

Using life-history traits of New Zealand sea lions, Auckland Islands to clarify potential causes of decline

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Abstract

Annual censuses of New Zealand (NZ) sea lions *Phocarctos hookeri* at the subantarctic Auckland Islands have indicated a decline in pup production of over 40% during the first decade of the 2000s. With this significant decline and likely decline in the population as a whole, population ecology theory hypothesizes that life-history traits such as reproduction rate, survival or growth should improve, particularly if density-dependency is playing a significant role in the population. This research examined whether changes in NZ sea lion pup production were associated with changes in adult abundance or population life-history traits in an attempt to clarify potential causes of decline. Since 1998/1999, daily surveys of Sandy Bay, Enderby Island, were undertaken during the NZ sea lion breeding season (December–February). These surveys confirm that the number of adults at the breeding area has significantly declined during the period of pup production decline. There was no difference between years in mean pup birth date, but the ratio of pups at birth also varied from year to year, but with no significant variation overall. Pup mortality varied significantly only during years of epizootic events (1997/1998, 2001/2002 and 2002/2003). Pup birth mass showed little variation between 2000/2001 and 2006/2007, increasing slightly in the last 3 years of study. Pup mass at 3 weeks, although highly variable, showed no trend during the period of decline. Despite the significant decrease in pup production and breeding animals, not all life-history traits relating to pup mass and survival or female fecundity improved. Research suggests that indirect fishing-related pressures may influence some of these traits and that the NZ sea lion population was unlikely to have been influenced by density-dependent factors or to have been at or near carrying capacity before the decline.

Introduction

Understanding the causes of population change within a species is essential for wildlife management, particularly for populations in decline or at risk of extinction. However, this has proven to be difficult for marine species (e.g. Steller sea lions *Eumetopias jubatus*; NRC, 2003). Population variation can result from changes in survival, reproduction, immigration and/or emigration. Impacts that cause changes in individuals' survival, reproduction ability or dispersal will affect a population as a whole (Kruuk *et al.*, 1999). For example, for marine mammals, decreases in prey abundance and therefore food intake can affect the growth and condition of individuals. For females, this will, in turn, affect reproductive condition, timing of breeding and offspring mass, growth and survival (Lunn, Boyd & Croxall, 1994; Mellish, Iverson & Bowen, 1999; Bowen *et al.*, 2001).

New Zealand (NZ) sea lions *Phocarctos hookeri* are long-lived, slow-breeding mammals in the family Otariidae,

with 99.9% of all breeding restricted to NZ's subantarctic Auckland and Campbell Islands (Chilvers, Wilkinson & Childerhouse, 2007a). The species has been classified as Nationally Critical, under the NZ Threat Classification System (Baker *et al.*, 2010), and 'Vulnerable' and projected in decline by the IUCN (2008; <http://www.iucnredlist.org/>). Adult females are highly philopatric (Chilvers & Wilkinson, 2008). They give birth on land to only one pup which they suckle for up to 10 months (Gales, 1995). Soon after giving birth, females are impregnated, although the blastocyst is not thought to implant until 3 months after impregnation (Gales, 1995). Females divide their time during lactation, spending ~1.5 days ashore feeding their pup and 2 days at sea foraging (Chilvers *et al.*, 2006). Once the current year's pup is weaned, it is thought that females return to forage extensively at sea to gain condition during the last 2–3 months of pregnancy before the next year's pup is born (Gales, 1995). This means that both maternal and offspring traits may be affected by variation in food supply occurring

