

**MOVEMENTS AND HOME RANGES OF HARBOR SEALS (*PHOCA VITULINA*)
IN THE INLAND WATERS OF THE PACIFIC NORTHWEST**

By

Sarah E. Hardee

Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

Moheb A. Ghali, Dean of the Graduate School

ADVISORY COMMITTEE

Chair, Dr. Alejandro Acevedo-Gutiérrez

Dr. Benjamin Miner

Dr. Merrill Peterson

MASTER'S THESIS

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Western Washington University, I grant to Western Washington University the non-exclusive royalty-free right to archive, reproduce, distribute, and display the thesis in any and all forms, including electronic format, via any digital library mechanisms maintained by WWU.

I represent and warrant this is my original work, and does not infringe or violate any rights of others. I warrant that I have obtained written permissions from the owner of any third party copyrighted material included in these files.

I acknowledge that I retain ownership rights to the copyright of this work, including but not limited to the right to use all or part of this work in future works, such as articles or books.

Library users are granted permission for individual, research and non-commercial reproduction of this work for educational purposes only. Any further digital posting of this document requires specific permission from the author.

Any copying or publication of this thesis for commercial purposes, or for financial gain, is not allowed without my written permission.

Signature _____
Date _____

**MOVEMENTS AND HOME RANGES OF HARBOR SEALS (*PHOCA VITULINA*)
IN THE INLAND WATERS OF THE PACIFIC NORTHWEST**

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Sarah E. Hardee

June 2008

**MOVEMENTS AND HOME RANGES OF HARBOR SEALS (*PHOCA VITULINA*)
IN THE INLAND WATERS OF THE PACIFIC NORTHWEST**

by

Sarah E. Hardee

ABSTRACT

Marine resources are under increasing human pressure and conservation managers are using tools such as marine reserves to increase target fish stocks. However, marine predators may respond to the resultant changes in fish abundance. Harbor seals, *Phoca vitulina*, are abundant marine predators in the inland waters of the Pacific Northwest with the potential to influence the recovery of depressed fish stocks, yet relatively little is known about their movement patterns and home range sizes in the region. To describe harbor seal behavior, I deployed satellite and time-depth recorder tags during April and May 2007 on 20 individuals at three haul-out sites in the inland waters of the Pacific Northwest: six at a rocky reef site in the eastern San Juan Islands, six at an estuarine bay site directly east of the San Juan Islands and eight at a rocky reef site in the Canadian Gulf Islands. Tags were deployed for a mean (\pm SD) of 110 (\pm 32) d and transmitted a mean 726 (\pm 382) satellite locations seal⁻¹. Satellite locations allowed me to quantify distances moved from the capture site, minimum convex polygon size, home range size, utilization of candidate marine reserve sites in the eastern San Juan Islands and haul-out site fidelity. This study used novel analysis techniques, including weighting satellite transmissions to account for autocorrelation within the data to calculate harbor seal home ranges using fixed kernel density estimates. Overall, harbor seals moved

farther than previously documented in the region and their behavior, including distance traveled, home range size and haul-out site fidelity, appeared to be influenced by haul-out site. There was no effect of month or season on the behavior of the harbor seals. Harbor seals from the rocky reef sites moved farther distances for longer periods of time and utilized haul-outs over a wider geographic distribution than seals from the bay site. Three individuals from the rocky sites traveled to the Pacific coast of Washington and British Columbia and then returned one to two months later, a roundtrip distance > 200 km. Additionally, seals from the rocky reef haul-outs had segmented home ranges, with core areas of use up to 100 km apart. Despite moving greater distances than previously estimated within the region, harbor seals rarely utilized the space within candidate marine reserves. Less than 4.5 % of all satellite transmissions fell < 3 km from the boundaries of the reserves. It is likely that harbor seals from rocky reef haul-outs moved greater distances than previously assumed in search of prey. The long-distance movements of tagged individuals suggest that seals from distant haul-outs could visit candidate marine reserves in the eastern San Juan Islands, consequently increasing the pool of predators that could potentially impact such sites. Combining these observations with synchronous diet and diving behavior analyses will provide comprehensive baseline behavior, which will allow us to determine how harbor seals interact with the recovery of target fish species within the inland waters of the Pacific Northwest.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Alejandro Acevedo-Gutiérrez for his patience, support, advice and for bringing me onto this project. I would also like to thank my committee members, Dr. Benjamin Miner and Dr. Merrill Peterson for their suggestions, questions, support with statistical analyses and most of all, for their time.

This project has been successful due to the support and advice of our collaborators: Steven Jeffries and Monique Lance from the Washington Department of Fish and Wildlife, Peter Olesiuk from the Department of Fisheries and Oceans, and Dr. Phil Levin, Dr. Greg Williams and their team at the National Marine Fisheries Service, to all of whom I am very appreciative of their constructive comments and guidance. Thank you so much to all of the members of the tagging crew, including Dyanna Lambourn, Bryan Murphie, Tom Cyra, Joe Gaydos and numerous others who spent many a cold day out on the water to help us catch the harbor seals we needed for this research. I would also like to thank the pilots who flew aerial surveys and Christina Ball from Washington Department of Fish and Wildlife for passing on her technical expertise counting harbor seals in digital images.

Gene McKeen and Nate Schwarck at Shannon Point Marine Center were instrumental in the support of our boating and logistics out of Anacortes. Many, many thanks to Pam Davis for providing us with dock space where we could leave our research vessel. Thanks to Peter Thut and the stockroom at Western Washington for other research materials.

I am greatly appreciative for the field and laboratory support provided by a number of wonderful undergraduate research assistants: Sara Cendejas-Zarelli, Amanda Chomos, Patrick Haggerty, Kelsea Peterman and Tyler Ritchie. Thanks also to my fantastic

colleagues in the Marine Behavior and Ecology Lab at Western Washington for support and advice through the duration of this project: Adria Banks, Jessica Farrer, Katie Luxa, Sasha McFarland, Sarah Schuster-Howard, Kenady Reuland and Austen Thomas.

I am grateful to the many funding sources that have supported this project and me over the last two years. I was supported by a Research Assistantship in Estuarine Science and Coastal Zone Management from the Padilla Bay National Estuarine Research Reserve, a GK-12 Fellowship from the National Science Foundation, the Biology Department, the Office of Research for Sponsored Programs, the Ross Travel Grant from Western Washington University and the National Science Foundation (Award #0550443 to A. Acevedo-Gutiérrez).

Lastly, I send out my heartfelt thanks to my fellow graduate students, GK-12 colleagues, my family and Michael Peterson for their friendship and support throughout this project.

TABLE OF CONTENTS

ABSTRACT	iv
ACKNOWLEDGEMENTS	vi
LIST OF FIGURES	x
LIST OF TABLES	xii
LIST OF APPENDICES	xiii
INTRODUCTION	1
Marine protected areas	3
The Georgia Basin	3
Predator abundance and movements relative to marine reserves	4
Harbor seal movements and home ranges	6
Research objectives	11
METHODS	13
Study site	13
Abundance	13
Data collection	13
Data analysis	17
Movement patterns and home ranges	18
Data collection	18
Captures	18
Satellite tags	19
Data analysis	21
Filtering methods	21
Geographic information systems	23
Linear mixed effects models	23
Movement patterns	25
Home ranges	26
Spatial use near candidate marine reserves	28
Data analysis	28
Site fidelity	29
Data analysis	29
RESULTS	30
Abundance	30
Movements and home ranges	30
Captures and filtering	30
Distance traveled	33

Bird Rocks	36
Padilla Bay	36
Belle Chain.....	36
Minimum convex polygons	36
Male minimum convex polygons.....	41
Sex comparison for Padilla Bay.....	41
Home ranges	41
Bird Rocks	42
Padilla Bay	47
Belle Chain.....	47
Male home ranges.....	50
Sex comparison for Padilla Bay.....	50
Spatial use near candidate marine reserves.....	50
Site fidelity.....	51
Bird Rocks	51
Padilla Bay	58
Belle Chain.....	58
DISCUSSION	59
Abundance	59
Movements.....	60
Home ranges	66
Interaction with candidate reserves.....	68
Haul-out site fidelity	70
Conclusions.....	72
LITERATURE CITED	75
APPENDICES	83

LIST OF FIGURES

Figure 1. The study site in the Pacific Northwest: the Georgia Basin..... 2

Figure 2. Harbor seal capture sites in the Georgia Basin..... 14

Figure 3. Harbor seal capture sites relative to haul-out sites and candidate marine reserves in the eastern San Juan Islands..... 15

Figure 4. Harbor seal abundance estimates for the San Juan Islands and the adjacent bays (between Bellingham Bay and Similk Bay) over the last 10 years. 31

Figure 5. The 95th percentile (maximum distance) traveled by harbor seals from their haul out site..... 34

Figure 6. Mean distance traveled by harbor seals from their haul-out site..... 35

Figure 7. Minimum convex polygons of harbor seals relative to season..... 40

Figure 8. Home ranges (95th percentile contours) of harbor seals relative to season..... 45

Figure 9. Core areas (50th percentile contours) of harbor seals relative to season..... 46

Figure 10. Home range and core areas of harbor seal male # B1695 from Bird Rocks relative to season 48

Figure 11. Home range and core areas of harbor seal male # B1699 from Padilla Bay relative to season..... 48

Figure 12. Home range and core areas of harbor seal male # B1704 from Belle Chain relative to season..... 49

Figure 13. Home range and core areas of harbor seal male # B1709 from Belle Chain relative to season..... 49

Figure 14. Location of satellite-tagged harbor seals during April – October 2007 in relation to the candidate marine reserves..... 52

Figure 15. Haul-out sites with harbor seals present during the aerial pupping surveys < 40 km from the candidate marine reserves..... 53

Figure 16. Haul-out regions with the highest percentage of haul-outs for each harbor seal with a recovered time-depth recorder tag (n = 11)..... 55

Figure 17. Location of haul-out bouts for satellite-tagged seals in the Georgia Basin..... 56

Figure 18. Location of haul-out bouts for satellite-tagged seals around the San Juan Islands... 57

LIST OF TABLES

Table 1. Harbor seals captured in April and May 2007 at three haul-out sites in the Georgia Basin.....	32
Tables 2a-d. Minimum convex polygon LME model summary relative to season.....	38
Table 3. Minimum convex polygon areas relative to month, season and the entire study period.....	39
Tables 4a-d. Home range LME model summary relative to season.....	43
Table 5. Haul-out regions used by seals from the three haul-out sites.....	54

LIST OF APPENDICES

Appendix 1. Filtering method comparison..... 83

Appendix 2. Distance from capture haul-out site..... 84

Appendix 3. Harbor seal minimum convex polygon size relative to month and duration
of study..... 104

Appendix 4. Male harbor seal minimum convex polygon and home range size..... 109

Appendix 5. Harbor seal movements and home ranges in Padilla Bay relative to sex and
season..... 114

Appendix 6. Individual harbor seal home ranges and core areas relative to season..... 117

Appendix 7. Harbor seal home ranges relative to month and the duration of study..... 119

Appendix 8. Harbor seal haul-out regions relative to individual..... 127

Appendix 9. Home range maps for each individual harbor seal relative to season..... 129

INTRODUCTION

Marine habitats are highly productive and economically valuable; however, they have suffered years of harmful fishing practices and habitat degradation, and are under increasing pressure to provide ecological goods and services (Griffis & Kimball 1996). Marine protected areas, especially marine reserves, are a conservation tool used to increase target fish stocks and improve habitat (Tuya et al. 2000, Eisenhardt 2002, Parnell et al. 2005). The inland waters of the Pacific Northwest include the inland marine waters of Washington State and British Columbia, Canada, and are often referred to as the Georgia Basin (Figure 1). This region contains numerous depressed fish species (Musick et al. 2001) of which populations of rockfish (*Sebastes* spp.) are of particular interest to conservation managers in the eastern San Juan Islands, which lead to the proposal of candidate marine reserve sites to aid in their recovery (McConnell & Dinnel 2002).

Predation by pinnipeds (seals, fur seals, sea lions and the walrus) has the capacity to impact the recovery of depressed fish stocks (Mohn & Bowen 1996, Fu et al. 2001, London et al. 2002). Harbor seals (*Phoca vitulina*) are abundant, resident marine predators in the Georgia Basin that consume a variety of fish and invertebrates (Scheffer & Sperry 1931, Everitt et al. 1981, Olesiuk 1993, Laake et al. 2002, Lance & Jeffries 2006, Lance & Jeffries 2007, Wright et al. 2007). As such, they have the potential to significantly affect depressed fish stocks (Bax 1998, London et al. 2002) and possibly impact the success of marine reserves. To understand the role of harbor seals and predict their foraging pressure upon certain fish species, such as rockfish, we must first describe their abundance and movements. However, these behaviors are not well understood in the Georgia Basin.

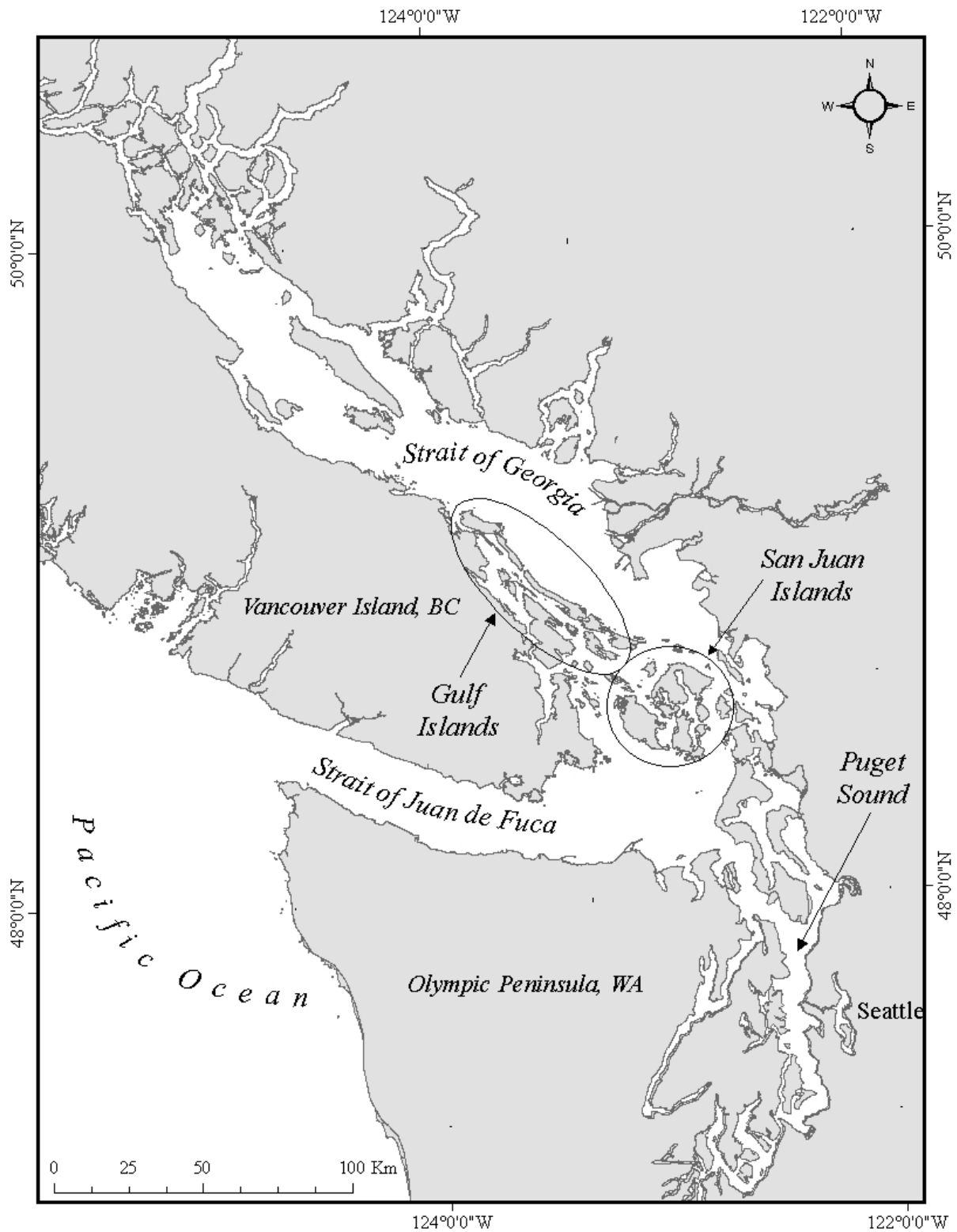


Figure 1. The study site in the Pacific Northwest: the Georgia Basin. The Georgia Basin encompasses Puget Sound, the San Juan Islands, the Canadian Gulf Islands, the Strait of Juan de Fuca and the Strait of Georgia.

Marine protected areas

Marine protected areas are a conservation management tool intended to increase target populations of marine organisms by providing varying levels of protection and resource extraction within their boundaries (Musick et al. 2001). Marine protected areas are defined as “any area of the marine environment that has been reserved by Federal, State, territorial, tribal, or local laws or regulations to provide lasting protection for part or all of the natural and cultural resources therein” (Clinton 2000). Higher densities and biomass of species are supported within the boundaries of marine protected areas relative to adjacent unprotected habitats (Eisenhardt 2002, Parnell et al. 2005, Guidetti 2007). Marine reserves, also known as ‘no-take’ marine protected areas, are a subset of marine protected areas that provide complete protection to biotic and abiotic resources found within the reserve.

Marine reserves are implemented to accomplish numerous goals, which include increasing the biomass and density of target organisms, protecting critical spawning stocks and improving community habitat (Yoklavich 1998, Palsson 2002). Depending on individual species’ mobility and life history stages, marine reserves may protect all of an organism’s life stages or certain vulnerable stages. Prohibiting the removal of abiotic or biotic resources may improve community composition by protecting the habitat for target and non-target organisms within the reserve.

The Georgia Basin

The Georgia Basin contains a wide array of biological diversity and economic interests. However, formerly viable and economically successful fisheries have collapsed in the region, including salmonids (family Salmonidae), Pacific herring (*Clupea pallasii*),

Pacific cod (*Gadus macrocephalus*), walleye pollock (*Theragra chalcogramma*), Pacific hake (*Merluccius productus*) and numerous rockfish species (*Sebastes* spp.) (Musick et al. 2001). These collapses have created the need to implement conservation strategies that will increase regional fish stocks to healthy and sustainable levels.

In the eastern San Juan Islands, the Skagit County Marine Resources Committee proposed eight candidate marine reserve sites, three of which have been recommended for implementation (Weispenning 2006). One impetus for recommending these reserves is to increase rockfish stocks, a previously important commercial fishery in Washington, which have declined to critically low levels (Mills & Rawson 2004). Creating reserves should protect fragments of the rockfish stocks from fishing as well as their habitat, theoretically allowing for stock recovery (Tuya et al. 2000).

Marine reserves and marine protected areas in general are well suited to rockfish life histories for several reasons. Rockfish can live up to 200 years, and there is evidence of infrequent recruitment success and therefore low reproduction rates (Love et al. 2002, Mills & Rawson 2004). Additionally, rockfish use small, localized areas; for instance, in the San Juan Islands 13 of 14 tagged adult rockfish stayed within a 100 m² area during a two month study (Mills & Rawson 2004). While reserves may work well for fish recovery, creating marine reserves raises questions regarding the potential impact of marine predators upon fish populations within the protected areas.

Predator abundance and movements relative to marine reserves

Before the potential effectiveness of the candidate marine reserves in the eastern San Juan Islands can be predicted, we need to understand the movements and foraging patterns of

predators that could impact stock recovery. Pinnipeds are marine predators requiring large quantities of fish and invertebrates to sustain their populations (Stenson et al. 1997, Trites et al. 1997). They consume depressed fish stocks in many places, including California (Stanley & Shaffer 1995), Oregon (Wright et al. 2007) and Washington (London et al. 2002).

While marine protected areas, specifically marine reserves, provide relief from human pressure, there is no guarantee as to how other predators will respond to increases in prey abundance within the reserve boundaries. Predators show two responses to changes in prey density: functional and aggregative. Aggregative responses are changes in predator spatial distribution in response to changes in prey abundance, while functional responses are shifts in diet composition, often attributable to an increased abundance of a particular prey species (Bax 1998, Middlemas et al. 2006). Both responses may occur in marine protected areas as prey abundance increases. As such, marine predators can prevent or inhibit stock increases of certain target species. For instance, marine protected areas in California contained decreased numbers of red abalone (*Haliotis rufescens*) where sea otters (*Enhydra lutris*) were present (Fanshawe et al. 2003).

California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) are all marine predators found within the Georgia Basin ecosystem; however, harbor seals are the most abundant of these pinnipeds in the region. Harbor seals are also the only year-round and non-migratory resident pinniped of the Georgia Basin, spending time in a variety of habitats that include estuarine mudflat-bays and rocky reefs (Olesiuk et al. 1990, Suryan & Harvey 1998, Huber et al. 2001, Jeffries et al. 2003). Numerous harbor seal haul-outs have been documented within close proximity to the three candidate marine reserve sites (Jeffries et al. 2000, Banks 2007). Haul-outs are sites where

harbor seals leave the water (“haul-out”) to thermoregulate, give birth to their pups and molt. Harbor seals are also opportunistic predators and prey upon more than 20 species of fish, including rockfish and invertebrates (Scheffer & Sperry 1931, Everitt et al. 1981, Olesiuk 1993, Laake et al. 2002, Lance & Jeffries 2006, Lance & Jeffries 2007, Wright et al. 2007). Thus they have the capacity to exert a negative impact upon marine reserves if they were to consume critically low populations of fish species found within their boundaries. To best predict the potential impact of harbor seals on the three candidate marine reserves we need an accurate estimate of current abundance and a comprehensive understanding of behavioral patterns in the region.

Harbor seal movements and home ranges

Harbor seal abundance in the Georgia Basin will affect estimates of foraging pressure, as larger populations require more resources. The inland waters of Washington contained more than 15,000 harbor seals as of 1999 (Jeffries et al. 2003), and the Strait of Georgia contained over 37,000 harbor seals as of 1998 (Olesiuk 1999). In both Washington and British Columbia harbor seal populations increased rapidly between the 1970s and the 1990s but have since stabilized (Olesiuk 1999, Jeffries et al. 2003), suggesting that foraging pressure has stabilized as well.

Harbor seal behavior, specifically movement patterns, home range size and haul-out site fidelity of harbor seals may affect their impact on depressed fish stocks and recovery efforts because the population may stay clustered in aggregations in a confined region (Thompson & Miller 1990) or seals may instead move diffusely and forage in multiple locations over a broader spatial scale (Lowry et al. 2001, Lesage et al. 2004). Haul-out type

may affect these behaviors and therefore affect foraging pressure by harbor seals. There are two types of haul-outs identified in the Georgia Basin: rocky reefs and estuarine mudflat-bays (Olesiuk et al. 1990, Jeffries et al. 2003). Both prey resources and suitability for pupping and molting may vary between these types of haul-outs. Harbor seal behavior has been studied at various sites around the world, including Scotland (Thompson 1989, Thompson et al. 1989), the Oregon coast (Bayer 1985, Harvey et al. 1990, Brown et al. 2005), Sweden (Harkönen et al. 1999), British Columbia (Olesiuk et al. 1990, Olesiuk 1993) and Washington (Suryan & Harvey 1998, Banks 2007). Previous research in the Georgia Basin examined movement patterns and haul-out site fidelity (McLanahan et al. 1984, Suryan & Harvey 1998, Huber et al. 2001). Data indicate that seals remain < 28 km of their haul-out sites with high haul-out site fidelity. This research relied on VHF radio-telemetry (McLanahan et al. 1984, Suryan & Harvey 1998, Huber et al. 2001), which provides an accurate description of movement at small spatial scales. Because VHF radio-telemetry requires line of sight to the tagged seals, it is difficult to track them over large spatial scales for extended periods of time or monitor them once they leave the study area. Additionally, research investigating movements was conducted on males during the pupping season from one haul-out site (Suryan & Harvey 1998). Consequently, we do not know how far away seals move when they are out of radio-telemetry range or if seals from estuarine mudflat-bays or rocky reef sites behave uniformly or whether haul-out type must be taken into account when predicting behavior.

Harbor seals, while described to be non-migratory (Scheffer & Slipp 1944), have been observed traveling different distances from a primary haul-out site. The majority of observations have placed seals < 50 km of a primary haul-out site (Brown & Mate 1983,

Thompson & Miller 1990, Thompson et al. 1996, Suryan & Harvey 1998, Huber et al. 2001). However, individual seals traveled > 220 km in Oregon (Brown & Mate 1983), 520 km in eastern Canada (Lesage et al. 2004) and 525 km in Alaska (Lowry et al. 2001). In the Georgia Basin, adult male seals radio-tagged and monitored between June and September of 1992 at Sucia Island traveled ≤ 28 km from their primary haul-out sites (Suryan & Harvey 1998). Further, the typical distance traveled to a foraging area was ≤ 5.6 km (Suryan & Harvey 1998). Although these results have informed future research and advanced knowledge of harbor seals in the region, the data were collected from males from one haul-out site during a four-month study beginning one month prior to pupping season. Consequently, it is unknown if the observed behaviors are indicative of foraging patterns of males during other temporal periods, of females in general or of seals from estuarine mudflat-bay sites. Male and female harbor seals radio-tagged and observed between June and September of 1983 in Padilla Bay were only observed < 15 km from their capture site (McLanahan et al. 1984). However, it is possible that VHF radio-telemetry in both studies was unable to capture all movements because the seals were moving farther than the reaches of the VHF-signal in the study area (Suryan & Harvey 1998). Satellite telemetry provides an alternative to VHF radio-telemetry that is able to pick up longer distance movements and more completely document spatial use.

Satellite telemetry is an increasingly useful method for determining movement patterns and home range size of animals ranging from sea turtles, *Chelonia mydas*, (Craig et al. 2004) to polar bears, *Ursus maritimus*, (Mauritzen et al. 2002), and has been used extensively with pinnipeds (Heide-Jørgensen et al. 1992, McConnell et al. 1992, Lowry et al. 1998, McConnell et al. 1999, Bonadonna et al. 2000, Guinet et al. 2001, Lowry et al. 2001,

Small et al. 2005, Austin et al. 2006). This technology allows data to be obtained over greater distances than is feasible using VHF-telemetry (Thompson et al. 1996, Suryan & Harvey 1998, Lesage et al. 2004). While there may be less fine-scale detail observed using satellite telemetry than VHF radio-telemetry, satellite technology documents animal locations and has been used to quantify movements, calculate home ranges and assess site-fidelity over the entire extent of an animal's range.

Home range size is an important indicator of how much space an animal is using for survival and has been defined as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943). Home ranges are often described using the 95th and 50th percentiles of a utilization distribution obtained from kernel density estimates, which give probabilities of finding an animal in a particular location. The 95th percentile is commonly treated as the home range of an animal and the 50th percentile describes the core area of use (Dickson & Beier 2002, Hyrenbach et al. 2002, Seminoff et al. 2002, Tougaard et al. 2003, Lesage et al. 2004). Harbor seals tagged in Denmark demonstrated variability in home range sizes and spatial use, with a range of 95th percentile contours from 2,300 to 67,900 km² and a range of 50th percentile contours from 300 to 6,500 km² (Tougaard et al. 2003). To my knowledge, this technical report is the only literature describing home ranges of adult harbor seals using kernel density estimates. In Alaska, minimum convex polygons, which enclose the outer-most locations and assume uniform distribution throughout the entire enclosed region (Mohr 1947), were used to calculate harbor seal home ranges and adult home ranges were estimated between 300 and 17,000 km², whereas juveniles had even larger home ranges (Lowry et al. 2001). To my knowledge, there is no published literature analyzing home ranges of harbor seals in the Georgia Basin using

any method. Describing home ranges of harbor seals in the Georgia Basin will elucidate regions of greater use and can be a powerful tool in predicting areas under higher foraging pressure.

Haul-out fidelity, defined as the preference for one site over all others, is another aspect of harbor seal behavior that may influence their foraging impact, as it determines where seals begin and end foraging trips. Seals observed using VHF-telemetry in California demonstrated high fidelity to one haul-out site but may have traveled further distances than could be observed with radio-tracking equipment and hauled-out at distant sites (Yochem et al. 1987). Female seals tagged in a Scottish estuary used multiple haul-outs within several km of each other (Thompson et al. 1994), indicating variability in haul-out fidelity within a region. Within the Georgia Basin, nine out of 13 male seals tagged at Sucia Island, a rocky reef site, were faithful to one haul-out site 75% of the time (Suryan & Harvey 1998), indicating that the majority of males were using one primary site. Seals in Padilla Bay demonstrated high fidelity to the bay but switched haul-outs within the bay regularly; only one of ten tagged seals, a sub-adult female, was spotted repeatedly outside of the bay at a haul-out site 15 km from Padilla Bay (McLanahan et al. 1984). Research is needed in the Georgia Basin to broaden the temporal scope of haul-out site observations for males, include females and determine whether haul-out site fidelity is affected by the type of haul-out from which a seal is captured. Satellite telemetry may illuminate previously undetected haul-out behavior. It will be valuable to determine whether seals captured at different haul-outs in the Georgia Basin overlap in their haul-out use and movement patterns, which could indicate areas of foraging pressure, and the relation of these areas to candidate marine reserves.

Behavioral differences based on haul-out type may also be critical in understanding the impact of harbor seals on depleted fish populations. Estuarine (soft-bottomed) and non-estuarine (rocky) habitats exist within the Georgia Basin and haul-outs can be grouped into these two categories (Olesiuk 1993). Seals tagged in an Oregon estuarine bay moved short distances to an adjacent bay, possibly pursuing food resources (Brown & Mate 1983), while seals in Alaska and eastern Canada moved large distances from both rocky reef and estuarine haul-outs (Lowry et al. 2001, Lesage et al. 2004). Seals tagged at Sucia Island travelled varying distances up to 28 km (Suryan & Harvey 1998) while seals tracked from Padilla Bay were located almost entirely within the bay and were observed a maximum 15 km from the bay (McLanahan et al. 1984). Variability in harbor seal movements may be attributable to haul-out type, the availability of food resources in a particular habitat or a combination of these factors. To accurately predict the movement patterns of harbor seals in the Georgia Basin, we need to know whether seals hauled-out in rocky reefs show similar or dissimilar movement patterns to those hauled-out in soft-bottomed sites. This comparison can be carried out using satellite telemetry technology.

Research objectives

To better understand harbor seal behavior in the Georgia Basin and their potential impact on the candidate marine reserves in the eastern San Juan Islands, I aimed to answer four questions. These questions were investigated on two spatial scales, the larger of which was the Georgia Basin, which allowed me to gather data regarding regional behavior of harbor seals. Within the Georgia Basin, I was specifically interested in predicting the

possible influence of harbor seals on candidate marine reserves in the eastern San Juan Islands.

To be able to predict regional harbor seal presence in candidate marine reserves, I wanted to know how many harbor seals are in the San Juan Islands and the adjacent bays during the pupping season. To answer this question, I conducted aerial surveys around the three candidate marine reserves to count the number of seals hauled-out and applied a correction factor to obtain an entire population estimate.

Secondly, I wanted to know the movement patterns and home range size of seals in the Georgia Basin. To answer this question, I attached satellite transmitters to individual seals at three haul-out sites to describe the distances that they covered and calculate the size of their home ranges.

To bring my first two questions into the context of marine reserves and conservation, I wanted to know the spatial use of harbor seals in and around candidate marine reserves in the eastern San Juan Islands. This question had two components. The first was to describe how frequently candidate marine reserve sites were used by satellite-tagged harbor seals. The second was to use estimated population abundance (objective one) and observed movements (objective two) to predict if one candidate reserve might be used more by regional harbor seals than the others.

Lastly, I wanted to determine if satellite-tagged seals hauled-out in one geographic region or if they used haul-outs in different regions (i.e. site fidelity). To answer this question, I used time-depth recorder tags from each seal to determine the timing for haul-out bouts and matched haul-out bouts with high quality satellite transmissions to determine the location of haul-out sites.

METHODS

Study site

This research took place in the Georgia Basin, which includes the inland marine waters of Washington State, including the San Juan Island Archipelago and Puget Sound, the Canadian Gulf Islands of British Columbia, the Strait of Georgia and the Strait of Juan de Fuca (Figure 1). Harbor seals were captured and tagged at two sites in Washington and a third in British Columbia (Figure 2). Padilla Bay, a characteristic estuarine-mudflat habitat (48°28.37'N, 122°30.88'W), and Bird/Belle Rocks, a rocky reef habitat in Rosario Strait (48°29.16'N, 122°45.61'W), are both located in the eastern San Juan Islands. The third site was the Belle Chain Islets, a rocky reef in the southeastern Gulf Islands of British Columbia (48°49.67'N, 123°11.56'N). The candidate marine reserves in the eastern San Juan Islands are located slightly northwest of Deception Pass, between Burrows and Allen Islands and north of Cypress Island (Figure 3).

Abundance

Data collection

Harbor seal surveys conducted between the beginning of seasonal harbor seal pupping and molting result in the highest numbers of animals counted on land (Bayer 1985, Olesiuk et al. 1990, Olesiuk 1993, Harkönen et al. 1999, Jeffries et al. 2003). Therefore, aerial surveys conducted during pupping can be used to estimate the population of a particular region (Huber et al. 2001). Aerial surveys were conducted with collaborators from the Washington Department of Fish and Wildlife. The survey area included the San Juan

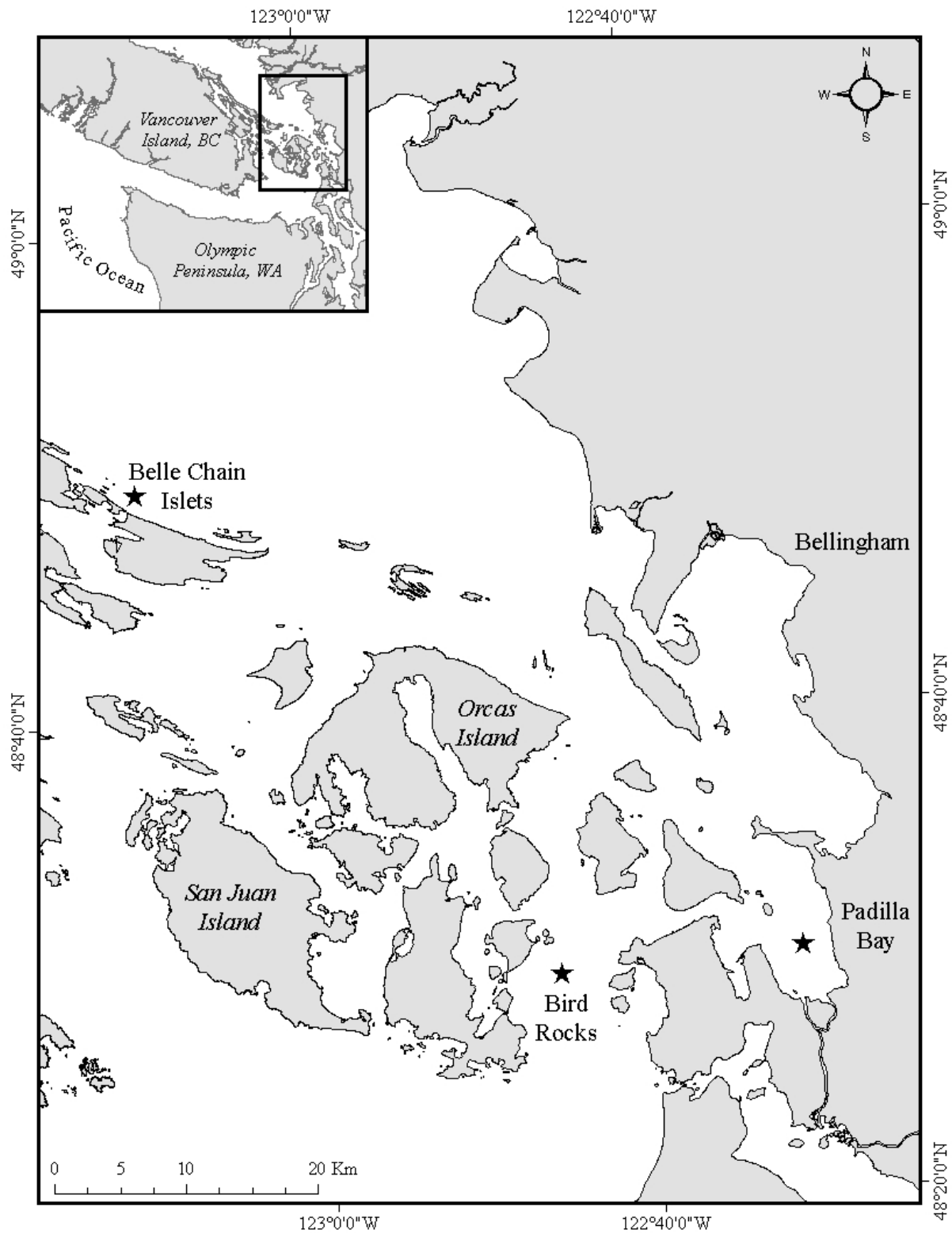


Figure 2. Harbor seal capture sites in the Georgia Basin. Each site is indicated by a star. Bird Rocks and the Belle Chain Islets are rocky reef sites and Padilla Bay is an estuarine mudflat-bay site.

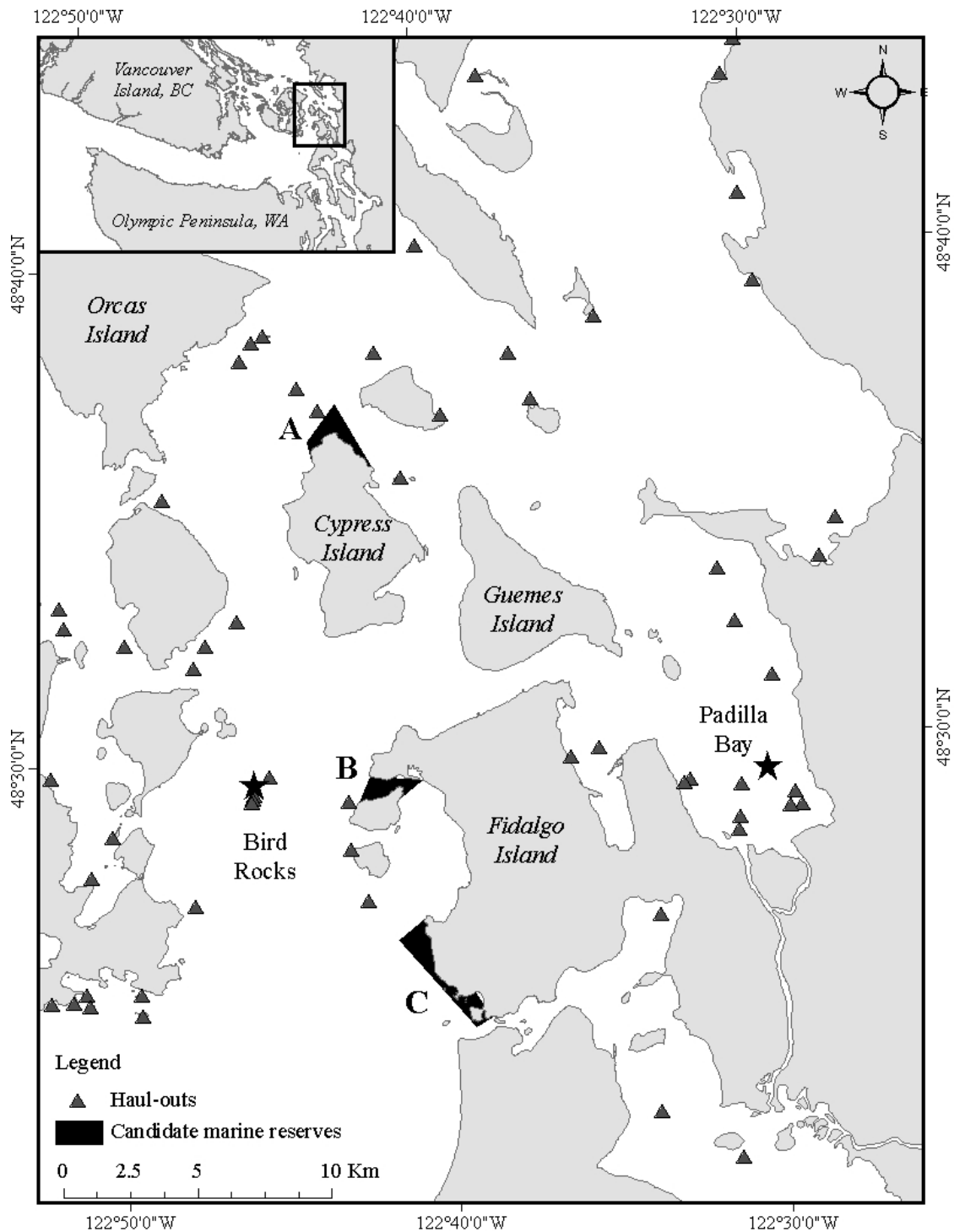


Figure 3. Harbor seal capture sites relative to haul-out sites and candidate marine reserves in the eastern San Juan Islands. Capture sites are indicated by stars. Bird Rocks is a rocky reef site and Padilla Bay is an estuarine mudflat-bay site. Haul-out sites are based on Jeffries et al. (2000). Candidate marine reserves are based on Weispfenning (2006): A = North Cypress Island, B = Burrows Channel and C = Sares Head.

Islands and eastern bays of Washington between Similk Bay and Bellingham Bay, encompassing a substantial section of the inland harbor seal stock (Jeffries et al. 2003). All of the proposed marine reserves and numerous harbor seal haul-out sites were located within the survey area. Counts were conducted only on hauled-out seals (Jeffries et al. 2003, Brown et al. 2005) during late July and mid-August (pupping season).

Harbor seal haul-out use and density in Washington have been surveyed previously with small aircraft at heights up to 350 m (Calambokidis 1979, Harvey et al. 1990, Olesiuk et al. 1990, Huber et al. 2001, Jeffries et al. 2003, Banks 2007). Following protocol from Jeffries et al. (2003), Washington Department of Fish and Wildlife collaborators and I flew surveys in a Cessna 185 at 200 – 300 m, moving at 90 kt, on two or three consecutive days during moderately low tides. We flew over the region moving with the tide, to cover the entire area within ± 2 h from low tide. Visual counts were taken on sites with < 25 seals and digital photographs and visual counts were taken concurrently at sites with > 25 animals, using a Nikon D100 with a 200 mm lens. The time was documented on the survey log for all haul-out counts, haul-out estimates and photographs. Surveys were conducted under permit 782-1702 awarded to the Washington Department of Fish and Wildlife by the Office of Protected Resources.

Selection of flight times was not only dependent on tidal conditions but also on time of day. In Scotland, time of day was more influential than tide height on the numbers of seals hauled-out (Thompson et al. 1989); however, along the British Columbia coast, relatively close to the study area, tide levels influenced haul-out behavior more than time of day (Olesiuk et al. 1990). If one chooses tidal heights that are extremely low, there is a risk that the survey underestimates the number of seals in the region because normal haul-out

sites may be inaccessible (Jeffries, pers. comm.)¹. Additionally, fog may become problematic for flying if the tide window, especially in August, is too early in the morning. We took these factors into account when selecting our survey dates.

Data analysis

In the lab, I used Photoshop and Photostudio to enlarge the digital photographs and count seals to obtain haul-out counts. Obtaining a visual count of seals on land records minimum numbers of seals; however total population size is more informative in determining foraging pressure. Counts for each haul-out site were averaged within a survey and the average counts were summed to obtain a total survey count. Difficulties arise in predicting total population size because there is no single time when the entire population is on land and it is challenging to determine the proportion in the water (Thompson & Harwood 1990). Nonetheless, a correction factor has been determined for the San Juan Islands for use during pupping where the total population of harbor seals is approximately 1.53 times the number of visible seals on land (Huber et al. 2001). Therefore, I used the correction factor with each total survey count to obtain a corrected total survey count. Corrected total survey counts were averaged between the two surveys to obtain a mean (\pm SD) count of harbor seals during pupping (July and August) and 95 % confidence intervals were calculated from these values. Confidence intervals did not include error in the correction factor. I also used the pupping counts to examine annual trends in seal abundance extending back to 1998 by comparing our yearly counts with historical Washington Department of Fish and Wildlife pupping counts.

¹ Steven Jeffries; Washington Department of Fish and Wildlife; 7801 Phillips Road SW; Tacoma, WA 98498; January 2007.

Movement patterns and home ranges

Data collection

Captures. To determine home range and movement patterns of harbor seals in the Georgia Basin, I utilized location data from adult satellite-tagged seals from three haul-out sites. Satellite tags have been successfully deployed on a variety of pinnipeds (Heide-Jørgensen et al. 1992, McConnell et al. 1992, Guinet et al. 2001, Lowry et al. 2001, Austin et al. 2004) and other animals (Mauritzen et al. 2002, Craig et al. 2004) to document behavior, and have not been shown to alter behavior of pinnipeds (Stewart et al. 1989). Six harbor seals were tagged in April and May 2007 from each of the Washington sites: Padilla Bay (n = 3 M, 3 F) and Bird/Belle Rocks (n = 5 M, 1 F). In May 2007, eight harbor seals were tagged in the Belle Chain Islets (n = 8 M). Seals were captured using several methods including beach seining, tangle-netting and boat rushes (Jeffries et al. 1993). Captures were led in Washington by our Washington Department of Fish and Wildlife collaborators and in Canada by a Department of Fisheries and Oceans collaborator. After entanglement in a net, seals were processed and tagged using the protocol developed by Jeffries et al. (1993). Seals were removed from the net and placed in individual hoop-nets. Individual seals were physically restrained while being sexed, weighed and measured (standard length), and to obtain samples of blood and blubber for our collaborators' work. Valium was administered to six males, dosages ranging from 3.0 – 4.4 ml, based on weight. Five seals were drugged intramuscularly and the sixth seal was given Valium intravenously. All animals were given a uniquely numbered cattle ear tag, attached to each hind flipper for future identification. The pelage of each animal was rinsed with seawater, washed with acetone, and dried using

compressed air, after which the instruments were attached using five-minute epoxy (Jeffries et al. 1993).

Satellite tags. SPOT5 satellite tags (Wildlife Computers, Redmond, WA) were placed on the heads of all 12 seals in Washington, six from Padilla Bay (n = 3 M, 3 F) and six from Bird and Belle Rocks (n = 5 M, 1 F). The tags emitted signals to receivers aboard polar-orbiting satellites thus obtaining the latitude and longitude locations for these seals while the tags remained attached. Mk10-F Fast-GPS time-depth recorder tags (Wildlife Computers, Redmond, WA) were placed on the upper backs of four individuals from Bird/Belle Rocks (n = 3 M, 1 F). Mk10-F time-depth recorder tags recorded depth and wet/dry status, which indicated if the animal was out of the water at the surface or underwater. The remaining eight animals were equipped with Mk9 time-depth recorder archival tags (Wildlife Computers, Redmond, WA), which recorded depth and wet/dry status analogous to the Mk10-F tags. SPLASH tags (Wildlife Computers, Redmond, WA), which incorporate satellite telemetry with depth and wet/dry status, were placed on the upper backs of the eight seals from the Belle Chain Islets (n = 8 M). The combination of tags attached to each animal provided me with satellite-derived locations over the course of the study and allowed me to determine when the seal was out of the water. The average number of locations day⁻¹, the average number of auxiliary locations day⁻¹ and the average number of standard locations day⁻¹ did not vary between SPOT5 and SPLASH tags (ANOVA p > 0.05, ANOVA p > 0.05 and Kruskal-Wallis p > 0.05, respectively). Therefore I combined the results obtained by both tags.

