

REVIEW

The population decline of the New Zealand sea lion *Phocarctos hookeri*: a review of possible causes

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ABSTRACT

1. The New Zealand (NZ) sea lion *Phocarctos hookeri* is NZ's only endemic pinniped and is listed as 'nationally critical'. The species breeds in the NZ sub-Antarctic: 71% of the population at the Auckland Islands (2010 pup production: 1814 ± 39) and the remaining 29% on Campbell Island (726 pups in 2010).

2. Pup production at the Auckland Islands has declined by 40% since 1998 (1998: 3021 pups produced): only 1501 pups were born in 2009. This decline is directly linked to philopatric females not returning to breeding areas. While the Auckland Island population has declined, the Campbell Island population appears to be increasing slowly.

3. Potential reasons for the decline in the Auckland Island population, but not in the Campbell Island population, include non-anthropogenic factors: (i) disease epizootics, (ii) predation, (iii) permanent dispersal or migration, (iv) environmental change; and anthropogenic impacts: (v) population 'overshoot', (vi) genetic effects, (vii) effects of contaminants, (viii) indirect effects of fisheries (i.e. resource competition) and (ix) direct effects of fisheries (i.e. by-catch deaths). Of the nine potential reasons examined here, six can be discounted (ii–vii). Bacterial epizootics (i) occur in the NZ sea lion population, but their impact has predominantly increased pup mortality, which is unlikely to cause the severe decline observed, as pup mortality throughout the species is naturally high and variable.

4. The most plausible hypotheses, based on available evidence, are that the observed decline, in particular, the decreasing number of breeding females in the Auckland Island population, is caused by (viii) fisheries-induced resource competition and (ix) fisheries-related by-catch. By-catch is the main known anthropogenic cause of mortality in the species. Competition with fisheries resulting in resource competition, nutrient stress and decreased reproductive ability in NZ sea lions should be a priority area for future research.

Keywords: decline, fisheries by-catch, Pinnipedia, population trends, resource competition

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INTRODUCTION

The New Zealand (NZ) sea lion *Phocarctos hookeri* is NZ's only endemic pinniped and is listed as 'nationally critical' under the NZ threat classification system (Baker et al. 2010) and as 'threatened in decline' by the International Union for the Conservation of Nature (Anonymous 2008). The species has the smallest population estimate of any otariid (9880, 95% CI: 8604–11297; Geschke & Chilvers 2009). Historically, NZ sea lions once ranged along the entire length of the NZ coast, from the north of the North Island through to Stewart Island and the NZ sub-Antarctic Islands (Fig. 1; Childerhouse & Gales 1998). Although a direct estimate of pristine abundance is not available, the present population size is thought to be reduced significantly from pre-sealing times (Childerhouse & Gales 1998).

Breeding colonies occur in only two areas in the NZ sub-Antarctic. The largest proportion of the species breeds at the Auckland Islands (50°30'S, 166°E; Fig. 1 and 71% of total pup production, 1814 ± 39 pups in 2010; Chilvers 2010). The remaining 29% breed 270km south-east of the Auckland Islands on Campbell Island (52°33'S, 169°09'E; 726 pups in 2010; A. Maloney, L. Chilvers, C. Muller & M. Haley, unpublished data). There is a tiny population starting to re-colonize Otago Peninsula, South Island, NZ, but it currently only produces four to five pups a year (<0.001% of the species' yearly pup production). The Otago Peninsula population derives from one matriarchal line, and this area is not yet recognized as an official NZ sea lion breeding area. The NZ sea lion's breeding season occurs mid-December to early January each austral summer; for clarity, breeding seasons in this review are referred to by the January year (i.e. the 1997/1998 season is referred to as 1998).

The Auckland Islands NZ sea lions have had a 40% decline in pup production in the last 12 years, from 3021 pups born in 1998, to 1814 in 2010 (Chilvers et al. 2007, Chilvers 2008a). In 2009, there was a 31% drop in pup production in 1 year, resulting in the lowest ever record for NZ sea lions at the Auckland Islands of only 1501 pups born. The 2009 drop was directly linked to philopatric females (Chilvers & Wilkinson 2008) not returning to breeding areas to reproduce, but the reason for this is unknown. For pinnipeds, estimates of pup production are the best index of relative population status and overall population size (Berkson & DeMaster 1985). Therefore, the decline in pup production at the Auckland Islands probably reflects a decline in overall population; however, this relationship is hard to confirm as estimation of pinniped population size directly is difficult. The long-term decline in pup production at the Auckland Islands means that the relative proportion of all pups born at each breeding area has altered significantly. In 2003, the first comprehensive estimate of pup production was undertaken on Campbell Island; results suggested that the proportion of pups produced on Campbell Island was 14% compared with 86% at the Auckland Islands. By 2010, these percentages had changed to 71% and 29%, respectively, due to the decreasing Auckland Island pup production and increasing estimates from Campbell Island.

A considerable body of research is available on NZ sea lions that can be used to investigate the cause or causes of their decline. The research includes long-term population studies to quantify life-history parameters (Lalas & Bradshaw 2003, Wilkinson et al. 2003, Chilvers et al. 2007, Chilvers & Wilkinson 2008, Childerhouse et al. 2010a, b, Chilvers & Mackenzie 2010, Chilvers et al. 2010); deployment of archival dive recorders and satellite telemetry systems to study foraging behaviour (Gales & Mattlin 1997, Costa et al. 1998, Costa & Gales 2000, Crocker et al. 2001, Chilvers et al. 2005,

