



Historical population size of the threatened New Zealand sea lion *Phocarctos hookeri*

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Marine mammal species were exploited worldwide during periods of commercial sealing in the 18th and 19th centuries. For many of these species, an estimate of the pre-exploitation abundance of the species is lacking, as historical catch records are generally scarce and inaccurate. Genetic estimates of long-term effective population size provide a means to estimate the pre-exploitation abundance. Here, we apply genetic methods to estimate the long-term effective population size of the subantarctic lineage of the New Zealand sea lion (NZ sea lion), *Phocarctos hookeri*. This species is predominantly restricted to the subantarctic islands, south of mainland New Zealand, following commercial sealing in the 19th century. Today, the population consists of ~9,880 animals and population growth is slow. Auckland Island breeding colonies of NZ sea lion are currently impacted by commercial trawl fisheries via regular sea lion deaths as bycatch. In order to estimate sustainable levels of bycatch, an estimate of the population's carrying capacity (K) is required. We apply the genetically estimated long-term effective population size of NZ sea lions as a proxy for the estimated historical carrying capacity of the subantarctic population. The historical abundance of subantarctic NZ sea lions was significantly higher than the target values of K employed by the contemporary management. The current management strategy may allow unsustainable bycatch levels, thereby limiting the recovery of the NZ sea lion population toward historical carrying capacity.

Key words: effective population size, genetic bottleneck, historic abundance, *Phocarctos hookeri*, pinniped, sea lion

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Throughout the 18th and 19th centuries, numerous marine mammal species were the target of aboriginal and commercial hunters worldwide, resulting in severe reductions in abundances (Yesner 1988; Hildebrandt and Jones 1992; Woodburne et al. 1995). The New Zealand sea lion (NZ sea lion), *Phocarctos hookeri* (Gray 1844), was hunted in the early periods of human colonization in New Zealand, resulting in extirpation from mainland New Zealand (Smith 1985; Collins et al. 2014a) and a drastic reduction in abundance on New Zealand's subantarctic islands (Childerhouse and Gales 1998). Historical records indicate that the species began to recover following the cessation of sealing around the subantarctic islands in the late 19th century, however, this recovery has been slow (Childerhouse and Gales 1998). Today, the NZ sea lion is one of the rarest otariid species in the world (Robertson and Chilvers 2011), and its status is listed as "nationally critical" by the New Zealand threat classification system (Baker et al. 2010) and "endangered" by the IUCN Redlist (Chilvers 2015).

Prior to human settlement, NZ sea lions were widely distributed along the New Zealand coastline (Fig. 1; Smith 1985; Childerhouse and Gales 1998; Collins et al. 2014a). NZ sea lions' remains are found extensively in early Māori middens but were absent from much of the New Zealand mainland at the time of European settlement (Smith 1985; Childerhouse and Gales 1998; Collins et al. 2014a). Recent genetic analyses revealed that this mainland NZ sea lion population comprised a distinct mitochondrial genetic lineage of NZ sea lions to those present in the subantarctic NZ sea lions, a lineage that is extinct today (Collins et al. 2014b). Commercial sealing within New Zealand's southern waters commenced following European settlers discovering the Auckland Islands in 1806, leading to a decline in the subantarctic NZ sea lions (Childerhouse and Gales 1998). Today, the largest population of NZ sea lions is centered on the subantarctic Auckland Islands (Fig. 1), contributing 73% of the species total annual pup production (Maloney et al. 2012).