Satellite tags transmitted from each animal until the animal molted and the tag fell off, usually occurring between August and October, or until there was a malfunction with the

tag itself and transmissions ceased. Satellite tags transmitted constantly, except during extended haul-out periods, which triggered a cessation of transmissions after an hour of transmissions from a dry tag until the tag was re-submerged in the water, at which point transmissions resumed. Mk10-F, Mk9 and SPLASH tags all had VHF-radio telemetry antennae on them, which allowed them to be located and then retrieved once they had been molted off the seals. A 19-ft steel-hulled inflatable research vessel was used in the San Juan Islands to track and retrieve these tags. If we were unable to locate the tags by boat we flew over the region in a small plane to search for the tags, which once located were retrieved by boat. We used additional vessels from the Washington Department of Fish and Wildlife or Department of Fisheries and Oceans to retrieve tags that fell off > 25 km from the haul-out sites in Washington.

Argos instruments, aboard polar-orbiting satellites, received transmissions from the tags and transmitted the locations back to a processing center, which then compiled data files with time, date, latitude, longitude and location quality of all transmissions on a monthly basis. Argos (2007) uses the Doppler effect on a transmission frequency to determine the location of a seal and assign a location quality based on the number of uplinks received by the passing satellite. Standard locations need more than four uplinks from the tag and are designated 1, 2 or 3, with assigned accuracies of approximately < 1000 m, 350 – 150 m, and < 150 m respectively (Argos 2007). Auxiliary locations receive four or less uplinks. Locations based on four uplinks are level 0, with > 1000 m accuracy and locations based on three and two uplinks are labeled as A or B, respectively, with no given accuracy (Argos 2007). The majority of satellite locations fall into the auxiliary location class (McConnell et al. 1992, Lowry et al. 1998, Bonadonna et al. 2000, Guinet et al. 2001) and have not been

extensively utilized in the literature for movement analysis, however removal of these auxiliary locations drastically reduces the size of data sets (McConnell et al. 1992, Lowry et al. 1998, Bonadonna et al. 2000, Guinet et al. 2001).

Data analysis

SATPAK 2003 (Wildlife Computers, Redmond, WA) was used to extract raw data from the Argos data files, converting them into analyzable data files. I removed Z locations, considered “failed” locations by Argos (2007), and converted the time from Greenwich Mean Time (GMT) into Pacific daylight time (PDT). Argos provides two possible locations for certain transmissions. I examined the second latitude and longitude pairs to see if they provided a better solution than the primary Argos provided solution. They were switched if it was obvious that the primary Argos solution was biologically improbable but the second Argos solution was biologically reasonable. Additionally, I removed the lower quality of two transmissions occurring ≤ 60 s of each other, and if both transmissions were of equal quality then the second transmission was removed. Afterwards, I employed filtering methods relying on speed thresholds to remove likely erroneous points from the data set.

Filtering methods. Data filtering techniques were designed to remove erroneous locations and allow for the utilization of acceptable auxiliary locations, thus doubling to tripling the size of the usable data set. The filtering method I used for final home range and movement analyses relied on the first two steps of a three-stage algorithm developed by Austin et al. (2003). To justify the use of the multi-step filter, I compared how my data responded to this multi-step filter with the filter created by McConnell et al. (1992), which is only the second step from Austin et al. (2003). (The results of this comparison are shown in

Appendix 1.) Use of the McConnell filter without the steps added by Austin et al. (2003) can result in the removal of biologically reasonable standard locations (Austin et al. 2003). This was observed in my data, as the McConnell filter removed more locations overall but a greater percent of standard locations than the multi-step filter.

The filter developed by Austin et al. (2003) has three distinct steps; however the third step was unnecessary for this study as there were not lengthy periods of time without any transmissions. To begin the filtering process, I used standard locations (1, 2 and 3) to calculate the 95th percentile of speed traveled by each animal, which became an individualized speed threshold used for the first step of the filter. Beginning with the third transmission, referred to as n , four speeds of travel were calculated between n and the surrounding four transmissions, $n-1$, $n-2$, $n+1$ and $n+2$. If all four speeds exceeded the individualized speed threshold, transmission n was rejected, and the process was repeated with $n-2$ becoming the new n . However, if all four speeds did not exceed the individualized speed threshold, transmission n was kept and the process was repeated with $n+1$ as the new n . This iterative back-and-forth algorithm continued, either accepting or rejecting transmissions, until the entire set was filtered. This first step was designed by Austin et al. (2003) to supplement the McConnell (1992) filter and remove the most biologically erroneous points right away so that they do not cause the removal of accurate standard locations during step two.

The second step of the Austin et al. (2003) filter is the filter designed by McConnell et al. (1992). It uses the same procedure to move through the data set as step one, taking n , $n-1$, $n-2$, $n+1$, and $n+2$. However, a geometric mean speed is calculated from the four individual speeds:

$$V_i = \sqrt{\frac{1}{4} \sum_{j=-2, j \neq 0}^{j=2} (v_{i,j+i})^2}$$

(Austin et al. 2003)

I squared each the four speeds, summed these speeds, divided the sum by four and then took the square root to obtain an average rate of travel (geometric mean). If this rate of travel exceeded the average maximum traveling speed of harbor seals of $< 2 \text{ m s}^{-1}$ (Williams & Kooyman 1985, Thompson & Miller 1990, Lesage et al. 1999), then transmission n was removed. The filter continued in the same iterative forward and backward manner as in step one until all remaining transmissions were filtered.

Geographic information systems. Once filtered, coordinates from the transmissions were input into ArcView 9.2 (Environmental Systems Research Institute, Inc. Redlands, CA) to create multi-dimensional movement and home range maps. These maps characterized individuals and sites (all individuals from one site). Sex was only investigated for Padilla Bay because it was the only site with an even sex distribution. I used the filtered data points in GIS to construct minimum convex polygons (Mohr 1947, Lowry et al. 2001) and kernel densities (Worton 1989) to investigate movement patterns and home range size for each animal over the whole study period as well as by month and season.

Linear mixed effects models. Linear mixed effects (LME) models combine fixed effects, which are repeatable levels associated with a population, and random effects, which are associated with individuals, to describe how a response variable and covariates in the data are related (Pinheiro & Bates 2004). LME models can be effectively run with unbalanced data and are commonly used for repeated measures (Pinheiro & Bates 2004). Before running a model, I used “R” to test normality using the Shapiro-Wilk test and variance using either

the Fligner test when the response variable violated normality or a Bartlett test when the response variable was normally distributed. If untransformed data violated assumptions of normality and homogeneous variance ($p < 0.05$), I used either a square-root or a cube-root transformation to obtain homogeneous variance ($p > 0.05$) and data that were either normally distributed ($p > 0.05$) or had a P-value within 0.02 of normality. Minimum convex polygon area and fixed kernel density contour areas were used as the response variables.

I ran complete LME models with all fixed effects and varying combinations of random effects including the number of transmission days, mass and sex. Models were run on three temporal scales: month (May, June, July and August), season (pre-pupping and pupping) and the entire tagging duration. July 1 was set as the first day of the pupping season (Huber et al. 2001) and data were divided accordingly. After the best combination of random effects was chosen for each model, using the Akaike Information Criterion (AIC) scores (Pinheiro & Bates 2004), models were run with the selected random effects and all combinations of fixed effects. Fixed effects included in the full models were haul-out site and an interaction with the temporal component, haul-out site and the temporal factor with no interaction and haul-out site by itself. The model with the lowest AIC score was chosen if the next lowest AIC score was not a significantly better fit. If there was a significant effect for any of the fixed effects, independent contrasts were run to compare the estuarine haul-out site (Padilla Bay) to the two rocky reef haul-out sites (Bird Rocks and Belle Chain) as well as to compare the rocky reef haul-out sites to each other.

Due to small and uneven sample sizes, LME models were also run with females removed to estimate how the removal of females affected the overall trends seen with all seals.

Movement patterns. For each seal I calculated the distance between each satellite-transmission and the location at which the seal was captured. This calculation gave a sequential straight-line distance from the transmission location to the haul-out site, which was used to approximate and compare seal movements between individuals and haul-out sites. To determine what I will refer to as “maximum distance traveled” I took the 95th percentile of the distances from the haul-out site. The possibility existed that biologically erroneous points slipped through the filtering method; therefore using the 95th percentile produced a conservative estimate of the maximum straight-line distances that seals moved from their haul-out site. I also calculated mean distance from the haul-out site for each seal.

All filtered transmissions for each seal were used to calculate minimum convex polygons using the Hawth’s tools extension for ArcGIS (Beyer 2004) by month, by season and for the entire study period. Land was removed from minimum convex polygons, to provide the area of water covered by the polygon. Untransformed minimum convex polygon area for the entire duration met assumptions of normality and homogeneous variance; however minimum convex polygon area for seasons and months did not meet assumptions and were transformed using a cube root. LME models were run to compare minimum convex polygon areas between the three haul-out sites on all three temporal scales: month, season and the entire study duration.

Padilla Bay had an even sex ratio of males ($n = 3$) to females ($n = 3$), therefore these individuals were compared to determine whether there was a detectable effect of sex on the size of their minimum convex polygons. These data were not normally distributed with homogeneous variance; hence, a non-parametric Kruskal-Wallis rank sum test was run to compare minimum convex polygon size.

Home ranges. Several independent steps and programs were required for the estimation of home range size. Fixed kernel density estimation of home ranges and calculation of 95th and 50th percentile contours were performed using Hawth's tools (Beyer 2004). However, this analysis required input of a smoothing parameter (h) and allowed me to weight each transmission. Assigning weights to the satellite-transmissions allowed me to include data with uneven sampling intervals without biasing the data towards transmissions close in time and space (Katajisto & Moilanen 2006b). Kernel density estimates are nonparametric and generate a probability density estimate, interpreted directly as a utilization distribution, which predicts where something will be at any given time based on a sample of locations (Seaman et al. 1998). The probability density estimate at any given point is the probability of finding an animal at that location. Animals often have “multiple modes” of higher use and, assuming that the correct smoothing parameter is selected, these activity centers are captured effectively by conducting kernel density estimates (Seaman & Powell 1996).

The smoothing parameter, also known as the smoothing width or bandwidth, determines the width of the kernel, which influences the density estimate. Narrower kernels are more influenced by points that are nearby, whereas wider kernels allow the more distant observations to have a greater influence in the density estimate (Seaman & Powell 1996). The smoothing parameter must be chosen carefully, based on the data themselves, as it helps to reveal the shape of the distribution. I used KernelHR software (Seaman et al. 1998) to calculate a smoothing parameter, using least-squares cross-validation. The same smoothing parameter must be used to compare multiple animals, therefore values for each seal in both

the x-direction and y-direction were calculated and an overall average smoothing parameter was obtained.

To utilize the entire filtered data set, each point was given a weighted value on a scale of zero to one, compensating for autocorrelation in the data set (Katajisto & Moilanen 2006b). Location data are received at uneven sampling intervals and therefore can be spatially and temporally aggregated. Previous studies tried to solve this issue by calculating an average daily location at the expense of the number of data points (Lowry et al. 2001, Austin et al. 2004, Small et al. 2005); however, this solution does not completely address autocorrelation in the data. I used the program B-Range (Katajisto & Moilanen 2006a) to calculate weights for each transmission, giving a lower weight to a transmission if it was spatially close to and temporally clustered with other transmissions (Katajisto & Moilanen 2006b). The temporal scale at which to make transmissions independent from one another was set at 12 hours. After 12 hours a harbor seal can cover about 85 km if moving straight at 2 m s^{-1} transit speed. At the same time, observations from individual seals in one of the candidate marine reserve sites indicate that seals moved away from the site after 3.5 h, suggesting that localized and likely dependent movements last $< 12 \text{ h}$ (Banks 2007). Consequently, I feel confident that the temporal scale I set is a conservative indicator of independent movements.

I used fixed-kernel density estimates to calculate the 95th and 50th percentile contours of seal locations. A contour encircles an area of equivalent density. For example, the 95th percentile contour is the “smallest area containing 95 % of the utilization distribution (Seaman & Powell 1996). That is, one would predict that area to be the smallest area used by the animal 95 % of the time. Contours for several individuals resulted in small doughnut

shaped holes within the middle of a contiguous area of estimated use and these were included in the total home range size estimates for analysis. Land was erased from the contours and area was calculated in km² for each seal. Areas of the contours were statistically compared between the three haul-out sites using LME models in the same manner as the minimum convex polygons. Untransformed data did not have homogeneous variance but a square root transformation met both assumptions of normality and homogeneous variance. Models were run for both the 95th and 50th percentile contours on all three temporal scales: month, season and the entire study duration.

Home ranges, 95th percentile contours, and core areas of use, 50th percentile contours, were compared between Padilla Bay males (n = 3) and females (n = 3) to determine whether there were differences based on sex. These data were analyzed using a non-parametric Kruskal-Wallis rank sum test.

Spatial use near candidate marine reserves

Data analysis

I used filtered satellite locations to analyze harbor seal presence in and around the top three candidate reserves (Weispenning 2006) (Figure 3). Using ArcGIS 9.2 as a visualization tool, I determined the total number of filtered transmissions from within the candidate reserves. I also determined total numbers of transmissions from within buffers of 1, 2 and 3 km of a candidate site because error in the location accuracy of the satellite tags may cause locations to appear adjacent to the candidate reserve even when a seal was actually inside the boundaries (White & Sjoberg 2002, Argos 2007). Using aerial survey

counts, I extrapolated the movements observed for the satellite tagged seals to the number of seals from haul-out sites up to 40 km from the candidate reserves to predict how they might utilize the candidate marine reserve sites.

Site fidelity

Data analysis

Site-fidelity was examined using haul-out statistics obtained from MK10-F, Mk9 and SPLASH tags on each animal. Animals were only analyzed for haul-out site fidelity if their time-depth recorder tag was recovered. Wet/dry sensors revealed whether the tag was in or out of the water. I identified haul-out bouts based on these wet/dry data. The beginning of a bout was triggered by four min of consecutive dry readings and was terminated after two min of consecutive wet readings. Any bout lasting ≥ 20 min was considered a haul-out bout (Austin et al. 2006). The time for a haul-out event was then paired with satellite transmission records to examine if a standard satellite transmission occurred during the haul-out bout. Haul-out bouts with coinciding standard transmissions, or transmissions < 60 s from either end of the haul-out bout, were included in the analysis. Due to error in the satellite tags, I had to assume that haul-out locations separated by a certain distance could represent the same haul-out site or different haul-out sites close together. Hence, I described distinct regions of haul-outs used by the seals. Haul-out sites were assumed to be in distinct regions if separated by > 5 km. I then determined the haul-out region with the greatest percentage of haul-out bouts and the percentage of haul-out bouts from the haul-out region where each seal was captured.

RESULTS

Abundance

Two sets of aerial surveys were conducted during July and August 2007; the first took place July 31 – Aug 2 and the second took place August 13 – 15. The average survey count (\pm SD), including pups, was 5,308 (\pm 205) harbor seals. The total population estimate was 8,121 (\pm 313) harbor seals in the San Juan Islands and the eastern bays from Bellingham Bay south to Similk Bay. This estimate fits within counts from the last 10 years of aerial surveys from the Washington Department and Fish of Wildlife database, which ranged from 6,669 to 11,823 harbor seals (Figure 4).

Movements and home ranges

Captures and filtering

Harbor seals were captured from three sites (Figure 2) on ten different days between April 4, 2007 and May 21, 2007 and a combination of satellite tags and time-depth recorders were deployed (Table 1). Tags were attached to seals a mean (\pm SD) 110 (\pm 32) d with a range of 46 – 179 d (Table 1). On average, tags provided a location 98 (\pm 3.5) % of days. The lowest transmission rate was 88 %, for an animal that failed to transmit on 12 of 102 d.

Based on unfiltered Argos data, seals transmitted a mean 8.9 (\pm 2.6) locations d^{-1} . On average, 77 (\pm 10) % of locations seal⁻¹ were auxiliary (A, B, 0 and failed Z transmissions). The means were 2.2 (\pm 0.8), 3.1 (\pm 1.0) and 1.5 (\pm 0.9) locations d^{-1} for A, B and 0 classes,

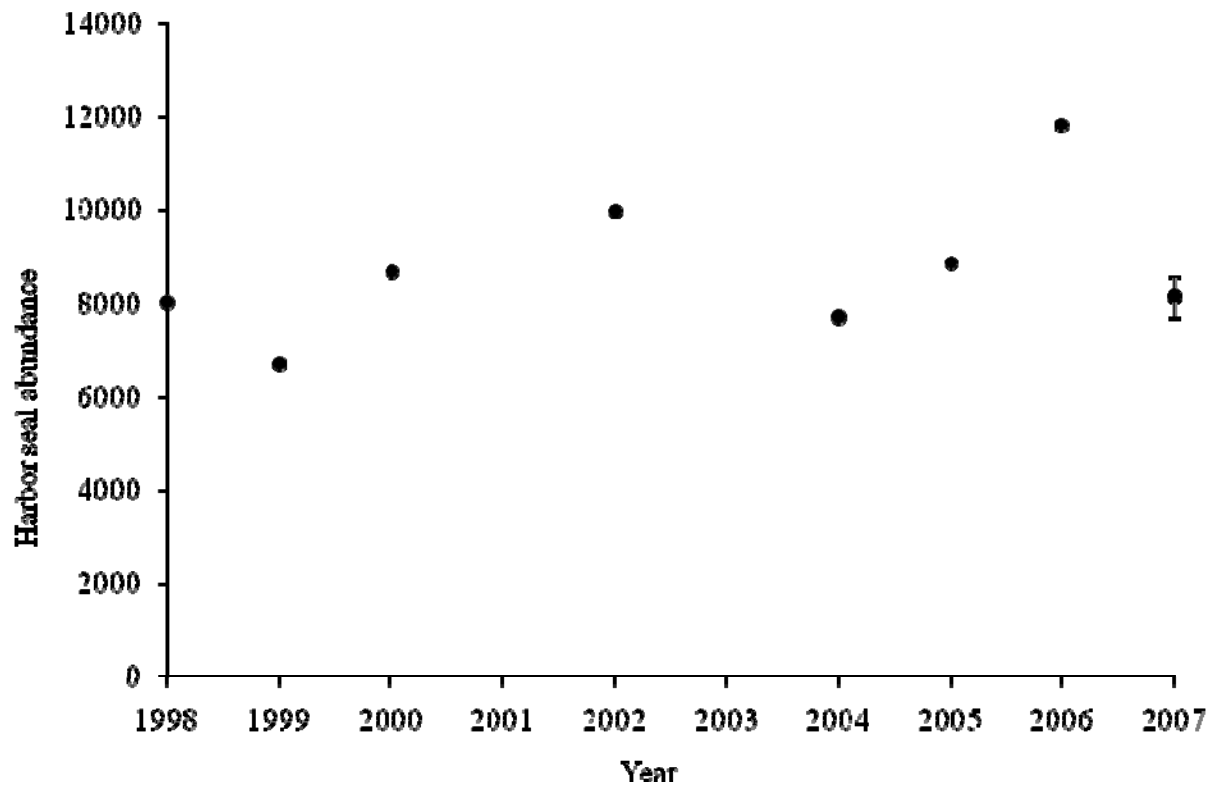


Figure 4. Harbor seal abundance estimates for the San Juan Islands and the adjacent bays (between Bellingham Bay and Similk Bay) over the last 10 years. Estimates obtained from aerial survey counts with a correction factor (1.53) applied (Huber et al. 2001). Error bars for 2007 represent the 95% confidence interval but do not include error in the correction factor.

Table 1. Harbor seals captured in April and May 2007 at three haul-out sites in the Georgia Basin. Seal ID indicates male (B) or female (Y) followed by a number unique to that individual. Length represents the total number of days from tag deployment to tag failure for each animal. Transmit is the percent of days resulting in at least one transmission. Locations d^{-1} is the mean number of transmissions d^{-1} for each seal.

Site	Seal ID	Deploy date	Mass (kg)	Satellite tag	TDR tag	Length (days)	Transmit (% days)	Locations d^{-1}
Bird Rocks	Y1455	4/4/07	76.5	SPOT5	Mk10-F	135	100	10.4
Bird Rocks	B1696	4/4/07	74.5	SPOT5	Mk10-F	58	100	11.2
Bird Rocks	B1695	4/5/07	71.5	SPOT5	Mk10-F	156	100	10.1
Bird Rocks	B1697	4/6/07	96.0	SPOT5	Mk9	94	98.9	5.4
Bird Rocks	B1698	4/6/07	90.0	SPOT5	Mk9	83	100	5.4
Bird Rocks	B1701	4/20/07	86.0	SPOT5	Mk10-F	179	100	12.1
Padilla Bay	B1699	4/18/07	64.0	SPOT5	Mk9	147	100	11.8
Padilla Bay	Y1459	4/19/07	83.0	SPOT5	Mk9	134	100	9.0
Padilla Bay	Y1460	4/19/07	62.5	SPOT5	Mk9	101	92.1	2.5
Padilla Bay	B1712	5/21/07	69.0	SPOT5	Mk9	107	100	9.4
Padilla Bay	B1713	5/21/07	54.0	SPOT5	Mk9	113	100	10.5
Padilla Bay	Y1462	5/21/07	77.5	SPOT5	Mk9	116	100	8.8
Belle Chain	B1711	5/3/07	70.5	SPLASH	SPLASH	99	100	9.8
Belle Chain	B1706	5/1/07	90.5	SPLASH	SPLASH	132	100	9.2
Belle Chain	B1707	5/2/07	58.5	SPLASH	SPLASH	102	88.2	7.5
Belle Chain	B1709	5/3/07	92.0	SPLASH	SPLASH	97	99.0	8.9
Belle Chain	B1702	5/1/07	81.5	SPLASH	SPLASH	76	90.8	6.4
Belle Chain	B1704	5/1/07	72.0	SPLASH	SPLASH	97	97.9	7.2
Belle Chain	B1710	5/3/07	77.0	SPLASH	SPLASH	46	100	9.3
Belle Chain	B1703	5/1/07	66.5	SPLASH	SPLASH	126	100	13.0

respectively. Conversely, the means were 1.2 (± 0.5), 0.6 (± 0.4) and 0.3 (± 0.3) locations d^{-1} for standard level 1, 2 and 3 transmissions.

After filtering, seals transmitted a mean 726 (± 382) locations, or approximately 6.4 (± 2.0) locations d^{-1} . Auxiliary quality locations accounted for a mean 74 (± 11) % of all locations and a mean 1.6 (± 0.7), 2.0 (± 0.6) and 1.0 (± 0.6) locations d^{-1} for location classes A, B and 0, respectively. Standard locations accounted for a mean 1.0 (± 0.5), 0.5 (± 0.4) and 0.3 (± 0.3) locations d^{-1} for location classes 1, 2 and 3.

Distance traveled

Overall, 12 seals ($n = 20$) moved > 28 km from their haul-out site and eight seals moved > 100 km from their haul-out site, including two seals from each of the two rocky reef sites that moved > 140 km. Roundtrip distances > 200 km were observed for 43% of males ($n = 16$). The distance between individual seal locations and their haul-out site over time is shown in Appendix 2.

Seals from Padilla Bay had the smallest variability in their maximum (95th percentile) straight-line distance traveled and did not travel as far as some individuals from Bird Rocks or Belle Chain (Figure 5). Seals from Padilla Bay had a range of 10 – 104.5 km (mean = 32.5, SD = 35.7) for maximum distance traveled while seals from Bird Rocks traveled 15 – 210 km (mean = 108, SD = 75) and Belle Chain seals traveled 16 – 145 km (mean = 70, SD = 75). The mean distance of seals from their haul-out site showed similar trends, with less variability in seals from Padilla Bay than for Bird Rocks or Belle Chain (Figure 6).

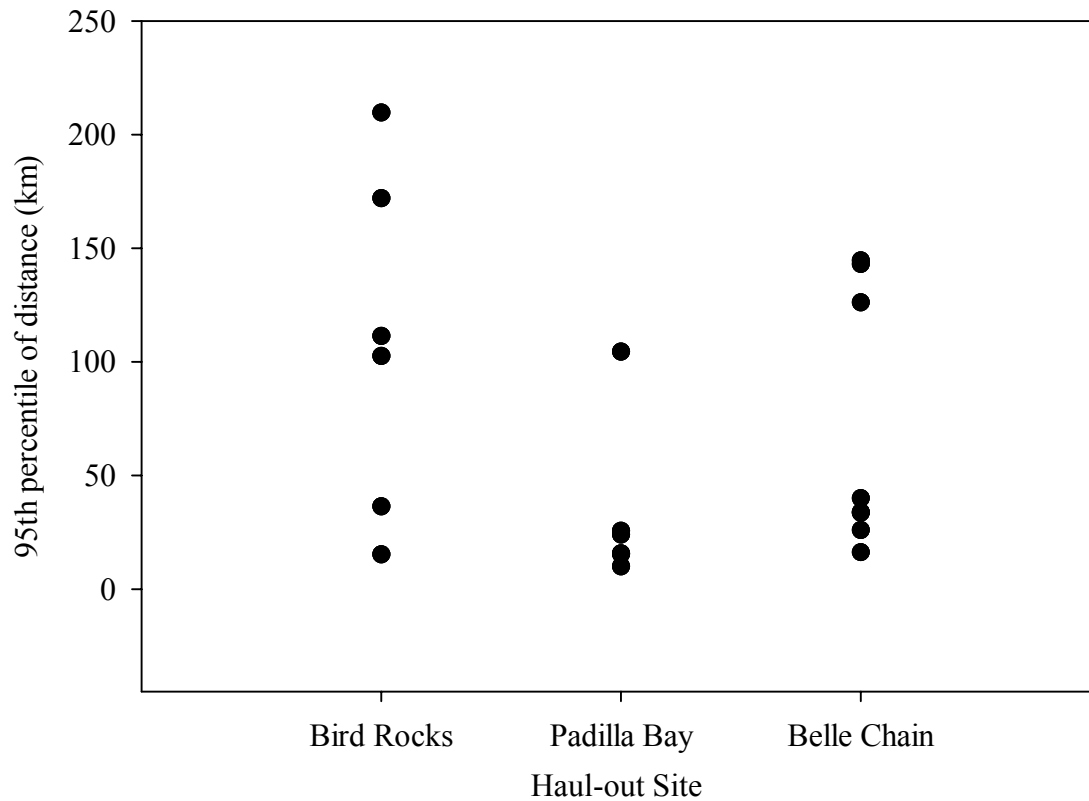


Figure 5. The 95th percentile (maximum distance) traveled by harbor seals from their haul-out site. Bird Rocks (n = 6), Padilla Bay (n = 6) and Belle Chain (n = 8). Each dot represents an individual seal and some dots overlap.

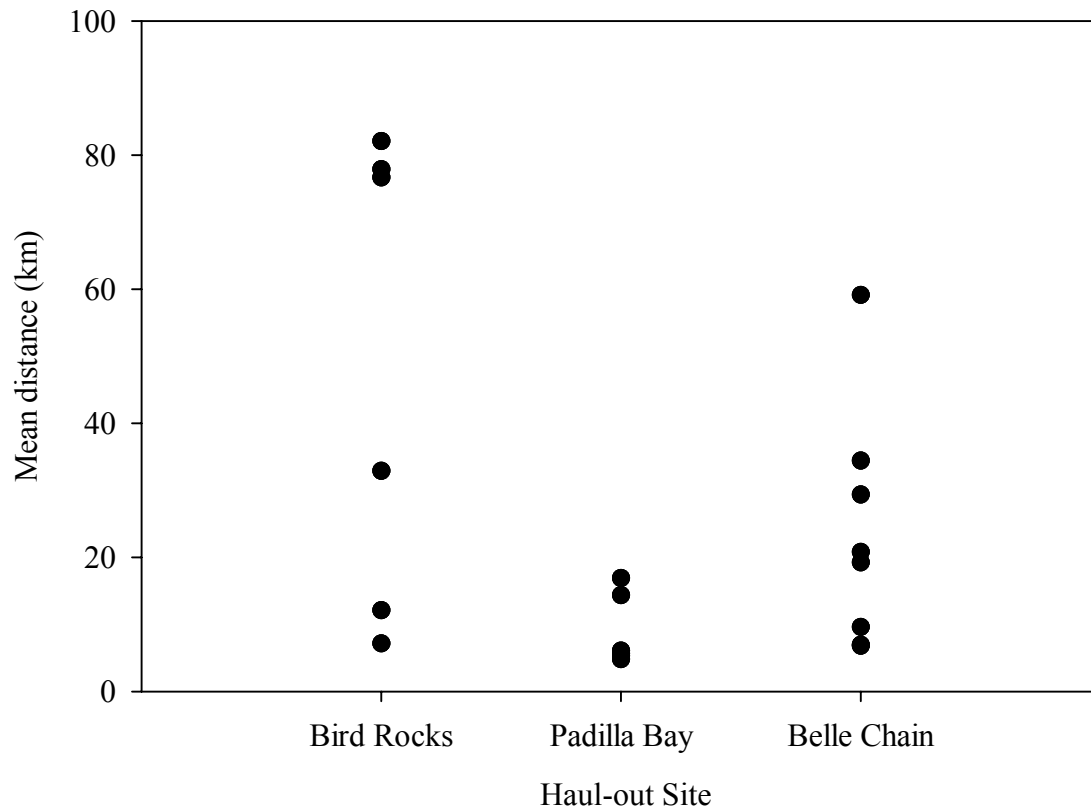


Figure 6. Mean distance traveled by harbor seals from their haul-out site. Each dot represents an individual seal.

Bird Rocks. Seals from Bird Rocks had the greatest variability in distances moved from their haul-out site. The mean distance away from the haul-out site was 48 (\pm 35) km ($n = 6$ seals). The sole female tagged at Bird Rocks stayed ≤ 15 km from her haul-out site for 95 % of the tagging duration, while four of the five males moved > 50 km one-way from the haul-out site. Two of five males made five trips each that put them > 50 km from the haul-out site, while one male had three lengthy trips (all > 100 km) and the remaining male moved > 140 km twice over the study period to different locations. These extended trips away from the haul-out site lasted 1 – 8 weeks in duration (Appendix 2).

Padilla Bay. Padilla Bay seals ($n = 6$) had a mean distance traveled of 9 (\pm 5) km from their haul-out site throughout the duration of the study. All but one seal made numerous short trips staying < 26 km of the haul-out site, while the sixth animal stayed within this distance for the majority of the study but then moved approximately 105 km away for the last three weeks of his tag deployment at the end of August (Appendix 2).

Belle Chain. The mean travel distance between transmissions and the Belle Chain haul-out site for the whole study was 23 (\pm 18) km ($n = 8$ seals). Three individuals had trips > 50 km from their haul-out site and each of these seals had at least one trip > 120 km that lasted between 1.5 and 6 weeks (Appendix 2). The five remaining animals had trips ranging from 15 – 40 km from their haul-out site (Appendix 2).

Minimum convex polygons

The size of minimum convex polygons varied significantly by haul-out site on a monthly, seasonal and entire study-period temporal scale (LME, $p < 0.023$, Table 2, Appendix 3). Transformed data were analyzed on the monthly and seasonal scales and

untransformed data were analyzed for the entire study period. There was no detectable effect of month, season or an interaction between month or season with haul-out site (LME, $p > 0.05$, Appendix 3). Because the entire study period was too large of a temporal window to reflect small changes in behavior over the course of the study, I will present the results for the model with minimum convex polygons for each season. Results for the models examining months and the entire study period are shown in Appendix 3.

The LME model that best explained the size of minimum convex polygons on a seasonal scale included haul-out site as the only fixed effect and mass as a random effect (Table 2). Independent contrasts indicated a significant difference between minimum convex polygon size for seals from the rocky reefs (Bird Rocks and Belle Chain) and seals from Padilla Bay (LME, $p < 0.001$) but did not detect a difference between seals from Bird Rocks and seals from Belle Chain (LME, $p = 0.315$) (Table 2).

Standard deviation of minimum convex polygon size was largest for Bird Rocks during prepupping and pupping (Figure 7). On the other hand, Padilla Bay seals demonstrated the least variability during both seasons. Untransformed minimum convex polygon sizes ranged from 580 – 7,224 km² for seals from Bird Rocks, 299 – 4,137 km² for Padilla Bay and 1,469 – 6,422 km² for Belle Chain. Overall, Bird Rocks had the highest mean area for both seasons, followed by Belle Chain (Table 3).

Tables 2a-d. Minimum convex polygon LME model summary relative to season. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Table 2a. Comparison of models with different random effects on a seasonal temporal scale with all fixed effects included.

Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
Mass	8	169.53	-76.77			
Sex and Mass	10	171.43	-75.71	1 vs 2	2.10	0.3490
Transmission Days and Mass	10	171.79	-75.89			
Sex	8	172.64	-78.32	3 vs 4	4.85	0.088
Transmission Days	8	172.99	-78.49			
Sex and Transmission Days	10	175.41	-77.70	5 vs 6	1.58	0.453
Transmission Days, Mass and Sex	10	176.64	-78.32			

Table 2b. Comparison of fixed effects on a seasonal temporal scale with mass as the random effect.

Model	df	AIC	logLik	Test	L.Ratio	p-value
1 - Site	5	181.26	-85.6			
2 - Site + season	8	182.09	-83.1	1 vs 2	5.16	0.160
3 - Site * season	6	183.11	-85.6	2 vs 3	5.02	0.081

Table 2c. Seasonal temporal scale model with site as the fixed effect and mass as the random effect.

	numDF	denDF	F-value	p-value
Intercept	1	17	505.90	< 0.0001
Site	2	17	9.68	< 0.002

Table 2d. Independent contrasts on the model with site as the fixed effect and mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
Intercept	13.50	0.61	17	22.30	0.000
Bird Rocks vs Belle Chain	0.77	0.74	17	1.04	0.315
Rocky Reefs vs Padilla Bay	1.88	0.43	17	4.36	< 0.001

Table 3. Minimum convex polygon areas relative to month, season and the entire study period.

Site	Area (km ²) ± SD for different temporal periods			
	Months			
	May	June	July	August
Bird Rocks	3425 ± 2180	3257 ± 1906	1988 ± 1477	1326 ± 877
Padilla Bay	409 ± 368	541 ± 408	775 ± 585	1189 ± 1656
Belle Chain	1627 ± 452	2506 ± 1835	2772 ± 1456	1255 ± 856
	Seasons			
	Prepupping			Pupping
Bird Rocks	5354 ± 2617			3310 ± 3088
Padilla Bay	736 ± 442			1565 ± 1422
Belle Chain	3317 ± 1750			3502 ± 1775
	Entire duration			
Bird Rocks	6468 ± 3703			
Padilla Bay	1831 ± 2488			
Belle Chain	4482 ± 2200			

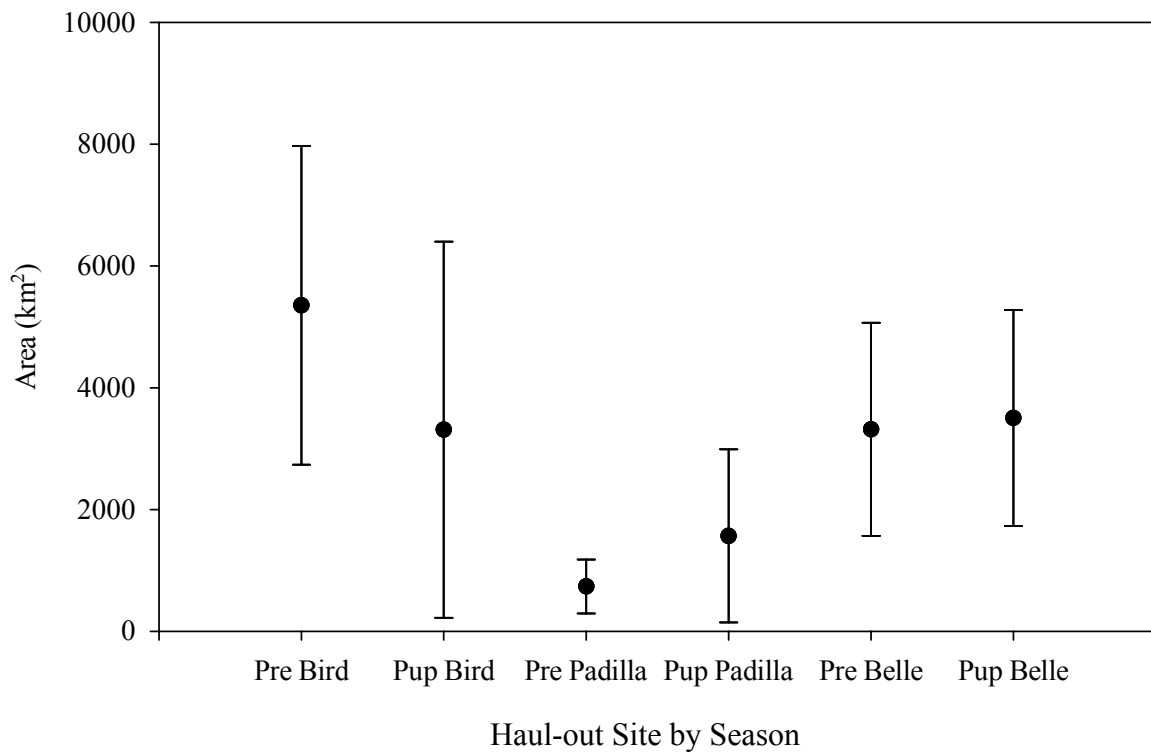


Figure 7. Minimum convex polygons of harbor seals relative to season. Untransformed data. Pre = prepupping and Pup = pupping.

Male minimum convex polygons. LME models were run with only males by excluding the female from Bird Rocks and the three females from Padilla Bay. Similar comparisons for females were not possible due to limited sample size. Haul-out site had a significant effect on minimum convex polygon size (LME, $p < 0.001$, Appendix 4). The best model included site as the fixed effect and mass as the random effect (Appendix 4). Independent contrasts for the seasonal temporal scale revealed significant differences between rocky reef sites and Padilla Bay (LME, $p < 0.001$, Appendix 4) as well as between the two rocky reef sites (LME, $p = 0.031$, Appendix 4). Padilla Bay males had the smallest minimum convex polygons (299 – 4138 km²), followed by Belle Chain males (1469 – 6422 km²) and finally Bird Rocks males (2690 – 8542 km²) (Appendix 4).

Sex comparison for Padilla Bay. Kruskal-Wallis rank sum tests did not reveal differences in the size of minimum convex polygons based on sex ($p = 0.262$, Appendix 5). Female minimum convex polygons ranged in size from 415 – 2223 km² while males ranged from 299 – 4138 km² (Appendix 5). Sex was not compared at Bird Rocks or Belle Chain due to the sex ratios of the satellite-tagged seals from those two haul-out sites.

Home ranges

Home range sizes varied significantly by haul-out site relative to month, season and throughout the study period for both the 95th and 50th percentile contours (LME, $p < 0.036$, Table 4, Appendix 6). Transformed data were used on the monthly and seasonal scales and untransformed data were used for the entire study period. There was no detectable effect of month or season or an interaction effect between month or season with haul-out site on home range size for either the 95th or 50th percentile contours. The entire study period did not

reflect small changes in behavior over the course of the study. I will present the results for the model with home ranges for each season. Results for the models examining individual months and the entire study period are shown in Appendix 6.

The best model on the seasonal temporal scale included mass as a random effect and site as the only fixed effect (Table 4). Independent contrasts from LME models showed significant differences between seals from the rocky reefs (Bird Rocks and Belle Chain) and Padilla Bay for the 95th (LME, $p < 0.001$) and 50th percentile contours ($p = 0.001$ but not between Bird Rocks and Belle Chain for either contour (LME, $p > 0.115$) (Table 4).

Bird Rocks seals demonstrated the greatest variability during both seasons for both the 95th (Figure 8) and 50th (Figure 9) percentile contours and Padilla Bay seals demonstrated the least variability during both seasons for both contours. Untransformed 95th percentile contours ranged in size from 209 – 1217 km² for seals from Bird Rocks, 57 – 464 km² for Padilla Bay and 84 – 856 km² for Belle Chain. Untransformed 50th percentile contours ranged from 34 – 307 km² for seals from Bird Rocks, 15 – 105 km² for Padilla Bay and 24 – 267 km² for Belle Chain. Overall, Bird Rocks had the greatest mean 95th and 50th percentile contours for both seasons, followed by Belle Chain and then Padilla Bay (Figures 8 – 9).

Bird Rocks. Four seals from Bird Rocks, all males, had segmented home ranges with multiple sections of their home ranges and their core areas of use (50th percentile contours) separated by > 20 km, sometimes > 100 km (e.g. Figure 10). Home ranges for each individual seal by season are shown in Appendix 7. One individual had a segment of his home range adjacent to Bainbridge Island in south Puget Sound, another seal utilized the region southeast of Victoria as well as the Strait of Juan de Fuca out to its mouth at the Pacific Ocean, the third male utilized the area south of Texada Island in the Strait of Georgia

Tables 4a-d. Home range LME model summary relative to season. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Table 4a. Comparison of models on a seasonal temporal scale with all fixed effects and combinations of random effects.

Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
95th percentile contours						
Transmission Days and Mass	10	193.23	-86.61			
Mass	8	198.93	-91.47	1 vs 2	9.70	0.008
Sex and Mass	10	201.99	-91.00	2 vs 3	0.93	0.627
Sex	8	205.43	-94.71	3 vs 4	7.44	0.024
Transmission Days	8	205.51	-94.75			
Transmission Days, Mass and Sex	10	209.43	-94.71	5 vs 6	0.08	0.961
50th percentile contours						
Transmission Days and Mass	10	156.74	-68.37			
Mass	8	160.52	-72.26	1 vs 2	7.77	0.021
Sex and Mass	10	163.91	-71.96	2 vs 3	0.60	0.739
Sex	8	174.40	-79.20	3 vs 4	14.49	0.001
Transmission Days	8	174.02	-79.01			
Transmission Days, Mass and Sex	10	178.40	-79.20	5 vs 6	0.38	0.827

Table 4b. Comparison of models on a seasonal temporal scale with different fixed effects and mass as the random effect.

Model	df	AIC	logLik	Test	L.Ratio	p-value
95th percent contours						
1 - Site	5	212.05	-101.02			
2 - Site + season	6	213.97	-100.99	1 vs 2	0.07	0.790
3 - Site * season	8	217.43	-100.72	2 vs 3	0.54	0.760
50th percent contours						
1 - Site	5	165.44	-77.72			
2 - Site + season	6	166.86	-77.43	1 vs 2	0.58	0.446
3 - Site * season	8	170.76	-77.38	2 vs 3	0.10	0.950

Table 4c. Models on a seasonal temporal scale including haul-out site as the fixed effect and mass as the random effect.

	numDF	denDF	F-value	p-value
95th percent contours				
Intercept	1	17	346.94	< 0.0001
Site	2	17	10.69	0.001
50th percent contours				
Intercept	1	17	244.86	< 0.0001
Site	2	17	8.01	< 0.004

Table 4d. Independent contrasts comparing sites for the best seasonal models with mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
95th percent contours					
Intercept	19.57	1.06	17	18.49	0.000
Bird Rocks vs Belle Chain	2.13	1.28	17	1.66	0.115
Rocky Reefs vs Padilla Bay	3.36	0.76	17	4.45	< 0.001
50th percent contours					
Intercept	9.98	0.64	17	15.48	0.000
Bird Rocks vs Belle Chain	1.16	0.78	17	1.49	0.154
Rocky Reefs vs Padilla Bay	1.77	0.46	17	3.83	0.001

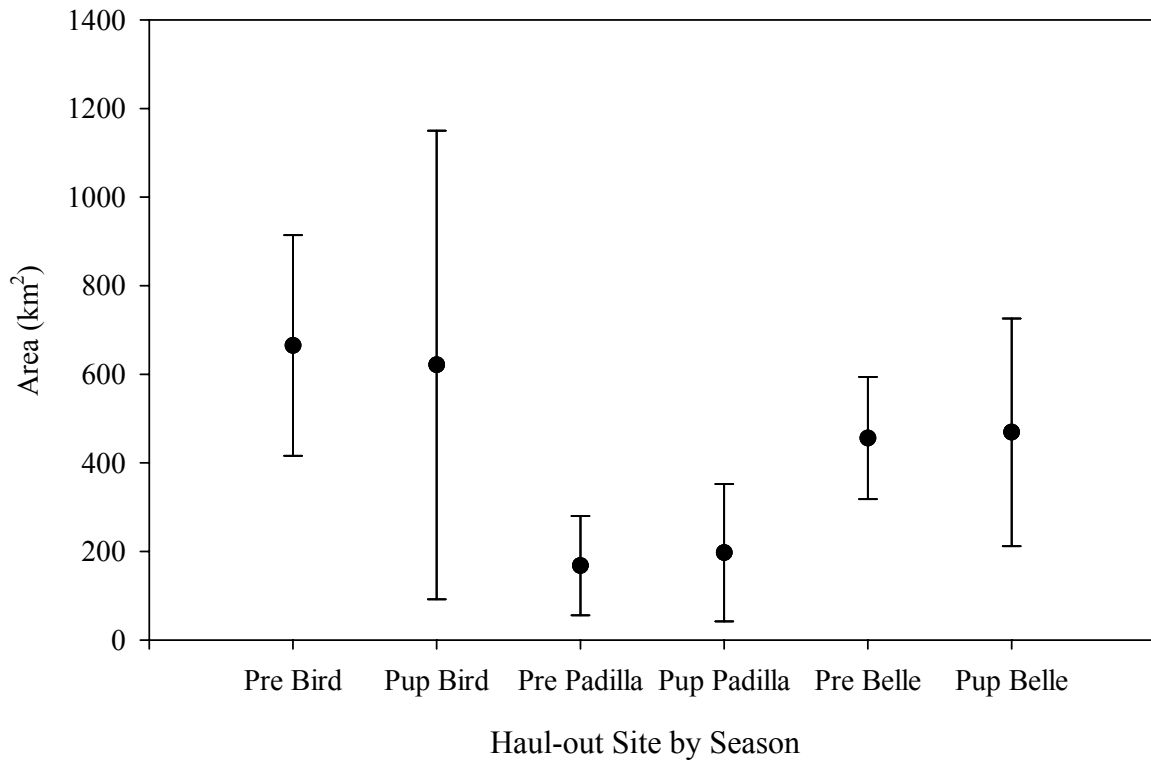


Figure 8. Home ranges (95th percentile contours) of harbor seals relative to season. Untransformed data. Pre = prepupping and Pup = pupping.

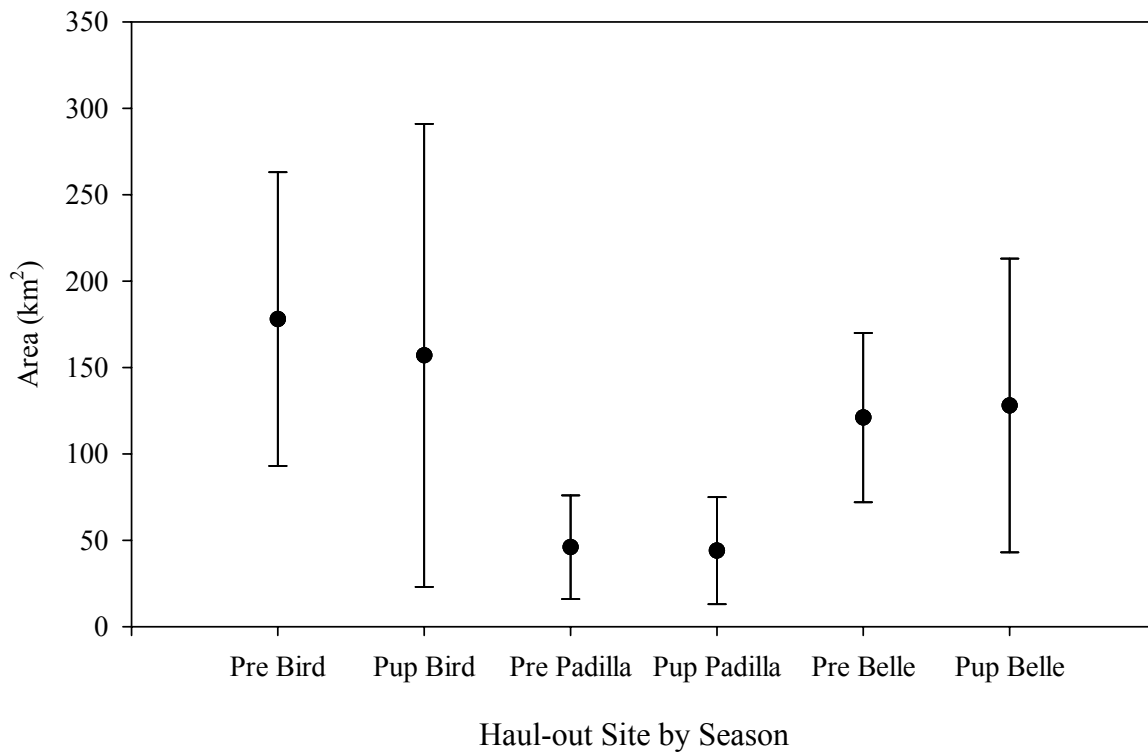


Figure 9. Core area (50th percentile contours) of harbor seals relative to season. Untransformed data. Pre = prepupping and Pup = pupping.

all the way north to the Campbell River, while the last male used the Strait of Georgia north to Hornby Island during prepupping and then went to the outer coast of Washington during the pupping season. The remaining two individuals, a male and a female, had smaller home ranges within the eastern San Juan Islands, focused around the haul-out site, Bird Rocks, and Rosario Strait east of Lopez Island.

