



# Projected impacts of climate change, bycatch, harvesting, and predation on the Aotearoa New Zealand tītī *Ardenna grisea* population

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**ABSTRACT:** Many factors have contributed to a decline in the tītī (sooty shearwater) *Ardenna grisea* population in Aotearoa New Zealand since at least the 1960s. The relative impacts of Southern Oscillation Index (SOI) variation, bycatch, predation, and traditional harvesting by Rakiura Māori were recently estimated in a study fitting population models to data from the period 1976–2005. Annual mean SOI was related to both adult survival and fecundity. We used the results from that study to project abundance of tītī under a range of management strategies and future SOI scenarios, based on 41 climate models. Projections over the period 2019–2070 showed marked variation across the climate models. When the proportion of chicks harvested and the level of depredation by weka *Gallirallus australis* were set at their historical means and the proportion of birds killed in bycatch was set at an upper bound based on current estimates, the probability of a decline ranged from 0.30 to 1.00, across all climate models. When both bycatch and depredation by weka were set to zero, the probability of a decline ranged from 0.11 to 1.00, across all climate models. Our results suggest that future abundance of tītī in Aotearoa New Zealand will depend to a large extent on SOI conditions over the coming decades. As climate-model uncertainty makes reliable prediction of future SOI conditions difficult, adaptive management is likely to be the best option for Rakiura Māori, the kaitiaki (environmental guardians) of the Rakiura Titi Islands, to maintain sustainable tītī harvests.

**KEY WORDS:** Harvest management · Population projection model · Southern Oscillation Index · Sooty shearwater

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## 1. INTRODUCTION

The vulnerability of many seabird populations to multiple threats can be attributed to several aspects of their life history (Gremillet et al. 2015, Paleczny et al. 2015). The high adult survival rates and low productivity of some seabird species result in low population growth rates (Hunter et al. 2000), which limits the ability of the population to recover from increases in mortality. This is particularly true for adult mortality, as population models for long-lived vertebrates show the importance of adult survival to population dynamics (Caughley 1966, Lebreton & Clobert 1991, Sæther & Bakke 2000, Mills 2006). Recently, the potential impact of climate change on seabird population dynamics has become an important focus of conservation management (Goyert et al. 2018, Jenouvrier et al. 2018, 2020, Dias et al. 2019, Iles & Jenouvrier 2019). Adult mortality in fisheries bycatch is also clear cause for concern in many seabird populations (Pott & Wiedenfeld 2017, Clay et al. 2019, Dias et al. 2019, Good et al. 2020). In addition, delayed maturation, low reproductive rates, and ease of exploitation at their breeding colonies make some seabird populations especially vulnerable (Russell 1999, Weimerskirch 2002, Moller 2006).

In recent decades, tītī (sooty shearwater) *Ardenna grisea*, long-lived procelliforms, have faced a suite of threats to their persistence in the Aotearoa New Zealand (A-NZ) region (Lyver et al. 1999, Jones 2000, Uhlmann 2003, Harper 2007). During the austral summer, tītī forage over a wide area of the Southern Ocean from their breeding colonies on islands to the south of A-NZ, and in the winter undertake a trans-equatorial migration to the North Pacific (Shaffer et al. 2006, Thompson et al. 2015). This behaviour has exposed individuals to several regions that have experienced significant climate-driven perturbations (Veit et al. 1997, Lyver et al. 1999, Humphries & Möller 2017, Humphries 2018) and high levels of fisheries bycatch (Uhlmann 2003, Uhlmann et al. 2005, Uhlmann & Jeschke 2011). Furthermore, predation of tītī chicks by both the native weka *Gallinula australis*, a flightless bird (Dillingham et al. 2007), and ship rats *Rattus rattus* that were introduced to some breeding islands (Harper 2007), as well as harvesting by humans (Bragg et al. 2007, Newman et al. 2009b, McKechnie et al. 2010) have all had an impact on the A-NZ population.

As a consequence of several agents having simultaneous impacts, tītī population dynamics have been characterised by large-scale declines and erratic fluctuations in abundance since at least the 1960s

(Veit et al. 1997, Lyver et al. 1999, Scofield & Christie 2002, Scott et al. 2008, Humphries & Möller 2017). A recent study by McKechnie et al. (2020) separated the relative impacts that the various sources of mortality have on demographic rates at the appropriate stage of the life cycle. This approach allowed for uncertainty in both the choice of projection model and the demographic parameters. They concluded that annual fluctuations in population size are closely related to large-scale climatic conditions, and that long-term declines were the result of a synergistic effect of fisheries bycatch, depredation by predators, human harvesting, and an unfavourable period of climatic conditions in the latter part of last century. Of these threats to tītī persistence, climate is perhaps the most difficult to address, owing to the difficulties in responding with appropriate management actions and uncertainty as to how tītī populations will respond to changes in conditions. Furthermore, mitigation of the effects of inter-annual and long-term climate change relies on international, policy-level decisions and global uptake by humans.

The Intergovernmental Panel on Climate Change (IPCC) has predicted that atmospheric global warming will continue over the coming decades, with a number of variables such as wind patterns, sea surface temperatures, and sea level also expected to change (Field 2014). Previous research has identified strong relationships between the El Niño Southern Oscillation Index (ENSO) and tītī demography (Lyver et al. 1999, McKechnie et al. 2020). It is therefore important to understand how future climate change will affect ENSO conditions and the resulting effects on tītī populations. Previous tītī projection models (Hamilton & Moller 1995, Hunter et al. 2000, Hunter & Caswell 2005) have not accounted for the influence of climate change on demography, thereby limiting our understanding of potential future dynamics of tītī populations. Robust methods for increasing our understanding of the likely responses of the population to short- and long-term climate variation are urgently needed to allow more efficient management of tītī populations.

Projections of the effects of changing climate conditions on animal populations are difficult, partly due to the challenges of relating climatically controlled physical variables to demographic rates (Jenouvrier et al. 2009, Hunter et al. 2010, Barbraud et al. 2011). This relationship is an important step in formulating models to simulate future population dynamics under a variety of climatic scenarios. Such an approach involves assuming that climate indices will follow the dynamics suggested by general circulation models,

and that the relationships between climate indices and animal demographic rates will be maintained in a similar manner to that estimated from past data. Difficulties in meeting these assumptions make it hard to reliably predict future population size (Ludwig 1999, Fieberg & Ellner 2000). However, quantitative projection models can have an important role in risk assessment when they are used to compare the relative performance of competing management strategies (Brook et al. 2000, 2002).

We used projection models to predict future tītī population dynamics over a range of potential management and Southern Oscillation Index (SOI) scenarios, using the posterior distributions for tītī demographic rates provided by McKechnie et al. (2020). We considered a range of scenarios for the proportion of chicks harvested, the levels of bycatch and weka-depredation, and future SOI conditions. In this study, we focus on differences between scenarios, in both annual growth rate and the probability of decline, in order to develop future management strategies. Understanding the performance of tītī populations across a range of SOI scenarios is important, owing to the high degree of uncertainty around future climatic conditions (Yeh et al. 2009). The IPCC has placed an emphasis on understanding the impacts of climate change on biodiversity (Field 2014). Case studies of the potential responses of species to changing climate conditions are therefore vital for indigenous peoples, conservation managers, and policy makers to grasp the consequences of their management decision-making and practices alongside climate-change impacts.