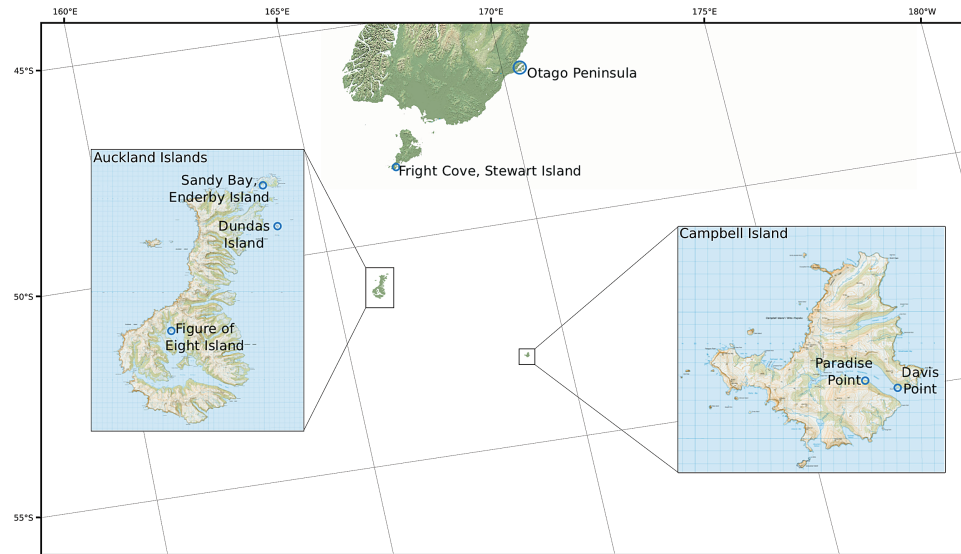


Fig. 1.—Geographic location of modern New Zealand sea lion colonies sampled. Inserts show enlarged map of sampling locations on the Auckland Islands (Sandy Bay, Dundas Island, and Figure of Eight Island) and Campbell Island (Paradise Point and Davis Point).

As a major contributor to the NZ sea lions total pup production, the Auckland Islands population is of particular importance for the persistence of this species. Consequently, the decline in pup production (48% between the 1994/1995 and 2013/2014 breeding seasons—[Childerhouse et al. 2013](#)) of the Auckland Islands population is of concern. Numerous factors have been hypothesized to be contributing to this decline, including disease epizootics, predation, permanent dispersal, genetic effects and resource competition, and bycatch deaths due to fisheries operating in the subantarctic region ([Robertson and Chilvers 2011](#)). In a recent review, [Robertson and Chilvers \(2011\)](#) identified the arrow squid (*Nototodarus sloani*) fisheries operating around the Auckland Islands (squid fishing area SQU6T) as likely to be contributing to the decline in numbers via both direct and indirect impacts. The squid trawl fishery overlaps both spatially and temporally with the foraging range of lactating female NZ sea lions (SQU6T—[Chilvers 2009](#)). NZ sea lions are caught as bycatch in the squid fishery, directly impacting the Auckland Island population ([Chilvers 2008](#)). In an effort to mitigate bycatch, sea lion exclusion devices (SLEDs) are now used in trawl nets, but uncertainty remains regarding the efficacy of SLEDs and the survival of sea lions exiting trawl nets via SLEDs ([Bradshaw et al. 2013](#); [Robertson 2015a](#)). Additionally, diet analysis suggests the fisheries operating in SQU6T may be in direct competition with NZ sea lions ([Meynier et al. 2009](#)), however, the magnitude of these effects is difficult to quantify ([Bowen 2012](#)). Other trawl fisheries in the New Zealand subantarctic catch NZ sea lions as bycatch, but the number of NZ sea lions deaths is lower than in SQU6T ([Thompson and Abraham 2010](#); [Thompson et al. 2013](#)).

Today, the population size of NZ sea lions is estimated to be around 9,880 (95% confidence interval [CI] 8,604–11,267) individuals ([Geschke and Chilvers 2009](#)). An estimate of the pre-exploitation abundance of NZ sea lions, which is presumed to represent the historical carrying capacity, K , of the subantarctic population is currently lacking. Ship records and personal

memoirs describing sealing in the early 19th century mention the presence (or apparent absence) of NZ sea lions and describe the decline in seal and sea lion numbers but are not quantitative. For example, “the seals, though not actually exterminated, became vastly reduced in number” ([McNab 1907:250](#)); however, the accuracy of these records is generally questionable and details are scant ([Childerhouse and Gales 1998](#)).

