New Zealand Journal of Zoology, 2009, Vol. 36: 307–323

1175-8821 (Online); 0301-4223 (Print)/09/3603–0307

Estimating regional population size and annual harvest intensity of the sooty shearwater in New Zealand

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Abstract Recent comprehensive survey data from multiple New Zealand offshore islands were combined with demographic population models to produce the first formal estimate of the total population of sooty shearwaters within New Zealand territory. We estimated the total population over 1994–2005 to be 21.3 (19.0–23.6) million individual birds in the New Zealand region. This population consisted of 12.8 (12.0–13.6) million adults, 2.8 (2.5–3.1) million chicks, and 4.4 (4.2–4.7) million breeding pairs. Breeding sooty shearwaters were concentrated primarily around the southern islands of New Zealand, with 53% breeding in the Titi Islands surrounding Rakiura (Stewart Island). Rakiura Maori muttonbirders were estimated to harvest 360 000 (320 000–400 000) sooty shearwaters per year, equivalent to 18% of the chicks produced in the harvested areas and 13% of chicks in the New Zealand region. Overall, 11% of the chicks within the Tītī Islands live on unharvested ground. Systematic and widespread surveys of breeding colonies in South America are needed before a reliable global sooty shearwater population estimate can be calculated.

Keywords harvest intensity; population size; population structure; sooty shearwater; sustainability

Z09027; Online publication date 2 September 2009
Received 27 July 2009; accepted 1 August 2009

INTRODUCTION

The sooty shearwater (*Puffinus griseus*, whose chicks are known as tītī or muttonbirds) is an abundant, burrow-nesting, colonial, trans-equatorial migrant seabird. The species has been described as one of the most numerous and widely distributed seabirds in the world (Warham & Wilson 1982; Marchant & Higgins 1990; Heather & Robertson 1996; Taylor 2000). However, no reliable estimate of the global or regional population size has been made, as is the case for most of New Zealand's seabird populations (Taylor 2000). Sooty shearwaters migrate to the Northern Hemisphere during the austral winter (Shaffer et al. 2006). They predominate amongst the seabirds along the western seaboard of North America, especially along the Californian current (Veit et al. 1997; Oedekoven et al. 2001). Sooty shearwater chicks are harvested by Rakiura Māori, the southernmost Māori community in New Zealand (Stevens 2006; Lyver et al. 2007). The harvest, strictly limited to chicks, takes place in April and May on a number of Tītī Islands around Rakiura (Stewart Island).

Reliable estimates of the total size of seabird populations are needed to determine the relative risk of threats such as bycatch, predation at breeding colonies and harvesting. Population estimation can be used to assess species contributions to ecosystem or global scale processes (Brooke 2002) and to evaluate the use of the species as an indicator of

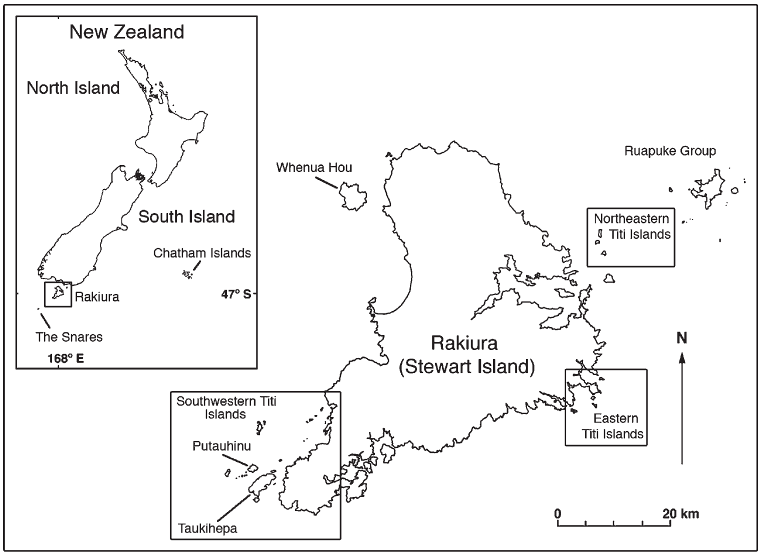

Fig. 1 Map of New Zealand showing North Island, South Island, The Snares Island chain, the Chatham Islands, and Rakiura (Stewart Island), including sooty shearwater breeding colonies (Tītī Islands) located around Rakiura.

global oceanic changes (Furness & Camphuysen 1997). Indications of a long-term decline of sooty shearwater numbers recently led the IUCN to upgrade their status from "Least Concern" to "Near Threatened" (Birdlife International 2004; Scott et al. 2008). We sought to provide a robust population estimate of sooty shearwaters from the past decade to provide a benchmark for future comparisons, conservation management, and to guide harvest limits.

The typically remote and inaccessible nature of the islands upon which many seabirds nest severely limits monitoring efforts (Knight et al. 2008). Burrow-nesting behaviour has also hampered reliable population estimation because of the difficulties inherent in relating burrow entrance density to the density of breeding pairs (McKechnie et al. 2007). The number of breeding pairs is a common measure of seabird population size (e.g., Marchant & Higgins 1990; Taylor 2000). Definition of a breeding pair can vary, and variation in population structure can affect the ratio between number of pairs and total population size. Accordingly, here we formalise an estimation method for sooty shearwaters and test a rule of thumb for extrapolating from breeding attempts suggested by Brooke (2004).

In this paper we (i) combine recent survey data and demographic population models to produce a formal estimate of the total New Zealand sooty shearwater population; (ii) compare and contrast the relative importance of the various colonies in the region; (iii) estimate the sooty shearwater population structure, (iv) detail the size of annual harvest and its intensity; and (v) list the gaps and key factors that must be addressed in order to further improve these estimates, facilitate the calculation of a global population estimate, and guide conservation management of sooty shearwaters.

METHODS

The main concentration of breeding sooty shearwaters in New Zealand is located on islands to the south of the South Island (Fig 1). There are sooty shearwater colonies on most of the 36 Tītī Islands located around Rakiura (Stewart Island), and a large population on The Snares island chain, c. 100 km further to the south-west. A colony also exists on Wheuna Hou (Codfish Island); a New Zealand nature reserve and the largest of the islands adjacent to Rakiura.

