New Zealand Journal of Zoology

ISSN: 0301-4223 (Print) 1175-8821 (Online) Journal homepage: https://www.tandfonline.com/loi/tnzz20

Mitochondrial DNA structure and colony expansion dynamics of New Zealand fur seals (*Arctocephalus forsteri*) around Banks Peninsula

A Emami-Khoyi, DA Hartley, AM Paterson, RH Cruickshank, LJ Boren, JG Ross, EC Murphy & TA Else

To cite this article: A Emami-Khoyi, DA Hartley, AM Paterson, RH Cruickshank, LJ Boren, JG Ross, EC Murphy & TA Else (2016) Mitochondrial DNA structure and colony expansion dynamics of New Zealand fur seals (*Arctocephalus forsteri*) around Banks Peninsula, New Zealand Journal of Zoology, 43:4, 322-335, DOI: 10.1080/03014223.2016.1179649

To link to this article: https://doi.org/10.1080/03014223.2016.1179649

Published online: 08 Jul 2016.

NEW ZEALAND JOURNAL OF ZOOLOGY, 2016
VOL. 43, NO. 4, 322–335
http://dx.doi.org/10.1080/03014223.2016.1179649

Taylor & Francis
Taylor & Francis Group

RESEARCH ARTICLE

Mitochondrial DNA structure and colony expansion dynamics of New Zealand fur seals (*Arctocephalus forsteri*) around Banks Peninsula

A Emami-Khoyi[a], DA Hartley[b], AM Paterson[a], RH Cruickshank[a], LJ Boren[c], JG Ross[a,d], EC Murphy[a,d] and TA Else[e]

[a]Department of Ecology, Lincoln University, Lincoln, New Zealand; [b]Micro-Seq Enterprises, Las Vegas, NV, USA; [c]New Zealand Department of Conservation, Wellington-Te Aro, New Zealand; [d]Centre for Wildlife Management and Conservation, Lincoln University, Lincoln, New Zealand; [e]Touro University Nevada, Henderson, NV, USA

ABSTRACT

New Zealand fur seals are one of many pinniped species that survived the commercial sealing of the eighteenth and nineteenth centuries in dangerously low numbers. After the enforcement of a series of protection measures in the early twentieth century, New Zealand fur seals began to recover from the brink of extinction. We examined the New Zealand fur seal populations of Banks Peninsula, South Island, New Zealand using the mitochondrial DNA control region. We identified a panmictic population structure around Banks Peninsula. The most abundant haplotype in the area showed a slight significant aggregated structure. The Horseshoe Bay colony showed the least number of shared haplotypes with other colonies, suggesting a different origin of re-colonisation of this specific colony. The effective population size of the New Zealand fur seal population at Banks Peninsula was estimated at approximately 2500 individuals. The exponential population growth rate parameter for the area was 35, which corresponds to an expanding population. In general, samples from adjacent colonies shared 4.4 haplotypes while samples collected from colonies separated by between five and eight bays shared 1.9 haplotypes. The genetic data support the spill-over dynamics of colony expansion already suggested for this species. Approximate Bayesian computations analysis suggests re-colonisation of the area from two main clades identified across New Zealand with a most likely admixture coefficient of 0.41 to form the Banks Peninsula population. Approximate Bayesian computations analysis estimated a founder population size of approximately 372 breeding individuals for the area, which then rapidly increased in size with successive waves of external recruitment. The population of fur seals in the area is probably in the late phase of maturity in the colony expansion dynamic.

ARTICLE HISTORY
Received 31 July 2015
Accepted 9 March 2016

KEYWORDS
Banks Peninsula; colony expansion; fine-scale population; mitochondrial DNA; New Zealand; New Zealand fur seal

CONTACT Adrian M Paterson Adrian.Paterson@lincoln.ac.nz

Introduction

The traditional view of a species as a single large, randomly mating unit is usually challenged when faced with actual field observations (Coltman et al. 2003). Many species consist of several sub-populations with different degrees of co-ancestry and relatedness (Sugg et al. 1996). In most mammalian species, males are the main dispersing sex. Female philopatric behaviour usually gives rise to matrilineal social groups (Greenwood 1980). Male-mediated gene flow, along with female philopatry and polygynous mating systems, are strategies that have evolved to avoid the impacts of inbreeding that can arise when both sexes exhibit philopatric behaviour (Chesser 1991). A high degree of co-ancestry among members of a matrilineal group may also facilitate kin selection and local adaptation with long-term beneficial evolutionary consequences (Coltman et al. 2003).

Marine environments provide animals with immense dispersal potential, with relatively few barriers to gene flow (Mirimin et al. 2011). Defining distinct populations in marine ecosystems has a major role to play in species management and conservation. Hoelzel (1998) suggested that in many marine mammals, fine-scale population genetic structure arises from specialisation of behaviour, which in turn could facilitate resource partitioning among individuals (Skulason & Smith 1995). Fine-scale population structure is more pronounced in species with socially structured or breeding-group population dynamics, where matrilocal females in stable social groups mate with males whose associations with females vary from permanent bond to semi-permanent association. This non-random dispersal of individuals in social groups will result in groups that are genetically similar due to co-ancestry, and differentiated from neighbouring groups (Sugg et al. 1996; Storz 2005). Such a population structure has been reported for numerous mammalian species including black-tailed prairie dog (*Cynomys ludovicianus*) (Chesser 1983), red howler monkey (*Alouatta seniculus)* (Pope 1992), several cercophithecine primates (Schwartz & Armitage 1980; Turner 1981; Dracopoli et al. 1983; Melnick 1987a, 1987b; Kawamoto 1996), the common vampire bat (*Desmodus rotundus*) (Wilkinson 1985), Richardson's ground squirrel (*Urocitellus richardsonii*) (van Staaden et al. 1994), European rabbit (*Oryctolagus cuniculus*) (Surridge et al. 1999), lion (*Panthera leo)* (Spong et al. 2002), bottlenose dolphin (*Tursiops truncatus*) (Urian et al. 2009) and many ungulates (Coltman et al. 2003).

