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Foraging behaviour indicates marginal marine habitat for New Zealand sea lions: remnant versus recolonising populations

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ABSTRACT: The New Zealand sea lion *Phocarctos hookeri* historically bred on the New Zealand mainland (South and North Islands). Subsistence hunting and later commercial sealing reduced its distribution to 3 breeding areas at the spatial edges of its historical distribution range, in the Auckland Islands (AI) and on Campbell Island. Here, we present foraging areas and foraging trips of female New Zealand sea lions from the Otago Peninsula, where a recolonising population has been found in the core of the historical range of the species. We compare the results with data from the AI in order to assess the theory that the spatial margin of a species' distribution represents the lower end of habitat suitability. Female New Zealand sea lions at Otago had significantly smaller foraging ranges than females at the AI (mean 65% Kernel ranges: 47 ± 25 km^2 versus 687 ± 109 km^2), made shorter foraging trips (mean 11.8 ± 2.3 h versus 66.2 ± 4.2 h), and spent 40% less time at sea overall. Juvenile females at Otago from age 2 onwards could access foraging grounds used by adult females nursing pups; this is unlikely to be the case at the AI due to the large distances and associated depths of foraging grounds. Our study illustrates the theory that spatial marginality is related to habitat marginality. Existing management measures to mitigate the impact of bycatch in fisheries on declining remnant colonies around the AI were modelled based on populations exploiting optimal habitat. They should now integrate this new information.

KEY WORDS: *Phocarctos hookeri* · Pinnipeds · Spatial · Marginal · Satellite tracking · Marine conservation

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INTRODUCTION

The New Zealand sea lion *Phocarctos hookeri* is endemic to New Zealand, and once bred from the northernmost cape of the North Island to the sub-Antarctic islands (Childerhouse & Gales 1998; Fig. 1). However, early Polynesian settlers extirpated the species from most of the New Zealand mainland (the 2 largest islands of New Zealand: North and South Islands) through subsistence hunting before European colonisation (Childerhouse & Gales 1998). Commercial sealing then wiped out the New Zealand sea lion from Stewart Island and depleted the remnant populations in the sub-Antarctic islands. Only 3 remnant breeding areas exist today (all below 50°S; Gales & Fletcher 1999, Robertson et al. 2006). Two are found in the Auckland Islands: the North Auckland Islands breeding area (comprised of 2 breeding colonies: Dundas Island and Enderby Island) and the Figure of Eight Island breeding colony (Robertson et al. 2006, DOC 2009). The third breeding area is Campbell Island (Maloney et al. 2009; Fig. 1).

The geographical locations of the remnant breeding colonies of New Zealand sea lions consequently correspond to the spatial edges of the historical breeding distribution of the species (see Fig. 1). Theories on influence of spatial marginality describe a decreasing gradient in suitability of the habitat for a species from

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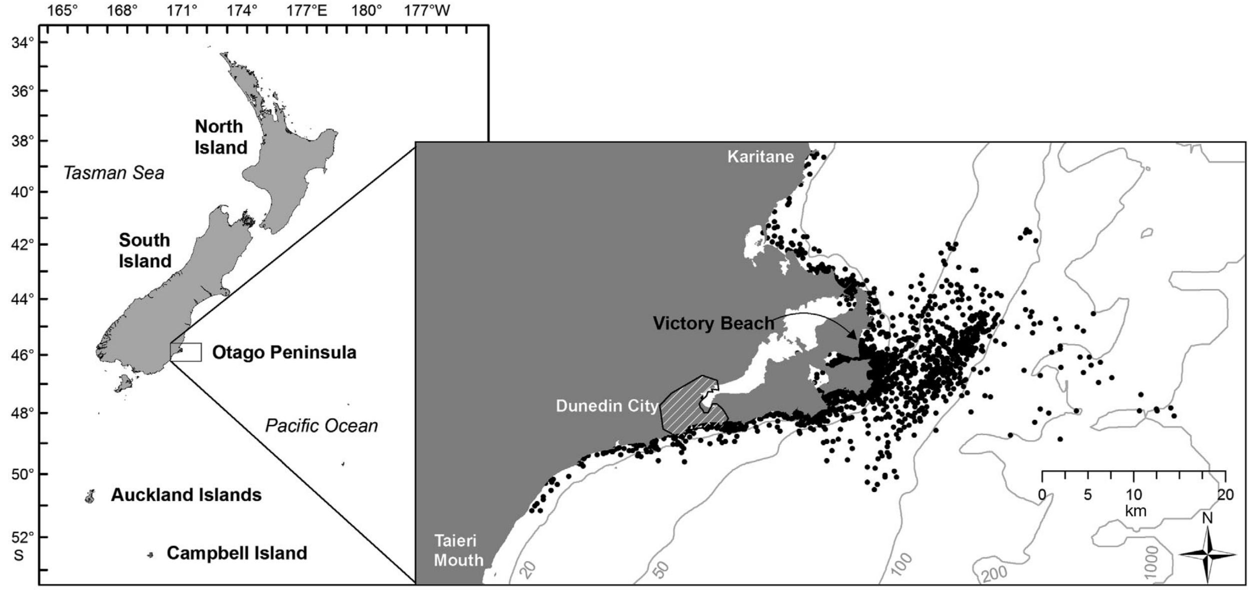

