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Age distribution of lactating New Zealand sea lions: Interannual and intersite variation

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ABSTRACT

The age distribution of 865 lactating New Zealand sea lions (NZSLs; *Phocarctos hookeri*) was investigated over 3 yr (1999–2001) at two breeding colonies, Sandy Bay and Dundas Island, New Zealand. Lactating females were aged between 3 and 26 yr with a maximum observed age of 28 yr. The mean age of lactating females was 11.1 (SE = 0.16) yr. Age distributions peaked at ages 8 and 9 with a strong

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skew toward younger females, likely indicative of maximum recruitment into the breeding population by this age. There were significant intersite differences in age structure and also significant interannual differences in age distributions at Sandy Bay, but not at Dundas Island. Given that the two colonies are less than 10 km apart, have some interchange, and share foraging areas, these differences are surprising. However, the colony at Dundas Island is almost four times larger than Sandy Bay and may therefore be less sensitive to demographic or environmental stochasticity. That age distributions of NZSLs vary significantly over small temporal and spatial scales has important implications for the extrapolation of data from one site or year to the population level, and hence for their management and conservation.

Key words: New Zealand sea lion, *Phocarctos hookeri*, lactating, age distribution, age structure, interpopulation variation, ageing.

Demographic models are widely used to study the dynamics of marine mammal populations (*e.g.*, Payne 1977, Barlow and Boveng 1991, York 1994, Boyd *et al.* 1995, Dabin *et al.* 2004, Evans and Hindell 2004). A fundamental step in many of these models is the characterization of the age structure of a population. Changes in the dynamics of populations are often reflected in age-specific changes in demographics that in turn will be reflected in the age structure (Caughley 1977). Age distributions can then be used to assess population stability, geographic or temporal variation, and to investigate demographic variables, such as survival, longevity, and reproduction (Caughley 1977, Barlow and Boveng 1991, Holmes and York 2003).

Demographic studies rarely sample the entire population and instead utilize subsamples that are assumed to be representative of the overall population. This assumption is rarely tested. Failure to meet such an assumption can have a significant impact on the overall understanding of population demographics (Fredrickson *et al.* 2005). As such, comparative studies of interpopulation variation in demographic parameters can improve our understanding of population dynamics and the evolution of life histories (Fredrickson *et al.* 2005). Therefore, an understanding of age structure and how it varies temporally and spatially across a population is essential in understanding population dynamics, especially for a threatened species.

New Zealand sea lion (NZSL) *Phocarctos hookeri* (also known as Hooker's sea lion) is endemic to New Zealand (NZ) and is currently listed as threatened (IUCN 2002). The most recent estimate of population size is 10,550 (CV = 0.04) individuals. Annual pup production, on which this estimate is based, is declining significantly (Chilvers *et al*. 2007). Sealing and subsistence harvesting has reduced the breeding distribution of NZSLs to the NZ sub-Antarctic (*i.e.,* Auckland, Campbell, Snares Islands)—fewer than 10 pups are born annually outside this zone (Childerhouse and Gales 1998, Chilvers *et al.* 2007). Most (64%) of the annual pup production for the species occurs at Dundas Island, with the second largest breeding colony being at Sandy Bay on Enderby Island (19%). Other breeding sites include Campbell Island (8%), Figure of Eight Island (3%), and Otago Peninsula (<0.1%) (Chilvers *et al.* 2007) (Fig. 1). NZSLs are regularly caught as bycatch in the southern squid (*Nototodarus sloanii*) trawl fishery. It is estimated that on average more than 70 NZSLs have been killed each year since observations began in 1988 (Ministry of Fisheries 2005).

Life history parameters for this species are poorly known. Most population modeling to date has either used life history parameters derived from other species

