

# Is management limiting the recovery of the New Zealand sea lion *Phocarctos hookeri*?

Bruce C. Robertson

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**Abstract** Pup production of the ‘nationally critical’ New Zealand sea lion *Phocarctos hookeri* has declined by 48 % since 1998, with fisheries bycatch playing a role in this decline. Current management of the sea lion population involves, amongst other measures, the setting of an annual bycatch limit based on Bayesian modelling of the sea lion population and fisheries information. Success of management scenarios is determined against two criteria, both of which involve keeping the sea lion population at or above 90 % of a modelled carrying capacity (6,987 mature individuals). Due to a lack of information on the pre-sealing abundance of the New Zealand sea lion, it is unclear whether the modelled carrying capacity represents a cap on sea lion recovery. Here, I use published estimates of genetic diversity based on microsatellite loci (expected heterozygosity,  $H_e$ ) of the New Zealand sea lion and other otariid species to estimate historical effective population size ( $N_e$ ). I then use existing knowledge of the ratio of  $N_e$  to census population size ( $N_C$ ) to determine a historical census population size of these species. Genetical estimates of historical  $N_e$  suggest that NZ sea lions were considerably more abundant (>68,000 individuals) historically than the current population estimate (11,855 animals). Importantly, the genetical estimate of historical population size suggests that the modelled carrying capacity (6,987 mature sea lions) is likely an underestimation of recovery potential of the species; hence, current management maybe limiting the recovery of the species.

**Keywords** *Phocarctos hookeri* · New Zealand sea lions · Species recovery · Management · Heterozygosity · Historical effective population size

## Introduction

The New Zealand (NZ) sea lion *Phocarctos hookeri* is New Zealand’s only endemic pinniped and is listed as ‘nationally critical’ under the NZ threat classification system (Baker et al. 2010) and ‘vulnerable’ and projected in decline by the IUCN (Gales 2008). Once widespread around the NZ coastline, the population was extirpated from much of this range by subsistence hunting and early nineteenth century commercial sealing (Childerhouse and Gales 1998). Breeding is now largely restricted to the NZ sub-Antarctic islands, where 71 % of pup production occurs at three breeding colonies at the Auckland Islands (Robertson and Chilvers 2011).

Pup production at the Auckland Islands has declined by 48 % since 1998 (Childerhouse et al. 2014), with the anthropogenic impacts of fisheries bycatch and resource competition playing a role in the decline (Robertson and Chilvers 2011; Chilvers 2012). For example, over 1,300 estimated sea lion mortalities have been attributed to fisheries bycatch in the Auckland Islands arrow squid (*Nototodarus sloanii*) trawl fishery (SQU6T) between 1992 and 2009 (Table 2 in Robertson and Chilvers 2011). Considerable effort has been expended by governmental and non-governmental agencies to mitigate and manage the sea lion–fisheries interactions (Chilvers 2008; Robertson and Chilvers 2011). These efforts have included designation of a 12 nautical mile no-take marine mammal sanctuary and marine reserve around the Auckland Islands, development of bycatch mitigation devices (sea lion

B. C. Robertson (✉)  
Department of Zoology, Allan Wilson Centre for Molecular Ecology and Evolution, University of Otago,  
PO Box 56, Dunedin 9054, New Zealand  
e-mail: bruce.robertson@otago.ac.nz

exclusion devices, SLEDs) and the setting of an annual fishing-related mortality limit (a FRML), which if exceeded can result in closure of the squid fishery for the year (Chilvers 2008).

Management of the species and squid fisheries interactions relies heavily on an age-structured Bayesian population model (the Breen–Fu–Gilbert (BFG) model; Breen et al. 2010), which models a range of sea lion, bycatch and fishing effort parameters simultaneously, including sea lion carrying capacity ( $K$ , carrying capacity of mature animals). Estimation of carrying capacity is pivotal for sea lion management, as the success, and hence, the choice of modelled management strategies ('harvest control rules') is determined against two criteria for future population projections: (1) based on 100-year runs, that the number of mature animals in a given year would be at least either 90 %  $K$  or 90 % of the mature numbers obtained in the absence of fishing; and (2) the average mature numbers from the second 50 years of 100-year runs should average at or above 90 % of  $K$  (Breen et al. 2010; Bradshaw et al. 2013).