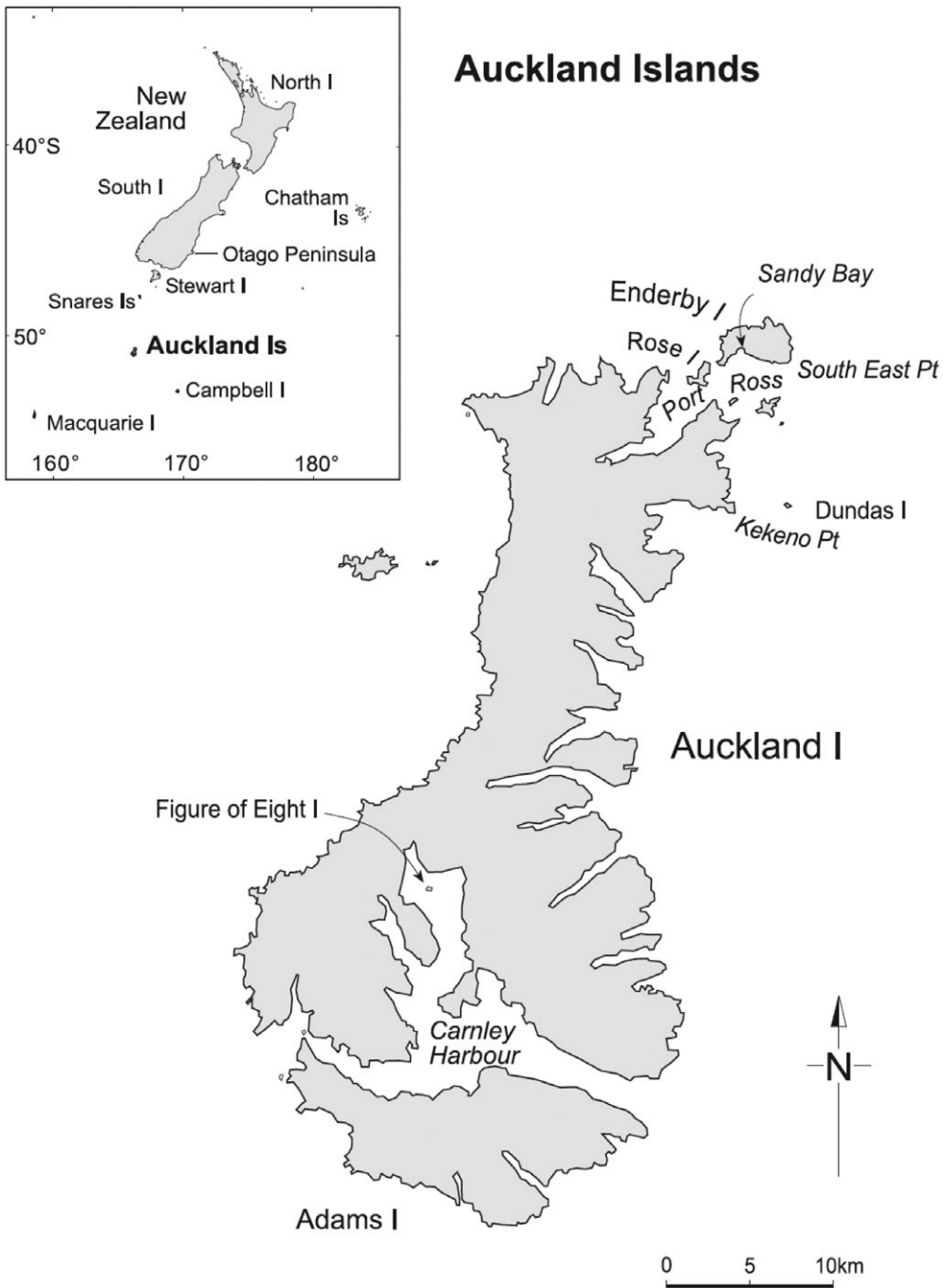


Fig. 1. New Zealand (NZ) mainland and sub-Antarctic showing Otago Peninsula, Stewart Island, Snares Islands, Auckland Islands and Campbell Island. Auckland Islands' main breeding areas for NZ sea lions are in Sandy Bay on Enderby Island, Dundas Island and Figure of Eight in Carnley Harbour.

2006, Chilvers 2008a, b, 2009, Chilvers & Wilkinson 2009); the analysis of milk composition (Riet-Sapriza 2007, Riet-Sapriza et al. 2009); investigation into diet through stomach, scat and fatty acid analysis (Lalas 1997, Childerhouse et al. 2001, Meynier et al. 2008a, b, 2009, 2010, N. McNally, unpublished data); investigation into the growth rates and causes of pup mortality (Chilvers et al. 2005, 2009, Castinel et al. 2006, 2007a, b, c, 2008); and breeding and dispersal behavioural studies (Chilvers et al. 2005, 2007, Robertson et al. 2006, Augé et al. 2009, Augé & Chilvers 2010). From these papers, much has been learned about demography, foraging and diving behaviours, diet and mortality, which has never been reviewed to determine the possible causes of decline.

The potential causes of decline for NZ sea lions include non-anthropogenic factors (disease epizootics, predation, dispersal or migration, and environmental change), and anthropogenic factors (population overshoot, genetic inbreeding, effects of contaminants, indirect effects of fisheries – resource competition and direct effects of fisheries by-catch deaths). The aim of this review is to evaluate the relative importance of these possible agents of decline using existing data in order to draw reasonable conclusions as to the contribution of each threat to the observed decline. In doing this, we hope to provide a synthesis of the impacts that each factor has had or is having on the NZ sea lion population.

It is timely to examine trends and to determine causes of decline for NZ sea lions as their threat classification under the NZ threat classification system (Townsend et al. 2008) increased to 'nationally critical' in 2010 (Baker et al. 2010). Furthermore, future research needs to be targeted to help understand and prevent the continued decline of the species. In this paper, the population status of the two breeding areas of NZ sea lions is assessed; the possible hypotheses for the observed pup production decline at the Auckland Islands are examined and compared with increasing pup production at Campbell Island; and suggestions are given for future research.

POPULATION SIZE AND TRENDS

Auckland Islands

The Auckland Islands were discovered by Europeans in 1806; commercial sealing of both fur seals *Arctocephalus* spp. and sea lions began the following year. Numbers of both species quickly declined. By 1830, fur seals could no longer be found for hunting and only low numbers of sea lions were reported (Childerhouse & Gales 1998). There are now three islands where sea lions breed at the Auckland Islands (Fig. 1): Dundas Island (50°35'S, 166°19'E; 54% of total pup production in 2010), Enderby Island (50°30'S, 166°17'E; 15% of total pup production in 2010) and Figure of Eight Island in Carnley Harbour (50°46'S, 166°01'E; 2% of total pup production in 2010). Dundas and Enderby Islands are considered one breeding area because adult males move between them and mate with females on both islands during single breeding seasons (Robertson et al. 2006).

The first observations and counts of NZ sea lions at the Auckland Islands were carried out at Sandy Bay, Enderby Island, intermittently between 1942 and 1979; the breeding population was reported to be about 1000 animals, and pup production was 350–400 pups per annum (Falla 1965, 1975, Falla et al. 1979). From the 1980s to 1995, counts were undertaken on Enderby Island at varying intervals and times of the season, and between 430 and 530 pups were counted (M. Cawthorn, unpublished data). Five counts were also done on Dundas Island during this time; however, they

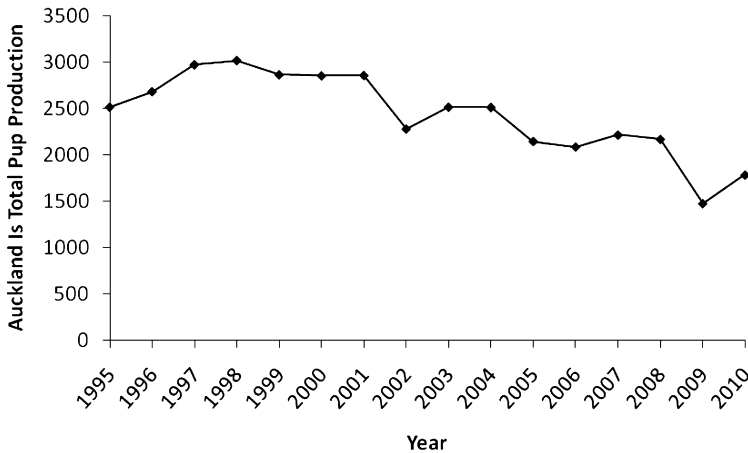


Fig. 2. Total estimated production of New Zealand sea lion pups, for the Auckland Islands, 1995 to 2010. Breeding seasons are referred to by the January year (i.e. the 1997/98 season is referred to as 1998).

