

SURVIVORSHIP IN FLESH-FOOTED SHEARWATER *PUFFINUS CARNEIPES* AT TWO SITES IN NORTHERN NEW ZEALAND

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SUMMARY

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The Flesh-footed Shearwater *Puffinus carneipes* is a widespread sub-tropical species, breeding on Southern Hemisphere islands managed by New Zealand, Australia and France. Recent concern over the population's stability and frequently noted bycatch in longline fisheries has prompted a review of its conservation status. Studies of nesting shearwaters at two sites presented here provide detail of survivorship rates for two populations, studied over 13 and 23 years, respectively, in northern New Zealand sites. Adult survival (0.93–0.94) is moderate to high compared with survival of congeners. Population growth rates estimated from marked individuals indicate stability for one site and decline at the other site. Average age of first return of banded chicks was 6.2 years of age in one study and 6.4 years in the other. Current threats affecting survivorship for the New Zealand populations of this species are reviewed.

Key words: shearwater, survivorship, New Zealand, bycatch

INTRODUCTION

Flesh-footed Shearwaters (FFSW, *Puffinus carneipes*) feature prominently and in an enduring manner in fisheries bycatch statistics (Gales *et al.* 1998, Trebilco *et al.* 2010, Reid *et al.* 2012). The species is documented in the bycatch of fisheries using trawl, longline and gillnet methods (DeGrange *et al.* 1993, Robertson *et al.* 2003, Gilman 2006, Waugh *et al.* 2008, Thompson 2010, Waugh *et al.* 2011, Richard & Abraham 2013, Pierre *et al.* 2013). They are being considered for review of conservation status by the Australian Government (Agreement for the Conservation of Albatrosses and Petrels [ACAP] 2013), and their population status and occurrence in fisheries mortality has led to a specific research interest in the status and trends of their populations, as well as their foraging ecology and overlap with fisheries (ACAP 2012).

From the 1950s to early 1990s, several thousand (6000 ± 8000) FFSW may have been killed annually in North Pacific salmon gillnet fisheries. These estimates were developed from bird mortality data collected in 1990, before the prohibition of gillnet fishing in high seas (DeGrange *et al.* 1993). Baker & Wise (2005) estimated that 1794–4486 FFSW, originating from the Lord Howe Island population, were killed every year in longline fisheries from 1998 to 2002 at rates that were likely to be unsustainable for the population. Dillingham & Fletcher (2011), using Potential Biological Removals (PBR) models and estimates of key demographic parameters from closely related species, estimated that removals of 600 individuals above the naturally occurring mortality from New Zealand fisheries, and of 11000 individuals internationally, could adversely affect the populations. Estimation of captures in commercial fisheries using fisheries data from 2006/07 to 2010/11 indicates 780 (95% confidence interval [CI] 523–1090) FFSW may be caught annually

within New Zealand waters and places this species at high risk of adverse population effects from fishing mortality (Richard & Abraham 2013).

Other potential risks identified for the species include plastics ingestion. Hutton *et al.* (2008) found that ca. 80% of chicks of this species at Lord Howe Island had plastics in their proventriculus, with loading of ~30% of the volume of the proventricular capacity, enough to seriously impede digestion. Lavers *et al.* (2014) also found high plastic loadings in chicks at this site and contamination at levels above those recorded for all other marine vertebrates. Plastic reduces the ability of chicks to ingest and digest foods during chick-rearing and can result in direct mortality; as well, both adults and chicks may be affected by contamination by heavy metals contained in plastics (Bond & Lavers 2011). FFSW from Australia and New Zealand were found to have high mercury loadings in their feathers, at a level that could lead to sub-lethal effects (Bond & Lavers 2011). However, compared with levels subsequently reported in other Procellariiforme species, the levels found for FFSW were in the middle of the range (Anderson *et al.* 2009, Seco Pon *et al.* 2011).