Little information is available to inform estimation of the pristine abundance of the New Zealand sea lion (i.e. the historical  $K$ ). Scant sealing records indicate that NZ fur seals (*Arctocephalus forsteri*) and NZ sea lions were present in large numbers when the Auckland Islands were discovered by Europeans in 1806, but by 1830 few individuals of each species remained to be hunted (Childerhouse and Gales 1998). The only mention of NZ sea lions being harvested from the NZ sub-Antarctic (3,670 sea lion skins) was by two ships in 1825 (Childerhouse and Gales 1998). With a lack of information to inform the estimation of carrying capacity, sea lion management relies on the BFG model to estimate  $K$ , which currently is estimated as 6,987 mature animals (Breen et al. 2010). For comparison, current estimates of total sea lion population size (mature and non-mature individuals) are between 8,604 and 13,061 (Geschke and Chilvers 2010; Breen et al. 2010). Management strategies for sea lions are deemed successful if they maintain the population at 90 % of 6,987 mature animals in future population projections.

Information on the genetic diversity in a population can be used to estimate past population size (e.g. Schwartz et al. 1998; Wang 2005; Alter et al. 2007; Luikart et al. 2010; Ruegg et al. 2010; Hare et al. 2011). The level of neutral genetic diversity in a population at mutation-drift equilibrium equals  $4N_e\mu$  for autosomal nuclear DNA, where  $N_e$  is the genetically effective population size and  $\mu$  is the mutation rate for the DNA marker examined (Wang 2005). Therefore, with knowledge of genetic diversity and a mutation rate, a genetical estimate of long-term effective population size ( $N_e$ ) can be determined for a population (Lehmann et al. 1998; Hare et al. 2011).  $N_e$  is defined as the

closed, idealised population size that would maintain the observed level of genetic diversity at mutation-drift equilibrium (Hedrick 2000; Leberg 2005) or, in other words, the number of individuals contributing to each generation over evolutionary time. The time period over which  $N_e$  relates to depends on the molecular markers used to quantify genetic variation and the methodology used, but ranges from the contemporary (recent, one to a few generations), the historical (past, tens to thousands of generations), to the ancient time frame (thousands to millions of generations) (Wang 2005; Luikart et al. 2010).

Here, I use published estimates of genetic diversity based on microsatellite loci (expected heterozygosity,  $H_e$ ) of the New Zealand sea lion and otariid species to estimate historical effective population size ( $N_e$ ). I then use knowledge of the ratio of  $N_e$  to a census population size ( $N_C$ ) (e.g. Frankham 1995) to determine a historical census population size for the species. The genetically derived, historical population size of New Zealand sea lion is then compared with values obtained from the other otariid species and with the modelled carrying capacity presently used to set management strategies for the recovery of the species (Breen et al. 2010). This approach provides a valid methodology to examine the abundance of NZ sea lions prior to sealing (Curtis et al. 2011).

## Materials and methods

### Estimation of historical effective population size

A range of approaches has been proposed to estimate  $N_e$  from genetic data (Leberg 2005; Luikart et al. 2010). Here, I estimate long-term  $N_e$  (hereafter called historical  $N_e$ ) using published estimates of expected heterozygosity ( $H_E$ ) for microsatellite loci in the nuclear DNA of various otariid species (Table 1) using a formula based on the stepwise mutation model (SMM):  $N_e = ((1/(1 - H_e))^2 - 1)/8\mu$  (Lehmann et al. 1998), where  $H_e$  is the expected heterozygosity and  $\mu$  is the mutation rate of the microsatellite locus. This method was chosen because genetic diversity information for other genetic markers (i.e. mitochondrial DNA) is presently unavailable for the New Zealand sea lion. The mutation rate employed can lead to an order of magnitude change in  $N_e$  (see below); consequently, I used a conservative rate for microsatellite loci of  $1 \times 10^{-4}$  (Dallas 1992; Weber and Wong 1993).