## 2. MATERIALS AND METHODS

### 2.1. Tītī in Aotearoa New Zealand

The tītī population in the A-NZ region was estimated to be 21.3 million individuals (95% CI: 19.0–23.7 million) on 31 March (post-breeding, i.e. including fledged chicks) in the 2005 breeding season (Newman et al. 2009a). The largest colonies are located on The Snares Islands, and on the Rakiura Tītī (Muttonbird) Islands, close to Rakiura (Stewart Island; Fig. 1). The breeding cycle begins with the return of adult birds to the colony in the early Austral spring season of late September to October. Eggs are laid in November to early January, and chicks hatch in the summer season of January and February. The adult migration period to the Northern Hemisphere commences in late March (Schaffer et al. 2006), while

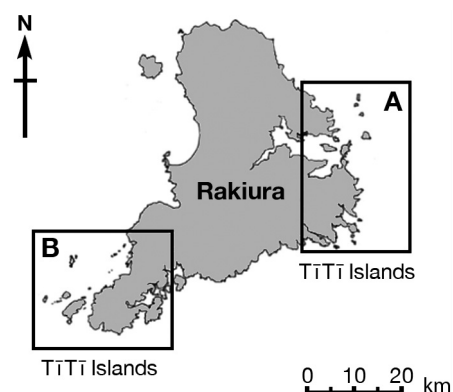


Fig. 1. Rakiura (Stewart Island), the (A) North-Eastern and Eastern Tītī Islands and the (B) South-Western Tītī Islands

the chicks fledge and migrate north in late April to May (Richdale 1963).

There are approximately 36 islands that constitute the Rakiura Tītī Islands, most of which are subjected to annual harvesting by Rakiura Māori. Harvesting is restricted to these islands and only occurs between 1 April and 31 May each year, in which pre-fledgling chicks are procured for human consumption (for a detailed account of the harvesting system, see Lyver 2002). The tītī, the islands, and harvest are also a key part of Rakiura Māori identity and linkage to place, ancestors, and future generations. The time spent on the islands enables the reaffirming of linkages and bonds within and between families, including connection back to the tītī, land, and sea.

### 2.2. Population model structure

The model we consider is exactly the same as that fitted to harvest catch per unit effort data for the period 1976–2005 in McKechnie et al. (2020). It is an age-structured matrix model with 15 age classes (0–14), where age class 0 represents fully developed chicks. It assumes a post-breeding census on 31 March, immediately before the start of harvesting. The final age class (14) is a recycling ‘plus group’ within which all individuals have identical vital rates, and thus accumulates all birds older than age class 13. The projection matrix for the transition from year  $t - 1$  to  $t$  is given by:

$$\begin{bmatrix} F_{0,t} & F_{1,t} & \cdots & F_{13,t} & F_{14,t} \\ P_{0,t} & 0 & \cdots & 0 & 0 \\ 0 & P_{1,t} & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & P_{13,t} & P_{14,t} \end{bmatrix}$$

with:

$$F_{i,t} = 0.5(1-w)f_t p_{i+1} (1-b)s_{t-1}^a \quad (i = 0, \dots, 13) \quad (1)$$

$$F_{14,t} = 0.5(1-w)f_t p_{14} (1-b)s_{t-1}^a \quad (2)$$

$$P_{0,t} = (1-h) (1-b)s_{t-1}^j \quad (3)$$

$$P_{1,t} = (1-b)s_{t-1}^j \quad (4)$$

$$P_{i,t} = (1-b)s_{t-1}^a \quad (i = 2, \dots, 14) \quad (5)$$

where:

$f_t$  = fecundity (number of fledged chicks alive per breeding adult) in year  $t$ ;

$s_t^a$  = probability of an adult bird alive in year  $t$  surviving to year  $t+1$ ;

$s_t^j$  = probability of a juvenile bird alive in year  $t$  surviving to year  $t+1$ ;

$p_i$  = probability that an individual in age class  $i$  is sexually mature;

$b$  = proportion of birds (juveniles + adults) caught as bycatch;

$h$  = proportion of chicks taken by humans during harvest;

$w$  = proportion of breeding attempts that fail due to weka-depredation.

In Eq. (1), fecundity is multiplied by 0.5 because we assume a 1:1 sex ratio and only 1 egg is laid per breeding pair. Note also that we assume a single survival rate for all individuals less than 2 yr old ( $s_t^j$ ) and for those aged 2 years or more ( $s_t^a$ ), due to the constraints that needed to be imposed when modelling chick banding data for this species (for details, see Fletcher et al. 2013 and McKechnie et al. 2020). In addition,  $s_t^j$  is assumed to be lower and proportional to adult survival, i.e.  $s_t^j = rs_t^a$  where  $r < 1$  is a scaling parameter. As some individuals aged 2 yr or more will not be sexually mature, we refer to  $s_t^a$  as the 'adult' survival rate purely for simplicity of terminology.

Based on the analysis in McKechnie et al. (2020), the probability of sexual maturity in Eqs. (1) & (2) needs to be assumed to be the same in all years; it is set to 0 for age classes 0–2,  $\Phi\left(\frac{i-\mu_p}{\sigma_p}\right)$  for age classes 3–12, and 1 for age classes 13 and 14, where  $\Phi(\cdot)$  is the cumulative distribution function for the standard normal distribution, and  $\mu_p$  and  $\sigma_p$  are the mean and standard deviation of the age at maturity, respectively.

Links between large-scale climatic events and tītī abundance have been reported by Lyver et al. (1999) and Humphries & Möller (2017). They showed that catch per unit effort of tītī chicks by human harvesters has a lagged relationship with the SOI, and that years of high and low shearwater abundance

pre-empt low (El Niño conditions) and high (La Niña conditions) SOI values, respectively. As described by McKechnie et al. (2020), we therefore assume that adult survival and fecundity in year  $t$  are related to SOI indices in year  $t$  by the equations:

$$s_t^a = \frac{s_m^a}{1 + \exp\{-(\alpha_s + \beta_s z_t^s)\}} \quad (6)$$

and

$$f_t = \frac{f_m}{1 + \exp\{-(\alpha_f + \beta_f z_t^f)\}} \quad (7)$$

respectively, where  $s_m^a = 0.98$  and  $f_m = 0.9$  are the maximum potential adult survival and fecundity,  $\beta_s$  and  $\beta_f$  are coefficients controlling the strength of the relationships with climate, and  $z_t^s$  and  $z_t^f$  are 2 choices of SOI index in year  $t$  (described below). For every choice of index, negative values are associated with El Niño conditions and positive values with La Niña conditions.

Table 1 shows the posterior means and 95% credible intervals (CIs) for the demographic parameters obtained by McKechnie et al. (2020) after fitting this model to harvest catch per unit effort data for the period 1976–2005. Details regarding the harvest data, the other data sources used to fit the model, the model-fitting procedures, and the methods used to specify  $s_m^a$  and  $f_m$  (Eqs. 6 & 7) are given in McKechnie et al. (2020).