Padilla Bay. Harbor seals from Padilla Bay had significantly smaller home ranges and more contiguous home ranges than seals from Bird Rocks or Belle Chain. Padilla Bay seals had home ranges that were mostly contained within Padilla Bay with only several adjacent regions (Vendovi Island and Eliza Rocks) that were included in the 50th percentile contours (e.g. Figure 11). One seal moved away from Padilla Bay near the end of the study and this was reflected in the home range analysis, as part of his home range was located in the Belle Chain Islets during the pupping season.

Belle Chain. Several seals from Belle Chain had segmented home ranges, similar to seals from Bird Rocks, several seals remained relatively close to their haul-out site and several seals demonstrated an intermediate home range pattern. Two individuals had segmented home ranges that included the Belle Chain Islets as well as the outer coast of Washington and Vancouver Island, BC (e.g. Figure 12). Three individuals stayed close to the haul-out site while the remaining individuals had segmented home ranges including areas around Hornby Island to the north, Lummi and Orcas Island to the south, over to the mainland between Point Roberts and Birch Bay and the northeastern corner of the San Juan Islands to the south (e.g. Figure 13).

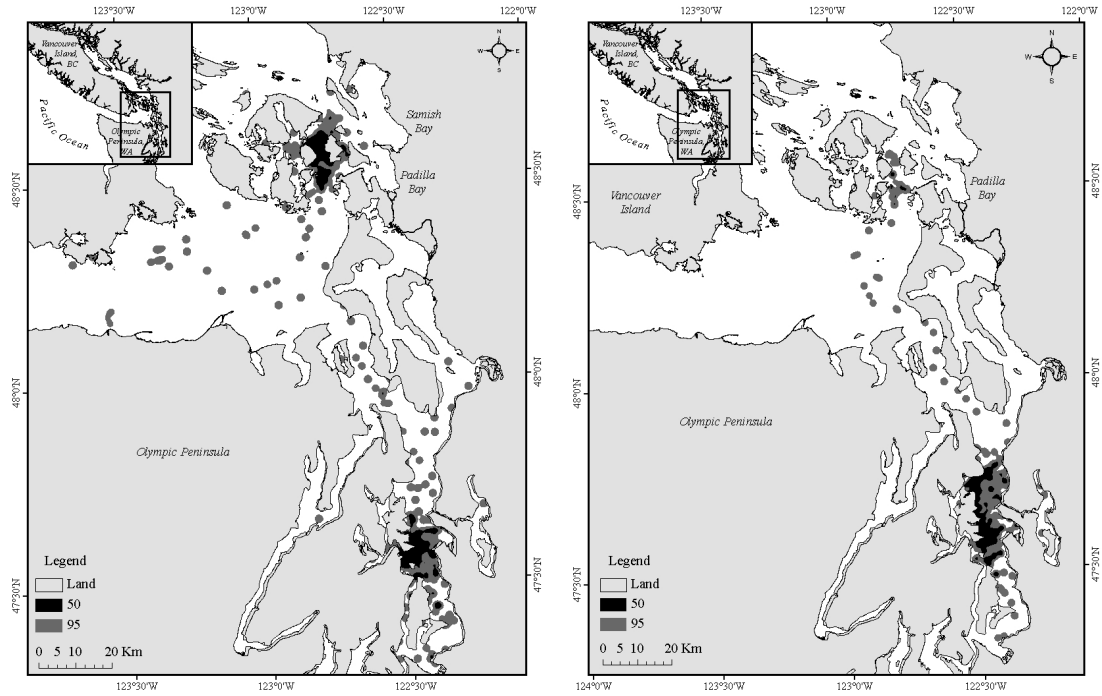


Figure 10. Home range and core areas of harbor seal male # B1695 from Bird Rocks relative to season. Home range = 95th percentile contour, core areas of use = 50th percentile contour, prepupping season (left), pupping season (right).

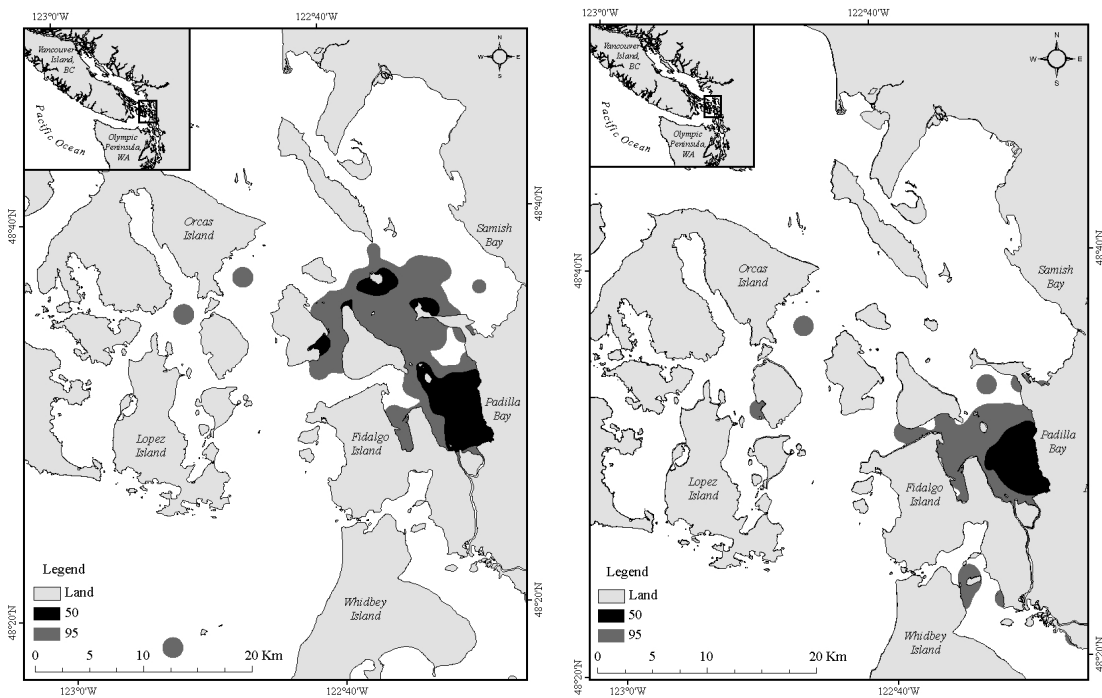


Figure 11. Home range and core areas of harbor seal male # B1699 from Padilla Bay relative to season. Home range = 95th percentile contour, core areas of use = 50th percentile contour, prepupping season (left), pupping season (right).

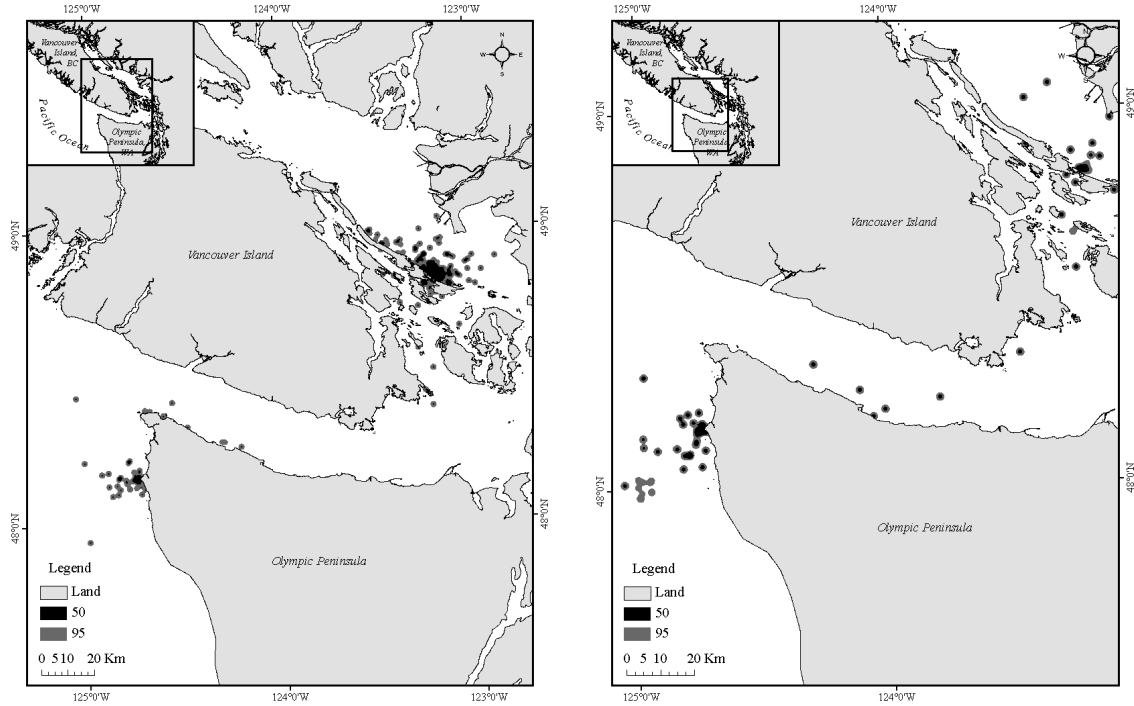


Figure 12. Home range and core areas of harbor seal male # B1704 from Belle Chain relative to season. Home range = 95th percentile contour, core areas of use = 50th percentile contour, prepupping season (left), pupping season (right).

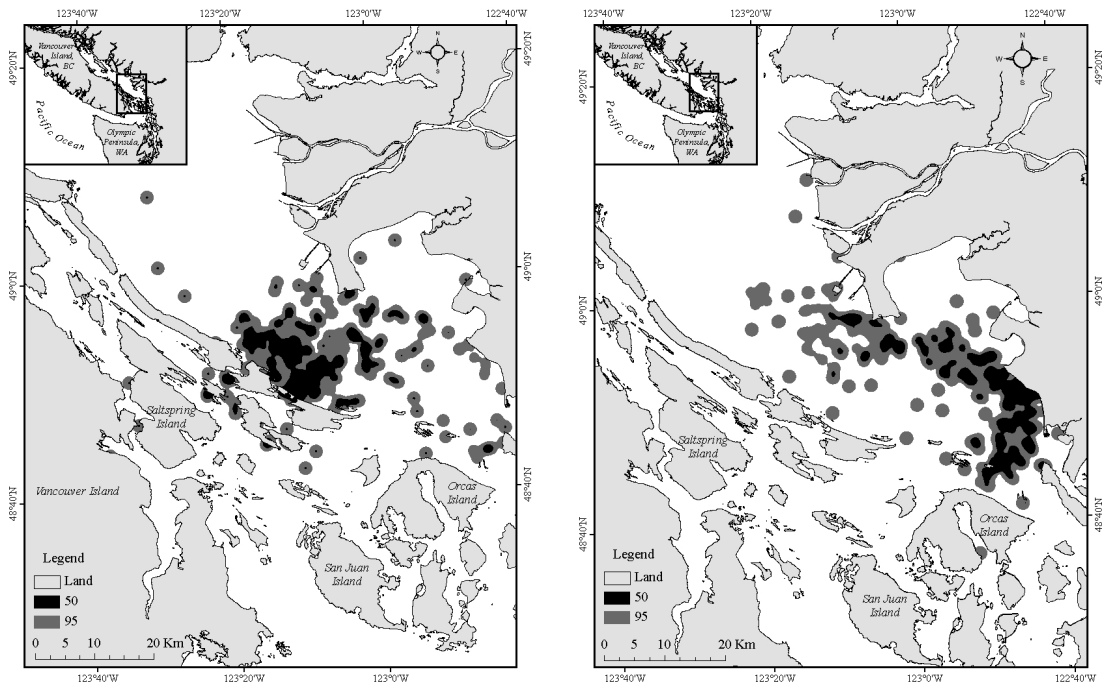


Figure 13. Home range and core areas of harbor seal male # B1709 from Belle Chain relative to season. Home range = 95th percentile contour, core areas of use = 50th percentile contour, prepupping season (left), pupping season (right).

Male home ranges. LME models were run for the seasonal temporal scale with only males by excluding the female from Bird Rocks and the three females from Padilla Bay. Similar comparisons for females were not possible due to limited sample size. Haul-out site had a significant effect on 95th and 50th percentile contours (LME, $p < 0.004$, Appendix 4). The best model included site as the fixed effect and mass as the random effect. Independent contrasts revealed significant differences between rocky reef sites and Padilla Bay (LME, $p < 0.002$) as well as between the two rocky reef sites (LME, $p < 0.038$) (Appendix 4). Padilla Bay males had the smallest home ranges and core areas of use (83 – 464 km² and 15 – 84 km², respectively), followed by Belle Chain males (195 – 856 km² and 28 – 267 km², respectively), and finally Bird Rocks males (436 – 1217 km² and 117 – 307 km², respectively) (Appendix 4).

Sex comparison for Padilla Bay. Kruskal-Wallis rank sum tests did not reveal differences based on sex on the size of the 95th percentile contour ($p = 0.745$, Appendix 5) or the 50th percentile contour ($p = 0.745$, Appendix 5). Female 95th percentile contours ranged from 57 – 388 km² while males ranged from 83 – 464 km². Female 50th percentile contours ranged from 15 – 105 km² while males ranged from 15 – 84 km² (Appendix 5). Sex was not compared at Bird Rocks or Belle Chain due to the sex ratios of the satellite-tagged seals from those two haul-out sites.

Spatial use near candidate marine reserves

All seals from Bird Rocks and Padilla Bay ($n = 12$) and one seal from Belle Chain transmitted at least one location within a 3-km buffer of the candidate marine reserves. Seal locations within a 1-, 2- or 3-km buffer were less than 1.1, 2.6 or 4.5 % of the total satellite

locations, respectively, for animals tagged at Bird Rocks and Padilla Bay. Locations from within the candidate marine reserves represented $< 0.2\%$ of the total satellite locations (Figure 14). Only one of the 17 transmissions from within the boundaries was of standard quality.

Aerial surveys conducted during pupping located seals hauled-out at 114 sites within the San Juan Islands and the adjacent bays < 40 km from the candidate marine reserves (Figure 15). The 40 km range was set after examining the movements of satellite tagged seals. All harbor seals from Padilla Bay, all but one of the seals from Belle Chain and three seals from Bird Rocks had mean distances from their haul-out site < 40 km.

Site fidelity

Haul-out bout times and durations were matched to standard satellite transmissions from SPOT5 tags for the three seals from Bird Rocks, six seals from Padilla Bay and two seals from Belle Chain with recovered time-depth recorder tags. These bouts ranged from 16 to 52 haul-out bouts seal⁻¹ ($n = 11$). Seals from the two rocky reef sites had a higher number of haul-out regions and a wider spatial distribution of haul-out regions than seals from Padilla Bay (Table 6). Regions were separated by > 5 km. Haul-out regions with the highest percent of haul-outs for each seal are listed in Table 6 and shown in Figure 16. All haul-out regions are shown in Figures 17 and 18 and individual seals are identified in Appendix 8.1 and 8.2.

Bird Rocks. The three seals from Bird Rocks used haul-outs that were more spread out spatially than seals from Padilla Bay (Figure 17). One male seal used four different regions for 17 haul-outs bouts, separated by up to 90 km (Figure 17). Another male used seven regions for 36 haul-out bouts, several of which were in the San Juan Islands and

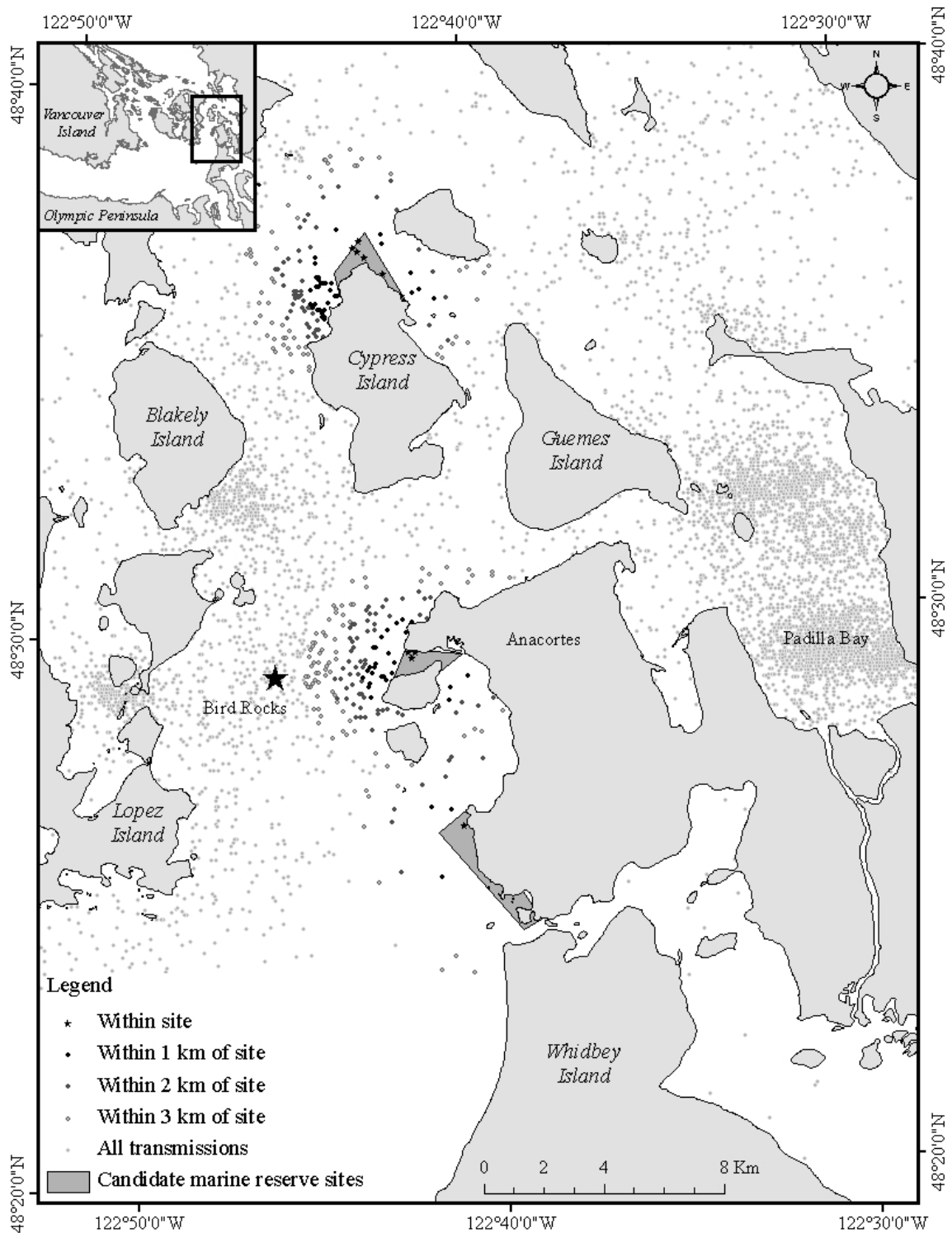


Figure 14. Location of satellite-tagged harbor seals during April – October 2007 in relation to the candidate marine reserves. Transmissions are shown from within the candidate reserve boundaries and within three different buffer widths: 1, 2 and 3 km. Locations ≤ 3 km from a candidate reserve represented 4.5 % of all satellite locations.

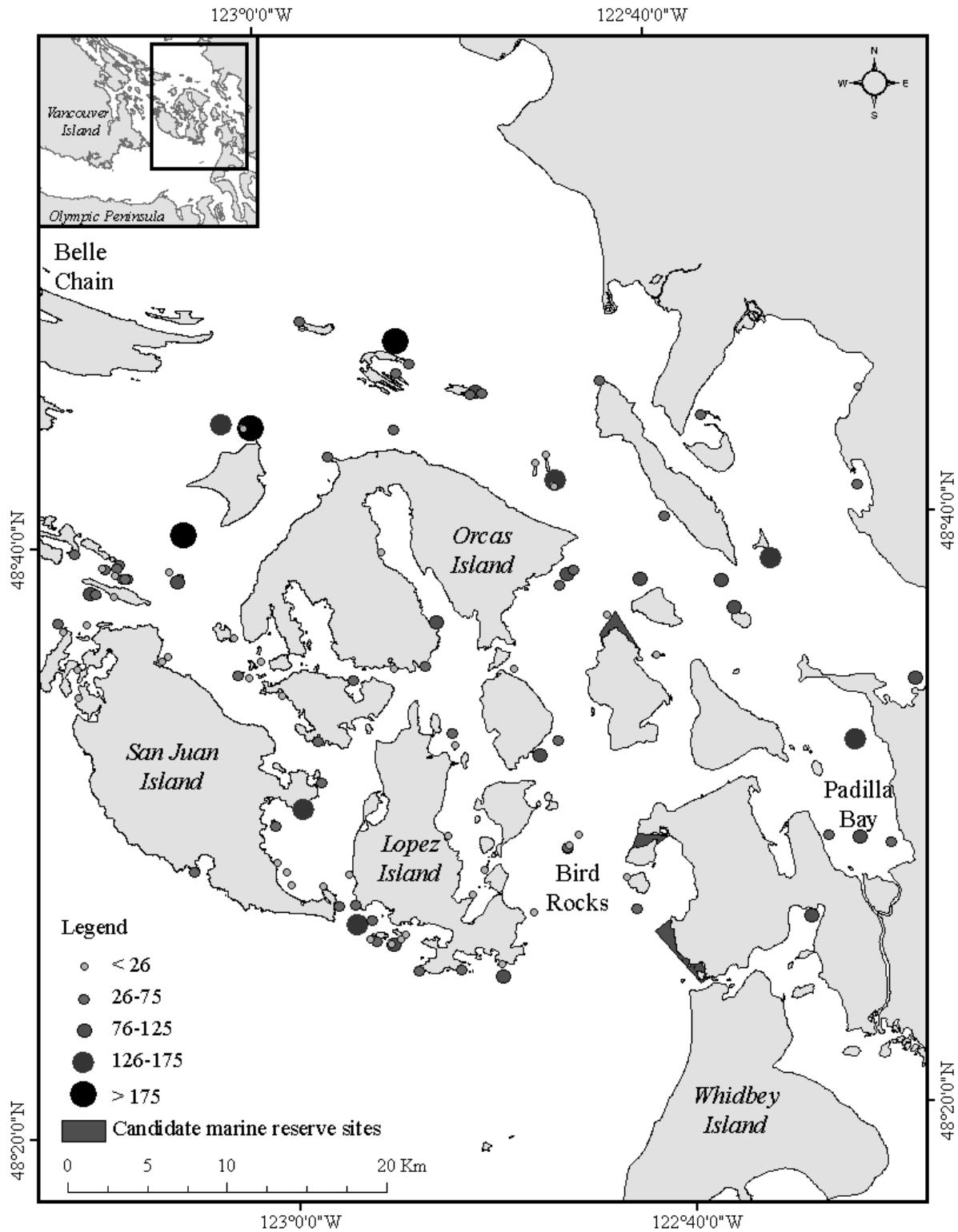


Figure 15. Haul-out sites with harbor seals present during the aerial pupping surveys < 40 km from the candidate marine reserves. Each circle represents one haul-out and the size is relative to the mean count for that haul-out site.

Table 5. Haul-out regions used by seals from the three capture sites. Haul-out site % indicates how many of the haul-out bouts were from the capture site. Regions are separated by > 5 km and the region with the greatest percentage of bouts is listed as ‘Highest % region.’ Highest % regions are shown in Figure 16.

Haul-out Site	Haul-out site %	Seal ID	Bouts	Regions used	Highest % region	Range of distance between regions (km)
Bird Rocks	6	Y1455	33	4	Pointer Island - 82	5 – 15
Bird Rocks	0	B1696	17	4	Ballenas Island - 53	20 – 90
Bird Rocks	19	B1695	36	7	Blakely Rocks - 50	10 – 80
Padilla Bay	93	B1699	29	2	Padilla Bay - 93	5 – 10
Padilla Bay	12	Y1459	25	4	Vendovi Island - 52	5 – 10
Padilla Bay	100	Y1460	20	1	Padilla Bay - 100	---
Padilla Bay	100	B1712	16	1	Padilla Bay - 100	---
Padilla Bay	100	B1713	19	1	Padilla Bay - 100	---
Padilla Bay	92	Y1462	25	2	Padilla Bay - 92	5 – 10
Belle Chain	6	B1707	52	> 10	Skipjack Island - 33	10 – 120
Belle Chain	68	B1709	47	2	Belle Chain Islets - 68	25

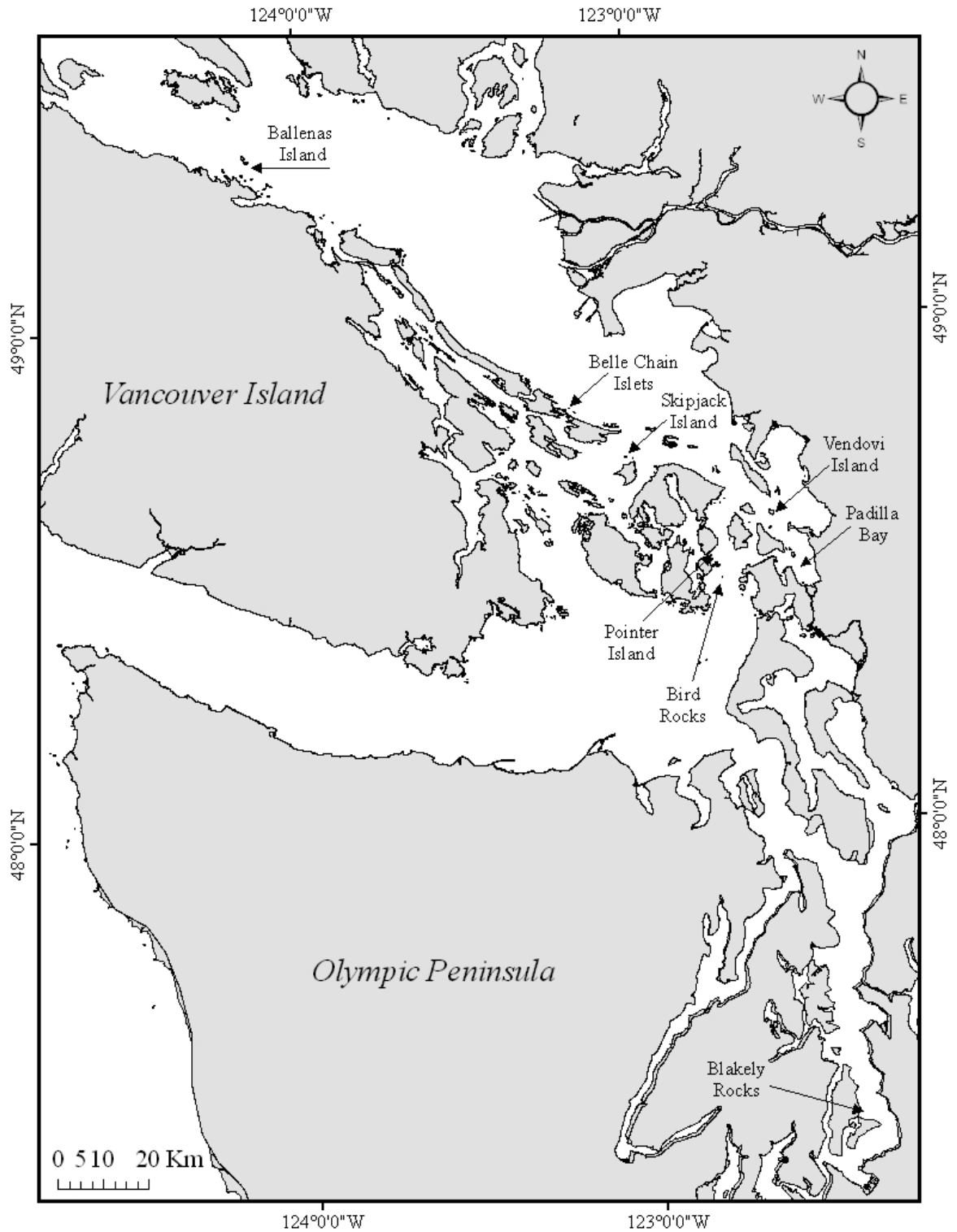


Figure 16. Haul-out regions with the highest percentage of haul-outs for each harbor seal with a recovered time-depth recorder tag (n = 11).

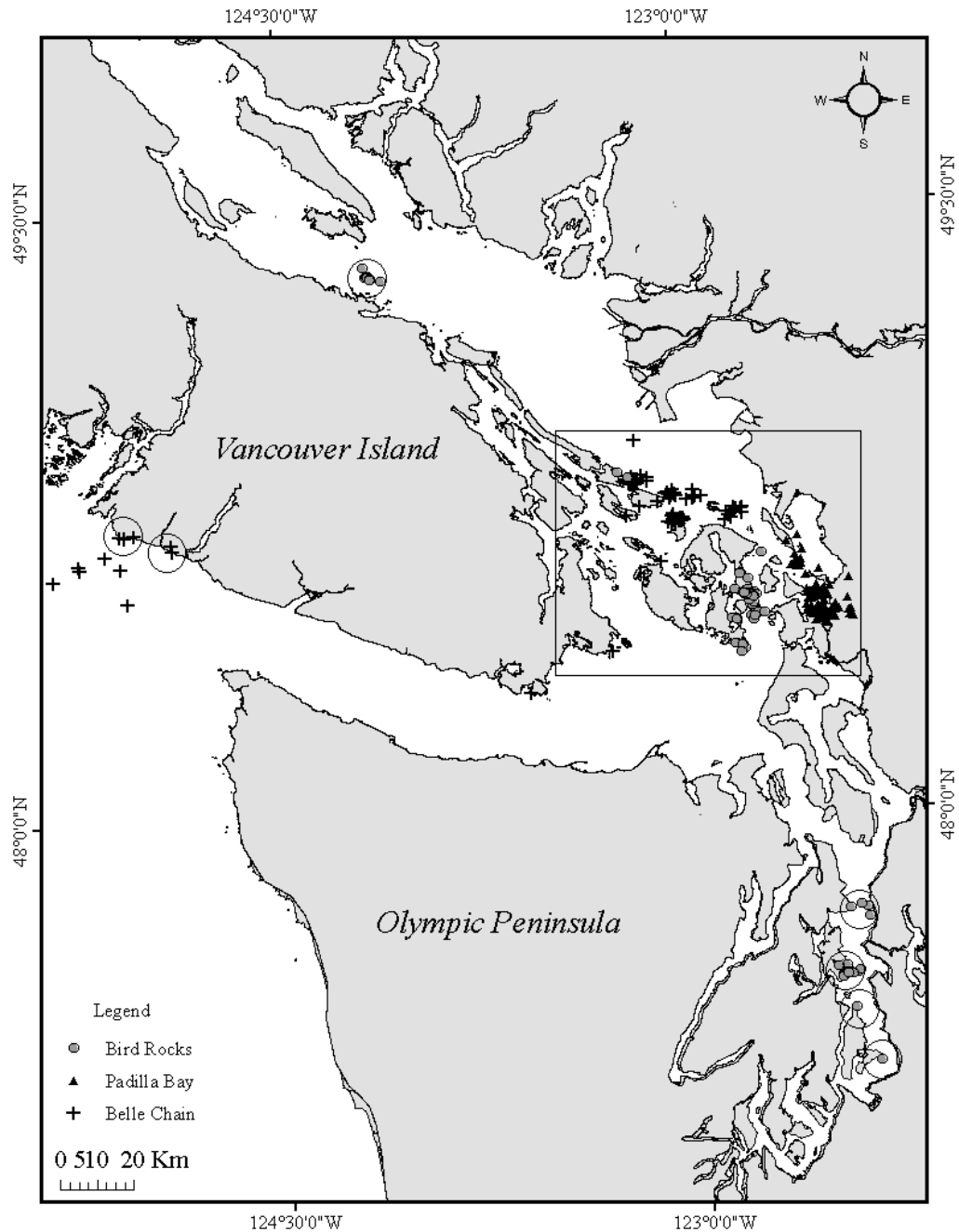


Figure 17. Location of haul-out bouts for satellite-tagged seals in the Georgia Basin. Circles encompass haul-out regions. Seals from Bird Rocks are indicated by (●), seals from Padilla Bay are indicated by (▲) and seals from Belle Chain are indicated by (+). ‘Haul-outs’ (+) offshore not enclosed in circles have been left out of this analysis. Haul-outs occurring within the enclosed square are enlarged in Fig 18.

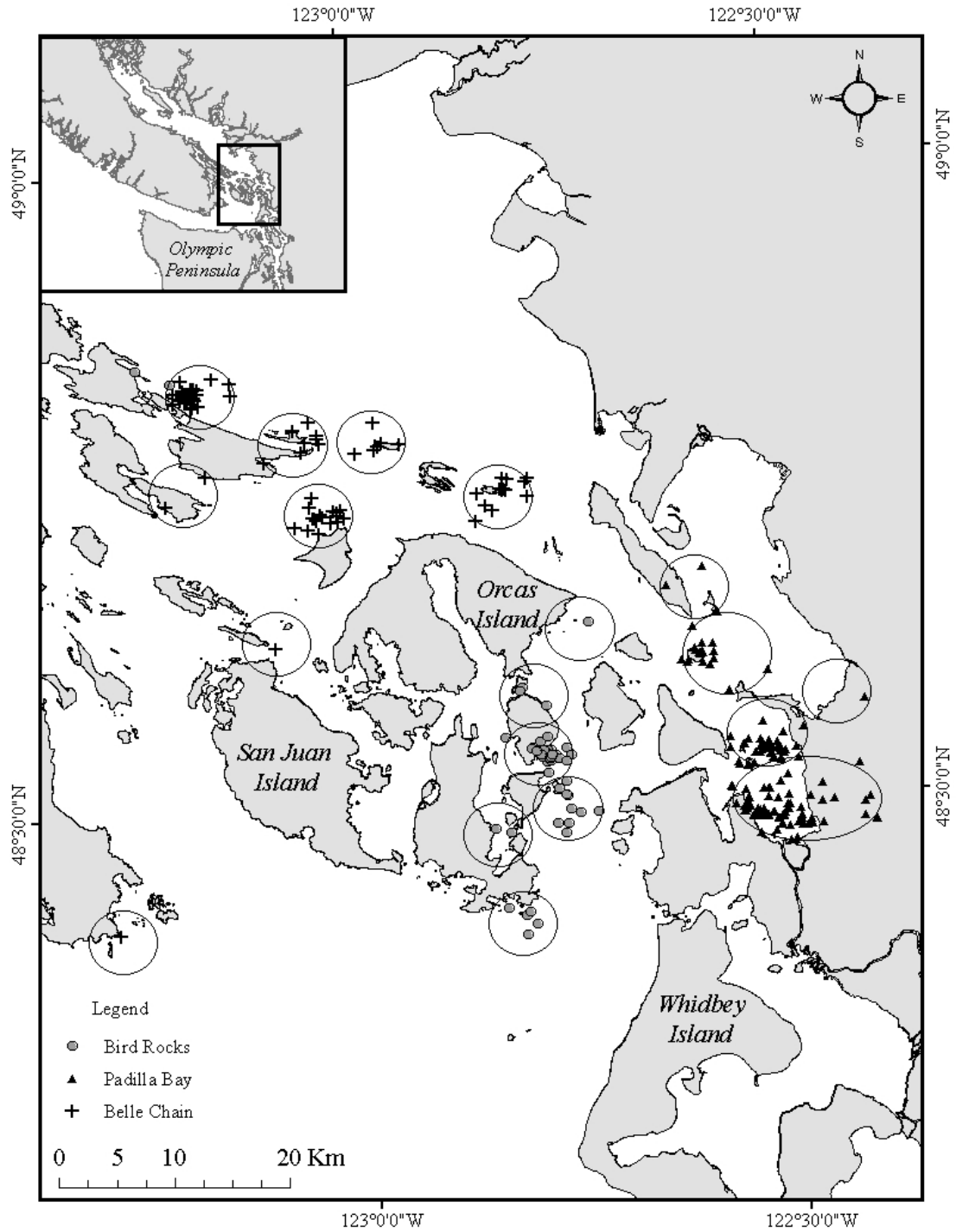


Figure 18. Location of haul-out bouts for satellite-tagged seals around the San Juan Islands. Circles encompass haul-out regions. Seals from Bird Rocks are indicated by (●), seals from Padilla Bay are indicated by (▲) and seals from Belle Chain are indicated by (+).

several of which were in south Puget Sound, over 80 km apart (Figure 17). The last individual, a female, had four distinct regions where haul-out bouts occurred but they were separated from each other by < 15 km. Of her haul-out bouts (n = 36), 75 % clustered around Pointer Island, which is north of Bird Rocks by about six km, and each of the remaining three regions had only two haul-out bouts (Figure 18).

Padilla Bay. The majority of haul-out bouts with corresponding standard satellite locations for Padilla Bay seals occurred within the main body of the bay (Figure 18). Haul-out bouts at sites outside of Padilla Bay (Vendovi Island and Viti Rocks) were observed two and three times for two male seals and 13 times for one female (Vendovi Island) (Figure 18). Within Padilla Bay, there was variability in the distribution of haul-out site usage for all seals, but three individuals had haul-out bouts clustered at the southern end of the bay, two seals had haul-out bouts clustered at the northern end of the bay and the last seal had the majority of haul-out bouts just north of Padilla Bay, around Vendovi Island (Figure 18).

Belle Chain. The two individuals from Belle Chain had differing patterns from each other; one seal used two regions of haul-outs approximately 25 km apart and the second seal used > 10 regions of haul-outs that were each separated by over 10 km with the farthest apart haul-outs separated by > 120 km (straight line distance) (Figure 17 – Figure 18). The seal that used > 10 regions utilized haul-outs from the Belle Chain Islets out to the outer coast of Vancouver Island (Figure 17).

DISCUSSION

The harbor seal population in the San Juan Islands and the bays directly east of the San Juan Islands was approximately 8,100 seals in 2007. Harbor seals tagged in the Georgia Basin moved longer distances than previously observed, including movements to and from the outer coast of Washington and British Columbia. Numerous harbor seals also had segmented home ranges, indicating that certain seals may concentrate their activities in multiple distinct spatial regions separated by substantial distances. Seals from rocky reef haul-out sites used haul-out sites in multiple regions sometimes separated by tens of km while seals from Padilla Bay demonstrated much higher haul-out fidelity and remained within 10 km of the bay. Seals moved between haul-out regions but rarely utilized the space within candidate marine reserve sites in the eastern San Juan Islands. Results also indicate that seal movement and spatial use differed by haul-out site. Seals from the two rocky reefs, Bird Rocks and Belle Chain, moved greater distances, spent more time farther away from their haul-out site and had larger home ranges than seals from Padilla Bay. There was no detectable effect of season (pre-pupping or pupping) or month (May – August) on the movements of harbor seals for any of the haul-out sites.

Abundance

The methods I used to estimate harbor seal population follow well documented protocols (Olesiuk et al. 1990, Thompson & Harwood 1990, Huber et al. 2001, Jeffries et al. 2003, Banks 2007) and the results fit into the trends seen over the past 10 years. Aerial surveys of harbor seals during pupping provided us with abundance estimates for a sub-region within the Georgia Basin adjacent to the candidate marine reserves. This estimate will

assist in predicting prey consumption based on diet and foraging behavior and therefore the potential impact of harbor seals on prey populations, particularly depressed fish stocks such as rockfish. Concurrent diet studies and bioenergetics models can use this population abundance to predict the amount of prey consumed by harbor seals.

Additionally, this abundance estimate assists in tracing the population growth trends of harbor seals for this area. The population of harbor seals in the Georgia Basin has stabilized, having recovered from the effects of a government financed bounty that ended in 1960 (Olesiuk et al. 1990, Jeffries et al. 2003). The population of seals increased threefold from 1978 – 1999 (Jeffries et al. 2003). The abundance estimate from 2007 was 8,121 (\pm 313), which fits into the last 10 years of estimates from the Washington Department of Fish and Wildlife, which ranged from 6,669 to 11,823 harbor seals for the same survey area (Figure 4.). The counts show slight fluctuations in estimated harbor seal abundance but support the hypothesis that the population is stable now after increasing significantly from the population observed during the 1970s. An increased population will require increased prey resources and could cause specific changes in behavior in response to this demand. It is possible that increased abundance of seals has caused movements and spatial use of the region to change over time as seals respond to increased competition for resources.

Movements

Three male harbor seals moved between inland waters and the Pacific Ocean, with roundtrip distances > 200 km. Preliminary data from harbor seals satellite-tagged in 2008 also indicated movements to the outer coast, with several individuals spending similar lengths of time in the inland waters and along the outer coast. The inland and coastal harbor

seals were separated into two distinct stocks based on differences in the timing of pupping (pupping clines) and differences in mitochondrial DNA (Lamont et al. 1996, Huber et al. 2001). These stocks have not been observed mixing with each other (Jeffries et al. 2003). Hence, movements between the inland waters and the outer coast were considered unlikely. Our results are unexpected and although it is likely that seal movements were related to foraging, it is possible that there is less genetic separation between these seal populations than previously assumed and that seals traveling to the coast are opportunistically mating. Previous genetic work compared seals from Grays Harbor, on the southern Washington coast, to Gertrude Island in south Puget Sound, haul-out sites separated by over 350 km. Current genetic analyses, comparing sites in between Grays Harbor and south Puget Sound, indicate no significant differences in mitochondrial DNA between seals from the northern Washington Coast and the San Juan Islands (Huber, pers. comm.)², suggesting the presence of gene flow between these populations. Mating happens approximately one month earlier on the outer coast than in the inland waters and two males tagged in this study were present on the outer coast at the onset of mating. Comparing non-mitochondrial genetic markers of harbor seals from the northern Washington coast and the Georgia Basin will investigate paternal lineage and conclusively ascertain whether gene flow is occurring between coastal and inland harbor seal stocks.

Female seal movements, < 26 km from haul-out sites, were consistent with previous studies in eastern Canada and Alaska (Lesage et al. 1999, Lowry et al. 2001); however, we observed male seals moving much farther distances, > 50 km, which was consistent with some studies (Lowry et al. 2001, Lesage et al. 2004) but differed from others (McLanahan et

² Harriet Huber; National Marine Mammal Laboratory; 7600 Sand Point Way N.E.; Seattle, WA 98115; May 2008.

al. 1984, Thompson & Miller 1990, Suryan & Harvey 1998). Adult male harbor seals have not been previously observed in the Georgia Basin moving as far as was observed in this study (McLanahan et al. 1984, Suryan & Harvey 1998). Previous observations may have been limited by radio-tracking technology (McLanahan et al. 1984, Yochem et al. 1987, Suryan & Harvey 1998) or a feature of the habitat, where additional haul-out sites were not located within close proximity to the study site (Thompson & Miller 1990).

The present study was conducted on adults during the late spring and summer; therefore it was surprising to see multiple roundtrip movements > 200 km for adult males not associated with a migratory over-wintering behavior. Harbor seals, in general, can travel distances > 100 km; however these movements have primarily been observed in juveniles (Brown & Mate 1983, Lowry et al. 2001) or been indicative of seasonal movements to overwintering sites (Lesage et al. 1999). Males in the Saint Lawrence River Estuary were observed to move up to 520 km between summer and wintering sites but were limited in their movements during the middle of a season; 90 % of standard satellite locations were < 10 km from their summer haul-out sites (Lesage et al. 1999). The longest duration of trips other than the seasonal switch was 12 d (Lesage et al. 2004). Conversely, in this study seven adult male seals from Bird Rocks and Belle Chain had long trips > 200 km roundtrip that lasted 1 – 8 weeks between April and August.

My results indicate that seals from the rocky reefs moved farther distances from their haul-out site than seals from Padilla Bay. Maximum and mean straight-line distances between satellite locations and each seals' haul-out site differed from previous research in the Georgia Basin for the rocky reef seals while Padilla Bay seals showed similar trends to previous research conducted in Padilla Bay. Sixty percent of seals, the majority of which

were from the two rocky reef sites, had a maximum straight-line distance from their haul-out site greater than the maximum distance of 28 km previously observed in the Georgia Basin (Suryan & Harvey 1998). Harbor seals from Bird Rocks and Belle Chain had mean distances of 48 km and 23 km from their haul-out site, respectively. Seals from Padilla Bay moved a mean distance of 9 km from their haul-out site and made relatively few excursions out of the bay, a behavior previously observed in Padilla Bay (McLanahan et al. 1984). Variability in harbor seal movements between different haul-out sites has been observed in several studies (Tollit et al. 1998, Small et al. 2005, Waring et al. 2006), indicating that these are not novel observations; however, the driving factors behind differing haul-out site behaviors are still not well understood. Two hypotheses include movement in search of prey resources or in search of ideal haul-out site locations at which to pup and molt (Brown & Mate 1983, Jeffries 1986). Prey resources appear to be the more likely factor influencing seal behavior in this study because males and females from Padilla Bay acted similarly and remained in the bay well before the onset of pupping or mating. If seals remained in Padilla Bay because of its function as a nursery and not because of prey availability then one would expect that only females would remain in Padilla Bay during pupping but not before. Thus, it is likely that their behavior would shift in the winter and that they would move greater distances when the bay was no longer being utilized as a nursery. Likewise, if harbor seals from the rocky reefs move in response to biological seasons such as pupping or molting then one would expect seals to make small movements during pupping and molting and then change their behavior in the winter. Future studies should examine winter harbor seal behavior, ideally with a larger sample size of females, and examine prey availability around both types of habitats to determine if differences in prey abundance might explain harbor seal behavior.

My sample size of females was small, especially outside of Padilla Bay, and may not reflect the trends of all females in the region or individual site-specific patterns. However, satellite technology did support previous research conducted in Padilla Bay using VHF-telemetry (McLanahan et al. 1984) and demonstrated that female seals from Padilla Bay spent the majority of their time in Padilla Bay.

Straight-line distance ignored the effect of land on the movement patterns of seals, underestimating the actual distances moved by individuals from Belle Chain and Bird Rocks. This effect was more pronounced in seals from Belle Chain than Bird Rocks. The actual water distance traveled by a seal to reach the outer coast from the Belle Chain Islets was > 210 km, an increase > 65 km from the calculated straight-line distance, indicating that differences observed between rocky reef sites and Padilla Bay were conservative and differences in the actual distances moved were most likely substantially larger than indicated by the results. Individual seals from Bird Rocks would have been moderately affected by using straight-line distance but it is unlikely that the overall trends between Bird Rocks and Belle Chain would change if water distance were used.