Historical  $N_e$  reflects a harmonic mean of the effective number of adults contributing to the gene pool of a population over a number of generations (Hare et al. 2011). However, historical population bottlenecks have an important effect on the level of genetic variation and consequently impact the  $N_e$ . Indeed, the reduced population

**Table 1** Genetic diversity of microsatellite loci (no. of loci, no. of samples, average heterozygosity,  $H_e$ ), historical effective population size ( $N_e$ ) and historical census population size ( $N_C$ ) for two ratios of  $N_e$  to  $N_C$  for the New Zealand sea lion *Phocarctos hookeri* and various other otariids

Species	No. loci	$N$	$H_e$	$N_e$	$N_C$ 0.45	$N_C$ 0.11	$N_{\text{current}}$	$N_e:N_{\text{current}}$
New Zealand sea lion <i>Phocarctos hookeri</i>	21	1,351	0.66 <sup>a</sup>	9,563	21,251	86,938	11,855	0.807
New Zealand sea lion <i>P. hookeri</i>	22	39	0.72 <sup>b</sup>	14,694	32,653	133,581	11,855	1.239
Australian sea lion <i>Neophoca cinerea</i>	5	217	0.54 <sup>c</sup>	4,657	10,350	42,340	13,790	0.338
California sea lion <i>Zalophus californianus</i>	12	58	0.61 <sup>d</sup>	6,968	15,485	63,348	355,000	0.019
Steller sea lion <i>Eumetopias jubatus</i>	13	668	0.66 <sup>c</sup>	9,563	21,251	86,938	143,000	0.067
South American fur seal <i>Arctocephalus australis</i>	19	20	0.71 <sup>d</sup>	13,613	30,252	123,757	250,000–300,000	0.049
Galapagos sea lion <i>Z. wolfebaeki</i>	10	20	0.73 <sup>d</sup>	15,897	35,326	144,516	20,000–40,000	0.539
New Zealand fur seal <i>A. forsteri</i>	10	114	0.77 <sup>d</sup>	22,379	49,732	203,450	200,000	0.112
Northern fur seal <i>Callorhinus ursinus</i>	7	~463	0.80 <sup>d</sup>	30,000	66,667	272,727	<1,100,000	0.027
Antarctic fur seal <i>A. gazella</i>	6	~102	0.80 <sup>d</sup>	30,000	66,667	272,727	≤6,200,000	0.005
Sub-Antarctic fur seal <i>A. tropicalis</i>	6	~102	0.82 <sup>d</sup>	37,330	82,956	339,366	>310,000	0.120

$N_{\text{current}}$  is the current estimate of population size based on the IUCN redlist and  $N_e:N_{\text{current}}$  is the ratio of effective population size to the IUCN estimate, which provides information on a possible otariid-specific ratio (mean  $0.14 \pm 0.18$  SD, all otariids, excluding the NZ sea lion)

<sup>a</sup> Osborne et al. (2013)

<sup>b</sup> Acevedo-Whitehouse et al. (2009)

<sup>c</sup> See Table 1 in Robertson and Chilvers (2011)

<sup>d</sup> See Table 3 in Curtis et al. (2011)

size of bottlenecked years greatly reduces historical  $N_e$  meaning historical  $N_e$  should be viewed as a minimum population size rather than an average (Frankham 1995; Akst et al. 2002).

A number of assumptions are used when estimating  $N_e$  (Hartl and Clark 2007): random mating, no variance in reproductive success, non-overlapping generations, stable population size, equal sex ratio, and negligible selection, migration and mutation. When these assumptions are met,  $N_e$  equals the observed number of individuals in the population (census population size,  $N_C$ ). However, many of these conditions are violated in natural populations leading to  $N_e$  being considerably smaller than  $N_C$ . For example, in polygynous species, such as the NZ sea lion, reproductive success is skewed to a few males dominating matings (Le Boeuf 1991). In a review of estimates of  $N_e$  and  $N_C$  for wild populations, Frankham (1995) found that ratios of  $N_e$  to  $N_C$  were typically below 0.5 (a median value of 0.11), with fluctuating population size, unequal sex ratio and variance in reproductive success as the main factors causing low  $N_e/N_C$  ratios. Here, I estimate the historical number of individuals (i.e.  $N_C$ ) for each otariid species based on the values of historical  $N_e$  using two ratios of  $N_e/N_C$ : (1) a ratio of 0.45, which is the average ratio for mammals in Frankham (1995); and (2) the median value of 0.11 (Frankham 1995). As ratios of  $N_e/N_C$  might be specific to certain groups of organisms, for example, some marine organisms can have ratios of 0.001 (Palstra and Ruzzante 2008), I estimated the ratio of  $N_e$  to current population estimates for each otariid species ( $N_{\text{current}}$ ) using data from

the IUCN red list (Gelatt and Lowry 2008). This otariid-specific ratio was then also used to determine the expected historical  $N_C$  of the NZ sea lion.