Based on the results of McKechnie et al. (2020), we considered 8 models which differ solely in terms of the choice of  $z_t^s$  and  $z_t^f$ ; see McKechnie et al. (2020) for details regarding the reasoning that led to these models. For the model denoted S0F0,  $z_t^s$  is the mean of the 12 monthly SOI values between April in year  $t$  to the following March (the period over which survival is calculated), and  $z_t^f$  is the 12 mo mean between October (just before the onset of egg-laying) in year  $t-1$  and the following September. Five of the models involve lagged versions of these definitions. Thus, the S0F0 model has a '0 lag' on adult survival and a '0 lag' on fecundity, and the equations relating these 2 rates to SOI are exactly as above. In contrast, an S-1 model has a '-1 lag' on survival, with the function involving  $z_t^s$  now being a model for  $s_{t-1}^a$ , i.e.:

$$s_{t-1}^a = \frac{s_m^a}{1 + \exp\{-(\alpha_s + \beta_s z_t^s)\}} \quad (8)$$

Likewise, an S1 model has a '+1 lag' on survival, with:

$$s_{t+1}^a = \frac{s_m^a}{1 + \exp\{-(\alpha_s + \beta_s z_t^s)\}} \quad (9)$$

Analogous definitions hold for an S-2 model, an F-1 model, and an F1 model. A model with a '-1 lag' on adult survival and a '0 lag' on fecundity is denoted S-1F0, with similar definitions for other lags. The

Table 1. Model-averaged posterior means and 95 % credible intervals (CI) for the demographic parameters estimated by McKechnie et al. (2020), with model averaging being carried out using the models and weights given in Table 2. For both adult survival and fecundity, results are given for the lowest and highest annual estimates, over the period 1976–2005, corresponding to El Niño and La Niña conditions, respectively

Parameter		Posterior mean	95 % CI
Adult survival ( $s_t^a$ )	Lowest	0.85	0.64–0.96
	Highest	0.96	0.90–0.98
Fecundity ( $f_t$ )	Lowest	0.43	0.35–0.53
	Highest	0.62	0.51–0.71
Probability of maturity at age $i$ ( $p_i$ )	Mean age at maturity ( $\mu_p$ )	7.5	7.0–8.0
	SD of age at maturity ( $\sigma_p$ )	1.9	1.7–2.1
Juvenile survival	Ratio to adult survival ( $r$ )	0.68	0.46–0.95

remaining 2 models involve no relationship between SOI and either fecundity (denoted NoF) or adult survival (denoted NoS). The full set of 8 models is shown in Table 2, together with model weights calculated using the Watanabe-Akaike information criterion (Watanabe 2010, Yao et al. 2018). These weights were used by McKechnie et al. (2020) to model average the posterior distributions obtained from each model, in order to allow for projection-model uncertainty; the posterior summaries in Table 1 are based on this model averaging.

The model with the highest weight (0.49) is S–1F0, which indicates a positive relationship between both fecundity and SOI during the breeding season, and between adult survival and SOI in the following 12 mo (see Fig. 3 of McKechnie et al. 2020). For this model, setting  $z_t^s = z_t^f = 0$  gives the following posterior medians (and 95 % CI) for the demographic parameters: adult survival = 0.95 (0.92–0.97); juvenile survival = 0.64 (0.44–0.87); fecundity = 0.54 (0.48–0.59); and mean age at first breeding = 7.5 yr (7.0–8.0 yr). Using the methods described by Dillingham (2010), we then obtained a posterior median for optimal mean generation time (Leslie 1966) of 15.5 yr (95 % CI: 13.3–18.4 yr) and for maximum annual growth rate of 6.7 % (5.6–7.8 %). The estimate of optimal mean generation time provides an update on the value of 21.2 yr used in the current IUCN

Red List (Scott et al. 2008, IUCN 2020), and on the most recent estimate of 13.1 yr (Fletcher et al. 2013). We projected tītī dynamics over the period 2019–2070, as this is approximately 3 generations, a timespan used in the IUCN Red List criteria.

### 2.3. Model parametrisation

We parametrised the 8 projection models directly from the posterior distributions obtained by McKechnie et al. (2020) (Section 2.2), and carried out

the following steps for each model. For each of the 10 000 sets of values from the joint posterior distribution for the demographic parameters, and for each SOI scenario, bycatch level ( $b$ ), harvest level ( $h$ ), and level of weka-depredation ( $w$ ) we:

- (1) Used the predicted number of birds in each age class in 2005 as the initial number in that age class for the projection;
- (2) Projected the population forward to 2019 using the observed values of  $z_t^s$  and  $z_t^f$ ;
- (3) Projected the population further forward to 2070, using the predicted values of  $z_t^s$  and  $z_t^f$  for that SOI scenario;
- (4) Calculated the annual population growth rate, the proportion of projections which led to a decline, and the proportion of projections which led to a decline of greater than 50 %, all calculated between 2019 and 2070. The latter is of interest, as it is estimates the probability that the population will be classified as Endangered at the end of the projection period (IUCN 2020).

We then used the model weights (Table 2) to generate a sample of size 10 000 from the model-averaged posterior distribution for each of the 3 projection-summaries in Step 4.

### 2.4. Future SOI scenarios

We obtained projections of monthly SOI values for 41 global climate models, based on the RCP8.5 emissions scenario (van Vuuren et al. 2011), from Dr. Brett Mullan of the National Institute of Water and Atmospheric Research (NIWA) in A-NZ. These models were all used in the Coupled Model Intercomparison Project Phase 5 (CMIP5), as part of the Fifth Assessment of the IPCC (Collins et al. 2013). Models from CMIP5 that did not make projections over a long

Table 2. Watanabe-Akaike information criterion (WAIC) model weights for 8 projection models. The notation for the models is described in Section 2.2

Model	Weight	Model	Weight
S–1F0	0.49	NoSF0	0.04
S–2F0	0.21	S–1NoF	0.02
S1F0	0.17	S–1F–1	0.02
S0F0	0.04	S–1F1	0.01



enough period for our purposes were excluded. We focus on the RCP8.5 emissions scenario in order to consider what is most likely to happen without strong policy intervention by multiple governments and economies. RCP8.5 has often been used as such a baseline, e.g. in Stage 1 of the A-NZ National Climate Change Risk Assessment (Mullan et al. 2018). Further details regarding the climate models and emission scenarios can be found in Section 2.2 of Mullan et al. (2018) and van Vuuren et al. (2011), respectively.

For each climate model, we calculated the projections of  $z_t^f$  and  $z_t^s$  for the period 2019–2070, separately for each of the 8 projection models. Figs. S1 & S2 in the Supplement at [www.int-res.com/articles/suppl/m670p223\\_supp.pdf](http://www.int-res.com/articles/suppl/m670p223_supp.pdf) show these projections as well as the observed values of  $z_t^f$  and  $z_t^s$  for the period 1976–2005; the latter were used by McKechnie et al. (2020) to fit the population model to the catch per unit effort data. The local polynomial regression curves in Figs. S1 & S2 show little or no trend in either index over the period 1976–2005. For both indices, the climate-model projections show either no trend, a small positive trend, or a clear positive trend in the latter part of the projection period. As the best fitting model (S–1F0) indicates a positive relationship between fecundity and  $z_t^f$  as well as between adult survival and  $z_t^s$  (Section 2.2), we would expect the climate-model projections with higher values of these 2 indices to provide more optimistic projections, particularly those with higher values of  $z_t^s$  (McKechnie et al. 2020).

The partial autocorrelations of the residuals from the local polynomial regressions are shown in Figs. S3 & S4. Over the period 1976–2005, these indicate evidence of negative autocorrelation at lags 2 and 8 for the observed  $z_t^f$  (–0.45 and –0.39, respectively), but no evidence of autocorrelation for the observed  $z_t^s$ . For both indices, the majority of the climate-model projections also show evidence of negative autocorrelation at lag 2 (range = –0.27 to –0.74), with a small number showing evidence of negative autocorrelation at other lags (range = –0.27 to –0.64) and/or positive autocorrelation at lag 1 (range = 0.28 to 0.50). These autocorrelations give some insight as to why the set of best projection models in McKechnie et al. (2020) includes models with different lags for the relationship between SOI and both adult survival and fecundity (Eqs. 6 & 7).