There is a lack of long-term mark-recapture studies and demographic parameter estimates reported in the literature for this species. A better understanding of the species demography to assess the impacts of fisheries mortality, plastics pollution, predation and other influences on the populations is warranted. This study examines mark-recapture data sets collected to monitor population changes in FFSW at two sites in northern New Zealand, over 13 and 23 years, respectively. While our data sets were not sufficient to enable a fully age-structured population model to be developed for either study population discussed here, they do adequately describe survival probability for nesting adult birds and give an indication

of age-at-first-return to the breeding colonies, age-at-first-breeding and population growth rates.

STUDY AREA AND METHODS

Study sites and species

FFSW were captured and banded at breeding burrows on two islands: Lady Alice Island / Mauimua in the Hen and Chickens' Group (35.89°S, 174.71°E), Northland, and at Kauwahaia Island, Te Henga (Bethells Beach; 36.54°S, 174.26°E) in West Auckland, both in northern New Zealand.

On Kauwahaia Island, the birds were studied for 23 consecutive years by one of us (G.A.T.) from 1989/90 (thereafter 1990) onwards with 102 individual adults banded, of which 69 females and 28 males were identified (5 birds were not sexed).

All seabird burrows on Kauwahaia Island (approximately 450) were checked annually between 26 November and 5 December, primarily to band Grey-faced Petrel (GFP) *Pterodroma macroptera* chicks. FFSW use the same burrows as the winter-nesting GFPs, and 58 different burrows were used by FFSW during the study, some for multiple years. Any early-laying FFSW were identified at this time. Two further day visits were made 7–10 days apart in late December and early January to identify all breeding shearwaters and their partners. Burrows were inspected through study hatches or by burrowscope for a few pairs inhabiting very deep nests. All adults handled were checked for bands or were banded for the first time. Presence of an egg was confirmed for each bird removed from burrows. On the day visits, all burrows used by FFSW over the previous three years were inspected. Also, any other active sites with fresh digging, white excreta outside or birds heard calling were checked. Non-breeding FFSW (birds in burrows without an egg) were less frequently encountered unless they were caught in burrows used by FFSW in the previous three years. A few FFSW of uncertain status were captured on the surface in the early evening or pre-dawn on 3–5 nights annually. All accessible chicks present in burrows in March or April each year were banded. FFSW were sexed by DNA methods from blood or feather samples. Some sexes were confirmed by cloacal examination immediately after laying or by palpable eggs felt in the abdomen. There were 119 FFSW chicks banded at this site in 1990–2012.

On Lady Alice Island / Mauimua, the birds were studied for 13 consecutive years from 1999/2000 (thereafter 2000) onwards by one of us (A.B.), with 583 individual adults banded and recaptured at either the surface of the colony or in burrows. Between 138 and 170 burrows were checked each year throughout the study, with the proportion of burrows occupied ranging between 0.19 and 0.33 (average occupancy 0.29, standard deviation [SD] 0.05), or 33–53 birds on eggs followed during the breeding season, except in 2004 and 2012, when no checks were made. Birds were not classed according to sex or breeding status.

Estimating survival

We used multistate capture-recapture (MS CR) modelling to estimate probabilities of adult survival (Kendall & Nichols 2002, Lebreton *et al.* 2009). Since capture-recapture protocols differed between both study sites, we built two MS CR models and analysed the data sets separately.

For Kauwahaia Island, our starting model [$S_{t^*sex}^s, \psi_{t^*sex}^s, p_{t^*sex}^s$] assumed that survival (denoted S), capture (p) and transition between states (ψ) varied independently over time (t), sex (sex) and states (s). This model distinguished two states: breeder and non-breeder. Given the limited size of the data set, this starting model was constrained to enable parameter estimation by assuming that survival and breeding transition probabilities were constant over time and by assuming that capture probabilities did not differ between sexes. These constraints led to the initial model [$S_{sex}^s, \psi_{sex}^s, p_t^s$] for Kauwahaia Island, and we then tested several hypotheses by considering constrained models for each parameter type. First, we tested whether capture probabilities were time- or state-dependent. We also tested whether a model in which capture probabilities were sex- and state-dependent was better fitted to the data than our initial model. We then tested whether transition probabilities were sex- or state-dependent, and tested whether survival probabilities were sex- or state-dependent.