The estimation of K is key to effective management of the subantarctic population of NZ sea lions, in particular for modeling the impact of fishing-related mortality limits on the persistence of the sea lion population. Currently, the success of management strategies is assessed against 2 criteria that aim to allow the NZ sea lion population to achieve 90% of the estimated carrying capacity, K ([Cryer et al. 2014](#)). In the absence of an estimate of the pre-exploitation abundance of the NZ sea lion, K is modeled with an integrated Bayesian management procedure evaluation model (the Breen–Fu–Gilbert [BFG] model) to be 6,987 mature animals ([Breen et al. 2010](#)). This model incorporates fishing and population components and is currently applied to assess the likely performance of bycatch rules. A recent, preliminary study provided an estimate of K of the subantarctic NZ sea lion population, based on published estimates of heterozygosity, and suggests that the population is currently unlikely to be near the historical K (estimated historical $K = 21,251$ – $133,581$ based on N_e/N_c ratios of 0.11 and 0.45 and estimated using 2 genetic datasets; [Robertson 2015b](#)). The 2- to 10-fold difference between this estimate of historical K and the current abundance (~9,880—[Geschke and Chilvers 2009](#)) highlights the need for a more detailed assessment of K of the subantarctic NZ sea lion population based on a comprehensive genetic dataset collected from the extant population.

In the absence of reliable historical estimates of NZ sea lion population size, estimates for long-term effective population size (N_e) based on contemporary genetic data can be used to estimate historical abundances ([Alter et al. 2007](#); [Ruegg et al. 2013](#)) and to infer historical K . Effective population sizes (short and long

term) can be estimated using contemporary genetic data, based on the balance between increasing variation due to mutation and genetic drift reducing variation (Charlesworth 2009). While there are uncertainties in applying these values to estimate a historical census size (N_c), due to N_c generally being greater than N_e (Frankham 1995), a species-specific estimate of N_e (and subsequently N_c/N_e) would assist NZ sea lion management. Genetic estimates of long-term N_e have previously been applied to the management of threatened species, including many marine species with a history of overexploitation (Waples 1991; Roman and Palumbi 2003; Alter et al. 2007; Ruegg et al. 2013).

Here, we estimate the long-term effective population size of the subantarctic NZ sea lions using mitochondrial sequence and microsatellite data to gain an approximation of the NZ subantarctic's historical carrying capacity (K). We test the hypothesis that both the current subantarctic abundance and the K used for the contemporary management of the population are less than the historical carrying capacity.

MATERIALS AND METHODS

Sampling

New Zealand sea lion pups from the 7 main breeding areas were included in this study: Sandy Bay (SB, Enderby Island), Dundas Island (DI), and Figure of Eight Island (FE) within the Auckland Islands; Paradise Point (PP) and Davis Point (DP) on Campbell Island; Stewart Island (SI); and the Otago Peninsula (OP; Fig. 1). All sites were sampled within a single breeding season (with the exception of the Otago Peninsula, where pup production is too low to sample a large numbers of pups in a single breeding season; Supporting Information S1) to overcome the bias that may be caused by the use of data from overlapping generations in the estimate of effective population size (Nunney 1993). Sampling pups from the same breeding season was not possible for the Otago Peninsula due to the small numbers of pups (4–5) born each year (Robertson and Chilvers 2011). Population subdivision can influence how demographic histories are interpreted within datasets from extant populations (Peter et al. 2010), however, no genetic structure is evident between the present day NZ sea lion breeding colonies (Collins 2014). Consequently, all breeding colonies were treated as a single population for effective population size estimates and bottleneck tests. The contemporary Otago Peninsula and Stewart Island populations are the result of a recent range expansion of the subantarctic NZ sea lions (McConkey et al. 2002; Collins 2014; Collins et al. 2014b). Consequently, genetic estimates of N_e derived from this dataset (i.e., contemporary NZ sea lion colonies breeding in the subantarctic region, Stewart Island and the Otago Peninsula) apply only to the historical subantarctic region.