Few studies have investigated the pattern of re-colonisation of an area by a species after an initial disappearance. Carr et al. (2007) found that fishers (small aquatic mustelids, *Martes pennanti*) in southern Ontario, Canada re-colonised the area from multiple source populations after initial removal in the 1950s. The multi-source nature of re-colonisation results in homogenisation of genetic variation at local scales. Recently, Bonin et al. (2013) reported the multi-source nature of re-colonisation of Livingston Island by Antarctic fur seals (*Arctocephalus gazella*), with obvious population differentiation between Livingston Island and the larger, nearby South Georgia Island populations, indicating the contribution of several source populations to the re-invasion history of Livingston Island, rather than a single spill-over event from larger South Georgia colonies to the smaller Livingston Island colonies.

New Zealand fur seals, *Arctocephalus forsteri* (Lesson, 1828), are a group of pinnipeds that show an extreme polygamous mating system in which a few males sire most of the

offspring in the next generation (Crawley & Wilson 1976). This mating system has important impacts on species demographic dynamic and colony expansion pattern.

Since the end of the large-scale commercial sealing of the eighteenth and nineteenth centuries, populations of many pinniped species, including New Zealand fur seals, have started to recover from the brink of extinction (Macdonald 2001). Roux (1987) suggested four successive phases for the process of fur seal re-colonisation: (1) survival, (2) establishment, (3) re-colonisation, and (4) maturity. Individuals surviving a large-scale human harvest initially form a few founding colonies during the establishment phase. This stage is immediately followed by a re-colonisation phase when shortage of space in the older colonies accelerates the formation of new colonies, primarily in the vicinity of the founder colonies. The process of older colonies spilling over into new colonies continues until density-dependent factors, such as absolute shortage of space on land or food resources at sea, limit the establishment of new colonies and subsequently the colonies enter the maturity phase.

Intra-regional fine-scale population genetics of New Zealand fur seals is poorly known. Two studies have previously investigated the broader population structure in this species. Lento et al. (1994) found limited gene flow across the broad geographical range of the New Zealand population. Similarly, Robertson and Gemmell (2005) reported moderate gene flow (an average F_{ST} value = 0.017 for all pairwise comparisons) between seven colonies throughout New Zealand. Despite providing valuable information at a broad scale, neither of these studies examined population structure at a smaller scale and its consequences on colony expansion dynamics.

Banks Peninsula (approximately 1150 square kilometres) is situated in the middle of the east coast of New Zealand's South Island. Originally formed from two extinct volcanoes, Banks Peninsula was isolated by the ocean as recently as 15,000 years ago, at the end of the last glacial epoch, and remained isolated from the mainland until the alluvial plains of Canterbury reached its base (McLintock 1966). A variety of species have colonised the area from different source populations throughout the New Zealand mainland (Burrows 1994; Banks et al. 2002).

Banks Peninsula offers an opportunity to study the fine-scale population genetics of New Zealand fur seals using mitochondrial DNA. The local bays provide suitable habitat for New Zealand fur seals and the relative timings of re-colonisations for the major colonies in the area are known. This area has been re-colonised by fur seals over the past 40 years (Wilson 1981). Many colonies are even younger and have established in the last decade (Baird 2011).

Wilson (1981) was the first researcher to report the re-appearance of four New Zealand fur seals pups, and one female, in haul-outs on the eastern side of Horseshoe Bay on Banks Peninsula in 1973. Despite observing seals at many other locations throughout the area, no pups or females were reported elsewhere; these locations were occupied by immature, subadult males. Ryan et al. (1997) subsequently found that many of the previously identified haul-out sites had become breeding colonies. Only two of the study sites ($n = 9$) in our research, Horseshoe Bay and Island Bay colonies, were reported as breeding colonies or haul-out sites by Ryan et al. (1997). Baird (2011) was the first to suggest that all of the colonies included in our research were well-established breeding colonies. Records suggest that many of these colonies were established between 1997 and 2010. The recent establishment

history of these colonies could provide an insight into the dynamic of colony expansion in New Zealand fur seals on a local scale.

We report here a study of matrilineal population structure and colony expansion dynamics in New Zealand fur seals on a local scale at Banks Peninsula, in the South Island of New Zealand. Alternative hypotheses of multiple source re-colonisation events versus a single re-colonisation event, and a spill-over pattern of colony expansion, previously reported as a potential model for colony expansion dynamics (Bradshaw et al. 2000), were thoroughly evaluated using genetic data from the mitochondrial control region.

Material and methods

Tissue collection

Tissue samples were collected from the interdigital web of fur seal pups' left fore-flipper using a medium-size piglet ear-notcher (Majluf & Goebel 1992). Nine or ten individuals from all major breeding colonies with more than 50 individuals from around Banks Peninsula were sampled (Figure 1). The samples were transferred to 99% ethanol immediately and kept cold until DNA could be extracted at Lincoln University, usually within a few weeks. The whole process was performed in accordance with permit 35069-MAR issued by the New Zealand Department of Conservation. DNA was extracted from tissue

