Chilvers BL, Wilkinson IS... Philopatry and site fidelity of New Zealand sea lions (Phocarctos hookeri). Wildlife Res 35: 463-470

Article *in* Wildlife Research · January 2008

DOI: 10.1071/WR07053

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CSIRO PUBLISHING

www.publish.csiro.au/journals/wr *Wildlife Research*, 2008, **35**, 463–470

Philopatry and site fidelity of New Zealand sea lions (*Phocarctos hookeri*)

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Abstract. The New Zealand sea lion (NZ sea lion), *Phocarctos hookeri*, is New Zealand's only endemic pinniped, and one of the worlds rarest otariids. It is classified as 'Threatened' based primarily on the low number of breeding sites and restricted distribution. In New Zealand, a species listed as 'threatened' is required to be managed to allow its recovery and removal from the list within 20 years. For NZ sea lions this is dependant on the establishment of new breeding areas. However, understanding the recolonisation processes for pinnipeds is still in its infancy with factors such as philopatry needing more research to understand individual dispersal and the recolonisation process. This paper presents the first quantitative investigation into the level of site fidelity and philopatry to breeding beaches in NZ sea lions. Data from resights of NZ sea lions marked as pups from the northern Auckland Island breeding area suggest that both site fidelity and philopatry are important characteristics of this species. Our results show that overall: (1) females have a higher resighting rate than males, particularly at natal sites; (2) female non-natal resightings are predominantly restricted to locations within the northern Auckland Island breeding area (an area of ~10 km^2), whereas male resightings are more widely dispersed (up to 700 km to NZ mainland); and (3) philopatry occurs for both sexes, but is more predominant in females than males, with males displaying delay related to sexual and social maturity. The colonisation of new breeding habitats rarely occurs when philopatry is strong and population density is low, stable or declining such as seen for NZ sea lions. Therefore, this research indicates that management of NZ sea lions needs to minimise anthropogenic mortality and encourage population growth to maximise density at breeding sites and encourage females to disperse to establish new breeding areas.

Introduction

Mammals that congregate to breed, such as polygamous seals, typically have discrete breeding sites. Interchange between these sites can be influenced by the extent to which offspring show site fidelity (repeat sightings at natal or non-natal sites) or philopatry (return to breed at their natal site). The prevalence, by each sex, of site fidelity and philopatry has fundamental consequences for the social and genetic structure within and between breeding sites and therefore for a species (Pomeroy *et al*. 2000). Site fidelity and philopatry can slow down the colonisation process and can temporarily restrict the entire population in a subset of available colonies. Under this situation new colonies occur only rarely because individuals must overcome their site fidelity and philopatry to found new colonies. This renders the entire metapopulation vulnerable to rare catastrophic collapses (Matthiopoulos *et al*. 2005).

The New Zealand sea lion (NZ sea lion) (*Phocarctos hookeri*) is New Zealand's only endemic pinniped, and one of the worlds rarest otariids. The population size is estimated at between 10 000 and 14 000 animals, including ~5000 adult animals (Campbell *et al*. 2006). NZ sea lions have one of the most restricted breeding ranges of any otariid limited to New Zealand's subantarctic waters between 50°S and 53°S on the Auckland (50°S, 166°E) and Campbell Islands (52°33′S, 169°09′E) (Gales and Fletcher 1999; McNally 2001; Childerhouse *et al*. 2005; Chilvers *et al*. 2007) (Fig. 1). There are only three recognised breeding areas for NZ sea lions. One area comprises the beaches at Sandy Bay and South-east Point (SEP) on Enderby Islands and Dundas Island (a 2-ha island) which are within a 10-km radius in the north of the Auckland Island group and account for 83% of the species' annual pup production (Chilvers *et al*. 2007) (Fig. 1). The other two breeding areas are Figure of Eight Island (a 4-ha island) at the southern end of the Auckland Islands and Campbell Island (a 11 000-ha island) (Fig. 1). Haul-out sites of NZ sea lions are more widespread, extending from Macquarie Island (54°30′S, 159°E) in the south (McMahon *et al*. 1999; Robinson *et al*. 1999), north to the Snares Islands (46°30′S, 169°45′E), Stewart Island (47°S, 168°E), the Catlins and Otago Peninsula, on the New Zealand mainland (46°S,170°40′E) (McConnell 2001; McNally 2001; McConkey *et al*. 2002*a*, 2002*b*) (Fig. 1). NZ sea lions are classified as 'Vulnerable' by the IUCN (Reijnders *et al*. 1993) and 'Threatened' under New Zealand's *Marine Mammals Protection Act 1978* primarily on the basis of their low number of breeding sites and restricted distribution (Hitchmough 2002).

The population is directly affected by the arrow squid (*Nototodarus sloanii*) trawl fishery, which incidentally drowns up to 140 adults a year (MFISH 2006). It is also assumed that the fishery affects the population indirectly through ecological competition for resources, and possibly through marine habitat

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alteration and biodiversity modification from bottom and mid-water trawling in the fishery (Wilkinson *et al*. 2003). Since 1997/98 this species has been affected by three episodic epidemics caused by bacterial infection (Duignan 1999; Wilkinson *et al*. 2003). These events have resulted in the deaths of 53%, 32% and 21% respectively of the 1998, 2002 and 2003 season's pup production within 6 weeks of the mean birth date, and at least 75 adult females during the 1998 epidemic (Duignan 1999; Wilkinson *et al*. 2003; Duignan, unpublished).

Under New Zealand's *Marine Mammals Protection Act 1978* animals with a 'threatened' status are required to be managed to allow their recovery and removal from the threatened list within 20 years. For NZ sea lions this is dependant on the establishment of new breeding areas because they are listed as threatened due to their restricted number of breeding sites within a restricted area (Reijnders *et al*. 1993; Hitchmough 2002). Current management is focussed on limiting anthropogenic impacts and monitoring natural environmental variability to encourage population growth and promote natural recolonisation processes. It is believed that for colonial breeders such as pinnipeds, recolonisation occurs when current breeding locations are affected by density-dependent factors, such as competition for breeding space, which initiates breeders to emigrate to other suitable sites (Roux 1987). This process assumes a level of philopatry within the species and the strength of such philopatry could determine whether individuals overflow to breeding sites close to natal sites or disperse randomly to other areas (Pomeroy *et al*. 2000).

