TERRESTRIAL SPATIAL ECOLOGY OF FEMALE NEW ZEALAND SEA LIONS

STUDY AT SANDY BAY, AUCKLAND ISLANDS, AND IMPLICATIONS FOR THE MANAGEMENT OF THE RECOLONISATION

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ABSTRACT

The New Zealand sea lion, *Phocarctos hookeri*, is endemic to New Zealand and has only three breeding colonies, all situated in the sub-Antarctic islands. This reduced breeding distribution is the result of human extirpation from most of its pristine range, which included the New Zealand mainland. In 1993, a female bred for the first time on mainland New Zealand, indicating the possible start of the recolonisation. The recolonisation of an urbanised coastline will create interactions between humans, infrastructures and sea lions. No study had however looked at how the New Zealand sea lion uses its terrestrial environment. This study thus aimed to characterise, in space and time, the terrestrial spatial ecology of the female New Zealand sea lions at a breeding colony.

Intensive fieldwork at the Sandy Bay breeding colony, Enderby Island, in the Auckland Islands, during two breeding seasons (between December 2001 and March 2003), produced a large dataset of daily Global Positioning System (GPS) locations of branded females onshore (4252 locations) within the study area (0.7 km²). A habitat type map and a Digital Terrain Model (DTM) of the study area were produced.

The analyses were conducted in ArcGIS at three scales: individual, population and habitat. A two-phase pattern, including a harem phase (aggregation of females, area used < 0.003 km²) and a dispersion phase (spread of females, area used > 0.550 km²), was revealed and characterised using Nearest Neighbour Indices. A dispersion model of an average female was produced based on cumulative Minimum Convex Polygons (MCP) and pup mortality was found to be affected by females' movements on pupping day. The female population was found to move and shift areas used throughout the dispersion phase while the gregariousness of females was considerably modified between the harem phase and the end of the dispersion phase (80 versus 0.3 females per 100 m²). Temporal analyses of habitat use demonstrated a radical change in habitat preferences between the two phases and a gradual change during the dispersion phase. At the end of the season, females preferred sites in forest and at more than 1.1 km from shore. Male aggressiveness and disturbance, habitat properties and parasite infections are thought to be some of the main factors that drive the terrestrial ecology of the females *P. hookeri*.

In conclusion, the presence and spatial extent of a female population at Sandy Bay, unusual for a pinniped species, was found to be predictable and thought to be species-specific rather than location-specific. The results of this study can thus be used as a basis for the management of the recolonisation. Human infrastructure and disturbance are likely to interfere with the establishment of new breeding colonies and the ecology of female New Zealand sea lions on mainland New Zealand. Some recommendations based on these results are immediate public awareness and education programs, the monitoring of the new population using a GIS database and the identification, protection against human disturbance and rehabilitation of suitable sites for the establishment of a new breeding colony on the mainland.

Key words: wildlife, GIS, movements, habitat, spatio-temporal, management, recolonisation

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INTRODUCTION

1. Research problem

The New Zealand sea lion, *Phocarctos hookeri*, is a threatened species endemic to the New Zealand region (Gales and Fletcher, 1999). It has been listed in the International Union for the Conservation of Nature (IUCN) inventory as vulnerable, and as a conservation priority by the New Zealand Department of Conservation (DoC) (IUCN, 2004; Suisted and Neale, 2004). The main reason for this is the occurrence of only three breeding colonies (Gales and Fletcher, 1999; Wilkinson *et al.*, 2003; Robertson *et al.*, 2006). Two of them are found in the Auckland Islands and represent more than 85% of the total pup production of this species each year (Chilvers, 2005a). However *Phocarctos hookeri* once bred all around the New Zealand mainland before extirpation in the 19th century. A possible natural recolonisation has recently started along the Otago coast, New Zealand mainland, with 28 pups born since 1993 (L.Chilvers pers. com.). The establishment of new breeding colonies on the mainland, or at other sites, is the critical step to remove this species from its threatened status. Unlike the remote sub-Antarctic islands, the coastal areas of the mainland have been modified and urbanised (Johnson, 1992; Hilton *et al.*, 2000). The management of this recolonisation thus requires knowledge, amongst other things, on how the species uses its terrestrial habitat. However the current extent of this information is found only as anecdotal observations in the literature.

The New Zealand sea lion is a marine mammal as it feeds at sea and has developed physical and physiological adaptations to marine life (Walker and Ling, 1981; Gales and Mattlin, 1997). Hence, to date, studies concerning its spatial behaviour have focussed on the marine environment, particularly as bycatch of sea lions in trawl fisheries is the current major source of mortality (Wilkinson *et al.*, 2003; Chilvers *et al.*, 2006a). Nevertheless, unlike most pinnipeds, this species exhibits significant terrestrial movements which was already noted by Eden (1955, p.35) and raised the start point of this thesis: "*It is interesting to note that sea-bears* [female sea lions] *in particular penetrate a considerable distance inland* […]". The marine environment is vital for the species as it is the foraging area. The terrestrial environment is however equally significant as it is the place of mating, breeding, nursing and resting. Considering the management of the recolonisation of the New Zealand sea lion back on mainland New Zealand, the challenge of dealing with interactions between humans and sea lions on land will depend on our understanding of their terrestrial spatial ecology. Knowing where, and why, female New Zealand sea lions move and the consequences on pup survival should help to develop better conservation measures.

The breeding strategy of the New Zealand sea lion is a colonial polygamy with female philopatry (i.e. females return where they were born to breed) and 'maternal care only' (Walker and Ling, 1981). The males do not play any role in the rearing of the pups. Moreover as a mammal species, the pups depend on their mothers for food in the form of milk for up to 12 months (Walker and Ling, 1981). Consequently females' behaviours have the greatest influence on pup survival and, therefore, on the overall fitness of the species. The recovery of the species also depends on the female's behaviour to initiate a new breeding colony. These are the reasons why the objectives of this study are focussed on New Zealand sea lion females' spatial ecology.

Modern technologies, such as Global Positioning System (GPS), satellite imagery and Geographic Information Systems (GIS), have been used to study wildlife movements in the last 15 years. They allow the spatio-temporal analysis of movements and habitat use based on large amounts of data. These tools were used in the present study to investigate the terrestrial spatial ecology of female New Zealand sea lions.

2. Objectives of study

This thesis primarily aims to fulfil the significant gap in the literature available for the New Zealand sea lion on its terrestrial ecology in order to help develop conservation measures for the management of the recolonisation.

The main objective of this research was thus to investigate females' movements onshore, the existence of predictable patterns and consequences on pup survival of these movements, and habitat use. To achieve this, the data were analysed at three spatial scales, each of which answered the main questions of this study. The results were then used to discuss the potential spatial problems due to the recolonisation of the New Zealand mainland by the species as well as possible management measures and considerations.

The first scale is the individual scale and aims to:

- Determine if there is a specific timing and a spatio-temporal pattern in the space use of a female New Zealand sea lion and if this behaviour can be modelled.
- Quantify the distances a particular female moved once ashore and how these movements influenced her pup survival.

The second scale is the population scale and aims to:

- Characterise the timing of the presence of a female New Zealand sea lion population at a breeding colony.
- Identify the seasonal movements of the population and the total area used by the population.
- Determine the consistency in the presence and movements of the female population between years.

The third scale is the habitat scale and aims to:

- Characterise, in terms of habitat, a breeding colony and the sites where females were found.
- Detect which kinds of habitats were preferentially selected by females.
- Determine if sites where females nursed a pup were more specific than resting only sites.

3. Organisation of the thesis

Chapter 1 presents a literature review encompassing the background on the New Zealand sea lion, the study area and general methods used. The first section focusses on the species, *Phocarctos hookeri*, including its distribution, ecology and current threats. A second section offers knowledge of the study site, Enderby Island and the Auckland Islands, from its history to its environment, in relation to the New Zealand sea lion population. The last section presents the concept of wildlife conservation and how spatial ecology is incorporated into it as well as brief descriptions of GPS, satellite imagery and GIS and how they are used in the study of wildlife spatial ecology.

The Material and Methods are presented in Chapter 2, including descriptions of the fieldwork and the data acquisition, the preparation of the datasets, the general data processing and the statistics on the data. However descriptions of more specific methods and analyses are presented at the start of each chapter of results in a methodology part.

The results of this thesis are organised into three different chapters based on a scale-orientated manner. From Chapter 3 to 5 the scale thus moves from individual, to population and to habitat. Chapter 3 presents the descriptive analysis of individual females' movements i.e. at individual scale, as well as a model of space use of an average female. Comparisons between age and status classes were made. How pup survival is influenced by movements was also investigated. The population scale is investigated in Chapter 4 to analyse the presence, movements and the space use of the whole female population. In this chapter the predictable patterns of the dynamics of the breeding female population is also covered. Chapter 5 is where information at the habitat scale is treated to give insights into the terrestrial habitat use of the species. Habitat use at a breeding colony and specific habitat preferences were determined and then compared to define the study site in term of suitability as a breeding environment.

Chapter 6 is the general discussion with a focus on how the results can be used for the management of the recolonisation of mainland New Zealand. A general summary of the results from the three scales is presented to gather the main patterns of the terrestrial spatial ecology of the female New Zealand sea lions. Methods, results, improvements and future potential researches are discussed as well as the implications that these results may especially have for the recolonisation of mainland New Zealand by the species.

CHAPTER ONE: LITERATURE REVIEW

THE NEW ZEALAND SEA LION AND SPATIAL ECOLOGY STUDIES

> *"A new baby is like the beginning of all things – wonder, hope, a dream of possibilities."*
>
> E.J. Le Shan

1. The New Zealand sea lion

1.1. Distribution and abundance

The New Zealand sea lion, *Phocarctos hooker*i (Gray, 1844; classification in Table 1.1), previously known as Hooker's sea lion, is the only species of pinnipeds endemic to the New Zealand region (Wilson, 1979). The species is thought to have been hunted to extinction in the North Island in the 1770s when Captain Cook and the first Europeans reached New Zealand increasing the hunting pressure of the Maori people (Higham, 1991). Before extirpation by Maori and European sealers, the New Zealand sea lion bred all around the North Island (up to North Cape), the South Island, Stewart Island, the sub-Antarctic islands of New Zealand and at least frequented the Chatham Islands (Worthy, 1992; Childerhouse and Gales, 1998). *Phocarctos hooker*i eventually disappeared from mainland New Zealand by the 1830s (Childerhouse and Gales, 1998) and the populations found in the Auckland Islands and other sub-Antarctic islands of New Zealand were severely depleted by European sealers and settlers from 1806 up to 1895 (McLaren, 1936). It however seems that, by the 1950s, the population of sea lions had already recovered as Eden (1955, p.33) noted that "*the sandy beach at Enderby Island is frequented by hundreds of the creatures* [sea lions]" during an expedition in 1944. The latest abundance estimate for the New Zealand sea lion was of 10,391-13,791 (95% CI) individuals for the 2004/05 season with a pup production estimate of 2533 (S.D.=44.5) (Chilvers, 2005a). The New Zealand sea lion is consequently one of the three least

Table 1.1: Classification of the New Zealand sea lion (source: Walker and Ling, 1981).

	Principal characteristics for classification
class *Mammalia*	-Warm-blooded vertebrates -Hair or fur -Females suckle their young with milk produced by mammary glands
order *Carnivora*	Prominent canines and carnassials
sub-order *Pinnipedia*	-Semi-aquatic mammals -Large flippers -Carnivorous feeding at sea
family *Otariidae*	-Small external ears -Walk on land with four flippers
sub-family *Otariinae*	Sea lions

abundant *Otariidae* species in the world (Gales and Fletcher, 1999); with the exceptions of the Guadalupe fur seal, *Arctocephalus townsendi* (Maravilla-Chavez and Lowry, 1999) and the Australian sea lion, *Neophoca cinerea* (Gales *et al.*, 1994), all other otariids are substantially more abundant.

The current breeding distribution of *Phocarctos hookeri* is restricted to the sub-Antarctic islands and is highly localised. Two of the three breeding colonies of *Phocarctos hookeri* are found in the Auckland Islands (Gales and Fletcher, 1999; Wilkinson *et al.*, 2003; Robertson *et al.*, 2006); Campbell Island is the only breeding colony outside this group (McNally *et al.*, 2001; Childerhouse *et al.*, 2005) (Figure 1.1). Solitary breeding sometimes occurs on the Snares Island (Crawley and Cameron, 1972) and a few pups have been born along the Otago coast and on Stewart Island during the last decade (McConkey *et al.*, 2002a; Lalas and Bradshaw, 2003). These areas are also used by adult and juvenile males while straggler adult males reach the Macquarie Islands in the South.

1.2. Ecology

The species exhibits a typical polygamous breeding system and thus shows a large sexual dimorphism, typical of otariid species (Boness, 1991). Males can weigh up to 410kg with a length of up to 3.5m. Females are smaller with a maximum length of 2.0m and a weight of up to 160kg (Walker and Ling, 1981). Adult males are also dark brown whereas females are light grey to creamy (Walker and Ling, 1981) (Figure 1.2). At birth pups weigh around 10kg with an average length of 70cm. Age of maturity is six and four year-old respectively for males and females (Walker and Ling, 1981). The maximum recruitment age for females is reached around eight year-old but the reproduction rate decreases when the females reach 13 year-old (Chilvers, 2005b).

Females give birth to a single pup suckled for up to 12 months during which the females alternate foraging trips at sea and nursing periods on land with an average period at sea of 1.7 days and 1.2 days ashore (Marlow, 1975; Gales and Mattlin, 1997). During foraging trips female New Zealand sea lions were found to dive to the greatest depths for the longest periods of all otariids, and to reach their physiological limits while foraging (Gales and Mattlin, 1997; Costa and Gales, 2000; Chilvers *et al.*, 2006a).

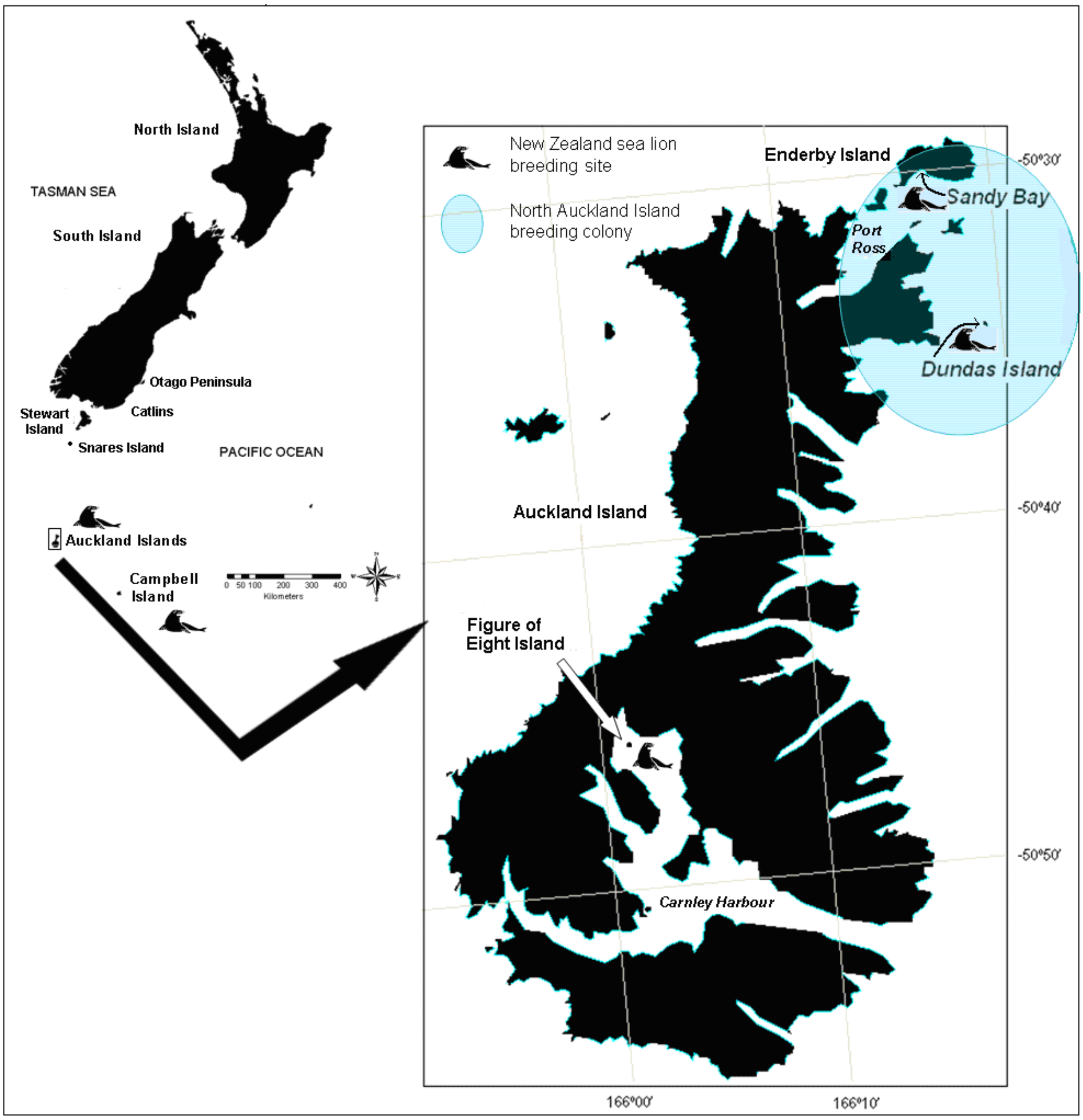


Figure 1.1: Breeding colonies of the New Zealand sea lion at the Auckland Islands: Figure of Eight Island breeding colony; Sandy Bay and Dundas Island breeding sites form one breeding colony regrouped as the North Auckland Island breeding colony.

Marlow (1975), who first studied the species at Sandy Bay, Enderby Island (see Figure 1.1) in the summer season 1972-73, qualitatively described the breeding period. His work was supported by later observations (Chilvers *et al*., 2005a). The species follows the typical breeding pattern of sea lions: polygamy and gregariousness (Peterson and Bartholomew, 1967). The breeding season starts at the end of November when adult males take up ‘harem territories’, from which females can move, at the breeding beach. Males hold these territories for an average of 7.5 days (S.D.=7 days) (Robertson *et al*., 2006). Females appear between December and early January to give birth. They aggregate around the site where the first females (usually a group of 2 to 6 females) land and

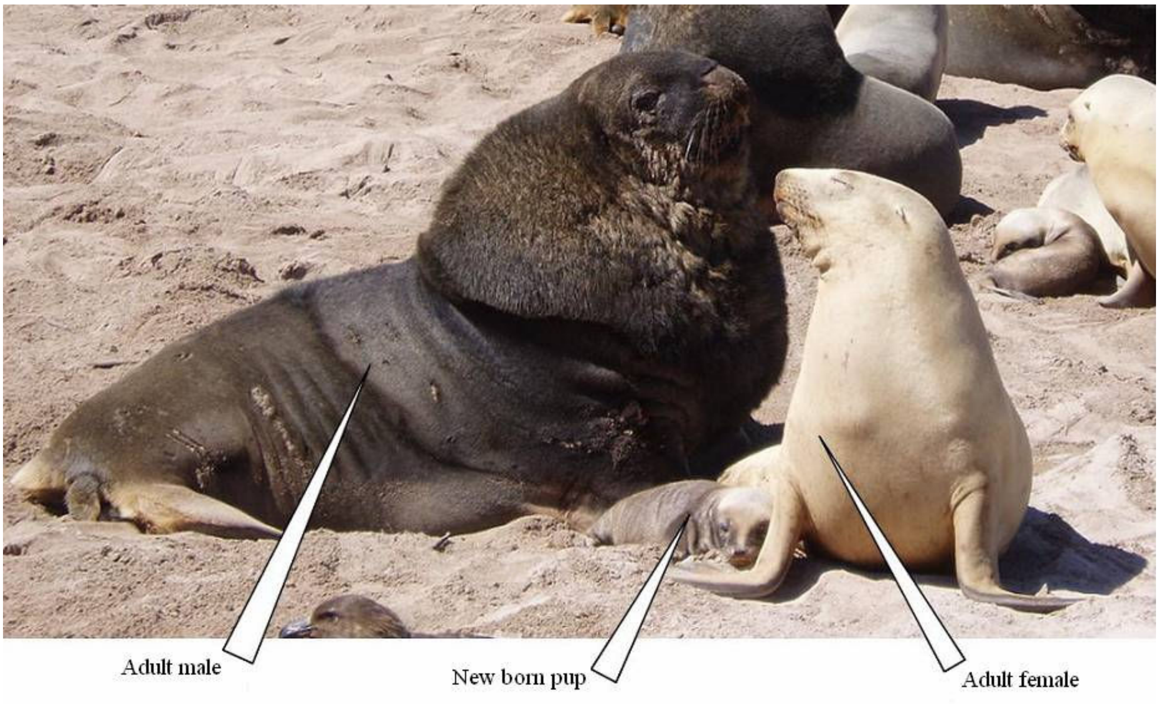


Figure 1.2: Dimorphism between male and female New Zealand sea lions and comparative sizes with a new born pup (photo taken on 24/12/05 at Sandy Bay).

eventually form a mass overlapping the males' territories, with the harem maximum extent reached by mid-December (Chilvers *et al*., 2005a). Marlow (1975, p.181) described the social behaviour of females as '*highly gregarious*'. Mating occurs within a week after the pup is born. After copulation, the females leave for their first trip at sea and the pups gather in pods on the beach. A few days after the last copulations occur (mid-January), the harem breaks up and males begin to leave the breeding beach. The beach is then almost deserted as females move their pups inland, to other beaches or islands (Marlow, 1975).

Females *Phocarctos hookeri* exhibit philopatry and site fidelity (McConkey *et al*., 2002a). This means that the breeding colonies of New Zealand sea lions occur at a permanent site each year. At these breeding colonies, causes of movements witnessed by Marlow (1975) mostly involved aggressiveness of males which was confirmed in Chilvers *et al*. (2005a). Marlow (1975) also noticed that females seemed to get restless around birth, staying in the same site within the harem. Once the harem breaks up, the terrestrial movements of females increase as they are found to go far inland in scrub and rata forest with their pups. This was reported by Marlow (1975) and earlier sailors including Eden (1955).

New Zealand sea lions are able to walk long distances. They have kept the same terrestrial locomotion as their terrestrial ancestors as shown in Beentjes (1989). He emphasised this by looking at the differences with the New Zealand fur seal, *Arctocephalus forsteri,* which does not exhibit the same ability to walk on land due to the use of a different gait. This terrestrial behaviour along with ease of access to the sites where breeding colonies and resting animals occur is one of the factors that led the species to its current threatened status due to past sealing.

1.3. A threatened species

Historically, the New Zealand sea lion was totally extirpated from the New Zealand mainland by the 1830s while the remaining colonies in the sub-Antarctic islands suffered from severe depletions during almost a hundred years (McLaren, 1948; Childerhouse and Gales, 1998).

In addition to the current low abundance of the species and the few breeding colonies, a high mortality of pups can be usual at the Auckland Islands (17% on average, Chilvers *et al*., 2005a, and up to 49%, Gales and Fletcher, 1999). Childerhouse *et al*. (2005) calculated a mortality of pups of 36% at Campbell Island.

The population of New Zealand sea lions also appears to be naturally vulnerable to pathogens. In 1998 a mass mortality due to a bacterial disease at the breeding colonies on Enderby Island and Dundas Island (in the Auckland Islands) claimed 60% of pups and over 20% of adults and juveniles (Baker, 1999). Lento *et al*. (2003) found evidence of low diversity of a gene involved in the Major Histocompatibility Complex (MHC). This result suggested that New Zealand sea lions may have a low resistance to bacterial infections which was suspected to be the major factor resulting in the high mortality due to the bacterial epizootic in 1998 (Lento *et al.,* 2003). In 2002 and 2003, bacteria outbreaks were then recorded (Wilkinson *et al*., 2003). A slow overall decline of 30% in the pup production during the last ten years was also highlighted by Chilvers (2005a).

Because of the vulnerability of the population, the limited distribution of the species, the low population estimate and the few breeding colonies, the New Zealand sea lion was declared as a threatened species by the International Union for the Conservation of Nature (IUCN) in 1997 and is protected by the New Zealand Marine Mammal Protection Act 1978 (Lalas and Bradshaw, 2003; Wilkinson *et al*., 2003). *Phocarctos hookerii* is listed as vulnerable under code D2 “less than five breeding locations” (IUCN, 2004). The species was also incorporated in the New Zealand Department of Conservation Marine Mammal Action Plan for 2005-2010 as a Priority 1 species alongside the Hector’s dolphin, *Cephalorhyncus hectori*, and the Southern right whale, *Eubalaena australis* (Suisted and Neale, 2004).

Indeed several threats contribute to endanger the species. On land, in its current distribution in the sub-Antarctic islands, the only indirect cause of mortality due to human actions was the entrapment of pups in rabbit burrows which killed around 3% of pups each season at Enderby Island before the eradication of rabbits in 1993 (Marlow, 1975; Gales and Fletcher, 1999). The New Zealand sea lion does not face any other threat except natural causes such as diseases, starvation of pups and aggressive behaviours of males towards pups and females (Wilkinson *et al*., 2000; Chilvers *et al*., 2005a).

On the mainland, however, New Zealand sea lions face human disturbance both direct by human activities and infrastructures and indirect through modifications or loss of habitats, pollution and human activities. Childerhouse and Gales (1998) reported six male New Zealand sea lions shot in the Catlins in 1993 and 1994. New Zealand sea lions seem to be tolerant to human disturbance and are recolonising sites close to urban areas such as the Otago Peninsula (Childerhouse and Gales, 1998; McConkey *et al*., 2002a,b). McConnell (2001) nevertheless reported a pup born at Ulva Island that a high number of tourists visit every summer. This human disturbance is thought to be the reason of the failure of this breeding event. McConkey *et al*. (2002b) also recorded a dog attack on a pup at Sandfly Bay, Otago Peninsula, and the disappearance of a pup at Blackhead Beach, Otago coast. The sandy beaches with dune areas along the New Zealand coastlines are also highly used by humans and have been severely modified. They are favoured areas for recreation activities from surfers, ecotourists or walkers, and introduced vegetation, such as marram grass, and sand mining have also led to modifications in topography of beaches and dunes (Johnson, 1992; Wright, 1998; Hilton *et al*., 2000).

At sea, bycatch in the fishing trawl fishery for squid is the most significant anthropogenic source of mortality around the Auckland Islands (Gales and Fletcher, 1999). In 1993, a Marine Mammal Sanctuary (within which commercial fishing is forbidden) was established over a zone of 12 nautical miles (22.2 km) around the Auckland Islands (Gales, 1995). Female New Zealand sea lions were found to use the entire continental shelf off the Auckland Islands as feeding grounds (Gales and Mattlin, 1997; Chilvers *et al*., 2005b), and so the squid fishery still overlaps with the feeding grounds and bycatch continues (Wilkinson *et al*., 2003) (Figure 1.3). A maximum allowable bycatch limit of sea lions was adopted in 1992 (Gales, 1995), which if exceeded, requires the fishery to be closed. This limit is referred as the MALFIRM or Maximum Allowable Level of FIshing Related Mortality. Its calculation, revised every year with the data from the preceding season, combines the minimum population estimate, the maximum net productivity and the recovery factor (Wilkinson *et al*., 2003). This measure was implemented to allow an increase of the number of pups and thus improve the recovery of the population (Wilkinson *et al*., 2003). Combined with adequate management of the recolonisation process, this represents the main conservation policy of the New Zealand Department of Conservation (Suisted and Neale, 2004).

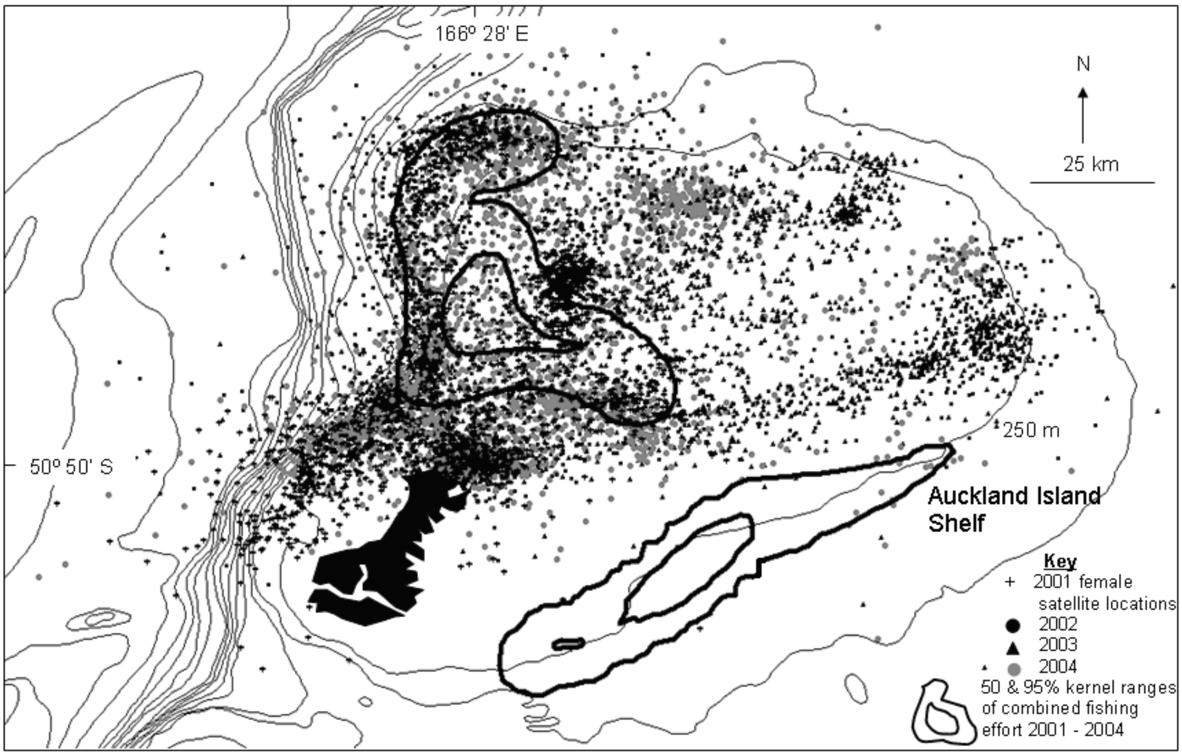


Figure 1.3: Locations of satellite-tagged female New Zealand sea lions (from the Sandy Bay breeding colony) during the breeding seasons 2001 to 2004, and Kernel ranges of fishing activities around the Auckland Islands for the same period (from Chilvers *et al*., 2005b).

1.4. Recolonisation of mainland New Zealand

Male New Zealand sea lions have regularly been reported on sandy beaches at the Otago Peninsula since 1972 (Wilson, 1979; see Figure 1.1), but evidence of adult males using the Otago coast date from the mid-1950s. A picture taken in 1954 at Papanui Beach represents the first confirmed record of adult male in the area since extirpation of the species from the mainland (McConkey *et al.*, 2002b). However, no record of female on the Otago coast was made before 1987 (Hawke, 1993).

The first recorded birth on the New Zealand mainland, since the extirpation of the species, occurred in 1992 (Hawke, 1993). The pup did not survive because of a premature birth (McConkey *et al.*, 2002a). In 1993, the same female gave birth at Taieri Mouth (50km south of the Otago Peninsula) to a second pup that survived (McConkey *et al.*, 2002a). Taieri Mouth was used as the 'pupping site' but 11 weeks after birth, the female and her pup swam to Victory Beach, Otago Peninsula, where the pup stayed afterwards (McConkey, 1997). Since then, it is the only known breeding area of the New Zealand sea lion on the mainland. This female had been tagged as a pup at the Auckland Islands in 1987 but did not show philopatry as she bred at a new site (Childerhouse and Gales, 1998). She was still breeding at Otago and used Victory Beach in 2006 along with her female offspring that have bred at Victory Beach since 1997 (McConkey *et al.*, 2002a). In 2005 the second generation of females born on the mainland also started breeding at Victory Beach with to date 25 pups born from the founder female's lineage, showing philopatry for this site.

A study by Lalas and Bradshaw (2003) indicated, in a stochastic model, that the new breeding group at Victory Beach is likely to be composed of 9 to 22 adult females by 2018, getting closer to the status of breeding population. The status of breeding population is accorded to a breeding group when it reaches 35 mature females exhibiting philopatry (draft New Zealand sea lion Population Management Plan). A new breeding colony would put the species nearer to removal from its threatened status and is one of the main objectives of the different documents where a species management plan is mentioned (Gales, 1995; Suisted and Neale, 2004). In 2006, six pups were born around, and nursed at, Victory Beach. The Auckland Islands are nevertheless the only current significant breeding grounds for the New Zealand sea lion and have a particular environment that influenced both sea lions' behaviour and the survival of the species in the sealing period.

2. Enderby Island, the Auckland Islands and the New Zealand sea lion

2.1. History

The Auckland Islands were discovered in 1806 by Captain A. Bristow of the whaling ship, *The Ocean* (Enderby, 1849). The islands soon became one of the most active sealing stations in the Pacific with up to 60,000 skins returned on a single ship after a season (McLaren, 1936). The main target was the fur seals as their skins were commercially valuable. Even if sea lions were not principally targeted for skins they were for oil and meat. An expedition led by Morrell searched the whole group of islands during the breeding season 1829-1830 and found not one fur seal and less than 20 sea lions. As cited in McLaren (1936, p.363) Morrell concluded "*American and English seamen* […] *have made such clean work* […] *there was not one fur seal to be found on the fourth of January 1830*." Although Morrell's works were not always found to be objective, it is unlikely that he would have lied about the number of sea lions he found (Childerhouse and Gales, 1998).

Following the end of the sealing activity, the islands were left uninhabited until, in 1846, Charles Enderby proposed a plan to create a whaling station and a new British colony at the Auckland Islands (Enderby, 1849). From the 1830s, the islands were already used by whaling ships to refit and wait for the whales to come through (McLaren, 1948). Yet no land base was established by the whalers apart from a few huts. In 1842 or 1843 around 70 Maori from the Chatham Islands had already established a few villages on the main island and one on Enderby Island (Eden, 1955). Following Enderby's project, a small town, Hardwicke, was built in 1849 in Port Ross facing Enderby Island (see Figure 1.1) where around 250 settlers were shipped including families with children (McLaren, 1936). The main activity of men during their spare-time became the capture and kill of the few sea lions still frequenting Port Ross. Unfortunately for Enderby, made Governor of the new colony, the populations of whales had already been significantly depleted and only a few whales were caught during the season. Moreover the soils were revealed to be unable to grow neither vegetables nor crops (Higham, 1991). The colony was eventually abandoned in 1852 and Maori also deserted the islands in 1856 leaving once more the Auckland Islands uninhabited (McLaren, 1948; Eden, 1955). Up to this date cats, mice, cattle, rabbits and pigs had already been introduced in some of the islands of the group, all on Enderby Island (McLaren, 1948).

Another European attempt to start a permanent settlement was drawn in 1874 (McLaren, 1936). Once again this failed after less than three months. This settlement however revealed that fur seals had started coming back to the islands and that sea lions were found in increased numbers (McLaren, 1936).

The New Zealand Government eventually decided to offer the Auckland Islands in auction in 1894 with leases for 20 years (McLaren, 1936). These leases were for grazing only and from this date, 1894, killing of seals (any species) was prohibited. Enderby Island was acquired by a pastoralist from Invercargill for grazing sheep. By the end of 1895 all pastoralists had however left the Auckland Islands as they experienced another failure in breeding sheep and growing crops. Some cattle however survived and were left breeding on Enderby Island (McLaren, 1948).

Human influence on the islands have yet stayed limited as since this last attempt the Auckland Islands have been uninhabited apart from temporary coastwatching during the Second World War (Dingwall, 1981). The group of islands was established as a National Nature Reserve in 1986 in order to preserve its flora and fauna (Penniket *et al.*, 1987). In 1993, a Marine Mammal Sanctuary was declared covering the territorial sea of the islands (12 nmi from the shores) within which commercial take of aquatic life is prohibited (Wilkinson *et al.*, 2003). This allowed protecting part of the feeding grounds of the New Zealand sea lion and limiting bycatch in squid fishery. The Auckland Islands were also listed in the World Heritage list in 1998 (Gary, 2002). In 2003, the area covered by the Marine Mammal Sanctuary was declared a Marine Reserve (Gary, 2002; DoC, 2005).

2.2. Environmental characteristics

The Auckland Islands group lies 465 km south of the New Zealand mainland and is composed of the main island, Auckland Island (51,000 ha), Adams Island (10,120 ha), Enderby Island (710 ha) and several smaller islands (Higham, 1991). They are located in the region of the "Roaring Forties" (-50º lat /166º long), where westerlies and cold fronts are almost persistent. From a weather station based on the main island, it was recorded average wind gusts of more than 35 knots during 280 days per year (Higham, 1991). Charles Enderby however wrote in his application for the new British colony "[…] *the agreeable temperature of the climate, which is very fine* […]. *There are occasional high winds, attended with rains*" (Enderby, 1849, p.11). However McLaren (1936, p.12) differently described the weather at the Auckland Islands as "[…] *astonishingly equable temperature, they are continually subject to wind* […]. […] *hours of sunshine coming as brief intervals between days of driving mist and falling rain*." The temperature is indeed consistent throughout the year with a usual range from 5 to 12 ºC with occasional snowfall anytime of the year as a temporary light cover (Higham, 1991). Periods of sunshine are only an average of 660 h per year (in Auckland City the average of sunshine per year is 2600 h) and rainfall occurs around 300 days per year as light rain or drizzle (but only 200mm rain more than in Auckland City) (Higham, 1991). The weather is very changeable within one day as Eden (1955, p.30) commented with "*The weather was lovely, quite warm with plenty of sunshine*. […] *was soon succeeded by stormy days with high wind and driving rain* […]."

The west coasts of the islands are made of cliffs whereas the east coasts are mostly a succession of deep inlets. Sandy Bay on Enderby Island is the only significant sand dune area in the Auckland Islands (McLaren, 1948; Higham, 1991). The maximum height of Enderby Island is 43 m whereas the summit of the main Auckland Island reaches 659m (LINZ, 1997). The vegetation of Sandy Bay, as well as the general pattern of vegetation of the island, have been modified through burning by farmers and introduced mammals (Taylor, 1970; Dingwall, 1981; Higham, 1991). The small surviving sheep population from the last settlement attempts naturally died out whereas both rabbits and cattle were successfully eradicated from Enderby in 1993 (Torr, 2002). This has led to the re-establishment of native plants (Torr, 2002). The natural pattern of vegetation at Enderby Island is typically tussock lands in exposed areas (*Poa litorosa* and *Poa foliosa* primarily) and forest more inland (dominated by *Metrosideros umbellata*, the Southern rata) with no ground cover, apart from some liverworts and mosses in the most protected zones (Higham, 1991).

Both terrestrial and marine habitats of the Auckland Islands are still considered as one of the least human-disturbed environments in the world (Gary, 2002). They are major resting, breeding and feeding sites for a range of marine mammals, including the New Zealand sea lion and the New Zealand fur seal, and a range of sea birds including the royal albatross, *Diomedea epomophora*, and the yellow-eyed penguin, *Megadyptes antipodes* (Higham, 1991). All species are found on Enderby Island. In order to keep the level of human disturbance at a minimum, the entry to the Auckland Islands Nature Reserve is by permit only delivered by the Department of Conservation. Moreover any visitor or scientific activity must be accompanied by a DoC officer and visitors' landing is limited to some sites, including Enderby Island (Penniket *et al*., 1987).

2.3. Sea lion population at Enderby Island

The history of the Auckland Islands showed that the population of sea lions at Enderby Island had been almost decimated by European sealers and settlers by the 1830s. In 1851, 42 sea lions were slaughtered in Carnley Harbour, likely from the Figure of Eight Island colony that had been less depleted during the European sealing period and settlements (Mackworth and Munce, 1999). A few decades later, reports from diverse sources already mentioned a recovery of the New Zealand sea lion. Childerhouse and Gales (1998) cited Musgrave (1866) who spent a year in the Auckland Islands after a shipwreck and Joyce (1894) who went on an expedition to the islands. Both reported great numbers of sea lions especially in Carnley Harbour, on Enderby Island and in inlets and harbours of the main island. Wilson (1907; cited in Childerhouse and Gales, 1998) commented on the presence of juvenile animals at Enderby Island which corresponded to the first evidence that the species was breeding at the Auckland Islands since the sealing period. Eden's (1955) comments on the number of sea lions at Enderby Island in 1944 seemed to indicate that the population had already built up to its current size which was confirmed through the research by Childerhouse and Gales (1998).

From the first officially recorded count of pups at Sandy Bay in 1965, an estimated 407 pups were born with no apparent increase since this date (Table 1.2). It has been hypothesised in some research on the species (Gales and Mattlin, 1997; Chilvers *et al.*, 2006a) that the Auckland Islands could be a marginal foraging habitat for New Zealand sea lions as it is thought to be the case for the remnant populations of the Hawaiian monk seal, *Monachus schauinslandi* (Baker and Johanos, 2004). This highlights the need of conservation measures that can help to protect the species around the Auckland Islands, mainly against bycatch in fishery, and to enhance the establishment of new breeding colonies on the mainland, which will depend in part of our understanding of the terrestrial spatial ecology of the species.

Table 1.2: Estimates of pup production at Sandy Bay, Enderby Island, between 1965 and 2005 (from Childerhouse and Gales, 1998, and Chilvers, 2005a).

Season	Date of count	Total	**Alive**	Dead
65-66	22/01	407	**407**	-
72-73	12/01	460	**460**	-
74-75	19/01	368	**368**	-
75-76	17/01	406	**406**	-
76-77	19/01	375	**375**	-
77-78	19/01	380	**380**	-
80-81	18/01	375	**375**	-
81-82	17/01	491	**450**	41
83-84	14/01	400	**-**	30
84-85	18/01	446	**446**	-
85-86	4/01	358	**358**	-
86-87	12/01	415	**415**	-
89-90	12/01	379	**379**	-
90-91	14/01	376	**376**	-
91-92	11/01	436	**436**	-
92-93	9/01	424	**408**	16
94-95	14/01	464	**418**	46
95-96	15/01	455	**417**	38
96-97	16/01	509	**473**	36
97-98	16/01	477	**468**	9
98-99	16/01	513	**473**	40
99-00	16/01	506	**482**	24
00-01	16/01	562	**527**	35
01-02	16/01	403	**320**	83
02-03	16/01	489	**409**	80
03-04	16/01	507	**473**	34
04-05	16/01	441	**411**	30

3. Global Positioning System (GPS), remote sensing and Geographic Information System (GIS): Applications in spatial ecology for wildlife conservation

3.1. The concept of wildlife conservation

In a world where human activities affect the environment in so many ways, wildlife are under threat in most parts of the world. Species, such as the New Zealand sea lion, have been hunted and populations dramatically reduced or brought to extinction. Habitats have been modified through urbanisation and agriculture leading to changes in ecosystems and their biodiversity in most areas. These human impacts have increased with the development of modern civilisations and eventually led to the modern concept of wildlife conservation as an attempt to lesser these effects.