were highly variable in both timing and number (Childerhouse & Gales 1998). From 1995 until 2010, mark–recapture estimates of pup population size at all breeding areas of the Auckland Islands have been undertaken annually on the same date each year (Fig. 2; Gales and Fletcher 1996, Chilvers et al. 2007). These ongoing mark–recapture estimates of pup production have shown that production at the Auckland Islands has decreased 40% since 1995 (Fig. 2). The 20% drop in pup production seen for the 2002 season (Fig. 2) was due to a bacterial outbreak of *Klebsiella pneumoniae* (Wilkinson et al. 2006, Castinel et al. 2007a, c). The 31% drop in pup production seen in 2009 was linked to philopatric females not returning to breeding areas to reproduce, but, as noted above, the reason for this is unknown.

Campbell Island

Campbell Island was discovered by Europeans in 1810, and both fur seals and sea lions were quickly reduced to low numbers by commercial sealing (McNab 1908, Warneke 1982). Opportunistic sightings since the 1940s appear to document a slow increase in the pup production of NZ sea lions on Campbell Island (Bailey & Sorenson 1962, Russ 1980, Moore & Moffat 1990, Cawthorn 1993, McNally et al. 2001, Childerhouse et al. 2005). Moore and Moffat (1990) reported a minimum of 51 pups for the 1988 season. During the 1992 season, 98 pups were tagged and 24 dead pups were counted, giving a minimum production of 122 (M. Fraser, unpublished data). Cawthorn (1993) estimated pup production to be 150 for the 1993 season, and McNally et al. (2001) estimated a minimum pup production of 78 and a pup mortality rate of 44%, based on an incomplete survey in 1998. In January–March 2003, Childerhouse et al. (2005) completed the first comprehensive survey of sea lions on Campbell Island, reporting a pup production of 385 pups and a pup mortality rate of 36% during that time. In December/January 2007/2008, Maloney et al. (2009) undertook the first pup surveys at the breeding sites of Campbell Island while breeding was occurring, reporting a pup production estimate of 583 and an early pup mortality rate of 40%. A similar survey at colonies during the pupping season was repeated during the 2009/2010 season and

produced a pup production estimate of 726 and a pup mortality rate of 64% (A. Maloney, L. Chilvers, C. Muller & M. Haley, unpublished data).

The two surveys by Maloney et al. (2009, unpublished data) are not directly comparable with previous estimates because these surveys were undertaken at colonial breeding sites during the height of the breeding season, before the dispersal of adults and pups. This difference in survey timing is likely to account for much of the increased pup production reported by Maloney et al. (2009, unpublished data) compared to Childerhouse et al. (2005). Maloney et al. (2009) confirmed that in 2008, the majority of NZ sea lion breeding was colonial on Campbell Island, at Davis and Paradise Point colonies on either side of Perseverance Harbour (Fig. 1). Only 3% of the known pup production on Campbell Island was non-colonial, which differs from previous research (Maloney et al. 2009). However, the two most recent pup production estimates for Campbell Island indicate that this breeding area did not experience the drop in pup production that the Auckland Island breeding area did during the 2009 season.

There has been limited tagging or re-sighting of the NZ sea lions on Campbell Island (748 pups tagged between 1988 and 2008); hence, there is no population dynamics information available. Apart from pup production estimates, the only population parameter known is the mortality rate of pups in the first months of life, which appears to be high, at between 36% and 64%, compared with 8% from the Auckland Islands (Chilvers et al. 2007).

POSSIBLE REASONS FOR THE NZ SEA LION DECLINE

One advantage of the different population trends observed between the two NZ sea lion breeding areas is that hypotheses for the species' decline can be examined by comparing the declining Auckland Island population with the Campbell Island population, which appears to be increasing slowly.

Non-anthropogenic factors

Disease epizootics

Disease may act as a regulator in pinniped populations (Harwood & Hall 1990, Visser et al. 1991). Disease outbreaks have caused mass mortality events in many pinniped populations, with severe consequences for some endangered species (Osterhaus et al. 1997, van de Bildt et al. 1999, Kennedy et al. 2000). The NZ sea lion has been recorded to have naturally occurring epizootic mass mortality events (Baker 1999, Duignan 1999, Wilkinson et al. 2003, 2006). Since the first accurate pup production and population estimates in 1996, NZ sea lions have been affected by two epizootics (one epizootic being the same bacteria over 2 years). At the Auckland Islands, epizootics resulted in the death of 53, 32 and 21% of pups in the first month of their lives in the 1998, 2002 and 2003 seasons, respectively; a 20% drop in pup production in 2002; and the deaths of at least 74 adult females during the 1998 epizootic (Baker 1999, Duignan 1999, Wilkinson et al. 2003, 2006). These epizootic events have not been linked to any known naturally occurring or anthropogenic influences (i.e. the bacteria implicated in the events are not known to have come from humans or domestic animals; P. Duignan, unpublished data). There is also no apparent link between the timing of events and environmental factors, such as El Niño/Southern Oscillation (ENSO) cycles (L. Meyneir, unpublished data).

These epizootic events are likely to have demographic consequences, such as the high early pup mortality, which may lead to reduced recruitment into the breeding

population 4–7 years later, but the presence or extent of this effect has not been seen in either population from current research. The disease outbreaks alone, however, are unlikely to be the cause of the continuing severe decline seen in NZ sea lions at the Auckland Islands, particularly as both the Auckland Islands and Campbell Island breeding areas have been impacted by the mass mortality events (McNally et al. 2001, Castinel et al. 2007a, c), and the Campbell Island population appears to be increasing slowly. It is likely that these epizootic events leave both populations more vulnerable to other factors impacting the population.

NZ sea lion pups are more susceptible to bacterial outbreaks than adults, as they possess the least developed immunity of individuals in the population. Pups are also the most susceptible to other factors that can impact disease resistance (e.g. small body size to skin area, low body fat for temperature regulation, restricted ability to move long distances to shelter from the weather). The reduction in pup production in 2002 was hypothesized to have been caused by the bacteria *K. pneumoniae*; however, the 2009 drop in pup production had no apparent link to an epizootic event (W. Roe, unpublished data). In 2009, early pup mortality was normal: 6% at 1 month of age and 12% at 2 months (the mean pup mortality at 1 and 2 months since 1995 excluding epizootics is 8 and 13%, respectively; Chilvers et al. 2007). There were 36 pups and 19 non-pups (subadults and adults) necropsied at Sandy Bay, Enderby Island, during the 2009 season to determine the cause of death. Although both pups and non-pups were diagnosed as dying from bacterial infections, the bacteria identified were already known within the population, and no single bacterial species was the dominant cause of the deaths, indicating that it was not an epizootic event (W. Rowe, unpublished data). Consequently, an epizootic was unlikely to be the cause of the 2009 decline in pup production or the reduction in breeding females returning to breeding areas.