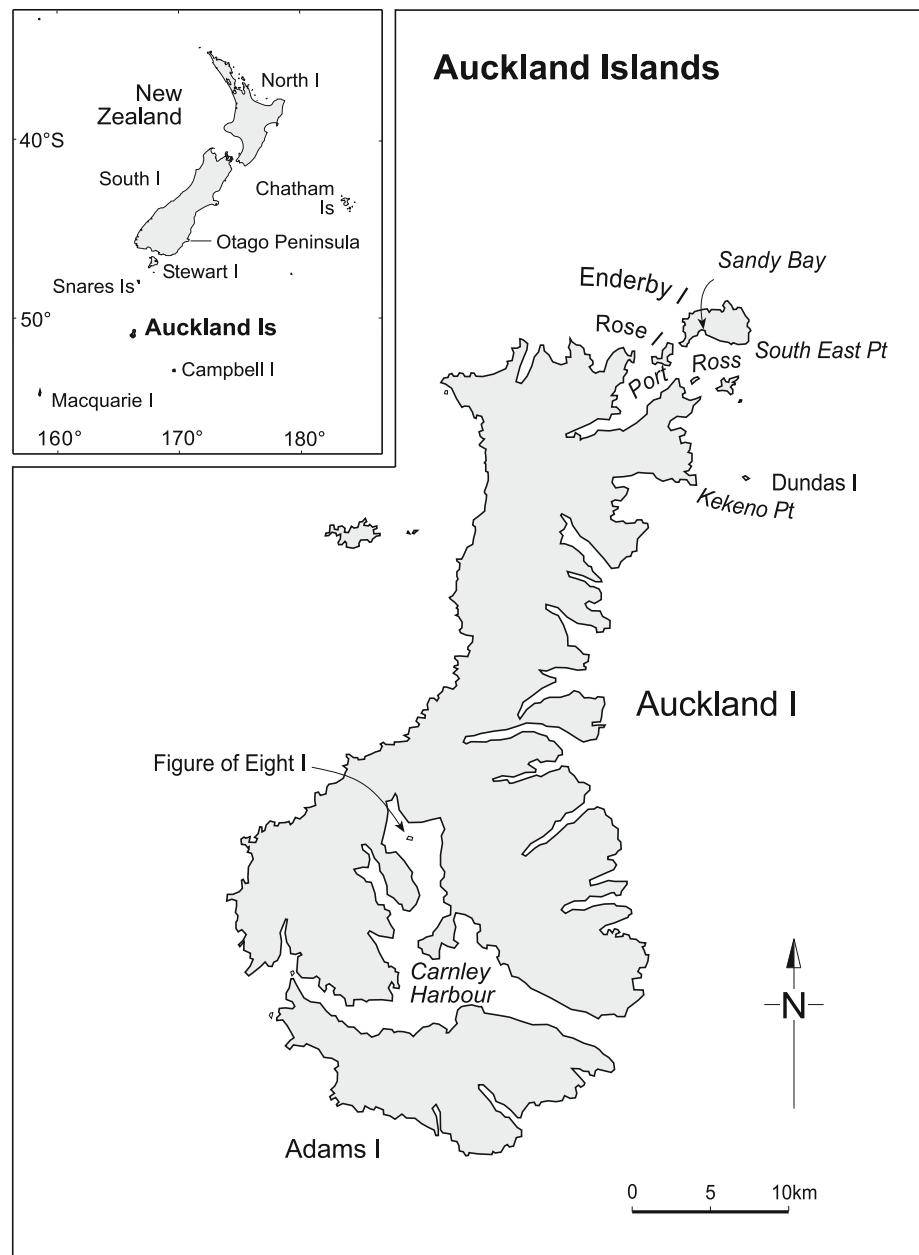
Two published estimates of  $H_e$  are available for the NZ sea lion (Table 1). One estimate (0.72) is based on 39 individual pups from a single breeding season at Sandy Bay breeding colony in the Auckland Islands (Acevedo-Whitehouse et al. 2009). The other estimate (0.66) is based on 1,351 individuals sampled over seven breeding seasons and includes live and dead pups of the year, as well as mothers and breeding male sea lions (potential fathers) from three breeding colonies on the Auckland Islands (Osborne et al. 2013). When inbred individuals or close relatives are included in a sample (as is the case for the large sample size),  $H_e$  has a downward bias (Weir 1989; DeGiorgio and Rosenberg 2009), which might account for the difference between the two  $H_e$  values (as could sampling bias associated with a small sample size) (Fig. 1).