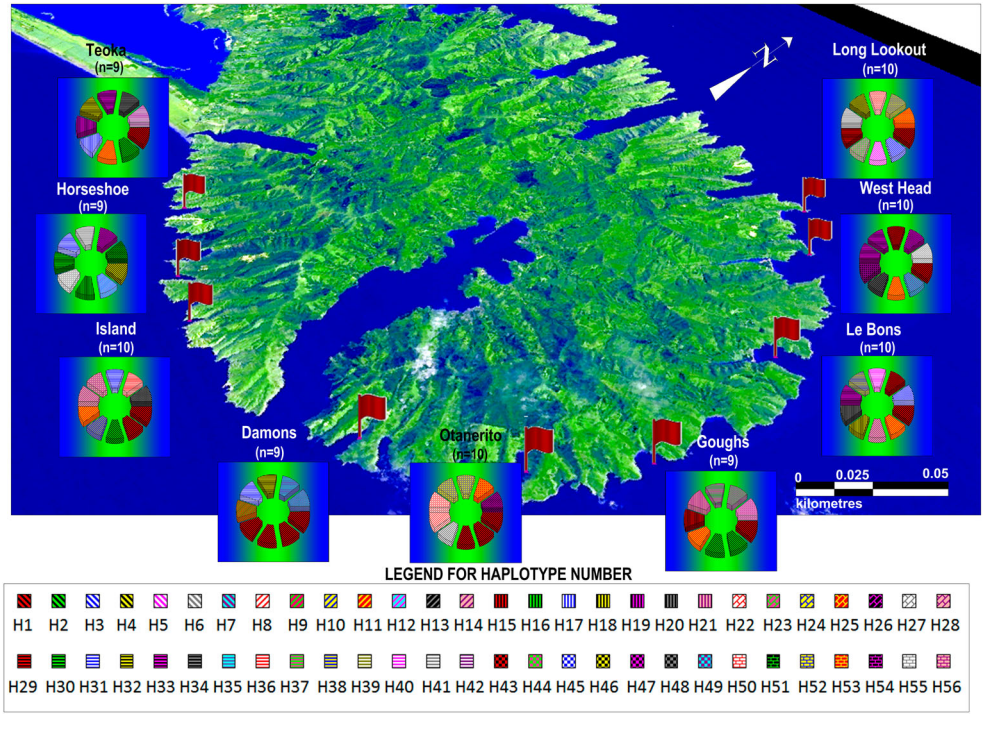

Figure 1. Locations of the fur seal colonies around Banks Peninsula and haplotype structure found within the colonies. Numbers inside parenthesis represent the number of sampled individuals from each colony.

samples using a Qiagen DNeasy Blood &Tissue Kit (Catalogue number 69506) according to the manufacturer's instructions, and DNA was then stored at –20 °C.

Control region amplification/analysis

An approximately 1 kilobase long fragment of the mitochondrial control region was amplified and sequenced using T-Thr and T-Phe primers as explained in Goldsworthy et al. (2000). These primers bind to tRNA gene regions on either side of the control region. Sequences were aligned using both Clustal W2 (Larkin et al. 2007) and MAFFT (Katoh & Standley 2013). After rigorous filtering of the sequences c. 600 base pairs of high-quality sequences were used in the subsequent analysis. Haplotype analyses were performed in Arlequin v.3.5 (Excoffier et al. 2005) using default settings except where explicitly stated otherwise. A multimodal (model averaging) phylogenetic tree was constructed using software package jModelTest (Posada 2008). A median-joining haplotype network was constructed using the software package Network (Rohl 2000), changing the default parameters to accommodate mitochondrial DNA's special dynamics (three times higher transition to transversion weight).

To estimate the parameter Θ (N_e μ) and exponential growth rate (g) for the New Zealand fur seal at Banks Peninsula the phylogenetic package LAMARC v2.1.10 (Kuhner 2006) was used in a Bayesian analysis mode using a single final long chain of 2.5×10^8 simulations with different temperature.

Three separate Approximate Bayesian Computations (ABCs) analyses were performed using DIYABC v2 (Cornuet et al. 2014). In the first model, it was assumed that the current Banks Peninsula population is descended from a founder population of around 1000 individuals that gradually increased to the current population size (c. 2500 breeding females). We chose 1000 individuals as the founder population size assuming that all immature males and females that Wilson (1981) observed in the area, in addition to the only lactating female, remained at Banks Peninsula, and other immigrant individuals have subsequently given rise to the current population. In the second model, the probability of a scenario with an instantaneous single massive re-colonisation event was investigated. In the third, model, a multi-source origin of re-colonisation of the area was evaluated. To test this model, a homologous region of mitochondrial DNA control region was sequenced from 50 additional fur seals chosen from around New Zealand and the sub-Antarctic islands and was subjected to Bayesian phylogenetic analysis using the phylogenetic package BEASTv1.8 (Drummond et al. 2012). Two clades identified by the analysis were considered as representative of the putative source populations for the re-colonisation of Banks Peninsula. The most likely size of the Banks Peninsula fur seal founder population was also estimated in this model.

Eight summary statistics were calculated from a single population: (1) number of haplotypes, (2) number of segregating sites, (3) mean pairwise genetic distance, (4) variance of pairwise genetic distances, (5) Tajima's D, (6) number of private segregating sites, (7) mean frequency of the rarest nucleotide at segregating sites, and (8) the variance of the frequency of the rarest nucleotide at segregating sites. In addition, five other summary statistics were calculated from a pool of all samples: (1) number of distinct haplotypes in the pool sample, (2) number of segregating sites in the pool sample, (3) mean of within-sample pairwise differences, (4) mean of between-sample pairwise differences, and F_{ST}

between two samples as explained in Cornuet et al. (2014). A maximum likelihood analysis adapted from Choisy et al. (2004) was used to estimate the coefficient of admixture of two putative populations that have probably given rise to the current Banks Peninsula population.

A Mantel test and spatial analyses of inter-colony genetic variation were performed on the data set using the software package AIS v1 (Miller 2005) to test for possible non-random patterns of genetic variation around the edge of Banks Peninsula. Two separate statistics are of special interest: spatial autocorrelation index and index of allelic aggregation (non-uniform dispersion of the alleles in the area) (Miller 2005). The genetic variation landscape of the area was also drawn from data using a specific approach applied in the software package AIS v1 (Miller 2005).