As part of our research programme assessing the sustainability of the tītī harvest, we have dedicated considerable research effort to surveying many of the colonies on these islands. Between 1999 and 2005 we surveyed 22 "*manu*" (Māori family harvesting areas on the breeding colonies) on 12 of the harvested Tītī Islands (Table 1). The manu covered varying areas and proportions of each island surveyed. In six cases the manu covered the entire island (Table 1) either because only one family harvests on the island, or because the island is harvested by several discrete families but is not split into individual manu (the "open" manu system, Kitson & Moller 2008). The remaining islands were split into two or more discrete manu. During this time we completed six other surveys within the Tītī Islands group on unharvested areas of islands (Table 1). For the two largest Tītī Islands, Taukihepa and Putauhinu, we have previously used this survey information to calculate estimates of the local sooty shearwater population and the tītī harvest on each island (Newman et al. 2008b; Bragg et al. 2009 this issue). After extensive surveys employing similar approaches we have also published formal estimates of the sooty shearwater colony sizes on The Snares and Whenua Hou (see Scott et al. 2008, 2009 for details of methods used). The information from these four published estimates (Table 2) is used alongside our additional measurements here to estimate the New Zealand regional population size.

Table 1 Location, area and number of harvested areas on 38 islands. Surveys on 22 manu took place between 1999 and 2005. Source shows papers in which specific individual island surveys have been previously reported.

	Island	Planar area (ha)	Area surveyed	Number of manu surveyed	Harvested	Source
Tītī Islands	Betsy	2.0	Entire	1	y	
	Big	17.3	Partial	1	y	
	Bunkers	10.7			y	
	Ernest	10.4	Partial	1	y	
	Herekopare	21.6			y	
	Horomamae	34.0			y	
	Joss's	16.1	Entire	1	y	
	Kaihuka	7.5			y	
	Kaimohu	9.4			y	
	Kaninihi	2.6			y	
	Kopeka	1.8			y	
	Kundy	17.1			y	
	Mokoiti	5.9			y	
	Mokonui	65.8	Partial	1	y	
	Pikomamaku nui	5.6	Entire	1	y	
	Pikomamaku iti	7.7			y	
	Pohowaitai	27.3	Entire	1	y	
	Pohutuatua	3.8			y	
	Poutama	25.9	Entire	1	y	Lyver (2000)
	Pukeweka	2.6	Entire	1	y	
	Pukuparara	1.0			n	
	Putauhinu	129.2	Entire	5	y	Bragg et al. (2009)
	Putauhinu nuggets	7.7	Entire		n	
	Solomon	21.0			y	
	Takawiwini	1.2			y	
	Taimaitemoika	7			y	
	Taukihepa	796.6	Partial	6	y	Newman et al. (2008b)
	Te Pohamatakiarehua	3.0			y	
	Tia	13.5	Partial	2	y	
	Timore	1.9	Entire		n	
	Wharepuaitaha	11.3			y	
Reserves	Whenua Hou / Codfish	1396.0	Entire		n	Scott et al. (2009)
	The Snares	280.0	Entire		n	Scott et al. (2008)
Ruapuke Group	Bird	1.0			y	
	Green	68.9			y	
	Hazelburgh	5.0			y	
	South	4.0			y	
	Topi	2.0			y	

General approach to population estimation

The overall approach we employed to estimate populations on each manu (or island) was as follows; we first measured area and burrow entrance density; second, we used an infrared burrowscope (see Lyver et al. 1998 for a detailed description) to check burrow occupancy and estimate chick density; third, we corrected estimates of chick density for known detection errors; and fourth, we used a population model to estimate the age-structure and proportion-at-age breeding in the population, and total population size for the manu. A detailed description of each stage is given below.

Calculating chick population size on individual manu

We subdivided each manu into between six and 14 strata. Boundaries of each strata, within the manu, were established using geographical features such as streams, ecotones and harvesting tracks. We randomly placed circular plots with a 3 m radius (28.27 m^2) within each stratum to sample burrow entrance density. The number of plots sampled ranged between 12 and 24 according to the size of the stratum. To estimate burrow occupancy we randomly established between 9 and 14 strip transects, each containing 20 entrances. We considered an entrance to be potentially viable if a tunnel extended >20 cm in length from the entrance, the shortest tunnel found to be occupied in previous studies (Lyver et al. 1998). We assessed all viable entrances within the transect with an infrared burrowscope to detect burrow occupants (Lyver et al. 1998).

The locations of section boundaries and transects were recorded using handheld GPS units. Two-dimensional (planar) areas for each island and manu were calculated from these points using GIS software (MapInfo Professional version 6.0) and aerial survey photographs (for more detail see Scott et al. 2008, 2009 this issue; Newman et al. 2008b; Bragg et al. 2009).

We estimated the total number of chicks on a manu $\hat{N}_a$ as

$$\hat{N}_a = \sum_i A_i \hat{c}_i$$

where A_i is the planar area, and $\hat{c}_i$ is the chick density (chicks m^{-2}), in stratum i, calculated as $\hat{c}_i = \bar{e}_i \bar{d}_i$ where $\bar{e}_i$ is the mean density of burrow entrances (entrances m^{-2}) in stratum i calculated

$$\bar{e}_i = \frac{1}{n_i} \sum_{j=1}^{n_i} e_{i,j}$$

where $e_{i,j}$ is the density of burrow entrances observed on plot j in stratum i ($j = 1,...,n_j$). Similarly, $\bar{d}_i$ is the mean number of chicks per burrow entrance in stratum i calculated

$$\bar{d}_i = \frac{1}{m_i} \sum_{k=1}^{m_i} d_{i,k}$$

is the number of chicks per burrow entrance observed on transect k in stratum i ($k = 1,...,m_j$).

Estimates of sooty shearwater burrow occupancy made using a burrowscope are known to be biased low (McKechnie et al. 2007). We calculated a manu-wide correction factor for burrowscope bias $\hat{K}$ using the method of McKechnie et al. (2007) such that

Table 2 Sooty shearwater population estimates (and range) on five Tītī Islands, from published surveys taken between 1994 and 2006. Source shows papers in which specific surveys have been reported.