## Results

The NZ sea lion displays comparable genetic diversity (expected heterozygosity) as other otariids (Table 1; Curtis et al. 2011; Robertson and Chilvers 2011): an average  $H_e$  of 0.716 (0.096, SD) (Table 1).

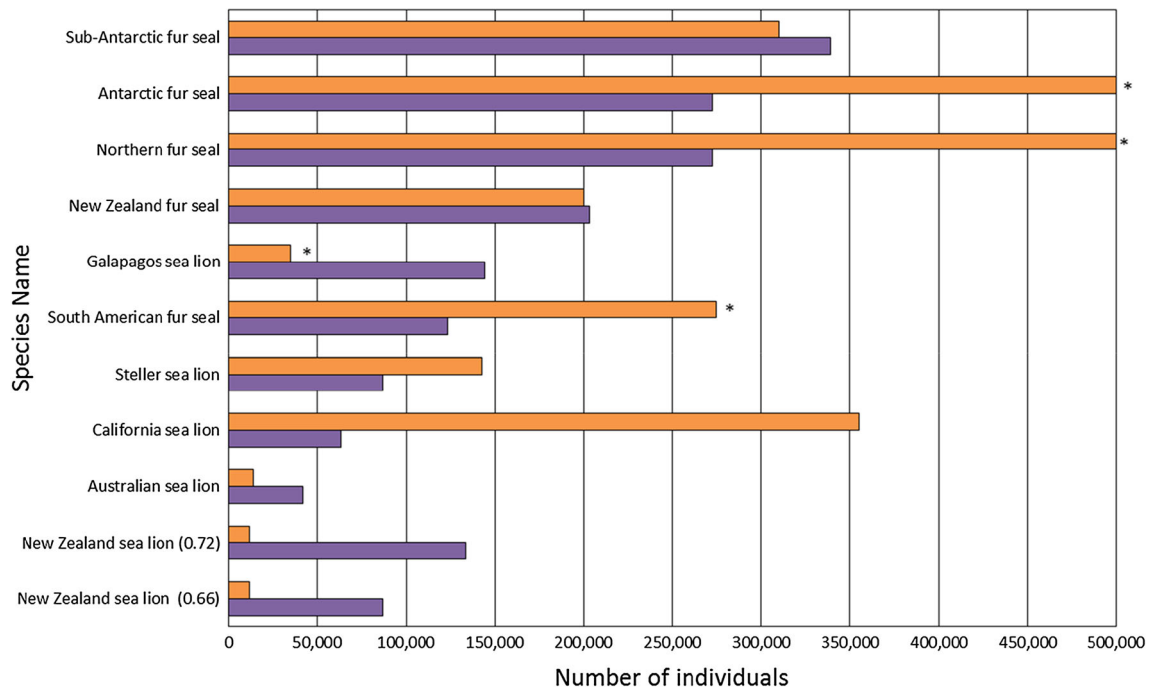
The historical  $N_e$  for the NZ sea lion was 9,563 or 14,694 (depending on the  $H_e$  value used), which resulted in a historical census population size ( $N_C$ ) in the range of 21,251–133,581 individuals (depending on the  $N_e/N_C$  ratio)

**Fig. 1** Auckland Islands showing the main breeding areas for New Zealand sea lions *Phocarcos hookeri*: Sandy Bay, Enderby Island; Dundas Island; and Figure of Eight Island. *Inset* New Zealand showing Otago Peninsula and New Zealand's sub-Antarctic islands showing the Auckland Islands and Campbell Island/Motu Ihupuku



at some point in the past (Table 1). Comparison of the historical  $N_C$  values with current estimated population sizes ( $N_{\text{current}}$ ) indicated that three species (NZ sea lion, Australian sea lion *Neophoca cinerea* and Galápagos sea lion *Zalophus wollebaeki*) have not attained the expected historical  $N_C$  (i.e. a pre-sealing population size) when the ratio of  $N_e/N_C$  is 0.11 (Fig. 2; Frankham 1995). For the NZ sea lion, this value is 86,938 or 133,581 individuals (Table 1). A number of otariid species have considerably exceeded the historical  $N_C$  0.11 estimate in their current abundance (e.g. the Antarctic fur seal *A. gazella* is at least 22 times as abundant as estimated by  $N_e$ ) (Fig. 2).