Defining wildlife conservation is challenging and differs with the general aims of people and organisations. Wildlife management tends to target species with an economic value and for which management involves influencing or modifying wildlife to meet our needs. Wildlife conservation, on the other hand, tends to consider the protection of all genetic diversity on Earth against our actions, present and past, where possible (Festa-Blanchet and Apollonio, 2003). Today, both concepts tend to be merged as one as wildlife management now also deals with endangered species (Sinclair *et al.*, 2006). All definitions found in literature share one major common point in that the aim of wildlife management and conservation is to ensure that future generations will benefit from wildlife, under the form of resources and recreational opportunities as we do, or did in the past if restoration is possible (Festa-Blanchet and Apollonio, 2003; Hambler, 2004; DoC, 2006; IUCN, 2006; Sinclair *et al.*, 2006).

Although several countries had earlier developed conservation organisations, it was not until the mid-1930s that the concept of wildlife conservation appeared in the vocabulary of international decision makers (Hambler, 2004). The first significant step was made in 1948, when following an international conference, the International Union for the Protection of Nature was founded (IUCN, 2006) followed one year later by the publication of the first Red Data list of threatened species (Hambler, 2004). The IUCN aims to link scientists that study wildlife to decision-makers and politicians in order to conserve and manage the world biodiversity (IUCN, 2006). Each nation is nevertheless responsible for its own wildlife conservation unless the issues concern international areas (high seas and Antarctica) or the species migrate or disperse over several countries (Sinclair *et al.*, 2006). In New Zealand, the Department of Conservation (DoC) is the link between wildlife researchers and decision makers to ensure adequate management decisions to protect New Zealand wildlife.

3.2. Integration of spatial ecology into wildlife conservation

Conservation organisations, including IUCN and DoC, base their lists of threatened species and measures for these species on biologists' work (Festa-Blanchet and Apollonio, 2003). Consequently in the last 50 years methods and equipment for the study of wildlife have been developed and improved to respond to the need to get valuable information on species and ecosystems. This has become a priority to define which, where and in what way wildlife are endangered. It soon became apparent that habitat use, distribution, and movement patterns, regrouped under the term of spatial ecology, play a significant role in wildlife conservation.

"*Spatial behaviour is of great importance to management* [of wildlife]" (Apollonio *et al.*, 2003, p.157). "*One of the main needs to conserve animal populations is to know where individuals go at different times and how far they can disperse*." (Festa-Blanchet and Apollonio, 2003, p.31). "*Habitat use is a critical facet in the management of a wildlife species*" (White and Garrott, 1990, p.183). "*Effective management of wildlife population largely depends upon understanding and predicting their habitat needs*." (Clark *et al.*, 1993, p.519). These are all quotations from books and papers discussing how spatial ecology can play a crucial role in wildlife conservation. This is especially relevant when considering large animals (e.g. Bian and West, 1997), migrating populations (e.g. Brower and Malcolm, 1991), or wide-ranging species (e.g. Marker and Dickman, 2005). As pointed out by Beissinger (1997), conservation of recovering species, such as the New Zealand sea lion through its current recolonisation of the mainland, greatly depends on our understanding of their spatial ecology. Taking the example of two species of large predators of North America, Apollonio *et al.* (2003) illustrated the importance of scientific knowledge about movements on conservation strategies for natural recolonisations.

Spatial ecology relies on methods to survey and analyse large areas and numerous entities over time to determine how animals use, move and migrate within these areas. Investigating individual differences is an important step that may identify what are the driving factors that lead to the spatio-ecological characteristics of a species. Festa-Blanchet and Apollonio (2003) outlined that it is not only important to investigate a population's spatial ecology but also to be able to detect individuals' behaviour as "*individual differences in age, sex* […] *can all affect how an animal reacts* […] *and may determine the* *success or failure of a management strategy*" (Festa-Blanchet and Apollonio, 2003, p.6). As a consequence spatial ecology studies require large amounts of detailed geographic and biological data, including identity and status of the animals as well as habitat data, and methods to combine all these data and draw appropriate conclusions. The lack of spatial methods of analyses has always been a challenge for biologists, and a technical obstacle to produce valuable scientific knowledge that may be applied to wildlife management and conservation. For the last 20 years GPS, satellite imagery, and GIS have provided significant advances to meet the requirements of such wildlife studies.

3.3. Insights into GPS, satellite imagery and GIS

3.3.1. GPS

GPS is a system that can give the geographic location of any point at the surface of the Earth based on a constellation of satellites. The theory of GPS was developed during World War II by the U.S. Department of Defence for purposes such as positioning of ships and planes as well as military mapping (Pace *et al.*, 1995). The TRANSIT system was available by 1967 but was slow and started to be replaced by the NAVigation System with Timing And Ranging (NAVSTAR) GPS in 1973 (Pace *et al.*, 1995). In 1994 the system was completed when all the 24 NAVSTAR satellites had been launched by the U.S. Air Force, and are nowadays orbiting at an approximate altitude of 26,000km in space around the Earth (Hofmann-Wellenhof *et al.*, 2001). GPS is thus composed of these 24 satellites, a master control station in Colorado, USA, and smaller ground stations around the world. The satellites are positioned such as at least four satellites are visible at any time and at any point around the globe (excluding screen effect of mountains, vegetation, buildings etc).

The user moves or positions itself on the ground with an individual receiver. The satellites send continuous signals, coding the times and their locations, towards the Earth. These signals are picked up by the user's receiver which, by triangulation, determines the parameters (latitude, longitude and altitude) of its location. The degradation of the signals through the atmosphere, changing over time and space, as well as orbit and satellite clock errors, leads to a decrease in the timing accuracy and, thus, in the accuracy of the point location (Hofmann-Wellenhof *et al.*, 2001). These main sources of inaccuracy can be reduced by using a Differential GPS (DGPS). DGPS uses a fixed base station of exact known location, equipped with a fixed GPS receiver. Since the location is known, variation in the atmosphere and its effects on the satellite signals are deduced and can be applied to correct locations obtained simultaneously from a roving receiver, which for the best results should be located less than 500km from the base station. The theory, errors and mathematics behind GPS and DGPS are explained in details in Hofmann-Wellenhof *et al.* (2001).

A wide range of GPS receivers are available for civilian users, each giving a location with various accuracies up to sub-centimetres for professional surveying purposes. The accuracy varies with the number and the geometry of the satellites used to compute a position. The more satellites are used the more accurate the location is. The accuracy is also related to the PDOP (Position Dilution Of Precision) determined by the geometry of the satellites visible from the receiver on the ground (Hofmann-Wellenhof *et al.*, 2001). This geometry is considered as good if PDOP is under six and very good if it is under three (Hofmann-Wellenhof *et al.*, 2001). Generally, the more satellites are used and the lower the PDOP is the better the accuracy of the location gets. Both PDOP and number of satellites can be predicted for a specific area from an almanac of the satellite positions giving, for any time of each day, these values. The user can thus determine when are the best periods to use the GPS in order to get the best accuracy as possible.

3.3.2. Satellite imagery

Satellite imagery is a remote sensing technique based on the electromagnetic radiations reflected or emitted by the ground surface of the Earth (Campbell, 2002). Unlike aerial photos, another remote sensing technique, satellite imagery uses the spectral differences in energy specific to a particular type of surface. The detailed principles behind satellite imagery and its interpretation are explained in Campbell (2002). Descriptions of aerial photography and its techniques are available in Lillesand and Kiefer (2000).

The first satellite imagery sensors, such as TIROS and Landsat, were launched in the 1960s and early 1970s for meteorology purposes (Campbell, 2002). To date, the spatial resolutions (the size of a pixel) of satellite images are still improving and already reached the sub-metre level. In Panchromatic imagery Ikonos gets 1.00m resolution while Quickbird gets up to 0.61m resolution, currently the highest public resolution available (see Infoterra, 2005). Satellite imagery allows mapping habitats over large areas with automated classifications based on sample points that indicate what spectral (radiance characteristics) and spatial (shapes and geometric patterns of the image) patterns correspond to which habitat (Lillesand and Kiefer, 2000). Quickbird images, with a higher spatial resolution than

Ikonos, were found to be as spectrally accurate in panchromatic format using an object-orientated classification as Ikonos images (Wang *et al.*, 2004).

Both satellite imagery and aerial photography can be used for habitat mapping through digital classification techniques (Lillesand and Kiefer, 2000). Despite the increase in accuracy of satellite imagery, aerial photography still produces more detailed maps. However they are not suitable for large areas or remote locations where flying is not possible or too expensive. Satellite imagery however can be used for any location on the Earth and can cover extensive areas.

3.3.3. GIS

Both GPS and satellite image techniques require a computerised system that allows users to deal with a high quantity of spatio-temporal information from various provenances. This system is called a Geographic Information System (GIS). Its development started in the 1980s when GIS softwares were produced (Schuurman, 2004). They are specialised in handling digital spatial information and proceed by overlay analyses of spatial information. Layers can contain information in the form of a *vector* i.e. discrete entity (point, line or polygon) or *raster* i.e. continuous field (made of pixels). Each vector is associated with attributes that define the object. ArcGIS is a GIS that can combine both types of data and compute spatial analyses (see ESRI, 2006).

GPS data are visualised and analysed with GIS although each GPS feature not only has a latitude, a longitude and an altitude, but also has a date and time associated to it. This consequently integrates a temporal component in spatial analyses that is still a challenge for GIS technologies. Rucker (1977; cited in Landgran, 1993) already clearly defined that every physical object is a state pattern in a four-dimensional space-time block and that time thus can not be eliminated as traditional cartography does. His thought already pointed out that time is an essential component of spatial analysis such as those computed by a GIS. Nevertheless time is still a difficult factor to incorporate into the rather non-dynamic GIS. Side extensions working under a GIS, such as the Hawth's Analysis tool working with ArcGIS (see Beyer, 2004), were specially designed for ecological studies and offer a range of pre-programmed functions to analyse wildlife spatial ecology e.g. analyses of movements in a temporal context.

3.4. Applications of GPS, satellite imagery and GIS in spatial ecology for wildlife conservation

The combined use of GPS data, satellite imagery and GIS now gives scientists the opportunity to investigate wildlife spatial ecology. Using GPS to get locations in space and time of individuals and satellite imagery to produce habitat maps and elevation models, GIS can highlight spatial patterns of wildlife not studied before because of a lack of appropriate tools. Numerous studies have shown the advantages and performances of advanced GIS functions and precise spatial data to investigate wildlife spatial ecology in a conservation context as presented in this section.

3.4.1. General applications

The study of wildlife movements and habitat use depends on our ability to get animals' locations over time. Two distinctive methods can be used. The 'homing-in' technique consists of an observer finding the animal and recording its GPS location whereas the 'satellite tracking' technique involves animals equipped with a transmitter, attached to them, that sends or records the satellite locations (White and Garrott, 1990). Both techniques have advantages and inconveniences. Requiring the presence of an observer makes the 'homing-in' technique time consuming and may disturb the animals. It also requires that individuals are identifiable. On the other hand this technique allows getting accurate locations and detailed comments on behaviours and state of the animals. A great advantage of the 'satellite tracking' is that it can be done in any environment (including marine) and with more complete data in time. However this technique necessitates expensive equipment and may be intrusive when the transmitters are placed and retrieved on wildlife. Due to the fact that the transmitters are expensive, fewer animals can be followed than with the 'homing-in' technique. White and Garrott (1990) highlighted that, consequently, the technique used for a study of wildlife movement must be carefully chosen depending on the target species, the environment and the questions to answer.

In Japan, the population of the gray-faced buzzard eagle, *Butastur indicus,* is currently declining and was studied through a 'homing'in' technique. Matsuura *et al*., (2005) investigated the species' habitat use by means of line transects to estimate where the species was found, and a digital model of the vegetation and landscape in order to assess the potential habitats to protect. In the same way, individuals of a freshwater turtle species of the East coast of North America, the spotted turtle, *Clemmys guttata* (populations are listed from vulnerable up to endangered depending on the geographic location), were radiotracked during three field seasons (Litzgus and Mousseau, 2004). At each radio location, a GPS position was taken as well as date, time, behaviour, habitat and weather. Two parts of the analyses focussed on habitat use and movement patterns comparing data amongst years and sex classes. The results helped in understanding the reproduction system of this threatened species. Several conservation recommendations were expressed in conclusion of this study (Litzgus and Mousseau, 2004).

Approaches using satellite images to characterise the habitat are also found in the study of wildlife spatial ecology for conservation purposes. Grizzly bears' habitat was classified using satellite images, and then integrated into a GIS to detect cover type or vegetation preferences (Agee *et al.*, 1989). This was done to determine the potential of grizzly bear encounters with humans in order to manage the human/bear interactions. Habitat characteristics important to species can be identified with satellite imagery to protect special habitat threatened by human activities but essential for wildlife (e.g. the wild turkeys in Glennon and Porter, 1999; e.g. the great bustards in Osborne *et al.*, 2001). Studies using high-resolution satellite imagery to map habitats showed that analysing habitat use and predicting the distribution of animals could also be done at finer scales whereas low-resolution satellite imagery only allows the detection of broad patterns (Shanahan, 2004; Wang *et al.*, 2004; Laurent *et al.*, 2005).

Satellite tracking has been extensively used to give insights into the marine spatial ecology of pinniped species using the combine method of satellite transmitters and GIS analyses. Twenty female and two male South American sea lions, *Otaria flavescens*, were satellite-tagged and followed during their trips at sea in order to understand where interaction with fishery happens (Campagna *et al.*, 2001). Huckstadt and Krautz (2004) completed this first research in using GIS and geostatistics to model the interactions with fisheries. Studies with the same aims were also realised for harbour seals, *Phoca vitulina* (Bjørge *et al.*, 2002), South American fur seals, *Arctocephalus australis* (Thompson *et al.*, 2003), crabeater seals, *Lobodon carcinophagus* (Southwell, 2004) as well as for New Zealand sea lions off the Auckland Islands (Chilvers *et al.*, 2005b). Even if most spatial ecological studies of pinnipeds took place in the marine environment, especially due to the negative interactions with fishery, the same valuable methods can also be used to investigate the terrestrial spatial ecology to acknowledge that conservation measures are also required in this environment.

3.4.2. Applications for pinnipeds in terrestrial environment

A few studies have already looked at terrestrial spatial behaviour of pinnipeds. Each of these incorporated GPS, remote sensing or/and GIS showing how these technologies can adequately be adapted for the study of terrestrial ecology. Satellite tagging of females can show where individuals go and haul-out however they do not give any insight into the spatial ecology once ashore, especially since satellite telemetry has a limited accuracy (e.g. mean best Argos accuracy 226m; Vincent *et al*., 2002) and transmitters are usually equipped with a dry switch off system to save the batteries (Lunn and Boyd, 1991; Trites and Porter, 2002; Raum-Suryan *et al*., 2004; Chilvers *et al*., 2006a). Such studies can give large scale site fidelity and philopatry for a site but, due to the low accuracy, can not assert the importance of fine-scale spatial patterns.

Godsell (1988) looked at the haul-out behaviour of harbour seals. Despite a fair amount of fieldwork and data collected, the analyses of this study did not effectively use the spatial information due to a lack of spatially orientated tool for analysis. The quality of data collected would have been better used nowadays with the development of GIS to analyse them. The same conclusion was drawn for another study by Pomeroy *et al.* (1994) that looked at spatial behaviour of the grey seal, *Halichoerus grypus*. The improvement of the analysis of spatial patterns ashore was then demonstrated in later studies with more powerful and accurate results with spatial analyses hardly feasible without the use of GIS (Pomeroy *et al*., 2000).

To study the fine-scale terrestrial spatial ecology of grey seals, locations of animals were obtained by observers in the field (Pomeroy *et al*., 2001) and with aerial photography (Twiss *et al*., 2000) with respectively mean accuracy of 5m and 0.2m. Both studies used a GIS database to digitise individuals' locations from sketch maps or aerial photos. By using aerial photos, Twiss *et al*. (2000) were unable to identify specific individuals whereas with the field observations, in the study by Pomeroy *et al.* (2001), branded females could be located and their behaviours recorded. Both studies gave valuable insights into spatial ecology. Being able to recognise individual females, Pomeroy *et al.* (2001) showed high site fidelity (median distances of breeding sites of 55m independent of the number of years) and a low daily movement of less than 10m around the pupping site. They also linked reproductive performance to spatial patterns and relatedness amongst females. Females within a 30m radius were found to be closely related indicating philopatry. With a high topographic resolution Twiss *et al.* (2000) were able to detect fine spatial patterns in the choice of a breeding site by females. Females chose slopes less than 45º, with the least ‘cost-distance to nearest access point’ sites being occupied by the first females that arrived. A seasonal variation in the mean distances amongst females was also detected showing a change in the degree of aggregation throughout the breeding season. As a whole fine-scale topography and individual recognition combined with GIS analyses of female grey seal locations were found to be highly valuable techniques to investigate terrestrial spatial ecology and relate it to species fitness through reproductive performance. Conservation of grey seals’ populations can be improved with the results of the studies mentioned above. Habitat use of grey seals is indeed an indication on how females choose where they breed and which kind of habitats allow a better fitness for the species.

Terrestrial spatial ecology of pinnipeds can thus effectively be investigated with GPS, remote sensing and GIS technologies. Results from such studies were significantly valuable to improve knowledge in spatial ecology and improve the conservation of endangered or threatened species. This is the reason why a method based on these similar techniques was adopted to investigate for the first time the terrestrial spatial ecology of the New Zealand sea lion in the present study.

Finally the objectives of the study were thus to use GPS, satellite imagery and GIS, in order to investigate female New Zealand sea lions’ movements at the Sandy Bay, Enderby Island, breeding colony. Quantifying in space and time these movements was necessary to gain knowledge on spatial ecology.

CHAPTER TWO: GENERAL METHOD

STUDY SITE, STUDY POPULATION AND GEODATABASE

> “*‘The scientific method,’ T.H. Huxley once wrote, ‘is nothing but the normal working of the human mind.’ That is to say, when the mind is working, that is to say further, when it is engaged in correcting its mistakes.*”
>
> N. Postman

1. Introduction

In this chapter, the study area, study population and sample population are described. The data acquisition during fieldwork and preparation of these data for analyses are also presented. The exploration of the spatio-temporal characteristics of the data was realised in order to decide on the best tools for analyses and determine the techniques that could be used to describe, quantify and model the principal features of the datasets. The construction of the geodatabase for incorporation into a Geographic Information System (GIS), which was used for the analyses in the following chapters, is then explained. The habitat type map, the Digital Terrain Model (DTM), the slope map, and the slope orientation map are illustrated at the end of the chapter after explanation on how they were produced.

2. Material

2.1. Study area

Enderby Island, in the Auckland Islands group, has an area of 7.1 km^2 and provides the only significant sandy beach and dune land of the Auckland Islands, named Sandy Bay (SB) (-50.50º S /166.28º E), where the second largest harem of New Zealand sea lions occurs. The study area covered an area of 0.7 km^2 (10% of the island) including beach, dune land, part of scrub and forest adjacent to SB (Figure 2.1). It was delimited using known occurrence of females from previous fieldwork as well as vegetation features limiting the access to both the observers and sea lions. The farthest point of the study area was situated at a straight-line distance of 780m from the beach. The sandy beach is 400m long and is bounded by rocky shores and cliffs (the type of shore habitat found around the rest of the island). The width of the sandy beach around where the harem occurred varied from 43m at low tide to 24m at high tide. At mean sea level the width of the beach was 34m.

The vegetation of Enderby Island was described in a review by Taylor (1970). From his results and field observations, the habitat of the study area was separated in eight classes: rock, sand, low sward, high sward, scrub, forest, tussock, water (descriptions in Table 2.1). These classes incorporated consideration of the potential influence of the vegetation on sea lions. Rock and sand are substrates where walking ability is differentially affected. In vegetated areas the walking is also affected depending on the height and the strength of the plants. Height and coverage of vegetation may also have an influence on the

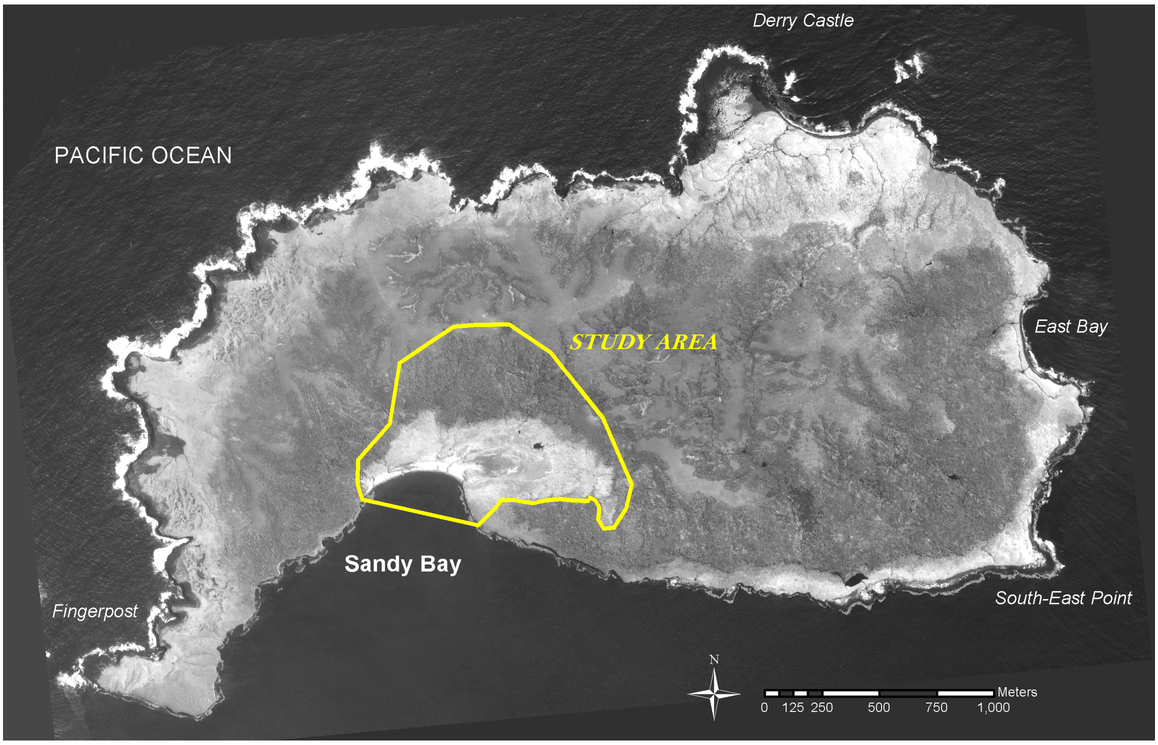


Figure 2.1: Outline of the study area at sandy Bay on the Quickbird panchromatic satellite image of Enderby Island.

protection that it offers against wind, rain and other individuals. For these reasons the sward was split into two classes: low sward where vegetation does not offer any protection and does not disturb walking, and high sward, where adult sea lions are not visible once laying on the ground. Scrub habitat was distinguished from forest due to its relative difficulty in going through, i.e. hard low branches where paths are limited, whereas in the forest the ground is only covered with mosses and grass plants. The access to both scrub and forest is reduced due to the belt of very dense and impenetrable scrub formed around most of the dune land. Some tracks and a few zones where there is not or less dense scrub were the only entrances to the forest from SB to both the observers and sea lions.

2.2. Study population

The study population was the female New Zealand sea lion population of the SB breeding colony. A total of 397 and 480 females bred respectively in 2002 and 2003 at SB. These numbers were obtained by counting the number of pups born at SB. Up to 20 January, 24% (in 2002) and 18% (in 2003) of pups did not survive. The number of non-breeding females using SB was not recorded as within the harem there was no possible distinction from breeding females. Non-breeding females were the females who were sighted at SB

Table 2.1: Definitions and illustrations of the different habitat type classes found in the study area at Sandy Bay (Enderby Island). The classification was based and adapted from the descriptions in Taylor (1970). Illustrations represent a sample and are not exhaustive as vegetation classes were based on morphology of the community and thus regroup several species.

Habitat type	Description		
Rock	Rocky shorelines and rocks emerged at mean sea level		
Sand	Sandy beach and sandy areas with pebbles		
Low sward	Short grassland (less than 30cm high) including *Rumex spp.* (A.), Bidi bidi (*Acaena minor*) (B.), liverworts, European daisy (a weed)...	 	
High sward	High grassland (where sea lions when lying on the ground are not visible) including introduced pasture grass (C. and D.), and megaherbs such as the Macquarie cabbage (*Stilbocarpa polaris, E.)*	 	
Scrub	Short woody vegetation (mostly *Myrsine divaricata, F., and Hebe elliptica, G.*) with no trunc, spreading on the floor up to 1.5m high and hard to go through		
Forest	Southern rata forest (*Metrosideros umbellata*)		
Tussock	Field of tussock (*Poa litorosa*) along the exposed shores (with low sward on the non-covered floor)		
Water	Ocean, lakes, streams, ponds		

each year without rearing a pup. These females were likely to be present at SB to mate in the harem and were thus temporary non-breeding for a particular season only.

As a Pinniped species, New Zealand sea lions need to go to sea regularly to feed. Breeding females look after their pups for up to 12 months during which they alternately nurse their pups onshore and leave their pups alone to feed at sea. Non-breeding females however do not have to exhibit this rhythm in the presence at breeding colonies as they do not have to nurse a pup. The time in between two departures at sea is called a ‘foraging cycle’ and is thus made up of a period at sea (a ‘foraging trip’) and a period ashore (a ‘nursing period’). Figure 2.2 illustrates these terms with the example of females from the study population. There is, however, a period including days before and after birth during which the females stay ashore all the time. This period is called the ‘pupping period’ and ends when the female goes to her first foraging trip after birth. The size of the study population thus varied everyday as the duration of foraging cycles varies. The mean length of a foraging trip at SB during seasons 2002 and 2003, was 4.0 days (n=12), with 3.0 ± 0.9 days at sea and 1.0 ± 0.4 day ashore while the minimum average recorded was 0.9 day at sea and 0.6 day ashore and the maximum average was 4.0 days at sea and 1.5 days ashore (data adapted from Chilvers *et al.*, 2005b). In order to deal with this variation, it was considered that the daily study population was formed by the females ashore during any one day without accounting for females at sea on this specific day. However the overall study population was the whole breeding population of females at SB each year.

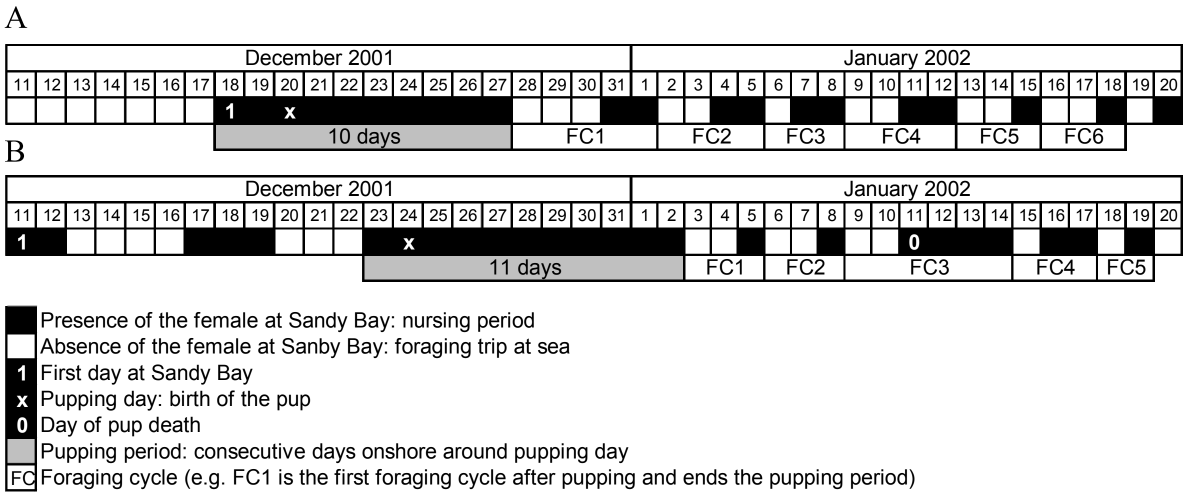


Figure 2.2: Illustrations of foraging cycles and pupping periods for two breeding females of the sample population in season 2002 from 11/12/01 to 20/01/02 (A: female 1369; B: female 1379, her pup died on 11/01/02).

The foraging cycle also implies that if a female was found within another habitat than the beach at SB, after she came back from a foraging cycle, she must have come ashore at the beach (only potential shore access within the study area) and walked to her current location from there. Conversely, when a female went to sea, she must also have used the beach and walked from where she was. Consequently, the 'pupping period' constituted a period when consecutive sightings calibrated the minimum distance a female moved. Before and after this period, two consecutive sightings, with one or more days of the females' absence at SB, represented the location where the females left the beach and the location where she went when she came back to SB after a foraging trip.

2.3. Sample population

In 2000, within the study population at SB, 135 adult females (ages based on the post canine method; see Childerhouse *et al.*, 2004) were branded by the New Zealand Department of Conservation in order to get precise data on population dynamics (see Wilkinson *et al.*, in press, for the method of hot-iron branding). During this season all 135 females had pupped at SB. Plastic flipper tags are also used for this purpose but have a high loss rate and can become unreadable, and consequently, are not as accurate as branding data for the management of the species. In rain or wet weather, tags are also covered with sand or pieces of vegetation and are therefore illegible whereas brands are still visible. The sample population was thus the group of branded females using Sandy Bay during the two study seasons (88 and 89 individuals, in total 117 different animals). Branded females were easily identifiable and sightings were independent of the weather. This sample population corresponded to 18% and 16% of the total breeding female population at SB respectively for the two study seasons. Brands were placed only on the left side of the female and are composed of four digits between 1364 and 1500 (Figure 2.3). Pups of branded females were also marked with non-permanent marker caps glued on their heads in order to detect if and where the pup died.

The sample population was composed of females aged 6 to 18. A status was given to each branded female of the sample population at SB for each study season: *breeding alive pup* (BR-if the pup survived), *breeding dead pup,* (BDP-if the pup died) and *non-breeding* (NB-when a female did not pup). Another temporary status was *expectant* which categorised breeding females until they gave birth and was mainly used to record the dates of birth. The average ages of the branded females were 10 and 11 years old respectively for the two study seasons. Table 2.2 summarises the numbers of individuals of each status

Figure 2.3: Photos of brands of female New Zealand sea lions at Sandy Bay (examples of females 1498 and 1445). The brand was only put on the left side of the animal.

depending on their ages. Considering the whole population of branded females (n=135), 57% of them bred during both seasons, 16% bred during one season but did not breed during the other season, 27% were non-breeding or not seen at SB during both seasons (including 3% known dead). Figure 2.4 shows the daily numbers of females at SB (study population) including the fraction represented by branded females (sample population) for the period 12 December to 20 January during both seasons (after this date females started leaving the beach and thus female counts were stopped). The sample population represented on average 13.5% per day (S.D.=3.0%) of the study population with a maximum of 25.0% and a minimum of 7.6%. The maximum number of branded females encountered at SB during one day was 59 on 31/12/03 (maximum harem extent) and the minimum was 1 on the first and last days of the study.

Table 2.2: Numbers of females of the sample population in cohort ages and numbers within each status cohort: bred and the pup survived (*Breeding alive pup*), bred but the pup died (*Breeding dead pup*), and females that did not breed during the season (*Non-breeding*).

			Breeding alive pup		*Breeding dead pup*		*Non-breeding*	
Age	**2002**	**2003**	**2002**	**2003**	**2002**	**2003**	**2002**	**2003**
6	1	0	1	0	0	0	0	0
7	3	1	2	1	1	0	0	0
8	6	3	3	1	2	1	1	1
9	16	7	13	5	2	1	1	1
10	24	17	13	12	4	3	7	2
11	12	19	11	15	1	1	0	3
12	9	15	7	12	2	2	0	1
13	4	11	2	9	1	1	1	1
14	1	5	1	5	0	0	0	0
15	5	1	1	1	0	0	4	0
16	2	2	2	1	0	1	0	0
17	1	2	1	1	0	0	0	1
18	0	1	0	0	0	1	0	0
unknown	4	5	2	3	1	1	1	1
total	***88***	***89***	***59***	***66***	***14***	***12***	***15***	***11***

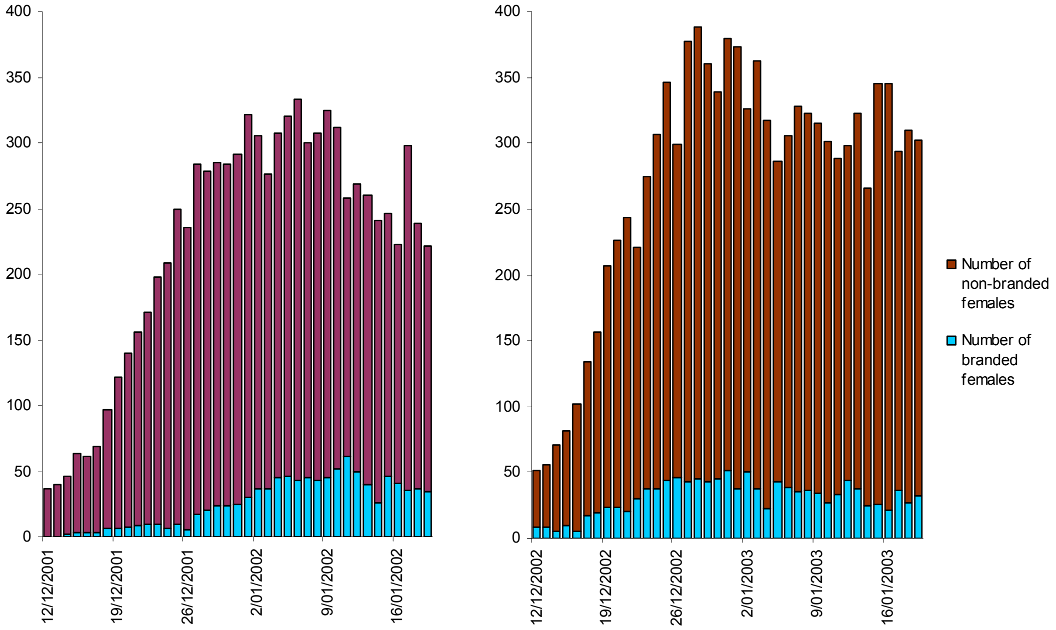


Figure 2.4: Numbers of branded and non-branded females on the beach at Sandy Bay from 12/12 to 19/01 for season 2002 and season 2003.

3. Data acquisition

3.1. Females' locations and harem extent

Surveys of the study area were undertaken by an observer every day during two breeding seasons, season 2002: from 6/12/01 to 18/02/02 (75 days), and season 2003: from 6/12/02 to 21/03/03 (106 days). The field method used was the 'homing-in' technique to gather individual information such as status and death of pups. During these daily surveys, a Global Positioning System (GPS) location, with the four digits of the female's brand and her status for attributes, was recorded for each of the branded females found onshore. These daily surveys were kept at four consecutive hours in order to keep the survey as a snapshot of the female population and the surveys as independent observations. The fieldwork was carried out with a handheld GPS Garmin 12, giving an accuracy of 2 to 3m (Garmin International Inc., USA) using the geographic coordinate system New Zealand Geodetic Datum 2000 (NZGD2000; based on the Geodetic Reference System 1980 ellipsoid). Due to the compactness of the harem, sketch maps of females' positions within the harem were hand drawn and GPS points of permanent ground indices (rocks, streams, sticks), and of the harem boundaries on the day, underlined the sketch maps and were later used to determine the latitudes and longitudes of the locations with a maximum error of 1 to 2 m. The sketch maps were drawn from a high observation point allowing an overview on the whole harem. A total of 1828 and 2424 GPS branded females' locations onshore were taken during seasons 2002 and 2003 respectively.

3.2. Terrain and habitat data

Prior to the field work, an almanac of the satellite positions and PDOP values was produced for SB with Trimble GPD-Pathfinder Office Software for the period during which the fieldwork was conducted in order to know when the best dates and times for the data acquisition were. A set of elevation points, based on transects spaced from 2 to 10 metres, was taken throughout the study area in December 2005 and January 2006 using a handheld GPS GeoExplorer 3 (Trimble Navigation Ltd., USA) with geographic coordinate system NZGD2000. Additional points were also taken all around lakes and following streams as well as around any significant terrain features. The vegetation types however limited the number of transects possible within some areas. The scrub areas were inaccessible if there were no sea lion or penguins' tracks that could be followed. Points within rata forest were also limited to a few areas only. Consequently the number of elevation points was smaller in these vegetation types. The set of elevation points is illustrated in Figure 2.5.

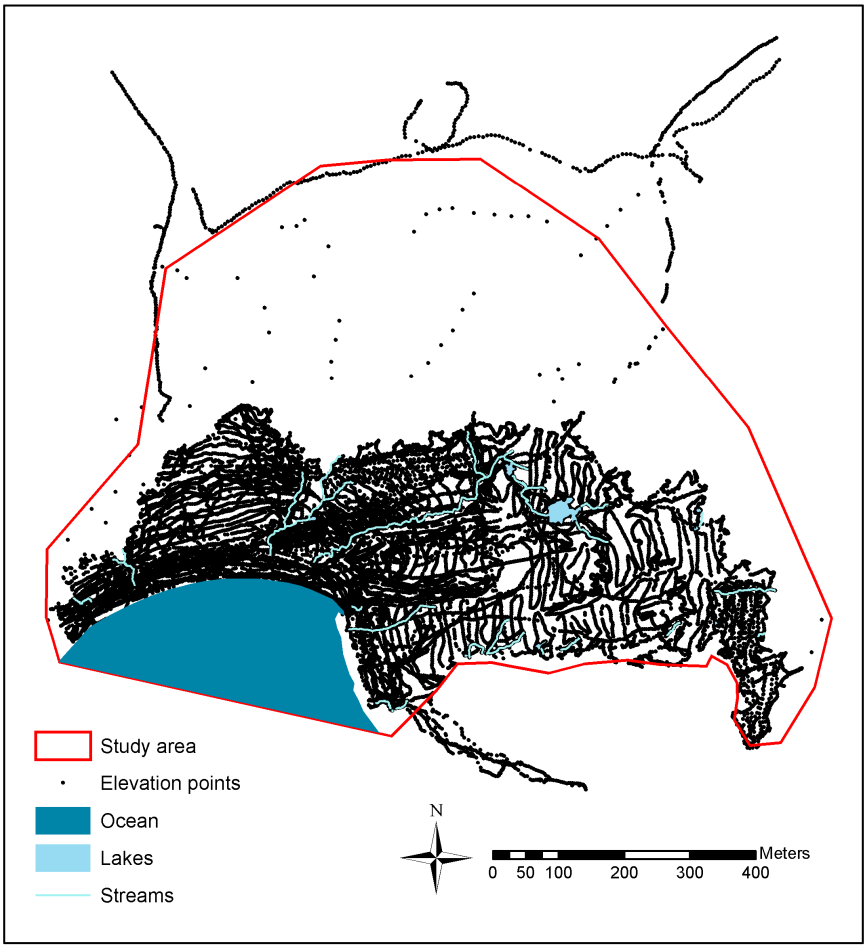


Figure 2.5: Elevation points used for the modelling of the terrain of the study area at Sandy Bay, Enderby Island with outline of the study area.

A Quickbird panchromatic satellite image (pixel size 62cm) of Enderby Island (in geographic coordinate system NZGD2000) was acquired on 31/12/05 with a total cloud free area. Forty Ground Control Points (GCP) were taken using the handheld GPS GeoExplorer 3 (Trimble Navigation Ltd., USA) in December 2005 and January 2006 at Enderby Island to georectify the Quickbird satellite image. Twenty-three habitat sample points were also taken with the GeoExplorer 3 to support the classification of the satellite image into the different habitat classes.

4. Data exploration and geodatabase preparation

4.1. Exploration of the spatio-temporal characteristics of the data

In order to adequately address the main objectives of the thesis, the datasets corresponding to the females' locations were explored using SPSS 14.0. Visualising the data in a spatio-temporal context was used in order to appreciate which analysis methods and tools would be the most appropriate. 3-D scatter plots (x, y, z) for each study season, with x as longitude, z as latitude and y as time, were produced. As Figure 2.6 demonstrates, the females used the study area according to a spatio-temporal pattern including two phases: a 'harem phase' and a 'dispersion phase'. These two phases similarly appeared on the graphs during both years. Consequently the analyses of the female New Zealand sea lions' spatial ecology at SB must include a temporal factor rather than static geographic analyses as GIS is mainly built for (O'Sullivan, 2005).

4.2. ArcGIS: main spatial tool

ArcGIS was used as the main tool, alongside SPSS 14.0 for advanced statistical analyses, in order to gather, visualise, organise, quantify and conduct spatial analyses. ArcGIS is composed of different modules. ArcCatalog is where the geodatabase and files are created, stored and accessed to be used within other modules of the program such ArcMap and ArcScene. ArcMap allows the visualisation of the layers within a 2-D environment, the modification and creation of entities within a layer, the creation of maps, the determination of areas and distances and the application of statistical and other analyses through diverse extensions. ArcScene allows 3-D visualisations based on elevation models. The geographic and projected coordinate system used throughout the thesis was NZGD2000.

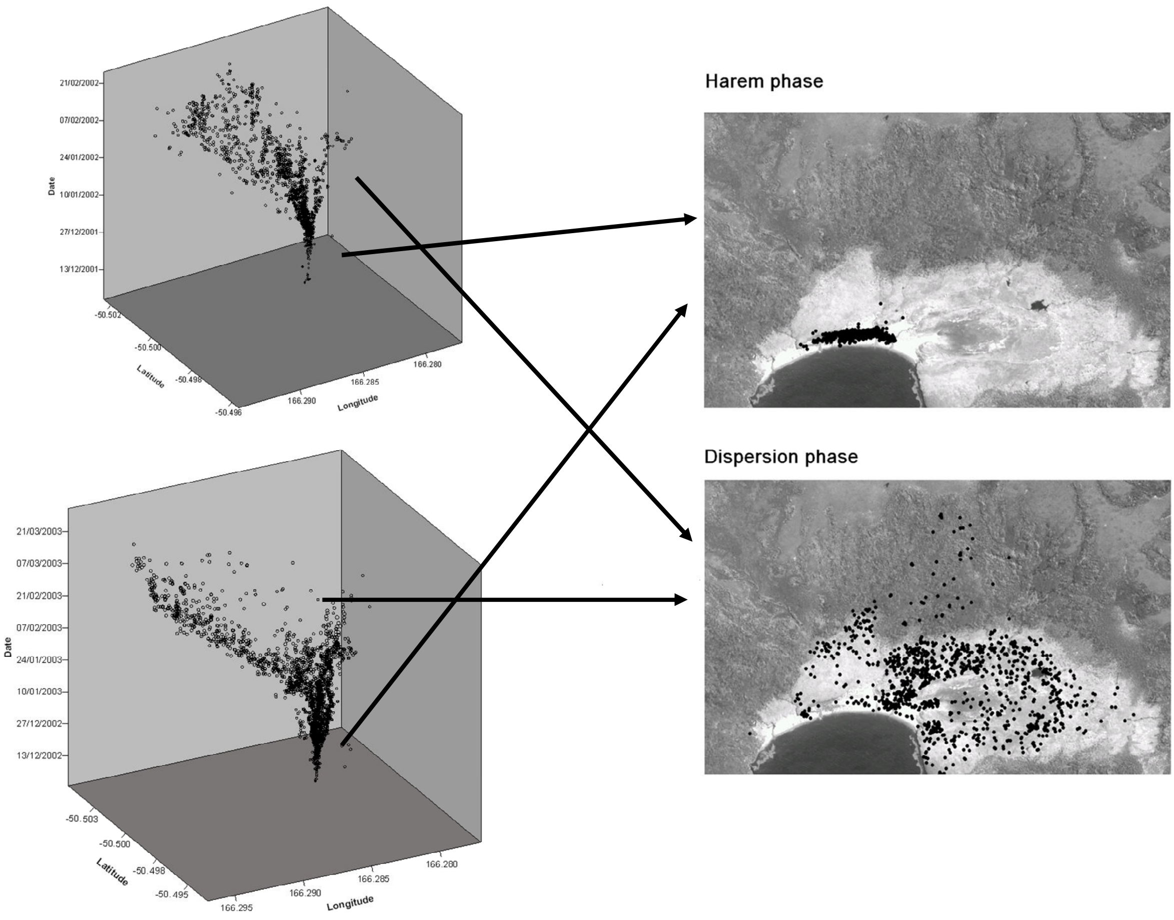


Figure 2.6: Space-time plot representations of the ‘harem phase’ and the ‘dispersion phase’, during both study seasons (until 18/02/02 and until 21/03/03), using 3-D scatter plots of the GPS points of the daily females’ locations with Latitude and Longitude as *x* and *z* axis, and time (Date) as *y* axis; and visualisation of the two phases at Sandy Bay.