Fig. 1. *Phocarctos hookeri.* The study site, the Otago Peninsula, and other breeding colonies of the New Zealand sea lion at Auckland Islands and Campbell Island. The detailed map shows the Otago Peninsula with all foraging locations of New Zealand sea lions obtained in autumns 2008 and 2009, over bathymetry (in m, light grey lines)

the core to the edge of natural distribution (Lawton 1993, Shreeve et al. 1996, Rhodes et al. 2008). The habitat beyond this edge is unsuitable and hence delineates the distribution of the species (Gaston 2009). As a consequence of this gradient, animals from populations found at the edges of distribution ranges may exploit poorer food resources (i.e. lower quality or quantity or less accessible) than in the core of their distribution (Shreeve et al. 1996, Marti 1997, Baker & Johanos 2004).

Since 1994, the first and currently only recolonising population of breeding female New Zealand sea lions on the New Zealand mainland has established itself on the Otago Peninsula (McConkey et al. 2002). This population was started by a single matriarch, which was born in the Auckland Islands but did not show the typical philopatry of females of this species (Chilvers & Wilkinson 2008) and moved to Otago to breed. From 1994 to 2010, 45 pups were born in this new population and female pups have remained and bred there. Breeding female New Zealand sea lions are permanent central place foragers as they use the same breeding site each year (Chilvers & Wilkinson 2008) and do not seasonally migrate with their pups (which they nurse for a minimum of 8 mo) except over short distances <25 km from breeding sites (Hawke 1993, A. A. Augé unpubl. data). Consequently, they exploit the same marine habitat throughout their lives. We hypothesised that breeding female New Zealand sea lions in the remnant populations found at the edges of the historical spatial distribution of the species exploit marginal marine habitat with low food resources and hence spend significantly more time foraging and search larger areas than animals of the same species inhabiting the core of their natural distribution.

Diving behaviour of female New Zealand sea lions around the Auckland Islands indicated that these animals surpassed their physiological limits during more than 60% of dives which led to the hypothesis that these animals may exploit marginal habitat (Costa & Gales 2000, Chilvers et al. 2006). Chilvers et al. (2005) presented foraging areas and trip characteristics of female New Zealand sea lions around the Auckland Islands. They showed that these animals also foraged for long periods and in large areas compared to other otariid species. However, the extensive foraging trips observed at this site may be typical of this species rather than resulting from the marginality of the marine habitat. The comparison of these data with results of foraging behaviour of New Zealand sea lions in areas found in the spatial core of the historical distribution is the only way to test the hypothesis that the remnant populations exploit marginal marine habitat.

The pup production of breeding colonies in the Auckland Islands has declined by over 30% since the mid 1990s (Chilvers et al. 2007, L. Chilvers unpubl. data). Deaths of female New Zealand sea lions occur in commercial fisheries around the Auckland Islands and may contribute to this decline, alongside bacterial epizootics (Castinel et al. 2007, Chilvers 2008). However, the cause of the decline is not well understood and potential competition for food resources with fisheries was recently revealed (Meynier et al. 2010). Establishing if the remnant populations exploit marginal marine habitat may help increase the effectiveness of management measures for the remnant populations of this threatened species (Baker et al. 2010).

In this paper, we present for the first time the foraging ranges and foraging trip characteristics of recolonising female New Zealand sea lions that breed on the Otago Peninsula. These data were then compared to results published for breeding female New Zealand sea lions from remnant populations in the Auckland Islands to determine the effects of spatial marginality on habitat suitability.

MATERIALS AND METHODS

Fieldwork, field site and studied population. From 8 April to 21 May 2008 and 30 March to 12 May 2009 (austral autumns), female New Zealand sea lions were satellite-tracked on the Otago Peninsula (Fig. 1). In 2009, the population of female New Zealand sea lions at the Otago Peninsula was composed of 9 known-to-be-alive breeding females and 7 known-to-be-alive juvenile females (i.e. sighted within the last 2 yr). The 11 females investigated in our study included all adult females and 3 of the juvenile females born on the Otago Peninsula. The eldest female that initiated the Otago population was born at the Auckland Islands and was not part of this study.

Each female was first caught in a specially designed hoop-net, secured by 2 handlers, and then anaesthetised with isofluorane delivered with oxygen using a field-portable vaporiser (Gales & Mattlin 1998). Captures were undertaken only after the females had been ashore for more than 6 h to limit the risk of regurgitation. Under anaesthesia, we equipped each of the study females with a SPLASH tag (10 × 4 × 4 cm, Wildlife Computers) placed behind the mid-shoulder line and a Very-High-Frequency (VHF) transmitter (7 × 3 × 1.5 cm, Sirtrack) close to the tail, using quick-setting epoxy. An observer stayed in proximity to the recovering sea lion until she was fully awake. All satellite-tracked females were recaptured at the end of the study each year to retrieve the tags.

