HOME RANGES AND DIVING BEHAVIOR OF NEW ZEALAND SEA LIONS ALONG THE CATLINS COAST, SOUTH ISLAND, NEW ZEALAND

A Dissertation

by

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ABSTRACT

New Zealand sea lions (*Phocarctos hookeri*) were extirpated from the North and South Islands of New Zealand during pre-European native hunting, and their numbers were greatly reduced on the Auckland and Campbell Islands during European commercial sealing. However, they began reoccupying South Island in 1994, and pup production remains low but steady. The home range, at-sea movements, and diving behavior of females at the breeding colony along the Catlins Coast of South Island have not been studied since its inception in 2006. The goal of the study was to: 1) evaluate the performance of home range models to identify the most accurate model(s) for a semi-aquatic distribution, 2) track movements to identify home ranges, and 3) record diving behavior of females to characterize foraging behavior and estimate energy expenditure. To accomplish this study, we attached satellite telemeters and video and data recorders to females along the Catlins Coast during austral winter of 2019.

Home ranges were most accurately modeled by separating inshore and offshore habitats and applying adaptive local convex hulls (LOCOH) and fixed kernel density with plug-in bandwidth selection (PKDE), respectively. This method minimized the ranges outside of used habitat, handled boundaries to movement, and performed accurately in cross-validation evaluation. The results showed the importance of home range model selection.

Total home ranges were small and restricted to coastal areas. Foraging cycles were frequent, with short times at sea and onshore. Dives were shallow, short in duration, and divided into three types based on variables derived from three-dimensional dive analysis. Dive characteristics indicated a benthic foraging strategy with transit periods between foraging patches. At-sea estimated metabolic rate varied by activity, with an estimated field metabolic rate lower than that of females at the Auckland Islands, possibly indicating differences in energetic expenditure among populations. It appears that females along the Catlins Coast consume nearshore, abundant prey and require less time and smaller home ranges for foraging compared to that for females in the Auckland Islands. Although reoccupation of their historic range on South Island will take decades, suitable habitat for breeding and prey availability along the southeast coast are encouraging.

DEDICATION

To the teachers, mentors, family, and friends who inspired me to ask questions and search for answers. This is for you all.

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The analyses depicted for Chapter 2 were conducted in part by Professor Sterba-Boatwright. All other work conducted for the dissertation was completed by the student independently.

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CHAPTER I

INTRODUCTION

Taxonomy

New Zealand sea lions (hereafter referred to as NZSL) are one of 14 extant species of sea lions and fur seals in the Family Otariidae (Order Carnivora, Clade Pinnipedia). Among the Otariidae, there are six species of sea lions, two of which occur in northern hemisphere (Steller [*Eumetopias jubatus*] and California [*Zalophus californianus*] sea lions), three in southern hemisphere (Southern [*Otaria byronia*], Australian [*Neophoca cinerea*] and New Zealand [*Phocarctos hookeri*] sea lions), and one along the equator (Galápagos sea lion [*Zalophus wollebaeki*]).

Evolution

Fossils of the arctoid ancestors of Pinnipedia (seals, fur seals, sea lions, walruses) can be traced to the Eocene (45 Mya), although fossil pinnipedimorphs only extend to the late Oligocene (27-25 Mya). The clade of Pinnipedia is a sister group to the Ursoidea, which includes the Ursidae (i.e., bears; Rybczynski et al., 2009; Berta, 2018). The earliest Otariidae fossils (17.1-15 Mya) are from southern California (Boessenecker and Churchill, 2015). The Otariidae probably evolved in the North Pacific with the divergence of the Otariinae (sea lions) and Arctocephaline (fur seals) clades in the late Miocene (6 Mya) (Boessenecker and Churchill, 2015). The southern hemisphere clade likely emerged in the southeastern Pacific and later dispersed globally (Churchill et al., 2014).

Stem Pinnipedia were a transitional link between early Arctoid carnivores and the more highly derived pinnipediformes such as *Enaliarctos*, in which both sets of limbs were already modified as flippers (Berta et al., 1989; Berta and Ray, 1990 Wang et al., 2005; Rybczynski et al., 2009). Early Otariidae were fish-eating, semi-aquatic carnivorans, which displayed the same foreflipper propulsive swimming technique seen in extant species, but were likely better adapted to terrestrial locomotion (Berta, 2018).

Abundance and Distribution

The historical abundance and distribution of NZSL is based on archaeological remains and historical records. Seal fossils in New Zealand are no older than the Pleistocene (2-3 Mya) (Fordyce, 1988). Most pre-European fossils date from the 12th-17th centuries and indicate that NZSL were used by indigenous Maori and Moriori for food (Childerhouse and Gales, 1998). While the historical distribution included both North and South Islands, almost half of the fossils were concentrated in southern South Island (Gill, 1998). Breeding colonies disappeared north of the Otago Peninsula on South Island by the 16th century, and NZSL were extinct on South Island by the end of the pre-European period (Smith, 1989).

Commercial sealing, which began in the Auckland Islands in the early 19th century, significantly reduced the population in the subantarctic islands by 1830 (Childerhouse and Gales, 1998). Commercial sealing ceased in 1893, and sea lion populations increased throughout the 20th century. From 1974-96, the estimated population of NZSL more than tripled, and females with pups were observed as far north as Otago Peninsula by the 1990s (Childerhouse and Gales, 1998; McConkey et al., 2002). However, the number of females and pups in the Auckland Islands declined from 1996-2009 (Chilvers, 2015; Melidonis and Childerhouse, 2020). The most recent population estimate was 11,767 (95% C.I.: 10,790-12,923), the smallest of any sea lion species (Chilvers and Meyer, 2017).

The International Union for Conservation of Nature (IUCN) classified New Zealand sea lions as ‘Endangered’ in 2015, and the New Zealand Department of Conservation currently lists the conservation status as ‘Nationally Vulnerable’. The current breeding distribution ranges from Campbell Island (52.5° S, 169.1° E) to the Otago region of South Island (45.9° S, 170.7° E) (Fig. 1.1), while males are occasionally observed farther north (Chilvers, 2018b). Breeding colonies exist on Dundas, Enderby, and Figure of Eight Islands within the Auckland Island archipelago (Melidonis and Childerhouse, 2020). Annual births decreased by 50% (from 2,975 to 1,501) from 1996-2009, with reductions at all three colonies (Chilvers, 2009a). More than 70% of sea lion births occur on the Auckland Islands (Maloney et al., 2012), and the total population estimate was significantly impacted by the decline. The population has stabilized, and numbers have recently increased. However, current pup production remains well below peak level during the early 1990s (Melidonis and Childerhouse, 2020). The most likely explanation for the decrease in breeding females is fisheries competition and by-catch around the Auckland Islands (Robertson and Chilvers, 2011). One hypothesis is that reduced prey availability in this area is contributing to the slow growth over the past decade (Auge et al., 2011b; Auge et al., 2012a).

Estimated annual pup production is increasing among other breeding colonies on

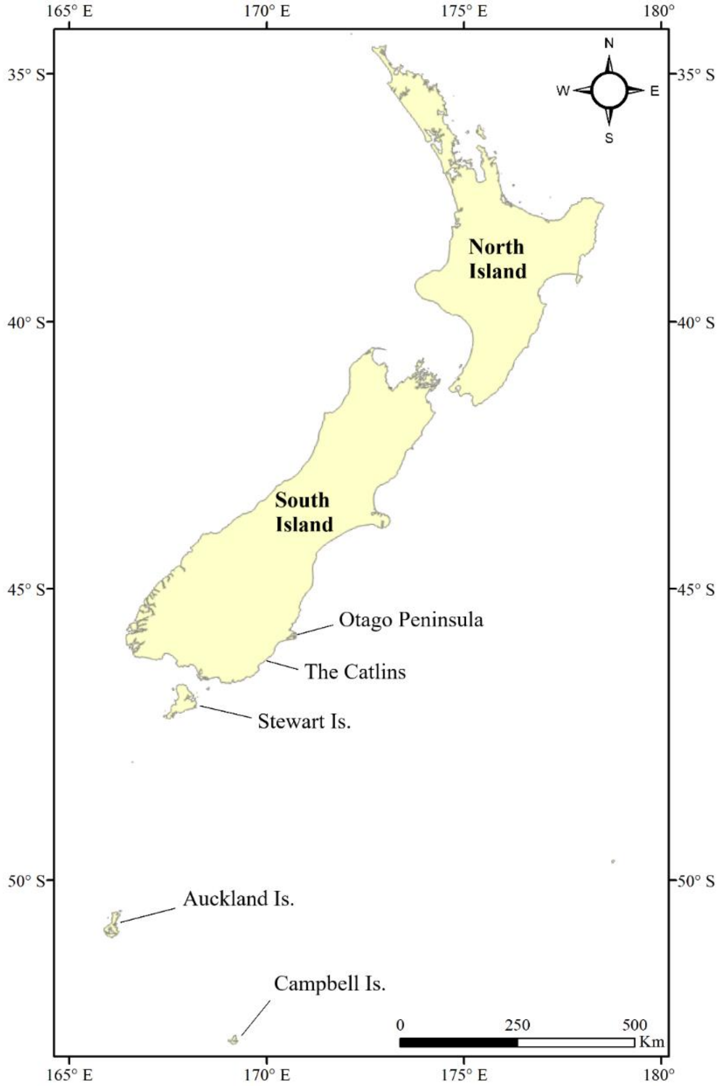

Figure 1.1. Breeding locations for New Zealand sea lions. This study occurred along the Catlins Coast.

Campbell, Stewart, and South Islands. An estimated 700 pups were produced on Campbell Island in 2018, an increase of almost 200 since 2008 (McNutt, 2020). Females on Stewart Island produced > 40 pups, and this area was declared an official breeding colony in 2018, the first in this region in over 150 years (DOC, 2018). Since the first recorded birth on the Otago Peninsula in 1994, pup production has slowly increased to 13 in 2018 (Jim Fyfe, DOC ranger, pers. comm.). The Catlins Coast breeding colony has grown from one pup in 2006 to seven in 2019 (Charles Barnett, DOC ranger, pers. comm.). Resource accessibility may be contributing to growth in these areas, particularly around South Island.

Despite the large geographic range of NZSL, no significant genetic differences exist among colonies (Collins et al., 2017), possibly because commercial sealing on the Auckland Islands created a genetic bottleneck resulting in low levels of mitochondrial genetic variation. Breeding groups on the Otago Peninsula and along the Catlins Coast were founded by immigrant females from the Auckland Islands, further supporting the small mitochondrial genetic diversity (McConkey et al., 2002; Auge, 2010). The movement of males between colonies during breeding season likely facilitates gene flow and prevents genetic isolation, as NZSL have moderate levels of nuclear genetic variation comparable to other sea lion species (Collins et al., 2017; Osborne et al., 2016).

Reproduction

NZSL are sexually dimorphic and have a polygynous mating system. Adult males have a body mass of 300-450 kg, while adult females range from 90-165 kg (Fig. 1.2; Chilvers, 2018b). Starting around the age of three years, females come ashore between mid-December to mid-January and give birth to a single pup approximately two days later (Childerhouse et al., 2010; Chilvers et al., 2007). Sexual dimorphism is present in pups: birth mass 10.6 kg for males and 9.7 kg for females (Chilvers et al., 2007). Female NZSL are philopatric, and frequently return to their natal colony to give

Figure 1.2. New Zealand sea lion harem consisting of one male (back right), five females, and one pup (front middle) along the Catlins Coast, South Island, New Zealand. Image courtesy of Charles Barnett.

birth (Chilvers and Wilkinson, 2008; Auge et al., 2014). Mature males defend harems of females during the breeding season, and copulation occurs about a week after parturition when females enter estrus (Cawthorn et al., 1985; Trillmich, 1990). Males may disperse during this period and travel among breeding colonies during a single season (Robertson et al., 2006). As with other Otariidae, NZSL are income breeders and make alternating foraging trips and time onshore while nursing a pup until weaning (Davis, 2019). Foraging trips are 0.5-2.8 days in duration followed by 0.6-1.3 days onshore (Gales and Mattlin, 1997; Chilvers et al., 2005; Chilvers et al., 2006; Auge et al., 2011b). Both periods vary geographically and seasonally as the pup matures (Gentry and Holt, 1986). Females wean pups around nine months of age (Gales, 1995), and the cycle repeats the next breeding season.

Foraging

NZSL in the Auckland Islands have the deepest recorded dives (~600 m) of any sea lion species, with mean depths of about 125 m and durations of 3.5 min (Gales and Mattlin, 1997; Costa and Gales, 2000; Crocker et al., 2001; Chilvers et al., 2006). These deep, long dives may be possible because of an increased blood volume, which increases the aerobic dive limit (ADL; Costa et al., 1998; Costa and Gales, 2000). Environmental variables may influence diving ability in Pinnipedia, as the negative correlation between body size and mass-specific oxygen stores in southern sea lions (*Otaria flavescens*) was hypothesized to be ecologically driven (Hückstädt et al., 2016). However, NZSL in the Auckland Islands may exceed their ADL on 69% of foraging dives (Chilvers et al., 2006). In contrast, the mean depth and duration of dives made by females on Stewart Island (60 m in depth, 2.5 min in duration) and the Otago Peninsula (20 m in depth, 1.8 min in duration) are more modest and remain within their ADL (Auge et al., 2011a; Chilvers, 2018c). The differences in diving behavior between subantarctic and South Island populations are apparent in juvenile NZSL as young as two years of age (Leung et al., 2013). Dives that appear to be benthic and mesopelagic have been identified among females throughout their range, so ocean depth influences dive behavior and performance (Chilvers and Wilkinson, 2009; Auge et al., 2011a). Similar contrasts have been identified among female southern sea lions on the Falkland Islands, as well as Galapagos sea lions (*Zalophus wollebaeki*), which can be separated by foraging strategy based on dive depth and distance traveled from the colony (Baylis et al., 2015; Villegas-Amtmann et al., 2008).

Differences in home range are reflected in the maximum distance from the breeding colony and total travel distance during foraging trips. Females on the Auckland Islands range > 100 km from the colony and travel over 400 km during a foraging trip (Chilvers et al., 2005). In contrast, females on Stewart Island range ~28 km from shore and swim an average of 45 km during foraging trips (Chilvers, 2018c). Foraging trips made by females on the Otago Peninsula are even closer to shore (~5 km), with short (26 km) travel distances (Auge et al., 2011b). Juvenile females (2-3 yrs) at the Auckland Islands have foraging trip distances and maximum distances from the colony 5-fold and 10-20-fold longer, respectively, than that of juvenile females on the Otago Peninsula (Leung et al., 2013). Female age positively correlated with foraging trip distance on the Auckland Islands (Chilvers et al., 2005), but not for females on the Otago Peninsula (Auge et al., 2011b). Australian sea lion (*Neophoca cinerea*) home ranges and trip distances positively correlated with age due to physiological limitations of young animals (Fowler et al., 2007). Most research on NZSL foraging behavior has been conducted during austral summer and autumn when females return frequently because of the short fasting duration of young pups. Although austral winter data are limited, foraging areas are similar, but home range may expand compared with summer (Fletcher, 2002; Chilvers, et al. 2013).

Diet varies geographically for NZSL, and the preferred prey of females on the Auckland Islands differs between mesopelagic and benthic foraging strategies, although blue hake (*Macruronus novaezelandiae*) and javelinfish (*Lepidorhynchus denticulatus*) comprise significant portions of the diet for both dive strategies (Meynier et al., 2014).

However, the mesopelagic diet includes higher proportions of red codling (*Pseudophycis bachus*), while the benthic diet has more pink lobster (*Metanephrops challenger*) (Meynier et al., 2014). Significant contributions of yellow octopus (*Enteroctopus zealandicus*) and opalfish (*Hemerocoetes* species) were found in scats and regurgitations on the Auckland Islands, likely part of a benthic diet (Meynier et al., 2008). The diet of females on the Otago Peninsula consists primarily of snake mackerel (*Thyrsites atun*) and jack mackerel (*Trachurus sp.*), with smaller percentages of other species including yellow-eyed penguins (*Megadyptes antipodes*) and New Zealand fur seals (*Arctocephalus forsteri*) (Auge et al., 2012a; Bradshaw et al., 1998). Male NZSL along the Catlins Coast consume high percentages of red codling and Maori octopus (*Octopus maorum*) (Milne, 1996). Diet may vary seasonally with availability of prey (Lalas, 1997), as is the case in southern sea lions (Suarez et al., 2005). Most prey species have high energy densities (6.1-8.5 kJ g^{-1}) except for pink lobster and yellow octopus (3.8 kJ g^{-1}), which are major diet components on the Auckland Islands and may contribute to the poor body condition observed in this area (Auge et al., 2012a; Meynier et al., 2014). The higher energetic costs of deep, long dives in the Auckland Islands plus less energy-dense prey may contribute to the slow recovery of subantarctic populations.

Management

Anthropogenic threats to NZSL are both direct and indirect. Commercial fisheries for arrow squid (*Nototodarus sloanii*) and pink lobster are active around the Auckland Islands during the early period of pup dependency. Their presence can lead to resource competition and by-catch mortality during this critical period. A maximum allowable level of fishing-related mortality (MALFIRM) was implemented in 1994, which would close the arrow squid fishery for the season if the by-catch limit was reached (Robertson and Chilvers, 2011). The MALFIRM was replaced by a fishing-related mortality limit in 2004, which calculated a larger number of allowable deaths using an alternative model (Breen et al., 2003). Arrow squid fishing vessels began using the sea lion exclusion device (SLED) the same year to deflect animals from trawl nets and reduce by-catch (Robertson and Chilvers, 2011). Annual reported mortalities decreased to a mean of 2.4 from 2013-2019 (Fisheries NZ, 2019), but the effectiveness of SLEDs is still debated because of potential injury and poor survival interactions with trawl nets (Wilkinson et al., 2003; Robertson and Chilvers, 2011). Additionally, a marine reserve was designated around the Auckland Islands in 2003, but lactating females regularly venture beyond the 12 nautical mile boundary during foraging trips (Chilvers, 2018b; Chilvers, 2009b). While no sea lion by-catch mortalities have been reported around Otago Peninsula, the potential for future sea lion-fishery interactions and competition is of concern (Auge et al., 2012b). NZSL on South Island are also threatened by human harassment, intentional harm, and vehicle strikes (Lalas, 2008). At least four sea lions have been killed by vehicles since 1992, most recently a female with a young pup in February 2020 along the Catlins Coast (Lalas, 2008; Charles Barnett, DOC ranger, pers. comm.). The New Zealand Department of Conservation and Ministry for Primary Industries constructed a Threat Management Plan (TMP) in 2017 with the goal of managing threats and promoting population growth, with the goal of reaching non-threatened status (DOC, 2017).

Research

Extensive research on NZSL on the Auckland Island has been conducted on population dynamics, fisheries interactions, movements, diving, life history, foraging, reproduction, disease and home range (Breen et al., 2003; Childerhouse and Gales, 2001; Childerhouse et al., 2010; Chilvers, 2009b; Chilvers, 2019; Chilvers and Wilkinson, 2008; Chilvers and Wilkinson, 2009; Chilvers et al., 2005; Chilvers et al., 2006; Chilvers et al., 2007; Chilvers et al., 2011; Costa and Gales, 2000; Costa et al., 1998; Crocker et al., 2001; Fletcher, 2002; Gales and Fletcher, 1999; Gales and Mattlin, 1997; Leung et al., 2013; Leung et al., 2014a; Leung et al., 2014b; Meyer et al., 2015; Meynier et al., 2014; Michael et al., 2019; Robertson and Chilvers, 2011). Females on the Otago Peninsula have also been the focus of research on foraging, diet, movements, genetics, recolonization, and disease (Auge et al., 2011a; Auge et al., 2011b; Auge et al., 2012a; Auge et al., 2012b; Auge et al., 2014; Foote et al., 2020; Hawke, 1986; Jackson, 2007; Lalas and Bradshaw, 2003; McConkey et al., 2002; Roe et al., 2017). In contrast, less research has been conducted on Campbell Island (Childerhouse et al., 2005; Maloney et al., 2009; Maloney et al., 2012; McNally et al., 2001; McNutt, 2020) and Stewart Island (Chilvers, 2018c). Because the breeding colony along the Catlins Coast is the most recent, research has been limited to onshore habitat assessments and demographics (MacMillan et al., 2016; McNally, 2001). The recent increase in breeding females in this area has prompted new interest in research as the colony expands.

In this study, I present results from the first biologging research on females along the Catlins Coast on South Island, New Zealand. The results provide insights into home ranges and diving behavior for pregnant and lactating females, which are compared with the results from other colonies that are geographically distant and have different habitats and prey resources. Direct conservation applications include inshore habitat associations, foraging areas, and potential fisheries conflict. A habitat-based application of home range models is also presented, which can be used in future studies to identify high-use areas.