For Lady Alice Island / Mauimua, our starting model [S_t^s, ψ_t^s, p_t^s] assumed that survival, capture, and transition between states varied independently over time and states. This model distinguished two states: individuals captured at the surface of the colony and individuals captured in burrows. Given the limited size of the data set, this starting model was constrained to enable parameter estimation by assuming that survival and breeding transition probabilities were constant over time. These constraints led to the initial model [S^s, ψ^s, p^s] for Lady Alice Island / Mauimua. There was no capture effort in 2004 and 2012, and therefore capture probability was 0 for these years. We then tested several hypotheses by considering constrained models for each parameter type. First, we tested whether capture probabilities were time- or state-dependent. We then tested whether transition and survival probabilities were state-dependent.

We based inference on information-theoretic model selection, using Akaike information criteria corrected for small samples (AICc) (Burnham and Anderson 2002) for model selection. Data analyses were conducted with the program E-SURGE 1.8.5 (Choquet *et al.* 2009a). Because multistate models are prone to local minima during the likelihood maximization routine, we ran each model 10 times from different initial values to ensure that they converged to the lowest deviance. For both models, we performed goodness-of-fit (GOF) tests for MS CR models using U-CARE (Choquet *et al.* 2009b). Estimates are given \pm standard error unless otherwise specified.

Estimating age-at-first-return and population growth rate

We assessed the age-at-first-return based on banding and recapture data for juveniles banded at the study sites, by calculating the average age at which recaptured juveniles were first seen at the colony, across all cohorts. The data sets were too limited to use capture-recapture approaches to estimate age-specific return probabilities (Pradel 1996).

We estimated the population growth rate of marked individuals using Pradel's models (Pradel 1996). For both study sites, our starting model [S, p_t, λ] assumed that survival and population growth rate (λ) were constant and that capture probability varied over time. This model considered only one state, corresponding to the observation of an individual during a given year.

RESULTS

For Kauwahaia Island, the GOF tests indicated that the multistate model was well fitted to the data (females: $\chi^2 = 72.3$, $df = 127$, $P = 1.00$; males: $\chi^2 = 52.8$, $df = 62$, $P = 0.79$; both sexes combined: $\chi^2 = 125.2$, $df = 189$, $P = 0.99$).

For the Kauwahaia Island population, model selection (Table 1) indicated that capture probability (p) was not time-dependent, and varied between states (0.880 ± 0.040 for breeders and 0.197 ± 0.024 for non-breeders) but not between sexes. There were sex-dependent transition probabilities between states, with females moving from non-breeding to breeding state with a probability of 0.312 ± 0.033 and from breeding to non-breeding with a probability of 0.371 ± 0.052 . The corresponding probabilities for males were 0.299 ± 0.051 and 0.164 ± 0.044 . The best models (MK9 and MK10) indicated that survival did not vary between years. Although models MK9 and MK10 had similar AICc, and were therefore closely ranked and both contenders for the best model, the confidence intervals of the survival estimates for males and females from model MK9 overlapped considerably. Thus, average annual survival obtained from model MK10 was 0.931 ± 0.010 .

The average age-at-first-return of banded chicks was 6.4 (1.1 SD) years for eight juveniles recaptured from 119 banded. Seven individuals were found breeding (5 males, 2 females), with an average age of 6.7 (0.8 SD) years.

Modelled population growth rate was 0.984 ± 0.009 (95% CI 0.967–1.002), suggesting that the marked population was stable or declining very slowly. The number of breeding pairs, noted by direct observation, increased from eight pairs in 1990 to 20 pairs by 1999, and remained at that level until 2012.

For Lady Alice Island / Mauimua, the GOF tests indicated that the multistate model was well fitted to the data ($\chi^2 = 52.0$, $df = 57$, $P = 0.66$, Table 2).

At Lady Alice Island / Mauimua, model selection suggested that capture probabilities varied between years and state. The average capture probabilities for surface-captured birds and burrow-captured birds were 0.154 ± 0.053 and 0.209 ± 0.061 , respectively. State transition probabilities were state-specific. The probability that a surface-captured bird was again captured at the surface the following year was 0.943 ± 0.016 , and the probability that a burrow-captured bird was again captured in a burrow the following year was 0.721 ± 0.083 , indicating birds were most likely to be re-sighted in the same environment if they were surface-caught. Finally, the best model had state-dependent survival probabilities. The survival rate estimated for burrow-caught birds was 0.940 ± 0.087 and for surface-caught birds 0.756 ± 0.027 .