Minimum convex polygons revealed variation in spatial distribution of seals between the three haul-out sites, supporting trends observed by looking solely at maximum and mean distances traveled from individual haul-out sites. Seals from Padilla Bay utilized significantly less of the Georgia Basin than seals from the two rocky reef sites. Minimum convex polygons assume uniform distribution; therefore this analysis did not indicate how the space within the polygon was used but merely that the rocky reef individuals as a group utilized a much larger area within the Georgia Basin than the seals from Padilla Bay. I did not detect a temporal effect, either on a seasonal or monthly scale, or a detectable interaction

effect of site with season or month, contrary to research conducted in Alaska where a significant monthly effect on minimum convex polygon size was detected (Lowry et al. 2001). However, my study also observed long-distance and long-duration movements throughout the study period that would be reflected in minimum convex polygon size and had not been noted in previous studies. These movements may be novel regional behaviors, less driven by temporal scales and more by the individual sites from which the seals originated.

All levels of satellite-transmissions were used to determine movements. It was possible that locations far away from the haul-out site represented erroneous locations that bypassed the filter. However, when analyzing only standard locations, the same movement patterns and distances were revealed. Minimum convex polygons are highly influenced by outliers (Freitas et al. 2008) and it is possible that erroneous points inflated the sizes of the polygons. Even so, transmission errors are likely random and therefore should not have influenced patterns seen between groups.

Seal body mass was included in the LME model as a random factor and this was biologically realistic as body size affects movements and foraging behavior of mammals, including harbor seals (McNab 1963, Thompson et al. 1998, Woodward et al. 2005). Sex was not detected as an important factor to include in the model for this study but this may have been due to the sample size of this study. Several males had polygons as small as females, and removing females from the analyses actually exaggerated differences seen between haul-out sites. Sex was an important factor influencing movements in some studies with larger sample sizes of males ($n = 23$) and females ($n = 14$) (Thompson et al. 1998). However, in Alaska harbor seal males ($n = 15$) and females ($n = 12$) of the same age class

had similarly sized minimum convex polygons between April – July (Lowry et al. 2001).

The small and unequal sample size of females in this study did not allow me to fully examine the influence of sex on movements, but this question should be addressed by future studies.

Home ranges

Harbor seals had home ranges that differed in size for different haul-out types and a number of individuals had segmented home ranges. Home range estimations using fixed kernel density estimates or very similar methods have been conducted on numerous marine mammal species but to my knowledge, the only study analyzing kernel density home ranges of adult harbor seals is a technical report describing harbor seals from the Wadden Sea, Denmark. Their study calculated home range size and individual variability of two adult and eight sub-adult/pup harbor seals (Tougaard et al. 2003). The Denmark observations were similar to those from my study and also contradict the traditional view that harbor seals are resident to a limited geographic area and do not leave that home area for extended periods of time. Harbor seals in Denmark moved between separated foraging areas and haul-out banks to a greater extent than previously assumed, spent more time in deeper water than previously documented and overlapped in distribution with a genetically distinct population, the German Wadden Sea population (Tougaard et al. 2003). To my knowledge, segmented home ranges of this nature have not been observed previously for harbor seals in the Georgia Basin. However, pinnipeds in other regions, such as grey seals, have segmented home ranges, which were interpreted as preferential use of certain habitats and bathymetry over others (Sjoberg & Ball 2000). Prey resources may differ between habitats in the Georgia Basin and harbor seals may move deliberately to exploit regions of higher prey abundance.

Home ranges (95th percentile contours) and core areas of use (50th percentile contours) were larger for seals from the rocky reefs than for seals from Padilla Bay, with large sections of their home range separated by distances > 20 – 100 km. Neither season nor months were detected as having a significant effect on home range size or the core area of use. Assuming that foraging was a main driver of seal movements, these results suggest that harbor seals from the rocky reef sites were unable to find enough resources or a particular food resource in one location and had to move over greater distances in search of these resources or resource whereas seals from Padilla Bay may not have been faced with the same challenges. Diet data indicate that seals from Padilla Bay have a more diverse diet than seals from rocky reef sites (Lance & Jeffries 2007) The lack of a temporal effect implies that it was either individual variability in the haul-out sites or habitat-specific characteristics driving the behavior of these seals and not biological seasons related to life history stages such as pupping or mating.

This study employed several novel techniques to assess the home range size and core areas of harbor seals. Kernel density estimates are not significantly affected by biologically improbable outliers; therefore satellite locations that passed the filtering methods but were most likely erroneous were retained to avoid introducing bias to this analysis. Kernel density estimates are less accurate as sample size decreases (Seaman & Powell 1996, Girard et al. 2002); therefore it was advantageous to include all quality levels of transmissions, as it increased the data set threefold, despite the heightened chance for greater error in the locations. Weighting the satellite transmissions based on time also increased the data set because it allowed the inclusion of all points instead of calculating a daily average or using the highest quality transmission. There were small, disjointed encircled areas included in the

95th percentile contour that most likely represent one or several satellite transmissions.

However, this is theoretically distributed evenly among all seals and is an expected feature of using fixed kernel density estimates with least-squares cross validation (Seaman & Powell 1996).

Interaction with candidate reserves

Harbor seals rarely utilized the space within candidate marine reserves. Only 4.5 % of satellite transmissions fell < 3 km from candidate reserves. Assuming that the haphazardly tagged seals were representative of the haul-out sites at which they were tagged, it seems unlikely that harbor seals had an impact on rockfish populations in the candidate marine reserves during the study period. Foraging data further support this statement. Rockfish were documented in 9 % of scat samples of harbor seals in the San Juan Islands during the summer (Lance & Jeffries 2007) and the diving behavior of the same seals that I studied indicate that they fed on forage fish, such as herring (*Clupea* spp.), and estuarine fish rather than rockfish (Reuland 2008). However, rockfish comprise a greater percent of the diet of harbor seals in the San Juan Islands during the winter, occurring in 23 % of scat samples (Lance & Jeffries 2007). Future studies should investigate movements during the winter to integrate with diet and foraging data to determine if harbor seals are traveling to the candidate reserve sites to consume rockfish.

Although there were only 17 transmissions from within the boundaries of the candidate marine reserves, it is possible that seals may have been inside the boundary and transmitted lower quality, auxiliary locations. Tag location error may have then placed the seal outside of the candidate marine reserve boundaries. Placing a buffer around the reserve

attempted to account for some of the tag error although it is possible that this did not account for all transmissions that could have occurred while a seal was actually within the boundaries but were placed farther away by the satellite estimation. Despite inherent error in the tags, investigating individual transmissions and home range maps allowed me to feel confident in inferring that these seals were spending the majority of their time elsewhere in the region and not within the boundaries of the candidate marine reserves.

There were 114 haul-out sites and approximately 8,100 harbor seals in the San Juan Islands and adjacent bays that were < 40 km from the candidate marine reserves during pupping. The selection of a 40 km buffer around the marine reserves was based on the movements observed from the satellite tagged seals. All seals from Padilla Bay, all but one of the Belle Chain seals and three of the Bird Rocks seals had mean distances from their haul-out site < 40 km. This may be an overestimate of the abundance of seals that may impact the candidate reserves but it provides us the capacity to examine where there are more or less dense aggregations of harbor seals in the region. Based on the proximity of haul-outs that we observed and the quantity of seals at those haul-outs it appears that the northern-most candidate reserve (Figure 15) is the most vulnerable of the three candidate reserves for utilization by harbor seals. There are several large haul-outs with over 100 seals within 10 km of this reserve whereas there are not as many seals within 10 km of the two other candidate reserves. It will be important to continue monitoring of these sites and harbor seal behavior to determine whether there are changes in harbor seal utilization which could indicate increased foraging pressure on the prey resources within these sites.

Predicting the foraging impact of regional harbor seals on candidate reserves may be more difficult than previously assumed. Harbor seals did not remain within a particular

distance of their haul-out, foraging only within that area. Instead, seals exhibited segmented home ranges and core areas of use separated by 20 – 100 km. My research suggests that seals can move into the area from far distances and could forage at candidate marine reserves. It is possible that the 20 seals observed in this study did not utilize the candidate reserves frequently but other seals from farther away, with segments of their core areas that encompassed the candidate reserves, could have had an impact on the fish populations found within their boundaries. This new knowledge will help conservation managers determine the spatial scale at which to consider the possible effects of predators, a scale which should be much larger than previously estimated.

Haul-out site fidelity

Harbor seals from the three haul-out sites showed differing haul-out patterns; seals from the rocky reef sites used haul-outs in distinctly separated geographic regions, whereas seals from Padilla Bay used haul-outs that were primarily concentrated within Padilla Bay. High site fidelity has been observed previously in harbor seals in other geographic regions (Yochem et al. 1987, Thompson et al. 1994), including previous research in the Georgia Basin (McLanahan et al. 1984, Suryan & Harvey 1998). However, the use of VHF radio telemetry may have prevented researchers from observing the use of haul-out sites away from their study site (McLanahan et al. 1984, Yochem et al. 1987, Thompson et al. 1994, Suryan & Harvey 1998). It is difficult to determine which, if any, haul-out is the “home” site for seals from the rocky reefs. While we cannot be certain that the capture sites were their “home site,” distance figures (Appendix 2) indicate that seals did move to and from the vicinity of where they were tagged throughout the duration of the study. Several seals did

not haul-out very frequently at the haul-out site at which they were captured but they did spend time repeatedly hauled-out within 10 – 15 km of those sites at similar rocky reef sites. Examining the data, I am confident describing these seals “rocky reef” seals and not animals from an estuarine bay haul-out. Conversely, based on the haul-out bouts of seals from Padilla Bay, I am confident referring to these individuals as “bay seals.”

Contrary to behavior demonstrated by the rocky reef seals, seals from Padilla Bay used haul-outs within the bay for the majority of haul-outs with only several forays away from the bay. The farthest away haul-out sites revealed by this analysis were 8 – 15 km of the bay and included Eliza Rocks, Viti Rocks and Vendovi Island. Seals showed preferences for one region within the bay over others, as their haul-out bouts clustered in different regions of the bay. Seals within estuarine systems, including Padilla Bay, have previously been observed using multiple haul-outs within several km from each other within the estuary (McLanahan et al. 1984, Thompson et al. 1994). Conversely, seals have also been observed moving between estuarine habitats on the outer coast, either following prey resources or searching for suitable pupping and molting sites (Brown & Mate 1983, Jeffries 1986). Conclusions from the present analysis align with those from movement patterns and home ranges, indicating that seals from Padilla Bay remained within the vicinity of the bay and that they most likely have adequate food resources and appropriate haul-out sites for pupping. Padilla Bay is a well-known nursery haul-out site for harbor seals (Jeffries et al. 2000).

There were caveats in this examination of haul-out locations. Not all haul-out bouts had corresponding standard locations; therefore the sample may not be representative of all bouts. Additionally, there is inherent error in locations, however this error is more likely to occur in the longitudinal direction (Vincent et al. 2002). Several haul-out bouts were not

located at a haul-out site but were directly east or west of a known haul-out (Figure 17), within the known longitudinal error of the tags (Vincent et al. 2002). Because I examined regions of haul-outs instead of individual haul-out sites to compensate for this location error I am confident in the conclusions drawn from the data.

Conclusions

Harbor seals moved farther than previously documented in the region and their behavior, including distance traveled, home range size and haul-out site fidelity, appeared to be driven by haul-out site. Harbor seals from the rocky reefs moved greater distances for longer periods of time and utilized haul-outs over a wider geographic distribution than seals from Padilla Bay. If movement patterns were driven by biological seasons, such as pupping or breeding, I would expect seals from all three haul-out sites to act similarly within a season and change behavior between seasons; however this behavior was not observed. Further, if differences in haul-out sites were attributed to female behavior, then removing females should have resulted in similar movement patterns among males regardless of haul-out type. Again, this behavior also was not observed. Consequently, results indicate that differences in movement behavior were attributed to the haul-out sites where the seals were captured. Foraging and diving behavior vary according to the habitat surrounding their haul-out (Tollit et al. 1998, Reuland 2008). This study indicates that seals also exhibit differences in movements and home ranges based on habitat type. Hence, haul-out type should be considered when predicting the predatory impact of harbor seals.

With the exception of one male that moved > 100 km at the end of the study, seals from Padilla Bay stayed < 15 km of the bay, which differed from the behavior exhibited by

seals from the rocky reef sites. Increased seasonal abundance of fish species smaller than salmonids and preferred habitat for pupping were suggested to regulate seal abundance and movements during the summer in an Oregon estuary (Brown & Mate 1983). Parous female harbor seals were observed moving from Columbia River haul-outs, where they were feeding, into estuaries at the onset of pupping (Jeffries 1986). These observations might explain why harbor seals remained in Padilla Bay during this study, while seals from the rocky reefs made larger regional movements. Padilla Bay is a protected estuary and seals within this habitat may remain there, using localized haul-out sites, due to adequate food resources or other habitat characteristics that make it a prominent nursery site for pupping (McLanahan et al. 1984, Jeffries et al. 2000). The timing of this study may not have captured changes in male behavior leading into mating because many tags ceased transmitting in late August, at the start of mating. Diet analysis of harbor seal scats from Padilla Bay revealed the presence of a wide diversity of smaller estuarine prey items in harbor seal scats, including gunnel (*Pholid* spp.), Pacific staghorn sculpin (*Leptocottus armatus*), plainfin midshipman (*Porichthys notatus*) and numerous other species (Luxa, pers. comm.)³, suggesting that harbor seals were foraging within the estuary on locally abundant estuarine prey.

Seals from Bird Rocks and Belle Chain made lengthy trips and it can be inferred that the use of multiple haul-outs in distinct regions is due to their wide-ranging movements. The movements of the satellite-tagged seals in this study did not appear to be random walks but instead appeared to be directed movement as described by (Austin et al. 2004). Therefore, I can infer that seals were moving intentionally either in pursuit of food resources or possible mating opportunities. Prey may not be consistently abundant locally, thus encouraging seals

³ Katie Luxa; Western Washington University Department of Biology; 516 High Street; Bellingham, WA 98225; May 2008.

to move farther to exploit different prey sources. Harbor seals with larger movements and larger home ranges also utilized haul-out sites over a broader geographic scale. Seals previously observed switching haul-out locations were theorized to move in search of food resources or haul-outs ideal for pupping or molting (Brown & Mate 1983, Jeffries 1986). Male harbor seals have not been previously observed traveling large distances to mate in a separate geographic region and then return to their original site. However, differences in the timing of pupping and mating between the coastal and inland waters make this another possible explanation for excursions to the outer coast. At this point, however, I am unable to conclusively determine the cause of these large movements and segmented home ranges. Further research examining oceanographic conditions indicative of increased productivity and prey abundances as well as genetic analysis of non-mitochondrial DNA may elucidate the motivations behind these newly observed behaviors.

Harbor seals are an abundant marine predator within the inland waters of the Pacific Northwest. My analysis of movements and home ranges in this study suggest that the candidate marine reserves in the eastern San Juan Islands were not frequently utilized by harbor seals. It will be important to continue monitoring of harbor seals if these reserves are implemented to assess whether there are changes in seal behavior if rockfish abundances increase. Additionally, future research should investigate harbor seal behavior during the winter to supplement this research and obtain a complete yearly prediction of harbor seal behavior in this region in order to properly inform conservation managers on the potential impact of harbor seals on the future success of candidate marine reserves as a conservation tool.

LITERATURE CITED

- Argos (2007) Argos User's Manual. CLS/Service Argos.
- Austin D, Bowen WD, McMillan JI (2004) Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *OIKOS* 105:15-30
- Austin D, Bowen WD, McMillan JI, Iverson SJ (2006) Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* 87:3095-3108
- Austin D, McMillan JI, Bowen WD (2003) A three-stage algorithm for filtering erroneous argos satellite locations. *Marine Mammal Science* 19:371-383
- Banks AS (2007) Harbor seal abundance and habitat use relative to candidate marine reserves in Skagit County, Washington. MS Thesis, Western Washington University, Bellingham, Washington
- Bax NJ (1998) The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Science* 55:997-1030
- Bayer RD (1985) Six years of harbor seal censusing at Yaquina estuary, Oregon. *The Murrelet* 66:44-49
- Beyer HL (2004) Hawth's Analysis Tools for ArcGIS. Available online at: <http://www.spatial ecology.com/htools>
- Bonadonna F, Lea MA, Guinet C (2000) Foraging routes of Antarctic fur seals (*Arctocephalus gazella*) investigated by the concurrent use of satellite-tracking and time-depth recorders. *Polar Biology* 23:149-159
- Brown RF, Mate BR (1983) Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook bays, Oregon. *Fishery Bulletin* 81:291-301
- Brown RF, Wright BE, Reimer SD, Laake J (2005) Trends in abundance and current status of harbor seals in Oregon 1977-2003. *Marine Mammal Science* 21:657-670
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352
- Calambokidis J (1979) Harbor seal census for the inland waters of Washington. *The Murrelet* 60:110-112
- Clinton WJ (2000) Executive Order 13158 -- Marine Protected Areas. *Weekly Compilation of Presidential Documents* 36:1230-1234
- Craig P, Parker D, Brainard R, Rice M, Balazs G (2004) Migrations of green turtles in the central South Pacific. *Biological Conservation* 116:433-438

- Dickson BG, Beier P (2002) Home-range and habitat selection by adult cougars in southern California. *The Journal of Wildlife Management* 66:1235-1245
- Eisenhardt E (2002) Inside and out of the San Juan Islands Marine Preserves: Demographics of nearshore rocky reef fish. *Puget Sound Notes* 46:4-8
- Everitt RD, Gearin PJ, Skidmore JS, DeLong RL (1981) Prey items of harbor seals and California sea lions in Puget Sound, Washington. *The Murrelet* 62:83-86
- Fanshawe S, VanBlaricom GR, Shelly AA (2003) Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: a case study with red abalones and sea otters. *Conservation Biology* 17:273-283
- Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science* 24:315-325
- Fu C, Mohn R, Fanning PL (2001) Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1613-1623
- Girard I, Oullet J, Courtois R, Dussault C, Breton L (2002) Effects of sampling effort based on GPS telemetry on home-range size estimations. *The Journal of Wildlife Management* 66:1290-1300
- Griffis RB, Kimball KW (1996) Ecosystem approaches to coastal and ocean stewardship. *Ecological Applications* 6:708-712
- Guidetti P (2007) Potential of marine reserves to cause community-wide changes beyond their boundaries. *Conservation Biology* 21:540-545
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonadonna F, Donnay J (2001) Spatial distribution of foraging in female Antarctic fur seals *Arctocephalus gazella* in relation to oceanographic variables: a scale-dependent approach using geographic information systems. *Marine Ecology Progress Series* 219:251-264
- Harkönen T, Harding KC, Lunneryd SG (1999) Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. *Journal of Applied Ecology* 36:825-841
- Harvey JT, Brown RF, Mate BR (1990) Abundance and distribution of harbor seals (*Phoca vitulina*) in Oregon, 1975-1983. *Northwestern Naturalist* 71:65-71
- Heide-Jørgensen MP, Stewart BS, Leatherwood S (1992) Satellite tracking of ringed seals *Phoca hispida* off northwest Greenland. *Ecography* 15:56-61

- Huber HR, Jeffries SJ, Brown RF, DeLong RL, VanBlaricom G (2001) Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. *Marine Mammal Science* 17:276-293
- Hyrenbach KD, Fernandez P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233:283-301
- Jeffries S (1986) Seasonal movements and population trends in harbor seals (*Phoca vitulina richardsi*) in the Columbia River and adjacent waters of Washington and Oregon: 1976-1982. Final report to the Marine Mammal Commission in partial fulfillment of contract No. MM2079357-5, Washington Department of Game, Olympia, WA
- Jeffries S, Brown RF, Harvey JT (1993) Techniques for capturing, handling and marking harbour seals. *Aquatic Mammals* 19:21-25
- Jeffries S, Huber H, Calambokidis J, Laake J (2003) Trends and status of harbor seals in Washington State 1978-1999. *Journal of Wildlife Management* 67:208-219
- Jeffries SJ, Gearin PJ, Huber HR, Saul DL, Pruett DA (2000) Atlas of seal and sea lion haulout sites in Washington, Washington Department of Fish and Wildlife, Wildlife Science Division, Olympia, WA
- Katajisto J, Moilanen A (2006a) B-Range. Metapopulation Research Group, Department of Biological and Environmental Sciences, University of Helsinki
- Katajisto J, Moilanen A (2006b) Kernel-based home range method for data with irregular sampling intervals. *Ecological Modelling* 194:405-413
- Laake JL, Browne P, DeLong RL, Huber HR (2002) Pinniped diet composition: a comparison of estimation models. *Fishery Bulletin* 100:434-447
- Lamont MM, Vida JT, Harvey JT, Jeffries S, Brown R, Huber HH, DeLong R, Thomas WK (1996) Genetic substructure of the Pacific harbor seal (*Phoca vitulina richardsi*) off Washington, Oregon, and California. *Marine Mammal Science* 12:402-413
- Lance MM, Jeffries S (2007) Temporal and spatial variability of harbor seal diet in the San Juan Island archipelago. Final report to U.C. Davis Wildlife Health Center, SeaDoc Society, Research Agreement No. K004431-25, Washington Department of Fish and Wildlife, Lakewood, WA
- Lance MM, Jeffries SJ (2006) Estimating the importance of rockfish, lingcod and other bottomfish in the diet of harbor seals in the San Juan Islands. Contract Report to SeaDoc Society Research Agreement No. K004431-2, Washington Department of Fish and Wildlife, Olympia, WA

- Lesage V, Hammill MO, Kovacs KM (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology* 77:74-87
- Lesage V, Hammill MO, Kovacs KM (2004) Long-distance movements of harbour seals (*Phoca vitulina*) from a seasonally ice-covered area, the St. Lawrence River estuary, Canada. *Canadian Journal of Zoology* 82:1070-1081
- London JM, Lance MM, Jeffries SJ (2002) Observations of harbor seal predation on Hood Canal salmonids from 1998 to 2000. Final report PSMFC Contract No. 02-15, Washington Cooperative Fish and Wildlife Research Unit, Seattle, WA
- Love MS, Yoklavich M, Thornsteinson L (2002) The rockfishes of the northeast Pacific. University of California Press, Berkeley, CA
- Lowry LF, Frost KJ, Davis R, DeMaster DP, Suydam RS (1998) Movements and behavior of satellite-tagged spotted seals *Phoca largha* in the Bering and Chukchi seas. *Polar Biology* 19:221-230
- Lowry LF, Frost KJ, Ver Hoef JM, DeLong RA (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William sound, Alaska. *Marine Mammal Science* 17:835-861
- Mauritzen M, Derocher AE, Wiig Ø, Belikov SE, Boltunov AN, Hansen E, Garner GW (2002) Using satellite telemetry to define spatial population in polar bears in the Norwegian and western Russian arctic. *The Journal of Applied Ecology* 39:79-90
- McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the southern ocean. *Antarctic Science* 4:393-398
- McConnell BJ, Fedak MA, Lovell P, Hammond PS (1999) Movements and foraging areas of grey seals in the North sea. *The Journal of Applied Ecology* 36:573-590
- McConnell BL, Dinnel PA (2002) Rocky reef bottomfish recovery in Skagit County: Assesment of eight potential marine reserves sites and final site recommendations, Skagit County Marine Resources Committee, Mount Vernon, WA
- McLanahan EC, Scholz AT, O'Laughlin K, Cassidy P (1984) Radiotelemetry investigations of harbor seal (*Phoca vitulina*) summer haulout activity at the Padilla Bay National Estuarine Sanctuary, Eastern Washington University, Cheney, WA
- McNab BK (1963) Bioenergetics and the determination of home range size. *The American Naturalist* 97:133-140
- Middlemas SJ, Barton TR, Armstrong JD, Thompson PM (2006) Functional and aggregative responses of harbour seals to changes in salmonid abundance. *Proceedings of the Royal Society B* 273:193-198

- Mills C, Rawson K (2004) Outlook grim for north Pacific rockfish: rockfish symposium, Friday Harbor laboratories, University of Washington, USA, September 25-26, 2003. *Fish and Fisheries* 5:178-180
- Mohn R, Bowen WD (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2722-2738
- Mohr CO (1947) Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-249
- Musick JA, M.M. Harbin, Berkeley SA, Burgess GH, Eklund AM, Findley L, Gilmore RG, Golden JT, Ha DS, Huntsman GR, McGovern JC, Parker SJ, Poss SG, Sala E, Schmidt TW, Sedberry GR, Weeks H, Wright SG (2001) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6-30
- Olesiuk PF (1993) Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fishery Bulletin* 91:491-515
- Olesiuk PF (1999) An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Canadian Stock Assessment Secretariat Research Document, Department of Fisheries and Oceans, Nanaimo, B.C.
- Olesiuk PF, Bigg MA, Ellis GM (1990) Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 47
- Palsson W (2002) Scientific approaches to designing a marine reserve network for Puget Sound. *Puget Sound Notes* 46:1-4
- Parnell PE, Lennert-Cody CE, Geelen L, Stanley LD, Dayton PK (2005) Effectiveness of a small reserve in southern California. *Marine Ecology Progress Series* 296:39-52
- Pinheiro JC, Bates DM (2004) *Mixed-effects models in S and S-Plus*. Springer, New York, NY
- Reuland K (2008) Seasonal variation in the foraging behavior of harbor seals in the Georgia Basin: implications for marine reserves. MS Thesis, Western Washington University, Bellingham, WA
- Scheffer TH, Slipp JW (1944) The harbor seal in Washington State. *American Midland Naturalist* 32:373-416
- Scheffer TH, Sperry CC (1931) Food habits of the Pacific harbor seal, *Phoca richardii*. *Journal of Mammalogy* 12:214-226

- Seaman DE, Griffith B, Powell RA (1998) KERNELHR: A program for estimating animal home ranges. *Wildlife Society Bulletin* 26:95-100
- Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075-2085
- Seminoff JA, Resendiz A, Nichols WJ (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series* 242:253-265
- Sjoberg M, Ball JP (2000) Grey seal, *Haliochoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? *Canadian Journal of Zoology* 78:1661-1667
- Small RJ, Lowry LF, Ver Hoef JM, Frost KJ, DeLong R, Rehberg MJ (2005) Differential movements by harbor seal pups in contrasting Alaska environments. *Marine Mammal Science* 21:671-694
- Stanley WT, Shaffer KE (1995) Harbor seal (*Phoca vitulina*) predation on seined salmonids in the lower Klamath river, California. *Marine Mammal Science* 11:376-385
- Stenson GB, Hammill MO, Lawson JW (1997) Predation by harp seals in Atlantic Canada: preliminary consumption estimates for Arctic cod, capelin and Atlantic cod. *Journal of Northwest Atlantic Fishery Science* 22:137-154
- Stewart BS, Leatherwood S, Yochem PK, Heide-Jørgensen MP (1989) Harbor seal tracking and telemetry by satellite. *Marine Mammal Science* 5:361-375
- Suryan RM, Harvey JT (1998) Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behavior, foraging activity, and haul-out site use. *Marine Mammal Science* 14:361-372
- Thompson PM (1989) Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haul-out groups. *Journal of Zoology* 217:281-294
- Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). *The Journal of Applied Ecology* 26:521-535
- Thompson PM, Harwood J (1990) Methods for estimating the population size of common seals, *Phoca vitulina*. *Journal of Applied Ecology* 27:924-938
- Thompson PM, Mackay A, Tollit DJ, Enderby S, Hammond PS (1998) The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology* 76:1044-1053

- Thompson PM, McConnell BJ, Tollit DJ, Mackay A, Hunter C, Racey PA (1996) Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N.E. Scotland. *The Journal of Applied Ecology* 33:1572-1584
- Thompson PM, Miller D (1990) Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina*. L.) in the Moray Firth, Scotland. *The Journal of Applied Ecology* 27:492-501
- Thompson PM, Miller D, Cooper R, Hammond PS (1994) Changes in the distribution and activity of female harbour seals during the breeding season: implications for their lactation strategy and mating patterns. *The Journal of Applied Ecology* 63:24-30
- Tollit DJ, Black AD, Thompson PM, Mackay A, Corpe HM, Wilson B, Van Parijs SM, Grellier K, Parlane S (1998) Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology* 244:209-222
- Tougaard J, Ebbesen I, Tougaard S, Jensen T, Teilmann J (2003) Satellite tracking of harbour seals on horns reef, Fisheries and Maritime Museum, Esbjerg
- Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *Journal of Northwest Atlantic Fishery Science* 22:173-187
- Tuya FC, Soboil ML, Kido J (2000) An assessment of the effectiveness of marine protected areas in the San Juan Islands, Washington, USA. *ICES Journal of Marine Science* 57:1218-1226
- Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. *Marine Mammal Science* 18:156-166
- Waring GT, Gilbert JR, Loftin J, Cabana N (2006) Short-term movements of radio-tagged harbor seals in New England. *Northeastern Naturalist* 13:1-14
- Weispfenning AJ (2006) Survey of nearshore demersal fishes within candidate marine reserves in Skagit County, Washington. MS Thesis, Western Washington University, Bellingham, WA
- White NA, Sjoberg M (2002) Accuracy of satellite positions from free-ranging grey seals using ARGOS. *Polar Biology* 25:629-631
- Williams TM, Kooyman GL (1985) Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiological Zoology* 58:576-589
- Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. *Trends in Ecology and Evolution* 20:402-409

- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168
- Wright BE, Reimer SD, Brown R, Ougzin AM, Bucklin KA (2007) Assessment of harbor seal predation on adult salmonids in a Pacific Northwest estuary. *Ecological Applications* 17:338-351
- Yochem PK, Stewart BS, DeLong R, DeMaster DP (1987) Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in Autumn. *Marine Mammal Science* 3:323-332
- Yoklavich MM (1998) Marine harvest refugia for West Coast rockfish: a workshop. NOAA Technical Memorandum NMFS-SWFSC-255, Pacific Grove, CA

APPENDICES

Appendix 1

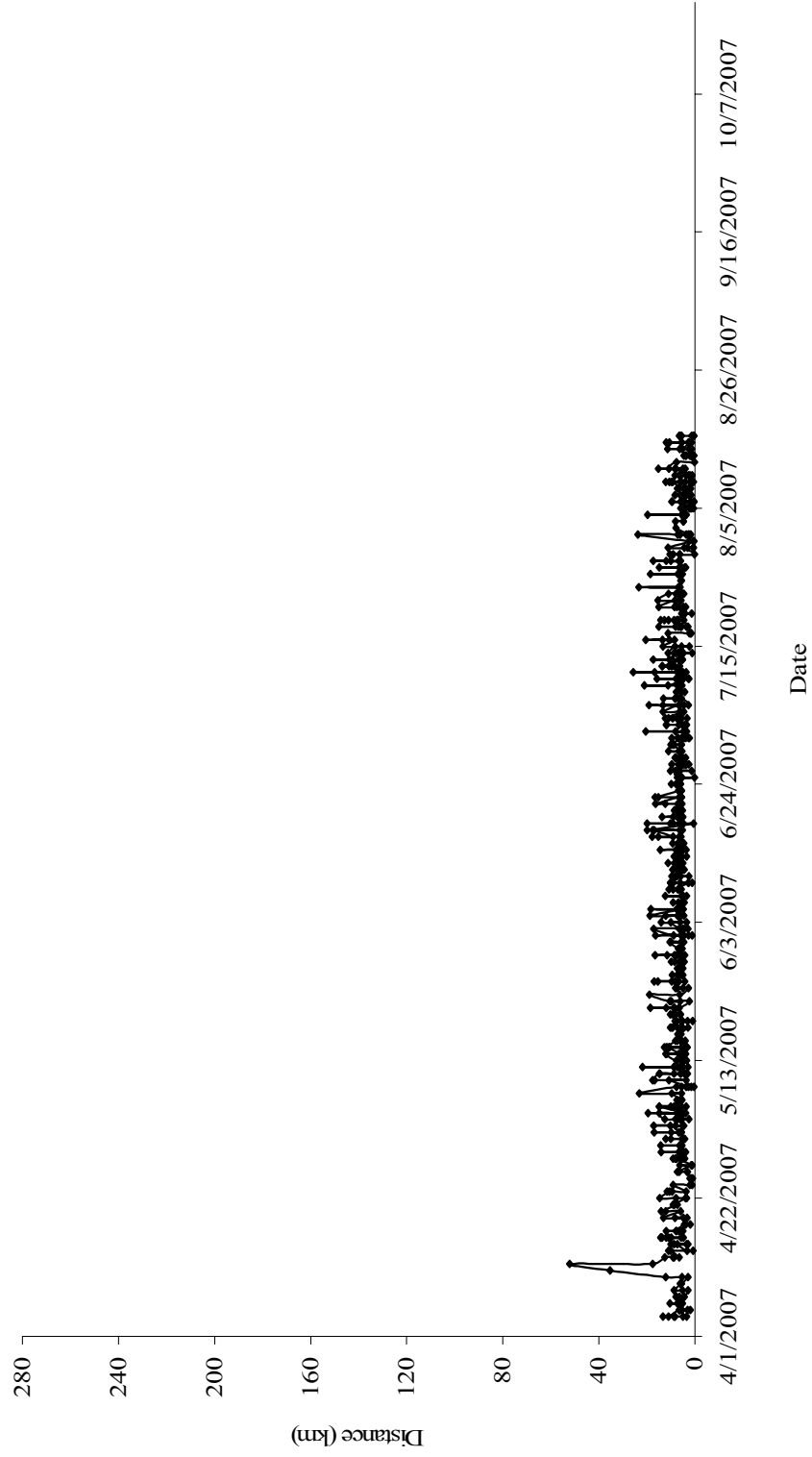
Filtering method comparison

Appendix 1.1. Two filtering methods used on auxiliary and standard satellite transmissions for all harbor seals ($n = 20$). Pre-filtered transmissions have had Z -transmissions and the lower quality of transmissions occurring within 60 seconds of each other removed. Post-filter is the mean \pm SD number of locations of each quality level seal¹ remaining after the locations were filtered. No. removed is the mean number \pm SD of removed locations for each quality level. Standard vs. auxiliary shows, out of the total removed locations, the mean percentages attributed to each of the two types of quality levels (standard vs. auxiliary). Of the removed locations, the Austin et al. (2003) filter removed a lesser percent of standard quality locations than the McConnell et al. (1992) filter.

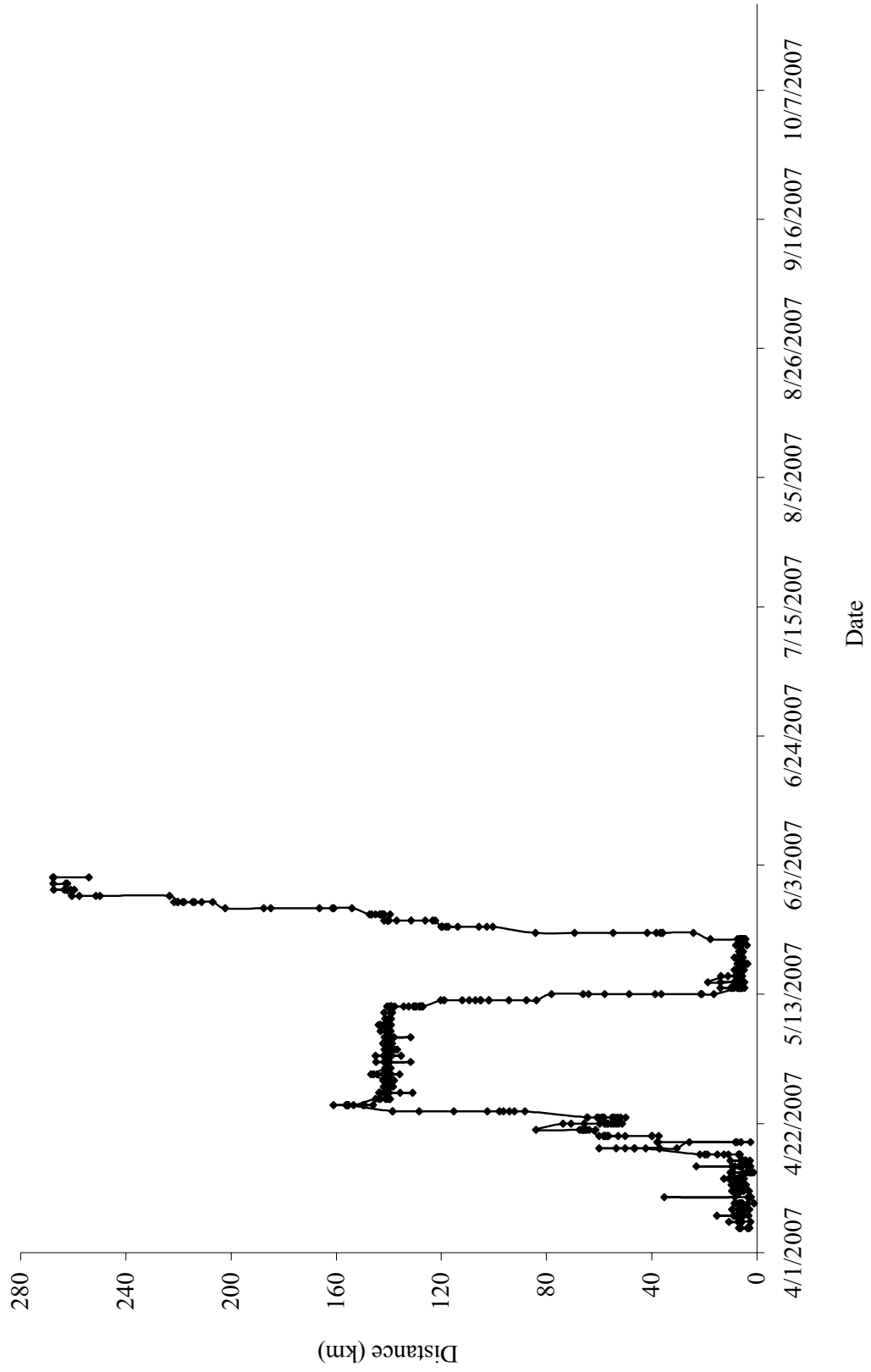
Filter	Transmission quality					Total	
	3	2	1	0	Auxiliary levels		
Pre-filtered \pm SD	36 \pm 40	65 \pm 55	128 \pm 77	170 \pm 132	241 \pm 136	340 \pm 167	980 \pm 494
Austin et al. (2003)							
No. removed \pm SD	3 \pm 3	7 \pm 5	19 \pm 10	50 \pm 39	60 \pm 41	117 \pm 87	254 \pm 165
Post-filter \pm SD	34 \pm 37	58 \pm 51	109 \pm 71	120 \pm 96	182 \pm 107	223 \pm 104	726 \pm 382
Standard vs. auxiliary		12.9 \pm 7.2			87.1 \pm 7.2		
McConnell et al. (1992)							
No. removed \pm SD	5 \pm 5	11 \pm 8	27 \pm 15	67 \pm 67	76 \pm 55	136 \pm 104	322 \pm 229
Post-filter \pm SD	32 \pm 35	55 \pm 49	101 \pm 69	103 \pm 75	165 \pm 97	203 \pm 95	658 \pm 353
Standard vs. auxiliary		14.6 \pm 7.4			85.4 \pm 7.4		

Appendix 2

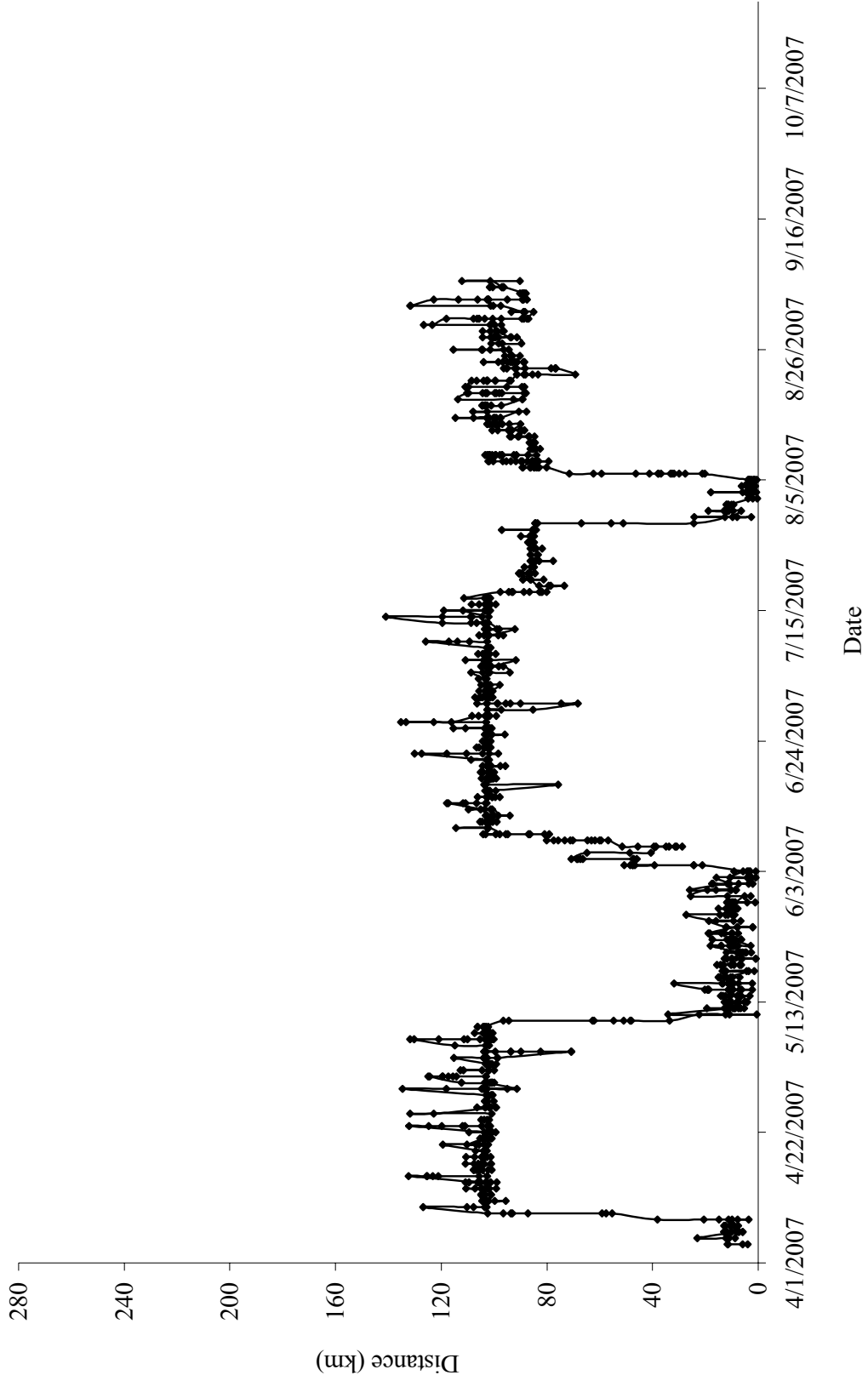
Distance from capture haul-out site



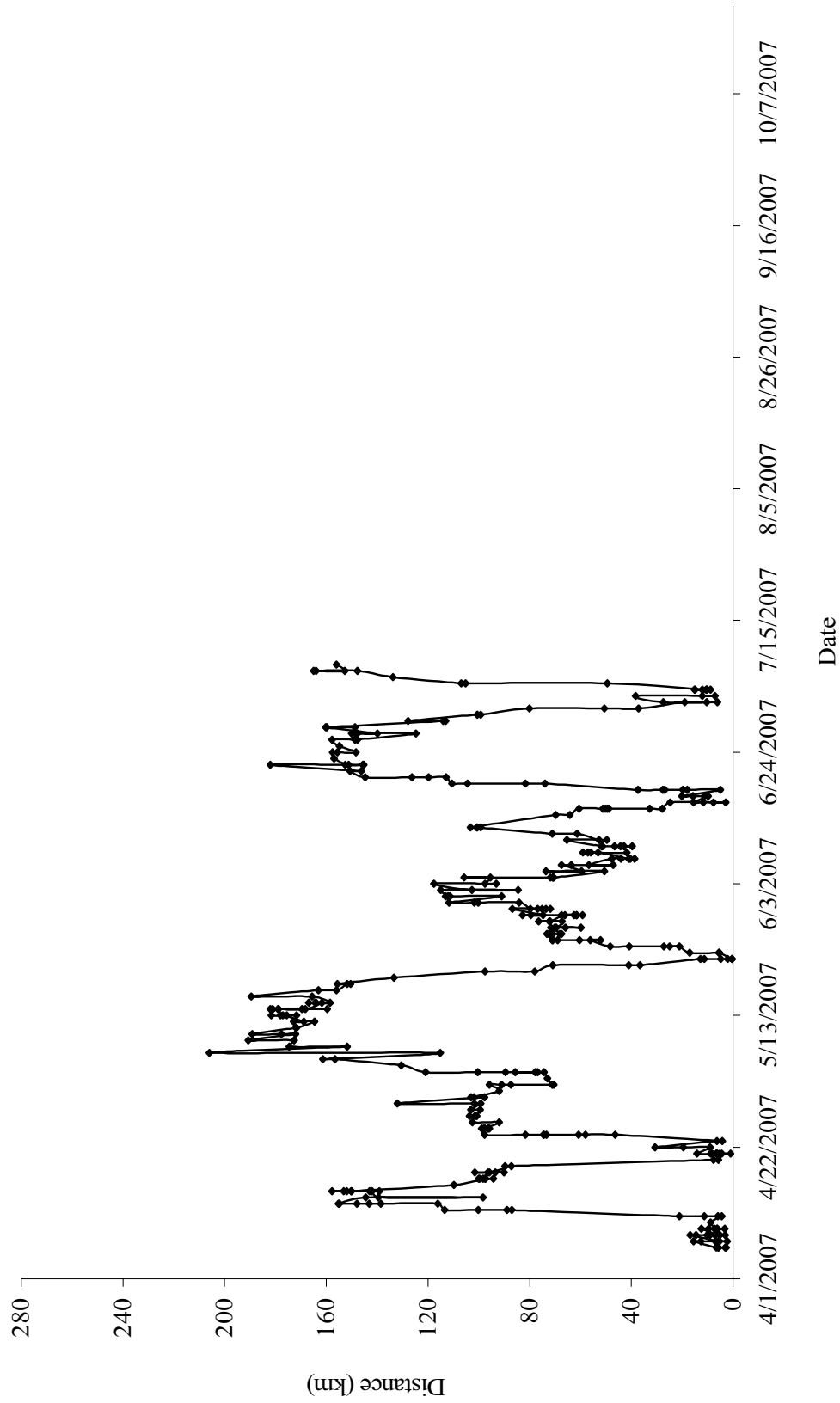
Appendix 2.1. Distance between sequential satellite locations for seal Y1455 and Bird Rocks.