The ratio of  $N_e$  to the current population estimate ( $N_{\text{current}}$ ) ranged from 0.005 to 0.454 (mean  $0.14 \pm 0.18$  SD) for otariids (excluding the NZ sea lion) (Table 1). The ratio  $N_e: N_{\text{current}}$  for the NZ sea lion was close to or greater than one, which contrasts noticeably with all other otariids (Table 1) and suggests that the current NZ sea lion population size of 11,855 is considerably lower than the pre-sealing, historical population size. Using the  $N_e: N_{\text{current}}$  for the other otariids (i.e. 0.14) as an otariid-specific estimate of the ratio of  $N_e/N_C$  (cf. 0.11 of Frankham 1995), the NZ sea lion population could be expected to number 68,307 or 104,957 individuals, which is at least an order of



**Fig. 2** Historical census population size ( $N_C$  0.11, purple bars) compared with current population estimate (IUCN redlist, orange bars) of various otariid species.  $N_C$  0.11 uses a ratio of 0.11 for effective population size ( $N_e$ ) to  $N_C$ . Asterisks denotes current population estimates averaged (Galapagos sea lion *Zalophus*

*wollebaeki* and South American fur seal *Arctocephalus australis*) or limited to 500,000 individuals (Antarctic fur seal *Arctocephalus gazella* and Northern fur seal *Callorhinus ursinus*) to facilitate graphical presentation. Values in brackets are average heterozygosity. (Color figure online)

magnitude greater than current model estimate of mature individuals (6,987 mature individuals; Breen et al. 2010).

## Discussion

Due to the lack of reliable sealing records, genetical estimates of historical effective population size ( $N_e$ ) provide the only presently available way to estimate the historical population size for the New Zealand sea lion and hence can inform our understanding of past carrying capacity (i.e. before nineteenth century sealing). The  $N_e$ -derived census population size of the NZ sea lion indicates that at some time in the past there were between 1.8 and 11.3 times (depending on the ratio of  $N_e/N_C$  used) more sea lions than the current IUCN population size estimate of 11,855 (Table 1). When an average otariid-specific  $N_e:N_{\text{current}}$  ratio of 0.14 is used, the pre-sealing population size of the NZ sea lion was at least 68,307 sea lions or 5.8 times the number observed today.

Estimating historical effective population size and consequently the estimated historical census population size is not without its challenges (e.g. Alter et al. 2007). For example, population size changes by an order of magnitude depending on the choice of mutation rate. Here, I used a conservative mutation rate for microsatellite loci

( $1 \times 10^{-4}$ : Dallas 1992; Weber and Wong 1993), but others have used a lower rate (i.e.  $1 \times 10^{-5}$ ) to examine historical  $N_e$  in pinnipeds (Curtis et al. 2011). Using a lower rate results in 10 times more NZ sea lions and only serves to reinforce the conclusion that the population has not yet increased to historical levels. A faster mutation rate ( $1 \times 10^{-3}$ ) leads to a tenth the number of NZ sea lions ( $N_C$  0.11 = 8,693), but unlikely  $N_C$  values for the other otariids. For example, the minimum number of NZ fur seal *A. forsteri* skins taken during sealing in the NZ sub-Antarctic was c. 440,000 (Lalas and Bradshaw 2001), but based on a faster mutation rate the  $N_C$  0.11 for the species was only 20,345 (Table 1). Thus, the use of a mutation rate of  $1 \times 10^{-4}$  appears appropriate for estimating  $N_e$  in NZ sea lions.

Population structure and gene flow can bias historical  $N_e$  when locally sampling a portion of a metapopulation (Hare et al. 2011). Currently, NZ sea lion breeding is restricted to the NZ sub-Antarctic islands with a few pups born annually on the NZ mainland (Robertson and Chilvers 2011), but prior to human arrival in New Zealand, sea lions were spread around the two main islands of New Zealand and then were subsequently extirpated (Collins et al. 2013). If the mainland and sub-Antarctic colonies were exchanging migrants, then the historical  $N_e$  reported here would reflect the global population size of NZ sea lions. However,

molecular genetic evidence from ancient DNA analyses of sea lion bones in archaeological deposits indicates strong genetic differentiation between the extirpated mainland sea lions and those from the sub-Antarctic (Collins et al. 2014), similar to the level of differentiation noted in the yellow-eyed penguin (*Megadyptes antipodes*), which had a similar history of extirpation and re-colonisation, in the same region and at approximately the same time (Collins et al. 2014). In the case of the penguin, the historical mainland NZ population was identified as a distinct taxon (*M. waitaha*) from the sub-Antarctic birds (Boessenkool et al. 2009). On this basis, it appears gene flow has been limited between the two sea lion taxa, and hence, the historical  $N_e$  reported here likely reflects a historical population size of the sea lion taxon in the NZ sub-Antarctic region.