Average age-at-first-return of banded chicks was 6.2 (1.0 SD) years, for 12 birds re-sighted as adults from 191 banded as chicks. None of these birds was found breeding.

Modelled population growth rate was 0.883 ± 0.016 (95% CI 0.852–0.916), suggesting that the marked population declined at a rate of 16% per year.

DISCUSSION

Our study provides detailed data about individual life-history outcomes, enabling demographic modelling approaches (Sibly & Hone 2003) to be applied, thus examining which part of a population is most likely to be experiencing pressure. The work presented here provides a first, preliminary assessment of survivorship for adult breeding FFSW, measured for two populations in northern New Zealand, with some indication of the age-at-first-breeding from very small data sets.

Little demographic detail for the species had been reported, despite strong conservation concern about the adverse effects of fishing on the populations. The species is listed fourth among species most at risk of the adverse effects of fishing for New Zealand commercial fisheries (Richard & Abraham 2013). These authors

TABLE 1
Modelling capture (p), transition (ψ) and survival (S) probabilities for
Flesh-footed Shearwaters (1990–2012) at Kauwahaia Island, New Zealand

Model	Description	Effect tested	Deviance	Model rank	AICc	Δ AICc
Modelling p						
MK1	$S_{sex}^s, \psi_{sex}^s, p_t^s$	–	1 623.6	54	1 744.5	4.1
MK2	$S_{sex}^s, \psi_{sex}^s, p^s$	No time dependence	1 717.7	12	1 742.3	1.9
MK3	$S_{sex}^s, \psi_{sex}^s, p$	No state dependence	1 786.5	11	1 809.0	68.6
MK4	$S_{sex}^s, \psi_{sex}^s, p_{sex}^s$	Sex and state dependence	1 717.2	14	1 746.1	5.7
Modelling ψ						
MK5	S_{sex}^s, ψ^s, p^s	No sex dependence	1 725.9	10	1 746.3	5.9
MK6	$S_{sex}^s, \psi_{sex}^s, p^s$	No state dependence	1 722.4	10	1 742.9	2.5
MK7	S_{sex}^s, ψ, p^s	No sex, no state dependence	1 726.2	9	1 744.6	4.2
Modelling S						
MK8	S^s, ψ_{sex}^s, p^s	No sex dependence	1 722.0	10	1 742.4	2.0
MK9	$S_{sex}^s, \psi_{sex}^s, p^s$	No state dependence	1 720.0	10	1 740.4	0.0
MK10	S, ψ_{sex}^s, p^s	No sex, no state dependence	1 722.1	9	1 740.5	0.1

cite lack of data about vital demographic rates as one of the major sources of uncertainty about the modelling of population changes in relation to fisheries mortality. FFSW are listed with a conservation status of “Least Concern” by the IUCN (IUCN 2013), whereas in New Zealand the threat classification is described as “At Risk, Declining” (Miskelly *et al.* 2008), and Vulnerable in New South Wales, Australia (Threatened Species Conservation Act 1995 [New South Wales]).

While the species’ breeding is widespread in southern Australia at 43 sites (Australian Government Department of the Environment 2013), repeat census counts of population numbers are restricted to Lord Howe Island, where it has been subject to detailed study. Most recently, Reid *et al.* (2013) conducted demographic modelling showing declines in burrow numbers of 26% since 1978 (1.3% per year on average over 30 years). These major changes were attributed to reduced availability of breeding habitat and lower burrow density at breeding sites. FFSW on Lord Howe Island appear to have high reproductive output, despite reduced breeding numbers compared with earlier periods (Reid *et al.* 2013). Productivity at Lord Howe Island, measured by Priddel *et al.* (2006) in 2003 across six sub-colonies, was between 0.13 and 0.44 chicks per breeding burrow. Reid *et al.* (2013) found fecundity of around 0.46–0.49 fledglings produced per year per burrow from 2006 to 2009 in one area only. They put forward the hypothesis that favourable breeding conditions, combined with reduced fishing mortality, in this period explained the difference in breeding output compared with Priddel *et al.*’s results.

