

A review of evidence for indirect effects of commercial fishing on New Zealand sea lions (*Phocarctos hookeri*) breeding on the Auckland Islands

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Abstract

The New Zealand (NZ) sea lion (*Phocarctos hookeri*) is a rare pinniped species with a highly restricted geographic distribution. They mainly breed on New Zealand's subAntarctic islands and currently about 71% of all births occur on the Auckland Islands. Pup production at the Auckland Islands colonies has been declining. Sea lions have been recently uplisted to 'Nationally Critical' under the New Zealand threat classification system. Sea lions are incidentally drowned each year in southern commercial trawl fishing operations, particularly those targeting arrow squid (*Nototodarus sloanii*). Satellite tagging studies indicate that foraging areas of juveniles and lactating females from the Auckland Islands overlap with commercial trawl fisheries, including arrow squid. Arrow squid are eaten by sea lions. Therefore, there may be indirect fishery effects on the NZ sea lion population through resource competition. Scientific literature pertaining to indirect effects was reviewed. Although there is overlap in the distribution of juvenile and adult female sea lions with commercial fisheries, this conclusion is based on data from only the first month of a 10-12 month lactation period. The short-term foraging distribution of juveniles has been studied at only one colony. Reliable estimates of diet, including the contribution of arrow squid, are not available, although the main prey species consumed are probably known. Despite the opportunity of indirect fishery effects, there is no evidence that competition with the squid fishery for food is negatively affecting the NZ sea lion population. Reliable estimates of diet and a better understanding of the foraging distribution of adult females later in lactation and juveniles is needed. Simultaneously testing competing hypotheses (including indirect fishery effects on food) about the causes of population decline may be a more effective approach than attempting to evaluate single factor explanations for the decline.

Keywords: New Zealand sea lion, indirect fishery effects, arrow squid, fishery interactions, diet, foraging behaviour

Introduction

The New Zealand (NZ) sea lion (*Phocarctos hookeri*), also known as Hooker's sea lion, is a relatively rare pinniped species with a highly restricted geographic distribution (Chilvers 2008a). Their population is one of the smallest reported for an otariid, estimated at < 9,880 (Geschke and Chilvers 2009). They mainly breed on New Zealand's sub-Antarctic islands between latitudes of 48 and 53° S (Gales & Mattlin 1997) and currently about 71% of all births occur on the Auckland Islands (Fig. 1). The only other significant breeding area is located on Campbell Island/Motu Ihupuku some 400 km southeast of the Auckland Islands (Chilvers et al. 2007a, Maloney et al. 2009). Given these characteristics, it has been classified as 'Vulnerable' by the International Union for Conservation of Nature, IUCN (Reijnders et al. 1993) and recently uplisted to 'Nationally Critical' under the New Zealand threat classification system (Baker et al. 2010).

NZ sea lions are incidentally drowned each year in southern commercial trawl fishing operations, particularly those targeting arrow squid (*Nototodarus sloanii*). Satellite tagging studies indicate that foraging areas of some lactating females from the Auckland Islands overlap both spatially and temporally with commercial trawl fisheries (e.g. Chilvers 2008a, 2009). It is also known that arrow squid are eaten by sea lions (Childerhouse et al. 2001). Therefore, in addition to the direct effects of the bycatch, there may be indirect effects on the NZ sea lion population through resource competition with the arrow squid fishery (Chilvers 2009), particularly in years of low squid abundance (e.g., Meynier et al. 2009).

Direct, fishing-induced mortality of NZ sea lions by the Auckland Island's trawl squid fishery (SQU 6T) is being managed by restricting the total number of mortalities per season. Since 1992, the Minister of Fisheries has set an annual limit, known as Fisheries Related Mortality Limit, on the number of sea lions that can be killed in the SQU6T fishery before it is closed. This limit is based on a harvest control rule that has been evaluated with demographic modelling using annual estimates of pup production and a wide range of fishery and sea lion biological data as input to the model (Breen and Kim 2005). However, current demographic models have not included potential indirect impacts of fisheries on sea lions. Sea lion exclusion devices, designed to allow caught sea lions to exit a trawl net, were introduced into the fishery from 2000–01 (Anon 2010). Management measures aimed at protecting the sea lions has resulted in the closure of the fishery five times since 1995. In another 6 years, the fishers voluntarily ended fishing (Anon 2010). Several other conservation management actions have also been taken. In 1995, the New Zealand Department of Conservation declared a Marine Mammal Sanctuary around the Auckland Islands extending to 12 nautical miles (22 km, i.e. the Territorial Sea) to protect NZ sea lions. In 2003, the Marine Mammal Sanctuary was also designated as a concurrent no-take full Marine Reserve (under the Marine Reserves Act 1971) (Chilvers 2008a).

Although area-based protection and the additional fisheries management measures in the surrounding waters have been taken to protect sea lions, pup production at the Auckland Island breeding colonies has declined significantly in the last decade. This is thought to have resulted from a decline in the number of breeding adults (Wilkinson et al. 2006, Chilvers et al. 2007a, Chilvers 2010). There are uncertainties about that impact of fishery-bycatch mortality on the NZ sea lion population. Several early models suggested that the estimated level of take may limit the capacity for NZ sea lions to increase in number and, under some scenarios, may result in population decline (Doonan & Cawthorn 1984, Woodley & Lavigne 1993), other more recent and comprehensive models as used by the Ministry of Fisheries to inform their decision making on management measures, suggest that there would be little population impact (Breen et al. 2003, Breen and Kim 2005). Neither the methods used to estimate the magnitude of bycatch in the arrow squid fishery nor the population models developed to evaluate their impact on the population dynamics were reviewed here.

The purpose of this paper is to review evidence for indirect effects of fisheries, mainly the arrow squid fishery, on the population dynamics of NZ sea lions. Indirect effects of fisheries could be manifested in a number of ways, with effects on reproduction and survival. A conceptual model of such effects is illustrated in Fig. 2. Hypotheses of indirect effects of fisheries either explicitly or implicitly involve changes in the diet or foraging behaviour of individuals which affect body condition which, in turn, negatively influence fecundity, provisioning of dependent offspring, or survival. Changes in the nutritional condition of foraging sea lions due to changes in the abundance of prey could arise through fishery removals, ocean climate variability affecting prey availability, other ecosystem changes affecting predator and prey or some combination of these.

Methods

Information for this review was collated and supplied from published reports either by DeepWater Group Ltd. or was obtained from searches of the Web of Science and websites of the New Zealand Ministry of Fisheries and Department of Conservation. Another piece of related work, a model of the population energetics of NZ sea lions, is forthcoming from L. Meynier, but was not available in time for consideration in this review.

Results

Prey abundance and associated fisheries

Although a number of species have been found in the diets of NZ sea lions (see below), relatively few species appear to be frequently consumed. This conclusion is tempered by the probable biases in estimates of the species composition of the diet and the limited seasonal sampling. Therefore, it is possible that some prey species may currently seem

more important that they are and others less important. Octopus (*Enteroctopus zelandicus*), hoki (*Macruronus novaezelandiae*), opal fish (*Hemerocoetes* sp), red cod (*Pseudophycis bachus*) and scampi (*Metanephrops challengerii*) are briefly reviewed because of their apparent importance in the diet or the size of the fishery.

Little is known about the abundance of octopus and opal fish as finfish and scampi surveys do not catch significant amounts of these species. The marine reserve around the Auckland Islands precludes sampling in this area so abundance is unknown. Although their abundance in the reserve is open to conjecture, it appears that these species are either not prevalent or not vulnerable to the sampling gear outside the reserve (DeepWater Group pers comm.).

Hoki is the dominant species in the bottom fish community of the upper slope (200–800 m) and is considered a key biological component of the slope ecosystem, particularly around the South Island (Anon 2010). Growth is fairly rapid with juveniles reaching about 27–35 cm at the end of the first year. Hoki are fished using both bottom and mid-water trawls, although the proportion of bottom trawling has increased in the last decade. There is a hoki spawning fishery that operates from mid-July to late-August and a second spawning fishery in Cook Strait from late-June to mid-September. Outside the spawning season, there is a substantial fishery on the Chatham Rise and a smaller fishery in the Sub-Antarctic, the area relevant to sea lions. In the Sub-Antarctic, catches typically peak in April to June. The hoki fishery was developed by Japanese and Soviet vessels in the early 1970s. Catches peaked at 100 000 t in 1977, but dropped to less than 20 000 t in 1978 when the EEZ was declared and quota limits were introduced. Annual catches ranged between 175 000 and 215 000 t from 1988–89 to 1995–96, increasing to 246 000 t in 1996–97, and peaking at 269 000 t in 1997–98, when the TACC was over-caught by 19 000 t. Catches have declined as the TACC has been reduced to about 100,000 t. The western stock experienced an extended period of poor recruitment from 1995 to 2001. However, the biomass of the western hoki stock is expected to increase over the next 5 years at 2007-08 fishery catch levels (Anon 2010).