Filtering of Argos data. SPLASH tags use the Argos satellite-tracking system to determine locations of the animals at sea when they surface. These tags also record when the animals dive and were set to switch off when not submerged in salt water for over 30 min (this is unlikely to happen when the animal rests at the surface while at sea as the tag is placed in the middle of the back). From these data, the date, time and length of foraging trips can be determined. A scale of accuracies from best (status LC3 < 250 m) to worst (status LCA or LCB with no accuracy) is given by the Argos system for each location obtained. Vincent et al. (2002) found that all accuracy status given by Argos contain large variations in accuracy. We consequently minimised the use of the status information but filtered the locations using a custom-designed algorithm based on Freitas et al. (2008).

First, we separated the locations for each foraging trip, defined as a period during which the animal was at sea for >2 h. All locations received when the animals were onshore were removed. The locations of each trip were integrated in ArcGIS (ESRI). The filter used threshold values of 3 m s^{-1} for the speed, based on Crocker et al. (2001), and of 30° for inside turning angle, classifying significant spatial outliers. Any location <500 m from a preceding correct location was kept. In addition to the Freitas et al. (2008) filter, we followed these steps: (1) last and first onshore locations of a foraging trip were used during filtering as start and end points of the trip but were removed to determine foraging ranges, (2) all LC3 locations (7.4% of total number of at-sea locations) were kept during filtering, (3) locations with no neighbouring location closer than 5 km (based on a value of 4.8 km for the 95% CI of nearest neighbour distances within each female's unfiltered dataset) in the dataset of a particular animal were removed, and (4) the remaining locations that were onshore but <1 km from shore were moved to the nearest location at sea. If 2 or more locations were taken <30 min apart, only the earliest was kept to reduce autocorrelation. Some autocorrelation remained in the datasets as locations were obtained from tracks. However, in 30 min, a female could have swum 3.6 km (based on a swim speed of 2 m s^{-1}) and the median of the nearest neighbour distances was calculated at 454 m. Hence, the foraging ranges were likely not affected by the remaining autocorrelation.

Analysis of foraging locations around the Otago Peninsula. Because of the small spatial scale of the data and based on personal observations of foraging activities of sea lions in inlets and within a few meters from shore during our study, all locations obtained while a female was at sea were assumed to represent foraging locations. However, feeding success was not assessed. Fixed Kernel density maps (single smoothing factor: 1 km) were produced for each female using the ArcGIS extension Hawth's Analysis tool (Beyer 2004). The areas of the 100% and 65% Kernel ranges, representing the maximal foraging ranges and the core foraging ranges for each female, respectively, were calculated. These areas excluded all land.

If the number of locations of a particular foraging trip was 2 or less, this trip was not used to determine trip characteristics due to lack of data. The minimum route was the minimum distance that a female travelled during each trip. Hawth's Analysis tool was used to create paths from the locations and these paths were manually modified to go around coastlines in the most direct manner when they intersected with the coastline. The maximum distance from shore was the maximum straight line between land and the farthest location of a trip. The maximum water depth corresponded to the bathymetry over which the female foraged during a trip. We calculated the duration of each trip and the time that the female spent onshore between trips.

Comparisons with the Auckland Islands. We used data from Chilvers et al. (2005) and Chilvers (2009) for comparison with our results. These studies reported the latest data available for the Auckland Islands at the 3 breeding colonies (Enderby, Dundas and Figure of Eight Islands). Only the foraging behaviour of adult females nursing pups was investigated. Consequently, for comparison purposes, only the results of adult females from the Otago population, all nursing a pup and one nursing a yearling, were used (n = 8). The data available for the Auckland Islands was obtained during 1, 2, and 4 yr, respectively, for Figure of Eight, Dundas and Enderby Islands. The satellite tracking technique used similar instruments. However, the methods used to filter the Argos locations differed between the studies (a speed-only filter was applied to Argos locations for the Auckland Islands data; Chilvers et al. 2005). The purpose of applying different filters was to obtain the best estimates of foraging ranges; the choice of filter depended on the configuration of the sites and the foraging characteristics of the animals. Due to the scale of the differences found in the results, this does not affect the validity of the comparison between the sites. The studies at the Auckland Islands were also conducted ~1.5 mo earlier in the year (from mid-January to end of February) than in our study. The implications of this difference are assessed in the discussion. We compared the 65 % Kernel ranges, i.e. core foraging areas, the routes, and the mean distances from shore amongst the 4 different sites.

Mapping and statistical analysis. All maps were produced using ArcGIS and all statistical analyses were conducted in R 2.10.0 (R Development Core Team 2009). All means presented are arithmetic means ± SE. Pearson's correlation tests were performed to determine relationships between 2 variables. Linear regression models, with 1 or 2 factors, were used to establish the effects of *Age* (age of the individual) and/or *ID* (individual identity) on foraging ranges and trip characteristics, and to test for differences in foraging ranges amongst sites. No interaction between factors was found to be significant. *Year* was not used as a factor as we sampled different females each year.