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CHAPTER II

CROSS-VALIDATION HOME RANGE MODEL SELECTION FOR A SEMI-AQUATIC SPECIES

Introduction

Scientific techniques to track animals originated with bird banding in the early 19th century (Davies, 2004). More recently, wildlife tracking has evolved into a variety of technology-driven methods including radar (Able, 1977), acoustic monitoring (Hayes et al., 1997; Espinoza et al., 2011), radio telemetry (Thomas, 1982; Kays et al., 2011), satellite telemetry (Stewart et al., 1989; Hofman et al., 2019), and satellite or cellular phone-linked GPS (Global Positioning System) tracking (Kuhn et al., 2009). Many of these techniques involve animal-borne instruments, which are referred to as biologging. As a result, extensive data are now available on the movements of numerous species globally (Luschi et al., 1998; Block et al., 2002; Shaffer et al., 2006; Costa et al., 2012).

The analysis and interpretation of these data have evolved simultaneously with biologging technology. Improvements in software and computing capabilities enable sophisticated statistical models for animal tracking. Questions regarding behavior (Schwager et al., 2007; Davis et al., 2013), habitat associations (Aebischer et al., 1993; Davis et al., 2014), physiology (Davis and Williams, 2012; Watanabe et al., 2015), foraging (Dragon et al., 2012; Davis et al., 2013), and conservation (Lennox et al., 2019) have been studied using large and fine-scale spatial and temporal analysis. Shared databases such as Satellite Tracking and Analysis Tool (STAT) (Coyne and Godley,

2005) and OzTrack (Dwyer et al., 2015) have made data sharing, analysis, and visualization easier and more accessible.

The home range of an animal is defined as the area (i.e., territory) where it lives and moves on a periodic basis in search of food or mates and which may be defended against conspecifics or heterospecies (Burt, 1943). Home ranges are dynamic and change temporally as animals seek different resources. As a result, tracking the same individual daily, seasonally, and interannually may lead to different conclusions about a home range. Most home range models use probability density functions, which predict occurrence over a spatial range (i.e., utilization distributions) (Anderson, 1982). Utilization distributions (UD) are the relative frequency distributions of animal locations throughout a range over time (Van Winkle, 1975; Millspaugh et al., 2006). Home range models produce probability density functions to estimate the frequency and intensity of spatial occurrence, and spatial contours are generated that encompass a percent probability of occurrence. The accuracy of various methods depends on multiple factors, and their performance can vary among species (Seaman et al., 1999; Boyle et al., 2009; Börger et al., 2006). There is no universally accepted method, and comparisons among models applied to the same data have been used to identify the most accurate (i.e., best) statistical fit (Horne and Garton, 2006; Cumming and Cornelis, 2012; Walter et al., 2015; Chirima and Owen-Smith, 2017).

Kernel Density Estimates (KDE) have been used to construct home ranges (Worton, 1989; Seaman and Powell, 1996), and their non-parametric nature can use data that may not meet parametric assumptions of normality and independence. Individual locations are assigned probability densities (i.e., kernels) within a gridded range. Weighted (i.e., probability) kernel densities for evaluating locations are based on the volume of kernels that overlap an area. Highly weighted densities are the result of many locations within an area, while fewer locations lead to lower probability densities (Seaman and Powell, 1996). Bandwidth parameter selection (*h*) (i.e., kernel width) for KDE significantly influences calculated home ranges (Jones et al., 1996). The bandwidth selection can vary based on statistical calculation (e.g., reference, least squares cross-validation, plug-in, solve-the-equation, etc.) and can be applied across all locations (i.e., fixed), or can vary by location (i.e., adaptive).

Minimum Convex Polygon (MCP) is another method used to estimate home ranges, but it is strongly influenced by sample size and outliers (Worton, 1995). A variation of MCP known as Local Convex Hulls (LOCOH) also has performed well (Getz and Wilmers, 2004; Getz et al., 2007; Downs, et al. 2012). LOCOH builds spatial polygons using one of three options: 1) k-1 nearest neighbors (k-method), 2) all points within a fixed radius *r* of a reference point (r-method) or 3) all points within radius *a* such that the summation of all distances from a reference point that are $\leq a$ (a-method) (Getz et al., 2007). Whereas KDE tends to expand estimated ranges into inaccessible areas, LOCOH connects points with straight lines, which can be more appropriate in habitats with hard boundaries (e.g., cliffs, rivers, etc.) when sampling is sufficient to demarcate the boundaries (Getz et al., 2007; Chirima and Owen-Smith, 2017).

In this study, we compared the performance of KDE (with two bandwidth parameters) and LOCOH using satellite telemetry data from New Zealand sea lions along the southeast coast of South Island, New Zealand. Model accuracy was assessed using cross-validation to identify the best fit. The objectives of this study were twofold: 1) To compare and evaluate the performance of three commonly used home range models applied to datasets of varying sample sizes and spatial distributions, and 2) To determine the most accurate model or combination of models for a semi-aquatic species using terrestrial and aquatic habitats.

Methods

Animals and Instrumentation

We tracked four female New Zealand sea lions (NZSL) along the coast of southeastern South Island (hereafter referred to as the Catlins Coast; Lat 46.5° S, Long 169.7° E), New Zealand during July-October, 2019 (Fig. 2.1). This area, which is located 95 km south of the Otago Peninsula, is composed of sandy beaches, rocky and reef intertidal, and estuaries (DOC, 2011). The continental shelf is ~30 km wide, and the 50 m isobath is < 5 km from the coast. After they were hunted to near extinction, female NZSL began reoccupying this area in the 1990s, but the current breeding population is small (~7 adult females) (Childerhouse and Gales, 1998; McNally, 2001)

We captured females (two had pups and all four were pregnant) onshore using a modified hoop net and then anesthetized them with 5% isoflurane using a field-portable vaporizer (Gales and Mattlin, 1998). Mean body mass was estimated to be 115 kg based on girth and standard length (Childerhouse et al., 2010). Satellite transmitters (SPOT-293, Wildlife Computers, Redmond, WA) mounted on nylon-backed neoprene were glued to fur on the head or back with quick-drying epoxy (Devcon® 10-minute, Danvers,

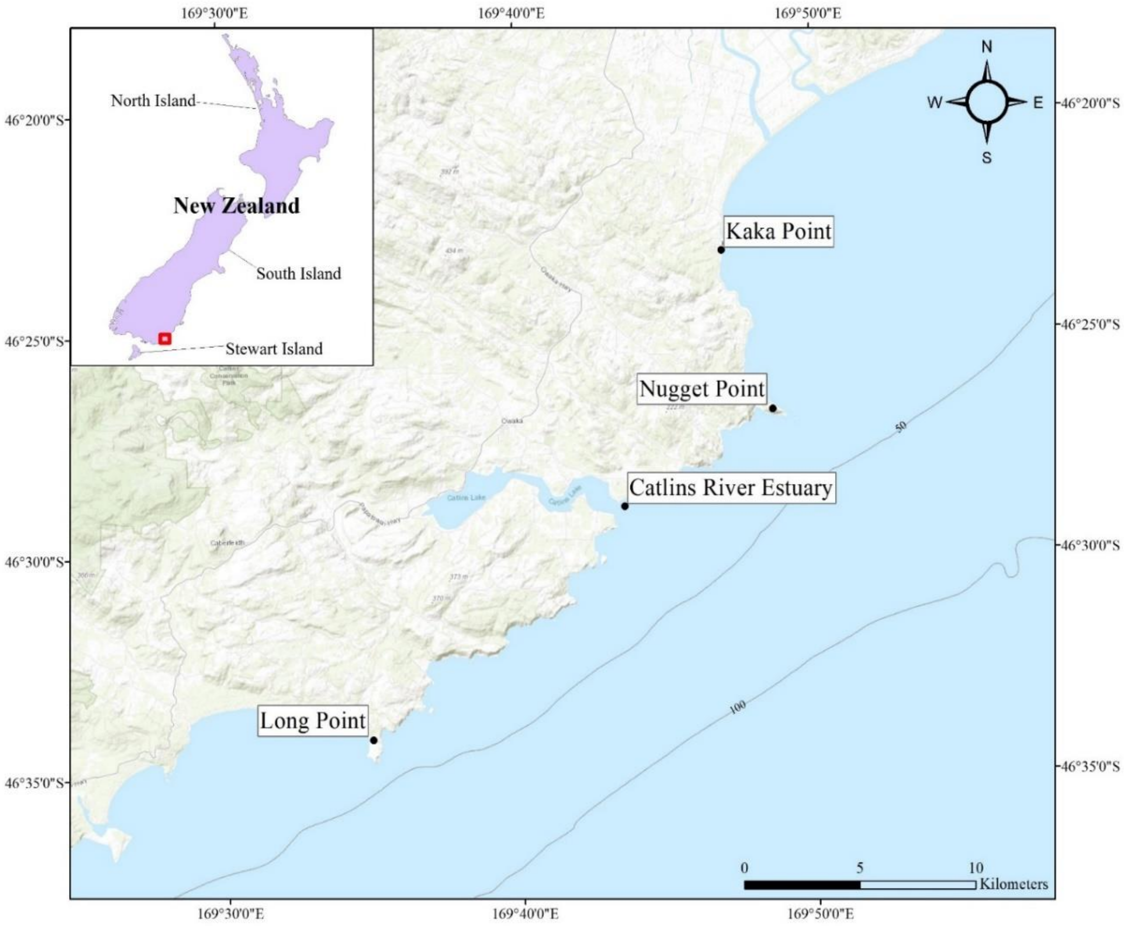

Figure 2.1. Study area in the southeast coast of South Island, New Zealand. Females were instrumented when they came ashore around the Catlins River Estuary, and most locations occurred between Kaka Point and Long Point.

MA). The duration of anesthesia was less than one hour, and recovery was rapid. The neoprene and satellite transmitters were shed 1-3 months later.

Sea lions were tracked using the Argos satellite system. The satellite transmitters were programmed to provide up to 250 locations at the surface in each of four, 6-hourly time-periods (dawn, day, dusk and night) for New Zealand time (GMT+12), which balanced the number of locations throughout the 24-hr period. A saltwater sensor on the transmitters prevented transmission while underwater to conserve battery power and maximize surface transmissions.

This study was conducted under a New Zealand Department of Conservation Permit to take Marine Mammals (Permit number: 70764-MAR). Animal protocols were approved by the University of Otago Animal Ethics Committee (AUP-18-91) and Texas A&M University Institutional Animal Care and Use Committee (AUP: IACUC 2017-0444).

Location Filters

Each animal location had an assigned Argos location class (LC), which is a measure of accuracy. The seven LC are ranked from best (most accurate) to worst as 3, 2, 1, 0, A, B, and Z, respectively. Locations were downloaded from the Argos portal and filtered to remove LC *Z* locations, which have no assigned accuracy. Four filtering methods were tested to remove potentially erroneous locations. Three filters retained either location classes 3 and 2 (LC32), LC 3, 2 and 1 (LC321), and LC 3, 2, 1 and A (LC321A). The fourth filter (hereafter referred to as SAL) used the R (R Core Team 2019) package *argosfilter* (Freitas, 2012) to remove erroneous locations based on speed (> 3 m s^{-1}), turning angle (< 15° and < 30° for locations 2,500 m and 5,000 m apart, respectively), and those onshore > 1 km from the coast in ArcMap (ESRI vers. 10.6). We selected the best filter based on highest retention of locations and used it in all home range models.

Home Range Models

We created probability density distributions for filtered locations using the R package *adehabitatHR* (Calenge, 2006) and code modified from Walter et al. (2015). Probability maps were created with 200 m resolution and 5,000 m extents. 95% and 50% home range contours were constructed using the R package *rhr* (Signer, 2019). We also examined home ranges by geographic area and sorted locations to compare model performance based on total, inshore, and offshore occurrence. Land locations and those ≤ 500 m offshore were classified as inshore while all others were considered offshore. This separation of inshore and offshore habitat was necessary because of the inaccuracy of Argos locations, which prevented us from distinguishing between those onshore and within 500 m of the shore. This resulted in a disproportionately large number of inshore locations, which caused a bias in estimated total home ranges.

We used KDE with two bandwidth parameters to create probability distributions: 1) KDE with reference bandwidth (RKDE) and 2) KDE with plug-in bandwidth (PKDE). These two variations of KDE use either a broad or narrow bandwidth selector (h) for generating probability densities. RKDE has been used in previous studies, but it can overestimate home ranges under certain circumstances (Seaman and Powell, 1996; Gitzen et al., 2006). PKDE has performed well in prior studies (Gitzen et al., 2006; Jones et al., 1996), but there have been problems with oversmoothing fine-scale home ranges (Millspaugh et al., 2006).

For the LOCOH, the a parameter for each animal was selected using the farthest measured distance between any two locations within the distribution (Getz et al., 2007).

LOCOH does not produce probability densities automatically, so we followed the method of Lichti and Swihart (2011) and converted isopleths into a probability grid by taking the contour density at a location and normalizing it for the entire grid.

Cross-Validation Comparisons

Model performance was evaluated using five-fold cross-validation. Probability density distributions were constructed for each model using 80% of the data for training and the remaining 20% for validation in each iteration. We tested model performance using 90% probability areas in congruence with previous model comparisons (Huck et al., 2008) and recommendation by Börger et al. (2006). The number of locations excluded from the 90% probability area were counted for each iteration. The expected exclusion value for each iteration was 10% of the test data (0.1 proportion) due to the use of 90% probability areas, which should include 90% of locations if accurate. Excluded proportions were then averaged by animal and habitat. We selected the most accurate model for each region based on performance compared to the expected 0.1 proportion. Models with values < 0.1 had oversmoothed, inflated distributions and included > 90% of test locations, while models with > 0.1 were overly restrictive and included < 90% of test locations. We used one-sample t-tests to compare model exclusion means to the expected 0.1 value and to compare model means between regions. One-way ANOVA tests were used to compare exclusion means, as well as 95% and 50% home range means among all models. 95% confidence intervals (CI) of exclusion means were used to further compare model performances. We used the Friedman test with a block on individual animals to compare mean home ranges for models when normality assumptions were not met. Values are presented as mean (± s.d.).

Results

Location Filters

The SAL filter retained 78% of animal locations for a mean of 795 locations for each sea lion (range 264-1,650; Fig. 2.2). LC321A retained the second highest percentage (58%) of locations. Both LC321 and LC32 filters retained < 50% of original locations. The LC filters removed a larger percentage of offshore locations because of their lower accuracy. Because the SAL filter retained a larger number of offshore locations, we used it in all subsequent home range models.

Total Home Range

The PKDE ($\bar{x}$ = 0.072, CI = 0.058-0.086) and RKDE ($\bar{x}$ = 0.034, CI = 0.00-0.071) probability distribution cross-validation results both deviated significantly from the expected 0.1 exclusion value when applied to entire ranges (One-sample t-tests $p < 0.05$; Fig. 2.3). LOCOH did not differ significantly from the expected value because of a wider 95% CI range ($\bar{x}$ = 0.067, CI = 0.00-0.143; One-sample t-test $p > 0.05$). Mean location exclusion proportions did not differ significantly among models (One-way ANOVA $p > 0.05$).

PKDE produced the smallest mean total home ranges for both 95% and 50% volume contours, while RKDE produced the largest (Table 2.1). Both RKDE isopleth areas were significantly larger than those of PKDE and LOCOH (Fig. 2.4; Friedman test $p < 0.05$). RKDE 95% and 50% mean home ranges (95% = 363 ± 246 km^2; 50% = 81 ±

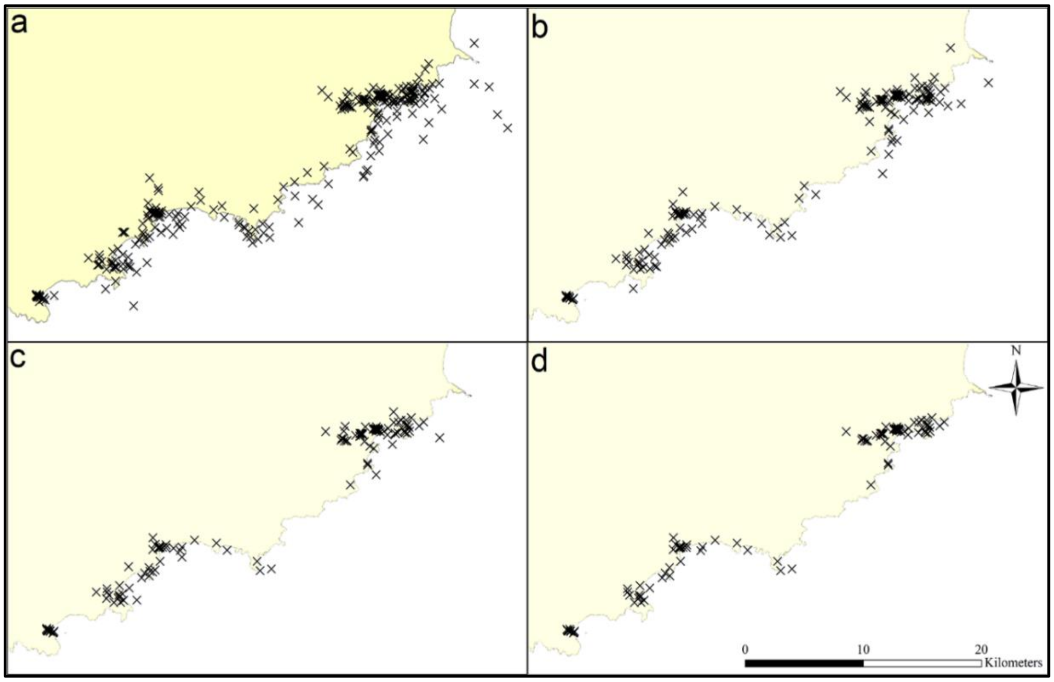

Figure 2.2. Location filtering results for one female (SL2): a) SAL filter retained the highest percentage of locations and the most offshore locations, b) LC321A filter retained inshore locations but removed more offshore locations than did SAL, c) LC321 and d) LC32 filters both removed a majority of locations and kept almost exclusively inshore locations with smaller error estimates.

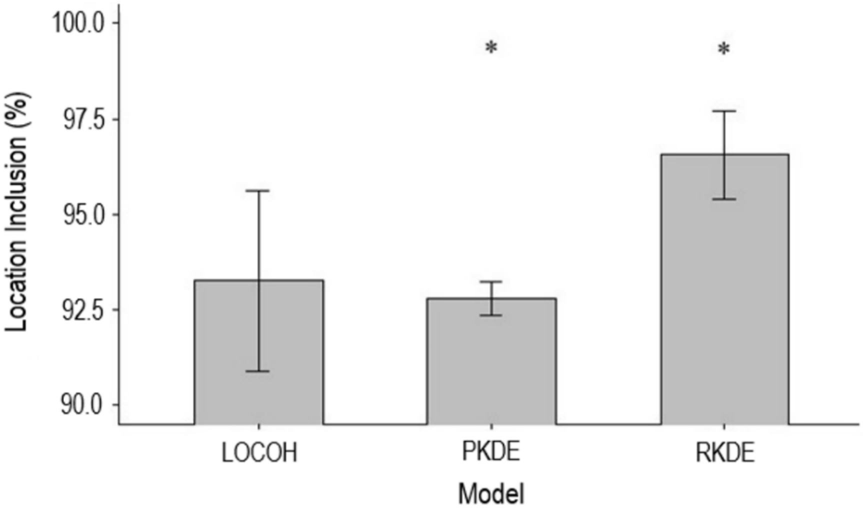

Figure 2.3. Results of model cross-validation as mean (± s.e.) percentage inclusion of locations within the training 90% probability areas. The three models included > 90% of test locations for estimated total home ranges for expanded probability densities (exclusion < 0.1). Asterisks denote significant differences of means from the expected 90% inclusion value (α = 0.05).

Table 2.1. Mean (± s.d.) total 95% and 50% home ranges (km2) based on LOCOH, PKDE, and RKDE. Superscript letters denote Friedman test statistical differences ($\alpha = 0.05$) between models within ranges.