Island	Population estimate	95% confidence limits		Year	Source
		Lower	Upper		
Putauhinu	374 000	331 000	417 000	2005	Bragg et al. (2009)
The Snares*	393 000	165 000	621 000	1996–2001	Scott et al. (2008)
Whenua Hou*	132 000	82 000	181 000	2001–06	Scott et al. (2009)
Taukihepa	807 000	713 000	901 000	1999–2005	Newman et al. (2008b)
Poutama 1994†	93 000	64 500	125 000	1994	Lyver et al. (2000)
Poutama 1995†	98 000	78 000	120 000	1995	Lyver et al. (2000)
Poutama re-estimated 1994†	62 000	38 000	85 000	1994	Current paper
Poutama re-estimated 1995†	68 000	53 000	83 000	1995	Current paper

*Population estimates from The Snares and Whenua Hou were calculated from the numbers of burrow entrances reported in Scott et al. (2008) and Scott et al. (2009) respectively, using the model described in the Methods. † Lyver's (2000) estimate of the number of chicks on Poutama in 1994 and 1995 utilised an area estimate for the island of unknown source which was substantially larger than our estimate using GIS software (60 versus 26 ha). We re-estimated the number of chicks on Poutama using the raw entrance density and occupancy data provided by Lyver (2000), our statistical methods, and the new area estimate.

$$\hat{K} = \frac{n_T}{\sum_x \frac{n_x}{\hat{g}(x)}}$$

where n_T is the total number of chicks detected, n_x is the count of chicks at each distance increment (10 cm intervals), both pooled over all transects on the manu, and $\hat{g}(x)$ is the detection probability at that distance, estimated using the simple detection function of McKechnie et al. (2007).

We can now estimate the population of chicks corrected for burrowscope bias $\hat{N}_b$ as $\hat{N}_b = \hat{N}_a / \hat{K}$. In the absence of three-dimensional estimates of the surface area of each manu, we used measurements of slope at each transect to correct for the negative bias incurred when relying on planar estimates. This assumes that slope measurements taken on transects provide a random representation of the actual slope of the manu. A corrected estimate of the population size, is now given by $\hat{N}_c = \hat{N}_b / \bar{b}$ where $\bar{b}$ is the mean over all transects of $b_k = 1/\cos(\theta_k)$ and θ_k is the slope measured on transect k using an inclinometer. Dividing $\hat{N}_C$ by the total area of the manu A gives an overall estimate of chick density $\hat{d}_C$. Note that this density overestimates true density slightly because A is a planar estimate of area. However, this simplifies, and is subsequently corrected for, in later calculations. Calculating the total number of entrances $\hat{N}_e$ is simply

$$\hat{N}_e = \sum_i A_i \bar{e}_i$$

Estimating chick population size on unsurveyed areas

Except on seven of the Tītī Islands where we surveyed a single manu covering the entire island (hence $\hat{N}_C$ is our estimate of population size of chicks on the entire island) we calculated the total population of chicks on partially unsurveyed islands as

$$\hat{N}_c = \hat{d}_c A$$

where $\hat{d}_C$ is the density of chicks on the surveyed manu on the island and A is the total planar area of breeding habitat on the island.

To estimate an appropriate general chick density $\hat{d}_g$ to apply to other islands in the region that could not be surveyed at all, we calculated an average across 12 of the surveyed Tītī Islands. We removed the density estimates of Whenua Hou and The Snares, as they display characteristics (distance from unsurveyed Tītī Islands, island size, extreme habitat differences) that make their suitability for extrapolation uncertain. We calculated $\hat{d}_g$ as a simple mean, unweighted by area, to prevent the density estimate from Taukihepa (Big South Cape) from dominating the calculation. For each of the unsurveyed islands, the total population size of chicks is now $\hat{N}_c = \hat{d}_g A$ where A is again the planar area of the island. As we are using $\hat{d}_g$, which accounts for three-dimensional surface area estimates on the surveyed islands, this is the correct population estimate and assumes that slope measurements made on surveyed islands are representative of the overall population of islands we are concerned with. Our estimate of the New Zealand population of chicks is now simply

$$\hat{\hat{N}}_c = \sum_i \hat{N}_{ci}$$

over the i islands.

Harvest estimates

As part of each Tītī Island manu survey we estimated harvest intensity (proportion of chicks harvested) from data on the total number of chicks removed in that year, as provided by the harvesters. From these 21 manu-specific estimates of harvest intensity we calculated the overall mean harvest intensity. For each of the harvested islands that were unsurveyed, we used this overall mean estimate of harvest intensity to estimate the total number of chicks harvested. On partially surveyed islands we assumed harvest intensity was the same on the manu that were not surveyed as on those that were surveyed on the same island.

Estimating total population size from a demographic model

We constructed a deterministic Leslie matrix model (Leslie 1945) assuming a post-breeding census counting 21 age-classes (0–20+), defined immediately before the start of the harvesting season (1 April). The first age-class (0) represented the almost fully developed chicks, and the twenty-first age-class (20+) was a recycling "plus group". The projection matrix A corresponding to the model was

$$A = \begin{pmatrix} f_0 & f_1 & \cdots & f_{19} & f_{20+} \\ s_0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{19} & s_{20+} \end{pmatrix}$$

Fecundity in each age-class i was calculated as

$$f_i = 0.5 s_{i-1} \pi_i p v$$

where s_i was the probability that an individual in age-class i survived to the next class, π_i was the probability that an individual in age-class i was an adult, p was the proportion of adults that laid an egg in any given year and v was the probability that an egg produced a chick on 1 April.

We constructed three projection matrices representing populations on The Snares, Whenua Hou, and a generic Tītī Islands population. Parameter estimates utilised for each model are specified in Table 3. The Snares projection matrix was modified so set the census immediately after egg laying, as this was the period when population monitoring was most consistent. Fecundity in this model then became

$$f_i = 0.5 s_{i-1} \pi_i p$$

and first year survival was modified to $s_0 v$.

We assumed that adult survival was constant across populations, because this parameter was generally related to broad-scale factors (Clucas et al. 2008). Survival probabilities $s_{>1}$ were assumed to be equivalent to the estimates given by Clucas et al. (2008). We allowed breeding success to be site-specific, as local conditions (e.g., population density, rainfall) could conceivably influence it. We used estimates by Newman et al. (2009) for The Snares and Whenua Hou as given in their respective models, while for the Tītī Islands model we utilised the mean of these estimates (weighted by their variance). We constructed a model for each individual Tītī Island based on the generic Tītī Islands model but allowing for site-specific estimates of h, the proportion of chicks present on 1 April that were harvested before fledging.

We assumed that survival in the first 2 years was constant (i.e., $s_0 = s_1$), and calculated it by parametising the projection matrix (for The Snares, Whenua Hou and the Tītī Islands separately), calculating the asymptotic population growth rate of the model λ_m (as given by the dominant eigenvalue of the matrix), and constraining $\lambda_m = \lambda_o$ by adjusting s_0/s_1, where λ_o is the observed population growth rate at that island over the period when the other population parameters were estimated (McKechnie et al. in press b). We assumed that the estimate of population growth rate observed on Putauhinu (McKechnie et al. in press b) was suitable to apply to the generic Tītī Islands model. Survival from age-class zero to age-class one was modified to $s_0(1–h)$ on those islands where chicks were harvested.