Red cod are a fast-growing, short-lived species, attaining sexual maturity at about 52 cm in both sexes at an age of 2–3 years. Red cod are fished primarily by domestic trawlers at depths of between 30 and 200 m and are also a bycatch of deepwater fisheries off the southeast and southwest coasts of the South Island. The domestic red-cod fishery begins in November and continues to May or June, with peak catches around January and May. Catches from the RC03 stock, which broadly overlaps with the distribution of NZ sea lions, have varied from about 2,000 t to 15,000 t during the period 1983 to 2008 (Anon 2010). Usually, landings have been lower than the TACC since 1999. There is no current stock assessment (2009 most recent), but yearly fluctuations in red cod catch seem to reflect changes in recruitment. Trawl surveys and catch sampling of red cod have shown that the fishery is based almost exclusively on two and three year old fish. Both catch and survey biomasses have declined substantially since the mid 1990s and a 2007 survey confirms that biomass remains low relative to the early 1990s.

Arrow squid are a large, muscular, schooling squid which live for about 1 yr then die after spawning, mostly in autumn, but also in spring (Uozumi & Ohara 1993). Arrow squid are found in and to the south of the convergence zone (Anon 2010). Because squid live for only about 1 year and stock size is highly recruitment driven, and the variables driving recruitment are unknown, it is not possible to predict stock size in advance of the fishing season. Hence, there are no current or reference biomass estimates of arrow squid and it is not possible to estimate a long-term sustainable yield for squid, nor determine if recent catch levels or the current Total Allowable Commercial Catch will allow the stock to move towards a size that will support the MSY (Anon 2010). Juvenile arrow squid, which were most common in summer, are found at peak abundance schooling in waters 50 to 100 m deep (Uozumi & Ohara 1993). Arrow squid appear to move offshore to deep water to spawn during the winter, and only juveniles are readily available to pinnipeds during that period (Uozumi & Ohara 1993, Uozumi et al. 1995, Fea et al. 1999).

The squid fishery began in the late 1970s, reached a peak in the early 1980s with over 200 squid jigging vessels and then declined to around 15 in 1994 (Anon 2010). There are several management areas for the squid fishery, but it is the Southern Islands trawl fishery (SQU 6T) that takes place in the waters around the Auckland Islands that is relevant to this review, as this is also the area where most fishery interactions with sea lions occur. Between 2001 and 2004, 56% of trawls in SQU6T were recorded in the area north of the Auckland Islands, resulting in 61% of the tonnage of squid caught and 72% of the incidental bycatch of sea lions (Chilvers et al. 2005). The remaining trawling occurs southeast of the Auckland Islands at the edge of the Auckland Island rise. From 1986 to 1998 the trawl catch fluctuated between about 30,000–60,000 t. With the exception of two years (1988-89 ~36,000 and 1990-91 ~42,000) the Total Allowable Commercial Catch (TACC) from 1997 to 2008 has been rather stable at between ~30,000 and 32,000 t/yr. However, catches during this period have been highly variable from less than 1,000 t to ~34,600 t. This variability presumably reflects squid abundance, markets, and sea lions management measures. The SQU6T fishery operates annually from 1 February to generally mid-May over the Auckland Island shelf in depths between 150 m and 250 m, with most fishing occurring at 180-220 m, using either mid-water (generally operated half closed in semi-pelagic mode) or bottom trawling nets.

Scampi are widely distributed around New Zealand, principally in depths between 200m and 500m on the continental slope. The species is found in sandy and muddy areas of the sea floor, where the scampi make burrows, in which they spend the majority of adult life. Directed bottom trawl fisheries for scampi were developed in the late 1980s in New Zealand's EEZ. The main fisheries take place around the east of the North Island, the Chatham Rise and the Auckland Islands. The Auckland Island fishery takes a relatively constant small catch of about 200-300 t at depths of 350-550 m. Bycatch of scampi in other trawl fisheries during the most recent 5-year period was low (<0.1%, of total scampi catch) (David Foster pers. comm.).

Ecosystem context

The potential impact of commercial fishing for arrow squid on the dynamics of NZ sea lions can only be meaningfully evaluated in the context of the supporting ecosystem. The area off southeast New Zealand is an important feeding area for birds, marine mammals, and fish and supports several commercial fisheries, including that for arrow squid. The Southern Plateau, which includes the Auckland Shelf, supports relatively low levels of phytoplankton biomass (Murphy et al. 2001), despite there being plenty of phytoplankton nutrients such as nitrates (Bradford-Grieve et al. 1999). One reason for this is the low levels of dissolved iron in these waters and the way this interacts with available light and silicate (Boyd et al. 1999) resulting in a system dominated by small phytoplankton, a relatively long food web, and only a small fraction of phytoplankton production reaching the highest trophic levels.

To better understand the functioning of this ecosystem, Bradford-Grieve et al. (2003) constructed a mass-balance ecosystem model of the Southern Plateau subantarctic region with 19 compartments from upper-trophic level predators to detritus and known predator-prey relationships. Omitting the large predators (birds, seals, whales), the model estimated that the pelagic domain contained 69% of total living biomass and benthic compartments contained 31%. Upper-trophic level predators represented about 0.3% of total biomass and account for about $0.24 \text{ g C m}^{-2} \text{ year}^{-1}$ of food consumed made up of 24% birds, 17% seals (sea lions and fur seals combined), and 60% whales. This amounted to an estimate of $\sim 106,000 \text{ t}$ carbon over the whole of the Southern Plateau, or about 17% of the total amount of food eaten by non-mesopelagic fish. Estimates adult fish production is almost completely accounted for by fisheries catches (32%), consumption by seals (7%), toothed whales (21%), other adult fish (13%), and squid (20%). The model indicated that adult fish abundance had the greatest impact on their prey and also negatively impacted birds and pinnipeds. This result is expected as these taxa were modeled as directly competing for resources. Increasing the fishing fleet had the greatest negative impact on bird and seal biomass, resulting incidental mortality and competition for the food. These changes cannot be interpreted as predictions as the model does not accommodate changes in diet composition of predators that could alter the potential for competition. The authors noted several limitations of their model, including the need to increase primary production using unrealistically high P/Q ratios for some compartments to balance the model. Other limitations of the model included the use of data for subAntarctic water just north of the Plateau that may not be representative of the Plateau itself, the use of literature values for a number of parameters, and a lack of data on production/biomass ratios and quantitative food consumption in relation to biomass for commercial fish species. The authors stressed that better estimates of the diets of birds, pinnipeds, and individual species of fish in the fishery might reveal less competition than currently assumed in the model.

NZ sea lions

Reproduction and abundance –

NZ sea lions are polygamous colonial breeders with a highly synchronized breeding season. At the Auckland Islands, mean pupping date is late December and about 70% of pups are born during a two week period (Chilvers et al. 2007b). Lactation lasts approximately 10-12 months (Gales 1995, Schultz and Bowen 2004) during which females alternate between foraging at sea and attending a single pup (Chilvers et al. 2005). Daily growth rate for the first 60 days of lactation is 151 g/d (Chilvers et al. 2007b). This growth rate is lower than that reported for other sea lion species (Higgins et al. 1988, Boness et al. 1991, Cappozzo et al. 1991, Schulz & Bowen 2004). Slow pup growth rate is associated with low lipid content of milk during early lactation (Riet-Saprizo 2007), but it is unclear to what extent this is a causal relationship. Mean energy density of NZ sea lion milk during early lactation is among the lowest measured in otariids (Riet-Saprizo 2007). The composition of milk from peak lactation is unknown.

Tag resighting data suggest that sea lions, particularly females, exhibit both site fidelity and philopatry (Chilvers & Wilkinson 2008). Males attend breeding grounds from early November to mid January before they disperse to Campbell Island (adult and subadult males), and north to the Catlins and Otago Peninsula (Robertson et al. 2006). Thus fewer males are present around the Auckland Islands during the fishing season, lowering their chances for interactions with fisheries and their dependence of prey in this area. Nevertheless, sea lions are present all year round at the Auckland Islands, at Campbell Island, and other islands groups in the region such as the Snares and Stewart Island and its associated islets.

Not much is known about the historical size of this population. The population had likely recovered from having been decimated by sealers in the early 1800s and was apparently stable through the 1990s. However, there is evidence that sea lions were hunted by indigenous human populations of New Zealand and that the geographic range, and presumably the abundance, of the species had been reduced prior to European contact (Childerhouse and Gales 1998). Pre-sealing population size is unknown and therefore it is not possible to know if the population observed through the 1990s had once been larger, although clearly the geographic range of the population was and so it seems reasonable to suggest that both the abundance and geographic range of NZ sea lions is smaller today than it was historically.

Currently, about 70% of New Zealand sea lions breed at the Auckland Islands, where pup production and resighting of marked animals have been collected since the 1990s. These data have been used to generate estimates of fecundity, survival and other components of population dynamics (e.g. Gilbert and Chilvers 2008; MacKenzie 2011; Chilvers and MacKenzie 2010). Within the last 10 years, a few individuals have started to breed on mainland New Zealand and Stewart Island, which may reflect a slow recolonisation of earlier breeding grounds. New Zealand sea lions have recolonized the Otago Peninsula,

South Island some 200 years after they had been extirpated from the area (Lalas 2008). Males began frequenting the area in the mid 1980s, increased in numbers through the late 1990s and have increased at about 10%/yr more recently (Lalas 2008). Breeding began at Otago in 1994 and the number of females has continued to increase at an annual rate of 13%, although the colony is still very small (Lalas 2008).