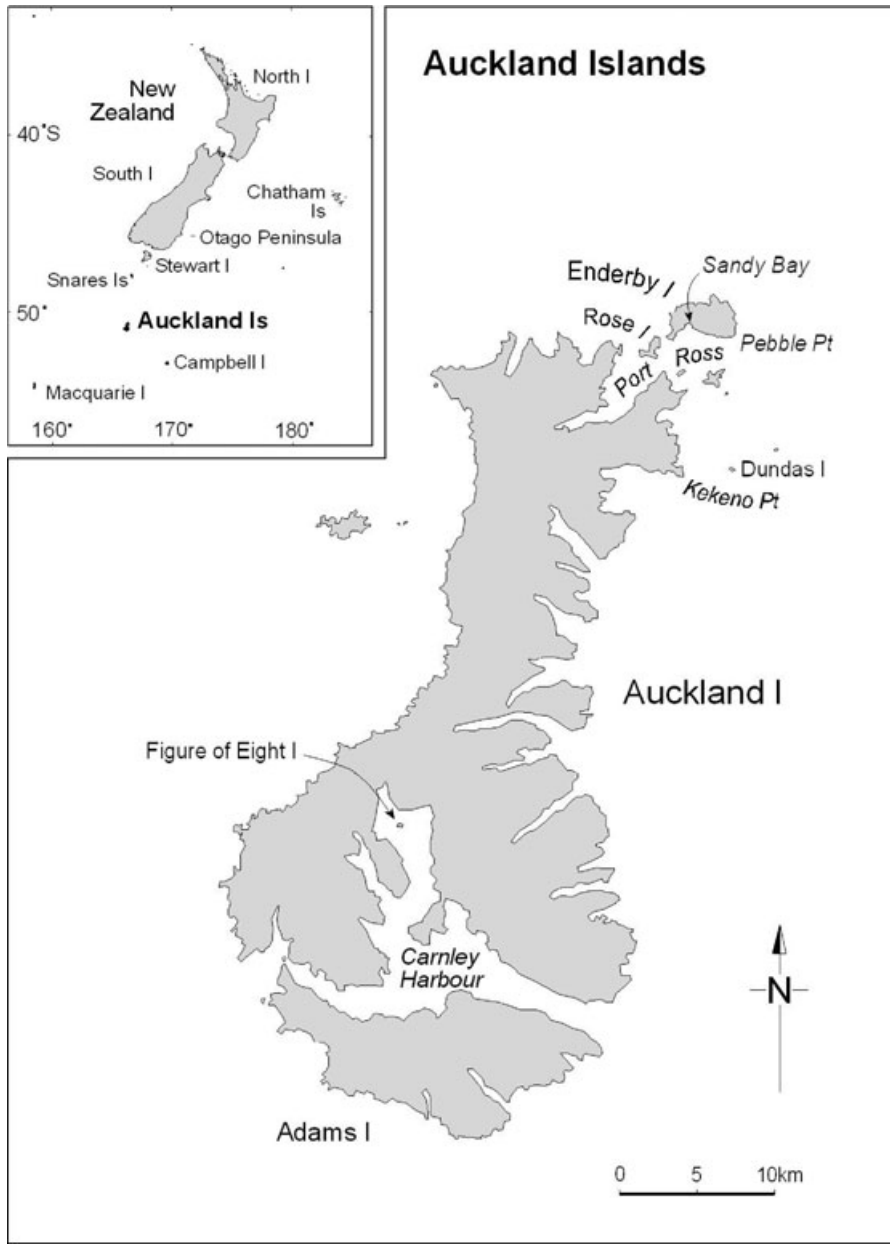

Figure 1. Map showing places mentioned in the text.

(Gales and Fletcher 1999) or has attempted to estimate them using a computationally intensive Bayesian approach (Breen *et al.* 2003). Maximum ages reported for NZSLs are 23 for males and 21 for females (Cawthorn *et al.* 1985, Dickie 1999), although these observations are based on a small number of individuals of estimated rather

than known ages. The minimum estimated age at first reproduction in females has been reported as four and age at last reproduction as 21 (Cawthorn 1993, Dickie 1999). The proportion of females that achieve maturity at these ages is not known and, to date, these values have been treated as a "knife edge" function in most models. The only estimate of the proportion of mature females giving birth to a pup is 0.75 (95% CI 66%–84%) from resightings of branded females (Chilvers, unpublished data). Without robust estimates of life history it is difficult to assess how closely the modeling, and the resulting management actions, corresponds to reality. In the context of ongoing bycatch, this ignorance constitutes a risk to appropriate management and the long-term survival of NZSLs.

From the perspective of population biology, understanding the demographics of reproductive females is one of the most fundamental questions, especially for a polygynous breeding species (Caughley 1977). For this reason, and because it is logistically feasible to capture and handle them, lactating females are the focus of this study. We chose to specifically sample lactating females rather than sexually mature females, as a proportion of non-breeding mature females do not return to the breeding colonies each year and are therefore unavailable for sampling, whereas all lactating females are thought to return (Chilvers and Wilkinson 2008). We investigated the age distribution of lactating NZSLs at two breeding colonies over 3 yr at the Auckland Islands. The aims of the study were to: (1) describe the age distribution of lactating NZSL, and (2) investigate temporal and spatial patterns in age distribution.

Methods

This study formed part of a wider study investigating demographics of NZSLs. To minimize disturbance to the colony and individuals, we estimated the minimum sample size required to estimate demographic rates (*i.e.*, survival) robustly (*i.e.*, CV = 0.10) to be approximately 150 individuals per site per year. This same sample was used in this study. Our study was conducted at two breeding colonies in the Auckland Island group (50°30′S, 166°17′E): Dundas Island and Sandy Bay (Enderby Island) with an annual pup production of 1,600–2,100 and 400–500, respectively (Chilvers *et al.* 2007). The colonies are approximately 10 km apart (Fig. 1).