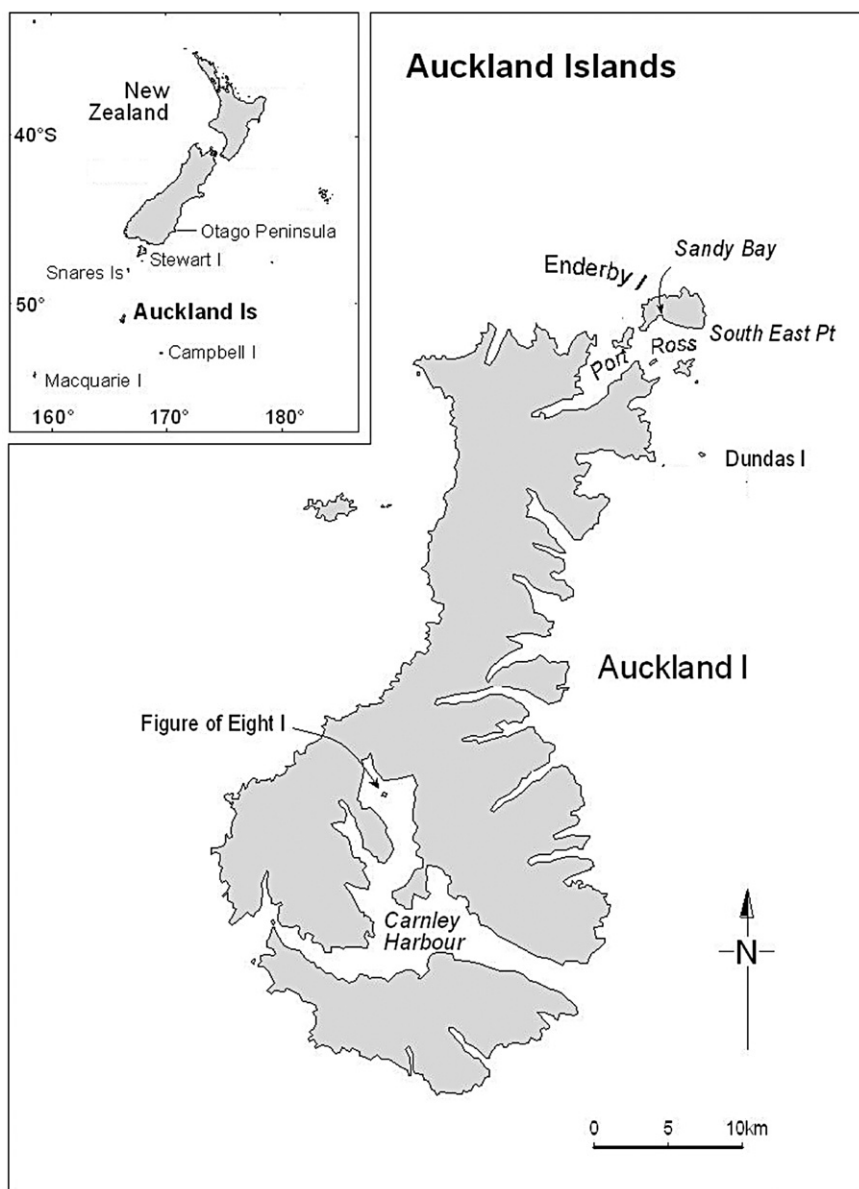


Figure 1 Auckland Islands showing the main breeding areas for New Zealand (NZ) sea lions *Phocarctos hookeri*: Sandy Bay and South East Point, Enderby Island, Dundas Island and Figure of Eight Island, Carnley Harbour. Inset: New Zealand's subantarctic area showing the Otago Peninsular, Stewart Island/Rakiura, Snares Island, Auckland Islands, Campbell Island/Motu Ihupuku and Macquarie Island (Australia), areas where NZ sea lions are known to occur.

during both pregnancy and the period of offspring provisioning (lactation).

The Auckland Islands (Fig. 1) are the main breeding area for NZ sea lions, with up to 86% of the species' pups being born there annually (Chilvers *et al.*, 2007a). Individuals in this population have been flipper tagged annually since 1997/98, and resighted and counted daily each breeding season since 1999 (Chilvers *et al.*, 2007a). Between 1998 and 2010, pup production decreased by 40% (from 3021 born in 1998 to 1814 in 2010; Baker *et al.*, 2010).

Population ecology theory hypothesizes that with this significant decline in births and likely decline in the population as a whole, life-history traits such as reproduction rate, survival or growth could improve due to decreasing intraspecific competition (particularly if the population is

influenced by density-dependent factors or is at carrying capacity) (e.g. Steller sea lions; Wolf & Mangel, 2008). It is predicted that increasing food availability for breeding females would increase offspring birth mass, growth and survival (Lunn *et al.*, 1994; Mellish *et al.*, 1999; Bowen *et al.*, 2001), could change implantation date, thus mean pup birth date (Bowen *et al.*, 2003), and could lead to male-skewed pup sex ratios (Clutton-Brock, 1989; Kruuk *et al.*, 1999).

This research investigated changes in life-history traits of NZ sea lions at the Auckland Islands during a period of pup production decline. It provides an opportunity to examine whether this decline could have affected maternal or offspring life-history traits, and to provide insight into the causes of the pup production decline.

Materials and methods

Sandy Bay, Enderby Island, Auckland Islands (50°30'S, 166°17'E; Fig. 1), is 400 m long, backed by a grass sward. During peak pupping, all breeding females and pups are on the beach (Augé *et al.*, 2009), while adult and sub-adult males can be found both on the beach and on the sward. The number of NZ sea lion pups born at Sandy Bay was determined annually using mark-recapture estimates and individual flipper tagging of neonates born at the breeding area (Chilvers *et al.*, 2007a). Annual pup tagging began in 1997/1998, although occasional tagging was conducted in previous years (Chilvers & MacKenzie, 2010). Pups were tagged at approximately 3 weeks of age each year, and gender was determined at the time of tagging by observation of genitalia, allowing calculation of the sex ratio at birth. Tagging and mark-recapture estimates have been collected and reported annually.

To document different age and gender components of the population, within and across years, daily counts were conducted between 5 December and 18 January annually from 1999. Each day, an observer surveyed the study area and counted the number of adult males, adult females, juvenile males (2–6 year olds) and pups. Juvenile females (below 4 years of age) and 1-year-old males are rarely observed in the harem during peak breeding (pers. obs.). These surveys provided a standardized index of numbers rather than absolute population size. To examine interannual trends, the mean of daily counts during attendance peaks for each sex each breeding season, 22 December and 8 January for males and 27 December and 18 January for females, was used. Mean counts over these time periods were used to reduce variation as a result of different weather conditions, that is, rain, high winds and large swells all reduce the number of sea lions hauled out. Different dates were used for adult males and females because males arrive at and depart from the breeding area earlier than females, and so their maximum abundance estimates occur earlier in the season.

The daily ratio of the number of pups to females at the breeding beach was calculated between 29 December and 18 January each season. This ratio is used as an indicator of the fecundity of females present, understanding that not all females present will have given birth to a pup and that not all females will be present on any given day: on any given day, up to 2/3 of the females at Sandy Bay could be away foraging at sea, whereas all the pups born will be present. Therefore, a ratio of 1.7 (pups : female) does not mean that each female had 1.7 pups but rather provides a reference with which to compare other ratios. This ratio is calculated for the period following the mean pup birth date (26–27 December; Chilvers *et al.*, 2007b) and during the period of highest pup and female numbers at the beach. Foraging studies of lactating females from Sandy Bay during the period of this research show no evidence that the proportion of time at sea/ashore for adult female NZ sea lions has changed (Chilvers *et al.*, 2005; Chilvers, 2009).