We estimated the proportion of individuals in age-class i that were adults π_i by a two-step procedure described in outline by Newman et al. (2008b), and in detail by Fletcher et al. "Age at first return to the breeding colony, juvenile survival rate and transience of sooty shearwater (*Puffinus griseus*)" (in prep). We first estimated the proportion of birds in each age-class that would be at the colony at a given time using a method proposed by Spendelow et al. (2002). This required fitting an age-specific model

Table 3 Parameters utilised in the construction of age-structured population models for sooty shearwater populations on The Snares (S), Whenua Hou (W) and the Tītī Islands (T). Parameters with Normal on logit distributions resulted from logit-transformed proportions being generated from a normal distribution. Standard errors (SE) for these parameters are presented as estimates on the normal scale calculated using the delta method. N/A, Not applicable.

Parameter	Notation	Distribution	Island	Estimate	SE	Source
Proportion adults breeding	p	Normal on logit scale	All	0.722	0.018	J. S. Bradley unpubl. data
Breeding success	v	Normal on logit scale	S	0.349	0.108	Newman et al. (2009)
			W	0.763	0.032	Newman et al. (2009)
			T	0.722	0.033	averaged from above
Proportion chicks harvested	h	Normal on logit scale	IS	0.168[a]	0.023	McKechnie et al. (in press a)
Juvenile survival	s_0, s_1	Normal on logit scale	S	0.709	0.260	See Methods for details
			W	0.506	0.147	See Methods for details
			T	0.525	0.183	See Methods for details
Adult survival	$s_2 - s_{14+}$	Normal on logit scale	All	0.952	0.019	Clucas et al. (2008)
Proportion of individuals that are adults	π_i	N/A	All			Fletcher et al. (in prep.)
Observed asymptotic population growth rate	λ_o	Normal	S	0.993	0.003	McKechnie et al. (in press b)
			W	0.998	0.003	McKechnie et al. (in press b)
			T	0.995	0.009	McKechnie et al. (in press b)

for "probability of first-return' to mark-recapture data obtained from banding chicks at The Snares and at Taiaroa Head on the Otago Peninsula. We then combined this model with an estimate of the delay between arrival at the colony and first breeding attempt using data from a long-term study of short-tailed shearwaters *Puffinus tenuirostris* (Temminck, 1835) on Fisher Island, Tasmania, to estimate the proportion of individuals in each age-class that were adult (J. S. Bradley unpubl. data). The net result was an estimate of 7.9 years as the mean age at first reproduction (Newman et al. 2008a; Fletcher et al. in prep.).

The asymptotic population growth rate λ was given by the dominant eigenvalue of the projection matrix A, while the stable age distribution w was given by the corresponding right eigenvector (Caswell 2001). The total population size was given simply by

$$N=\sum_{i=0}^{20+} n_i$$

where n_1 was the number of individuals in age-class i. Given that we could calculate the stable age distribution, and n_0 had already been estimated above ($\hat{N}_C$), then it was simple to estimate the total population size as

$$\hat{N}_T = \hat{N}_c / w_0$$

where w_0 was the first element of the stable age distribution (vector) corresponding to the chick age-class (0).

We defined breeding pairs as the number of eggs laid in the breeding season being surveyed, calculated as $\hat{N}_{BP} = \hat{N}_C / v$. For comparative purposes we also calculated the total adult population (including sexually mature birds not breeding in the current season as well as breeding pairs) as

$$\hat{N}_A=\hat{N}_c \sum_{i=0}^{20+} \pi_i \frac{w_i}{w_0}$$

where w_i was the element of the stable age distribution corresponding to age-class *i.*

We obtained confidence intervals for the harvest, number of breeding pairs, adults and total population estimates by Monte Carlo simulation, in which each model parameter was resampled 1000 times from its estimated sampling distribution (Davidson & Hinkley 1997). Throughout this paper we report the calculated (empirical) means. No correction was deemed necessary, as the difference between the calculated mean and bootstrapped mean was small (typically less than 2%).

Assessing the size of colonies elsewhere in New Zealand

In order to extend our local estimate out to the rest of the New Zealand region we searched extensively for other current or historical information on sooty shearwater colonies around the New Zealand coast and islands. As part of this research effort we sent requests to 21 ornithologists, seabird researchers, and wildlife managers around New Zealand in 2006, asking for any information about sooty shearwater colonies. The pooled information they supplied is summarised in Appendix 1. Most of the known colonies located beyond our study area are small; few were estimated to number more than a few thousand birds: the largest was Rangatira Island, The Chathams, with only 17 000 burrow entrances in 1994 (Nilsson et al. 1994). Many of these informal records were difficult to incorporate into our regional population estimate because they were anecdotal, ambiguous, or over 40 years old.

The Otago and Southland coastlines have been given more recent and detailed attention (Hamilton & Moller 1995; Hamilton et al. 1997; Jones 2000, 2001; Jones et al. 2003). Jones (2000) found that most of the mainland petrel breeding sites he studied were small and declining rapidly, fitting the general pattern of decline since the first arrival of introduced predators (Taylor 2000). Although not all of the historical records in the region were checked, most were considered to be small or extinct (Hamilton et al. 1997). Taiaroa Head was the only colony reported by Jones (2000) along the entire mainland coastline that had more than 150 entrances. It contains around 2000 entrances, and benefits from the predator control focused on the nearby royal albatross (*Diomedea epomophora*) colony.

RESULTS

Population estimates

Our model estimated that 2.8 (2.5–3.1) million chicks, and 4.4 (4.2–4.7) million breeding pairs, inhabited the nesting colonies of the New Zealand region during the breeding seasons of 1994–2006. This equated to a total regional population of 21.3 (19.0–23.7) million sooty shearwaters, of which 12.8 (12.0–13.6) million birds were adults.

Examining the regional distribution of this total population, we estimated that there were 3.1 (2.9–3.3) million breeding pairs of sooty shearwater nesting each year in the Tītī Islands group surrounding

Rakiura. This equated to an estimated 8.9 (8.2–9.5) million adults, 2.2 (2.1–2.3) million chicks and a total population of 14.6 (12.9–16.3) million individual birds. This Tītī Islands population represented 69% of all sooty shearwaters in New Zealand in those years (Table 4).