Predation

Sea lions around the world have two common predators: killer whales *Orcinus orca* and large sharks. Killer whales have never been sighted around the NZ sub-Antarctic islands. The only natural predator known to NZ sea lions is the great white shark *Carcharodon carcharias*. Twenty-seven per cent of all adult NZ sea lions at Sandy Bay, Enderby Island, have scarring from near-miss shark attacks (A. Augé, personal communications), and great white sharks have been satellite tracked around the Auckland Islands. It is not known what the relationship between near-misses and mortality rates is for NZ sea lions, but 8 years of observations of the scarring and fresh wounds on NZ sea lions at Sandy Bay have not shown an increase (A. Augé, unpublished data). Consequently, an increase in predation is unlikely to be the cause of the decline of the Auckland Islands population either long term or in 2009.

The shark scarring rate on NZ sea lions on Campbell Island has not been quantified, although shark scarring has been observed (A. Maloney, personal communications). There has also been a great white shark attack on a person at Campbell Island, so the species is known to be found in the area (<http://www.nzgeographic.co.nz/articles.php?ID=284>).

Permanent dispersal or migration

There has been extensive tagging and re-sighting of NZ sea lions throughout their range to help determine levels of site fidelity, philopatry and dispersal (i.e.

Robertson et al. 2006, Chilvers & Wilkinson 2008). NZ sea lion pups have been tagged at 1 month of age as part of a demographic study at the Auckland Islands since 1980 on Enderby Island, 1986 on Dundas Island and 1987 on Figure of Eight Island. Tagging has been intermittent and the numbers of animals tagged annually have varied from 0 to over 500 (1980–96). From 1996, all pups on Enderby Island have been tagged and 400 each year on Dundas Island (between 20% and 36% of all pups annually), while tagging of at least 50% of all pups on Figure of Eight Island has occurred since 2005. In the years 1988, 1992, 1998, 2003, 2008 and 2010, between 50 and 500+ pups have been tagged on Campbell Island. The three latter years had the most comprehensive tagging: 42, 68 and 59% of the estimated pup production was tagged each year, respectively. For all tagging, the sex ratio detected in the population was 50:50 at all locations, except on Dundas Island, where from 2004 onwards, 300 female and 100 male pups have been deliberately tagged annually, because research was focused on understanding female philopatry.

Until the 1998 season, data on the presence and breeding status of marked animals were collected opportunistically at NZ sea lion breeding sites and other haul-out sites. Since 1998, daily tag re-sightings have been carried out on Enderby Island between 1 December and 20 February each season (1999–2010). Additionally, a minimum of 4 days of re-sighting has been undertaken on Dundas Island each season. Since 1990, Campbell and the Snares Islands have had high levels of opportunistic re-sightings during austral summers from scientific expeditions researching species other than NZ sea lions (S. McConkey, P. Sagar and P. Moore, personal communications). The NZ mainland has been extensively, and continuously, surveyed by the University of Otago and the NZ Sea Lion Trust since the early 1990s (McConkey et al. 2002a, b). The occasional sightings from Macquarie Island come from the permanently staffed Australian sub-Antarctic research station that has been operating since 1948 (McMahon et al. 1999, Robinson et al. 1999, Robertson et al. 2006).

From these re-sightings and other research, it is clear that many male sea lions disperse and migrate away from their birth islands, including between Campbell and Auckland Islands (McConkey et al. 2002a, Robertson et al. 2006, Chilvers & Wilkinson 2008). However, no female has ever been recorded to travel between Campbell and the Auckland Islands (Chilvers & Wilkinson 2008, Maloney et al. 2009). It is also unusual for females to disperse or breed in any area other than their birth beach or colony (Enderby and Dundas Islands are deemed one breeding colony). For example, females are known to travel between Enderby and Dundas Islands (10km), but have never been re-sighted on Figure of Eight Island (60km), Campbell Island (250km) or on the NZ mainland (500km; Chilvers & Wilkinson 2008). There is one notable exception. One female NZ sea lion, tagged in 1987 on Dundas Island, pupped on Otago Peninsula, NZ (c. 700km) in 1993 and has shown breeding-site fidelity to that new area for the subsequent 17 years, as have her female offspring (McConkey et al. 2002a, S. McConkey, personal communications).

Consequently, the continuing decline in the Auckland Island population and the reduction in pup production due to decreased numbers of females returning to breed in 2009 are most unlikely to be due to dispersal or migration of female NZ sea lions between breeding areas.

Environmental change

Changes in the ocean environment that affect the abundance or availability of NZ sea lion prey species could affect NZ sea lion populations. The Southern Hemisphere sub-Antarctic climate is affected by irregular fluctuations in climatic conditions called ENSO, which is an approximately 7- to 8-year cyclic pattern of anomalous sea temperatures (Allan et al. 1996). ENSO may affect NZ sea lions by directly modifying the availability of a food source or by changing ocean productivity (Priddle et al. 1998).

Both NZ sea lion breeding areas (Auckland and Campbell Islands) are on the Southern Plateau (Bradford-Grieve et al. 2003); hence, any large-scale environmental change, such as ENSO, should affect both populations similarly. Therefore, environmental change is unlikely to be the cause of the decline of the Auckland Island population of NZ sea lions; however, it is an area where more research could be focused.

Anthropogenic impacts

Population 'overshoot'

The population 'overshoot' hypothesis, as proposed to explain the decline of southern elephant seal *Mirounga leonine* populations (Hindell 1991), suggests that the decrease in a predator population allows its prey to increase to over-abundance. Once the pressure on the predator population ceases, the recovering predator increases to numbers sufficient to 'overshoot' prey availability, resulting in another decline in predator numbers to a smaller, sustainable population size. Under this hypothesis, it must be assumed that the population size of the NZ sea lion has 'overshot' the carrying capacity of prey availability. Consequently, the declines noted in sea lion numbers at the Auckland Islands represent the species returning to a sustainable population size. This is unlikely to be the case.