An important consideration when using  $N_e$ -derived historical population size to inform species recovery is that the carrying capacity of the environment can change over time. Anthropogenic impacts, such as fishing and climate change, may decrease oceanic productivity leading to declines in abundance of prey species (Hirons et al. 2001; Hilton et al. 2006; Newsome et al. 2007; Jaeger and Chérel 2011). However, not all predator populations appear to respond similarly to decreases in primary productivity. For example, populations of fur seals are reported as increasing or stable in many areas across their respective ranges in the southern oceans, including the New Zealand fur seal *A. forsteri* in the NZ sub-Antarctic region (Gelatt and Lowry 2008). Currently, there is no evidence for a general decrease in the carrying capacity of NZ sea lions. NZ sea lions are suggested to display a flexible diet involving prey switching in times of low prey abundance, and hence, evidence for food limitations is elusive (Bowen 2012). Over the last 17 years, there appears to have been a shift in prey species of the NZ sea lion at the Auckland Islands (Stewart-Sinclair 2013).

Is current management limiting sea lion recovery?

Current management of fisheries bycatch of the NZ sea lion uses Bayesian modelling to first determine a carrying capacity ( $K$ ) for the species based on pup counts and then whether specific management strategies maintain sea lions at a minimum of 90 % of this  $K$  (Breen et al. 2010; Bradshaw et al. 2013). Presently,  $K$  is modelled as 6,987 mature individuals (i.e. 57.9 % of a total modelled population size: 12,065 individuals, 90 % CI 11,160–13,061) (Breen et al. 2010). Therefore,  $K$  is a very important value for sea lion management. Assuming that mature individuals always make up 57.9 % of the total population for the NZ sea lion, we could expect there to have been 39,550 mature sea lions in the past when using an otariid-specific estimate of census population size based on the  $N_e$  reported here

(c. 68,307 sea lions). For that matter, all  $N_e$ -derived census population sizes for the NZ sea lion give a mature number of animals that are between 2 and 11 times the modelled  $K$  of 6,987 mature individuals (Table 1), indicating that sea lion management is using a carrying capacity lower than the historical census population size of the NZ sub-Antarctic environment.

Available evidence supporting the modelled value of  $K$  is limited and equivocal (hence the need for the present study). Indeed, it is acknowledged that the lack of information about pre-sealing sea lion numbers or numbers killed (e.g. Childerhouse and Gales 1998; Maloney et al. 2009) hinders the assessment of the accuracy of the estimate of  $K$  (Breen et al. 2003). An important implication of using an incorrect  $K$  is that sea lion bycatch limits can be set at unsustainable levels, especially if model parameterisation is leading to optimistic conclusions of management success (Bradshaw et al. 2013). Furthermore, placing a cap on the sea lion population's recovery might hinder important density-dependence effects that play a role in the colonisation dynamics of the species. For example, otariids have shown four successive phases of recolonisation post-sealing, dictated by rate of increase, spatial distribution and density (Roux 1987). Phase three (recolonisation) occurs when density reaches a particular level that promotes the movement of breeding individuals to new areas (Roux 1987), hence a management cap on sea lion numbers may stop the population from reaching this critical density threshold and hence recolonisation may be hindered. With the species currently being range restricted, recolonisation is necessary to move the species from the present threat status of 'nationally critical'.

## Conclusion

Genetical estimates of historical effective population size suggest that NZ sea lions were considerably more abundant (>68,000 individuals) historically than the current IUCN population estimate of 11,855. While environmental changes can result in changes in abundance over time, there is no evidence for or against a decrease in the carrying capacity of NZ sea lions that could explain the low current population size estimate. Importantly, the genetical estimate of historical population size suggests that the modelled carrying capacity of 6,987 mature sea lions is likely an underestimation of recovery potential of the species. Therefore, current sea lion management that targets recovery to around 7,000 mature sea lions is likely placing a limit on the recovery of the species and could expose the population to unsustainable fishing impacts further exacerbating the species' extinction risk (Robertson and Chilvers 2011; Chilvers 2012).

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