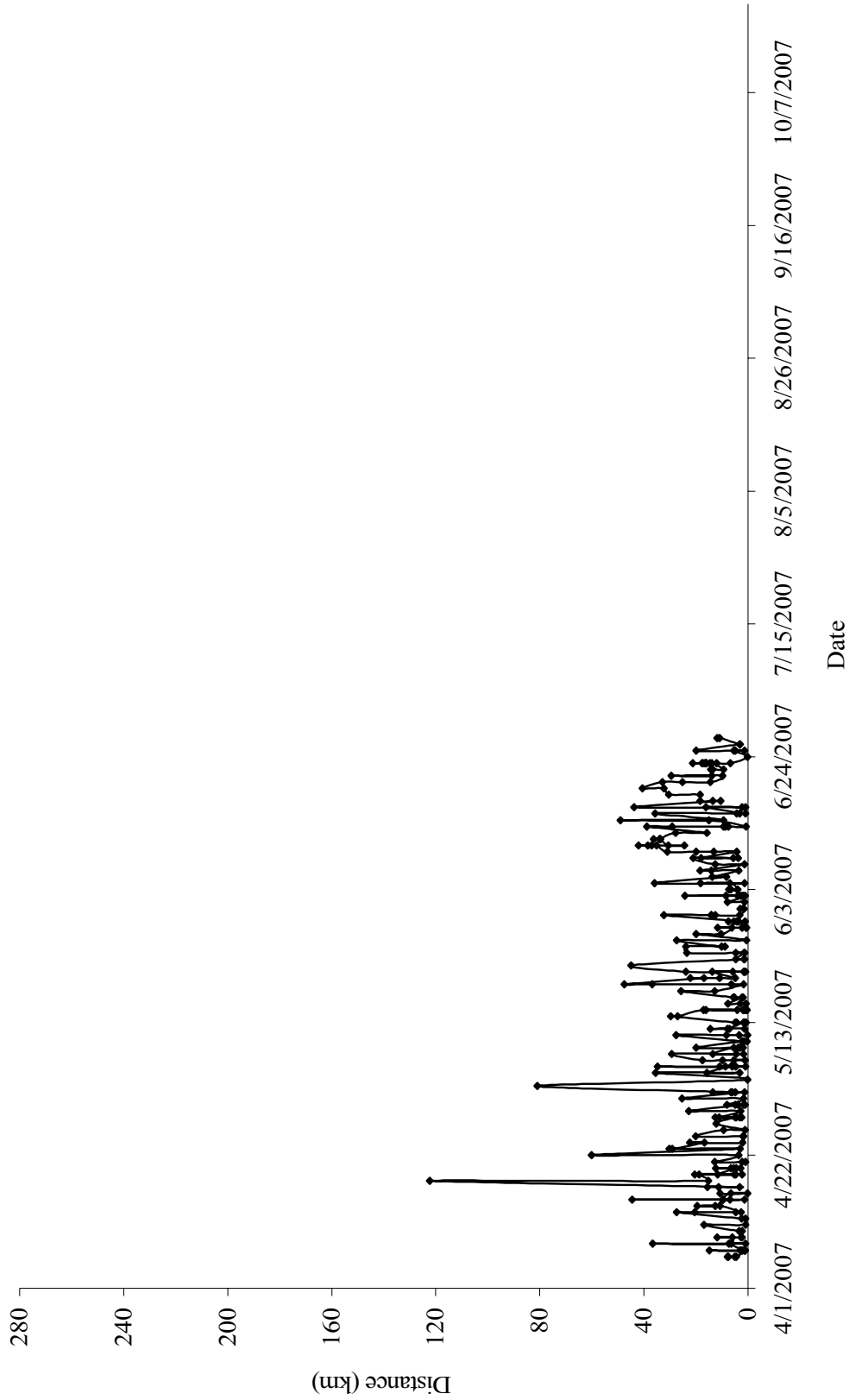
Appendix 2.2. Distance between sequential satellite locations for seal B1696 and Bird Rocks.



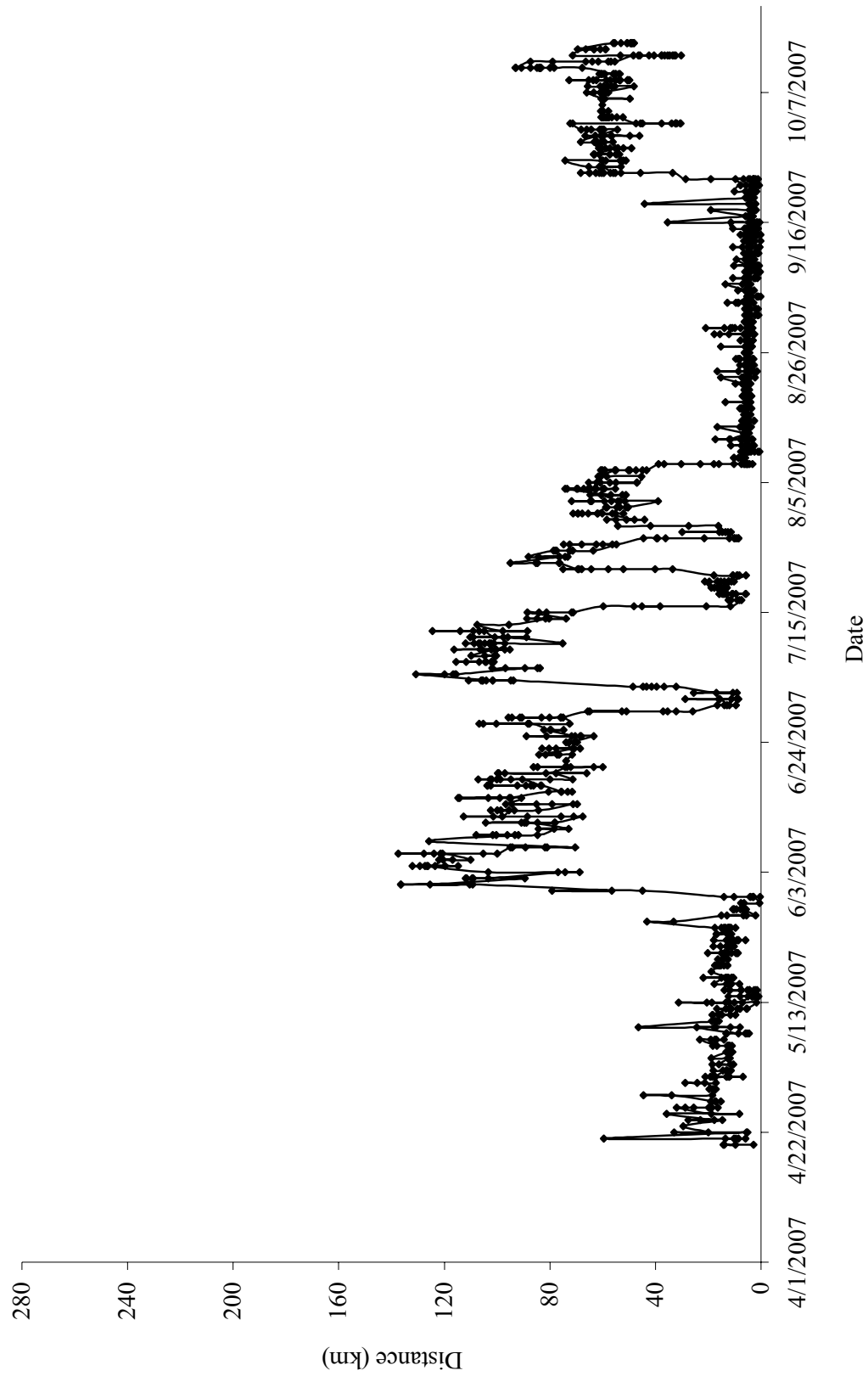
Appendix 2.3. Distance between sequential satellite locations for seal B1695 and Bird Rocks.



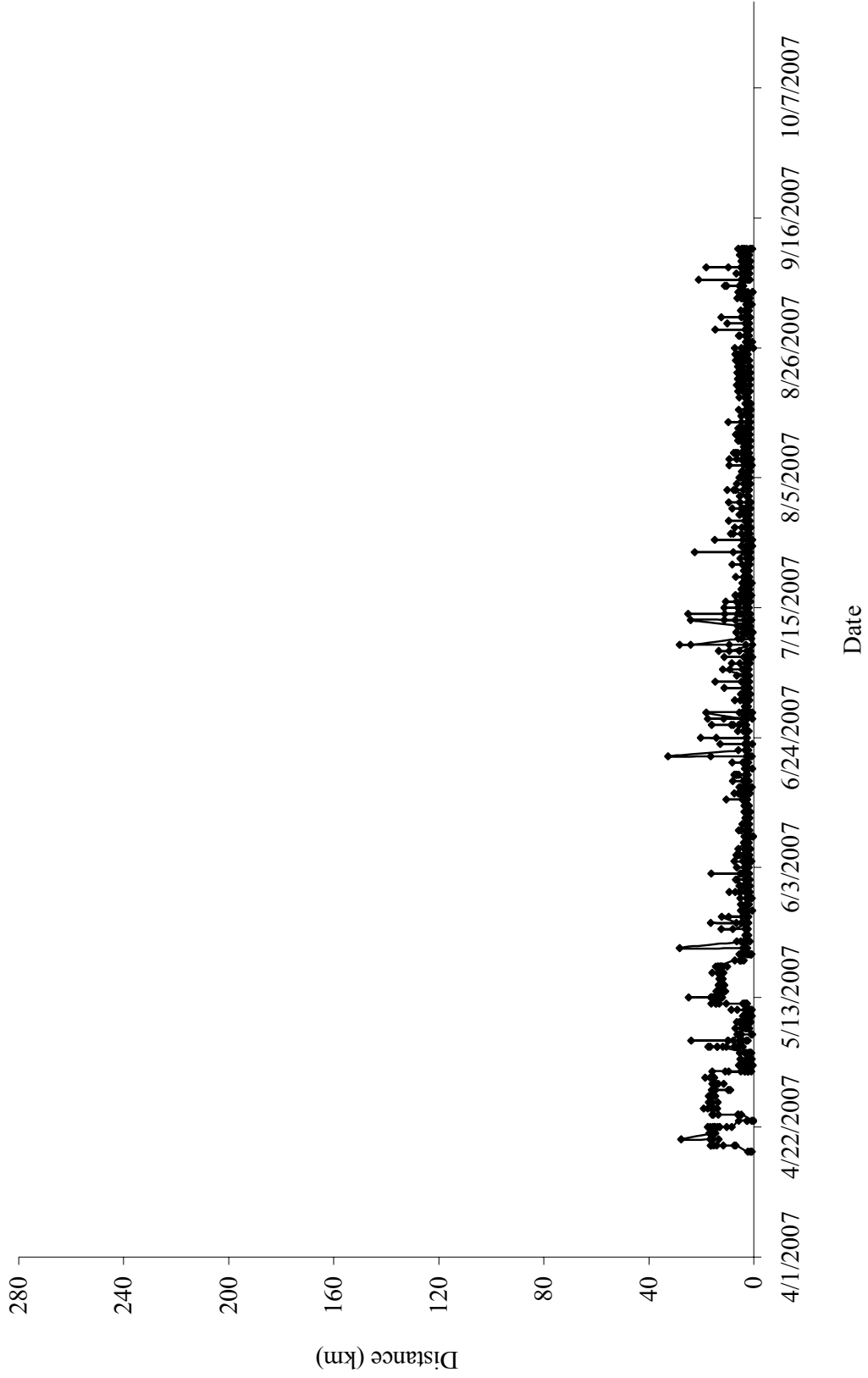
Appendix 2.4. Distance between sequential satellite locations for seal B1697 and Bird Rocks.



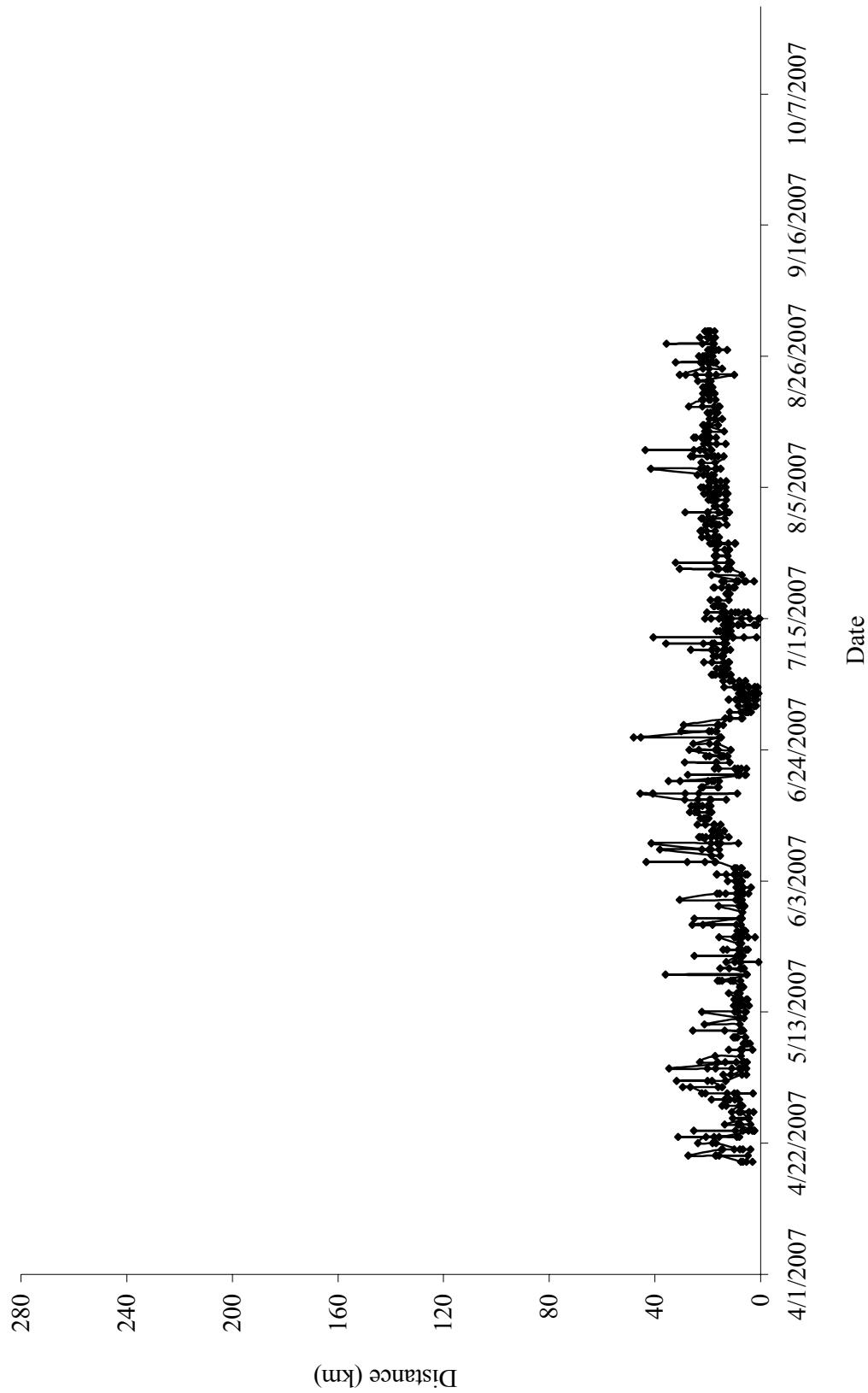
Appendix 2.5. Distance between sequential satellite locations for seal B1698 and Bird Rocks.



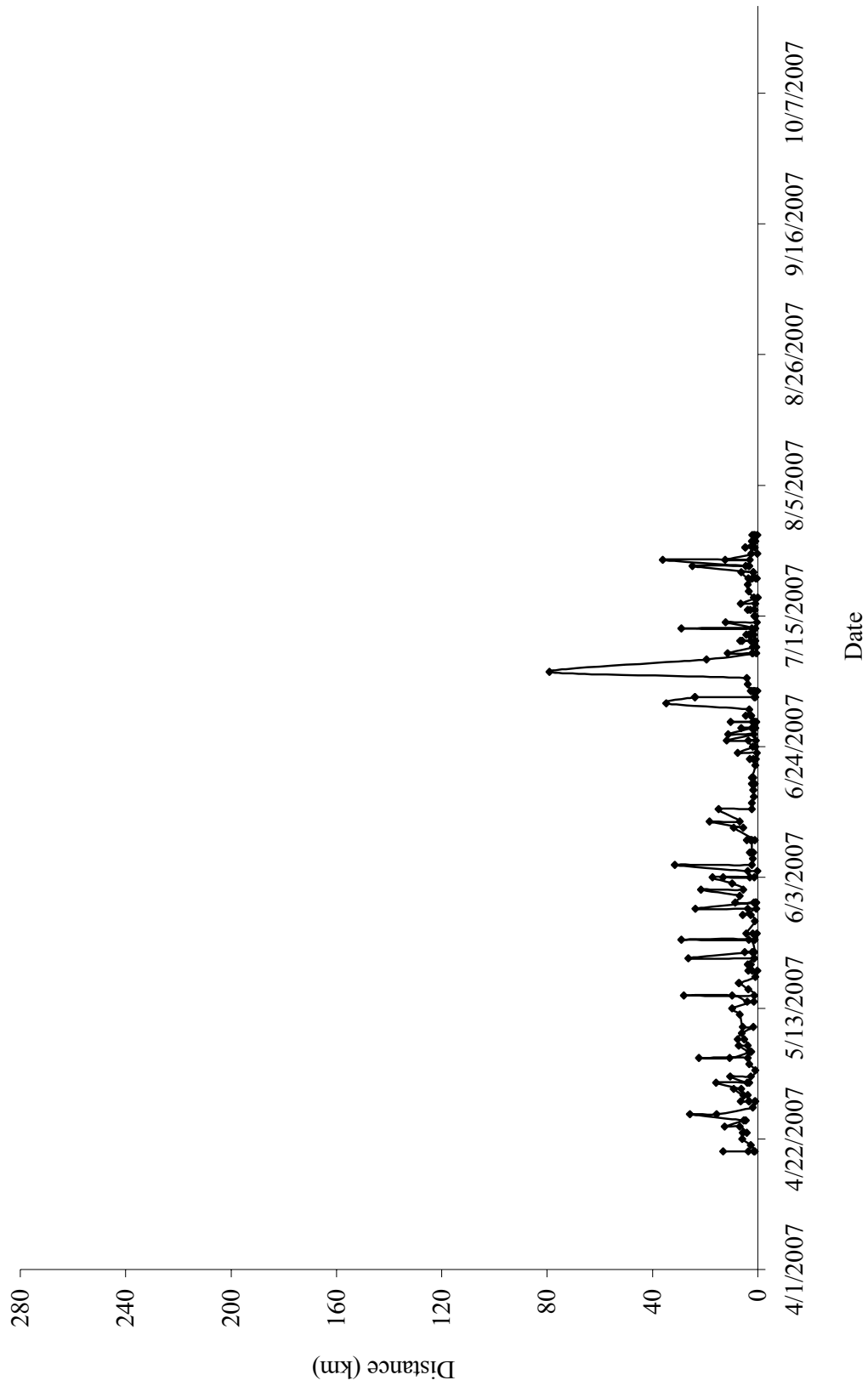
Appendix 2.6. Distance between sequential satellite locations for seal B1701 and Bird Rocks.



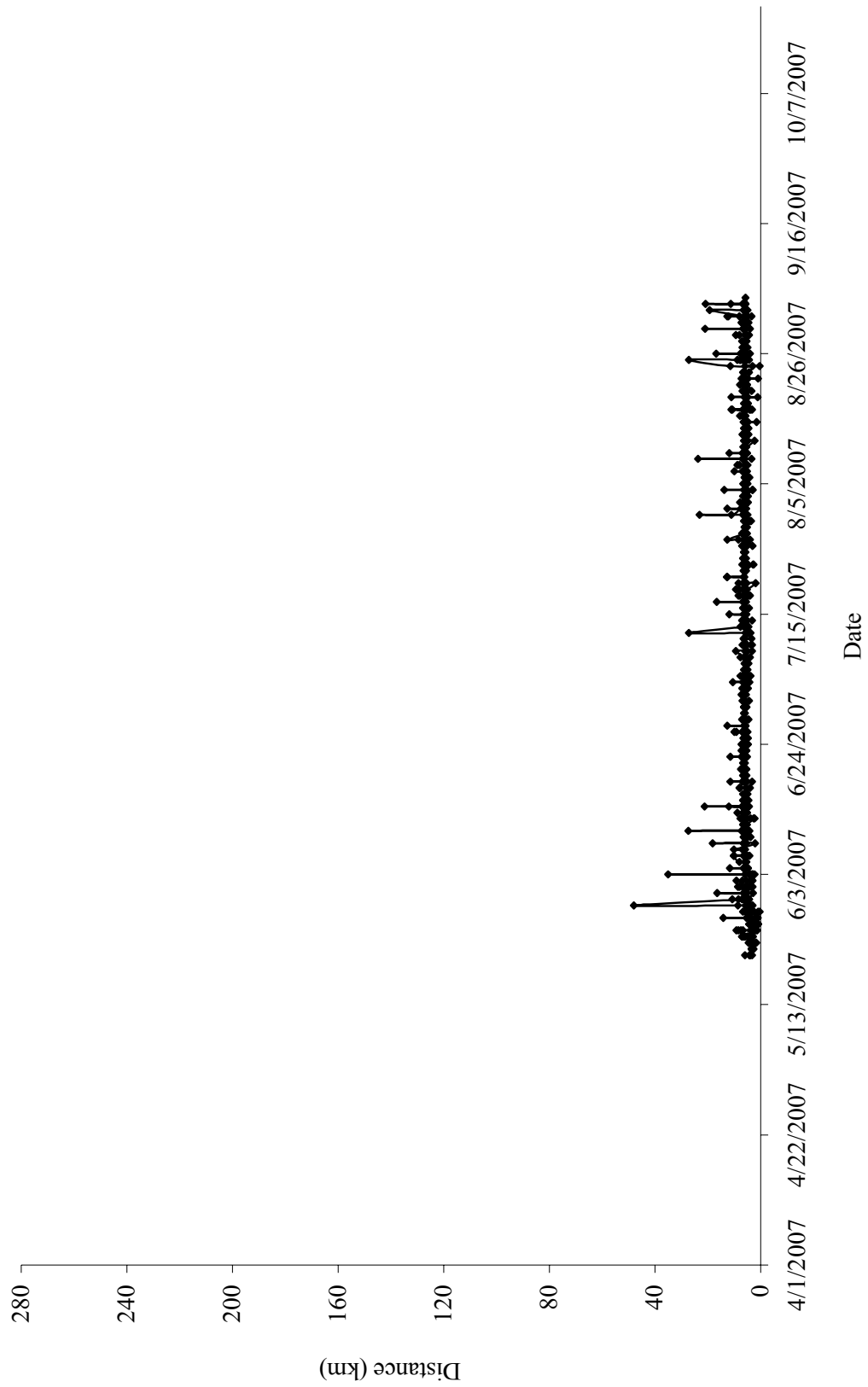
Appendix 2.7. Distance between sequential satellite locations for seal B1699 and Padilla Bay.



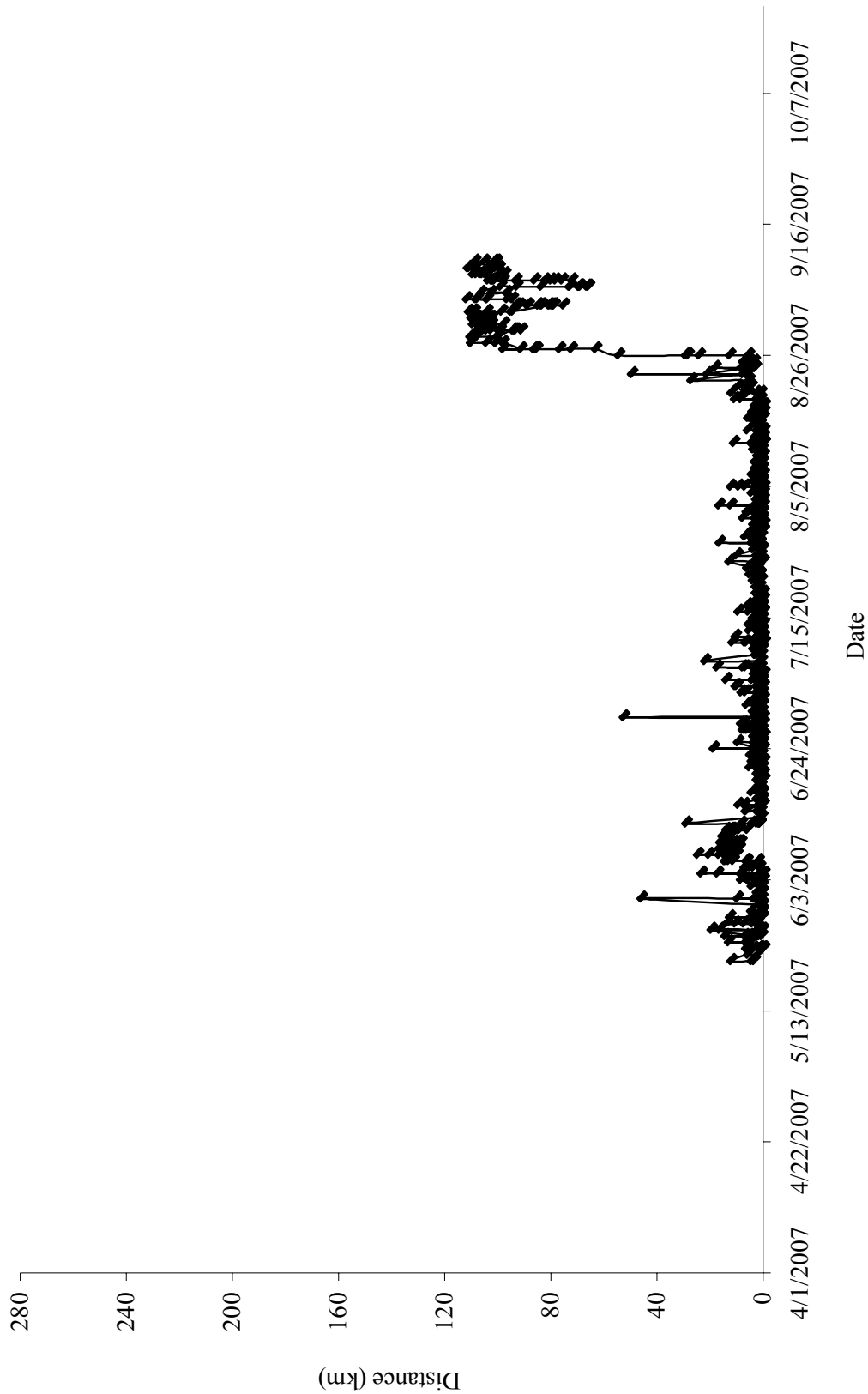
Appendix 2.8. Distance between sequential satellite locations for seal Y1459 and Padilla Bay.



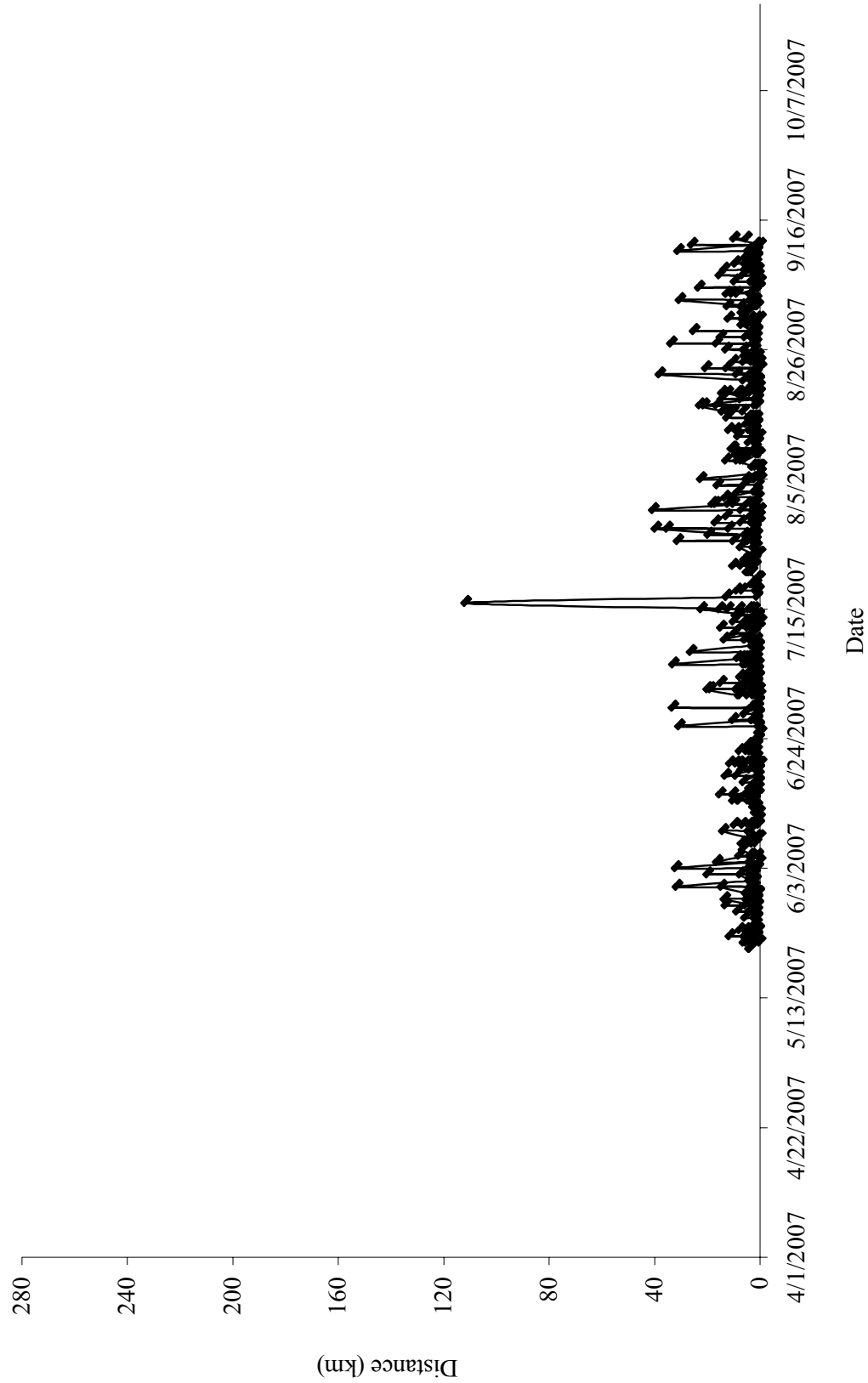
Appendix 2.9. Distance between sequential satellite locations for seal Y1460 and Padilla Bay.



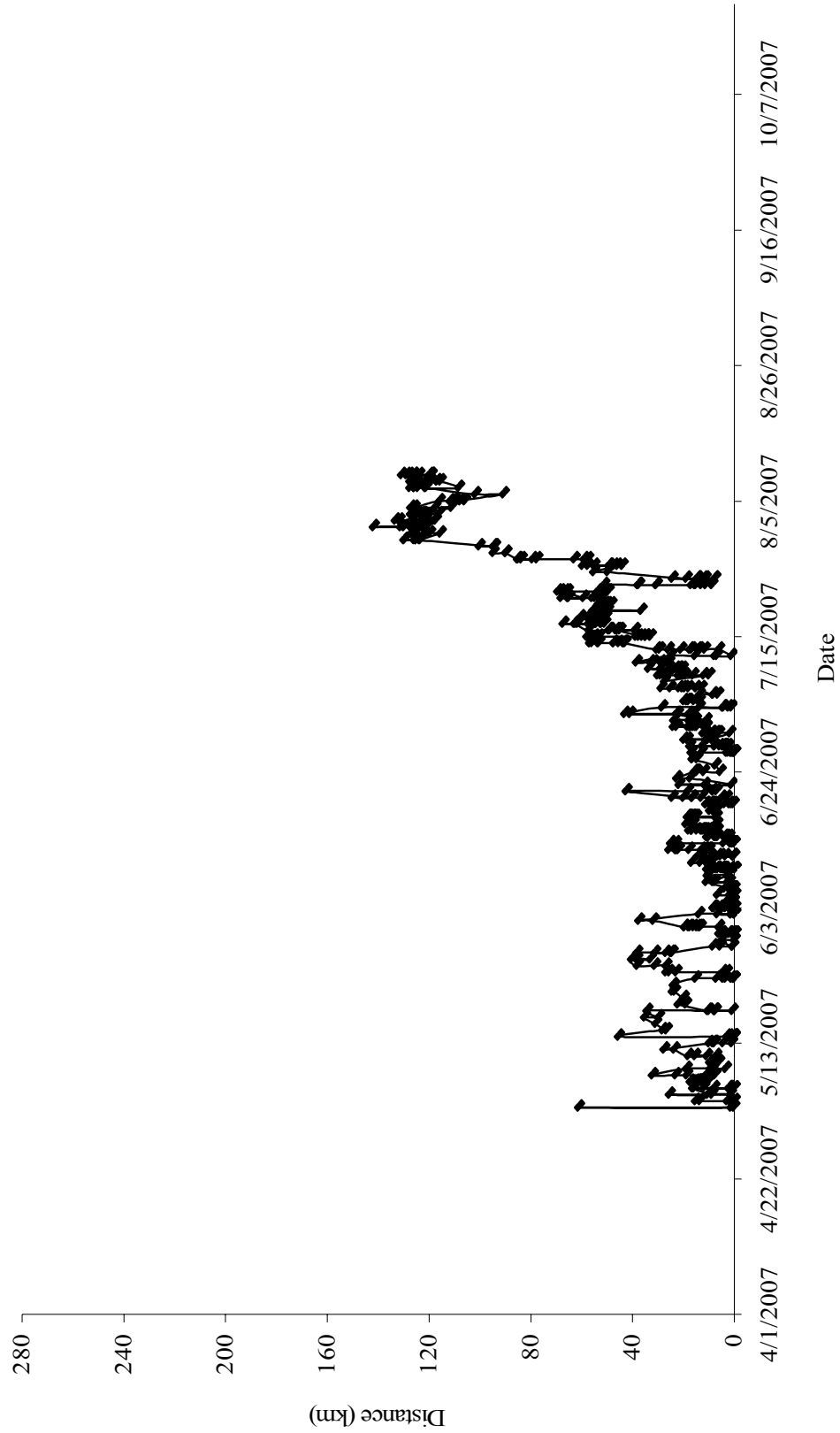
Appendix 2.10. Distance between sequential satellite locations for seal B1712 and Padilla Bay.



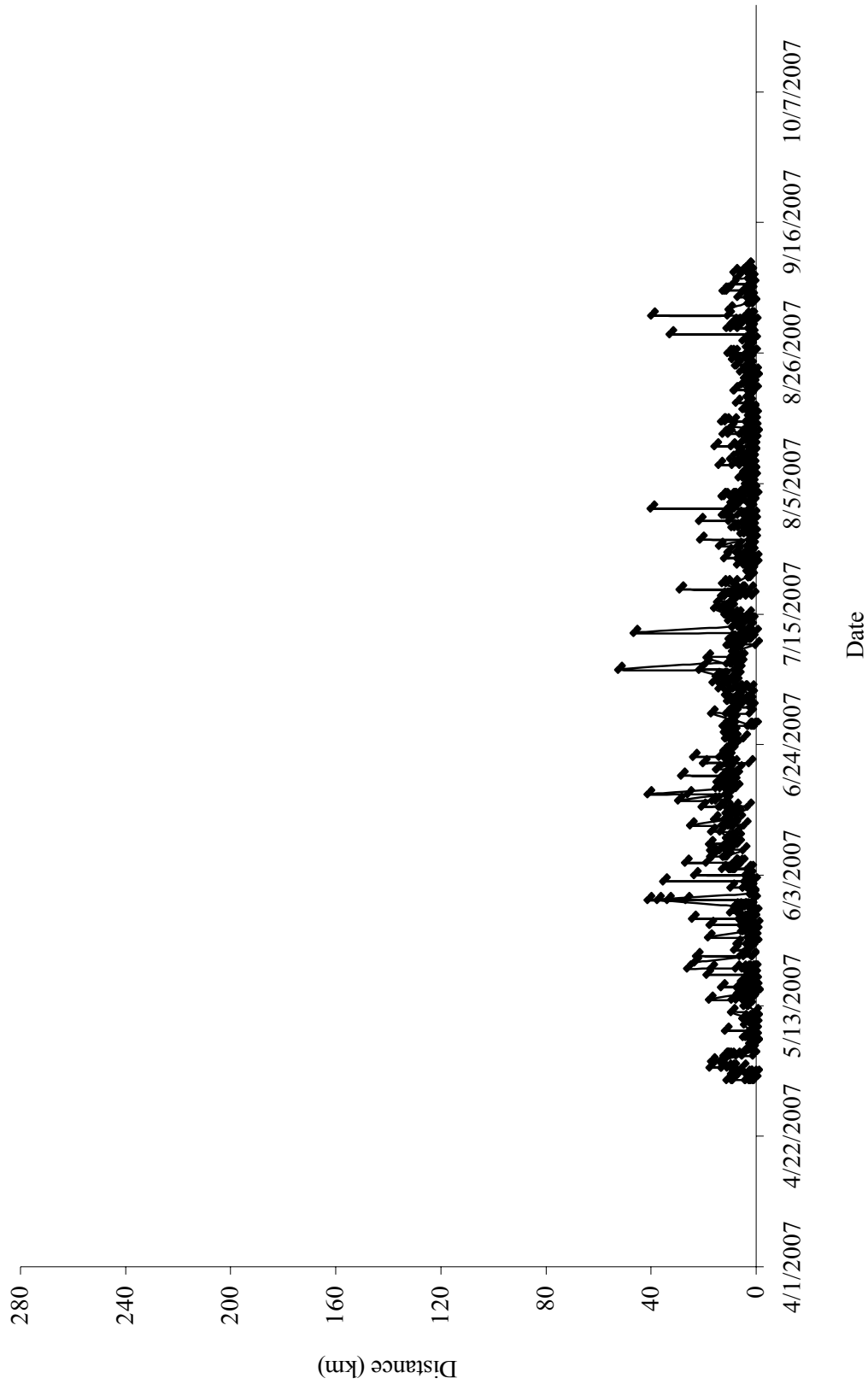
Appendix 2.11. Distance between sequential satellite locations for seal B1713 and Padilla Bay.



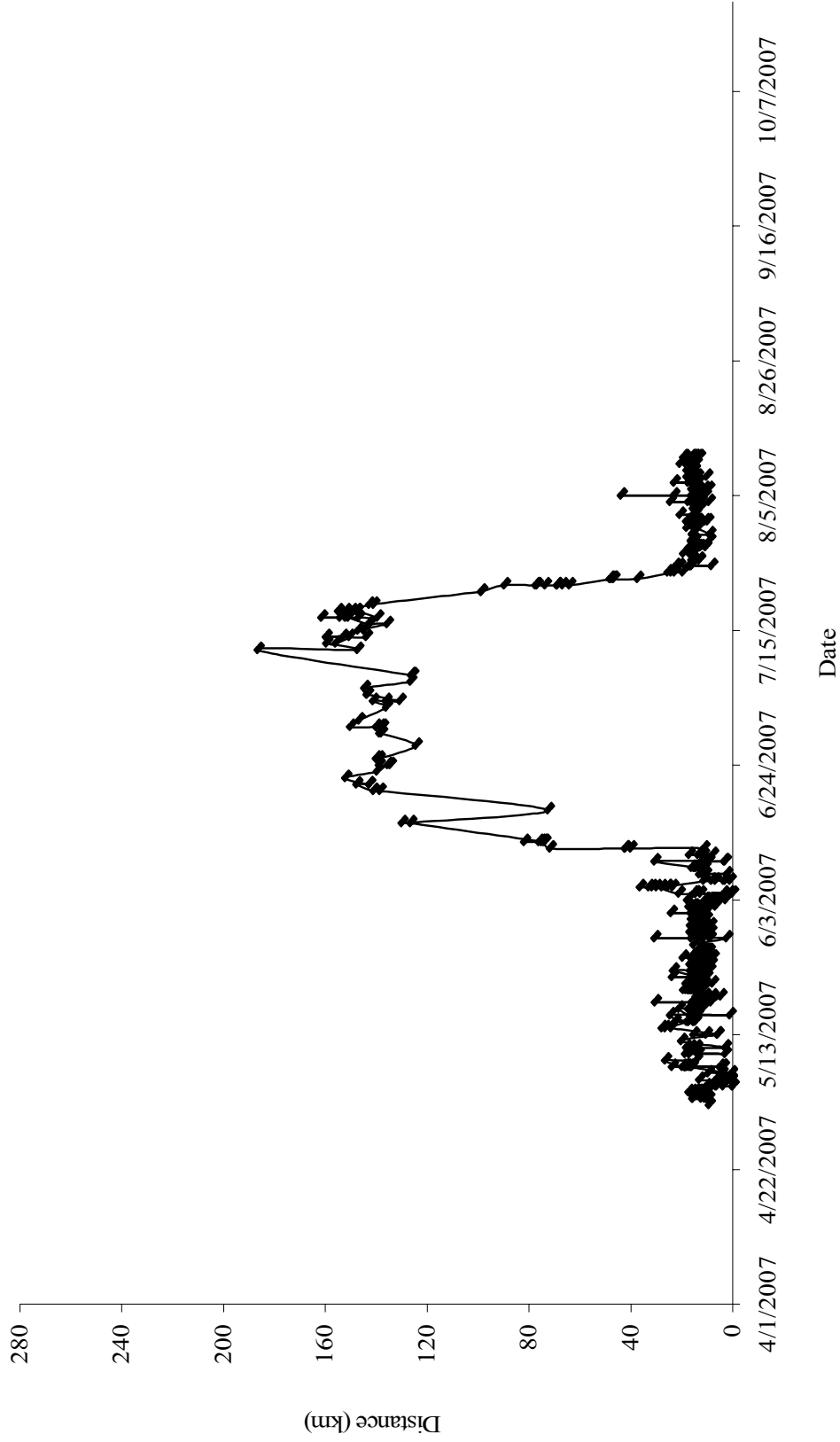
Appendix 2.12. Distance between sequential satellite locations for seal Y1462 and Padilla Bay.



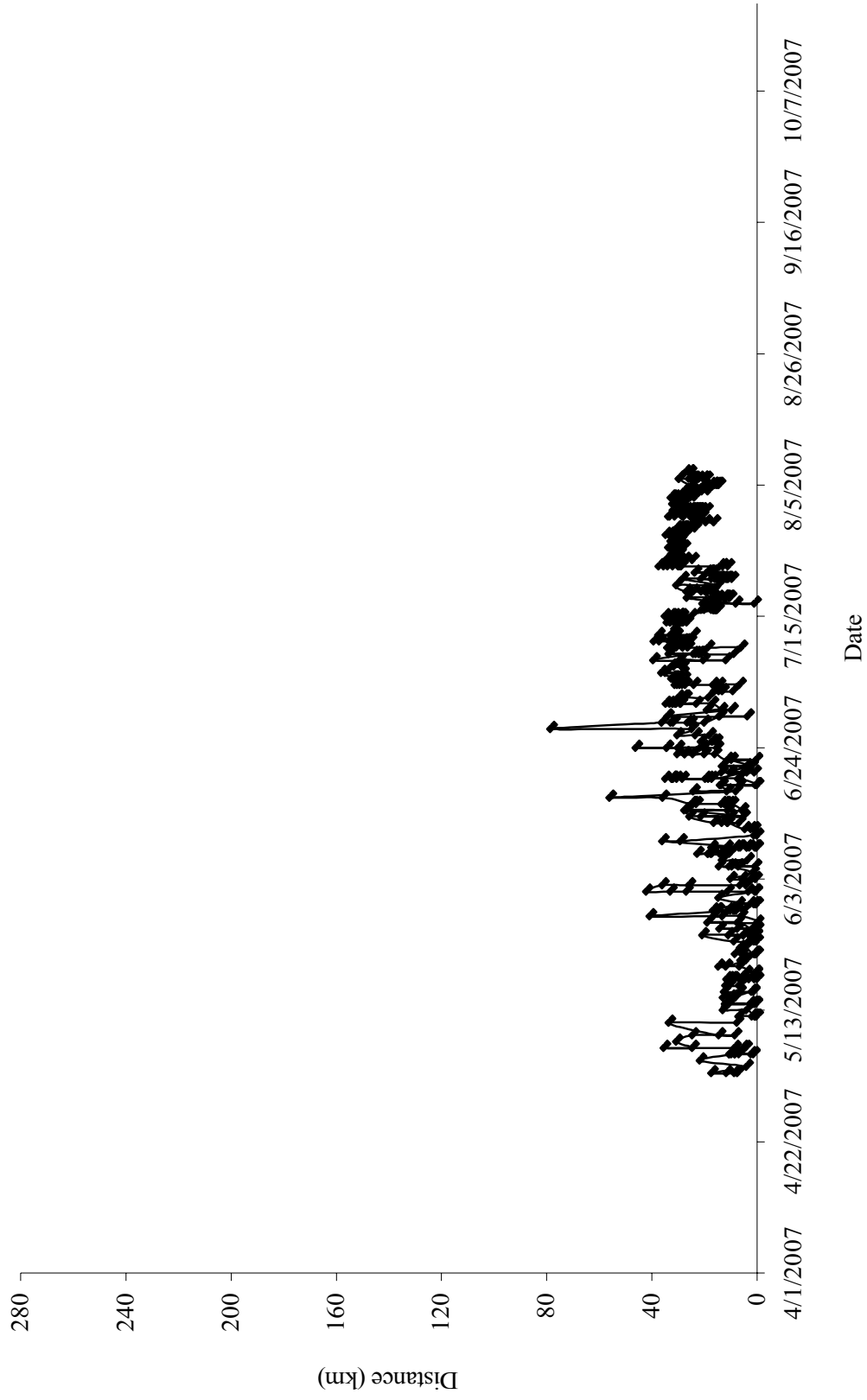
Appendix 2.13. Distance between sequential satellite locations for seal B1711 and the Belle Chain Islets.



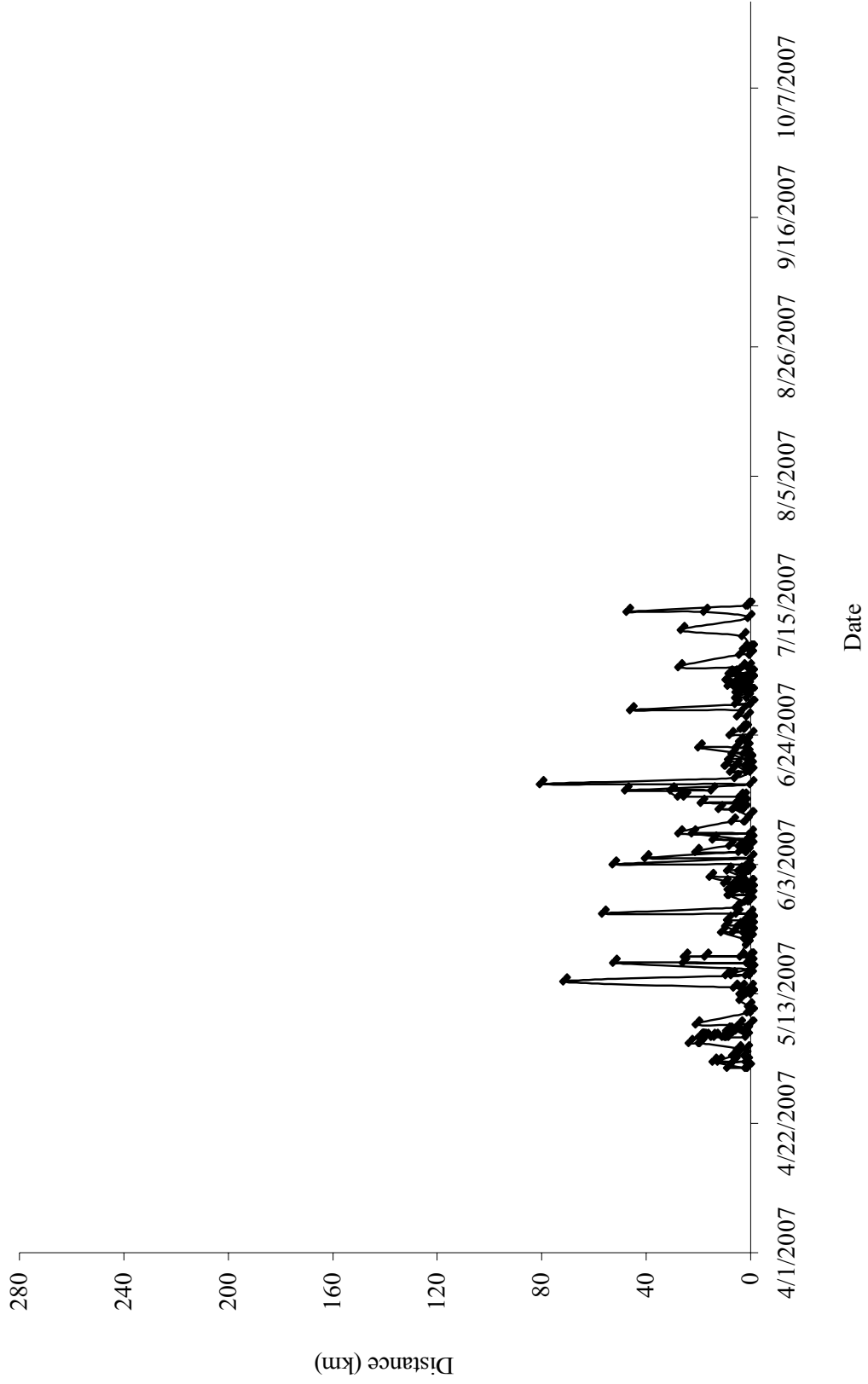
Appendix 2.14. Distance between sequential satellite locations for seal B1706 and the Belle Chain Islets.