RESULTS

Foraging ranges around the Otago Peninsula

Table 1 contains the details of captures, studied animals, and data structures. The rate of locations per hour after the application of the filter was on average 1 location for every 2.1 h at sea. Satellite coverage was low during the mornings (from 06:00 to 11:00 h) and consequently fewer locations (on average 1 location every 5.2 h at sea) were obtained during this period.

Female New Zealand sea lions inhabiting the Otago Peninsula foraged at maximal straight-line distances from the breeding site of 40.3 km to the South, 35 km to the East and 21.7 km to the North (Fig. 1). There was no correlation between the numbers of locations and the areas of 65 % Kernel ranges (Pearson's coefficient = 0.43, p = 0.181), but there was a significant positive correlation between this number and the areas of

Table 1. *Phocarctos hookeri.* Maximal foraging ranges and core foraging ranges (km^2, based on the 100 % and 65 % Kernel ranges, respectively) used by each studied female New Zealand sea lion at the Otago Peninsula, mainland New Zealand, in autumns 2008 and 2009. A foraging trip was defined as any period at sea of >2 h. Year = satellite-tracked in 2008 or 2009

ID	Age (yr)	Year	Tagged on:	Deployment of tags (d)	No. of trips with >2 locations	No. of locations	Locations kept by filter (%)	65 % Kernel range (km^2)	100 % Kernel range (km^2)
F0350	14	08	8 Apr	26	19	175	77.8	52	400
F0351	12	08	9 Apr	39	31	258	73.9	95	492
F2578	7	09	31 Mar	42	31	207	77.2	54	193
F2580	7	09	1 Apr	40	39	171	75.7	13	53
F2582	5	08	8 Apr	43	37	315	78.9	76	331
F2584	4	08	8 Apr	43	34	237	66.2	45	378
F2587	4	09	30 Mar	31	26	147	79.9	52	220
F2588	4	09	1 Apr	38	32	230	77.7	40	108
F2591	3	09	30 Mar	46*	11	52	78.8	15	64
F2594	3	09	30 Mar	32	16	140	62.5	58	520
F3451	2	09	2 Apr	40	26	104	76.5	20	70

*The satellite tag lost its aerial after 26 d so no location data was retrieved but data on trip length were available (total 40 trips)