4.3. Female location datasets

The fieldwork produced a set of point locations containing one location per female per day when she was onshore on this day during the survey. The GPS points of the females’ locations were stored as Excel files separately for the two study seasons. Firstly, individual females’ locations were gathered, copied, ordered by date, and separated in different workbooks called ‘*Locations per female’*. This file was used in order to investigate differences amongst individuals. Secondly, locations on the same day were copied and separated in different workbooks called ‘*Locations per day*’ that were created in order to look at the spatial changes overtime at the population level. Each GPS points had thus two attributes: date or female brand and status. The geodatabase was composed of 177 ‘*Individual female*’ shapefiles, each of them labelled with the brand number of the females and organised per season, and 181 ‘*Day*’ shapefiles labelled with the corresponding dates.

4.4. Harem extent

During the peaks of the harem phase, observers collected GPS points of the boundaries of the harem. The Excel files containing the points were transformed in shapefiles and integrated in ArcGIS. In season 2002 the harem boundaries were marked from 7 December until 7 January; in 2003 they were taken from 13 December to 9 January. Harem polygons were digitised (i.e. created in a new shapefile) and labelled with the corresponding dates as '*Harem*' shapefiles in the geodatabase. Areas of the harem polygons were calculated for each day and the maximum value found was kept as the maximum harem extent for each season.

4.5. Habitat type map

The satellite image was georectified, using a polynomial first order function, with the set of 40 GCPs including 19 within the study area (Root Mean Square error = 50cm). The image classification was realised with *e*-Cognition (object-orientated image classification software), first operating a segmentation of the image into polygons, and then, a classification based on sample polygons of each habitat class. These sample polygons were derived by the software from the habitat sample points surveyed on the ground. Each polygon was classified in one of the eight habitat classes sand, low sward, high sward, scrub, forest, tussock, rock and water (as described in Table 2.1). The classification scheme was, last, manually improved using old aerial photos, field notes and photos. The habitat type map of the study area is presented in Figure 2.7.

4.6. Digital Terrain Model (DTM), slope map and aspect map

The elevation points were first exported and filtered in Pathfinder (PDOD<5 and satellite number>4). A total of 21709 points were retrieved. Differential correction of the points was then performed using the Bluff Trimble base station (-45˚53' S/ 168˚17' E; 450km from SB). After this operation, the expected average horizontal and vertical maximum errors were 1.5m and 3m respectively. In order to get the precise altitudes from the edge of the water, i.e. from where females came ashore, the ocean, as the mid-tideline, was set up as elevation 0. The points were incorporated in ArcGIS and a kriging technique was used to interpolate the terrain surface (ordinary kriging with spherical semivariogram model, search radius 10 points, cell size 3m) using the elevation points. The DTM of the study area is presented in Figure 2.8. The slope map was created for a smaller area, the reduced study area, including only some of the areas made of scrub and forest, where the DTM was accurate enough. Slopes were calculated from the DTM in ArcGIS using Spatial Analyst with a cell size of 3m (Figure 2.9 A). The aspect (i.e. slope orientation) map was also produced for the reduced study area using Spatial Analyst (cell size 3m), and is shown in Figure 2.9 B.

5. Conclusion

The data exploration revealed a significant spatio-temporal pattern in the spatial ecology of female New Zealand sea lions, and especially emphasised the apparent existence of two phases (harem and dispersion). A geodatabase, made of the '*Individual female*' dataset, the' '*Day*' dataset, the '*Harem*' dataset, a habitat map, a DTM, a slope map and a slope orientation map was produced. Different elements from this database were used depending on the scale analysed in the following chapters. It is the reason why specific analyses and the datasets they were applied to are described at the start of each of the three next chapters of results.

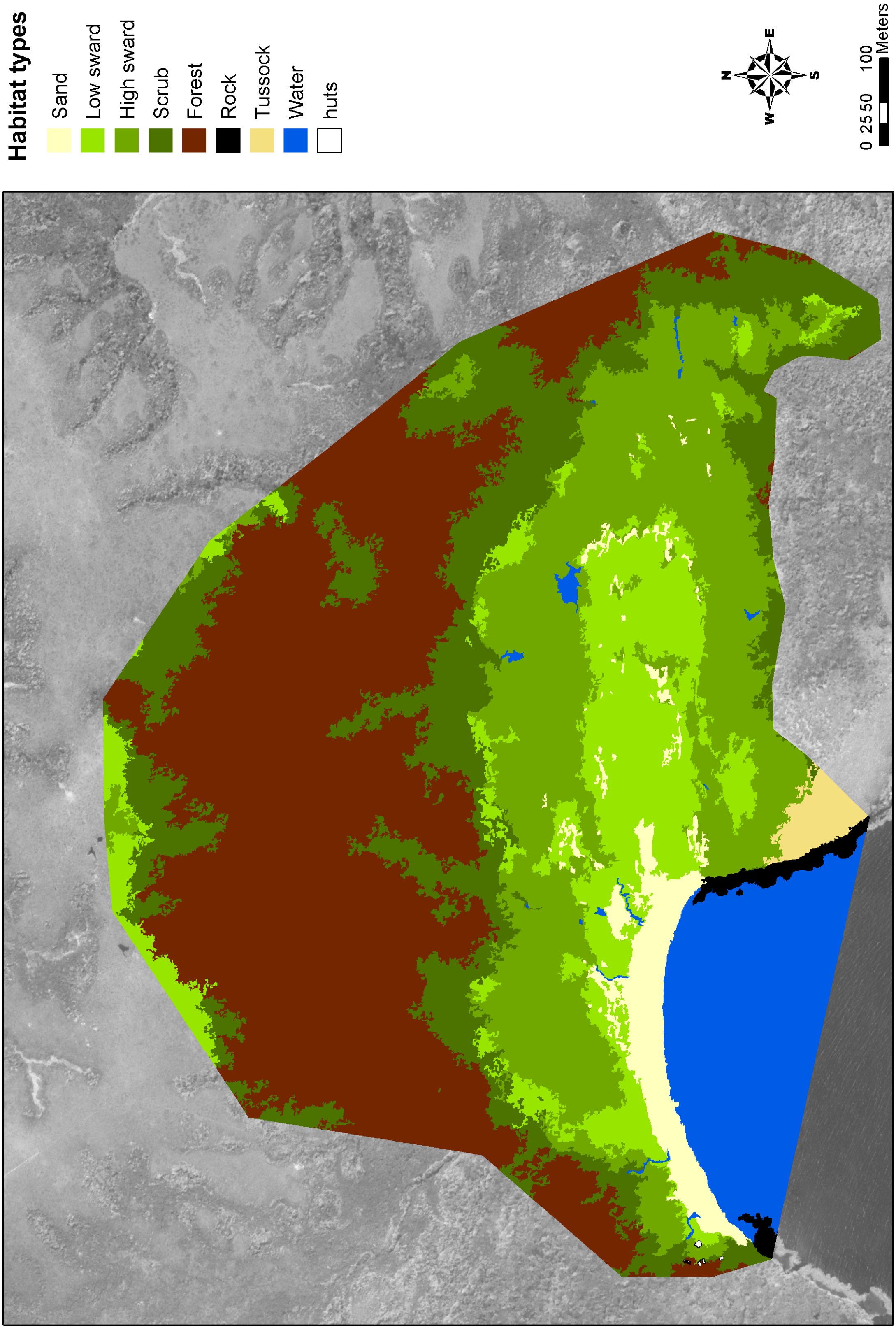


Figure 2.7: Habitat type map of the study area at Sandy Bay, Enderby Island.

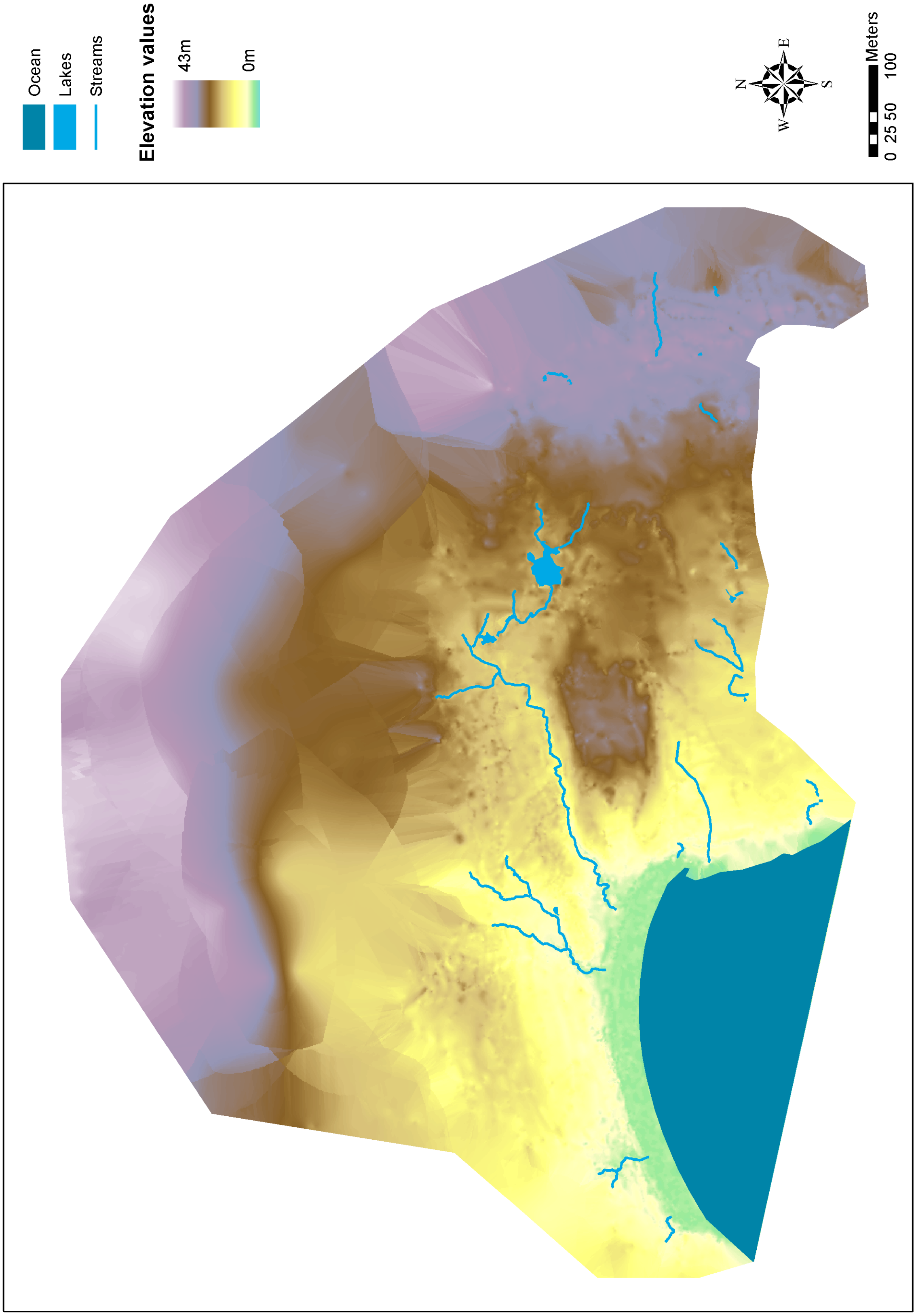


Figure 2.8: Digital Terrain Model of the study area at Sandy Bay, Enderby Island.

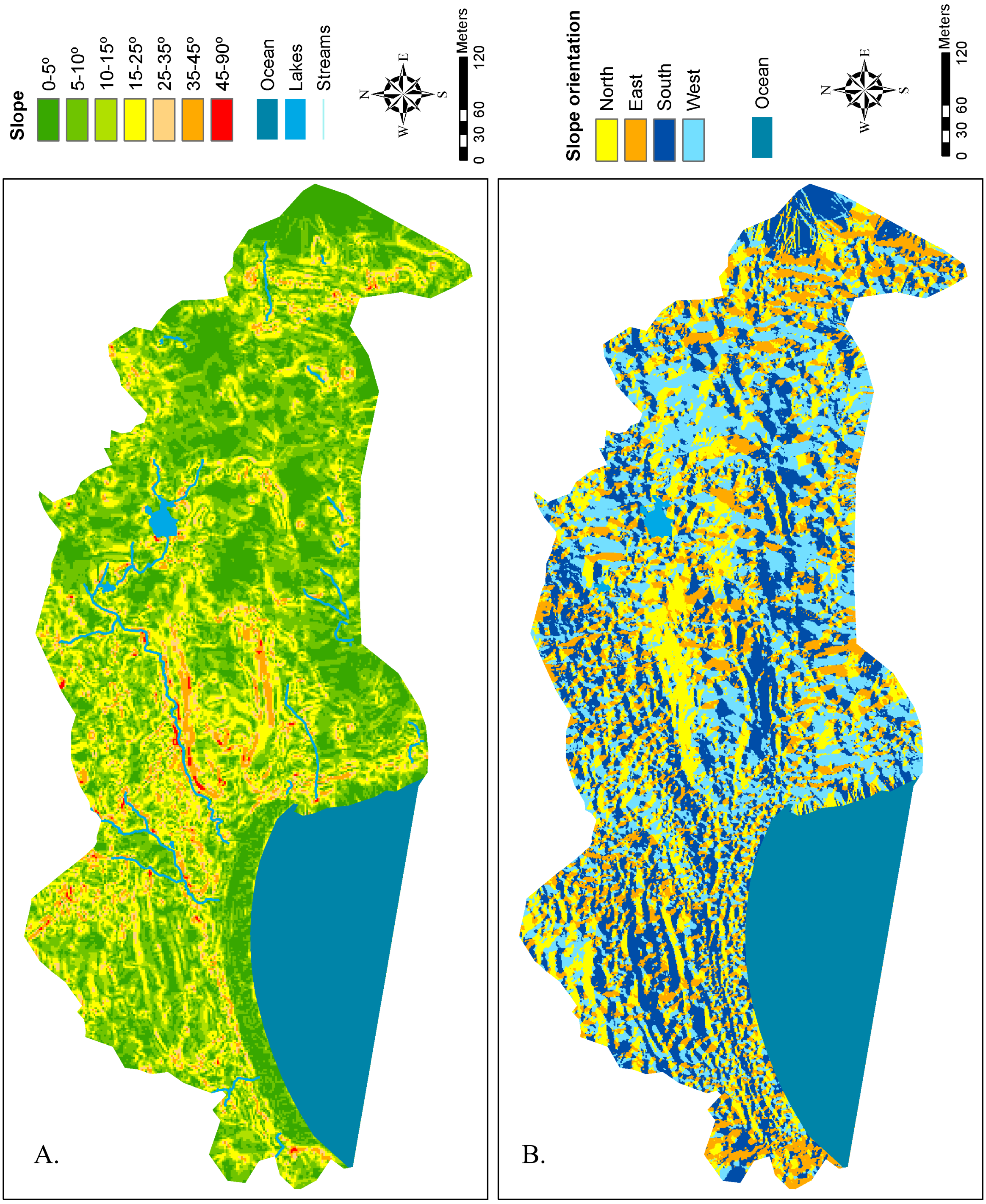


Figure 2.9: Slope map (A.) and slope orientation map (B.) of the reduced study area at Sandy Bay, Enderby Island.

CHAPTER THREE: INDIVIDUAL SCALE

MOVEMENTS OF INDIVIDUAL FEMALES

“*The Behaviour of individuals and the strategies they adopt to maximize fitness plays an important role when a species’ natural behaviour can lead to conservation problems.*’’

Festa-Blanchet and Apollonio

1. Introduction

In this chapter the individual females' presence and movements at Sandy Bay (SB) were analysed to determine the timing of the main events and the main patterns driving the spatial ecology of a female on land. A model of an average female's space use was then produced and how movements of a female influenced the survival of her pup was investigated. The analyses looked at timing, distribution of locations, dispersion and distances moved. These results are discussed at the end of the chapter.

2. Methodology

2.1. Aims

- Determining if there are specific timing and patterns in the distribution of locations of a female New Zealand sea lion; if it is related to her age and if it influenced the survival of her pup
- Producing a model of an average female's spatio-temporal use of SB
- Quantifying the distances a particular female moved during the pupping period and how this influenced pup survival

2.2. Timing of arrival, pupping and departure at Sandy Bay (SB)

The '*Locations per female*' Excel files were explored in order to determine for each female during each season her first day of presence at SB, the length of her pupping period, the date of pupping, the number of days of this pupping period after pupping, the date of pup death, her last day of presence at SB, and the total number of days she stayed at SB. The mean, Standard Deviation (S.D.), maximum and minimum were calculated for each of these variables. The influence of these timing variables on pup survival could be tested. Single-factor ANOVAs (factor: status) were produced on the timing variables: first day at SB, pupping date, pupping period length and period ashore after birth (Sheskin, 2004). Both variables first day at SB and pupping date were first transformed in a numeric form (Julian days). Prior to analyses the data were checked for normality in distribution (test of Kolmogorov-Smirnov) and homogeneity of variance (test of Hartley; Sheskin, 2004).

2.3. Point pattern analyses for location of individual females: Nearest Neighbour Indices (NNI)

In order to characterise the two phases revealed in the data exploration, point pattern analyses were conducted on the set of locations of each female during each season. The NNI were first presented in Clark and Evans (1954) as a measure of spatial relationship of a set of points corresponding to a wildlife pattern of distribution. The objective was to detect how the points were spatially distributed compared to spatial randomness within a selected area. The NNI are calculated for a set of points using the study area, *S*, the total number of points, *N*, and the distance to the nearest location for each location, *d*, as $NNI = \left(\sum_{i=1}^{N} \frac{d}{N} \right) / 0.5 \sqrt{\frac{S}{N}}$. The NNI reflect the variation of the point distribution pattern from spatial randomness. NNI range from 0 (complete aggregation, all points are at the same place) to 2.149 (uniformity, the points are as sparse as possible). A value of 1 corresponds to complete spatial randomness. Clark and Evans (1954) emphasised that the comparison of the NNI calculated from a different set of points is possible and shows the relative difference in spatial organisation of the points.

In this section, NNI were used to characterise the distribution of the daily locations of each female. The set of points represented the same animal at different dates rather than a population at one time. The NNI thus characterised the spatial distribution of a female's locations over time. If a female was always located within the same area once ashore, the index was close to 0. If she was located at sparse sites during her periods onshore, the index was closer to 1 or higher. For each female the NNI were separately calculated for the harem phase and the dispersion phase. The dispersion date, for each female, was visually determined by displaying the maximum extent of the harem of the season and overlaying the female's locations to find when the first location was outside the harem (i.e. dispersion date). This was done because it was detected, during data exploration, that the harem phase corresponded to an aggregation of the females whereas the dispersion phase was a spatial spread of the females' locations. The calculation of the NNI for the dispersion phase was done using only the locations recorded before the end of season 2002 (18 February) in order to be able to compare results from both seasons. The Arc Tool box module contains a function that calculates the NNI for a point shapefile for a given area. This function was applied to the shapefile containing the locations of a female during the harem phase and to the shapefile containing the locations of a female during the dispersion phase to determine the NNI for each female for the two phases.

NNI values were analysed with single-factor ANOVAs and General Linear Model GLM) using year, status, age as factors. This allowed determination of differences in behaviours between the two study seasons and the influence of status or age of a female on the distribution of the locations she used onshore. Prior to these analyses the data were checked for normality in distribution (Kolmogorov-Smirnov test) and homogeneity of variance (Hartley test). The main results were graphed using box-plots showing the median, quartiles and extreme data values of the data.

2.4. Time-dispersion model

In this section, the changes in time of the area used by an average breeding female were modelled. The females' locations were used to create the areas a female has used since the beginning of the season by cumulating her daily locations. It must be understood that this area represents the females' home range only at SB. It does not imply that a female would not have come ashore elsewhere on Enderby Island or at another site during her foraging trips. Minimum Convex Polygon (MCP) was the technique used to quantify the area, and regression models were applied to model the changes in area over time.

2.4.1. MCP: quantifying home ranges

Mohr (1947) first described the possibilities of determining the home range of an animal by creating a line, that connects the outer most locations where an animal was found to create an area called the minimum home range. Now known as MCP, this is the smallest convex polygon containing all points from a set. Figure 3.1 illustrates the creation of the MCP for a hypothetical set of points. Since then, MCPs were used in numerous wildlife studies looking at home range (recent examples in Litzgus and Mousseau, 2004; Franzreb, 2006; Righton and Mills, 2006). However it was discussed that the MCP technique, by using the outer most locations, may bias the results by possibly using outliers (i.e. an animal may have been to a location only as an irregular behaviour; MCP may contain habitat that the animal never or would never used; Worton, 1987).

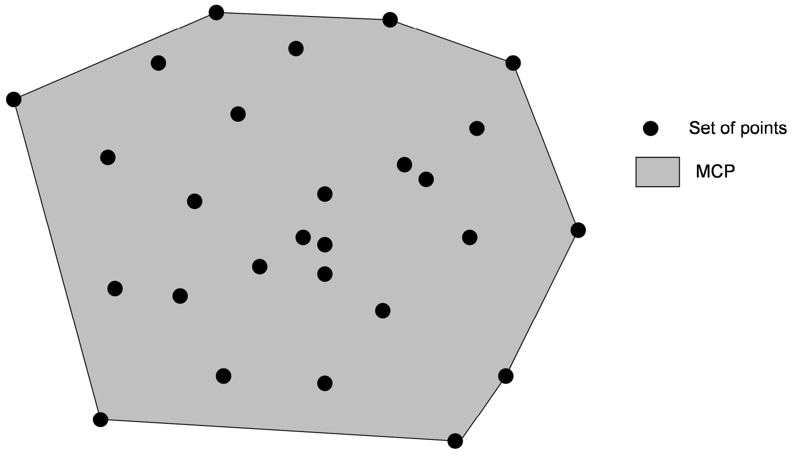


Figure 3.1: Creation of the Minimum Convex Polygon (MCP) for a hypothetical set of points based on Mohr's (1947) method of the minimum home range.

In the present study, MCP was the method applied to the females' locations to model the change in the area used by each female during the season. A new MCP was created for each day a location of a female was measured. This was done by cumulating the new point to all previous locations of the female since the start of the season, and was denominated as the cumulative MCP of the female (e.g. in Figure 3.2). Using cumulative MCP gave the opportunity to include, in the study, not only the location of the females and her distance from the ocean, but also where she likely walked or went before to get to her new location after a foraging trip at sea.

The cumulative MCPs were created using the Hawth's analysis tool in ArcGIS (see Beyer, 2004). Any MCP incorporating ocean area was digitally modified in order to exclude the ocean area from it. A total of 3840 cumulative MCPs were digitised. The areas of each of these MCP (MCPA) were then computed in square meters using the Arc Toolbox. The results were organised per female per day in an Excel file and the cumulative means of MCPA were eventually calculated for the two study seasons.

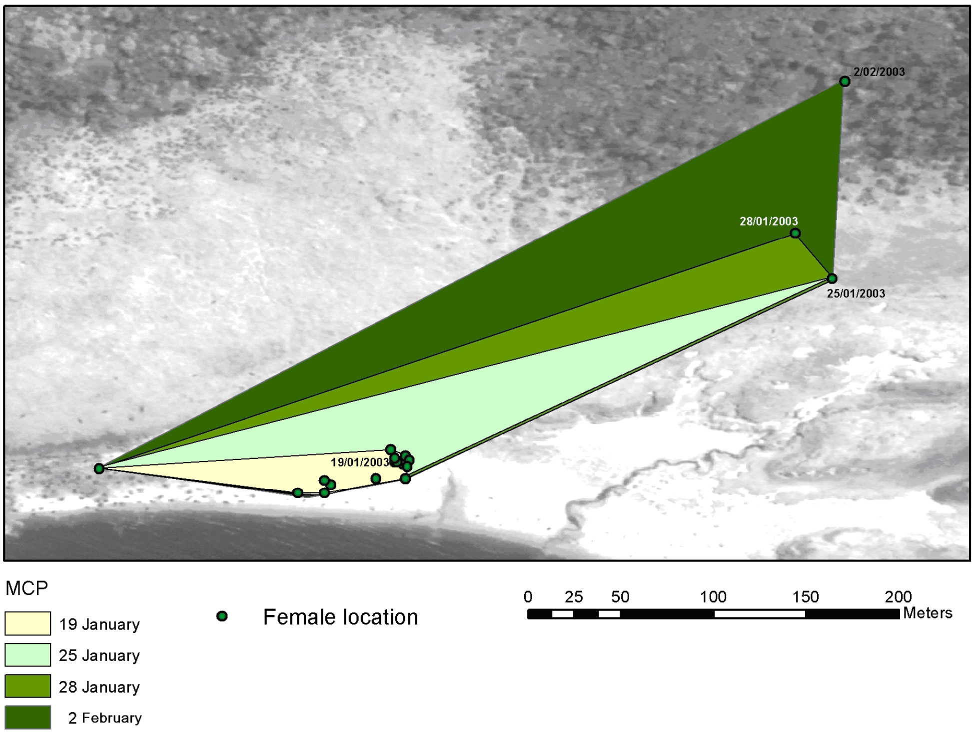


Figure 3.2: Example of the creation of the cumulative Minimum Convex Polygons (MCP) of a female during season 2003 (from 10/12/01 to 2/02/03) at Sandy Bay.

2.4.2. Regression analyses: modelling

A regression analysis is a statistical method that allows building a regression model based on data previously acquired (Bowerman *et al.*, 2005). Time series (i.e. values of a specific variable over time) can be analysed through regression analyses which leads to the production of forecasting models (Bowerman *et al.*, 2005). In order to characterise the increase of MCP of female New Zealand sea lions at SB, univariate forecasting models were performed. The same number was assigned for each date of both seasons such as Day1 was 8 December, Day 73 was 18 February (end of season 2002) and Day 104 was 21 March (end of season 2003). A different model was developed for each of the study seasons to identify the data pattern and detect the possibility to predict the values of the MCPA.

The exponential regression model used was under the form (MCPA in m^2):

$$\text{MCPA}(\text{Day } i) = \text{b.a}^{i}$$

A logarithmic transformation was first realised on the data to linearise them as:

$$\text{MCPA}(\text{Day } i)' = \log 10\ (\text{MCPA}(\text{Day } i))$$
$$\text{With a}' = \log 10\ (\text{a})$$
$$\text{b}' = \log 10\ (\text{b})$$

The transformed variables were then analysed with a linear regression model such as:

$$\mathrm{MCPA}(\mathrm{Day}\ i)' = a'i + b'$$

The parameters of the linear regression equation, a', the slope, and b', the y-intercept, were determined in each analysis. The coefficient of determination, R^2, was used to show the proportion of the variation of the data that the regression model explains (Bowerman *et al.*, 2005). Statistical significances were tested with analyses of variances for the regression model and t-tests for the parameters a' and b'.

Once a' and b' were determined, the reverse logarithmic transformation was calculated to get a and b ($a=10^{a'}$ and $b=10^{b'}$), parameters of the exponential regression model, giving, for each day, the expected MCPA. Because the model was built using the mean MCP of the sample population, it thus described the behaviour of an average female of the SB population.

The data from Day 74 to Day 104 of season 2003 were separately analysed as no data was available from season 2002. It was found that they followed a linear regression model of the form:

$$\mathrm{MCPA}(\mathrm{Day}\ i) = a_2 i + b_2$$

Parameters a_2 and b_2 were determined and statistical significance calculated as for a' and b'.

2.5. Distances moved during the pupping period

The distances a particular female moved during each day of her pupping period were calculated and compared between status. During the pupping period females stayed onshore. Consequently by determining the Euclidean distance between two consecutive daily points, the minimum distance that a female moved per day was determined. This was done using the function 'Distance between points' in the Hawth's Analysis tool (see Beyer, 2004). This function produces a table containing the Euclidean distances between all pairs of points within a point shapefile. For each female the dates of start and ends of the pupping period as well as the pupping day were known from the precedent analyses on timing of events. From the tables created for each '*Individual female*' shapefile, the distances for each day before the pupping day, on the pupping day, on the first day after pupping (day 1) and until the end of the pupping period were extracted. Mean distances moved, during each day, were then calculated for the different statuses of breeding females (BR and BDP). A GLM was performed using year and status as factors for each day from the days before pupping until day 5. Prior to analyses the data were checked for normality of distribution (Kolmogorov-Smirnov test) and homogeneity of variances (Hartley test).

3. Results

3.1. Timing of arrival, pupping and departure at Sandy Bay (SB)

Tables 3.1 summarises the mean dates and periods with associated statistics for the first day a particular female was found at SB, the length of the pupping period, the length of the portion of this period after the birth of the pup, the date of pupping, the date of pup death, the last day the female was found at SB and the total number of days a female used SB. The means were separately calculated for breeding and non-breeding females. The resultant timings of all variables investigated were highly similar between the two seasons.

For the last day at SB and the total number of days at SB, comparisons between seasons were not possible as the length of the study period varied. However the results can be used to look at differences between breeding and non-breeding females. Non-breeding females were found at SB only half the number of days (42.2% in 2002 and 48.3%) of an average breeding female. The lowest number of days for a non-breeding female was 3 and the maximum was 26 days, which is 5 days less than the mean for breeding females (31.6 days). Based on the 2003 season, the non-breeding females also stopped using SB earlier than breeding females (21/02/03 versus 1/03/03).

Due to the high similarity in timing, all results from both seasons were gathered to produce statistical analyses. Status was not found to have any effect on any of the timing variables. The survival of a pup was not found to depend on the date the female arrived at SB (F=0.300, d.f.1, p= 0.585) or gave birth (F=0.210, d.f.1, p=0.648), neither on the length of the pupping period (F=0.034 ,d.f.1, p=0.854) or the number of days of the pupping period after birth (F=0.631 ,d.f.1, p=0.428).

	Season	First day at SB	Pupping period (in days)	Period ashore after birth (in days)	Date of pupping	Date of pup death	Last day at SB	Total number of days at SB
Mean	**2002**	**21/12/01**	**8.14**	**6.33**	**26/12/01**	**12/01/02**	**13/02/02**	**26.22**
	2003	**21/12/02**	**8.35**	**6.23**	**25/12/02**	**13/01/03**	**1/03/03**	**31.64**
S.D. (in days)	2002	7.97	2.99	2.84	6.97	7.34	6.12	5.87
	2003	6.94	3.07	3.28	6.85	24.23	15.03	8.19
Minimum	2002	2/12/01	1.00	0.00	7/12/01	4/01/02	14/01/02	14.00
	2003	6/12/02	2.00	0.00	8/12/02	12/12/02	26/12/02	14.00
Maximum	2002	6/01/02	14.00	13.00	8/01/02	1/02/02	18/02/02	46.00
	2003	6/01/03	15.00	14.00	8/01/03	27/02/03	21/03/03	61.00

A.

	Season	First day at SB	Last day at SB	Total number of days at SB
Mean	**2002**	**25/12/01**	**2/02/02**	**11.07**
	2003	**27/12/02**	**21/02/03**	**15.27**
S.D. (in days)	2002	15.18	13.38	7.86
	2003	13.83	14.85	5.75
Minimum	2002	8/12/01	1/01/02	3.00
	2003	16/12/02	2/02/03	8.00
Maximum	2002	9/02/02	18/02/02	25.00
	2003	3/02/03	17/03/03	26.00

B.

Table 3.1: Timing and length of the main events at Sandy Bay (SB) breeding colony during season 2002 and 2003. A: breeding females (in 2002, N=73, with N= 14 for date of pup death; in 2003, N=78, with N=12 for date of pup death) and B: non-breeding females (in 2002, N=15; in 2003, N=11). The fieldwork was stopped on 18 February in 2002. Consequently, the last days at SB and the total numbers of days are just given as indicative as females were still using SB at this date.

3.2. Point pattern analyses on locations

The mean NNI for each season and each phase, arranged by status, are presented in Table 3.2. The NNI values characterised the two phases as the NNI during the harem phase were closer to 0 (aggregation) whereas the NNI during the dispersion phase were around 1 (randomness in spatial distribution; Figure 3.3). During both seasons a significant difference in NNI was found between the harem and dispersion phases (in 2002: F=210.077, d.f.1, p<0.001 and in 2003: F=274.788, d.f.1, p<0.001).

The status of a female did not have any effect of the NNI values however the year had an effect during each of the phase (harem phase, GLM, status F=6.347, d.f.=1, p=0.460, year F=15.296, d.f.1, p<0.001; and dispersion phase, status F=0.117, d.f.1, p=0.733, year F=6.347, d.f.1, p<0.001; Figures 3.4 and 3.5). The NNI values during the 2002 season were overall greater than the values from the 2003 season. This also indicated that females with dead pups exhibited the same pattern of distribution of their locations ashore as females who kept nursing a pup during the whole length of the study.

No effect of the age of a female was found on the distribution of her locations either during the harem phase (F=0.755, d.f.11, p=0.682) nor during the dispersion phase (F=1.725, d.f.11, p=0.087).

Table 3.2: Means NNI during seasons 2002 and 2003 for each breeding status during the harem phase (NNI harem) and the dispersion phase (NNI dispersion). With BR: breeding females with alive pups, BDP: breeding females with pups that died before the end of the season, NB: non-breeding females. Remark: NB did not show a harem phase and thus only the NNI during dispersion was calculated.

		2002			*2003*		
		BR	*BDP*	*NB*	*BR*	*BDP*	*NB*
		N=54	N=14	N=15	N=59	N=12	N=11
NNI harem		**0.236**	**0.244**	**-**	**0.159**	**0.178**	**-**
	S.D.	0.1	0.103		0.064	0.56	
NNI dispersion		**1.155**	**1.098**	**1.899**	**0.838**	**0.882**	**0.929**
	S.D.	0.735	0.445	0.771	0.33	0.434	0.362

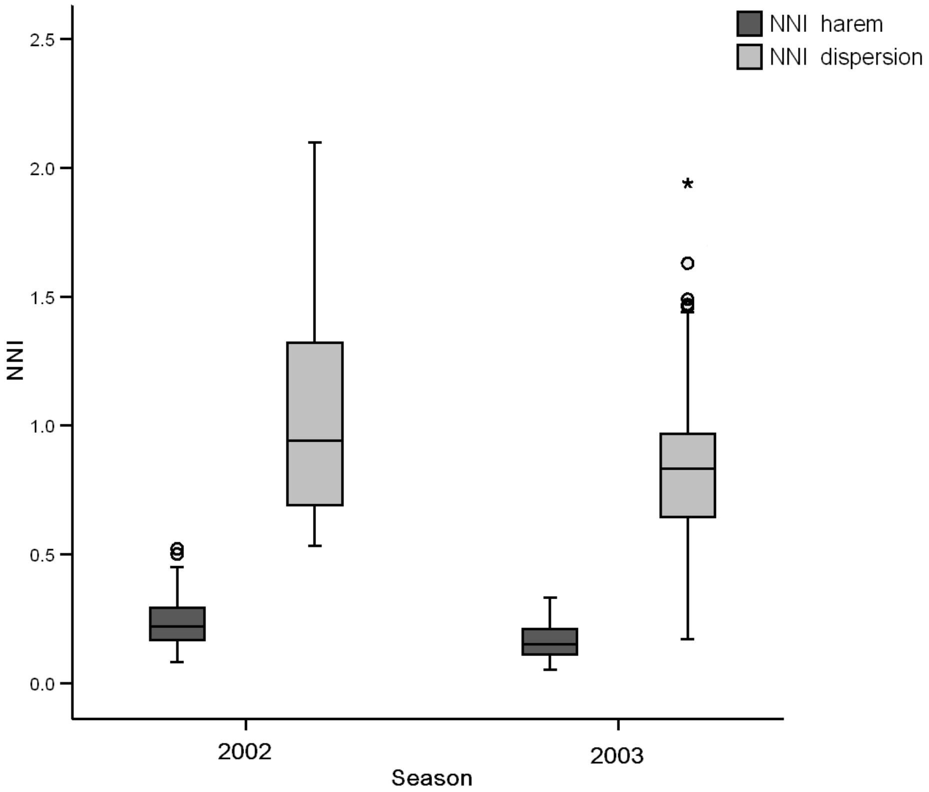


Figure 3.3: Differences in point distribution between the harem phase and the dispersion phase during season 2002 and 2003. Mean NNI values of BR and BDP together. The circles and stars indicate extreme values.

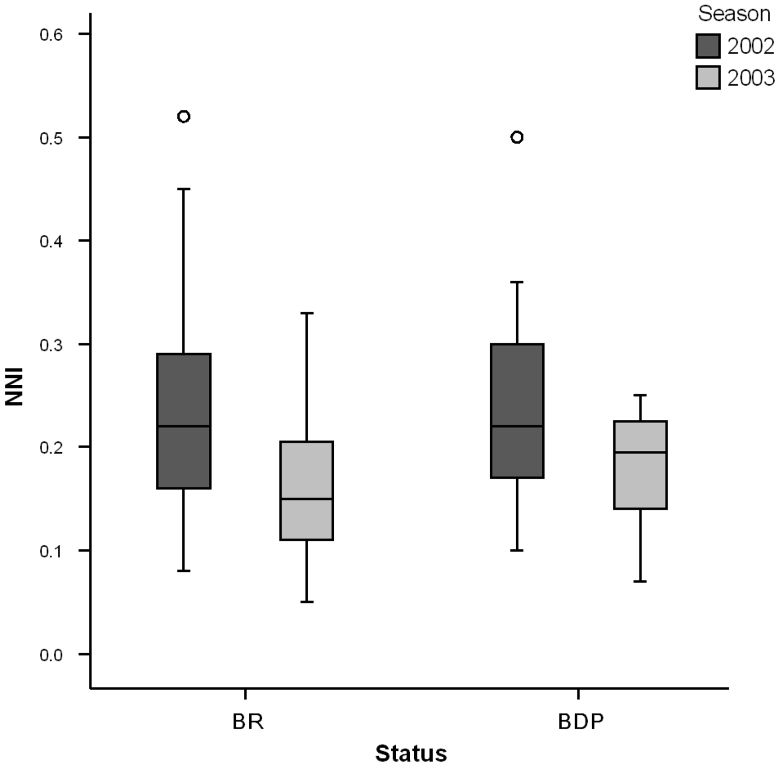


Figure 3.4: Box plot graphs (median, quartiles and extreme values) of mean NNI values during the harem phase for each status for the seasons 2002 and 2003. The circles indicate extreme values.

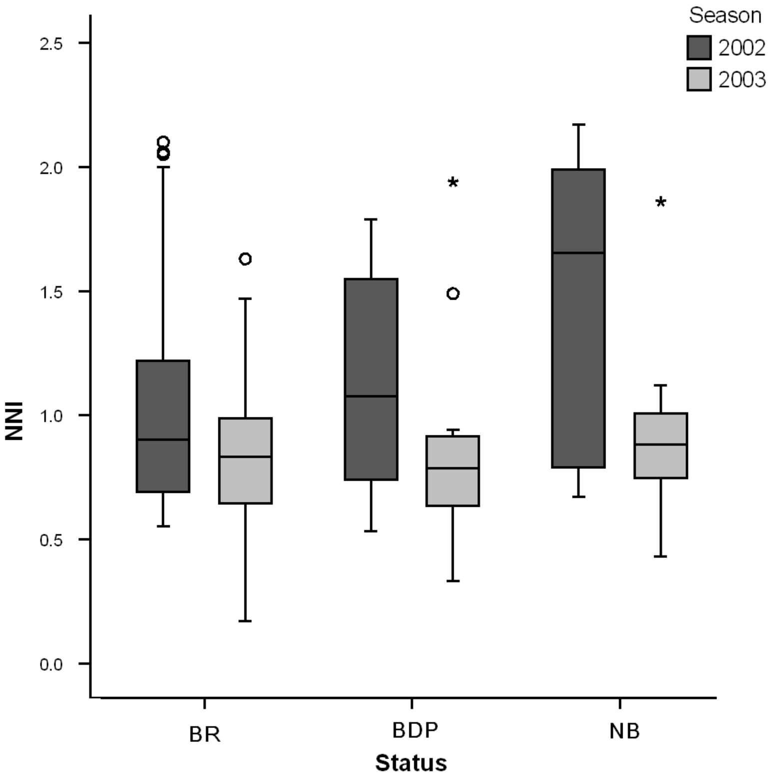


Figure 3.5: Box plot graphs (median, quartiles and extreme values) of mean NNI values during the dispersion phase for each status for the seasons 2002 and 2003. The circles and stars indicate extreme values.

3.3. Time-dispersion model

Because no difference was found in the spatial distribution of locations amongst females of the three statuses, results for all females were used to produce a time-dispersion model. The mean (with standard deviation) and maximum MCPA per day are illustrated in Figure 3.6 for season 2002 and in Figure 3.7 for season 2003. During season 2003 the study lasted until 21 March (Day 104) on which day the mean MCPA was 185756 m^2 and the maximum MCPA calculated for an individual female reached 246131 m^2. The pattern of increase of the MCPA coincided with the two phases described in the preceding sections. During the first half of the graph, the mean MCPA during both seasons stayed very low (harem phase when locations were all aggregated in the same area) whereas during the second half of the curve there is an exponential increase in the mean MCPA (dispersion phase when locations were spread).

The increase in MCPA was found to follow a logistic exponential model during both seasons (Figure 3.8).