Mitochondrial DNA analyses

DNA was extracted, amplified, and sequenced according to the methods described in Supporting Information S2. Mitochondrial DNA sequences for *D-loop* and cytochrome *b* (*Cytb*) were edited and trimmed using Geneious v6.1 (Kearse

et al. 2012). Ambiguous bases were visually checked and corrected. Sequences resulting from sequencing with both forward and reverse primers were concatenated for the respective loci. Sequences for each mitochondrial locus were then aligned using the ClustalW algorithm (Larkin et al. 2007) in Geneious for further analyses. The number of polymorphic sites, nuclear diversity (π), number of haplotypes, and haplotype diversity (h) was determined for each colony in Arlequin v3.5 (Excoffier et al. 2005). The additional 7 nuclear regions (Supporting Information S3) were tested for sequence variation, however, no variation was observed in sequence data from the initial samples preventing further analyses with these nuclear regions.

Microsatellite analyses

A total of 16 dinucleotide microsatellite loci were amplified and genotyped according to the methods described in the Supporting Information (S2). Genotype files were scored using the Microsatellite plug-in available for Geneious. The frequency of scoring errors was checked by genotyping and scoring 10% (30 individuals) of the samples for the 2nd time and comparing the 2nd scores to original scores according to the methods described by Hoffman and Amos (2005). Allelic richness (k), observed and expected heterozygosity (H_o and H_e) were calculated with Fstat v2.9 (Goudet 1995). Microchecker v2.2 (van Oosterhout et al. 2004) was used to estimate the frequency of null alleles at each locus. Departure from Hardy–Weinberg equilibrium was tested with exact tests implemented in Genepop v4.2 (Raymond and Rousset 1995). Exact tests were performed in Genepop to assess allele frequency differences.

Effective population size estimates

Effective population sizes were calculated based on data for both mitochondrial and nuclear loci separately. Approximately 1.2kb and 800 base sequences of the mitochondrial regions *Cytb* and *D-loop*, respectively, were included in estimates of long-term effective population size, $2N_{ef}$ (where N_{ef} represents female effective population size—Wright 1931). Fifteen unlinked microsatellite loci (Supporting Information S4; locus ZcCgDh1.8 was monomorphic and was removed from the analysis) were used for estimates of autosomal, long-term effective population size, N_e (Wright 1931), as well as an estimate of short-term N_e and the effective number of breeding parents, N_b (Schwartz et al. 1998; Luikart et al. 2010).

Short-term effective population size.—The effective number of breeders, N_b , of NZ sea lions was estimated using the microsatellite dataset and an unbiased linkage disequilibrium method (Weir 1979; Waples 2006) applied in LDNe (Waples and Do 2008). This method generally performs well in populations with skewed sex ratios or non-random variance in reproductive success, as is the case in the NZ sea lion and other otariid species displaying polygynous mating systems (Le Boeuf 1991). Short-term N_e was then estimated using the approximate Bayesian computation (ABC) method implemented in ONeSAMP (Tallmon et al. 2008), a method expected to estimate an N_e that would apply to the last few generations (Luikart et al. 2010; but see Skrbinek et al. 2012) of N_e . Priors of 100 and 5,000

(minimum and maximum N_e) were used in the estimation of N_e , as ONeSAMP requires an estimate of the upper and lower bounds of N_e based on values estimated by the user. These priors were selected based on the current estimate of abundance and the assumption that the ratio N_e/N_c will be small due to the polygynous mating system. A 2nd ONeSAMP analysis was run using the default priors (min. N_e 2; max. N_e 10,000) on the same dataset to investigate the impact of the selected priors on the estimation of short-term N_e (see [Supporting Information S2](#)).