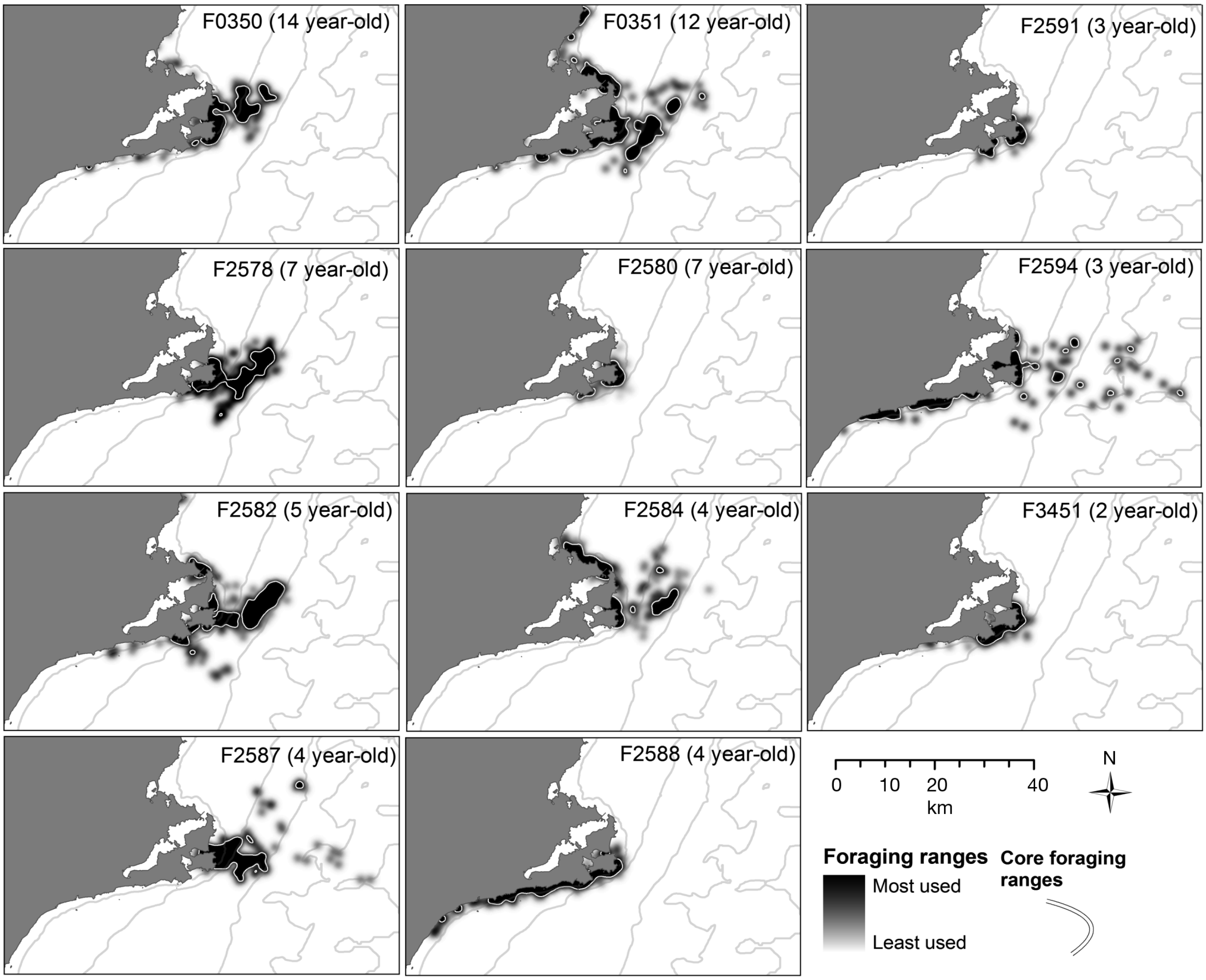

Fig. 2. *Phocarctos hookeri.* Foraging ranges (Kernel densities of foraging locations) and core foraging ranges (65% Kernel contours) of 11 female New Zealand sea lions satellite-tracked in April and May 2008 and 2009 at the Otago Peninsula. The female ID and her age (in brackets) are presented in the top right corner

100% Kernel ranges (Pearson's coefficient = 0.70, p = 0.016). All the 65% Kernel areas were consequently considered a useful index of the females' core foraging ranges during autumn.

The foraging ranges differed amongst sea lions with the largest area being 10 times the size of the smallest (Table 1, Fig. 2) but there was no apparent effect of *Age* on the areas of the foraging ranges (F = 1.837, df = 1, p = 0.208).

Overall, 68.4% of the foraging trips were in coastal areas (<3 km from shore), and 30.3% were on the continental shelf (depth < 200 m). The oceanic area (depth > 200 m) was only explored by 2 females (F2587 and F2594) during 5 trips, in an area close to the edge of the zone (i.e. mainly above the continental slope; Fig. 2).

Foraging trips at the Otago Peninsula

The minimal route and the duration of foraging trips were correlated (F = 75.0, df = 1, p < 0.001). The longer a female stayed at sea, the more distance she travelled. The duration of a foraging trip had no effect on the time onshore between foraging trips (F = 1.942, df = 1, p = 0.164) or on the distance from shore (F = 1.739, df = 1, p = 0.188).

The mean duration of a foraging trip of female New Zealand sea lions at Otago was 11.4 ± 2.3 h (Fig. 3). *Age* did not affect the length of foraging trips but there were significant differences amongst females (*Age*: F < 0.005, df = 1, p = 0.982 and *ID*: F = 5.614, p < 0.001). The mean time onshore between foraging trips was

13.4 ± 2.8 h (Fig. 3). *Age* did not affect this characteristic but there was a significant difference amongst females (*Age*: $F = 0.995$, df = 1, $p = 0.319$ and *ID*: $F = 1.956$, $p < 0.043$). The significant difference among females were found to be due to the fact that animal F0350 had longer onshore periods. When this individual was excluded from this analysis, no significant difference amongst females was found (*ID:* $F = 0.848$, df = 8, $p = 0.568$).

The mean minimal route travelled by a female during a foraging trip was 23.7 ± 3.8 km. *Age* of the study animals did not influence the distance that they travelled during a foraging trip (*Age*: $F = 1.797$, df = 1, $p = 0.213$), however there were significant variations amongst individuals (*ID*: $F = 11.454$, df = 9, $p < 0.001$). The mean maximum distance from shore reached by female New Zealand sea lions at Otago was 4.1 ± 2.1 km (max. = 34 km). No effect of *Age* on maximum distance reached by an individual was found ($F = 0.545$, df = 1, $p = 0.465$) but differences amongst individuals were high (*ID*: F = 7.706, df = 9, $p < 0.001$). Depth and maximal distance from shore are physically correlated (Pearson's coefficient = 0.77, $p < 0.001$) hence effects of *Age* and *ID* on maximum depth were similar. The mean maximum depth over which female New Zealand sea lions foraged at Otago was 41.7 ± 5.7 m.