Over the last decade there has been a 31% decline in pup production at the Auckland Islands (Chilvers 2009). Although disease has resulted in mass mortalities of pups and an unknown number of adult females (Castinel et al 2007), the reasons for the longer-term decline remain unclear. In contrast, pup production may have increased on Campbell Island, the second major breeding location for the species (Maloney et al 2009). This conclusion is tentative as earlier estimates were not systematic and thus it is not possible to say anything about trends with any confidence.

Foraging behaviour and at-sea distribution during lactation –

Indirect effects of fisheries on sea lions could be manifested through reduced body condition affecting natality and survival; each of these being mediated through foraging success. Although any age and sex group in the population could suffer reduced foraging success because of competition with fisheries, lactating females and juveniles might be more severely affected, the former because their foraging range is constrained by the needs of their dependent offspring and their energy requirements are elevated by the cost of milk production, the latter because of their inexperience at finding and capturing prey.

Considerable progress has been made in understanding the foraging behaviour of female otariids and the limits that physiology imposes on behaviour (e.g., Boness and Bowen 1996, Boyd 1999, Costa and Gales 2003, Schulz and Bowen 2005). Among otariids, the period of maternal care and energy investment in offspring varies from 3-4 months on several high latitude species to a year or more in lower latitude species (Schulz and Bowen 2004, 2005). Comparative analyses support the hypothesis that the prolonged lactation duration of most otariids may have evolved in response to relatively low and unpredictable levels of food availability (Boness and Bowen 1996, Schulz and Bowen 2005). Within species, foraging trip duration and the rate of energy transfer to offspring are influenced by distance to foraging locations from the breeding colony (Boness and Bowen 1996). It is within this broader context that one needs to evaluate the foraging ecology of lactating NZ sea lions. NZ sea lions exhibit a typical otariid lactation strategy (Schulz and Bowen 2005). Females give birth to a single offspring, and subsequently remain on land for about one week during which they suckle their pup with high-fat milk derived from maternal nutrient stores. They then alternate between foraging trips to sea with feeding their pups on land for the remainder of a prolonged lactation of about 10-12 months.

Several studies have examined the diving and spatial behaviour of lactating NZ sea lions at Enderby Island. To date, 58 females have been fitted with time-depth recorders to

study diving behaviour and about 50 females have been fitted with satellite-linked tags to study characteristics of foraging trips. These studies have shown that NZ sea lion females have the deepest and longest dives recorded for any otariid (e.g., Gales & Mattlin 1997). They dive almost continuously while at sea with no evidence of diel variation (Gales & Mattlin 1997). Although some dives are <100 m, most occur from 101 to 180 m, accounting for 50.4% of all dives and 60.7 % of total dive time. Still deeper dives to depths of 181 -474 m (14.6 % of all dives) accounted for 21.1 %. Dives tend to be so-called “flat bottomed”, suggesting benthic feeding, and sea lions spend about half of their time submerged at the bottom of the dive. A large fraction of dives exceed the estimated aerobic dive limit (ρ ADL) suggesting that many deep dives are anaerobic. The implication here is that such dives require considerably longer recovery time at the surface and may impose a limit on foraging time (Fedak and Thompson 1993).

Given the observation of deep diving, Costa et al. (1998) tested the hypothesis that NZ sea lions were physiologically better equipped for prolonged, continuous diving than other fur seals and sea lions. They found that NZ sea lions have the highest blood volume yet reported for an otariid, supporting the hypothesis that NZ sea lions have a physiological capability suited to their deep-diving behavior. To further understanding diving behaviour, Costa and Gales (2000) simultaneously measured diving and metabolic rate in adult females. They found that at-sea field metabolic rate (FMR) was 5.8 times the predicted standard metabolic rate of a terrestrial animal of equal size. This is similar to the 4.8–7 times BMR previously reported for Australian sea lions *Neophoca cinerea*, California sea lions (*Zalophus californianus*), Northern fur seals (*Callorhinus ursinus*) and Antarctic fur seals (*Arctocephalus gazella*) (Costa 1993). However, individual females appeared to adjust their FMR based on depth of diving as indicated by an inverse relationship between dive depth and FMR (one female was excluded as an outlier). Even so, compared to other otariid species, estimates of at-sea metabolic rates of these females suggested that were operating near their physiological maximum (Costa and Gales 2000). Chilvers et al. (2006) also studied the diving behaviour of lactating females to determine if a large percentage of their dives exceeded the estimated ρ ADL, given that environmental variation, continued fishery effects, and demographic effects may have changed how females were exploiting their environment. They fitted 18 adult females with both an Argos satellite tag and a TDR. Results of that study were similar to that found previously. Although 68% of dives exceeded the ρ ADL, they exceeded this limit by only 20% on average. Chilvers et al. (2006) echoed earlier conclusions that their research showed that lactating female NZ sea lions are “close to their maximum physiological capacity for their foraging behaviour during early lactation.” But there is no simple way to know what limits female performance in the wild. Consistent deep diving may simply reflect what it takes to make a living in this environment. The lack of relationship between surface time and these putative anaerobic dives would seem to indicate that ρ ADL has been consistently underestimated. Furthermore, all of these studies of diving behaviour were conducted during early lactation when the demands of offspring are less than they would be later in lactation. Therefore, it is unlikely that females are operating at or near a physiological limit. Although the short duration of

these studies is understandable, it does mean that much of the foraging performance of lactating females is unknown.

High at-sea metabolic rate and deep diving led to the conclusion that sea lions must use anaerobic metabolism for a proportion of their dives (e.g., Chilvers et al. 2006). However, contrary to that conclusion, Costa and Gales (2000) found no relationship between the ratio of observed dive duration to ρ ADL and mean dive depth. This result does not support the hypothesis that deep diving is achieved by incorporating anaerobic metabolism. Crocker et al. (2001) confirmed this in a study of swim speeds of adult females during diving which found that patterns of swimming speed and acceleration suggested that females glided during descent such that extended duration of deeper dives did not impact on surface times indicating the use of aerobic metabolism during diving.

Understanding the spatial distribution of foraging is relevant not only to an evaluation of the indirect effects of fishing, but to determining how variability in food availability might impact the population. Most pups in the Auckland Island are born at two sites – Enderby Land (~19%) and Dundas Island (~64%). Thus understanding the foraging distribution of lactating females at these sites is critical to test hypotheses about indirect effects of fisheries. During the period 2001 and 2007, 55 satellite tags have been fitted to females from these two islands (Chilvers et al. 2005, Chilvers and Wilkinson 2009, Chilvers et al. 2011). At Enderby Island, at-sea locations were determined for an average of about 1 month, ranging from 5 days to 36 days, whereas at Dundas Island, only one to two foraging trips could be studied for each female given the difficulty of landing and living on the Island. Characteristics of these early lactation foraging trips are given in Table 1. The only significant difference between the two islands was total trip distance. There was substantial overlap between the Enderby and Dundas Island female foraging areas in the north-east of the Auckland Island shelf. There were also two distinct foraging areas where the females from each breeding island did not overlap (Chilvers et al. 2011): the area north-west of Enderby Island, where only Enderby Island females occur, and the area south and south-east of Dundas Island, where only Dundas Island females are found (Fig 3). In addition to this general pattern of foraging, interannual differences on the location of foraging areas and older females making longer trips were also suggested by the data (Chilvers et al. 2005, Chilvers and Wilkinson 2009). Although there is evidence of interannual variability in foraging distribution, another study suggests that some individual females do exhibit fidelity to foraging areas between years (Chilvers 2008b).

Current studies have revealed much about the behaviour of NZ lactating females. However, it is important to remember that these studies only cover the first month of a prolonged lactation period during which the energetic demands of growing offspring steadily increase. There are no studies of NZ sea lions during the latter portion of lactation, but a study on NZ fur seals (*Arctocephalus forsteri*) at the Otago Peninsula has investigated the response of lactating females to seasonal and interannual changes in

food availability (Harcourt et al. 2002). Comparison with NZ fur seals should be useful because, in both species, adult females are central place foragers that support most of lactation from feeding rather than previously stored lipids. In addition, as many of the same prey are eaten by sea lions and fur seals, changes in the seasonal and interannual behaviour of fur seals females may provide insight into the expected responses of sea lions. The fur seal study simultaneously measured the spatial distribution of foraging, diving, and associated diet over several years. Harcourt et al. (2002) found that foraging trip duration of NZ fur seal females differed among seasons becoming 2-3 times longer through autumn and winter. There were also significant differences among seasons and years in the relative proportion of three types of bouts, thought to reflect differences in foraging behaviour. Travel distance to foraging patches also increased through the year. During the study, the estimated diet of the females differed significantly among seasons, shifting from mixed fish and cephalopods in autumn to a fish dominated diet in winter. Arrow squid was an important percentage of the diet in summer and autumn, but not in winter. As in the case of NZ sea lions, arrow squid was over-represented in regurgitates, relative to scats. Comparison of the diet of fur seals with estimates of prey abundances from trawl surveys showed little correspondence and thus provided little insight into the foraging tactics used during lactation. Harcourt et al. (2002) concluded that seasonal changes in foraging behaviour of lactating NZ fur seals may indicate changes in prey selection as targeted species become more or less available within the foraging range from the breeding colony. This ability of generalist predators to switch among selected prey species to meet the energetic requirements of maintenance and reproduction may mask large scale changes in the environment. Given the known variability in squid abundance and the variability in ocean processes in the sub Antarctic waters in the vicinity of the Auckland Islands, we should expect NZ sea lion to have a flexible foraging strategy involving prey switching. By analogy, we might also expect changes in the characteristics and distribution of adult female foraging trips later in lactation. This suggests that existing studies, which are limited to early lactation, may not be representative of the behaviour of females over the entire lactation period.