	95% Home Ranges			50% Home Ranges		
Animal	LOCOH	PKDE	RKDE	LOCOH	PKDE	RKDE
SL1	70	42	159	7	6	18
SL2	109	97	663	14	14	156
SL3	102	99	467	14	16	113
SL4	82	69	164	11	9	35
Mean	**91 (18)^a**	**77 (27)^a**	**363 (246)^b**	**12 (3)^a**	**11 (5)^a**	**81 (65)^b**

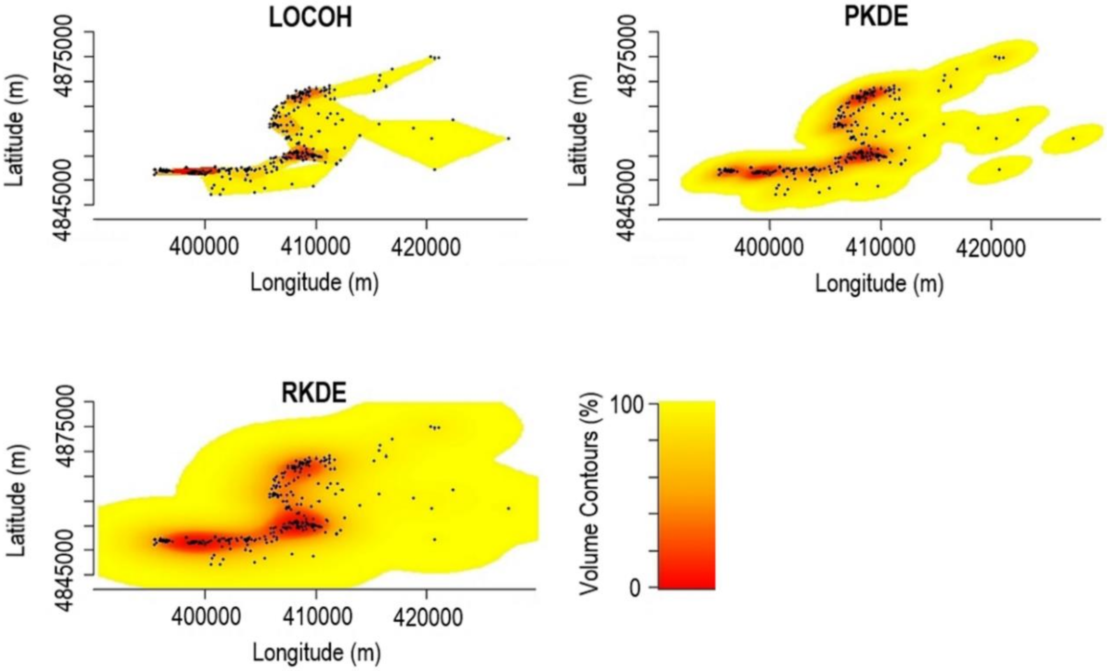

Figure 2.4. Total home range volume contours for female SL3 using local convex hulls (LOCOH), plug-in bandwidth kernel density estimation (PKDE), and reference bandwidth kernel density estimation (RKDE).

65 km^2) were 5-fold and 7-fold larger than those of PKDE (95% = 77 ± 27 km^2; 50% = 11 ± 5 km^2), respectively. LOCOH 95% mean home range (91 ± 18 km^2) was 1.2-fold larger than that of PKDE, while the 50% area (12 ± 3 km^2) was nearly identical.

The 95% total home ranges decreased as individual sample sizes increased for the three models (Fig. 2.5). The RKDE 95% home range (663 km^2) with the smallest sample size was 4-fold larger than that (159 km^2) with the largest sample size. Over the same range of sample sizes, the PKDE (97-70 km^2) and LOCOH home range differences (109-82 km^2) showed < 30% variation.

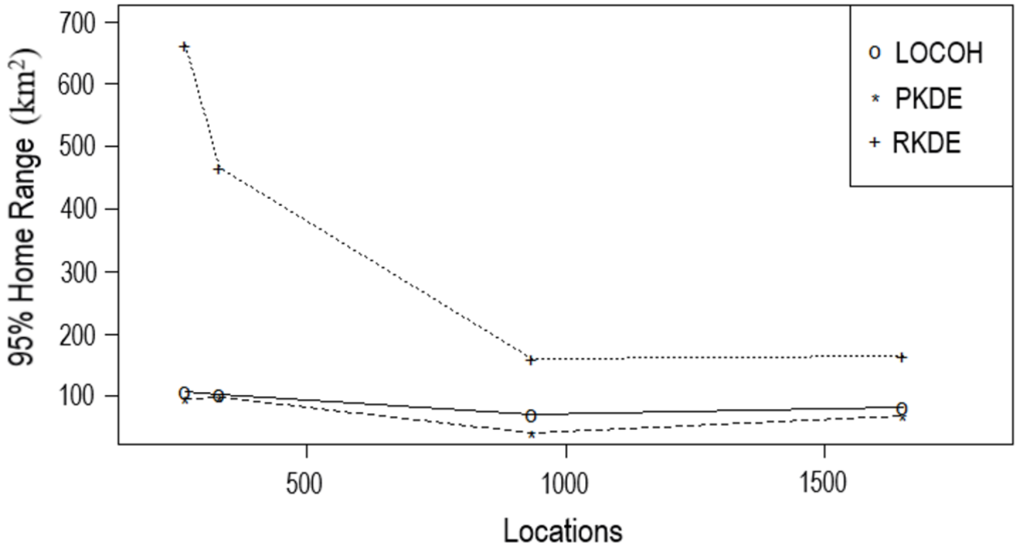

Figure 2.5. 95% total home ranges for the three models as a function of sample size. LOCOH and PKDE models produced stable areas across all sample sizes, while RKDE home ranges increased with decreasing sample size.

Inshore and Offshore Home Ranges

The SAL filter retained a mean of 561 inshore locations (range 215-1,118) for the four females. Inshore LOCOH performance did not differ significantly from the expected 0.1 ($\overline{x}$ = 0.073, CI = 0.0-0.163; One-sample t-test $p > 0.05$; Fig. 2.6). Both PKDE and RKDE means were significantly lower than 0.1 (PKDE: $\overline{x}$ = 0.046, CI = 0.024-0.068; RKDE: $\overline{x}$ = 0.025, CI = 0.0-0.06; One-sample t-tests $p < 0.05$). Exclusion means did not differ significantly among models (ANOVA $p > 0.05$), but 95% and 50% inshore home ranges were significantly different (Friedman $p < 0.05$). The mean LOCOH 95% home range (32 ± 9 km^2) was 10% of that for RKDE (317 ± 253 km^2; Table 2.2). The 50% home ranges showed a similar reduction (LOCOH $\overline{x}$ = 6 ± 2 km^2; RKDE $\overline{x}$ = 75 ± 64 km^2). PKDE mean 95% and 50% home ranges were not significantly different from LOCOH (95% = 41 ± 14 km^2; 50% = 6 ± 3 km^2; Friedman $p > 0.05$).

The SAL filter retained a mean of 234 offshore locations (range 49-532) for the four females. Offshore PKDE and LOCOH cross-validation means were not statistically different from 0.1 (PKDE: $\overline{x}$ = 0.086, CI = 0.061-0.112; LOCOH $\overline{x}$ = 0.142, CI = 0.013-0.271; One-sample t-tests $p > 0.05$; Fig. 2.6). RKDE was significantly below the expected 0.1 exclusion mean ($\overline{x}$ = 0.036, C.I. = 0.0-0.077; One-sample t-test $p < 0.05$). LOCOH and RKDE offshore home range cross-validation means were significantly different (One-way ANOVA $p < 0.05$). The PKDE exclusion mean was not significantly different from the other two models (One-way ANOVA $p > 0.05$). 95% home ranges differed significantly among RKDE and the other two models (Friedman $p < 0.05$), but

50% home ranges did not (One-way ANOVA $p > 0.05$). LOCOH had the smallest mean 95% and 50% home range areas (95% = 77 ± 26 km^2, 50% = 15 ± 11 km^2) while PKDE home ranges were ~10% larger (95% = 84 ± 44 km^2, 50% = 18 ± 11 km^2; Table 2.2). RKDE offshore home ranges means were ~6-fold larger (95% = 436 ± 304 km^2, 50% = 103 ± 103 km^2) than predicted by the other two models.

PKDE cross-validation exclusion means were statistically different by habitat (T-test $p < 0.05$). Offshore means were higher and closer to the expected 0.1 value than were inshore means. Neither LOCOH nor RKDE exclusion means differed by habitat (T-tests $p > 0.05$).

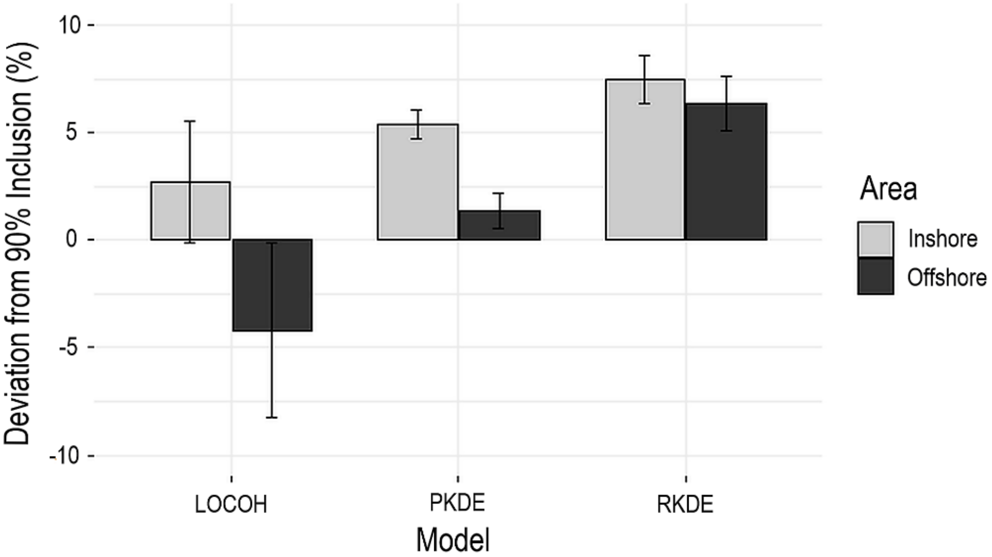

Figure 2.6. Cross-validation performances of models for inshore (gray) and offshore (dark) habitats as mean deviation (± s.e.) from the expected 90% inclusion. The most accurate model for each habitat approached 0% deviation. LOCOH performed the best for inshore habitat while PKDE performed best for offshore habitat.

Table 2.2. Mean (± s.d.) 95% and 50% home ranges (km2) for inshore and offshore habitats. Superscript letters denote Friedman and one-way ANOVA tests statistical differences (α = 0.05) between models within ranges and areas.

		95% Home Ranges			50% Home Ranges		
Animal	Area	LOCOH	PKDE	RKDE	LOCOH	PKDE	RKDE
SL1	Inshore	32	23	119	3	3	16
	Offshore	74	37	198	5	7	23
SL2	Inshore	40	56	365	7	8	100
	Offshore	62	133	521	25	23	100
SL3	Inshore	19	46	656	8	9	153
	Offshore	114	106	831	24	31	249
SL4	Inshore	38	37	128	5	5	31
	Offshore	56	59	195	7	9	41
Mean	Inshore	**32 (9)^{a}**	**41 (14)^{a}**	**317 (253)^{b}**	**6 (2)^{a}**	**6 (3)^{a}**	**75 (64)^{b}**
	Offshore	**77 (26)^{a}**	**84 (44)^{a}**	**436 (304)^{b}**	**15 (11)^{a}**	**18 (11)^{a}**	**103 (103)^{a}**

Discussion

Total home ranges were most accurately modeled by LOCOH. This method did not significantly deviate from the expected 0.1 exclusion value during cross-validation evaluation. However, LOCOH performance varied among females, as evidenced by the large 95% CI range compared to PKDE and RKDE models. LOCOH produced 90% probability areas that encompassed ~97% of test locations for SL1 and SL4, possibly because of boundaries around highly clustered distributions adjacent the Catlins River Estuary (Fig. 2.1). Total home ranges using all locations (i.e., inshore and offshore) created sampling bias. LOCOH 50% total home ranges were primarily onshore even though females spent ~57% of time at sea. The disproportionately large percentage of onshore locations created total home ranges centered around these areas, which likely did not reflect the actual UD of females. Because of this bias, we modeled inshore and offshore home ranges separately.

The most accurate inshore and offshore home range estimates for female sea lions used LOCOH and PKDE models, respectively (Fig. 2.7). The LOCOH model, which was the most accurate for the inshore home range, consistently excluded unused areas. Inshore locations were characterized by clusters separated by gaps. Cliffs and rocky shorelines presented barriers to inshore movement, which interspersed with high-use sandy beaches and estuaries. The distribution was restricted by the shore to the west and deeper, offshore areas to the east. These geographic boundaries to inshore home range were most appropriately handled by the LOCOH model. KDE methods created probability distributions that extended beyond habitat boundaries (Getz and Wilmers, 2004). This expansion led to lower exclusion values for both PKDE and RKDE inshore home ranges. Alternatively, LOCOH used outlying locations to create volume boundaries, modeling gaps and barriers in the distribution more accurately (Fig. 2.7; Lichti and Swihart, 2011). LOCOH outperformed fixed KDE for urban badger (*Meles meles*) home range modeling based on suitable habitat inclusion and avoided habitat exclusion (Huck et al., 2008). For locations constrained spatially by complex environments, LOCOH home range models may perform more accurately than traditional KDE methods.

PKDE probability distributions were consistently the most accurate with the smallest variation among the three models for offshore distributions. LOCOH

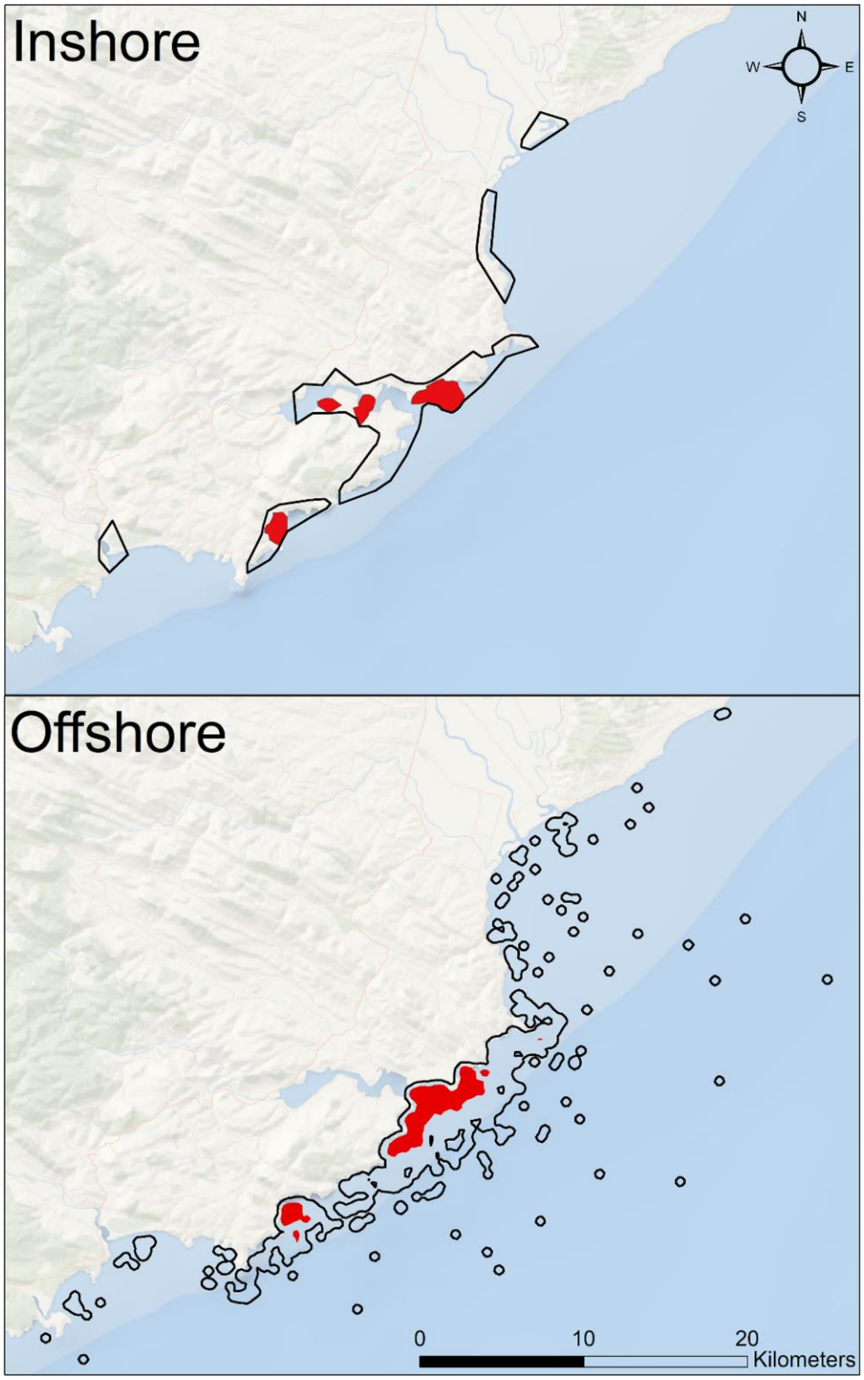

Figure 2.7. Total 95% (black lines) and 50% (red polygons) home ranges for inshore habitat using LOCOH and offshore habitat using PKDE.

underestimated home ranges on average and had a wide exclusion CI. LOCOH excluded both unused and used areas (type II error) in previous studies, indicating that the restrictive home ranges can be problematic (Pebsworth et al., 2012). In environments with less restrictive barriers to movement, kernel density models may more accurately reflect distributions. The application of LOCOH to home ranges of fully aquatic species may not best represent true distributions and could lead to unrealistic home range estimates (Davis et al. 2014). While both LOCOH and PKDE exclusion means were close to the expected value in this study, the consistent precision of PKDE made it a better choice for offshore home ranges. Our results agree with Lichti and Swihart (2011) that the PKDE bandwidth selector handles distributions with multiple centers of activity and linking corridors more accurately than other estimators. Fragmentation of offshore home ranges modeled by PKDE implied the presence of undersmoothing (Fig. 2.7; Hemson et al., 2005). However, the cross-validation results support this method of offshore home range modeling over the other two models.

RKDE home ranges were larger than the other two methods for both inshore and offshore habitats. This method overestimated areas and included unused portions of ranges (type I error). The difference in cross-validation performance between PKDE and RKDE indicated the importance of smoothing parameters for KDE methods. Bandwidth selection directly influenced the resulting probability distributions, and factors such as distribution and sample size should be evaluated during the selection of smoothing parameter (Gitzen et al., 2006). Reference bandwidth selection consistently performed poorly and produced overestimated home ranges compared to other methods (Walter et al., 2015; Gitzen et al., 2006; Reinecke et al., 2014; Kie et al., 2010). However, *ad hoc* techniques to select modified reference bandwidth values have been applied in previous home range studies (Bowman, 1985; Pebsworth et al., 2012). Studies employing kernel home range methods should consider the underlying UD and study goals in choice of smoothing parameter. Too small of a bandwidth can create inaccurate features in the probability density estimate and large bandwidths may lose detail and overestimate home ranges (Jones et al., 1996; Gitzen et al., 2006). The bandwidth selection likely accounted for the poor performance and larger home ranges of RKDE compared to the other two models in this study, making it less desirable (Lichti and Swihart, 2011; Seaman and Powell, 1996).

Home ranges varied among models and individuals within our study. Sample size can affect home ranges in KDE and LOCOH models, as the precision of both increase with sample size (Seaman et al., 1999; Boyle et al., 2009; Lichti and Swihart, 2011; Gitzen et al., 2006). Although the true home ranges may differ among individual sea lions, the difference is likely less than the RKDE model implied. Both PKDE and LOCOH 95% home ranges decreased with increased sample sizes, but much less severely than did RKDE. Between 30-100 locations have been recommended to reach a home range asymptote (Seaman et al., 1999; Girard et al., 2002). Our smallest dataset was within that range, and the rest were all > 100 locations, which should reflect the true UD and limit sample size bias.

Location filtration methods influence home ranges as models rely on the number of locations for estimation of the underlying UD. Inclusion of poor location estimates will negatively affect home range models through inflation of error. Marine mammal tracking studies regularly collect high percentages of low-quality locations (i.e., LC < 1), ranging as high as 90% of entire datasets (McConnell and Fedak, 1996). This makes LC filters undesirable as they remove large percentages of locations. The resulting home ranges are biased toward areas of best transmitter signal receptions. Location filters incorporating movement parameters have been used as an alternative to LC filters (McConnell, Chambers & Fedak, 1992; Keating, 1994). The SAL filter used in this study removed biologically unfeasible locations but retained large percentages of locations. This was a benefit to offshore home ranges and allowed sufficient sample sizes to estimate the UD. Studies with large location error estimates should filter data using species-specific parameters of movement to retain enough locations for analysis.

The acquisition of locations from satellites was not spatially uniform, with 2-fold more inshore than offshore locations. This resulted primarily because the inaccuracy of Argos locations prevented us from distinguishing between locations onshore and those < 500 m from shore. This inshore bias would have reduced total home ranges and the identification of core areas. To avoid any sampling bias, we divided the home range analysis into inshore and offshore habitats. The separation of inshore and offshore habitats and habitat-specific home range modelling has not been attempted before with sea lions or fur seals. Baylis et al. (2015) separated inshore and offshore home ranges for southern sea lions (*Otaria flavescens*) in the Falkland Islands, but individuals were assigned solely to one group and the same bandwidth selection was applied for both habitats. Future home range studies should consider modeling home ranges with a combination of models to achieve the overall greatest accuracy. Choice of transmitter attachment location and transmission schedule also are important and should be evaluated to ensure consistent sampling on species with transmission barriers or limitations (e.g., water, canopy, etc.).