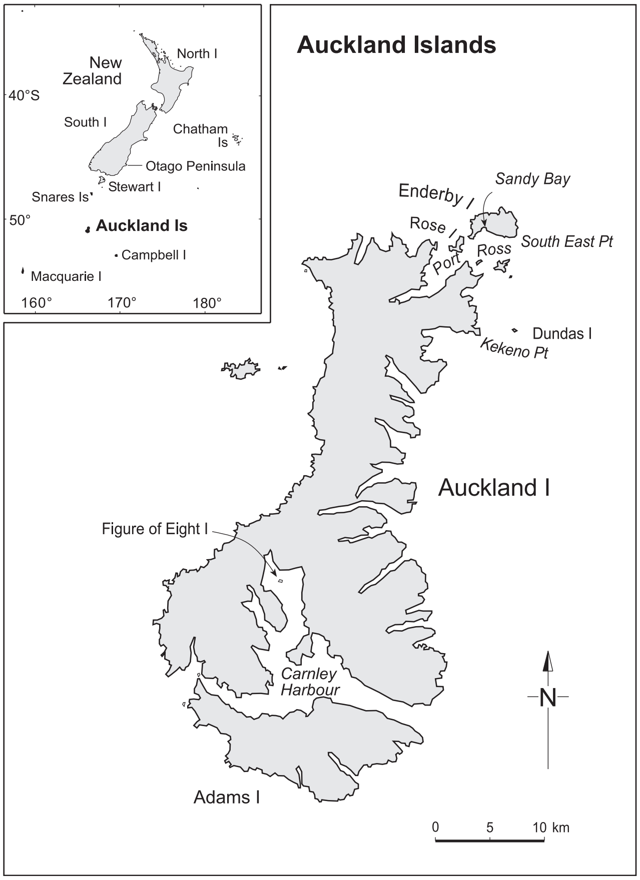

Fig. 1. New Zealand sea lion breeding and haul-out distribution. Northern Auckland Island pupping sites shown at Sandy Bay, South-east Point and Dundas Island.

In this paper we examine philopatry (returning to breed at the natal site) and site fidelity (repeated sightings at either natal or non-natal sites) of both male and female NZ sea lions from the breeding beaches at the north of the Auckland Islands. The levels of philopatry and site fidelity to breeding beaches exhibited by NZ sea lions will be examined in the context of the implications of possible recolonisation process and overall management of NZ sea lions.

Methods

Study sites

Sandy Bay (50°30′S, 166°17′E) and South East Point (SEP; 50°30′S, 166°19′E) on Enderby Island, and Dundas Island (50°35′S, 166°19′E) are located in the north of the Auckland Islands group and are recognised as a single breeding area for management (Robertson *et al*. 2006; Fig. 1). Together they contribute 83% of the total pup production for the NZ sea lions and are located within 10 km of each other (Chilvers *et al*. 2007). Enderby Island is 210 ha in size, with the two pupping sites (beaches) located on the south side of the island separated by ~3 km. The Sandy Bay NZ sea lion pupping site produces 400–500 pups each year, while the SEP pupping site produces less than 50 pups each year. Dundas Island is 2 ha in size with only one breeding beach and pup production is 1500–2000 pups annually or 64% of the pup production for the species (Chilvers *et al*. 2007).

Sandy Bay has been identified as a sea lion breeding site since early in the 19th century, with pup-production estimates intermittently recorded since 1942 (Childerhouse and Gales 1998). Sea lions were first reported on Dundas Island in 1941, with the first pup-production estimate made in 1974 (Childerhouse and Gales 1998). SEP is considered an inadvertent pupping site, in that it is an initial haul-out site for pregnant females that eventually pup at either Sandy Bay or Dundas Island (Cawthorn *et al*. 1985). However, pupping does occur at SEP, earlier than at the other two sites and usually by young females (B. L. Chilvers, pers. obs.).

Marking study

Sea lion pups have been tagged at one month of age as part of a demographics study since 1979/80 at Sandy Bay, 1985/86 on Dundas Island and 1992/93 at SEP. Tagging has been intermittent and the numbers of animals tagged annually have varied from 0 to over 500 since 1979/80. Between 1979/80 and 1992/93 flipper tags used were uniquely numbered Alflex laser-marked button tags (Alflex NZ Ltd, Palmerston North, NZ), tagged in the right pectoral flipper only. In the 1997/98 and 1998/99 seasons the same tags were used but animals were tagged in both pectoral flippers. Since 1999/2000, uniquely numbered Dalton DAL 008 Jumbotags® coffin-shaped tags (Dalton Supplies Ltd, Henley-on-Thames, UK) have been used to tag animals in both pectoral flippers. During the 1999/2000 season 297 pups and 135 adult females from Sandy Bay were also hot-iron branded (I. S. Wilkinson, P. J. Duignan, C. J. A. Bradsahw and B. L. Chilvers, unpubl. data).

Presence and breeding status of marked animals

Presence and breeding status data were collected opportunistically from marked animals at all breeding sites and other haul-out sites before the 1998/99 breeding season. Subsequently, daily tag resightings were conducted at Sandy Bay and SEP between 1 December and 20 February each season (1998/99 to 2005/06). A minimum of five days' resighting has been undertaken at Dundas Island each season after the tight breeding congregation of adult males and females had broken up, with breeding males leaving the island and females spreading out into the grass areas behind the beach. While the breeding congregation is operating (mid-December to early January), conditions on Dundas Island are too crowded and dangerous for tag resighting, and only counts of animals present are undertaken. Since 1989/90, Campbell and The Snares Islands have had high levels of opportunistic resightings during austral summers from scientific expeditions that were on the islands for research other than on NZ sea lions (S. McConkey, P. Sagar and P. Moore, pers. comm.). The NZ mainland (comprising the Otago Peninsula and the Catlins area) has been extensively, and continuously, surveyed by students from Otago University since the early 1990s (McConkey *et al.* 2002*a*, 2002*b*). The occasional sightings from Macquarie Island come from a year-round Australian sub-Antarctic research station that has been operating since 1948 (McMahon *et al.* 1999; Robinson *et al.* 1999). The resighting data presented here from our research is up to the 2005/06 season.