Diet -

The extent to which NZ sea lions may compete for food with the arrow squid and other fisheries depends, among other things, on both on the spatial distribution of the foraging with respect to those fisheries and on the diet of sea lions. The species composition of the diet of sea lions has been estimated mainly using the analysis of prey hard parts from scats and regurgitates (spewings) (Table 2). More recently, fatty acid profiles and quantitative fatty acid signature analysis have been used to make inferences about the diet (Meynier et al. 2008, 2010). Given the importance of diet in evaluating the squid and other fishery-competition hypotheses, below is a critique of our current understanding of diet and the limitations of present data.

Before discussing what existing studies have revealed about the diet, it is useful to briefly consider the methods used to estimate the diets of pinnipeds and their strengths and weaknesses. Diet estimation in free-ranging marine mammals relies mostly on

indirect methods (Tollit et al. 2010). The most common, and still widely used, methods are the recovery of hard parts from stomach contents, intestines, and faeces. Less commonly, prey hard parts recovered from spewings (regurgitates) are also used (e.g., Gales and Pemberton 1994, Longenecker 2010). Several chemical methods also have been developed, including analysis of stable isotopes of carbon and nitrogen (Hobson et al. 1997), quantitative fatty acid signature analysis (QFASA, Iverson et al. 2004), and the analysis of prey DNA recovered from stomachs and faeces (Deagle and Tollit 2007).

All of the indirect methods currently in use are subject to bias arising from both features of the methods and our ability to sample the diet representatively from wild populations (Tollit et al. 2010). Experimental evidence shows that digestion strongly influences both the number and size of otoliths that can be recovered in stomachs, intestines and faeces. Experiments on fur seals and sea lions indicated that there are strong predator-species effects on the magnitude of biases caused by otolith digestion. Recovery rates from several species of otariids were considerably lower than that found in harbour seals, *Phoca vitulina* (e.g., Gales and Cheal 1992, Casper 2006). Digestion also reduces the number of cephalopod beaks that are recovered in scats, but the effects are less than with otoliths. Without accounting for bias, large errors in the estimated diet are expected. Number correction factors (NCF) and digestion coefficients have been developed to reduce the biases caused by the effects of digestion on otoliths and squid beaks recovered from faeces. Although necessary, such correction factors have not been developed for prey material recovered from stomachs. QFASA requires information of the fatty composition of prey species, the fatty acid composition of the predator fat stores (e.g., blubber in the case of marine mammals), a subset of fatty acids that come mainly from dietary sources only, calibration coefficients (CC) to account for predator metabolism of fatty acids prior to their deposition in blubber, and a statistical model to minimize the distance between the predator and a mixture of prey species representing the diet. Estimates of the species composition of the diet are sensitive to how well prey fatty acids signatures are known, the calibration coefficients used, and to a lesser extent, the fatty acid subset used in the statistical model.

In addition to the methods used, there are differences in the way diet estimates are expressed (reviewed in Tollit et al. 2010). Energy intake is of primary interest in most studies of pinniped diets. However, estimating the energy contribution of each prey species to the diet is often extremely difficult and in many cases is not possible. Some ways of expressing the results of diet studies are more useful than others. Percent frequency of occurrence (percentage of samples containing a given prey taxon) is the simplest and least informative method. Occurrence indices may overestimate the importance of small or trace prey. Numerical counts of prey (percentage of the number of individuals for each prey taxon as a percentage of the total number of individuals found in all samples) are susceptible to overestimating the importance of small prey, mainly due to differences in the number of prey consumed per meal. Estimates of biomass consumed (percentage of prey species by wet mass) may overestimate the

importance of large prey. This last method requires the development of prey regressions to convert otolith and squid beak size into an estimate of the mass of prey ingested.

Most of what we know about the diet of NZ sea lions comes from the Auckland Islands and the Otago Peninsula. Childerhouse et al. (2001) conducted the first study of the diet of NZ sea lions using prey hard parts recovered from scat and regurgitates (Table 2). They analyzed mainly summer samples over the three-year period in the mid 1990s and found significant differences in the prey species composition of scat and regurgitate samples, with scats having a higher frequency of occurrence and number of fish remains and regurgitates having a higher occurrence of cephalopod remains. Studies on captive pinnipeds show that cephalopod beaks may accumulate in the stomach over several meals before being regurgitated whereas otoliths tend to be digested and/or passed relatively quickly (Harvey 1989; Tollit et al. 1997). Thus, it is difficult to compare the relative importance of prey items from regurgitates as a single sample may represent a significantly higher number of meals than a single scat sample. Due to these and other potential biases in using scats and regurgitates to determine diet, as the authors of the study noted, their diet estimates represented a qualitative account of the main species eaten rather than a reliable quantitative estimate of the prey species providing for the energy requirements of the population. This study indicated that arrow squid was an uncommon prey with opalfish, octopus, lobster krill and hoki accounting for most of the diet, expressed as frequency of occurrence (Table 2).

Meynier et al. (2009) examined the stomach contents of 121 NZ sea lions incidentally drowned by the squid fishery during the summer/autumn 1997–2006 around the Auckland Islands. Given the origin of these samples, it is certainly possible, even likely, that the proportion of squid in the diet was positively biased. Video observations from the SQU 6T fishery have shown that sea lions are observed around trawls, and feeding on meshed squid or fish, relatively frequently (e.g. in 7 of 39 trawls from which video footage was obtained in 2008; Middleton & Banks 2008). Another potential source of bias results from the way hard parts that could not be identified by species were assigned. Hard parts were attributed to the most abundant species in the waters where the sample was taken rather than prorating the hard part based on the species estimated to have been consumed. The former approach makes a strong assumption about the feeding tactics used by sea lions whereas that later is simply an accounting based on empirical data. Although the authors attempted to minimize bias by only using digested squid in their calculations, the rapid digestion of squid makes it unlikely that this approach would remove the bias toward squid from having sampled from the squid fishery. The main species in the estimated diet, expressed as percent mass, are listed in Table 2. Octopus was the main prey, followed by squid, opalfish and red cod. There was some evidence the males and females differed in the consumption of opal fish, but for the most part, no differences in the species composition of the diet were found in the samples. The lack of significant variation in the diet may reflect the source, small number of samples, and the averaging of any year effects for the 10 years of sample collection.

Meynier et al. (2010) used QFASA on 82 blubber samples to estimate the diet of NZ sea lions incidentally caught in the NZ arrow squid fishery from 2000 to 2006. Over all years, the most important prey species were southern arrow squid, hoki, rattails, and possibly scampi (Table 2). Most of the identified prey were demersal species living mainly at depths >200 m on the slopes of the Auckland Islands shelf. Although the number of samples available for analysis is rather small to fully capture interannual and other sources of variability in the diet, unlike scats or stomach contents, they may be less biased by their origin as bycatch from a commercial fishery. This is because fatty acids represent an integration of diet over longer periods of feeding (Iverson et al. 2004). Nevertheless, sea lions that have been foraging in association with the squid fishery for several weeks will have begun to express that diet in their blubber, with the result that the proportion of squid could be artificially elevated. QFASA estimates of diet are sensitive to the calibration coefficients used to account for predator metabolism. They are also influenced by which fatty acids are used in the estimation model, how distinct prey species are in their fatty acid signatures and well the samples characterize the species. Meynier et al. (2010) conducted extensive simulations to select the best combination of input data from which to estimate the diet. Nevertheless, NZ sea lion specific calibration coefficients are not known and most reference prey were represented by 10 or fewer individuals raising concern that the fatty acid signatures of prey may not be as well sampled, as acknowledged by the authors.

The Auckland Island estimates of diet are based mostly on samples collected in summer. Therefore, the recent unpublished study by Lalas and McConnell of winter collected samples is an important addition (Table 2). They found that the main prey species, expressed on a wet mass basis, were octopus, fur seals, rough skate, and red cod. Arrow squid accounted for only a minor part of the diet. Again, the importance of these prey depended heavily on the source of the material, i.e., scats vs. regurgitates.