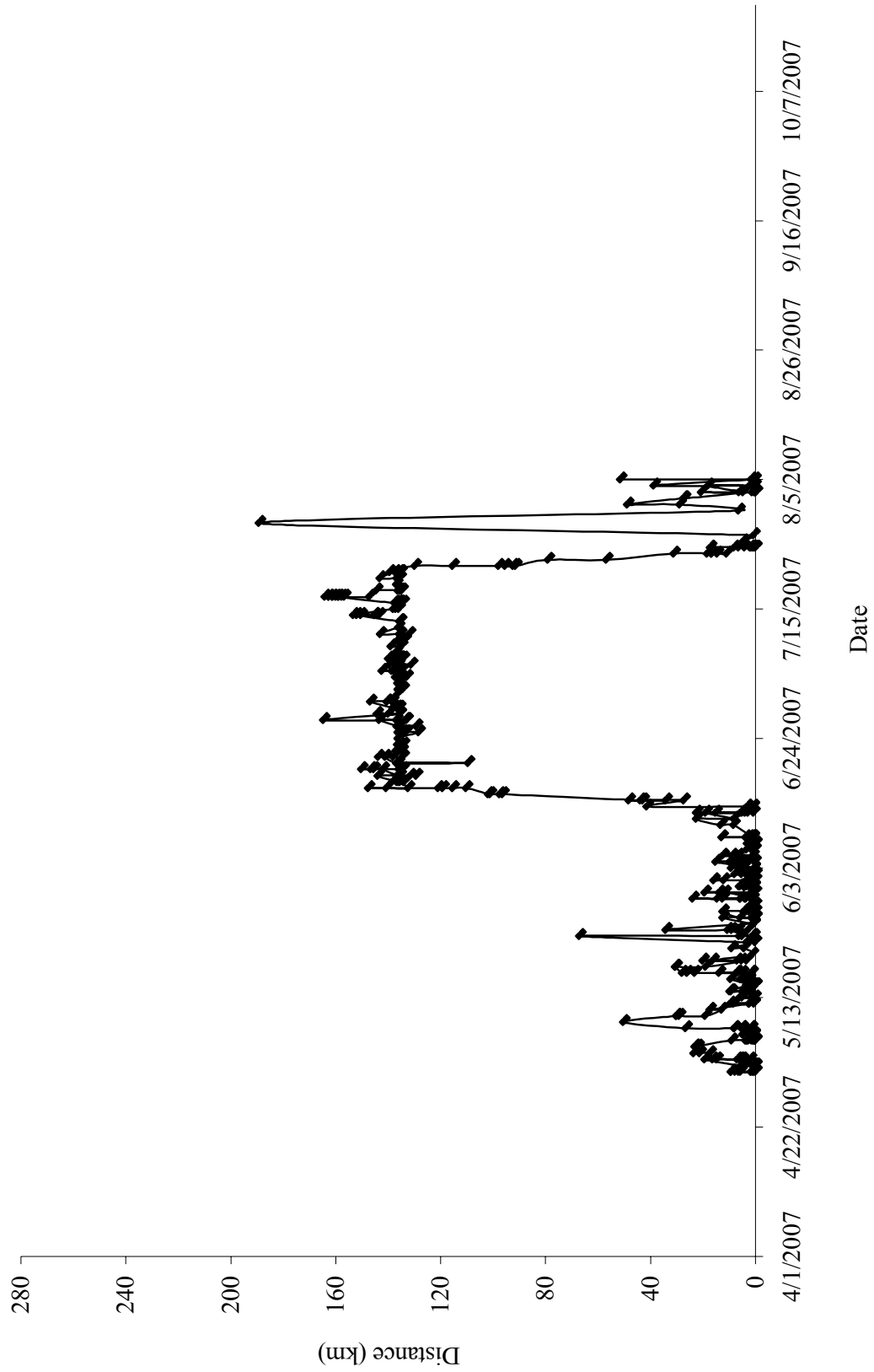
Appendix 2.15. Distance between sequential satellite locations for seal B1707 and the Belle Chain Islets.



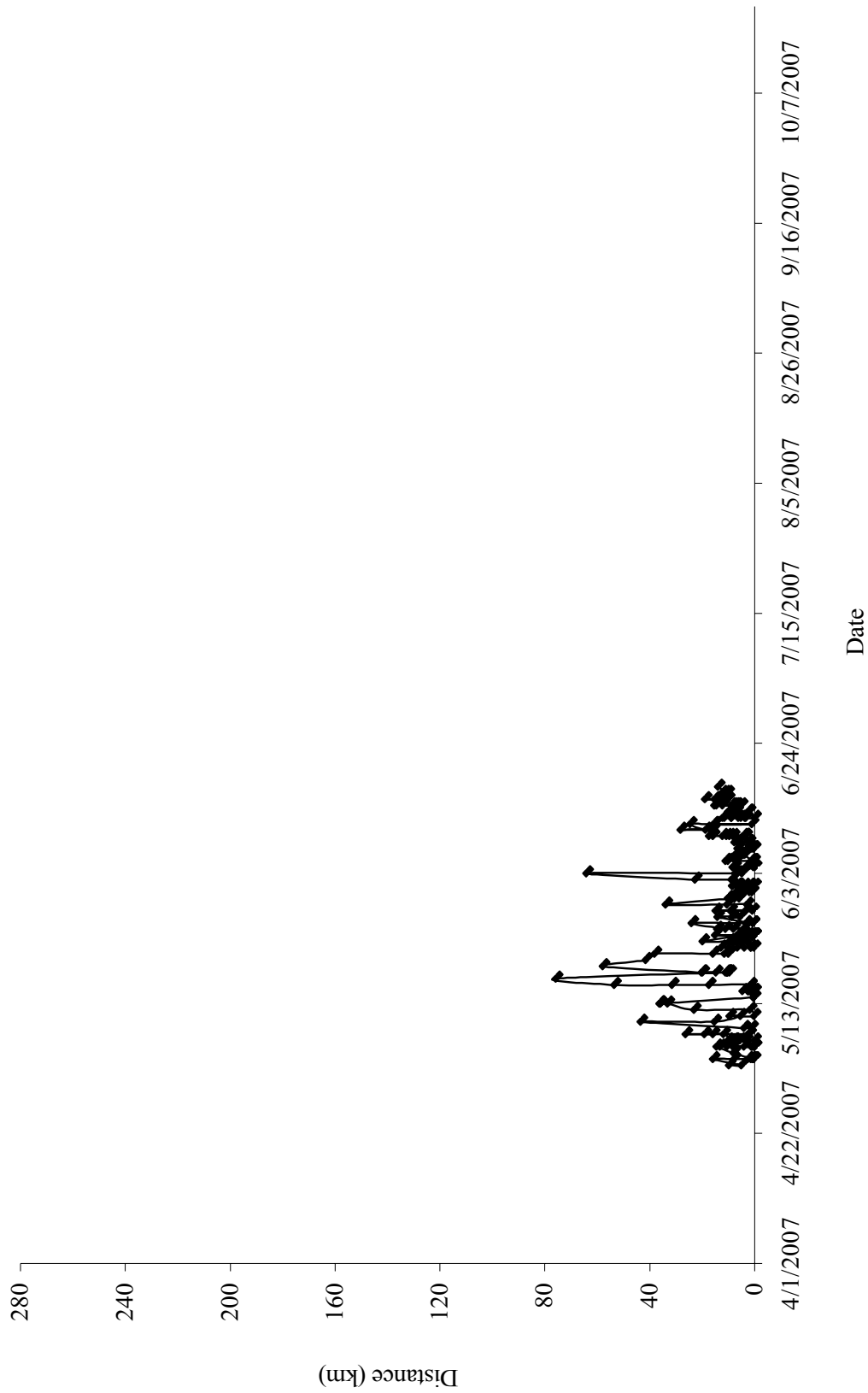
Appendix 2.16. Distance between sequential satellite locations for seal BI709 and the Belle Chain Islets.



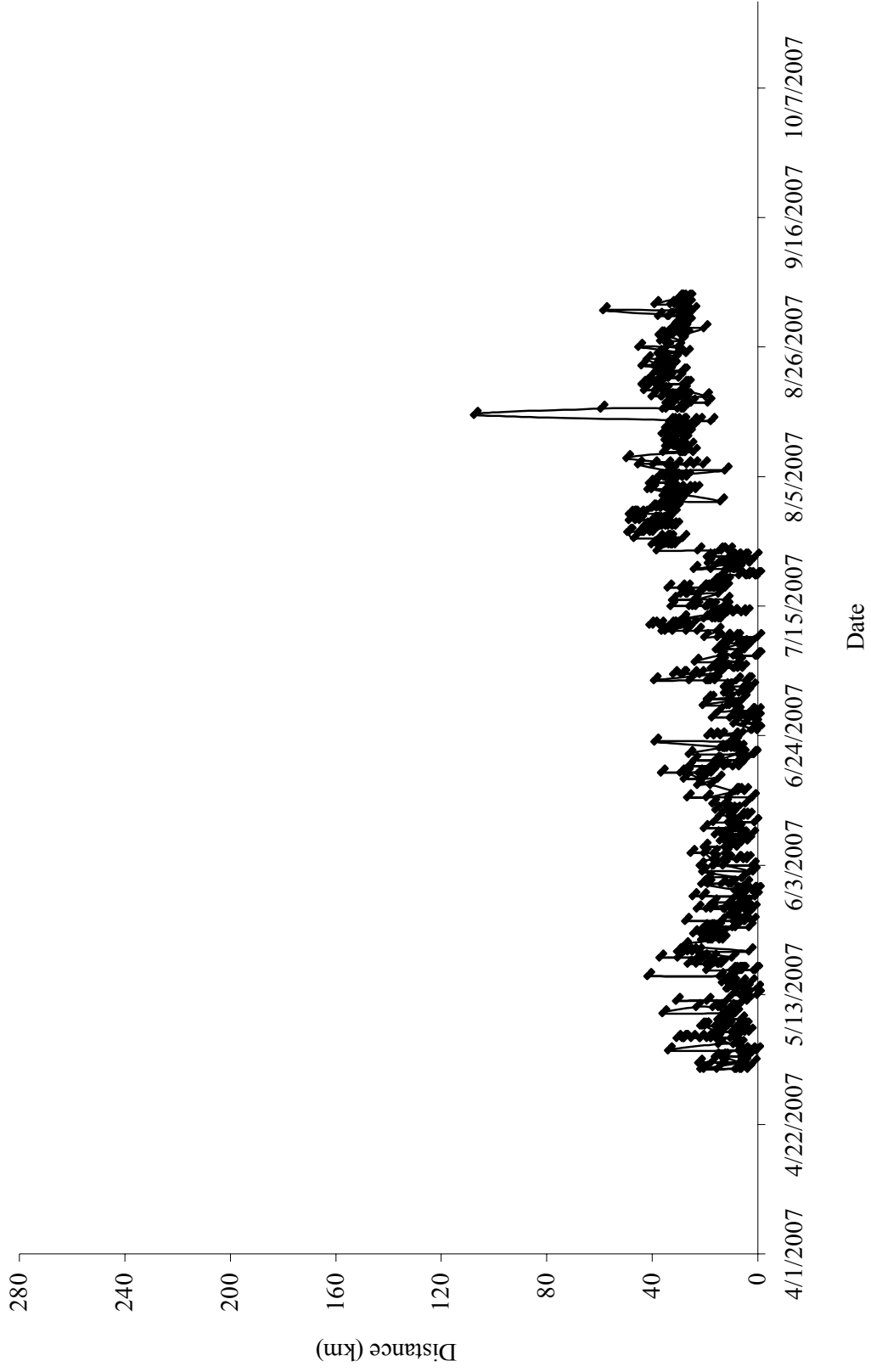
Appendix 2.17. Distance between sequential satellite locations for seal B1702 and the Belle Chain Islets.



Appendix 2.18. Distance between sequential satellite locations for seal B1704 and the Belle Chain Islets.



Appendix 2.19. Distance between sequential satellite locations for seal B1710 and the Belle Chain Islets.



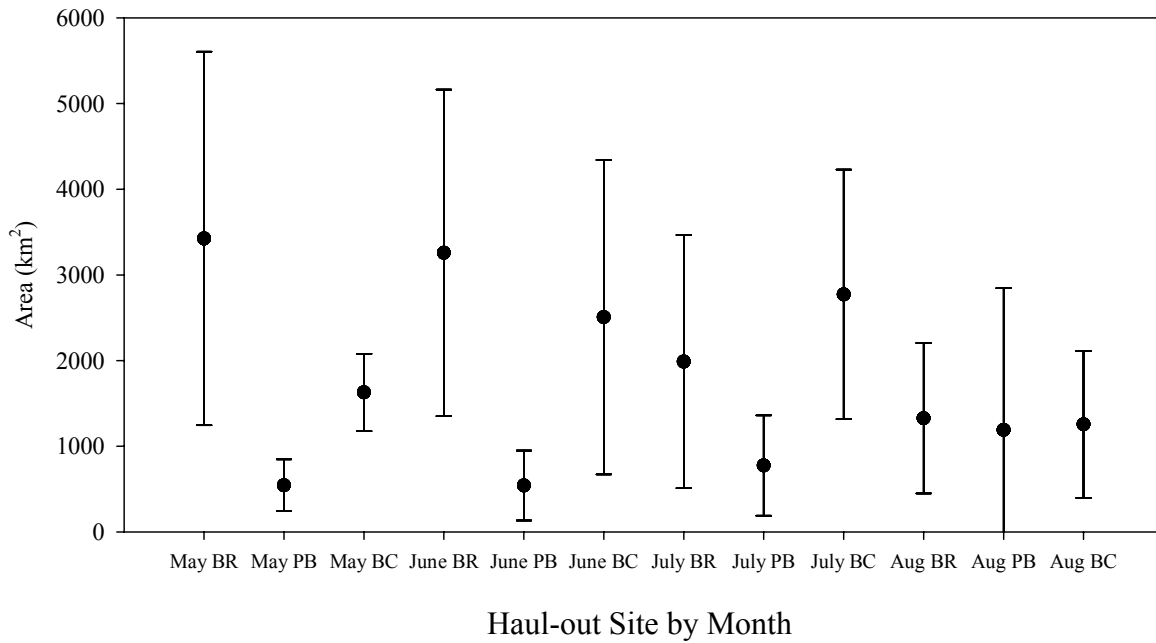
Appendix 2.20. Distance between sequential satellite locations for seal B1703 and the Belle Chain Islets.

Appendix 3

Harbor seal minimum convex polygon size relative to month and duration of study

Monthly temporal scale. Transformed data on a monthly temporal scale revealed that seals from Bird Rocks had the greatest variability in minimum convex polygon size for all months except August, when Padilla Bay seals were most variable. Padilla Bay seals showed the least variability from April – July (Appendix 3.1). Transformed minimum convex polygon sizes varied significantly by site (LME, $p < 0.002$, Appendix 3.2) with site as the fixed factor and mass as the random factor. Independent contrasts revealed a significant difference between seals from the rocky reefs (Bird Rocks and Belle Chain) and Padilla Bay (LME, $p < 0.001$, Appendix 3.2) but did not detect a difference between seals from Bird Rocks and Belle Chain (LME, $p = 0.367$, Appendix 3.2). Untransformed minimum convex polygon sizes ranged from 441 – 6105 km² for Bird Rocks, 923 – 5590 km² for Belle Chain and 80 – 4100 km² for Padilla Bay (Table 3).

Whole study period temporal scale. Untransformed minimum convex polygon size for the whole study period varied significantly by haul-out site, including sex as a random factor (LME, $p = 0.023$, Appendix 3.3). Independent contrasts detected a significant difference between seals from the rocky reefs and Padilla Bay (LME, $p = 0.011$, Appendix 3.3) but did not detect a difference between seals from Belle Chain and Bird Rocks ($p = 0.183$; Appendix 3.3). Minimum convex polygon sizes for Bird Rocks ranged from 1142 – 11759 km², while Belle Chain ranged from 2191 – 8133 km² and Padilla Bay ranged from 787 – 4196 km² (Table 3). Bird Rocks had the highest mean area of 6404 km², almost 1.5 times the mean of Belle Chain and 3.5 times the mean of Padilla Bay (Appendix 3.4).



Appendix 3.1. Minimum convex polygons of harbor seals relative to month. Untransformed data. BR = Bird Rocks, PB = Padilla Bay and BC = Belle Chain.

Appendix 3.2a-d. Minimum convex polygon LME model summary relative to month. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 3.2a. Comparison of models with different random effects on a monthly temporal scale with all fixed effects included.

Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
Mass	14	281.75	-126.87			
Transmission Days and Mass	16	285.74	-126.87	1 vs 2	0.00	1.000
Sex	14	289.44	-130.72	2 vs 3	7.70	0.021
Transmission Days	14	290.02	-131.01			
Transmission Days, Mass and Sex	16	293.44	-130.72	4 vs 5	0.58	0.749
Mass and Sex	16	293.44	-130.72			
Sex and Transmission Days	16	294.02	-131.01			

Appendix 3.2b. Comparison of fixed effects on a monthly temporal scale with mass as the random effect.

Model	df	AIC	logLik	Test	L.Ratio	p-value
3 – Site	5	298.32	-144.2			
2 - Site + month	8	302.65	-143.3	1 vs 2	1.67	0.643
1 - Site * month	14	306.93	-139.5	2 vs 3	7.72	0.260

Appendix 3.2c. Monthly temporal scale model with site as the fixed effect and mass as the random effect.

	numDF	denDF	F-value	p-value
Intercept	1	41	521.07	< 0.0001
Site	2	17	9.40	< 0.002

Appendix 3.2d. Independent contrasts on the model with site as the fixed effect and mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
Intercept	11.59	0.51	41	22.54	0.000
Bird Rocks vs Belle Chain	0.58	0.62	17	0.93	0.367
Rocky Reefs vs Padilla Bay	1.58	0.37	17	4.30	< 0.001

Appendix 3.3a-c. Minimum convex polygon LME model summary relative to the entire study period. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 3.3a. Comparison of models with different random effects on an entire duration temporal scale with all fixed effects included.

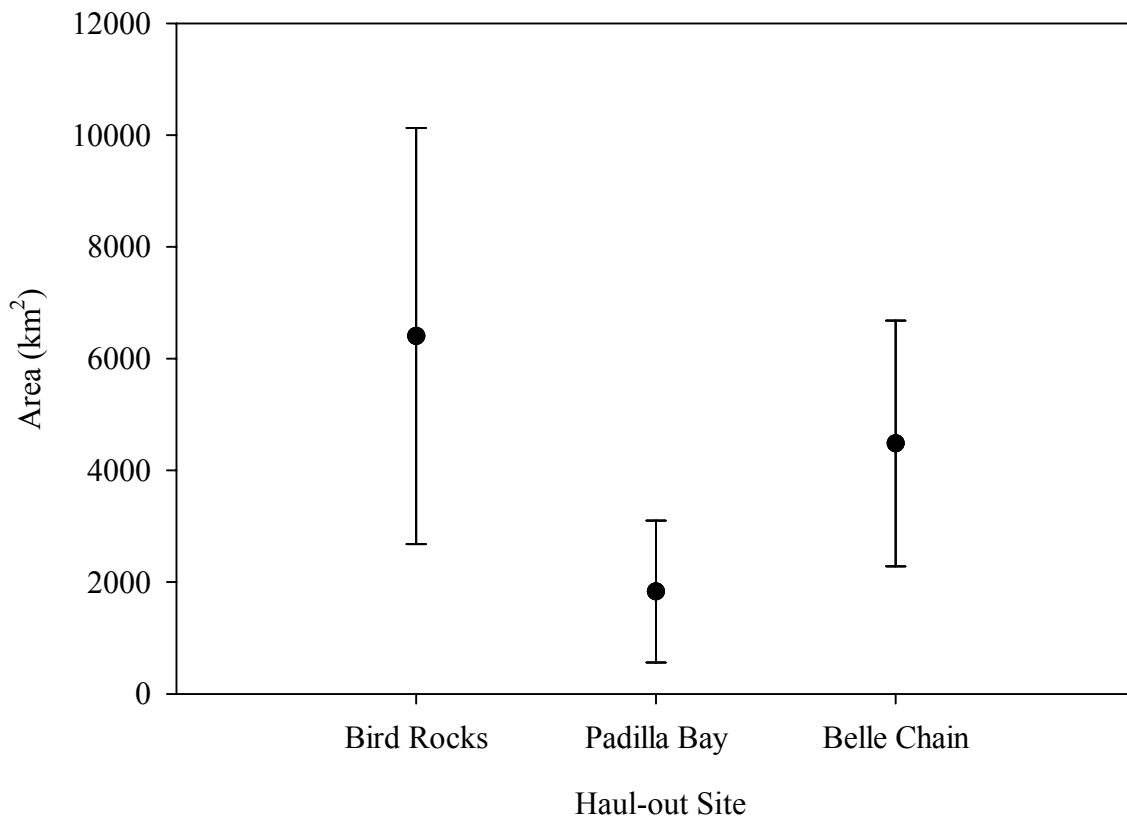
Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
Sex	5	330.30	-160.15			
Mass	5	330.71	-160.35			
Transmission Days	5	330.71	-160.35			
Transmission Days and Sex	7	334.27	-160.14	3 vs 4	0.43	0.805
Transmission Days, Mass and Sex	7	334.30	-160.15			
Mass and Sex	7	334.30	-160.15			
Transmission Days and Mass	7	334.71	-160.35			

Appendix 3.3b. Entire duration temporal scale with site as the fixed effect and sex as the random effect.

	numDF	denDF	F-value	p-value
Intercept	1	16	55.54	< 0.0001
Site	2	16	4.84	0.023

Appendix 3.3c. Independent contrasts on the model with site as the fixed effect and sex as the random effect.

	Value	Std. Error	DF	t-value	p-value
Intercept	4238.88	577.30	16	7.34	0.0000
Bird Rocks vs Belle Chain	960.77	690.79	16	1.39	0.183
Rocky Reefs vs Padilla Bay	1204.02	417.39	16	2.88	0.011



Appendix 3.4. Minimum convex polygons of harbor seals relative to the entire study period. Untransformed data.

Appendix 4

Male harbor seal minimum convex polygon and home range size

Appendix 4.1a-c. Minimum convex polygon LME model summary relative to season for males (n = 16). Statistically significant values (p < 0.05) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 4.1a. Comparison of models with different random effects on a seasonal temporal scale with all fixed effects included.

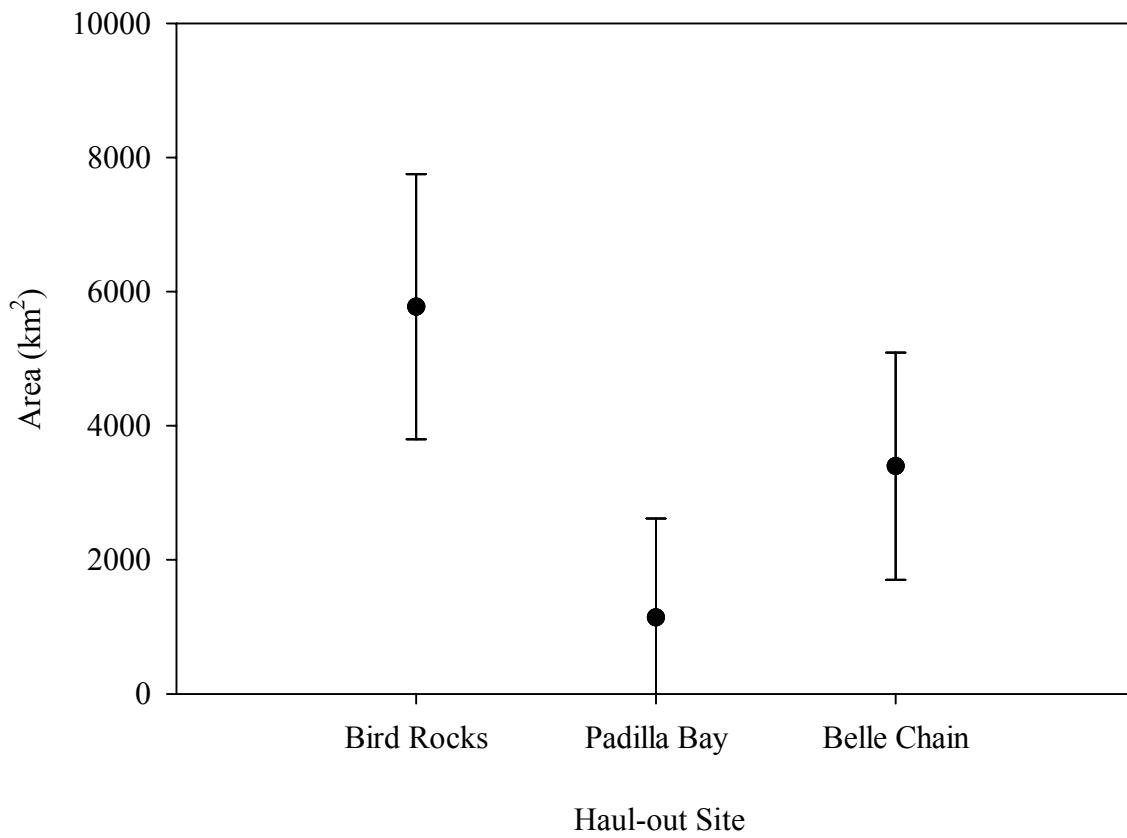
Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
Mass	8	124.87	-54.43			
Transmission Days	8	125.59	-54.79			
Mass and Transmission Days	10	128.81	-54.40	2 vs 3	0.78	0.68

Appendix 4.1b. Seasonal temporal scale model with site as the fixed effect and mass as the random effect.

	numDF	denDF	F-value	p-value
Intercept	1	13	689.83	< 0.0001
Site	2	13	14.2	< 0.001

Appendix 4.1c. Independent contrasts on the model with site as the fixed effect and mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
Intercept	13.94	0.59	13	23.79	0.0000
Bird Rocks vs Belle Chain	1.57	0.65	13	2.42	0.031
Rocky Reefs vs Padilla Bay	2.28	0.45	13	5.05	< 0.001



Appendix 4.2. Minimum convex polygons of harbor seals relative to season. Prepupping and pupping are pooled together. Untransformed data.

Male home range size

Appendix 4.3a-c. Home range LME model summary relative to season for males (n = 16). Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 4.3a. Comparison of models on a seasonal temporal scale with all fixed effects and combinations of random effects.

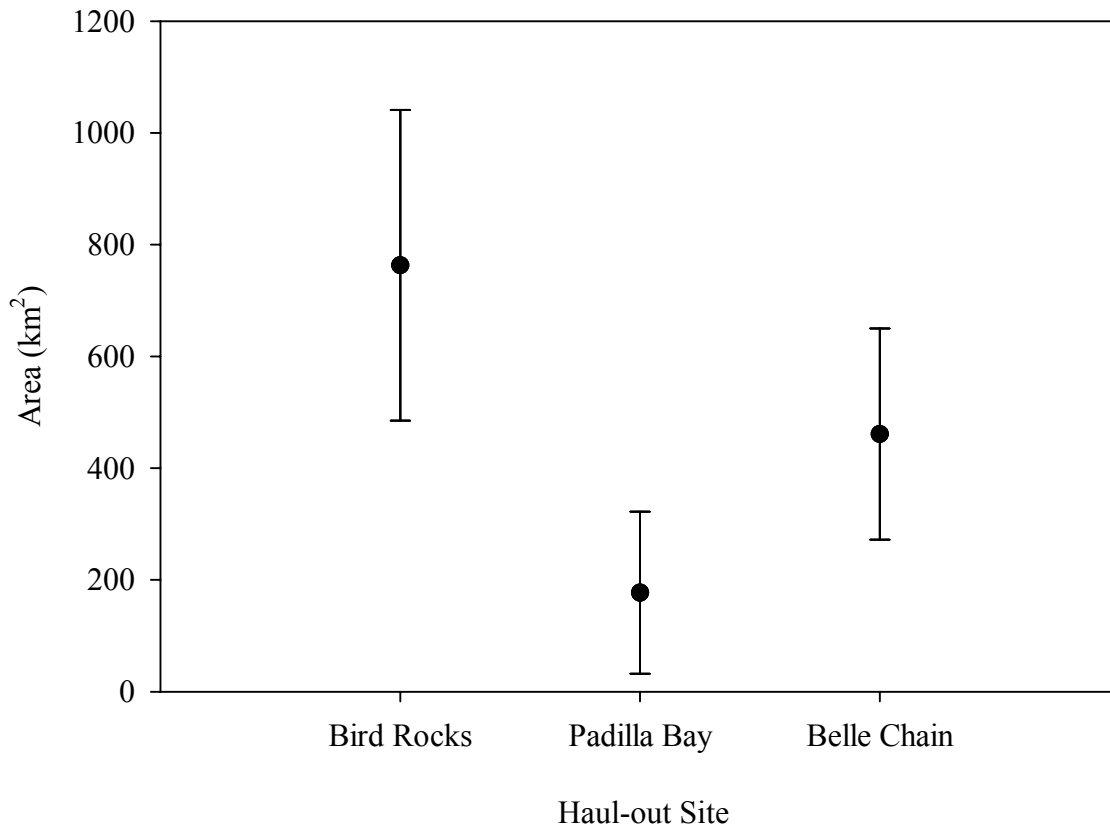
Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
95th percentile contours						
Mass	8	148.56	-66.28			
Transmission Days	8	151.03	-67.52			
Mass and Transmission Days	10	154.88	-67.44	2 vs 3	0.16	0.925
50th percentile contours						
Mass	8	122.24	130.6			
Transmission Days	8	129.28	137.64			
Mass and Transmission Days	10	131.90	142.35	2 vs 3	1.38	0.501

Appendix 4.3b. Comparison of models on a seasonal temporal scale with different fixed effects and mass as the random effect.

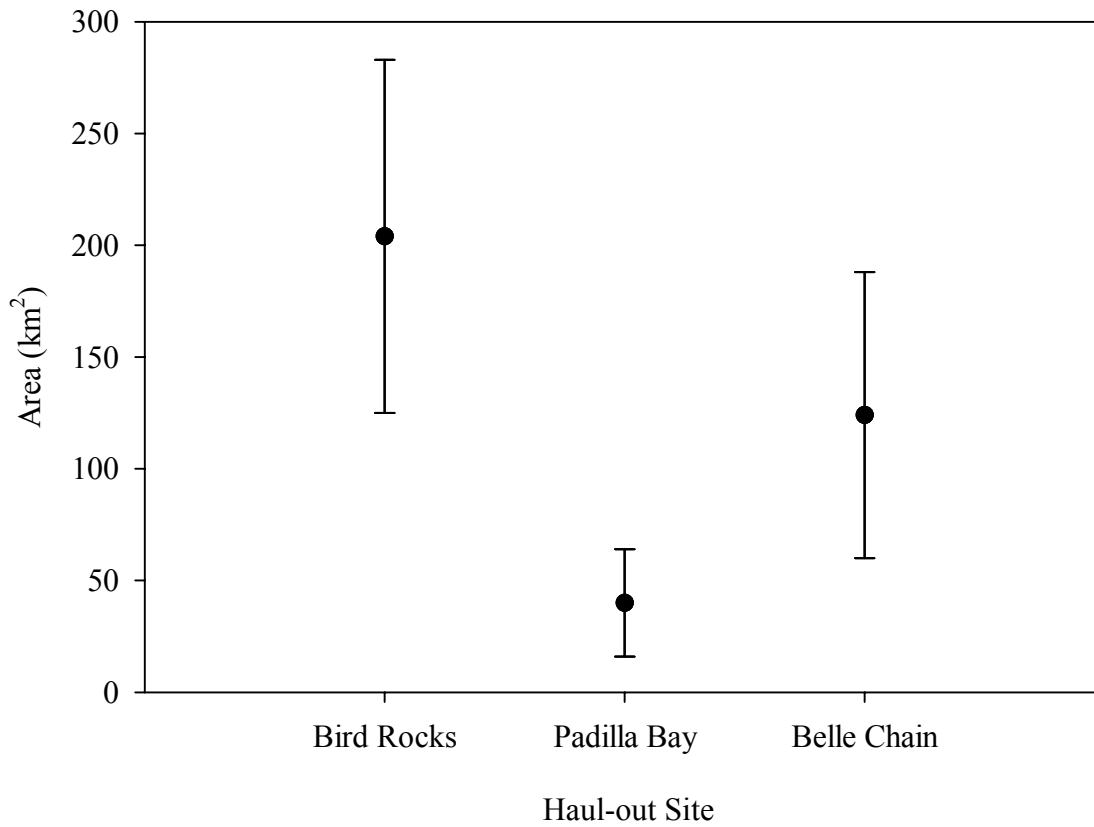
	numDF	denDF	F-value	p-value
95th percentile contours				
Intercept	1	13	406	< 0.001
Site	2	13	11.63	0.001
50th percentile contours				
Intercept	1	13	272.31	< 0.001
Site	2	13	8.97	0.004

Appendix 4.3c. Independent contrasts comparing sites for the best seasonal models with mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
95th percentile contour					
Intercept	20.21	1.11	13	18.10	0.000
Bird Rocks vs Belle Chain	3.15	1.21	13	2.59	0.023
Rocky Reefs vs Padilla Bay	3.79	0.87	13	4.37	< 0.001
50th percentile contour					
Intercept	10.25	0.70	13	14.60	0.000
Bird Rocks vs Belle Chain	1.74	0.75	13	2.31	0.038
Rocky Reefs vs Padilla Bay	2.09	0.55	13	3.79	0.002



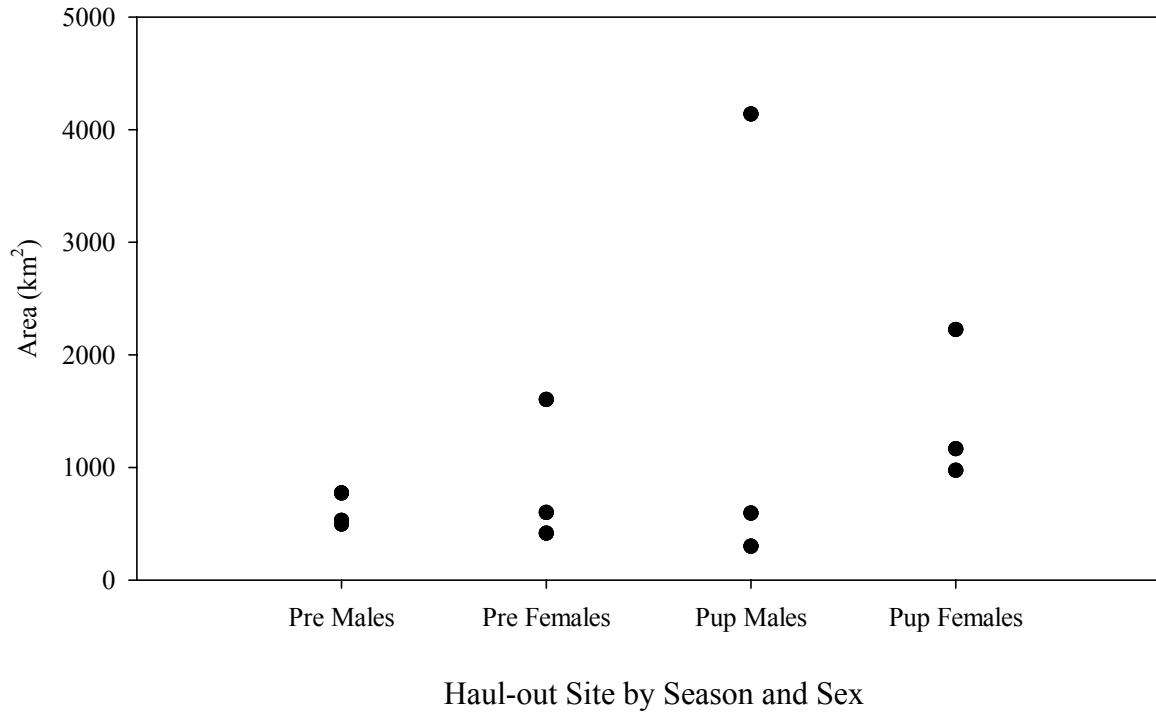
Appendix 4.4. Home ranges (95th percentile contours) of harbor seals relative to season. Prepupping and pupping are pooled together. Untransformed data.



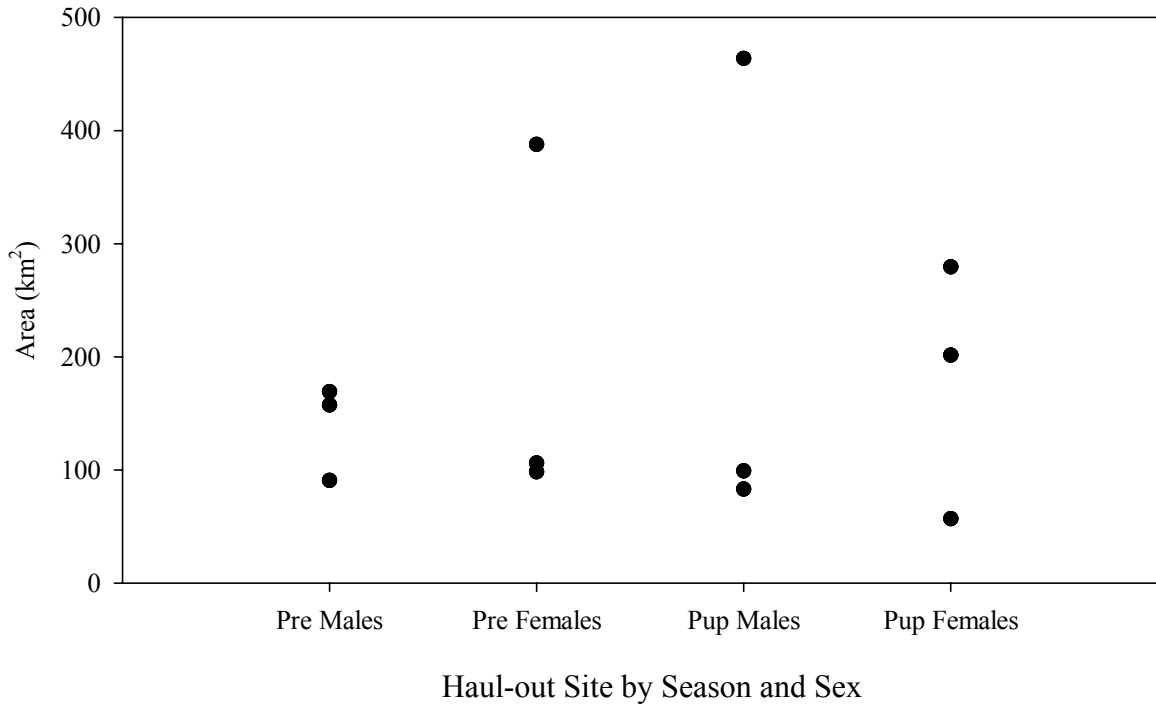
Appendix 4.5. Core areas (50th percentile contours) of harbor seals relative to season. Prepupping and pupping are pooled together. Untransformed data.

Appendix 5

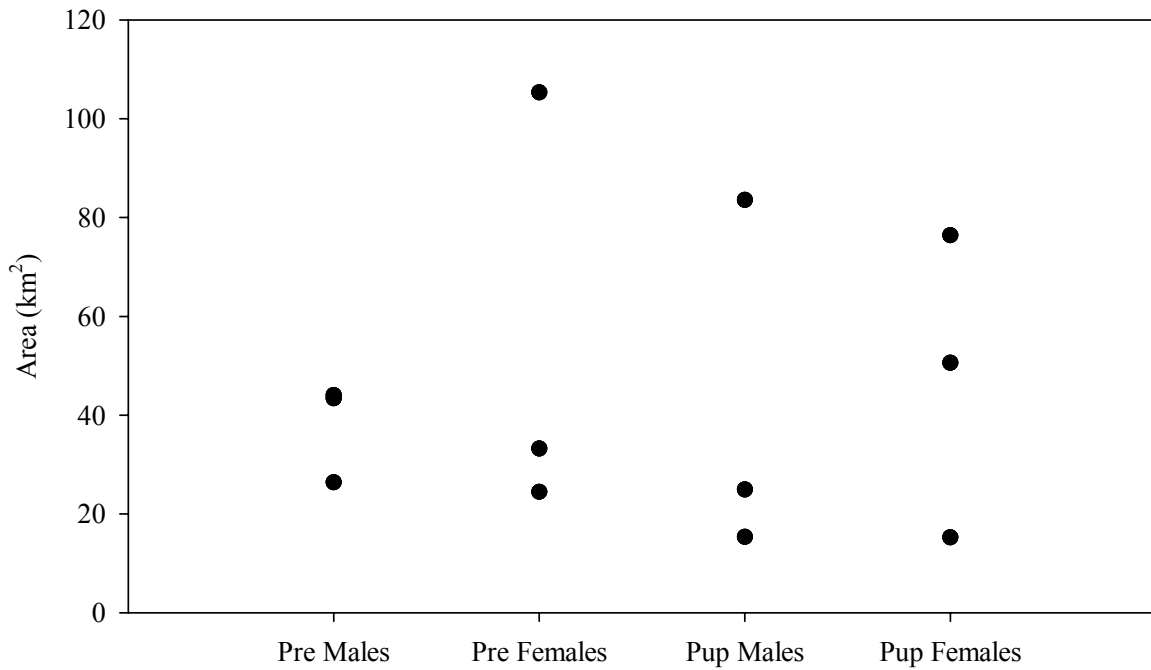
Harbor seal movements and home ranges in Padilla Bay relative to sex and season



Appendix 5.1. Minimum convex polygons of male ($n = 3$) and female ($n = 3$) harbor seals from Padilla Bay relative to season. Untransformed data. Pre = prepupping and Pup = pupping. Each dot represents an individual seal.



Appendix 5.2. Home ranges (95th percentile contour) of male (n = 3) and female (n = 3) harbor seals from Padilla Bay relative to season. Untransformed data. Pre = prepupping and Pup = pupping. Each dot represents an individual seal.



Haul-out Site by Season and Sex

Appendix 5.3. Core area (50th percentile contour) of male (n = 3) and female (n = 3) harbor seals from Padilla Bay relative to season. Untransformed data. Pre = prepupping and Pup = pupping. Each dot represents an individual seal.

Appendix 6

Individual harbor seal home ranges and core areas relative to season

Appendix 6.1a. Home range sizes of harbor seals during the prepupping season. Seal ID indicates male (B) vs. female (Y).

Site	Seal ID	Mass (kg)	Contour (km ²)	
			95th pct	50th pct
Bird Rocks	Y1455	76.5	298	59
Bird Rocks	B1696	74.5	843	221
Bird Rocks	B1695	71.5	640	141
Bird Rocks	B1697	96.0	914	283
Bird Rocks	B1698	90.0	446	118
Bird Rocks	B1701	86.0	846	242
Padilla Bay	B1699	64.0	157	44
Padilla Bay	Y1459	83.0	388	105
Padilla Bay	Y1460	62.5	98	24
Padilla Bay	B1712	69.0	91	26
Padilla Bay	B1713	54.0	169	43
Padilla Bay	Y1462	77.5	106	33
Belle Chain	B1711	70.5	591	185
Belle Chain	B1706	90.5	269	45
Belle Chain	B1707	58.5	558	146
Belle Chain	B1709	92.0	514	154
Belle Chain	B1702	81.5	260	57
Belle Chain	B1704	72.0	451	117
Belle Chain	B1710	77.0	397	112
Belle Chain	B1703	66.5	610	155

Appendix 6.1b. Home range sizes of harbor seals during the pupping season. Seal ID indicates male (B) vs. female (Y).

Site	Seal ID	Mass (kg)	Contour (km ²)	
			95th pct	50th pct
Bird Rocks	Y1455	76.5	209	48
Bird Rocks	B1695	71.5	436	117
Bird Rocks	B1701	86.0	1217	307
Padilla Bay	B1699	64.0	83	25
Padilla Bay	Y1459	83.0	280	76
Padilla Bay	Y1460	62.5	57	15
Padilla Bay	B1712	69.0	99	15
Padilla Bay	B1713	54.0	464	84
Padilla Bay	Y1462	77.5	201	51
Belle Chain	B1711	70.5	856	267
Belle Chain	B1706	90.5	195	28
Belle Chain	B1707	58.5	346	100
Belle Chain	B1709	92.0	492	143
Belle Chain	B1704	72.0	248	65
Belle Chain	B1703	66.5	674	167

Appendix 7

Harbor seal home ranges relative to month and the duration of study

The best model on the monthly temporal scale and for the entire study period temporal scale included site as the only fixed effect (LME, $p \leq 0.032$, Appendix 7.1 and 7.2) and mass as a random effect (Appendix 7.1 and 7.2) with one exception; at the monthly scale the best model with which to examine the 50th percentile contours was a model including both site and month (Appendix 7.1). Independent contrasts from LME models on a monthly scale and for the entire study period for both 95th and 50th percentile contours showed significant differences between seals from the rocky reefs (Bird Rocks and Belle Chain) and Padilla Bay (LME, $p < 0.018$, Appendix 7.1 and 7.2) but not between Belle Chain and Bird Rocks (LME, $p > 0.354$, Appendix 7.1 and 7.2). Seals from Bird Rocks had the largest mean 95th and 50th percentile contour for all months except for July, when seals from Belle Chain had the greatest mean (Appendix 7.3 and Appendix 7.4). Seals from Padilla Bay had the smallest mean 95th and 50th percentile contours for all months (May – August) (Appendix 7.3 and Appendix 7.4). Seals from Bird Rocks had the highest mean 95th and 50th percentile contours for the entire study period followed by seals from Belle Chain and then seals from Padilla Bay (Appendix 7.5)

Appendix 7.1a-d. Home range LME model summary relative to month. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 7.1a. Comparison of models with different random effects on a seasonal temporal scale with all fixed effects included.

Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
95th percentile contours						
Mass	14	287.93	314.12			
Sex and Mass	16	290.22	320.16	1 vs 2	1.71	0.426
Transmission Days and Mass	16	291.93	321.87			
Sex	14	309.97	336.17	3 vs 4	22.04	< 0.001
Transmission Days	14	309.97	336.17			
Transmission Days, Sex and Mass	16	313.97	343.91	5 vs 6	0.00	1.000
Sex and Transmission Days	16	313.97	343.91			
50th percentile contours						
Mass	14	240.25	-106.12			
Sex and Mass	16	242.17	-105.09	1 vs 2	2.07	0.345
Transmission Days and Mass	16	243.72	-105.86			
Sex	14	263.47	-117.74	3 vs 4	23.76	< 0.001
Transmission Days	14	263.47	-117.74			
Transmission Days, Sex and Mass	16	267.47	-117.74	5 vs 6	0.00	1.000
Sex and Transmission Days	16	267.47	-117.74			

Appendix 7.1b. Comparison of fixed effects on a monthly temporal scale with mass as the random effect.