## 2.5. Scenarios projected

We investigated a number of scenarios where the levels of bycatch ( $b$ ), chick harvest ( $h$ ), and weka-depredation ( $w$ ) were varied. For the projections from

2005 to 2019 we set  $h = 0.11$ , the estimate of the mean proportion of chicks harvested over the period 1976–2005 (McKechnie et al. 2020), and  $w = 0.11$ , the estimate of recent weka-depredation (Dillingham et al. 2007). We obtained an order of magnitude estimate of global bycatch of tītī during the period 2005–2019 using the Seabird Information for Fisheries Assessment Tool of the American Bird Conservancy ([www.fisheryandseabird.info](http://www.fisheryandseabird.info); accessed May 2020). We consulted all of the relevant literature listed therein, and additional references retrieved from other sources (S. Uhlmann unpubl. data). Reported annual rates were in the order of hundreds or thousands (e.g. Waugh et al. 2008, Dietrich et al. 2009, Alfaro-Shigueto et al. 2010, Calvert et al. 2013, Žydelis et al. 2013), except for driftnet fisheries in the Russian Far East which were in the order of tens of thousands (Artukhin et al. 2010). This led us to use an estimate of between 10 000 and 100 000 tītī having been killed per annum by global fishing operations between 2005 and 2019; the upper estimate of 100 000 was chosen as deliberately conservative, in order to allow for illegal, unreported, or unregulated fishing (Oliver & Jacobs 2019). These estimates of annual bycatch are equivalent to between 0.1 and 0.8% of the A-NZ adult population in 2005 (posterior median = 12.6 million). We therefore set  $b$  at an intermediate level of 0.005 in the projections from 2005 to 2019. Our final results should be robust to the above choices for  $b$ ,  $h$ , and  $w$ , as they will only affect the estimate of the initial population size in 2019, not the projections from 2019 onwards.

The effects of future harvest levels were determined by setting  $h$  after 2019 at one of the following levels: 0, 0.05, 0.1, 0.11 (the estimate for 1976–2005), 0.15, 0.2, 0.3, 0.4, 0.6, 0.8, and 1.0. We investigated the effects of weka-depredation after 2019 by setting  $w = 0$  (weka-eradication) or  $w = 0.11$  (the most recent estimate). Likewise, we assessed the impact of bycatch after 2019 by setting  $b = 0$  or  $b = 0.01$  (the latter being the higher of the 2 estimates for 2005–2019). We considered all 1804 combinations of the 41 SOI scenarios, 11 harvest levels, 2 weka-depredation levels, and 2 bycatch levels.

## 2.6. Sensitivity analyses

The 8 projection models in Table 2 do not allow for annual variation in adult survival and fecundity other than that due to the relationships with SOI (Eqs. 6 & 7). McKechnie et al. (2020) found that addition of an error term in Eqs. (6) & (7), as a means of representing non-SOI sources of annual variation,

led to lack of convergence to a stationary posterior distribution. In order to assess the extent to which their results might be affected by this constraint, they carried out a sensitivity analysis in which they modified the best-fitting model (S-1F0) so that Eqs. (6) & (7) included normal errors with specified (rather than estimated) standard deviations. Thus they set:

$$s_t^a = \frac{s_m^a}{1 + \exp\{-(\alpha_s + \beta_s z_t^s + \varepsilon_t^s)\}} \quad (10)$$

and

$$f_t = \frac{f_m}{1 + \exp\{-(\alpha_f + \beta_f z_t^f + \varepsilon_t^f)\}} \quad (11)$$

where  $\varepsilon_t^s \sim N(0, \sigma_s^2)$  and  $\varepsilon_t^f \sim N(0, \sigma_f^2)$ , and the error standard deviations were set at ‘high’ values of  $\sigma_s = 0.37$  and  $\sigma_f = 0.72$ . These values were determined by specifying plausible ranges for the true annual adult survival and fecundity rates over the period 1976–2005 and then calculating the values of  $\sigma_s$  and  $\sigma_f$  that would lead to the modified model predicting that the annual adult survival rates and the annual fecundity rates for 1976–2005 cover the specified ranges (McKechnie et al. 2020). We used the posterior distributions obtained by McKechnie et al. (2020) from the modified S-1F0 model to carry out an extra set of projections over the period 2019–2070, and compared these with the projections from the original S-1F0 model.

We also calculated the ‘sensitivity’ associated with each component of the S-1F0 model, i.e. the amount by which we would expect the population growth rate to change for every unit change in that component, assuming that the other components remain fixed (Caswell 2001, 2019). As long as we bear in mind the plausible range of values for each component, these sensitivities provide a useful summary of their relative influence on the population growth rate.

All calculations were performed using the statistical programming language R, v. 4.0.3 (R Core Team 2020).

### 3. RESULTS

#### 3.1. Variation between climate models

The model-averaged projection-summaries show a high degree of variation across the 41 SOI scenarios (Figs. 2–4). We focus here on the case where the proportion of chicks harvested each year is 0.11, the estimate of the mean for 1976–2005. If the level of weka-depredation is 0.11 and bycatch is 0.01, the posterior median growth rate ranges from  $-2.8$  to  $+0.6\%$

across all 41 SOI scenarios; if there is no bycatch, this range becomes  $-1.8$  to  $+1.7\%$  (right-hand column, Fig. 2). Even more variation occurs for the probability of a decline (as estimated by the proportion of projections that show a decline): if weka-depredation is again 0.11, it ranges from 0.30 to 1.00 when bycatch is 0.01, and from 0.14 to 1.00 when there is no bycatch (right-hand column, Fig. 3). For the probability of a decline greater than 50 % and weka-depredation = 0.11, the range is from 0.12 to 1.00 when bycatch = 0.01, and from 0.04 to 0.93 when there is no bycatch (right-hand column, Fig. 4).

If weka-depredation is reduced to 0, the posterior median growth rate ranges from  $-2.3$  to  $+1.2\%$  when bycatch is 0.01, and from  $-1.3$  to  $+2.2\%$  when there is no bycatch (left-hand column, Fig. 2). Likewise, the probability of a decline ranges from 0.20 to 1.00 when bycatch = 0.01, and from 0.11 to 1.00 when there is no bycatch (left-hand column, Fig. 3); the probability of a decline greater than 50 % ranges from 0.08 to 1.00 when bycatch is 0.01, and from 0.01 to 0.41 when there is no bycatch (left-hand column, Fig. 4).

As expected, the climate-model projections with higher mean values of  $z_t^f$  and  $z_t^s$  led to the more optimistic population projections: there were clear linear relationships between the posterior median growth rate and the mean value of both of these indices (not shown), for each combination of bycatch, harvest, and weka-depredation, with the correlation coefficients ranging from 0.86 to 0.90.