Summaries of the population estimates for the four intensively studied islands are given in Table 5. The largest colony was on The Snares, where there were an estimated 5.5 (3.9–7.1) million birds, or 26% of the total New Zealand population. By contrast, the estimated number of chicks, 393 000 (166 000–621 000) on the island, represented just 14% of the New Zealand estimate. On Taukihepa alone, the largest of the Tītī Islands, we estimated that there were 5.3 (3.9–6.7) million individuals, or 25% of the total number of individuals in New Zealand.

Harvest intensity estimates

We estimated that 360 000 (320 000–400 000) chicks were harvested each year during our survey. Ninety-eight percent of these were from the Tītī Islands, with the remaining 2% harvested from the nearby Ruapuke Group. Overall we estimated that 294 000 (254 000–333 000) chicks were harvested per year on the Tītī Islands in the southwestern group (see Fig. 1 for location). The harvest intensity reduced to 16% (14–18%) as a proportion of all chicks on the Tītī Islands, and further still to 13% (11–15%) as a proportion of all chicks produced each year in the New Zealand region (Table 4). We estimated that, within the Tītī Islands, only 11% of all chicks are hatched on the unharvested areas between the birded manu or on the unharvested islands (Fig. 2).

DISCUSSION

Survey coverage of islands

There were 56 manu on the 36 Tītī Islands, of which we surveyed 21. We visited 14 islands in total, and estimated sooty shearwater population

Table 4 Total sooty shearwater population estimates for New Zealand and sub-regions. Standard error (SE) and coefficient of variation (CV) are given.

	Total New Zealand population	
Chicks	2 790 000 ± 132 000 (0.05)	
All birds	21 300 000 ± 1 170 000 (0.05)	
Adults	12 800 000 ± 398 000 (0.03)	
Breeding pairs	4 410 000 ± 127 000 (0.03)	
Harvested	360 000 ± 19 900 (0.06)	
Harvest intensity	0.129 ± 0.009 (0.07)	
	Total Tītī Islands population	Proportion of total New Zealand population
Chicks	2 210 000 ± 62 300 (0.03)	0.79
All birds	14 600 000 ± 843 000 (0.06)	0.69
Adults	8 880 000 ± 316 000 (0.04)	0.69
Breeding pairs	3 060 000 ± 103 000 (0.03)	0.69
Harvested	351 000 ± 19 900 (0.06)	0.98
Harvest intensity	0.159 ± 0.01 (0.06)	
	Only harvested areas of Tītī Islands	Proportion of Tītī Islands population
Chicks	2 010 000 ± 59 500 (0.03)	0.91
All birds	13 300 000 ± 826 000 (0.06)	0.91
Adults	8 080 000 ± 232 000 (0.03)	0.91
Breeding pairs	2 790 000 ± 99 900 (0.04)	0.91
Harvested	351 000 ± 19 900 (0.06)	1.00
Harvest intensity	0.175 ± 0.011 (0.06)	
	All harvested areas in New Zealand	Proportion of total New Zealand population
Chicks	2 220 000 ± 62 000 (0.03)	0.80
All birds	14 600 000 ± 843 000 (0.06)	0.69
Adults	8 910 000 ± 316 000 (0.04)	0.70
Breeding pairs	3 070 000 ± 103 000 (0.03)	0.70
Harvested	360 000 ± 19 900 (0.06)	1.00
Harvest intensity	0.162 ± 0.010 (0.06)	

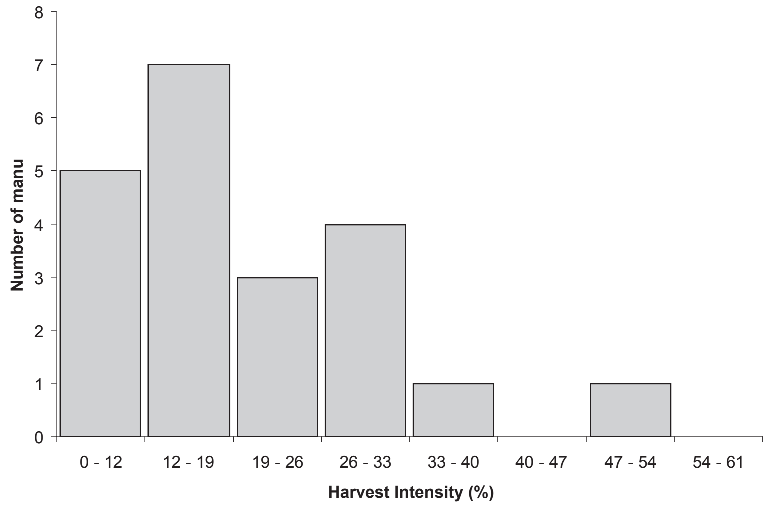

Fig. 2 Levels of harvest intensity on 21 surveyed manu, expressed as a percentage of chicks available removed during the harvest. Manu were surveyed between 1999 and 20005.

Table 5 Total sooty shearwater population estimates on four islands. Standard error (SE) and coefficient of variation (CV) are given. Harvest on Putauhinu comes from a total count rather than an estimate, so SE or CV are not reported.

		Proportion of total New Zealand population	Proportion of Tītī Islands population
	The Snares		
Chicks	393 000 ± 141 000 (0.29)	0.14	
All birds	5 520 000 ± 790 000 (0.14)	0.26	
Adults	3 200 000 ± 221 000 (0.07)	0.25	
Breeding pairs	1 100 000 ± 66 600 (0.06)	0.25	
	Whenua Hou		
Chicks	132 000 ± 24 300 (0.18)	0.05	
All birds	870 000 ± 189 000 (0.22)	0.04	
Adults	510 000 ± 97 200 (0.19)	0.04	
Breeding pairs	170 000 ± 33 160 (0.20)	0.04	
	Taukihepa		
Chicks	807 000 ± 47 100 (0.06)	0.29	0.37
All birds	5 310 000 ± 689 000 (0.13)	0.25	0.36
Adults	3 240 000 ± 251 000 (0.08)	0.25	0.36
Breeding pairs	1 120 000 ± 81 400 (0.07)	0.25	0.37
Harvested	138 000 ± 17 200 (0.12)	0.38	0.39
Harvest intensity	0.171 ± 0.024 (0.14)		
	Putauhinu		
Chicks	374 000 ± 21 600 (0.06)	0.13	0.17
All birds	2 520 000 ± 300 000 (0.12)	0.12	0.17
Adults	1 510 000 ± 110 100 (0.07)	0.12	0.17
Breeding pairs	520 000 ± 34 100 (0.07)	0.12	0.17
Harvested	31 300	0.09	0.09
Harvest intensity	0.084 ± 0.005 (0.06)		

size for 31 of the 36 Tītī Islands. The 14 islands we visited were spread throughout the Tītī Islands group; the five islands for which we did not estimate populations were not known to contain any sooty shearwater burrows. We therefore consider our survey coverage and effort comprehensive for the Tītī Islands, and any systematic bias seems unlikely. The only potential gap was the inclusion of islands in the Ruapuke group in Foveaux Strait (not formally defined as Tītī Islands, but subject to some limited harvesting) within the harvested islands group. In order to estimate the number of birds on these islands and the number harvested, we applied the chick density and harvest intensity that we had measured on the Tītī Islands to 10% of the area of Green Island—the only large birded island within the Ruapuke group. This value was informed by discussions with muttonbirders in the area, who estimated that only this proportion of the island contained colonies by the time of our survey. Given that the estimated total area of the Green Island colonies was only 81 ha, we are confident that their contribution to overall bird numbers and harvest totals was relatively minor.