Resightings of animals were accepted for inclusion in analysis only if the tag number or brand had been recorded twice in one breeding season (December–February, Sandy Bay, SEP, Dundas Islands, The Snares and Campbell Island) and twice within one year on the NZ mainland or a single sighting that was confirmed by photograph, presence of a subcutaneous identification chip or identified by two independent observers simultaneously. This was to minimise the potential bias from the misreading of tags on resighting analysis.

Resights of females at SEP early in the breeding season (early December) that eventually pupped at Sandy Bay or Dundas Island were not considered site-fidelity resights. This is because SEP is an early-season 'staging post' for females from where they move on to pup at either Sandy Bay or Dundas Island. Recording of females at SEP that go on to pup at another site are considered a false positive. Similarly, Dundas Island females that are sighted at Sandy Bay in late January (after 26 January – one month after mean pupping day: Chilvers *et al.* 2006*a*) with pups but that have never been sighted at Sandy Bay previously that season are not considered to have bred at Sandy Bay. Dundas Island females swim with their month-old pups to Sandy Bay (and other locations near Dundas Island) during late January (B. L. Chilvers, pers. obs.), and recording them as having pupped at these locations would result in false positives for Dundas Island females breeding at Sandy Bay.

Although tagging has occurred since 1979/80, this study only considered animals tagged and resighted since 1989/90, as resightings recorded in this period are more consistent, reliable, frequent and widespread. The proportions of animals (by sex) that were considered to show site fidelity at natal or non-natal sites were calculated by dividing the number of animals resighted at each breeding site by the number of animals tagged as pups at each breeding site since 1989/90. Animals needed to be sighted at least two years at a breeding beach, consecutively or without being sighted at a different breeding beach in between, to be considered to show site fidelity. These proportions were then also calculated taking into consideration mortality and tag-loss estimates for those animals double-tagged (i.e. from 1998 onwards). Philopatry rates were calculated as the proportion of animals (by sex) that pupped (for females) or were associated with females – held harem (therefore had access to females to breed – for males) at natal or non-natal sites calculated by dividing these animals at each breeding site by the number of animals tagged as pups at each breeding beach since 1989/90. A female had to breed only once at a natal or non-natal site (and never be seen to breed at an alternative site) to be called philopatric. Philopatry rates were then also calculated, taking into consideration mortality and tag-loss estimates for double-tagged animals (from 1998 onwards). Data were analysed using SPSS12 (SPSS, Chicago, IL) and Microsoft Excel. Generalised linear models (GLM) and one-way ANOVAs were used to examine data for potential statistical differences. Differences were considered significant at $P < 0.05$ for all tests. All means are presented ± s.e.

Results

Resightings

The number of pups tagged at each pupping site since 1989/90 ranged from 0 to 522 (Table 1). Since 1997/98 all pups born at Sandy Bay and SEP have been tagged, while ~400 pups have been tagged on Dundas Island (Table 1). The proportion of animals in a tagged cohort (cohort refers to all pups born and tagged in the same year, therefore they are the same age) that were resighted ranged from 0.06 to 0.5, varying with sex, age and location of tagging. For those animals that were double tagged (from 1998 onwards) tag-loss rates from two tags or one tag to no tags (given that animals that change from two tags to one tag can still be identified) has previously been estimated at 12% for pups in their first year and thereafter 1% annually with no differences in sex (unpubl. data). Females were more likely to be resighted than males (females 0.30 ± 0.044, males 0.15 ± 0.023; GLM: $F_{1,37} = 10.7$, $P = 0.003$). Similarly, a higher proportion of tagged animals were resighted if they were originally tagged at Sandy Bay followed by SEP and then Dundas (SB 0.30 ± 0.034, SEP 0.22 ± 0.074, Dundas 0.13 ± 0.023; GLM: $F_{2,37} = 5.6$, $P = 0.008$). There was no interaction between sex and location in relation to the proportion of tagged animals resighted (GLM: $F_{2,37} = 1.8$, $P = 0.35$). There was a significant difference in the proportion of animals resighted between cohorts (GLM: $F_{7,37} = 3.8$, $P = 0.004$), with younger cohorts having lower resight probabilities than older cohorts; however, there was no significant interaction between year and sex or location (GLM: year/sex, $F_{7,37} = 1.3$, $P = 0.28$; year/location, $F_{9,37} = 0.024$, $P = 0.98$). Resighting rates at natal and non-natal sights for Sandy Bay, SEP and Dundas are shown in Fig. 2.

Site fidelity

Males

Male NZ sea lions showed a slightly higher proportion of site fidelity at non-natal sites than natal, although this was non-significant (proportion of sightings at natal 0.11 ± 0.024, at non-natal 0.18 ± 0.025; one-way ANOVA: $F_{1,37} = 3.6$, $P = 0.06$). These proportions increase to 0.13 and 0.21 when tag loss is taken into consideration. Males were less likely to have site fidelity at natal sites than females (GLM: $F_{1,37} = 6.7$, $P = 0.014$). The probability of site fidelity of a male at either natal or non-natal sites was not affected by the location at which the male was born and tagged. The age of males (cohort) similarly had no effect on the probability of site fidelity at natal or non-natal sites (GLM: natal site, $F_{7,18} = 0.49$, $P = 0.82$; non-natal, $F_{7,18} = 2.4$, $P = 0.09$).