Comparison between the Otago Peninsula and the Auckland Islands

Table 2 highlights the contrasting differences between the foraging ranges and trips of breeding female New Zealand sea lions around the Auckland Islands and around the Otago Peninsula. Within the Auckland Islands, females from Figure of Eight Island were reported as having significantly shorter trips, smaller foraging ranges, and travelling smaller distances from shore than the females from Dundas or Enderby Islands (Chilvers 2009). However, the results from this study at the Otago Peninsula were appreciably lower, and differences between Otago and the Auckland Islands dwarfed those amongst the populations of the Auckland Islands. Females from Figure of Eight Island travelled longer routes ($F = 25.58$, df = 1, $p < 0.001$) that took them farther from shore ($F = 186.6$, df = 1, $p < 0.001$; Fig. 4) than the Otago females, and their core (65% Kernel) foraging

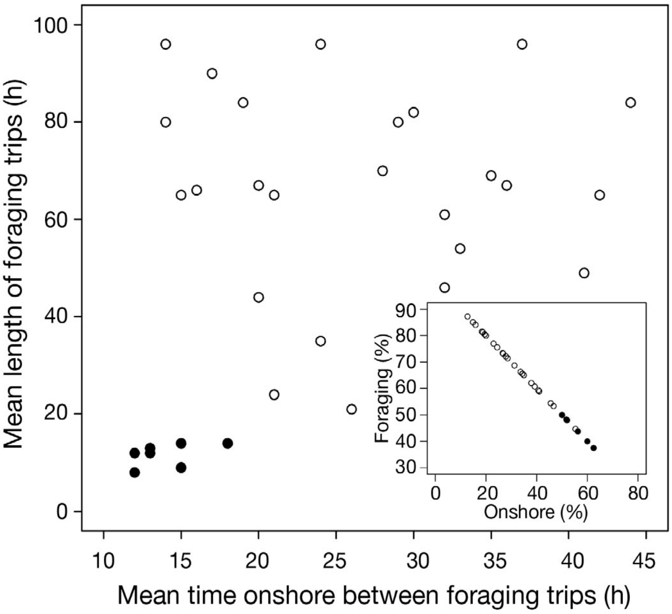

Fig. 3. *Phocarctos hookeri*. Comparison of length of foraging trips and time spent onshore between trips by female New Zealand sea lions at (●) the Otago Peninsula and (○) Enderby Island (Auckland Islands). The inset box presents the same data as percentages of time

Table 2. *Phocarctos hookeri.* Mean time of foraging trips, mean time onshore between foraging trips, mean route travelled, mean maximal distance from shore during foraging trips and core foraging range (65% Kernel range) between adult female New Zealand sea lions nursing pups on mainland New Zealand (historical range), and in the Auckland Islands (remnant colonies). The distance from shore corresponds to distance from colony for the Auckland Islands, as females there did not come ashore anywhere else, whereas females at Otago rested on multiple sites along the coast. All means ± SE; na: not available

Breeding sites	N	No. of locations	No. of trips	Time at sea (h)	Time onshore (h)	Route travelled (km)	Max. distance from shore (km)	65% Kernel area (km^2)
Mainland New Zealand								
Otago Peninsula	8	1740	247	11.8 ± 1.5	13.8 ± 1.4	26.4 ± 2.7	4.7 ± 1.6	47 ± 5.0
Auckland Islands								
Enderby Island[a]	26	9200	183	66.2 ± 4.2	26.8 ± 1.8	423.0 ± 43.9	102.0 ± 7.7	643 ± 131
Dundas Island[b]	29	na	na	na	na	302.0 ± 21.5	87.0 ± 5.3	1213 ± 139
Figure of Eight Island[b]	4	1677	50	na	na	214.0 ± 17.9	45.0 ± 4.5	207 ± 58

[a]Data from Chilvers et al. (2005) and [b]Chilvers (2009)

ranges were larger ($F = 3.641$, df = 1, $p = 0.001$; Table 2).

The females inhabiting the Auckland Islands spent more time at sea (70.0 ± 11.0% of total time) than the females at the Otago Peninsula (45.7 ± 4.5%) and thus proportionally less time onshore (Fig. 3). Moreover, satellite-tracking data indicated that nursing females in the sub-Antarctic area spend time onshore only at the breeding site where their pups were left (B. L. Chilvers unpubl. data). The females nursing pups at Otago, however, spent between 12 and 49% (mean 23 ± 3.5%) of their time onshore at other beaches than Victory Beach (where the pups were). Based on the mean values of times spent onshore and at sea, females at the Auckland Islands spent on average 29% of their time onshore where their pups were. Accounting for the time that females at Otago spent onshore at other sites than Victory Beach, they spent on average 36% of their time where their pups were. Additionally, the Otago females were onshore during approximately half of this time at 2 beaches <3 km away from Victory Beach, and at maximal distances of 7 km.

Female New Zealand sea lions at Otago foraged almost exclusively in coastal and mid-shelf waters within a narrow continental shelf. Females at the Auckland Islands foraged within a wide continental shelf (narrower on the west of the group of islands, see maps in Chilvers et al. [2005]), mostly at the edge of the shelf or above the continental slope.