Capture and sampling of lactating female NZSLs were undertaken in January and February during the austral summers of 1999, 2000, and 2001 at Dundas Island and Sandy Bay (we refer to each austral breeding season, which straddles two calendar years, as the date in which sampling took place, *i.e.*, 1998/1999 season as 1999). Random sampling of lactating females was not possible during January as some inner parts of the colonies, and therefore some individuals, were not accessible due to highly territorial and aggressive males (Chilvers *et al.* 2005*a*). We attempted to mitigate this potential bias by spreading capture effort evenly throughout the accessible parts colony each day. Effort was also spread over three periods between 10 January and 13 February each year (see Fig. 2a, b for exact timing of sampling), to allow for temporal and spatial mixing of individuals between sampling days. All females were available for capture in February when territorial males departed. Recent detailed observations of marked females show they are highly mobile within the breeding colonies over short periods, suggesting that females inaccessible for sampling on one day, may have been available on subsequent days (Augé *et al*. in press).

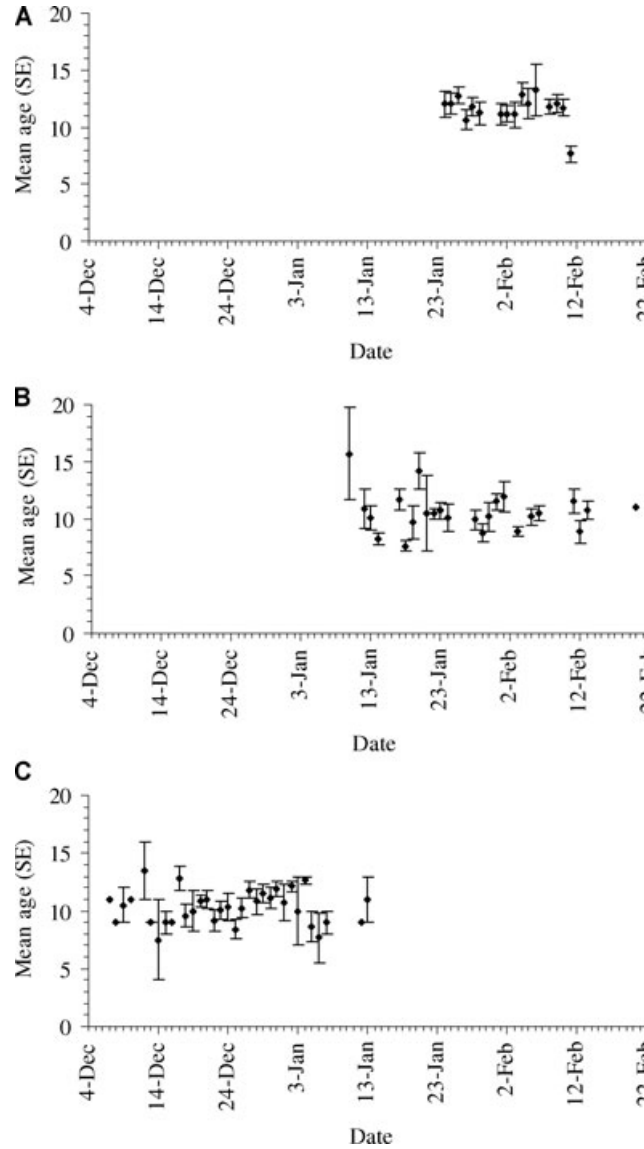

Figure 2. Daily mean age (±SE) of sampled females by date of capture for (a) Dundas Island ($n = 438$), (b) Sandy Bay ($n = 427$), and (c) daily mean age of known- or estimated-age females observed giving birth at Sandy Bay ($n = 159$). (a) and (b) are from sampling between 1999 and 2001, and (c) are from observations between 1998 and 2005.

Sampling refers to both the capture of an individual for tooth ageing and the resighting of a previously aged individual. Individuals were considered as lactating by either expressing milk from captured individuals or if seen nursing a pup if resighted and not captured. If a previously tagged or branded female (and therefore the age was already known or estimated) was selected for sampling, it was not physically

captured, but its number was recorded and it was included in the sample. Individuals were only sampled once per season. The same selection criteria for sampling were used to ensure that an individual's capture probability was equal across years, sites and between individuals of known and unknown age.

NZSLs were captured in specially designed nets (Fuhrman Diversified, TX), physically restrained, and anaesthetized using an isoflurane gas anesthetic machine (Gales and Mattlin 1998). After physical restraint, and being mildly sedated *via* gas anesthesia, an intravenous injection of 2.5 ml of midazolam (Hypnoval, Roche Products Ltd, Welwyn Garden City, UK) at 5 $mgmL^{-1}$ concentration was administered. Once anaesthetized, individuals were strapped to a custom-made restraint frame to prevent movement if they awakened prematurely. All individuals were tagged on both flippers with individually numbered Allflex cattle ear tags (1999) or Dalton jumbo tags (2000 and 2001). In addition, an individual coded PIT chip (Trovan, London, UK) was inserted subcutaneously dorsal and anterior to the pelvis. Females caught at Sandy Bay in 2000 were also hot branded on the left side of their body (see Chilvers and Wilkinson 2008 for details).