Long-term effective population size.—Long-term effective population size was estimated using both the mitochondrial and microsatellite datasets. The diversity parameter Θ was estimated for *D-loop* and *Cytb* sequences independently and as linked loci using the Bayesian method implemented in LAMARC ([Kuhner 2006](#)). In LAMARC, 10 independent replicates, each consisting of 10 short chains of 50,000 iterations and 2 long chains of 1,000,000 iterations, were performed in order to ensure model convergence. Mutation rates per generation for *D-loop* and *Cytb* were estimated by comparing pairwise genetic distances between species of otariids based on mitochondrial sequence data ([Arnason et al. 2006](#)) and their corresponding divergence times ([Higdon et al. 2007](#)). These mutation rates were then compared to mutation rates estimated based on *D-loop* and *Cytb* sequence data in other pinniped and mammalian taxa in order to ensure that mutation rates were suitable for N_e estimation ([Supporting Information S5](#)), and a generation time of 10 years was assumed ([COSEWIC 2010](#)). Following the estimation of Θ and μ , the formula $\Theta = 2N_e\mu$ was solved to provide an estimation of long-term effective population size for the 2 mitochondrial loci, using their respective mutation rates ([Supporting Information S5](#)).

To estimate N_e , with the microsatellite data, Θ was estimated for the 15 microsatellite loci using a Bayesian algorithm implemented in IMA2 ([Hey 2010](#)). A conservative mutation rate of 1×10^{-4} mutations per site per generation was assumed for microsatellite loci, following the rate selected for previous estimates of N_e in pinniped species ([Palo et al. 2001](#); [Curtis et al. 2011](#)). Fifteen independent replicates were completed in IMA2, each with 1,000,000 iterations following a burn in of 50,000. Ratios of N_e/N_c vary between populations and can be difficult to predict when inferring census sizes from genetically estimated effective population sizes. [Frankham \(1995\)](#) estimated a mean N_e/N_c for mammals of 0.45, while values as low as 0.06 have been reported in pinniped species ([Curtis et al. 2009, 2011](#)). In a species with a polygynous breeding system, such as the NZ sea lion, it is expected that the N_e/N_c will be low ([Nunney 1993](#); [Storz et al. 2001](#)). Consequently, we applied [Frankham's \(1995\)](#) median of N_e/N_c of 0.11 estimated from wild populations, as a conservative estimate of N_e/N_c to determine the historical census size of the NZ sea lion ([Robertson 2015b](#)), in addition to a more realistic N_e/N_c of 0.05 and the mean mammalian N_e/N_c of 0.45.

Assessing the impact of the 19th century bottleneck

Approximate Bayesian computation was used to assess the impact of the 19th century bottleneck resulting from commercial

sealing. ABC allows the use of informed priors (based on historical records, contemporary population, etc.) and was performed on microsatellite dataset, in DIYABC v2 ([Cornuet et al. 2014](#)). The support for 2 alternative historical scenarios was evaluated to assess the impact of a population bottleneck (see [Supporting Information S2](#) and [S6](#) for details of each scenario). The 1st modeled scenario assumed a severe historical population bottleneck, with prior distributions selected to encompass values from sealing records and previous N_e estimates ([Supporting Information S6](#)). The 2nd scenario described a stable population over time, with the same prior parameters. DIYABC analyses were run for 1,000,000 generations. Two summary statistics were selected for the data: mean genic diversity ([Nei 1987](#)) and mean Garza–Williamson's M ([Garza and Williamson 2001](#)). Following the initial ABC analysis using tight priors based on historical records and estimates of N_e from mitochondrial data (this study), the analysis was run again using a wider set of priors to assess the influence that the prior distributions had on posterior distributions ([Supporting Information S6](#)).

RESULTS

A total of 4 haplotypes were detected at the mitochondrial *D-loop* (haplotype diversity 0.411; [Supporting Information S7](#)) and 5 haplotypes were detected at *Cytb* (haplotype diversity 0.375; [Supporting Information S7](#)). Nucleotide diversity was similarly low, with 4 polymorphic sites in the 1,027bp *D-loop* sequence (nucleotide diversity 0.000553; [Supporting Information S7](#)) and 5 polymorphic sites in the 1,189bp *Cytb* sequence (nucleotide diversity 0.0008804; [Supporting Information S7](#)).