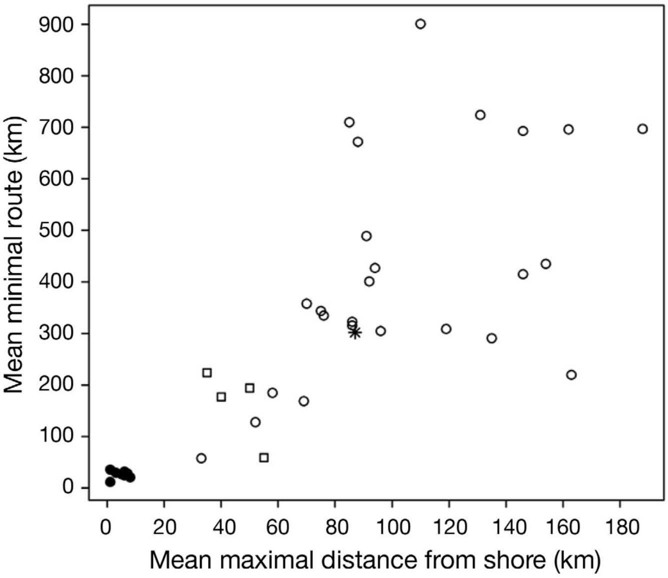

Fig. 4. *Phocarctos hookeri.* Comparison of minimal route travelled and maximal distance reached during foraging trips by female New Zealand sea lions at (●) Otago Peninsula and the Auckland Islands: (□) Figure of Eight Island, (○) Enderby Island and (✱) Dundas Island. At Dundas Island, only the overall mean was available

DISCUSSION

Remnant versus recolonising populations: impact of spatial marginality on habitat quality

There were large individual variations in foraging ranges and trips amongst female New Zealand sea lions around the Otago Peninsula. Although at different spatial scales, our results highlighted individual preferences for different foraging areas, as was reported at the Auckland Islands (Chilvers et al. 2005). However, when put in perspective, in comparison with females at the Auckland Islands that foraged in areas up to almost 100 times larger than at the Otago Peninsula, these variations were insignificant. Overall, breeding female New Zealand sea lions exhibited contrasting foraging behaviours at the 2 different geographical locations. Around the Auckland Islands, at the edges of the historical breeding distribution of the species, they foraged farther from shore within larger areas and for larger proportion of their time than the females around the Otago Peninsula, in the core of the historical distribution. This paper consequently demonstrates that the spatial marginality of a population within the natural range of a species can be related to habitat quality, with a decrease from the core (Otago Peninsula) to the edges (Auckland Islands). Differences in foraging behaviour between populations of pinnipeds within various areas in the core of their distribution range are often observed; however, the scale of the differences is minimal compared to that reported in our study (Baylis et al. 2008, Lea et al. 2008, Lowther & Goldsworthy 2010, Staniland et al. 2010). This indicates that optimality of the local marine habitat may vary within the entire range of a species' distribution, but corroborates that the habitats at the edges of the historical distribution often represent the lower end of suitability.

While there were individual variations amongst female New Zealand sea lions' foraging ranges at the Otago Peninsula, they were not related to ages of the animals. A young adult female nursing a healthy male pup (i.e. having one of the highest energy requirements; Winship et al. 2002) confined her foraging range to coastal waters within a stretch of 23 km of the coastline. This indicates that food resources close to shore in shallow waters, and hence accessible to juvenile sea lions as well, are of high quality and abundance. Even though the only 2-year-old female in this study had a small foraging range, it was still larger than the foraging range of the adult female nursing a pup. Consequently, all juvenile females at the Otago Peninsula can theoretically exploit foraging areas of high quality.

Female New Zealand sea lions at the Auckland Islands spent time onshore exclusively at the breeding site with their pups, while females at Otago spent a large portion of time onshore without their pups. This supported the assumption that females at the Auckland Islands had to maximize their limited time onshore to feed their pups between foraging trips whereas females at Otago did not have this constraint. The proximity (often <5 km away) of the beaches that the Otago females used when they were not at Victory Beach (where their pups were) showed that they could have gone back to their pups instead without incurring high-energy costs if it was essential for pup health. Finally, all results presented in this paper corroborate the theory that the spatial marginality of the Auckland Islands within the historical range of the New Zealand sea lion is associated with habitat marginality for this species.

Methodology considerations

The total area used by female New Zealand sea lions at the Auckland Islands may not represent the actual maximum available habitat to them. These animals may be able to go farther and extend their foraging ranges around other sites where food resources would be less abundant or distributed farther away than the 2 sites studied. This is not an option that can be ruled out as we cannot test this with the available data. However, studies on diving behaviour of breeding female New Zealand sea lions at the Auckland Islands concluded that these females frequently operated at their physiological limits (Costa & Gales 2000, Chilvers et al. 2006). Chilvers et al. (2005) also found that distances from shore reached by female New Zealand sea lions at the Auckland Islands were typical of otariid species, but that they covered greater distances during foraging trips than any other species. This likely indicates that breeding females at the Auckland Islands may have to exploit a large part of the available area to them, and may not be able to increase their foraging effort further.