Results

The genetic data identified 56 control region haplotypes from 86 Banks Peninsula individuals. Forty-six of the 56 haplotypes occurred only once. A haplotype with 14 counts (16% of the total) was the most abundant haplotype in the region. The mean number of pairwise nucleotide differences between haplotypes was estimated as 23.53 (SD ± 10.45). Mean nucleotide diversity over all loci was 0.0426 (SD ± 0.021). Tajima $\hat{\theta}_{(T)}$ (Tajima 1983) and Watterson $\hat{\theta}_{(W)}$ (Watterson 1975) were calculated as 23.53 (SD ± 11.58) and 16.12 (SD ± 4.33), respectively. Colonies throughout Banks Peninsula showed differing degrees of shared haplotypes. Most of the colonies showed the highest number of shared haplotypes with their adjacent colonies, rather than colonies farther apart (Figure 2). In general, samples from adjacent colonies had a mean of 4.4 shared haplotypes whereas samples collected from colonies separated by between five and eight bays had a mean of 1.9 shared haplotypes. For example, the Damons Bay colony at the entrance of Akaroa Harbour, a busy recreational port, showed the highest number of shared haplotypes with the Otanerito and Island Bay colonies, which are in its immediate vicinity.

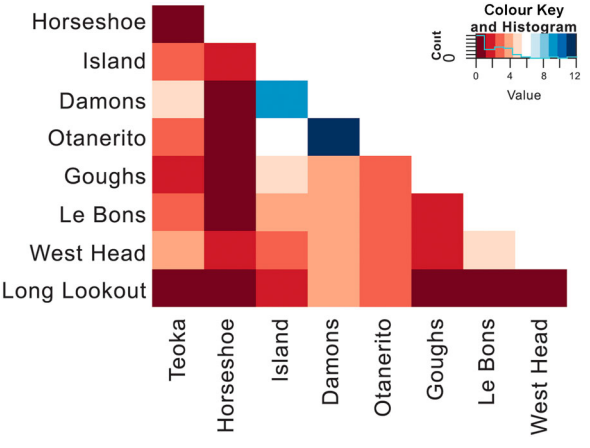

Figure 2. A heat map showing number of shared pairwise haplotypes among different colonies in Banks Peninsula. Different colours show the absolute counts of the shared pairwise haplotypes.

The Horseshoe Bay colony had the fewest number of shared haplotypes with any other colonies in the area (Figure 2).

Analysis of molecular variance (Excoffier et al. 1992) found that almost all of the variation was within populations. The null hypothesis of a lack of population structure around Banks Peninsula ($F_{ST} = 0$) could not be rejected ($P = 0.675$). The pairwise F_{ST} was only significant between Otanerito–Te Oka (0.13), Otanerito–Le Bons (0.18) and Otanerito–Horseshoe (0.12). The remaining pairwise F_{ST} values between the other colonies were not statistically different from zero. Spatial analysis of molecular variance (Dupanloup et al. 2002) identified the Otanerito Bay colony as maximally differentiated from the remaining eight colonies ($F_{ST} = 0.08$), although the result was not statistically significant when performing a permutation test (P value = 0.6).

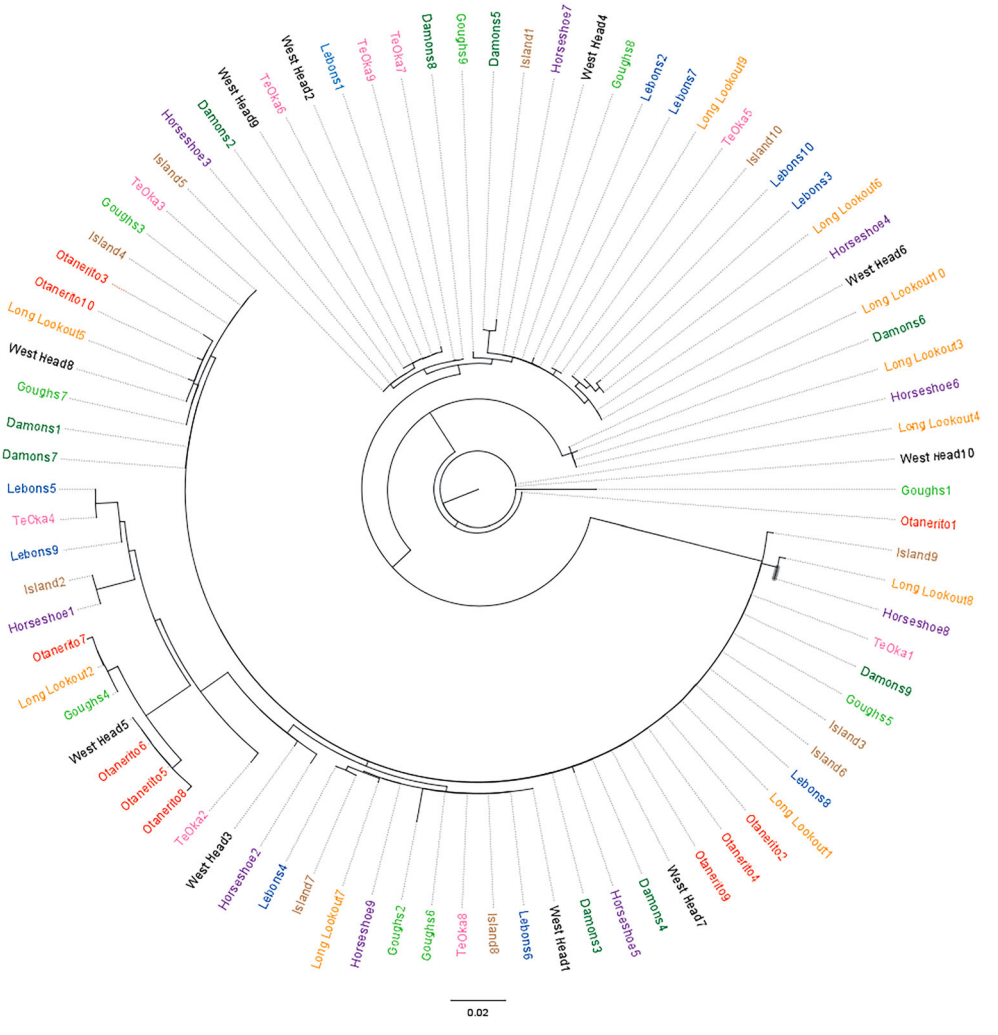

Figure 3. A multimodal (model averaging) phylogenetic tree of the mitochondrial DNA at Banks Peninsula. The haplotypes from the same colony share the same colour. Scale bar in standardised nucleotide substitution per generation.