Lalas (1997) described the diet of NZ sea lions that haul out on the Otago Peninsula from scats and regurgitates collected fortnightly over the period of one year. This area is regularly used by males throughout the year and is a relatively new small breeding colony. Although collections were made regularly throughout the year, the largest samples were collected from February to May. Prey sizes were reconstructed by “interpolation from diagnostic remains”. The author states that this “compensated for erosion or breakage of remains (especially otoliths)” but it is not clear what was actually done. Expressed as reconstructed mass of prey eaten, the diet comprised mostly fish, and cephalopods, with over 70% of estimated diet biomass represented by only 5 taxa (Table 2). Although expressing the diet by mass is a more informative measure than frequency of occurrence, sources of bias remain unaccounted for and therefore, as the author stated, these data should be regarded only as an indication of the relative importance of different prey species in the diet.

Based on the studies to date (Table 2), the most frequently eaten species by adult females during summer are presumably known, however, their contribution to the energy requirements of females remains poorly understood. Limited data are available for adult males and juveniles (sea lion older than 1 yr). Spatial and temporal components of variation in diet are also poorly understood. The recent winter sample suggests that seasonal variation in diet may be large. Although some attempt has been made to minimize biases resulting from the source of samples and the methods of analysis, other important sources of bias remain, such as the effects of digestion of hard parts, which could be large. Also, despite the statement by Childerhouse et al. (2001) that “Lake (1997) showed, from feeding trials with New Zealand fur seals (*Arctocephalus forsteri*), that despite these biases scats and regurgitates can provide a reliable estimate of diet.”, the Lake study showed only that the length of several fish species could be reliably estimated. No attempt was made to estimate the diet from the recovered material and it is clear from the data presented in the paper that without applying NCFs to account for complete digestion of otoliths, any estimates of diet would have contained serious bias. I conclude that our understanding of the contribution of arrow squid and other prey to the energy requirements of sea lions is highly uncertain and certainly is not sufficient to indicate that competition with the fishery for arrow squid or other prey may be negatively affecting the population.

Evaluating the evidence for indirect fishery effects

Identifying causes, and their relative importance, for declining of pinniped populations has proven difficult (e.g., the western stock of Steller sea lions, *Eumatopis jubatus*, NMFS 2008; harbour seals, *Phoca vitulina*, Bowen et al. 2003; southern elephant seals, *Mirounga leonina*, McMahon et al. 2005;) except where the cause produced a rapid and large decline, as was the case with the phocine distemper epizootics (e.g., harbour seals, Harwood and Hall 1990). There are several reasons for this. First, individuals within wild populations are subject to multiple sources of mortality acting at different spatial and temporal scales. This vastly compounds the difficulty of identifying sources and their relative importance. In attributing causation to a particular factor, it is important to understand the extent to which it alone can account for the observed changes. Factors other than direct and indirect fishery-effects that might negatively affect NZ sea lions include disease, predation (e.g., great white sharks (*Carcharodon carcharias*), dispersal, lack of genetic variation, natural variation in food supply, human disturbance, and pollution. These have been reviewed most recently by Robertson and Chilvers (2011) and although some may contribute to the decline, none of these are thought to be the single underlying cause. A similar list of potential factors, with a focus on indirect fishery effects, have been investigated as underlying the dramatic declines in the western stock of Steller sea lions in Alaska (reviewed in NMFS 2008). Ship, offshore oil and gas construction, and seismic survey noise could be a source of disturbance that might influence foraging distribution and behaviour of marine mammals, but there is little evidence of effects on pinnipeds (Richardson et al. 1995). Furthermore, in their

review of threats, Robertson and Chilvers (2011) did not identify noise as a threat to NZ sea lions.

The second reason it has been difficult to determine the cause for pinniped declines is that it is usually not possible to make measurements at the appropriate scales or in many cases to know what the appropriate scales are. A third reason is that time series of what are thought to be informative response variables are often not available for testing alternative explanations for declines and many of these variables are uninformative by themselves or as a group (i.e., they are predicted to respond in similar ways under different hypotheses, Table 3, modified from Bowen et al. 2001). For example, all response variables in Table 3 are predicted to change in the same fashion under the indirect-effects hypothesis, the competition with native-predators hypothesis, and the ocean climate-variation hypothesis.

A number of studies have investigated the nature of the interactions between the arrow squid fishery and NZ sea lions (e.g., references in Chilvers 2008a). Evidence that there are indirect negative effects of the squid fishery on the sea lion population has been difficult to find, but could take a number of forms (see Chilvers 2008a, Robertson and Chilvers 2011). It has been suggested that the following provide evidence or at least raise concern about the potential for negative effects: the spatial and temporal overlap of lactating females from Enderby Island and the fishery (Chilvers et al. 2005, 2006), that arrow squid is eaten by NZ sea lion females (Meynier et al. 2010), declining pup production in the Auckland Islands, low pup growth rates in 2001 and low energy density of milk (Chilvers et al. 2007), low reproductive rates (Chilvers et al. 2010), lower survival rates of adult females compared to adult males (Chilvers and MacKenzie 2010), foraging effort of lactating adults near physiological limits (Costa and Gales 2000), and remnant colonies in marginal habitats (Auge et al. 2011). The implication of the last points is that reduced female foraging success could reduce fecundity and impair lactation performance. Given that females are thought to be performing near physiological limits, it is hypothesized that fishery effects on food availability serve to push females “over the edge”, resulting in reduced lactation performance or reduced fecundity (e.g., Chilvers 2008a).

Spatial and temporal overlap with fisheries –

Based on the distribution of satellite locations from animals fitted with Argos tags, there is broad overlap in the foraging areas used by female sea lions during early lactation and fishing effort (Chilvers et al. 2005, 2006, 2009, 2011). Overlap between females from Enderby and Dundas Islands and the arrow squid fishery during the period 2001-2007 is summarized in Chilvers et al. (2011). Enderby Island females that forage directly north and west of Enderby Island, 9 of 26 or 35%, have significant overlap with the north-west fishery operations (Fig 4.). However, there is no apparent overlap between Enderby Island females and the south-east part of the fishery. By contrast, about 31% of Dundas Island females forage east to south-east of the island and do overlap with the south-east

fishery area, but females from Dundas appear to overlap little with the north-west fishery.

Although there is evidence of overlap in space and time between lactating females from both islands and the squid fishery, it is important to note that existing data are limited to early lactation only. Given the squid fishery operates for 3.5-4.5 months, additional data are needed to determine if or how the degree of overlap may change during later lactation. Overlap with other fisheries appears to be even less based on a visual inspection of the distributions of fishing and sea lion females from Enderby Island and Dundas Islands. Not specifically considered here are any potential effects of bottom modification due to trawling impacting prey habitats in the area of the fishing grounds themselves.

Juveniles represent a large fraction of the food intake of the population and are likely to be sensitive to variation in food availability, thus knowing where they feed could provide further insight onto the extent to which the squid fishery might be impacting the sea lion population. Chilvers (2010) studied the at-sea distribution of 26 juveniles (15 females, ages 2-3 years; 11 males, ages 2-5 years) tagged at Sandy Bay, Enderby Island during January and February 2008, 2009 and 2010. Juveniles foraged close to the Auckland Islands on the Auckland Island shelf, predominantly in the north and north-east areas of the shelf. As in the case of adult females, there was significant overlap between some juvenile foraging locations and the 6T squid fishery. By contrast, there was little overlap of juveniles foraging locations with scampi or other fisheries activities around the Auckland Island area. However, juveniles from other breeding sites at the Auckland Islands and Dundas Island have not been studied and the foraging distribution of juveniles during the remainder of the year is unknown.

I conclude that these spatial overlap data indicate an opportunity for the squid fishery to indirectly affect sea lions, but alone they do not provide evidence that indirect effects have occurred or continue to take place.

Squid is eaten by sea lions –

The studies in Table 2 clearly indicate that arrow squid are eaten by lactating females during the summer. However, the contribution of squid to the energy requirements of lactating females is highly uncertain. Squid is estimated to have been an important prey only in the fatty acid and stomach content analyses, both based on sea lions incidentally drowned in the arrow squid fishery (Meynier et al. 2008, 2010). Although attempts were made to reduce the positive bias toward squid, there is no way of knowing if those attempts were successful. Other sources of significant bias, arising from complete or partial digestion of hard parts, have not been addressed. There is also little information on seasonal or interannual variation in the contribution of squid to the diet. To the extent that sea lions consume squid, there is potential for competition with the fishery, but existing data fall short of providing any evidence that competition with this fishery has had a negative impact on the seal lion population.

Also, there is little information about the diets of juveniles. Because of their small size and more limited foraging experience, juveniles are expected to be sensitive to changes in food availability. The lack of data from juveniles represents a significant gap. Therefore, effort should be directed towards ascertaining the diet of this population component.