One of the main limits of our study is its restricted time scale, being strictly based during autumn. Foraging locations of many female otariids vary depending on the season and growth of the pups; typically the size of foraging areas and distances travelled by breeding females increase during the period from birth to weaning of the pups (Beauplet et al. 2004, Baylis et al. 2008). Consequently, the comparison of our data (females nursing 3 to 5-mo-old pups and 1 yearling) with the data from the Auckland Islands (females nursing 3-wk-old to 2-mo-old pups; Chilvers et al. 2005, Chilvers 2009) is only enhanced by this difference in timing between the studies, as foraging effort at the Auckland Islands would be expected to further increase as pups get older.

Another limit of our study that cannot be currently assessed is related to the current small size of the recolonising population of female New Zealand sea lions at the Otago Peninsula. Absence of intraspecific competition may affect the foraging behaviour of individuals and this should be considered when comparing our data with the Auckland Islands where the largest breeding colony of New Zealand sea lions is found (Chilvers et al. 2007). However, it is estimated that up to 150 male New Zealand sea lions are found around the Otago Peninsula during most of the year (McConkey unpubl. data). In addition, there are already large numbers of other marine carnivores which forage around the Otago Peninsula, including New Zealand fur seals *Arctocephalus fosteri* (>20 000 individuals; Lalas 2008). The contrasting foraging ranges observed between female New Zealand sea lions at the Otago Peninsula and at the Auckland Islands are consequently unlikely to be due to differences in competition. Moreover, while a significant decline (~30%) in pup production and related population numbers of New Zealand sea lions has occurred at the Auckland Islands over the last 15 yr, the foraging behaviour of females there has not changed over this period (Chilvers et al. 2006). This is further refutation of the possibility that intraspecific competition may be the reason why they forage more remotely and for longer periods.

Fishing competition: impact on the differences observed and management implications

Around the Auckland Islands, large fisheries operate within the foraging ranges of female New Zealand sea lions and target species that are known to be important in the sea lions' diet (Childerhouse et al. 2001, Wilkinson et al. 2003, Meynier et al. 2009). Consequently, fishing competition may deplete food resources around the Auckland Islands and amplify the marginality of the marine habitat for the species. However, although the area 22 km around the Auckland Islands has been fully protected from fishing activities as a Marine Reserve since 2003, New Zealand sea lions forage almost exclusively outside this area (Chilvers et al. 2005, Chilvers 2009). Around the Otago Peninsula, all foraging activities took place within 25 km from shore. Consequently, if food resources were available in the 22 km buffer zone around the Auckland Islands, this area would be exploited by female New Zealand sea lions.

Competition between sea lions and commercial fisheries may occur around the Auckland Islands (Meynier et al. 2010) as reported for other large marine carnivores interacting with fisheries (Alonzo et al. 2003, Trites & Donnelly 2003, Drago et al. 2009). However, the management of the Auckland Islands populations of New Zealand sea lions currently focuses on reducing the bycatch rate in squid fisheries but does not take into consideration the impact of resource competition with fisheries (Chilvers 2008). In the latest model used to determine the MALFIRM (Minimum Allowable Level of Fishing Related Mortality; see Chilvers 2008) that sets the number of sea lions allowed to be killed as accidental bycatch each year before the fishery is closed, Breen et al. (2010) admitted that 2 of the most important factors in the model (maximal rate of population increase and the parameter that determines the shape of density-dependent pup survival) are given arbitrary values that are generally used for seal species. They also wrote that 'it remains a substantial concern that current pupping rates may be too low to replace the population' (p. 44). This model assumes that the population of New Zealand sea lions at the Auckland Islands follows typical population fluctuation due to natural variation in the food resources of a population exploiting a good quality marine habitat. However, as expressed by Shreeve et al. (1996), animals living at the edges of the natural distribution of a species likely have poorer life-history traits (i.e. lower fitness) due to marginal habitat. Despite the MALFIRM and other management measures to prevent bycatch of sea lions in squid fisheries, the Auckland Islands colonies have been declining since the mid-1990s (Chilvers et al. 2007). In the light of the results presented in this paper, models used to develop these measures (see Breen et al. 2010) likely overestimate the rate of population increase of the remnant populations of New Zealand sea lions exploiting a marginal habitat and fail to account for the suitability of this habitat.

CONCLUSIONS

The first investigation of the foraging behaviour of female New Zealand sea lions around the Otago Peninsula in the core of the historical range of the species revealed, by comparison, that the remnant populations of the species, found at the spatial margins of the historical breeding distribution of the species, exploit marginal marine habitat where food resource is suboptimal. Around the Otago Peninsula, even though female New Zealand sea lions exhibited various types of foraging behaviours (e.g. fully coastal or mix between coastal and mid-shelf foraging), they all had access to easily accessible foraging grounds in coastal waters. For many species of marine animals that have had their distribution areas reduced to small remnant parts, similar configurations are expected. However, because of the usual financial and methodological limitations that make it difficult to accurately assess available food resources in the marine environment, food requirements of individual animals and the amount taken by fisheries, fishing impact may be masked by the marginality of the habitat. Comparisons between populations of the same species in the core and at the edges of their historical distribution, when possible, can increase our understanding of their status and improve conservation measures for threatened species.

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