Demographic parameters and population modelling

Our extrapolation from the estimated number of chicks to total population sizes on each colony used an age-based demographic model, incorporating sampling uncertainty. All but one of the parameters used in this model were obtained as part of this study (Table 3). Nevertheless, some simplifying assumptions were necessary. The proportion of adults breeding was borrowed from the short-tailed shearwater study (J. S. Bradley unpubl. data), but elasticity analyses suggest that any error in this parameter is unlikely to greatly affect our conclusions (Hunter et al. 2000). As it was not possible to measure breeding success directly on the Tītī Islands, we chose to apply the weighted average of estimates from The Snares and Whenua Hou, even though breeding success on these two islands is highly variable (0.35, 0.20–0.52 on The Snares and 0.76, 0.70–0.82 on Whenua Hou; Newman et al. 2009).

New Zealand regional estimate

The size of the sooty shearwater population breeding around New Zealand (or worldwide) has never been reliably estimated; a common situation for many New Zealand seabird species (Taylor 2000). Rough estimates (obtained by unspecified means) suggested "about five million pairs" for the New Zealand sooty shearwater population (Taylor 2000), and more than 20 million birds worldwide (Robertson & Bell 1984; Heather & Robertson 1996; Brooke 2004). Both figures compare favourably with our formal estimate of 21.3 (19.0–23.6) million individuals or 4.4 (4.2–4.7) million breeding pairs within the New Zealand region (including fledgling chicks).

Even if we adopt a generous approach and include all of the colony records in Appendix 1, the additional number of breeding pairs or birds around the rest of New Zealand is likely to be very small. Summing all of the colony estimates by attributing one breeding pair per entrance (likely to be an overestimate) only added 87 000 more pairs, while multiplying this by 4.84 (our estimate of the ratio of breeding pairs to individuals) adds only 421 000 more individuals. These possible additions represent 2% of our reported totals.

Logistically it was not possible to survey the entire New Zealand coastal region in detail. Large regions of South Westland, for example, remain inaccessible and rarely visited even today. Nevertheless, we consider it unlikely that any large colonies remain undetected on mainland New Zealand, although we cannot rule out entirely the possibility that some might have escaped the general decline and extinction of colonies accessible to introduced mammalian predators. Our population estimate should be considered a conservative estimate of the total New Zealand population, so supports an environmental precautionary principle in conservation management. Nevertheless, our estimate is the most comprehensive made for sooty shearwaters, and one of the more detailed ever made for any super-abundant and widely distributed seabird. The remaining uncertainty (5.5% coefficient of variation, CV) is small when scaled against the magnitude of the task of estimation.

Population structure

Our population model assumed that approximately 60% of all individuals in the New Zealand population were adult birds (defined as birds that have bred at least once), of which 41% of all individuals were breeding in the years surveyed; their chicks comprised 13% of the population. Brooke (2004) adopts the simple approach of multiplying the number of breeding pairs of each species by three in order to estimate the total numbers of each species of seabirds in the world (following Meininger et al. 1995; Hashmi 2002). However, he does suggest that for longer-lived species this multiplier should be around five. Our modelling results support his assumption, indicating that a multiplier of 4.84 for sooty shearwaters is appropriate.

Population decline

Despite sooty shearwaters retaining high abundance in New Zealand at present, numerous strands of evidence point toward a large population decline over the last three decades (Veit et al. 1997; Oedekoven et al. 2001; Scofield & Christie 2002; Scott et al. 2008; Moller et al. 2009). Unsurprisingly, most mainland colonies are rapidly disappearing or are already extinct (Hamilton & Moller 1995; Hamilton et al. 1997; Jones 2001; Jones et al. 2003), but island colonies are declining too. Over the 27 years between 1976 and 2001 surveys at one of the largest known colonies on the main (predator-free) Snares Island, there was a 37% decline in density of burrow entrances (Warham & Wilson 1982; Scott et al. 2008). Moller et al. (2009) report a similar rate of decline on six Tītī Islands (an overall annual rate of change in burrow entrance density of –1.0% (95% CI –2.3% to –0.1%) between 1961 and 1976 and 1994 and 2006. Clucas (2009), analysing eight birders' diaries, found that harvest tallies declined by 39% between 1978 and 2004.

Population decline triggered a recent IUCN decision to change the status of the sooty shearwater to "Near Threatened" (Birdlife International 2004). Suggested causes for these observed declines have commonly included climate change, fisheries bycatch, colony predation and habitat loss, and overharvest (e.g., Veit et al. 1997; Lyver et al. 1999; Uhlman et al. 2005; Scott et al. 2008). Fisheries bycatch has been estimated to have killed between 1.0 and 12.8 million sooty shearwater between 1952 and 2001 (Uhlmann et al. 2005). The large amount of uncertainty in these figures was attributed to the paucity of available observer data, lack of reported detail and inconsistencies among data sources. Such large uncertainly makes it difficult to assess the full impact bycatch may have had.

The bycatch threat was much reduced or removed in 1991 when an international ban on driftnet fishing was introduced (Uhlmann et al. 2005). Similarly, while predation remains an issue on most mainland colonies (Jones 2001), the recent eradication of ship rats (*Rattus rattus*) from Taukihepa (Coote & Blackwell 2006), means that 90% of the Tītī Islands (by area) and 93% of the regional population now nest on rat-free islands. Proposed eradication of weka (*Gallirallus australis*, a rail endemic to New Zealand but introduced to the Titi Islands, that depredates sooty shearwater eggs and chicks (Harper 2006), is a potentially very important conservation management action to help slow or reverse sooty shearwater population decline (Dillingham et al. 2007).