Movement models (e.g. movement-based KDE, Brownian bridges, Markov chain Monte Carlo, etc.) are alternatives to location-based home range models and incorporate the correlation of locations (Buchin et al., 2015; Cumming et al., 2012; Walter et al., 2015; Walter et al., 2011; Christ et al., 2008; Fleming et al., 2015). Incorporation of movement processes allows researchers to incorporate the path of a mobile animal over time (Horne et al., 2007). Future applications of home range movement models to Otariidae are possible for offshore locations collected with global positioning systems (GPS) because of their higher acquisition rate and accuracy of locations for tracking movements and spatial use at sea.

Offshore home ranges for this study were considerably smaller than those for NZSL in the Auckland Islands (Table 2.3). While PKDE can undersmooth home ranges (Walter et al., 2011), this is not likely the primary explanation. PKDE cross-validation results were consistently accurate and balanced the inclusion of high-density locations with the exclusion of unused areas (i.e., minimized type I and type II errors). Auge et al. (2011) observed reduced home ranges for South Island NZSL compared to more southern populations. They used a single smoothing value of one kilometer for home range modeling, which could partly explain the home range differences from our study, and identified the group as coastal foragers with reduced home ranges. Foraging strategy and habitat availability have influenced home ranges for other marine mammals. Sea otter (*Enhydra lutris nereis*) home ranges were limited by bathymetry and constrained to coastal waters around Monterey Bay, California, resulting in mean home ranges of ~10 km^2 (Tarjan and Tinker, 2016). NZSL can exploit deeper waters to forage, but the high availability of prey in shallow, coastal waters may be sufficient to meet energetic demands. The restricted offshore home ranges on South Island may be a likely indicator of prey availability and habitat accessibility differences compared to subantarctic colonies and not an artifact of smoothing parameter choice.

Various home range models have been used in studies of Otariidae (Table 2.3). Fixed KDE methods have been used, but the choice of smoothing parameters rarely have been evaluated or justified. The results of our study indicate that the KDE bandwidth selection can have large effects on resulting home ranges for Otariidae. The studies that used least squares cross-validation bandwidth selection may have undersmoothed their distributions and produced smaller home ranges (Horne and Garton, 2006). Comparisons among studies need to consider methodological differences and their effects. Home ranges can differ based on smoothing technique rather than actual distribution differences. We recommend comparing KDE smoothing parameter errors through cross-validation during the home range model selection process to ensure accuracy of results.

The use of minimum convex polygons (MCP) for home range modeling should be abandoned in favor of more accurate models. MCP can overestimate home ranges due

Table 2.3. Otariidae home range studies, including location, age category and sex of animals, tagging method, model selection, home range isopleths, and ranges.

Species	Location	Age/Sex Class	Field Method	Model	Home Range (%)	Area (km^2)	Source
Neophoca cinerea	Kangaroo Island, AU	Adult Females	Satellite transmitters	Fixed KD LSCV[1]	75	596	Fowler et al. 2007[5]
		Juvenile Mix				353	
		Pup Mix				281	
Eumetopias jubatus	Prince William Sound and Resurrection Bay, AK, US	Juvenile Mix	Satellite transmitters	Fixed KD CV[2]	95	852	Bishop et al. 2018[6]
					Individually calculated core	167	
	Hazy and Forester Islands, AK, US	Adult Females		MCP	90	183	Rehberg et al. 2009[6]
Phocarctos hookeri	Enderby Island, Auckland Islands, NZ	Juvenile Females	Satellite transmitters	Fixed KD ad hoc	95	5836	Leung et al. 2012[5]
					50	523	
		Juvenile Males			95	12149	
					50	1742	
		Adult Females	Satellite transmitters	Fixed KD LSCV	65	643	Chilvers et al. 2005[6]
					50	378	
	Dundas Island, Auckland Islands, NZ	Adult Females	Satellite transmitters	Fixed KD LSCV	65	1213	Chilvers et al. 2011[6]
					50	691	

Table 2.3. Continued

Species	Location	Age/Sex Class	Field Method	Model	Home Range (%)	Area (km^2)	Source
	Otago Peninsula, South Island, NZ	Adult Females	Satellite transmitters	Fixed KD 1 km smoothing	100	257	Auge et al. 2011[6]
					65	47	
	Catlins, South Island, NZ	Adult Females	Satellite transmitters	Fixed KD plug-in	Offshore 95	84	This study[6]
					Offshore 50	18	
				a-LOCOH	Inshore 95	32	
					Inshore 50	6	
Otaria flavescens	Isla de Lobos, UY	Adult Females	Satellite transmitters	MCP[3]	100	10150	Rodriguez et al. 2013[5]
				KD 70% reference	95	12878	
					50	3121	
		Juvenile Females		MCP	100	9362	
				KD 70% reference	95	11531	
					50	2892	
	Northern and central Patagonia, AR	Adult Females	Satellite transmitters	MCP	100	6584	Campagna et al. 2001[6]
		Adult Males				11732	
	Falkland Islands, AR	Adult Females	Satellite/GPS transmitters	Fixed KD ad hoc	Offshore 90	7400[4]	Baylis et al. 2015[5]
					Offshore 50	1500	
					Inshore 90	278	
					Inshore 50	50	
Zalophus californianus	San Miguel Island, CA, US	Juvenile Mix	Satellite transmitters	MCP	100	6521	Orr et al. 2012[5]
		Yearling Mix				10130	

Table 2.3. Continued

Species	Location	Age/Sex Class	Field Method	Model	Home Range (%)	Area (km^2)	Source
		Pup Mix				8610	
	Monterey, CA, US	Adult Males	Satellite transmitters	MCP	100	832	Weise et al. 2006[5]
Callorhinus ursinus	Probilof Islands, AK, US	Adult Females	Satellite transmitters	Fixed KD	95	115572	Robson et al. 2004[5]
Arctocephalus pusillus doriferus	Kanowna Island, AU	Adult Females	GPS loggers	KD	50	49534	Hoskins et al. 2017[5]

[1] Least squares cross validation

[2] Cross-validation

[3] Minimum convex polygon

[4] Estimated from Fig. 1

[5] Home range estimates calculated per group

[6] Home range estimates calculated per individual

to the simplistic connection of outlying locations to form polygon borders and bias associated with sample size (Burgman and Fox, 2003). Davis et al. (2014) indicated this overestimation when comparing home ranges of Heaviside's dolphins (*Cephalorhynchus heavisidii*) modeled by MCP and LOCOH. MCP 100% home ranges were 1.5-fold larger than LOCOH estimates and overlapped impassable terrestrial habitats. MCP ignores the UD structure and should be used only as an estimate of maximum range. The availability, accuracy and relative ease of newer home range models (see Tetreault and Franke, 2017 and Walter et al., 2011 for more detailed overview) make MCP an undesirable choice in the future.

Our results indicate that home range model selection varied by habitat for NZSL. LOCOH modeled the fragmented landscape of inshore habitats more accurately than KDE methods, while PKDE fit offshore distributions with greatest accuracy. Combining LOCOH and PKDE created a more accurate representation of spatial use than did total home ranges for this semi-aquatic species. Previous studies have largely ignored inshore locations in favor of aquatic foraging home ranges and have modeled home ranges using inconsistent methods. Dividing home ranges into habitats and verifying model selection will better represent spatial use.

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CHAPTER III

HOME RANGES, FORAGING BEHAVIOR, AND ENERGETICS OF NEW ZEALAND SEA LIONS ALONG THE CATLINS COAST

Introduction

New Zealand sea lions (hereafter referred to as NZSL; *Phocarctos hookeri*) primarily breed (98% of pup production) on the subantarctic Auckland and Campbell Islands, where commercial sealing was conducted during the 19th century (Fig. 1.1; Robertson and Chilvers, 2011; Chilvers, 2018b). As a result, NZSL are one of the rarest of the six extant sea lion species, with an estimated population of ~12,000 (Chilvers and Meyer, 2017) and an IUCN classification of Endangered (Chilvers, 2015). The population of NZSL on South Island became extinct, and only a small number remained on Stewart Island by the time Europeans arrived in the mid-18th century (Smith, 1989). Recolonization of South Island began when male NZSL returned to the southeastern coast in the mid-20th century (Wilson, 1979; Hawke, 1986). Small breeding colonies have reoccupied Stewart Island, the Otago Peninsula, and along the Catlins Coast. The first female to pup on the Otago Peninsula in 1994 was originally tagged in the Auckland Islands, so expanding populations on South Island may result from local pup production and immigration from subantarctic populations (McConkey et al., 2002; Robertson and Chilvers 2011). The first pup along the Catlins Coast was observed in 2006 (McNally, 2001; Auge, 2010). Seven pups were produced in this area during the 2019 breeding season.

As with other Otariidae (sea lions and fur seals), NZSL are income breeders, which give birth on land and feed throughout lactation with alternating periods of nursing on shore and feeding at sea (Auge et al., 2011b; Chilvers et al., 2006). Females give birth (birth mass ~10 kg) from December-January followed by a perinatal period of 8-9 days (Chilvers et al. 2007) when the female remains on shore nursing the pup, establishes female-pup recognition (Trillmich 1981), and copulates. The female then goes to sea and feeds for 0.5-2.8 days, which varies geographically and seasonally (Chilvers et al. 2005; Auge et al. 2011b; Chilvers et al. 2018a). While the female is foraging, lipid-rich milk (21%; Riet-Sapriza et al. 2012) is produced and stored in the mammary glands. The female then returns to shore to nurse the pup for 0.6-1.3 days until weaning occurs ~9 months later (Chilvers et al., 2007). During the period of pup dependency, the female may make over 90 foraging trips.

Females on the Auckland Islands make deep (mean maximum depth 125 m), long (mean duration 3.5 min) dives during extended (1.7-2.8 days) foraging trips (Gales and Mattlin, 1997; Costa and Gales, 2000; Crocker et al., 2001; Chilvers et al., 2006; Chilvers et al., 2005). Swim speed during dives is ~2 m s^{-1} and varies with depth and dive phase (Crocker et al., 2001). These deep, long dives and extended foraging trips indicate low-density prey that are sparsely distributed, which may require dives that are longer than their aerobic dive limit (ADL; Costa and Gales, 2000; Chilvers et al., 2006; Auge et al., 2011; Chilvers et al., 2020). In contrast, females that forage around the Otago Peninsula make short (1.8 min), shallow (20 m) dives during short (0.5 days) foraging trips, which indicates accessible and abundant prey compared to the Auckland Islands (Auge et al., 2011a; Auge et al., 2011b).

Female NZSL in the Auckland Islands have large home ranges (65% range = 643-1213 km^2), and they may travel long distances (> 100 km) from the breeding colony (Chilvers et al., 2005; Chilvers et al., 2011). Females on Stewart Island have smaller home ranges (65% range = 440 km^2), which are 64% of those around the Auckland Islands. Maximum distance from shore (~28 km) is < 30% of that for females in the Auckland Islands (Chilvers et al. 2018a). Finally, females on the Otago Peninsula have the smallest home ranges (65% range = 47 km^2) and travel the shortest maximum distance (~5 km) from the colony when foraging (Auge et al., 2011b).

The home ranges and diving behavior of NZSL along the Catlins Coast have not been studied, primarily because this is a new breeding colony. The objective of this study was to track the movements and record the diving behavior of females to identify home ranges, characterize diving behavior, and estimate energy expenditure. In addition, inshore habitat-associations were assessed to identify suitable areas for re-colonization, though full reoccupation of all historical habitat is still many decades away.

Methods

Animals and Instrumentation

We captured and instrumented four female New Zealand sea lions along the southeastern coast (hereafter referred to as the Catlins Coast; Lat 46.5 S, Long 169.7 E) of South Island, New Zealand during July 2019 (Fig. 2.1). Two females had dependent pups, and all four females were pregnant at the time of capture. Animals were captured using a modified hoop net and anesthetized with 5% isoflurane using a field-portable vaporizer (Gales and Mattlin, 1998). Mean body mass was estimated to be 115 kg based on girth and standard length (Childerhouse et al., 2010). We glued a neoprene-mounted satellite transmitter (SPOT-293, Wildlife Computers, Redmond WA) and very high frequency (VHF) radio transmitter (R1930, Advanced Telemetry Systems, Isanti MN) to the fur on the back of each sea lion using quick-drying epoxy (Devcon® 10-minute, Danvers, MA). The duration of anesthesia was less than an hour, and recovery was rapid. The transmitters were shed 1-3 months later.

Two females were instrumented additionally with a video and data recorder (VDR; Pisces Design, La Jolla CA). However, one VDR was lost at sea and data were not recovered. The VDR and battery were mounted on a piece of neoprene, which was glued to the fur behind the head (Fig. 3.1d). The VDR (12 cm long, 5.7 cm wide, and 4.6 cm high; mass 60 g) was encased in polyurethane and depth-rated to 2000 m (Fig. 3.1a, b, c). It had a low-light sensitive, monochrome video camera, a 3-axis accelerometer and magnetometer, and sensors for depth, speed, temperature, and sound (50 Hz to 16 KHz). Sensor data were recorded at 1 Hz, except speed (4 Hz) and the 3-axis accelerometer (16 Hz). Data from the 3-axis accelerometer and magnetometer were used to determine compass heading, pitch, and roll. Data were recorded in New Zealand Standard Time (GMT +12). We relocated animals when they returned to the beach using VHF radio transmitters and remotely released the VDR two days after initial capture.

This study was conducted under a New Zealand Department of Conservation Permit to take Marine Mammals (Permit number: 70764-MAR). Animal research protocols were approved by the University of Otago Animal Ethics Committee (AUP-18-91) and Texas A&M University Institutional Animal Care and Use Committee (AUP: IACUC 2017-0444).

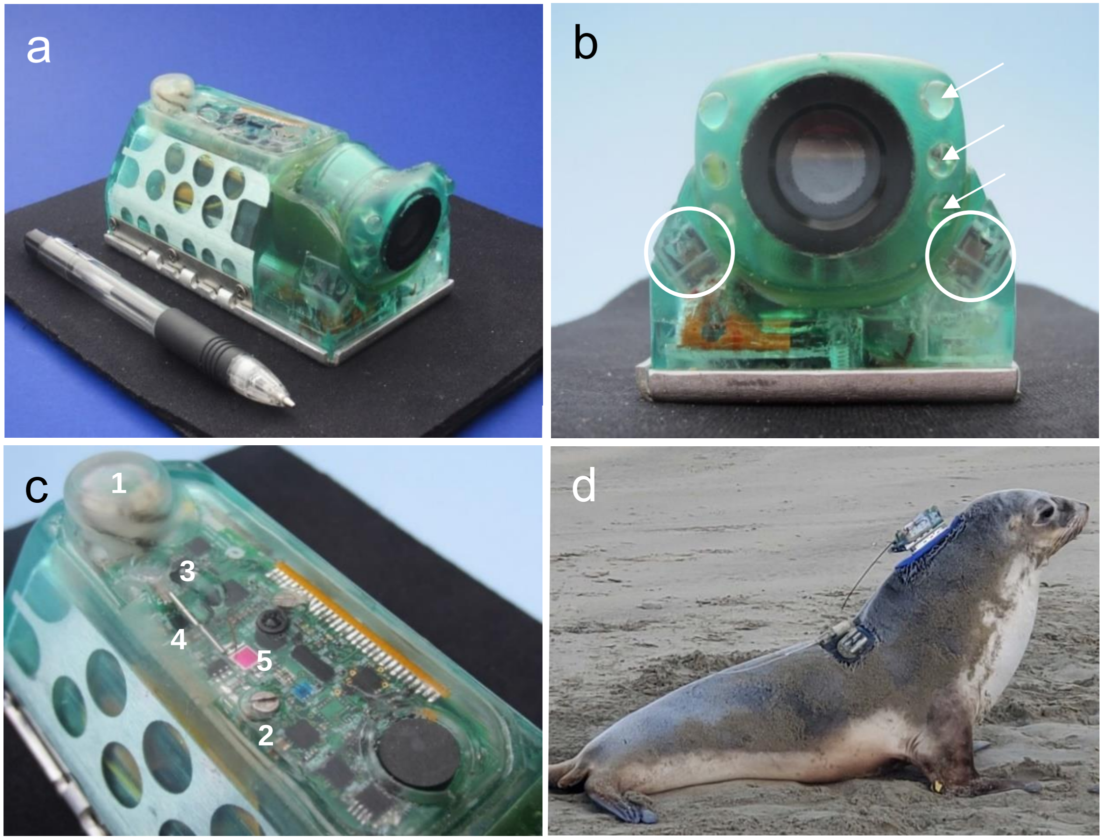

Figure 3.1. Video and data recorder (VDR) showing: (a) size, (b) six near-infrared LEDs (three on either side, arrows) for illumination and two speed sensors (circles), (c) GPS (1), seawater sensor (2), pressure sensor (3), temperature thermistor (4), light sensor (5), and (d) attachment of the VDR, satellite transmitter, and VHF radio transmitter to a female New Zealand sea lion.

At-Sea Movements

We used the Argos system to track sea lions using satellite telemetry. Argos assigns a location class (LC; 3, 2, 1, 0, A, B, and Z) to each geolocation indicating accuracy, with LC3 being the most accurate and LCZ with no accuracy indicated (i.e., invalid). Class *Z* locations were eliminated from the data, and the remaining locations were filtered using the *argosfilter* algorithm adapted from Auge et al. (2011) in R (Freitas, 2008, 2012). Exclusion criteria were based on speed (> 3 m s^{-1}) and turning angle (< 15° and < 30° for locations > 2,500 m and > 5,000 m apart, respectively). The remaining locations were imported into ArcMap (ESRI vers. 10.6, Redlands CA), and inland locations greater than one km from shore were removed. Locations were mapped using the Universal Transverse Mercator Zone 59 South (UTM 59S) coordinate system.

Foraging trip departure and return times were based on Argos location prior to and after foraging trips. One foraging cycle (T_{total}) was defined as the sum of the time at sea (T_{sea}) and subsequent time ashore (T_{land}) until the next trip. All cycles with T_{sea} durations < 2 h were removed from the analysis (Auge et al., 2011b). We calculated the surface transit distance for each foraging trip using the measured straight-line distance between at-sea locations.

Home Ranges

All locations were divided into inshore and offshore groups to calculate home ranges (see Chap. 2). Locations on land < 1 km from shore or at sea within 500 m of the shoreline were classified as inshore, while all other points were considered offshore. This division was necessary because the majority of locations were collected inshore, which may have biased estimates of home range. We performed cross-validation for multiple home range models and found that the local convex hull (a-LOCOH; Getz et al., 2007) method was the most accurate for inshore areas, while kernel density estimation with plug-in bandwidth selection (*h*) (PKDE; Walter et al., 2011) provided the best accuracy for offshore ranges (see Chap. 2). We calculated the 95% home range and 50% core range (200 x 200 m resolution and 5000 m extent) for each sea lion using R (RStudio Team, 2019; vers. 1.2.5033) package *rhr* (Signer, 2019).

Shoreline habitat composition was identified within inshore 95% and 50% home ranges for all animals using a coastal habitat map (DOC, 2011). The percentage compositions of 95% and 50% home range shorelines were calculated by measuring the length (km) of each habitat relative to entire shoreline distance.

Dive Analysis

Dives ≥ 3 m in depth were identified from the VDR time-and-depth profile for two foraging trips using a custom MATLAB (MathWorks vers. 8.0 R2012b) program (Fig. 3.2a; Auge et al., 2011a). Descent, bottom, ascent, and surface phases were identified for each dive. The bottom phase was defined as the continuous duration spent at depths ≥ 75% of maximum dive depth, as opposed to an 85% threshold which had been used in previous dive studies (Gales and Mattlin, 1997; Chilvers et al., 2006; Auge et al., 2011a). Descent and ascent phases were defined as the intervals between surface and bottom phases, and surface interval was the duration at depths < 3 m until the animal began the next dive.