Once under full anesthesia, a single post-canine tooth was removed. Following capture and processing, females were carried back into the colony and monitored until they retained consciousness. Pups were captured at the same time as the mother and reunited after sampling. A veterinarian oversaw all captures and no antibiotics or any other medication were given. All work was conducted under a Marine Mammal and Animal Ethics Permit issued by the NZ Department of Conservation. Fifty-five individuals were recaught up to 9 yr after tooth extraction as part of other studies and all had completely healed extraction wounds. There was no indication of any long-term detrimental effect (as has also been reported from other species, *e.g.*, Arnbom *et al.* 1992, Blundell and Pendalton 2008).

A single post-canine tooth was removed from all individuals of unknown age. All teeth were sectioned, stained and aged using readings of growth layer groups (GLGs) in the cementum. Methods for the removal, preparation and ageing of teeth are fully described in Childerhouse *et al*. (2004). Some individuals of known age were captured and a tooth was collected for validation of the ageing methodology. Teeth were read "blind" three times by the same reader (SC). Precision in estimated age was improved via adopting the decision rules of Dickie and Dawson (2003) and discarding sets of readings with low precision (*i.e.*, range of three readings >2 yr) and re-reading the tooth until a precise set of estimates was made. While there was some variation in assigning exact age to individuals, it was possible to age 94% of individuals to the exact age or to within 1 yr of actual age based on a study of teeth from individuals of known age (Childerhouse *et al.* 2004). There was no significant difference in the slope of the regression line of actual and estimated age using this technique, but we used the fitted regression line to estimate the age of individuals of unknown age because it uses the best information available (Childerhouse *et al.* 2004). For the purposes of this study, individuals were considered known age only if they were tagged at birth (*i.e.*, individuals between the ages of 3 and 26 yr in this study), otherwise they were of estimated age. Given the lack of significant difference between known and estimated ages, we combined all ages for analysis.

ANOVAs and a *G*-test were used to investigate differences in age distributions between and within colonies and over years. Regressions and ANOVAs were used to investigate possible trends in age at capture and age at parturition through the breeding season. Analysis was completed in SPSS version 10 (2004). Statistical significance was at the 0.05 level.

Results

A total of 865 lactating females were sampled during January and February over the 3 yr (Table 1, Fig. 3). Most (81%) individuals sampled were captured and a tooth removed. The remaining 19% were not captured as they were identified from existing tags or brands and therefore were already of known or estimated age. Overall, 3,435 individual tooth readings were made from 636 individuals of unknown age with a mean number of 4.5 (SE = 0.03) readings per individual tooth. All teeth extracted were aged successfully with most (59%) teeth only requiring one set of readings but some required two (39%) and three (2%) sets of readings before a precise set was achieved.

The estimated mean age from GLG readings (mean = 11.1, SE = 0.16) was slightly lower after correction via the regression in Childerhouse *et al.* (2004) (mean = 10.8, SE = 0.13) (Fig. 3). While there was no significant difference between means of estimated and corrected ages (ANOVA: $F = 3.15$, $df = 1$, $P = 0.07$), the age ranges and modes were different (*e.g.*, 4–23 yr and 3–26 yr; 8 and 9 yr for estimated and corrected ages, respectively).

Overall, 20% of all sampled females in this study were of known age. The age distribution of known age and estimated-age females was significantly different (*G*-test: $G = 46.7$, df = 23, $P = 0.04$) with known age individuals having a much younger mean age (mean = 8.5 *vs.* 11.8) and smaller age range (6–15 yr *vs.* 3–26 yr). This significant difference is due to the limited number of tagged individuals in the population that did not span all the ages, with no younger (*e.g.*, tagging stopped in 1992 so the minimum tagged age was 6) and few older tagged individuals (*e.g.*, tag loss in older individuals is high) available for sampling.

There was no evidence of any trend in mean age at capture for either colony across the sampling period (ANOVA: Dundas, $F = 0.06$, df = 437, $P = 0.80$; ANOVA: Sandy Bay, $F = 0.06$, df = 426, $P = 0.80$; Fig. 2a, b). Births occurred during December to February, but we were unable to sample in December due to the strongly territorial nature of males at this time. Resighting records ($n = 160$) of females observed giving birth during December and January at Sandy Bay between 1999 and 2005 (Fig. 2c) show no evidence of mean age varying through the breeding season (ANOVA: age, $F = 0.37$, df = 158, $P = 0.56$).

A two-way ANOVA confirmed a significant colony effect and a significant year effect but no interaction effect (two-way ANOVA: colony, $F = 14.6$, df = 1, 864, $P < 0.001$; year, $F = 4.6$, df = 2, 864, $P < 0.01$; colony year, $F = 0.01$, df = 2, 864, $P = 0.39$). Each colony was then investigated separately for year effect and while a significant difference in mean age was found for Sandy Bay (one-way ANOVA: year, $F = 4.7$, df = 426, $P < 0.01$), no such effect was detected for Dundas Island (One-way ANOVA: year, $F = 1.3$, df = 437, $P = 0.28$). The significant difference in age distribution between colonies was characterized by Dundas Island having an older mean age and being more variable over a greater range of ages with a greater spread than at Sandy Bay, which has a distinct peak (Table 1, Fig. 4).