Climate change, however, remains a serious suspected threat (Newman et al. 2008a). Lyver et al. (1999) first reported a link between climate and the harvesters' annual tally of chicks, suggesting that climate change was affecting the birds' productivity. More recently, population modelling has indicated that the declining numbers seen over the last few decades can be simulated only by variations in climatic parameters. Although the exact mechanism driving this link needs to be further investigated, the fact that the small changes in climate observed so far appear to have such a large effect on the birds signals a warning, given the much larger climate changes currently predicted for the next 50 years (IPCC 2007).

Harvest intensity

The first published estimates of the total number of tītī harvested date back to newspaper reports from the *Western Star*, a newspaper based in Invercargill and published from 1873 to 1942. This newspaper published numerous articles relating to muttonbirding over the years (Russell & Gaw 1998), and often reported the annual harvest. The *Western Star* reported that 65 000 birds were harvested in 1901, and 200 000 birds in 1909. Several ornithological texts mention totals from the 1930s onwards (e.g., Howard 1940; Anglem 1969) and all estimate the total harvest at c. 250 000–300 000 chicks a year, but without mentioning how these estimates were made. Many of the historical publications listing harvest figures appear to refer back to these historical and published but unsystematic estimates (Scott & Moller 2001), so comparison with our estimate is problematic. The only semi-formal survey we know of estimated that 61 parties on all the southwestern islands harvested approximately 240 000 chicks in 1961 (Moller et al. 2009). Harvest was estimated to be reduced by 25% that year because the chicks were small and thin. If so, c. 320 000 chicks would have been harvested from the southwestern Tītī Islands in the late 1950s, compared to our current estimate from those same islands of 294 000 in 1994–2005. Lyver (2000) reported harvests of 13–24% and 17–28% on the island of Poutama in 1994 and 1995 seasons. We have previously reported harvest intensities of between 7 and 12% on Putauhinu (Bragg et al. 2009) and 16–21% on Taukihepa (Newman et al. 2008b). These estimates were incorporated into the calculations used to make the overall estimates we report here (Table 4; Fig. 2).

The level of population mixing (immigration/emigration) between islands remains a crucial consideration when interpreting our harvest intensity estimates. If the total regional population can be considered as one homogenous group, then the total regional harvest intensity is much less than the harvest intensity for only the harvested regions of the Tītī Islands (13% cf. 18%). If the global population can be considered one homogenous group, then the overall harvest intensity would drop yet again after allowing for the numerous unharvested populations supplying chicks from elsewhere. Despite the urgent need to know the level of mixing between sooty shearwater populations, the technical difficulties estimating it mean that we currently have no reliable estimate of this important parameter.

Hunter & Caswell (2005) assessed the sustainability of the tītī harvest by employing an algorithm developed under the United States Marine Mammal Protection Act. This approach essentially calculated the maximum reduction in population growth rate (λ) due to harvest that could be permitted. They estimated that, in the absence of any additional adult mortality (for example caused by fisheries bycatch), a reduction in λ of 2% should be sustainable—which roughly translates to a harvest intensity of around 31% (see fig. 7, Hunter & Caswell 2005). Based on their estimates, our highest mean harvest intensity estimate (18%) is likely to be sustainable. However, there was considerable variation in harvest intensity between manu (Fig. 2) which relates partly to variation in the density of chicks, but mainly to the number of "person-days" spent hunting in a season on that area (McKechnie et al. in press a). A more detailed assessment of harvest sustainability is currently in preparation and should better specify safe levels of harvest, but in the meantime our preliminary conclusion is that (a) average harvest intensity is potentially sustainable, but (b) two of the 21 manu we surveyed may well be exerting unsustainable localised impacts on tītī abundance (Fig. 2), unless the harvesting there is entirely compensated by rapid immigration from surrounding areas.

Global estimate of sooty shearwater population

One major barrier to reaching a reliable estimate of the global sooty shearwater population is a lack of knowledge about the distribution of colonies within the wide breeding range of the species throughout the southern temperate zones. Australian populations are few, and all are smaller than 1000 breeding pairs (Marchant & Higgins 1990). In a global perspective this means that the Australian population is relatively trivial. The South American population is relatively unknown, even though Reyes-Arriagada et al. (2007) recently published a population estimate for the island of Guafo, located off the west coast of Chile. They estimated that this comparatively large island (30 000 ha) supported 3.98 million (±3.87 million, 95% CI) breeding pairs. We recommend that this estimate be treated with extreme caution, for several reasons.

First, it appears that the estimated number of burrow entrances on the island was extrapolated from sampling in a single 7 ha area, located in one small region on the island. The CV of the estimate is 98%, a particularly large margin. Second, they estimated occupancy by monitoring toothpicks set in burrow entrances, a method which has been found to be an unreliable and seasonally variable indicator of occupancy (Hamilton 1998; Scott et al. 2008). Third, Clark et al. (1984) previously estimated the population on Guafo to be just 200 000 individuals, two orders of magnitude less than the figure reached by Reyes-Arriagada et al. (2007). Furthermore, Reyes-Arriagada et al. (2007) found little information on other South American colonies. Aside from the few unpublished reports and personal observations, Lawton et al. (2006) estimate the Diego Ramirez archipelago contains "several thousand pairs" and Clark et al. (1984) presumed the species was nesting on a few other islands in the area. Despite this paucity of data, Reyes-Arriagada et al. (2007) suggest that the South American population may be larger than that of New Zealand. Without further detailed information it is impossible evaluate this hypothesis. A reliable estimate for the South American region together with a better understanding of how populations from these two regions interact is considered a research priority.

CONCLUSION

We consider the methods employed here and the resulting population estimates to be reliable baselines for future monitoring of New Zealand's regional sooty shearwater population. Although comparisons with historical estimates are unreliable, numerous other strands of evidence point towards a significant population decline over the last 30 years. Recent trends indicate a stabilisation or even gradual increase (McKechnie et al. in press b), but it is too early to be certain. Although the threat of fisheries bycatch has now been virtually eliminated, and introduced predators have also been eradicated from most breeding areas, the full historical impact of these threats cannot yet be properly assessed. Because of the high likelihood of ongoing climate change impacts, the population trends of this abundant ecosystem engineer species (McKechnie 2006) still needs monitoring.

Monitoring is also needed for the ongoing assessment of harvest sustainability (Newman et al. 2008a). Harvesting alone is an inadequate explanation for the observed declines in the past three decades, because declines have been faster on unharvested colonies (Moller et al. 2009). The current level of overall harvest intensity across all Tītī Islands appears sustainable based on a preliminary assessment, however harvesting could be depressing breeding density on a few manu where some birders exert much higher than average harvest pressure (see Fig. 2).