#### 3.2. Aggregation over climate models

In order to obtain an overall assessment of risk, we aggregated the posterior distributions over all SOI scenarios, a posterior sample of size 410 000 (Fig. 5). We focus on the following levels of bycatch, harvest, and weka-depredation:  $b = 0$  or 0.01,  $h = 0$  or 0.11, and  $w = 0$  or 0.11. Over all 4 combinations of harvest and weka-depredation, the effect of reducing bycatch from 0.01 to 0 is to increase the posterior median growth rate by 1 percentage point, decrease the probability of a decline by 0.25–0.29, and decrease the probability of a decline greater than 50 % by 0.09–0.20. The effect of reducing harvest from 0.11 to 0 is somewhat smaller: over all 4 combinations of bycatch and weka-depredation, the effect is to increase the posterior median growth rate by 0.5 percentage points, decrease the probability of a decline by 0.12–0.15, and decrease the probability of a decline greater than 50 % by 0.02–0.12. Finally, as we might expect, the effect of reducing weka-depre-

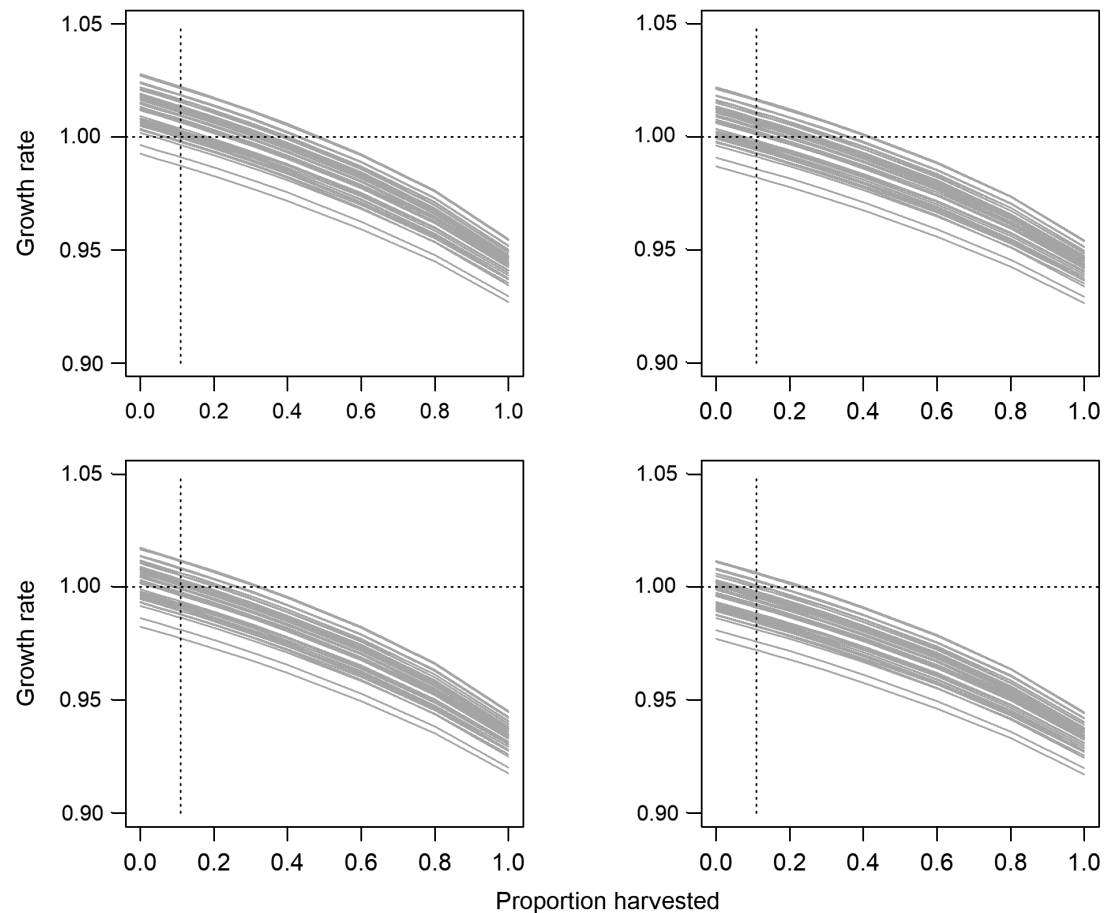


Fig. 2. Posterior median for annual growth rate over the period 2019–2070 versus proportion of chicks harvested each year when there is no bycatch (top row), bycatch is 0.01 (bottom row), and there is no weka-depredation (left column), or weka-depredation is 0.11 (right column). Each line represents 1 of 41 Southern Oscillation Index (SOI) scenarios. For each SOI scenario, the projections were based on model-averaged posterior distributions for the demographic parameters obtained by modelling data for the period 1976–2005. The estimate of the mean annual proportion of chicks harvested during this period (0.11) is indicated by a vertical dotted line, and a stable population (growth rate = 1) is indicated by a horizontal dotted line

duction from 0.11 to 0 is almost identical to that for reducing harvest: over all 4 combinations of bycatch and harvest, the effect is to increase the posterior median growth rate by 0.5–0.6 percentage points, decrease the probability of a decline by 0.12–0.16, and decrease the probability of a decline greater than 50% by 0.02–0.12.

With no bycatch, harvest, or weka-depredation, the posterior median growth rate is +1.3%, the probability of a decline is 0.17, and the probability of a decline greater than 50% is 0.01. Conversely, the probability of a decline is at least 0.76 when the proportion of chicks harvested is 0.6 or greater, for both levels of bycatch and weka-depredation.

Gauthier et al. (2016) advocated assessing what proportion of the variance in population projections is due to different components of the projection pro-

cess. We therefore estimated the proportion of the variance in the posterior sample (of size 410 000) of the logarithm of growth rate that was attributable to the climate models (as the logarithm of population growth rate will have a posterior distribution that is close to normal, this scale is more suitable for comparing variances). Over all combinations of bycatch, harvest, and weka-depredation, between 20 and 39% of the variance was due to the climate models, the remainder being due to the projection models and the uncertainty associated with the parameters in each projection model. The majority of the uncertainty is therefore associated with estimation of the demographic process, a conclusion akin to that of Gauthier et al. (2016) for a climate-dependent projection model of a greater snow goose *Chen caerulescens atlantica* population.