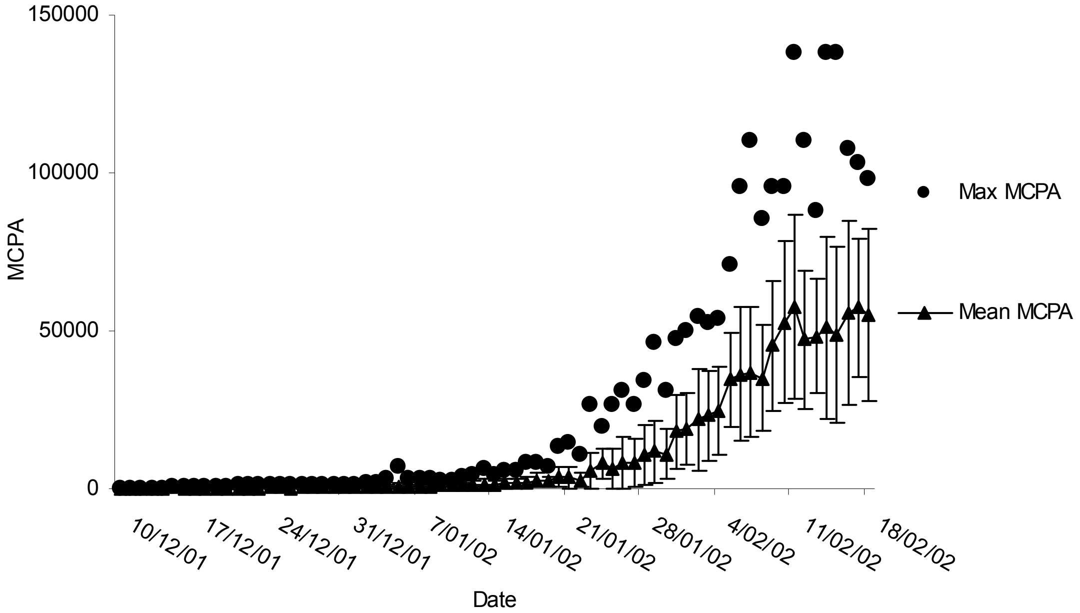


Figure 3.6: Maximum (Max MCPA), mean (Mean MCPA) and standard deviation of Minimum Convex Polygon Areas (MCPA; in m^2) along season 2002 (n=1 for the maximum and 1<n<41 per day for the mean).

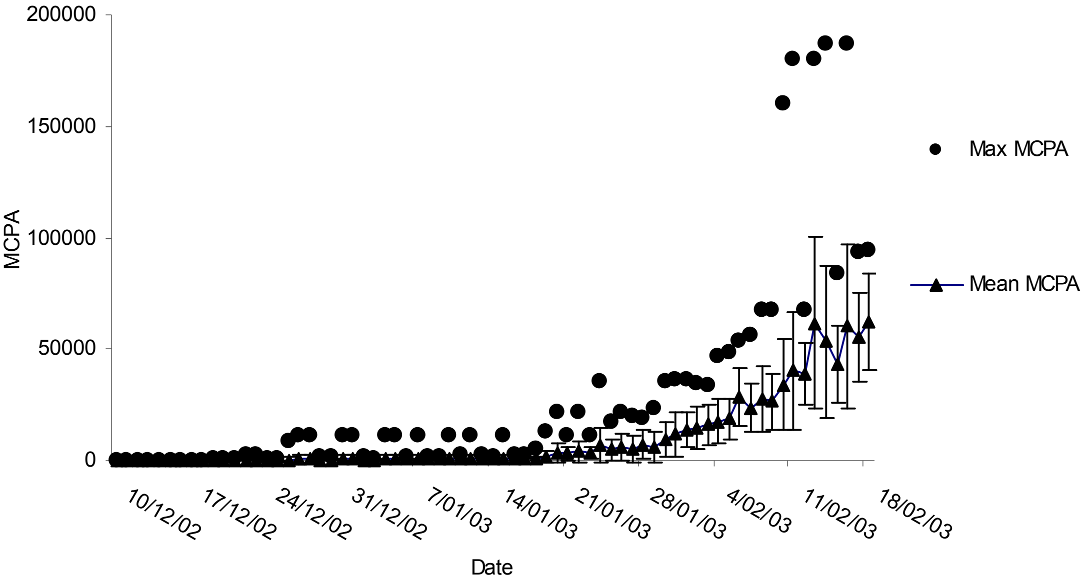


Figure 3.7: Maximum (Max MCPA), mean (Mean MCPA) and its standard deviation of Minimum Convex Polygon Areas (MCPA; in m^2) along season 2003 ($n=1$ for the maximum and $1<n<55$ per day for the mean).

The linearisation of the variables from both seasons was realised and linear regression analyses computed on the new variable MCPA'. The linear regression models for each season were:

$$\text{Season 2002:} \quad \text{MCPA(Day } i)' = 0.042i + 1.768$$
$$\text{Season 2003:} \quad \text{MCPA(Day } i)' = 0.047i + 1.410$$

Due to the similarity of the two models, the final linear model was produced by combining data from both seasons to increase the robustness of the model (Figure 3.9). The statistical significance of the regression model as well as the parameters and associated statistics are summarised in Table 3.3.

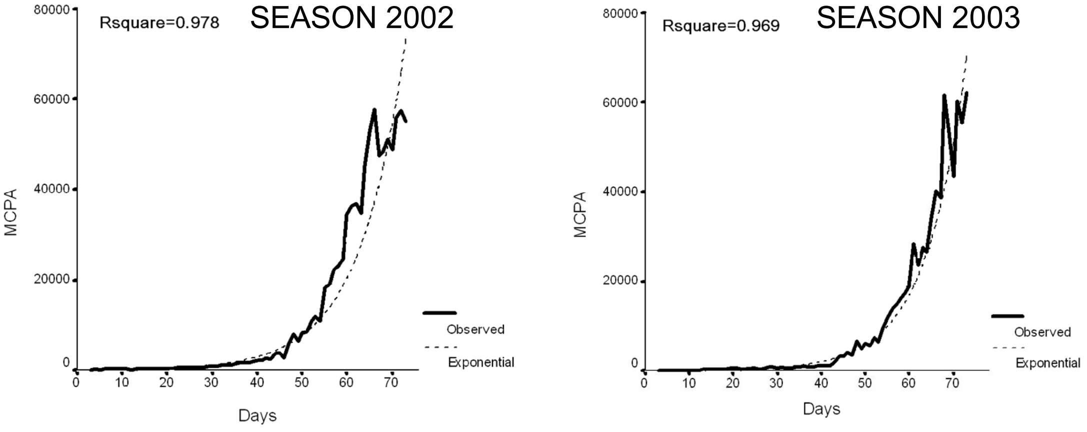


Figure 3.8: Representation of the logistic exponential models to best fit the regression analyses of MCPA over time with R^2 values, from Day 3 to Day 73. The significance of both models is $p<0.001$.

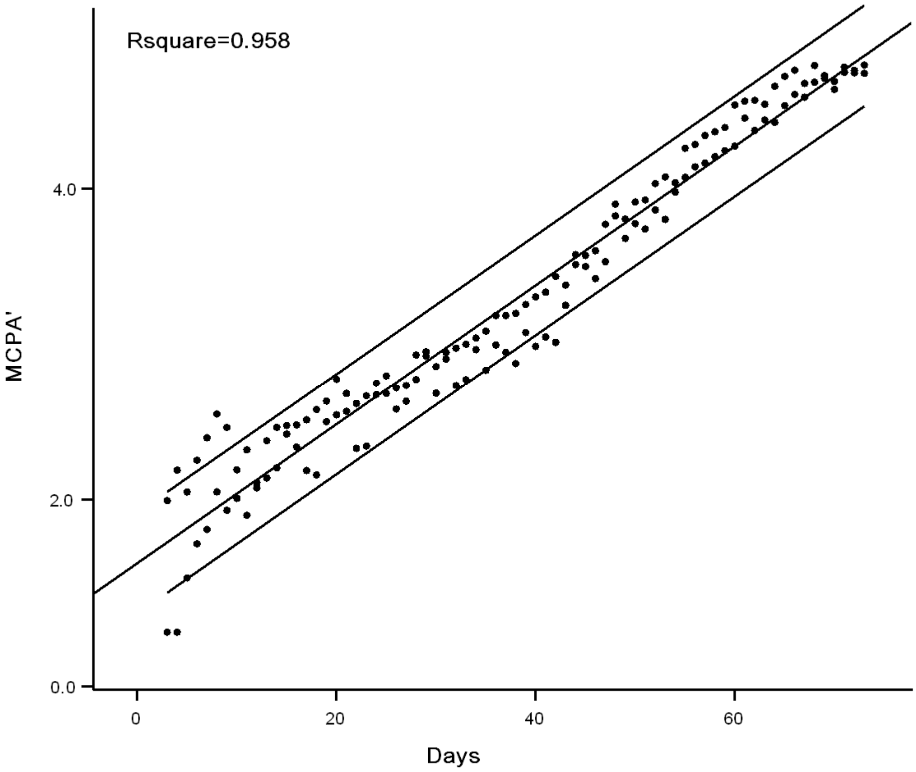


Figure 3.9: Linear regression fit line of MCPA' for the time-dispersion model, from Day 3 to Day 73. The linear regression (central line) is surrounded by the regression prediction lines with a C.I. 95% for the individual values.

After inverse transformation of the parameters a' and b' to a and b, the time-dispersion model, from Day 3 to Day 73, giving for each day the predicted area, in m^2, of the MCP of an average female of the population at SB, based on an exponential regression model, was deduced:

$$\text{MCPA(Day } i) = 38.815*1.109^{i}$$

The regression analysis conducted on the results of season 2003 from Day 74 to Day 104 revealed that during this period the increase in MCPA slowed down and followed a linear regression model, less robust due to the use of only data from one season (significance in Table 3.4):

$$\text{MCPA(Day } i)=2751i-120655$$

Table 3.3: Significance of the model and parameters of the linear regression of the MCPA' from Day 3 to Day 73.

	Sum of squares	d.f.	mean square	F	p
regression	119.239	1	119.239	3193.860	<0.001
residual	5.227	140	0.037		

	B	Standard Error	t	p
b'	1.589	0.034	46.517	<0.001
a'	0.045	0.001	56.514	<0.001

Table 3.4: Significance of the model and parameters of the linear regression analysis of the means MCPA from Day 74 to Day 104.

	Sum of squares	d.f.	mean square	F	p
regression	1.900*10^10	1	1.876*10^10	77.156	<0.001
residual	7.100*10^9	29	2.431*10^8		

	B	Standard Error	t	p
b_2	-120655	28010	-4.307	<0.001
a_2	2751	313	8.784	<0.001

The time-dispersion model gives for each day the MCPA of an average female and thus forecasts this area based on the number of days since the first day of her presence at SB (Figure 3.10).

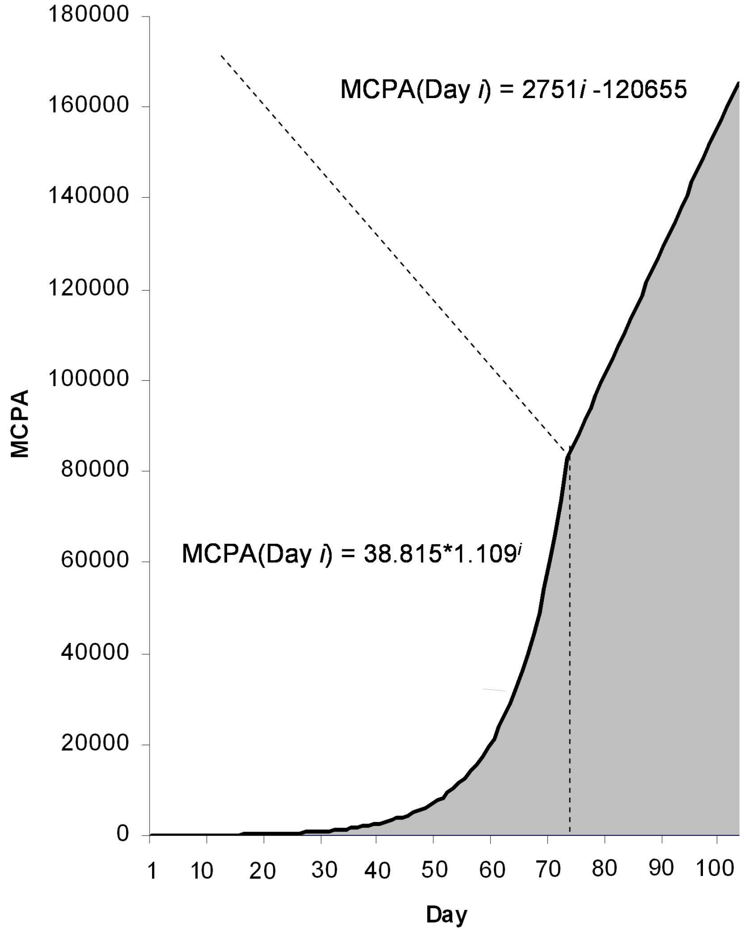


Figure 3.10: Time-dispersion model of an average breeding female New Zealand sea lion at Sandy Bay. The model gives for each day (starting Day 1 as 8 December and ending Day 104 as 21 March) the expected MCPA (in m^2).

3.4. Distances moved during pupping period

Table 3.5 contains the mean daily distances that females moved during the pupping period up to the fifth day after pupping (day 5). The results are separated between study seasons as there were significant differences between results for the day of pupping, day 1 and day 2. The amount of movements was significantly higher during the 2002 season than the 2003 season for these three days. This pattern could also be detected for the other days however no significant statistical difference was found. During both seasons and for both statuses, the distances moved on the pupping day (6.7m, S.D.=5.5m) dropped by 69% the distance a female moved during a day before giving birth (21.8m, S.D.=36.5) (Figure 3.11). Then the daily mean distances a female moved per day re-increased. Females thus became highly sedentary on the day of birth, and then started moving more and more until the end of the pupping period.

Year was found to have an effect on the GLM for day 1 and day 2 whereas status had an effect on the model for pupping day only (Table 3.6). During the pupping day, females who later lost their pups moved greater distances than females whom pups survived, with no difference between the seasons. Pup survival was thus affected by the movements of the females during the pupping day. On the other side, all females moved more during the 2002 season than the 2003 season during the two days following the day of pupping.

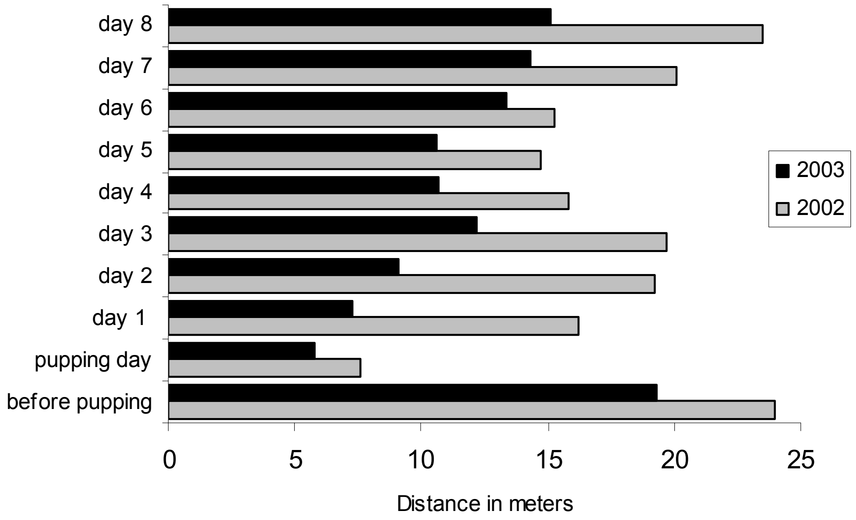


Figure 3.11: Mean daily distances (in metres) moved by the breeding females during the pupping period up to day 8 (remark: "before pupping" shows the mean distance per day).

		mean distance per day before pupping	pupping day			day 1			day 2			day 3			day 4			day 5		
		All	All	BR	BDP	All	BR	BDP	All	BR	BDP	All	BR	BDP	All	BR	BDP	All	BR	BDP
Mean	**2002**	**24.0**	**7.6**	**7.2**	**9.3**	**16.2**	**17.0**	**28.1**	**19.2**	**18.4**	**22.8**	**19.7**	**20.1**	**18.1**	**15.8**	**16.9**	**11.0**	**14.7**	**15.3**	**11.2**
	2003	**19.3**	**5.8**	**5.3**	**8.5**	**7.3**	**7.8**	**4.9**	**9.1**	**8.8**	**11.1**	**12.2**	**12.1**	**13.2**	**10.7**	**11.7**	**6.4**	**10.6**	**10.0**	**13.6**
Max	*2002*	221.9	22.8	22.8	15.0	74.1	74.1	223.0	101.3	96.7	101.3	182.0	182.0	72.0	171.4	171.4	25.8	43.7	43.7	27.3
	2003	163.9	28.9	19.2	28.9	65.5	65.5	12.7	78.5	78.5	56.9	236.4	236.4	52.0	238.6	238.6	18.0	106.0	106.0	50.0
Min	*2002*	0.0	1.3	1.3	3.7	0.0	0.0	4.9	2.3	3.3	2.3	0.7	0.7	6.1	1.8	1.8	2.3	1.1	1.1	2.6
	2003	0.0	0.0	0.0	2.3	0.7	0.7	1.1	0.0	0.0	1.8	0.0	0.0	2.3	1.3	1.3	1.4	0.7	0.7	5.8
S.D.	*2002*	42.0	5.1	4.9	4.3	13.3	12.2	56.4	21.7	17.5	26.2	33.8	28.6	18.7	30.9	25.0	7.8	12.4	12.3	8.3
	2003	30.9	5.4	3.5	8.9	10.4	8.7	3.2	14.6	11.7	15.6	39.9	31.6	15.6	43.0	34.6	4.9	21.8	17.9	14.9
N	*2002*	72	72	58	14	69	56	14	63	51	12	59	47	12	54	44	10	43	36	7
	2003	78	78	66	12	76	64	12	73	61	12	66	56	10	56	46	10	47	39	8

Table 3.5: Mean distances (in meters) per day for all breeding females of each season (All), only for breeding with alive pups (BR) and only for the females with dead pups (BDP) during pupping period up to the fifth day after birth (day 5). Max, Min, S.D. (Standard deviation) and N (number of females) are also given.

Table 3.6: Results of the General Linear Model (GLM) produced on the distances moved by breeding females during the pupping period for pupping day, day 1 and day 2. Same analyses were produced for days before pupping, day 3 up to day 8 but the models were not significant.

		FACTORS					
		Year			**Status**		
	N	F	d.f.	p	F	d.f.	p
Pupping day	150	1.953	1	0.164	6.493	1	**0.012**
Day 1	139	14.453	1	**<0.001**	0.939	1	0.334
Day 2	136	7.620	1	**0.007**	1.370	1	0.244

4. Discussion: spatial behaviour of a female New Zealand sea lion at Sandy Bay

4.1 Timing of presence

The presence of a female New Zealand sea lion at a breeding colony is a temporary phenomenon involving a precise and consistent timing. On average females first arrived at Sandy Bay on 21 December. The birth of a pup occurred during the second day (mean pupping date 26 December) of the pupping period that lasted for 8.2 days. After the first departure to sea the female alternated foraging trips at sea and nursing periods onshore. The total number of days of presence of an average female at Sandy Bay was 31.6 days during the whole study season (up to 21 March). The mean date of definitive departure from Sandy Bay was 1 March. A non-breeding female, present at Sandy Bay for mating only, exhibited a different behaviour as she arrived later (26 December, which corresponded to the pupping peak and thus mating peak which happens within a few days after birth; Marlow, 1975). A non-breeding female was sighted during only 15.3 days at Sandy Bay on average up to 21 March. The mean date of definitive departure from Sandy Bay was also earlier than that of females who had a pup (21 February).

No timing of any event was found to affect survival of pups in this study. The date of birth was however found to significantly affect the survival of pups of Southern sea lions, *Otaria byronia*, as the pup mortality was higher if the pup was born during the early part of the breeding season (Campagna *et al.*, 1992). In this species the period during which births occurred was yet long and thus implied an early time contrary to the New Zealand sea lion for which births are concentrated during 30 days with most births occurring around 26 December.

The absence of difference in the distribution of locations between females with a pup that survived and females whose pup had died also indicated that females who lost their pups kept using Sandy Bay as if they still had a pup in the colony.

4.2 Spatio-temporal use of Sandy Bay

The main feature of the spatial ecology of a female New Zealand sea lion was the two-phase pattern involving a harem phase, during which the female came ashore and used a small area of the beach, and a dispersion phase, during which the female used a large area behind the beach. Before the start of the dispersion phase a female's locations were aggregated whereas after this date the locations were randomly distributed within the study area. This randomness must be interpreted as the absence of influence of the previous locations on the new nursing site a female chose when she came back ashore after a foraging trip. Instead during the harem phase, the female came back to where she was on her previous onshore day.

The increase in the area used by an average female followed an exponential model called the time-dispersion model. This model gives the area of the Minimum Convex Polygon (MCP) corresponding to the area used by an average female on a specific day. The exponential increase matched the two phases as the sudden increase in area happened after the start of the dispersion. All births occurred during the harem phase. The amplitude of the dispersion phase appears as being particularly unusual for a marine mammal species. An average female, based on the time-dispersion model, was found to use an area of 73961m^2 (21% of the total area used by the female population) up to 18 February and 165249m^2 (29% of the total area used by the female population) up to 21 March.

A significant difference was found between the results in point distribution pattern of females' locations of the two study seasons. The NNI values were overall higher in season 2002 than in season 2003 whereas the general pattern of difference between harem phase (aggregation) and dispersion phase (randomness) was detected with the same intensity in both seasons. Consequently, an average female generally varied her nursing sites more during 2002 than during 2003. The main recorded dissimilarity between the two study seasons was the breeding female population size. During season 2002, the female population at Sandy Bay was down by 17% compared with the female population during season 2003. In a colonial breeding system, disturbance and harassment from males are the main elements for the formation of a harem, within which females are protected from disturbance by the dominant adult males keeping other males away (Campagna *et al.*, 1992). Smaller groups of females thus tend to have a higher harassment rate by males than bigger groups. The reduced number of females in 2002 may have engendered a higher male harassment rate per female and therefore imposed females to move more to avoid disturbance. During the 2002 harem phase, females were likely to move to different sites, depending on where the males were less aggressive. During the 2003 harem phase a less intense disturbance could have allowed the females to be more sedentary. During the 2002 dispersion phase, a female would go farther from her last site than in 2003 due to more disturbance to avoid created by a higher ratio of sub-adult males per female present at Sandy Bay (Marlow, 1975). This potential interpretation is also supported by the fact that the pup mortality was higher in 2002 (24% of pups died) than in 2003 (18% of pups died). A higher harassment level from males i.e. greater female disturbance and more aggressions would lead to a higher pup mortality through higher movement rates and an increased level of male-related pup deaths (Campagna *et al*., 1992).

4.3 Distances moved around the time of birth

The pupping period is critical for a breeding otariid female as it includes the birth of the pup and also the time during which the female and the pup get familiar before the female leaves for her first trip at sea. The female and pup must learn how to recognise each other; acoustical recognition was found to be the main mean by which a female and a pup otariid can find themselves within the colony with an ultimate olfactory recognition before acceptance (Bowen, 1991).

In this study, as it was already observed by Marlow (1975), females were very sedentary during the day of pupping (minimum average movements of 5.8m). The amount of movements dropped off by 70 % during the pupping day compared to the days onshore prior to birth. The distances moved per day rapidly increased and, by the eighth day of the pupping period after birth, they were almost equal to those before birth. Females thus reduced their movements on the day of birth, probably in order to stay in contact with their pups and avoid the pup to have contact with other sea lions (Lawson and Renouf, 1987). There is in fact, in mammalian species, a so called ‘sensitive period’ after birth during which the imprinting between the mother and the offspring occurs (Lévy *et al*., 1996). Disturbance of the mother-pup pair during this period may thus influence the survival of the pup.

The present study showed that there was a significant difference between the distances moved during the pupping day by females with a pup that survived and by females with a pup that died. This result could emphasise the existence of a sensitive period during the first day after the pup is born in this species. Gisiner and Schusterman (1991) had recorded that Californian sea lion, *Zalophus californianus*, mother-pup pairs with pups aged less than a day could already acoustically recognise each other. Lawson and Renouf (1987) even recorded that amongst harbour seals, *Phoca vitulina*, pups were able to orientate towards their mothers within 45 minutes of birth. This reinforces the hypothesis that the sensitive period of sea lions happens very soon after birth. The sensitive period of sheep was found to be between 4 and 12 hours after birth (Lévy *et al*., 1996). Nonetheless, it is likely that this period would be earlier and shorter for a colonial species such as the New Zealand sea lion. Indeed the quicker a mother-pup pair can recognise each other within the harem, the less the effect of separation should affect the pup survival. The female New Zealand sea lions that moved the most during this period had a higher level of pup death. This could come from a weak bond between the pair and thus difficulties to find each other after the first trip at sea of the female or later in the season. The same hypothesis was drawn by McCulloch and Boness (2000) for grey seals, *Halichoerus grypus*. They mentioned that separation soon after birth could induce an unsuccessful acoustical recognition due to the perturbation to the sensitive period. However neither the cause of the death of pup or the behaviour of the mother-pup pairs was recorded in the present study.

On the other side, females moved more during the two days following the day of pupping during 2002 than during 2003. This follows the discussion of the precedent section that the female population had a smaller size in 2002 and thus females may have endured more male disturbance per individual and had to move more to avoid aggression. The fact that, during the pupping day, this was not found also reinforces the idea of a sensitive period shortly after birth during which the females may try to stay as sedentary as possible even if males cause them more disturbance and may be aggressive towards them.

5. Conclusion

The analyses at the individual female scale suggested that the spatial ecology of an average breeding female at Sandy Bay could be modelled, stressing the predictability of this behaviour. This behaviour was indeed consistent during the two seasons of the study and all breeding females showed a similar spatio-temporal behaviour based on the two-phase pattern. The harem phase consisted of the use of a small area by the female followed by the dispersion phase during which the female exponentially increased the area she used behind the beach until she left Sandy Bay.

The existence of a sensitive period soon after birth for the New Zealand sea lion tended to be demonstrated as movements during this critical period influenced the pup survival. It was described that the survival of pups may also be affected by the female population size through higher male disturbance in smaller populations involving a higher movement rate per female.

Non-breeding females were found to behave differently as they were mostly at the colony only for mating and did not have to rear a pup. Both females with a pup that survived and those with a pup that died during the study periods exhibited the same behaviour. Consequently in the next chapter, involving study at the population scale, only breeding females were used in the analyses.

CHAPTER FOUR: POPULATION SCALE

SPACIAL DYNAMIC OF THE FEMALE POPULATION

"Le commencement de toutes les sciences, c'est l'étonnement de ce que les choses sont ce qu'elles sont.''

Aristote

1. Introduction

In this chapter, the presence and the spatio-temporal dynamic of the population of female New Zealand sea lions were investigated to characterise how, as a group, the females used Sandy Bay (SB). The density of females was also analysed as it reflected the way the female population was distributed. From the preceding chapter it was found that all breeding females used the same general spatio-temporal strategy. Consequently, this chapter aims to understand how this pattern impacts the population as a whole and what areas were used throughout the breeding season. In this chapter only breeding females were investigated as non-breeding females behaved differently.

2. Methodology

2.1. Aims

- Characterising the timing of the presence and the extent of the female New Zealand sea lion population at SB.
- Identifying the movements of the population throughout the season.
- Exploring the consistency in the presence and movements of the female population.

2.2. Presence of a female population New Zealand sea lion at Sandy Bay

The presence of female New Zealand sea lions at SB is variable throughout the breeding season (Marlow, 1975). To detect a pattern or cycle in this presence, the daily number of females found at SB was graphed, showing the trend of the presence over the two seasons in the numbers of females found onshore each day. The number of females was manually counted by observers during the peak of the harem phase for each season (from 8 December to 20 January). The ratio of branded females within the female population was calculated for each day as shown in Table 4.1. The mean ratio for each season was determined and was thus used to estimate the female population size for each day of the two seasons once the manual counts had stopped. An estimation of the error of the calculated population size was worked out by determining the mean percentage of difference between manual counts and the estimated population sizes during the days when manual counts were undertaken. The coefficients used to estimate the daily population size, after the manual counts stopped,

Table 4.1: Estimation of the ratio between the number of branded females and the total female population size onshore. *Daily ratios of branded females in the population onshore: manual population count/number of branded females; **estimation of the daily population based on this ratio; ***ratio between the number of branded females and the total population size (i.e. population size=number of branded females x coefficient).

	2002				2003			
	Manual female counts	Number of branded females	*Ratio	**Estimated female population	Manual female counts	Number of branded females	* Ratio	**Estimated female population
8-Dec	30	6	5.00	45.7				
9-Dec	38	5	7.60	38.1				
10-Dec	46	6	7.67	45.7	36	4	9.00	30.9
11-Dec	51	8	6.38	60.9	40	5	8.00	38.6
12-Dec	47	9	5.22	68.5	51	6	8.50	46.3
13-Dec	50	9	5.56	68.5	56	7	8.00	54.0
14-Dec	50	5	10.00	38.1	71	11	6.45	84.9
15-Dec	70	10	7.00	76.1	81	12	6.75	92.6
16-Dec	63	5	12.60	38.1	102	15	6.80	115.7
17-Dec	83	17	4.88	129.4	134	20	6.70	154.3
18-Dec	111	19	5.84	144.7	157	23	6.83	177.5
19-Dec	140	24	5.83	182.7	207	29	7.14	223.7
20-Dec	156	24	6.50	182.7	226	30	7.53	231.5
21-Dec	172	20	8.60	152.3	243	32	7.59	246.9
22-Dec	191	30	6.37	228.4	221	27	8.19	208.3
23-Dec	225	37	6.08	281.7	275	39	7.05	300.9
24-Dec	240	37	6.49	281.7	307	42	7.31	324.1
25-Dec	285	44	6.48	335.0	346	48	7.21	370.3
26-Dec	277	46	6.02	350.3	299	47	6.36	362.6
27-Dec	310	43	7.21	327.4	378	44	8.59	339.5
28-Dec	303	45	6.73	342.6	388	54	7.19	416.6
29-Dec	304	43	7.07	327.4	360	51	7.06	393.5
30-Dec	305	45	6.78	342.6	339	52	6.52	401.2
31-Dec	318	52	6.12	396.0	380	59	6.44	455.2
1-Jan	352	38	9.26	289.3	373	47	7.94	362.6
2-Jan	318	50	6.36	380.7	326	39	8.36	300.9
3-Jan	279	37	7.54	281.7	363	40	9.08	308.6
4-Jan	288	22	13.09	167.5	317	34	9.32	262.3
5-Jan	320	43	7.44	327.4	286	40	7.15	308.6
6-Jan	370	39	9.49	297.0	306	36	8.50	277.8
7-Jan	291	35	8.31	266.5	328	43	7.63	331.8
8-Jan	301	36	8.36	274.1	323	41	7.88	316.3
9-Jan	366	34	10.76	258.9	315	37	8.51	285.5
10-Jan	287	27	10.63	205.6	301	33	9.12	254.6
11-Jan	230	33	6.97	251.3	288	52	5.54	401.2
12-Jan	263	44	5.98	335.0	298	42	7.10	324.1
13-Jan	257	37	6.95	281.7	323	32	10.09	246.9
14-Jan	240	25	9.60	190.4	266	42	6.33	324.1
15-Jan	226	26	8.69	198.0	345	45	7.67	347.2
16-Jan	203	21	9.67	159.9	345	48	7.19	370.3
17-Jan	298	36	8.28	274.1	294	32	9.19	246.9
18-Jan	229	27	8.48	205.6	310	37	8.38	285.5
19-Jan	219	32	6.84	243.7	302	28	10.79	216.0
20-Jan	241	29	8.31	220.8	227	32	7.09	246.9
			***Mean ratio 7.61	Mean difference with manual count 16.9%			***Mean ratio 7.72	Mean difference with manual count 10.1%

were 7.61 and 7.72 females for each branded female found onshore, in 2002 and 2003 respectively.

Within each season the female population also varied in composition depending on the status of the females found onshore each day. The composition of the female population was determined by calculating the percentage of females of each status each day from the '*Locations per day*' Excel files and graphically represented in a stacked area graph.

2.3. Dynamics in space and time of the female population

In order to detect the patterns in the space use of the females at SB the maximum area of the harem during the two seasons were calculated from the 'Harem' shapefiles. The maximum extent of the harem was 2810 m^2 in 2002 and was 2561 m^2 in 2003. When the MCPA as determined by the time-dispersion model of an average female gets greater than the harem area it is thus considered to be the mean dispersion date of the population. The area used by the female population during the harem phase and the dispersion phase was calculated in square metres by producing the Minimum Convex Polygons (MCP) of all breeding females' locations before (harem phase) and after (dispersion phase) the dispersion date.

The dynamics of the female population was investigated by analysing the 'day' shapefiles. For each of these shapefiles the 'Mean center' function (in the Arc Toolbox) was applied to the set of points. A new point corresponding to the centre of the female population on this day was created. The Hawth's analysis tool was used to convert these points to lines based on the chronological order (date) of the points (with the function 'Convert locations to path'). A path for each season thus illustrated the mean movement of the female population along the season. The 'Linear Directional mean' (from the Hawth's analysis tool) was produced for each season. This function creates a straight line that symbolises the mean direction of a path. All results were visually displayed on maps in order to show the patterns of movements and compared between the two seasons.

The maximum straightline distances from the nearest ocean access (going around known obstacles that females could not pass e.g. cliffs) to the location of a mean centre and a female of the population were also calculated to highlight the extent of the dispersion. Only results from season 2003 were taken into consideration as they corresponded to the whole period of presence of the females at SB.

In order to characterise the changes in time in the sections of the study area that the female population used, all breeding females' locations for the two seasons were gathered into the same shapefile. The dates in the attribute table were transformed into a numeral format (e.g. 8/12/01 is 1) such as the day numbers were the same during each season independently of the year (i.e. 8/12/02 was also coded as 1). An ordinary spherical kriging method (set up on 12 points and using the values of the field ‘day number’) was used to interpolate a map representing during what periods the different sections of the study area were used as nursing sites by the female population. The gradual temporal change in nursing area used by the female population along the season was thus visualised on this map. Nevertheless the females’ locations were not uniformly distributed; some sections of the study area were indeed not or less used than others. An error prediction map was also produced with the Geostatistical Analyst Wizard (extension of ArcGIS). This map gives a mean error in number of days that was assigned to the period at which each section was used by the female population (see Fortin and Dale, 2005, for the concepts). This mean error highlights the areas of the study area not or less frequented by females (very high errors) as well as areas that females may have used during different periods (errors within sensitive ranges).

2.4. Determination of the density of females

The daily density of breeding females (number of females per 100 m^2) was calculated using the female population size (manual counts or estimated; as described in Section 2.2.) and the area of the MCP of the locations of all branded females found onshore on each day. The ‘day’ shapefiles were used to obtain the MCP and their areas. These values were used to extrapolate the density of breeding females within the area of occurrence in the study area. The area used by the sample population (branded females) on a specific day was assumed to be representative of the actual area used by the female population. Consequently, the density of females per 100 m^2, on each day, was derived by:

$$\textit{Density in females (per 100 } m^2\textit{) = Population size * 100 / MCP area}$$

Figure 4.1 shows the examples of the MCP and the locations of branded females that were used to determine the density of females during two days. On 25/12/02 the manual count of females was 346 and the MCP area was 943 m^2 whereas on 1/02/03 the estimate population size was 194 and the MCP area was 66927 m^2. Consequently the densities were 37 and 0.3 females per 100 m^2 respectively. The density could also be converted into an area per female by dividing the MCP area by the number of females within the population (an ‘individual area’). Even if the females were not totally dispersed

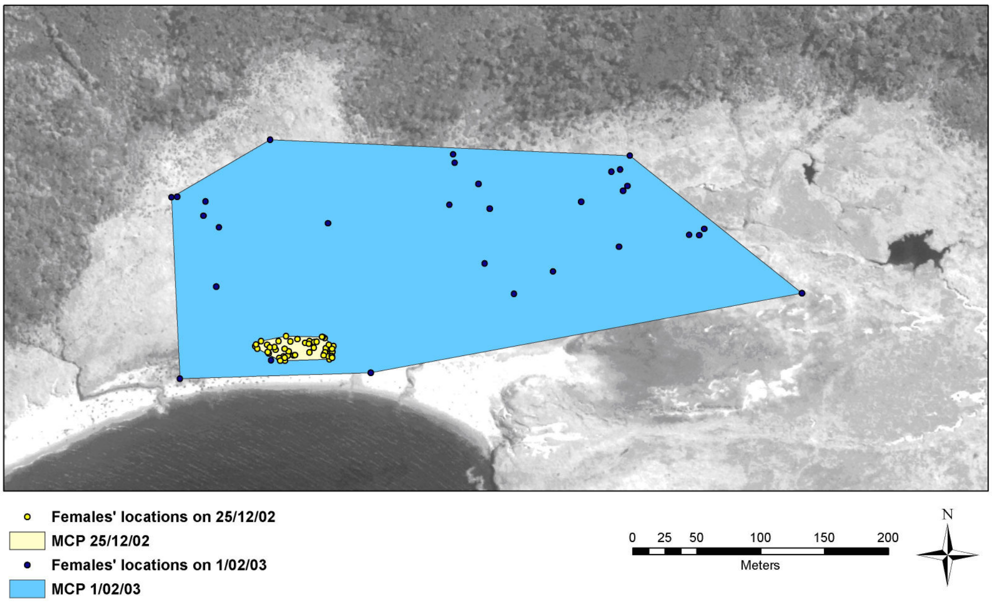


Figure 4.1: Visualisations of the density of branded females during a day of the harem phase (25/12/02) and a day of the dispersion phase (1/02/03).

within the area and form small isolated groups (see Figure 4.1), this gave a model of the temporal changes in the gregariousness of the females.

3. Results

3.1. Seasonal and cyclical presence of female New Zealand sea lions at Sandy Bay

The cyclical seasonal occurrence of female New Zealand sea lions at SB is presented in Figure 4.2. This is an annual cycle with presence of females during the summer months of the year: mainly December, January and February. One female and a small group of three females landed first at SB on 30/11/01 and 1/12/02. Then the number of females increased rapidly. On 18/12/01 and 16/12/02, more than 100 females formed the harem; eight days after these dates, more than 300 females were found in the harem. Shortly after, the breeding female population sizes gradually decreased until 21/03/03, when an estimate of only eight females was still using SB. Figure 4.3 illustrates the composition of the female population for each day of the study seasons based on the daily percentage of branded females of each status found onshore.

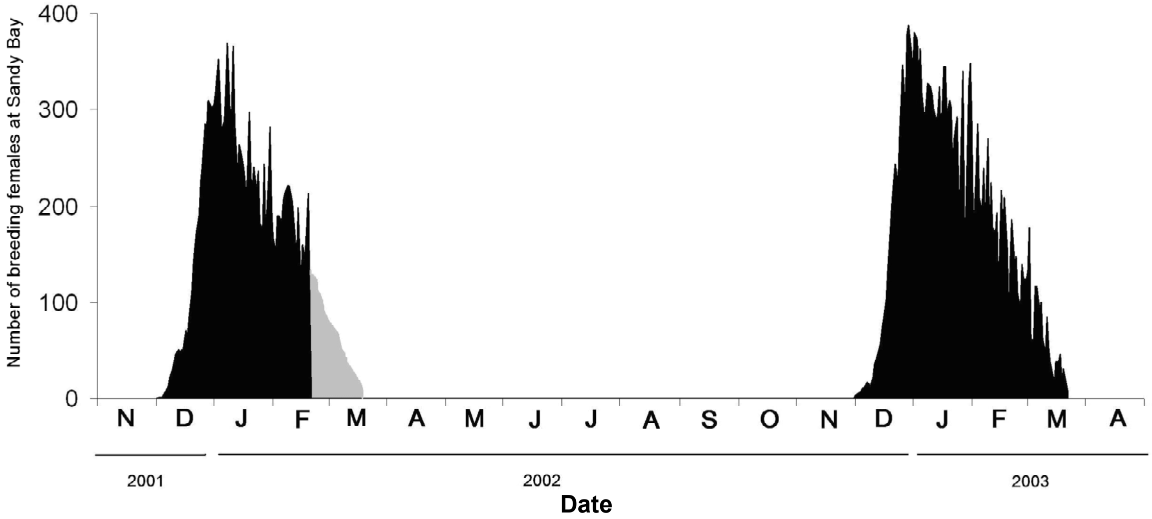


Figure 4.2: Year-round presence and size of the population of female New Zealand sea lions at Sandy Bay. The grey area marks the missing values for the season 2002 that were evaluated from the 2003 results.

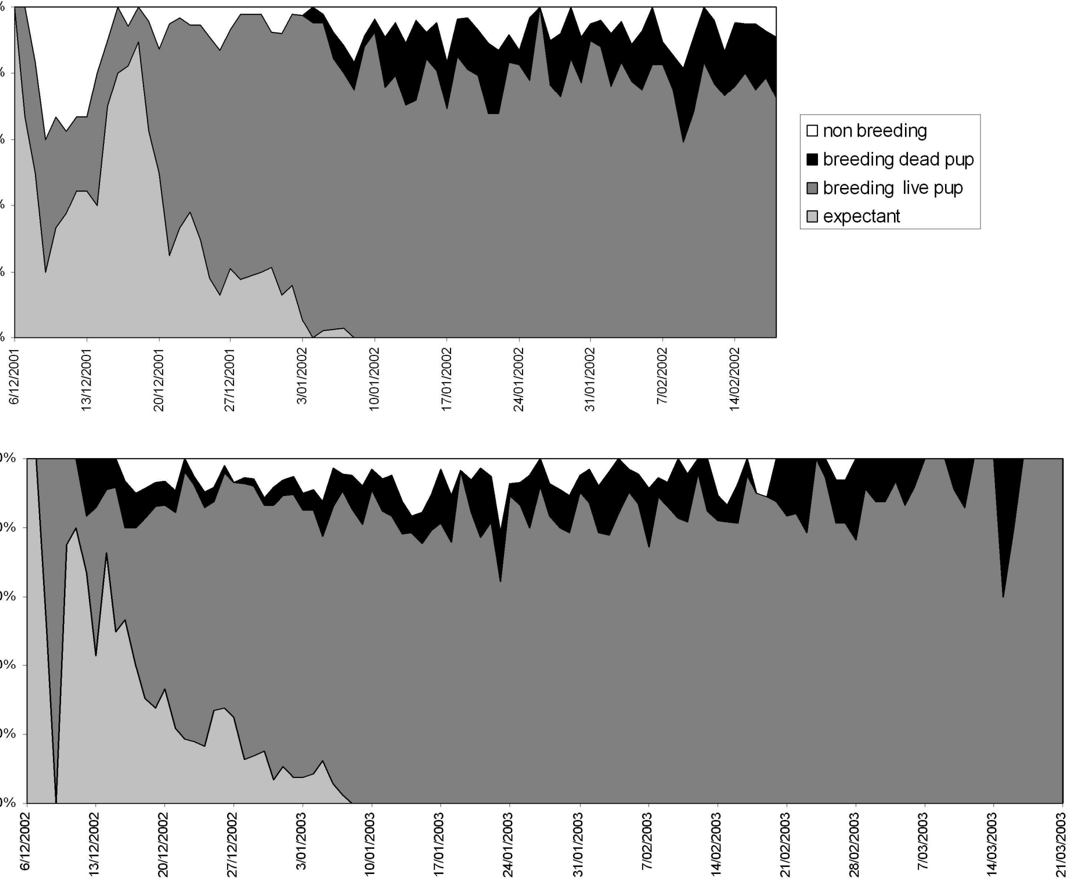


Figure 4.3: Percentages of branded females of each status (expectant, breeding with alive pup, breeding with dead pup and non-breeding) found ashore everyday at Sandy Bay from 6/12/01 to 18/02/02 and from 6/12/02 to 21/03/03.