Females

Female NZ sea lions showed a higher proportion of site fidelity at natal sites than non-natal (proportion at natal 0.19 ± 0.034, at non-natal 0.11 ± 0.031; one-way ANOVA: $F_{1,37} = 3.0$, $P = 0.08$). These proportions increased to 0.22 and 0.13 when tag loss is taken into consideration. Most females that showed site fidelity to non-natal sites were at the sites in the Auckland Islands closest to the original tagging site, i.e. those tagged at Sandy Bay were seen most at SEP or those tagged at SEP at Sandy Bay. Females had significantly higher site fidelity at natal sites than males (GLM: $F_{1,37} = 6.7$, $P = 0.014$). There was no relationship between tagging location and the probability of site fidelity of females at either natal or non-natal sights. The age of females (cohort) similarly had no effect on the probability of site fidelity at natal or non-natal sites (GLM: natal resighting, $F_{2,18} = 0.28$, $P = 0.7$; non-natal, $F_{2,18} = 1.03$, $P = 0.38$).

Philopatry

Males

Male NZ sea lions breed (interact with females and hold territory at the edges of, or within the breeding congregation of, males and females during the breeding season) from 9 years of age (Cawthorn *et al*. 1985; Robertson *et al*. 2006). Therefore philopatry, in terms of males holding territory in, and directly surrounding the breeding congregation at, the site they were born, could really only be determined for the 1990–93 cohorts and only for Sandy Bay and SEP (as tag resighting does not occur on Dundas Island when the breeding congregation is active). All sightings of males were considered for inclusion in philopatry estimates; however, no males less than 9 years of age were sighted breeding. No males tagged at SEP have shown philopatry ($n = 12$ tagged), whereas there have been 22 (or 2.8% of males) confirmed holding harem territory at Sandy Bay that were tagged at Sandy Bay between 1990 and 1993 ($n = 780$ tagged). Taking into consideration estimated tag-loss rates, this estimate increases to 3.4%. All of those males were between 9 and 13 years of age, with four animals observed to hold territory for two consecutive years. Male survival has not been estimated; however, if it is assumed to be the same as for females (see below) the rate of philopatry at Sandy Bay when mortality and tag-loss estimates are taken into account would increase to 6.8–12% of males tagged at Sandy Bay. There have been seven males tagged on Dundas Island confirmed to have held a harem territory at Sandy Bay and one that held harem territory at SEP. There is no evidence of males migrating between breeding areas (northern Auckland Islands, Figure of Eight Island and Campbell Island) within breeding seasons; however, resightings do occur between these areas outside the breeding season (February–October).

Females

In total, 293 females have been confirmed to be philopatric to Sandy Bay (defined as born at Sandy Bay and returned to give birth and breed at Sandy Bay). These 293 females represent

Table 1. Tagging and sighting records of NZ sea lions tagged at the northern Auckland Island breeding sites 1990–2005

Tag year	Age in 2005	Location of tagging	Number of pups tagged			Number of females showing fidelity to natal site		Number of females showing philopatry to natal site	Number of females known to breed at non-natal site
			Total	Female	Male	Female	Male		
1990	15	Sandy Bay	335	154	181	52	31	33	0
1991	14	Sandy Bay	376	192	183	65	20	62	1[A]
		Dundas	200	88	111	12	2	6	2[B]
1992	13	Sandy Bay	448	233	215	125	46	79	0
		Dundas	248	100	148	15	3	6	2[B]
1993	12	Sandy Bay	396	195	201	92	60	76	3[A]
		SEP	23	11	12	2	0	2	2[B]
1998	7	Sandy Bay	480	255	225	40	13	10	0
		SEP	36	23	13	0	0	0	1[B]
		Dundas	399	185	214	5	2	0	0
1999	6	Sandy Bay	485	210	274	63	60	19	4[A]
		SEP	39	23	16	4	1	0	0
		Dundas	510	231	279	16	5	4	1[B]
2000	5	Sandy Bay	482	240	242	48	36	10	2[A]
		SEP	37	16	21	2	1	0	0
		Dundas	421	192	229	5	3	0	0
2001	4	Sandy Bay	522	267	255	62	34	4	0
		SEP	44	23	21	2	0	0	0
		Dundas	408	190	218	7	2	0	0
Totals			5886	2828	3058	617	319	311	

[A]South East Point; [B]Sandy Bay.

16.8% of the female pups tagged at Sandy Bay since 1990. This proportion increases to 18.7% when tag loss is taken into consideration. Only 10 (or 0.5% of females that were born and tagged at Sandy Bay) have been recorded to breed at a non-natal site, with all of these births occurring at SEP. One female returned in two consecutive years to pup at SEP. All other females tagged at Sandy Bay that pupped at SEP had previously or subsequently pupped at Sandy Bay. There are no records of females pupping at any of the other breeding areas (Figure of Eight or Campbell Island). The estimated survival of female NZ sea lions for the first five years of life (in years without mass mortality events) ranges from 0.778 to 0.89 per year (Wilkinson *et al.* 2006). Given these figures, we would expect 560–1120 of the 1746 females tagged at Sandy Bay to return to breed at their natal site by the age of five years (including tag-loss estimates), increasing philopatry to 32–64% of all tagged female alive, compared with 18.7% philopatry if mortality is not considered.

At SEP, there have been only two females confirmed to have returned to breed (2% of total pups tagged, $n = 96$), while three females have bred at non-natal sites (3%), all at Sandy Bay. Dundas Island has had only 16 females confirmed to have breed at Dundas (1.6% of pups tagged), with five females confirmed to have bred at non-natal sites (0.5%), all of which were at Sandy Bay and all were once-only occasions.

