Summer space use of Southern Resident killer whales (*Orcinus orca*) within Washington and British Columbia inshore waters

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Abstract

Summer space use of Southern Resident killer whales (*Orcinus orca*) within Washington and British Columbia inshore waters

Donna D.W. Hauser

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Marine environments are heterogeneous across a range of spatial and temporal scales thereby influencing the ecological processes that govern the use of space by organisms and populations. Often animals respond to dynamic environments and patchy resources with variations in distribution pattern. Here I consider variations in space use for an endangered population of killer whales (*Orcinus orca*) within Washington and British Columbia inshore waters. First, I consider the application of sightings by whalewatchers for spatial analyses. Next, I study the effects of temporal scale on patterns of distribution. Finally, I describe similarities and differences in space use among distinct social units called pods.

Commercial whalewatching has been used as an opportunistic data source for some studies of cetacean distribution, but there are few comprehensive analyses of the biases and assumptions implicit in such methodology. My goal was to evaluate the utility of data generated by commercial whalewatch operators using a case study of whalewatchers targeting killer whales. Within Washington, USA and British Columbia, Canada inshore waters, many whalewatch vessels work cooperatively in a small, semi-enclosed area to locate and identify well-known killer whales. To address search biases and examine the accuracy in killer whale locations and pod identifications by whalewatchers, I conducted an independent field study. The whalewatch data were 91.7% accurate in locating killer whales, but only 74.1% of those sightings were correctly identified to pod. However, identification accuracy increased to 92.6% when errors due to sub-pod mis-identification were excluded and 96.3% when early morning (before 10:30) unknown pod sightings were additionally excluded. Recommendations

for specific uses of these data are presented, and it is suggested that these data can be used for description of spatial use patterns by killer whales, with recognition of dataset limitations. Results of this study indicate that examination of biases is necessary before initiating research using data generated by commercial whalewatchers, but such data sources can be effective for specific study questions if limitations are known. Although the whalewatch situation described here is relatively unique because it targets a small, well-known population, this study presents a practical methodology for evaluating the efficiency of whalewatch vessels in detecting and identifying cetaceans. Globally, whalewatching industries are increasing in number and geographic scope, and capitalizing on these platforms of opportunity represents potentially valuable and accurate data for studies of cetacean distribution.

Understanding animal responses to the patchy, dynamic marine ecosystem is linked to our ability to quantitatively understand the variability in animal distribution along a gradient of spatial and temporal scales. Furthermore, managing the core areas of use (i.e. the most frequently used areas of animal distribution) within dynamic marine systems requires the use of a repeatable method for description of how space use varies temporally. Using the validated dataset of whalewatch sightings, I apply innovative techniques of spatial pattern analysis from the field of landscape ecology to quantify the core areas of an endangered killer whale population. Patterns of core space use for Southern Resident killer whales (SRKW) were modeled on weekly, monthly, and summer temporal scales. Results indicated that SRKW exhibit dynamic, non-random distribution patterns across all scales during the summer period. The proportion of core area used relative to total area used declined as temporal scale increased, and dispersion from common core regions (weighted maximum distance to the edge) also declined as temporal scale increased. Dispersion was highest at the monthly temporal scale. The influence of temporal scale on the highest use regions, indicated by variability among scales in average proportion and dispersion from core areas, suggested that SRKW core area use of finer temporal scales (weekly) was more unpredictable than coarser scales (seasonal). This work identifies the use and variability of SRKW core areas along a gradient of temporal scales and highlights areas that are most frequently used within the SRKW summer range. I suggest focusing

conservation and management efforts in these core areas and subsequent research to identify risk factors in these areas that ultimately may affect SRKW population viability.

Modeling distribution patterns of wide-ranging, highly dispersed marine organisms such as cetaceans becomes even more complicated due to the influence of complex social structures. I next considered differential space use among social units of SRKW. Southern Resident killer whales are comprised of three distinct matrilineally-related social units termed pods, and recent population declines have prompted conservation actions in the United States and Canada. Habitat protection, such as critical habitat designation, is a major component of recovery planning. While extensive, long-term demographic studies have provided a framework for conservation, little is known about pod-specific patterns of space use for this population. Using whalewatcher sighting information, I modeled pod-specific summer distribution and measured relative variation in the density of sightings on a uniform spatial grid. My goals were to determine similarities in space use among pod assemblages, compare pod-specific distribution and high use regions, and evaluate degree of spatial overlap and specialization among pods using novel spatial measures of geographic distribution to describe variations among pods. My results indicate that SRKW pods exhibit complex, non-uniform summer space use patterns important to habitat management schemes. Although there were regions similarly used by pods, there were also areas used almost exclusively by certain pods, indicating specialization to particular areas. Taken as a whole, my results indicate that pods displayed differential patterns of space use and, therefore, each pod may experience unique habitat conditions or exposure to potential risk factors. This result is highly relevant when considering pod-specific mortality rates and the relative contribution of each pod to overall population trends. My analyses highlight areas of conservation interest and indicate that pod-specific designation of critical habitat may be warranted.

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Introduction

This thesis has a purposefully general title, where 'space use' is an extension upon the common biological concept of 'habitat use.' Rather than considering the myriad of potential biological and physical factors defining habitat characteristics or the selection of particular habitats, I have focused on describing the patterns of distribution in space for a particular population of killer whales (*Orcinus orca*), the so-called 'Southern Residents'. Description of space use is a necessary and important preliminary step to understanding how or why Southern Resident killer whales are using key areas, particularly for application to conservation and management planning. I have focused on the summer range of Southern Residents within the inshore waters of Washington state and British Columbia for two reasons: first, the whales are very commonly sighted and many data are available within this region during the summer period; and, second, because this population has much more potential for human impacts or disturbance within this region when they are common during the summer. Thus, data are readily available for spatial analyses, and such analyses will likely have the greatest relevance to conservation of critical areas for this small population. However, the winter distribution of Southern Resident killer whales should remain an important area of continued future research, particularly because the whales are more likely to be food-limited during that period.

The overall objective of this thesis is to describe variations and patterns in the use of space among multiple temporal scales and social groups ('pods') of Southern Resident killer whales, with an emphasis on the most frequently used areas during the summer. I have approached this objective in three chapters. Chapter One presents a validation study of opportunistic sightings of killer whales by a centralized and cooperative whalewatch network. I present a potential approach to other similar validations of opportunistic cetacean sightings and also describe how I came to the conclusion that such whalewatcher sightings are suitable, given a few acknowledgments of data limitations, for spatial analyses. Chapters Two and Three proceed to use the

whalewatch sightings in detailed descriptions of Southern Resident killer whale space use. In particular, Chapter Two considers the effect of observational temporal scale on the description of distribution and the most frequently used areas. Chapter Three illustrates the similarities and differences in space use among pods, which are distinct Southern Resident killer whale social units that are cohesive and stable over time.

Each chapter has been written as a distinct and independent manuscript for current or eventual submission to different scientific journals. As a result, some information and methodology is repetitive. Some of the methods are also relatively streamlined, but I have expanded on many of my spatial modeling techniques in an extended methods appendix. I have also included an appendix detailing additional analyses that were conducted to consider the relationship of Southern Resident killer whale distribution and a few physical environmental factors (water depth, bottom slope, and distance to nearest shore). Lastly, I have included an appendix with examples of the visual maps from each temporal scale that were produced for analyses in Chapter Two. Using 1998 as an example for weekly and monthly temporal scales and all maps for the summer scale, these maps give a visual representation of the degree of variation in distribution from week to week, month to month, or summer to summer.

Chapter One

Evaluating the use of whalewatch data in determining killer whale (*Orcinus orca*) distribution patterns[1]

Introduction

Assessing distributions of highly mobile, wide ranging marine mammals presents a challenge to marine ecologists. Depending on the species or population of interest and available resources, there are a number of possible assessment methods. Standardized line-transect aerial or vessel surveys are commonly used to determine distribution of cetaceans (e.g. Griffin, 1999; Baumgartner *et al.*, 2003b; Drouot *et al.*, 2004; Zerbini *et al.*, 2004), but such methods may not be feasible for all populations due to budgetary or other restrictions. Opportunistic information, such as historical stranding or whaling catch and sighting information, have been used to illustrate seasonal patterns of distribution (e.g. Jaquet *et al.*, 1996; Gregr & Trites, 2001; Dalebout *et al.*, 2003; Clapham *et al.*, 2004; Maldini *et al.*, 2005). Similarly, sighting data from platforms of opportunity, like whalewatch vessels, have provided broad-scale information on distribution (e.g. Darling *et al.*, 1998; Weinrich *et al.*, 2000) without expensive survey effort. However, precautions must be applied in using data collected from platforms of opportunity. Specifically, Evans & Hammond (2004) have argued that to generate useful data, observers must provide correct species identification and sighting biases must be limited in space and time. Potential biases in data collected from platforms of opportunity will be minimized with more observers and broad spatial coverage. Newly developing industries for commercial whalewatching, often with highly localized spatial and temporal effort, present a chance to test the applicability of data opportunistically collected by whalewatchers for studies of cetacean distribution.

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[1] This chapter has been submitted for publication in *The Journal of Cetacean Research and Management*. Please contact D.D.W. Hauser for the most current citation and text of this chapter.

Within the semi-enclosed marine waters of Washington and British Columbia, an extensive whalewatching industry has developed for killer whales (*Orcinus orca*). Whalewatchers have established a centralized method for locating whales on a daily basis that is available to any subscriber, between mid-May and October each year. In 2004, fifty American and Canadian whalewatch companies were estimated to operate 91 vessels on a frequent basis in the region (K. Koski, pers. comm.). Centralized observers from these companies have accumulated location data for killer whales across several years, creating prospects for distribution analyses. The killer whales in this region have been researched intensively over the last four decades, and there is substantial information on their behavior, population structure and demographics. Studies have identified three distinctive, sympatric ecotypes of killer whales, known broadly as 'residents' (or fish-eating), 'transients' (or mammal-eating) and 'offshores' (Bigg *et al.*, 1987; Ford, 1990; Hoelzel & Dover, 1991; Ford *et al.*, 1998; Hoelzel *et al.*, 1998; Ford *et al.*, 2000). Every individual resident and transient killer whale can be identified using photo-identification methods focused on unique pigmentation patterns and dorsal fin morphology (Bigg *et al.*, 1987; Baird & Stacey, 1988). Although whalewatch companies will view and report sightings of any killer whale ecotype, the so-called Southern Resident killer whales are most frequently encountered. Southern Resident killer whales are particularly well-studied and every individual is separated into one of three pods of matrilinealy related families (termed J, K and L pods) (Ford *et al.*, 2000; van Ginneken *et al.*, 2004), although some argue that L pod can be subdivided into multiple pods (Hoelzel, 1993, Baird *et al*., 2005). Published identification guides, regular occurrence in the relatively benign waters of this region, and proximity to urban centers facilitate viewing opportunities and identification of Southern Resident and transient killer whales from centralized observers and whalewatch vessels. Because the Southern Resident killer whales of the coastal eastern North Pacific are such a well-studied population in which all individuals are uniquely photo-identified and reside during the summer in a region that can be surveyed easily from land, they provide a unique opportunity to study the accuracy and applicability of data garnered from

whalewatching platforms. In addition, the whalewatching data could provide detailed information on habitat use in this region. However, there has not yet been any attempt to quantify effort biases, proper identification, or limitations for distribution analyses in the data, all of which are necessary before the data are used (Evans & Hammond, 2004).

The goals of this study are to evaluate biases in whalewatch data on killer whales from inshore waters of Washington and British Columbia, and to determine the quality and utility of this platform of opportunity for multi-scale analyses of distribution patterns. A validation study of these data was designed using independent field work with land-based spotters using a systematic search and identification of killer whale pods. This systematic search overlapped in time and space with the opportunistic data from the whalewatch industry. Data from this land-based network were used to determine biases in whalewatcher effort and evaluate the applicability of whalewatch data to spatial analyses. The specific objectives were to: (1) quantify efficiency of killer whale group detection by whalewatch data; (2) quantify whalewatch data accuracy in Southern Resident killer whale identifications; (3) identify inconsistencies in resident pod identifications; (4) describe general daily patterns in the whalewatch data; and (5) provide general and region specific recommendations for the use of whalewatch data for describing cetacean distribution patterns.

Methods

Whalewatch data

Data on killer whale locations were compiled daily from May to October 2004 by monitoring reports of a commercial whalewatch sighting network, referred to hereafter as the Pager Network. Commercial whalewatch operators created this centralized spotting service to cooperatively locate whales for their customers. Searches were made daily from approximately 08:00-17:00 by at least one land-based observer near Victoria, B. C. and several Canadian and American whalewatch vessels from throughout the region (Fig. 1.1). Whale identifications (i.e. Southern Resident J,

K or L pod, transient or unidentified), time of day, location and direction of travel were provided to subscribers of the Pager Network for all sightings. Sightings of unknown pod or ecotype were reported as unidentified killer whales. Location was described via pre-established grids throughout the study region and generalized to standard 25km^2 cells for analyses (Fig. 1.2).

The Pager Network represents a potentially useful platform of opportunity for collecting data on cetacean distribution, but search effort was not randomized. Effort was often concentrated in areas where whales were thought likely to be, and areas far from ports were less frequently searched. However, vessels were traversing throughout the region from home ports multiple times a day (morning, noon, and evening), and had the opportunity to intercept any previously un-reported whales. Sightings by the Pager Network are also typically a series of related events on a given day. It is in the best interest of whalewatching companies to locate whales early in a day and maintain group follows throughout a day. The ability to locate killer whales 'early' may involve expectations of the location and direction of movement of groups at the end of the previous day or a higher likelihood of detecting larger groups. To maintain whale follows, sightings are reported approximately every 30 minutes to the Pager Network throughout a day. Although several participants cooperatively searched for whales, an observation of a whale pod was only reported by the Pager Network once per time unit as a matter of standard protocol, such that sightings of a pod were not artificially inflated by multiple reports of the same whales.

Field evaluation

An independent field study was conducted to address possible violations of key assumptions and consider biases in effort, in the context of assessing utility of the Pager Network data for distribution analyses. Mis-identification and sampling bias are two common forms of error introduced by whalewatching platforms. Mis-identification can be either fully incorrect identification or partial mis-identification. The Pager Network assumed that every individual of a pod was present during each sighting, based on the definition of pods as long-term, stable associations (Bigg *et al.*, 1990). Sampling bias is

affected by the lack of documentation on search effort. It was assumed that there was sufficient effort throughout the region during the summer such that a pod would be detected by the Pager Network during a given 24hr period if whales were anywhere within the study area (Fig. 1.1). Information was reported when whales were located, but it was rarely known when, for how long and where whalewatchers looked before locating whales. Therefore, it was difficult to determine if apparent pod distribution patterns reflect bias in searching patterns by commercial operators or true animal distribution.

To study the Pager Network data, a land-based survey was designed in order to provide a systematic spatial and temporal search for killer whales in the study region over the same time period as the Pager Network data. The survey used trained observers in a uniform search protocol. The field study examined: (a) whether pods were being mis-identified, partially or wholly, and if mis-identification was affected by time of day or location; and (b) whether pods were present in areas less commonly seen by the Pager Network but not reported due to lack of effort, and if missed sightings were related to a particular time period. The land-based study sites (Fig. 1.2) were primarily chosen to cover the maximum extent possible of the primary whalewatch operations within the inshore waters of Washington and British Columbia. To identify whether lack of sightings by whalewatchers represented low search effort or a true deficiency of sightings in a particular area, some sites were chosen where there have been few killer whale sightings in past years (D. Hauser, unpubl. data) but which are nonetheless visible, at least in part, by Pager Network participants.

From July to September 2004, the network of land-based observers scanned for killer whales on a daily basis for 10 days per month (separated into two distinct five day blocks) for comparison with the Pager Network. At each of five spatially distinct sites (Fig. 1.2), observers simultaneously conducted an approximately five minute long scan of the surrounding area every 15 minutes using 10 x 50 magnification binoculars. Visual surveying via binoculars is a standard technique for spotting and censusing killer whales (Zerbini *et al.*, in press) and, in addition, the killer whales in this region are

primarily resident killer whales which have active surface behaviors and large pod size which makes them especially visible (Ford *et al*., 2000). Killer whale scans occurred throughout a five hour period of each observation day. The start time of each daily five hour scan period was staggered such that each hour from 08:00-17:00 was sampled at least once during a five day survey period. Sighting conditions (i.e. Beaufort sea state, glare, visibility, cloud cover) were recorded for each scan, and scans were aborted if sighting conditions were poor (i.e. Beaufort state of three or more, less than 100m visibility). Killer whales were identified to pod using the total number of individuals, number of adult and adolescent males, number of calves, any visually identified animals and ecotype (i.e. resident, transient, or offshore). Additionally, Photo-ID pictures were taken when possible. Subset groups of L pod whales often occur separate from one another, so subset groups were identified to 'sub-pod' if necessary. Additionally, other cetaceans (such as porpoises) and pinnipeds were also recorded. Regular spotting of other species helped confirm that the scans were successful at sighting animals in the water even if no killer whales were sighted. Pod location was estimated based on the same grid system used by the Pager Network to facilitate comparisons. Continuous daily killer whale monitoring occurred at a sixth site, Lime Kiln State Park on San Juan Island, where a large staff of researchers and a hydrophone provided continuous daytime visual and acoustic detection of whales. Hereafter, all scan and Lime Kiln data will be referred to as the land-based survey. Lime Kiln observations will be mentioned as 'during survey' for sightings co-occurring with the scheduled surveys at other sites and 'non-survey' periods for sightings occurring during times when there was not simultaneous sampling at other survey sites. Concurrently throughout the summer, sightings by the Pager Network were recorded independently from the field surveys. Although recorded independently from one another, it should be noted that the presence of whalewatch vessels could alert land-based observers of killer whale presence. However, scans were conducted systematically and for a fixed amount of time for killer whales regardless of the presence of whalewatch vessels, and the land-based scans used

standard survey methods that are regularly used to spot killer whales in the absence of vessels.

Data analysis

Land-based surveys at each of five land-based sites consisted of a total of 150 hours, on 30 days (10 days per month July to September 2004), and comprised a total of 2,941 scans. In cases where multiple sightings of a pod occurred during a day, the first Pager Network pod sighting on a sampling day at each site was selected to avoid pseudoreplication in analyses. There were a total of 34 independent killer whale group sightings during scans, 73% of which occurred at Lime Kiln Lighthouse. Killer whales were also observed at South Pender Island and Deception Pass survey sites. All killer whale sightings occurred in excellent-good sighting conditions (100% visibility, Beaufort sea state of one or two), and mean scan length was 5.1min (0.02 standard error). Only survey scans occurring in fair sighting conditions (three kilometer or more visibility, Beaufort sea state of three or less, little or no fog or glare) were used in comparisons to the Pager Network. Sightings of killer whale groups were identified to pod(s) using current, established Pacific Northwest killer whale Photo-ID guides (Ford & Ellis, 1999; Ford *et al.*, 2000; van Ginneken *et al.*, 2004). Percentages of pod sightings by land-based observers corresponding to the Pager Network were calculated to evaluate the land-based survey's ability to detect killer whale groups. Additionally, pod sightings were compared to the corresponding day of the Pager Network data to establish the percentage of correct locations and pod identifications by the Pager Network. It should be noted that the accuracy rates for the land-based survey and Pager Network are calculated in different ways; land-based accuracy will first look for Pager Network sightings that occurred during the survey period and compare those to the actual land-based detections, whereas Pager Network accuracy first looks for the land-based sightings during the surveys and compares those to the actual Pager Network sightings. Therefore, the number of detections may be different for each comparative method.

Pager Network pod mis-identification rates were examined by comparing Pager Network and land-based pod identifications for all sightings that corresponded in time and location. Observers from the land-based survey were assumed to have 'correct' killer whale identifications to test Pager Network identification accuracy against the land-based survey. This assumption is supported by: (a) the use of trained observers or experienced local killer whale researchers for sightings, (b) an explicit emphasis on pod identification by the land-based observers as opposed to the Pager Network observers who are primarily focused on killer whale presence rather than pod identification, (c) capture of photo-ID pictures when possible, and (d) observations of proportions of calves, juveniles, adult males, and easily identified individuals for comparisons with known pod compositions. Criterion (d) was particularly useful for establishing identification when land-based sightings occurred at a distance. The percentage of correctly identified pods by the Pager Network was calculated, and likely causes of any mis-identification errors were considered. Identifications between the Pager Network and land-based surveys were compared directly by creating a matrix of concurrent sightings. The Pager Network did not distinguish among possible sub-pods, while the land-based study did. Therefore, the matrix recognized identification inconsistencies between the Pager Network and the land-based study related to sub-pod mis-identification. Descriptive statistics of all 2004 Pager Network sightings were explored to produce Pager Network data use recommendations. Timing of daily sightings was described, and variations in mean sighting time were compared among pods and ecotypes.

Results

The Pager Network searched for whales on 166 days from 19 May to 31 October 2004, resulting in a total of 2,554 killer whale sightings. Of all the 2004 Pager Network data, 74% of sightings were identified as Southern Resident killer whales, while transient and unidentified killer whales each contributed 13% of the sightings.

Killer whale detections by land-based survey

Before examining the accuracy of the Pager Network data, it is first necessary to evaluate how well our land-based survey detected killer whale groups known to be present. In this case, whales reported by the Pager Network represent killer whales known to be present. Land-based sightings were compared to the number of Pager Network sightings co-occurring during the times and locations that were surveyed from shore. A total of 27 Pager Network observations occurred within areas visible from land-based sites during survey periods. During fair or better sighting conditions, the land-based survey detected 25 of the 27 Pager Network observations, or 92.6%. No Pager Network observations were made at survey locations in poor sighting conditions during the land-based study. These results indicate that the land-based surveys had a high detection probability for killer whale groups that are reported by the Pager Network. However, it is possible that a subset of killer whale groups may exhibit highly cryptic behavior, particularly transient killer whales that neither systematic land surveys nor opportunistic boat surveys would detect. It is unlikely, in our opinion, that killer whale groups would have been missed by the land surveys during good conditions, since smaller, more cryptic cetaceans like harbor and Dall's porpoise (*Phocoena phocoena* and *Phocoenoides dalli*, respectively) and pinnipeds were routinely observed (Table 1, columns five and six). Scans were short but frequent, making it extremely unlikely that killer whale pods would pass the scan area undetected.

Killer whale presence/absence accuracy of the Pager Network

To address whether the Pager Network failed to observe detectable killer whales, killer whale sightings detected by the land-based observers were compared to killer whales detected by the Pager Network. The Pager Network detected 31 of 34 killer whale groups observed at land-based locations, or 91.7% (Table 1.1, columns three and four). All sightings occurred in fair or better sighting conditions. Therefore, the Pager Network has a high probability (>90%) of detecting groups that were also detected as present by the land-surveys. Additionally, when no killer whales were

reported by the Pager Network in an area being surveyed from land, no whales were seen during nearly 3,000 scans of the systematic land surveys either (Table 1.1, column two). Overall, this suggests that deficient or low numbers of Pager Network reports within a particular area indicates a lack of killer whales rather than a lack of Pager Network search effort in that area. This is particularly important because prior to this study, it could be assumed that presence of killer whales in the Pager Network data represented presence, but absence of killer whales could not be assumed to mean that no whales were present.

Pod identification accuracy of the Pager Network

Of the killer whale sightings that corresponded between the Pager Network and the land-based survey, the Pager Network correctly identified 74.1% (N=20 of 27) of the pods at land-based sites and Lime Kiln lighthouse (Table 1.2). Of the incorrectly identified sightings, problems associated with L sub-pods appeared to be the most common reason for incorrect identification by the Pager Network. Seventy-one percent (N=5 of 7) of incorrect pod identifications occurred when either (a) all of L pod was reported when only a sub-pod was present or (b) a sub-pod was not present during a sighting of the rest of L pod. An inability to identify pods early in the morning (before 10:30) was also associated with incorrect pod identifications (14% of incorrect identifications). Pod identification inconsistencies were further compared using a matrix with counts of identified pods from all land surveyed sites and times corresponding to Pager Network sightings (Table 1.3). When sightings that mis-identified an L sub-pod were excluded, pod identification accuracy increased to a total of 92.6% (N=25 of 27) (Table 1.2, center panel). Pods were further correctly identified a total of 96.3% (N=26 of 27) of the time when mis-identifications of both L sub-pods and early morning un-identified killer whales were excluded (Table 1.2, right panel). Although the number of sightings (N=27) is small, the high correspondence suggests that the Pager Network has a high probability of correctly identifying Southern Resident pods, given exclusions of systematic mis-identifications.