The first females to land at SB in both seasons were all expectant. The presence of expectant females ended on 9 January during both years. After 26 December the majority of the females were nursing a pup making up on average 79% and 85% of the daily female population using SB during season 2002 and 2003. A maximum of 40% of the female population was composed of breeding females that had lost their pups on 15/03/03 but on a daily average over the season they represented 15% (in 2002) and 10% (in 2003). Non-breeding females were part of the female population a few days after the start of the season until 17 February. On 23/01/03 these females contributed 21% of the female population, the highest percentage since the population was more than 50 females in the harem. At the start of the 2002 season, two out of five (40%) branded females were non-breeding on 9/12/01.

3.2. Spatio-temporal dynamics of the female population

The spatial use of SB by the population of female New Zealand sea lions was found to be highly dynamic and changed during the season according to the two phase pattern. In 2002, the population started dispersing on 20 January, and on 19 January in 2003. The maximum areas used by the females before these dates were 29529 m^2 and 16646 m^2 respectively, while the area reached 568471 m^2 by the end of the dispersion phase in 2003. The total areas that the female population used during both years are presented in Figure 4.4 for comparison. The area the females used, up to the same date (18 February), was similar. The dynamic (movements and general direction) of the female population during the harem phase and during the whole season were mapped in Figure 4.5 and Figure 4.6 and depict the way the female population moved.

During the 2002 harem phase, an overall gradual shift of the female population (i.e. harem) towards the east along the beach was revealed. However this movement did not seem to appear during the 2003 harem phase as the population mean centre stayed within the same area. Unlike during 2002, the mean centre of the female population was found on the beach several days after the start of the dispersion, until 29/01/03. The dynamic of the female population during the whole season was different in the two years in the way the mean centre moved (movements of the female population) but overall the general orientations (mean directions) of these movements were similar.

Figrue 4.4: Comparison of the total area used by the female population during the two study seasons up to 18 February.

The maximum distances from a mean centre of the female population to its nearest access to the ocean reached 725m on 16/03/03 (sample population made of four BR and one BDP females i.e. population estimate of 39 females). The maximum distance from an individual female's location to its nearest access to sea was 789m on 20/03/03 (a BR female).

Figure 4.5 also highlighted that the locations where the first female or group of females (founder females) landed at the start of the breeding seasons determined where the harem was formed. The mean centre of the population on the first day of presence of females at SB corresponded to the location of the first female(s) on the beach. Subsequently, the mean centres of the population during the harem phase were all based around this first site. Females thus accreted around this initial site to form the harem.

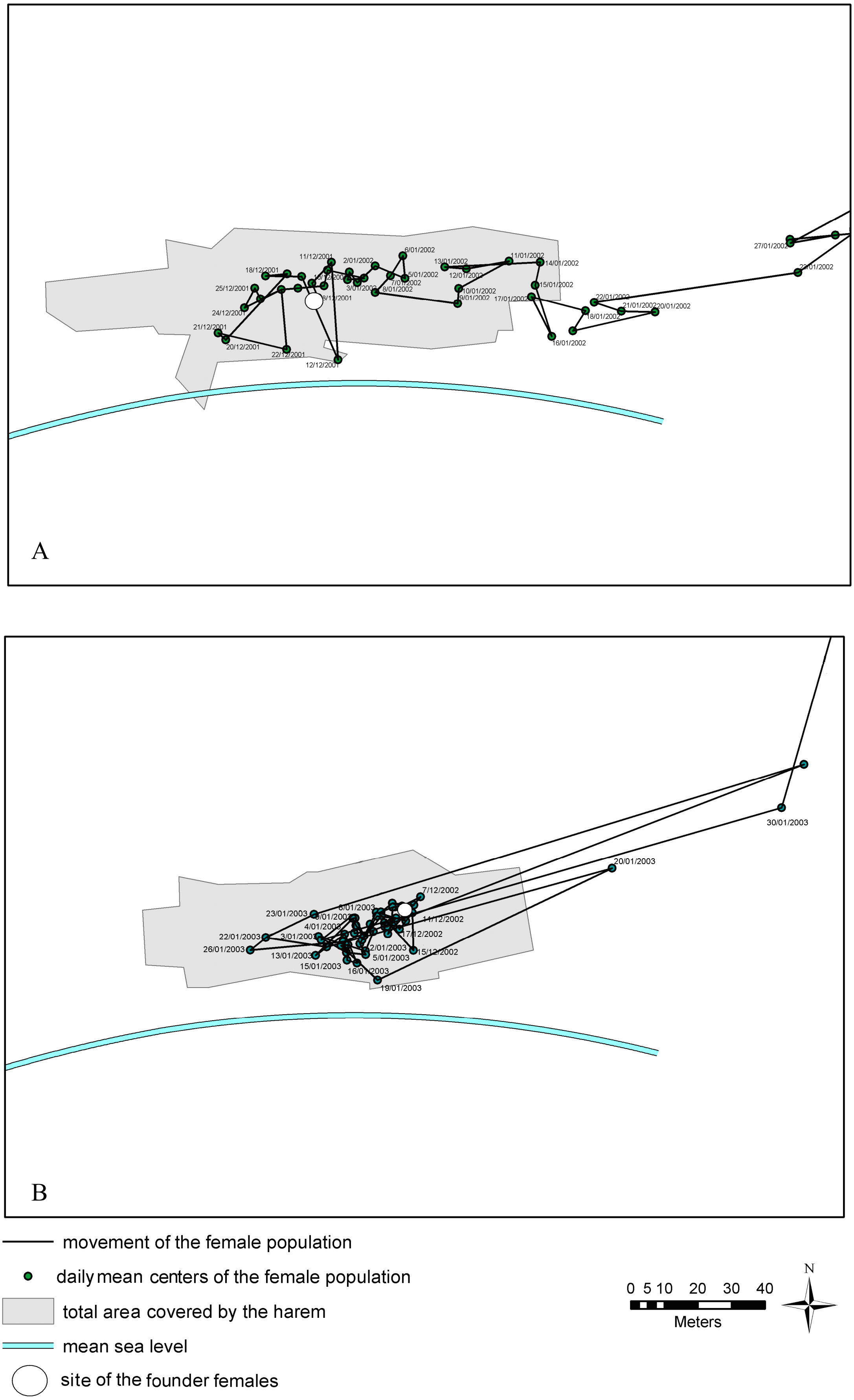


Figure 4.5: Mean movements of the female population at Sandy Bay during the harem phase and early dispersion phase 2002 (A) and 2003 (B) at the same scale.

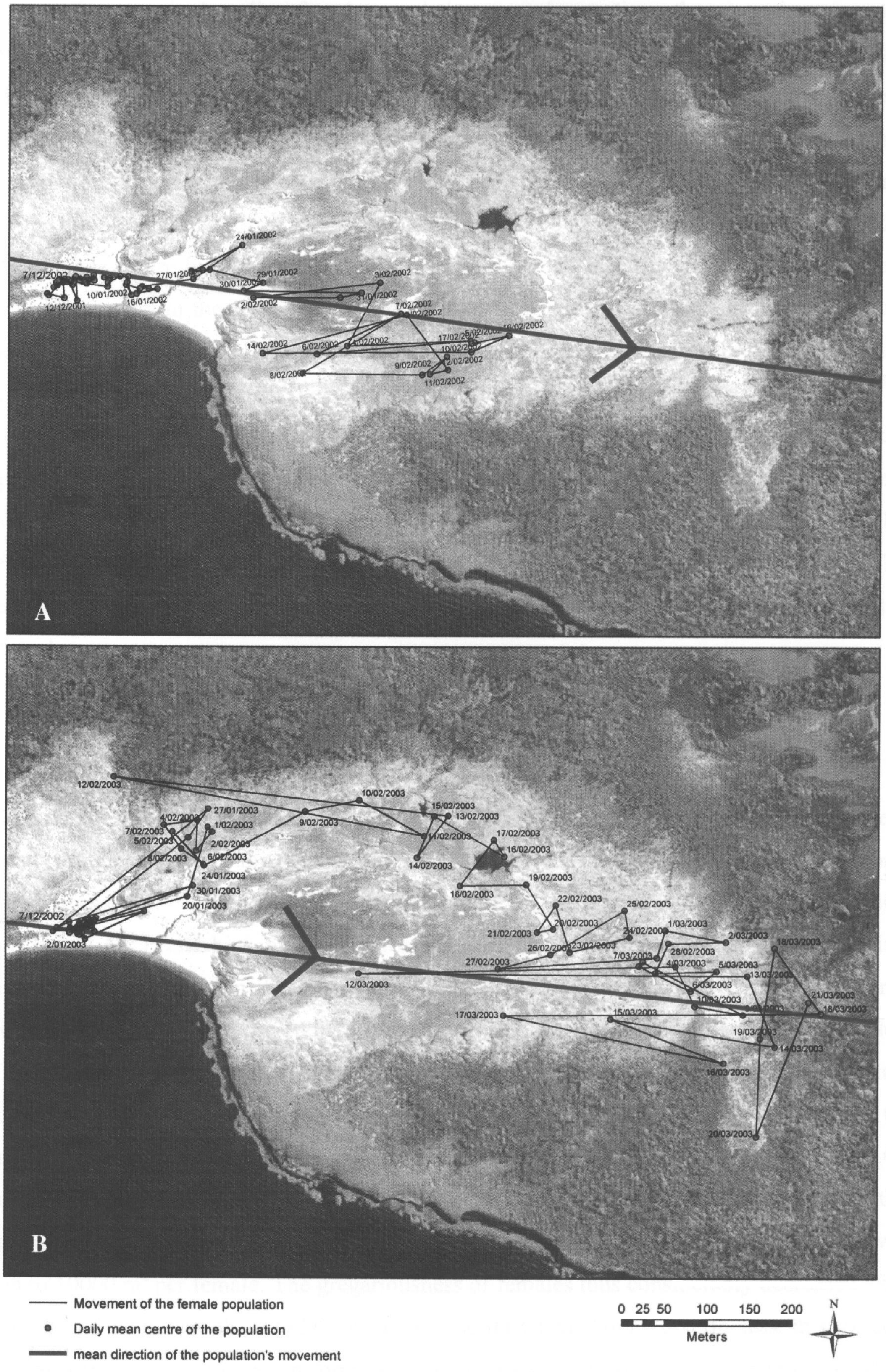


Figure 4.6: Movements and mean directions of the female populations at Sandy Bay during season 2002 (A, from 8/12/01 to 18/02/02) and season 2003 (B, from 8/12/02 to 21/03/03) at the same scale.

Because the breeding female population moved over time, the area where females were found nursing their pups changed throughout the season. Figure 4.7 shows when the different sections of the SB study area were used by the female population as nursing areas during the two study seasons. Until 20 January (yellow) the section used by the female population was confined to a small area close to the ocean corresponding to the harem. After this date, the sections used expanded and were found farther and farther from the ocean. The figure highlights that there was a change, and not only a spread, as areas that were used early in the season were seldom used later in the season. A shift in the nursing areas clearly occurred. Nevertheless all the areas closer to the ocean were still used by the females to travel to and from the nursing sections between foraging trips.

The error prediction map (in Figure 4.7) shows the mean error associated with the periods of use of the various sections. The average standard error was overall 8 days and was as low as 4 days. The error can come from two sources: utilisation of the area by females during periods far apart and a lack of data i.e. females seldom used the area. The areas with the largest errors (20+ days) indeed reflect areas that were not used by the females.

3.3. Changes in female density at Sandy Bay

The number of females and the area they used changed over time as shown in preceding analyses. Consequently the density of females within the area they used also varied along the season (Figure 4.8). There was a rapid increase in density while the harem was building up (small MCP and high number of females) until around 26 December (mean pupping date). The maximum density of females (85 females per 100 m^2 and 87 females per 100 m^2) was reached on 23/12/01 and 20/12/02 respectively. The density then decreased to around 30 females per 100 m^2. The density slowly kept lowering until around the 19 January (start of the dispersion phase) when the female density dropped to less than one female per 100 m^2. This decrease led to a very low density at the end of the season with values around 0.01 to 0.30 female per 100 m^2. These densities can be related to the 'individual area' that, at the maximum peak in density, was 1.15 m^2 per female, and, at the lower densities recorded, was up to 10000 m^2 per female. The gregariousness of females thus considerably decreased after the end of the harem phase to levels closer to solitary behaviour. Nevertheless, this solitary behaviour usually consisted in forming small groups of two to four females rather than females being totally solitary.

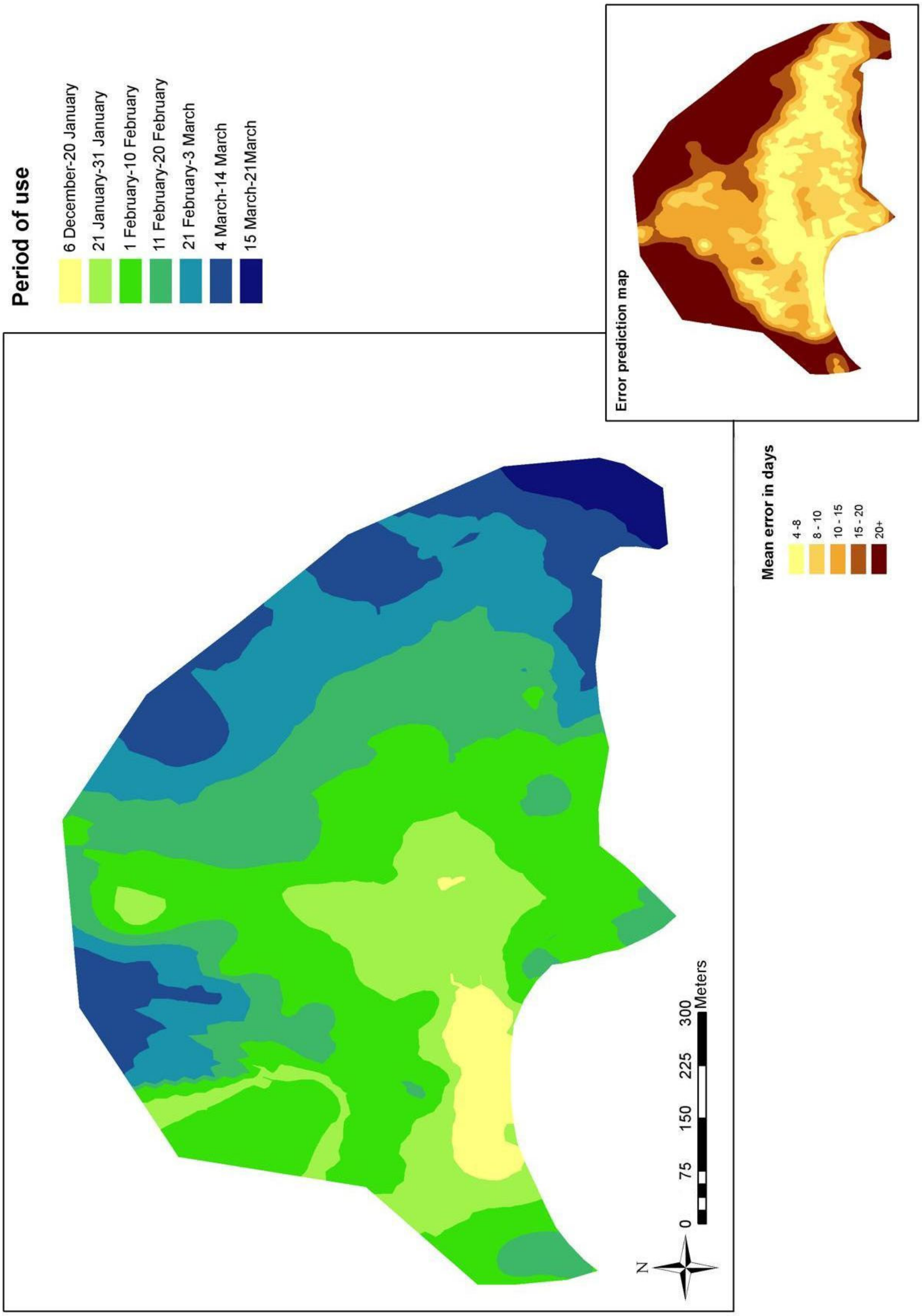


Figure 4.7: Visualisation of the gradual change of the sections used by the females to nurse their pups along the season. The map was produced with a kriging interpolation technique applied to the date of the females' locations (time-kriging).

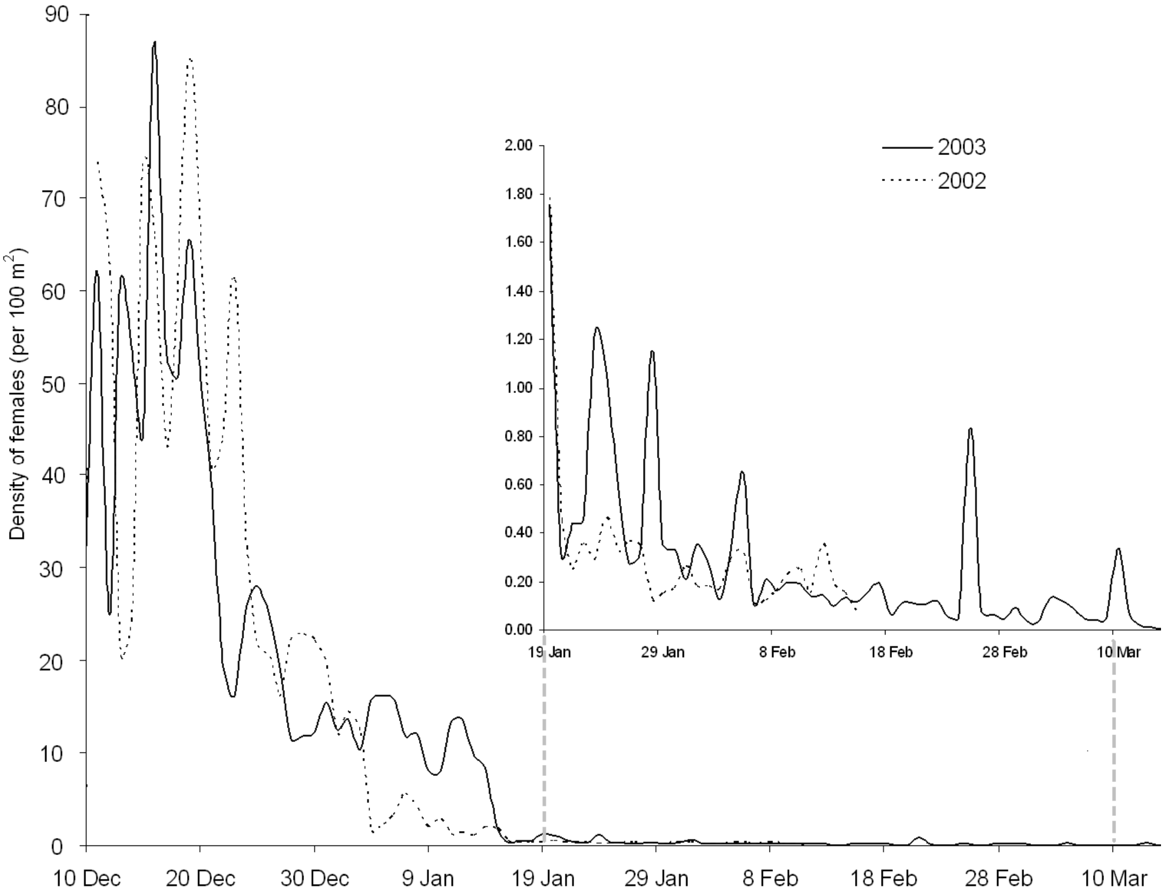


Figure 4.8: Changes in the density of female New Zealand sea lions per 100 m^2, within the MCP on this day at Sandy Bay, from 10 December to 18 February (season 2002) and to 21March (season 2003).

4. Discussion

4.1. Female New Zealand sea lion population at Sandy Bay: cyclical presence

The presence of female New Zealand sea lions at Sandy Bay was found to be an annual cyclical phenomenon. The cycle started between the last days of November and the first days of December when one or a few expectant females landed on the sandy beach. The first females pupped within a few days. The population (i.e. harem) built up quickly by accretion of other expectant females and some non-breeding females. Within 24 days from the start, the daily female population reached its maximum size with more than 300 females forming the harem onshore at one time. This count did not include all breeding females as, at this stage, pregnant females represented less than 30% meaning that some females had already started their foraging trips after pupping. These females were thus not present within the population during foraging periods. Once pupping had occured the population was predominantly composed of females nursing a pup and 10 to 40% of females who had lost their pups. The population significantly decreased after the start of the dispersion phase as females also gradually stopped using Sandy Bay in the same time.

The presence of female New Zealand sea lions was not investigated outside the periods of fieldwork of this study (30 November to 21 March). The assumption that females seldom used Sandy Bay outside this period was based on the fact that no female was found at Sandy Bay at arrival at the study site and that, at the date of departure, only eight females remained following a slow gradual decrease. Several reports from early explorers, shipwreck survivors and later research expeditions to the Auckland Islands also confirm this. They all recorded Sandy Bay as mostly deserted by the sea lions outside the breeding period (December to March) with individuals found on other sites at Enderby Island (Eden, 1955; Marlow, 1975; I. Wilkinson pers. com.). These records confirmed the cyclical nature of the occurrence of female New Zealand sea lions at Sandy Bay.

Outside the breeding season, or as soon as a female left the population at Sandy Bay after pupping, it is likely that there was thus a wider dispersion of the females taking their pups to other sites or other islands. Eden (1955) reported females with pups on the main island after the end of the breeding season. These pairs were likely to have bred in one of the colonies and then changed their nursing sites. Tagged pups from Sandy Bay with their mothers were found at Rose Island (next to Enderby Island) after mid-January (L. Chilvers pers. com.). Three marked pups that were born at Sandy Bay in 2003 were also resighted with their mothers on the main island by mid-March (L. Chilvers, pers. com.). In spring 2003, an expedition also revealed that a tagged female and her pup born at Sandy Bay had then moved to the Snares Island by mid-October (I. Wilkinson pers. com.).

4.2. The female population: a shifting population

The main original phenomenon detected in the spatio-temporal dynamics of the female population was a shift in the areas of Sandy Bay that were used as nursing sites. Following the two-phase pattern of the spatial ecology of an average female New Zealand sea lion, this revealed that the movements of the whole population were based on these individual strategies. During the harem phase the population was centred in the middle of the harem whereas after the start of the dispersion phase the population started moving away from the beach towards the east. At the end of the breeding period, when the female population size was reduced to only about 30 individuals, the centre of the population was found to be at a straight-line distance of over 700m from the nearest access to sea. The shift of the mean centre of the population was coupled with the increase in area used as, before the mean dispersion date (19 January), the population only used a maximum of almost 30,000 m^2 whereas at the end of the season the area used was more than 550,000 m^2. While the population moved towards the east of the study area, the area used thus also increased around the mean centres. The females were also found to shift the areas they used and seemed to avoid the sections of Sandy Bay that the female population had used before during the season.

Several reasons could explain this shifting in areas. First of all, females may want to go away from the beach as the summer ends and storms are more frequent. Storms can wash up the whole beach and being farther from the ocean would prevent pups and the females during nursing periods from suffering from these storms. Then by moving farther inland, the females may also attenuate the adversity of strong winds. Secondly, the likelihood of being harassed by the sub-adult males, which stay around Sandy Bay after the end of the harem (Marlow, 1975), may decrease if the females and the pups are not visible from the ocean i.e. being behind the beach; regular changes in nursing sites would also avoid males to know where females and pups are. Another cause may explain why females would avoid areas that the population previously used. The shifting of the nursing areas may indeed be related to the avoidance of parasite infected zones. Pinnipeds are indeed host of a range of endoparasites that are more or less pathogenic (Geraci and St Aubin, 1987). Hookworms, *Uncinaria* spp., were found in New Zealand sea lion adult females (Marlow, 1975) and pups (Castinel *et al.*, 2006). The adult form of this parasite is well known to colonise the small intestine of the pups and are a significant source of pup mortality in otariid species (Olsen and Lyons, 1965; Lyons *et al.*, 1997; Lyons *et al.*, 2003). The parasite is originally transmitted by the mother through suckling under the form of an infective form. The infective form becomes adult in the pup and produces eggs that are excreted on the ground by the pup with its faeces and hatch under the form of free-living larvae, staying in the soil until any sea lion rests on the soil where the larvae are (Geraci and St Aubin, 1987). Then the larva penetrates the skin and migrates to the blubber. If it infests an adult female, then the infection will be transmitted to the next generation of pups (Geraci and St Aubin, 1987). It is thus evident that, by shifting the areas they use, female New Zealand sea lions would avoid using areas that have been previously infested by the parasite during the season and thus would limit the risk of infection i.e. increasing the survival of their next pup. A. Castinel (unpublished data) showed that infective forms of hookworms in the New Zealand sea lion become adult forms producing eggs around mid-January. The mean start date of the dispersion phase (19 January) thus also supports this hypothesis as it is similar to when the adult hookworms start producing eggs and thus to the beginning of the infection during a breeding season. Other potential reasons for such movements as exhibited by the female population of New Zealand sea lions at Sandy Bay are however probably outside the scope of this study.

Another shift at smaller scale was revealed as there was also a shift towards the east side of the beach of the whole harem during season 2002. This shift was not identified in 2003. Marlow (1975) also noticed this shift and has put forward the theory, through behavioural observations, that the harem would move because of the tendency of non-breeding females to gather at one end, creating a social dynamic due to male aggressiveness and a movement of the breeding females. In this study, no sign of aggregation of the non-breeding females at one side of the harem was found. Nevertheless, the results may have been biased by the sample population as branded females were all mature animals. Only a small portion each year did not breed whereas, within the harem, there must have been more young females who came to mate for the first time at Sandy Bay and thus were not breeding during this season. These females may have created a movement of the harem by grouping at the west end of the harem in 2002. This behaviour was not perceptible during the 2003 season though. This may also be related to the results found at the individual scale. Overall, females moved less within the harem in 2003 than in 2002, thought to be due to a higher number of females present in the harem. Based on this, a smaller ratio of male aggressiveness per female would have not required the non-breeding females to group on the side of the harem but to mix within the breeding females. Therefore, movement of the harem would not have been instigated.

The female population also progressively shifted their nursing areas to other sites, leaving Sandy Bay almost deserted by the species during the months outside the breeding period. This behaviour highly contrasts with the strategy adopted by the Australian sea lion, *Neophoca cinerea*. Females of this species were indeed found to nurse their pups and use the same island as they gave birth year round (Gales *et al*., 1992). This difference is unlikely to be caused by a male aggressiveness factor. Male Australian sea lions are more aggressive towards pups and cause more pup deaths than the male New Zealand sea lions (Marlow, 1975). Consequently female Australian sea lions would be more susceptible to move to other sites to avoid aggressions towards themselves or their pups left alone, especially if it was the cause of this behaviour. New Zealand sea lion females are thus unlikely to shift nursing sites because of the presence of males. Other hypotheses that could be stated include, firstly, a shift in prey species in the winter months (diet was found to seasonally vary depending on the prey species available around the mainland; Lalas, 1997) or, secondly, a competition avoidance. Pup Steller sea lions, *Eumetopias jubatus,* were found to prey near shore in the vicinity of the nursing sites during the first year of their lives (Raum-Suryan *et al*, 2004). Juvenile Australian sea lions were still found to have limited diving abilities at two-year old which was thought to lessen their available foraging habitat (Fowler *et al.*, 2006). Consequently by spreading, females would avoid competition amongst pups for food resources close to shores.

4.3. Gregariousness of female New Zealand sea lions: harem creation and temporality

The density of females per 100 m^2 of the area they used each day defined the degree of gregariousness of the female New Zealand sea lions and how it varied throughout the season. Marlow (1975, p.181) described the female New Zealand sea lions as "highly gregarious". This observation was confirmed with densities estimated of up to 85 females per 100 m^2. A single female would only have an area of 1.15 m^2, which is close to the average surface covered by a female resting on the ground (length 1.7m; Walker and Ling, 1981; width estimated around 0.6m thus area of 1 m^2). The females in the harem are not orientated parallel to each other, causing a lot of overlap amongst females' bodies which confirms the extreme tolerance amongst females described in Marlow (1975) (Figure 4.9). The spatial arrangement and density of the females within the harem thus confirmed the high gregariousness of the female New Zealand sea lions.

Figure 4.9: Illustration of the high gregariousness of female New Zealand sea lions, during the harem phase, with a non-parallel organisation involving considerable body contact (photo taken at Sandy Bay, Enderby Island on 17/12/05).

This gregariousness created a continual accretion of the females to the harem as females go to sea and then come back within the harem. The harem was formed by the gradual addition of females around the landing site of the founder females. This was already mentioned in Marlow (1975) and Chilvers *et al.* (2005a). In 2003 season, during which there was no shift of the harem, the location where the founder females landed almost stayed at the centre of the population during most of the harem phase. In 2002 this phenomenon was less obvious as a shift occurred. However, the early centres of the population stayed close to where the first female was found on the beach. Anderson *et al.* (1975) suggested that the same phenomenon happens amongst grey seals and that the position of the first female ashore during a breeding season decides the distribution of the colony because of their gregariousness. This phenomenon seems likely to be consistent for any species of pinnipeds exhibiting colonial breeding as an initial group of females must always be required to start a harem.

The New Zealand sea lion females were however found to modify their gregariousness later in the season. Marlow's (1975) statement that they are 'highly gregarious' should thus be completed with the term 'temporary'. Indeed the breeding females at Sandy Bay decreased their degree of gregariousness markedly during the dispersion phase. The females then exhibited a behaviour close to solitariness by forming isolated small groups (of two to five individuals) with corresponding areas of up to 10,000 m^2 per female found onshore at Sandy Bay. This degree of solitariness was also found in the movements to other sites as discussed in the precedent section. The extreme gregariousness of the female New Zealand sea lions is thus a seasonal characteristic that allows the formation of the harem and protection of the females against male aggressiveness (Chilvers *et al.*, 2005a). One of the main causes for the shifting of nursing areas during the dispersion phase can also be applied to the solitary behaviour of the females during the dispersion phase. Indeed parasite infections are known to exponentially increase the risk of death in groups where a large number of offspring stay in close proximity (Daan and Tinbergen, 1997). In a bird species, the great tit, *Parus major*, significantly greater infection rates causing higher mortality rates were detected in nests supporting bigger broods than in nests with a brood of only two or three chicks (Daan and Tinbergen, 1997). Relating to the New Zealand sea lion, females, by forming small groups from two to five female-pup pairs, would even more limit the risk of hookworm infections combined with the avoidance of previously used areas. Yet the presence of other pups would still allow the pups to interact and socialise contrary to a pup whose mother would be totally solitary.

4.4. Kriging time: visualisation of some wildlife movements

As the results of this study strengthened, time is a significant factor for wildlife spatial ecology when movements are investigated. New Zealand sea lion females exhibited a highly dynamic spatial behaviour. This behaviour is however a seasonal behaviour and it is repeated in the same way each year. This corresponds to characteristics of another wildlife movement: migration. Dispersion and migration are two spatio-temporal phenomena that are based on a gradual shift of the area used by a population and are also predictable. Population movements driven by these processes tend to generate a high vulnerability to the animal population to anthropogenic interactions and disturbance (Brower and Malcolm, 1991, Simons *et al.*, 2000, Philips *et al.*, 2005). Mapping these phenomena in space and time would give an advantage to wildlife managers as it would give visual support to show when and in which areas the animals of a population move during the process. Issues arising from migration or dispersion processes could then be addressed with more efficiency, especially in the case of threatened or endangered wildlife.

Kriging was developed by geostatisticians in order to interpolate values over a surface, for the field of interest, from a set of sample points (Cressie, 1989). The main assumption for the development of such a technique was the spatial auto-correlation present in most geographical phenomena (i.e. what is closer in space is likely to be alike, and what is farther apart is likely to be more different; Cressie, 1989). The values in between sample points can thus be evaluated based on the sampled values and how far the sample points are situated from the interpolated locations (see details in Webster and Oliver, 2001). Following O'Sullivan's (2005) discussion, kriging the time values (i.e. 'time-kriging') could be useful to visualise and map in 2-D wildlife movements involving a shift in used areas (e.g. dispersion and migration) but would not be suitable for other types of wildlife spatio-temporal phenomena (e.g. if a population stays within the same area). 'Time-kriging' used to map the dispersion process of the female New Zealand sea lions at Sandy Bay was also based on the assumption that locations close to each other were closer in time than locations that were found farther apart. The kriging technique can thus be applied on the field value 'time' to create a prediction map of the gradual change in area used by a population (or an individual) to visualise dispersion or migration processes in space and time.

5. Conclusion

The occurrence of a population of female New Zealand sea lions at Sandy Bay is temporary and cyclical. It occurs from December to the end of March, with a quick increase during the first half of December and a gradual decrease of the population size from mid-January onward. Most of this population is composed of breeding females nursing a pup once all pupping has occurred but is initiated by the founder females that are still expectant.

The analyses at the population scale demonstrated that, following the results from the analyses at the individual scale, the female population of New Zealand sea lions follows a consistent movement coupled to a spread of the population once the harem phase finishes. During the harem phase the female population was entirely contained in a restricted area on the beach because of males' aggressiveness. During the dispersion phase the population dispersed over a large area, observed during both seasons, and its centre moves farther and farther from the beach in the same time as the area used by the population increases. This reveals a shift of the areas where females nurse their pups which is thought to be an adaptive behaviour to decrease the impact of storms, to avoid sub-adult males disturbance and to minimise hookworm infections as well as other potential unknown reasons.

Female New Zealand sea lions exhibit a temporary high gregariousness during the harem phase. This gregariousness allows the formation of the harem as females continually aggregate where the founder females landed on the beach at the start of the breeding season. Once the harem breaks up the females become less and less gregarious and exhibit behaviours close to solitariness which may also be behaviour to lesser the risk of being detected by males and other females and of hookworm infections.

Specific habitat needs and preferences may also require females to move and thus play a role in the creation of these dynamic phenomena. The habitat use of the females is thus investigated in the next chapter: habitat scale.

CHAPTER FIVE: HABITAT SCALE

HABITAT USE OF THE FEMALES

"When one moves through the forest,
his sense of discovery is quickened…''
W. O'Douglas

1. Introduction

The low number of breeding colonies of the New Zealand sea lion indicates that these areas are likely to have specific characteristics required for the breeding females. The general characteristics of the habitat at Sandy Bay (SB) were likely to have played a considerable role in the establishment of a breeding population. Within SB, females had a range of habitats (based on terrain and vegetation) available for use but appeared to choose specific sites. The existence of a preferential selection for sites with specific characteristics by the females should reveal what are the most suitable habitats for the species. Furthermore this should also help to determine the overall suitability of SB as a breeding environment. Females nursing pups may also have more particular preferences for some habitats than females without the requirements to nurse a pup. If such preferences exist, they should reflect which habitat characteristics are the most significant for optimal nursing behaviour and thus survival of pups.

2. Aims

- Characterising, in term of habitat, SB and the sites where females were found.
- Determining which kinds of habitats were preferentially selected by females in a temporal context.
- Detecting if nursing sites were more specific than resting only sites.

3. Sandy Bay: general habitat features

The general characteristics of SB are, first of all, a long, fine-sand, wide and relatively flat beach. The general slope of the beach is 6° and the beach is bounded on each side by rock cliffs. The bay, facing south, is sheltered by the east part of the island and the main Auckland Island in the south protecting against high southerlies and main swells. The beach is backed inland by a duneland consisting of a few major high dunes behind the east part of the beach. The rest of the duneland gently goes up with a few streams producing several small ‘canyon-like’ formations one to three meters deep. Overall the general pattern of small dunes creates an alternation of high and low slopes. From the shore to the highest point of the study area, SB has an average slope of 7.4° with a range from 0° (flat) to 80° (cliffs). A large flat area is found behind the big dunes on the east of the beach, then the terrain keeps going up towards the dead end of the duneland that is enclosed by a large belt of scrub with the rata forest found behind this scrub. A major lake is found around 400m from shore towards the east of SB. Another eight less significant lakes (i.e. ponds) are spread within the duneland. The areas around these lakes are usually swampy with water running underneath the sward. The general elevation at SB increases with the distance from the ocean; nevertheless these two values are not overall correlated due to the presence of high dunes close to shore. Most of the terrain within the study area (73%) is south and west facing. The 3-D views of SB draped with an old vertical aerial photo (from 1993 i.e. vegetation has changed) and with the habitat type map illustrate the general features of SB (Figures 5.1 and 5.2). The first view shows the part of the sandy beach where the harem occurred and the middle part of the duneland, including, on the right, some of the major dunes as well as some of the 'canyon-like' formations created by streams.

The study area thus gave the females a choice within a range of habitats, from sand to forest habitat type, from flat to cliff, from elevation 0 to 40m altitude, any orientated terrain, from the edge of the water to inland zones, and from lake and swampy areas to dryer zones.

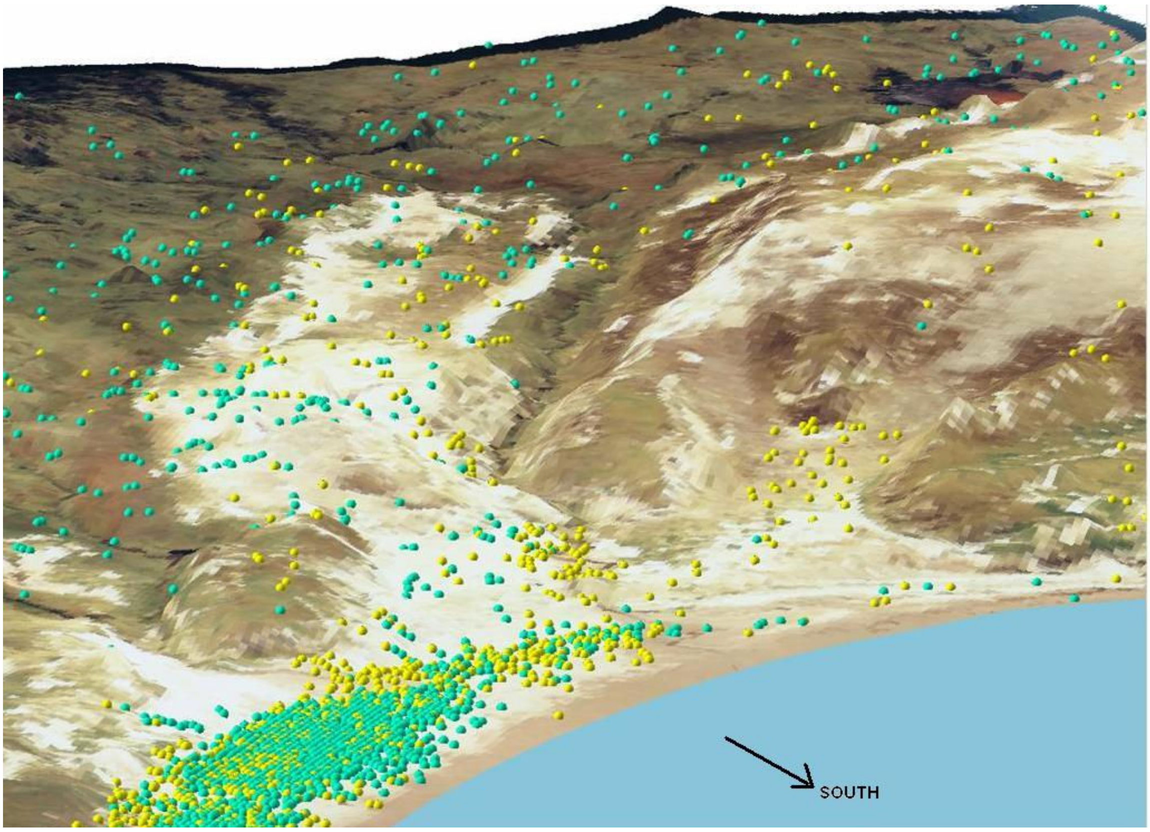


Figure 5.1: 3-D view of the east part of the sandy beach and the mid-part of the duneland at Sandy Bay, Enderby Island. It was created in ArcScene using the Digital Terrain Model of the study area. The blue area delimitates the mid-tide line of the ocean (elevation 0). The dots represent some of the locations of females recorded during the study seasons (yellow in 2002, blue in 2003). Where the harem occurred is clearly visible with the aggregation of the locations on the sandy beach. The duneland and scrub/forest area extended farther than showed on this model.

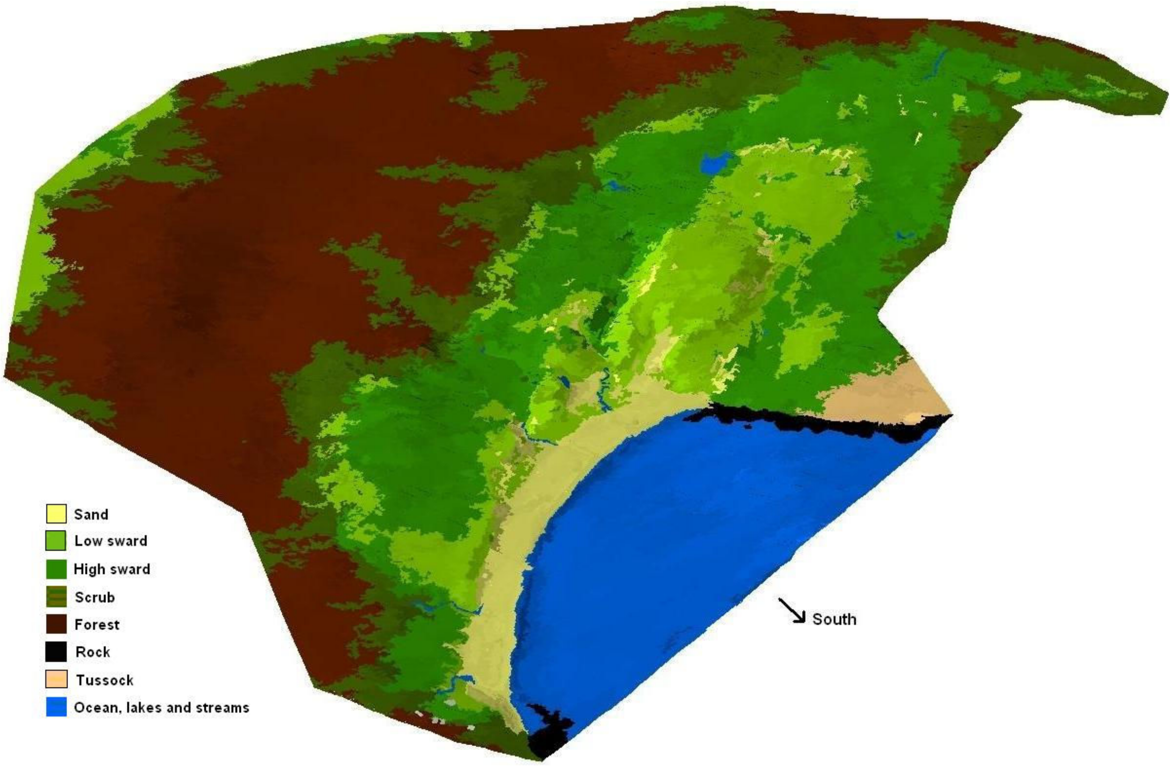


Figure 5.2: 3-D view of the study area at Sandy Bay with the different habitat types. The shadows were created from a sun location set up at azimuth 315° (North-West) and altitude 30°.