Low and declining pup production –

The decline in pup production at the Auckland Islands is no doubt real, as there seems to be a consistent series of estimates on which this conclusion is based. Unfortunately, this declining trend is not helpful in distinguishing among possible causes. NZ sea lions have been directly affected by three epidemics over the past 13 yr caused by bacterial infections. These disease events resulted in the deaths of 53, 32, and 21% of annual pup production at the Auckland Islands for the 1998, 2002, and 2003 seasons, respectively, and at least 75 adult females during the 1998 epidemic (Anon. 1999, Wilkinson et al. 2003, 2006). Because some adult females would have been at sea foraging, and many of the adult males would have left the islands by January, the total mortality of adults is not known. Exhaustive investigations into the cause of these mortalities lead to hypotheses that the deaths might have been caused by a previously unknown bacterium, or that some event predisposed the sea lions to a suite of bacterial infections (Anon. 1999). According to L. Meynier (unpublished, not seen) there appears to be no link between the timing of these disease events and environmental factors (cited in Robertson and Chilvers 2011). Robertson and Chilvers (2011) concluded that as both Campbell Island and the Auckland Island colonies were affected by the disease events, and Campbell Island continues to increase, the cause of the decline at the Auckland Islands lies elsewhere. Although the evidence for increasing pup production at Campbell seems problematic (see above, Reproduction and Abundance), there is no evidence for declining production at Campbell Island and so the conclusion about contrasting trends seems secure. No evidence has been brought forward to link these epidemics with indirect fishery effects on pups and their susceptibility to disease.

In the absence of other explanations, it is inferred that food limitation acting on adult females must be the principle indirect cause for the decline in pup production (see Robertson and Chilvers 2011). However, the diet of females from the largest pupping colonies have not been studied and studies of the diet and foraging distribution of females elsewhere (mainly Enderby Island) cover only about the first month of a 10-12 month lactation period, and therefore may not be representative of the later stages of lactation. There also is large uncertainty about the biomass of prey that might be available to sea lions, given the difficulty in estimating the abundance of many of their prey species. Population energetics modelling could provide insight, but any such modelling will be hampered by the lack of input data on diets and prey abundance. Thus, it is not possible to draw conclusions about the role of food limitation on declining pup production at this time.

Low pup growth and milk energy density –

Low pup growth rate and low milk energy density have been advanced as evidence of reduced foraging success in lactating females (Chilvers et al. 2007b). In Antarctic fur seals, interannual variation in milk energy density reflected interannual variability in food availability (Arnould and Boyd 1995). It is not known if a similar relationship might hold in the case of NZ fur seals. More generally, pup growth rates in pinnipeds are positively related to daily milk energy intake. However, milk energy intake has not been measured in NZ sea lions. Furthermore, existing data on the composition of NZ sea lion milk were collected over roughly the first two months of lactation, such that differences among years in average stage of lactation of the female sampled might account for some of the interannual variability. The ages of pups of females sampled each year were not provided in Riet-Sapriza (2007), but females sampled for milk appear to have ranged in age from 5 to 64 d postpartum. Although the low pup growth rates observed in 2001 correspond to the year when the lowest energy density of milk was measured, available data are only sufficient to formulate a hypothesis, not to rigorously test it, as milk energy density is only one factor affecting energy delivery to and growth rate of offspring.

Growth and reproduction –

Childerhouse et al. (2010) estimated growth and reproductive rates of females from two colonies in the Auckland Islands. Although there was some evidence of differences in body mass at age between the two colonies, there was no evidence of interannual variability over the four years of the study. The study found that age-specific growth rates of females were lower than that estimated in Steller sea lions. This may be a species-specific difference, but Chilvers et al. (2010) suggested that it might reflect the results of occupying marginal habitat. This notion that the habitat is marginal for the species is pervasive throughout the literature – but there seems little direct evidence to support this conclusion (see below). There is evidence that sea lions currently inhabit an area of comparatively low productivity (see Murphy et al. 2001), but this has most likely been the case for sometime, perhaps over much of their evolutionary history, and there seems no a priori reason to think that they are not somewhat adapted to this environment, as suggested by their comparatively deep diving behaviour and associated physiology. Childerhouse et al. (2010) also make the inference that lighter animals at Sandy Bay are in poorer condition. Leaner animals are not necessarily in poorer condition (i.e., less healthy), we can only conclude that they are lighter. As the difference was small, this could result from any number of effects on body mass at age. That the observed differences might result in differential juvenile mortality between the two sites, as suggested by Childerhouse et al. (2010), seems unwarranted given the small magnitude of the estimated differences.

Robertson and Chilvers (2011) and Chilvers et al. (2010) stated that NZ sea lions have “low reproductive ability” compared to other sea lion species, inferring that this could be the result of indirect effects of fisheries on food availability to females. But this contradicts the study by Childerhouse et al. (2010) which concluded that in NZ sea lions

“reproductive rate for this species is consistent with rates reported for other sea lions”. In fact that the age-specific patterns of birth rate reported in Childerhouse et al. (2010) and Chilvers et al. (2010) for NZ sea lion are quite similar to comparable data from California sea lions (Hernandez-Camacho et al. 2008) and the mean estimate for NZ sea lions is similar to that estimates in Steller sea lions (Pitcher et al. 1998). Therefore, the conclusion about unusually low reproductive rates does not appear to be strongly supported by the evidence.

Adult female survival lower than adult males –

Differences in the magnitude and trend in survival rates of components of the population could provide indirect evidence for fishery effects. Chilvers and MacKenzie (2010) estimated that the survival rate of adult males, ages 4–15 years, was 0.98 and for similarly aged female was lower at 0.94. An unusual feature of these estimates is that adult male survival is usually lower than female survival in other size-dimorphic pinnipeds. Taken at face value, this might indicate that adult females were experiencing unusual mortality. However, as the authors noted, their estimate for adult males is unusually high, while that for females is similar to that found in other species of sea lions. Furthermore, Chilvers and MacKenize (2010) also point out that direct and any indirect impacts from the local squid trawl fishery on the Auckland Islands NZ sea lion population affect adult females and juveniles, but do not affect adult males (Chilvers 2008). Adult females also appear to have been more heavily impacted by the bacterial epizootics that occurred in 1998 and 2002 (Wilkinson et al. 2006). Together these factors may account for the observed sex-specific differences in estimated survival rates. This does not rule out the possibility that there are indirect effects of the squid fishery on the survival rates of adult females, but it does not provide evidence of those effects.

Foraging energetics and lactation –

A central issue with respect to the possible impacts of the squid, or any other, fishery on NZ sea lions is the observation that a large fraction of lactating female dives exceed the calculated aerobic dive limit (cADL) suggesting that NZ sea lions may be operating at their physiological limits (Gales & Mattlin 1997, Costa et al. 1998, Costa & Gales 2000). The implication from this is that anything that makes it more difficult to find or capture food could push individuals into a negative energy balance. On the surface this is a reasonable hypothesis. The problem with this hypothesis is twofold. First, the lack of relationship between surface time and these putative anaerobic dives would seem to indicate that cADL has been consistently underestimated. The energy efficient swim-and-glide behaviour apparently used during diving (Crocker et al. 2001) presumably is one mechanism that could lead to an overestimate of O_2 expenditure and an underestimate of ADL. If this turns out to be true then females may not be operating as close to the limit as has been assumed. This hypothesis is further supported by the fact that, on average, females gained weight during the deployment of instruments (Crocker et al. 2001) or maintained their body mass (Chilvers et al. 2006). Thus, another interpretation of the data is that the observed diving behaviour reflects a successful physiological adaptation for exploiting deep benthic prey. The second problem is that studies done to

date have been limited to essentially the first month of a prolonged lactation. The energetic demands of offspring increase steadily throughout lactation implying that few females would be able to successfully wean offspring if they were operating at or near some physiological limit so early on.

Remnant colonies are in marginal habitat –

Recently, Auge (2010) and Auge et al. (2011) have argued that the Auckland Islands colonies represent remnant colonies at the southern extreme of the species historical distribution and therefore are presumably occupying marginal habitat (low food availability) requiring females to work harder satisfy their energy requirements. In such a habitat, indirect effects of fishing could be detrimental to the foraging success of sea lions. To test this hypothesis, in 2008 they studied the at-sea movements of 8 females (all the adult females) from the Otago colony, a recolonizing site considered to be part of the core of the species historical distribution and thus in good habitat. Comparison of the Otago and Auckland Islands' colonies revealed that Otago females had shorter foraging trips, closer to the colony, smaller core foraging areas, and spent less time at sea than Auckland Island females. Auge et al. (2011) interpret their results as confirming that females in the Auckland Islands occupy marginal habitat. Although the behavioural differences between these colonies seem clear enough, the conclusion about habitat quality would be strengthened by data on the extent of interannual variation in foraging behaviour (which can be large in other otariid species (Boyd 1999) and the consequences of these behavioural differences on reproductive success. Although adult females at the Otago colony were studied in two years, 4 in 2008 and 4 in 2009 (Auge 2011), the number of females in this colony is too small to draw inferences about interannual variability in foraging behaviour. Estimates of prey abundance will also be needed to confirm the conclusion that habitat quality and not some other feature, such as the spatial distribution of prey underlie the observed differences.

Conclusions and Recommendations

Over the past 10-15 years, there has been a large effort to better understand the diving physiology, population biology, and foraging ecology (diet and distribution) of NZ sea lions. Along with this ecological research, there have been efforts to better estimate the level of bycatch, particularly in the arrow squid fishery, and to reduce incidental mortality through various management actions. Without this ecological research, firm conclusions about the magnitude of the decline in pup production at the Auckland Islands would not be possible. However, despite what has been learned about NZ sea lions, our understanding of changes in life history traits, foraging behaviour, and diet of this small population is insufficient to provide convincing evidence for the causes underlying the observed decline in pup production. Part of the reason for this, is that little is known about juveniles and what is known about lactating females is confined largely to the first month of a ~10 month lactation period. There are good reasons for these gaps, both financial and logistic, but the reality is that there is much more we

need to know. Apart from the time series of pup production estimates at the Auckland Islands, there are few time series with which to test competing hypotheses about causes of the decline.