Temporal trends in Pager Network sightings

Trends in the timing of all (N=2,554) Pager Network sightings were also examined. Among all of the 2004 Pager Network data, sightings of killer whales occurred between 06:00-20:00. The majority of sightings (87.3%) occurred and maintained a relatively constant frequency level from 10:00 to 16:30 (Fig. 1.3). There was no variation in mean time of sightings among Southern Resident pods and transients, except for un-identified killer whale sightings which occurred significantly earlier than all other pods (ANOVA with Tukey's HSD post-hoc, F=80.3, p=0.000). Mean un-identified killer whale sighting time occurred at nearly 10:00 ($\bar{x}$ = 9.97, SD =1.77) and exhibited a positive skew (Fig. 1.4). Excluding un-identified killer whales, mean sighting time occurred at nearly 13:00 ($\bar{x}$ = 12.99, SD =2.00). This suggests that killer whale pod identification tends to be known by midday, and that unknown pod identifications are skewed to 10:00 and earlier.

Discussion

Implications for the use of Pager Network data for study of Southern Resident killer whale distribution

These results suggest that the Pager Network can provide accurate locations of killer whale pods, but the Pager Network's ability to correctly identify Southern Resident pods is less certain. The primary cause of pod mis-identification by the Pager Network occurred because sub-structure of L pod was not recognized by the Pager Network. Instead, they reported L sub-pods only as 'L pod' even when the entire pod was not necessarily present. Pods are considered long-term and consistent social associations among Southern Resident killer whales where individuals spend 50% or more of their time together (Bigg *et al.*, 1990). Smaller groups, often referred to as sub-pods, also occur within L pod. Although only three Southern Resident pods (J, K and L) are usually recognized, some suggest that L sub-pods are actually two recently split pods (Hoelzel, 1993; Baird *et al.*, 2005). If the sub-pod concept is dissolved and, instead, it is assumed that at least 'some' of L pod is present in a Pager Network L pod

sighting, then accuracy in Pager Network sightings improves from 74 to 93% correct. While it is recommended that future Pager Network operators distinguish among L sub-pods, this allowance in sub-pod ambiguity facilitates confidence in past Pager Network identifications. Both J and K pod follow the Bigg *et al.* (1990) definition of pods, and it can be assumed that the entire pod is present during Pager Network sightings of J or K pod.

Unknown pod identity of early morning sightings was another reason for pod mis-identification by the Pager Network. Identification is not necessarily a priority of operators, since killer whales, irrespective of pod, are their target. Some animals are very distinctive and easily identified by experienced observers. Although published identification guides are available and used by whalewatchers, vessels cannot be assumed to have equal identification ability. Unknown identity killer whale sightings occurred significantly earlier in the day than all Southern Resident pod and transient sightings. These patterns likely represent the search strategy of whalewatch operators. Operators search for killer whales until they are located in the morning, and an increasing number of operators, and thus number of experienced observers, searches for whales as the day proceeds. There appears to be a short transition period before pod identity is determined and unknown killer whale sightings decline after 10:00. Whalewatchers often locate whales in the morning and consistently follow them throughout a day, thereby maintaining recognition of pod identity and location. This behavior promotes the whalewatcher's ability to locate and maintain relatively high confidence in pod identity after 10:00. The majority of sightings occur from 10:30-16:00, and during this time period, sighting frequency remains relatively constant before abruptly discontinuing after 16:00. This suggests that sighting effort throughout a day was consistent and stable among pods from mid-morning to afternoon and supports the conclusion that pod identity is typically determined by mid-morning. If the previous allowances for L sub-pods are accepted and unknown identity sightings before 10:30 are also excluded, the Pager Network identification accuracy increases to 96%.

To evaluate whether the observed killer whale distribution reflects bias in whalewatch operator search patterns, areas where sightings are rare must be sampled. In 166 days of surveys, no killer whales were sighted during the land-based surveys from Clover Point, Fort Ebey, or Olympic Peninsula sites, and there were few sighted at Deception Pass. During the same periods, no killer whales were reported by the Pager Network for the grids which were searched from these sites. The possibility that whalewatch operators still miss killer whales in these areas where sightings are infrequent cannot be eliminated since we have few to no land sightings to compare. However, hundreds of scans were conducted at each site and no killer whales were ever observed, nor reported by the Pager Network. With nearly 100 vessels originating from over 22 ports throughout the study region, the area is transited by whalewatchers throughout the day. Therefore, it is suggested that there is sufficient effort throughout the region during the summer that a pod would be detected by the Pager Network during a 10:30-16:00 period if whales were anywhere within the study area.

Southern Resident sightings occurred in the 2004 Pager Network data significantly more frequently than transient or unidentified killer whales. This pattern can be attributed primarily to the higher likelihood of sighting residents than transients (Ford *et al.*, 2000). Total transient population size within this region is unknown and is assumed to be in the low hundreds, and there is a protracted resighting interval (up to ten years) for many individuals (Baird & Dill, 1995; Baird, 2001). Additionally, the divergent foraging strategies of transients and residents contribute to overall likelihood of sighting animals. Average transient pod size in this region is two individuals, and ranges from one to four individuals (Baird & Dill, 1996), while Southern Resident pod sizes range from 11 individuals in an L sub-pod to all 91 individuals when the pods assemble as a single group (van Ginnekan *et al.*, 2004). Larger group size presumably contributes to greater sighting probability of residents, but transients are also less vocal, have more erratic surface behavior and are more difficult to detect at the surface than their resident counterparts (Ford and Ellis, 2004). Therefore, it is expected that the Pager Network is more likely to miss sightings of transients than residents, and care

should be taken in future research employing Pager Network transient sightings. Furthermore, variation in ecotype behavior, with residents often exhibiting more noticeable surface behaviors and occurring in large groups (typically greater than 20 individuals among Southern Residents), promotes sightability of Southern Residents. Poor weather could reduce sightability for both land and whalewatch observers, but was not a factor considered in this study since all land-based observations occurred in fair or better conditions.

These results suggest that the Pager Network can be used for future research of killer whale distribution and habitat analyses within this region, particularly for identified Southern Resident sightings. The Pager Network was able to detect whales within the region, and a lack of Pager Network detection in an area was assumed to be due to a true lack of whales instead of poor effort. However, it is recommended that researchers recognize the limitations, biases and assumptions associated with these data. Specifically, it is proposed that researchers may rely on Pager Network pod identifications given three conditions: (a) awareness that a small (<5%) degree of error due to unambiguously incorrect pod identifications exists; (b) assumption that a Pager Network L-pod sighting does not necessarily represent all of L-pod but rather may represent only one of its sub-pods; and (c) restriction of analyses of Pager Network data to sightings occurring between 10:30 and 16:00 when there is consistent search effort and pod identity is more likely already known. Finally, future studies should not extrapolate these results beyond the region bounded by the extent of the land-based survey sites.

Broader Implications

Globally, whalewatching is a growing enterprise, and research opportunities using whalewatching as a platform are likely to increase. In 1998, over nine million participants were involved in whalewatching in 87 countries and territories, and the number of participants was growing by an average of 12% per year (Hoyt, 2001). Although ecological tourism has been regarded by some as a possible disturbance source to cetacean populations, it is beyond the scope of this study to examine potential

impacts of whalewatching. If managed responsibly, ecological tourism may also have local economic and educational benefits. A more dispassionate analysis of such activities seems appropriate, and researchers should consider whether ecological tourism can be utilized to gather technical data of value in understanding, conserving and managing target species. Using whalewatching as an avenue of research represents a more affordable approach to distribution studies, which traditionally require labor and cost intensive line transect, aerial or vessel surveys.

In this case, whalewatching companies have a high level of self-interest in maintaining a sighting network. The Pager Network is a somewhat unique situation where whalewatchers target a small, well-known population of a single species in a very localized, semi-enclosed area. However, as shown with the Pager Network, such data can be accurate enough to be useful for describing whale distribution. Particularly in developing nations with expanding ecotourism endeavors, whalewatch platforms may present a cost-effective method to accumulate basic information as a segue into more intensive research. There is clearly a need for testing data quality from platforms of opportunity, as well as acknowledgment of data limitations and biases before such research is pursued. These should be tested on a regular basis if long-term use of platforms of opportunity is planned. Although there may be situation-specific considerations for each whalewatching platform, this research provides an example of possible approaches to validation. It is proposed that data provided by commercial whale operations can be applied to spatial analyses, with proper evaluation and understanding of limitations.

Table 1.1. Information on effort (number of scans) at each site, the Pager Network's accuracy in correctly locating killer whales (indicated as the number of land detections matched by the Pager and percent accuracy) and the number of non-killer whale marine mammal observations (small cetacean and pinniped). Sites are Clover Point, near Victoria, BC (CP), Deception Pass State Park, WA (DP), Fort Ebey State Park on Whidbey Island, WA (FE), Lime Kiln State Park on San Juan Island, WA (LK) during the survey periods and non-survey periods, Dungeness National Wildlife Refuge on the Olympic Peninsula, WA (OP) and Higg's Point on South Pender Island, BC (SPI). Lime Kiln State Park was under continuous surveillance during Pager Network operations via acoustic and visual detection, but did not record non-killer whale sightings.

	Land-based effort	Pager Network accuracy		Non-killer whale marine mammal observations	
Survey site	Number of land-based scans	Number of land-based observations	Number of land-based observations detected by Pager Network (% accuracy)	Number of small cetacean observations	Number of pinniped observations
CP	474	0	0	9	75
DP	631	2	1 (50%)	309	255
FE	605	0	0	268	89
OP	599	0	0	11	95
SPI	632	8	8 (100%)	173	472
LK	continuous	18	16 (88.9%)	N/A	N/A
LK non-survey	continuous	6	6 (100%)	N/A	N/A
Total	2941	34	31 (91.7)	770	986

Table 1.2. Information on the Pager Network's accuracy to correctly identify Southern Resident killer whale pods at survey locations, including Lime Kiln State Park during and not during land-based survey periods, based on correctly located sightings as listed in Table 1.1. South Pender Island and Deception Pass sites were pooled for the non-Lime Kiln survey sites. Counts and relative percent accuracy are shown for all observations (left panel), those excluding errors due to mis-identification of an L sub-pod (center panel) and for all excluding L sub-pod and early morning (before 10:30) errors (right panel).

	All Observations			**Excluding L subpod Errors**			**Excluding L subpod & early morning errors**		
Observation Period	**Total**	**# Correct**	**Percent**	**Total**	**# Correct**	**Percent**	**Total**	**# Correct**	**Percent**
Non Lime Kiln survey	5	4	80.0	5	5	100	5	5	100
Lime Kiln: survey	16	13	81	16	15	93.8	16	16	100
Lime Kiln: non-surveys	6	3	50.0	6	5	83.3	6	5	83.3
Overall	27	20	74.1	27	25	92.6	27	26	96.3

Table 1.3. Matrix showing counts of killer whale identifications by pod (bold) for the land-based survey (correct identification) and Pager Network (test identification). Pods observed traveling together are noted with double (e.g. 'JK') or triple (e.g. 'JKL') pod designations. L sub-pod (called L12s) identification errors are shown. Survey information, listed horizontally, includes sightings corresponding to the Pager Network from all surveyed sites and Lime Kiln during survey & non-survey periods. The Pager Network sightings are listed vertically. Correct identification correspondence between the survey and Pager Network should fall along the highlighted horizontal.

		SURVEY											
	Pod	**J**	**JK**	**JKL**	**JL**	**K**	**KL**	**L**	**L12s**	**JKL12s**	**transient**	**Un-ID**	**SUM**
PAGER NETWORK	**J**	0	0	0	0	0	0	0	0	0	0	0	0
	JK	0	**7**	0	0	**1**	0	0	0	**1**	0	0	9
	JKL	0	0	**8**	0	0	0	0	0	**1**	0	0	9
	JL	0	0	0	0	0	0	0	0	0	0	0	0
	K	0	0	0	0	0	0	0	0	0	0	0	0
	KL	0	0	0	0	0	0	0	0	0	0	0	0
	L	0	0	0	0	0	0	**2**	**3**	0	0	0	5
	L12s	0	0	0	0	0	0	0	0	0	0	0	0
	JKL12s	0	0	0	0	0	0	0	0	0	0	0	0
	transient	0	0	0	0	0	0	0	0	0	**3**	0	3
	Un-ID	0	0	**1**	0	0	0	0	0	0	0	0	1
	SUM	0	7	9	0	1	0	2	3	2	3	0	27

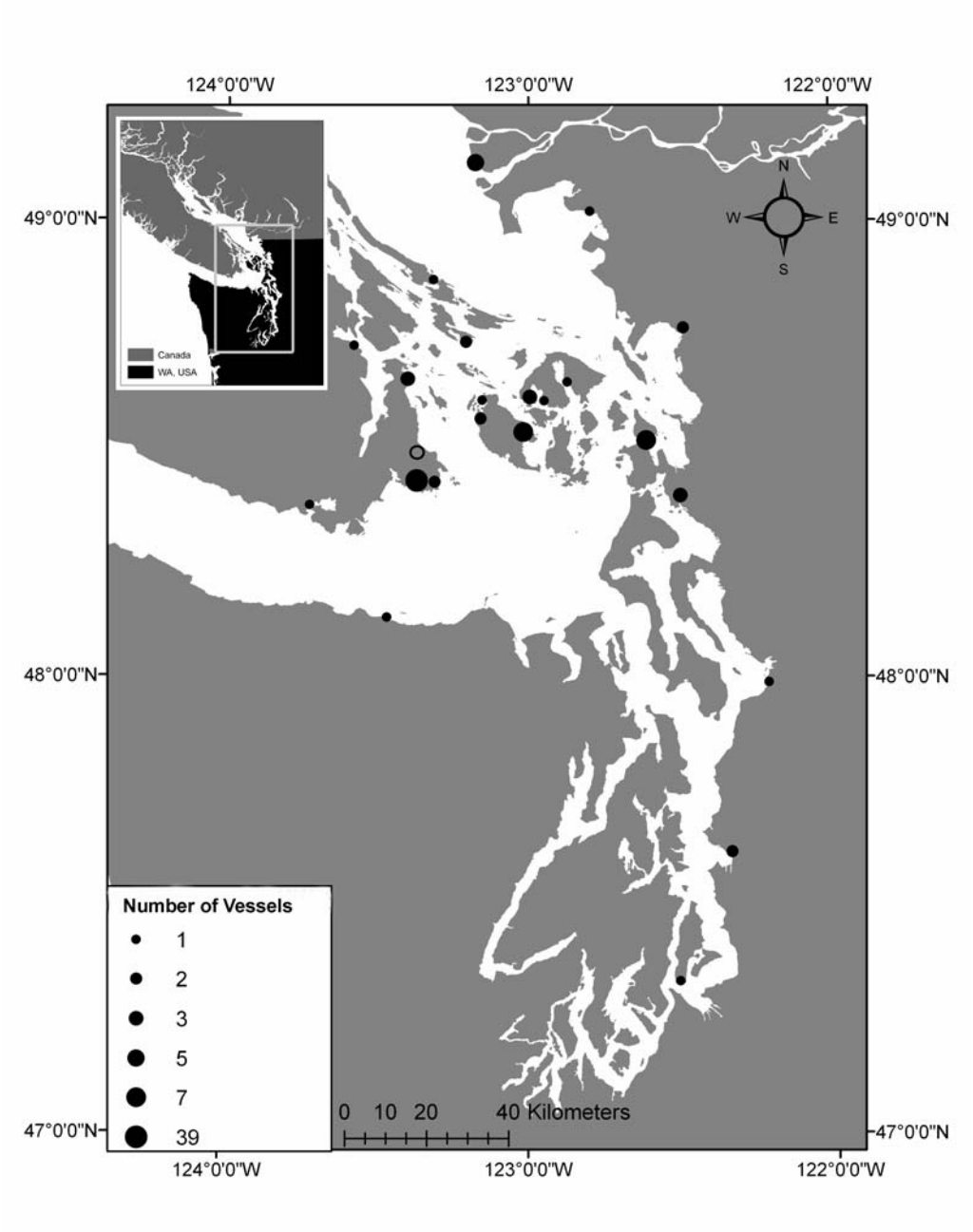

Figure 1.1. Map of Washington and British Columbia 2004 whalewatch ports. Solid circle diameter indicates the total number of vessels originating from each port (data courtesy Kari Koski, The Whale Museum Soundwatch Program), and the open circle signifies the location of the land-based Pager Network observer. Vessels transit throughout the region and to/from their ports on a daily basis, contributing sightings to the Pager Network.

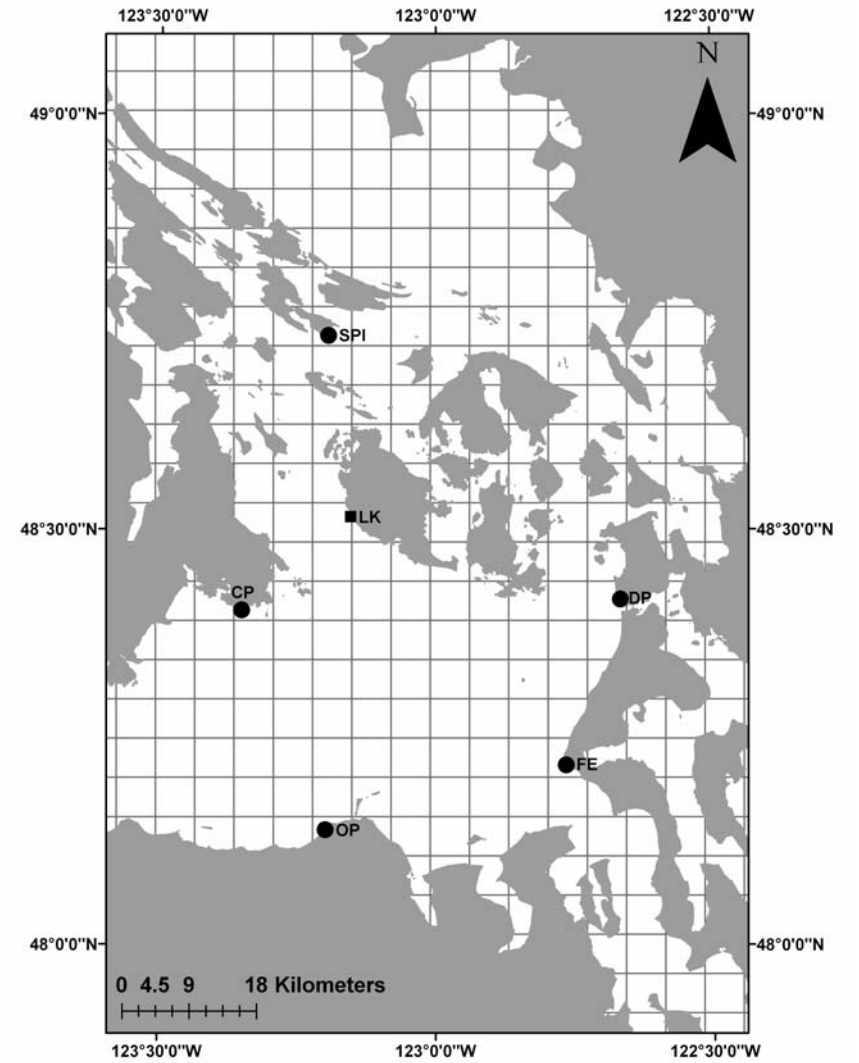

Figure 1.2. Detail map of study area and standardized grids indicating survey sites referenced in the text. Solid circles represent sites that were surveyed according to the study schedule and the square represents Lime Kiln State Park (LK) that was continuously surveyed during the day (i.e. constant surveillance for killer whales). Study sites include Clover Point near Victoria, BC (CP), Deception Pass State Park, WA (DP), Fort Ebey State Park on Whidbey Island, WA (FE), Lime Kiln State Park on San Juan Island, WA (LK), Dungeness National Wildlife Refuge on the Olympic Peninsula, WA (OP) and Higg's Point on South Pender Island, BC (SPI).

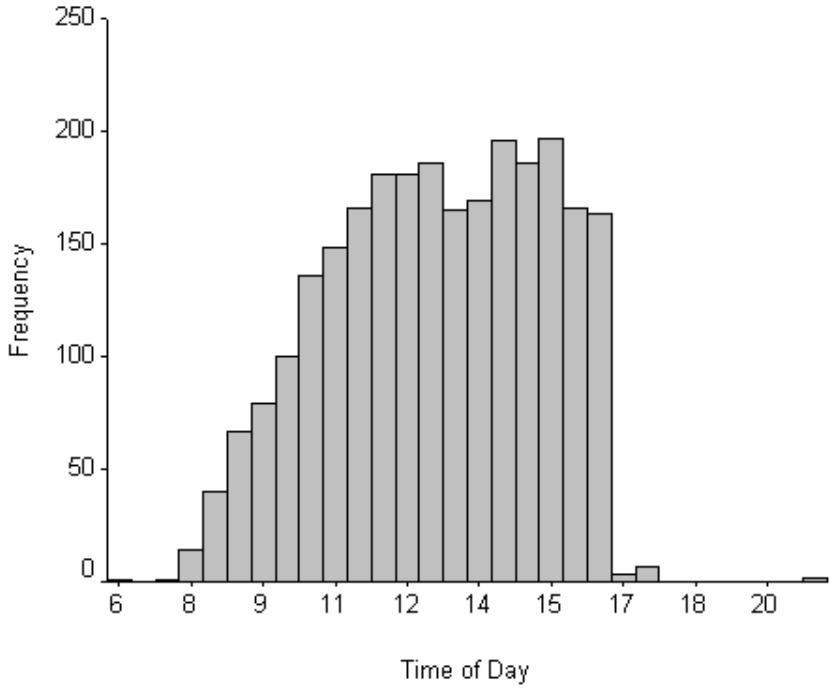

Figure 1.3. Frequency histogram of all Pager Network killer whale sightings during 2004 ($\bar{x}$=12.6, *SD*=2.22, N=2,554).

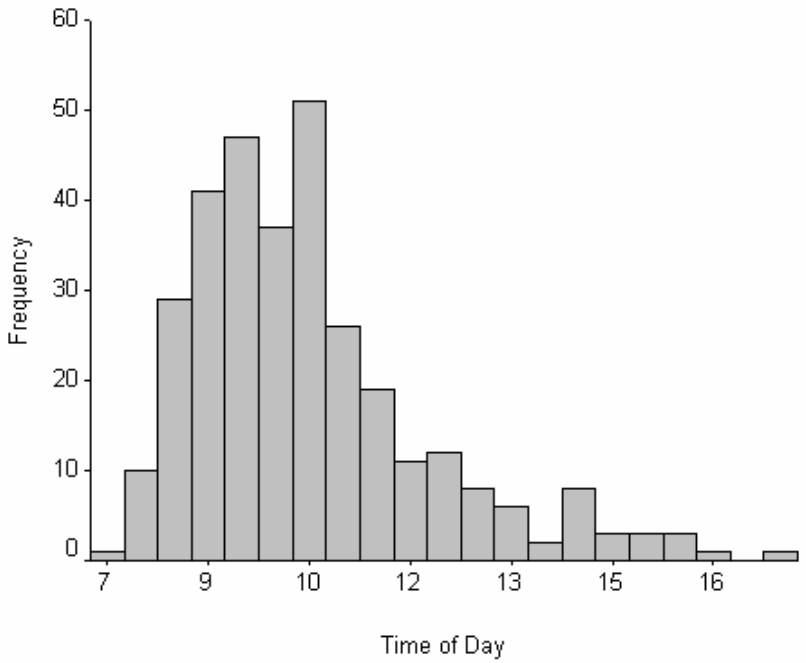

Figure 1.4. Frequency histogram of all 2004 Pager Network sightings listed as unidentified killer whales ($\bar{x}$=9.97, *SD*=1.77, N=319).