The overall mean age of all lactating females sampled was 11.1 (SE = 0.16) yr (Table 1). The youngest individual observed giving birth was at age 3. All the age distributions followed the same general pattern, showing a rapid increase in the number of lactating females from age 3 to 8 or 9, and then declining slowly until age 26 (Fig. 3b). Overall, individuals of age 8 and 9 comprised 26% of the total age distribution and those of between the ages of 7 and 11 yr comprised 51% of the total age distribution. The cumulative frequency distribution of sampled females shows

Table 1. Summary statistics for observed age distribution of lactating NZSLs at two breeding colonies (Dundas Island, Sandy Bay) for 3 yr (1999, 2000, 2001) at the Auckland Islands. SE = standard error.

Breeding colony	Year	*n*	Mean	SE	Minimum	Mode	Median	Maximum
Sandy Bay	1999	146	9.7	0.3	3	8	9	21
Sandy Bay	2000	138	10.6	0.4	3	8	9	24
Sandy Bay	2001	143	11.2	0.4	4	9	10	26
Sandy Bay	1999–2001	427	10.5	0.2	3	8	9	26
Dundas Island	1999	140	11.2	0.4	3	8	10	25
Dundas Island	2000	149	12.1	0.4	4	9	11	26
Dundas Island	2001	149	11.8	0.4	4	9	11	23
Dundas Island	1999–2001	438	11.7	0.2	3	9	11	26
Combined	1999–2001	865	11.1	0.2	3	9	10	26

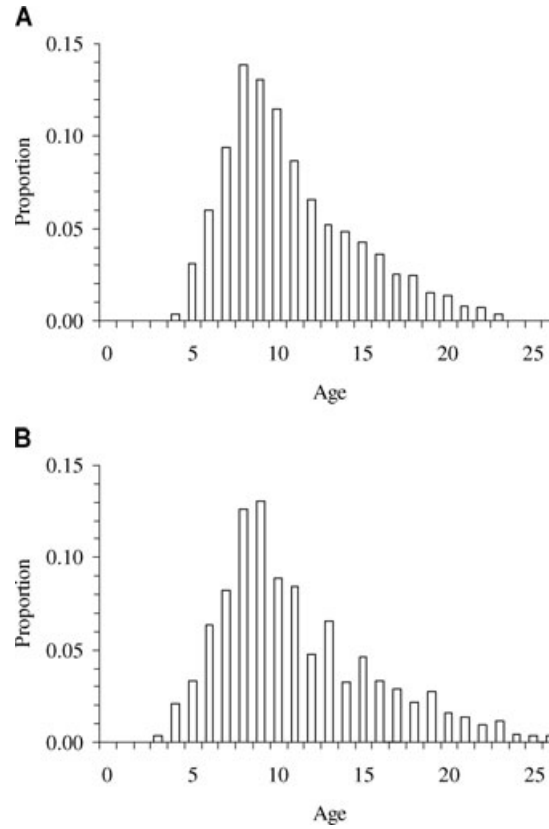

Figure 3. Estimated age distribution of lactating NZSLs ($n = 865$) from (a) mean reading of GLGs in post-canine teeth, and (b) after correction using the regression equation in Childerhouse *et al.* (2004).

the younger age distribution at Sandy Bay than at Dundas Island (Fig. 5). Fifty three percent of individuals sampled at Sandy Bay were aged 9 yr (the peak of the overall age distribution) or less. At Dundas Island this same age group corresponds to only 39%. In addition to the information from sampling of lactating females, there were resightings of two females of estimated age 27 and 28, but these individuals were not included in the data as they were not lactating.

Discussion

This is the first description of the age distribution of lactating NZSLs; showing an age range from 3 to 26 yr of age. This is considerably wider than previous estimates (*i.e.*, 4–21, Dickie 1999). This is the first time that 3-yr olds have been reported with pups, indicating that NZSLs can become sexually mature as early as 2 yr of age. This work also extends the previous maximum age recorded for a female from 21 to 28 yr, with maximum observed age at last reproduction of 26. This estimate of maximum age may also be biased low if reproductive senescence is a strong feature of this species