The multimodal phylogenetic tree indicated several distinct clades in the area (Figure 3). In parallel, two obvious genetic clades were observed in the median-joining haplotype network analysis (Figure 4).

Approximate Bayesian Computations analysis was consistent with a population that has formed from the admixture of at least two separate clades from the New Zealand mainland and sub-Antarctic island populations. The most likely admixture coefficient from the above-mentioned clades to form the Banks Peninsula population was estimated at 0.418. The most probable estimate (MPE) of the parameter Θ and exponential growth rate (g) were estimated as 0.069 and 30.544, respectively. The direct and logistic regressions of the posterior probabilities of ABC analysis strongly rejected both the expansion from a small founder population without an external recruitment model, and the model with a single massive re-colonisation event. The simulations favoured significantly the multi-source re-colonisation dynamics ($P < 0.0001$). All estimated summary statistics for the two other models were significantly less than the observed value.

The Mantel test results did not show significant correlation between genetic and geographical distances ($r = 0.014$, $P = 0.35$). The lack of significant spatial correlation is also obvious in the spatial autocorrelation test, which was not significant. However, the allelic aggregation analysis showed that the most abundant allele in the area, which is probably the oldest allele, has a significant allelic aggregation index at 94% confidence level ($P = 0.06$), suggesting a slightly aggregated allelic structure. The landscape of the genetic variation suggested two peaks in the southern edge of the genetic landscape surface at Banks Peninsula (Figure 5).

Discussion

Re-colonisation of Banks Peninsula by New Zealand fur seals has happened in the past 40 years. Wilson (1981) reported the presence of only 50–100 individuals around Banks Peninsula in 1973, mainly non-breeding males and immature juveniles.

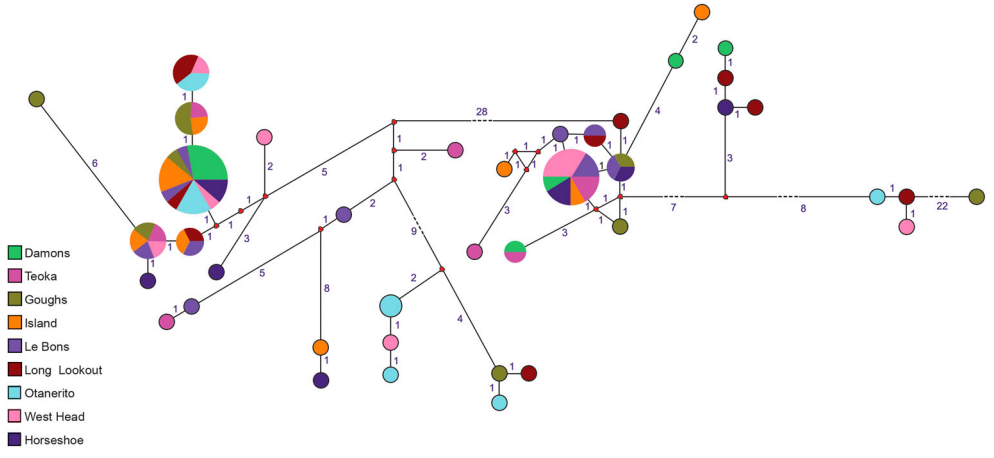

Figure 4. A median joining haplotype network reconstructed from New Zealand fur seal mitochondrial DNA control region at Banks Peninsula. The numbers are mutation steps and small red circles are median haplotypes.

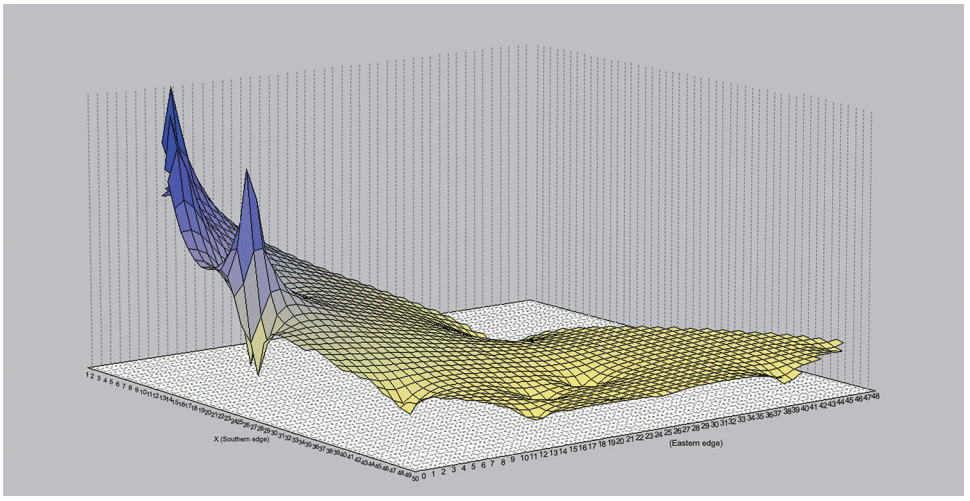

Figure 5. Genetic landscape of mitochondrial DNA control region from Banks Peninsula. The *x* and *y* coordinates are the midpoints of each edge in the triangulation. The *z* axis is a reflection of the genetic distance among haplotypes found at the vertices of triangles according to Miller (2005).