Chapter Two

Linking spatial patterns of core area use with temporal scale for an endangered killer whale (*Orcinus orca*) population

Introduction

The importance of pattern and scale is a central tenant of ecology (Levin, 1992). Scale, or the indexing of a variable in a particular spatial and temporal context (Schneider, 2001), often affects the interpretation of ecological patterns. Study of ecological systems depends on the perception of spatial and temporal scales, and a single scale cannot encompass the range of variability within a system. Basic aspects of population ecology, such as animal distribution and space use, are thus affected by the scale of observation as animals respond to a broad array of scales (Wiens, 1989). Since the mechanisms driving animal movement and distribution are likely scale dependent, a wide range of spatial and temporal scales should be considered when describing how animals use space.

Marine environments exemplify ecosystems that are heterogeneous in time and space, and marine organisms, from zooplankton to large apex predators, are known to alter distributions in response to these patchy, dynamic conditions across multiple scales (e.g. Stommel, 1963; Haury *et al.*, 1978; Schneider & Duffy, 1985; Rose & Leggett, 1990). The ability to respond to changing environments by shifting distribution or movement patterns has been suggested as an adaptation to environmental heterogeneity to produce more viable life histories (Ferguson *et al.*, 1998; Laidre *et al.*, 2004a). Although the importance of temporal scale in describing space use patterns and core areas is widely recognized by ecologists, analyses of animal distribution at multiple scales are relatively rare for wide-ranging marine wildlife with low reproductive rates and high body mass like cetaceans (Schneider, 1994; Jaquet, 1996). Of those studies that investigate the importance of scale, most focus on spatial scale (e.g. Jaquet *et al.*, 1996;

Whitehead, 1996; Jaquet & Gendron, 2002) and few examine the effects of temporal scale (e.g. Whitehead, 1996; Baumgartner *et al.*, 2003a).

Many cetacean populations are of conservation concern, and management efforts for cetaceans are increasingly protecting key areas and habitats (Hooker *et al.*, 1999; Ingram & Rogan, 2002; Wilson *et al.*, 2004). Thus, the importance of scale cannot be disconnected from management and natural resource conservation. Management strategies, such as the determination of critical habitats for endangered cetacean conservation, necessitate knowledge of variability in distribution. Accordingly, it is unlikely that a single scale of management can encapsulate the range of ecological phenomena important to wide-ranging organisms. When solely considering spatial distribution, habitat management may fail to incorporate temporal processes of cetacean distribution and movements (Wilson *et al.*, 2004). Ultimately, the ability to manage key areas at critical times may be limited and yield less than sufficient protection for population sustainability.

In the case of the so-called Southern Resident killer whales (*Orcinus orca*), recent population declines have led to a variety of conservation listings, including Endangered Species listing under the U.S. Endangered Species Act and Canada's Species at Risk Act (Baird, 2001; Krahn *et al.*, 2004). Protection of key areas, or 'critical habitat', is a component of each management action. Over three decades of research within inshore waters of Washington, USA and British Columbia, Canada has provided much knowledge on individual and population biology of killer whales. Three distinctive, sympatric ecotypes of killer whales have been identified as fish-eating 'residents', mammal-eating 'transients', and 'offshores' (Bigg *et al.*, 1987; Ford, 1990; Hoelzel & Dover, 1991; Ford *et al.*, 1998; Hoelzel *et al.*, 1998; Ford *et al.*, 2000). Furthermore, every individual can be identified from unique pigmentation patterns and dorsal fin morphology using photo-identification methods (Bigg *et al.*, 1987; Baird & Stacey, 1988), facilitating analyses of distribution patterns of individuals and groups.

While extensive long-term knowledge of population status and demographics exists for the fish-eating Southern Resident killer whales (SRKW), strikingly little is

known about any consistent patterns of spatial and temporal variability in key areas used by this population. Winter distribution of SRKW is poorly understood, but their summer (May to September) range is primarily restricted to the semi-enclosed inshore waters of Washington, USA and British Columbia, Canada (Osborne, 1999; Ford *et al.*, 2000). Summer distribution of SRKW is primarily understood through the combined observations of a number of researchers and whalewatch operators over the last 30 years. SRKW are easily accessed by observers due to their regular occurrence in the relatively calm waters of this region, appearance in near-shore waters, and proximity to large cities. This availability has resulted in the development of an extensive network of whalewatch operators who work collaboratively to locate and report whale observations on a daily basis. We utilize this unique dataset to investigate the influence of temporal scale on our understanding of spatial distribution of SRKW. Differences in SRKW use of core areas (i.e. most frequently used regions) and dispersion from those core areas among temporal scales can provide a measure of variability of core regions within their summer range, offer a spatially-explicit description of core space variation, and highlight locations for future research on potential factors impacting this population.

The overall goal of this study was to identify and quantify core area use for Southern Resident killer whales and quantify temporal variation in the use of these areas. Applying concepts from landscape ecology and spatial pattern analysis, I used a relatively new approach to describe how spatial distribution of this endangered population changes across multiple temporal scales, particularly in the use of core areas. My specific objectives were to: (1) quantify the amount of and distance, or ‘dispersion’, from SRKW core areas along a gradient of temporal scales (i.e. week, month, summer season, and all data pooled); (2) quantify variability in core area use at each temporal scale; and (3) identify the locations within the SRKW summer range that can be considered core areas across all temporal scales. I also considered how an applied understanding of the effects of temporal scale may affect management of key areas.

Methods

Location Data

Daily locations of SRKW were reported from May to September 1996-2001 by a centralized spotting network of commercial whalewatchers working cooperatively to locate whales for their customers (Chapter One). Operators searched throughout the study region for killer whales from approximately 08:00-17:00 using both U.S. and Canadian vessels and at least one land-based observer. Identification of killer whale group (i.e. Southern Resident pod, transient, or unidentified killer whale), time, and location of each sighting were compiled. Sightings were reported roughly every thirty minutes, and locations were described as the center point of pre-established grids ranging throughout the study region and generalized to standard 25 km^2 cells for analyses. Sightings were standardized to occur in a given cell once per day to reduce pseudo-replication.

Biases and assumptions associated with using whalewatch information were considered in Chapter One, and these data were deemed valid for use in killer whale distribution studies within this region. Chapter One identified data use guidelines to minimize errors in the location data. Specifically, only sightings between 10:30 and 16:00 were used, and unidentified killer whale sightings were excluded. It should be noted that these are also the best available spatial data for summer SRKW distribution studies. Tagging studies are currently not politically feasible for this population given its endangered status, and therefore the best available opportunistic data were used with recognition of the potential limitations and biases. While Chapter One only validated these data based on samples collected during 2004, I assumed that conclusions regarding data applicability and whale watcher effort have been consistent through time.

Modeling space use

The process of identifying and quantifying SRKW core area use involved several steps. First, overall space use was modeled for multiple samples of each temporal scale using kernel density estimation. For direct comparison among samples, each sample was

then normalized. Next, I derived the core area of each sample and calculated the relative amount of core area as well as the degree of dispersion around the core area. These metrics stem conceptually from theory of landscape ecology. I calculated averages and coefficients of variation of relative core area amount and dispersion for each temporal scale to compare among scales. Finally, the locations identified as core space were also mapped for each temporal scale. Each step is outlined in detail below.

SRKW locations at four temporal scales (week, month, full summer season, and all data pooled) were sub-sampled from May to September 1996-2001. Thus, each week of every year, each month of every year, and each summer of every year represent a single 'sample' for the respective temporal scales. Using the selected locations, I modeled space use for each sample with fixed kernel density estimators in ArcGIS (ESRI, v9.0). Kernel density estimators provide a two-dimensional representation of the frequency distribution of animal locations during some period of time as well as the configuration of space use throughout a study area (Silverman, 1986; Worton, 1989; Appendix A). Kernel estimators are favored over other methods for describing animal distribution because they appear to be least biased by sample size or outliers, and consist of a nonparametric probability density function not requiring a particular statistical distribution (Kernohan *et al.*, 2001). I applied the fixed kernel instead of the adaptive kernel because it is computationally simplified, and produces less biased results in simulations (Seaman & Powell, 1996). Kernel density distributions were derived for each week of each year, each month of each year, the entire summer of each year, and a single distribution to represent all available data.

I used fixed kernel density estimators to represent the relative frequency distribution of SRKW locations over each temporal sample as well as to provide estimation of the how differential space use was configured throughout the study region for each sample. Kernel density estimates in wildlife ecology are typically used to estimate animal 'home ranges' or overall ranging pattern (e.g. Gubbins, 2002; Flores & Bazzalo, 2004), but, while the application to my study is analogous, I was not explicitly attempting to determine home ranges. The overall summer ranging patterns of SRKW

are described elsewhere (Heimlich-Boran, 1988; Ford *et al.*, 2000), and I use kernel density as a method of spatial representation and relative space use for location data.

To directly compare kernel density distributions among samples of temporal scale, normalization was necessary. Normalization was accomplished by classifying each sample into five bins ranging from low to high density based on a quartile reclassification scheme that chose breakpoints with an equal count of cells in each class. Locations with no sightings (0 density) were excluded. In this way, I compared the range of density classes as well as the highest densities among samples of a given temporal scale.

I defined 'core areas' to be those locations that were used most frequently by SRKW, and core areas are often thought to contain important features or resources (Samuel *et al.*, 1985). I delineated core areas in our study as the highest density class resulting from kernel density classification. This allowed core space to be self-selected for each sample rather than basing it on the arbitrarily set limit of 25 or 50% of the kernel range that is common in other wildlife distribution studies (e.g. Gubbins, 2002; Heide-Jorgensen *et al.*, 2002; Owen *et al.*, 2002). Therefore, I identified core space based on *locations* with a high frequency of use, not the magnitude of the density value itself. Given this definition of core, there would be no designation of core space for animals that use space uniformly.

Quantitative description of core use

We applied the conceptual framework and quantitative metrics from the field of landscape ecology to describe changes in the pattern of SRKW core areas. Landscape ecology is focused on the interface of spatial pattern and ecological processes, and is now broadly employed by many ecologists (Turner, 2005) including those in marine research (e.g. Tokeshi, 1995; Teixido *et al.*, 2002; Laidre *et al.*, 2004a). We apply the definition of a 'landscape' as an area that has at least one feature that is spatially heterogeneous (Turner *et al.*, 2001). In our case, the 'landscape' is the inshore waters of Washington and British Columbia that features SRKW core area use across temporal scales. Following a landscape ecology framework, the spatial relationships among relative SRKW density levels for each temporal sample can be characterized by their spatial

composition and configuration. Composition refers to the makeup, presence, and amount of a feature while configuration indicates the physical distribution and arrangement of features.

I used two metrics to consider the composition and configuration of core space use across temporal scales. Using FRAGSTATS 3.3 (McGarigal & Marks, 2002), I calculated the percent composition of core relative to total space for each temporal sample to provide a relative measure of core quantity. Mean core quantity was then calculated for each temporal scale by averaging the core composition of each sample of that scale. I also developed a two step procedure to derive a measure of spatial configuration for each sample, referred to as 'dispersion.' The dispersion from core regions first required identification of the region that was always classified as core for each sample of a temporal scale (referred to as common core), and, secondly, the distance from the common core to the furthest extent of every sample was calculated using a cost-weighted Euclidean distance function. Calculations of distance were forced to select measurements around land forms by heavily weighting (1000 times more likely) travel through water. Similar to core quantity, mean dispersion from common core for each temporal scale was determined by averaging the distance of each sample of that scale. Mean dispersion from common core and relative percent core composition were compared among temporal scales using standard parametric tests (ANOVA and linear regression), and standard variation in metrics was considered using the coefficient of variation (Zar, 1999). We also mapped the proportion of samples classified as core for the week, month, and summer temporal scales to visually represent the spatially-explicit variation in core space.

Results

A total of 90 weeks, 27 months, and 6 summers were sampled across the six year dataset for these analyses, and SRKW were available to whalewatchers within the region for a total of 776 days (May to September) over the entire study. Throughout the summer

season, SRKW were observed on an average of 79.3% of the days each year that they were available to whalewatchers (SD=11.2%, N=6). An average of 35.2 sightings occurred per week (SD=12 sightings), 127.0 sightings per month (SD=44 sightings), and 576.5 per year (SD=148 sightings) after eliminating repeat sightings within a grid cell.

Spatial patterns of core area composition and configuration varied significantly among temporal scales. The simple metric of relative core quantity, or core percent composition, suggests that core area contributed the greatest amount to total space at the finest temporal scales (week) and varied significantly (p= 0.00001, F = 51.3) among weekly, monthly, and summer scales (Table 2.1, Fig. 2.1). There was also a linear decrease in core percent composition from the finest to coarsest temporal scales (summer and pooled data). Tukey's HSD post-hoc tests indicated significant variation (p<0.05) between core compositions for each combination of week, month, and summer scales.

Mean dispersion (the average maximum distance from the area of common core to the greatest extent of an individual sample) also varied significantly (p = 0.006, F = 5.4) among temporal scales, but there was not a significant linear trend between scales and the monthly temporal scale had the greatest mean dispersion value (Table 2.1, Fig. 2.2). Post-hoc tests indicated that weekly mean dispersion varied significantly from monthly. Similarly, summer mean dispersion varied significantly from monthly, but week and summer mean dispersion were not significantly different from one another.

The greatest standard variation (coefficient of variation) in dispersion occurred at the weekly temporal scale and decreased as scale became increasingly coarse (i.e. to the seasonal scale). The coefficient of variation for core composition was relatively stable across temporal scales (Fig. 2.3). Mean values of dispersion and core composition fell above the 1:1 relationship for all temporal scales (Fig. 2.4), suggesting that dispersion was always greater than expected for a given percent core composition.

The spatial location of core areas also varied among temporal scales (Fig. 2.5). For each mapped grid cell, we found the relative frequency of assignment as a core area. Proportion of areas classified as core in a given temporal scale ranged from 0-1, where 1 represented locations that were considered core in each sample of that temporal scale, or

common core. When comparing among temporal scales, there were some areas that were always considered core in the highest proportion (shown in red) regardless of temporal scale, suggesting that these locations were nearly always considered a core area. Other locations were always classified as core in the lowest proportion (blue regions), indicating that these areas were also always a core area except they only get used in a small proportion of samples for each temporal scale. Similarly, there were locations that were never regarded as core (no coloration). Some areas were only deemed core at one temporal scale but not others, so these regions were judged as ephemerally core regions.

Discussion

SRKW used space non-randomly, non-homogenously, and dynamically during the summer period. Two descriptive measures, percent composition and dispersion, were presented as compliments to one another, which in combination provide a general depiction of the range, compactness, and consistency of SRKW space use. In addition, these metrics identify and describe variation in specific core area locations and provide a foundation for continued studies into potential processes motivating use of core areas.

The SRKW core areas varied in percent composition and dispersion among temporal scales, but there were certain locations that can be considered common core areas at all temporal scales. The total amount of core area varied among temporal scales and dominated a greater proportion of the total space used at finer temporal scales. The proportion of core area declined as the temporal scale increases. Thus, there is a greater probability of incorporating core area at the finer temporal scales when managing total space since finer temporal scales consist of a greater proportion of core area than coarser scales. At coarse temporal scales, so much more total space is used by SRKW that core contributes a smaller proportion. In other words, total space use at coarser temporal scales (summer) is large and the core area only makes up a small component of the overall area, resulting in a small core percent composition. Dispersion generally declines as temporal scale increases; however, dispersion peaks at the monthly temporal scale.

Southern Resident killer whales were observed at greater distances away from the core areas at the monthly scale despite a greater amount of core area quantity. This is consistent with a visual inspection of the mapping of the total amount of monthly core space and the spatially explicit location of core areas at finer temporal scales.

There was little relative variation in the amount of core area among temporal scales. Regardless of the relative amount of core space, however, SRKW were found to have much more variation in their ranging patterns at finer temporal scales. Dispersion varied greatest from week to week, suggesting that the range of SRKW movements is more variable at finer temporal scales. However, there was higher dispersion than would be expected for each temporal scale, regardless of the measure of core percent composition. At the monthly scale, there was elevated exploration and movement away from core areas relative to other temporal scales because there was the greatest range in dispersion. The weekly temporal scale had the greatest degree of variation from its mean.

In addition to greater variability in core area use at finer temporal scales, less concentrated movements around the core space, or greater dispersion, suggests that SRKW search at a greater distance from their core area at the monthly scale. Chinook salmon (*Oncorhynchus tshawytscha*) are the most frequently observed prey of SRKW during summer months (Ford *et al.*, 1998; Ford & Ellis, 2005), so it would be reasonable to consider variations in chinook salmon availability at each temporal scale as a potential driver for SRKW space use. Within this region, multiple chinook salmon populations exhibit unique migration pathways through the inland waters overlapping with SRKW summer distribution (Quinn, 2005). Some populations are considered ‘resident’ throughout the year, but multiple other populations of chinook salmon are transiting through this region towards their divergent natal rivers at different rates throughout the summer (Quinn, 2005). The observed variability in dispersion along the gradient of temporal scales likely relates to the distribution of their prey.

Numerous factors may act as environmental constraints and controls on the spatial behavior of SRKW. An understanding of the variability in locations that are most frequently used within SRKW summer range allows focused research into the

relationship between biological and physical environmental conditions driving space use. Southern Resident killer whales are more likely to be responding to highly variable processes, such as prey movements, from week to week than at coarser scales where variability in motivating factors would be expected to even out the use of space. Description of where and how prey vary in relation to SRKW distribution is a potential next step for incorporating similar metrics of spatial and temporal behavior. It is equally important to expand our understanding of the relationships to physical environmental characteristics that may also serve as proxies for prey distribution. For example, cetacean distribution has been related to static physical characteristics such as water depth or slope as well as dynamic processes like eddies or primary productivity (e.g. Jaquet *et al.*, 1996; Griffin, 1999; Jaquet & Gendron, 2002), with each representing a potential feature that motivates or concentrates prey distribution. Although there are indications that SRKW forage in areas with high relief sub-surface bottom topography where prey presumably concentrate (Heimlich-Boran, 1988), some research disagrees (Hoelzel, 1993), and there has not yet been any clear link with other environmental factors.

Describing patterns in variability of the location of core areas among temporal scales provides a spatially-explicit description of geographic consistency. Mapping of core areas, and frequencies at which a given location was considered core, show that SRKW always used some locations as core and highlights areas that could be target regions for protection, regardless of temporal scale. Other areas were also always considered core regardless of temporal scale, but only in a small proportion of samples, and there were other locations that SRKW used as core at one temporal scale but not others. In addition, there were also regions that were never considered core at any temporal scale. With this knowledge of variability in SRKW core space use, researchers can potentially evaluate spatial overlap with possible risk factors, like reduced prey quantity and quality, influence of anthropogenic contaminants, and vessel impacts (Alvarez-Flores & VanBlaricom, 2001; Baird, 2001; Krahn *et al.*, 2004; Ross, 2006). Thus, relative impacts of each on population viability can be considered. In the case of another critically endangered cetacean, the North Pacific right whale (*Eubalaena*

glacialis), an understanding of distribution as it relates to patchy, variable prey (Baumgartner *et al.*, 2003b; Baumgartner & Mate, 2003) has been compared to space use patterns of shipping traffic (Ward-Geiger *et al.*, 2005), which can be a direct source of mortality to right whales. This work can then be used to develop methods for reducing mortality of right whales induced by ship strikes. Similarly for SRKW, the spatial distribution and relative intensity of contributing risk factors can be measured as they relate to variations in SRKW core space use. In addition, we document high use of this region, but SRKW were not observed in this area on approximately 20% of the summer days, suggesting that there should be continued research into other key areas used by SRKW during the summer.

Protection of core areas, or areas of concentrated use, is an increasingly common management technique on a global scale. This is demonstrated with the recent emphasis on management involving designation of critical habitat, essential fish habitat, and marine protected areas. Some have argued that such space-based management does not provide functional boundaries for many marine species that respond to variable environments (Boersma & Parrish, 1999). Marine ecosystems are highly dynamic with poor predictability and processes occurring over multiple scales, and it has been suggested that dynamic protected areas (Hyrenbach *et al.*, 2000), localized protection that is closely related to the biology of the species and key characteristics of the environment (Hooker *et al.*, 1999), or incorporation of the unique spatial attributes affecting life history and demographics (Hooker & Gerber, 2004) are key aspects of protecting mobile marine predators.

From a SRKW management perspective, variability decreases and predictability increases at larger temporal scales. This suggests that perhaps managing at the summer scale would be ideal. Management at the summer temporal scale, however, suggests management of a larger total amount of core area, as seen in the amount of red core areas for the summer scale. Protection of a large summer-scale core area with sub-regions that are used differently on a weekly and monthly basis may impose complications as managers act to mitigate impacts on SRKW. This study suggests that a dynamic

management plan could be developed that recognizes the temporal dynamics of SRKW distribution, and is simultaneously the first to offer an estimate of the anticipated locations and range of core areas. Ultimately, decisions of which temporal scale to manage should depend on the goals and objectives of management for SRKW distribution.

Our results suggest that SRKW are another example of cetaceans with dynamic space use that could be incorporated into habitat management planning. Summer critical habitat designations for SRKW may not necessarily be the most effective means of protection if implemented in a static fashion. Similar to pelagic protected areas, managers may instead be able to institute changing boundaries or buffers for SRKW habitat management. Furthermore, SRKW core areas span across international borders. Perhaps a synergistic approach that can incorporate an attention to the temporal and spatial variability in the space use requirements of SRKW at multiple levels of government (e.g. county, state, provincial, and federal) as well as intergovernmental agencies (i.e. United States and Canada) will be most beneficial to effective protection of this population.

Table 2.1. Summary statistical results for ANOVA and linear regression of core composition and dispersion relationships among temporal scales.

Statistic	Core composition	Dispersion from core
ANOVA		
F statistic	51.312	5.405
p-value	0.00001	0.006
Linear Regression		
F statistic	97.691	0.087
p-value	0.00001	0.769
R^2	0.441	0.001

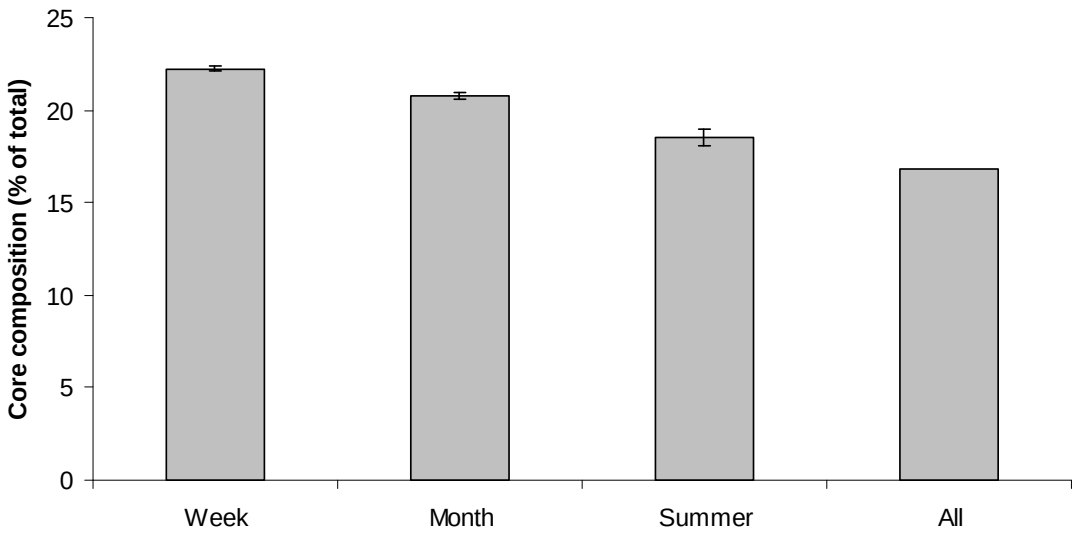

Figure 2.1. Mean composition of core (+/- 1 se), measured as the percent of core space to total space used, at each temporal scale, and all data pooled ("All").