The results from standard tests to assess for Hardy–Weinberg equilibrium, linkage, expected and observed levels of heterozygosity, and the polymorphism of each locus confirmed that the microsatellite loci were not linked and all were suitable for further analyses ([Supporting Information S8](#)). The average expected heterozygosity across all 15 loci was 0.60, and an average of 7.4 alleles was detected per locus ([Supporting Information S9](#)). A scoring error of 2.13% was estimated across all 15 loci, following the method of [Hoffman and Amos \(2005\)](#).

Effective population size

Estimate of short-term effective population size.—Approximate Bayesian computation analyses based on microsatellite data in ONeSAMP estimated a mean short-term N_e of 842.89 for NZ sea lions, however, this estimate has wide CIs (95% CI 294.68–4,429.05). Applying wider priors to the ONeSAMP analysis resulted in a less realistic short-term N_e ([Supporting Information S10](#)), consequently a short-term N_e of 842.89 was used in subsequent analyses. The linkage disequilibrium method implemented in LDNe to estimate N_b provided an estimate of mean $N_b = 452.8$ (95% CI 269.4–1,094.8).

Estimate of long-term effective population.—Estimate of long-term effective population size based on mitochondrial DNA. Mutation rates of 2.41×10^{-7} and 6.31×10^{-8} base pairs per year (2.41×10^{-6} and 6.31×10^{-7} per generation, assuming a

generation time of 10 years; [Supporting Information S5](#)) were estimated for *D-loop* and *Cytb*, respectively, by comparing pairwise genetic distances and divergence times of pinniped species (7 species were included in the estimation of mutation rate for *D-loop* and 9 for *Cytb*). Assuming the above mutation rates, a long-term N_e of 10,284 individuals was calculated ([Supporting Information S11](#)).

Estimate of long-term effective population size based on microsatellite data. A value of $\Theta = 3.151$ across all microsatellite loci was estimated in IMA2. If a mutation rate of 1×10^{-4} substitutions per site per generation is assumed, rearranging the formula $\Theta = 4N_e\mu$ indicates a long-term effective N_e of approximately 7,875 NZ sea lions for the subantarctic region ([Supporting Information S12](#)).

Conversion of N_e to N_c .—An estimate of the historical N_c for the subantarctic region was obtained by applying an N_e/N_c ratio of 0.11 ([Frankham 1995](#)). Historical census population sizes of 93,490 and 71,590 were estimated for the subantarctic region, based on mitochondrial and microsatellite data, respectively ([Supporting Information S13](#)). Applying a wider range of N_e/N_c ratios (0.05 and 0.45) provides a historical N_c of 17,300–203,000; ([Supporting Information S13](#)). Comparing the estimates of short-term N_e and N_b to the current population size results in an observed N_e/N_c ratio for NZ sea lions of 0.07 (95% *CI* 0.02–0.37) and N_b/N_c ratio of 0.04 (95% *CI* 0.02–0.09).

Impact of 19th century population bottleneck

Two alternative scenarios were modeled using ABC in DIYABC ([Cornuet et al. 2014](#)). The scenario modeling a population bottleneck around the time of commercial sealing ([Supporting Information S6, S10, and S12](#)) was better supported than the alternative model assuming a constant population size. The bottleneck model received a posterior probability between 0.9992 and 0.9998, whereas the model inferring a constant population size through time received a posterior probability between 0.0002 and 0.0008 ([Supporting Information S6](#)). The posterior distributions of the bottleneck model indicate a genetic bottleneck that ended approximately 21.0 generations ago (=31.8, median=32.0, mode=32.0, 95% *CI*=28.9–34; [Supporting Information S6, S12](#)) with a N_e of 487 (=487, median=479, mode=501, 95% *CI*= 254–753; [Supporting Information S6 and S12](#)) following the 19th century sealing bottleneck. This post-bottleneck N_e is lower than the mean short-term N_e estimate calculated using ABC methods in ONeSAMP (842.49), but within the short-term N_e 95% *CI* (294–4,489). The 2nd DIYABC analysis using a wider set of priors resulted in a similar distribution of posterior values to the initial priors ([Supporting Information S6](#)).