At present, there is little evidence that negative indirect effects of fisheries are contributing to the observed decline in Auckland Island pup production. Both arrow squid and scampi are seasonally fished in the waters near the Auckland Islands and both are prey species are eaten by sea lions, but scampi does not appear to be an important food. Although these observations underscore the opportunity for ecological interactions, as noted most recently in Robertson and Chilvers (2011), we know little about the contribution of either of these or other prey species to the energy requirement of sea lions and therefore there is little that can be concluded. We also have a rather poor understanding of the quantity of food available to sea lions and so testing hypotheses involving the effects of food competition is problematic.

What might be done in the short- to medium-term to better understand the factors influencing the demography of NZ sea lions? In lieu of conducting replicated field experiments, which would be both difficult to design and to carry out, studying contrasting time series might provide insight into underlying causes. Therefore, the apparent contrast in the abundance trends at Campbell Island and the Auckland Islands, and other sites such as Otago Peninsula (assuming continued growth of this new colony), should be more fully exploited. Given the distance between Campbell Island and the Auckland Islands, differences in fishing effort and prey characteristics, such size composition, numbers, biomass and spatial distribution, could be used to test hypotheses about causes underlying the different population trajectories. This would require studies of the foraging behaviour and diet of females, pup growth rate, and pup production at both sites during the same years and to extend studies of lactating females to include a large fraction of the lactation period. Such studies would serve also to test if current conclusions about foraging distribution and diet based on studies in early lactation are representative of the whole lactation period.

The comparative lack of information on the foraging ecology (distribution and diet) of juveniles seems an important gap as juveniles ought to be sensitive also to changes in food availability. Linking foraging ecology to body condition and survival probability of juveniles at contrasting sites could also lead to insights about the causes of differing population trends. Further mark-resighting studies of individuals with long-term marks will be needed at both sites to link foraging performance and diet to demography.

Estimating the diet of any marine mammal is difficult. The challenges of estimating the diets of NZ sea lions are no less daunting, and although much has been learned by the studies conducted to date, we still do not have good estimates of the contribution of different prey species to the energy requirements of sea lions. Current estimates suffer from known biases, some of which could be large. Thus, experimental feeding studies of the type conducted with Steller sea lions (Tollit et al. 2007) will be needed to estimate

correction factors to account for the effects of digestion on prey hard parts used to reconstruct the diet. Although digestion correction factors are available for many prey species (e.g., Bowen 2000, Grellier and Hammond 2006, Tollit et al. 2007), additional experiments will be needed using prey species thought to be important in the diet of NZ sea lions. Experimental feeding studies, to estimate NZ sea lion-specific calibration coefficients, will also be needed to provide more confidence in estimates of diet composition from the use of fatty acids and DNA. The design of future diet studies, regardless of the methods used, should weight sampling by the spatial distribution of the population and for seasonal and demographic effects on the diet.

Finally, it is important to underscore how difficult it has been for ecologists to determine the causes of population declines of other pinnipeds. Nowhere is this better illustrated than the decades of ambitious, large-scale research on the causes of population declines of Steller sea lions in Alaska (reviewed recently in revised recovery plan, NMFS 2008). Although much has been learned about Steller sea lions, there is still great uncertainty about what caused the decline or why numbers are now increasing in some areas, while others continue to decline (NMFS 2008). The difficulties of determining the potential indirect effects of fisheries on NZ sea lion food are no less daunting. In both species, it has proven extremely difficult to find strong evidence for food limitation on the one hand, and the causes (including fisheries) of food limitation on the other. As large-scale, manipulative experiments in the open ocean have proven difficult or impossible to undertake, one of the most promising approaches has been the use of stochastic statistical models and formal model selection to simultaneously test multiple hypotheses about the causes underlying population trends (Wolf et al. 2006). However, this approach requires time series of response variables linked to the competing hypotheses and predictor variables. For example, to test competing hypotheses, one would require time series of relevant prey species abundance from fisheries surveys, fishing effort, bycatch of sea lions in fisheries, and sea lion pup production at all major colonies. Other series might include pup growth rates (a good indication of maternal foraging success), reproductive rates, juvenile survival rates (more sensitive to environmental variability than adults), and diet composition. The variables included in the analysis will depend both on the nature of the hypotheses to be tested and what can be measured. In the longer term, this approach, or something comparable, serves to help determine what research should be of the highest priority and provides a framework for evaluating hypotheses about the causes of population trends using those new data.

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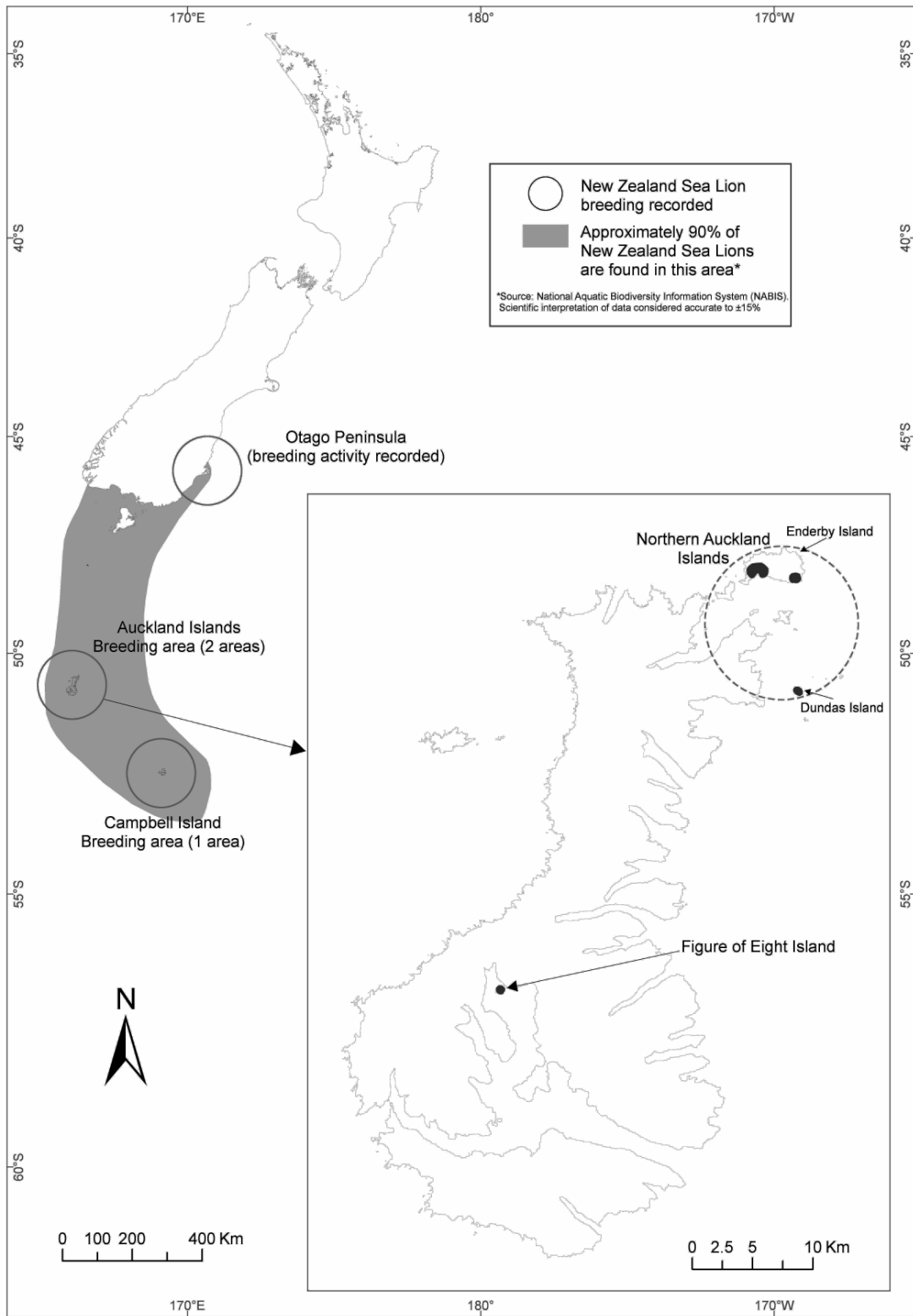


Fig. 1. Map showing place names in the text and the range of New Zealand sea lions.