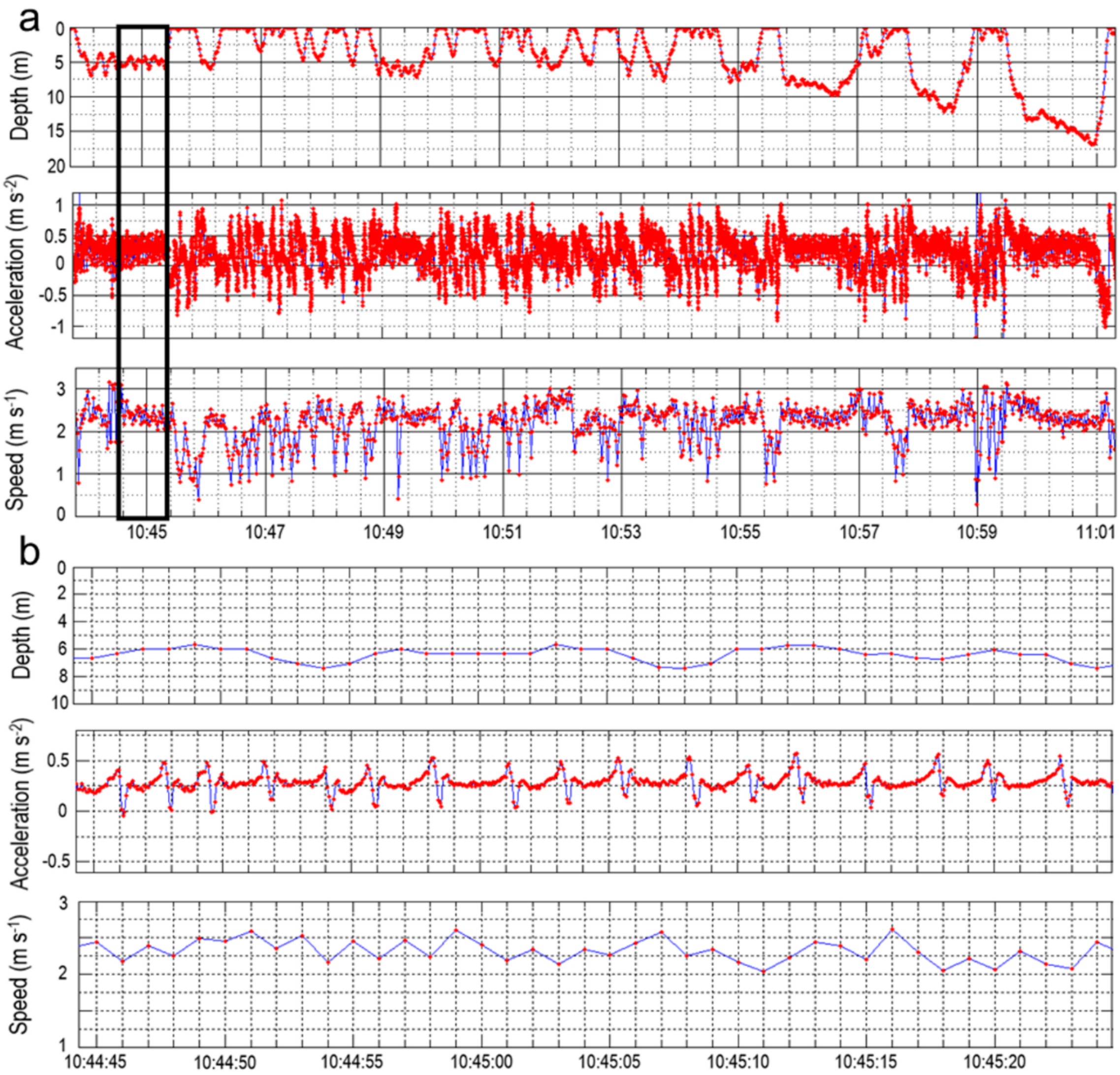

Figure 3.2. (a) Data for depth, X-axis acceleration, and speed behavior during a period of ~18 min. (b) Enlargement of the area in the black rectangle showing 17 individual flipper strokes in the X-axis accelerometer and simultaneous pulses in speed associated with each stroke.

Table 3.1. Dive variables used in the K-means clustering analysis

Variable	Units	Definition
Total Dive Duration	min	Total submergence duration of a dive
Descent Duration	min	Time from submergence until bottom phase
Bottom Duration	min	Time from descent end to ascent begin
Ascent Duration	min	Time from bottom end to surface
Surface Duration	min	Time spent at depths < 3 m following a dive
Descent Percentage	%	Percentage of dive devoted to descent phase
Bottom Percentage	%	Percentage of dive devoted to bottom phase
Ascent Percentage	%	Percentage of dive devoted to descent phase
Maximum Dive Depth	m	Maximum depth reached during dive
Mean Bottom Depth	m	Mean depth of the bottom phase of a dive
Total Strokes	N	Total number of flipper stroke during a dive
Stroke Rate	Hz	Total strokes converted to strokes sec^{-1}
Descent Pitch	°	Mean pitch during descent phase of dive
Bottom Pitch	°	Mean pitch during bottom phase of dive
Ascent Pitch	°	Mean pitch during ascent phase of dive
Descent Speed	$m\ s^{-1}$	Mean speed during descent phase of dive
Bottom Speed	$m\ s^{-1}$	Mean speed during bottom phase of dive
Ascent Speed	$m\ s^{-1}$	Mean speed during ascent phase of dive
Surface Speed	$m\ s^{-1}$	Mean speed during surface phase following dive
Distance	m	Total distance swam during dive, calculated by summation of dive phase durations times mean speeds
Net-to-Gross Displacement Ratio		Ratio of the net displacement (m) at the surface between the beginning and end of a dive and the total distance swam (m). The most linear dives have a value approaching 1 and the least linear dives a value approaching 0.

The x-axis accelerometer and corresponding variations in swim speed were used to determine flipper stroke frequency (strokes sec^{-1}) and total strokes during a dive (Fig. 3.2b). Three-dimensional dive measurements were calculated based on heading, speed, and depth. The percentage of time spent diving, surface swimming, and resting onshore were determined for each of the two foraging trips.

Twenty-one variables were extracted from three-dimensional dive profiles and used to classify dives using k-means clustering in the R package *NbClust* (Table 3.1; Charrad et al., 2014). We used principal component analysis to identify dimensional contributions to variance within the data and identified three clusters (i.e., dive types) as the optimal number with little overlap. We then used linear discriminant analysis (LDA) within package *MASS* (Venables and Ripley, 2002) to generate a cluster predictor model using all explanatory variables. The LDA model was trained using cross-validation, with 80% of the data used for training and evaluation conducted on the remaining 20% via a confusion matrix. Forward stepwise variable selection was used to determine primary explanatory variables within the LDA model using Euclidean distance threshold provided in R package *klaR* (Weihs et al., 2005). The simplified model performance was assessed using the same methods of cross-validation.

Energetics

The estimated mass specific metabolic rate for the 126 kg female with the VDR while resting onshore (6.0 ml O_2 min^{-1} kg^{-1}) was based on the mass adjusted resting metabolic rate in air for Southern sea lions (*Otaria flavescens*) and in water for California sea lions (*Zalophus californianus*) of similar body mass (Dassis et al., 2012;

Liwanag et al., 2009). To estimate surface swimming and diving metabolic rates, we assumed an underlying resting metabolic rate for normal physiological function and added the additional cost of flipper stroking for locomotion based on the number of strokes and cost-per-stroke (CPS) for Southern sea lions (Williams et al., 2004; Dassis et al., 2012; Davis, 2019). The mass specific metabolic rate for surface swimming ($\dot{V}O_{2swim}$) was calculated from the equation:

Equation 3.1 $\dot{V}O2swim = ((\dot{V}O2rest\ air\ x\ Swim\ Duration) + (Total\ Strokes\ x\ 0.38\ ml\ O2\ kg\text{-}1\ stroke\text{-}1)) \div Swim\ Duration$

where $\dot{V}O_{2rest\ air}$ was the mass specific metabolic rate while resting in air (6.0 ml O_2 min $^{-1}$ kg^{-1}; Dassis et al., 2012), *Swim Duration* was the total surface swimming duration determined from the VDR record, and 0.38 ml O_2 kg^{-1} stroke^{-1} was the CPS. Flipper stroking at the surface could not be obtained from the VDR record, so *Total Strokes* was estimated as the product of the mean stroke frequency (0.37 strokes sec^{-1}) for the three dive types and the *Swim Duration*.

The mass specific metabolic rate for each dive type ($\dot{V}O_{2dive}$) was calculated from the equation:

Equation 3.2 $\dot{V}O_{2dive} = ((\dot{V}O_{2rest\ air}\ x\ Dive\ Duration) + (Total\ Strokes\ x\ 0.38\ ml\ O_2\ kg^{-1}\ stroke^{-1})) \div Dive\ Duration$

where $\dot{V}O_{2rest\ air}$ was the mass specific metabolic rate while resting in water (6.0 ml O_2 min^{-1} kg^{-1}; Dassis et al., 2012), *Dive Duration* was the product of the mean duration and the number of each dive type, *Total Strokes* was the product of the duration and mean flipper stroke frequency for each dive type, and 0.38 ml O_2 kg^{-1} stroke^{-1} was the CPS.

Statistical Analyses

All statistical analyses were performed within R statistical software. The correlations of diving and foraging trip variables were analyzed using Pearson's correlation or Kendall's rank correlation depending on normality. One-way analysis of variance (ANOVA) and Kruskal-Wallis tests with Tukey and Dunn post-hoc testing, respectively, were used to compare foraging trip and diving means with a significance value of $\alpha = 0.05$. Linear mixed-effects models (LME) were used to assess effects of presence/absence of a dependent pup (*Pup*) on foraging trip characteristics while treating individual (*ID*) as a random factor. Values are presented as mean (± s.d.).

Results

At-Sea Movements

We tracked 267 foraging trips (mean = 67 ± 47) for the four females using satellite telemetry with a mean duration of 58 ± 39 days (Table 3.2). The mean T_{sea} and T_{land} were 11.3 ± 1.5 h and 8.7 ± 1.8 h, respectively, for a mean foraging cycle duration of 20.0 ± 2.7 h. There was no correlation between T_{sea} and subsequent T_{land} (Kendall's T $p > 0.05$). Mean T_{land} differed significantly among females (Kruskal-Wallis $p < 0.05$), but T_{sea} did not (Kruskal-Wallis $p > 0.05$). Neither T_{sea} nor T_{land} showed a significant correlation with the presence of a pup (LME $p > 0.05$).

Foraging trip departures occurred throughout the 24-hr. cycle (Fig. 3.3a). The time of return showed a bimodal distribution, with peaks occurring between 5:00-10:00 and 21:00-0:00 local time (Fig. 3.3b). The maximum distance from shore (mean = 12 ± 5.7 km) varied among females, although 93 ± 6.5% of all locations occurred < 3 km

Table 3.2. Foraging cycle characteristics for four female NZSL. Mean ± s.d.

[1]Animal	[2]Age (yr)	[3]Tracking duration (days)	[4]Locations (N)	[5]Locations < 3 km from shore (%)	[6]Foraging Cycles (N)	[7]T_{sea} (hr)	[8]T_{land} (hr)	[9]Distance (km)	[10]Speed ($m\ s^{-1}$)	[11]Max Distance (km)
SL1	3	76	936	94	79	11.9	9.8	14	0.4	13
SL2	3	21	264	96	28	9.1	7.4	13	0.4	7
SL3	7	31	330	84	32	11.7	10.6	20	0.5	19
SL4	8	104	1650	99	128	12.3	6.8	18	0.4	7
Mean	-	**58 ± 39**	**795 ± 645**	**93 ± 6.5**	**67 ± 47**	**11.3 ± 1.5**	**8.7 ± 1.8**	**16 ± 3.3**	**0.4 ± 0.05**	**12 ± 5.7**

[1] Female sea lion identification number

[2] Age in years

[3] Duration of tracking before the satellite telemeter was shed or stopped transmitting (days)

[4] Number of satellite locations used in the analysis

[5] Percentage of locations that were < 3 km from shore

[6] Number of foraging cycles, which included the time at sea and onshore

[7] Time at sea during a foraging trip (hr)

[8] Time on shore between foraging trips (hr)

[9] Transit distance during a foraging trip (km)

[10] Horizontal transit speed ($m\ s^{-1}$)

[11] Maximum distance from shore during a foraging trip (km)

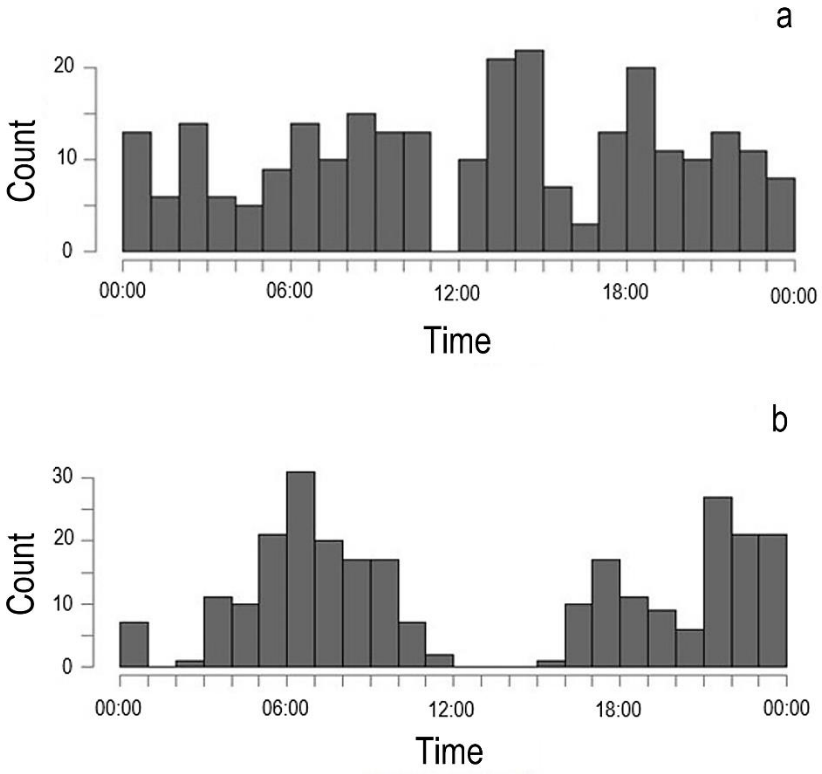

Figure 3.3. Foraging trip departures (a) and returns (b) as a function of time. Departures were distributed evenly throughout the day, while returns centered around two main peaks in morning and at night (GMT +12)

from shore (Table 3.2). Most foraging trips occurred in waters < 50 m in depth, and only one female (SL1) swam in an area with a water depth > 100 m.

Mean surface transit distance during a foraging trip was 16 ± 3.3 km at a mean transit speed of 0.4 ± 0.05 m sec^{-1} (Table 3.2). Distance traveled was positively correlated with both T_{sea} and subsequent T_{land} (Kendall's T $p < 0.05$). Mean trip distance did not correlate with the presence of a pup (LME $p > 0.05$). Mean T_{sea} differed significantly among months. The mean trip duration in August (14.0 h) was significantly

Table 3.3. Total, inshore, and offshore home ranges. Mean ± s.d.

Animal	Total 95% Home Range (km^2)	Total 50% Home Range (km^2)	Inshore Locations (N)	95% Inshore Home Range (km^2)	50% Inshore Home Range (km^2)	Offshore Locations (N)	95% Offshore Home Range (km^2)	50% Offshore Home Range (km^2)
SL1	61	8	692	32	3	244	29	5
SL2	138	30	215	40	7	49	98	23
SL3	103	26	219	19	8	111	84	18
SL4	85	12	1118	38	5	532	47	7
Mean	**97 ± 32.4**	**19 ± 10.6**	**561 ± 434**	**32 ± 9.5**	**6 ± 2.2**	**234 ± 215**	**65 ± 32.2**	**13 ± 8.7**

longer than that of September (9.9 h) (Dunn's test $p < 0.05$), but mean minimum distance travelled did not differ among months (Kruskal-Wallis $p > 0.05$).

Home Ranges

Mean total (inshore and offshore) 95% and 50% home ranges were 97 ± 32.4 km^2 and 19 ± 10.6 km^2, respectively (Table 3.3). The mean inshore 95% home range was 32 ± 9.5 km^2, and the 50% core range was 6 ± 2.2 km^2, which represented ~33% of total 95% and 50% home ranges, respectively. Inshore 95% and 50% home ranges showed moderate variability among females (Fig. 3.4; 95% CV = 29%; 50% CV = 42%). The four females had 50% core ranges that included the Catlins River Estuary (CRE). The coastline habitat-associations for the mean inshore 50% home range included rocky/reef (20%), sandy beaches (34%), and estuaries (46%), whereas those for the mean inshore 95% home range included rocky/reef (40%), sandy beaches (32%), and estuaries (28%) (Fig. 3.5).

The mean offshore 95% home range was 65 ± 32.2 km^2, and the 50% core range was 13 ± 8.7 km^2 (Table 3.3), both composing ~67% of total 95% and 50% home ranges, respectively. Offshore 95% and 50% home ranges showed high variability among females (Fig. 3.6; 95% CV = 50%; 50% CV = 68%). There were not significant correlations among the number of locations, transit distance, and T_{sea} for either 95% or 50% offshore home ranges (Pearson's r $p > 0.05$). Offshore 50% home ranges included waters adjacent to the CRE. All offshore 95% home ranges were in water depths < 100 m except for one female.

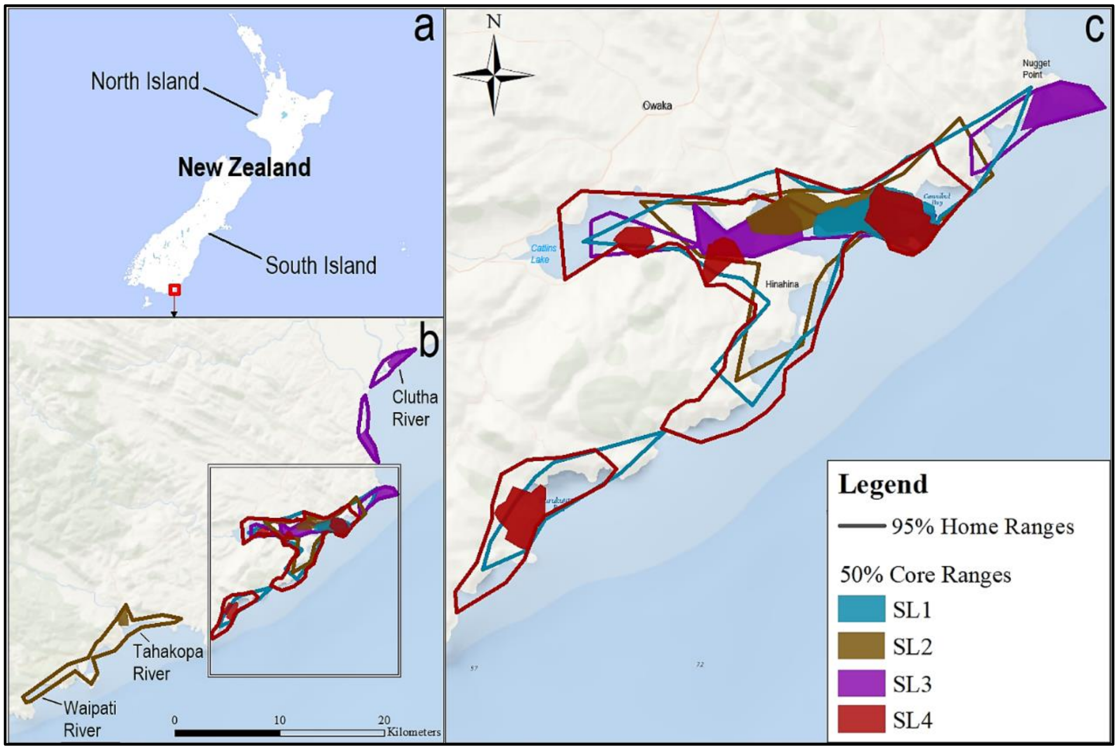

Figure 3.4. Inshore home ranges of the four female NZSL. (a) Study area (red box). (b) Inshore 95% home ranges and 50% core ranges for four females based on local convex hulls (LOCOH). (c) Enlargement of home ranges around the Catlins River Estuary.

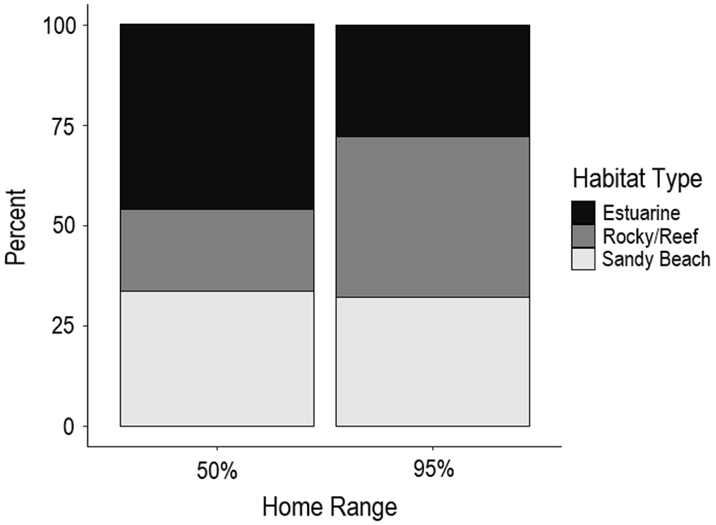

Figure 3.5. Adjacent coastline habitat for the inshore 50% and 95% home ranges.