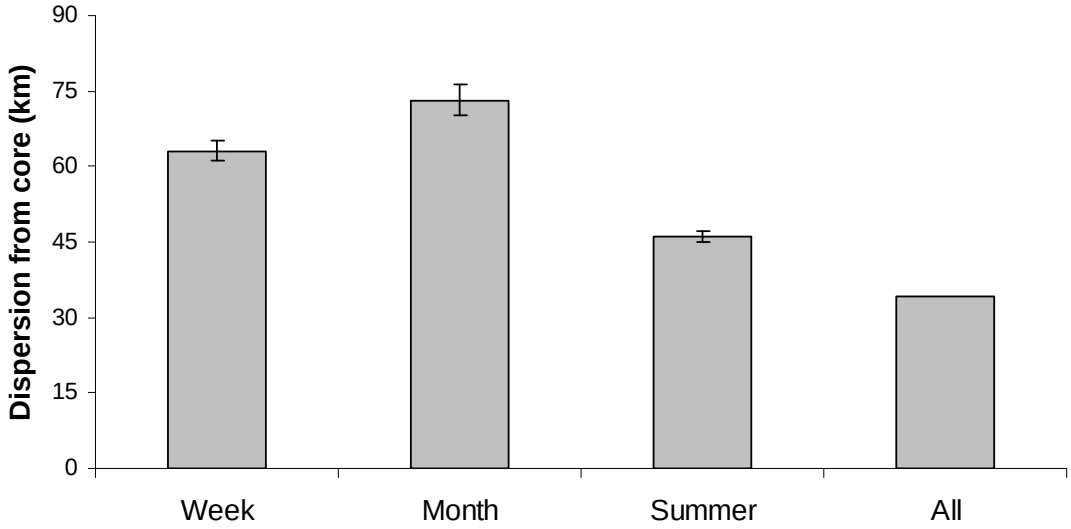

Figure 2.2. Mean dispersion from common core (+/- 1 se) of each temporal scale and all data pooled ("All"). Dispersion from core was measured as the Euclidean distance, weighted to avoid travel through land masses, to maximum extent from the common core space of a given temporal scale.

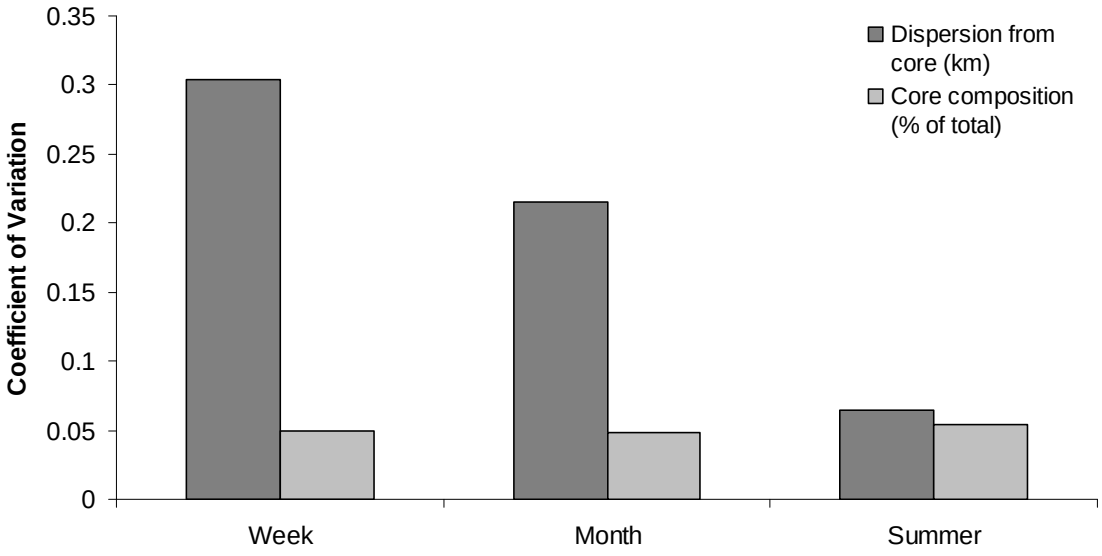

Figure 2.3. Coefficient of variation in SRKW dispersion and core composition for each temporal scale.

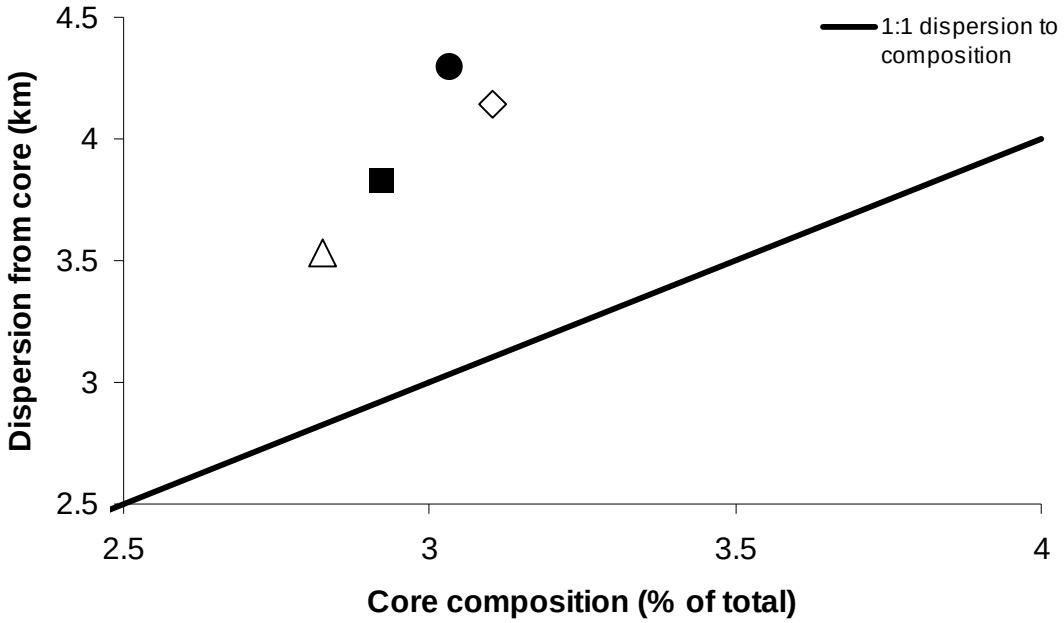

Figure 2.4. Relationship of mean dispersion from and composition of core space for weekly (open diamond), monthly (closed circle), summer (closed square), and pooled data (open triangle) temporal scales, natural log transformed, and indicating the 1:1 line of dispersion to composition. Points falling on the line would predict dispersion based on core composition.

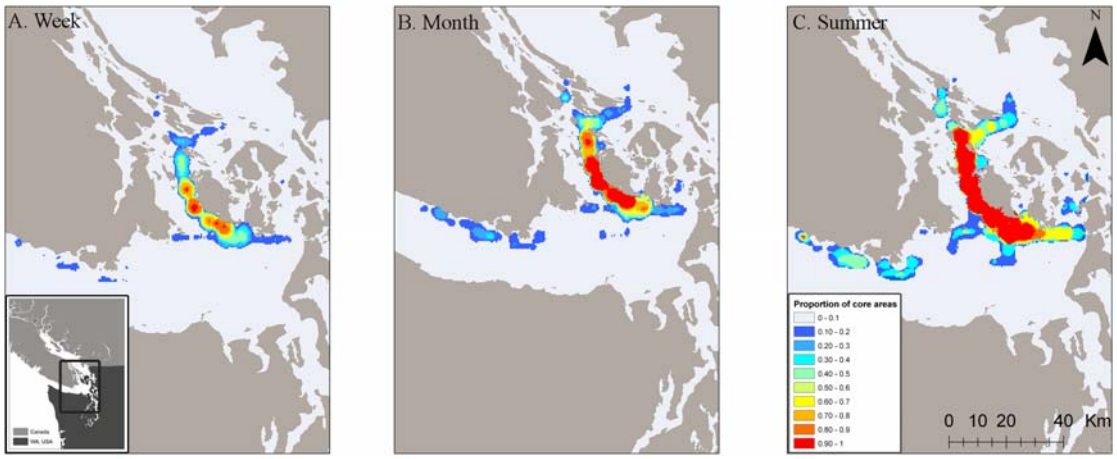

Figure 2.5. Areas within Washington state, USA and British Columbia, Canada inshore waters classified as core at the (a) weekly, (B) monthly, or (C) summer temporal scale, as relative proportion of samples classified as core. Red coloration represents locations that were classified as core in 90% or greater of the samples at a given temporal scale while dark blues are locations that were also classified as core, but only in 10-20% of the samples at the specified temporal scale.

Chapter Three

Differential space use among matrilineal pods of Southern Resident killer whales (*Orcinus orca*)

Introduction

Understanding the processes driving animal distribution is a fundamental issue in ecology and highly relevant to conservation and management. In the marine environment, organisms are confronted with dynamic environmental conditions and patchy resources that range across spatial and temporal scales. Many marine predators, such as cetaceans, respond to ecosystem variability by modifications in distribution pattern to limit reductions in survival or reproductive success (Forney, 2000). Understanding the distribution patterns of cetaceans becomes more complicated when the social organization and behavior of these species is considered (Redfern *et al.*, 2006) because space use can vary for distinct populations and population segments (e.g. Baird & Dill, 1995; Whitehead, 1997). For example, habitat preferences of humpback whales (*Megaptera novaeangliae*) on a wintering ground are influenced by social structure, with mother-calf groups preferring consistent habitat types relative to variable preferences by paired adults or competitive groups (Ersts & Rosenbaum, 2003).

Differential space use among cetacean social units can be a result of unique responses to physical characteristics of the habitat, anthropogenic and non-anthropogenic risk factors, and other conditions driving animal distribution. In some cases, differences in habitat use and movement patterns among social units of sperm whales (*Physeter macrocephalus*) have been associated with variable feeding success and effects of climate change (Whitehead & Rendell, 2004). Furthermore, social structure and associated variations in spatial distribution can affect reproductive success and gene flow among population segments, making social structure an important variable for analyses of space use (Dobson & Poole, 1998). Thus, unique distribution patterns among different population segments may be critical components of space-based management and

conservation initiatives. In this study, we focus on the description and comparison of space use among distinct population segments of an endangered killer whale (*Orcinus orca*) population in the coastal eastern North Pacific.

Early studies of fish-eating killer whales in this region used individual recognition to describe a complex social system with multiple stages of stable, long-term associations and limited dispersal (Bigg *et al.*, 1990). The so-called Southern Resident killer whale (SRKW) population, found within inshore marine waters of Washington (USA) and British Columbia (Canada) during summer months, is composed of three matrilineally-related population segments termed 'pods' and identified as 'J', 'K', and 'L'. Pods are considered long-term, consistent social associations among SRKW, and individuals spend 50% or more of their time together (Bigg *et al.*, 1990). Every individual can be identified using photographic identification of unique pigmentation patterns and dorsal fin morphology (Bigg *et al.*, 1987; Baird & Stacey, 1988), and several decades of annual censuses provide thorough long-term demographic studies (Ford *et al.*, 2000; van Ginneken *et al.*, 2004). Recent declines in the total SRKW population have prompted several conservation listings in both the United States and Canada, including listing as 'Endangered' under the U.S. federal Endangered Species Act and Canada's federal Species At Risk Act (Baird, 2001; Krahn *et al.*, 2004). Identification of key areas within the SRKW range and protection of 'critical habitat' are central components of SRKW recovery planning.

Southern Resident killer whale summer range within Washington and British Columbia is generally described for the population (Heimlich-Boran, 1988; Ford *et al.*, 2000), but detailed knowledge of variations among pod distribution patterns is poorly known. There are seasonal variations among pods in proportion of time spent within the inshore waters of Washington and British Columbia and some evidence of niche partitioning on a large scale (Osborne, 1999). Southern Resident killer whale pods have distinct acoustic call types, cultures, population trajectories, and mortality trends (Ford, 1990; Rendell & Whitehead, 2001; Foote *et al.*, 2004; Krahn *et al.*, 2004), so it is possible that these unique social units also display fine-scale variations in their

distribution patterns. In addition, knowledge of pod-specific distribution and use of key areas is important if conservation efforts will be focused on pods. Within their summer range, it is possible that SRKW use space disproportionately, and 'core areas', or areas used most frequently, may contain important resources (Samuel *et al.*, 1985; Barg *et al.*, 2005). Although there is some information on variations in core space for SRKW (Chapter Two), there is no information on core area delineation or variation among pods.

My overall goal was to describe variations in space use among SRKW pods, including identification of core areas, using six years of sighting data collected throughout their summer range within Washington and British Columbia inshore waters. I utilized conventional and innovative approaches for describing pod distribution. Pods are also known to combine briefly, primarily for socialization (Osborne, 1986), and many sightings of combined pods exist in our database. Therefore, I also considered similarities in distribution for pod combinations. My specific objectives were to: (a) distinguish groupings of SRKW pod combinations based on similar space use patterns; (b) determine and compare pod-specific distribution patterns and core space; and (c) evaluate degree of spatial overlap and specialization among pod groupings.

Methods

SRKW location data

Chapters One and Two extensively describe data collection techniques, so data will only be briefly described here. From May to September 1996-2001, SRKW daily locations were reported by an organized spotting system of commercial whalewatchers functioning cooperatively to find whales for their customers. Canadian and US vessels and at least one shore-based observer searched Washington and British Columbia inshore waters for killer whales from 08:00-17:00 (Fig. 3.1). Approximately every thirty minutes, the sighting network collected pod identification (J, K, L or some combination of pods, transient, or unidentified killer whale), time, and location for each killer whale sighting. Potential limitations and biases related to the use of these whalewatch data for

distribution studies were evaluated in Chapter One. For this analysis, I follow the data use guidelines developed in Chapter One to ensure high pod identification accuracy. The number of days between the first and last sighting of each year were calculated as the minimum number of days that whales were available to whalewatchers. Using this information, I determined the percentage of days that each pod was located within the study region as well as the number of sightings per pod.

Describing space use: kernel density and core areas

Distribution for each pod and pod combination (J alone, K alone, L alone, J and K, J and K and L, J and L, and K and L) was modeled using fixed kernel density estimators in ArcGIS (ESRI, v9.0). Fixed kernel density estimators were used to represent the two-dimensional relative frequency of summer pod locations across the six year data period and describe the configuration of differential space use for each pod (Silverman, 1986; Worton, 1989). Kernel density estimator theory and application to SRKW distribution analyses are described in Chapter Two and Appendix A.

Distinguishing spatial distributions among pod combinations

Similarities in spatial distributions can be compared in a number of ways. Two multivariate methods of data reduction, hierarchical cluster analysis and non-metric multidimensional scaling analysis, were applied to determine the degree of similarity in kernel density distribution patterns among pod combinations. Each pod combination's kernel density was normalized from 0-1, where 1 represents the maximum density value, and values were standardized for pod abundance in each cell of the study region as suggested for species similarity analyses (Clarke & Warwick, 2001). Thus, standardized, geographically-referenced density distributions were compared among pod combinations. Using the Bray-Curtis similarity coefficient (Bray & Curtis, 1957), 'similarities' were next calculated between pod combinations to create a similarity matrix which was then used in both hierarchical cluster and non-metric multidimensional scaling analyses. Bray-Curtis similarity ranges from 0-100, where 100 implies completely identical distribution patterns among pod combinations and 0 suggests completely distinct

patterns. When considered as a pair, clustering and ordination techniques are effective methods for checking the adequacy and mutual consistency of results from both analyses (Clarke & Warwick, 2001).

Hierarchical cluster analysis was used initially to find natural groupings among the density distribution patterns of the pod combinations. Hierarchical agglomerative methods using the group-average link on the similarity matrix (Everitt, 1980; McGarigal *et al.*, 2000; Clarke & Warwick, 2001) were used to describe groups of pod combinations that tend to co-occur in an analogous manner across cells in the study region. The resulting dendrogram was compared to non-metric multidimensional scaling ordination results. Non-metric multidimensional scaling (NMDS) is an ordination method well-suited to many types of ecological community data because data can be non-parametric and do not require continuous scales or linear relationships among variables (Kruskal & Wish, 1978; Clarke, 1993). Through an iterative process, NMDS was used to compute coordinates for each pod combination in *n*-dimensional space. 'Stress' values are calculated as a measure of goodness-of-fit for the non-parametric regression, where low stress is optimal (i.e. <0.1 is considered a "good" final ordination result and <0.05 is "excellent") (Kruskal, 1964; Clarke, 1993; Clarke & Warwick, 2001). To effectively choose an adequate number of groupings, cluster results were superimposed upon the final NMDS ordination and examined for mutual consistency.

Modeling pod-specific space use

The groupings of pod combinations that resulted from clustering and NMDS were used for all other comparisons of pod-specific space use. Sightings of grouped pod combinations were pooled and kernel density was recalculated for each new pod group. For direct comparisons of kernel density distributions among pod groups, each pod group was normalized into five density classes ranging from low to high density. Quartile separation was used to select breakpoints such that there was an equivalent count of grid cells in each of the five density classes. Locations with no sightings (0 density) were not included in normalization. This normalization scheme allowed for comparisons among

pod groups across the range of low to high density classes as well as comparisons of the highest density regions.

To determine core space use, I delineated core areas as the newly classified highest density region. In this way, core space was self-selected for each pod group instead of arbitrarily set to a proportion of the kernel range as has been done in other wildlife distribution studies (e.g. Gubbins, 2002; Owen *et al.*, 2002). Core space use was considered of high management interest because it represents the most frequently used regions by each pod group.

I applied several techniques to compare core and total space use among pod groupings. First, kernel density was mapped, normalized as the proportion of maximum density, for each pod group to generally describe variations in use of particular areas and differences in the extent of distribution for each pod group. Next, I used the classified normalization to determine areas where one pod group specialized in space use relative to the other groups by finding all of the locations classified in the highest density class for one pod group that were simultaneously classified as the lowest density of all other groups. The identified cells were mapped, and generalized polygons were added over the identified locations to indicate the broad region of specialization by one pod group. I also considered common space use patterns among pod groups by mapping all of the unique locations where each pod group shared the same density classification. Variations in core area among pod groups were compared by mapping the unique and overlapping core areas for each group. Finally, I measured the spatially explicit central tendencies, or geographic distribution, of each pod group and pooled SRKW locations by calculating the mean center and directional distribution.

The geographic distribution is somewhat analogous to the more conventional biostatistical measurement of a mean and standard deviation for a data set. Spatial statistics, including calculation of mean center and directional distribution, is an extension of traditional statistics that incorporates the distribution of descriptive values as well as how those values are arranged in space (Haining, 2003). In this case, I considered the description of kernel density value in spatially explicit locations for each pod group.

The mean center represents the average x- and y-coordinate for all cells with a density greater than 0, weighted by the density value (Mitchell, 2005). Directional distribution describes variation and spatial trend around the mean center as standard distance and spatial orientation from the mean center, weighted by density values greater than 0 (Mitchell, 2005).

Results

Southern Resident killer whales were observed on 611 days throughout the six-year study period, with sightings first occurring in May in each year but 1996 and ending in September in each year except 1998 (Table 3.1). Assuming that whalewatchers searched for whales each day between the first and last sightings, there were a total of 776 searched days. SRKW were observed within the study region 78.7% of those days each year, with yearly percentages ranging from 64.5% (2000) to 96.7% (2001). Additionally, each pod combination occurred within the region at varying levels, from KL and JL (each only seen approximately 6% of the available days) to the most frequent sightings of J or L pods (22.8 and 38.9%, respectively) (Fig. 3.2).

Similarities among pod combinations

Hierarchical cluster analyses of similarities in distribution patterns among pod combinations indicated that there were 3 natural groupings of pod combinations with similar density patterns (Fig. 3.3). Non-metric multidimensional scaling results corroborate clustering results and provide an “excellent” two-dimensional graphical configuration (stress=0.04) of space use similarities among pod combinations (Clarke & Warwick, 2001; Fig. 3.4). J pod alone, J pod combined with K pod, and J pod combined with L pod were pooled together for a new pod variable hereafter called J group. The new K group pod variable was composed of K pod alone and K pod combined with L pod, and the L group pod variable combined L pod alone and J combined with K and L pods. Therefore, these three new pod groups were used in subsequent spatial analyses.

Upon combination, L group was sighted the greatest percentage of days available, followed by J and then K groups (Table 3.2).

Pod-specific variations in distribution

Generally, there were several similarities and variations in space use among pod groups (Fig. 3.5). All pod groups shared similarly high density regions throughout Haro Strait, but distinctions in space use were particularly noticeable for J and L groups. J group exhibited higher density ranging further north, with exaggerated use of Swanson Channel into Active Pass, relative to the other two pod groups. While J group also used Boundary Pass, it appears that use of Swanson Channel and Active Pass was more common. In addition, J group's higher density ranged further east to the South of San Juan and Lopez Islands and north into Rosario Strait. Space use by K group appeared to be an intermediate form of J and L groups. There was near-equal relative use of Swanson Channel and Active Pass as Boundary Pass, and no exaggerated use of any other area relative to J and L groups. L group showed the greatest variation relative to J and K groups, with rather extensive use of the Strait of Juan de Fuca off Southern Vancouver Island. L group also appeared to use Boundary Pass rather than Swanson Channel and Active Pass.

Both J and L groups exhibited regions used at their highest density classes which the other two pod groups simultaneously used at their lowest density classes (Fig. 3.6). No areas of such specialization were identified for K group. J group specialized in use of northern Rosario Strait and near Active Pass while L group specialized south of Vancouver Island in the Strait of Juan de Fuca. There were also several areas of common space use among all three pod groups, described as the unique cells with matching density classifications for each pod group (Fig. 3.7). All three pod groups shared highest use in Haro Strait, representing a common core region regardless of pod. This highest use area was also the largest shared region (360 km^2), followed in succession by each lower shared use category (the 4th highest use class was 116 km^2, 3rd was 69 km^2, 2nd was 53 km^2, and the lowest use category comprised 31 km^2). The common core region was primarily composed of a single, large and connected area, whereas the other shared areas

were rather discontinuous and patchily distributed. Each pod group also shared regions that were never used (0 density). Beyond the common core region identified in Figure 3.7, there were variations in pod-specific core areas (Fig. 3.8). J and K groups shared some core regions surrounding the common core area to the north and south. J group's core region extended into Swanson Channel, K group's core region largely overlapped with the common core except for a small extension in Boundary Pass, and additional core areas for L group were identified in the Strait of Juan de Fuca south of Vancouver Island.

The mean center for each pod group was slightly displaced from the pooled SRKW mean center, with J group furthest displaced in a northeastern direction (Fig. 3.9, Table 3.3). K group's mean center showed the least displacement from the pooled SRKW mean center with the least distance and smallest angle, near directly east. L group's mean center was displaced to the southwest of the pooled SRKW mean center. However, the greatest variation in geographic distribution was identified by comparing directional distributions among pod groups. L group's directional distribution was largest, but oriented most similarly to the pooled SRKW distribution along a northeast-southwest axis. Directional distributions for both J and K groups were near perfect circles, with no clear directional orientation. However, K group's distribution was the most concentrated, with the smallest total area, around its mean center.

Discussion

This study is the first long-term, fine-scale study identifying spatially-explicit overlap and variation among killer whale pods as well as the core areas of their range. The results suggest that SRKW pods display some similarities as well as important distinctions in their overall and core space use. Such similarities and variations in pod-specific distribution may be a response to variable ecological processes or killer whale cultural differences among pods, and differences may contribute to differences in population parameters, highlighting regions critical to recovery planning of endangered SRKW. Although the mechanisms underpinning the observed distribution patterns are

unknown, my analyses provide the critical first step to describe core area and variability of pod-specific SRKW distribution patterns. This analysis focuses on SRKW distribution patterns within inshore waters of Washington and British Columbia, constituting a minimum of 80% of summer days. While this area is obviously a prominent component of SRKW summer space use, the other 20% of their summer as well as winter distributions may contain key habitat areas and should continue to be researched.