For the two study populations, adult annual survival was within the range reported for other shearwaters, at 0.93 for Kauwahaia Island adjacent to the Tasman Sea and at 0.94 for burrow-caught birds at Lady Alice Island / Mauimua with birds exploiting primarily the Pacific Ocean. The low survival for surface-caught birds may be due to the presence of transients (i.e. birds visiting the colony but not resident) and/or to a different age structure among surface-caught birds than among burrow-caught birds. These rates of survivorship recorded for FFSW compare well with adult survivorship rates within stable populations for other *Puffinus* shearwaters estimated using comparable methodologies (Manx Shearwater *P. puffinus*, 0.93 [Perrins *et al.* 1973]; Hutton’s Shearwater *P. huttoni*, 0.93 [Cuthbert *et al.* 2001]; Sooty Shearwater *P. griseus*, 0.94 [Clucas *et al.* 2008]; and Short-tailed Shearwater *P. tenuirostris*, 0.92 [Skira 1991]). Populations in decline have been noted: adult survivorship

for breeding birds is 0.7–0.94 for Yelkouan’s Shearwater *P. yelkouan* in France, and 0.85 for the same species in Malta (Oppel *et al.* 2011).

Average age-at-first-return was estimated at 6.2 years at Lady Alice Island / Mauimua and 6.4 years Kauwahaia Island, with age-at-first-breeding of 6.7 years at Kauwahaia Island. These estimates should be treated with caution as they are based on very small sample sizes, but are similar to those found for other shearwater species, with 6.8 years and 7.0 years for female and male Manx Shearwater (Brooke 1990), and 6.9 years and 7.0 years for female and male Short-tailed Shearwater, respectively (Serventy & Curry 1984). Fletcher *et al.* (2013) noted that use of simple proportions of birds resighted breeding from cohorts banded, not taking into account recapture probability, was likely to falsely estimate age-at-first-return or breeding, and provided corrected estimates of 7.7 years for Short-tailed Shearwater from Australian sites. These authors also re-estimated age-at-first-return of 4.8 years for Sooty Shearwater at southern New Zealand sites compared with estimates ranging from 5.4 to 5.7 years calculated using proportions of recaptures reported in the literature (see Fletcher *et al.* 2013 for details).

Overall, our data support the trends in breeding numbers observed at Kauwahaia Island, a colony that has been stable at around 20 pairs since 1998. In contrast, the Lady Alice Island / Mauimua population does not appear to be faring so well and may be in decline, as suggested by our results and also by burrow-transect estimates of population size (Museum of New Zealand Te Papa Tongarewa, unpublished data).

Population estimates for the species at 20 sites in New Zealand indicate that the breeding populations may be decreasing (Waugh *et al.* 2013). This estimate put the total breeding population at 10 000–15 000 birds, although further surveys at key sites are still ongoing to quantify recent population changes. This more accurate estimate (Waugh *et al.* 2013) is much smaller than previous accounts that 25 000–50 000 pairs (Taylor 2000) or 50 000–100 000 pairs exist at New Zealand breeding sites (Robertson & Bell 1984). These differences likely reflect the more quantitative count methodology in recent estimates than in earlier work, rather than a change in breeding numbers. Unfortunately, we are unable to test which of those two hypotheses is most likely, due to the poor documentation of the methodologies of early surveys.

TABLE 2
Modelling capture (p), transition (ψ) and survival (S) probabilities for
Flesh-footed Shearwaters (1990–2012) at Lady Alice Island / Mauimua, New Zealand

Model	Description	Effect tested	Deviance	Model rank	AICc	Δ AICc
Modelling p						
MLA1	S^s, ψ^s, p_t^s	–	1 847.8	25	1 899.4	0.0
MLA2	S^s, ψ^s, p^s	No time dependence	2 192.7	7	2 206.8	307.4
MLA3	S^s, ψ^s, p_t	No state dependence	1 904.5	15	1 935.1	35.7
Modelling ψ						
MLA4	S^s, ψ, p_t^s	No state dependence	1 861.2	24	1 910.7	11.3
Modelling S						
MLA5	S, ψ^s, p_t^s	No state dependence	1 851.7	24	1 901.2	1.8