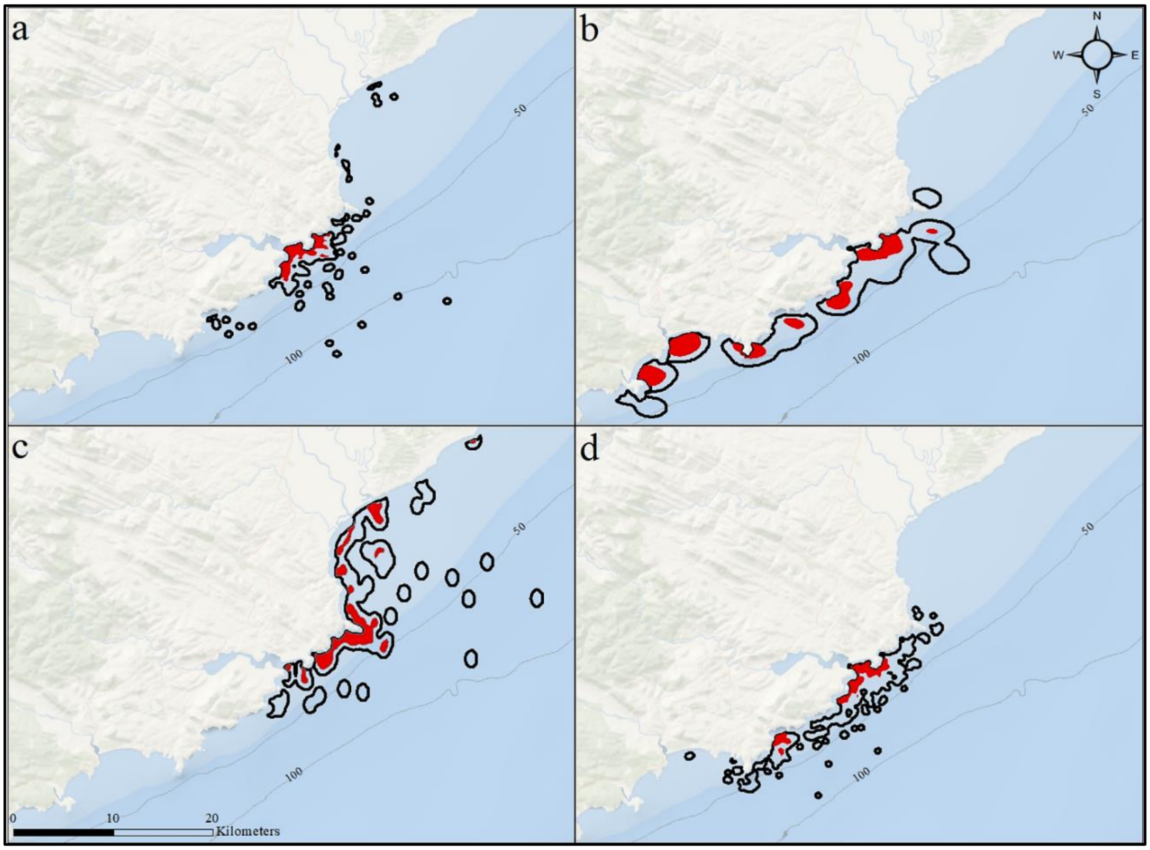

Figure 3.6. Offshore home ranges for four female sea lions. 95% home ranges (black lines) and 50% core ranges (red polygons) represented for SL1 (a), SL2 (b), SL3 (c), and SL4 (d).

Diving Behavior

We recorded 813 dives during two foraging trips for one female. Dives were frequent (30.6 dives h^{-1}) and occurred during 72% of the time at sea. All dives occurred between 06:30-23:59 local time. Sunrise occurred at 08:20 and sunset at 17:10, so 71% of dives occurred when the sun was above the horizon. Mean maximum dive depth and dive duration were 8.9 ± 5.2 m and 1.4 ± 1.1 min, respectively (Fig. 3.7). Eighty-nine percent of dives were < 15 m in depth, and 72% were < 2 min in duration. Mean surface time between dives was 0.5 ± 0.9 min. The maximum dive depth and duration were 27 m and 7.1 min, respectively. Mean flipper stroke rate during dives was 0.4 ± 0.09 Hz with a mean swim speed of 1.5 ± 0.51 m s^{-1}.

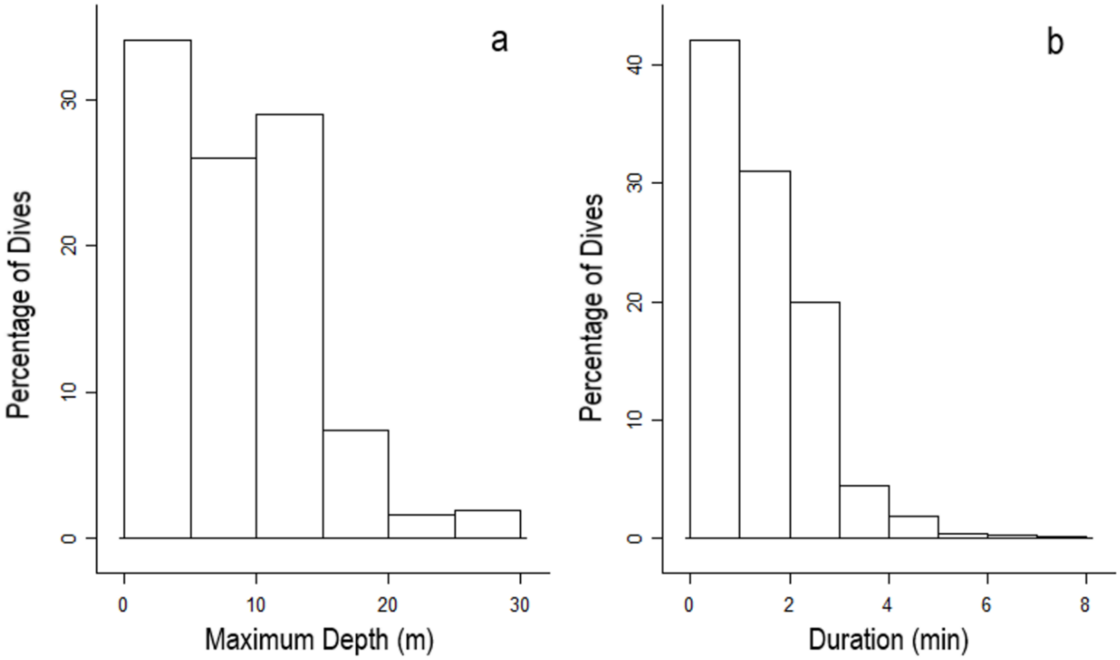

Figure 3.7. Histograms for all recorded dives displaying maximum depth (a) and duration (b). No dives > 30 m or > 8 min were recorded.

K-means cluster analysis identified three dive clusters, hereafter referred to as Dive Types 1, 2, and 3 (Fig. 3.8). Significant differences existed among all variables for these dive types (Table 3.4). LDA correctly assigned dives for 96% of test dataset predictions using four variables identified through forward stepwise variable selection as primary contributors to accuracy: 1) total dive duration, 2) maximum depth, 3) total distance swam, and 4) net-to-gross displacement (NTGD).

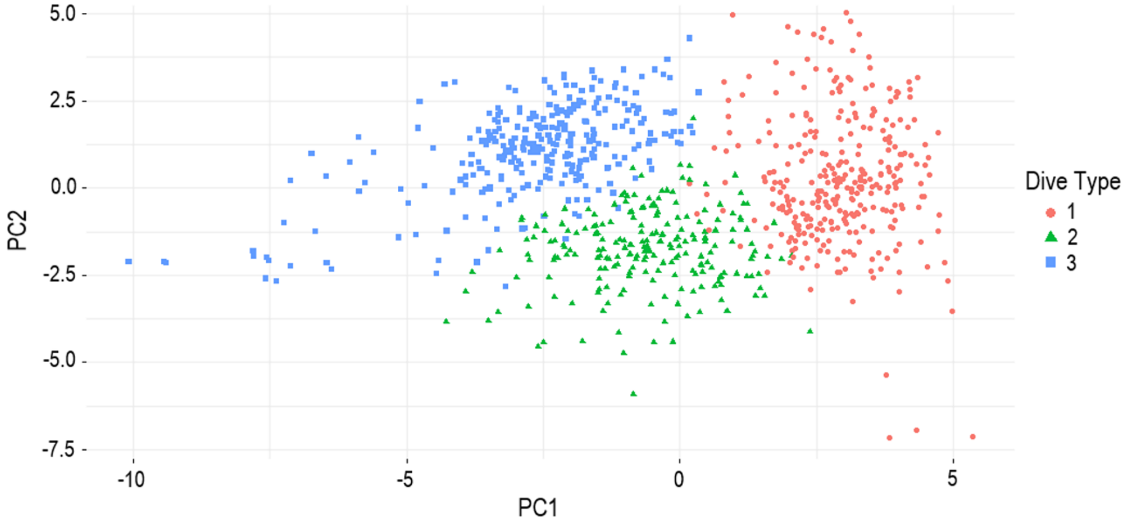

Figure 3.8. K-means cluster analysis results identifying three dive types. Principal component one (PC1) accounted for 36.2% of variation while principal component two (PC2) accounted for an additional 17.1%.

Table 3.4. Comparison of Type 1, 2 and 3 dives. Mean values for each variable with different superscripts are significantly different. (α = 0.05). Values are presented as mean (± s.d.).

Variable	**Dive Type**		
Dives	**1**	**2**	**3**
N	284	311	218
% total	35%	38%	27%
Depth (m)			
Mean maximum depth	14.1 (4.1) ^{a}	5.3 (2.6) ^{b}	7.3 (3.4) ^{c}
Mean bottom depth	11.8 (3.9) ^{a}	4.0 (2.2) ^{b}	5.9 (2.9) ^{c}
Duration (min)			
Total duration	2.3 (1.0) ^{a}	0.4 (0.2) ^{b}	1.7 (0.6) ^{c}
Descent	0.2 (0.2) ^{a}	0.1 (0.1) ^{b}	0.1 (0.1) ^{c}
Bottom	1.8 (1.0) ^{a}	0.2 (0.1) ^{b}	1.4 (0.6) ^{c}
Ascent	0.2 (0.1) ^{a}	0.1 (0.1) ^{b}	0.2 (0.2) ^{c}
Duration (%)			
Descent	11 (8) ^{a}	29 (12) ^{b}	10 (7) ^{a}
Bottom	77 (12) ^{a}	41 (17) ^{b}	79 (13) ^{a}
Ascent	12 (7) ^{a}	30 (11) ^{b}	12 (9) ^{a}
Speed (m sec^{-1})			
Total dive	1.1 (0.3) ^{a}	1.7 (0.5) ^{b}	1.8 (0.3) ^{c}
Descent	1.5 (0.3) ^{a}	1.6 (0.5) ^{b}	1.8 (0.3) ^{b}
Bottom	1.0 (0.4) ^{a}	1.8 (0.6) ^{b}	1.8 (0.3) ^{c}
Ascent	1.4 (0.4) ^{a}	1.6 (0.4) ^{b}	1.7 (0.4) ^{b}
Angle (°)			
Descent	-36 (7) ^{a}	-26 (10) ^{b}	-26 (8) ^{b}
Ascent	22 (15) ^{a}	15 (10) ^{b}	10 (11) ^{b}
Strokes			
Total dive	42.4 (18.5) ^{a}	8.8 (5.4) ^{b}	40.3 (15.0) ^{a}
Stroke frequency (Hz)	0.31 (0.06) ^{a}	0.39 (0.10) ^{b}	0.40 (0.08) ^{b}
Dive path			
Total distance (m)	153 (93) ^{a}	37 (22) ^{b}	184 (69) ^{c}
[1]Net-to-Gross Displacement (NTGD)	0.6 (0.2) ^{a}	0.5 (0.2) ^{a}	0.8 (0.1) ^{b}

[1] The most linear dives have a value approaching 1 and the least linear have a value approaching 0

Type 1 Dives

Type 1 dives accounted for 35% of all dives, comprising 89% of dives ≥ 20 m maximum depth and 41% of the total time at sea. Compared with Type 2 and 3 dives, Type 1 dives were deeper (mean maximum depth = 14.1 m) and longer in duration (mean duration = 2.3 min) (Fig. 3.9a and Table 3.4). Because of their greater depth and duration, Type 1 dives had the longest descent (0.2 min), bottom (1.8 min) and ascent (0.2 min) durations and the steepest descent (-36°) and ascent (22°) angles. Type 1 dives had the slowest mean swim speed (1.1 m s^{-1}), especially during the bottom phase (1.0 m s^{-1}), which represented 77% of dive duration. Mean flipper stroke frequency (0.31 Hz) was modestly but significantly less than for Type 2 and 3 dives. Mean distance swam (153 m) was 4.1-fold greater than that for Type 2 dives, but 83% of that for Type 3 dives. The NTGD ratio was 0.6, which indicated a tortuous swim path, especially during the bottom phase (Fig. 3.9b). The mean surface time following Type 1 dives was 0.7 ± 0.5 min.

Type 2 Dives

Type 2 dives accounted for 38% of all dives, but only 8% of the time at sea because of their shorter duration. Compared with Type 1 and 3 dives, Type 2 dives were the shallowest (mean maximum depth = 5.3 m) and shortest in duration (mean duration = 0.4 min) (Fig. 3.9c and Table 3.4). As a result, Type 2 dives had the shortest descent (0.1 min), bottom (0.2 min) and ascent (0.1 min) durations with gradual descent and ascent angles (-26° and 15°, respectively). Type 2 dives had a faster swim speed (1.7 m sec^{-1}) than Type 1 dives, especially during the bottom phase (1.8 m sec^{-1}), which represented 41% of dive duration. Mean flipper stroke frequency (0.39 Hz) was similar to Type 3 dives but modestly higher than that for Type 1 dives. Mean distance swam was only 37 m, which was 20-24% of that for Type 1 and 3 dives. The NTGD ratio was 0.5, indicating a tortuous swim path (Fig. 3.9d). The mean surface duration following Type 2 dives was 0.3 ± 0.6 min.

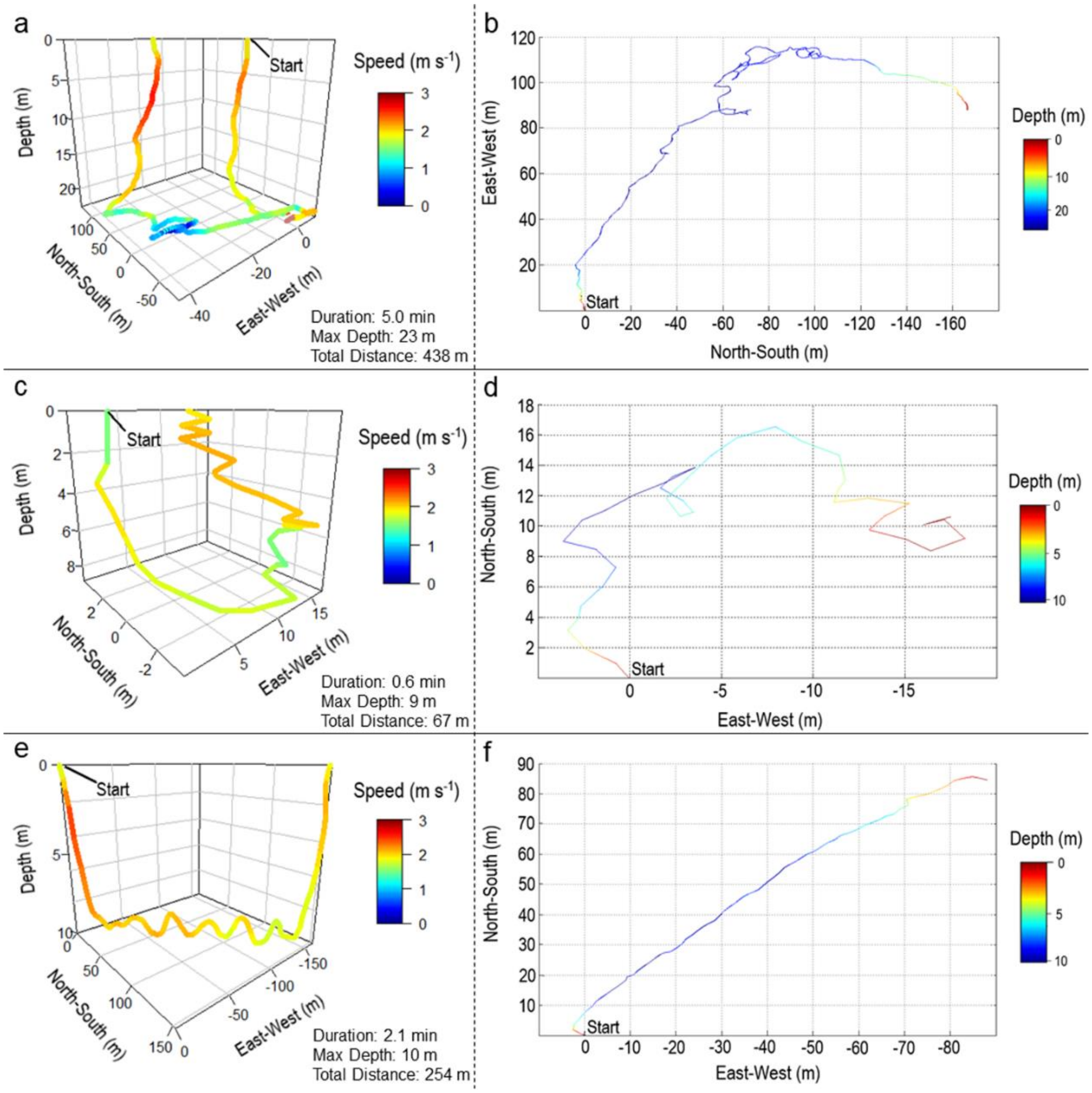

Figure 3.9. Three-dimensional and aerial plots of Type 1 (a, b), Type 2 (c, d) and Type 3 (e, f) dives.

Type 3 Dives

Type 3 dives accounted for 27% of all dives and 23% of the time at sea. Compared with Type 1 and 2 dives, Type 3 dives were intermediate in depth (mean maximum depth = 7.3 m) and duration (mean duration = 1.7 min), and this was reflected in descent (0.1 min), bottom (1.4 min) and ascent (0.2 min) durations (Fig. 3.9e and Table 3.4). Type 3 dives had the most gradual descent (-26°) and ascent (10°) angles but fastest swim speed (1.8 m sec^{-1}) and the longest percentage bottom duration (79%). Mean flipper stroke frequency (0.40 Hz) was similar to that for Type 2 dives. Mean distance swam (184 m) was 1.2-fold greater than that for Type 1 dives and 5.0-fold greater than that for Type 2 dives. The NTGD ratio was 0.8, indicating a more linear swim path throughout the dive (Fig. 3.9f). The mean surface time following Type 1 dives was 0.7 ± 1.4 min.

Energetics

The estimated mass specific metabolic rate while resting ashore was 6.0 ml O_2 min^{-1} kg^{-1} based on the mass adjusted resting metabolic rate in air for Southern sea lions (Dassis et al., 2012). The estimated mass specific metabolic rate for surface swimming was 14.5 ml O_2 min^{-1} kg^{-1}, while that for Dive Types 1, 2, and 3 was 13.0, 14.4 ml, and 15.0 ml O_2 min^{-1} kg^{-1}, respectively. The estimated net energy expenditure (E_{net}) for the 33.6 hr VDR record was 61,749 kJ, which was equivalent to a mean mass specific metabolic rate (i.e., power) of 4.0 W kg^{-1} (Tables 3.5 and 3.6). Minimum power (2.0 W kg^{-1}) occurred while resting onshore, and maximum power (4.9 W kg^{-1}) occurred during Type 3 dives, which had the highest (1.8 m sec^{-1}) mean swim speed (Table 3.4).

Table 3.5. Activity and energy budget for a female NZSL (BM = 126 kg) during two foraging trips.