Data on newborn pup mass were collected annually (2001 season onwards) from females who were branded either as adults or pups in 2000 (Chilvers *et al.*, 2006; Wilkinson, Chil-

vers & Duignan, 2011). Females branded as adults were considered a random sample of the lactating female population in 2000, with ages ranging from 4 to over 18 years (Childerhouse *et al.*, 2010). Pups from these females were weighed and sexed 24 h after birth and then returned to their mothers (Chilvers *et al.*, 2007a). Data on pup mass at 3 weeks of age have been collected annually since 2000 during pup tagging (16 and 17 January). The first 50 male and 50 female pups caught during tagging were weighed. This is considered to be a random sample, as pups mix and move daily and there is no apparent age or sex clumping of pups (pers. obs.). Mean parturition date was estimated by taking the total pup production estimate for each year (total number of pups born) and then calculating on which day half of all pups had been born using the daily counts (Chilvers *et al.*, 2007b).

During daily counts, pups on the beach were observed and noted as alive or dead, and all dead pup carcasses were removed so double counting did not occur. This continued throughout the entire season, allowing 1- and 2-month mortality rates relative to total pup production to be determined (i.e. Chilvers *et al.*, 2007a).

Statistical analyses were performed using SPSS statistical software version 15.0 (SPSS, 1997, SPSS Inc., Chicago, IL, USA) and R software (R Development Core Team, 2006). One-way analysis of variance (ANOVAs) were used to test annual differences in daily averages of animals present at the Sandy Bay breeding area. Pearson's chi-square test was used to determine whether sex ratios differed from 1:1. Univariate ANOVAs with Tukey's *B*-test were used to test differences in pup weights at birth and 3 weeks. Means are reported with standard errors (SE). The significance level for all tests was $P \leq 0.05$.

Results

During the period of severe pup production decline (1998–2010; Figs 2 & 3), there was a comparable decline in the number of females, sub-adult males and adult males seen ashore at Sandy Bay during peak breeding (Figs 3 & 4). Between 1999 and 2009, the average number of females observed ashore at Sandy Bay during peak breeding (29 December–18 January; see Fig. 5a) declined significantly from 333 females to 220 females per day (ANOVA $F_{(11,264)} = 17.8$, $P < 0.0001$; Fig. 3). A similar decline was observed for adult males (22 December–8 January; see Fig. 5b) (ANOVA $F_{(11,204)} = 38.3$, $P < 0.0001$; Fig. 4) and sub-adult males observed daily over the entire breeding season (10 December–20 January) between 1999 and 2010 (ANOVA $F_{(11,567)} = 25.9$, $P < 0.0001$; Fig. 4).

The pup to female ratio of animals on the beach varied significantly from year to year, from 1:1 in 2002 and 2009 to 1.7:1 in 2005 (ANOVA $F_{(11,240)} = 7.8$, $P < 0.0001$; Fig. 3); however, there was no trend across all years. This variation appeared to follow the variation in pup production estimates between 1999 and 2004 (i.e. ratio of pups to females increasing with increasing pup numbers and decreasing with decreasing pup numbers), but following 2004, the pup to female ratio varied markedly relative to pup production (Fig. 3).

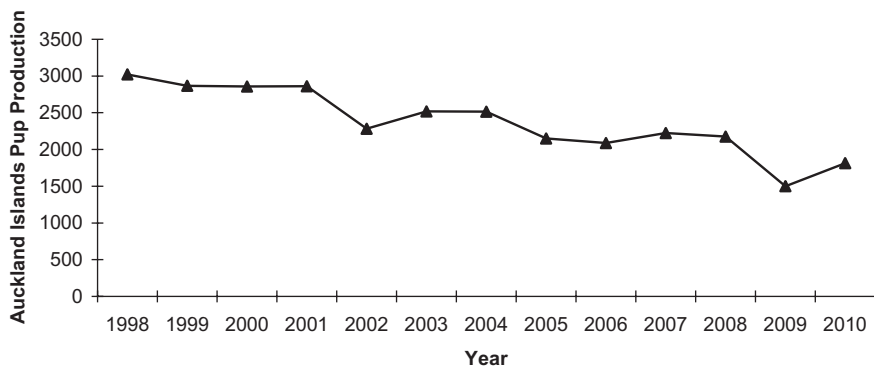


Figure 2 Total pup production for Auckland Islands, 1998–2010.

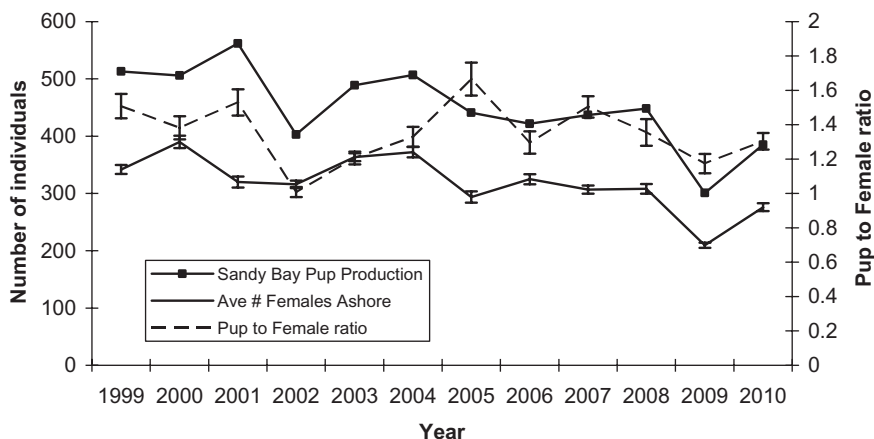


Figure 3 Mean \pm SE pup production (1999–2010), average daily number of female New Zealand sea lions *Phocarctos hookeri* counted annually (27 December–18 January) and average daily pup to female ratio counted annually during peak pup production (29 December–18 January) at Sandy Bay, Enderby Island.