The 'overshoot' hypothesis has two main assumptions: (i) a simple and direct predator-prey relationship exists; and (ii) prey populations of the predator are not exploited or regulated by other predators, which in the case of the NZ sea lion would be small cetaceans, sea birds, other seals, fish species or humans. From diet analysis, it is known that predator-prey relationships for the NZ sea lion are not simple, as individuals eat many different fish, squid and octopus species (Childerhouse et al. 2001, Meynier et al. 2008a, 2010). Also, complex relationships are known to exist for seals even with simple diets (e.g. Yodzis 2000, 2001). Additionally, scat and vomit analysis from NZ sea lions on Campbell Island shows that individuals eat the same prey species as sea lions at the Auckland Islands (N. McNally, S. Heinrich, C. Lallas, unpublished data), yet the two populations show differing population trends. If it is assumed that the exploitation of prey by other predators (cetaceans, sea birds, other seals, fish and humans) is similar in these two areas, then it should be expected that both populations of sea lions would be in decline, given that they have had a similar recovery time since the cessation of sealing. The 'overshoot' hypothesis, however, leads to the unlikely conclusion that the Auckland Island population has 'overshot' prey availability, while the Campbell Island population has not.

Genetic factors

Small populations and those that have been through severe bottlenecks tend to have reduced genetic diversity due to more severe and/or prolonged genetic drift and

Table 1.

Microsatellite genetic diversity in otariid seals, based on expected heterozygosity (H_e) and average number of alleles per locus (A)

Species	No. individuals	No. loci	H_e	A
New Zealand fur seal <i>Arctocephalus forsteri</i> *	383.0	11	0.75	11.8
Antarctica fur seal <i>Arctocephalus gazella</i> †	2106.0	9	0.80	12.4
Australian fur seal <i>Arctocephalus pusillus</i> ‡	183.0	5	0.58	8.0
Sub-Antarctic fur seal <i>Arctocephalus tropicalis</i> §	76.0	8	0.60	11.1
Northern fur seal <i>Callorhinus ursinus</i> ¶	462.7	8	0.80	17.0
South American fur seal <i>Arctocephalus australis</i> **	226.0	8	0.77	8.4
Australian sea lion <i>Neophoca cinerea</i> †	217.0	5	0.54	4.5
New Zealand sea lion <i>Phocarctos hookeri</i> ‡‡	40.0	22	0.72	5.9
California sea lion <i>Zalophus californianus</i> §§	58.0	12	0.61	6.8
Galapagos sea lion <i>Z. c. wollebacki</i> ¶¶	20.0	10	0.72	6.7
Steller sea lion <i>Eumetopias jubatus</i> ***	668.0	13	0.66	7.9

Low values for H_e and A indicate low genetic diversity in the population.

*B. Robertson, A. Kalinin, H. Best, N. Gemmell (unpublished data).

†Hoffman and Amos (2005).

‡Lancaster et al. (2010) (H_o only).

§L. Wynen, S. Goldsworthy, R. White, R. Slade (unpublished data) (H_o only).

¶Dickerson et al. (2010).

**Oliveira et al. (2008).

††R. Campbell (unpublished data).

‡‡Acevedo-Whitehouse et al. (2009) (H_o only).

§§Hernandez-Velazquez et al. (2005).

¶¶Hoffman et al. (2007).

***Hoffman et al. (2006).

inbreeding (see Allendorf & Luikart 2007). These genetic factors can lead to reduced fitness, or inbreeding depression, due to increased homozygosity or reduced heterozygosity, which can impact on population growth and persistence over time (e.g. Vila et al. 2003).

Although the NZ sea lion has been through a population bottleneck during 19th century sealing, like most otariid seal species, it does not display low levels of genetic diversity at microsatellite loci (Table 1, NZ sea lion genetic samples from the Auckland population). While caution must be used when comparing microsatellite variation between species (e.g. Väli et al. 2008), this molecular marker type is indicative of low levels of genetic diversity in species that have been exposed to strong genetic drift and inbreeding (e.g. Jamieson et al. 2006, Robertson et al. 2009, Schultz et al. 2009). Importantly, the NZ sea lion does not have lower than expected heterozygosity ($H_e = 0.72$) or numbers of alleles per locus ($A = 5.9$) relative to other otariid species, which indicates that the species has not been exposed to strong and prolonged genetic drift and inbreeding due to small population size. Sea lions, in general, appear to have slightly lower levels of genetic diversity than fur seal species (Table 1), which might be a consequence of the greater post-sealing population growth of fur seals relative to sea lions (especially the southern hemisphere sea lion species; Reijnders et al. 1993, Childerhouse & Gales 1998). Indeed, the rate of population increase following a bottleneck is positively related to the retention of genetic diversity (Allendorf & Luikart 2007).

Given that the NZ sea lion does not have low genetic diversity, and hence has not been exposed to severe genetic drift and inbreeding, it is unlikely that the

population is being negatively influenced by inbreeding depression. Consequently, the decline of the Auckland Island population cannot be attributed to genetic factors. Furthermore, if such genetic factors were causing the observed decline, they could reasonably be expected to have a similar impact on the Campbell Island population.

Contaminants

Contaminants have the potential to exert population-level effects on pinniped populations in two ways (Reijnders 1986, Ross 2002, Tanabe 2002, Ylitalo et al. 2005). First, acute toxicity can cause mass mortality, usually affecting the entire population in an area over a short period of time. Second, chronic sub-lethal exposure can cause toxicity, which manifests as health problems, such as immune and reproductive dysfunction.

Toxicity in mammals is usually due to persistent organochlorines (OCs), such as polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDT) and dichlorodiphenyldichloroethylene (DDE). Persistent PCBs and other OCs were tested for in the thoracic blubber from seven NZ sea lions (five females and two males) caught in the Auckland Island arrow squid *Nototodarus sloanii* fishery in 2007 (Donaldson 2008). The average Σ PCBs was 0.075mg kg^{-1} (range $0.034\text{--}0.192$). The Σ OCs (i.e. DDT, DDE) ranged from 0.067 to 0.51mg kg^{-1} . Compared to a proposed threshold for adverse effects in marine mammals of Σ PCBs 17mg kg^{-1} (Kannan et al. 2000), the NZ sea lions' range of $0.034\text{--}0.192\text{mg kg}^{-1}$ can be considered insignificant. The levels of OCs and PCBs in NZ sea lion blubber are lower than those reported for NZ cetacean species (Stockin et al. 2007) and for most northern hemisphere pinnipeds (e.g. California sea lion *Zalophus californianus*, up to 1.4mg kg^{-1} DDT and 0.41mg kg^{-1} PCBs; Le Boeuf et al. 2002, Fillmann et al. 2007, Wang et al. 2007).

Based on the available evidence, the levels of PCBs or OCs in NZ sea lions are unlikely to play a role in lower pup production or mortality levels in the species. However, contaminant testing of a greater number of NZ sea lions should be undertaken to confirm this finding.

Indirect effects of fisheries: resource competition

The degree of overlap between the spatial distribution of commercial fishing and the foraging diversity and effort of marine mammals determines the likely rate of spatial encounters between them, and is the key component in the evaluation of the extent of competition between marine mammals and fisheries (Matthiopoulos et al. 2008). Therefore, to try and understand potential resource competition, a description of the diet, the foraging behaviour at sea and the distribution of NZ sea lions is given and compared with the fisheries activities and prey take around the Auckland and Campbell Islands.