DISCUSSION

The lack of detailed catch records for historically harvested species, such as the NZ sea lion, prevents a reliable estimation of the species' historical abundance. Such an estimate is important for the management of threatened populations, as it provides a "historical baseline" for interpretation of the current

abundance. The analysis of neutral genetic variation from contemporary populations provides a means to estimate historical effective population sizes pre- and post-commercial sealing, in addition contemporary effective population sizes. Genetically estimated effective population sizes can then be used to estimate census population sizes for time periods surrounding commercial sealing, and, by extension, provide an approximation of the historical carrying capacity of the subantarctic population of NZ sea lions. This allows conservation managers to evaluate the extent of the recovery of the NZ sea lion population since commercial sealing ceased and also the success of current management strategies.

The long-term estimates of N_e determined here imply a much larger historical carrying capacity of NZ sea lions in the subantarctic islands than the current estimate of the population size (~9,880—[Geschke and Chilvers 2009](#)). These estimates suggest that the historical population could have been as large as 17,300–205,000 individuals (based on N_e/N_c ratios of 0.45 and 0.05; [Supporting Information S13](#)). Regardless of uncertainties in choosing an appropriate N_e/N_c ratio, the short-term estimates of N_e (842.49, 95% *CI* 294–2,249) and N_b (452.8, 95% *CI* 269–1,094) are both much smaller than the estimates of long-term N_e , indicating that the NZ sea lion population has not reached pre-harvest levels, following the 19th century commercial sealing. Based on the estimates of short-term N_e and N_b , an N_e/N_c ratio of 0.03–0.22 would be required to equal the current abundance estimate of ~9,880 individuals. An N_e/N_c ratio of 0.03–0.22 is within the range of N_e/N_c ratios calculated for other species, including other otariids, and given the polygynous mating system of the NZ sea lion, a low N_e/N_c ratio is expected. Additionally, comparison of the N_e of the post-bottleneck population from ABC analyses (95% *CI* 254–753; [Supporting Information S6](#)) with the N_b (452.8; 95% *CI* 269.4–1,094.8) provides further support for a population that is still recovering from the 19th century bottleneck, with the *CI*s for the post-bottleneck N_e and the current N_b largely overlapping.

While it is valuable to estimate the K of a population based on long-term N_e values, it is also important to consider that the carrying capacity of the environment can change over time (e.g., [Hilton et al. 2006](#)). It is possible that the K of the subantarctic NZ sea lion population has declined since the historical (pre-commercial sealing) population, and hence the current environment may not be able to sustain the estimated historical population size. An increase in anthropogenic impacts (e.g., fishing, climate change) has been demonstrated to lead to declines in suitable prey species for other systems ([Hirons et al. 2001; Hilton et al. 2006; Newsome et al. 2007; Jaeger and Cherel 2011](#)) and is a possibility for the NZ sea lion population ([Roberts and Doonan 2014](#)). Declines in the K of other subantarctic species have been recorded, for example, in the rockhopper penguin (*Eudyptes chrysocome*) population ([Hilton et al. 2006](#)). Numbers of rockhopper penguins in the subantarctic islands have declined, possibly due to a reduction in food resources available in the subantarctic marine ecosystem, as indicated by declining $\delta^{13}\text{C}$ in the rockhopper diet over time ([Thompson and Sagar 2002; Hilton et al. 2006](#)). However,

the population of a generalist feeder, such as the NZ sea lion (Meynier et al. 2009; Bowen 2012), might be expected to be more robust to changes in the availability of food resources, as NZ sea lions demonstrate a flexible diet and are capable of prey switching (Stewart-Sinclair 2013). Indeed, fur seal species in the southern Indian Ocean have been reported to have a stable or increasing population size (Gelatt and Lowry 2008), despite a decline in penguin populations in the same region (Jaeger and Cherel 2011), suggesting that the impact of a decrease in primary productivity can vary between species.