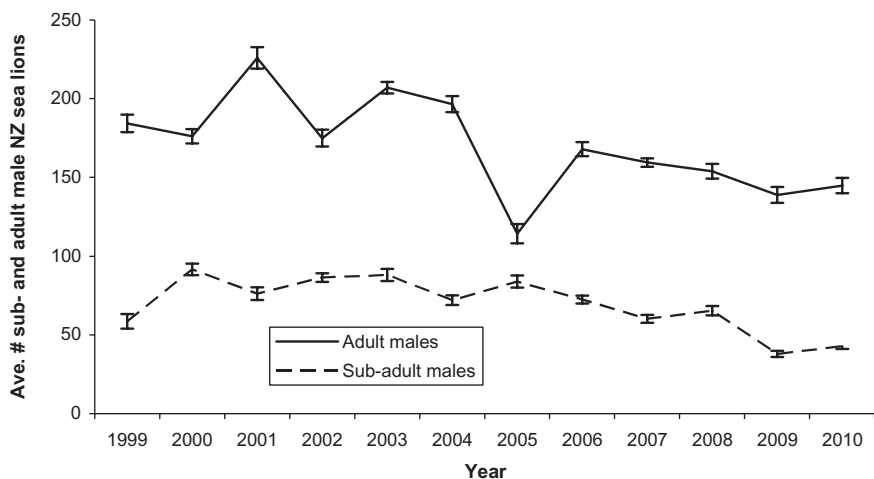


Figure 4 Mean \pm SE average daily number of sub-adult and adult male New Zealand (NZ) sea lions *Phocarctos hookeri* counted at Sandy Bay, Enderby Island, between 20 December and 8 January, 1999–2010.

There was no interannual difference in mean birth date for NZ sea lion pups born at Sandy Bay between 1998 and 2010, with mean birth dates always falling either on 26, 27 or 28 December. Pup sex ratio at birth varied from 54% females to 44% females born (Table 1). The largest skew in ratio from 1:1 was in 1999, the year after the first bacterial epizootic mass

mortality in pups, when more male than female pups were born; however, overall, there was no significant difference between years ($\chi^2_{(1)} = 16.5773$, $P = 0.1210$).

Between 22 and 70 pups (of equal sex ratio) have been weighed within 24 h of birth annually since 2001. The mean pup birth mass was 10.2 ± 1.2 kg. Males were consistently

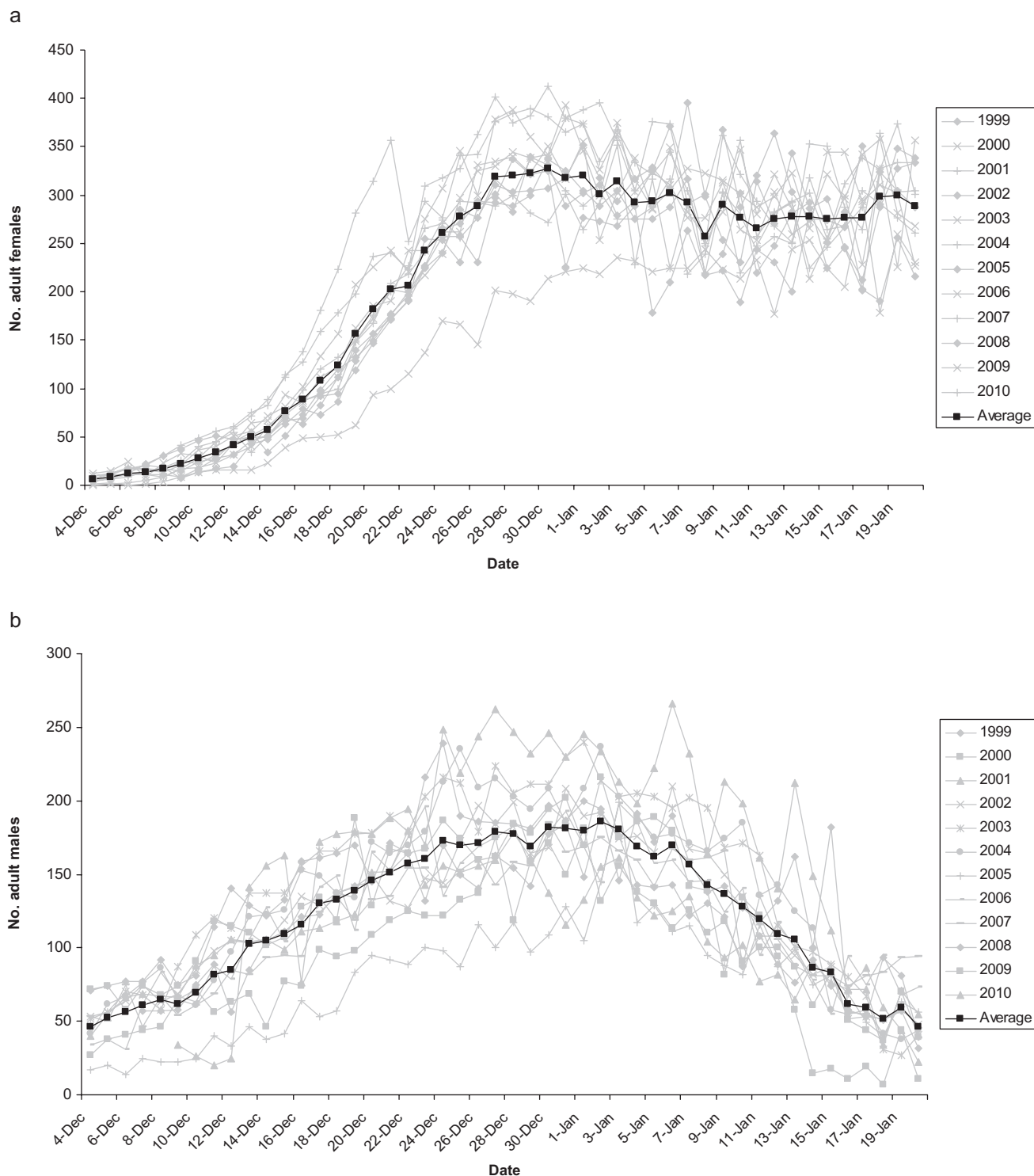


Figure 5 Daily counts of (a) female and (b) male New Zealand sea lions *Phocarctos hookeri* at Sandy Bay, Enderby Island, between 4 December and 18 January, 1999–2010.