The value of the parameter Θ estimated in the current research, assuming a mutation rate of 2.7×10^{-5} per site per generation (Schneider & Excoffier 1999), corresponds to a maximum effective population size of 2500 breeding individuals for the fur seal population at Banks Peninsula. The value of exponential growth rate (g) (Kuhner 2006) is positive and consistent with an expanding population that had a smaller effective population size in the past. Extra caution is necessary when interpreting the exponential growth rate becausee the 95% credibility interval estimated for the population includes a value of zero, indicating a lack of information in the data to definitely reject a constant population size.

The lack of significant local population structure in the New Zealand fur seal population at Banks Peninsula is consistent with observed patterns reported for fur seals at other locations (Matthee et al. 2006; Dickerson et al. 2010; Lancaster et al. 2010; Berry et al. 2012). This finding indicates substantial matrilineal gene flow among neighbouring colonies, causing a homogeneous dispersion of genetic variation at a local scale.

The presence of two well-separated haplotype groups (clades) around Banks Peninsula strongly supports the hypothesis of the existence of two separate population refuges for New Zealand fur seals that escaped the large-scale human harvest, as was initially suggested (Lento et al. 1994). The fact that both of these hypothetical haplotype groups have been identified at a local scale may suggest the random initial re-colonisation of Banks Peninsula by individuals originating from these different clades.

The ABC results also strongly support the presence of at least two putative source populations re-colonising the area in the past 40 years. The same ABC analysis suggests a founder population size of approximately 300 individuals that rapidly increased in size due to both exponential population growth and successive waves of external recruitment.

The Horseshoe Bay colony haplotype structure was genetically the most different from other colonies in the area. Most of the haplotypes in this colony are private haplotypes that are found in no other colony. The Horseshoe Bay colony was the first colony reported

from Banks Peninsula after recent re-colonisation of the area (Wilson 1981). It is possible that the origin of the first re-colonisation event in the area was different from subsequent re-colonisation events. Alternatively, this colony might represent a relict lineage that survived human harvest in hard-to-access population refuges around Banks Peninsula.

The number of haplotypes at Banks Peninsula was also substantial for a population that has passed through a bottleneck and mirrors the pattern observed in other seal species (Lento et al. 1997; Weber et al. 2004; Baker et al. 2005; Matthee et al. 2006; Coltman et al. 2007). To what extent the observed pattern reflects pre-sealing demographic dynamics in this species is unknown. A high level of genetic diversity has already been reported for this region. Banks et al. (2002) found that little penguins (*Eudyptula minor*) around Banks Peninsula originated from populations all around New Zealand and suggested that the particular location of Banks Peninsula in New Zealand makes it an ecological hotspot for marine species travelling through New Zealand waters.

The observed pattern in the mitochondrial data is consistent with the spill-over theory of colony expansion suggested first by Bradshaw et al. (2000). The first founder colonies on Banks Peninsula probably profited from an abundance of vacant space and food resources available in the area, and increased rapidly in numbers. At some stage, a shortage of space in a colony forced some breeding females, probably first-time breeders (Roux 1987; Bradshaw et al. 2000), to emigrate to suitable habitat in the vicinity of the founder colonies. These newly established colonies may have been further re-colonised, to a lesser extent, by immigrants from other colonies around New Zealand and the sub-Antarctic islands (Taylor et al. 1995). Accepting this hypothesis requires the assumption of some degree of site philopatry (repeated return to natal sites) and site fidelity (repeated return to non-natal sites), which is not unusual for otariids (Kenyon & Wilke 1953; Trites & Antonelis 1994; Gentry 1998). The spill-over dynamics of colony expansion is obvious in most of the colonies as the highest numbers of shared haplotypes are usually found in colonies situated in close proximity to one another. This pattern is particularly obvious in the Island Bay, Damons Bay and Otanerito Bay colonies. The Island Bay colony is one of the oldest colonies in the region, as reported by Wilson (1981) as a potential haul-out site. However, two other colonies in the vicinity of Island Bay (Damons Bay and Otanerito Bay) were not reported as breeding colonies until 2011 (Baird 2011). Interestingly, both of these colonies show the highest number of shared haplotypes with the older Island Bay colony, and a pairwise $F_{ST} = 0$, which strengthens the idea of spilling over of older colonies in to new colonies in their vicinity.

The populations of New Zealand fur seals on Banks Peninsula are probably in the late stages of the maturity phase of re-colonisation dynamics. There is growing evidence that population genetic parameters may vary through time (Viard et al. 1997; Piertney et al. 1999; Garant et al. 2000; Nussey et al. 2005), for example fixation index estimations are considerably influenced by factors such as dispersal, mating system and effective population size (Nussey et al. 2005). The fact that most of the F_{ST} values in the current study are not significantly different from zero does not definitively rule out the presence of some kind of population structure in the earlier stages of the re-colonisation of the area or later on when new mutations start accumulating in the recently established colonies.

In conclusion, the level of diversity observed on Banks Peninsula could be representative of the overall genetic diversity of the species observed throughout New Zealand. The data also support the idea that there is enough diversity in mitochondrial DNA for this

marker to be useful in answering questions of conservation importance, especially when used in conjunction with high-throughput computation analysis pipe lines like massive population simulations. These results also provide the first step for more detailed population genetics studies of New Zealand fur seal.

Acknowledgements

The authors are grateful to New Zealand Department of Conservation and its local rangers. The contributions of all local Iwi, Ngāi Tahu, Ngāti Mamoe, Ngāti Apa, Ngāti Koata, Ngāti Rārua, Ngāti Tama, Ngāti Kuia, Te Ati Awa, Waitaha, Ngāti Kahungunu ki Wairarapa, Taranaki, Te Ati Awa, Ngāti Mutunga, Ngā Ruahine, Ngā Ruanui, Ngā Rauru and Te Āti Hau, are acknowledged. The contributions of Sudipta Kundu for GIS analysis and Mehdi Mahjoob for graphical re-creation of the figures are acknowledged. We are thankful to two anonymous reviewers for their constructive comments on the initial version of the manuscript.