Genetical estimates of short-term N_e and N_b of the NZ sea lion in the subantarctic region are much smaller than the current estimate of population size (~9,880—Geschke and Chilvers 2009). The estimated N_e/N_c ratio from these data (0.07) is toward the lower end of the spectrum of expected N_e/N_c ratios (Frankham 1995), however, it is still within previously observed estimates (Waples 2005; Curtis et al. 2011; Hare et al. 2011). Furthermore, a strongly polygynous breeding system is likely to lead to a low N_e/N_c (Nunney 1993; Storz et al. 2001). The mutation rate applied in N_e estimations is also crucial and can significantly alter results. The mutation rates applied here for mitochondrial markers were comparable with mutation rates recorded in other marine mammals (Supporting Information S5), and a mutation rate of 10^{-4} substitutions per site per generation was applied for microsatellite loci (Palo et al. 2001; Curtis et al. 2011; Robertson 2015b). If the mutation rate was to be increased or decreased by a factor of 10, the resulting N_e estimates would also increase or decrease by a factor of 10 providing estimates that would be incongruent with mitochondrial N_e and unrealistic based on our understanding of the population's history (Chilvers 2012; Robertson 2015b).

The estimation of long-term N_e is of particular importance to the management of NZ sea lions in the subantarctic region. Management strategies are assessed against 2 criteria that aim to allow the NZ sea lion population in the subantarctic region to achieve 90% of K (Cryer et al. 2014). Currently, K is estimated to be 6,987 mature animals based on the BFG model incorporating both population and fishery components (Breen et al. 2010). The estimate of long-term N_e (~7,800–10,300; Supporting Information S13) presented here suggests that the historical K (71,590–93,490, if $N_e/N_c = 0.11$; Supporting Information S13) of NZ sea lions is much greater than the estimate of K currently used to assess the impact of bycatch limits. If the value of K used to assess the success of management strategies is underestimated, then there would be a risk that the target population size is set too low. As such assuming that the NZ sea lion population is nearing K (Breen et al. 2010) may be limiting the recovery of the species (Robertson 2015b).

The estimates of a historical K for subantarctic NZ sea lions using multiple genetic markers and an estimate of a post-bottleneck N_e close to the current abundance of this population suggest that the population is still recovering from the population bottleneck caused by commercial sealing in the 19th century. If a value of K smaller than what is historically true is used to model the impact of bycatch on the NZ sea lion population, an overly optimistic view of the status of the NZ sea lion

population may be presented. Consequently, current bycatch mitigation practices may be effectively “capping” the growth of the NZ sea lion population and inhibiting population recovery.

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SUPPORTING INFORMATION

Supporting Information S1.—Table of sampling locations and number of samples per colony included in microsatellite and mitochondrial analyses.

Supporting Information S2.—Supplementary methods.

Supporting Information S3.—Table of oligonucleotide sequences for nuclear regions tested for genetic variation in extant *Phocarctos hookeri*.

Supporting Information S4.—Table of oligonucleotide sequences, multiplex number, and dye label of microsatellite loci used.

Supporting Information S5.—Table of mutation rates recorded in marine mammal species.

Supporting Information S6.—Table of priors used in approximate Bayesian computation analyses and numerical ABC results.

Supporting Information S7.—Table of mitochondrial genetic diversity in otariid seals.

Supporting Information S8.—Table of number of successfully genotyped individuals per locus and polymorphism characteristics of microsatellite loci.

Supporting Information S9.—Table of microsatellite genetic diversity in otariid seals, based on expected heterozygosity average number of alleles per locus.

Supporting Information S10.—Supplementary methods.

Supporting Information S11.—Table of mutation rate estimates and effective population size estimates calculated from mitochondrial data.

Supporting Information S12.—Posterior density curves of model parameters used in ABC analyses.

Supporting Information S13.—Table of estimate of historical abundance of *Phocarctos hookeri* in the subantarctic region based on genetically estimated long-term N_e .

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