Analysis of scats, vomit and stomach contents indicates that NZ sea lions at the Auckland and Campbell Islands have similar, varied diets containing both fin fish (i.e. rattails *Macrouridae* spp., hoki *Macruronus novaezelandiae* and red cod *Pseudophycis bachus*) and cephalopods (squid *Nototodarus* spp. and octopus *Enteroctopus zealandicus*; Childerhouse et al. 2001, Meynier et al. 2008a, 2010, N. McNally, S. Heinrich, C. Lalas, unpublished data). Meynier (2008a), using the novel technique of blubber fatty acid analysis, showed similar results to scat and stomach analysis for the Auckland Island region, indicating that in this area, the diet of sea lions is consistent throughout the year.

Research on foraging by adult males (Geschke & Chilvers 2009) and adult females (Gales & Mattlin 1997, Chilvers et al. 2005, 2006, Chilvers 2008a, b, 2009, Chilvers & Wilkinson 2009) has been undertaken at the Auckland Islands. Here, the research focus is on female foraging behaviour, as females are the most comprehensively studied of the sexes and have the most restricted foraging areas.

Female NZ sea lions forage over the entire Auckland Island shelf (Chilvers 2008a, b, 2009). They are restricted in their area and duration of foraging by their need to return to dependent pups ashore. Individuals show either benthic (foraging on the sea floor) or mesopelagic (foraging at various, but usually deep, depths in the water column) diving behaviours (Chilvers & Wilkinson 2009). NZ sea lions have the deepest and longest dive durations recorded, plus the longest distances travelled during foraging trips, of any otariid (Chilvers et al. 2005, 2006). They dive almost continuously when at sea, and their diving behaviour is at or close to their physiological limits (Gales & Mattlin 1997, Chilvers et al. 2006, Chilvers & Wilkinson 2009). They show high levels of individual variation in foraging location and diving behaviour, but individuals show strong fidelity to foraging areas and strategies (i.e. either being benthic or mesopelagic foragers) within and between breeding seasons (here defined as December–February each year; Chilvers et al. 2005, 2006, Chilvers 2008a, b, Chilvers & Wilkinson 2009). This consistent fidelity is thought to occur even with differences in prey distribution and environmental conditions between years (Chilvers 2008a, b). Populations composed of long-term individual foraging strategy specialists, such as female NZ sea lions, are thought to be highly susceptible to, and less able to respond to, environmental changes or anthropogenic impacts (Costa 1993, 2007, Gales & Mattlin 1997, Bolnick et al. 2003, Chilvers et al. 2006).

Meynier (2008a), using a simple energetic model, estimated that the daily food requirement of a lactating female NZ sea lion is approximately 20% of its body mass, taking into account the average intake of each prey species (squid, hoki and octopus) and their estimated energy value. During years of low arrow squid recruitment, such as in 2001, the amount of squid estimated to be required by the NZ sea lion population as a component of their diet would have been similar to the amount harvested by the fishery, indicating that resource competition between the arrow squid fishery and NZ sea lions is likely to occur, particularly when squid abundance is low.

The Auckland Islands area has two main fisheries: the arrow squid trawl fishery and the NZ scampi *Metanephrops challengerii* trawl fishery. The arrow squid fishery around the Auckland Islands is trawl-only, and is called SQU6T. The SQU6T fishery operates annually from 1 February to between mid-May to mid-August over the Auckland Island shelf, in depths between 150 and 250m, in two concentrated areas north of Enderby Island and south-east of the main Auckland Islands (Chilvers 2009). Therefore, the fishery operates for between 4 and 7 months during the majority of the lactation period for female NZ sea lions, and overlaps both spatially and in terms of water depth with female NZ sea lions (Chilvers 2008a, 2009). The total allowable commercial catch each year for SQU6T is 32369 metric tonnes (1 metric tonne = 1000kg); actual catches between 2001 and 2009 have ranged from 3254 metric tonnes in 2001 to 34635 metric tonnes in 2004 (<http://fs.fish.govt.nz> – stock status). The scampi fishery in the Auckland Island area is called SCI6A. The total allowable commercial catch each year for this area is 306 metric tonnes, and catches are fairly consistent between years, ranging from 234 to 302 metric tonnes between

2002 and 2009 (<http://fs.fish.govt.nz> – stock status). This fishery operates in water between 250 and 500m deep, south-east of the main Auckland Islands, and so also overlaps with foraging female NZ sea lions (Chilvers 2009).

The spatial and temporal overlap of the Auckland Island trawl fisheries with female NZ sea lions during the breeding and lactation periods, when foraging is most restricted due to dependant pups and energy needs peak due to lactation, signals that indirect impacts of fishing are likely to affect NZ sea lions, particularly females, around the Auckland Islands. The indirect effects of fishing in the form of resource competition lowering food quantity and quality have been shown to influence reproduction in Steller sea lions *Eumetopias jubatus* (Trites & Donnelly 2003) and in southern elephant seals (Atkinson et al. 2008). Female NZ sea lions at the Auckland Islands have low reproductive ability compared with other sea lion species, indicating that this same affect maybe occurring at the Auckland Islands (Pitcher & Calkins 1981, Calkins & Pitcher 1982, Boyd 1992, Higgins & Gass 1993, York 1994, Melin 2002, Childerhouse et al. 2010a, Chilvers et al. 2010). At the Auckland Islands, NZ sea lion absolute pup growth rate is also low compared to that of Steller sea lions, Californian sea lions and southern sea lions *Otaria flavescens* (Higgins et al. 1988, Boness et al. 1991, Cappozzo et al. 1991, Schulz & Bowen 2004, Chilvers et al. 2007). The lower pup growth rate of NZ sea lions is likely to be linked with unusually low mean milk lipid content during early lactation, the lowest reported for any otariid species (19%; Riet-Saprizza 2007). Competition for prey with fisheries and low energy content of available prey are thought to be the major factors affecting NZ sea lion milk fat content (Riet-Saprizza 2007, Chilvers 2008a). Low reproductive rates and low pup growth, as seen in the Auckland Island NZ sea lion population, have been shown to lead to lower survival and reproductive ability in individuals, and hence affect overall population size and growth (McMahon et al. 2005). Consequently, indirect effects of fisheries through resource competition between fisheries and NZ sea lions are likely to occur, but to what extent they are contributing to the severe decline in the population is undetermined.