4. Methodology

4.1. Classification of the habitat

Six habitat variables were selected based on the general features of SB and the known ecology of the New Zealand sea lion and other pinniped species (as detailed in Chapter 1) to investigate the habitat use of the female New Zealand sea lions. Habitat type (HT), slope (SL), elevation (EL), orientation of the slope (OR), 3-D straight-line distance from the nearest access to the ocean (DO) and distance to nearest lake (DL) were the six classified habitat variables chosen in this study (Table 5.1).

Table 5.1: Habitat variables: range within the study area, class numbers (nb) and descriptions.

	Habitat variables											
	HT		**SL** (in degrees)		**EL** (in meters)		**OR**		**DO** (in meters)		**DL** (in meters)	
Range in study area	-		0 to 90		0 to 43		-		0 to 1410		0 to 455	
	nb	description	nb	description	nb	description	nb	description	nb	description	nb	description
Classes	1	sand	1	0 - 5 (flat)	1	0 - 5 (sea level)	1	North	1	0 - 100	1	0 - 20 (at lake)
	2	low sward	2	5 - 10 (almost flat)	2	5 - 10	2	East	2	100 - 200	2	20 - 30
	3	high sward	3	10 - 20 (low slope)	3	10 - 20	3	South	3	200 - 500	3	30 - 40
	4	scrub	4	20 -30 (gentle slope)	4	20 - 30	4	West	4	500 - 800	4	40 - 50
	5	forest	5	30 - 50 (medium slope)	5	30 +			5	800 - 1100	5	50 + (outside lake area)
	6	tussock	6	50+ (high slope)					6	1100 +		
	7	rock										

Maps of the variables DO and DL were created in ArcGIS (Figure 5.3). All other maps are presented in Chapter 2 as part of the geodatabase. The map of the 3-D straight-line distances from the nearest access to the ocean was created by using the function 'Cost-weighted distance' of Spatial Analyst on the slope habitat raster map with as base feature the mean tideline running all along the beach. These distances thus integrate the energy cost, induce by slopes, for a female to walk to the site. The map of the distances to nearest lake was produced by creating the raster of the Euclidean distances around the edges of the lakes. Both maps were produced with a cell size of 3m. The analyses were only carried out within the reduced study area (due to the less accurate data outside this area as explained in Chapter 2). The variables HT and OR were qualitative variables whereas the four other variables were quantitative. For these four variables, classes were created based on the range of the variables available within the study area (see Table 5.1).

4.2. Analyses

In this chapter the females' locations on land were analysed as sites (i.e. the 9 m^2 cell on which the females were found) independently of the female identity. Sites could be split between nursing sites (where a breeding female with a live pup (BR) was found) and resting sites (where a non-breeding female (NB) or a breeding females who lost her pup (BDP) was found). In this study, habitat use thus referred to the choice of a female for a site once she came ashore. Unlike satellite-tracking data, the data in this study also included a behaviour component as the aim was to determine for each habitat variable which class was preferred over others for a behaviour. The results presented in this chapter characterised the habitat use for resting and nursing pup. Tracking data do not discriminate animals' behaviours but quantify the percentage of time and area that an individual spends in a particular habitat (White and Garrott, 1990).

Advanced methods such as Principal Component Analysis (PCA; see Aebischer *et al*., 1993) or the resource selection function (Manly *et al*., 2002) for habitat use studies are nowadays available using powerful and complex statistical softwares. Nevertheless, due to the purpose of this study, the non-availability of random sites and the temporal component to include in the analysis, a simpler method was found more suitable and used to analyse the data. The statistical method used to discriminate preferences for classes within each habitat variable was based on stratified Chi-square analyses with associated coefficients of preference for each class (White and Garott, 1990), which also allowed integrating a temporal factor to describe changes in preferences throughout the season.

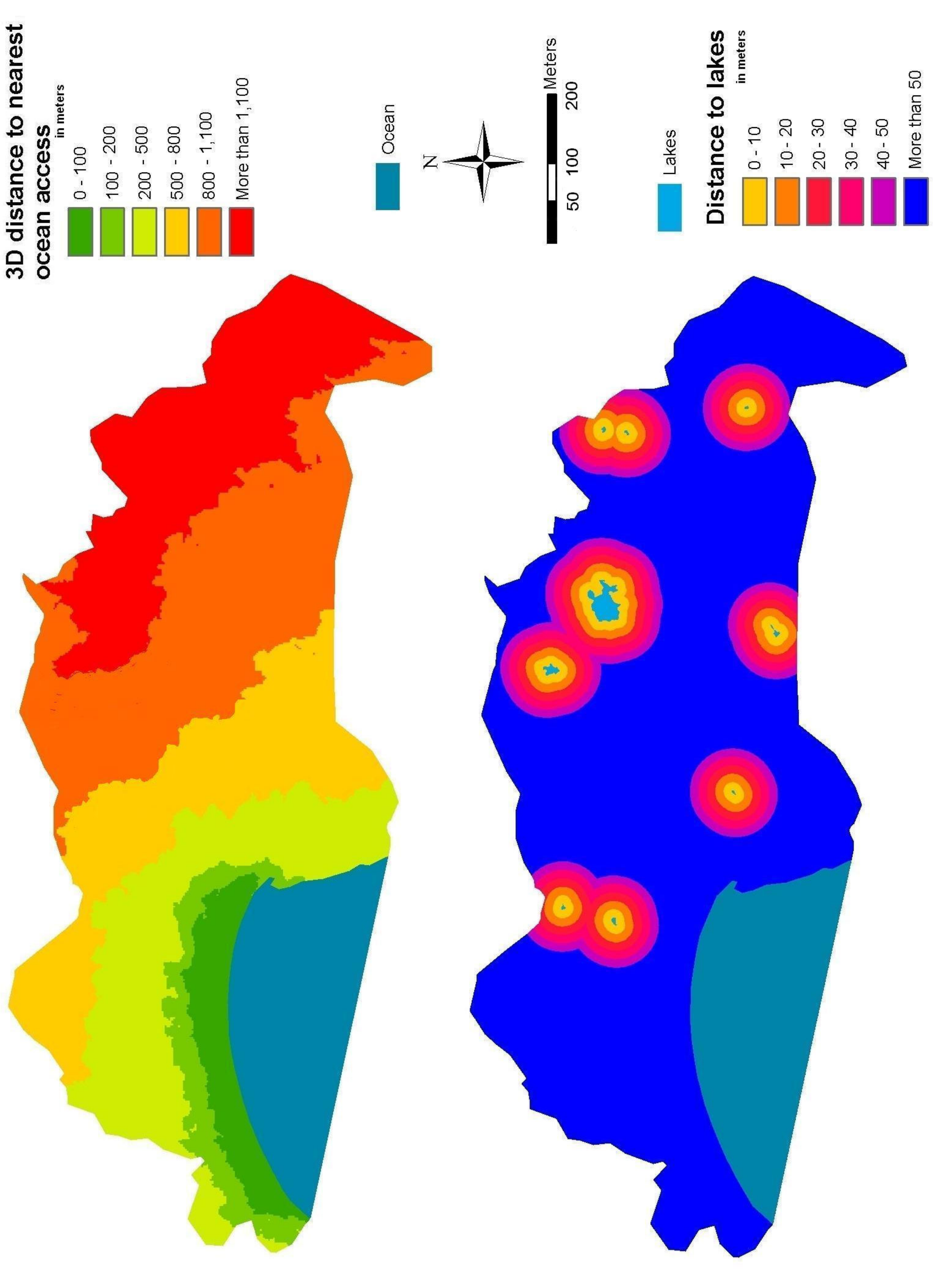


Figure 5.3: Maps of the reduced study area showing the 3-D distances from nearest access to the ocean and the Euclidean distances from lakes.

Two approaches were applied on the data for analyses on habitat use: descriptive and comparative. The first approach is based on the fact that the female population had first chosen SB as a permanent breeding site. The descriptive approach corresponds to the question: '*What is the degree of utilization of each habitat?*' (White and Garrott, 1990, p.183). This approach thus corresponds to the first level of habitat use: the use of this particular breeding site (Manly *et al*., 2002). The second approach is related to the fact that, within SB, the classes of each habitat variable represented different areas, and thus, were differentially available to the females. Comparing the observed distributions of sites, amongst habitat classes, to the distributions proportionally correlated to the habitat availability, highlighted the preferential habitat selections by the females. This approach thus answers another major question for a habitat use analysis: '*What is the preference for each habitat?*' (White and Garrott, 1990, p.183). This corresponds to the second level of habitat use: the preference of the individual of the species for certain habitat classes (Manly *et al*., 2002).

4.2.1. Descriptive method

4.2.1.1 During the harem phase

As demonstrated in previous chapters, the sites chosen by females were only found within a restricted part of the sandy beach. Consequently habitat use during this phase could be stressed through the description of this small area, which also reflected a complete preference for this kind of habitat.

4.2.1.2 During the dispersion phase

In a first part the descriptive analyses were based on determining the percentage of sites within each class for each habitat variable during the entire dispersion phase. The highest the percentage in a class, the greater its level of use at SB was.

As highlighted in the preceding chapters, females' space use consisted in a shift of the area they used during the dispersion phase. In a second part, temporal patterns were thus examined by investigating the same percentages but during four different periods of the dispersion phase (periods based on 10 days gathered to form periods represented by more than 200 sites). Three habitat variables were susceptible to be temporally influenced due to the large unmixed patches they formed in the reduced study area: HT, EL and DO.

4.2.2. Comparative method with habitat availability

The reduced study area was included in the Minimum Convex Polygon (MCP) of all sites where females were found at SB. Accordingly, the reduced study area was thus identified as available used habitat for sites.

Descriptive analyses gave an indication of the range and level of use of each habitat variable by the females at SB. It was nevertheless necessary to include the comparison with the observed habitat use with what was available to the females. Preferential selections for some habitat characteristics of sites could thus be revealed (Manly *et al.*, 2002). If a habitat covered a small area but was highly represented in the characteristics of the sites, it thus implied that, proportionally to the total number of sites recorded, females preferentially chose this habitat. A consequent expectation is thus that if the habitat class would have represented a greater part of the reduced study area, more sites would have been included in this habitat class than in other classes.

The area of each class was calculated in ArcGIS from the maps of each habitat variable. The total area of the reduced study area (TA) was 314572 m^2 and the total number of sites was 1540 (TS). For each habitat variables, the expected number of sites within each class was calculated with (similar technique in White and Garrott, 1990):

$$\text{Expected number in class } i = \text{TS/TA*area of the class } i$$

Chi-square tests of preference were performed on the observed and expected number of sites of the classes for each habitat variable (Sheskin, 2004). Significance identifies the habitat variables for which females preferentially selected some classes and avoided others. In order to determine a ranked level of preference for each class of the habitat variable, the coefficient of deviation, d, was determined:

$$d = \text{(observed number-expected number)/expected number}$$

This coefficient allowed comparison of the level of preference amongst classes and consequently determining if a habitat class was preferred or avoided, as well as classifying the classes from least to most preferred (e.g. if $d>0$ the class was preferred, if $d<0$ the class was avoided, and if $d_i>d_{ii}$ then the class i was preferentially selected over or less avoided than class ii). This relative scale of preference is necessary as females preferred different classes but preferentially selected some with more intensity (Aebischer *et al.*, 1993).

In a first part, this method of analysis was conducted on data including all sites recorded during the dispersion phase. In a second part the method was applied to the same data dividing into the four different periods (same as in section 4.2.1.2). Indeed females tended to extent their area i.e. shifting areas where sites were found along the season (see preceding chapter). Three habitat variables (HT, EL and DO) were constituted of classes made of large and not mixed patches within the reduced study area and were consequently subject to a different level of availability by the females. Analyses were conducted on these three habitat variables.

4.2.3. Characteristics of nursing sites

Another level of habitat use analysis to investigate was determining whether or not nursing sites had different characteristics or were more represented in some classes than resting sites only. This would thus highlight that females who had to nurse a pup chose the sites they used more selectively.

Statistical tests were realised to compare the characteristics of resting and nursing sites. Mann-Whitney U tests were conducted on the four quantitative variables (SL, EL, DO and DL) to compare the medians between the two types of sites (Sheskin, 2004). Chi-square tests for homogeneity were conducted on the two qualitative variables (HT and OR) to determine if the repartition of sites within each class of these variables was similar between the two types of sites (Sheskin, 2004).

If no significant difference was found between nursing and resting sites for one of the three variables potentially affected by the temporal dynamic pattern (as explained in the precedent section i.e. HT, EL or DO) then further analyses were conducted to explore the potential effect of the temporal factor. Using the previously defined four periods dividing the dispersion phase, same analyses were conducted for each of these periods.

5. Results

5.1. Descriptive habitat use

5.1.1. Habitat use during the harem phase

During the harem phase, almost all sites were included in the small area of the harem occurring on the sandy beach. During this phase, 93% of all sites recorded were thus on sand habitat type, with the remaining 7% on low sward. The mean elevation and distance from ocean (mid-tide line) were 3.2m and 17.6m respectively. The beach is characterised by an overall slope at the level where the harem occurred of 7.3° facing south.

5.1.2. Habitat use during the dispersion phase

5.1.2.1. Whole dispersion phase

Female New Zealand sea lions totally avoided sites where the slope was higher than 50° and sites made of rock. They also very seldom used sites covered with tussock; only two sites were recorded in this habitat type during 2003. These three classes (class 6 of variable SL, classes 6 and 7 of variable HT) were thus discarded in further analyses which reduced the number of classes of both variables SL and HT to 5 and the total number of sites to 1526.

Apart from the two classes totally avoided, sites were found in all classes of each habitat variable but for four of the six variables, the majority of sites were found in one or two classes (Figure 5.4). Classes 2 and 3 contained 84% of the sites for the variable HT; 85% of the sites were included in classes 2, 3 and 4 of the variable EL (with 45% corresponding to class 3); and 75% of sites were categorised in class 5 of the variable DL. Sites were thus in three-quarters or more of the cases found in sward habitat (low and high), in almost flat to gentle slope and outside the 50m lake area. Sites were distributed equally within the classes of the variable DO apart from low representations of the classes 1 and 2 (less than 8%). Sites during the dispersion phase were thus generally found farther than a 200m 3-D straight-line distance from the nearest shore access. The results for the variable OR corresponded to between 17% and 31% of the sites in each class. Females thus did not seem to specifically choose a site for its orientation of the slope.

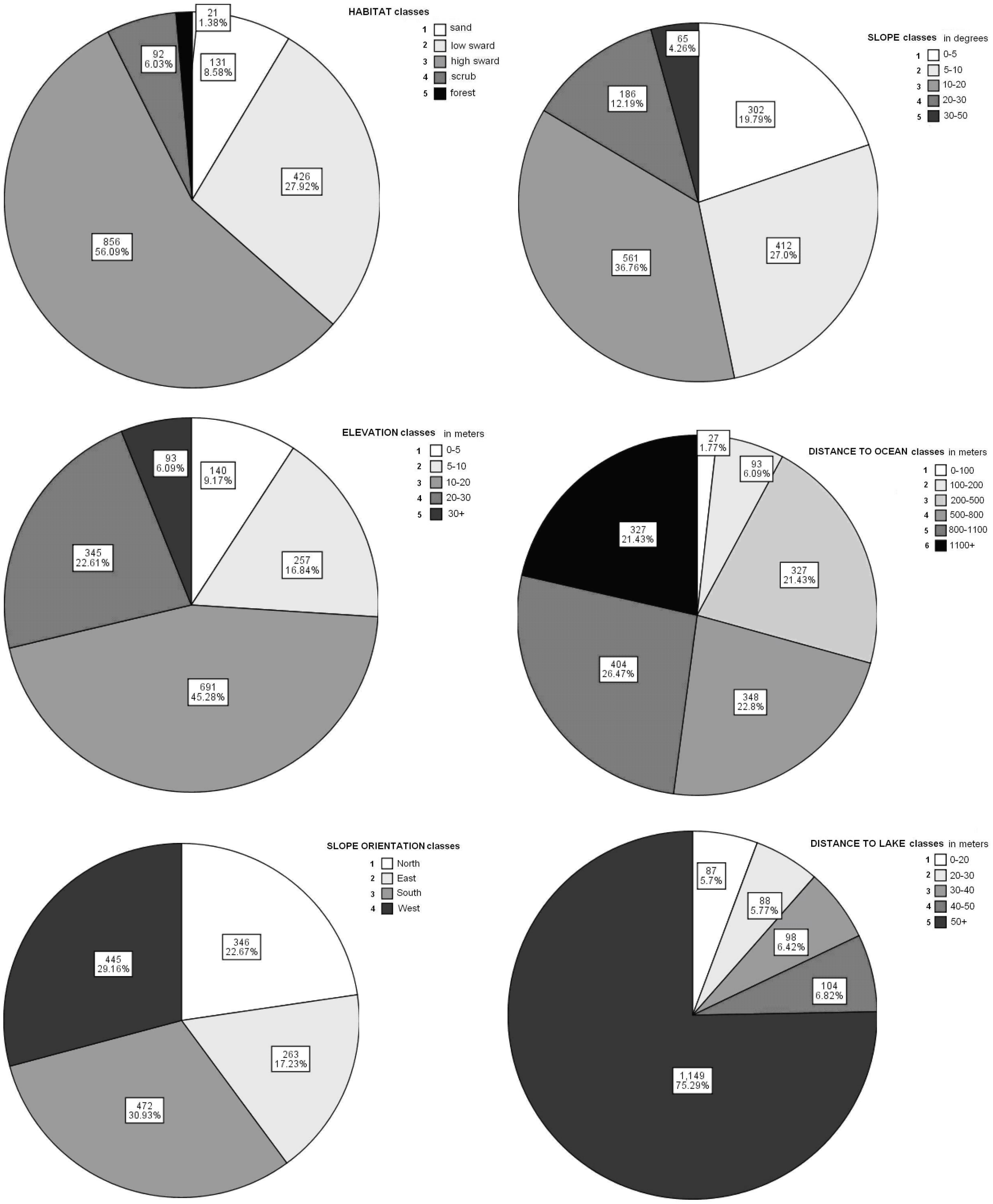


Figure 5.4: Distribution and percentage of all the sites recorded during the dispersion phase within the classes of the six habitat variables. The first line for each class shows the count and the line below the percentage that it represented. The total number of sites was 1526.

5.1.2.2. Changes in level of habitat use throughout the dispersion phase

The level of use of the different habitats shifted over time during the dispersion phase as expected for the three variables: HT, EL and DO (Figure 5.5). For the habitat type, sand and low sward represented smaller and smaller percentage to the credit of high sward from the second period (more than 50% of sites were in high sward habitat type) and scrub and forest from the third period. For the elevation, while sites at elevation 10-20m made up more than 50% of sites during the first three periods, 53% and 19% of sites were later found at altitudes from 20 to 30m or greater than 30m respectively. Sites less than 500m from an access to the ocean represented 54% of sites during the first period of the dispersion phase; during the last period, sites situated farther than 1100m from the access to the ocean made up 55% of sites with only 5% of sites situated at less than 500m.

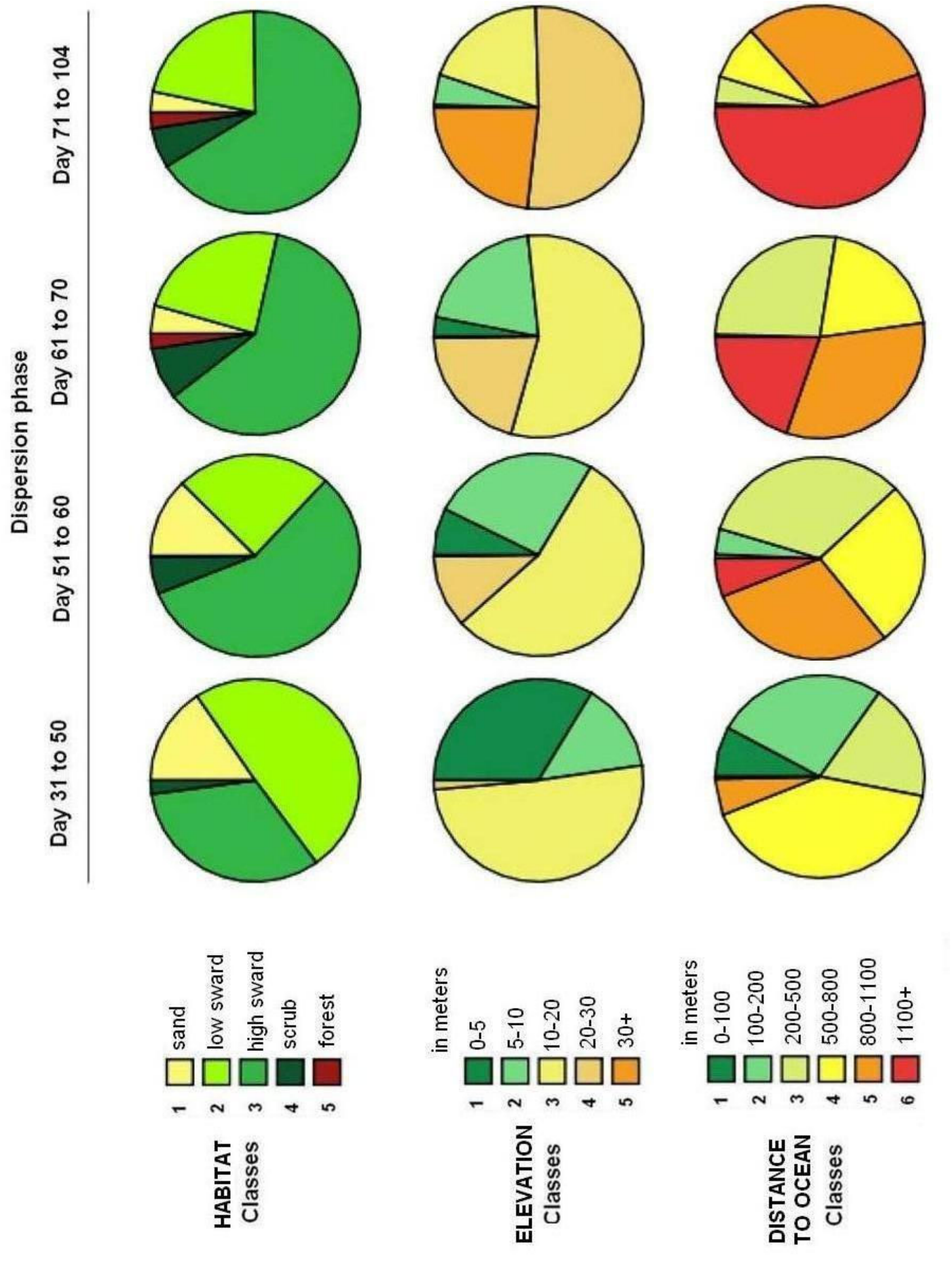


Figure 5.5: Percentage of sites in each class of the habitat variables: habitat type (HT), elevation (EL) and distance to ocean (DO) during four periods of the dispersion phase.

5.2. Preferences for habitat characteristics

5.2.1 During the whole dispersion phase

Of the six habitat variables, a significant deviation was found in the distributions of the sites in the classes from the number of sites expected for four: HT, SL, EL and DO (Table 5.2). The sites were distributed proportionally to the area of each class of the variables OR and DL. Consequently the orientation of the slopes and the distance to a lake of a site did not influence its selection by a female.

For the four significant variables the coefficient of deviation, *d*, defined if, and by what degree, habitat classes were preferentially selected over others (i.e. more sites were found in these classes than expected; Figure 5.6). For the variable HT, class 4 was the least preferred class with a high negative coefficient of deviation (-0.65), tending to show an avoidance by the females for scrub, while class 5 (forest) was the second least preferred class. The three other classes had close positive *d* reflecting an indiscriminate preference by the females for sand, low and high sward. The coefficients of deviation determined for the classes of the variable SL showed that classes 3 and 4 (low to gentle slopes, in this order) were preferentially selected over class 1 and 2 (flat). For the variable EL it was highlighted that mid classes in the range of the availability (classes 2 and 3, 5 to 20m altitude) were more preferred than extreme classes (classes 1, 4 and 5). To a lesser extent this phenomenon was also discriminated for the variable DO. Its class 1 (less than 100m) had a high negative coefficient of deviation (-0.72) which illustrated that this class was avoided by the females. The mid classes (2, 3 and 4) were preferentially selected at close levels whereas the extreme classes (5 and 6, more than 800m) were less preferred.

As a whole, during the entire season, sites seemed to be preferentially selected by females if they were in habitat types sand and sward (low and high), with a low to medium slope, at a mid-elevation (10 to 30m altitude), and at a 3-D straight-line distance from shore between 200 and 800m.

Table 5.2: Habitat variables investigated: range within data, description, percentage of cover of each class, observed and expected numbers of sites with results of Chi-square tests. The area of the tussock patch (5990 m^2) was excluded from the reduced area.

Habitat variables	Range within data	Number of classes	Descriptions of classes	Part of the reduced study area (in m²)[1]	Observed number of sites[2]	Expected number of sites[3]	Chi-square	d.f.	p
HABITAT TYPE**	-	5	1 sand	23719	131	115.06	133.249	4	<0.001
			2 low sward	75712	426	367.28			
			3 high sward	155544	856	754.55			
			4 scrub	54142	92	262.64			
			5 forest	5455	10	26.46			
SLOPE* (in degrees)	0.0 - 48.9	5	1 0 - 5	72902	302	353.65	45.637	4	<0.001
			2 5 - 10	94687	412	459.33			
			3 10 - 20	101500	561	492.38			
			4 20 -30	34613	186	167.91			
			5 30 - 50	12543	65	52.74			
ELEVATION* (in meters)	0.4 - 36.7	5	1 0 - 5	33732	140	163.63	70.730	4	<0.001
			2 5 - 10	43907	257	212.99			
			3 10 - 20	117962	691	572.24			
			4 20 - 30	93619	345	454.15			
			5 30 +	25354	93	122.99			
SLOPE ORIENTATION**	-	4	1 North	68447	346	332.04	5.446	3	0.142
			2 East	61378	263	297.75			
			3 South	93417	472	453.17			
			4 West	91329	445	443.04			
DISTANCE TO OCEAN* (in meters)	60.7 - 1403.0	6	1 0 - 100	18743	27	90.92	71.845	5	<0.001
			2 100 - 200	15346	93	74.44			
			3 200 - 500	59168	327	287.03			
			4 500 - 800	59260	348	287.47			
			5 800 - 1100	88524	404	429.43			
			6 1100 +	73532	327	356.70			
DISTANCE TO LAKE* (in meters)	0.0 - 424.3	5	1 10 - 20	17069	87	82.80	3.660	4	0.454
			2 20 - 30	15469	88	75.04			
			3 30 - 40	18715	98	90.79			
			4 40 - 50	20996	104	101.85			
			5 50 +	242322	1149	1175.51			

* quantitative variables with classes created for analyses

** qualitative variables

[1] total reduced area: 314572 m²

[2] total number of observed sites: 1526

[3] expected numbers if the 1526 sites were proportionally distributed within each class based on the areas they covered

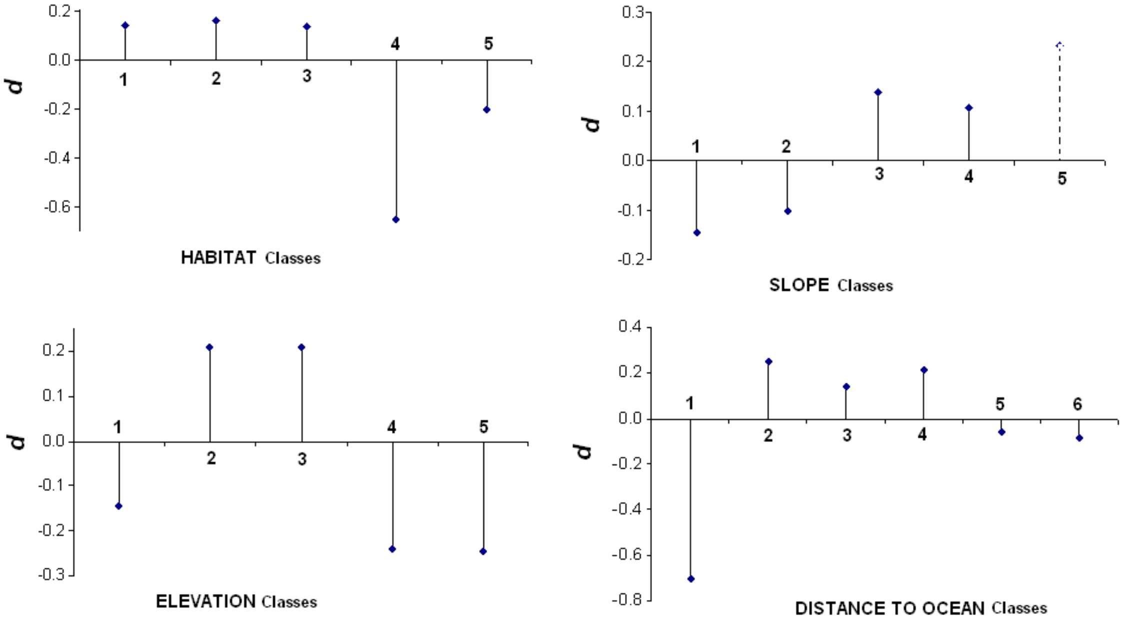


Figure 5.6: Coefficients of deviation, *d*, from the expected number of sites for each class of the habitat variables habitat, slope, elevation and distance to ocean. The coefficient for the class 5 of the variable SL was discarded as the number of sites creating the difference was very low (12).

5.2.2. Including a temporal factor along the dispersion phase

All chi-square tests showed significant differences between the distribution of the expected and observed numbers of sites within the classes of the habitat variables HT, EL and DO, for the four periods (Table 5.3). Three classes were not represented in the sites during one or two periods. Class 5 of variables HT and EL, during period Day 31 to 50, and class 1 of variable DO, during periods Day 61 to 70 and Day 71 to 104, did not include any site. This means that during the first period of the dispersion phase, no site was yet found in either forest habitat type or elevation higher than 30m, and that during the last period of the dispersion phase no site was found closer than 200m from an ocean access. Even with values 0 the coefficient of deviation, *d*, could still be determined and was equal to -1. Results on preferences amongst classes were written as, for instance, class1(+)>class3(-)>class2(--) with positive *d* values indicating with (+), and with (++) if *d*>1, and negative values with (-), and with (--) if *d*<-0.5.

Gradual shifts in the preferential selections for the classes of all three habitat variables along the dispersion phase were revealed; most classes with negative *d* during the first period progressively got a higher *d* value, and vice-versa (Figures 5.7, 5.8 and 5.9).

For the HT variable (Figure 5.7), class 4 consistently had a high negative *d* (-0.87 to -0.51). Both classes 1 and 2 had a high positive *d* (1.07 and 1.05) during the first period of

Table 5.3: Observed and expected number of sites within the classes of habitat variables habitat, elevation and distance to ocean during four periods of the dispersion phase (all chi-square tests between observed and expected values: $\chi^2 > 33$, d.f. 3 to 5, $p < 0.001$; classes 5 of variables habitat and elevation during period Day 31 to 50, and class 1 of variable distance to ocean during periods Day 61 to 70 and Day 71 to 104 were excluded from analyses as there was no site in these classes).

	Period							
	Days 31 to 50		Days 51 to 60		Days 61 to 70		Days 71 to 104	
Classes	observed	expected	observed	expected	observed	expected	observed	expected
HABITAT TYPE								
1	43	20.74	56	33.25	19	31.59	13	29.48
2	136	66.19	106	106.14	100	100.85	84	94.11
3	90	135.97	252	218.06	255	207.17	259	193.33
4	6	47.33	26	75.90	35	72.12	25	67.30
5	0	4.77	1	7.65	10	7.27	10	6.78
ELEVATION								
1	92	29.49	33	47.29	13	44.93	2	41.93
2	39	38.38	114	61.55	85	58.48	19	54.57
3	140	103.13	242	165.37	234	157.12	75	146.62
4	4	81.84	51	131.25	86	124.70	204	116.36
5	0	22.16	1	35.54	1	33.77	91	31.52
DISTANCE TO OCEAN								
1	22	16.39	3	26.28	0	24.97	0	23.30
2	73	13.42	18	21.51	2	20.44	2	19.07
3	51	51.72	146	82.95	113	78.81	17	73.54
4	112	51.81	117	83.08	85	78.93	34	73.66
5	16	77.38	130	124.10	136	117.91	122	110.03
6	1	64.28	27	103.08	83	97.94	216	91.40
Total	275		441		419		391	

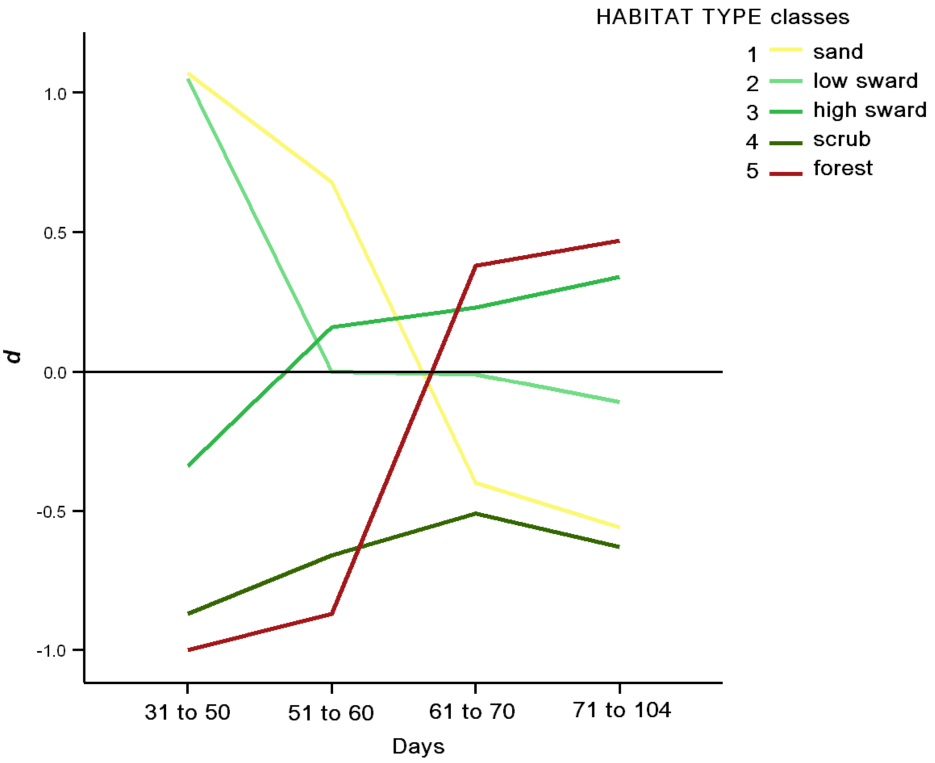


Figure 5.7: Coefficients of deviation, *d*, of each class of the habitat type variable (HT) during the dispersion phase.

the dispersion phase whereas during the last period the *d* became negative. On the contrary the *d* of class 3 became positive from the second period, and the *d* of class 5 went from -1.00 (smallest *d*) during the first period to 0.47 (highest *d*) during the last period. A preferential selection such as

class1(++)>class2(++)>class3(-)>class4(-)>class5(-)

shifted to a preferential selection such as

class5(+)>class3(+)>class2(-)>class1(--)>class4(--)

For the EL variable (Figure 5.8), the main pattern detected was an almost complete shift of preference from class 1 to class 5 between the first and the last periods of the dispersion phase. The *d* values for class 1 dropped from 2.12 to -0.95 whereas the *d* values for class 5 increased from -1.00 to 1.89. The *d* value of class 4 also increased along the dispersion phase while the *d* values of classes 2 and 3 tended to decreased but both classes had the highest *d* respectively during the second and the third period (0.85 and 0.49). The preferences thus shifted from

class1(++)>class3(+)>class2(+)>class4(--)>class5(--) to

class5(++)>class4(+)>class3(-)>class2(--)>class1(--)

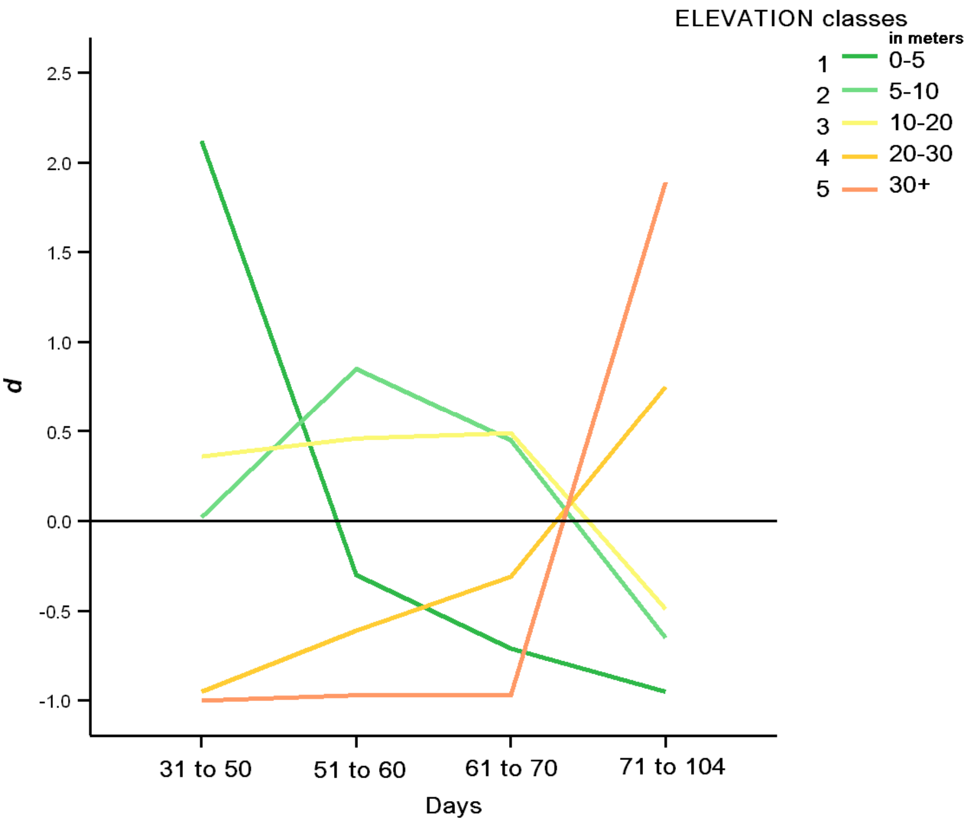


Figure 5.8: Coefficients of deviation, *d*, of each class of the elevation variable (EL) during the dispersion phase.

For the variable DO (Figure 5.9), the same major shift between two classes was also detected as class 2 had a very high positive *d* value (4.44) during the first period and had no site during the last period (*d*=-1.00). On the other hand, class 6 had a very high negative *d* value at the start of the dispersion phase (-0.98) which became highly positive during the last period (1.36). The *d* values for class 3 were the highest during the second and the third period (0.76 and 0.41). The class 1 was overall avoided with *d* values between 0.34 to -1.00. The shift in preferences thus went from

class2(++)>class4(++)>class1(+)>class3(-)>class5(--)>class6(--) to
class6(++)>class5(+)>class4(--)>class3(--)>class2(--)>class1(--)

As a whole female New Zealand sea lions shifted their habitat type preferences from sites in sand and low sward to sites in forest and high sward, with scrub habitat always avoided. They progressively preferentially selected less sites at low elevation (0 to 20m altitude) and more sites at higher elevation (20m altitude and more), as well as less sites close to shore (less than 200m) and more sites far from the ocean (more than 1100m). The area within 100m from shore was consistently avoided from the second period (after Day 51) of the dispersion phase.

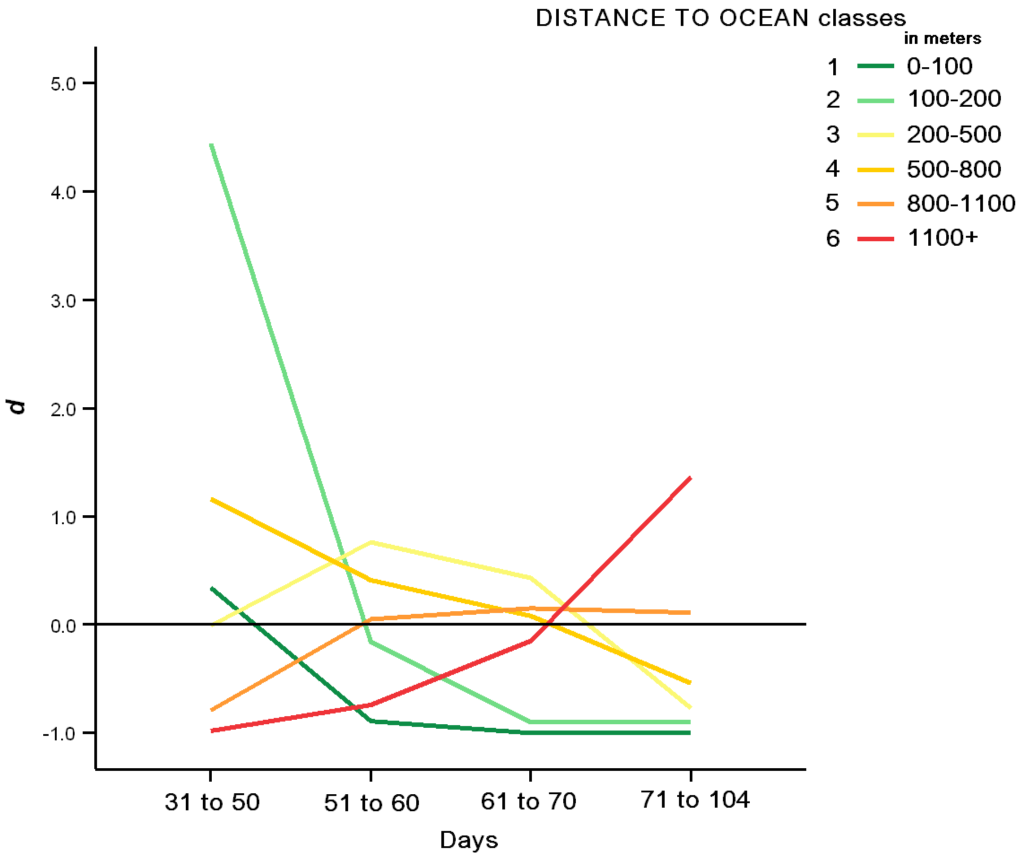


Figure 5.9: Coefficients of deviation, *d*, of each class of the distance to ocean variable (DO) during the dispersion phase.