Activity	[1]Number (N)	[2]Duration (min)	[3]Rest MR (ml O_2 min^{-1} kg^{-1})	[4]Rest O_2 (ml O_2 kg^{-1})	[5]Strokes (N)	[6]Stroking O_2 (ml O_2 kg^{-1})	[7]Total O_2 (ml O_2 kg^{-1})	[8]E_{net} (kJ)	[9]E_{ingested} (kJ)
Rest onshore	N/A	426	6.0	2570	N/A	N/A	2570	6380	8752
Surface swim	N/A	444	6.0	2679	9857	3746	6424	15947	21875
Dive Type 1	284	653	6.0	3941	12042	4576	8517	21141	29000
Dive Type 2	311	124	6.0	751	2737	1040	1791	4445	6097
Dive Type 3	218	371	6.0	2236	8785	3338	5574	13837	18981
Total							24877	61749	84704

[1] Number of each dive type for two foraging trips (Total time = 33.6 hr)

[2] Duration for resting onshore, surface swimming, and each dive type, which for dives is the product of the number and mean dive duration of each type (Table 3.3)

[3] Resting (basal) metabolic rate (MR) in air based on the mass adjusted value for Southern sea lions (Dassis et al. 2012)

[4] Resting (basal) oxygen consumed (i.e., not including stroking) for each activity or dive type, which is the product of resting MR and the duration of each activity or dive type

[5] Number of flipper strokes, which is the product of the duration and mean flipper stroke frequency for surface swimming or each dive type (Table 3.3)

[6] Total metabolic cost for stroking, which is the product of the number of strokes for surface swimming and each dive type and the cost-per-stroke (CPS) of 0.38 ml O_2 kg^{-1} stroke^{-1} (Dassis et al. 2012)

[7] Total oxygen consumption (ml O_2 kg^{-1}) for resting onshore, surface swimming, and each dive type

[8] Net energy (E_{net}) for resting and stroking for each activity or dive type, which is the product of total oxygen consumption (ml O_2 kg^{-1}), 19.7 J ml O_2^{-1}, and a body mass of 126 kg

[9] Minimum prey energy ingested ($E_{ingested}$) required to offset the energetic cost of foraging and time onshore (not including lactation). $E_{ingested}$ is the E_{net} adjusted for: 1) the Heat Increment of Feeding, 2) energy used for the synthesis of urea from protein nitrogen, and 3) the assimilation efficiency using the equations:

Metabolizable energy (E_{met}) = $E_{net} \div 0.9$ (Heat Increment of Feeding; Winship et al. 2002)
Digestible energy (E_{dig}) = $E_{met} \div 0.9$ (Urinary Energy; Winship et al. 2002)
$E_{ingested} = E_{dig} \div 0.9$ (Assimilation Efficiency; Fadely et al.. 1994; Winship et al. 2002)

Table 3.6. Estimated metabolic rate (power) for resting onshore, surface swimming, and diving for a 126 kg female NZSL during a 33.6 hr monitoring period that included two foraging trips.

	[1]Time (sec)	[2]Time (%)	[3]Net E (kJ)	[4]Power (W)	[5]Mass Specific Power W/kg	[6]Ratio to Resting Onshore
Rest onshore	25560	21%	6380	250	2.0	1.0
Surface swim	26640	22%	15947	599	4.8	2.4
Dive type 1	39192	32%	21141	539	4.3	2.2
Dive type 2	7464	6%	4445	595	4.7	2.4
Dive type 3	22236	18%	13837	622	4.9	2.5
Total	121092	100%	61749	510	4.0	2.0

[1] Total time for resting onshore, surface swimming, and each dive type

[2] Percentage time for resting onshore, surface swimming, and each dive type (Total time = 33.6 hr)

[3] Net energy (E_{net}) for resting onshore, surface swimming, and each dive type based on Table 3.5

[4] Power (watts) for resting onshore, surface swimming, and each dive type, which is the quotient of E_{net} and the total time for each activity with a conversion factor of 1000 for kJ to J, with mean of all activities

[5] Mass specific power for resting onshore, surface swimming, and each dive type, which is the quotient of power and a body mass of 126 kg, with mean of all activities

[6] Ratio of mass specific power for resting onshore, surface swimming, and each dive type relative to resting power onshore, with mean of all activities

Discussion

Home Ranges

Mean total home ranges were small and restricted to coastal areas (Table 3.3). The frequent use of the CRE and adjacent habitats created overlapping 50% core ranges among females, which was expected because females often haul out in the same areas (C. Barnett, pers. comm.). Pinnipedia commonly display seasonal and yearly philopatry, often associated with breeding and rearing offspring (Auge et al., 2014; Campagna et al., 2001; Chilvers and Wilkinson, 2008; Hoffman and Forcada, 2012). The females with and without pups had inshore 50% core ranges within the CRE, indicating that this area is used for reasons in addition to pupping. SL4 also consistently returned to the CRE through mid-October, presumably after weaning had occurred (Cawthorn et al., 1985; Auge et al., 2011a). Associations with estuaries have been recorded for other Pinnipedia. The home range of Southern sea lions at Isla de Lobos, Uruguay included foraging areas created by ecological and bathymetric conditions around the La Plata River Estuary (Rodriguez et al., 2013). Similarly, the St. Lawrence Estuary is used by multiple Phocidae species both seasonally and year-round for foraging and pupping (Dube et al., 2003; Lesage, 1999). The same ecological associations are likely for NZSL around the CRE. The frequency and time with which these females use the CRE make it an important area for management and conservation efforts that enhance breeding and population recovery.

Individual variation among females was evident for home ranges. Although the CRE was within the 50% core ranges for all females, individual core ranges occurred up to 20 km north and south of the CRE, and 95% home ranges spanned ~60 km of the Catlins coastline (Fig. 3.4). SL3, which had a pup, spent time onshore ~20 km north of the CRE, and SL4 used inshore habitat 10 km south of the CRE. Although female Otariidae often haul out on certain breeding rookeries (Rodriguez et al., 2013; Chilvers et al., 2005; Werner and Campagna, 1995), some species use other sites, especially as pups approach weaning (Thompson et al., 1998; Auge et al., 2011b; Villegas-Amtmann et al., 2008). Lactating NZSL females on the Otago Peninsula spent 23% of their time onshore at locations away from their pups onshore (Auge et al., 2011b). Compared to the NZSL on the Auckland Islands, the females in our study had shorter foraging trips, leading to onshore time budgets less constrained by nursing requirements. The results indicate that the females in our study foraged and spent time onshore within smaller temporal and spatial scales, perhaps because of access to greater food resources.

The inshore 50% core ranges bordered estuarine habitats with adjacent sandy beaches, which are two important variables associated with NZSL breeding aggregations (Fig. 3.5; Auge et al., 2012b; Macmillan et al., 2016). SL3 spent time around the Clutha River estuary on the northern end of the range, and SL2 frequented the Tahakopa River mouth on the southern end (Fig. 3.4b). SL4 also was tracked around Purakaunui River and Bay. Tahakopa and Waipati Bays have been identified as potential future breeding areas based on the estuarine and beach habitat (Macmillan et al., 2016). The inshore 50% and 95% home ranges of SL2 overlapped with these two bays, despite the absence of a pup. These habitat associations indicate that the Catlins Coast contains areas suitable for

NZSL throughout the year. The frequent use of these areas emphasizes the importance of coastal habitat for hauling out regardless of whether a female has a pup.

The mean total 95% offshore home range for the four females was 65 ± 32.2 km^2 (Table 3.3). In contrast, the 100% home range of females around the Otago Peninsula (257 km^2) was ~4-fold larger (Auge et al., 2011b), although this estimate would have been inflated by outlying locations because of the kernel density model that was used. Our results indicate that South Island NZSL have smaller home ranges compared to those in subantarctic populations and that of other Otariidae (Table 2.3). Chilvers et al. (2005) calculated a mean 50% core range of 378 km^2 for NZSL females at Enderby Island in the Auckland Islands, which is 29-fold larger than that in this study. Southern sea lions at Isla de Lobos had a 50% core range mean of 3,121 km^2 (Rodriguez et al., 2013), and Australian sea lions (*Neophoca cinerea*) had a mean 75% home range of 596 km^2 around Kangaroo Island (Fowler et al., 2007). While these home ranges are considerably larger than that of our study, they were still confined to the continental shelf. Benthic foraging habitat for the females in this study was constrained within a bathymetric range that was < 150 m in depth (*viz*. 2.3 min x 60 sec min^{-1} x 1.1 m sec^{-1}; Table 3.4) for dives that were within their ADL. Benthic divers are constrained by bathymetry and their ADL, so species inhabiting environments with an extended continental shelf may have larger foraging areas. The continental shelf along the Catlins Coast extends ~35 km offshore (Moore et al., 1995), which is much narrower than other areas occupied by NZSL. The combination of a narrow shelf and resource abundance in newly reoccupied coastal waters may partly explain the smaller home ranges observed for South Island NZSL studies.

Foraging Trips

The mean T_{sea} during foraging trips along the Catlins Coast was short in duration (11.3 hr) and with satellite locations primarily (93%) nearshore (< 3 km from the coast), which was similar to that for females in the Otago Peninsula (Table 3.2; Auge et al., 2011b). The four females spent a large percentage of time around the CRE, although individual variation occurred once animals left the area. SL3 travelled north of the estuary, while SL2 traveled almost exclusively south. Females on the Otago Peninsula also remained nearshore with 68% of locations < 3 km from shore, although two individuals traveled to the edge of the continental, which was ~35 km from the coastline (Auge et al., 2011b). Likewise, females on nearby Stewart Island had a mean T_{sea} of 15 hr and a mean maximum distance of 28 km, which were 1.3 and 2.3-fold longer and farther, respectively, which indicate coastal foraging and locally accessible resources in newly reoccupied areas. In contrast, the T_{sea} of females on the Auckland Islands was 6-fold longer because they traveled > 100 km from the colony and foraged in deeper waters (mean water depth = 371 m) (Chilvers et al., 2005).

Compared with the females in our study, the mean T_{land} for females on the Otago Peninsula and Stewart Island was 1.7-fold longer and that for females in the Auckland Islands ~3-fold longer (Auge et al., 2011b; Chilvers et al., 2005; Chilvers, 2018a). Part of this difference may have resulted from seasonality. Previous tracking studies were conducted during the summer-autumn (December-May), while our study occurred later in the winter (July-October). Females give birth from December-January (Chilvers et al., 2005), so pups in our study would have been 3-7 months older than pups in previous studies. Research on Galapagos fur seals (*Arctocephalus galapagoensis*) showed that T_{land} was negatively correlated with pup age (Gentry and Kooyman, 2014). Females with dependent pups in our study may have spent less time onshore and more time foraging than they would have earlier in the year with young pups. It also is possible that pups in our study were capable of foraging. Yearling NZSL pups in the Auckland Islands had mean dive depths (19.3 m) and durations (1.4 min) that were similar to the adults in our study (Leung et al., 2014). Pups were of weaning age (8-10 months) by the end of our study and they may have foraged in addition to nursing (Cawthorn et al., 1985). However, this observation does not completely account for the differences in T_{land}, because two of our females did not have pups. T_{land} was not correlated with the presence of a pup, so other factors affecting onshore duration warrant further investigation.

Dive Behavior

Although dive data were obtained from only one female, we recorded 813 dives during two ~13 hr foraging trips. Dives were frequent (30.6 dives h^{-1}) and represented most (72%) of the time at sea. Although dive effort was intense, most dives were shallow (< 15 m) and short duration (< 2 min) with a moderate swim speed (1.5 m s^{-1}) and short interdive interval (0.6 min).

Our analysis identified three dive types. Compared with Type 2 and 3 dives, Type 1 dives were 1.9 to 2.7-fold deeper and 1.4 to 5.8-fold longer in duration, especially during the bottom phase (Fig. 3.9a and Table 3.4). They had the steepest descent and ascent angles, longest bottom phase (77% of dive duration), slowest bottom speed, and a tortuous dive path over a mean distance of 153 m with small fluctuations in dive depth. This dive behavior, which is indicative of area intensive searching behavior with prey pursuit on the seafloor, is similar to that for benthic-foraging NZSL in the Auckland Islands and Otago Peninsula based on time-depth recorders (Chilvers and Wilkinson, 2009; Crocker et al., 2001; Auge et al., 2011a). This behavior also resembles the foraging behavior (based on VDR recorded three-dimensional dive path with video) of female Steller sea lions (*Eumetopias jubatus*) in the Kuril Islands in Russia, which feed predominately on demersal Atka mackerel (*Pleurogrammus monopterygius*) (Olivier, 2015). Unfortunately, the camera on our VDR failed to record, so we were unable to document prey capture.

During the summer and autumn, NZSL in the Otago Peninsula feed predominately on snake mackerel (*Thyrsites atun*) and jack mackerel (*Trachurus* sp.), which occur on the continental shelf (Fig. 3.10a, b; Auge et al., 2012a). However, the winter diet of the females in our study may differ, as jack mackerel were absent from prior analysis of scat collected during the winter (Lalas, 1997; Auge et al., 2012a). Swimming speed may vary with prey and dive type (Bowen et al., 2002; Le Boeuf et al., 1992) among Pinnipedia. Crocker et al. (2001) recorded significantly slower bottom phase swim speeds than descent and ascent speeds for NZSL during flat-bottomed dives in the Auckland Islands. Bottom speed decreased by 22% compared to descent and ascent speeds during their study, similar to the 31% decrease in swim speed during our Type 1 dives. These slower bottom speeds may occur while searching for demersal prey.

Red codling (*Pseudophycis bachus*), wrasses (*Labridae spp.*), Maori octopus (*Macroctopus maorum*), and squat lobster (*Munida gregaria*) are demersal species identified in the diet of NZSL from the Otago Peninsula and Catlins Coast (Fig. 3.10c, d, e, f; Table 3.7; Auge et al., 2012a; Milne, 1996).

Compared with Type 1 and 3 dives, Type 2 dives were the most common, but they were the shallowest and shortest in duration, with a high swim speed and tortuous dive path (Fig. 3.9b and Table 3.4). Without video recorded behavior or prey capture, we cannot be certain of their purpose. Their very short bottom duration and swim path make it unlikely that they are benthic foraging dives. However, their prevalence may indicate that Type 2 dives involve searching behavior or mid-water feeding on benthopelagic species such as snake mackerel, spiny dogfish (*Squalus acanthias*), and arrow squid (*Nototodarus sloanii*) (Table 3.7). Females from the Otago Peninsula also exhibited potential mid-water foraging dives (Auge et al., 2011a). Mixed pelagic and benthic foraging strategies are evident in other species of Pinnipedia (Hindell et al., 1991; Kuhn et al., 2010; Szpak and Buckley, 2020).

Finally, Type 3 dives were intermediate in depth, total duration, and bottom duration compared to Type 1 and 2 dives (Fig. 3.9c and Table 3.4). Based on their high swim speed, linearity, high percentage of time in the bottom phase, and shallow ascent angle, Type 3 dives may be associated with transiting. These dives were most abundant during the first foraging trip, especially at the beginning and end, which occurred in coastal waters 10 km north of the CRE. During the second trip, the female remained closer to

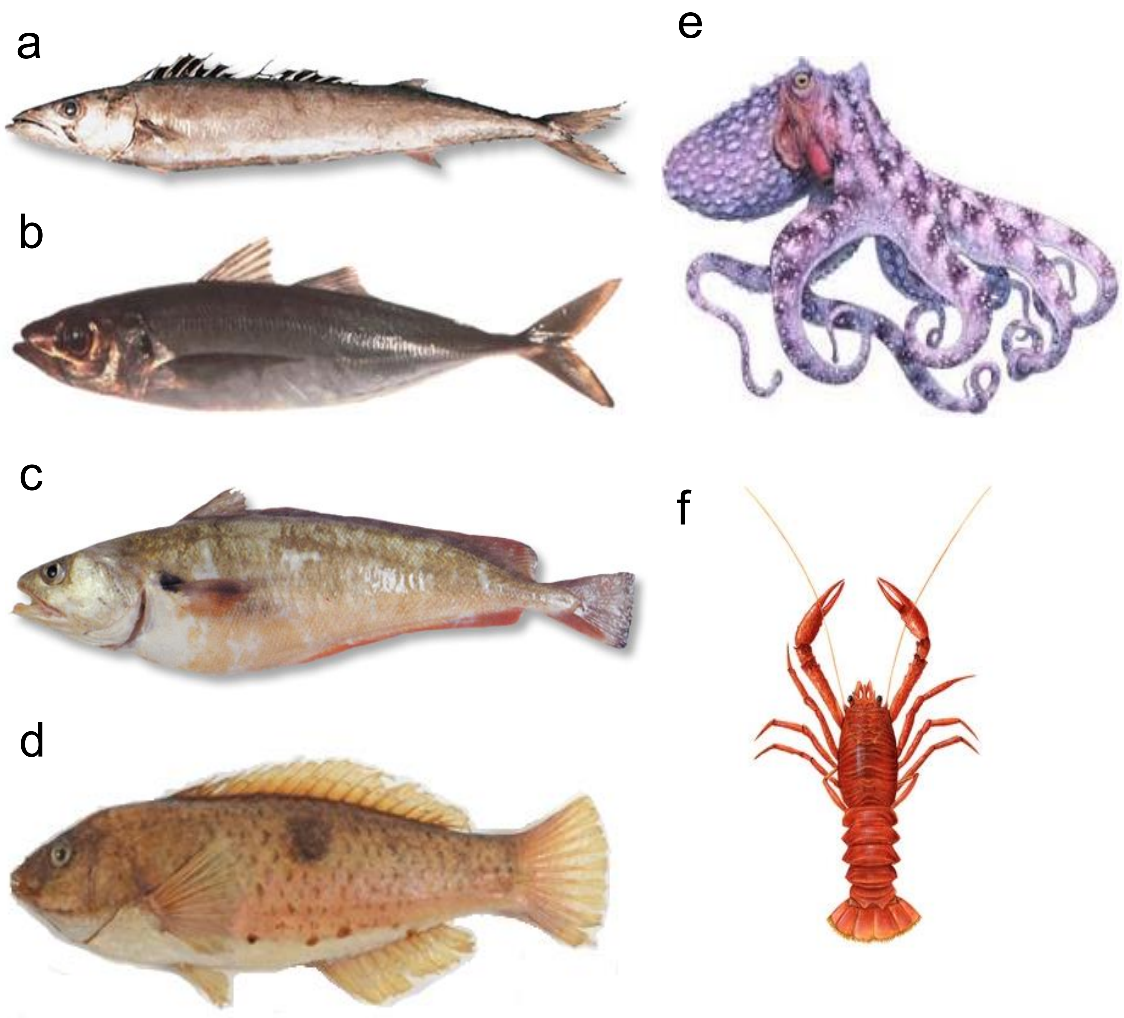

Figure 3.10. Prey species of NZSL along Catlins Coast and Otago Peninsula identified from scats and regurgitations. (a) snake mackerel (*Thyrsites atun*), (b) jack mackerel (*Trachurus sp.*), (c) red codling (*Pseudophycis bachus*) (d), wrasse (*Labridae sp.*), (e) Maori octopus (*Macroctopus maorum*), and (f) squat lobster (*Munida gregaria*). Images (a, b, c) courtesy of 2019 United Fisheries. Image (d) courtesy of Otago Museum. Image (e) courtesy of Institute for Marine and Antarctic Studies. Image (f) courtesy of ScandPosters.

Table 3.7. Prey species of NZSL. Species were identified through stomach, scat, regurgitation, and fatty acid analysis. Abbreviations: Auckland Islands (AI), Catlins Coast (CC), Campbell Island (CI), Otago Peninsula (OP), The Snares (S), and all five locations (Entire range).