Colony-based and marine threats to New Zealand populations

The survival rates of FFSW at our study sites need to be considered in the context of mortality-causing factors on and around their breeding and foraging areas. Introduced mammals no longer pose threats to the existing 20 populations, as these have been removed from all the major breeding colonies since threats were first assessed by Taylor (2000). However, FFSW have experienced local extinctions at four sites in northern New Zealand (G. Taylor & A. Tennyson, pers. obs., in Waugh *et al.* 2013): Taranga Island (Hen Island, 35°57'S, 174°43'E); Red Mercury Island (Whakau Island, 36°21'S, 175°56'E); Hongiora Island (36°57'S, 176°3'E); and Whakaari (White Island, 37°31'S, 177°11'E), which may be due to a combination of factors. Pacific rats *Rattus exulans* were present at three sites (all but Hongiora Island), and competition for burrows with other seabirds, reducing breeding outputs, along with additional mortality of adults at sea, are likely factors across these sites. Competition at burrows may be non-negligible, with FFSW breeding in mixed colonies with Sooty Shearwater, Grey-faced Petrel, and Little Penguins *Eudyptula minor* at many of their breeding sites. FFSW chicks are vulnerable to eviction or mortality by the aggressive winter-breeding Grey-faced Petrels when they return to colonies in April to clean out burrows (Taylor 2000).

The most important source of mortality documented for FFSW in New Zealand is fisheries mortality, which is at high levels in some fisheries, affecting potentially both the adult breeding population and younger birds. Fisheries mortalities of FFSW are known from a range of commercial fisheries in New Zealand, Australia, and internationally. These include gillnet fisheries (DeGrange *et al.* 1993, Baker & Wise 2005, Richard & Abraham 2013), longline fisheries (Baker & Wise 2005, Trebilco *et al.* 2010, Thompson 2010, Richard & Abraham 2013), and trawl fisheries (Thompson 2010, Richard & Abraham 2013). For New Zealand commercial fisheries, trawl, bottom longline and surface longline fisheries contribute most to the fisheries mortality documented, in descending order of importance (Richard & Abraham 2013). Commercial fisheries mortality alone in New Zealand is sufficient to result in population decreases for the species at New Zealand breeding sites (Richard & Abraham 2013). Despite the relatively small numbers of this species nesting in New Zealand compared with other species of seabird in the region (e.g. Sooty Shearwaters, ca 5 000 000 pairs), it is the sixth most commonly caught in commercial fisheries (Ministry for Primary Industries 2013). Consequently, improving knowledge of the FFSW population's status and finding means to reduce bycatch are high priorities nationally, identified in recent government policy on managing the effects of fishing on the environment (Ministry for Primary Industries 2013). Bycatch mitigation in Australian fisheries has been a focus for some years for this species (Baker & Wise 2005). The species mortality rates were used as an indicator of overall success in mortality reduction for the Australian Eastern Billfish and Tuna Fishery (Australian Government 2006).

In New Zealand, recreational fishing is estimated to catch around 40 000 birds annually (Abraham *et al.* 2010) based on surveys of fishers, mainly in northern New Zealand. Around 53% of birds caught by Abraham *et al.* (2010) were petrels (including shearwaters), although up to 82% of birds may in fact have been petrels, but were reported as seagulls or unidentified birds. In recreational fisheries, birds can be killed or injured by becoming entangled, sustain fatal injuries by becoming hooked, or be injured by people, either deliberately or through inappropriate handling.

Dead FFSW with fishing hooks embedded have been observed at breeding colonies (AB, pers. obs; G. Hedley, pers. comm.) or on beaches (Taylor 1996). Beach birds sampled following the 2011 container ship *Rena* oil spill were found with crushed or broken bones, puncture wounds and other lesions, possibly as a result of interactions with people at sea (Massey University & Museum of New Zealand Te Papa Tongarewa, unpublished data).