Model	df	AIC	logLik	Test	L.Ratio	p-value
95th percent contours						
1 - Site	5	310.35	-150.2			
2 - Site + month	8	312.25	-148.1	1 vs 2	4.1	0.251
3 - Site * month	14	315.12	-143.6	2 vs 3	9.14	0.166
50th percent contours						
1 - Site + month	5	251.12	-117.56			
2 - Site	8	251.80	-120.90	1 vs 2	6.69	0.083
3 - Site * month	14	255.43	-113.72	2 vs 3	14.36	0.110

Appendix 7.1c. Monthly temporal scale model with site (95th percentile contour) or site and month (50th percentile contour) as the fixed effects and mass as the random effect.

	numDF	denDF	F-value	p-value
95th percent contours				
Intercept	1	39	455.11	< 0.0001
Site	2	39	10.61	< 0.001
50th percent contours				
Intercept	1	36	325.97	< 0.0001
Site	2	36	6.50	0.004
Month	3	36	2.17	0.109

Appendix 7.1d. Independent contrasts on the selected models.

	Value	Std. Error	DF	t-value	p-value
95th percent contours					
Intercept	15.14	0.72	39	20.94	0.000
Bird Rocks vs Belle Chain	0.51	0.84	39	0.61	0.543
Rocky Reefs vs Padilla Bay	2.09	0.46	39	4.58	< 0.001
50th percent contours					
Intercept	7.31	0.64	36	11.41	0.000
Bird Rocks vs Belle Chain	0.49	0.53	36	0.92	0.363
Rocky Reefs vs Padilla Bay	1.07	0.29	36	3.75	< 0.001

Appendix 7.2a-c. Home range LME model summary relative to whole study period. Statistically significant values ($p < 0.05$) or the best model are indicated by bold text. Rocky reefs include both Bird Rocks and the Belle Chain Islets.

Appendix 7.2a. Comparison of models with different random effects on a whole study period temporal scale with all fixed effects included.

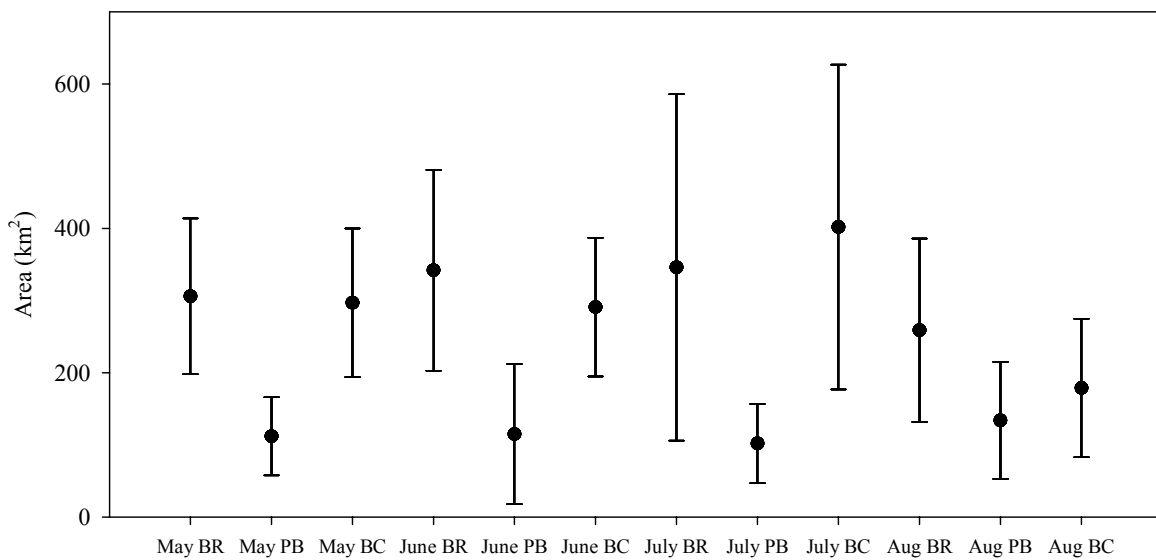
Random Effects	df	AIC	logLik	Test	L.Ratio	p-value
95th percentile contours						
Sex	5	264.1621	-127.08			
Mass	5	264.1624	-127.08			
Transmission Days	5	264.1624	-127.08			
Transmission Days and Mass	7	264.36	-125.18	3 vs 4	3.80	0.150
Sex and Transmission Days	7	266.59	-126.30			
Sex and Mass	7	267.97	-126.99			
Transmission Days, Mass and Sex	7	268.16	-127.08			
50th percentile contours						
Mass	5	111.91	-50.95			
Sex	5	111.91	-50.95			
Transmission Days	5	111.91	-50.95			
Sex and Transmission Days	7	114.49	-50.25	3 vs 4	1.41	0.493
Transmission Days and Mass	7	114.63	-50.31			
Sex and Mass	7	115.86	-50.93			
Transmission Days, Mass and Sex	7	115.91	-50.95			

Appendix 7.2b. Comparison of fixed effects on a monthly temporal scale with mass as the random effect.

	numDF	denDF	F-value	p-value
95th percent contours				
Intercept	1	16	56.77	< 0.0001
Site	2	16	4.31	0.032
50th percent contours				
Intercept	1	17	154.59	< 0.0001
Site	2	17	5.43	0.015

Appendix 7.2c. Independent contrasts on the model with site as the fixed effect and mass as the random effect.

	Value	Std. Error	DF	t-value	p-value
95th percent contours					
Intercept	601.38	81.55	16	7.37	0.000
Bird Rocks vs Belle Chain	93.25	97.56	16	0.96	0.354
Rocky Reefs vs Padilla Bay	167.56	58.96	16	2.84	0.018
50th percent contours					
Intercept	11.27	0.93	17	12.17	0.0000
Bird Rocks vs Belle Chain	0.82	1.11	17	0.74	0.469
Rocky Reefs vs Padilla Bay	2.18	0.67	17	3.26	0.005



Haul-out Site by Month

Appendix 7.3. Home ranges (95th percentile contours) of harbor seals relative to month. Untransformed data. BR = Bird Rocks, PB = Padilla Bay and BC = Belle Chain.

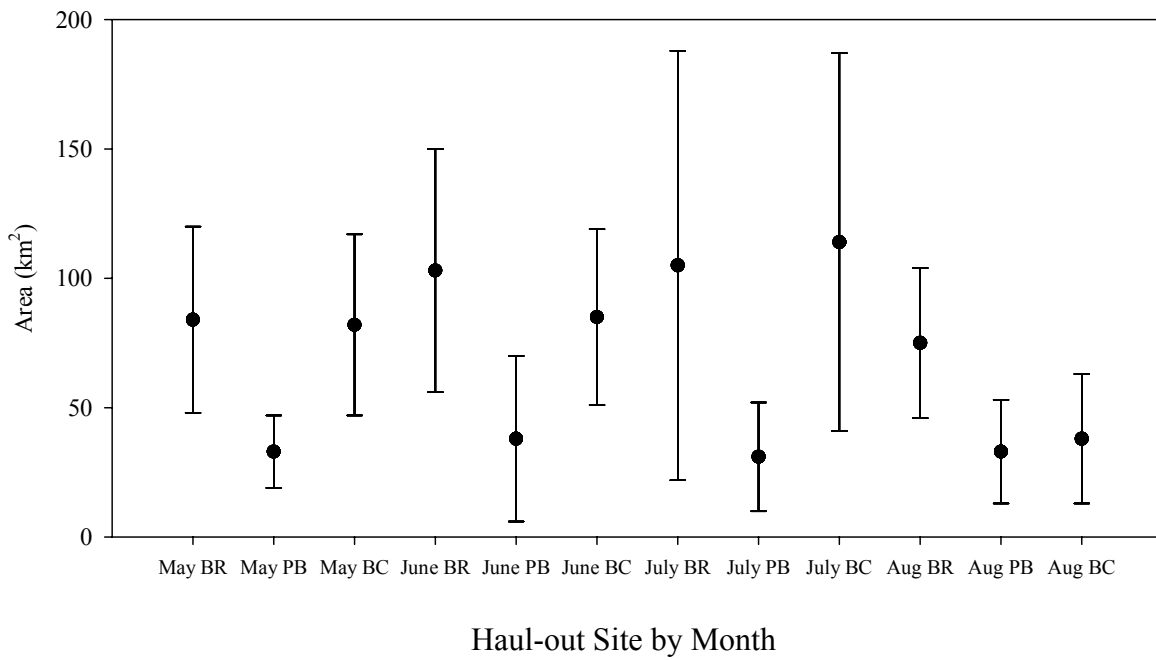


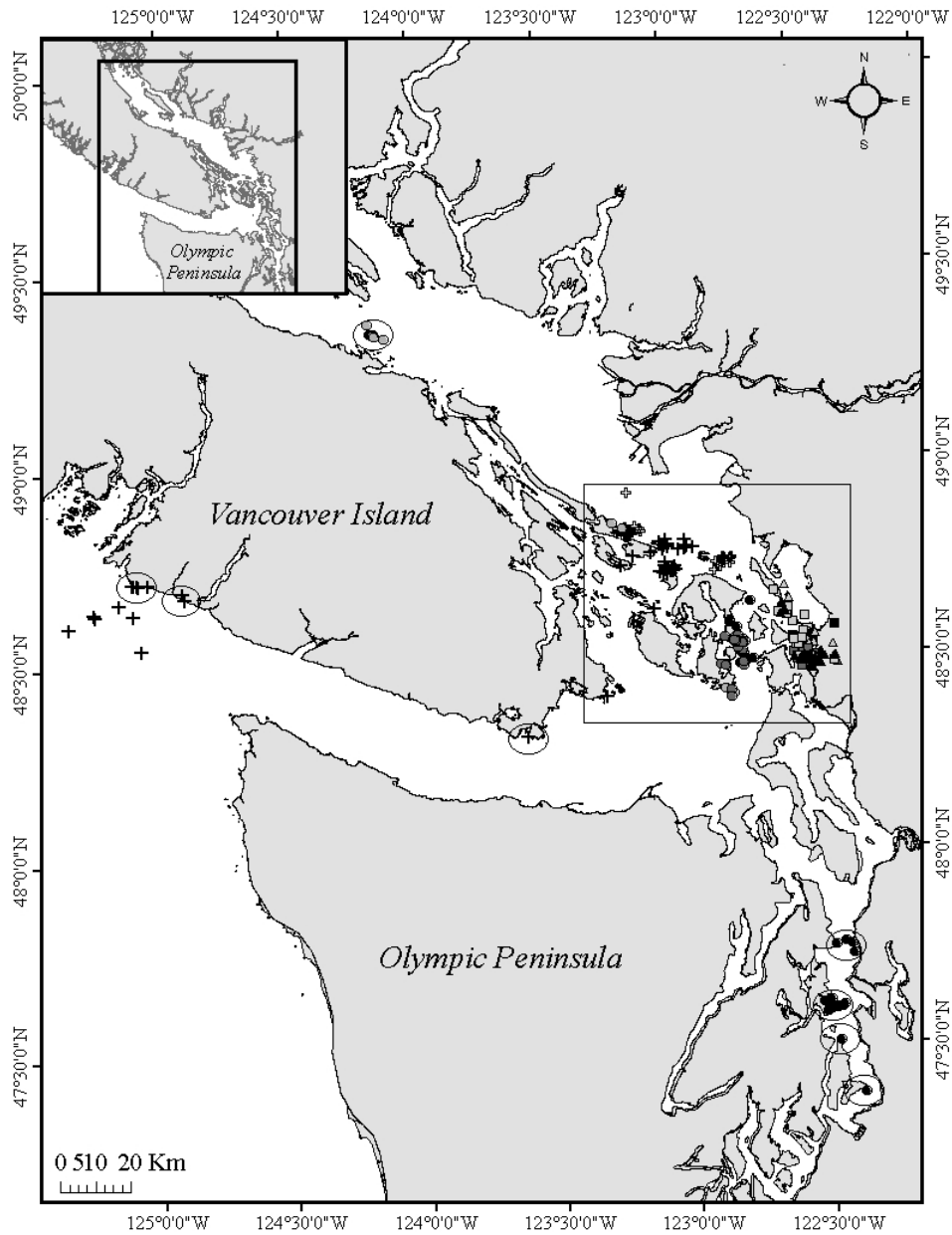
Fig 7.4. Core area (50th percentile contours) of harbor seals relative to month. Untransformed data. BR = Bird Rocks, PB = Padilla Bay and BC = Belle Chain.

Appendix 7.5. Home range area (means \pm SD) relative to the entire study period. Seal ID indicates male (B) vs. female (Y).

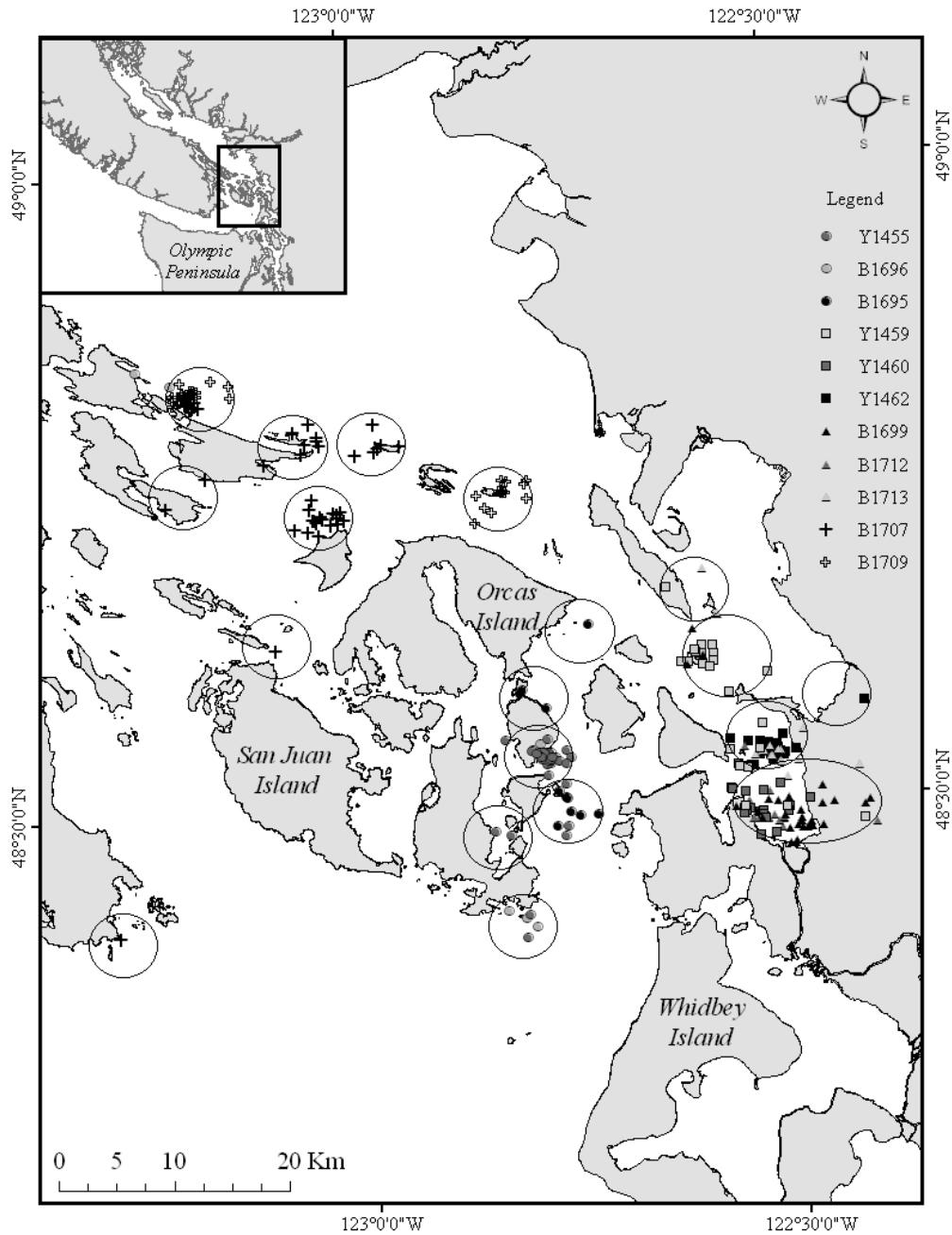
Site	Seal ID	Mass (kg)	Contour (km ²)		Mean contour \pm SD (km ²)	
			95th pct	50th pct	95th pct	50th pct
Bird Rocks	Y1455	76.5	338	58	862 \pm 504	223 \pm 140
Bird Rocks	B1696	74.5	839	221		
Bird Rocks	B1695	71.5	799	183		
Bird Rocks	B1697	96.0	992	307		
Bird Rocks	B1698	90.0	446	118		
Bird Rocks	B1701	86.0	1759	450		
Padilla Bay	B1699	64.0	173	33	266 \pm 180	52 \pm 37
Padilla Bay	Y1459	83.0	432	119		
Padilla Bay	Y1460	62.5	118	23		
Padilla Bay	B1712	69.0	114	22		
Padilla Bay	B1713	54.0	546	71		
Padilla Bay	Y1462	77.5	215	46		
Belle Chain	B1711	70.5	1231	384	676 \pm 335	177 \pm 115
Belle Chain	B1706	90.5	323	37		
Belle Chain	B1707	58.5	798	198		
Belle Chain	B1709	92.0	820	248		
Belle Chain	B1702	81.5	277	56		
Belle Chain	B1704	72.0	609	141		
Belle Chain	B1710	77.0	397	113		
Belle Chain	B1703	66.5	949	243		

Appendix 8

Harbor seal haul-out regions relative to individuals



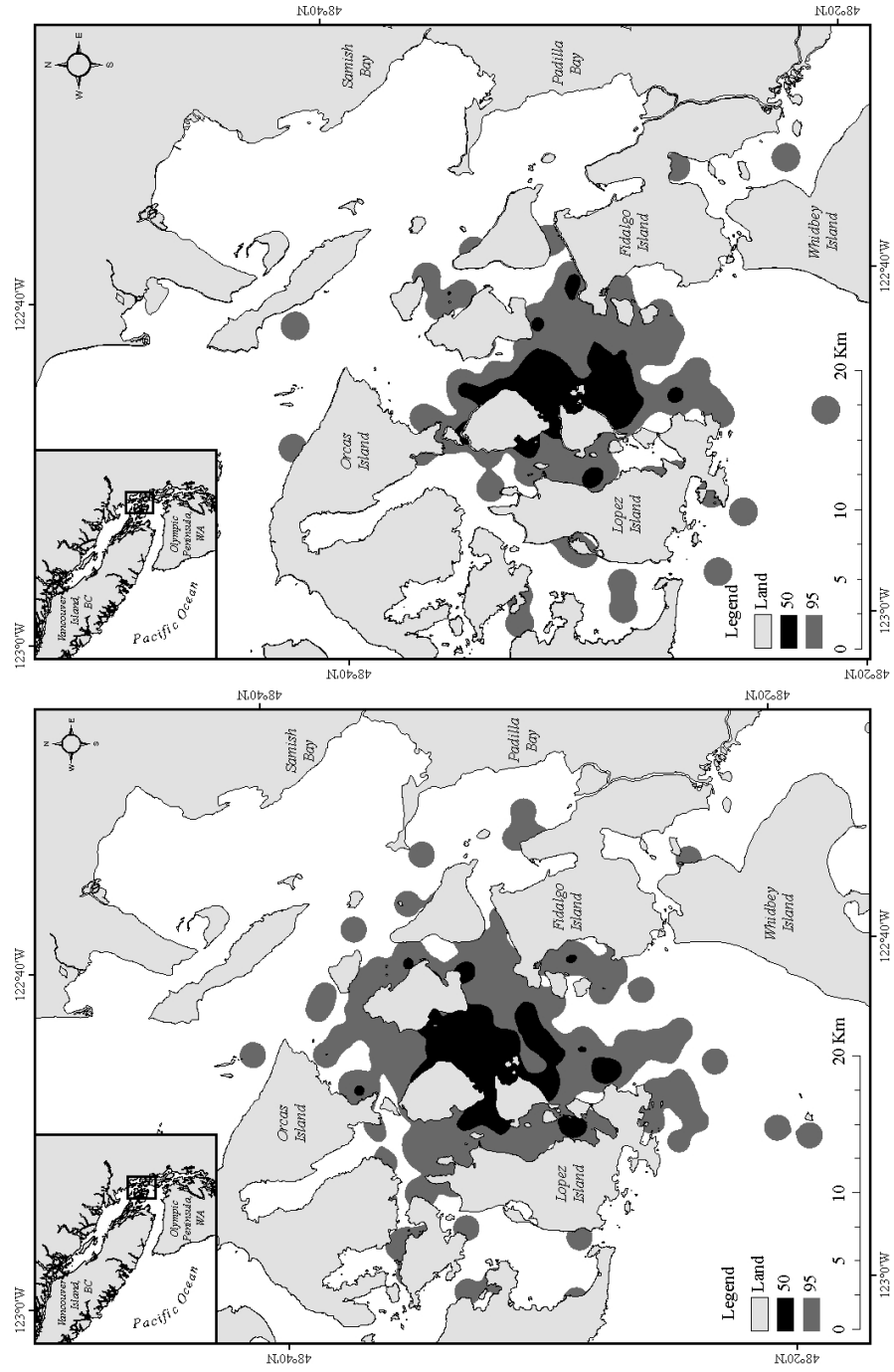
Appendix 8.1. Locations of haul-out bouts for satellite-tagged seals in the Georgia Basin. Circles encompass haul-out regions. ‘Haul-outs’ (+) offshore not enclosed in circles have been left out of this analysis. Haul-outs occurring within the enclosed square are enlarged in Appendix 8.2.



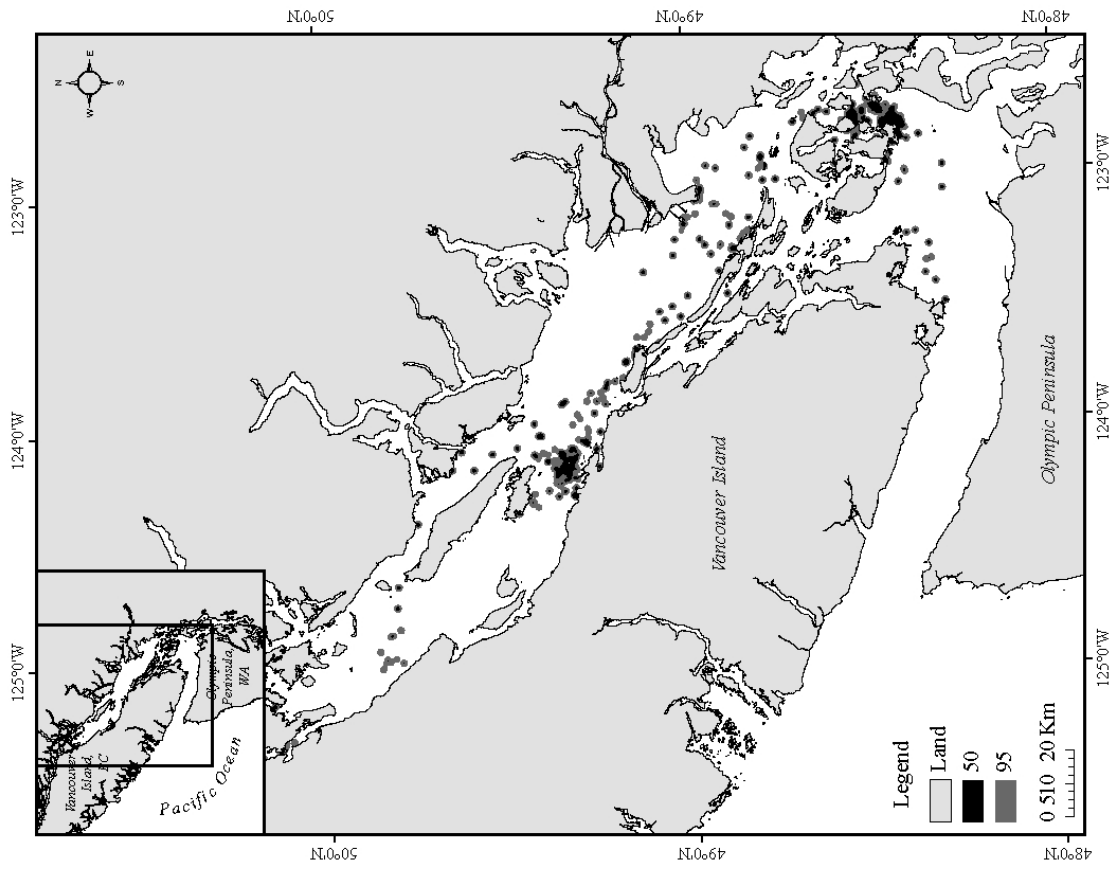
Appendix 8.2. Locations of haul-out bouts for satellite-tagged seals around the San Juan Islands. Circles encompass haul-out regions. Seals from Bird Rocks are indicated by (●), seals from Padilla Bay are indicated by (■) for females and (▲) for males and seals from Belle Chain are indicated by (+). Different seals are represented by different shadings of those symbols.

Appendix 9

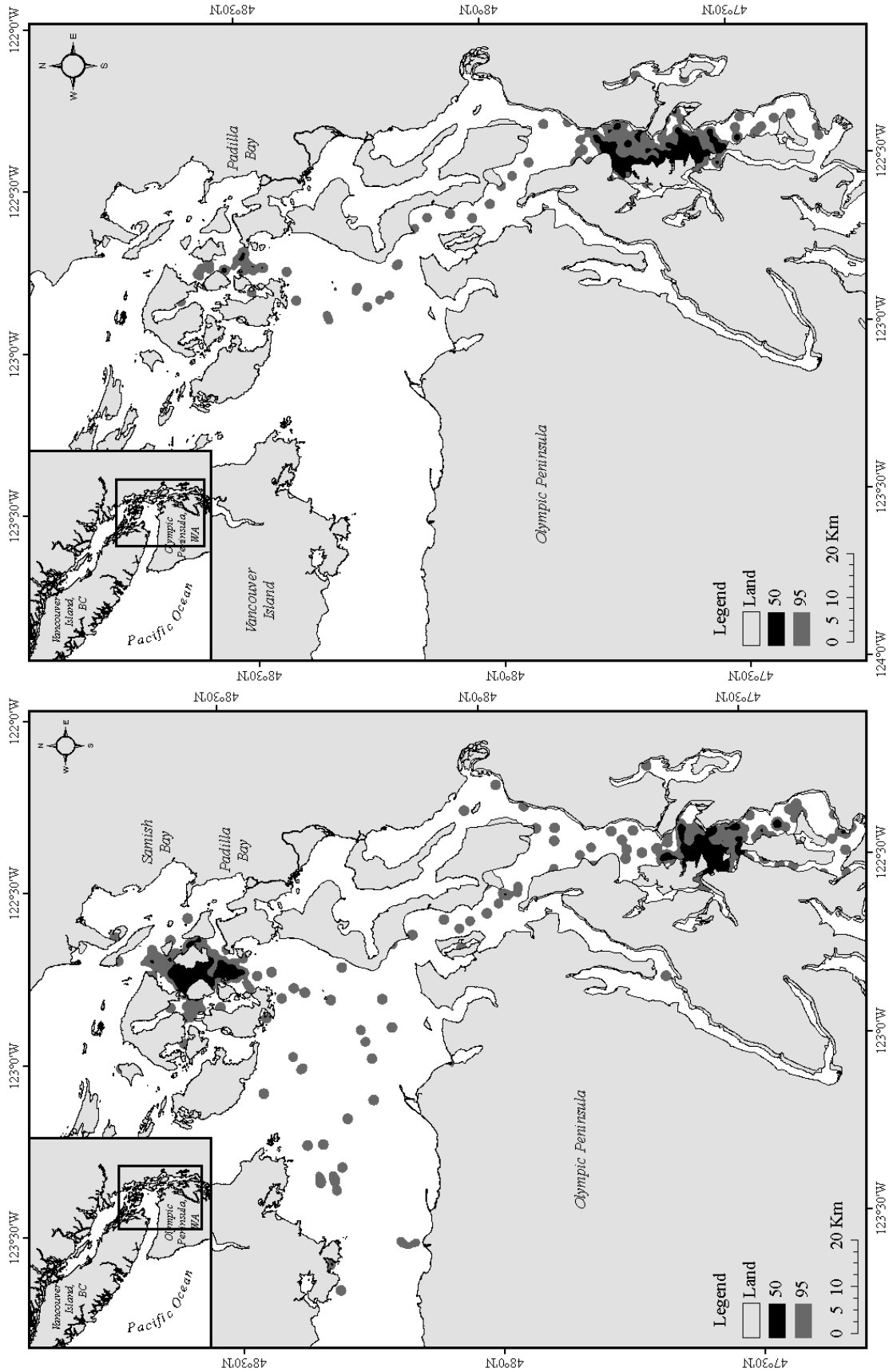
Home ranges maps for each individual harbor seal relative to season



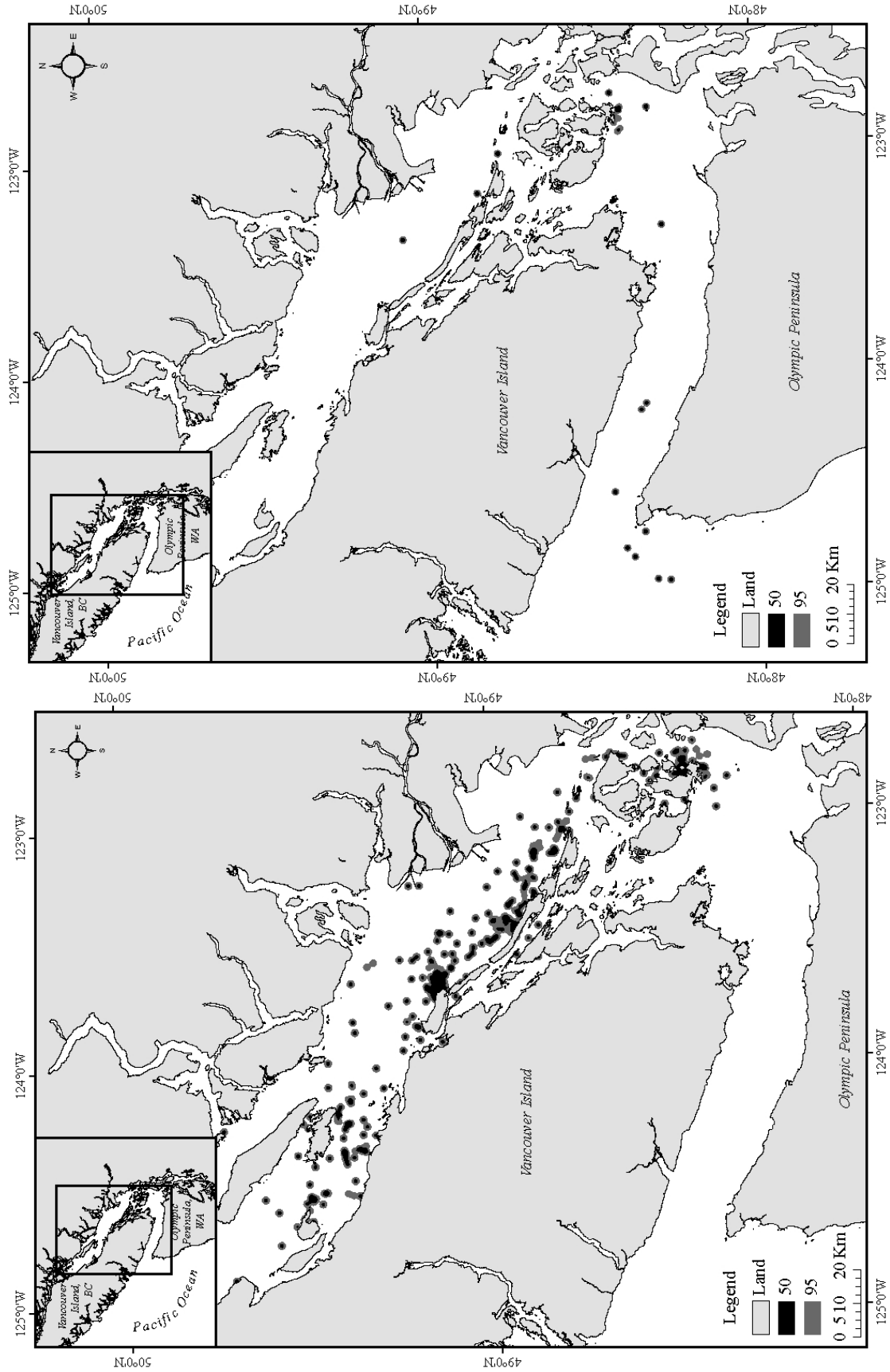
Appendix 9.1. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal Y1455 from Bird Rocks.



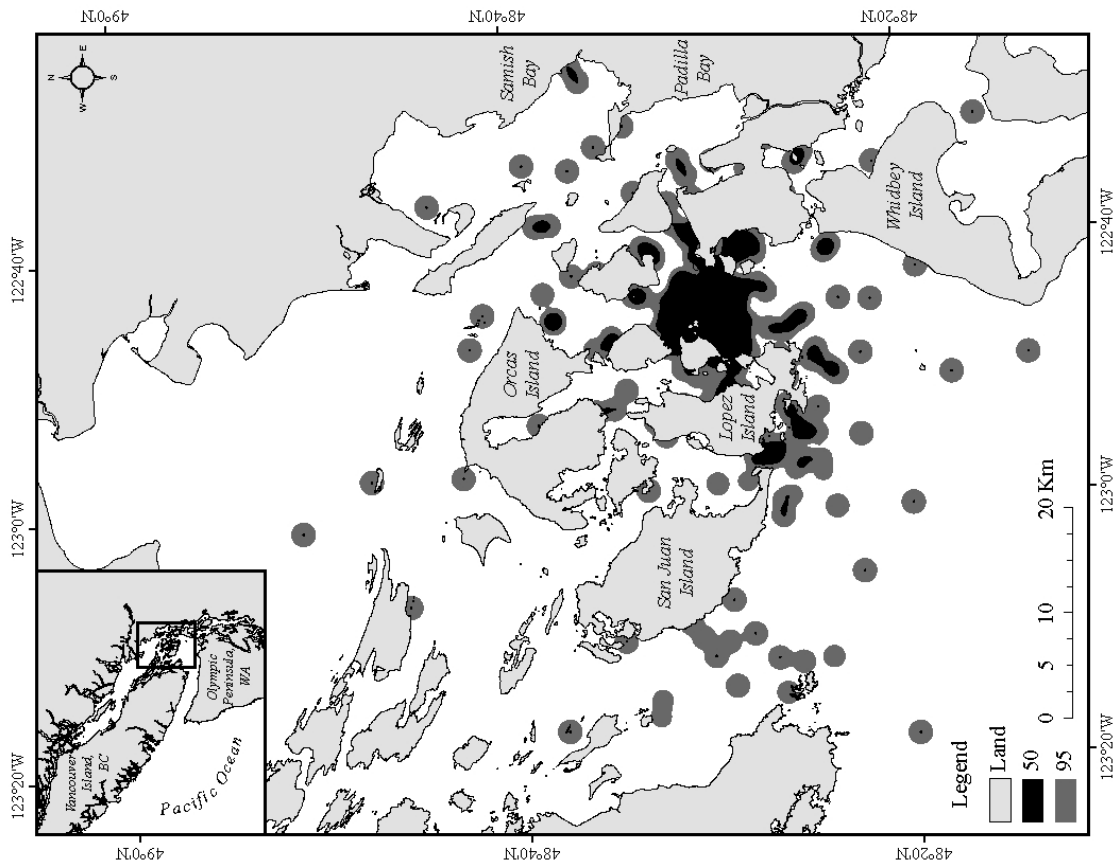
Appendix 9.2. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepping for seal B1696 from Bird Rocks.



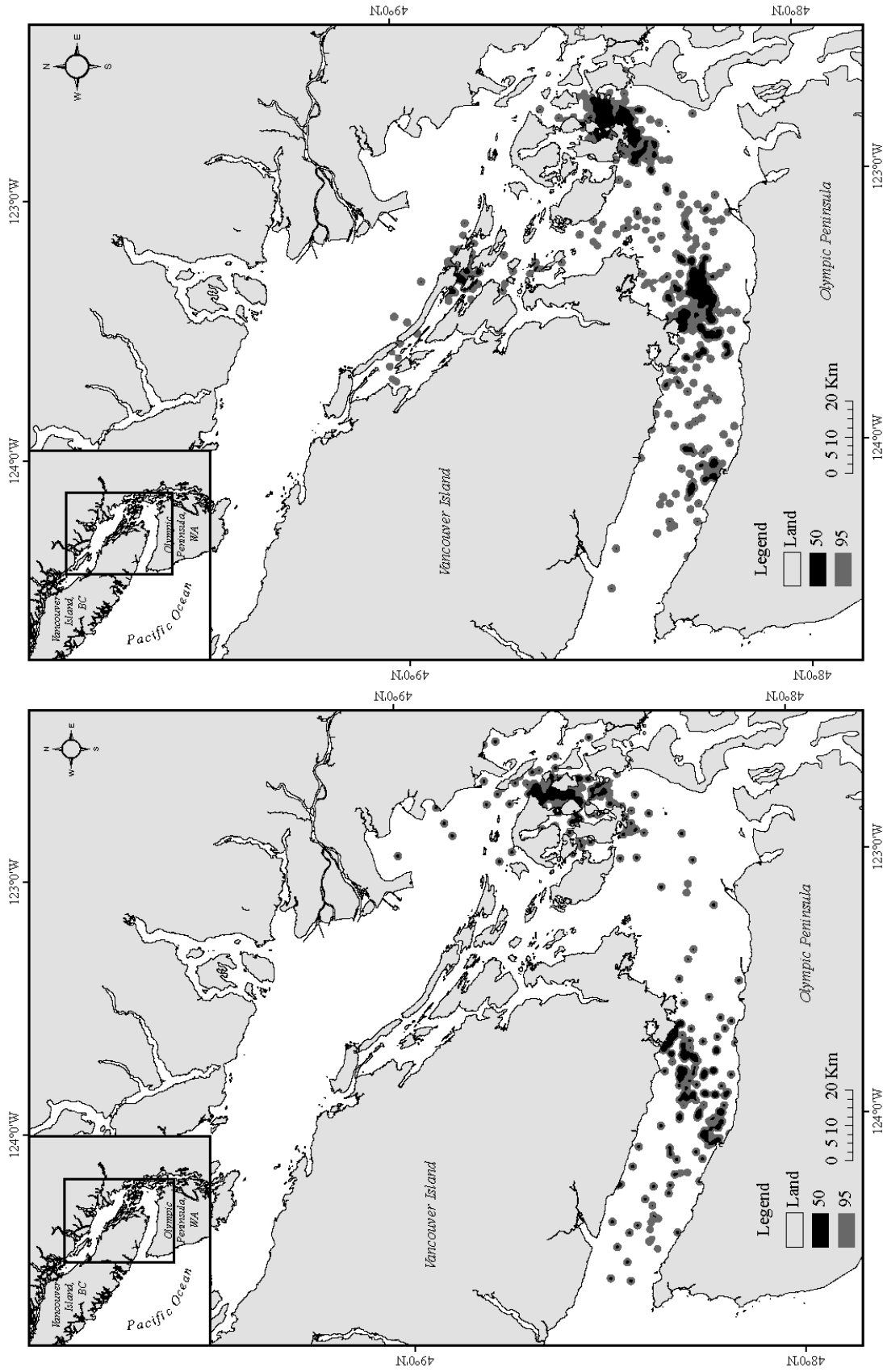
Appendix 9.3. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1695 from Bird Rocks.



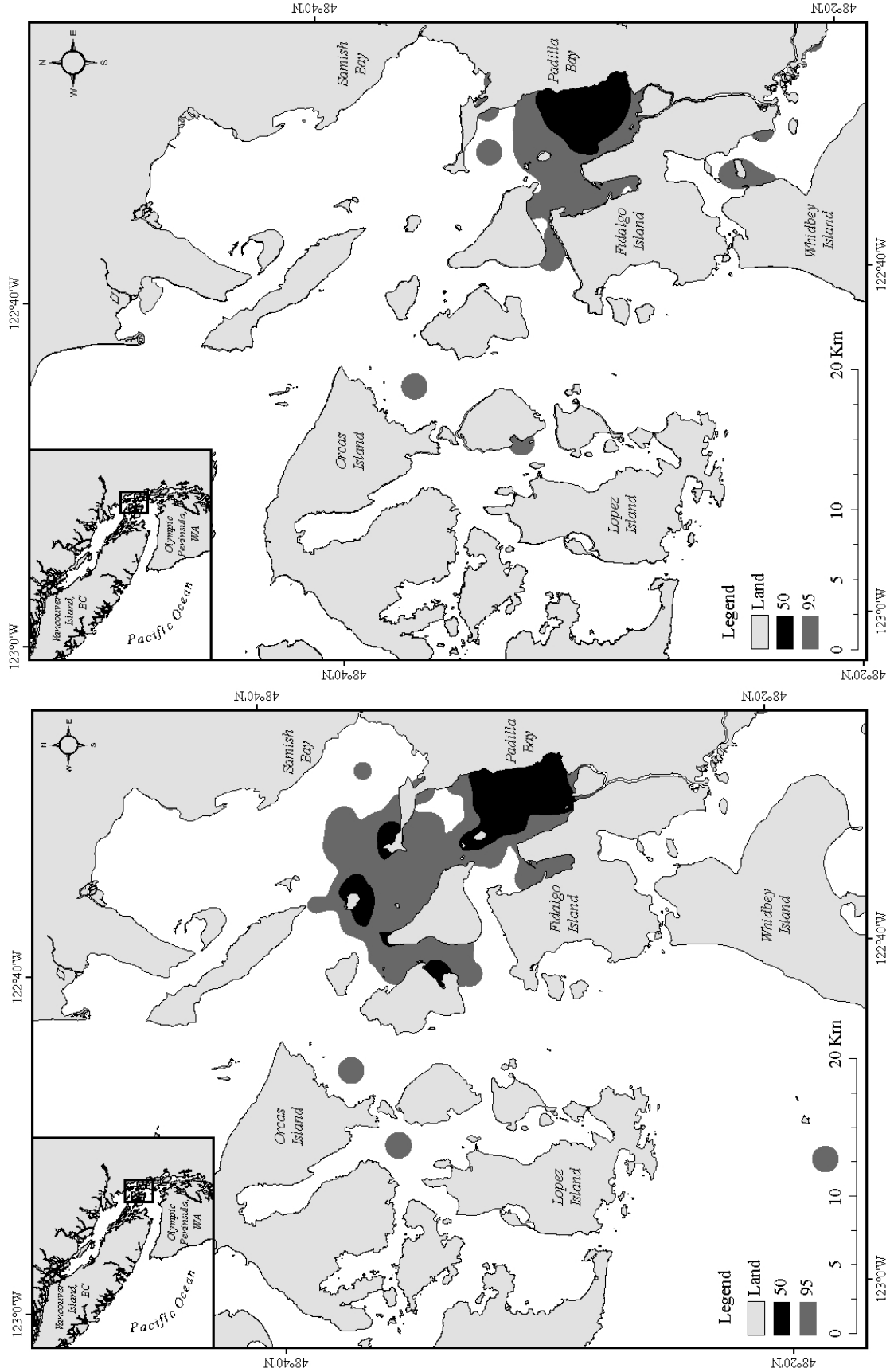
Appendix 9.4. The home range (95th percentile contour) and core areas of use (50th percentile contour) during pre-pupping (left figure) and pupping (right figure) seasons for seal B1697 from Bird Rocks.



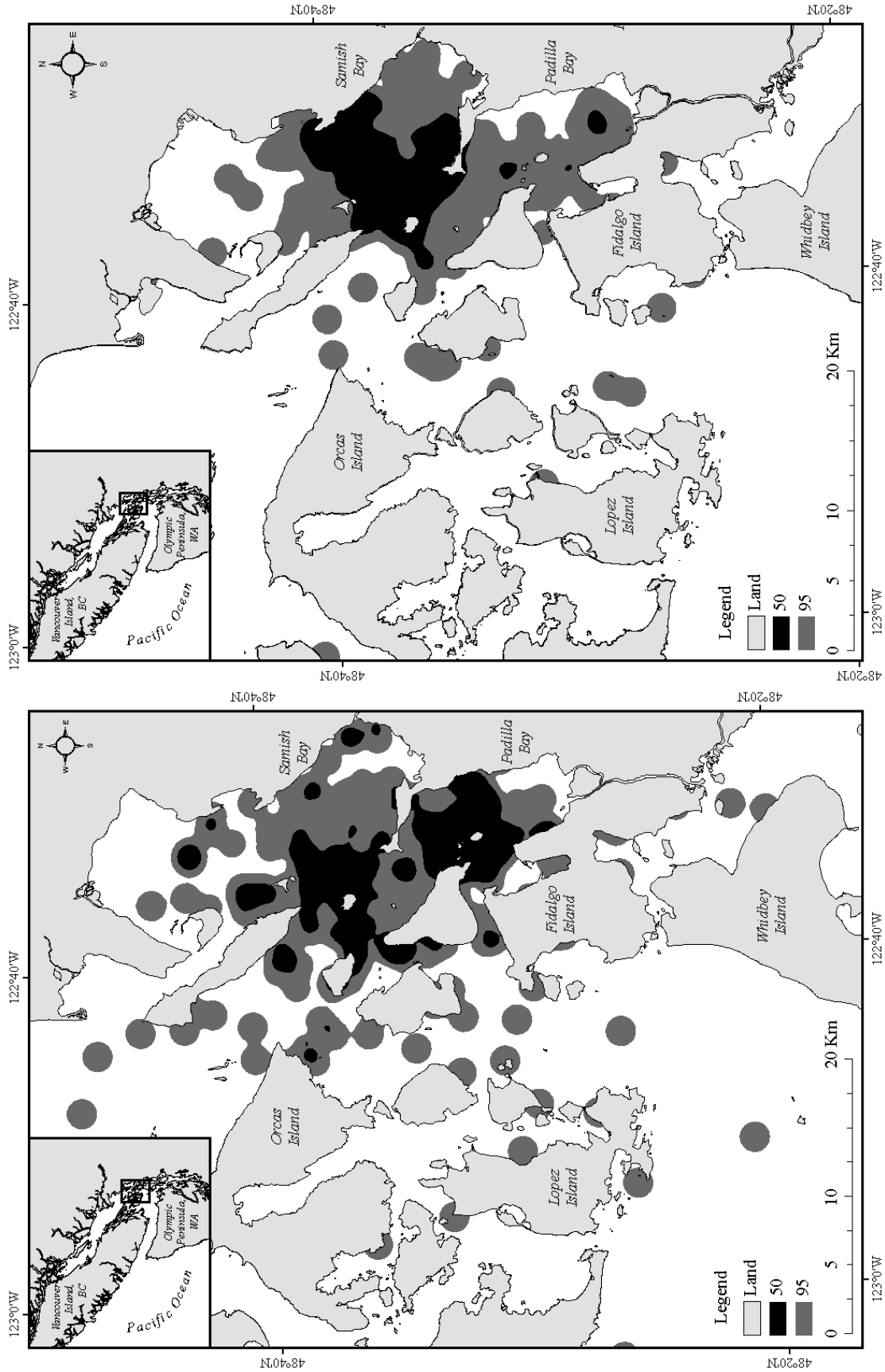
Appendix 9.5. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepping for seal B1698 from Bird Rocks.