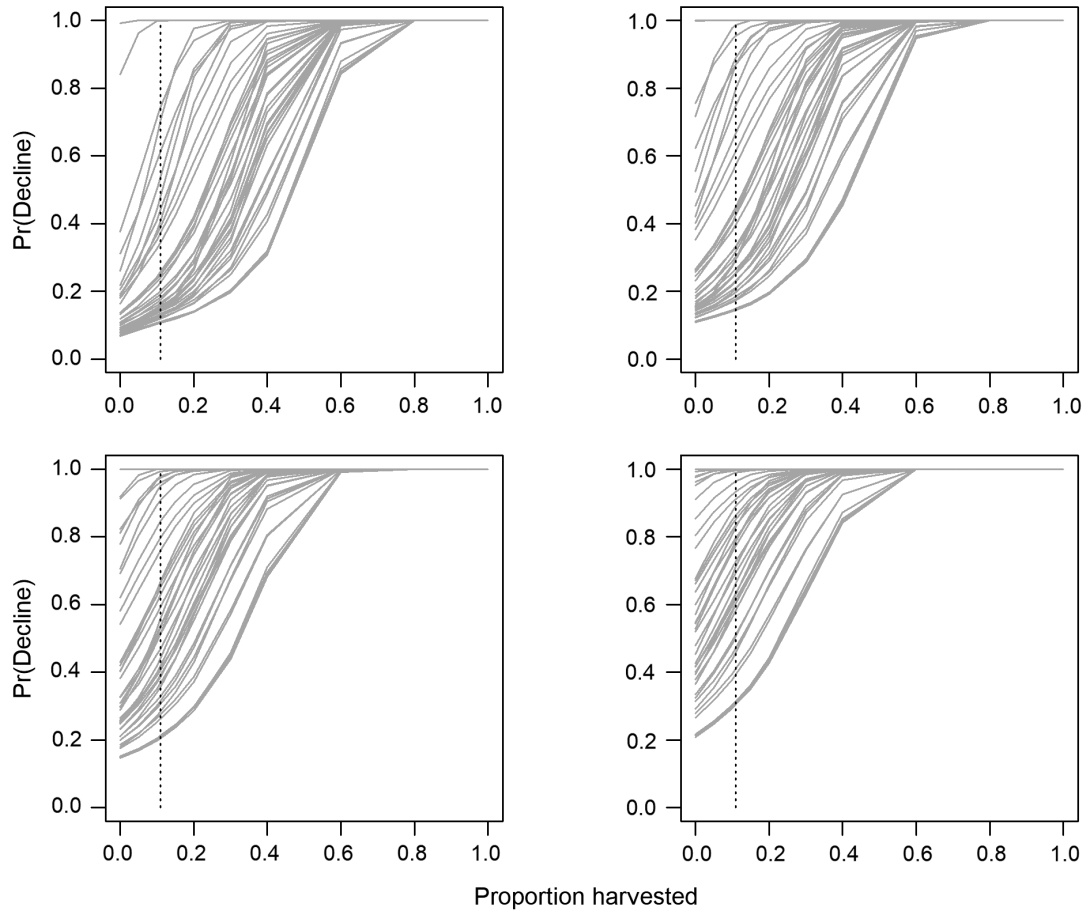


Fig. 3. Posterior probability of a decline over the period 2019–2070 versus proportion of chicks harvested each year when there is no bycatch (top row), bycatch is 0.01 (bottom row), and there is no weka-depredation (left column), or weka-depredation is 0.11 (right column). Other details as in Fig. 2

### 3.3. Sensitivity analyses

The effect of including ‘high’ levels of non-SOI annual variation in adult survival and fecundity (Eqs. 10 & 11) on the projections obtained using the best-fitting model (S-1F0), aggregated across all 41 climate models, are shown in Figs. S5–S7. For all combinations of harvest, weka-depredation, and bycatch, the posterior median annual growth rate decreased by 0.2–0.8 percentage points (Fig. S5), the width of the 95% CI for annual growth rate increased by 3.1–4.1 percentage points (Fig. S5), the change in the probability of a decline ranged from a decrease of 0.05 to an increase of 0.25 (Fig. S6), and the probability of a decline greater than 50% ranged from a decrease of 0.06 to an increase of 0.25 (Fig. S7). As we deliberately chose high values for  $\sigma_s$  and  $\sigma_f$ , we would expect that including the true amount of non-SOI variation would lead to the same qualitative changes, with the effects being less marked than in Figs. S5–S7.

If we again focus on the levels  $b = 0$  or 0.01,  $h = 0$  or 0.11, and  $w = 0$  or 0.11, the effects of changing bycatch, harvest, and weka-depredation were very similar for the original and modified versions of the S-1F0 model. The effects of such changes on the posterior median growth rate were almost identical for the 2 versions of the model, and also identical to the effects for the model-averaged projections in Section 3.2. The corresponding effects for the probability of a decline, and the probability of a decline greater than 50%, were slightly more variable for the modified S-1F0 model, compared to the original S-1F0 model, reflecting the increase in uncertainty caused by the addition of non-SOI annual variation.

Overall, the effect of including non-SOI annual variation was to decrease the estimate of the annual growth rate, increase the uncertainty in this estimate, and increase the probability of a decline. However, there was little impact on the effects associated with changing bycatch, harvest, and weka-depredation levels, especially in terms of the posterior median

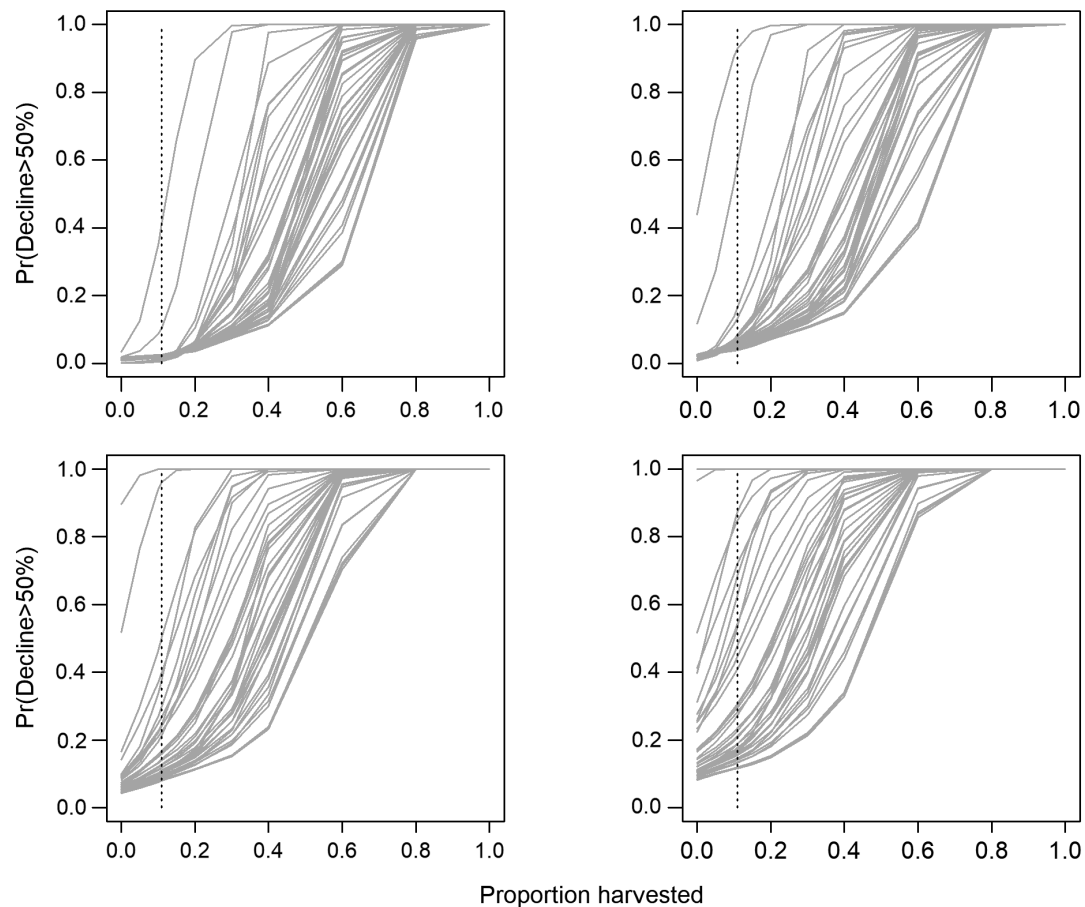


Fig. 4. Posterior probability of a decline greater than 50% over the period 2019–2070 versus proportion of chicks harvested each year when there is no bycatch (top row), bycatch is 0.01 (bottom row), and there is no weka-depredation (left column), or weka-depredation is 0.11 (right column). Other details as in Fig. 2

growth rate. Although we focus here on the effect of adding non-SOI annual variation to the best model (S–1F0), we obtained qualitatively similar effects for the other 7 models in Table 2, which implies that these conclusions will also apply to the results in Section 3.2, which are based on averaging over all 8 models.