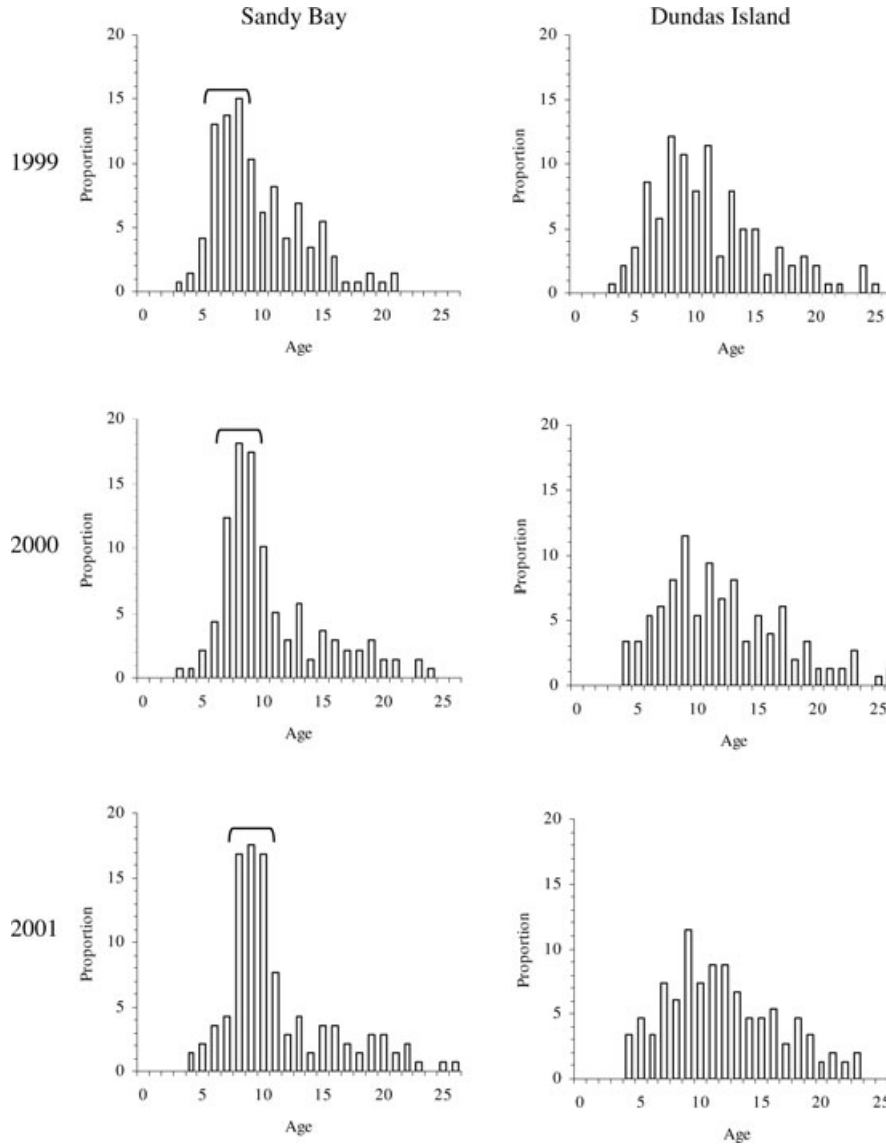

Figure 4. Relative age distributions of lactating female NZSLs by breeding colony (Sandy Bay, Dundas Island) and year (1999, 2000, 2001) in the Auckland Islands. Figures are for Sandy Bay in 1999 ($n = 146$), 2000 ($n = 138$), and 2001 ($n = 143$) and Dundas Island in 1999 ($n = 140$), 2000 ($n = 149$), and 2001 ($n = 149$), respectively. The three strong cohorts seen at Sandy Bay are designated by the horizontal brackets.

as only breeding females were sampled in this study, and any senescent females would have been excluded. However, this potential bias is unlikely to be important for population modeling, as it appears that there are few individuals older than 28 and if they are senescent, their impact on a population model would be negligible.

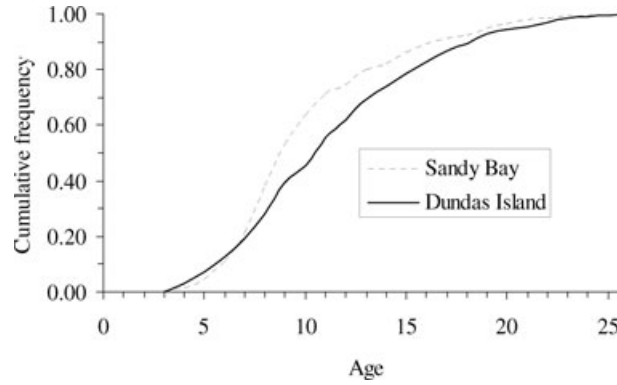

Figure 5. Cumulative age frequency (%) of lactating NZSLs by breeding colony: Sandy Bay ($n = 427$) and Dundas Island ($n = 438$).

The age range of lactating NZSLs is larger than that reported from other sea lion species (Table 2). Age at first reproduction is similar across sea lion species but the maximum breeding age for NZSLs is older than that reported from other species. While methodologies differed between these studies they provide useful comparisons, although the other studies had considerably smaller sample sizes. There is a large difference between maximum reported age and maximum breeding age for Steller's sea lion that could be indicative of reproductive senescence, or be due to low sampling, tagging or resighting effort. As only reproductive females were sampled in this study of age distribution, it is difficult to determine the effect of any senescence in NZSLs. However, preliminary analysis of age-specific reproductive rates indicates that reproductive senescence is likely to be a strong feature of NZSLs (Childerhouse *et al.* in press).