Common name	Species	Location	Habitat	Mean Length (cm)	Length Range (cm)
Silverside[1]	*Argentina elongata*	AI, CI	demersal	25	≤ 37
Rattails[1]	*Coelorinchus spp.*	AI, CI	demersal	19	5-44
Pigfish[1]	*Congiopodus coriaceus*	AI, CI	demersal		6-27
Cape bonnetmouth[2]	*Emmelichthys nitidus*	S	benthopelagic	25	16-35
Yellow octopus[3]	*Enteroctopus zealandicus*	AI, CI	demersal		≤ 140
Little penguin[4]	*Eudyptula minor*	OP	N/A	43	41-45
Pink cusk-eel[5]	*Genypterus blacodes*	AI, CI, OP	demersal	66	23-95
Opalfish[6]	*Hemerocoetes spp.*	AI, CI, OP, S	demersal	12	9-25
Wrasses[7]	*Labridae spp.*	CC, OP	demersal	20	6-33
Lanternfish[8]	*Lampanyctodes hectoris*	AI, S	pelagic	6	3-8
Striped trumpeter[4]	*Latris lineata*	OP	demersal	64	62-65
Javelinfish[9]	*Lepidorhynchus denticulatus*	AI, S	demersal	39	38-72
Maori octopus[10]	*Macroctopus maorum*	CC, OP, S	demersal	14	6-21

Table 3.7. Continued

Common name	Species	Location	Habitat	Mean Length	Length Range (cm)
Blue hake[11]	*Macruronus novaezelandiae*	AI, CI	benthopelagic	70	50-97
Yellow-eyed	*Megadyptes antipodes*	OP	N/A	70	62-79
Southern hake[12]	*Merluccius australis*	AI	demersal	92	78-120
Pink lobster[13]	*Metanephrops challenger*	AI	demersal	16	13-25
Codfish[14]	*Micromesistius australis*	AI, CI	benthopelagic	31	17-41
Greater hooked	*Moroteuthis ingens*	AI	pelagic		≤ 94
Squat lobster[16]	*Munida gregaria*	AI, CC, S	demersal		≤ 8
Swimming crab[17]	*Portunidae spp.*	AI, CC, CI, S	demersal		1-7
Dark toadfish[3]	*Neophrynichthys latus*	AI, CI	demersal	18	7-28
Black cod[3]	*Notothenia microlepidota*	AI, CI	benthopelagic		≤ 70
Arrow squid[18]	*Nototodarus sloanii*	AI, OP, S	pelagic	23	7-37
Octopus[3]	*Octopus campbelli*	AI, CI	demersal		
Butterfish[4]	*Odax pullus*	OP	demersal	31	23-49
Blue cod[19]	*Parapercis colias*	OP, S	demersal	28	16-43

Table 3.7. Continued

Common name	Species	Location	Habitat	Mean Length	Length Range (cm)
Red codling[20]	*Pseudophycis bachus*	Entire range	demersal	25	5-55
Warehou[21]	*Seriolella spp.*	AI, S	demersal		≤ 90
Spiny dogfish[19]	*Squalus acanthias*	OP, S	demersal/benthopelagic		40-110
Snake mackerel[22]	*Thyrsites atun*	AI, CC, OP,	demersal/benthopelagic	68	38-93
Antarctic flying squid[23]	*Todarodes fillippovae*	AI	pelagic		
Jack mackerel[18]	*Trachurus spp.*	AI, OP, S	pelagic	42	27-50
Skate[24]	*Zearajid spp.*	AI, CI, OP,	demersal	72	65-85

Data from: [1]Meynier et al. (2009), Roberts and Lalas (2015); [2]Lalas and Webster (2014); [3]Childerhouse et al. (2001), Roberts and Lalas (2015); [4]Auge et al. (2012); [5]Auge et al. (2012), Meynier et al. (2009), Roberts and Lalas (2015); [6]Auge et al. (2012), Lalas and Webster (2014), Meynier et al. (2009), Roberts and Lalas (2015); [7]Auge et al. (2012), Milne (1996); [8]Childerhouse et al. (2001), Lalas and Webster (2014); [9] Lalas and Webster (2014), Meynier et al. (2014); [10]Auge et al. (2012), Lalas and Webster (2014), Milne (1996); [11]Childerhouse et al. (2001), Meynier et al. (2009), Roberts and Lalas (2015); [12]Meynier et al. (2009); [13]Meynier et al. (2014); [14]Childerhouse et al. (2001), Meynier et al. (2009), Roberts and Lalas (2015); [15]Childerhouse et al. (2001), Meynier et al. (2009); [16]Childerhouse et al. (2001), Lalas and Webster (2014), Milne (1996); [17]Childerhouse et al. (2001), Lalas and Webster (2014), Milne (1996), Roberts and Lalas (2015); [18]Auge et al. (2012), Childerhouse et al. (2001), Lalas and Webster (2014), Meynier et al. (2009); [19]Auge et al. (2012), Lalas and Webster (2014); [20]Auge et al. (2012), Childerhouse et al. (2001), Lalas and Webster (2014), Meynier et al. (2009), Milne (1996), Roberts and Lalas (2015); [21]Lalas and Webster (2014), Meynier et al. (2009); [22]Auge et al. (2012), Childerhouse et al. (2001), Lalas and Webster (2014), Meynier et al. (2009), Milne (1996); [23]Childerhouse et al. (2001); [24]Auge et al. (2012), Childerhouse et al. (2001), Lalas and Webster (2014), Roberts and Lalas (2015) the CRE, which resulted in shorter transits to and from shore. Type 3 dives resembled Weddell seal (*Leptonychotes weddellii*) presumptive transit dives with extended durations at shallow depths for efficient locomotion while remaining within the ADL (Schreer and Testa, 1996; Williams, 2001).

The depth and duration of dives in this study were similar to those of females near the Otago Peninsula (Auge et al., 2011a). In contrast, females from the Auckland Islands made deeper (dive depth ~125 m) and longer (dive duration > 3 min) dives, with maximum depths up to nearly 600 m (Chilvers et al., 2006; Crocker et al., 2001; Costa and Gales, 2000; Chilvers and Wilkinson, 2009). The short dive durations in our study resulted in more frequent dives and a higher percentage of time spent diving than observed for females (8.1 dives h^{-1} and 45% of at sea time spent diving) in the Auckland Islands (Costa and Gales, 2000). Longer dive durations may require longer interdive intervals if the ADL is exceeded (Kooyman et al., 1980; Kooyman et al., 1983). During a dive bout, the total time spent submerged is increased by making many repetitive dives that are within the ADL because the recovery time at the surface replenishing blood and muscle oxygen stores is short (Kooyman et al., 1981; Davis 2019). However, Pinnipedia may make deep, long dives that exceed their ADL and require longer, post-dive recovery if prey capture is enhanced. Ultimately, foraging strategy will depend on the rate of prey ingestion (i.e., catch per unit effort or CPU). Submerged time is maximized at the individual dive-scale by prolonging dive duration but maximized at the bout-scale by remaining within the ADL to shorten surface recovery periods between dives (Kooyman et al., 1981). Stewart Island females perform dives of intermediate depth (~60 m) and duration (~2.5 min), indicating a different foraging strategy (Chilvers, 2018a). These regional differences in the diving behavior in NZSL indicate spatio-temporal differences in prey type and availability (Auge et al., 2011a). Regional differences in the diving behavior have been observed at San Cristobal Island for Galapagos sea lions (*Zalophus wollebaeki*), which display two main foraging behaviors. Individuals that forage north of the island have greater dive depths and durations, while those that travel west have increased bottom durations and total number of dives (Paez-Rosas et al., 2017). The diving and foraging behavior of Antarctic fur seals (*Arctocephalus gazella*) also differ throughout their range based on food availability (Staniland et al., 2010).

The metabolic cost of surface swimming and the three dive types were similar. Type 1 dives, which may have been associated with benthic foraging, had the lowest metabolic rate (10-13% less than Type 2 and 3 dives) because of reduced swim speed and flipper stroke frequency, primarily during the bottom phase. As a result, Type 1 dives had a longer ADL, which increased time for benthic foraging (Table 3.1). However, the slower swimming speed resulted in the highest cost-of-transport (COT; 3.9 J m^{-1} kg^{-1}) for Type 1 dives compared to that for Type 2 and 3 dives (2.8 and 2.7 J m^{-1} kg^{-1}, respectively), which were similar to that of captive Southern sea lions (Dassis et al., 2012).

We estimated the mass specific metabolic rates (power) for resting onshore, surface swimming, and diving during the 33.6 hr monitoring period recorded by the VDR (Table 3.6). Resting onshore accounted for 21% of the monitoring period with a metabolic rate of 2.0 W kg^{-1}, which was 2.2-fold higher than the predicted resting metabolic rate of 0.9 W kg^{-1} for a terrestrial carnivore of similar body mass (Davis, 2019). Surface swimming accounted for 22% of the monitoring period with a metabolic rated 4.8 W kg^{-1}, which was 2.4-fold higher than the resting metabolic rate onshore. The metabolic rate for diving ranged from 4.3-4.9 W kg^{-1}, with a maximum for Type 3 dives and a minimum for Type 1 dives (Table 3.6). However, because of their frequency and long duration, Type 1 dives represented 32% of the total time and 34% of the total energy expenditure. The overall mean metabolic rate or Field Metabolic Rate (FMR; 4.0 W kg^{-1}) during the monitoring period was 2.0-fold higher than that for resting onshore. Our estimated FMR was 27% less than that for Auckland Islands females (5.5 W kg^{-1}), possibly due to differences in methodology or at-sea behavior (Costa and Gales, 2000).

To balance the estimated total energy expended during the 33.6 hr monitoring period, the female needed to ingest 84,704 kJ (Table 3.5), which is the equivalent of 12.3 kg of prey assuming a mean energy content of 6.9 kJ g^{-1} for snake mackerel and jack mackerel (*viz*. 84704 kJ ÷ 6.9 kJ g^{-1} ÷ 1000 g kg^{-1}) (Auge et al., 2012a). This is equivalent to 8.8 kg day^{-1} or 7.0% of body mass daily (*viz*. 8.8 kg ÷ 126 kg), which is 1.4-fold larger than the mean consumption (~5% body mass daily), but less than the maximum food consumption (~10% body mass daily) for captive female California sea lions (*Zalophus californianus*) of similar body mass and energy-dense diet, primarily of mackerel (*Scomber scombrus*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*) (Kastelein et al., 2000). Our estimated prey consumption does not include the energetic cost of lactation in the two females with pups. However, the predicted daily food consumption of pregnant female Steller sea lions (*Eumetopias jubatus*) with pups is 11 ±

1.9% of body mass on a mixed diet (Winship et al., 2002). If this percentage were true for the pregnant, lactating females in our study, then food consumption would be 13.9 kg day^{-1}.

This was the first study of the home range and diving behavior of NZSL along the Catlins Coast. Mean total home ranges were small and restricted to coastal areas compared with that for females in the Auckland Islands. The inshore home ranges primarily occurred along local estuarine and sandy beach habitats. Three dive types were identified, and Type 1 dives were consistent with shallow benthic foraging on demersal prey with surface swimming among foraging areas. Differences in diving behavior and estimated FMR indicated spatio-temporal differences in prey type and availability between populations of NZSL on South Island and Auckland Islands. Compared with other populations, females along the Catlins Coast spent less time and energy foraging, which indicates plentiful, nearshore prey. Although reoccupation of their historic range on South Island will take decades, suitable habitat for breeding and prey availability along the southeast coast are encouraging.

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CHAPTER IV

SUMMARY AND CONCLUSIONS

Background and Project Basis

In this study, I focused on home range model selection, as well as home ranges and diving behavior of female New Zealand sea lions (hereafter referred to as NZSL) along the Catlins Coast. Home range model selection varies among Otariidae studies, with little justification of methods or evaluation of performance. Models are applied to entire distributions, and land locations are often removed from analysis. Kernel density estimators (KDE) are used to model home ranges for many species. These models depend on the choice of bandwidth parameter to produce probability density functions. Home ranges can vary widely based on differences in this parameter (Jones et al., 1996). Reference bandwidth kernel density estimation (RKDE) and plug-in bandwidth kernel density estimation (PKDE) use either broad or narrow bandwidth selection to generate probability densities and have displayed wide variations in performance in previous studies (Seaman and Powell, 1996; Gitzen et al., 2006; Jones et al., 1996; Millspaugh et al., 2006). Local convex hulls (LOCOH) connect locations with straight lines to produce spatial polygons and can be more appropriate in habitats with hard boundaries (Getz et al., 2007; Chirima and Owen-Smith, 2017). LOCOH models have not been applied to Otariidae distributions.

NZSL are income breeders and females make alternating foraging trips and time onshore while nursing a pup until weaning (Davis, 2019). The home ranges, total distanced travelled, maximum distance from the colony, trip duration, and diving behavior during foraging trips vary geographically among colonies. Females in the Auckland Islands have expanded home ranges and swim longer total distances and maximum distances from the colony than do females on Stewart and South Islands. Dives are deeper and longer in duration around the Auckland Islands than those of females on Stewart and South Islands, and females exceed their aerobic dive limit (ADL) on a higher percentage of dives. Hypotheses for these contrasts include marginal habitat around the Auckland Islands, with less accessible, energy-dense prey compared to Stewart and South Islands (Auge et al., 2011a; Auge et al., 2011b; Auge et al., 2012a).

The home ranges and diving behavior of the recently established Catlins Coast breeding colony have not been studied. The number of breeding females is low but increasing along this coast, contributing to the increasing pup production on South Island after a nearly 300-year absence. Understanding the movements and ranges of NZSL along the Catlins Coast is a crucial part of protecting and promoting the reoccupation of their historical range. Based on this information, my research objectives were:

1) To evaluate the performance of home range models applied to NZSL semi-aquatic distributions in order to determine the most accurate model or combination of models.

2) To track the movements and record the diving behavior of females to identify home ranges, characterize diving behavior, estimate energy expenditure, and identify inshore habitat associations.

I hypothesized that home ranges, foraging trip characteristics, and diving behavior would resemble those of females at Otago Peninsula due to geographic proximity and habitat similarity. To accomplish these objectives, I attached satellite telemeters and animal-borne video and data recorders (VDRs) to female NZSL to collect locations during foraging cycles and monitor foraging and diving behavior. Three home range models [1) LOCOH, 2) PKDE, and 3) RKDE] were applied to filtered satellite locations and evaluated over total, inshore, and offshore ranges using cross-validation. The VDRs provided high-resolution data on dive characteristics, foraging behavior, and swimming performance, including three-dimensional movements based on speed, heading, and depth.

Home Range Model Evaluation

Total home ranges were most accurately modeled by LOCOH. However, LOCOH performance varied among females, as evidenced by the large 95% CI range compared to PKDE and RKDE models. Total home ranges using all locations (i.e., inshore and offshore) reflected sampling bias. The disproportionately large percentage of onshore locations created total home ranges centered around these areas, which likely did not reflect the actual utilization distribution (UD) of females. Because of this bias, total home ranges were not preferred, and we modeled inshore and offshore home ranges separately.

The most accurate inshore and offshore home range estimates for female sea lions used LOCOH and PKDE models, respectively. The LOCOH model, which was the most accurate for the inshore home range, consistently excluded unused areas. Cliffs and rocky shorelines presented barriers to inshore movement, which interspersed with high-use sandy beaches and estuaries. These geographic boundaries to inshore home range were most appropriately handled by the LOCOH model compared to the KDE models, which expanded into unused areas. For locations constrained spatially by complex environments, LOCOH home range models may perform more accurately than traditional KDE methods.

PKDE probability distributions were consistently the most accurate with the smallest variation among the three models for offshore distributions. In environments with less restrictive barriers to movement, kernel density models may more accurately reflect distributions. The PKDE bandwidth selector handled distributions with multiple centers of activity and linking corridors more accurately than did other estimators.

RKDE home ranges were larger than the other two methods for total, inshore, and offshore habitats. This method overestimated areas and included unused portions of ranges (type I error). The difference in cross-validation performance between PKDE and RKDE indicated the importance of smoothing parameters for KDE methods. Bandwidth selection directly influenced the resulting probability distributions, and factors such as distribution and sample size should be evaluated during the selection of smoothing parameter. Studies employing kernel home range methods should consider the underlying UD and study goals in choice of smoothing parameter.

The separation of inshore and offshore habitats and habitat-specific home range modelling has not been attempted before with sea lions or fur seals. Future home range studies should consider modeling home ranges with a combination of models to achieve the overall greatest accuracy. Combining LOCOH and PKDE created a more accurate representation of spatial use than did total home ranges for this semi-aquatic species.

Previous studies have largely ignored inshore locations in favor of aquatic foraging home ranges and have modeled home ranges using various models and smoothing parameters (Auge et al., 2011b; Baylis et al., 2015; Bishop et al., 2018; Chilvers et al., 2005; Chilvers et al., 2011; Fowler et al., 2007; Leung et al., 2012; Robson et al., 2004; Rodriguez et al., 2013). Dividing home ranges into habitats and verifying model selection will better represent spatial use.

Home Ranges and Diving Behavior

Total home ranges of female NZSL along the Catlins Coast were small and restricted to coastal areas. The females with and without pups had inshore core ranges within the Catlins River estuary (CRE) and overlapped estuarine and sandy beach habitats along the coastline, indicating that the Catlins Coast contains areas suitable for NZSL throughout the year. The offshore home ranges were largely restricted to areas < 3 km from shore, though individual variation existed along the Catlins Coast. The frequency and time with which these females use the CRE and adjacent habitats make it an important area for management and conservation efforts that enhance breeding and population recovery. The results indicate that the females in our study foraged and spent time onshore within smaller spatial scales compared with those for females in the Auckland Islands, perhaps because of access to greater food resources. These characteristics are consistent with female NZSL foraging and time onshore in breeding colonies at Otago Peninsula and Stewart Island.

Compared to female NZSL on the Auckland Islands, females along the Catlins Coast made short foraging trips and spent less time onshore, which may be explained by a combination of prey accessibility and seasonality. Times at sea were comparable to those of females at Otago Peninsula, which indicate coastal foraging and locally accessible resources in newly reoccupied areas. They also indicate the lack of a seasonal shift from coastal to offshore prey during the pup dependency period as seen in southern sea lions (*Otaria flavescens*) (Drago et al., 2010). Females on the Auckland Islands forage for periods up to 6-fold longer. The shorter times on land along the Catlins Coast compared to those of females at Otago Peninsula and Stewart Island may have been associated with the stage of reproduction, as time on land is negatively correlated with pup age within Otariidae (Gentry and Kooyman, 2014). Females with dependent pups in our study may have spent less time onshore than they would have earlier in the year with young pups, in part because older pups are capable of foraging.

Most dives were shallow (< 15 m) and short duration (< 2 min) with a moderate swim speed (1.5 m s^{-1}) and short interdive interval (0.6 min). I identified three dive types within the dive record. Type 1 dives were the deepest and longest in duration, had the steepest descent and ascent angles, the longest bottom phase (77% of dive duration), the slowest bottom speed, and a tortuous dive path with small fluctuations in dive depth. This dive behavior was indicative of area intensive searching behavior with prey pursuit on the seafloor. Possible prey species included snake mackerel (*Thyrsites atun*), jack mackerel (*Trachurus* sp.), red codling (*Pseudophycis bachus*), and Maori octopus (*Macroctopus maorum*) (Auge et al., 2012a; Milne, 1996). Type 2 dives were the most common, but they were the shallowest and shortest in duration, with a high swim speed and tortuous dive path. Their prevalence may indicate that Type 2 dives involve searching behavior or mid-water feeding on benthopelagic species. Type 3 dives were intermediate in depth, total duration, and bottom duration compared to Type 1 and 2 dives. Based on their high swim speed, linearity, high percentage of time in the bottom phase, and shallow ascent angle, Type 3 dives may be associated with transiting.

The depth and duration of dives in this study were similar to those of females around the Otago Peninsula (Auge et al., 2011a). In contrast, females from the Auckland Islands made deeper and longer dives, with maximum depths up to nearly 600 m (Chilvers et al., 2006; Crocker et al., 2001; Costa and Gales, 2000; Chilvers and Wilkinson, 2009). The short dive durations in our study resulted in more frequent dives and a higher percentage of time spent diving than observed for females in the Auckland Islands (Costa and Gales, 2000). These regional differences in the diving behavior in NZSL indicate spatio-temporal differences in prey type and availability (Auge et al., 2011a).

The metabolic cost of surface swimming and the three dive types were similar. The metabolic rate for at-sea activities ranged from 4.3-4.9 W kg^{-1}, with a maximum for Type 3 dives and a minimum for Type 1 dives due primarily to differences in flipper stroke frequency. Our estimated FMR was 27% less than that for Auckland Islands females, possibly due to differences in methodology or at-sea behavior (Costa and Gales, 2000). To balance the estimated total energy expended during the 33.6 hr monitoring period, the female needed to ingest 8.8 kg day^{-1} or 7.0% of body mass daily. This estimate does not include the energetic cost of lactation in the two females with pups, which may increase daily food consumption to ~14 kg day^{-1}.

Final Thoughts

Physical and biological environmental conditions influence the foraging behavior of Pinnipedia (Melin et al., 2008; Burns et al., 2004; McConnell et al., 1992; Villegas-Amtmann et al., 2011; Saijo et al., 2017) and Cetacea (Torres and Read, 2009; Davis et al., 1996; Wells, 2019). While foraging, marine mammals are constrained by their physiological requirements and oxygen stores necessary to maintain aerobic metabolism (Ladds et al., 2020). Deep diving Phocidae and Odontoceti forage in oceanic (i.e., meso- and bathypelagic) zones, while Otariidae and small Odontoceti often forage in the neritic (i.e., epipelagic) zone (Davis, 2019 Appendix 3). Within species, diving behavior can vary spatiotemporally, reflecting the influence of environmental variables (Aurioles-Gamboa and Zavala-González, 1994; Paez-Rosas et al., 2017; Staniland et al., 2010). Many marine mammals forage in environments where prey is patchy and must travel among prey patches to acquire energy. In these cases, predators are hypothesized to maximize the net rate of energy gain, represented by the equation (Sinervo, 2013):

Equation 4.1 *Net Energy Gain = Total Energy Gain - (Energetic cost of Travel + Foraging)*

Animals can maximize net energy gain by increasing energy intake (e.g., consume more prey mass, select energy-dense prey), decreasing the energetic cost of traveling or foraging, or a combination of the two. For South Island NZSL, prey appears to be abundant and locally available, which enhances the rate of energy gain. In contrast, Auckland Islands NZSL travel farther and longer while foraging, which reduces net energy gain and affects body condition. NZSL at the Auckland Islands may then be more susceptible to fisheries competition because the energetic cost of foraging may have been elevated before commercial fisheries reduced prey availability (Costa et al., 2004; Robertson and Chilvers, 2011). Differences in environmental and anthropomorphic conditions between these populations have direct impacts on energy acquisition, recent population trends, and fitness.

Compared with NZSL on the Auckland Islands, the small home range and short foraging trips with shallow dives of females along the Catlins Coast indicate a group of animals meeting their energetic requirements with relative ease. The southeastern coast of South Island appears to have ample habitat for breeding colonies and further reoccupation of historic habitat. Future research and monitoring should focus on annual foraging ecology, specifically the identification of prey species, and habitat associations. As breeding colonies expand, competition and interactions with commercial and recreational fisheries will increase. Onshore conservation policies should reduce negative interactions with humans (e.g., disturbance, injury, vehicle strikes), as these incidents pose the greatest current threat on South Island. Although reoccupation of their historic range will take decades, the results of this study are encouraging for the future of NZSL on South Island.

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