The sub-Antarctic arrow squid fishery and scampi fisheries do not normally operate around Campbell Island. Only one main trawl fishery operates in the area (SBW61): southern blue whiting *Micromesistius australis*. While no foraging studies of NZ sea lions have been undertaken at Campbell Island, southern blue whiting is known to be an absent or negligible component of the NZ sea lion's diet (Lalas 1997, Childerhouse et al. 2001, Meynier et al. 2008a, 2010, N. McNally, unpublished data). The southern blue whiting fishery also operates in deeper waters and further from Campbell Island than either of the Auckland Island trawl fisheries; hence, it is unlikely to overlap as much with foraging NZ sea lions. Fishing effort in SBW61 is also concentrated in August–October annually, which does not overlap with the NZ sea lion breeding and lactation season; the total allowable commercial catch is currently 23000 metric tonnes, and actual catches ranged from 19039 to 33444 metric tonnes between 2002 and 2009 (<http://fs.fish.govt.nz> – stock status). Fisheries competition may also impact on the Campbell Island population of NZ sea lions, but to a lesser extent than around the Auckland Islands, as the spatial and temporal overlap with foraging areas is less. Therefore, the greater influence of indirect competition with fisheries on the Auckland Islands than on Campbell Island could be a factor affecting the differing population trends. More research into this effect both at the Auckland and Campbell Islands should be a priority in the future.

Direct effect of fisheries: by-catch deaths

Fisheries by-catch is the largest documented anthropogenic impact on NZ sea lions. The first NZ sea lion captures and mortalities reported in fisheries were in 1978, when 10 NZ sea lions were killed during 58 research tows in the northern Auckland Island area (Baird 1994). While NZ sea lions are fully protected under the NZ Marine Mammals Protection Act 1978, incidental captures during fisheries operations are not an offence, provided that captures are reported and handled as directed. Government observers have been placed on a proportion of commercial fishing vessels in an effort to determine the number and location of NZ sea lions captured by the SQU6T squid fleet since 1992 (observer coverage of the fleet ranges from 8% to 100%, 1992–2009; Table 2). Between 1992 and 2003, by-catch mortality of NZ sea lions in the arrow squid fishery was estimated by extrapolating the number of captures ($n = 3\text{--}38$ NZ sea lions, average $n = 15$; Table 2) reported by government observers on a proportion of fishing boats to the entire fleet each year ($n = 14\text{--}123$ dead by-catch sea lions; Table 2). Between 1993 and 2004, this estimated by-catch was compared annually with a by-catch limit called a maximum allowable level of fishing-related mortality (MALFIRM), derived using the formula used to calculate the potential biological removal (maximum number of animals that may be removed while allowing the stock to reach or maintain its optimum sustainable population), as developed by the US National Marine Fisheries Services (Wade 1998). If the estimated by-catch exceeded the MALFIRM within a season, the squid fishery was closed. Closures occurred in 1996, 1997, 1998, 2000 and 2002, and were attempted, but overturned by court orders, in 2003 and 2004 (Table 2). In 2004, the potential biological removal model was superseded by the fisheries-related mortality limit, established by using an 'adaptive' rule derived from a Bayesian model (Breen et al. 2003). This model allowed a higher number of NZ sea lions to be by-caught in the fisheries (Table 2).

In the same year, sea lion exclusion devices (SLEDs) were used by the entire fleet in the arrow squid fishery in the Auckland Island. A SLED is a metal separation grid fixed inside the trawl net at a 45° angle to the water flow, just before the cod end of the net (the collection area at the end of the trawl net that holds the captured target species, i.e. squid). SLEDs allow smaller objects, such as squid, to pass through the metal grid into the cod end, while larger objects, such as sea lions, are directed to an escape hatch opening at the top of the net. Trials of SLEDs during 2001 suggested that 91% of NZ sea lions were ejected through the escape hatch. However, examination by a veterinary pathologist indicated that an estimated 55% of animals that went through this ejection process (but were then intentionally drowned by cover nets sewn over the escape hatches) had suffered traumatic internal and head injuries that would have significantly compromised their chances of survival (Wilkinson et al. 2003). Therefore, uncertainty about the efficacy of SLEDs remains, but between 2004 and 2009, all fishing vessels used a SLED during SQU6T fishing. The use of SLEDs prevents direct counts of the number of sea lions injured or killed in the fishery.

Between 1992 and 2009, 234 NZ sea lions were captured by observed vessels; 59% of these animals were female (Table 2). However, since SLEDs have been used (2004 onwards), the proportion of females captured on observed vessels has been reported at 71% (Table 2). The implications of this increased female-biased by-catch may be seen in the estimated survival rates of adult NZ sea lions at the Auckland Islands; females 3 years old and over have lower survival estimates than their male

Table 2.

By-catch statistics for New Zealand (NZ) sea lions in Auckland Island arrow squid *Nototodarus sloanii* fisheries (SQU6T), showing the annual percentage of fishing boats carrying government observers (observer coverage), numbers of NZ sea lions captured on observed fishing vessels, number of observed tows, number of total tows within SQU6T and estimated total number of NZ sea lions captured per fishing season between 1992 and 2009

Season	% Observer coverage	Total number and numbers of female (F) and male (M) NZ sea lions caught on observed boats	% Female by-catch	Observed tows	Total tows	Estimated total number of NZ sea lion mortalities	Sea lion MALFIRM or FRML limit	Fisheries closure
1992	10	8 (3F, 5M)	38	218	2153	82	32	
1993	29	5 (3F, 2M)	60	197	656	17	63	
1994	10	4 (2F, 2M)	50	433	4677	32	63	
1995	8	8 (4F, 4M)	50	286	4000	109	69	
1996	13	13 (10F, 3M)	77	555	4460	105	73	4 May
1997	20	29 (9F, 20M)	31	731	3708	123	79	28 March
1998	23	15 (4F, 11M)	27	337	1442	62	63	27 March
1999	37	5 (4F, 1M)	80	156	401	14	64	
2000	35	25 (11F, 13M)	44	438	1208	71	65	8 March
2001	100 ^a	38 (22F, 16M)	58	576	582	67	75	^a
2002	33	22 (16F, 6M)	73	563	1647	84	79	13 April
2003	23	10 (6F, 4M)	60	420	1466	39	70	^b
2004	31	16 (14F, 2M)	88	792	2595	118	62	^c
2005	29	9 (6F, 3M)	67	805	2693	115	115	^d
2006	28	11 (10F, 1M)	91	688	2459	110	96/150	^e
2007	41	8 (6F, 2M)	75	540	1318	56	91	
2008	47	5 (3F, 2M)	60	586	1247	46	81	
2009	38	3 (2F, 1M)	66	728	1916	72	113/95	^f
Total		234 (136F, 98M)	59 (71*)			1322		

Also shown are maximum allowable level of fishing-related mortality (MALFIRM; until 2003) and fisheries-related mortality limit (FRML; from 2004) on by-catch, and dates of fisheries closure as a result of exceeding these limits.

^aPercentage of females captured since 2001 when sea lion exclusion devices were used on most, if not all, trawls undertaken in SQU6T fisheries; data obtained from Vicky Reeve/Aoife Martin Ministry of Fisheries (personal communications), Baird (1996, 1999), Baird and Doonan (2005), Smith and Baird (2005), and Baird (2005a, b).