Discussion

This is the first quantitative investigation into the level of site fidelity and philopatry at breeding beaches for NZ sea lions. Data from resights of NZ sea lions marked as pups from the northern Auckland Island breeding area suggest that both site fidelity and philopatry are characteristics of this species. Our results show that: (1) overall, females had higher resighting rates than males; (2) female non-natal sight locations were predominantly restricted to locations within the northern Auckland Island breeding area, whereas male resightings were more widely dispersed (Fig. 2); (3) females had significantly higher site fidelity at natal locations than males; and (4) philopatry occurs for both sexes, but is significantly more predominant in females, with males showing only weak philopatry with a time delay related to sexual and social maturity.

Limitations of research and resightability

All resighting results reported here are considered minimum estimates because: (1) animals that were recorded only once without confirmation were not included in the analysis to reduce possible bias from tag misreading; and (2) resightings at locations outside of the breeding areas in the northern Auckland Islands were only opportunistic, although all other known sites surrounding the northern Auckland Island breeding areas are checked during each breeding season. It must also be noted that these measures of site fidelity and philopatry have been taken during a period when the NZ sea lion population in the Northern Auckland islands (determined from yearly pup-production estimates) were in a low-density slow decline (Chilvers *et al.* 2007) and this needs to be considered when interpreting these results. Populations at stable low population densities or in slow decline are likely to show higher levels of site fidelity and philopatry than those with rapidly increasing or high population density (Matthiopoulos *et al.* 2005). Resighting data from Dundas

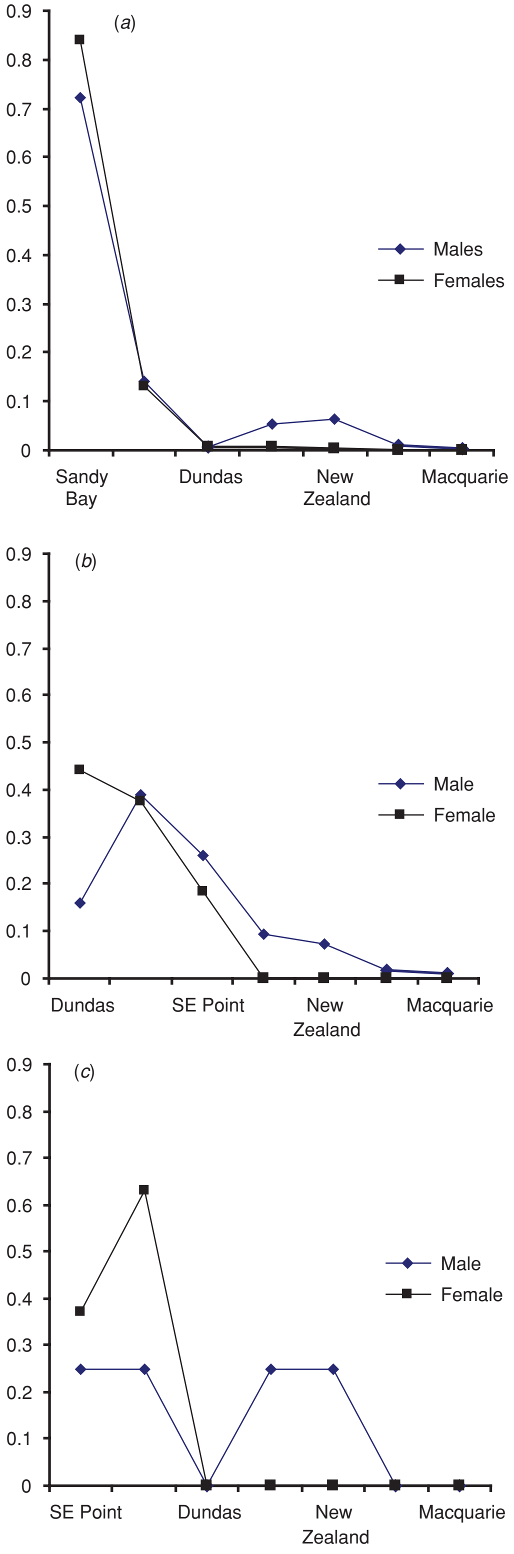

Fig. 2. The proportion of resights at natal and non-natal sites of tagged male and female NZ sea lions from (*a*) Sandy Bay, (*b*) South-east Point and (*c*) Dundas. The natal site is represented by the first site listed along the *x*-axis.

Island were limited by logistical and health and safety constraints when working on this island. This resulted in the lowest resighting rate for all three breeding sites studied and limited information available for this site. The lack of this information restricts the data available to calculate accurate site fidelity and philopatry at this breeding site.

Site fidelity and philopatry

Males

Male resighting rates and site fidelity were slightly higher at non-natal sites than at natal sites, although not significantly so ($P = 0.06$). This may be indicative of a possible trend towards a higher level of site fidelity at non-natal sites than at natal sites, which may be resolved by further observations. Consistent, both intra- and interannual, resights of adult males at haul-out sites indicate site fidelity to haul-out areas but not necessarily to breeding beaches. It is common for individually marked NZ sea lion males to be consistently sighted at haul-out sites such as the Snares, Macquarie Island and NZ mainland when they are juveniles and subadults and during the non-breeding season, but returning to the Auckland Islands to mate during the breeding season (Robertson *et al.* 2006). This suggests that males are the migrant sex for NZ sea lions, as is the case with Californian sea lions (*Zalophus californianus*), northern fur seals (*Callorhinus ursinus*) and subantarctic fur seals (*Arctocephalus tropicalis*) (Reidman 1990; Bowen and Siniff 1999; Gearin *et al*. 2004).

Only low levels of philopatry (3.4% or 6.8–12% when estimated tag loss and mortality rate is accounted for) were found for NZ sea lion males, with an obvious time delay relating to age (sexual and social maturity). Male philopatry appears to be delayed in many fur seal species (*Arctocephalus* spp.), which correlates with their sexual and social maturity (Gentry 1998). This result may be low due to this research only having four years of resighting data for males sexually and socially old enough to breed (i.e. >9 years of age). Studies on otariid males report that once males have ‘chosen’ a breeding location, inter- and intra-annual site fidelity is strong (McCann 1980; Gentry 1998). This is not the case for NZ sea lions (Robertson *et al.* 2006). Male NZ sea lions have been shown to have significant daily change in the breeding males at the breeding sites and within breeding congregations (18% of marked individuals per day, n = 202), and interchange of breeding males between pupping areas within a season (32% of marked individuals changed breeding sites within a season: Robertson *et al.* 2006).