Table 1 Pup sex ratio in New Zealand sea lions *Phocarctos hookeri* born at Sandy Bay, Enderby Island, 1998–2010

Year	Total pups	% female
1998	513	53
1999	498	44
2000	492	50
2001	549	51
2002	394	49
2003	470	52
2004	554	48
2005	451	54
2006	423	53
2007	435	49
2008	434	49
2009	318	50
2010	385	45

and significantly heavier than females, with an average birth mass of 10.8 ± 0.07 kg compared with 9.7 ± 0.07 kg (Sex $F_{(1,414)} = 135.6$, $P < 0.001$; Fig. 6). Birth mass appeared to be stable between 2001 and 2007, with only small variations, but has increased in the last 3 years across both sexes (Year $F_{(9,414)} = 4.7$, $P < 0.001$, Sex \times Year $F_{(9,414)} = 0.9$, $P = 0.49$; Fig. 6).

The first 50 pups of each sex tagged at approximately 3 weeks old have been weighed since 1999. In 2000, pups were also branded at this time, so an additional 30 pups (13 male and 17 female) were also weighed. The average mass of all pups at 3 weeks was 11.9 ± 0.05 kg. As for birth mass, male pups were consistently and significantly heavier than female pups, with an average mass of 12.5 ± 0.08 and 11.4 ± 0.08 kg, respectively (Sex $F_{(1,1206)} = 107.2$, $P < 0.001$; Fig. 6). Mass at 3 weeks of age varied significantly between years, but with no overall trend and no variation between the sexes (Year $F_{(11,1206)} = 7.8$, $P < 0.001$, Sex \times Year $F_{(11,1206)} = 1.2$, $P = 0.3$; Fig. 6).

Pup mortality at 3 and 7 weeks after mean pup birth date are shown in Fig. 7. In non-epizootic years (epizootic years 1998, 2002 and 2003), early pup mortality ranged between 5% and 9% at 3 weeks, 9% and 16% at 7 weeks.

Discussion

Demographic trends

The 40% decline in the number of NZ sea lion pups produced at the Auckland Islands during the early 2000s has not previously been observed in this population since commercial sealing (Childerhouse & Gales, 1998). The present research shows that the average number of male and female NZ sea lions returning to the Sandy Bay breeding area has also significantly declined. Chilvers & Wilkinson (2008) and Maloney *et al.* (2009) showed that there is extremely limited or no migration of breeding females between breeding areas and strong philopatry within the species. Therefore, this decline in adults is likely to represent a true decline in this population.

Life-history traits – females

During the period of significant decline in all age classes (Figs 2 & 3), the index of fecundity for this research (pup to female ratio at the breeding beach) varied significantly (Fig. 3). From 1999 to 2004, the pup to female ratio at Sandy Bay followed the same trend as pup production (Fig. 3). However, from 2005 onwards, this pattern changed, with the ratio fluctuating significantly different from pup production. Despite pup production being relatively constant between 2005 and 2008, the pup to female ratio oscillated (Fig. 3). The fecundity of females in 2005 and 2007 was higher than during the following years 2006 and 2008 (i.e. a high proportion of females at the breeding area did not breed). This suggests that the ability of females to reproduce was being influenced by a factor that was not present before 2005. Similar results were found from mark-recapture analyses of this population, for female NZ sea lions aged ≥ 4 years that were known to have bred (MacKenzie, 2010).

Meynier *et al.* (2010) identified a significant shift in diet composition of female NZ sea lions starting in 2004 using fatty acid analysis. The proportion of hoki *Macruronus novaezelandiae*, the main fin fish prey species identified for female NZ sea lions at the Auckland Islands, dropped from approximately 30% of their diet to below 5%. At the same time, hoki catches around NZ, including at the Auckland Islands, also decreased significantly, indicating a drop in biomass of hoki available to NZ sea lions rather than a change in food preference of the animals (Meynier *et al.*, 2010). At the same time, the percentage of arrow squid *Nototodarus sloanii* in their diet increased from approximately 15% to over 40%, also corresponding to higher squid catches in the Auckland Island area (<http://fs.fish.govt.nz>). Hoki has higher protein and lipid content values than arrow squid and, consequently, higher overall energy as a prey (7.1 kJ g^{-1} compared with 6.3 kJ g^{-1} for squid; Meynier *et al.*, 2008). This significant shift in female diet to a lower quality food source may have influenced factors such as fecundity (the pup to female ratio) and resulted in the fluctuations seen since 2004.

Life-history traits – pups

Spikes in early mortality of NZ sea lion pups can be linked to the epizootic outbreaks that have occurred within the NZ sea lion population, occurring in 1998, 2002 and 2003 (Baker, 1999; Fig. 7). During non-epizootic years, early pup mortality ranged from 5% to 9% at 3 weeks of age, from 9% to 16% at 7 weeks (Chilvers *et al.*, 2007a; Fig. 7), and from 40% to 70% by 1 year (Chilvers & MacKenzie, 2010).

Pup sex ratio at birth did not significantly depart from 1:1. The largest sex ratio bias was observed in 1999 with 56% male pups (Table 1), following the 1998 epizootic that killed 53% of pups within 8 weeks of birth (Chilvers *et al.*, 2007a). For polygamous mammals, it has been documented that better condition in breeding females often leads to male-skewed sex ratios in populations that are below carrying capacity (Clutton-Brock, 1989; Kruuk *et al.*, 1999).