The effects of plastics on the species at New Zealand sites are unknown; however, there is potential for FFSW populations to be affected by plastics at Ohinau Island, while negligible quantities were found at other sites where FFSW breed in the north of New Zealand (Buxton *et al.* 2013). Researchers at Lord Howe Island have expressed concern about the incidence of plastic in chicks (Hutton *et al.* 2008, Reid *et al.* 2013). Recent work on this topic by Lavers *et al.* (2014) indicates severe problems for FFSW at Lord Howe Island, with contamination rates for the species higher than those reported for any other species of marine vertebrates.

In the absence of long-term demographic data sets on FFSW at many of the breeding sites internationally, modelling research has been used to estimate the effects of a number of potential threats to the populations. Survivorship and age-at-first-breeding data are vital in the studies to estimate population response to pressures, such as additional mortality through fisheries (Cuthbert *et al.* 2001). The PBR approach indicates the additional mortality above natural levels before adverse population effects occur (Wade 1998). Dillingham & Fletcher (2011) estimated a PBR of 600 for the New Zealand FFSW population, using values of 93% survival for FFSW, and six years for the average age of first breeding. These demographic rates were proxies from related species, and the total population estimate was based on older data sets (e.g. Brooke 2003, Taylor 2000). However, the inputs chosen were not substantially different from the estimates, based on more recent surveys by Waugh *et al.* (2013) and this study. Using Bayesian modelling approaches, Richard & Abraham (2013) produced updated PBR analyses, with similar substitute variables to those of Fletcher & Dillingham (2011) and more recent population estimates. Richard & Abraham (2013) estimated the PBR for New Zealand FFSW was 590 birds, noting that demographic rates for survivorship and age-at-first-breeding were highly uncertain. Moreover, they estimated the probable catch of birds from New Zealand commercial fisheries was 780 (95% CI 523–1 090) for 2012, and exceeded the PBR. Our assessment of population growth rates, estimated from marked birds using a capture-recapture approach, is coherent with the modelling outcomes of their work. These findings taken together suggest that breeding populations are under pressure nationally from fisheries mortality. Indeed, our results indicate that the Kawahaua Island population appears to be stable or slightly declining and that at Lady Alice Island / Mauimua is probably declining. However, the relatively high adult survival estimate for Lady Alice Island / Mauimua burrow-caught birds suggests that the demographic causes of the decline at this site, at least, may be linked to low productivity and/or low juvenile/immature survival, rather than to adult breeder survival.

Although small, the data sets used here were sufficient to produce survivorship estimates with relatively small error estimates, owing to their relatively long time-series. The data set from Lady Alice Island / Mauimua showed that both burrow- and surface-captures can be used to estimate annual survival. However, because information on the breeding status of the birds was lacking, it

was not possible to estimate breeding probability. Efforts to reproduce study sites to examine inter-colony effects and to better understand variability within a population (e.g. between breeders and non-breeders or between sexes) should be considered in future study designs. Multiple factors are likely to be affecting these populations, including at-sea and colony-based threats such as multiple fisheries mortality and intra-specific competition for nest sites. Therefore, examining demographic outcomes through a combination of measures is pivotal to determining the principal causes of change. This should include mark-recapture studies, foraging ecology, assessment of fisheries mortality and census work on colonies to examine overall population change.

Our research provides much-needed data to help understand the demographic responses of FFSW populations to changing pressures in the marine environment. Although the results of this study are not likely lead to in major changes in modelling outcomes for FFSW, our empirical estimates are coherent with survival and age-at-first-breeding estimates used in modelling studies and substantially reduce the uncertainty around the estimates. Efforts to reduce fishing pressure in commercial longline and trawl fisheries as well as recreational fisheries in New Zealand should therefore continue in the knowledge that the serious problem of population declines identified by modelling exercises for the population is likely to be real and ongoing. FFSW are listed with a conservation status of “Least Concern” by the IUCN based on their wide geographic spread and perceived large population sizes (IUCN 2013). However, lower-than-expected population sizes and observed declines on Lord Howe Island and at New Zealand colonies (Priddel *et al.* 2006, Reid *et al.* 2013, Waugh *et al.* 2013) indicate that the IUCN status of this species needs to be reassessed urgently.

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