Table 3 gives the sensitivities for each component of the best-fitting model (S–1F0), with the parameters set to their posterior medians, both  $z_t^s$  and  $z_t^f$  set to 0, and the levels of bycatch, harvest, and weka-depredation set to 0, 0.11, and 0.11, respectively (the sensitivities are relatively robust to the choice of these levels). The largest sensitivities are for bycatch and adult survival, as we would expect for a long-lived species, since these are the 2 components that directly affect the adult portion of the population. The adult survival sensitivity is very close to +1, which implies that a one percentage-point increase in adult survival will lead to the same increase in growth rate. Likewise, the sensitivity for bycatch is close to –1, so a one percentage-point decrease in bycatch level will also lead to a

one percentage-point increase in growth rate, exactly as we saw for the projections in Section 3.2. Thus elimination of bycatch worldwide would lead to at most an increase of one percentage point in the growth rate. The sensitivities for all of the other components are much smaller, with those for the mean and standard deviation of age at first breeding being negligible. However, some components of the model will vary more with environmental factors. For example, the sensitivity for fecundity (0.076) is much smaller than that for adult survival (1.020), but in a long-lived species, we expect fecundity to be more variable, in both space and time, than adult survival. For this reason, Table 3 also includes sensitivities for the 2 SOI indices, which summarise the relative effects of these indices on the population growth rate. The sensitivity for  $z_t^s$  is 0.032, while that for  $z_t^f$  is 0.005; thus a decrease from 0 to –2 (strong El Niño) in  $z_t^s$  will lead to a decrease of  $2 \times 0.032$  in the growth rate, a dramatic reduction of 6.4 percentage points, compared with the same change in  $z_t^f$  leading to a de-

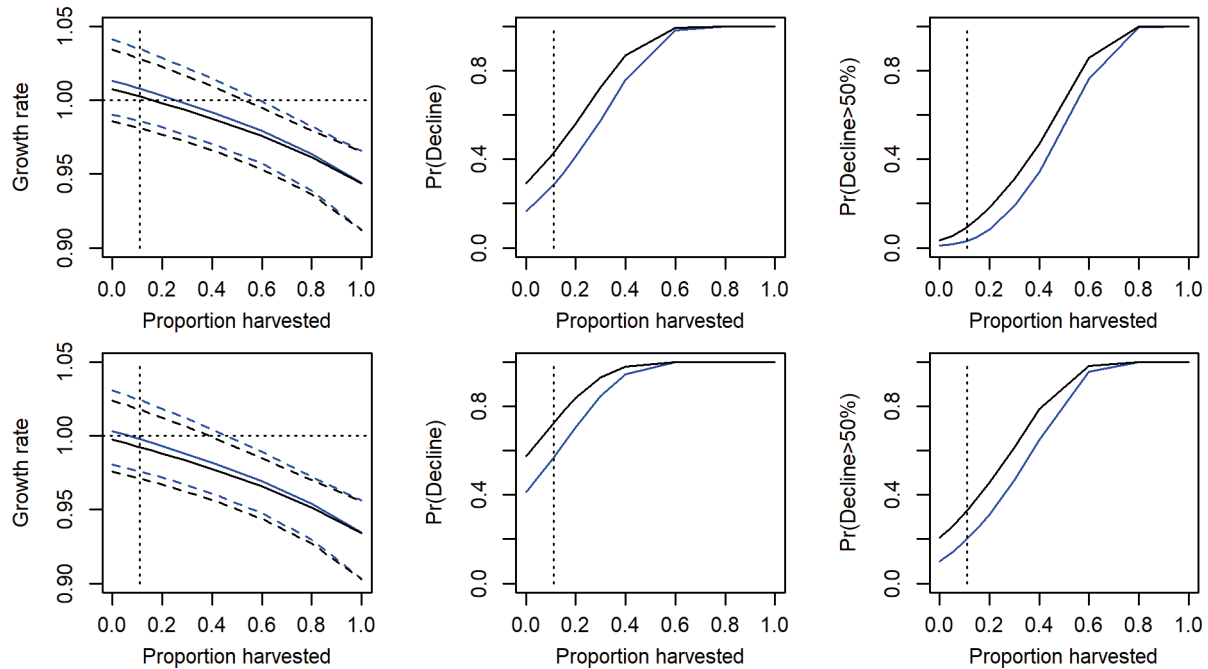


Fig. 5. Summaries of population projections over the period 2019–2070 versus proportion of chicks harvested each year, aggregated over 41 Southern Oscillation Index (SOI) scenarios. The plots show annual growth rate (left column), posterior probability of a decline over the projection period (middle column), and posterior probability of a decline greater than 50% over the projection period (right column), when there is no bycatch (top row) or bycatch is 0.01 (bottom row). The plots of annual growth rate indicate the posterior median (solid) and 95% credible limits (dashed), for no weka-depredation (blue) or weka-depredation is 0.11 (black). The plots of the posterior probability of a decline, and the posterior probability of a decline greater than 50% are also given for no weka-depredation (blue) or weka-depredation is 0.11 (black). The projections were based on model-averaged posterior distributions for the demographic parameters obtained by modelling data for the period 1976–2005; the estimate of the mean annual proportion of chicks harvested during this period (0.11) is indicated by a vertical dotted line, and a stable population (growth rate = 1) is indicated by a horizontal dotted line

crease of  $2 \times 0.005$  in the growth rate, a reduction of 1 percentage point. Thus the combined effect on adult survival (and hence juvenile survival) and fecundity of going from a scenario with  $z_t^f = z_t^s = 0$  to a

strong El Niño is much greater than elimination of all bycatch. Finally, the sensitivities for harvest and weka-depredation are both  $-0.046$ , indicating that a 10 percentage-point decrease in harvest or weka-depredation level will lead to a  $-0.046 \times -0.1 \approx +0.005$  change in growth rate, an increase of half a percentage point, again matching what we saw for the projections in Section 3.2.

Table 3. Sensitivity coefficients for the deterministic version of the S-1F0 model (see Section 2.2), when the parameters of the model are set to their posterior medians,  $z_t^f$  and  $z_t^s$  are both set to 0, and the levels of bycatch, harvest, and weka-depredation are set at 0, 0.11, and 0.11, respectively. SOI: Southern Oscillation Index

Component	Model notation	Sensitivity
Bycatch	$b$	-0.967
Harvest	$h$	-0.046
Weka-depredation	$w$	-0.046
Mean age at first breeding	$\mu_p$	-0.002
SD age at first breeding	$\sigma_p$	0.000
Fecundity	$f$	0.076
Ratio of juvenile to adult survival	$r$	0.121
Adult survival	$s^a$	1.020
SOI index for fecundity	$z^f$	0.005
SOI index for adult survival	$z^s$	0.032

#### 4. DISCUSSION

In this study we have used population projection models (which allow for separate effects of SOI, bycatch, weka-depredation, and harvest) and climate-model projections of SOI, to assess the potential impact of different management strategies for the vast majority of the A-NZ tītī population, which is on the Rakiura Tītī Islands. We found that the variation between climate model projections of SOI was large enough to lead to a wide range of outcomes for levels of bycatch, harvest, and weka-depredation that are of interest to management. Despite this, the effect of

changing these levels of bycatch, harvest, and weka-depredation on the population growth rate were fairly consistent over all 41 projections of SOI over the period 2019–2070. For example, over all SOI projections, the elimination of global bycatch would lead to an increase of approximately 1 percentage point in the growth rate (regardless of the levels of harvest and weka-depredation), but the population growth rate that would result from such an intervention varies substantially between SOI projections. In addition, we estimate that strong El Niño events will have the greatest impact on population growth rate, particularly via their impact on adult survival rate.