5.3. Nursing sites: special characteristics?

Significant differences were found in the analyses comparing the distribution of the nursing and resting sites within the three variables: elevation (EL), distance to ocean (DO) and distance to lake (DL) (Table 5.4). The nursing sites were overall found at higher elevations and greater distances to shore. Nursing sites were also significantly closer to lakes than resting sites. By looking at the number of sites within the classes of the variable DL, only 8.7% of resting sites were within 40m from lakes whereas 19.8% of nursing sites were closer than 40m from a lake. Females nursing pups did not distinctively choose a site more than females with no pup for its slope or slope orientation.

The statistical test for the variable habitat type (HT) gave a difference close to a significant level between nursing and resting sites (p=0.068). The same analyses were thus conducted for the four periods of the dispersion phase. A significant difference was produced for the period Day 61 to 70 (Table 5.5). A higher percentage of the nursing sites were found in class 4 and 5 (scrub and forest, 12.5%) than the percentage of resting sites (3.7%) whereas a higher percentage of resting sites (7.4%) was found in class 1 (sand) compared to the percentage of nursing sites (3.8%; Figure 5.11).

As a whole, more females who had to nurse a pup chose sites with more singular characteristics: higher elevations, higher distances from shore, closer to lakes and towards the end of the season scrub and forest habitat types.

Table 5.4: Results of the Mann-Whitney U tests conducted between nursing sites (n=1263) and resting sites (n=263) for the quantitative habitat variables: slope (SL), elevation (EL), distance to ocean (DO) and distance to lake (DL), and results of the Chi-square tests conducted between the distribution of nursing and resting sites in classes of the qualitative habitat variables: habitat type (HT) and orientation (OR).

Habitat factors	Sites	Mean	s.d.	**U**	Z	p
SL	nursing	12.5	8.4	156289.5	-1.507	0.132
	resting	11.5	7.5			
EL*	nursing	16.1	8.2	142460.5	-3.634	**0.000**
	resting	13.9	6.5			
DO*	nursing	756	355.6	141383	-3.799	**0.000**
	resting	673.6	312.8			
DL*	nursing	91.6	58	144978.5	-3.246	**0.001**
	resting	102.6	56.3			

Habitat factors	**Pearson Chi-square**	d.f.	p
HT**	8.726	4	**0.068**
OR	3.702	3	0.296

*significance at level 0.01

** close to significance

Table 5.5: Results of the Chi-square tests conducted on the variable habitat type (HT) between nursing and resting sites during four periods.

Period	Number of sites		Chi-square	d.f.	p
	nursing	resting			
Days 31 to 50	215	60	1.211	3	0.750
Days 51 to 60	368	73	4.746	4	0.314
Days 61 to 70	338	81	10.276	4	**0.036**
Days 71 to 104	342	49	5.935	4	0.204

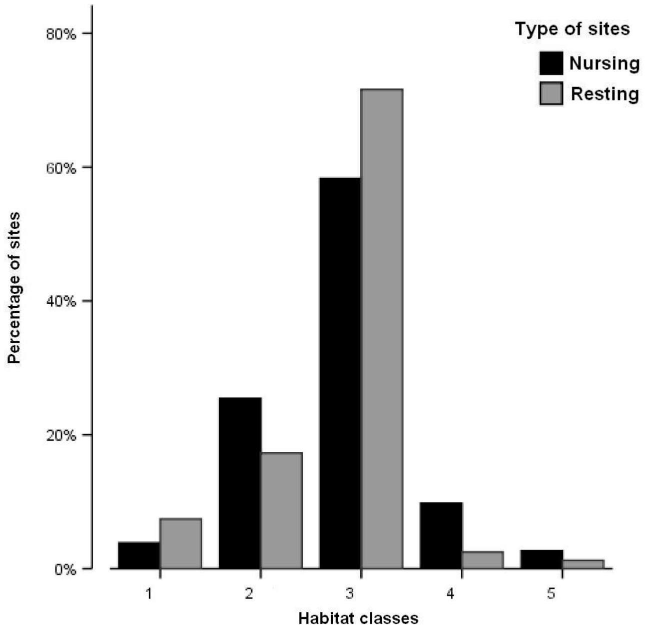


Figure 5.11: Percentages of each site type (nursing and resting) in the different habitat type (HT) classes during the period with significant difference (Days 61 to 70).

6. Discussion

6.1. Descriptive and comparative methods needed to fully understand female New Zealand sea lions' relationships to their habitats

6.1.1. Descriptive habitat use: habitat characteristics of Sandy Bay and how female New Zealand sea lions used it

Only two habitat characteristics: high slopes (more than 50°) and rock substrate (which corresponded to rocky shores and cliffs) were totally avoided by female New Zealand sea lions at Sandy Bay in this study. These habitats were avoided both during the harem and the dispersion phases and whether or not the females nursed a pup. New Zealand sea lion females thus avoided high slopes and rock habitats but it does not mean that they did not use these habitats for traveling or for short periods of time. The *zero* does not imply *no use at all* but rather a non-detected use due to the sampling method (Aebischer *et al*., 1993). The New Zealand sea lion is however known to avoid rock habitat due to better ability to walk on sand which contrasts with the New Zealand fur seals, *Arctocephalus forsteri*, that haul-out and breed in rock habitat type almost exclusively (Beentjes, 1989).

During the harem phase, sites were entirely located on the sandy beach (sand, low slope, sea level and close to shore) whereas after the start of the dispersion (7 January with mean dispersion date on 19 January; see Chapter 4), female New Zealand sea lions increased the variety of habitats they used. During the dispersion phase, sites of females were found in all habitats (excluding the two mentioned above) with a level that varied amongst habitats as well as different periods. Female sea lions were thus found in the same range of habitats as reported on Campbell Island: '*tussock meadows, dwarf forest, herbfields and coastal sward*' (McNally *et al*., 2001, p.82). Even if female New Zealand sea lions were found to use such a diverse type of habitats they however exhibited preferences for some habitat characteristics.

6.1.2. Preferential habitat selections of female New Zealand sea lions

Throughout the comparison of habitat use and its availability in the study area, it was found that by the end of the dispersion phase the female New Zealand sea lions would preferentially select sites in forest habitat type, at 3D distances ranging between 1100 and 1400m from the nearest access to the ocean with slopes between 10 and 20°, and elevations greater than 30m. No preferential selection was found for the distance of a site to a lake or the orientation of the slope. Nevertheless these habitat preferences were gradually obtained from preferences corresponding more to the harem phase (sand, low sward, close to ocean and low elevation) at the start of the dispersion phase. The preference for medium slopes was consistent throughout the dispersion phase. There would thus be the existence of a transitional phase during which females exhibit the dramatically change in habitat preferences.

Forest habitat corresponds to a very unusual habitat to be preferentially selected by a marine mammal. This habitat however seems to be adequate for the female's solitary behaviour as it allows hiding from other groups of females and, especially, hiding from males (i.e. avoiding aggression). It may also be adequate for the thermoregulation of the pup through protection against high winds and solar radiations in the same way that small rocks and crevices were thought to help in thermoregulation in the rocky environment chosen by the New Zealand fur seal to establish breeding colonies (Bradshaw *et al.*, 1999). The preferences for higher elevations and greater distances from shore, which induce a large energy dispense to reach, may be the results of the combination of the avoidance of sub-adult males, weather protections and parasite infections.

This study also highlighted that studies of habitat use that do not take into consideration the temporal changes in space use would definitely lead to biased conclusions (Manly *et al.*, 2002). Considerable differences in the classes classified as preferred were found between the results using the whole dispersion phase and the results taking into consideration the existence of a change in habitat preference. This consideration was based on the results of the previous chapters and was thus necessary to produce valuable results on habitat preferences. Indeed classifying the habitat preferences for the dispersion phase led to the mistaken conclusion that preferred habitats would have been sand and sward, elevations from 5 to 20m and distances from ocean from 100 to 800m. Instead, classifying the habitat preferences using previous knowledge on the New Zealand sea lion females' space use led to a more valuable conclusion that, after a transition phase, the habitats preferentially selected during the dispersion phase were forest, elevations and distances from ocean greater than 30m and 1100m respectively.

6.1.3. Classification of Sandy Bay in term of habitat suitability: comparing the two results

The differences in results from the descriptive and comparative methods may be an indicator of the quality of the study area in terms of the terrestrial environment. If descriptive and comparative analyses give the same results, it means that females are able to use their preferred habitats and that the area is suitable. If the results are not similar it consequently involves that the availability of the habitat within the study area does not allow the females to use the habitat they prefer.

During the harem phase, as females only used a small area of the beach, used and preferred habitats were totally merged showing that the sandy beach at Sandy Bay is likely to represent the best habitat for the occurrence of a harem of New Zealand sea lions. Sand is a soft substrate and would thus lesser the effects on pups when males trample them during fights or are thrown away by females. As Marlow (1975) reported, pups seemed to escape safely from these kinds of behaviours in *Phocarctos hookeri* whereas pups were likely to die from these behaviours in an Australian sea lion, *Neophoca cinerea*, colony occurring on a rocky shore. New Zealand sea lion is also known to have evolved walking adaptations for softer and less rough substrates than rocks (Beentjes, 1989). The preference for sites close to shore comes from the high rate of male aggression that females endure during their travel out and to sea (Chilvers *et al.*, 2005a). The shortest the distance between shore and harem, the least aggression the females deal with. Consequently, the location of the harem close to shore is conditioned by females' avoidance to male aggressiveness.

During the dispersion phase, however, differences between most used and preferred habitat classes were revealed for three out of the four habitat variables (Table 5.6). These

Table 5.6: Most used classes (from descriptive method) and preferred classes (from comparative method) for the habitat variable habitat type (HT), slope (SL), elevation (EL) and distance to nearest ocean access (DO) during the first and the last periods of the dispersion phase.

	Day 31 to 50		Day 71 to 104	
method	descriptive	comparative	descriptive	comparative
Habitat variables				
HT	low sward	sand/low sward	high sward	forest
SL	10-20˚	10-20˚	*no change*	
EL	10-20m	0-5m	20-30m	30-40m
DO	500-800m	100-200m	1100-1400m	1100-1400m

differences may accordingly indicate that Sandy Bay can be relatively successfully used by a breeding population of female New Zealand sea lions but does, however, not represent the best environment. The slope habitat at Sandy Bay is thought to represent an optimum for the species whereas the combination of distances to ocean, elevations and habitat types is unlikely to offer the best environment.

The results for the last period of the dispersion phase in this study represent the best indicator on habitat preference as females have a transition phase, after the harem phase ends, during which they gradually exhibit their radical change of habitat preferences. Consequently, the best terrestrial environment for the dispersion phase, in terms of habitat, is thought to be a coastal forest (dispersion phase preferences) spreading close behind a long, flat and fine-sand beach (harem phase preferences) accompanied by a duneland area (allowing for the transition in habitat preferences), with a low elevation and a terrain with slopes no greater than 50˚ and mainly 10 to 20˚. The presence of the large belt of scrub limiting the access to the forest is thus likely to be one of the factors reducing the suitability of Sandy Bay during the dispersion phase. Nevertheless scrub habitat can be composed on a variety of species and thus be more or less penetrable. The scrub at Sandy Bay is mainly made of *Myrsine divaritica* which is a very hard and compact scrub species (Taylor, 1970) which considerably reduces its penetration by sea lions. Where the scrub is dominated by other species e.g. *Hebe elliptica*, more flexible and less dense, access is easier. Consequently scrub habitat composed of less hard species would not be an obstacle for the movements and may be a more preferred habitat by the female New Zealand sea lions.

The information that can be gathered by looking at the differences between most used and preferred habitats should thus be valuable when one or only a few sites of an endangered or threatened species remain. This method relates to the two-stage approach of the example of the habitat use of squirrels mentioned in Aebischer *et al*. (1993) that showed that the comparison between different methods for habitat use studies can improve our understanding of the suitability of habitat for a species. This study thus showed that, even if Sandy Bay offers an optimum habitat suitability for the harem phase, it is unlikely to represent the most suitable type of environment for the dispersion and could thus be classified as a marginal terrestrial habitat in relation to the previous finding that the Auckland Islands may also be a marginal habitat for the species in term of marine environment (Gales and Mattlin, 1997; Chilvers *et al*., 2006a). Sandy Bay indeed offers one of the only significant sandy beaches within the Auckland Islands (Higham, 1991) i.e. was the only and most suitable site for a breeding colony relative to the overall marginality of the environment at the Auckland Islands. Dundas Island, where the biggest breeding colony of *Phocarctos hookeri* occurs (Gales and Fletcher, 1999), offers a long flat sandy beach suitable for the harem phase. However, the small area and habitat of the island do not appear to be suitable for the dispersion phase; females leave Dundas Island with their pups soon after the end of the harem (Gales and Fletcher, 1999; L. Chilvers, pers. com.). Another conclusion drawn from these results is that the female New Zealand sea lions likely choose to establish a breeding colony first of all based on the suitability of the beach to host a harem. Sandy Bay was indeed thought to include an optimal habitat for the harem phase but not for the dispersion phase. A highly suitable habitat for the harem would thus have been the priority for the establishment of a breeding colony at Sandy Bay.

Nevertheless, the fact that Sandy Bay may not represent the best environment for a population of breeding female New Zealand sea lions demonstrates an ability of a relative successful adaptation to a large and less favorable range of habitats. Indeed females used most of the habitats present at Sandy Bay with a relatively successful breeding (17% pup mortality; Chilvers, 2005a).

6.2. Optimum habitat selection for nursing sites

Due to the maternal care only strategy exhibited by the New Zealand sea lion, the survival of the pup depends entirely on its mother's behaviour, including her choice for a nursing habitat (Bowen, 1991). Females who had to nurse a pup selected sites at higher altitudes and greater distances to ocean than females without a pup. It thus indicates that nursing females are likely to spend more energy to find a suitable site.

The conclusion of the previous chapters highlighted that the dispersion phenomenon could be first driven by a density-related process. Females were found to form more and more isolated small groups around which a large area must be free of other groups. In order to find a suitable habitat, including this density factor, a female may thus have to go farther from shore, as previously used areas may not be suitable anymore (due to parasite infections; Castinel *et al*., 2006). Nevertheless the female also has the choice to take her pup to another place and leave Sandy Bay. Indeed if a female had more cost getting to a suitable nursing site (walking energy) than benefit (better pup survival and growth), she may have to decide to swim with her pup to another area where the nursing site would be closer to shore and requires less energy to reach. As Morris (2003) wrote '[...] *the optimal decision will be based on a cost/benefit analysis*'. This behaviour of definitive departure includes a risk for the survival of the pup (due to low swimming ability, predation and reduced thermoregulation) but this cost would be less significant for the female than walking long distances at Sandy Bay as it was found that some females exhibited this behaviour early in the season.

A female New Zealand sea lion thus has to make a compromise when the high demand in energy to walk to a suitable nursing site at Sandy Bay increases and becomes more costly for her reproductive success than the cost of the risk to swim her pup of the year to another place. This conclusion follows the concept of the trade-off (Daan and Tinbergen, 1997). The physiological limits of an individual can, in fact, lead to the adoption of a behaviour that may be negative for the current reproduction (death of the pup of the year) but will be positive for future reproduction (survival of the female) and overall increases the fitness of the individual (Daan and Tinbergen, 1997).

Nursing sites were also found in higher percentage within 40m of lakes during the dispersion phase. Although a low distance to lakes was not found to be a preferentially selected habitat by the females, this would mean that it is not an essential element in the choice of a site but females tended to be closer to lakes if they nursed a pup. The presence of pools was found to be a critical element for the establishment of fur seal breeding colonies to allow thermoregulation of pups (Bradshaw *et al.*, 1999). No female New Zealand sea lion was found in a lake; however, pups are known to swim in lakes during the dispersion phase (Eden, 1955, L. Chilvers pers. com.). Consequently the presence of lakes could be an advantage for pup survival, through the possibility to develop swimming abilities in a safe environment as well as being a mean of thermoregulation. Towards the end of the dispersion phase, a greater percentage of nursing sites were also found in forest habitat than the percentage of resting sites. This reinforces the overall preferential selection detected for this habitat and would increase its significance as an optimum suitable nursing habitat.

7. Conclusion

The analyses at the habitat scale confirmed the significance of the two-phase pattern in the spatial ecology of the female New Zealand sea lions. Indeed, two almost complete different habitats were preferred during the two phases. Overall orientation of slopes was not found to have an effect on the choice for a site, but slopes more than 50° were avoided and between 10 and 20° were preferred. During the harem phase, sand was the only habitat type used with a complete preference for sites close to shore whereas during the dispersion phase females used sward, scrub and forest with preferences for sites far from shore and at higher elevations, with the highest preference for forest habitat towards the end of the phase, and permanent avoidance to scrub. The habitat preferences during the harem phase are, however, highly induced by the avoidance of male aggressiveness by females towards themselves or their pups. Forest environment gives protection against weather as well as males and allows isolation from other small groups of females. Proximity to lakes was also detected as a possible benefit for the optimum of suitability of a nursing site.

From the investigation of the habitat use over time and between actual use and preferences, a better understanding of the causes of the definitive departure from Sandy Bay of a mother-pup pairs were drawn. This behaviour is likely to be the results of a trade-off exhibited by the female to benefit her fitness. The cost to find a suitable nursing site at Sandy Bay is indeed likely to progressively outweigh the actual benefit a female can gain and thus creates her decision to move with her pup to another site.

As a whole it is thought that Sandy Bay may represent a marginal terrestrial environment for the female New Zealand sea lions during the dispersion phase; such a hypothesis was also formulated by other studies for the marine environment. This overall marginality of the environment at the Auckland Islands may be part of the decline of the population. The best terrestrial environment for a breeding colony would thus be a long and flat sandy beach, for the occurrence of the harem, with a duneland in background to allow the transition in habitat preferences, and a forest spreading beyond to allow the dispersion phase. Nevertheless the behaviour of definitive departure from this optimum environment would take place because it is also caused by other factors than habitat.

CHAPTER SIX: GENERAL DISCUSSION

MANAGEMENT OF THE RECOLONISATION

> “The *important thing in science is not so much to obtain new facts as to discover new ways of thinking about them.*’’
>
> Sir W. Bragg

1. Introduction

This thesis represents the first quantitative insight into the spatial ecology of the New Zealand sea lion on land. Through the use of three different scales to investigate this behavioural ecology, the main patterns driving the female's timing and movements, their impact on the population's spatial dynamics and the potential causes of these patterns were revealed. The first scale, the individual female level, allowed the discrimination of the two-phase pattern that regulates the presence onshore of a female New Zealand sea lion. The population scale indicated how this two-phase pattern determined the use of Sandy Bay by the female population as well as how the population can influence an individual's behaviour. The last scale highlighted the habitat preferences and how habitat use can be integrated in the two-phase pattern and explain further the causes of the movements of the female population. Each scale thus offered a different way of looking at these patterns and allowed a better understanding of the spatial process regulating female New Zealand sea lions' use of the terrestrial habitat. The results of this thesis were found pertinent for application at other sites and are thus a valuable knowledge to understand and manage the recolonisation of the mainland by *Phocarctos hookeri*.

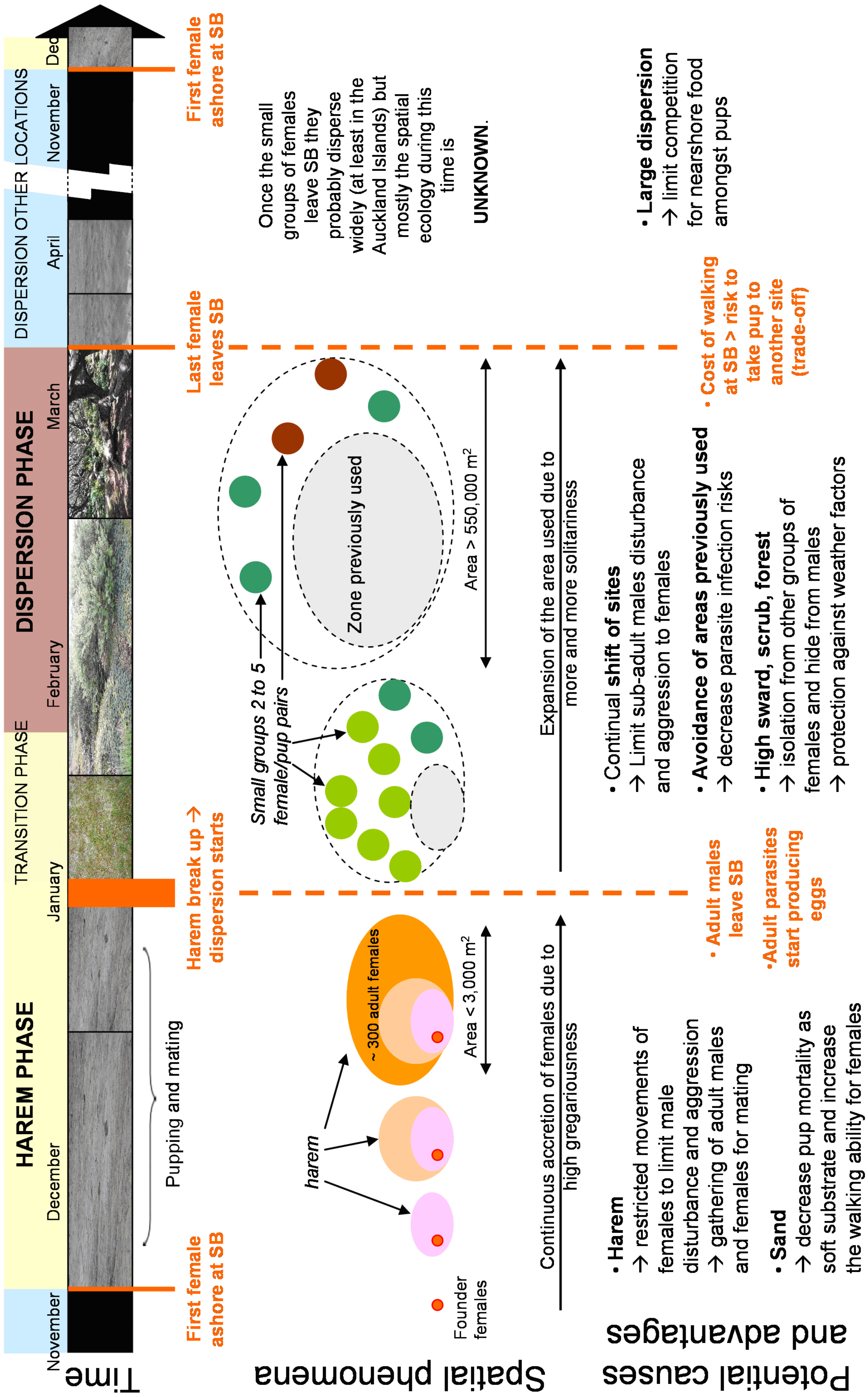
2. Synthesis of the terrestrial spatial ecology of the New Zealand sea lion with characteristics, predictability and potential biological causes and advantages

By investigating first the use of space of an individual female, the two-phase pattern for female New Zealand sea lions was determined and therefore more relevant analyses could be undertaken at the population and habitat scale. Indeed the two-phase pattern is a dynamic pattern which indicates that the female New Zealand sea lions' behavioural ecology changes throughout the breeding season. The two other scales gave more insights in the causes that may constrain this ecology while presenting other aspects of the females' ecology such as the shift of the area used by the population at Sandy Bay and the unusual habitat preferences.

The predictability of formation of breeding colonies is common amongst colonial polygamous breeders as a specific timing and site is required for breeding individuals to gather (Boness, 1991). The comparison between two seasons within this study allowed the determination of the predictability of the terrestrial ecology of female New Zealand sea lions. Timing of pupping was already known to be extremely similar every year (see Wilkinson *et al.*, 2003). Similarity in timing but also in the increase in the areas used allowed the production of a model of female space use along the season at Sandy Bay: the time-dispersion model. The predictability of the terrestrial spatial ecology was also emphasised at the population and habitat level as the female population used similar total areas during both seasons and the general population movements followed the same direction. Knowing where and when individuals are found and disperse to is thus possible. A graphical representation summarises the main patterns of the terrestrial spatial ecology of the female New Zealand sea lions at Sandy Bay and some of the potential causes as found or discussed in the thesis (Figure 6.1).

The harem phase lasts from the beginning of December, when the founder females (all expectant) come onshore at Sandy Bay, until mid-January. During this phase, breeding females always come back close to where they were found on their previous period onshore. Only a small area (less than 3,000 m^2) is thus used by the female population. The movements of females during this phase are indeed constrained to this small area due to the aggressiveness of adult males outside the harem (Chilvers *et al.*, 2005a). The harem phase occurs on the sandy beach and the presence of the harem is maintained by the continuous accretion of the females exhibiting a high gregariousness when they return from foraging trips. This gregariousness creates a high density (up to 80 females per 100 m^2) within the small area used. This level of female density in a harem of otariids is common (Boness, 1991). As outlined in Anderson *et al.* (1975), due to this gregariousness, the permanence of the location of the colony and the pre-defined timing, where and when the female population occurs is extremely predictable during the harem phase.

This harem phase is a typical phase for a species with a colonial breeding system (Boness, 1991). This is indeed the only time of the year during which adults of both sexes congregate and can mate for the production of the next year's offspring; it is thus an important part of the species perpetuation. Within the harem, females are relatively protected against male aggressiveness through the presence of dominant males preventing other males to interact with the females (Campagna *et al.*, 1992; Chilvers *et al.* 2005a). All pups are born within the harem during this phase and it may reflect an advantage for the survival of pups. Firstly, sand is a soft substrate and may limit the risk of death when males trample on pups. Secondly, this study revealed that the sensitive period during which the bond between a female and her pup is established, takes place during the first day after birth. If this imprinting is not thoroughly done, the vital process of recognition when the female comes back from a foraging trip is thus hard or even impossible, eventually leading to the death of the pup (McCullock and Boness, 2000).



Once the small groups of females leave SB they probably disperse widely (at least in the Auckland Islands) but mostly the spatial ecology during this time is **UNKNOWN**.

- **Harem**
  → restricted movements of females to limit male disturbance and aggression
  → gathering of adult males and females for mating
- **Sand**
  → decrease pup mortality as soft substrate and increase the walking ability for females

- **Adult males leave SB**
- **Adult parasites start producing eggs**

- Continual **shift of sites**
  → Limit sub-adult males disturbance and aggression to females
- **Avoidance of areas previously used**
  → decrease parasite infection risks
- **High sward, scrub, forest**
  → isolation from other groups of females and hide from males
  → protection against weather factors

- **Cost of walking at SB > risk to take pup to another site (trade-off)**

- **Large dispersion**
  → limit competition for nearshore food amongst pups

Figure 6.1: Terrestrial spatial ecology of female New Zealand sea lions at Sandy Bay, with some of the associated potential reasons and advantages detected in this study. The expansion in the area (MCPA in m^2) used by a female at Sandy Bay, since the founder females landing (Day 1) until the last females departed, is given by the time-dispersion model.

Around the birth of the pup, all breeding females also exhibit a pupping period during which they stay ashore for an average length of 8.2 days, including 1.9 days ashore before the pupping day (mean date 26 December). It is expected that this reflects that a female tries to exhibit the longest period ashore as her physiology permits to stay with the new born pup. The harem effect is, for this reason, also a benefit for the females. They endure fewer disturbances from males within the harem which means they can limit their movements and save energy to exhibit the longest pupping periods.

The dispersion phase starts once the harem breaks up (adult males leave; Marlow, 1975). The first few weeks (from mid-January to the beginning of February) were found to be a transition phase during which females exhibit a radical change in their space and habitat use. The main change of space use is that females now choose a site with no relation to where they were on their previous period onshore. Instead of coming back into the harem they now expand the area they use by moving inland. This change in space use generates a spread of the females and thus a decline in density (to 30 females and, by end of the phase, to less than 0.3 female per 100 m^2). The level of gregariousness hence decreases.

The dispersion phase takes place outside the sandy beach in other habitat types: sward, scrub and forest. Females not only change their space use but also their habitat use. From a strong preference to the sandy beach, their habitat preferences turn to forest habitat far from shore. They start using low sward during the transition phase. Then they are found in high sward which is the main habitat type used at Sandy Bay. Nevertheless the results of this study are likely to indicate that, due to the configuration of vegetation at Sandy Bay (i.e. presence of a dense and compact belt of scrub around the duneland), females cannot easily reach the forest. This is thought to be the reason why they mainly use high sward habitat. Forest habitat would seem to offer adequate properties against weather adversities (storms, high winds, sun radiations, high temperatures), and against males' disturbance by hiding the groups of females from each other and to the males. Females showed preferences for sites that have a low slope (10 to 20°) which was consistently chosen over others throughout the dispersion phase. The female population also tends to avoid areas that have been previously used during the season. This creates a shift in areas where the population is found. Overall movements of the population lead to the use of areas farther and farther from shore and induce a strong preference for sites further than 1km from shore (3D distance) and at more than 20m altitude by the end of the dispersion phase. One of the potential causes could be the avoidance of parasite infected zones. Nevertheless due to the fact that, during this phase, the only access to the ocean from Sandy Bay is the beach, all the area between where the females are found and the ocean is still used for travelling. By the end of the dispersion phase, the female population has used a total area of more than 550,000 m^2. This dispersion phase onshore and the preferences for forest habitat are exceptional for a pinniped and are not reported in the literature for any other species of this group. They are indeed unusual behaviours, involving the use of areas that would not be thought to be required for a marine mammal.

While the dispersion phase is occurring, females also progressively leave Sandy Bay with their pups. By the end of March the female population, that had built up since the founder females came ashore and slowly decreased after the end of the harem phase, has virtually deserted Sandy Bay. The small solitary groups of female-pup pairs formed during the dispersion phase at Sandy Bay thus later disperse outside Sandy Bay. This second and wider dispersion may be the results of the combination of the configuration of Sandy Bay in terms of habitat and the cost of walking for the females to avoid already parasite-infested grounds. Females are likely to exhibit trade-off behaviour by taking their pups to other locations. This dispersion may also limit competition for food amongst the pups when they start foraging near shore. Nevertheless this dispersion has not been studied and the locations where females take their pups are mostly unknown.

The results from this study also indicated that the movements that a female exhibits are likely to be affected by population size. Overall the space use of individual females was characterised by higher movement rates during the harem phase and greater distances between sites during a season when the population is smaller. Fewer females present in the colony during a season may thus induce a higher male disturbance rate per female and require females to move more to avoid aggression. This may be related to the theory that a harem may not form until a specific number of females breed at the colony which should be enough to reduce the aggression rate per female compared with the risk induced by solitary breeding (Boness, 1991; McNally *et al.*, 2001). No effect of population size on the area used by the population was however found in this study. During both seasons the population used the same area.

Both harem and dispersion phases were found to be similar year to year. Therefore, the spatial ecology of female New Zealand sea lions is highly predictable at Sandy Bay. This is an advantage when considering a wildlife management point of view. Nevertheless the results from this study are based on only one breeding colony with no validation site for comparison. It is thus important to evaluate the relevance of this study at a species level to understand if these results can be considered as representative to the species more than being specific to Sandy Bay only.

3. Relevance and limitations of the study for conservation and management purposes

The space and habitat use described in this thesis are only based on one breeding colony: Sandy Bay on Enderby Island. This colony represents the only significant seasonal pup production (around 400) with formation of a harem outside Dundas Island (around 1700; see Figure 1.1 for the locations of the breeding colonies mentioned in this section) (Gales and Fletcher, 1999). The Campbell Island colony produced 385 pups in 2003 but there was no detection of a real harem (McNally *et al*., 2001; Childerhouse *et al*., 2005). The Figure of Eight Island colony only produced 65 pups in 2006 (L. Chilvers pers. com.). Dundas Island is a small island (300m in length) with no forest and only the harem phase takes place there with most females leaving the island before early February (Gales and Flecther, 1999). Due to the fact that the sub-Antarctic islands are likely to be a marginal part of the pristine breeding area of the New Zealand sea lion (Childerhouse and Gales, 1998), the difficulty determining if the population at Sandy Bay reflects the way that the species would behave elsewhere, and especially in other environments, is a major issue. This is nevertheless a major problem for wildlife species that have been severely depleted and survived only in a few marginal areas. It is indeed important to understand to which extent the ecology of the remnant populations can be used to address problems such as the management of recolonisation. The case of the New Zealand sea lion appears particularly unique as there is virtually no evidence of where the species bred before extirpation. Indeed, Maoris, who hunted the species for food, have no written literature and the only available data on where *Phocarctos hookeri* colonies may have occurred is based on archeological evidence. Documentation on characteristic behaviour or habitat for the New Zealand sea lion around the mainland is only contained in a few early European settlers' reports and diaries. The species was however thought to have been already depleted by Maoris (Childerhouse and Gales, 1998). Understanding the ecology of the New Zealand sea lion is consequently restricted to the knowledge gained from the remnant populations.

Several papers gave insights into the timing of occurence of breeding colonies and pupping dates at the other breeding colonies in the Auckland Islands and on Campbell Island. Gales and Fletcher (1999) showed that the timing of presence of a breeding colony as well as the pupping peak were not different between Sandy Bay and Dundas Island breeding colonies. They also described the occurrence of what was named the dispersion phase in this study at Dundas Island around 24 January (as they reported '*ten days after the cessation of pupping* [14 January]') which is close to the mean dispersion date for the females at Sandy Bay (19 January). The period for the expedition to Campbell Island to count the pup production had been based on known timing from Sandy Bay and indicated that pups were born around the same time at Sandy Bay as well (McNally *et al*., 2001; Childerhouse *et al*., 2005). The Figure of Eight Island colony is likely to have the same timing of occurrence, as pups from new born to a few weeks old are encountered during the annual counts that takes place within the first weeks of January (Gales and Fletcher, 1999; Chilvers, 2005a). The presence of new born pups with recolonising females on the New Zealand mainland during the two first weeks of January suggests that these females gave birth around the same period as the pupping peak at Sandy Bay (McConkey *et al*., 2002a). These similarities in timing amongst Sandy Bay and the other current breeding colonies or solitary individuals show that the occurrence of breeding colonies of the New Zealand sea lion as described in this thesis is consistent and species-specific rather than location-specific. The breeding seasons is spread all year round in the Australian sea lion, *Neophoca cinerea*, depending on the geographic location of the colony (Gales *et al*., 1994). This phenomenon does not seem to exist in the New Zealand sea lion as all breeding events are synchronous, including at Campbell Island and around mainland New Zealand, which are geographically more separated from the major colonies in the Auckland Islands than two colonies of Australian sea lions with several months of difference.

No previous studies have looked at space or habitat use at other breeding colonies but sparse information from the literature can be gathered to understand if what happens at Sandy Bay is common. At Dundas Island, the harem occurs on the sandy beach (100m long and 50m wide) as at Sandy Bay (Gales and Fletcher, 1999). At Campbell Island, even if no real harem occurs, McNally *et al.* (2001, p.28) reported that '*the most commonly used haul-outs included an area of sandy beach*'. Though, Childerhouse *et al.* (2005) suggested that significant colonial breeding occurred at Davis Point, Campbell Island, on a bedrock platform. They also estimated the pup mortality at 36% (more than double compared with the Auckland Islands; Chilvers *et al*., 2005a) with 99% of the dead pups from this location. This suggests that the rocky environment is not suitable for New Zealand sea lion pups and creates high pup mortality. Females on the New Zealand mainland principally used sandy beaches, if not to pup, then to haul-out (McConkey *et al*., 2002a).

Inland movements and type of habitat reported at other breeding colonies than Sandy Bay were found to be consistent with the results of this study. At Campbell Island, females with pups were found up to 1.5km inland (McNally *et al*., 2001). It confirms that female New Zealand sea lions use to penetrate far inland with their pups, and may also suggest the existence of the same kind of dispersion inland as at Sandy Bay. The fact that females quickly leave Dundas Island once the harem breaks up also supports the requirement of exhibiting a dispersion phase for the females (Gales and Fletcher, 1999). The area of the island being so limited, females can not spread inland and thus move to other locations. The colony at Figure of Eight Island is radically different than all others as the harem occurs in the forest, which covers most of the island (Gales and Fletcher, 1999). The very small island only has rocky shores and no sandy beach and is found in the south of the Auckland Islands. The lack of beach for the occurrence of a harem in this area may have constrained the establishment of a breeding colony in the forest. The Figure of Eight Island colony is however the smallest colony, and is currently decreasing (Chilvers, 2005a). Even if this case implies that female New Zealand sea lions can exhibit different space and habitat use during the harem phase, it also confirms a strong preference for forest habitat as it is what they chose when no sand habitat was available. Preference for coastal forest habitat and avoidance for rock habitat is also found in McNally *et al*. (2001). They reported that the least commonly used habitats, at Campbell Island, were bedrock platforms with scrub and tussock on the shore whereas females were found more often in dwarf forest. McConkey *et al*. (2002a) also suggested that recolonising females chose the specific beach where most of the pups were born on the mainland (Victory Beach) because it is the only sandy beach with an abutted forest on the Otago Peninsula.

Archeological evidence showing where breeding colonies occurred on the New Zealand mainland is rare (Childerhouse and Gales, 1998). The timing cannot be determined but one site was identified as a breeding area: Delaware Bay on the north coast of the South Island. Here, remains of pups were found in the dunes behind a sandy beach. The habitat type of Delaware Bay coincides with what was asserted in this study as the most suitable habitat for breeding females: sandy beach backed by a duneland and coastal forest. This scarcity of evidence is due to a lack of systematic investigation for sea lions' remains; the information was mainly obtained from studies on Maori settlements (Childerhouse and Gales, 1998). Early European explorers and settlers were also cited by Childerhouse and Gales (1998) as they mentioned where breeding still occurred on the mainland before total extirpation of the species. Stewart Island seemed to have been where most sea lions still bred before 1850, and although it is not known if and where a harem occurred, reports of Maori killing great numbers of sea lions at Lord's River and Port Pegasus were made. Both locations contain the same type of environment i.e. sandy beach with adjacent bush that Wilson (1979) also described as main haul-outs of males *Phocarctos hookeri*.

As a whole all these observations concur to indicate that the patterns of terrestrial spatial ecology of the New Zealand sea lion observed at Sandy Bay should thus be considered as representative of a characteristic of the New Zealand sea lion. The two-phase pattern, including the timing and space use, as well as habitat preferences as described at Sandy Bay, are thought to be species-specific rather than location-specific. The results from this study can thus be used to portray the terrestrial spatial ecology on mainland New Zealand to anticipate how female New Zealand sea lions will use the terrestrial habitat along the mainland coastline and the associated problems that will arise.

The main limit of this study is thus that it was based only on the behaviour of females at one breeding location. As discussed above, the results are likely to be applicable to new breeding colonies. Nevertheless the size of the population may also affect the behaviour of the female population. With Sandy Bay being the only breeding colony where such a study could be conducted, it was not possible to describe what effects population size may have on the spatial ecology in generic terms. The comparison between the two seasons showed, for instance, that a smaller population size caused greater movement to the individual females. This study was also restricted to Sandy Bay. Due to logistic limits, movements of females outside Sandy Bay, either before gathering at Sandy Bay, during the presence of the female population at Sandy Bay or once the females definitely departed from Sandy Bay with their pups, were not investigated.

Due to only daily records of females' locations, investigation of movements at a smaller scale was not possible. This limited the interpretation of movements within the harem. The distance moved by a female during the pupping day was detected to affect pup survival which shows that the sensitive period occurs on this day. If the database contained locations taken closer in time, the detection of the sensitive period would have likely been improved including when exactly it takes places.

Another limit of this study is the low number of records of pups of branded females that died during the dispersion phase. This number was too low to detect a potential impact on pup survival of females' choices for specific sites (e.g. close to lakes, farther from ocean or in forest habitat). Even the two study years with a large sample size did not produce enough data for analyses. This comes from two facts: the females leave Sandy Bay during the dispersion phase, reducing the sample size, and dead pups are harder to find than during the harem phase due to the sparse distribution of females as well as the dense habitat in which they are found. Several years of compiled data are likely to be necessary to obtain significant results on what impacts terrestrial factors can have on the pups' survival during the dispersion phase.

These limits do not however decrease the importance and the significance of the results of this thesis as they were found relevant to be used as a base for the management of the recolonisation. The thesis described, in space and time, the ecology of female New

Zealand sea lions at a breeding colony which is valuable information when considering the implication for recolonisation, potential associated problems as well as conservation and management measures to lessen these problems.

4. Implications of the terrestrial spatial ecology for conservation and the management of the recolonisation of the New Zealand mainland by *Phocarctos hookeri*

New Zealand sea lions were totally extirpated from mainland New Zealand before European settlements were significant. Today's New Zealanders have thus never interacted with the species, and the New Zealand sea lion is recolonising an urbanised and modified coastline. Combined with the dynamic and unusual terrestrial spatial ecology revealed in this study, numerous problems may arise from the recolonisation. Interactions between humans and sea lions represent a new challenge for wildlife managers while they also have to deal with a species with unusual space and habitat requirements. Through the knowledge gathered in this thesis, the management can be improved and necessary management measures, immediate and future, be drawn up.

4.1 Potential interactions between humans and sea lions on the mainland: a new challenge for the managers

4.1.1 A spatio-temporal pattern to be addressed

Unlike in the Auckland Islands, which are isolated Nature Reserves with no permanent human presence (Penniket *et al.*, 1987), interactions between New Zealand sea lions and humans are now occurring and will increase on New Zealand mainland due to the recolonisation process. These interactions with humans may disturb or threaten both females and pups.

The terrestrial spatial ecology of the female New Zealand sea lions indicate that, in a population where a harem forms (December and January), the presence of the females and the pups will be obvious to any visitors to beach as the population is concentrated in a small area. However, once the dispersion phase starts, the spread of the females and pups will make their presence less obvious even if they are still vulnerable to human disturbances during this phase. As long as the females disperse inland from the breeding colony, the area in which they are likely to be found would be predictable through the time-dispersion model built in this study. Interactions between humans and sea lions would thus still be restricted to a limited and known area.

Numerous large wildlife species breeding in coastal habitats (with emphasis on the beach habitat especially) were found to be affected by significant level of human visits. Disturbances included changes in patterns of activity at the breeding beach to avoid the busiest periods (turtles; Jacobson and Figueroa Lopez, 1994), avoidance of beaches where human presence is greater (monk seals; Baker and Johanos 2004) and decrease in breeding success (penguins; Ellenberg *et al.*, 2006). The Otago Peninsula, where the females currently breed and nurse their pups (McConkey *et al.*, 2002a), is a favoured ecotourism site by visitors to Dunedin with a growing demand for viewing sea lions (Wright, 1998). A synchronous increase of both the sea lion population and number of visitors, on the Otago Peninsula for instance, would thus require preventive measures for a species of which little is known about the impact on even a small level of human presence.