Different pods often intermingle for brief periods, discussed as pod combinations in these analyses, and likely represent periods of socialization and possibly reproduction between pods (Osborne, 1986). By applying two multivariate techniques I allowed pod combinations to naturally cluster into groups and used these groups for analyses. A common problem for clustering techniques is the difficulty of choosing an objective number of groups to accept (McGarigal *et al.*, 2000), but accuracy in groupings can be verified by superimposing hierarchal clustering results on the NMDS ordination (Clarke & Warwick, 2001). The combination and comparison of clustering and ordination techniques is considered an effective method for examining the adequacy and mutual reliability of groupings by both analyses (Clarke & Warwick, 2001). At 70% similarity, space use of all 7 pods or pod combinations could not be grouped, but three groups were identified as similarity increased to 75%. The next break into six groups does not occur until 85% similarity. This suggests that space use of all pod combinations cannot be distinguished from one another to some degree, but there are also patterns suggesting that some pod combinations have more similar distribution patterns than others. I took the latter approach and investigated the present questions assuming there were three pod groupings which were used for subsequent comparisons of distribution patterns.

It is also worth considering which pod combinations were most closely linked with one another as an indication of potential dominance and separation among the pod combinations. All J pod combinations, other than J plus K and L, were most closely associated with J pod alone. Therefore, it appears that J pod may be driving the movements and space use relative to K or L pod when combining. K pod alone is most closely associated with K plus L pod, indicating that K pod may most influence space use

patterns when K and L pods combine. However, when all SRKW whales are together (i.e. J plus K plus L pods), distribution patterns paradoxically most closely resemble those of L pod alone. Mechanisms of partitioning among pod assemblages were not considered, but clearly may be a factor contributing to differences among pods. Culture and social learning have been recognized as aspects of SRKW social behavior (see Whitehead *et al.*, 2004), and may contribute to associations and variations in distribution patterns among pod assemblages. Aggregations of two or more SRKW pods may result from temporary or permanent dominance among pods. SRKW are a clear example of cetaceans influenced by culture, and behavioral choices are influenced by such culture (Rendell & Whitehead, 2001; Whitehead *et al.*, 2004). Thus, behavioral decisions among pods should be considered as a potential mechanism driving the variations described here.

Differences in the use of Active versus Boundary Pass may represent one example of partitioning among pods and changes in distribution over time. Historically there was apparently no use of Swanson Channel or Active Pass, and the first consistent use of this region occurred in the mid-1990s (R. Osborne, personal communication). Furthermore, Heimlich-Boran (1988) did not include any use of this region in analyses. J group appears to be leading use of Active Pass, with a preference for this region over Boundary Pass. K group has an intermediate use, where both Active and Boundary Passes are represented in their distribution patterns. L group maintains preferential use of Boundary Pass, with rare sightings in Active Pass. It is unclear what motivated novel use of Active Pass by J group or what propels some use by K group, nor why L group does not use this region, but such partitioning has been suggested as a consequence of a change in J pod's matriarchs during the mid-1990s (R. Osborne, personal communication). Following deaths of old matriarchs, new females may have started leading the exploration of novel regions. Potentially, decision-making and learning in this maternal society were altered by such a transformation, and managers may need to incorporate conservative habitat protection to allow for such changes in space use due to variable social dynamics.

Several areas were identified as places that were used at the same intensity, regardless of pod. Each pod group uses these regions at a matching level. The common core area throughout Haro Strait, regardless of pod, clearly indicates that this is a key component of SRKW summer range, but we also identified regions of lesser use yet common to each pod group. The common core area is not only spacious in terms of total area relative to the other density classes, but it is also highly contiguous. Therefore, it may be easier to consider factors that may be motivating common use of the core region than other common areas as well as manage the core area. Identical usage of particular locations by all SRKW pod groups indicates common cultural responses, likely to ecological factors (Whitehead *et al.*, 2004). Whether these common core areas represent areas of foraging, traveling, or socializing remains unclear, and additional research that combines observed distribution patterns with behavioral observations could be very insightful.

This study also describes specializations in space use of particular pod groups. Both J and L groups had unique core areas in addition to the common core region as well as locations they used frequently relative to low use by the other two pod groups. These variations are likely to be the consequence of some fundamental difference among pods, like foraging specializations or preferences for particular habitat characteristics. For example, pod-specific foraging specializations and resultant variations in space use have been described for mammal-eating transient killer whales within the same region (Baird & Dill, 1995). Currently there is insufficient information to compare diets of different SRKW pod groups, but this may be an important consideration in understanding pod-specific distribution patterns. Social groups of other cetacean populations are also known to segregate space use, with links to differential foraging success or reproductive status (Ersts & Rosenbaum, 2003; Whitehead & Rendell, 2004). While associations to foraging and reproduction cannot be made here, these remain important potential implications of pod-specific space use.

Simultaneous behavioral observations in relation to pod-specific distribution would highlight the importance of particular locations within the SRKW summer range.

Functional mechanisms, such as foraging, could then be linked to core areas (Hastie *et al.*, 2004). With information on behaviors that are characteristic in each region, the relative importance of different core areas could be distinguished by pod and higher status given to foraging and reproduction areas that directly influence population viability. Prey availability and distribution likely affect SRKW pod distribution. Chinook salmon (*Oncorhynchus tshawytscha*) are the most frequently observed prey items of SRKW, but the whales also feed on other salmonids and bottomfish at least occasionally (Ford *et al.*, 1998; Ford & Ellis, 2005). There is no information on pod-specific diet other than similar use of the vertical water column (Baird *et al.*, 2005), and diet studies are limited to a small number of SRKW observations. It is quite possible that there are small scale variations in proportions of prey items among pods not yet reflected in our knowledge of SRKW foraging habits.

Slight variations in foraging ability or availability of prey items in different core areas among SRKW pods may be contributing to the observed differences in pod population trends and mortality rates, thus affecting population viability. L pod displayed distinct core areas as well as specialization in the Strait of Juan de Fuca along southern Vancouver Island, and L pod also displays lower survival rates than J and K pods (Krahn *et al.*, 2004). Furthermore, L pod also most directly influences the overall SRKW population trends primarily because of its large population size relative to the other two pods (Ford *et al.*, 2000; Baird, 2001; Krahn *et al.*, 2004; van Ginneken *et al.*, 2004). Thus, L pod represents a potential conservation target pod, and protection actions focused on L group may have the most implications for overall SRKW recovery.

L group also exhibited the least concentrated movements around its mean center and greatest dispersion of all pod groups as well as the greatest variation in general space use. Furthermore, as the largest pod with the most summer sightings in the whalewatcher dataset, L group directional distribution matched the overall SRKW directional distribution, suggesting that L group is largely driving overall space use among SRKW. Several factors could be motivating these patterns, including an increased search effort for resources, larger pod size, or further divisions in the social structure of L pod. For

many cetaceans, it is clear that additional movement and dispersion is needed to locate and procure prey as resources become sparse (Jaquet & Whitehead, 1999; Hooker *et al.*, 2002; Laidre *et al.*, 2004a). Certainly several wild stocks of chinook salmon and other salmonid species are considered endangered or at risk in this region and exhibit decreasing size at age over time (Bigler *et al.*, 1996; NRC, 1996; Quinn, 2005). In addition, McCluskey (2006) suggests that SRKW, in general, have more complex, broader movement patterns during periods of population decline than growth. However, unless L pod is foraging on a unique prey species or population, it is unlikely that prey availability would drive greater dispersion by L group relative to the other pod groups. L pod was nearly twice the population size of the other two pods throughout the study period (Krahn *et al.*, 2004; van Ginneken *et al.*, 2004), and larger group size may simply also require the greater overall space use and dispersion that is documented here. In addition, studies have traditionally only recognized J, K, and L pods among SRKW, but there is increasing evidence of subpods in L pod that actually fissured into two new pods following the Bigg et al. (1990) pod definition (Hoelzel, 1993; Baird *et al.*, 2005). I had insufficient information to determine if L subpods exhibited distinct distribution patterns with the available data, but it is possible that the extensive space use and specializations of L group really reflect differences of distinct L subgroups. In addition, the relatively high proportion of L pod sightings during summer seasons is likely inflated by sightings of multiple subgroups that are not explicitly distinguished by the whalewatcher dataset. Thus, multiple 'L pod' sightings can occur at a given time if subgroups are reported at spatially distinct locations. Lastly, some combination of all or some of these factors may be contributing to L group's distribution patterns, and the ultimate cause remains unclear.

Additionally, each pod may be exposed to different levels of risk factors within the specialized portions of their summer range. Prey quality and quantity, toxins, vessel impacts, random small population fluctuations, or cumulative effects are most frequently implicated in SRKW declines (Alvarez-Flores & VanBlaricom, 2001; Baird, 2001; Krahn *et al.*, 2004; Ross, 2006). Knowledge of the relative spatial distribution of each factor compared with pod-specific distribution may provide valuable insight into conservation

and management recovery planning as well as the establishment of potential protected areas. These results certainly emphasize areas where the potential for human-whale conflicts may occur, particularly within key components of SRKW distribution. Depending upon management goals, this work provides a descriptive framework for pod-specific protected areas and conservation initiatives within these inshore waters.

Table 3.1. First and last days when SRKW were observed within the study region each year, and the number of days it can be assumed that whales were potentially available to whalewatchers. Using the number of days whales were actually observed, the percentage of sighting days per available days was calculated.

Year	First sighting day	Last sighting day	No. days available	No. days observed	% Sighting days /days available
1996	13-Jun-96	27-Sep-96	107	85	79.4
1997	24-May-97	28-Sep-97	128	91	71.1
1998	01-May-98	07-Oct-98	160	125	78.1
1999	29-May-99	23-Sep-99	118	101	85.6
2000	11-May-00	28-Sep-00	141	91	64.5
2001	03-May-01	29-Sep-01	122	118	96.7
Total			*776*	*611*	*78.7*
Average					*79.3*

Table 3.2. Number of sighting days for each pod group, percent of days each group was sighted relative to the number they were potentially available, and total number of sightings for each pod group throughout the study period.

Pod group	Total no. days sighted	Percent of days sighted/days available	Total no. observations
J group	379	48.8	2246
K group	157	20.2	1043
L group	473	61.0	3317

Table 3.3. Measures of spatial central tendency for J, K, and L pod groups as well as all SRKW, including mean center and one standard deviation in dispersion from the mean center.

	Mean center		Dispersion from mean center (1sd)			
Pod grouping	Distance from SRKW mean (km)	Angle from SRKW mean	Total area (km^2)	X standard distance (km)	Y standard distance (km)	Rotation angle
J	5.623	65.059	875,699	16.834	16.559	346.750
K	4.019	13.724	643,778	14.830	13.819	308.203
L	4.522	-125.122	1,016,679	14.789	21.884	292.957
All SRKW	-	-	973,009	15.754	19.661	295.563

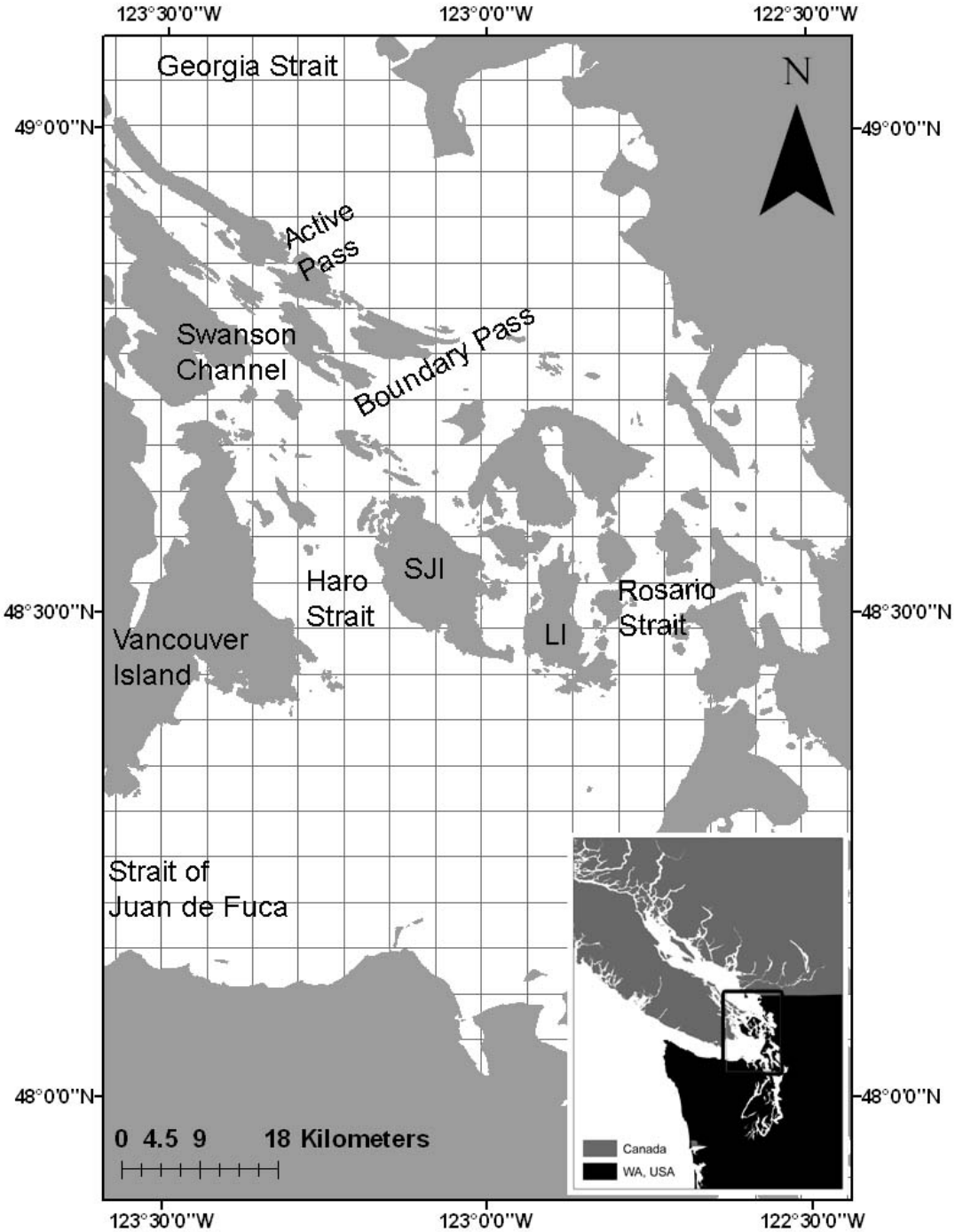

Figure 3.1. Generalized sampling grids within Washington and British Columbia inshore waters for SRKW sightings by commercial whalewatchers and regional location map. Several place names mentioned in the text are also identified. SJI represents San Juan Island, WA and LI identifies Lopez Island, WA.

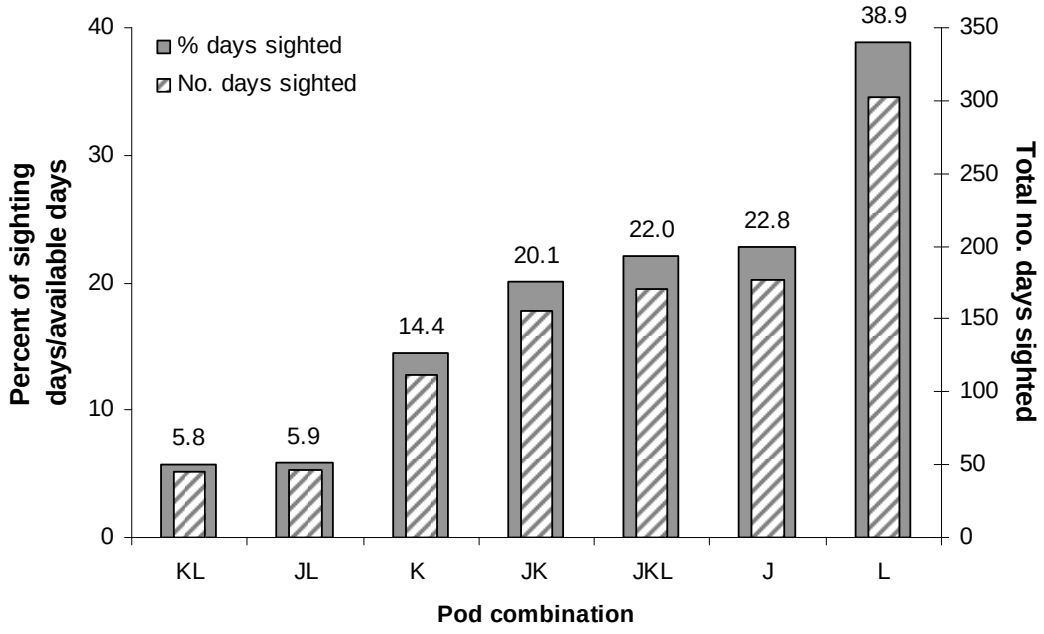

Figure 3.2. Percent of sighting days relative to available days and total number of sightings for each pod combination. Data labels represent the percentage value.

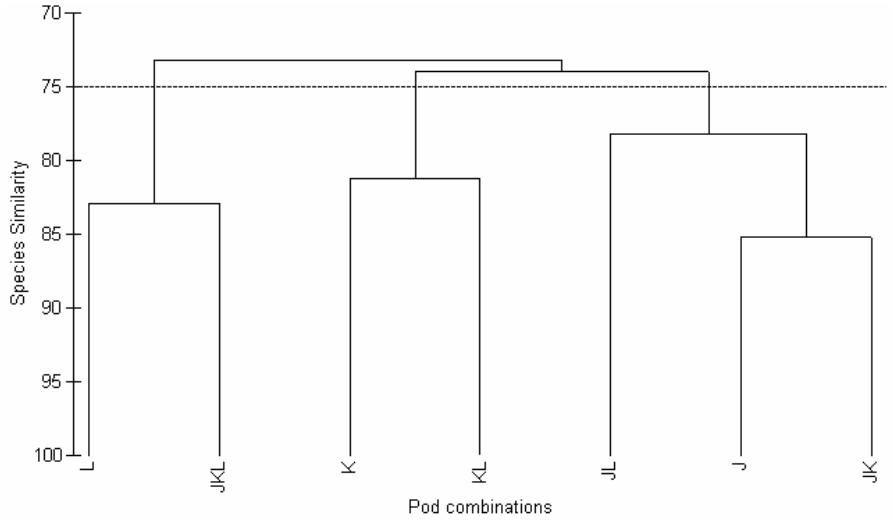

Figure 3.3. Dendrogram showing similarity in spatially-referenced density values among pod combinations as result of hierarchal clustering with group-average linking on Bray-Curtis pod combination similarities from standardized relative density values. Note the dashed line at 75% similarity indicating the presence of three groupings. Pod combinations are L pod alone (L), J, K, and L pods assembled together (JKL), K pod alone (K), K with L pod (KL), J with L pod (JL), J pod alone (J), and J with K pod (JK).

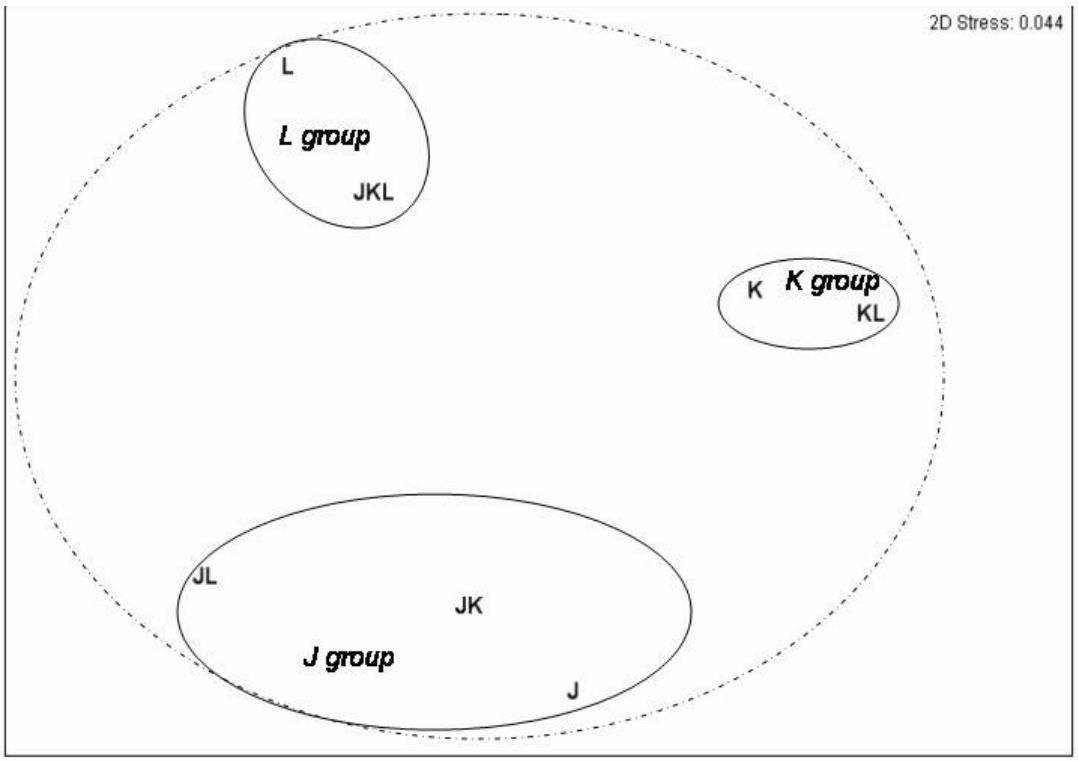

Figure 3.4. Two-dimensional non-metric multidimensional scaling configuration of similarities among pod combinations based on standardized Bray-Curtis similarity indices for spatially-referenced densities of each pod combination, with groupings from hierarchal clustering superimposed (stress=0.04). One group (composed of all pod combinations) is indicated by the dashed line at 70% similarity, three groups at 75% similarity are shown by the solid lines and referred to as J, K, and L group (shown in italics). Pod combinations are L pod alone (L), J, K, and L pods assembled together (JKL), K pod alone (K), K with L pod (KL), J with L pod (JL), J pod alone (J), and J with K pod (JK).

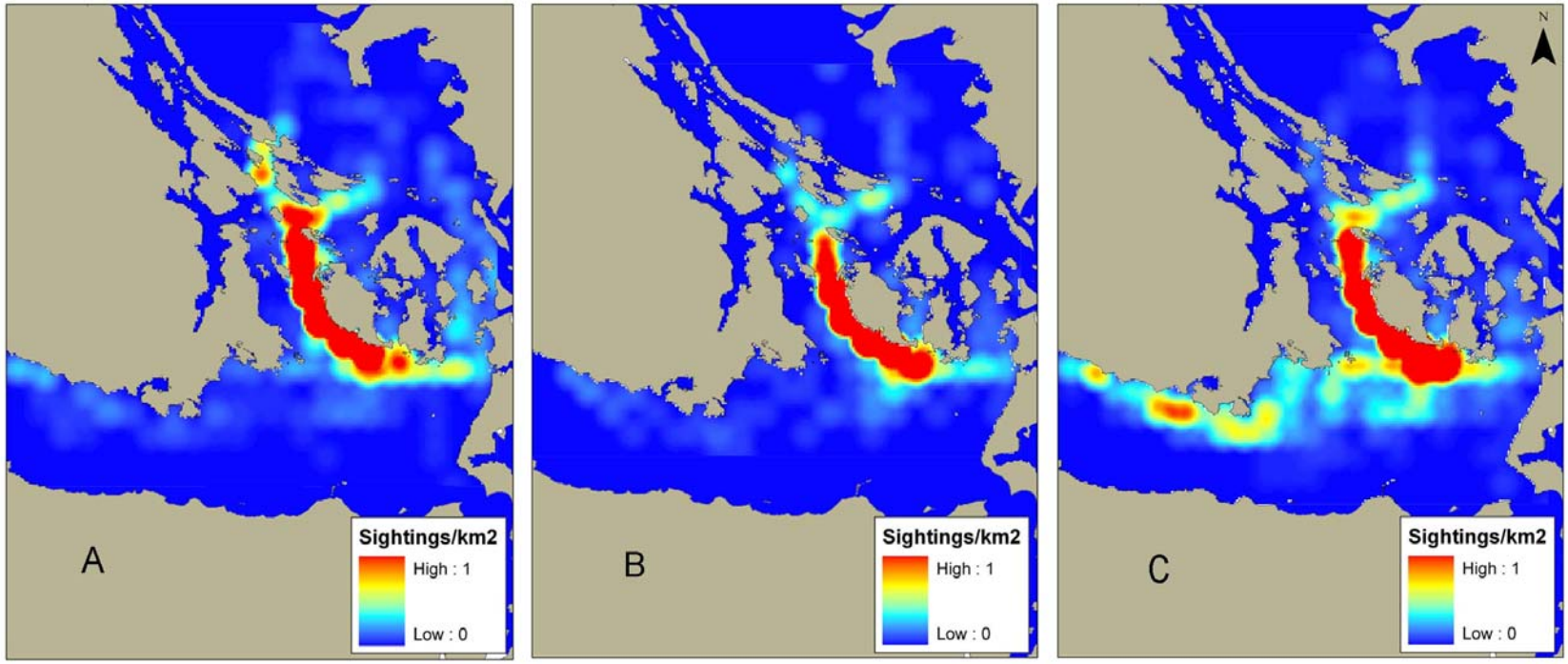

Figure 3.5. Kernel density (sightings/km^2) distributions for (A) J group, (B) K group, and (C) L group, normalized as proportion of maximum density. Reds or warmer colors represent highest sighting frequency while blues or cooler colors represent low or no sighting frequencies.