^bThe fishery was not officially closed in 2000/01. Industry voluntarily withdrew the majority of vessels on 7 March 2001 – note the low number of total tows and the high by-catch rate.

^cSQU6T fishery was closed on 29 March 2003. However, a High Court Ruling in April 2003 allowed for continued fishing.

^dSQU6T fishery was closed on 22 March 2004. However, a Court of Appeal ruling in April 2004 allowed for continued fishing.

^eFishers withdrew from the SQU6T fishery upon reaching the 115 animal FRML on 17 April 2005.

^fThe FRML was initially set at 97 animals, and the Minister of Fisheries chose to increase this mid-season to 150.

^gFisheries voluntarily reduced the FRML level to 95 mid-season due to reports of 30% drop in pup production at Auckland Islands in that season.

counterparts (Chilvers & Mackenzie 2010). Adult female otariids rarely have lower survival estimates than their male counterparts. For example, in both Californian and Steller sea lions, adult females have higher survival rates than adult males (Pendleton et al. 2006, Hernandez-Camacho et al. 2008). Sexual selection on males in polygamous breeding species, such as otariids, favours morphological traits and behaviours that increase reproductive fitness of the individual, but such reproductive investments lower long-term survival (Selander 1964, Clinton & Le Boeuf 1993, Mills 2006). Given the evolutionary expectation that female survival should be greater than male survival in otariids, the causes of lower female survival in NZ sea lions should be investigated and managed urgently.

Given the breeding cycle of the NZ sea lion, in which adult females give birth to a pup, mate and are hence pregnant again within the same breeding season (December–January each year), many of the 71% of by-caught animals that are female may have a dependent pup ashore and may also be pregnant. Consequently, one female by-catch death can result in up to three sea lion deaths rather than a single death when a male is captured, thereby having an even greater impact on the overall population.

NZ sea lions are by-caught in the southern blue whiting commercial fishery around Campbell Island, in predominantly August–September each year, at the end of the lactation period (Rowe 2008, Thompson & Abraham 2009). The average number of tows per year in the fishery is 656; observer coverage was 36% between 1996 and 2008. One to six sea lions have been reported captured each year between 2002 and 2008. The estimated total number of captures is between 4 and 16 animals (Thompson & Abraham 2009). Southern blue whiting fishing activities occur two to three times further offshore and in deeper water around Campbell Islands, and therefore further from sea lion colonies, than either the arrow squid or scampi fisheries around the Auckland Islands (Thompson & Abraham 2009). The majority of animals caught in the southern blue whiting fisheries are males (Thompson & Abraham 2009). There is no squid trawling in the Campbell Island area.

The available information indicates that fisheries by-catch of predominantly female NZ sea lions around the Auckland Island is negatively impacting the Auckland Island population and is hence a major contributing factor towards the observed decline at the Auckland Islands. The impact of fisheries by-catch at Campbell Island is less understood and may be as large relative to the NZ sea lion population size at Campbell Island. However, it may have a lesser impact, as by-catch is predominantly of males, and takes place outside the breeding and lactation season.

DISCUSSION

Untangling hypotheses for the decline of long-lived, slow-breeding pinnipeds is difficult at best (Trites & Donnelly 2003, McMahon et al. 2005, Atkinson et al. 2008). A fundamental component of assessing and managing any species in decline is the long-term monitoring of changes in numbers and population dynamics in each population of the species. Anthropogenic and natural influences, which may impact upon populations differently, must also be taken into account.

This review indicates that monitoring of the Auckland Island population of NZ sea lions over the last 15 years has provided many important demographic parameters and information on the foraging behaviours for the population, but it also reveals

the need for more research and, as the population continues to decline, greater conservation management. For research, a greater understanding is required regarding the influences of indirect impacts of fisheries on all age classes and sexes of the population. Continued monitoring is essential to examine future trends in pup production, changes in population parameters, and influences on mortality rates for all age and sex classes of this long-lived species. In contrast, the Campbell Island population has been the subject of minimal research, and only pup production, early pup mortality and some diet information are available. This lack of research has mainly been due to the low proportion of the total NZ sea lion population known to have bred at Campbell Island (until 2008, less than 14% of population was considered to breed on Campbell Island; Chilvers et al. 2007) and due to the difficulty of accessing breeding areas (Childerhouse et al. 2005, Maloney et al. 2009). With the decline of the Auckland Island population, the Campbell Island population is becoming a larger, increasing component of the species, and hence requires greater and more frequent research and monitoring.

This review also reveals that of the nine potential causes of decline of NZ sea lions proposed and examined, six can be discounted by comparing the Auckland Island NZ sea lion population with the Campbell Island population: predation, dispersal or migration, population overshoot, environmental change, genetic effects and effects of contaminants. Another potential cause, bacterial epizootics, is known to occur in the population, but as epizootics occur in both areas (Auckland Islands and Campbell Island) and predominantly only impact pup mortality, which is naturally highly variable, they are likely to be affecting both populations' resilience to other impacts, but are unlikely to be the cause of the severe decline in the Auckland Island population. Regardless, non-anthropogenic threats such as disease are not easily managed, and the feasibility of mitigating their impact is typically low to zero (McMahon et al. 2005).

Based on the available evidence, the two most parsimonious hypotheses for the decline seen at the Auckland Islands are indirect effects of fisheries in the form of resource competition and direct effects of fisheries in the form of by-catch mortality.

The indirect effects of fishing on NZ sea lions remain unclear and should be a priority for future research at both Campbell and Auckland Islands. Despite our lack of thorough understanding, it is clear that indirect effects can impact on the population dynamics of pinnipeds, including affecting reproductive ability, milk composition and, hence, pup growth rates and survival (Trites & Donnelly 2003, Atkinson et al. 2008). Low reproductive ability, low milk fat composition and low pup growth are all seen in the Auckland Island NZ sea lion population (Chilvers et al. 2007, 2010, Riet-Sapriza 2007, Chilvers 2008a). The NZ sea lion's lowered reproductive ability will make the Auckland Island population even less resilient to any unusual or anthropogenic increase in mortality in the population.

Fisheries by-catch is the main anthropogenic cause of mortality known for NZ sea lions, and the majority of mortalities in recent years are of females (Chilvers 2008a). Importantly, small changes in adult female survival probability, as seen in the Auckland Island NZ sea lion population (Chilvers & Mackenzie 2010), significantly affect population stability and population trend in large, long-lived mammals (Caughley 1966, Mills 2006, Pendleton et al. 2006). It is clear that the reduction of by-catch, particularly of female NZ sea lions, must be the highest priority for NZ sea lion management, a management goal already highlighted in the NZ Department of

Conservation NZ Sea Lion Species Management Plan 2009–14 (<http://www.doc.govt.nz/upload/documents/science-and-technical/sap251entire.pdf>).

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