Females

Site fidelity for female NZ sea lions was higher at natal sites than at non-natal sites. Philopatry was high, at up to 64% of females tagged at Sandy Bay returning to breed at their natal site, and when estimates of tag loss and survival are taken into consideration (Wilkinson *et al.* 2006). Site fidelity and philopatry has been documented at 60–80% for females of several otariid species, including Guadalupe fur seals (*A. townsendi*) (Peterson *et al.* 1968), antarctic fur seals (*A. gazella*) and subantarctic fur seals (Wilkinson and Bester 1990; Lunn and Boyd 1991), northern fur seals (Gentry 1998), California sea lions (Maldonado *et al.* 1995) and Australian sea lions (*Neophoca cinerea*) (Campbell 2005). Generally, female philopatry is substantially stronger than male philopatry, and in the case of Australian sea lions female philopatry is thought to be almost exclusive (Campbell 2005).

There have been few incidents of non-natal breeding observed in NZ sea lions (Table 1). The non-natal breeding that has occurred was at breeding sites close to natal locations (Table 1). Apart from one female born at Sandy Bay that bred twice at SEP, all other non-natal breeding showed no site fidelity. One notable exception was a female NZ sea lion tagged in 1987 at Dundas Island that pupped at Otago Peninsula in 1993 and has shown breeding-site fidelity to that area for the subsequent 12 years (McConkey *et al.* 2002*a*; McConkey, pers. comm.). There is no evidence of interchange of females between breeding areas (northern Auckland islands, Figure of Eight Island, and Campbell Island) either within or between breeding seasons.

Implications for recolonisation and management

In keeping with many mammals and other pinnipeds (Greenwood 1980), female NZ sea lions show high philopatry to their natal pupping sites and breeding areas, while male NZ sea lions appear to be the dispersing sex. The key criterion for removing the threatened species status from the NZ sea lion is the founding of new distinct breeding areas away from the current Auckland and Campbell Island populations. Notwithstanding the previously recorded movement of a female from the northern Auckland Islands breeding area to the Otago Peninsula (McConkey *et al.* 2002*a*), the female philopatry and small declining population numbers seen in this species may hinder the establishment of any new colonies unless there is strong population growth in the NZ sea lion population at the Auckland Islands.

The colonisation of new breeding habitats is a fundamental process in species that exhibit metapopulation dynamics, as most pinniped species do (Gaggiotti *et al.* 2002). When philopatry is strong and population density is low, stable or declining, geographic population expansion occurs only rarely because individuals must overcome their site fidelity to found new breeding areas (Matthiopoulos *et al.* 2005). This results in the metapopulation being vulnerable to rare catastrophic collapses, such as has been seen with mass mortality epidemics in NZ sea lions in the Auckland Island area (Baker 1999; Wilkinson *et al.* 2003, 2006). With female NZ sea lions showing a high level of philopatry, the dispersal of breeding animals from their natal site is probably a compromise between philopatry and density-dependent reproductive success. Individuals may ‘weigh-up’ the suitability of a new site with the loss of mate choice, density-dependence costs of aggressive interactions with adult males and other breeding females at the current pupping site, aggressive behaviour of males if the only female at a new site (Cassini and Fernandez-Juricic 2003), mother–pup separation costs (Campagna *et al.* 1992), pup mortality (Chilvers *et al.* 2005*a*) and distance to, and effort required to forage at, current breeding sites (Chilvers *et al.* 2005*b*, 2006*b*).

There is currently no evidence that density-dependent factors are operating at the Sandy Bay breeding beach. For example: (1) there is high availability of space for breeding females and pups; and (2) pup mortality is low (averaging 9.7% in the first month of life in the last 11 years excluding episodic mortality events: Wilkinson *et al.* 2006; Chilvers *et al.* 2006*a*) relative to other sea lion species that are showing the effects of known density-dependent factors such as parasite load and hookworm on pup survival (Lyons *et al*. 2000, 2001). Therefore, management of the northern Auckland Island population of NZ sea lions needs to result in an increase in population to a point where the pressures of density dependence at the breeding sites facilitate the dispersal of females to form new colonies, as has been described for other pinniped species (Roux 1987; Gentry 1998; Bradshaw *et al*. 2000; Gaggiotti *et al*. 2002; McConkey *et al*. 2002*a*). This process can be helped through a clearer understanding of breeding behaviour and habitat requirements at all current and potential breeding sites and by limiting, or preferably eliminating, avoidable anthropogenic mortality currently impacting this species from the subantarctic squid fishery. Minimising incidental mortality and encouraging population growth to maximise density at breeding sites could tip the scales and encourage females to disperse from current breeding areas to establish new breeding areas (Roux 1987).

Acknowledgements

The work was conducted under research and entry permits from the New Zealand Department of Conservation (DOC), and was funded by DOC, Research, Development and Information Unit and Conservation Services Providers. DOC Southland are thanked for their logistical assistance. We thank J. Amey, H. Best, A. Castinel, S. Childerhouse, P. Duignan, W. Hockley, C. Lalas, A. Maloney, S. McConkey, F. Riet Sapriza, B. Robertson, P. Sagar and other people who helped with resighting or reported resights from outside the Auckland Islands. A special thanks to M. Cawthorn for the early tagging and resights of the Auckland Island sites and C. Edkins for graphics help. Approval for work was obtained from DOC Animal Ethics Committee – Approval AEC86 (1 July 1999). I. West and two anonymous reviewers all provided helpful, critical reviews of the manuscript.