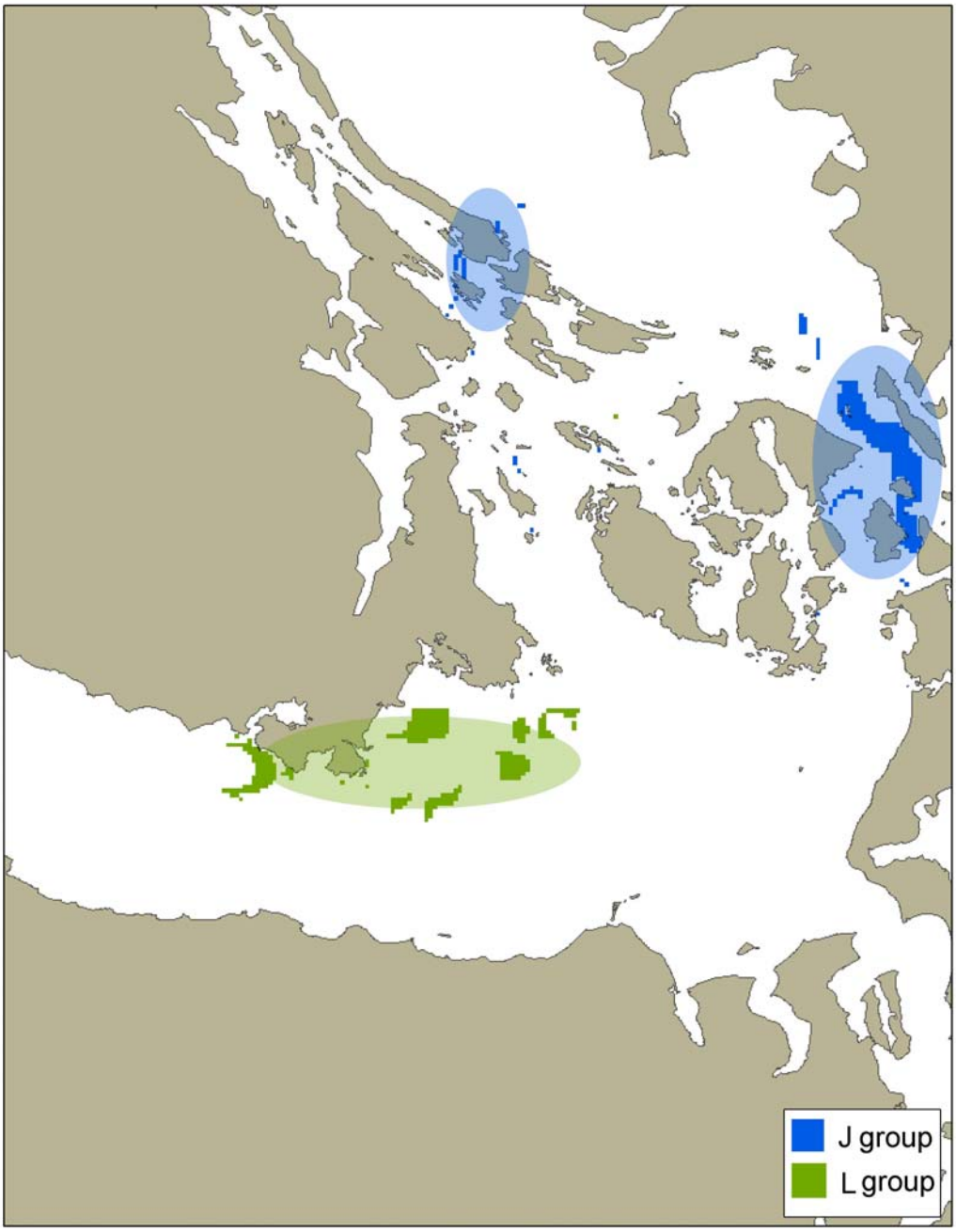

Figure 3.6. Locations representing specialization by one pod grouping. Locations were classified as high density by one pod grouping while simultaneously classified as low density for the other pod groupings. Overlaid ovals are generalized regions of specialization based on the exact locations identified. No areas of specialization were identified for K group.

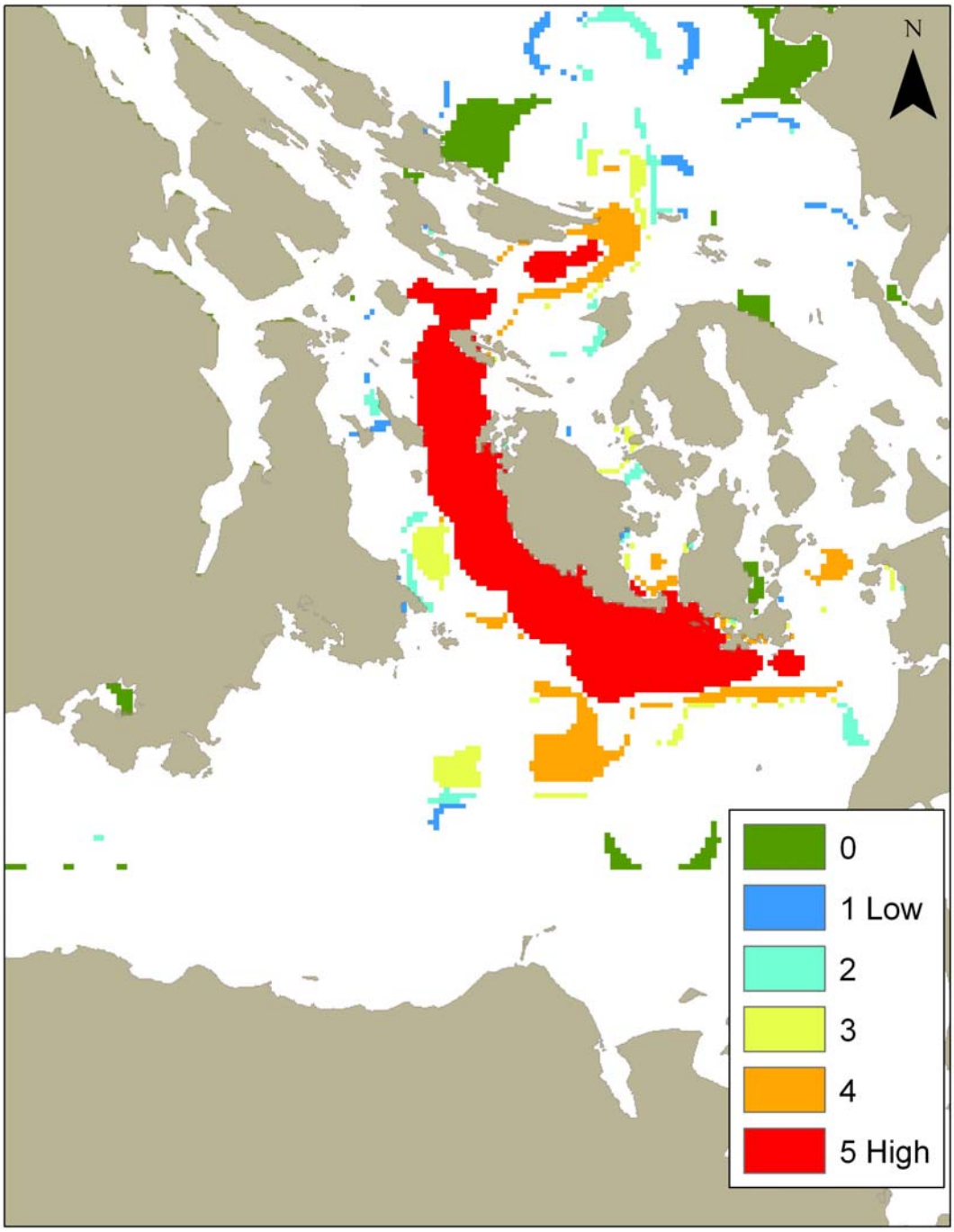

Figure 3.7. Common space use among all pod groupings of locations classified from low (1) to high (5) kernel density as well as 0 density (not used). Note that regions commonly classified as the highest density class is also considered a common core region among all pod groupings.

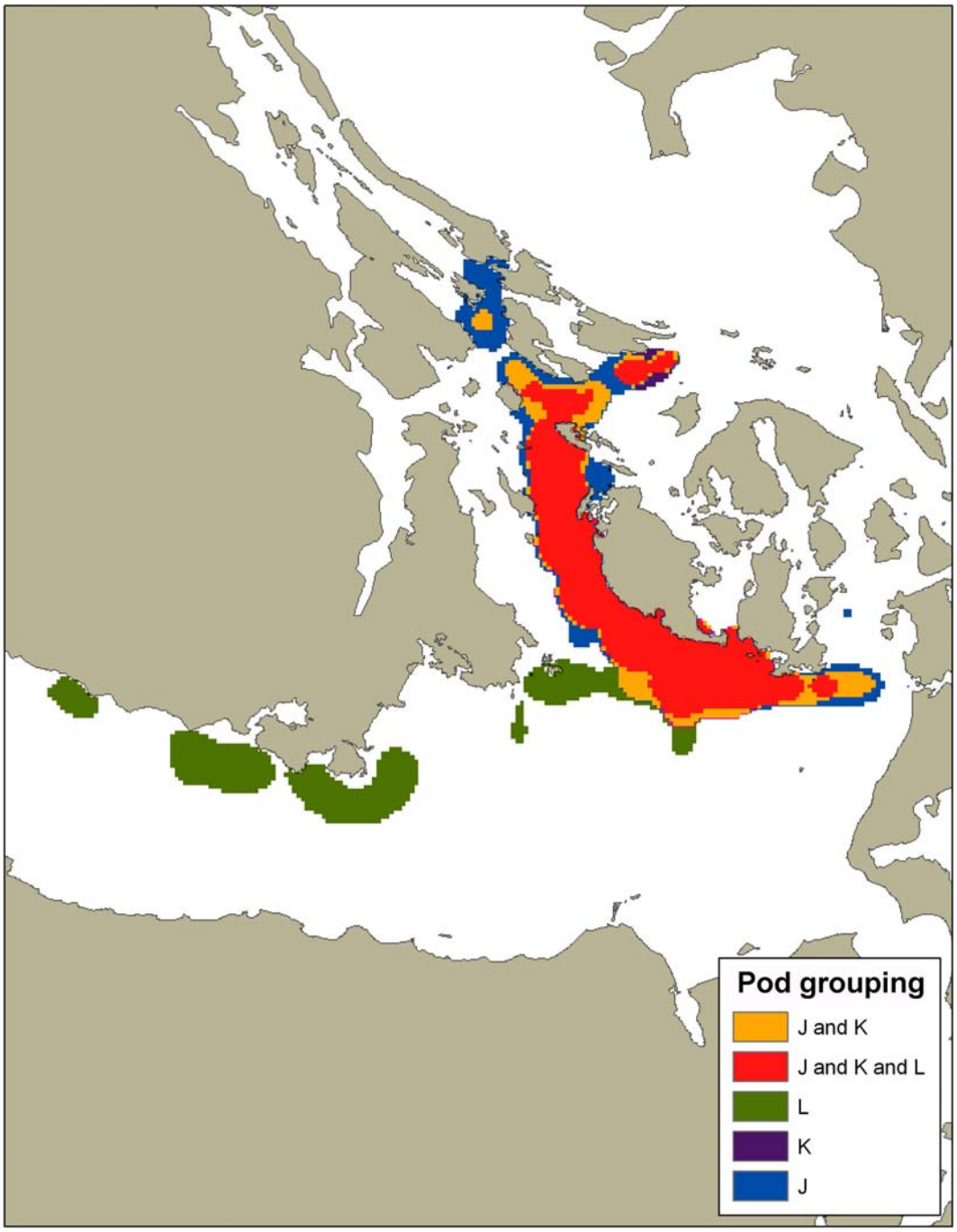

Figure 3.8. Core area locations for each pod grouping, including core area locations that were simultaneously designated for two or more pod groupings.

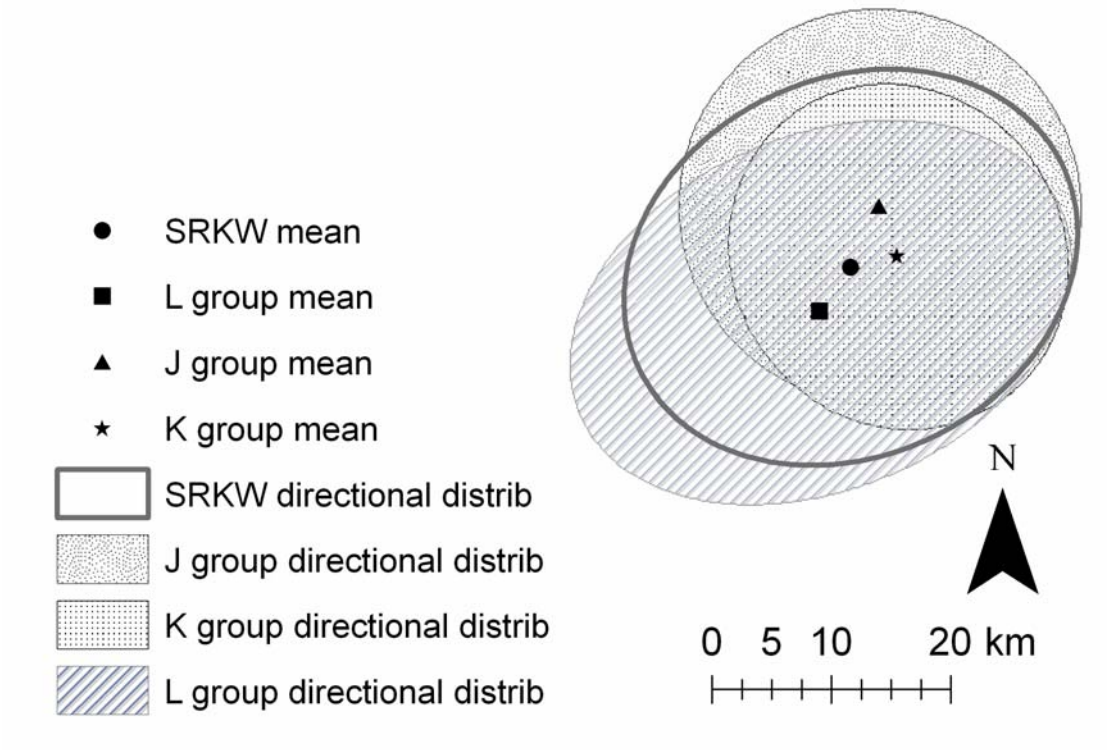

Figure 3.9. Orientation and placement in space of mean centers and directional distributions of all SRKW, J, K, and L group kernel densities. Landscape context is not included, because land will equally influence all pod groupings and its inclusion may lead to misinterpretation of land as core use areas.

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Appendix A

Extended Methodology

Introduction

As indicated in my thesis introduction, each subsequent chapter was written in manuscript form. As a result, I constrained the details of my methods sections to accommodate the space limitations common to scientific publications, particularly in Chapters Two and Three. This appendix consists of additional methods description and reference information that will prove valuable to those who wish to learn more about my spatial or multivariate modeling approaches.

Spatial data representation: fixed kernel density estimators

My goal was to describe space use, or distribution, patterns of SRKW. In spatial ecology, this is often referred to as the utilization distribution (UD) (Samuel & Garton, 1985; Samuel *et al.*, 1985; Mills & Knowlton, 1991; Kernohan *et al.*, 2001; Barg *et al.*, 2005). A UD represents the two-dimensional relative frequency of animal locations over a specific amount of time (Van Winkle, 1975; Silverman, 1986) and provides an estimation of the configuration of differential space use within the extent of the study. Several analysis techniques have been used to describe a UD from observed wildlife locations. Kernel density estimators are currently most heavily applied to many studies, including several recent cetacean studies (e.g. Gubbins, 2002; Heide-Jorgensen *et al.*, 2002; Owen *et al.*, 2002; Flores & Bazzalo, 2004).

First suggested as an estimator for UDs by Worton (1989), the fixed or adaptive kernel estimator is a nonparametric probability density function not requiring a particular distribution (Silverman, 1986):

$$\hat{f}(x) = \frac{1}{nh^2} \sum_{i=1}^{n} K\left[\frac{x - X_i}{h}\right]$$

where $\hat{f}(x)$ is the estimated probability density function (UD), n is the number of locations (sightings, in this case), h is the smoothing parameter, X represents the x and y coordinate locations for the n observed locations, x is the location or point for which the kernel estimate is being calculated, and the K [] function is the kernel function, such as the bivariate normal function used here. I applied the fixed kernel instead of the adaptive kernel because it is computationally simplified, and produces less biased results in simulations (Seaman & Powell, 1996). One can consider the density analysis as summed ‘hills’ over a point location, and the kernel function controls the hill’s shape while the smoothing parameter, or bandwidth, determines the width or how abruptly

each kernel tapers. As a result, point processes that are non-uniform or multimodal will have high density where there is a concentration of points (many hills) and low density in areas where there are few points (few hills). I used ArcGIS v9.0 (ESRI) for each of my kernel density calculations.

Kernel-based estimates are cell-based, but cell size has little effect on UD calculation relative to the smoothing parameter. The smoothing factor value determines how abruptly each kernel tapers and accentuates or minimizes regional variation depending on the set value. A small smoothing parameter allows the estimates to break into constituent kernels while a large parameter breaks local peaks and valleys into a single smoothed surface. To most appropriately represent my spatial data, I selected a smoothing parameter matching the approximate width (5 km) of each grid cell at which SRKW were originally sampled by the Pager Network. Such a parameter was chosen to prevent predicting space use beyond the unit of measurement (constituting a larger, smoother parameter value), nor underestimate space use less than the sampling unit (by using a smaller parameter value). For other studies without clearly identified sampling units, many have used least squares cross-validation to determine the best smoothing parameter value (e.g. Silverman, 1986; Worton, 1989; Seaman & Powell, 1996; Barg *et al.*, 2004). Kernel, or cell, size illustrates the level of data resolution certainty. The spatial resolution (grain), or cell size, of my representations was set to 500 m because my point distribution represents the center point of a Pager Network grid, and a sighting could have occurred anywhere within a given grid. Therefore, my grain size allows the greatest certainty about sighting locations to occur at the center point and decay as cells move away.

Kernel estimators are favored over other methods because they appear to be least biased by sample size or outliers, and are nonparametric (Kernohan *et al.*, 2001). However, there are still concerns about temporal autocorrelation and sample size, and there is no option to generate a variance expression. Although kernel estimation assumes independence between observed locations, several studies suggest that strict independence has been overemphasized. In reality, ecological relationships often depend on underlying spatial or temporal structure, and autocorrelation can be used to help understand such relationships (Legendre, 1993). Many studies suggest that a kernel-based UD should be estimated using sampling methodology that depicts organism-specific, biologically independent data instead of eliminating statistical autocorrelation (Hansteen *et al.*, 1997; Barg *et al.*, 2005). De Solla *et al.* (1999) even suggest that subsampling or restrictive sampling to reduce autocorrelation reduces the quality of UD estimates, and that kernel densities do not require serial independence of observations as long as it is consistently sampled. Accordingly, I assumed that Pager Network sampling frequency was consistent and adequate for estimating UDs. Simulation studies suggest that a minimum of 30 observations per animal should be used for kernel density estimates, but 50 is preferred (Seaman *et al.*, 1999). Each of my analyses was conducted on a minimum of 30 observations, but many more than 50 were typical.

Bray-Curtis Similarity Coefficient

I examined similarities in kernel density distribution patterns among pod assemblages (i.e. J, K, or L pod alone and in combination as JK, JKL, JL, or KL) using two multivariate approaches, hierarchal clustering and non-metric multidimensional scaling. Both multivariate approaches depend on the use of a similarity matrix, and I used the Bray-Curtis species similarity coefficient (Bray & Curtis, 1957). PRIMER 6.0 was used for all multivariate analyses (Plymouth Routines in Multivariate Ecological Research; Clarke & Warwick, 2001). The Bray-Curtis similarity coefficient measured the similarities in distribution between pairs of pod assemblages, and was calculated as:

$$S_{jk} = 100\left(1 - \frac{\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}(y_{ij} + y_{ik})}\right)$$

where S_{jk} is the similarity in pod assemblages between grid cell *j* and *k*, y_{ij} is the kernel density for the *i*th pod assemblage in the *j*th cell, and y_{ik} is the kernel density for the *i*th pod assemblage in the *k*th sample. Thus, the Bray-Curtis similarity coefficient is a calculation of the absolute value of the sum of differences divided by the sum of the totals for all pod assemblages in cells *j* and *k*, and it is favored in ecological studies (Clarke & Warwick, 2001; Wang, 2005). Similarity will equal zero if two pod assemblages have no cells in common, and it will range up to 100 if the density values are equal across cells. Kernel density for each pod assemblage was first normalized as the proportion of each pod assemblage's maximum density value. Next, Clarke & Warwick (2001) recommend standardizing by species for species similarity analyses, so we standardized among pod assemblages before calculating the Bray-Curtis similarity coefficient.

Appendix B

Physical environmental characteristics within core areas of Southern Resident killer whale pods

Introduction

Many physical, biological, and anthropogenic factors may affect the distribution of cetaceans in complex marine environments. The relationship of space use and environmental determinants is inherently dynamic, and a range of environmental variables have been correlated with cetacean distribution, including sea surface temperature (Baumgartner *et al.*, 2001; Hamazaki, 2002; Hastie *et al.*, 2005), salinity (Selzer & Payne, 1988; Forney, 2000), water depth (Selzer & Payne, 1988; Hooker *et al.*, 2002; Hastie *et al.*, 2004; Hastie *et al.*, 2005), seabed gradient (Selzer & Payne, 1988), distance from the nearest shore (Laidre *et al.*, 2004b), and tidal eddies or currents (Baumgartner *et al.*, 2003a; Baumgartner & Mate, 2003; Johnston *et al.*, 2005). In addition, many studies have linked cetacean distribution with prey distribution or availability (Jaquet & Gendron, 2002; Baumgartner *et al.*, 2003a; Benoit-Bird & Au, 2003; Hastie *et al.*, 2004) or indicators of prey productivity (Jaquet *et al.*, 1996; Rendell *et al.*, 2004). Finally, the effects of anthropogenic disturbance or global climate changes are increasingly of concern for many cetacean species and populations and may lead to shifts in space use (Hastie *et al.*, 2005; Laidre & Heide-Jorgensen, 2005; Ward-Geiger *et al.*, 2005).