Associate Editor: Dr Jonathan Banks.

Disclosure statement

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

Funding

This work was supported by Lincoln University postgraduate funding.

References

Baird S. 2011. New Zealand fur seals: summary of current knowledge. Wellington: Ministry of Fisheries.

Baker AR, Loughlin TR, Burkanov V, Matson CW, Trujillo RG, Calkins DG, Wickliffe JK, Bickham JW. 2005. Variation of mitochondrial control region sequences of Steller sea lions: the three-stock hypothesis. J Mammal. 86(6):1075–1084.

Banks JC, Mitchell AD, Waas JR, Paterson AM. 2002. An unexpected pattern of molecular divergence within the blue penguin (*Eudyptula minor*) complex. Notornis. 49(1):29–38.

Berry O, Spiller LC, Campbell R, Hitchen Y, Kennington WJ. 2012. Population recovery of the New Zealand fur seal in southern Australia: a molecular DNA analysis. J Mammal. 93(2):482–490.

Bonin CA, Goebel ME, Forcada J, Burton RS, Hoffman JI. 2013. Unexpected genetic differentiation between recently recolonised populations of a long-lived and highly vagile marine mammal. Ecol Evol. 3(11):3701–3712.

Bradshaw CJ, Lalas C, Thompson CM. 2000. Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). J Zool. 250(1):105–112.

Burrows C. 1994. Fruit, seeds, birds and the forests of Banks Peninsula. New Zeal Nat Sci. 21:87–87.

Carr D, Bowman J, Kyle CJ, Tully SM, Koen EL, Robitaille JF, Wilson PJ. 2007. Rapid homogenization of multiple sources: genetic structure of a recolonising population of fishers. J Wildlife Manage. 71(6):1853–1861.

Chesser RK. 1983. Genetic variability within and among populations of the black-tailed prairie dog. Evol. 37(2):320–331.

Chesser RK. 1991. Gene diversity and female philopatry. Genet. 127(2):437–447.

Choisy M, Franck P, Cornuet JM. 2004. Estimating admixture proportions with microsatellites: comparison of methods based on simulated data. Mol Ecol. 13:955–968.

Coltman D, Pilkington J, Pemberton J. 2003. Fine-scale genetic structure in a free-living ungulate population. Mol Ecol. 12(3):733–742.
Coltman D, Stenson G, Hammill M, Haug T, Davis C, Fulton T. 2007. Panmictic population structure in the hooded seal (*Cystophora cristata*). Mol Ecol. 16(8):1639–1648.
Cornuet J-M, Pudlo P, Veyssier J, Dehne-Garcia A, Gautier M, Leblois R, Marin J-M, Estoup A. 2014. DIYABC v2. 0: a software to make approximate Bayesian computation inferences about population history using single nucleotide polymorphism, DNA sequence and microsatellite data. Bioinformatics. 30(8):1187–1189.
Crawley MC, Wilson GJ. 1976. The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). Tuatara. 22:1–29.
Dickerson BR, Ream RR, Vignieri SN, Bentzen P. 2010. Population structure as revealed by mtDNA and microsatellites in northern fur seals, *Callorhinus ursinus*, throughout their range. PLoS ONE. 5(5):e10671. doi:10.1371/journal.pone.0010671
Dracopoli N, Brett F, Turner T, Jolly C. 1983. Patterns of genetic variability in the serum proteins of the Kenyan vervet monkey (*Cercopithecus aethiops*). Am J Phys Anthropol. 61(1):39–49.
Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol. 29(8):1969–1973.
Dupanloup I, Schneider S, Excoffier L. 2002. A simulated annealing approach to define the genetic structure of populations. Mol Ecol. 11(12):2571–2581.
Excoffier L, Laval G, Schneider S. 2005. Arlequin (version 3.0): an integrated software package for population genetics data analysis. Evol Bioinform. 1:47–50.
Excoffier L, Smouse PE, Quattro JM. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genet. 131(2):479–491.
Garant D, Dodson JJ, Bernatchez L. 2000. Ecological determinants and temporal stability of the within-river population structure in Atlantic salmon (*Salmo salar* L.)*. Mol Ecol. 9(5):615–628.
Gentry RL. 1998. Behavior and ecology of the northern fur seal. Princeton, NJ: Princeton University Press.
Goldsworthy S, Francis J, Boness D, Fleischer R. 2000. Variation in the mitochondrial control region in the Juan Fernandez fur seal (*Arctocephalus philippii*). J Hered. 91(5):371–377.
Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav. 28(4):1140–1162.
Hoelzel A. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. J Hered. 89(5):451–458.
Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol. 30(4):772–780.
Kawamoto Y. 1996. Population genetic study of Sulawesi macaques. In: Shotake T, Wada K, editors. Variations in the Asian Macaques. Tokyo: Tokai University Press; p. 67–88.
Kenyon KW, Wilke F. 1953. Migration of the northern fur seal, *Callorhinus ursinus*. J Mammal. 34(1):86–98.
Kuhner MK. 2006. LAMARC 2.0: maximum likelihood and Bayesian estimation of population parameters. Bioinformatics. 22(6):768–770.
Lancaster M, Arnould J, Kirkwood R. 2010. Genetic status of an endemic marine mammal, the Australian fur seal, following historical harvesting. Anim Conserv. 13(3):247–255.
Larkin MA, Blackshields G, Brown N, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R. 2007. Clustal W and Clustal X version 2.0. Bioinformatics. 23 (21):2947–2948.
Lento G, Haddon M, Chambers G, Baker C. 1997. Genetic variation of southern hemisphere fur seals (*Arctocephalus* spp.): investigation of population structure and species identity. J Hered. 88(3):202–208.
Lento GM, Mattlin RH, Chambers GK, Baker CS. 1994. Geographic distribution of mitochondrial cytochrome b DNA haplotypes in New Zealand fur seals (*Arctocephalus forsteri*). Can J Zool. 72 (2):293–299.
Macdonald DW. 2001. The Encyclopedia of mammals. Oxford, UK: Oxford University Press.