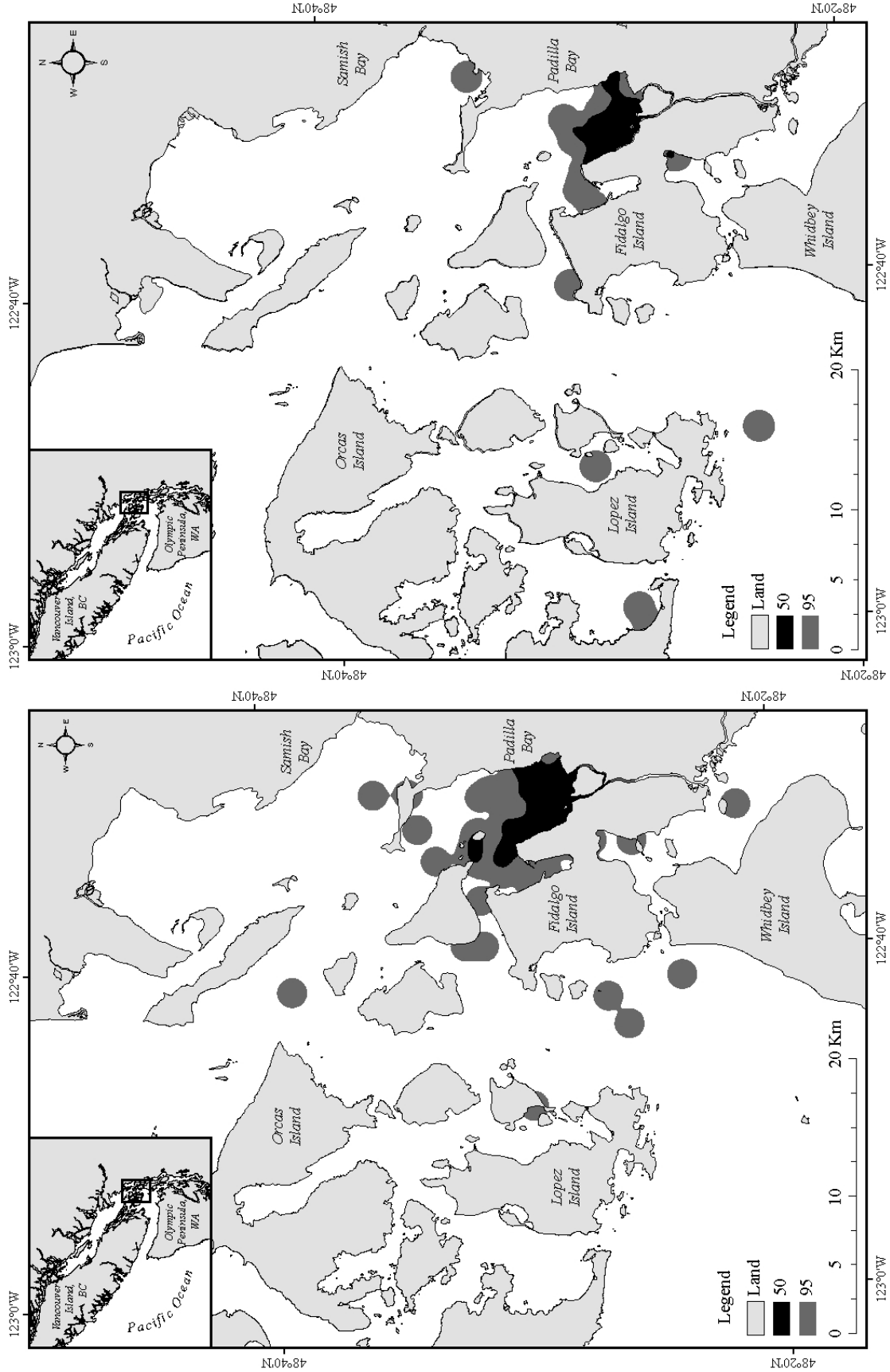
Appendix 9.6. The home range (95th percentile contour) and core areas of use (50th percentile contour) during pre-pupping (left figure) and pupping (right figure) seasons for seal B1701 from Bird Rocks.



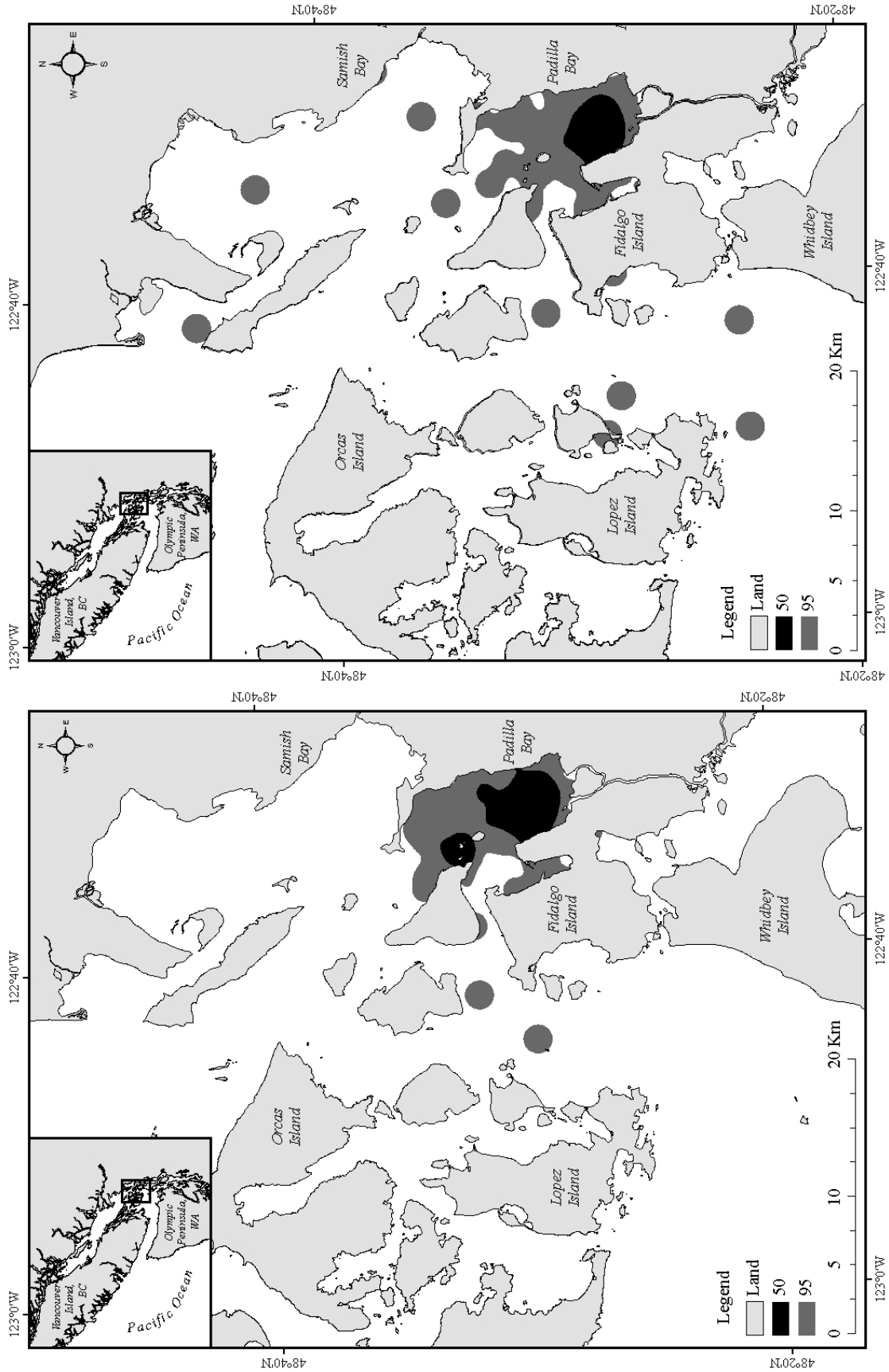
Appendix 9.7. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1699 from Padilla Bay.



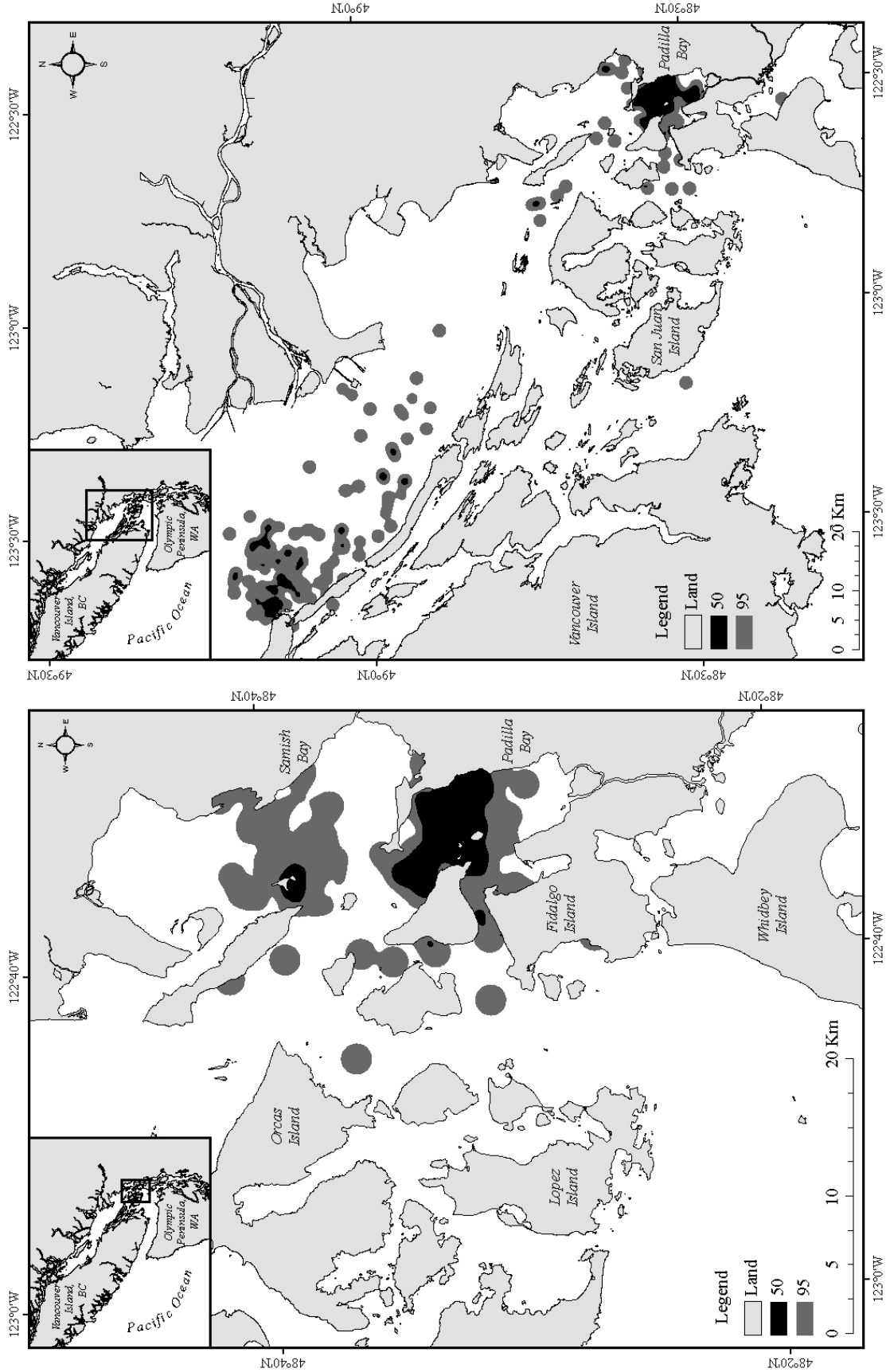
Appendix 9.8. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal Y1459 from Padilla Bay.



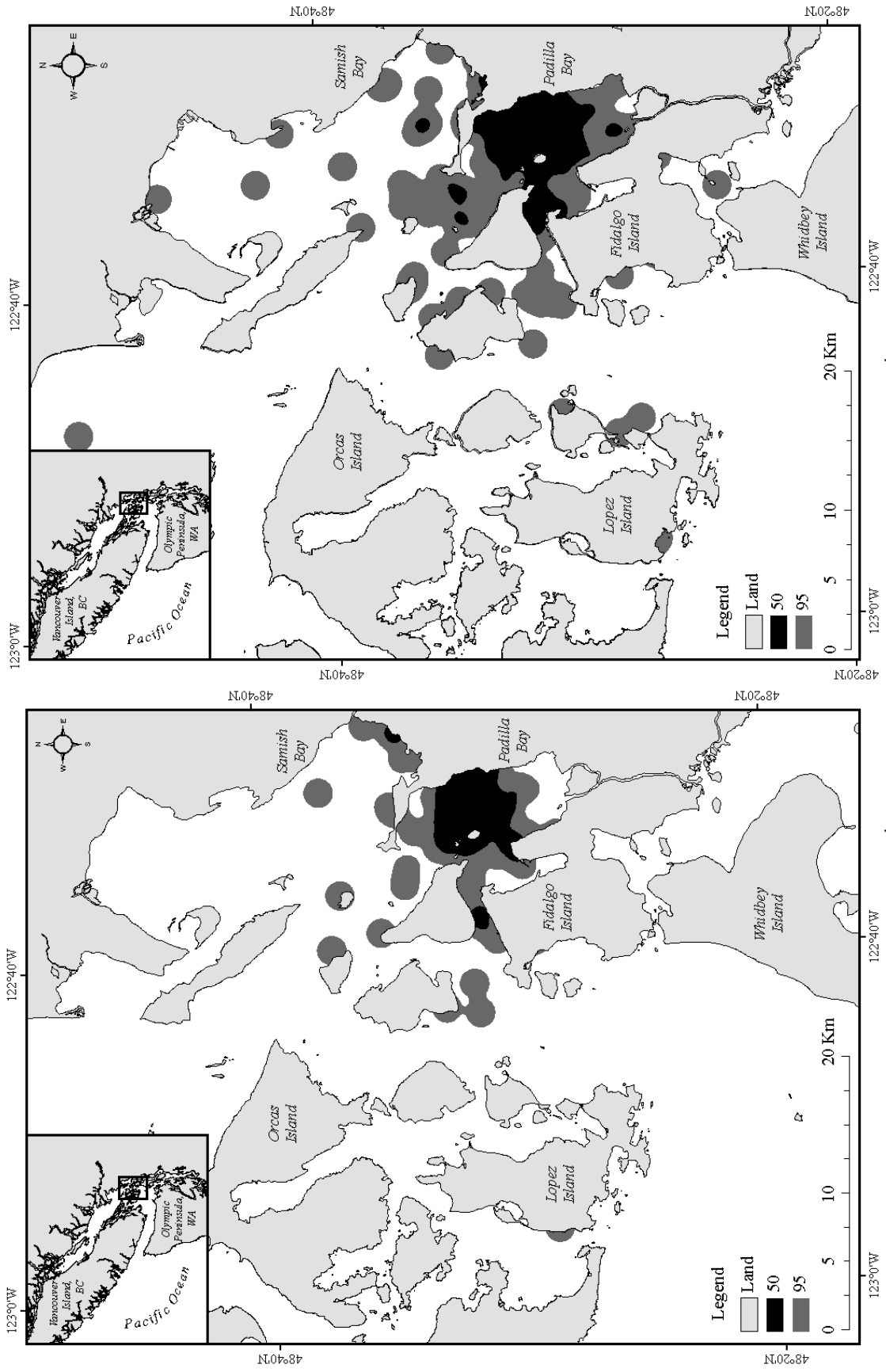
Appendix 9.9. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal Y1460 from Padilla Bay.



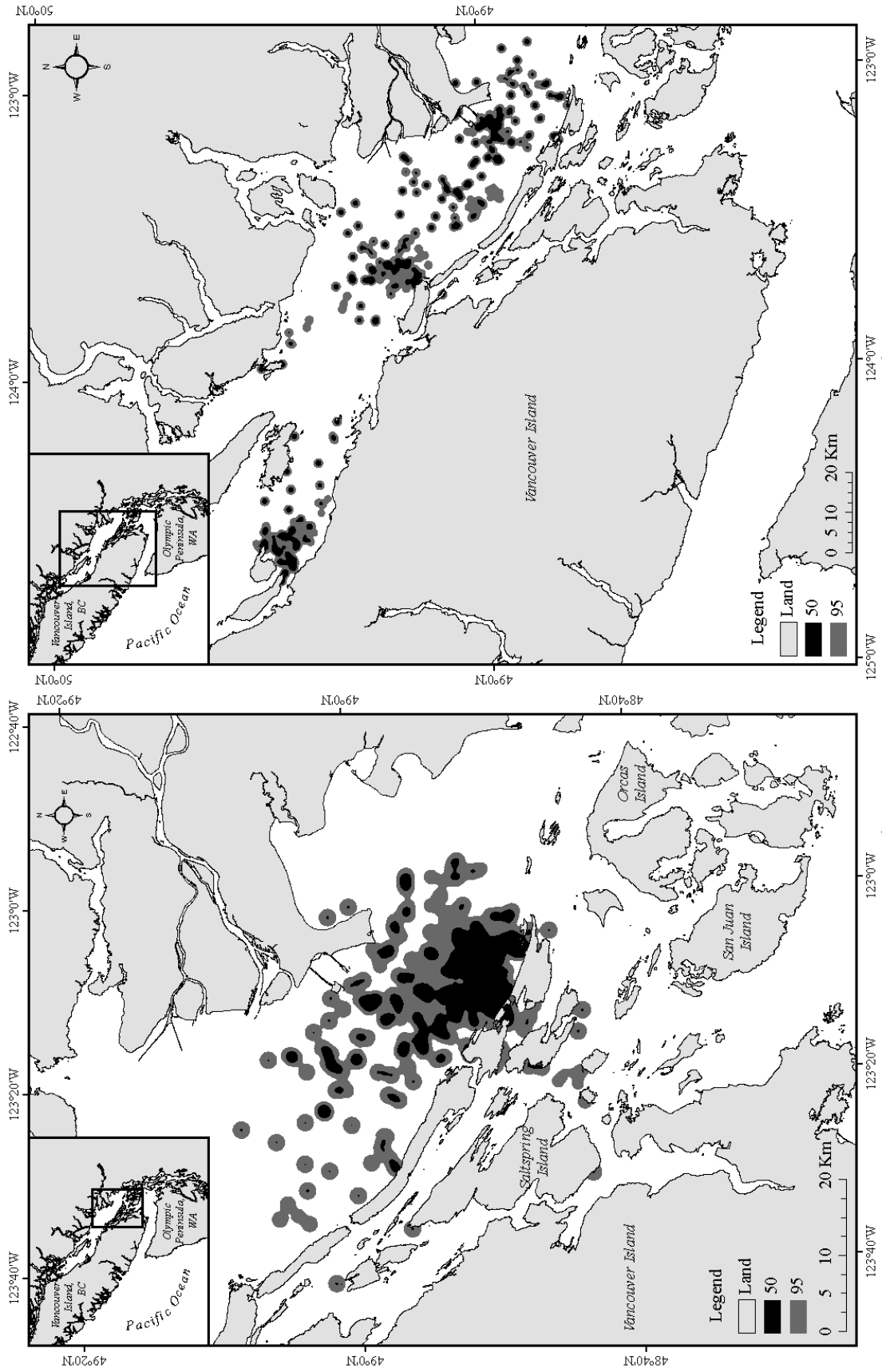
Appendix 9.10. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1712 from Padilla Bay.



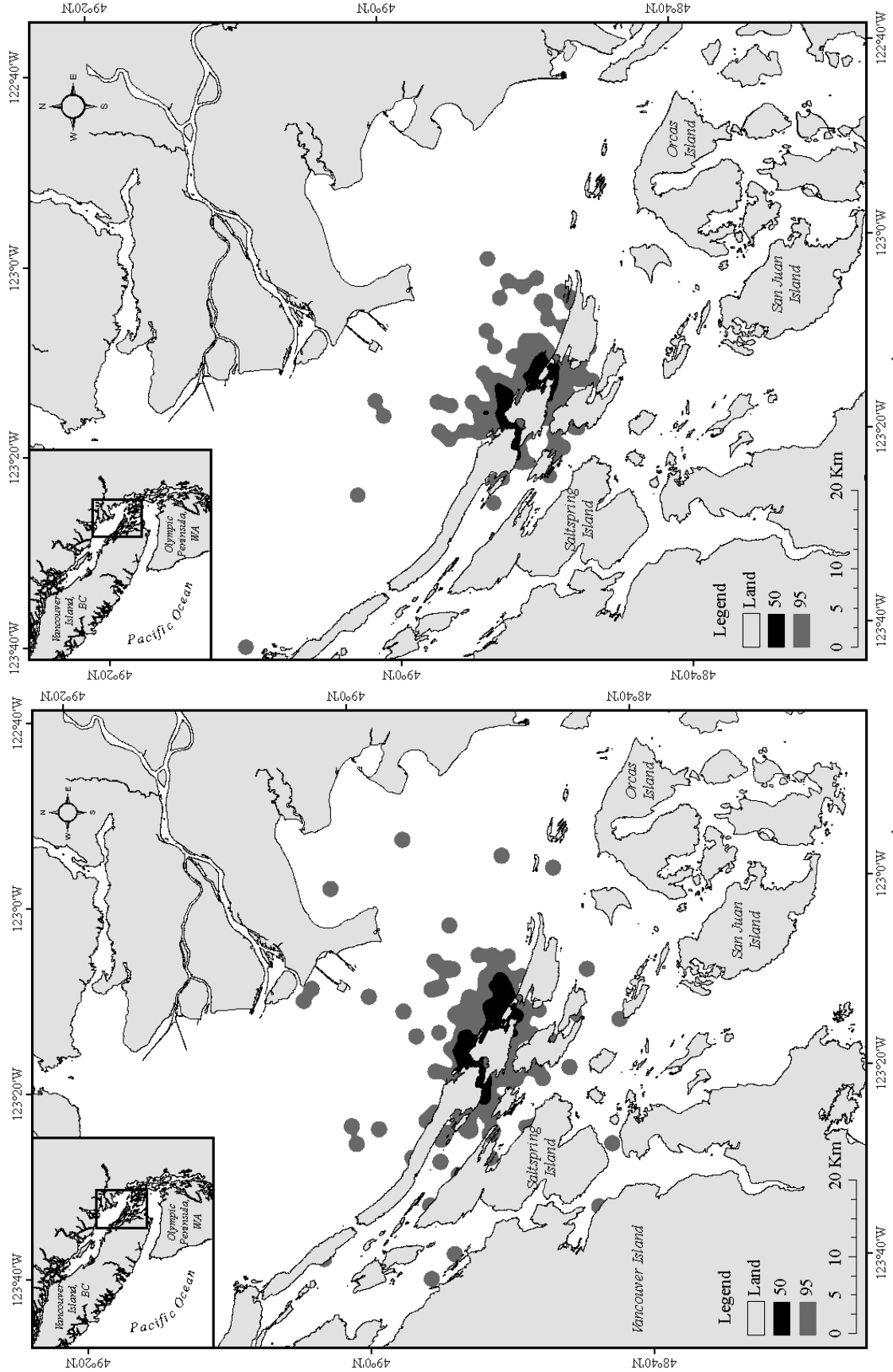
Appendix 9.11. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1713 from Padilla Bay.



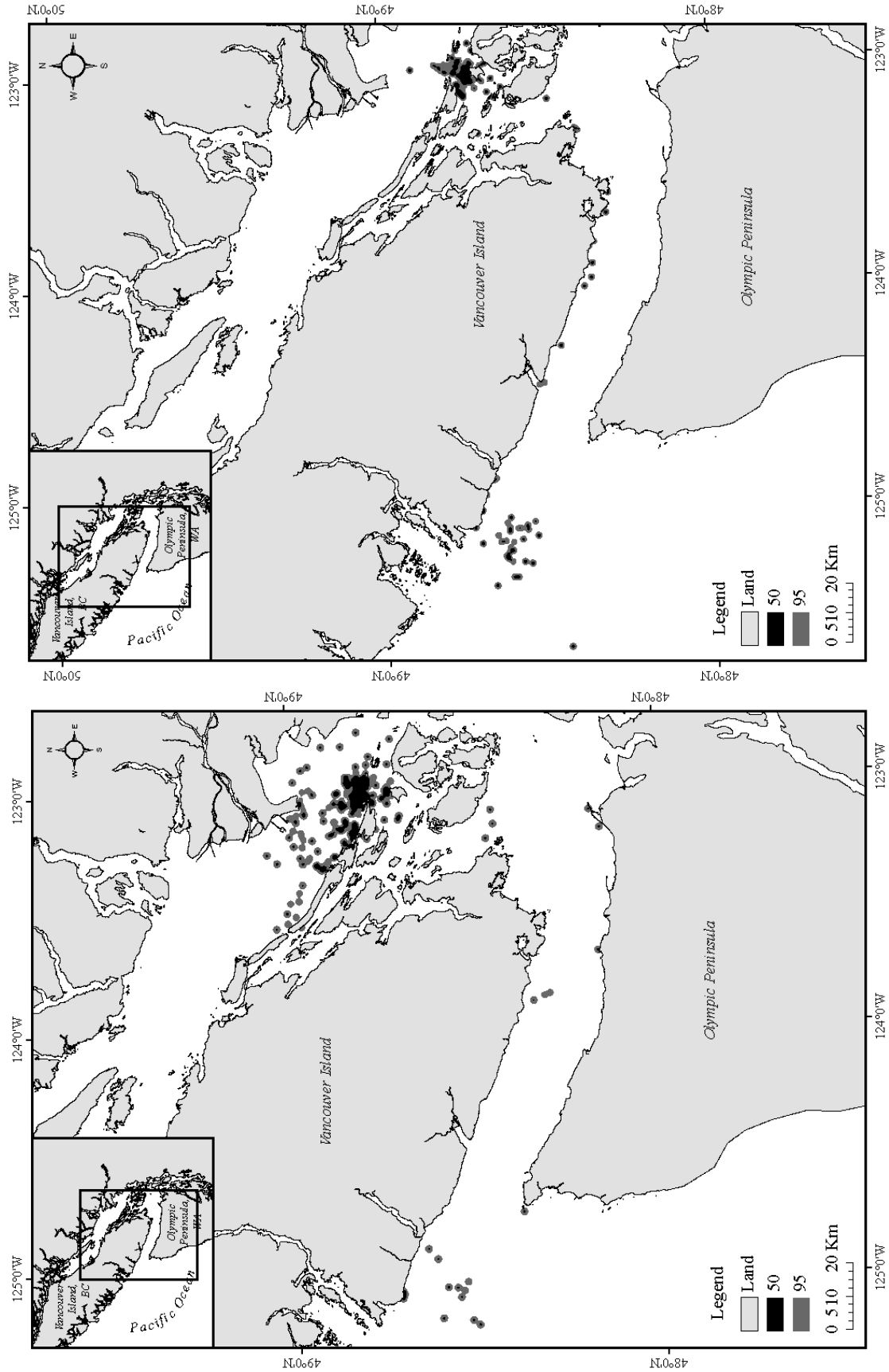
Appendix 9.12. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal Y1462 from Padilla Bay.



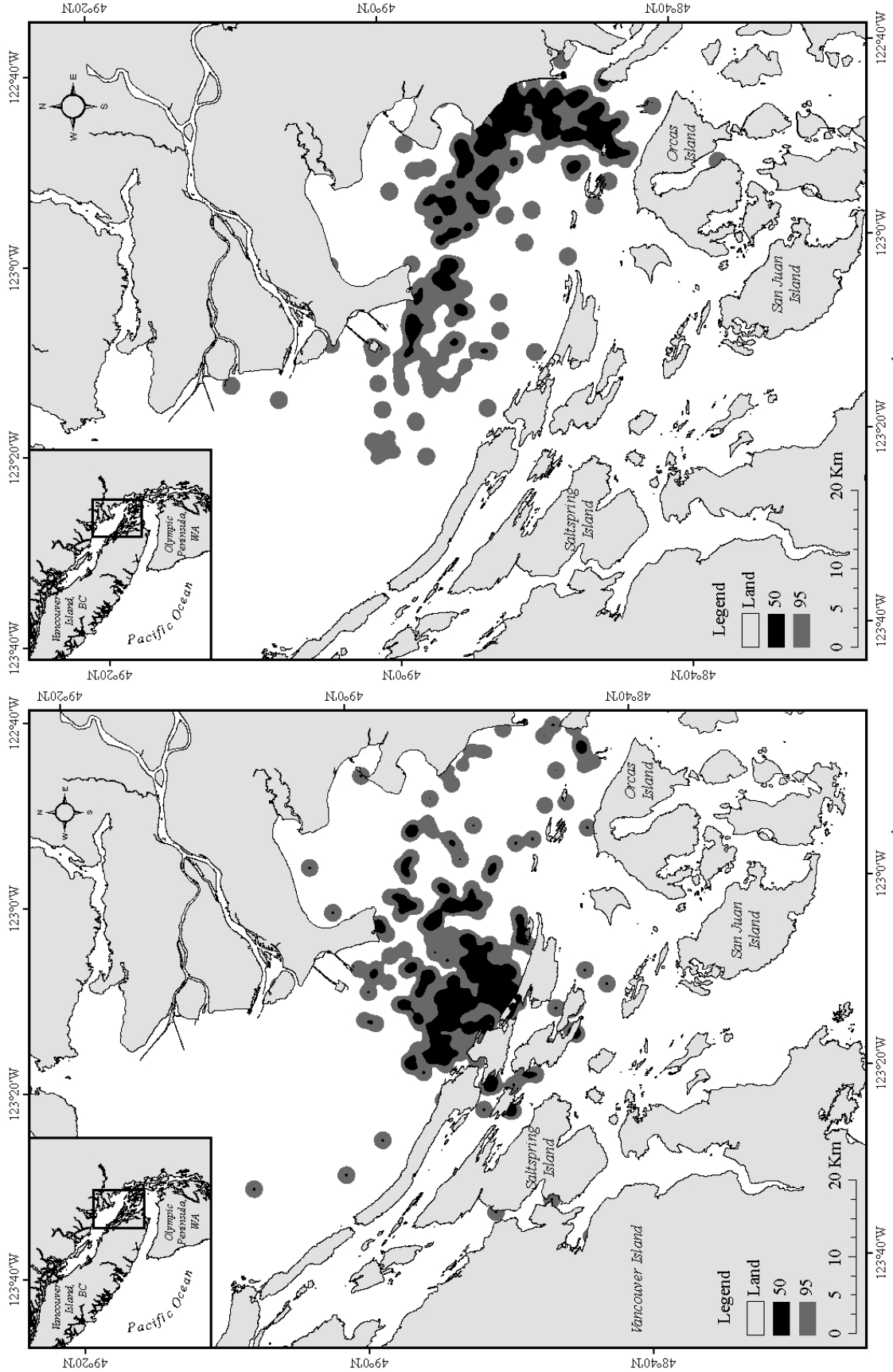
Appendix 9.13. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1711 from the Belle Chain Islets.



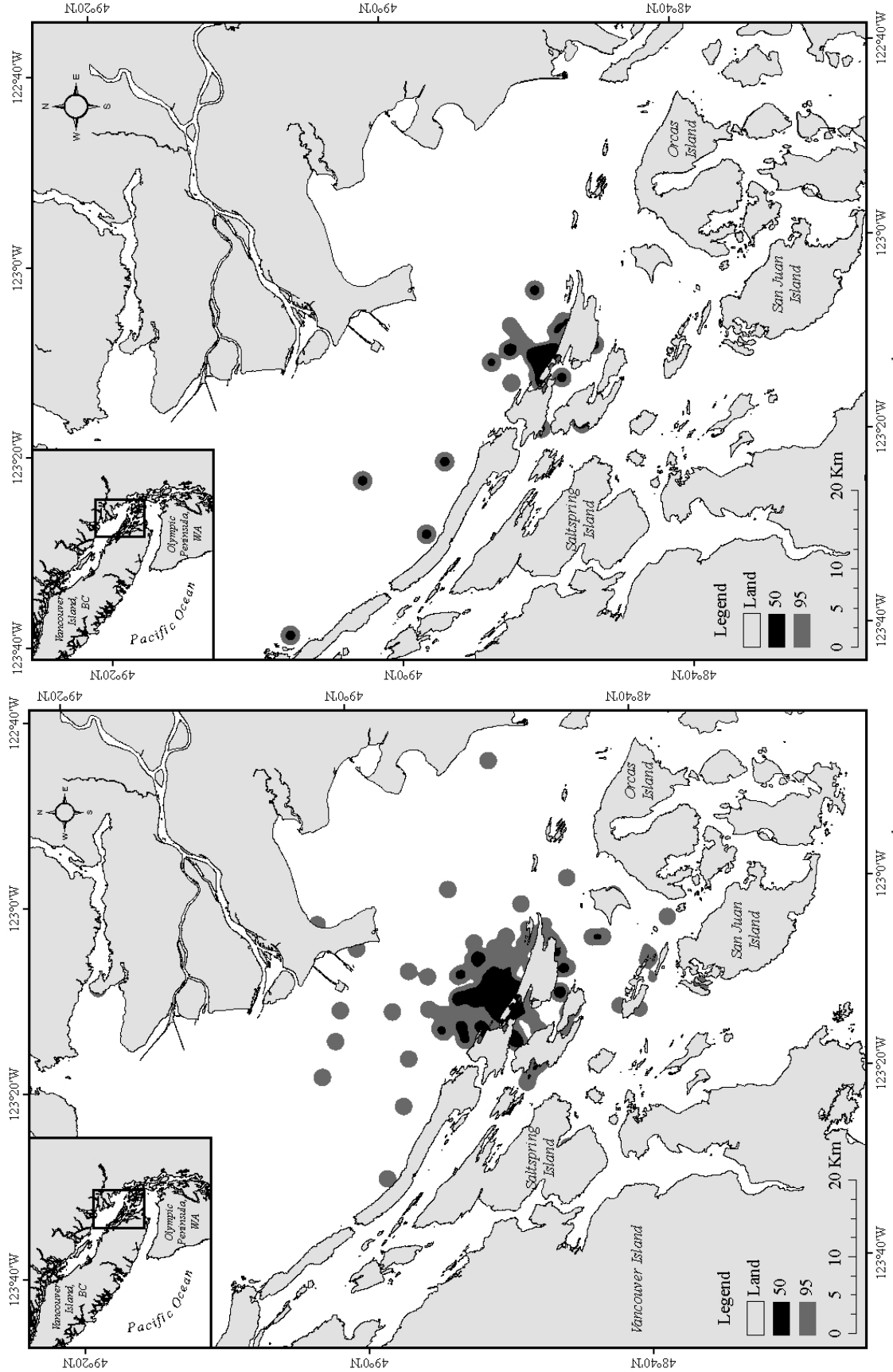
Appendix 9.14. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1706 from the Belle Chain Islets.



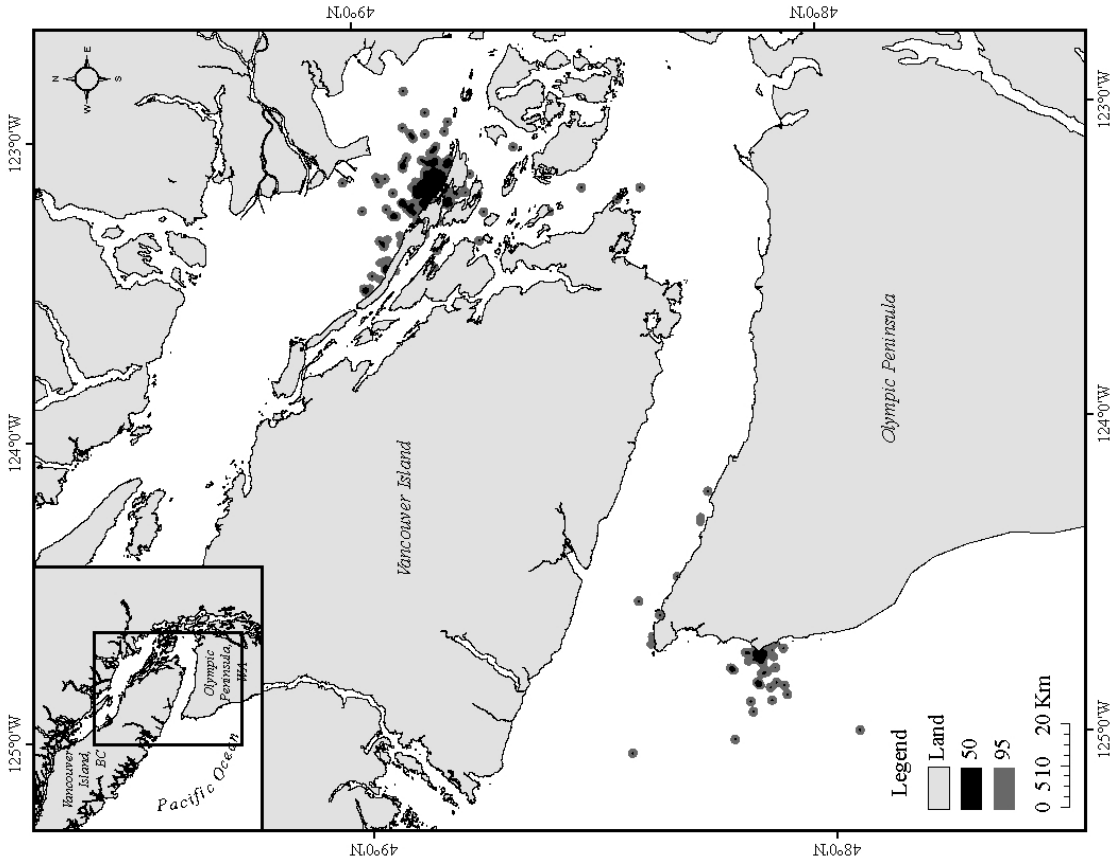
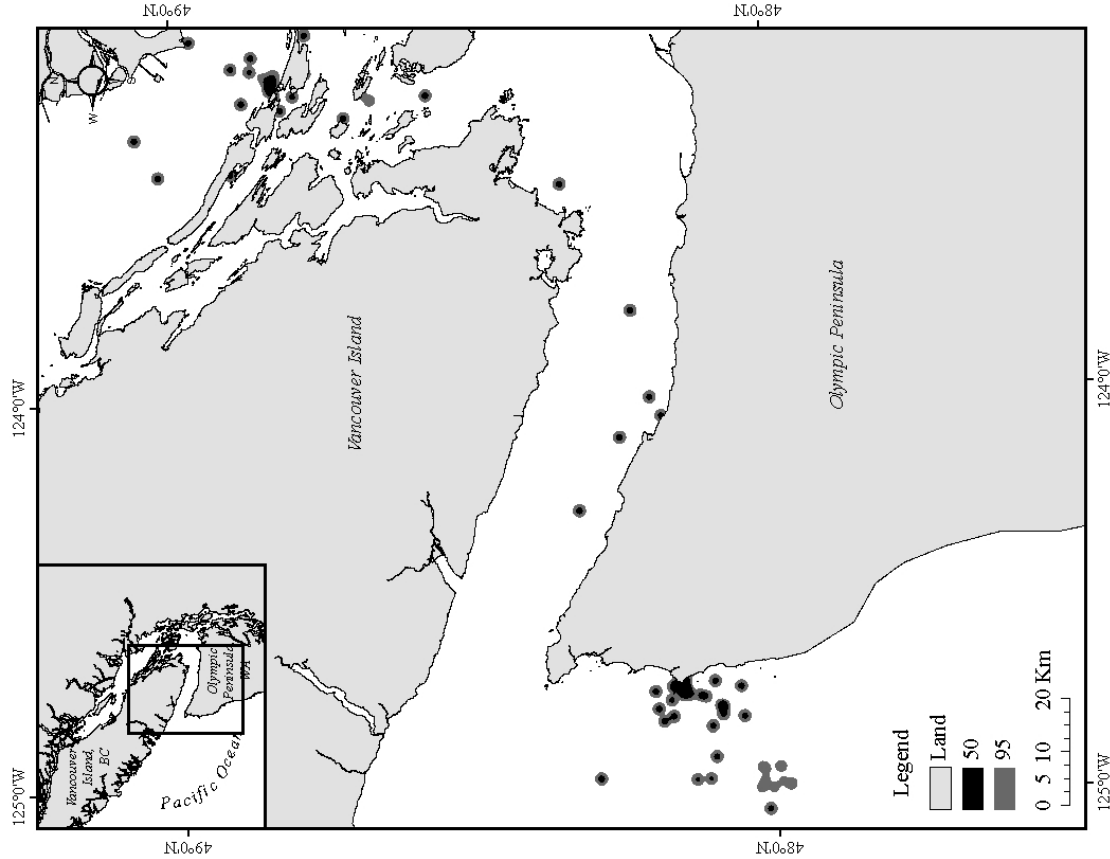
Appendix 9.15. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1707 from the Belle Chain Islets.



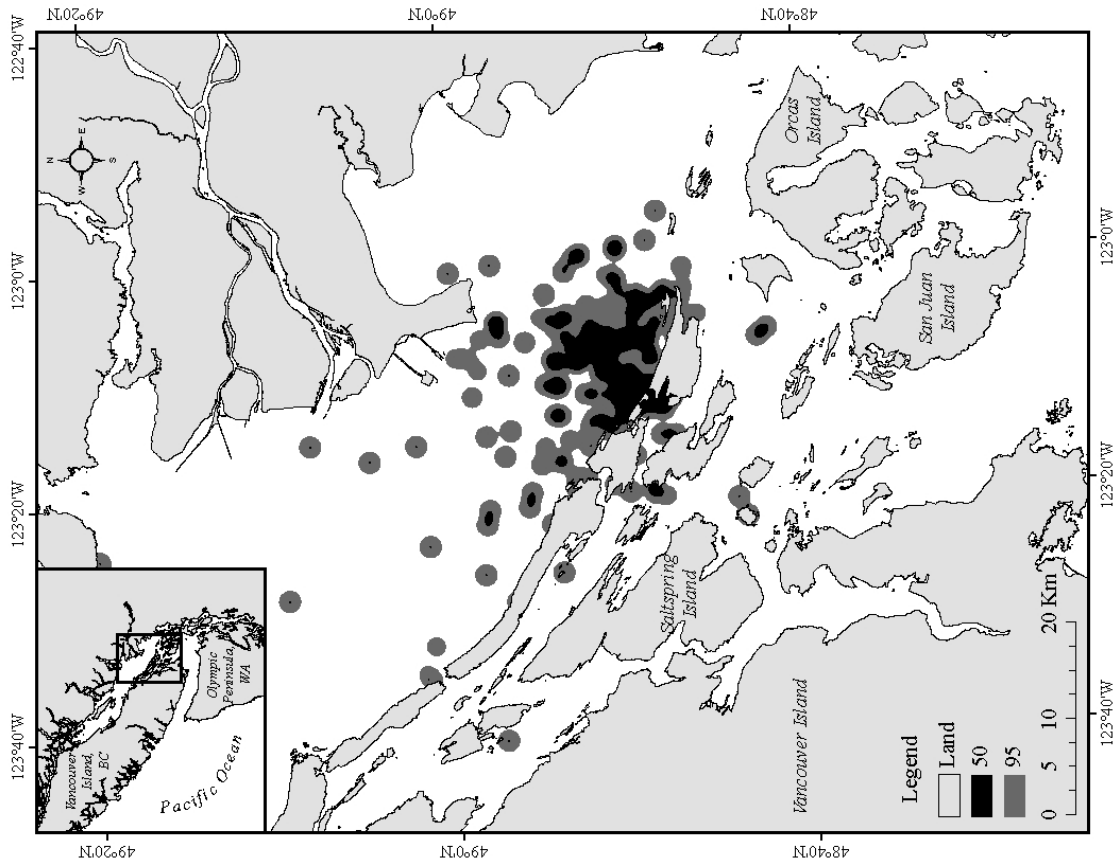
Appendix 9.16. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1709 from the Belle Chain Islets.



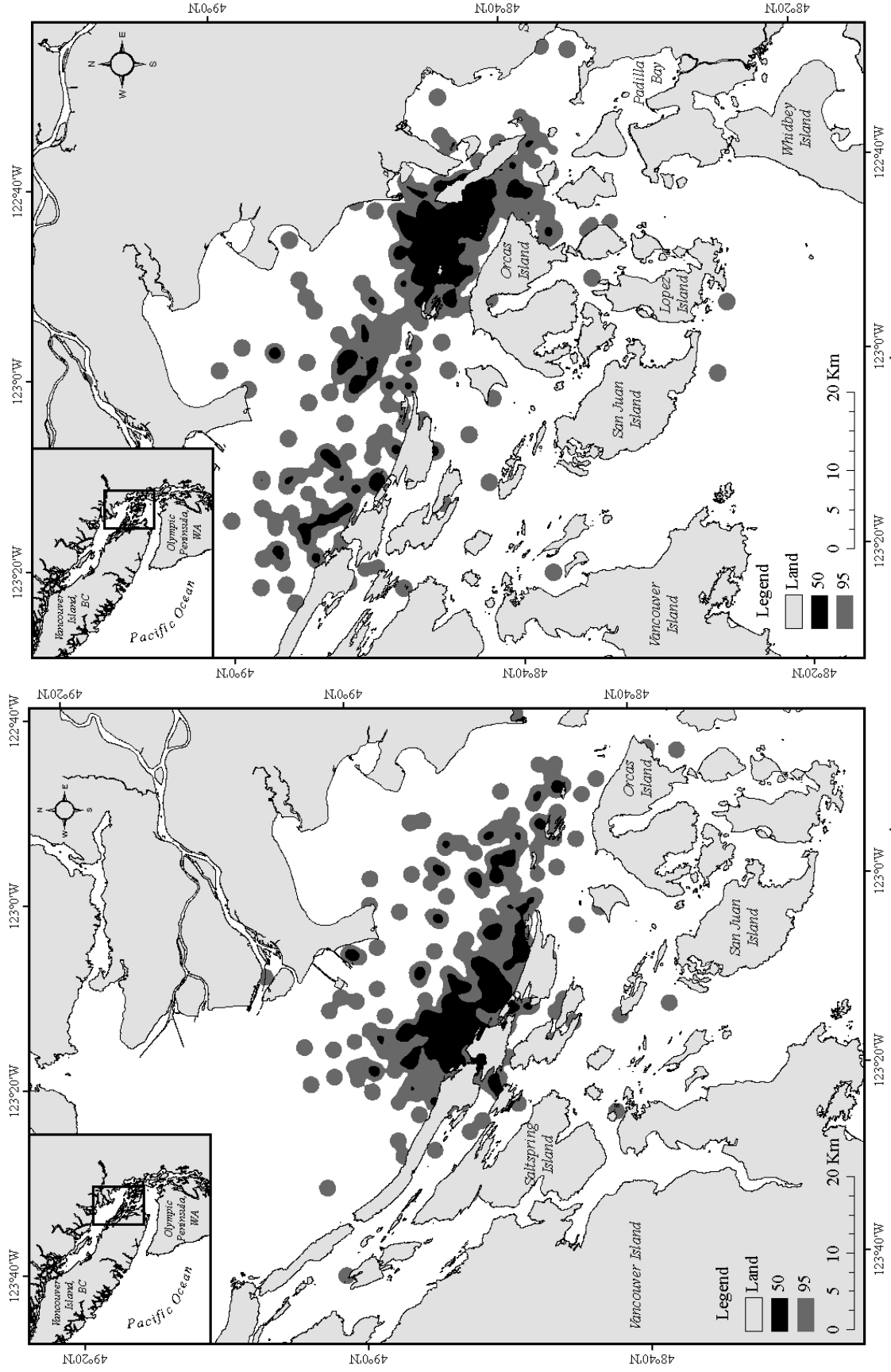
Appendix 9.17. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1702 from the Belle Chain Islets.



Appendix 9.18. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1704 from the Belle Chain Islets.



Appendix 9.19. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping for seal B1710 from the Belle Chain Islets.



Appendix 9.20. The home range (95th percentile contour) and core areas of use (50th percentile contour) during prepupping (left figure) and pupping (right figure) seasons for seal B1703 from the Belle Chain Islets.