The age distribution of breeding females shows a strong negative skew towards younger age classes (*i.e.*, <10). This is consistent with a slow recruitment into the breeding pool followed by a reasonably consistent level of mortality once all females are recruited, although it is not possible to confirm this pattern from the age distribution information alone. A striking feature of the distribution is the peak at ages 8 or 9. This suggests full recruitment into the breeding population by about this age that is consistent with the age specific reproductive rate reaching a plateau at ages 7–8 (Childerhouse *et al.* in press). This peak is influenced by the three strong cohorts (*i.e.*, individuals born in 1991–1993) seen moving through the age distribution at Sandy Bay that were years of slightly lower pup production. The majority of breeding females are aged between 7 and 11 yr of age. All females older than this, despite spanning 15 year classes, contribute only a little more than a third of total pup production, highlighting the importance of these younger individuals.

It was assumed that sampled individuals reflected random sampling of the lactating female population although, in practice, it is very difficult to achieve random sampling when sampling territorial pinnipeds at breeding colonies (Boyd *et al.* 1995). A consistent selection methodology was used over years and colonies, with sampling effort spread throughout the breeding season to minimize any possible bias. One of the features of the sampling design was the consistent selection criteria applied to both marked and unmarked females in both colonies. This ensured that there was no

Table 2. Estimates of reproductive parameters of breeding female sea lions, including age at first reproduction (AFR), and maximum observed female age.

	Breeding age females							
Species	AFR	Min	Max	Mean (SE)	Median	Mode	Max female age	Reference
NZSL		3	26	11.1 (0.16)	8	9	28	This study
Steller's sea lion	3–8	3	19				30	Pitcher and Calkins 1981[a]
		3	19	8.8 (0.44)	8	4, 7	29	Winship *et al.* 2001
		4	21				31	Holmes *et al.* 2007
Californian sea lion		4	23+				25	Melin 2002, Hernández-Camacho *et al.* 2008*a*, *b*
	5–9							Peterson and Bartholomew 1967, Odell 1975, Atkinson 1997
Australian sea lion	3.8–6.1	3.8	24	11			24	Higgins 1993; McIntosh, unpublished data
Southern sea lion	3–4	3	15				15	Rosas *et al.* 1993, Atkinson 1997

[a]This age frequency refers to females with fetus rather than females with a pup or pregnant.

bias from capture probability, which was especially important at Sandy Bay where a high proportion of marked females were sampled each year. While sample size was the same between colonies, a significantly higher proportion of marked females were sampled at Sandy Bay (mean ~28%) than Dundas Island (mean ~7%) each year. As the selection criterion for known and unknown age individuals in the sample was consistent, there is no reason to suspect that this would be a source of bias. Given the robust sampling strategy and, that all females were available for sampling in February, the sampling methodology is assumed to be unbiased.

The ageing technique used here is validated by blind reading of teeth of known age individuals. Age estimates are precise and estimated ages were modified to account for minor (but not significant) biases in ageing to improve accuracy (Childerhouse *et al.* 2004). In fur seals, with a shorter lactation period, the mean age of breeding females has been observed to change through the season (Boyd and McCann 1989, Lunn and Boyd 1993). This could have biased the age distributions we report here, as we were unable to sample across the full season, but this was not the case as mean age did not to change through the season for NZSL. We pooled across years due to small samples sizes to investigate this trend, which could have masked interannual variation, but given the large combined sample size (*e.g.*, >1,000 observations, Fig. 2) we do not believe this to be the case.

The two colonies in this study had significantly different age distributions, with Dundas Island having an older mean (1.2 yr older) and median (2 yr older) than Sandy Bay, although the age range was the same for both colonies. Sandy Bay had a more skewed age distribution with a higher proportion of young individuals. This is puzzling given that the colonies are less than 10 km apart. While males are known to move between the colonies regularly, females are highly philopatric and are rarely recorded breeding away from their natal colony (Chilvers *et al.* 2005*a*, Robertson *et al.* 2006). This variation between the colonies indicates that there are one or more factors influencing them differently.

Pup production at both colonies has been reasonably constant since at least the 1980s until 1998, but has declined since (Childerhouse and Gales 1998, Wilkinson *et al.* 2003, Chilvers *et al.* 2007). The rate of decline from 1998 to 2006 at Dundas Island (−4.8% per annum) is significantly higher than at Sandy Bay (−1.2% per annum) for the same period (t-test, $t = 0.001$, df $= 18$, $P < 0.01$). Different rates of decline may have given rise to the differences in age distributions reported here. The reason behind the decline at both colonies remains unknown. Research on demographics (*e.g.,* adult survival and reproduction, pup mortality) has been undertaken at Sandy Bay but not at Dundas Island, meaning that it is not yet possible to investigate intersite differences in demographics.