Although a significant amount of uncertainty in the projected population growth rate was caused by differences between SOI projections, the majority of this uncertainty was caused by the estimation process, i.e. the choice of population projection model and estimation of the demographic parameters in each model.

Our results showed that when the proportion of chicks harvested was high (0.6 or greater), population decline was inevitable, regardless of future SOI conditions. Historically, harvest levels appear to have been below this level: for one of the islands surveyed by McKechnie et al. (2010), the estimate of the proportion of chicks harvested was as high as 0.54, but this estimate was at least 0.2 higher than those for the other islands in the same study. Predation by introduced mammals has led to chick mortality at very high levels on the mainland of A-NZ, with rapid declines and localised extinctions of breeding colonies having been observed (Jones 2000, Lyver et al. 2000).

In order for our population projections to provide a reliable assessment of the effects of alternative management strategies, a number of assumptions must be made. We need to assume that the relationship between adult survival and SOI in the future will be similar to that estimated over the period 1976–2005. The same applies to fecundity, but to a lesser extent, as the sensitivity of population growth rate to the SOI index associated with fecundity is much smaller (Table 3 and Section 3.3). We also need to assume that the 41 SOI projections reflect the true range that will occur in the future. For the period for which we fitted the demographic models (1976–2005), all of the climate models provided projections that were generally more positive than those observed, for each choice of lag for both  $z_t^s$  and  $z_t^f$ . However, simple comparison of the distribution of projections of the SOI values over the period 1976–2005 with those that were observed may be misleading. For example, the projections might be seen as more reliable if one

allowed for asynchrony between the projected and observed SOI values. We did not pursue this issue further, due to the inherent system-level uncertainties associated with climate models. Although projections from such models have improved greatly in the past decade (Rashid et al. 2013, Zhang et al. 2020), the recent CMIP5 models that we used are still known to be prone to errors in ENSO amplitude, period, irregularity, skewness, spatial patterns, or teleconnections (Flato et al. 2013, Bellenger et al. 2014, L. Chen et al. 2016, X. Chen et al. 2019). Complex potential interactions between wind, cloud, air, and sea surface temperature, thermoclines, upwelling, ocean currents, waves, and volcanic eruptions have been postulated as reasons for uncertainty in projections of future SOI frequency and intensity under global climate change mitigation scenarios (Chen et al. 2015, Hua et al. 2019). Thus it is currently impossible to predict with certainty whether El Niño events will be more frequent and/or more intense in the future. It is therefore unknown whether climate conditions will ensure an abundant and sustainable tītī harvest, or make this difficult in the coming decades, no matter what other harvest management interventions occur.

Even if the SOI does not change in frequency and intensity, population trajectory may change if the population responds to changes in climate fluctuations in new ways. Based on current evidence, it appears that survival and fecundity are most likely being affected by food availability or wind patterns during foraging trips in the Southern Ocean, although the timing and location remain uncertain (Raymond et al. 2010, Humphries 2015). Changes in food abundance and location may alter the shape of the function between survival and/or fecundity and SOI (Section 2.2). Also, long-term change in population abundance may release or impose density-dependent influences on survival and/or fecundity that alter the relationships observed during the 1976–2005 period.

Another important consideration when interpreting our results is that density-dependent changes in fecundity or adult survival may limit population growth rate, within the range of abundances predicted for some of the SOI scenarios. For example, with bycatch, harvest, and weka-depredation all set to 0, just over 9% of the projections (over all 41 SOI scenarios) led to a greater than 5-fold increase in population size over the period 2019–2070. Without empirical estimates of density-dependent relationships, it is impossible to predict how high densities will affect demographic rates and abundance. However, as tītī population density is currently consid-

ered to be well below historical carrying capacities (McKechnie et al. 2020), it seems likely that compensatory feedback would not occur until after significant increases in abundance.

A lack of fine-scale information on demographic rates, human-induced mortality, and migration rates between colonies (Coulson & Coulson 2008, Ludwig & Becker 2012) prevented us from considering spatial structure in our projection models. Consequently, our results must be considered as generalizations across the whole A-NZ population. For example, if fecundity on a particular island is considerably lower than assumed in the model, the effects of harvesting and predation there will be underestimated. Having said that, the demographic rates most likely to display variation between islands, such as fecundity, have less impact on population growth rate than adult and juvenile survival (Table 3), which are likely to be more influenced by factors acting at larger spatial scales.

Given the above assumptions, our projections must be interpreted in the vein of Caswell (2001), i.e. they are potential predictions, conditional on these assumptions being met. We have deliberately focussed on relative changes (e.g. annual growth rate rather than actual abundance) and on the effects of different management strategies (e.g. reducing bycatch or weka-depredation), as these are likely to be robust to failure of the assumptions (Fieberg & Ellner 2000, Caswell 2001, Coulson et al. 2001).

With the current levels of uncertainty associated with future SOI conditions, adaptive management (Holling 1978, Walters 1986, Berkes et al. 2000, Moller et al. 2009) is likely to be the only viable approach for safe-guarding both the tītī population and the cultural and ecological systems associated with the species. Traditional Rakiura Māori teachings and management conventions have greatly protected the tītī population through the centuries (e.g. killing of adult birds prohibited; access to the islands only allowed in the latter part of the season, to avoid disturbance of breeding adults; Kitson & Moller 2008). There is firm control of who can harvest tītī, and some regulation of where on the islands the birders can establish workhouses. Also, an assemblage of traditional teachings on habitat care and minimising disturbance are in place. Particularly important is the *rāhui* (temporary access ban) that prevents the birders from accessing the islands until late in the breeding season, and the total prohibition on harvesting or disturbing the adults. The 2 Rakiura Māori tītī committees, and their associated constitutions, bylaws, knowledge, commitment, and respect from the ma-

jority of birders are fundamentally important community assets. Most management systems would characterise these attributes as the keystones in the 'social capital' that will enable the birding community to protect the 'natural capital' (a thriving tītī population) on which sustainable harvesting depends. If depredation by weka and customary harvest continue to slow the population recovery, and El Niño events like those experienced in the 1990s become commonplace, the expected pattern could be the gradual slippage of the resource through a '2 steps forward and 3 steps back' trajectory. The critical question for the community is whether the passive mechanisms used in the past can adequately protect the birding tradition into the future. Adoption of an active adaptive management approach, led by Rakiura Māori, is likely to become increasingly important.

Links between southern feeding locations/conditions and lagged SOI measurements in the equatorial region were at first surprising, but are consistent with recent modelling that demonstrates correlations and dependencies of several widespread atmospheric and oceanic perturbations, including with the atmospheric variability in high latitudes of the Southern Hemisphere (Morioka et al. 2013, Lu & Liu 2018). Further monitoring and tracking of individuals with electronic devices (Shaffer et al. 2006) and close monitoring of adult survival, fecundity, and tītī abundance would perhaps be the most effective means of discovering these mechanisms. Ecological fluctuations linked to temporal and spatial shifts in bird feeding and movements can 'biomagnify' significant oceanic and atmospheric perturbations at the incipient stage of climate fluctuations (Humphries et al. 2015, Humphries & Möller 2017). They provide valuable clues for climate scientists to test and improve models of coupled oceanic and atmospheric drivers of climate perturbations. Improved understanding of where, when, and how El Niños start is not just the key to understanding whether a culturally-defining customary harvest of a seabird by Rakiura Māori will continue. It could also help predict and mitigate widespread impacts of El Niño on fisheries, agriculture, species recovery, environmental resilience, storm events, disease, and human wellbeing of the Pacific Ocean and Pacific Rim nations (IPCC 2014).

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