During the recolonisation process and while a new colony is establishing, it is likely that most breeding will be solitary, despite an observed tendency of the females to gather at Victory Beach, Otago Peninsula, due to the high philopatry exhibited by colonial female pinnipeds (Boness, 1991). Some females, however, pupped at Victory Beach but others gave birth at another site and later swam to this beach with their pups (McConkey *et al.*, 2002a). The more predictable pattern is likely to appear as the population of breeding females increases. The mechanism for the establishment of a new breeding location may thus comprise a first step during which females are mostly solitary breeders but stay in close proximity. As suggested in McNally *et al.* (2001) and Campagna *et al.* (1992), once the female population reaches a '*critical mass*', a colony with the formation of a harem should occur. Even if the two-phase pattern is not clearly exhibited during the first step of the recolonisation, it is likely that females will spread inland. They are already known to frequent several beaches and to go far behind the beach if duneland is available as well as in the forest at Victory Beach (McConkey *et al.*, 2002a). Interactions with humans can thus happen at various sites and in different habitats where the general public may not expect the presence of sea lions.

4.1.2. Public awareness and interest as a management measure

As stated in the Marine Mammal Action Plan of the New Zealand Department of Conservation (Suisted and Neale, 2004), public awareness is the primary measure for the management of interactions between humans and sea lions. It seems indeed essential to educate people about how to interact with sea lions, and also to help residents to live with sea lions. No such issue took place while the New Zealand fur seal, *Arctocephalus forsteri*, started recolonising the New Zealand mainland because breeding colonies occur exclusively on rocky shores (Bradshaw *et al.*, 1999). Rocky shores are seldom frequented by humans and are also mostly not easily accessible, which limits interactions between fur seals and humans. On the other hand, sandy beaches are a favoured environment for recreational activities or housing and have easy access which creates frequent interactions between sea lions and humans.

During the first step of recolonisation, where and when sea lions will be may not be as predictable as once the colony is established. Public awareness should therefore include education about this recolonisation process and the basic ecology of the species. Emphasis should be put on educating people on the nursing ecology especially. One of the first pups born on the mainland seemed to have vanished from the beach where it was born while its mother was foraging at sea (McConkey *et al.*, 2002a). This was a highly frequented location and it is thought that the disappearance of the pup may be related to human presence. People need to be educated that finding sea lion females or lonely pups on beaches, in dunes, in scrub or in coastal forest, and at great distances from ocean is a natural behaviour. The possible habituation to human presence of the species (mentioned by several researchers who worked with sea lions on the mainland in Wright (1998)), especially for the females who will mostly all be mainland-born and thus will grow up with human presence, combined with a better understanding of its ecology by the public, may be a significant advantage in managing the interactions between humans and sea lions.

On the other hand, people, and especially residents, have to be alerted that the beach at which females choose to establish a new breeding location will be virtually inaccessible during the harem phase due to the high density of females and males. In conclusion a large public awareness program, through signs and managers' presence at beaches, should be initiated to inform visitors on the ecology of the New Zealand sea lion as well as about the possible consequences their disturbance can have. Another type of wider public awareness should focus on local communities and should be started as soon as possible to allow a slow acceptance of several conditions of use of some sandy beaches that the presence of sea lions will induce, both for the protection of the sea lions against human disturbance but also to prevent aggressions from breeding sea lions to humans.

4.1.3 Possible effects of human disturbance on female New Zealand sea lions and associated potential management solutions

As a whole New Zealand sea lions were found to be tolerant of humans, with no evidence of being highly disturbed by human presence (Wright, 1998). In all cases, females tended to have a tolerance to human presence and did not usually exhibit aggressive behaviour. Some females may move towards or farther from the observer. It does not mean that a higher rate of human presence cannot create a significant disturbance if visitor numbers increase. Wright (1998) expressed the necessity to monitor a possible change in the sea lions' behaviour towards humans, based on the example of sea lions at the Galapagos Islands, which became more aggressive towards humans at highly visited sites.

Direct disturbance from human presence may include direct antagonistic human behaviour towards females or pups, especially vulnerable during the dispersion phase when they are relatively solitary and sparsely located along the coastline. Deliberate killing of sea lions had already happened on the mainland (McConkey *et al.*, 2002a). Although the public awareness and interest program should limit this type of human behaviour, it is a hazard that cannot be thoroughly avoided. Protection is possible during the harem and dispersion phases at the breeding colony but cannot be monitored outside this period due to a large spread of the females and pups.

Other potential disturbances due to human activities at breeding colonies are also revealed through the results of this study. The harem phase represents the time of pupping, which includes the sensitive periods during which the females must limit their movements just after giving birth. In the harem, disturbance to females mostly come from male aggressiveness (Marlow, 1975). Any more disturbance than that caused by interactions within the harem is likely to increase the amount of movements per female, and consequently, disrupt sensitive periods and force the females to use their energy reserves for another aim than nursing her pup. Disturbance could thus lead to higher movement of the females, a decrease in pup survival, and may induce the definitive departure of females. Some breeding colonies of southern fur seals, *Arctocephalus australis*, were abandoned because of human disturbance (Stevens and Boness, 2003). This phenomenon has already been recorded for two solitary females that had pupped at Otago and Stewart Island but did not re-use the sites where human presence seemed to have led to the failure of their breeding at a previous time (McConnell, 2001; McConkey *et al.*, 2002a).

The harem phase with the formation of a colony and an aggregation of the females may create the impression that there is less risk for human induced disturbance. On the contrary, this phase should be considered as vulnerable, firstly due to the possible significant consequence of human disturbances, and, secondly, because it is most likely the phase where tourists will view the species (summertime and insurance of seeing the females and pups). During the first step of the recolonisation, the breeding female population will be small. It is suggested in this study that smaller female population size probably leads to greater amounts of female movements due to higher male aggression rate per female. This was found to significantly affect the maternal performance in other pinniped species (Boness *et al*., 1995). Additional disturbance due to human presence may increase the dynamics of the individuals within the harem, as Heinrich reported in Wright (1998), and cause more movement of the females.

Cassini *et al*. (2004) suggested the use of fences to allow visitors to view colonial breeding pinnipeds in their coastal environments with significantly reduced disturbance. This solution may be adapted to most of the species with such colonial breeding but does not appear as an appropriate option for the management of human-sea lion interactions for *Phocarctos hookeri*. The large terrestrial movements exhibited by the female New Zealand sea lions do not allow the use of fences behind the locations of breeding colonies. Fences would prohibit the ability of females to move inland during the dispersion phase. Even if temporary fences were to be put up and taken down before the females start dispersing, males that are not in the harem haul-out in the area behind the beach and must have free access to this area (Marlow, 1975; pers. obs. at Sandy Bay). Males are also scattered all along the breeding beach which would initially reduce the accessibility for visitors (Figure 6.2). The only potential option if managers are required to reduce interactions between humans and sea lions during the harem phase may be the closure of the beach and its surroundings to the public. This would avoid human disturbance to the harem as well as potential aggression of adult males towards humans (males in and peripheral to the harem can threaten humans).

During the dispersion phase, direct human disturbance should be self-limited as females and pups are mostly hiding in denser habitats and are thus less visible. Due to the fact that females are less susceptible to male harassment during this phase, the addition of human disturbance may not have such a negative effect. However, during this phase, females nurse their pups, which require more and more energy as they grow and gain on average 151g per day (Chilvers *et al*., 2006b). Consequently females are likely to increase the intensity of their foraging patterns and thus would require as little disturbance as possible while they are nursing their pups onshore to recover before their next foraging trip. In the Auckland Islands, breeding females are indeed thought to dive to their physiological

Figure 6.2: Illustration of the occupancy of the beach at Sandy Bay during the harem phase. Males are scattered along the whole beach outside the harem (photo taken at Sandy Bay on 26/12/05).

limits indicating that periods onshore are vital for the survival of the females (Chilvers *et al*., 2006a). Monitored access to the area in which the dispersion phase takes place behind the breeding beach would thus be still necessary. It is also during the dispersion phase that pups are left alone or in small groups at inland sites while their mothers forage at sea. While humans are unlikely to see the pups, or even the females, in a dense habitat such as forest or scrub, dogs can smell and find the pups and thus be potential threats. Dogs have already been reported biting pups and could easily kill a pup (McConkey *et al*., 2002a).

The formation of the harem may also be disrupted by human activities on beaches. Anderson *et al*. (1975) had already expressed concern about this negative interaction that is not obvious as animals stay mostly in the water. They stated that disturbance during the initial selection for a site by the founder females of a harem can cause the females to use alternative sites. As described in this study, the founder females determine where a harem of the New Zealand sea lion is formed. Consequently if the selection process by which they choose the most suitable site is disrupted, they may use substitute locations. This selection process can be applied at two levels: during the recolonisation process and the establishment of a colony, and later, once the colony becomes permanent at a specific beach as the harem can still be formed in different areas of the beach. During the recolonisation process, females must choose to gather on a specific beach. At Sandy Bay, females chose a location that does not appear to provide the best environment for the dispersion phase. Nevertheless it is thought to be due to a lack of more suitable sites in a marginal habitat. On the mainland where more beaches are available and where the species bred before, there must be some locations representing a more suitable habitat for both phases of the spatial ecology of the female New Zealand sea lions. If the level of human presence is too high on these most suitable beaches, the recolonising females may choose a less adequate environment to establish a colony. Once a permanent colony is established, a certain amount of space is still available for the founder females to land on the breeding beach. Nevertheless some areas of a beach can present some advantages compared to others due to terrain and vegetation distribution. Some preventative limitations in human visitation of potential suitable sites around the mainland (Victory Beach, Otago Peninsula, being the only current such known location; McConkey *et al.*, 2002b) during the last few days of November and first few days of December, should be taken before any female can actually be seen at the site. This short period corresponds to when the founder females land at the breeding beach. These limitations should be maintained even once a permanent colony is established to avoid displacement of the harem. It is thus important to understand where suitable sites for the recolonisation of the New Zealand mainland by the breeding female population are found to take these preventive measures during the recolonisation process.

4.2 What are the suitable terrestrial sites for the establishment of new breeding colonies on the New Zealand mainland?

Female New Zealand sea lions were found to require a particular and unusual association of terrestrial habitats to breed and nurse their pups. The most suitable terrestrial habitat as defined this study is a sandy beach backed with a small area of vegetated duneland with high sward and soft scrub species and a coastal forest. These types of habitat have been largely lost along the mainland coastline. Moreover the area that the female New Zealand sea lion population used behind the beach was found to cover more than 500,000 m^2. This second specificity implies that urbanisation of coastal areas in New Zealand will interfere with this spatial behaviour as well.

4.2.1 Coastal mainland New Zealand: significant habitat loss and introduced vegetation since the species' extirpation

The sub-Antarctic islands of New Zealand are considered to be some of the most pristine environments on Earth with only a few short contacts with humans (Gary, 2002). The habitats available to the New Zealand sea lions at the Auckland Islands are consequently natural with only some introduced vegetation (Higham, 1991). Enderby Island is, however, the island of the group that has suffered most human-induced changes in vegetation due to farming and the introduction of rabbits that heavily modified the pattern of plant distribution around Sandy Bay (Taylor, 1970). Even with this unnatural vegetation cover at Sandy Bay, the breeding colony of the New Zealand sea lion persisted and females now use the high sward, mostly composed of introduced grasses, during the dispersion phase. This may reinforce the proposed idea that the species can adapt and use a range of vegetation types even in a modified environment. Nevertheless the population at Sandy Bay was established before the changes happened and thus the establishment of the colony took place in a still undisturbed site. Later changes may have been slow and females progressively adapted.

The coastal regions of mainland New Zealand, in contrast, have been highly modified due to human colonisation and settlement while the species was absent. Both sandy beaches with sand dunes and coastal forests are listed as some of the most depleted habitats along the coast. Hilton *et al*. (2000) reported that since the 1940s, the area of active duneland along the coastlines of the North and South Islands and Stewart Island has been reduced by 70%. The change in distribution of native forests in the South Island was compiled by Seddon (1988) for the period 1840 to 1976 and revealed an almost complete loss of this type of habitat all along the east coast, while the coastal forests of the west coast stayed almost intact. Human settlements reduced the native forest of New Zealand to only 23% of its pristine area (Fleet, 1986). Coastal forest was described to grow extensively around the North Island and parts of the South Island while "[…] *today only remnants survive as patches* […] (Fleet, 1986, p.229). Both sandy beaches with dunelands and coastal forests were thus still abundant before the total extirpation of the New Zealand sea lion from the mainland by the 1830s (Childerhouse and Gales, 1998). Nowadays the preferred breeding habitats available for the species around mainland New Zealand is extremely reduced and unequally distributed along the coasts. The fact that the west coast forests are still intact may not indicate a higher level of potential breeding habitats because sandy beaches and dunes are usually backed with cliffs or high slope terrains in Fiordland. The west coasts of both islands are indeed subject to stronger swells and oceanic conditions than the east coasts (Hilton *et al*., 2000). This is also a factor that might reduce the suitability of the west coasts for breeding as the beaches are likely to be washed up often by large swells. No archeological record but one in the top north of the South Island was found along the west coasts of New Zealand (Childerhouse and Gales, 1998).

The loss in habitat is not only what can affect the potential for a site to be recolonised. Indeed plant species have also been introduced in the coastal zones of New Zealand to a large extent. The main invasive and aggressive introduced species to sand dune processes is thought to be the Marram grass, *Ammophila arenari* (Johnson, 1992). In 1951 it has started being used as a strong sand-binder, with the New Zealand government promoting its planting in sand dunes to reclaim land for pastoral development and forestry

(McKelvey, 1999). Pine trees, *Pinus radiata*, were then planted in the backdunes while marram grass stabilised the foredunes. A total of 52,000 hectares of coastal foredunes are nowadays invaded by marram grass and 200,000 hectares of backdunes used as pastures and radiata pine tree plantations (McKelvey, 1999). The presence of marram grass species changes the process of the duneland, notably creating sand cliffs along beaches due to its strong sand-binding properties (Hilton *et al*., 2000). Figure 6.3 shows an example of cliff sand created by the presence of marram grass in the foredune of a beach at Otago. These sand cliffs may greatly reduce the accessibility to backdunes by wildlife including sea lions as the females would not be able to easily move inland during the dispersion phase. The presence of introduced vegetation on the mainland can thus limit the suitability of the already few potential sites remaining due to habitat loss.

Alternatively, the native coastal forest has been replaced by introduced pine plantations behind sandy beaches (McKelvey, 1999). The female sea lions breeding at Victory Beach, Otago Peninsula, are known to use the pine forest which was planted in the backdune in the 1950s as nursing sites (McConkey *et al*., 2002a). It thus seems possible that the ability of the female New Zealand sea lions to use a wide range of habitats, described in this study, may also imply that they could recolonise an unnatural environment. They may indeed be able to use pine tree plantation as nursing habitat instead of native coastal forest during the dispersion phase. Pine tree plantations in coastal sand dunes may thus be regarded as a potentially suitable habitat for recolonisation as the availability of coastal native forest is nowadays highly limited.

Figure 6.3: Illustration of one of the effects of marram grass on sand dune processes: formation of sand cliffs along the foredune (photo taken at Victory Beach, Otago Peninsula on 30/07/04).

The loss of a potential suitable habitat for the establishment of new breeding colonies, especially around the south-east coast of the South Island, where the species is currently recolonising, emphasises the need to manage the recolonisation carefully and efficiently. Suitable sites in relation to preferred habitat configuration are nowadays certainly highly limited, even if the species appears to be able to recolonise modified environments. Habitat rehabilitation through re-vegetation of potential suitable sites along the current extent of the area used by the breeding females (Catlins and Otago coast), during the current early stage of the recolonisation, should be recommended to enhance the suitability of potential breeding sites. Nevertheless the lost native coastal forest cannot be replaced in a short term and other habitats such as sward and soft scrub as well as coastal pine forest can be sought as alternative habitats that females could use.

4.2.2 Coastal urbanisation: another factor decreasing habitat suitability

Before the extirpation of the New Zealand sea lion, the country was mostly still only inhabited by Maoris. Nevertheless within 150 years, urbanisation has occurred and consequently the species is recolonising a more human-made environment that includes roads and cities. The distribution of human population in New Zealand is not uniform. Most urban and sub-urban areas are found on the coast as the examples of the two main cities in the South Island, Dunedin and Christchurch, reflect. Both cities grew out to long sandy beaches and sand dunes. Even in rural areas, sandy beaches are usually targeted for housing. The area of 550,000 m² found to be used by the female New Zealand sea lions at Sandy Bay gives a potential indication of the area required to be free of human habitations and infrastructures behind a new breeding colony on the mainland. The presence of habitations along sandy beaches is a problem for management as such areas used by female sea lions could include residential areas creating a high rate of interactions for wildlife managers to deal with.

Due to the coastal distribution of the human population in New Zealand, roads were also built close to shores. The example of road distribution within the area currently used by the New Zealand sea lion on the mainland (from the Catlins to Dunedin) reveals a significant spatial problem between the female spatial ecology and urbanisation (Figure 6.4). Few parts of the coast are indeed free of secondary roads within 1.5km of the ocean in this area. The female New Zealand sea lions were found at distances to ocean greater than 1km behind the breeding beach. Consequently the presence of roads makes sites with adequate habitats for breeding unsuitable. Roads consistently stay a potential hazard for

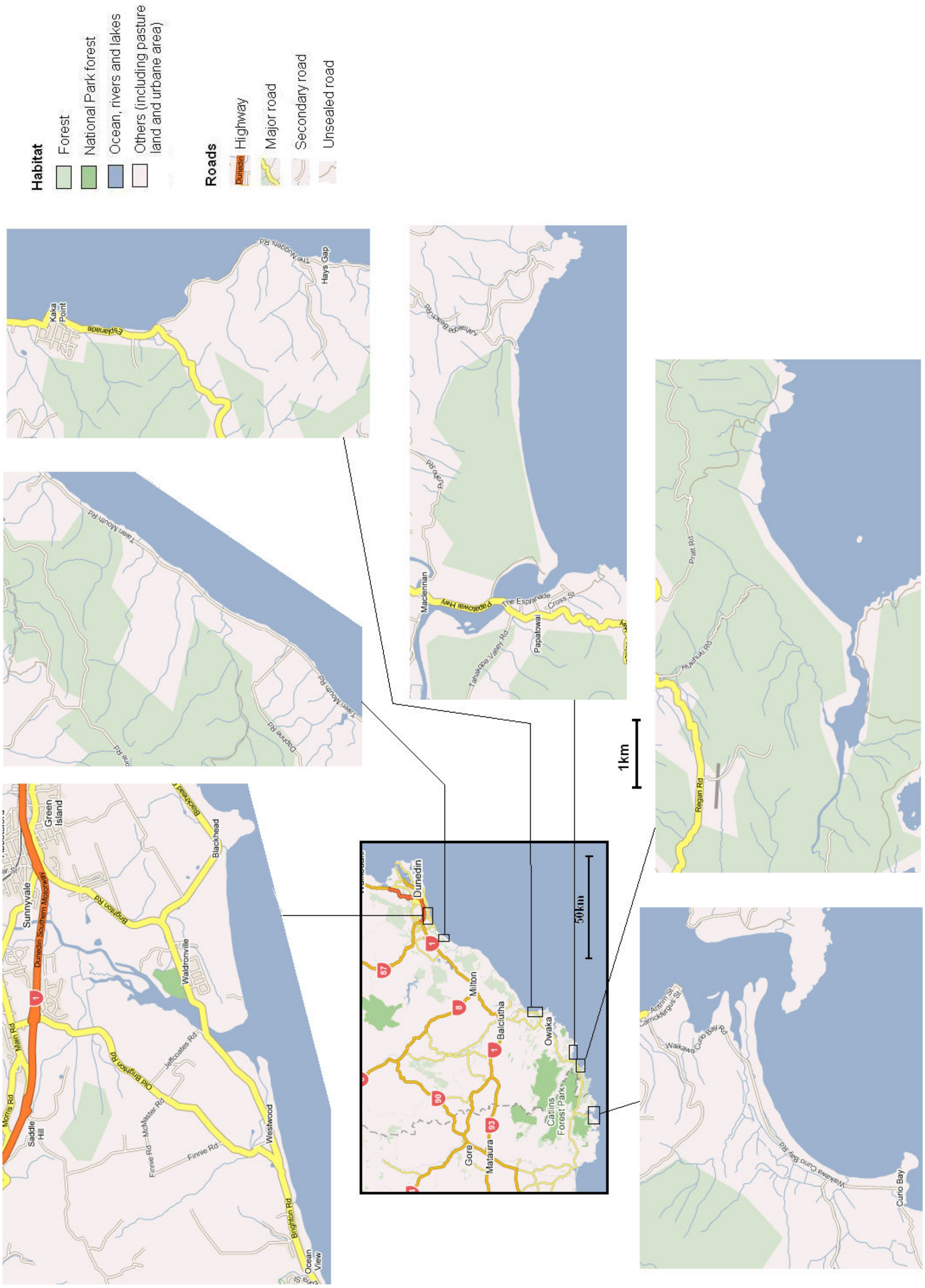


Figure 6.4: Example of urbanisation, especially distribution of roads, within selected coastlines between Dunedin and the Catlins, South Island, New Zealand. The maps were extracted and modified from Google maps (www.google.com).

females once they disperse to other and numerous locations; no protection can be made apart from signposting for 'sea lion crossing' in areas known to be used. A female has already been reported hauling out on a farm at more than 1km inland and had to cross roads to reach the site where she was found before being transported back to the coast. Her presence was indeed dangerous, both for her and the traffic (H. McConnell, pers. com.).

Both the distribution of populated areas and roads are thus added to habitat loss and modifications to decrease the potential number of breeding sites for the New Zealand sea lion. Not only do breeding colonies require a specific habitat within a large area, but it is also necessary for managers to try to orientate the establishment of a new breeding colony in areas where interactions between humans and sea lions could still be limited. This includes areas preferably free of roads or inhabitations.

Currently Victory Beach, Otago Peninsula, is thought to host the first population of New Zealand sea lion in the initial stage of a breeding colony on the mainland (McConkey *et al*., 2002a; Lalas and Bradshaw, 2003). From the results of this study it also appears that this location would be suitable for the establishment of a breeding colony both in terms of habitat and human activities. The habitat at Victory Beach is made of a sandy beach backed with foredunes and a radiata pine forest in the backdunes behind some scrub (Figure 6.5). The terrain is relatively flat with the presence of an inlet to the south of most of the sea lion's sites (McConkey *et al*., 2002a; Augé A., unpublished report). The inlet is a potentially safe water body for pups in the same way as the lakes at Sandy Bay. Victory Beach, even if relatively close (25km) to an urban area, also has a low human presence due to the existence of the Okia Reserve covering most of the land behind the beach in which there is no road nor habitation (DCC, 1991). The access to visitors to the southern part of the beach is also limited as it requires a long walk either from the northern part of the beach or all along Papanui Inlet from the road. The female New Zealand sea lions may thus have chosen the southern part of Victory Beach to breed, in part, for these terrestrial characteristics that correspond to the overall best suitable habitat as described in this study.

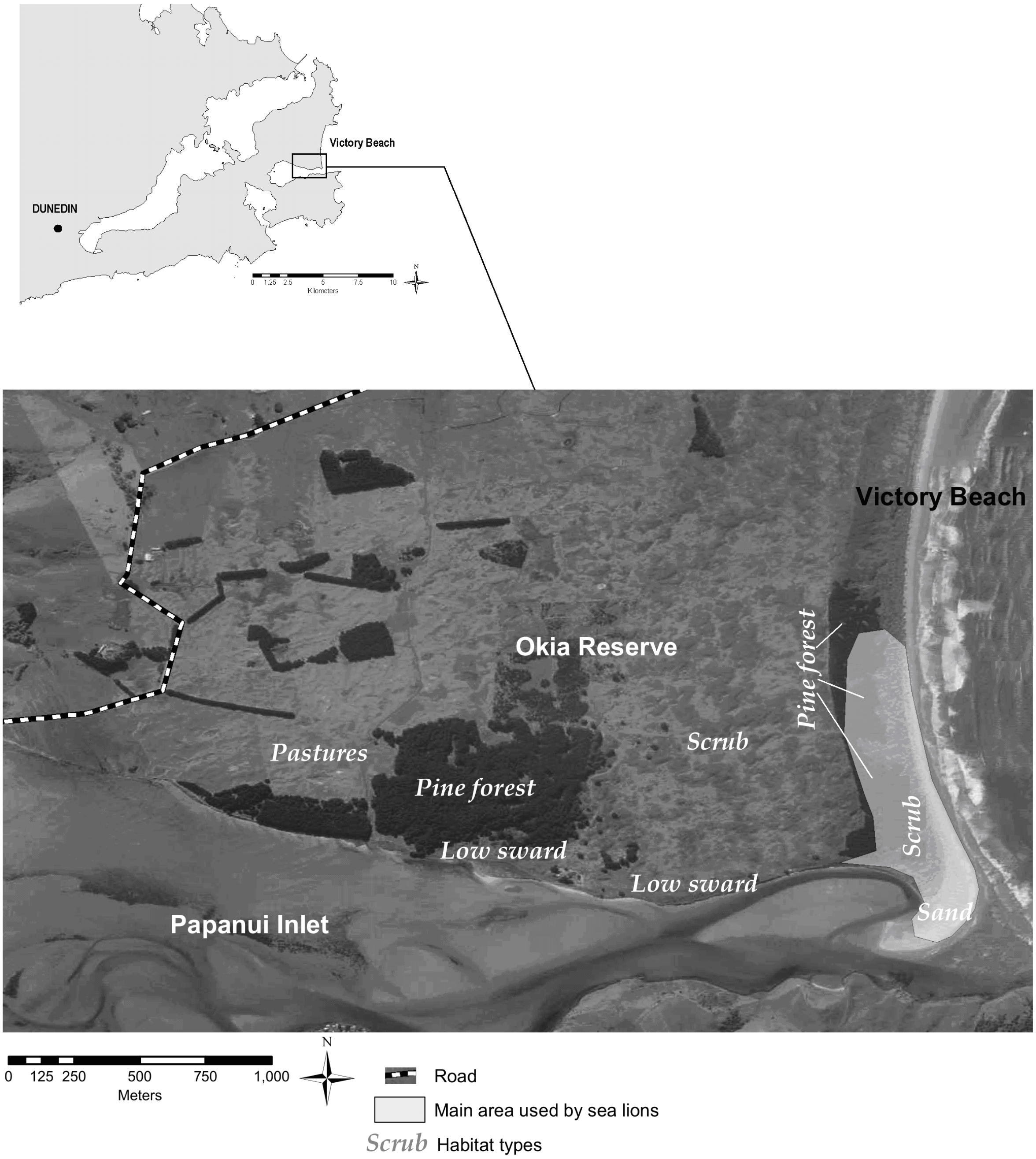


Figure 6.5: Victory Beach, Otago Peninsula: habitat types and area mostly used by the New Zealand sea lion.

5. Spatial ecology and Geographic Information System (GIS): benefits, current limits and further use for the management of the recolonisation

5.1 GIS benefits to spatial ecology research

The use of GIS to analyse the terrestrial spatial ecology of female New Zealand sea lions around a breeding colony revealed patterns that would have been hardly detected by other methods. Indeed the use of GIS to analyse the GPS locations of females onshore was valuable in order to deal with this large amount of spatio-temporal data. It also facilitated the combination of these data with the spatial organisation of the habitat. In the last 20 years, GIS has been successfully used to investigate wildlife spatial ecology and habitat use for various species (Millington *et al*., 2001). These types of studies helped to understand the amount and direction of movements (elk, Bian and West, 1997; grey seal, Twiss *et al*., 2000; spotted turtle, Litzgus and Mousseau, 2004; New Zealand sea lion at sea, Chilvers *et al*., 2005b).

The need for GIS in spatial ecology comes from the improvements in field techniques for wildlife ecology studies that are now involving the construction and analysis of large geodatabases. Using GIS allows data gathering and analysing in a relatively easy and fast way. This is especially useful in conservation applications as measures for threatened species are often required in a reasonably short term. Furthermore, mapping and modelling with GIS provides visual representations to reinforce conservation issues dealing with habitat or space use. As pointed out in Tarantino (2000), visualisation is a key part of the decision-making process in modern society. This concept is also valuable in wildlife conservation where maps are tools for scientific transmission of information that can also be used to raise awareness from the public.

5.2 Temporal analyses in GIS: significant limit for use in ecological studies

This study showed that the female New Zealand sea lion's terrestrial spatial ecology cannot be thoroughly analysed without integrating time and space. As such they exhibit a highly dynamic behaviour with specific timings and distinct patterns. This timing is of significant importance if conservation measures are taken to protect breeding areas. Time is a central factor in most wildlife studies whether it involves the period of a migration (Phillips *et al*., 2006), the timing of dispersion (Raum-Suryan *et al*., 2004; Phillips *et al*., 2005) or the seasonal differences in movement (Fergusson and Elkie, 2004). Ecological studies have benefited from the development of GIS as it has given the opportunity to investigate spatial behaviour (Millington *et al*., 2001). However GIS in the main still needs improvement to handle time and ease the spatio-temporal analysis of ecological and environmental data (Langran, 1993; Peuquet, 2001). Unlike standard GIS, no broadly applicable temporal GIS has been produced after almost two decades of time-based GIS research. O'Sullivan (2005, p.754) discussed that "*there may not be a readily generalized* […] *way to represent dynamic geographic phenomena or at any rate none that is widely considered adequate*." In this study, the use of kriging interpolation to characterise dynamic wildlife spatial patterns was explored and successful in representing the shift in areas used by the females during the dispersion phase. As discussed and in relation to O'Sullivan's (2005) statement, this technique is however only applicable to a restricted number of wildlife movements that would involve a shift in the distribution of the whole population i.e. dispersion and migration.

Prototype temporal GIS have been produced within the last ten years and are successful in the visual representation of temporal phenomena with advanced querying functions involving time (Morris *et al.*, 2000; Shaw and Xin, 2003). These GIS are actually specific to a research area and may not be adapted for spatial ecology. Some of the main GIS analyses functions involving time, missing from current GIS, have to do with movements i.e. distance and direction of each individual of a group to detect temporal patterns to model migrations or dispersions (see Laube and Purves, 2006, for the theory of the REMO approach). They have to do with a lack of statistical tools based on time to be able to distinguish between, for instance, clustering or dispersion during specific times or periods. As suggested by O'Sullivan (2005) in his review on time in geographic information science, the methods to integrate time into GIS should be re-approached with simple functions for basic temporal data as currently researchers seem to work on complex systems with already high focus on a particular issue. Geographic information science should also focus on improving the level of analysis involving time for ecological studies to adequately benefit from the advances in this domain.

5.3 Further use of GIS for the management of the recolonisation

Detection of suitable locations for natural recolonisation or reintroduction using GIS and based on habitat type, topography and human presence, were produced for several large threatened species in terrestrial environments (e.g. grey wolf, Mladenoff *et al.*, 1995; landbird migrants, Simons *et al.*, 2000; grey-faced buzzard, Matsuura *et al.*, 2005). Protection or measures in specific areas made of suitable habitats for the species was then sought to help the species' recovery. Due to the specific requirements of female ecology for a breeding colony of New Zealand sea lion to successfully establish, it seems essential to identify the most suitable locations so that wildlife managers could orientate their measures with priority. The same process as proposed in the above studies could be realised for the recolonisation of the New Zealand mainland by *Phocarctos hookeri*. Indeed the present research describes what combination of habitat types, topography and human presence represents the best suitable environment for the establishment of a new breeding colony.

A systematic survey of the coasts within the current known extent of the recolonisation (e.g. Stewart Island and the coastline of the South Island from the Catlins to the Otago Peninsula; McConnell, 2001) could be undertaken to map potential breeding sites. A stratified mapping technique from the shore could be used to reduce the mapping effort. Indeed, a mapping of the sandy beaches abutted with sand dunes could be first performed. More complex mapping of habitat types and terrain could then be done only for those parts of the coastline with contiguous areas of $500,000m^2$ going up to 1.5km from shore. The final addition would be to map human presence in the area including roads, habitations, pasture land with fences, and any other infrastructures. Selection within the GIS database using simple criteria could be executed to detect all locations that exhibit the most suitable habitat.

Ordering the suitability of sites will then depend on a range of factors such as the areas and distributions of the different habitats available, the presence of water bodies (lakes, ponds, inlets, estuaries…), and the degree of human presence. The current level of use by New Zealand sea lions could also be incorporated to determine some potential preference for locations by the species. As a whole this technique should allow the detection of the most suitable sites for the establishment of new colonies which should thus be prioritised if management measures are taken for the enhancement of the recolonisation.

Alternatively a GIS database could be used to monitor and map the recolonisation process of the New Zealand sea lion females. Records of locations and dates of females as well as the presence of pups could be incorporated in a GIS to create a spatio-temporal database such as the one used in this study. This database could be, firstly, used to understand the mechanism in space and time of the recolonisation process of the New Zealand sea lion females as well as to detect, as soon as possible, the exhibition of the two-phase pattern which would indicate the establishment of a new breeding colony and allow the strengthening of management measures. Secondly, this database could also be integrated with the habitat mapping suggested in the last paragraph. The identification of the females would be an additional advantage to investigate the space use of the recolonising population. Consequently further use of GIS to manage the recolonisation process would certainly be very beneficial to wildlife managers, based on the results from this thesis as well as females' locations on the mainland. Nevertheless, the results of this study still need to be combined with further research on the ecology of the New Zealand sea lion to acquire a sufficient and necessary understanding to better manage the recolonisation.

6. Recommendations for further research to improve the management of the recolonisation

6.1. Methods of data acquisition

A 'homing-in' technique was used in the present study to gather the females' locations. This technique allowed following the daily movements of more than 80 individuals for up to 106 days. On the other hand, a 'satellite tracking' technique allows investigating individuals' movements at a finer temporal scale. Due to logistical constraints (need to catch the animals to put on and retrieve the tag, battery lifespan, and budget limitations) there is, however, a restriction on the number of animals that can be studied and the number of days the study can last. As a remote technique there is also no knowledge on the type of behaviour exhibited by the animals when the location is taken. Most studies using satellite tracking have small sample sizes and look at movements during a period only rather than during a whole season (e.g. 22 individuals were followed for 34 days on average during different periods in Campagna *et al.*, 2001). Both techniques thus offer different ways of investigating spatial behaviour.

In the present study the large sample population permitted the production of a powerful model of an average female's spatial ecology on land and density of the female population during a period of three months as well as the exploration of the fine changes in habitat preferences over the whole breeding season. This kind of result could not have been obtained using satellite tracking. Nevertheless high resolution tracking data gained by this later technique would be valuable to investigate detailed spatial movements such as travelling in different habitat types, landing sites and timing at the beach, walking patterns (e.g. terrain related) and strategies for the search of the pups. All these aspects could enhance the knowledge on how females use their terrestrial habitat and what they require. Such additions to the results of this thesis would increase the potential for more sensible management measures to be taken.

Only the adult females' ecology was investigated in this study. This gave a valuable and required insight into their spatial ecology for management purposes but it is likely that the pups' spatial ecology induces a constraint to the breeding females on how they use their habitat. Indeed during the first few weeks pups are more sedentary whereas when they grow up they become more and more mobile, can move long distances and start going to sea alone (Raum-Suryan *et al.*, 2004). A study of terrestrial spatial ecology of pups from birth to the end of the dispersion phase, based on the same technique as the one used in this study would help to understand the relationship that exists between females and pups' requirements for the definition of a suitable breeding site. The study of males' ecology could also enhance the processes involved in the movements within the harem as well as some of the driving factors for the spread of the females during the dispersion phase.

6.2. The marine environment: requirements for foraging habitat interact with terrestrial habitat requirements for the suitability of breeding locations

Pinnipeds are almost unique amongst mammals as they use both terrestrial and marine (including both coastal and pelagic) environments for their vital behaviours. The only two other mammals that also rely on both environments for their survival are the sea otter, *Enhydra lutris*, and the polar bear, *Ursus maritimus*, both listed as endangered by the IUCN (Reeves, 2002). The status of these two species combined with the high number of endangered and threatened species of pinnipeds highlight their vulnerability (Reeves, 2002). Indeed the fact that they use both terrestrial and marine habitats doubles the pressure due to human activities, especially visitors and tourism on one hand (Wright, 1998) and fishery interactions on the other hand (Wilkinson *et al.*, 2003). This study only focused on the terrestrial spatial ecology to detect suitable sites from land-based factors. Nevertheless it is inevitable that these factors interact with marine factors for the suitability of a site. Proximity of foraging grounds, seasonal distribution of prey species, presence of currents, bathymetry and presence of prey species along the coast are amongst the reason why females choose a location to breed (Raum-Suryan *et al.*, 2004).

This study must thus be completed by an investigation of the possible foraging grounds around the current recolonised part of the coastline. Previous studies on the foraging ecology of female New Zealand sea lions in the Auckland Islands showed that females can travel up to 175km to reach foraging grounds that are thought to be mostly at the edge of the continental shelf (Chilvers *et al.*, 2005b). Nevertheless the marine environment and prey availability around the New Zealand mainland is significantly different from the sub-Antarctic islands. Childerhouse *et al.* (2001) described the New Zealand sea lion as a generalist feeder at the Auckland Islands which does not allow focusing on the distribution of one particular prey species to detect foraging grounds. Lalas (1997) confirmed this generalist feeding by looking at the diet of New Zealand sea lions at the Otago Peninsula. Investigating where females forage around mainland New Zealand would help determine the suitability of the different parts of the coastline as breeding habitat. Females are indeed likely to choose a location as close as possible to foraging grounds (Raum-Suryan *et al.*, 2004).

As suggested in this study the females may also disperse to various locations. The coastal marine environment is thus also likely to be of significant importance for the suitability of a breeding location of the New Zealand sea lion. Raum-Suryan *et al.* (2004) and Fowler *et al.* (2006) also highlighted the importance of coastal waters near breeding colonies as it is where pups and juveniles learn and improve their foraging skills. Requirements for both terrestrial and marine environments must consequently be integrated to detect suitable sites with complete consideration of the ecology of a pinniped species such as the New Zealand sea lion.

7. Conclusion

The results of this study are significant and relevant to be used to manage the recolonisation of the New Zealand sea lion back to the New Zealand mainland. They highlighted some management measures that should be implemented as soon as possible to enhance the first stage of the recolonisation. Future measures are also recommended to protect breeding colonies and avoid potential negative interactions for both humans and sea lions. It seems that the unusual amount of movement on land of the female New Zealand sea lions necessitates a large understanding of terrestrial spatial ecology to be correctly managed. Public awareness and education about the species' uncommon ecology is the first management step to be taken. The preferred habitat for a breeding colony is nowadays limited due to habitat loss and urbanisation. Consequently, measures should be taken to manage and monitor potential sites that could be detected using the present results. GIS could be a valuable tool to monitor the evolution of the recolonisation process until the start of the distinct two-phase pattern that signifies the establishment of a breeding colony. Then, some of the management measures to ensure little disturbance to the growing population are likely to include limited access or closure to the breeding beach and its surroundings, some days before and during the harem phase, but also during the dispersion phase. More detailed research on terrestrial spatial ecology, especially outside the breeding colony, as well as foraging spatial ecology could help to better predict the suitability of sites and to better manage the interactions between humans and sea lions.

CONCLUSION

The investigation of the terrestrial spatial ecology of the female New Zealand sea lions gives the first quantitative insights into their behaviour and their relation to the environment. The use of a large sample size and daily data acquisition for a period of up to 106 days during two breeding seasons allowed the gathering of a considerable amount of spatio-temporal data. These data were made of Global Positioning System (GPS) locations of females onshore within the study area. These positions were inserted into a Geographic Information System (GIS) and analysed in conjunction with habitat data. The habitat maps were obtained through a surveying technique to obtain a Digital Terrain Model of the study area and a Quickbird satellite image to map the habitat type.

The analyses at three different scales (individual, population and habitat) revealed both common and unusual behaviours of this species, fundamentally based on a predictable two-phase pattern comprising a harem phase and a dispersion phase. The predictability of this pattern was revealed through the production of the time-dispersion model that gives the average area that a female used each day of the breeding season since her first landing at the beach.

The harem phase, when adult of both sexes congregate to reproduce, is common amongst polygamous colonial species. It lasts 41 days in the New Zealand sea lion population at Sandy Bay. Pupping and mating exclusively took place during this phase within a small area of sandy beach (less than 3,000 m^2). The dispersion phase was characterised by the spread of the female population in a wide area (more than 550,000 m^2) with females found to walk more than 1km from the ocean to nurse their pups at suitable sites. Females also showed a surprising preferential selection for the forest habitat during this phase. Knowing that the New Zealand sea lion is considered to be a marine mammal, these are particularly unusual ecological characteristics that are not exhibited by any other pinniped.

Movements of an individual female during the harem phase were found to significantly influence the survival of her pup through the existence of a sensitive period during the day of pupping, and overall movements may induce a decrease in maternal efficiency. The first pregnant females to come ashore at the start of the breeding season (the founder females) determined where the harem was formed. From their initial landing sites, the timing of the establishment of a female sea lion population showed a close consistency between years. The areas used during the two seasons were also highly similar. A shift in area used by the female population was also detected after the start of the dispersion phase. At Sandy Bay most females also took their pups to other locations before the end of March.

This spatial terrestrial ecology is thought to be caused by various factors. The avoidance of aggression from adult males during the harem phase creates the formation of a high density of females close to shore (up to 80 females per 100 m^2) to reduce the aggression rate per female, including during the travel to and from the ocean, and the movements induced within the harem. The sand habitat may be preferred because its softness allows pups to better survive the interactions with males in the harem. The avoidance of perturbation from sub-adult males during the dispersion phase may cause the spread of the female population and the consistent change in sites used by a specific female. The constraint of parasites (hookworm) infections in the ground is certainly one of the factors that could explain the shift in areas. The habitat preference for forest during the dispersion phase can be attributed to the thermoregulation properties of this habitat as well as the possibility for the females to hide from males and from other groups of females.

The characteristics of the two-phase pattern of the spatial ecology on land of female New Zealand sea lions generate conservation issues when considering the management of the recolonisation, due to human infrastructure, presence and habitat modifications on the New Zealand mainland. However, the predictability of this ecology is a significant advantage for the management of such a dynamic and large scale behaviour. The results of this study should thus be used to develop management measures for the recolonisation. It is recommended that some of the main measures include a program of rehabilitation and protection of potential sites to enhance the recolonisation, a continuous and systematic monitoring of the spatial behaviour of the animals already breeding on the mainland to determine predictable patterns, and a large campaign of public awareness both to visitors to beaches to avoid disturbance, and to residents in recolonised areas to increase the understanding of the species' ecology and recolonisation process.

The use of GIS to analyse the terrestrial ecology of female New Zealand sea lions was found to be valuable, allowing the identification of detailed spatio-temporal patterns. Further uses of GIS for the management of the recolonisation are recommended, including the construction of a geodatabase to understand the recolonisation process, and detect where and when a new breeding colony appears, so that conservation measures can be taken.

In conclusion, the unusual characteristics of the female New Zealand sea lions' terrestrial spatial ecology revealed in this study highlighted the need for immediate and effective conservation measures for the success of the recolonisation, and for more research undertaken to better understand this unusual terrestrial ecology.

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