References

Baker, A. (Ed.) (1999). 'Unusual Mortality of the New Zealand Sea Lion, *Phocarctos hookeri*, Auckland Islands, January–February 1998: A Report of a Workshop Held 8–9 June 1998, Wellington, and a Contingency Plan for Future Events.' (Department of Conservation: Wellington.)

Bowen, W. D., and Siniff, D. B. (1999). Distribution, population biology, and feeding ecology of marine mammals. In 'Biology of Marine Mammals'. (Eds J. E. Reynolds and S. A. Rommel.) pp. 423–484. (Smithsonian Institution Press: Washington.)

Bradshaw, C. J. A., Lalas, C., and Thompson, C. M. (2000). Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Zoology* **250**, 105–112. doi:10.1111/j.1469-7998.2000.tb00581.x

Campagna, C., Bisioli, C., Quintana, F., Peres, F., and Vila, A. (1992). Group breeding in sea lions: pups survive better in colonies. *Animal Behaviour* **43**, 541–548.

Campbell, R. (2005). Historical distribution and abundance of the Australian sea lion (*Neophoca cinerea*) on the west coast of Western Australia. Fisheries Research Report No. 148.

Campbell, R. A., Chilvers, B. L., Childerhouse, S., and Gales, N. J. (2006). Conservation management issues and status of the New Zealand (*Phocarctos hookeri*) and Australian (*Neophoca cinerea*) sea lions. In 'Sea Lions of the World'. (Eds A. W. Trites, D. P. DeMaster, L. W. Fritz, L. D. Gelatt, L. D. Rea and K. M. Wynne.) pp. 455–471. (Lowell Wakefield Fisheries Symposium: AK.)

Cassini, M. H., and Fernandez-Juricic, E. (2003). Costs and benefits of joining South American sea lion breeding groups: testing the assumptions of a model of female breeding dispersion. *Canadian Journal of Zoology* **81**, 1154–1160. doi:10.1139/z03-098

Cawthorn, M. W., Crawley, M. C., Mattlin, R. H., and Wilson, G. J. (1985). Research on pinnipeds in New Zealand. WRLG Research Review No. 7. Pinniped Research Review Sub-committee, Wellington, New Zealand.

Childerhouse, S., and Gales, N. J. (1998). Historical and modern distribution and abundance of the New Zealand sea lion (*Phocarctos hookeri*). *New Zealand Journal of Zoology* **25**, 1–16.

Childerhouse, S., Gibbs, N., McAlister, G., McConkey, S., McConnell, H., McNally, N., and Sutherland, D. (2005). Distribution, abundance and growth of New Zealand sea lion *Phocarctos hookeri* pups on Campbell Island. *New Zealand Journal of Marine and Freshwater Research* **39**, 889–898.

Chilvers, B. L., Wilkinson, I. S., Duignan, P. J., and Gemmell, N. J. (2005*a*). Male harassment of female New Zealand sea lions, *Phocarctos hookeri*: mortality, injury, and harassment avoidance. *Canadian Journal of Zoology* **83**, 642–648. doi:10.1139/z05-048

Chilvers, B. L., Wilkinson, I. S., Duignan, P. J., and Gemmell, N. J. (2005*b*). Summer foraging areas for lactating New Zealand sea lions, *Phocarctos hookeri*. *Marine Ecology Progress Series* **304**, 235–247. doi:10.3354/meps304235

Chilvers, B. L., Robertson, B. C., Wilkinson, I. S., and Duignan, P. J. (2006*a*). Growth and survival of New Zealand sea lions, *Phocarctos hookeri*: birth to 3 months. *Polar Biology* **30**, 459–469. doi:10.1007/s00300-006-0203-9

Chilvers, B. L., Wilkinson, I. S., Duignan, P. J., and Gemmell, N. J. (2006*b*). Diving to extremes: are New Zealand sea lions pushing their limits in a marginal habitat? *Journal of Zoology* **269**, 233–241.

Chilvers, B.L., Wilkinson, I. S., and Childerhouse, S. (2007). New Zealand sea lion pup production –1995 to 2005. *New Zealand Journal of Marine and Freshwater Research* **41**, 205–213.

Duignan, P. J. (1999). Gross pathology, histopathology, virology, serology and parasitology. In 'Unusual Mortality of the New Zealand Sea Lion, *Phocarctos hookeri*, Auckland Islands, January–February 1998: A Report of a Workshop Held 8–9 June 1998, Wellington, and a Contingency Plan for Future Events'. (Ed. A. Baker.) pp. 29–33. (Department of Conservation: Wellington.)

Gaggiotti, O. E., Jones, F., Lee, W. M., Amos, W., Harwood, J., and Nichols, R. A. (2002). Patterns of colonization in a metapopulation of grey seals. *Nature* **416**, 424–427. doi:10.1038/416424a

Gales, N. J., and Fletcher, D. J. (1999). Abundance, distribution and status of the New Zealand sea lion, *Phocarctos hookeri*. *Wildlife Research* **26**, 35–52. doi:10.1071/WR98022

Gearin, P. J., Melin, S. R., DeLong, R. L., and Gosho, M. E. (2004). Migration and movements of adult male California sea lions. Abstract. In 'Sea Lions of the World: Conservation and Research in the 21st Century'. (22nd Wakefield Fisheries Symposium: Anchorage, AK.)

Gentry, R. L. (1998). 'Behavior and Ecology of the Northern Fur Seal.' (Princeton University Press: Princeton, NJ.)

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**, 1140–1162. doi:10.1016/S0003-3472(80)80103-5

Hitchmough, R. A. (2002). New Zealand Threat Classification Systems List 2002. Threatened Species Occasional Publication No. 23. Department of Conservation, Wellington.