The two colonies have significantly different annual pup production: Dundas Island with approximately 1,600–2,100 and Sandy Bay with approximately 400–500 (Chilvers *et al.* 2007). Given this difference in size, density-dependent factors (*e.g.*, availability of pupping space) may be less intense at Sandy Bay than Dundas Island. If this were true, Sandy Bay may have a better recruitment when conditions were favorable (*e.g.*, plentiful prey), as is seen with the 1991–1993 cohorts. While we do not understand what constitutes an acceptable pupping environment, there is plenty of unoccupied beach at both colonies during the breeding season suggesting that space is not limiting for both colonies. Both sites also have similar environmental conditions (*e.g.*, exposure to storm events). It is also possible that density dependence may be influencing age classes other than pups (*e.g.,* juvenile survival), and data are presently being collected to investigate this.

Another possible scenario is that females from Dundas Island and Sandy Bay have different foraging strategies and/or feeding grounds and that Sandy Bay females had several above-average years of foraging, compared to Dundas Island. Colony specific foraging areas have been documented in other pinniped species (Merrick and Loughlin 1997, Bonadonna *et al.* 2001). However, this seems unlikely for NZSLs as foraging studies suggest lactating females from Sandy Bay forage widely over the Auckland Island's shelf, and that recent work at Dundas Island has documented similar patterns (Chilvers *et al.* 2005*b*, L. Chilvers[2]).

Interannual differences in age distributions were not apparent from Dundas Island, which suggests that Dundas Island has a stable and more mature population structure. Sandy Bay, on the other hand, shows signs of strong cohorts moving through the age distribution, indicative of an unstable population, or at least a population with more variable population demographics. The three strong cohorts (*i.e.*, females born from 1991 to 1993) seen at Sandy Bay derive from years of slightly lower than average pup production (Wilkinson *et al.* 2003) suggesting that subsequent recruitment and survival may have been higher than normal rather than reflecting an increase in pup production. These three cohorts appear to be driving the intercolony differences in age distribution and most likely reflect higher than normal recruitment of these cohorts into the breeding population. These same three cohorts do not stand out in the age distribution at Dundas Island suggesting that there are different factors affecting juvenile recruitment into the Dundas Island breeding population.

There are several potential factors that may be influencing differential age distributions. It has been suggested that Sandy Bay is a younger colony than Dundas Island. However, this is not consistent with the reports, stretching as far back as the 1940s, in which both colonies were known to exist with reasonable numbers of NZSL present (Childerhouse and Gales 1998). Before observed declines (*i.e.*, pre 1998, Chilvers *et al.* 2007), annual pup production at both colonies had remained reasonably consistent over the last 30 yr, although monitoring at Dundas Island has been less regular and robust (Chilvers *et al.* 2007).

Another factor may be the direct and indirect harassment of breeding females by males (*e.g.*, female injury or mortality, pup mortality) that has a significant impact on breeding females with observed rates higher at Sandy Bay than Dundas Island (Chilvers *et al.* 2005*a*). Southern sea lion females benefit from group breeding through increased survival of their pups (Campagna *et al.* 1992) and also through reduced male–female agonistic interactions (Cassini and Fernandez-Juricic 2003), both factors leading to an increased net reproductive performance in larger colonies. Any or several of these factors could influence the age distributions at the two colonies but the exact mechanism, or combination of mechanisms, remains unclear.

The number of sea lions killed in the southern squid fishery around the Auckland Islands is managed *via* a bycatch limit of sea lions. Total sea lion catch is estimated from observer coverage (Ministry of Fisheries 2005) while the catch limit itself is estimated using an age-structured Bayesian model (Breen *et al.* 2003). The previous model uses a breeding age distribution of females between 4 and 19 yr with a maximum age of 21 yr. This study has extended these estimates considerably and the model is presently being revised to include these new estimates. Such revisions are likely to result in reduced estimates of survival rates, reproductive rates and population growth rate from those estimated in the previous version of the Breen

[2]Personal communication from L. Chilvers, Department of Conservation, P.O. Box 10-420, Wellington, New Zealand, lchilvers@doc.govt.nz, 10 September 2008.

and Kim model, and will likely lead to a reduced estimate of sustainable bycatch. The proportion of bycatch from the Sandy Bay and Dundas Island colonies is unknown, so the specific impact of this bycatch on each colony remains unresolved.

Another critical issue is that all of the biological data presently used in the Bayesian model are derived from observations at Sandy Bay. This study has demonstrated that the age distribution of Sandy Bay is significantly different from Dundas Island. It is therefore probable that female demographics from the two sites are also different, and the application of rates from one site to the other is inappropriate. A key finding from this study is that it has demonstrated that age distributions of wild populations can vary significantly over reasonably small temporal and spatial scales. This has broad implications for the extrapolation of data from one site and year to the wider scale. Failure to fully explore this temporal and spatial variation can have a significant impact on the overall understanding of population demographics (Fredrickson *et al.* 2005).

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