Pup birth mass changed little over most of the period of decline, with a slight increase between 2008 and 2010. In con-

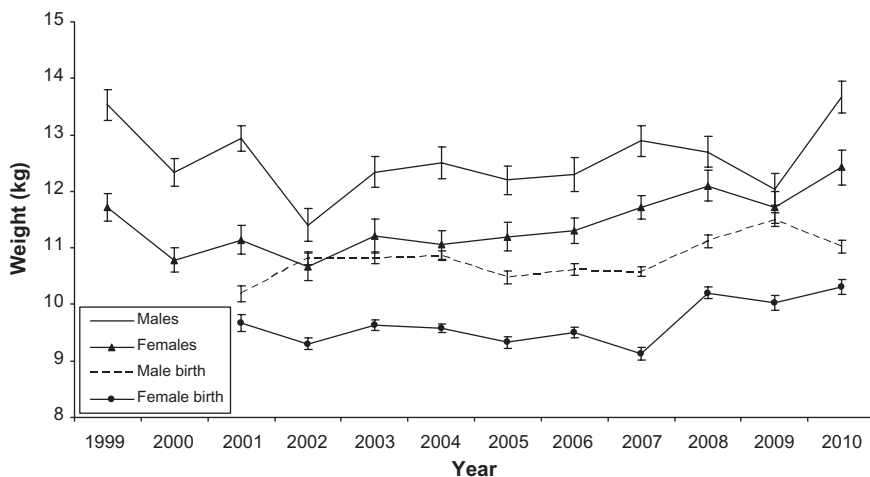


Figure 6 Mean \pm SE average birth mass (2001–2010) and 3-week mass (1999–2010) for New Zealand sea lion *Phocarctos hookeri* pups born at Sandy Bay, Enderby Island.

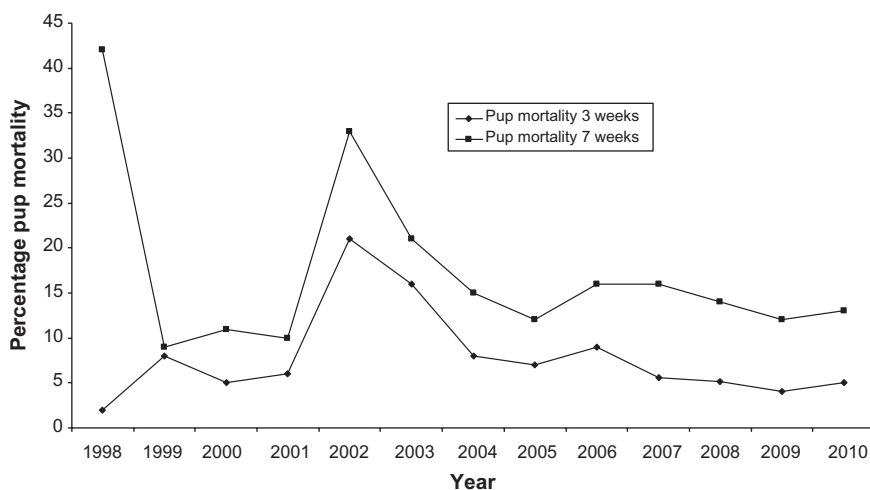


Figure 7 Percentage New Zealand sea lion *Phocarctos hookeri* pup mortality at 3 and 7 weeks after the mean pupping date, 1998–2010.

trast, pup mass at 3 weeks of age showed high variability, no corresponding increase between 2008 and 2010, and no overall trend. NZ sea lion females need to forage during lactation, so food shortage or low-quality food during pregnancy or lactation could result in reduced offspring birth mass or growth rate. The small change in birth mass across this period of decline indicates that females were either getting enough food during late pregnancy, when most fetal pup growth occurs, or had a strategy to ensure that they had sufficient energy during late pregnancy. This strategy may include weaning the previous pup earlier, aborting slow developing foetuses or not producing a pup every year. This latter strategy is seen in NZ sea lions, with, on average, only 65–67% of females giving birth each year (Childerhouse *et al.*, 2010; Chilvers, Wilkinson & MacKenzie, 2010). However, the variability in pup mass across years after birth indicates that females may not be able to compensate for interannual variability in food availability during the period of early lactation, when their foraging ability is severely restricted due to the need to return to young dependent pup ashore.

The mass of offspring at birth and early growth rates can influence many vital individual and population characteristics, from future reproductive ability to survival (Boltnev, York & Antonelis, 1998; Georges & Guinet, 2000). More interestingly, none of the pup life-history parameters studied here were related to the hypothesized change that appears to have occurred for adult females in 2004. This relationship may be difficult to detect, however, as female body condition, foraging ability and ability to alter maternal behaviour (i.e. wean the previous year's pup earlier) could be buffering impacts on pup parameters.

Population decline

There are many reasons why pup production and the population could have declined at the Auckland Islands, for example, emigration of adult females, increased predation, increasing intra- or interspecific competition, environmental change, genetic inbreeding or increased effects of contaminants.

However, all of these factors have previously been considered and determined to be unlikely or low impact (Robertson & Chilvers, 2011).

Bacterial epizootics are known to occur in this population, affecting predominantly only the life-history trait of pup mortality (Baker, 1999; Chilvers *et al.*, 2007a; Fig. 7). Pup mortality is naturally highly variable in NZ sea lion populations (Maloney *et al.*, 2009; Chilvers & MacKenzie, 2010), and populations with high pup mortality (e.g. Campbell Island 40–55%) still show population stability or increases (Maloney *et al.*, 2009). Sensitivity trials in the NZ sea lion – arrow squid fisheries management model also showed that changes in pup mortality (particularly as a density-dependent indicator) had little impact on population parameters (Breen, Fu & Gilbert, 2010).