Likewise, several factors could be motivating the space use patterns of Southern Resident killer whales (SRKW) described in the previous chapters, but analysis of each potential contributing aspect is beyond the scope of this thesis. Salmonid prey populations have been linked to Northern Resident killer whale distribution (Nichol & Shackleton, 1996), and there are indications of a relationship in prey availability and distribution for SRKW (McCluskey, 2006). In addition, many potential risk factors have been identified that may affect the space use patterns of SRKW, including vessel impacts and reductions in prey quality or quantity (Baird, 2001; Krahn *et al.*, 2004). SRKW foraging behavior has been observed over high relief subsurface topography where salmon presumably concentrate, while traveling most frequently occurred from headland to headland (Heimlich-Boran, 1988). In contrast, other studies have found that SRKW foraging behavior was not correlated with bottom topography within the same study area as that for Heimlich-Boran (1988), and foraging was equally likely over all bottom topographies (Hoelzel, 1993). The discrepancies between these studies are unclear and require clarification. I conducted initial investigations into the relationship of SRKW distribution patterns and three physical environmental factors (water depth, Euclidean distance to nearest shore, and bottom slope). My overall goal was to describe the environmental attributes found within each pod group's core area

relative to the available environment throughout the study area. Such analyses provide an indication of habitat preferences among SRKW pods.

Methods

Bathymetry data was obtained from the University of Washington, School of Oceanography, with mean depth converted to meters and described for 0.25 km^2 cells (Figure B1). Euclidian distance from the nearest shore was calculated from the center of every 0.25km^2 cell using ArcGIS Spatial Analyst distance tools and set to match the extent of the depth and slope data (Figure B2). Percent change in slope was derived from the bathymetry data, with 0.25 km^2 grain cell size (Figure B3). Slope was calculated as the maximum rate of change between each depth cell and its adjacent neighboring cells. Slope can range from 0 to 100 percent change, where a low slope value indicates flatter topography and a high value indicates a steep ocean bottom. The center point of each raster environmental grid cell was converted to a vector point, and the value for each location represented the 'available' suite and extent of environmental characteristics within the study area for habitat selection by SRKW.

To consider relationships between environmental characteristics and pod distribution, pod groups were first distinguished and I found their normalized density (proportion of maximum), as described in Chapter Three. Raster density data was converted to vector points and overlapping depth, distance, and slope was extracted for each point. Locations with zero density or a lack of sightings were excluded from analyses. First, density values were plotted against each environmental variable. A simple linear relationship was fit for depth. Next, I selected only the points that were considered within core areas for each pod group and extracted the overlapping depth, distance, and slope. Frequency histograms of the depth, distance, and slope distributions were constructed for each pod group's core area as well as what was available within the study region. Lastly, mean, standard deviation, and standard error of depth, distance, and slope was calculated for the core area of each pod group as well as what was available within the study region.

Results and discussion

Scatterplots of SRKW pod density and environmental variables suggest that SRKW had distinct relationships with depth, distance, and slope (Figure B4). In the case of each environmental characteristic, there was always low SRKW density across the entire range of the environmental parameter, and no regression lines were fitted for comparisons with distance and slope. There was a slight, yet significant ($p<0.05$), positive linear relationship with depth for each pod group, where pods tended to have higher density in deeper cells. Highest density cells for each pod group also occurred closer to shore, and there appeared to be little relationship with slope. These analyses, however, did not consider what was available within the study region.

The next step in analyses considered habitat choices (i.e. the environmental parameters within the core areas of each pod group) relative to what was available. Frequency histograms describe the relative distribution of chosen habitat (core areas) for each pod group and the available habitat (Figure B5), and Figure B6 shows mean depth, distance, and slope for each pod group's core area and the overall study region. With these analyses, it appears that each pod group selected core areas with slightly deeper waters than the available depth distribution, as well as steeper waters. Again, core areas that were closer to shore than what was available were somewhat preferred, but it is clear that everything is near-shore within the study region and this may be a spurious result. I did not use any standard statistical analyses to test the power of these relationships because independence and parametric assumptions are broken in this case. In addition, results would be confounded by cross-correlations among environmental variables. Such analyses would require extensive additional statistical modeling, but the general trends described here provide initial interpretation of SRKW habitat choices within their core areas.

Each pod appeared to respond similarly to each environmental variable. Although Chapter Three described distinctions among the pod groups, particularly J and L groups, each group also shares a large common core area in Haro Strait. As a result, it is not surprising that there were very similar mean environmental values for each pod group or indistinct relationships of density and environment. Considering the scatterplots, we see the greatest variance for L group, which would be expected given L group's high level of spatial dispersion as described in Chapter Three. Despite similar use of areas (in terms of depth, distance, and slope) among the three pod groups, there was some variability in the actual spatial location of core areas. Thus, these analyses enhance the need to actually consider spatial distribution as a component of habitat modeling for species of interest. In addition, these habitat variables are likely very different in areas outside of the SRKW summer range, so these relationships may not necessarily extend directly to the other areas used by SRKW.

Each environmental factor is considered as a proxy or contributor to more likely factors that are motivating the distribution patterns of SRKW, like prey distribution. Potentially, depth, distance from shore, or slope affect how prey distribute within this region, such that SRKW may be responding to prey rather than actual physical structure. Likewise, there are several other environmental conditions that are worthy of continued research, such as eddies, tides, currents, and water temperature that may effectively concentrate or affect distributions of prey in predictable ways for SRKW. Future research into the functional mechanisms driving SRKW distribution could consider the behavioral use of core areas as well as the relationship to the physical environment. For example, perhaps SRKW are foraging in deeper water within their core areas and resting in shallow areas. Behaviors that directly influence population survival, particularly foraging or reproduction, may be primarily associated with key environmental characteristics within core areas, possibly making them higher priority for management.

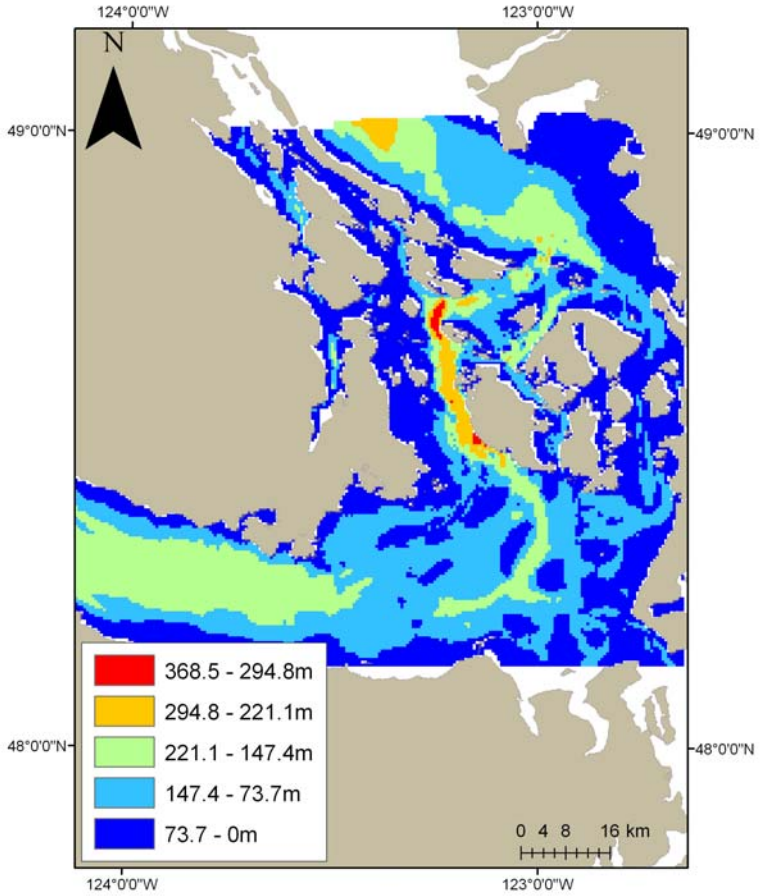

Figure B1. Depths (m) within the study area.

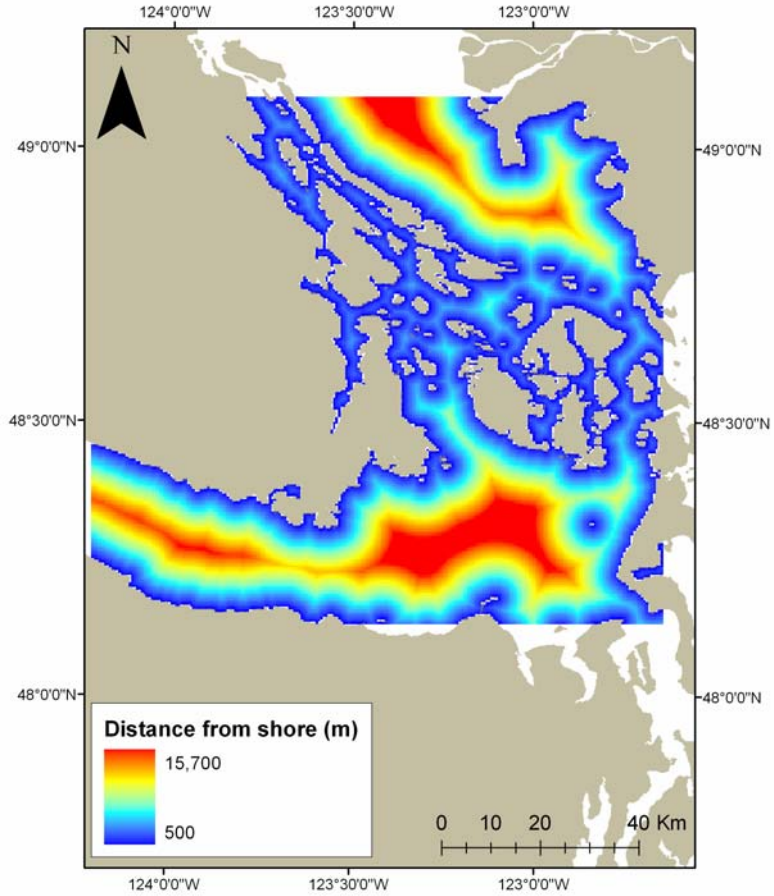

Figure B2. Distribution of distance from shore (m) within the study region.

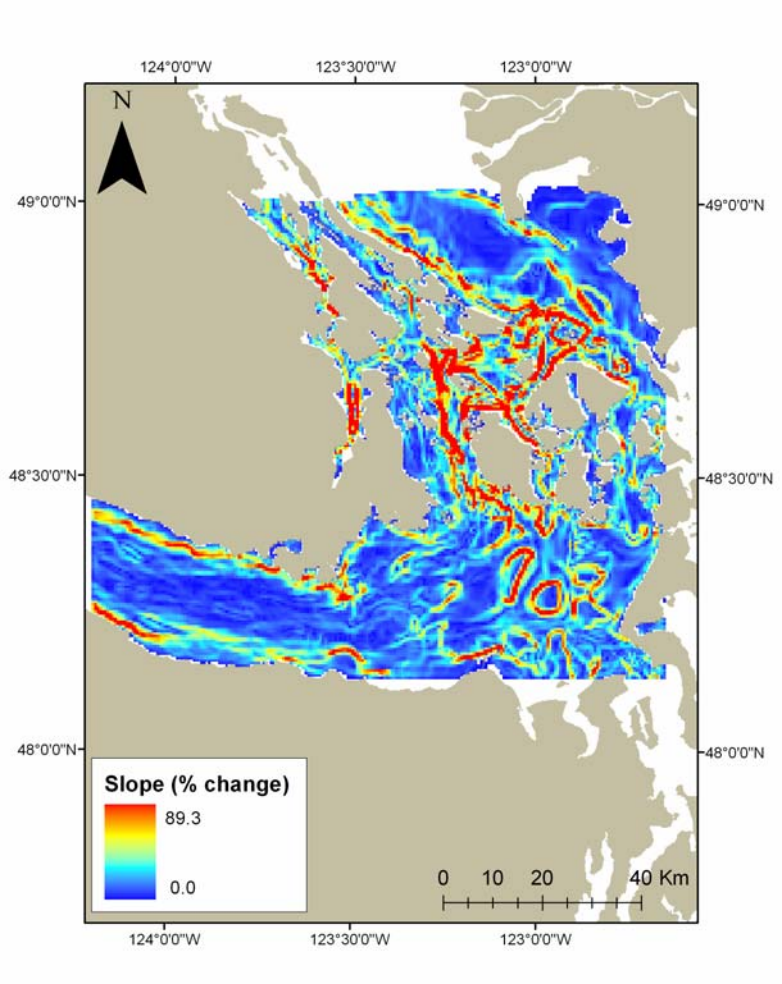

Figure B3. Bottom slope (% change) distribution within the study area.

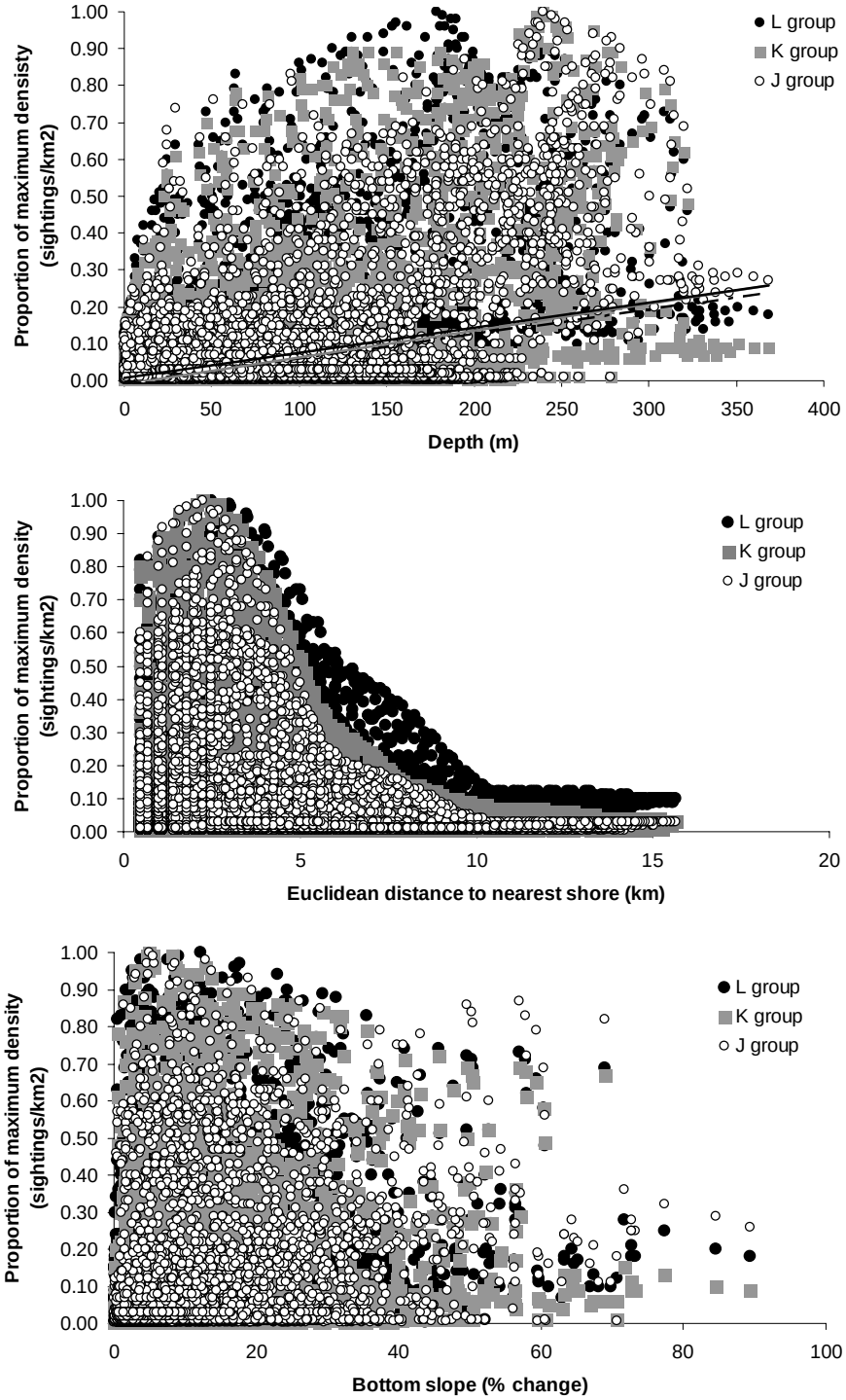

Figure B4. Scatterplots of the depth (m), distance to nearest shore (km), and bottom slope (% change) and relative density of each J, K, or L group sighting. Linear relationships were fit for depth and J (R^2=0.114), K (R^2=0.106), and L (R^2=0.095) groups.

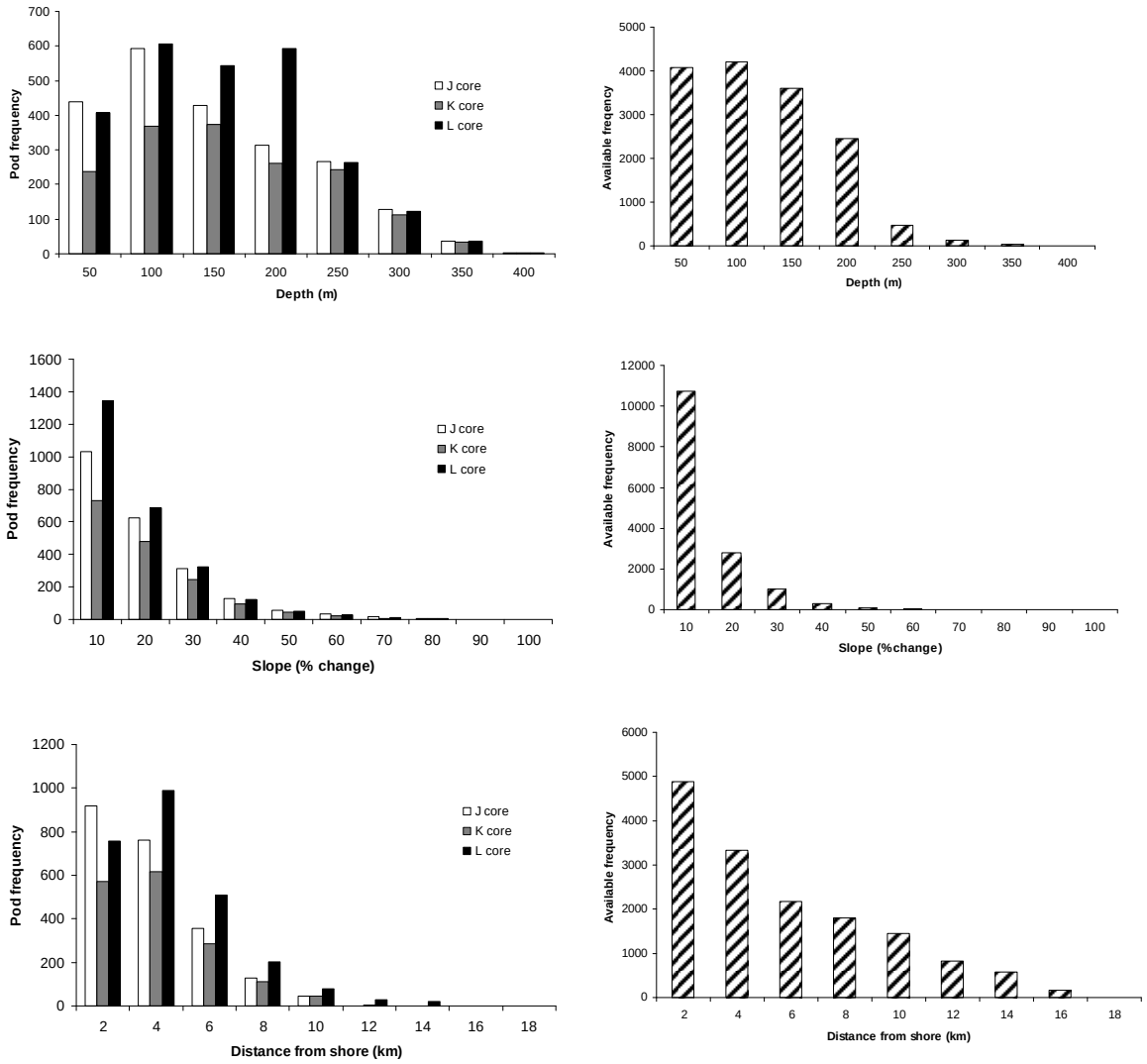

Figure B5. Frequency histograms of the distribution of depth (m), slope (% change), and distance from the nearest shore (km) for J, K, and L group core areas as well as what was available throughout the study area.

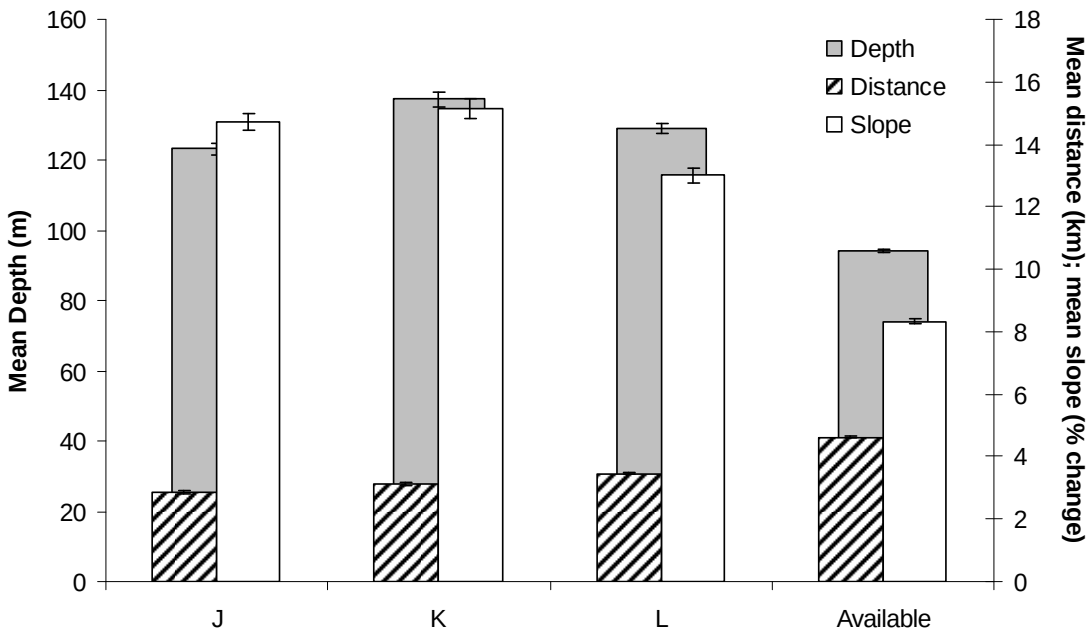

Figure B6. Mean depth (m), distance from nearest shore (km), and slope (% change) within J, K, and L pod groups' core area as well as what was available throughout the entire study area. Error bars represent standard error.

Appendix C

Example visual representations of Southern Resident killer whale space use at each temporal scale

As described in Chapter Two, I sampled and modeled space use as kernel density for every week, month, and summer season of each year of data (1996-2001). Here, I present examples of the maps that were produced for each temporal scale. Each shows normalized density after classification into five density classes, ranging from low to high kernel density (excluding zero density). Each is color scaled, where blue represents the lowest density class ranging to red as the highest density class. It should be noted that red regions were also considered the core area for the given sample. First, the normalized density of each week of 1998 is included to represent examples of variability in the weekly temporal scale. Next, only the core areas are included for the monthly temporal scale, and samples from 1998 are used as an example. Finally, normalized density for each summer season is included.