Our conservative estimate of 8.8 million sooty shearwaters breeding in the New Zealand region suggests that the species remains a superabundant apex predator in the South Pacific, despite a major episode of decline in the late 1980s and early 1990s. The largest barrier to making a reliable global estimate of population size, and setting a firm benchmark for future comparisons, is lack of information on South American populations, and their degree of mixing with New Zealand populations.

ACKNOWLEDGMENTS

We thank scores of volunteers who helped conduct the scientific surveys described here; and the Rakiura Māori muttonbirders who hosted the research team and shared data to make this study possible. The overall project was directed by the Rakiura Tītī Islands Administering Body. Ben Knight made helpful comments on an earlier version of this manuscript and prepared it for publication. This survey was funded mainly by a Foundation for Research, Science and Technology PGSF grant to Rakiura Māori, but generous additional financial and logistic support for the overall project has been provided by the University of Otago, New Zealand Aluminium Smelters Ltd, Te Runanga o Ngāi Tahu and South West Helicopters.

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Appendix 1 Locations other than those mentioned in the text where sooty shearwaters have been recorded in the New Zealand region. Population estimate calculated from number of breeding pairs (where available) multiplied by our estimated ratio of breeding pairs to adults (4.84; see text for details). Where only the numbers of entrances were available, the number of breeding pairs was estimated using the ratio of breeding pairs to number of entrances of Taukihepa (0.67). When number of entrances or breeding pairs was given as an order of magnitude rather than a specific value, we took the middle value of that order. For example, "100s" was recorded as 500, "1000s" as 5000 etc.

Location	Region	Entrances	Breeding pairs	Population estimate	Source
South West	Three Kings	40		130	McCallum et al. (1985)
Three Kings	Three Kings				McCallum et al. (1985)
Motuopao	Northland	30		100	Pierce & Parrish (1993)
Motokawanui	Cavalli Group				Falla (1934)
Poor Knights	Northland				Harper (1983)
Mauitaha	Hen and Chickens		10	50	Tennyson & Pierce (1995)
Whatupuke	Hen and Chickens				McCallum et al. (1985)
Taranga	Hen and Chickens		500	2420	Skegg (1964)
Motumuka	Hen and Chickens		5000	24 150	McCallum et al. (1985)
Araara	Hen and Chickens		5000	24 150	McCallum et al. (1984)
Coppermine	Hen and Chickens				Merton & Atkinson (1968)
Kauwahaia	Auckland		40	190	G. Taylor (pers. comm.)
Cuvier	Cuvier	200		650	P. Scofield (pers. comm.)
Little Barrier	Hauraki Gulf				Imber (1987)
Mokohinau	Hauraki Gulf				Hicks et al. (1975)

Appendix 1 (*continued*)

Location	Region	Entrances	Breeding pairs	Population estimate	Source
Whakau	Mercury Group	225		730	Taylor & Parrish (1993)
Kawhitihu	Mercury Group		50	240	Skegg (1972)
Korapuki	Mercury Group				Hicks et al. (1975)
Ruamahua-nui	Aldermen Islands		50	240	Hicks et al. (1975)
White Island	Middle North Island				Hicks et al. (1975)
Moutohora	Bay of Plenty				Department of Conservation
Kapiti	Lower North Island		12	60	Susan Waugh (pers. comm.)
Pipinui Pt	Wellington				Bartle (1974)
Ko Areao	Chathams				Gaze (1986)
Little Mangere	Chathams		5000	24 150	Flack (1976)
Rabbit	Chathams		500	2420	Imber & Lovegrove (1982)
Rangitira/South East Island	Chathams		17 000	82 110	West & Nilsson (1994)
Fossil Point	West Coast, Golden Bay	16		50	Nelson Marlborough Conservancy
Tunnel Island	West Coast, Golden Bay	50		160	Ibid.
Nguroa Island	West Coast, Golden Bay	100		320	Ibid.
Kokomohua	Marlborough Sounds		20	100	Ibid.
Long Island	Marlborough Sounds		60	290	Ibid.
Middle Trio	Marlborough Sounds		200	970	Ibid.
Motuanauru	Marlborough Sounds	100		320	Ibid.
Motuara	Marlborough Sounds		60	290	Ibid.
Motungarara	Marlborough Sounds		100	480	Ibid.
Otuhaereroa	Marlborough Sounds	20		60	Ibid.
Penguin	Marlborough Sounds		20	100	Ibid.
Pepin Stack	Marlborough Sounds	10		30	Ibid.
Puangiangi	Marlborough Sounds		20	100	Ibid.
Stewart	Marlborough Sounds	20		60	Ibid.
Takapourewa/ Stephens Island	Marlborough Sounds		200	970	Ibid.
Takawhero	Marlborough Sounds		20	100	Ibid.
Titi Island	Marlborough Sounds	800		2590	Ibid.
Tonga Island	Marlborough Sounds		50	240	Ibid.
Victory	Marlborough Sounds	100		320	Ibid.
Motunau Island	Canterbury	230		750	K. Wilson (pers. comm.)
Stony Bay	Canterbury	55	17	80	Ibid.
Island Bay Island	Canterbury				O'Donnell (1995)
Otago-Southland*	Otago-Southland	3814		12 350	Jones (2001)
12 Mile Bluff	Westland		50	240	Paul Scofield (pers. comm.)
Mt Oneone	Westland	53	6	30	Kerry-Jayne Wilson (pers. comm.)
Greymouth	Westland		50	240	Booth (1982)
Open Bay Islands	Westland	10		30	Stirling & Johns (1969)
Perpendicular Pt, Punakaiki	Westland	10		30	Jackson (1957)
Te Kakahu	Fiordland	500		1,620	D. Scott (pers. obs.)
Open Bay	Fiordland				Hamilton et al. (1997)
Breaksea Island	Fiordland				Ibid.
Ackers Point	Rakiura	200		650	B. Bevan (pers. comm.)
Centre Island	Rakiura	100		320	Cooper et al. (1991)
Solander	Solander Islands				Cooper (1984)
Antipodes Islands	Subantarctic Islands	1000		3240	Tennyson et al. (2002)
Dent Island	Subantarctic Islands		5000	24 150	J. Timms (pers. comm.)
Macquarie	Subantarctic Islands	1777		5760	Brothers (1984)
Auckland Islands	Subantarctic Islands				Hamilton et al. (1997)
Campbell Island	Subantarctic Islands	2000		19 320	M. Charteris (pers. comm.)
			Total	240 000	

*Estimate is for entire Otago-Southland region.