Results from this research and Meynier *et al.* (2010) indicate that food availability and/or quality, particularly during lactation, may be influencing this population. This variability potentially could cause fluctuations in female condition or in their ability to supply high-quality milk for their pups (Riet-Sapriza *et al.*, 2009; Augé, 2010), leading to variation in pup mass at 3 weeks of age. The impacts of food shortage during lactation on pup growth have been well documented in other otariids (Boness, Oftedal & Ono, 1991; Boltnev *et al.*, 1998). Changes in food quantity and quality as a result of fisheries have been shown to influence reproduction of Steller sea lions (Trites & Donnelly, 2003) and southern elephant seals *Mirounga leonina* (Atkinson, Demaster & Calkins, 2008).

Female NZ sea lions forage over the entire Auckland Islands shelf and its edges; all Auckland Island commercial fishing occurs within their foraging area during lactation (Chilvers, 2009). Female NZ sea lions are restricted in foraging range and time because of their need to return to dependent pups ashore. NZ sea lions diving behaviour is reported to be at their physiological limits (Chilvers *et al.*, 2006). Individuals have distinct foraging strategy, with individual strategies being constant both within and between years during summer, despite environmental and fisheries catch variability (Chilvers & Wilkinson, 2009). Animals that operate at or near their maximum physiological abilities, such as NZ sea lions, do not have the capacity to increase their foraging effort in response to reductions or significant changes in food availability, even if temporal (Bolnick *et al.*, 2003).

The arrow squid trawl fishery (SQU6T) is the dominant fishery around the Auckland Islands operating annually from 1 February to mid-May (Chilvers, 2009). Bycatch mortality is a known concern for this population. An estimated 89 deaths occurred annually of NZ sea lions in SQU6T (both arrow squid and scampi fisheries) between the austral summers of 1995–1996 and 2009–2010 (Thompson, Oliver & Abraham, 2010). Between 2004 and 2009, 82% of the animals retrieved dead were female sea lions (Robertson & Chilvers, 2011). The arrow squid fishery is also removing prey from the area and during the time in which lactating female NZ sea lions foraging behaviours are most restricted. Given that NZ sea lions have been shown to have no physiological or temporal ability to alter their foraging behaviour,

this removal of prey could indicate that resource competition could occur and may result in the changes in life-history parameters reported here.

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References

- Atkinson, S., Demaster, D.P. & Calkins, D.G. (2008). Anthropogenic causes of the western Steller sea lion *Eumetopias jubatus* population decline and their threat to recovery. *Mamm. Rev.* **38**, 1–18.
- Augé, A.A. (2010). Otago New Zealand sea lions foraging ecology. PhD thesis, Otago University, Dunedin, New Zealand.
- Augé, A.A., Chilvers, B.L., Moore, A., Mathieu, R. & Robertson, B. (2009). Aggregation and dispersion of female New Zealand sea lions at the Sandy Bay breeding colony, Auckland Islands: how unusual is their spatial behaviour? *Behaviour* **146**, 1287–1311.
- Baker, A. (1999). *Unusual mortality of the New Zealand sea lion, Phocarctos hookeri, Auckland Islands, January–February 1998*. Wellington: Department of Conservation.
- Baker, C.S., Chilvers, B.L., Constantine, R., DuFresne, S., Mattlin, R., van Helden, A. & Hitchmough, R. (2010). Conservation status of New Zealand Marine Mammals (suborders Cetacea and Pinnipedia), 2009. *N. Z. J. Mar. Freshwater Res.* **44**, 101–115.
- Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. & Forister, M.L. (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28.
- Boltnev, A.I., York, A.E. & Antonelis, G.A. (1998). Northern fur seal young: interrelationships among birth size, growth and survival. *Can. J. Zool.* **76**, 843–854.
- Boness, D.J., Oftedal, O.T. & Ono, K.A. (1991). The effects of El Niño on pup development in the California sea lion (*Zalophus californianus*). I. Early postnatal growth. In *Pinnipeds and El Niño: responses to environmental stress*: 173–184. Trillmich, F. & Ono, K. (Eds). Berlin: Springer-Verlag.
- Bowen, W.D., Boness, D.J., Iverson, S.J. & Oftedal, O.T. (2001). Foraging effort, food intake and lactation