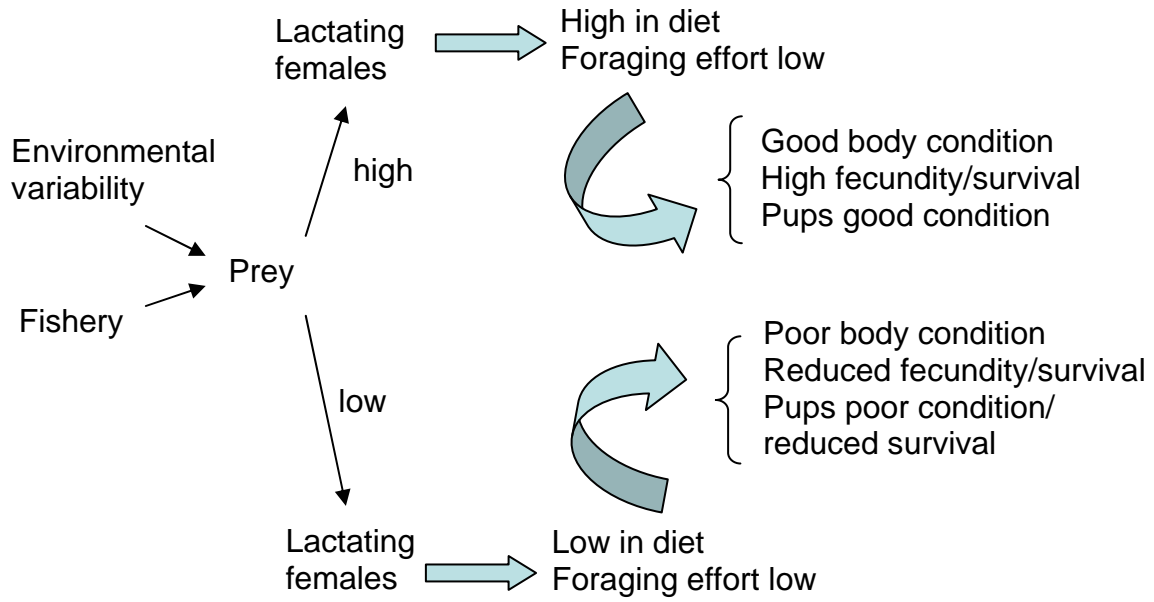


Fig. 2. Conceptual model of the indirect fishing-effects hypothesis.

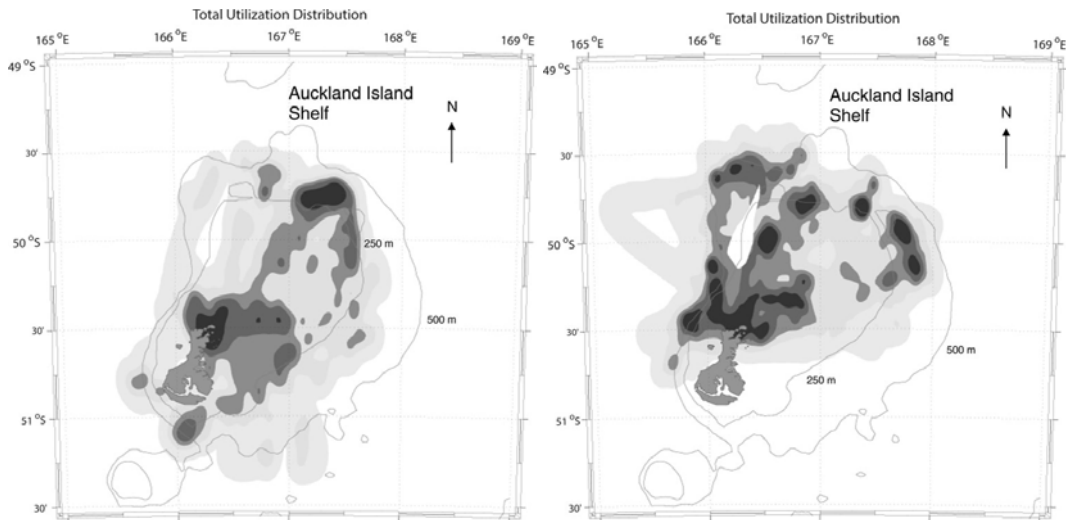


Fig. 3. Distribution of satellite locations for 29 and 26 sea lion females tagged at Dundas (left) and Enderby (right) Islands, respectively. (from Chilvers et al. 2011).

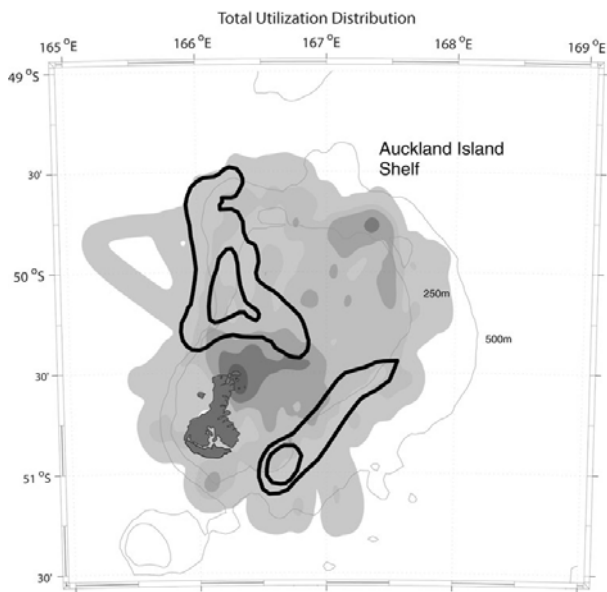


Fig. 4. Overlap of NZ female foraging areas (shades of grey, Enderby and Dundas Islands animals combined data) with squid fisheries (thick black lines). See Chilvers et al. 2011 for details.

Table 1. Characteristics of foraging by adult females at Enderby and Dundas Islands (modified from Chilvers et al. 2011).

Behaviour	Enderby	Dundas
Trip distance (km)	423	302
Max distance from colony (km)	102	87
50% Kernel home range size (km ²)	378	691
Distance to center 50% Kernel range (km)	64	74
CV of 50% Kernel home range (%)	109	66
# trips	2-15	1-2
# females	26	29

Table 2. Estimates of diet of New Zealand sea lions, whereby the contribution of major prey are expressed as **N** (percent by number), **M** (percent by wet mass), and **FOC** (percent frequency of occurrence). The use of number correction factors (NCF) and digestion coefficients (DC) to reduce bias due to digestion of hard parts is also indicated.

Location	Dates	Method	n	Major prey	NCF/DC	Source
Auckland Islands	1994-1997; 82% summer samples	Scat/regurgitates	142/64	%N ; opalfish (<i>Hemerocoetes</i> species), octopus (<i>Enteroctopus zelandicus</i>), lobster krill (<i>Munida gregaria</i>), hoki (<i>Macruronus novaezelandiae</i>), oblique-banded rattail (<i>Coelorhynchus aspercephalus</i>), and salps (<i>Pyrosoma atlanticum</i>)	no	Childerhouse et al. 2001
	2000-2006	Fatty acids; bycatch in squid fishery	82	N/A	N/A	Meynier et al. 2008
	2000-2006	QFASA	82	%M ; arrow squid 18–28%, hoki 10–27%, rattails (Macrouridae), 7–27%, and possibly scampi (Metanephrops)		Meynier et al. 2010

				challengeri) 1–19%		
	1997-2006; summer/autumn	Stomachs; bycatch squid fishery	121	%M; octopus 27.8, arrow squid 17.9, opalfish 4.7, red cod (<i>Pseudophycis bachus</i>) 4.3, rattail 2.4	Measure select, no DC	Meynier et al. 2009
	2010 winter	Scats/regurgitates	113/95	%M; octopus (30% in casts, 10% in scats), New Zealand fur seal (32% in casts, 6% in scats), rough skate (26% in scats, 10% in casts) and red cod (28% in scats, 2% in casts).	? ¹ , no DC	Lalas and McConnell unpubl.
Macquarie Island	1996-1997	Scats, 5 males	49	%FOC, <i>Zanclorhynchus spinifer</i> 62.5, <i>Dissostichus eleginoides</i> 41.7, <i>Notothenia squamifrons</i> 25.0, <i>Electrona subaspera</i> 22.9, <i>Chaunax</i> spp. 2.5	Measure select, no DC	McMahon et al. 1999
Otago Peninsula	June 1991 – May 1992; fortnightly collections	Scats/regurgitations, non-breeding males	490/29	%M; barracouta 33, , jack mackerel 11, flounder 11, octopus 9, skate 8	? ¹ , no DC	Lalas 1997

¹ how hard part erosion was handled was not stated by the authors

Table 3. Expected direction of change in response variables under various hypotheses for the decline in NZ sea lions (modified from Bowen et al. 2001).

Response variable	Hypothesis					
	Indirect effects fishing	Native competitors	Climate reducing food	Disease	Predation	Pollution
Pup growth rate	R	R	R	NC/R	NC	NC/R
Body condition	R	R	R	NC/R	NC	NC/R
Female trip duration	I	I	I	U	NC/R	NC
Foraging effort	I	I	I	U	NC/R	NC
Milk output	R	R	R	NC/R	NC	NC/R
Diet composition	C; lower squid	C	C	U	NC	NC
Birth rate	R	R	R	NC/R	NC	NC/R
Age at first birth	I	I	I	NC/I	NC	NC/I
Juvenile survival	R	R	R	R	R	R
Adult survival	R/NC	R/NC	R/NC	R	R	R

R=reduced; I=increased; C=changed; NC=no change; U=unknown