Lunn, N. J., and Boyd, I. L. (1991). Pupping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **72**, 202–206. doi:10.2307/1381999

Lyons, E. T., DeLong, R. L., Gulland, F. M., Melin, S. R., Tolliver, S. C., and Spraker, T. R. (2000). Comparative biology of *Uncinaria* spp. in the California sea lion (*Zalophus californianus*) and the northern fur seal (*Callorhinus ursinus*) in California. *The Journal of Parasitology* **86**, 1348–1352. doi:10.2307/3285025

Lyons, E. T., Melin, S. R., DeLong, R. L., Orr, A. J., Gulland, F. M., and Tolliver, S. C. (2001). Current prevalence of adult *Uncinaria* spp. in northern fur seal (*Callorhinus ursinus*) and California sea lion (*Zalophus californianus*) pups on San Miguel Island, California, with notes on the biology on these hookworms. *Veterinarian Parasitology* **97**, 309–318. doi:10.1016/S0304-4017(01)00418-6

Maldonado, J. E., Davila, F. O., Stewart, B. S., Geffen, E., and Wayne, R. K. (1995). Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from southern California and the Gulf of California. *Marine Mammal Science* **11**, 46–58. doi:10.1111/j.1748-7692.1995.tb00273.x

Matthiopoulos, J., Harwood, J., and Thomas, L. (2005). Metapopulation consequences of site fidelity for colonially breeding mammals and birds. *Journal of Animal Ecology* **74**, 716–727. doi:10.1111/j.1365-2656.2005.00970.x

McCann, T. S. (1980). Territoriality and breeding behaviour of adult Antarctic fur seal, *Arctocephalus gazella*. *Journal of Zoology* **192**, 295–310.

McConkey, S. D., McConnell, H., Lalas, C., Heinrich, S., Ludmerer, A., McNally, N., Parker, E., Borofsky, C., Schimanski, K., and McIntosh, G. (2002*a*). A northward spread in the breeding distribution of the New Zealand sea lion, *Phocarctos hookeri*. *Australian Mammalogy* **24**, 97–106.

McConkey, S. D., Heinrich, A., Lalas, C., McConnell, H., and McNally, N. (2002*b*). Pattern of immigration of New Zealand sea lion, *Phocarctos hookeri* to Otago, New Zealand: implications for management. *Australian Mammalogy* **24**, 107–116.

McConnell, H. (2001). New Zealand sea lions on the South Island and Stewart Island: abundance, decolonisation status and management considerations. M.Sc. Thesis, Otago University, Dunedin.

McMahon, C. R., Holley, D., and Robinson, S. (1999). The diet of itinerant male Hooker's sea lions, *Phocarctos hookeri*, at subantarctic Macquarie Island. *Wildlife Research* **26**, 839–846. doi:10.1071/WR98079

McNally, N. (2001). New Zealand sea lion abundance, demographics and movements in southern New Zealand. M.Sc. Thesis, Otago University, Dunedin.

MFISH (2006). 2006–07 SQU 6T Sea lion Operational plan initial position paper. Ministry of Fisheries, Wellington, New Zealand. http://www.fish.govt.nz.

Peterson, R. S., Hubbs, C. L., Gentry, R. L., and DeLong, R. L. (1968). The Guadalupe fur seal: habitat, behaviour, population size, and field identification. *Journal of Mammalogy* **49**, 665–675. doi:10.2307/1378727

Pomeroy, P. P., Twiss, S. D., and Redman, P. (2000). Philopatry, site fidelity and local kin association within grey seal breeding colonies. *Ethology* **106**, 899–919. doi:10.1046/j.1439-0310.2000.00610.x

Reidman, M. (1990). 'The Pinnipeds: Seals, Sea Lions and Walruses.' (University of California Press: Berkeley, CA.)

Reijnders, P., Brasseur, S., van der Toorn, J., van der Wolf, P., Boyd, I., Harwood, J., Lavigne, D., and Lowry, L. (1993). Seals, fur seals, sea lions and walrus, status survey and conservation plan. IUCN/SSC Seal Specialist Group. IUCN, Gland, Switzerland.

Robertson, R. C., Chilvers, B. L., Duignan, P., Wilkinson, I. S., and Gemmell, N. J. (2006). Dispersal of breeding, adult male *Phocarctos hookeri*: implications for disease transmission, population management and species recovery. *Conservation Biology* **127**, 227–236. doi:10.1016/j.biocon.2005.08.011

Robinson, S., Wynen, L., and Goldsworthy, S. (1999). Predation by Hooker's sea lion (*Phocarctos hookeri*) on a small population of fur seals (*Arctocephalus* spp.) at Macquarie Island. *Marine Mammal Science* **15**, 888–893. doi:10.1111/j.1748-7692.1999.tb00855.x

Roux, J.-P. (1987). Recolonization processes in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. In 'Status, Biology and Ecology of Fur Seals. Proceedings of an International Symposium and Workshop. Cambridge, England, April 1984'. (Eds J. P. Croxall and R. L. Gentry.) *NOAA Technical Reports NMFS* **51**, 189–194.

Wilkinson, I. S., and Bester, M. M. (1990). Continued population increase in fur seals, *Arctocephalus tropicalis* and *A. gazella*, at the Prince Edward Islands. *South African Journal of Antarctic Research* **20**, 58–63.

Wilkinson, I. S., Burgess, J., and Cawthorn, M. W. (2003). New Zealand sea lions and squid – managing fisheries impacts on a threatened marine mammal. In 'Marine Mammals: Fisheries, Tourism and Management Issues'. (Eds N. Gales, M. Hindell and R. Kirkwood.) pp. 192–207. (CSIRO Publishing: Melbourne.)

Wilkinson, I. S., Duignan, P. J., Grinberg, A., Chilvers, B. L., and Robertson, B. C. (2006). *Klebsiella pneumoniae* epidemics: Possible impact on New Zealand sea lion recruitment. In 'Sea Lions of the World'. (Eds A. W. Trites, D. P. DeMaster, L. W. Fritz, L. D. Gelatt, L. D. Rea and K. M. Wynne.) pp. 385–404. (Lowell Wakefield Fisheries Symposuim: Alaska.)

Manuscript received 10 May 2007, accepted 31 March 2008