- performance depend on maternal mass in a small phocid seal. *Funct. Ecol.* **15**, 325–334.
- Bowen, W.D., Ellis, S.L., Iverson, S.J. & Boness, D.J. (2003). Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *J. Zool. (Lond.)* **261**, 155–163.
- Breen, P.A., Fu, D. & Gilbert, D.J. (2010). *Sea lion population modelling and management procedure evaluations: final research report for SAP2008/14*. Wellington: Ministry of Fisheries.
- Childerhouse, S. & Gales, N. (1998). Historical and modern distribution and abundance of the New Zealand sea lion, *Phocarctos hookeri*. *N.Z. J. Zool.* **25**, 1–16.
- Childerhouse, S.J., Dawson, S.M., Fletcher, D.J., Slooten, E. & Chilvers, B.L. (2010). Growth and reproduction of female New Zealand sea lions. *J. Mammal.* **91**, 165–176.
- Chilvers, B.L. (2009). Foraging locations of a decreasing colony of New Zealand sea lions (*Phocarctos hookeri*). *N.Z. J. Ecol.* **33**, 106–113.
- Chilvers, B.L. & MacKenzie, D. (2010). Age and sex specific survival estimates incorporating tag loss for New Zealand sea lions, *Phocarctos hookeri*. *J. Mammal.* **91**, 758–767.
- Chilvers, B.L., Robertson, B.C., Wilkinson, I.S. & Duignan, P. (2007b). Growth and survival of New Zealand seal lions, *Phocarctos hookeri*: birth to 3 months. *Polar Biol.* **30**, 459–469.
- Chilvers, B.L. & Wilkinson, I.S. (2008). Philopatry and site fidelity of New Zealand sea lions, *Phocarctos hookeri*. *Wildl. Res.* **35**, 463–470.
- Chilvers, B.L. & Wilkinson, I.S. (2009). Diverse foraging strategies in lactating New Zealand sea lions. *Mar. Ecol. Prog. Ser.* **378**, 299–308.
- Chilvers, B.L., Wilkinson, I.S., Duignan, P.J. & Gemmill, N.J. (2005). Identifying the distribution of summer foraging areas for lactating New Zealand sea lions, *Phocarctos hookeri*. *Mar. Ecol. Prog. Ser.* **304**, 235–247.
- Chilvers, B.L., Wilkinson, I.S., Duignan, P.J. & Gemmill, N. (2006). Diving to extremes: are New Zealand sea lions (*Phocarctos hookeri*) pushing their limits in a marginal habitat? *J. Zool. (Lond.)* **269**, 233–241.
- Chilvers, B.L., Wilkinson, I.S. & Childerhouse, S. (2007a). New Zealand sea lion, *Phocarctos hookeri*, pup production – 1995 to 2005. *N. Z. J. Mar. Freshwater Res.* **41**, 205–213.
- Chilvers, B.L., Wilkinson, I.S. & MacKenzie, D. (2010). Predicting life-history traits for female New Zealand sea lions, *Phocarctos hookeri*: intergrating short-term mark-recapture data and population modelling. *J. Agric. Biol. Environ. Stat.* **15**, 259–264.
- Clutton-Brock, T.H. (1989). Mammalian mating systems. *Proc. Roy. Soc. Lond. Ser. B.* **235**, 339–372.
- Gales, N.J. (1995). *Hooker's sea lion recovery plan (Phocarctos hookeri)*. Threatened Species Recovery Plan Series No. 17. Wellington: Department of Conservation.
- Georges, J.-Y. & Guinet, C. (2000). Early mortality and perinatal growth in the sub-Antarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. *J. Zool. (Lond.)* **251**, 277–287.
- Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999). Population density affects sex ratio variation in red deer. *Nature* **399**, 459–461.
- Lunn, N.J., Boyd, I.L. & Croxall, J.P. (1994). Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *J. Anim. Ecol.* **63**, 827–840.
- MacKenzie, D. (2010). Estimation of demographic parameters for New Zealand sea lions breeding on the Auckland Islands – Final Report: 1997/98–2009/10 Objective 3: POP2007/1. www.doc.govt.nz/publications/conservation/marine-and-coastal/marine-conservation-services/csp-reports/estimation-of-demographic-parameters-for-nz-sea-lions-breeding-on-the-auckland-islands/.
- Maloney, A., Chilvers, B.L., Haley, M., Muller, C.G., Roe, W. & Debski, I. (2009). Distribution, pup production and mortality of New Zealand sea lion *Phocarctos hookeri* on Campbell Island, 2008. *N.Z. J. Ecol.* **33**, 97–105.
- Mellish, J.-A.E., Iverson, S.J. & Bowen, W.D. (1999). Individual variation in maternal energy allocation and milk production in grey seals and consequences for pup growth and weaning characteristics. *Physiol. Biochem. Zool.* **72**, 677–690.
- Meynier, L., Morel, P.C.H., MacKenzie, D.D.S., MacGibbon, A., Chilvers, B.L. & Duignan, P.J. (2008). Proximate composition, energy content, and fatty acid composition of marine species from Campbell Plateau, New Zealand. *N. Z. J. Mar. Freshwater Res.* **42**, 425–437.
- Meynier, L., Morel, P.C.H., Chilvers, B.L., Mackenzie, D.D.S. & Duignan, P.J. (2010). Quantitative fatty acid signature analysis on New Zealand sea lions: model sensitivity and diet estimates. *J. Mammal.* **91**, 1484–1495.
- NRC (National Research Council) (2003). *Decline of the Steller sea lion in Alaskan waters*. Washington, DC: National Academies Press.
- R Development Core Team (2006). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Riet-Sapriza, F.G., Lopez-Villalobos, N., Mackenzie, D.D.S., Duignan, P.J., Macgibbon, A., Chilvers, B.L. & Wilkinson, I.S. (2009). Comparison of methods for the analysis of New Zealand sea lion (*Phocarctos hookeri*) milk. *N. Z. J. Mar. Freshwater Res.* **43**, 997–1006.
- Robertson, B.C. & Chilvers, B.L. (2011). New Zealand sea lions *Phocarctos hookeri* possible causes of population decline. *Mamm. Rev.* **41**: 253–275.

- Thompson, F.N., Oliver, M.D. & Abraham, E.R. (2010). Estimation of the capture of New Zealand sea lions (*Phocarctos hookeri*) in trawl Fisheries from 1995–96 to 2007–08. New Zealand Aquatic Environment and Biodiversity Report No. 52. <http://fs.fish.govt.nz>.
- Trites, A.W. & Donnelly, C.P. (2003). The decline of Steller sea lions in Alaska: a review of the nutritional stress hypothesis. *Mamm. Rev.* **33**, 3–28.
- Wilkinson, I.S., Chilvers, B.L. & Duignan, P.J. (2011). An evaluation of hot-iron branding as a permanent marking method for adult New Zealand sea lions, *Phocarctos hookeri*. *Wildl. Res.* **38**, 51–60.
- Wolf, N. & Mangel, M. (2008). Multiple hypothesis testing and the declining-population paradigm in Steller sea lions. *Ecol. Appl.* **18**, 1932–1955.