Majluf P, Goebel ME. 1992. The capture and handling of female South American fur seals and their pups. Mar Mammal Sci. 8(2):187–190.
Matthee C, Fourie F, Oosthuizen W, Meyer M, Tolley K. 2006. Mitochondrial DNA sequence data of the Cape fur seal (*Arctocephalus pusillus pusillus*) suggest that population numbers may be affected by climatic shifts. Mar Biol. 148(4):899–905.
McLintock AH. 1966. Encyclopaedia of New Zealand. Wellington: Government Printer.
Melnick D. 1987a. The genetic consequences of primate social organization: a review of macaques, baboons and vervet monkeys. Genetica. 73(1–2):117–135.
Melnick DJ. 1987b. Cercopithecines in multimale groups: genetic diversity and population structure. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, editors. Primate societies. Chicago, IL: University of Chicago Press; p. 121–134.
Miller M. 2005. Alleles In Space (AIS): computer software for the joint analysis of interindividual spatial and genetic information. J Hered. 96(6):722–724.
Mirimin L, Miller R, Dillane E, Berrow S, Ingram S, Cross T, Rogan E. 2011. Fine-scale population genetic structuring of bottlenose dolphins in Irish coastal waters. Anim Conserv. 14(4):342–353.
Nussey D, Coltman D, Coulson T, Kruuk L, Donald A, Morris S, Clutton-Brock T, Pemberton J. 2005. Rapidly declining fine-scale spatial genetic structure in female red deer. Mol Ecol. 14 (11):3395–3405.
Piertney SB, MacColl AD, Lambin X, Moss R, Dallas JF. 1999. Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). Biol J Linn Soc. 68(1–2):317–331.
Pope TR. 1992. The influence of dispersal patterns and mating systems on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evol. 46(4):1112–1128.
Posada D. 2008. jModelTest: phylogenetic model averaging. Mol Biol Evol. 25(7):1253–1256.
Robertson BC, Gemmell NJ. 2005. Microsatellite DNA markers for the study of population structure in the New Zealand fur seal *Arctocephalus forsteri*, Department of Conservation.
Rohl A. 2000. Network: A program package for calculating phylogenetic networks, Version 4.1. Mathematisches Seminar, University of Hamburg, Hamburg. Available from: http://www.fluxus-engineering.com.
Roux JP. 1987. Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amstedam Island. In: Croxall JP, Gentry RL, editors. Status, biology and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, 23–27 April 1984. NOAA Tech. Rep. NMFS. 51:189–194.
Ryan CJ, Hickling G, Wilson K-J. 1997. Breeding habitat preferences of the New Zealand fur seal (*Arctocephalus forsteri*) on Banks Peninsula. Wildlife Res. 24(2):225–235.
Schneider S, Excoffier L. 1999. Estimation of past demographic parameters from the distribution of pairwise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics. 152(3):1079–1089.
Schwartz OA, Armitage KB. 1980. Genetic variation in social mammals: the marmot model. Science. 207(4431):665–667.
Skulason S, Smith TB. 1995. Resource polymorphisms in vertebrates. Trends Ecol Evol. 10 (9):366–370.
Spong G, Stone J, Creel S, Björklund M. 2002. Genetic structure of lions (*Panthera leo* L.) in the Selous Game Reserve: implications for the evolution of sociality. J Evolution Biol. 15(6):945–953.
van Staaden MJ, Chesser RK, Michener GR. 1994. Genetic correlations and matrilineal structure in a population of Spermophilus richardsonii. J Mammal. 75(3):573–582.
Storz JF. 2005. Nonrandom dispersal and local adaptation. Jay F. Storz Publications: 11.
Sugg DW, Chesser RK, Stephen Dobson F, Hoogland JL. 1996. Population genetics meets behavioral ecology. Trends Ecol Evol. 11(8):338–342.
Surridge A, Ibrahim K, Bell D, Webb N, Rico C, Hewitt G. 1999. Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). Mol Ecol. 8(2):299–307.

Tajima F. 1983. Evolutionary relationship of DNA sequences in finite populations. Genetics. 105 (2):437–460.
Taylor R, Barton K, Wilson P, Thomas B, Karl B. 1995. Population status and breeding of New Zealand fur seals (*Arctocephalus forsteri*) in the Nelson-northern Marlborough region, 1991–94. New Zeal J Mar Fresh Res. 29(2):223–234.
Trites AW, Antonelis GA. 1994. The influence of climatic seasonality on the life cycle of the Pribilof northern fur seal. Mar Mammal Sci. 10(3):311–324.
Turner T. 1981. Blood protein variation in a population of Ethiopian vervet monkeys (*Cercopithecus aethiops aethiops*). Am J Phys Anthropol. 55(2):225–232.
Urian KW, Hofmann S, Wells RS, Read AJ. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. Mar Mammal Sci. 25(3):619–638.
Viard F, Justy F, Jarne P. 1997. Population dynamics inferred from temporal variation at microsatellite loci in the selfing snail *Bulinus truncatus*. Genetics. 146(3):973–982.
Watterson G. 1975. On the number of segregating sites in genetical models without recombination. Theor Popul Biol. 7(2):256–276.
Weber D, Stewart B, Lehman N. 2004. Genetic consequences of a severe population bottleneck in the Guadalupe fur seal (*Arctocephalus townsendi*). J Hered. 95(2):144–153.
Wilkinson GS. 1985. The social organization of the common vampire bat. Behav Ecol Sociobiol. 17 (2):123–134.
Wilson GJ. 1981. Distribution and abundance of the New Zealand fur seal *Arctocephalus forsteri*. Fisheries Research Division Occasional Publication 20. Wellington: Ministry of Agriculture and Fisheries.