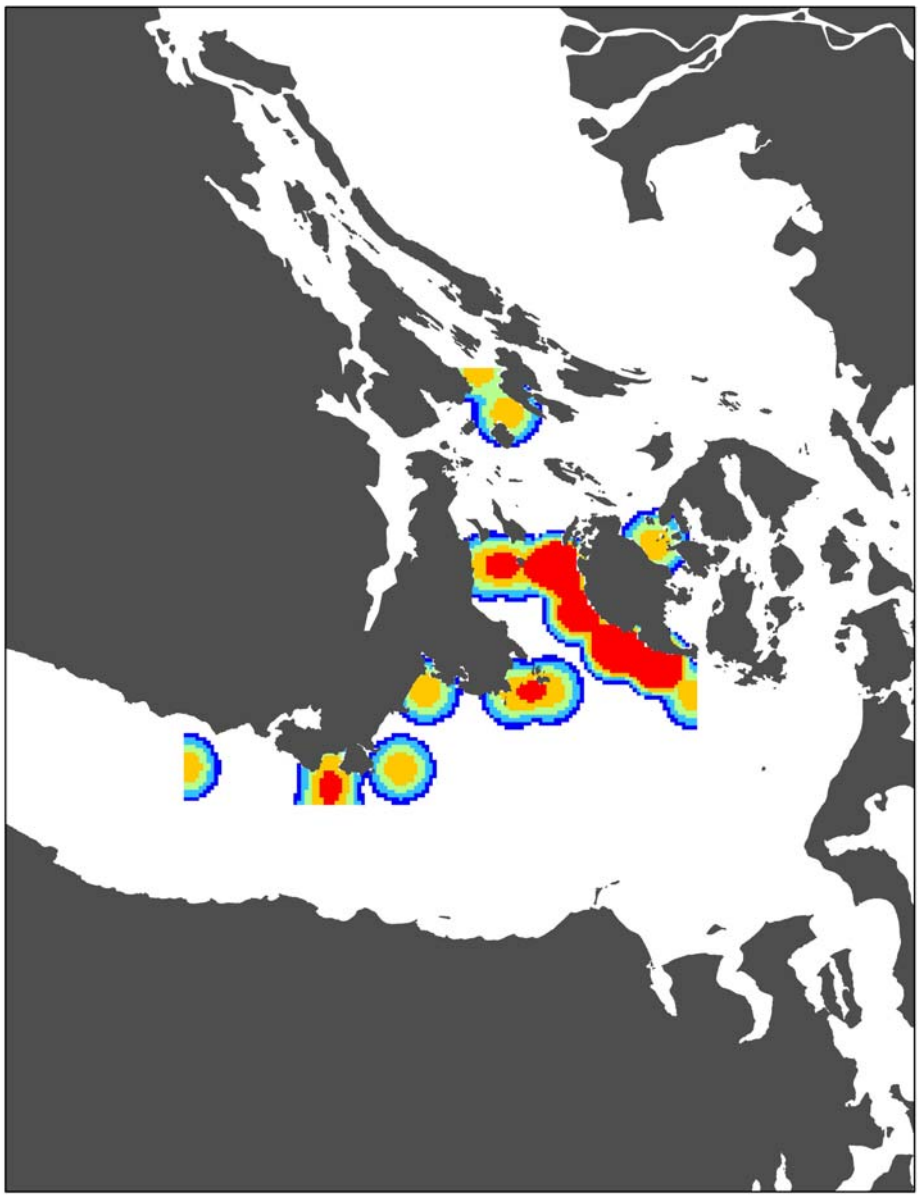

Figure C1. Week 22 of 1998 total space use by SRKW.

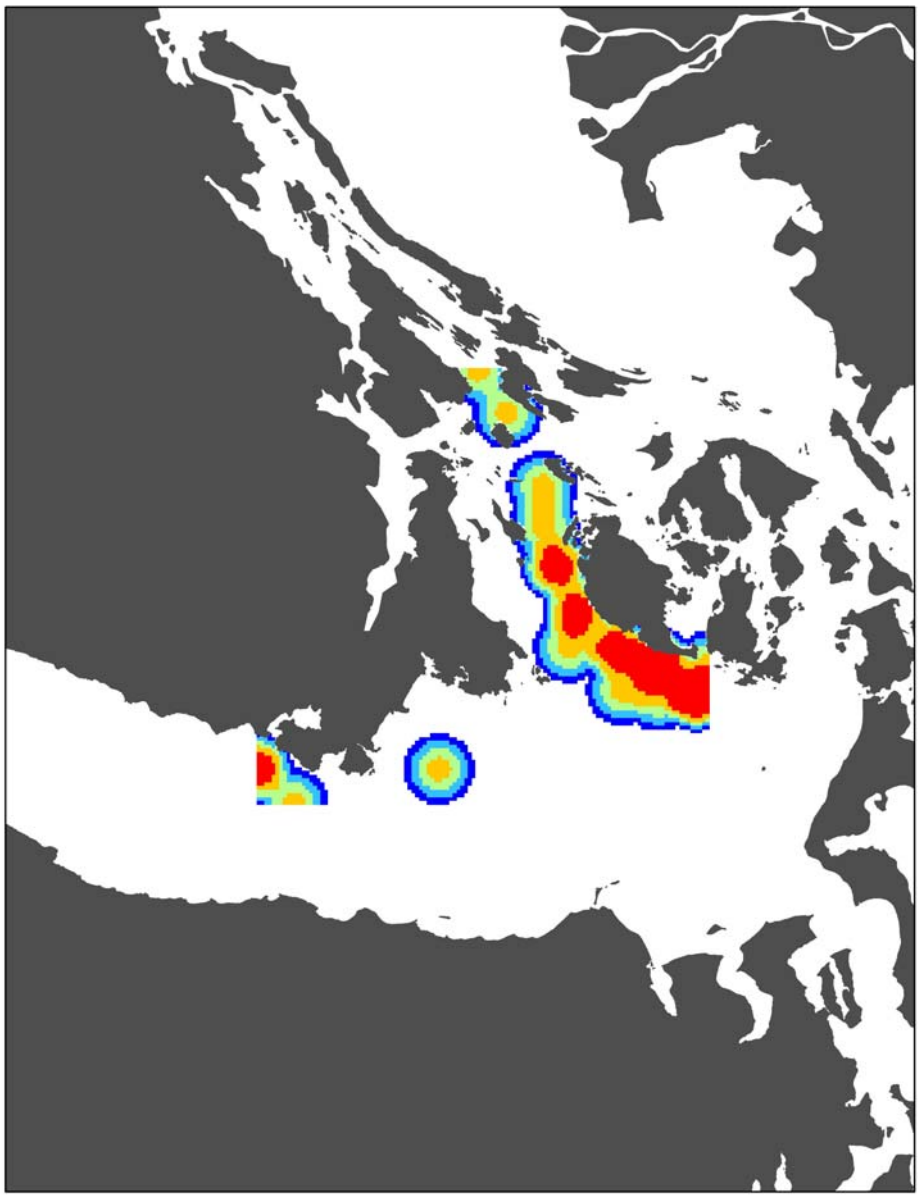

Figure C2. Week 23 of 1998 (early June) total space use by SRKW.

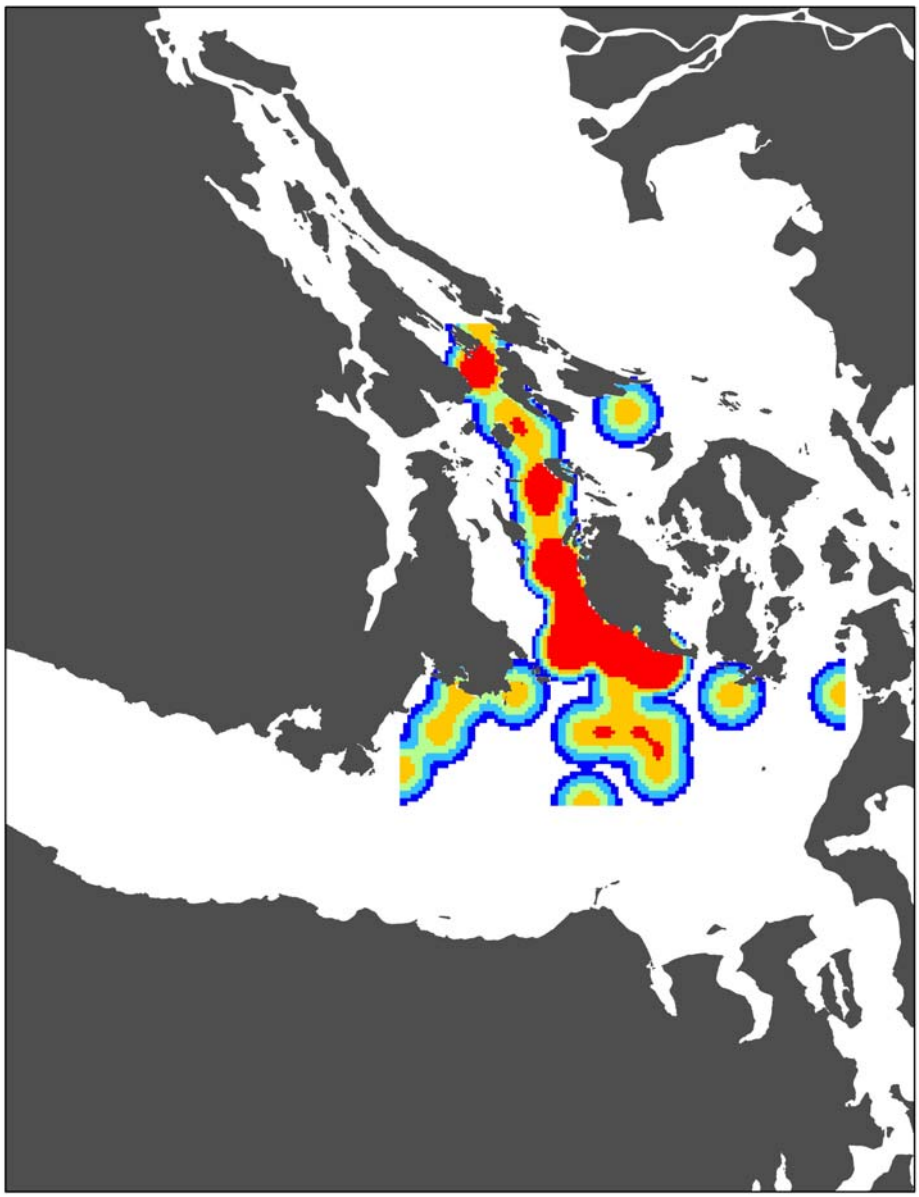

Figure C3. Week 24 of 1998 total space use by SRKW.

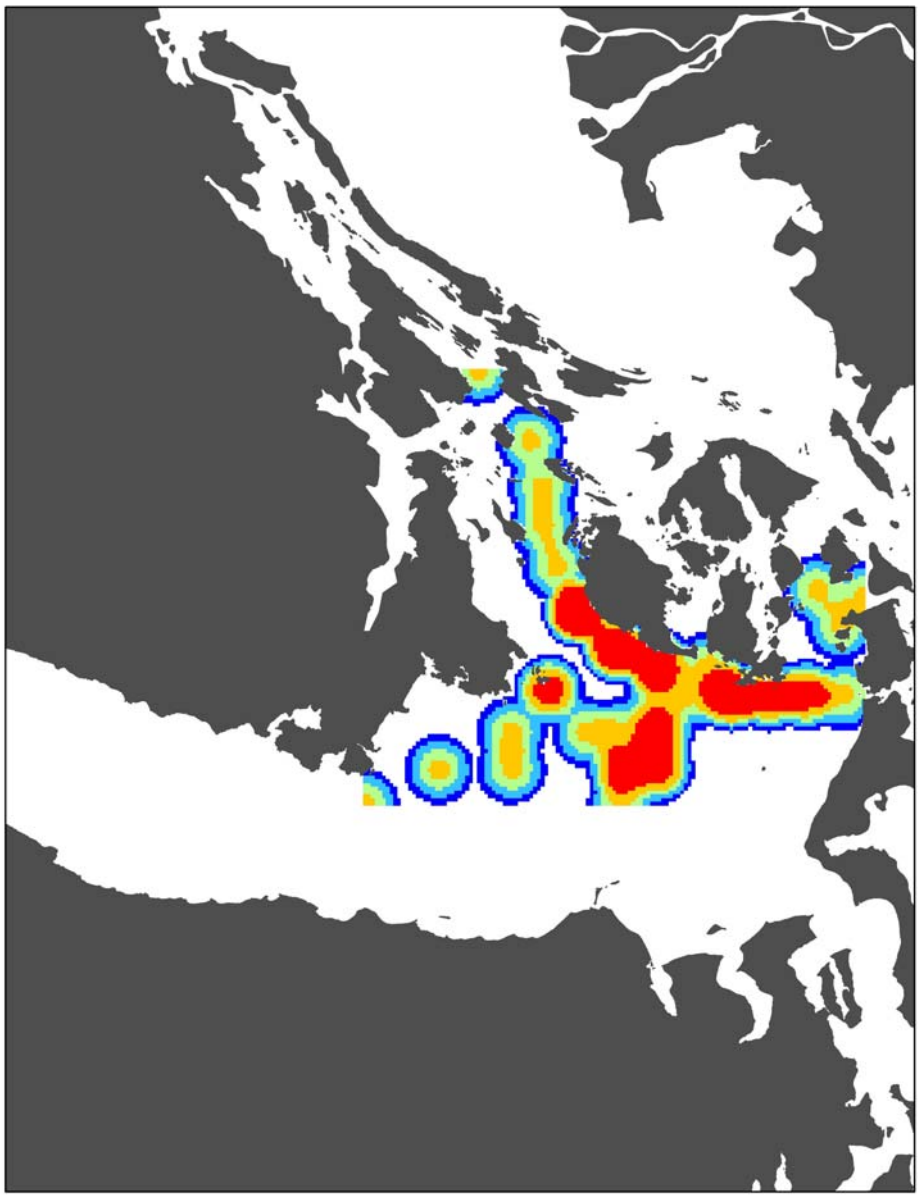

Figure C4. Week 25 of 1998 total space use by SRKW.

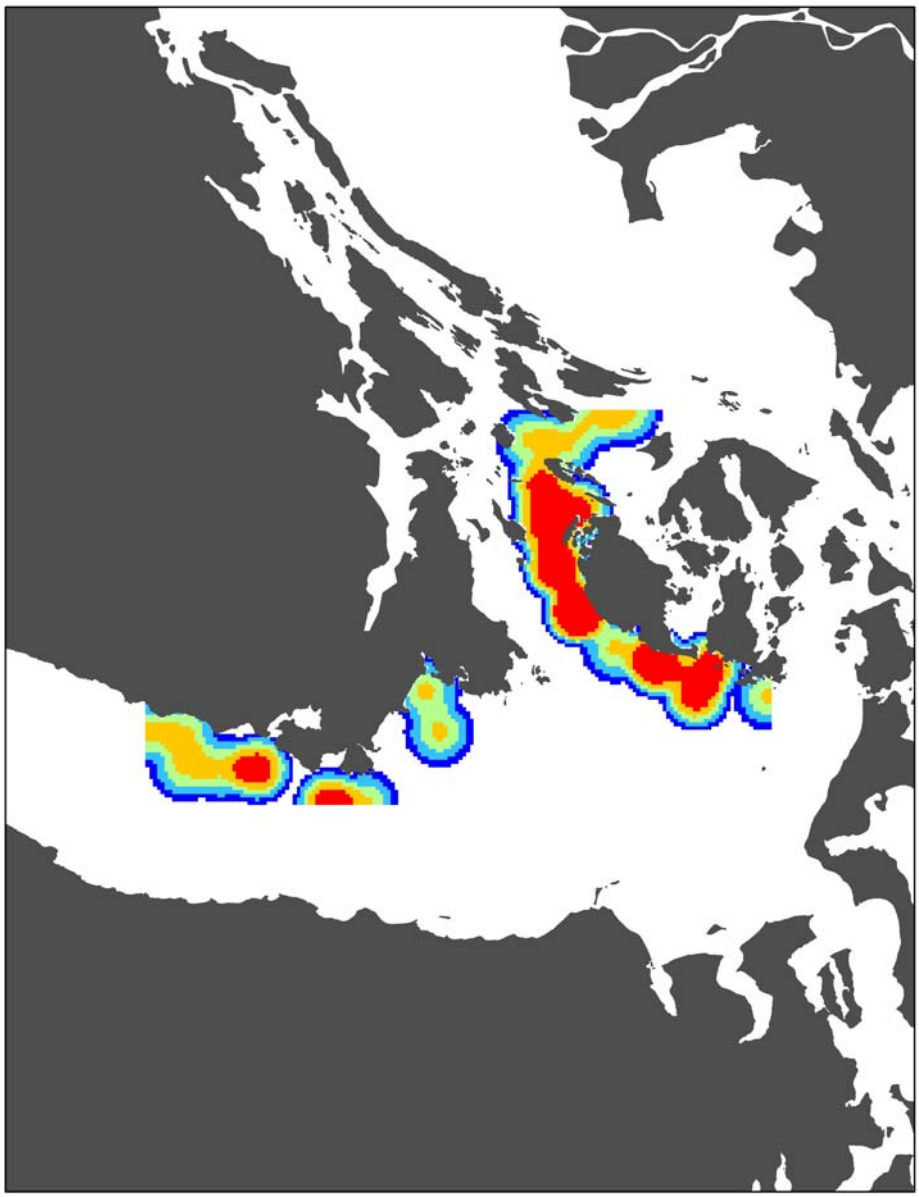

Figure C5. Week 26 of 1998 total space use by SRKW.

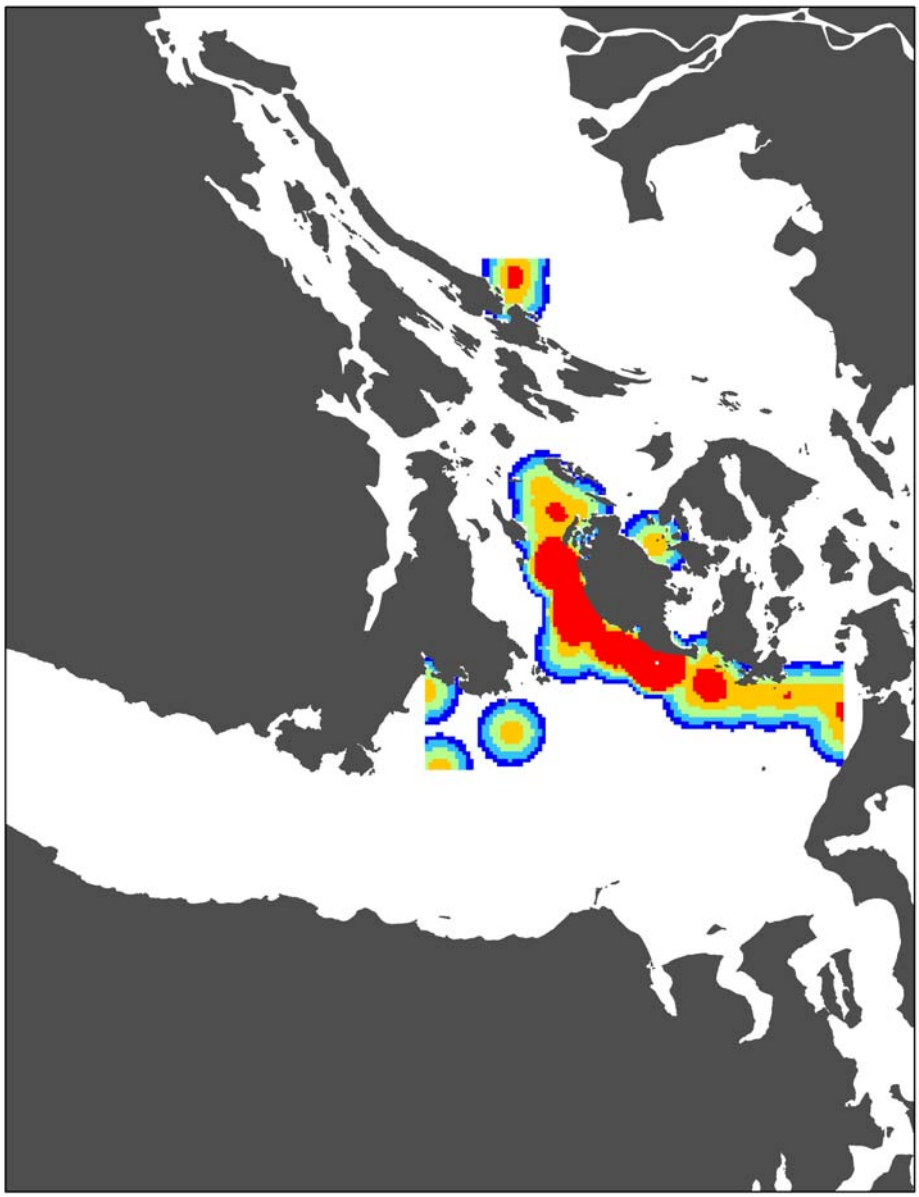

Figure C6. Week 27 of 1998 (early July) total space use by SRKW.

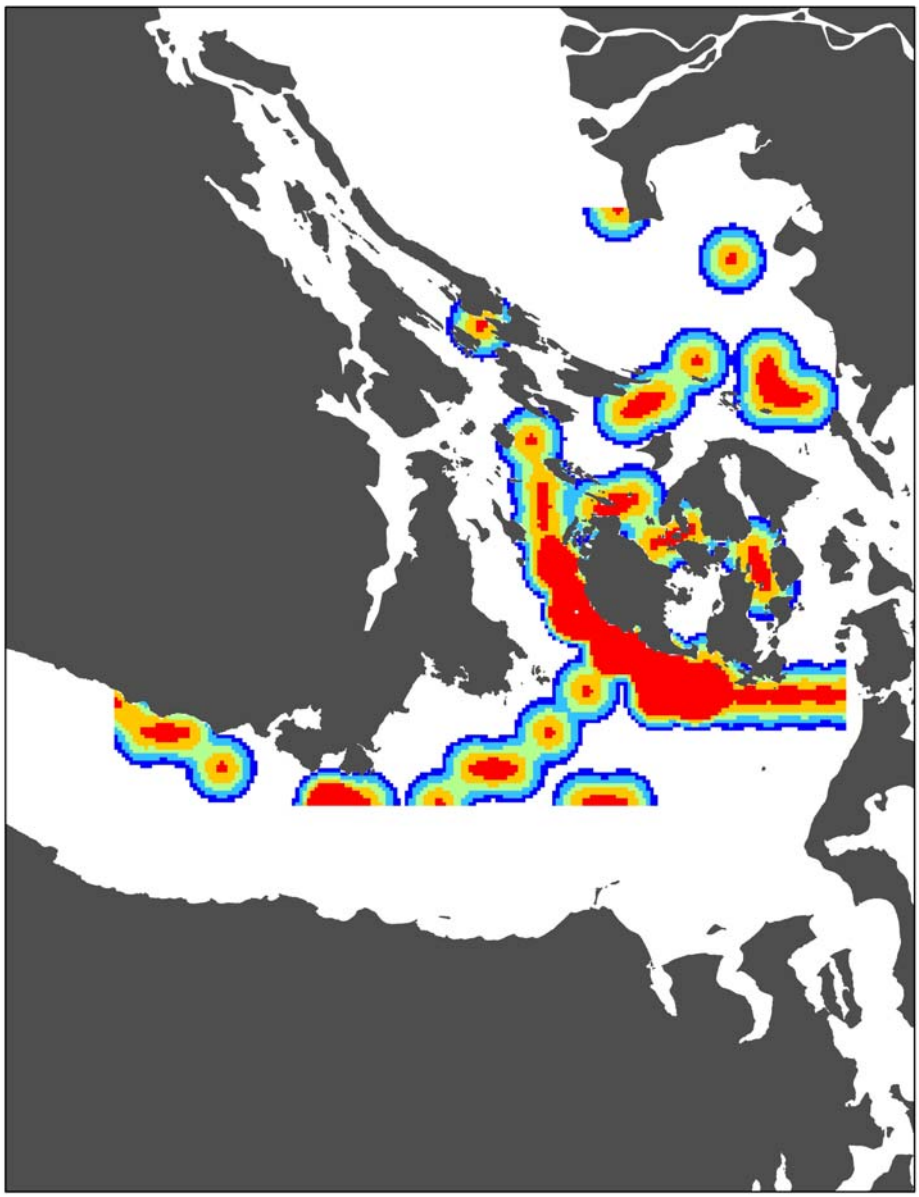

Figure C7. Week 28 of 1998 total space use by SRKW.

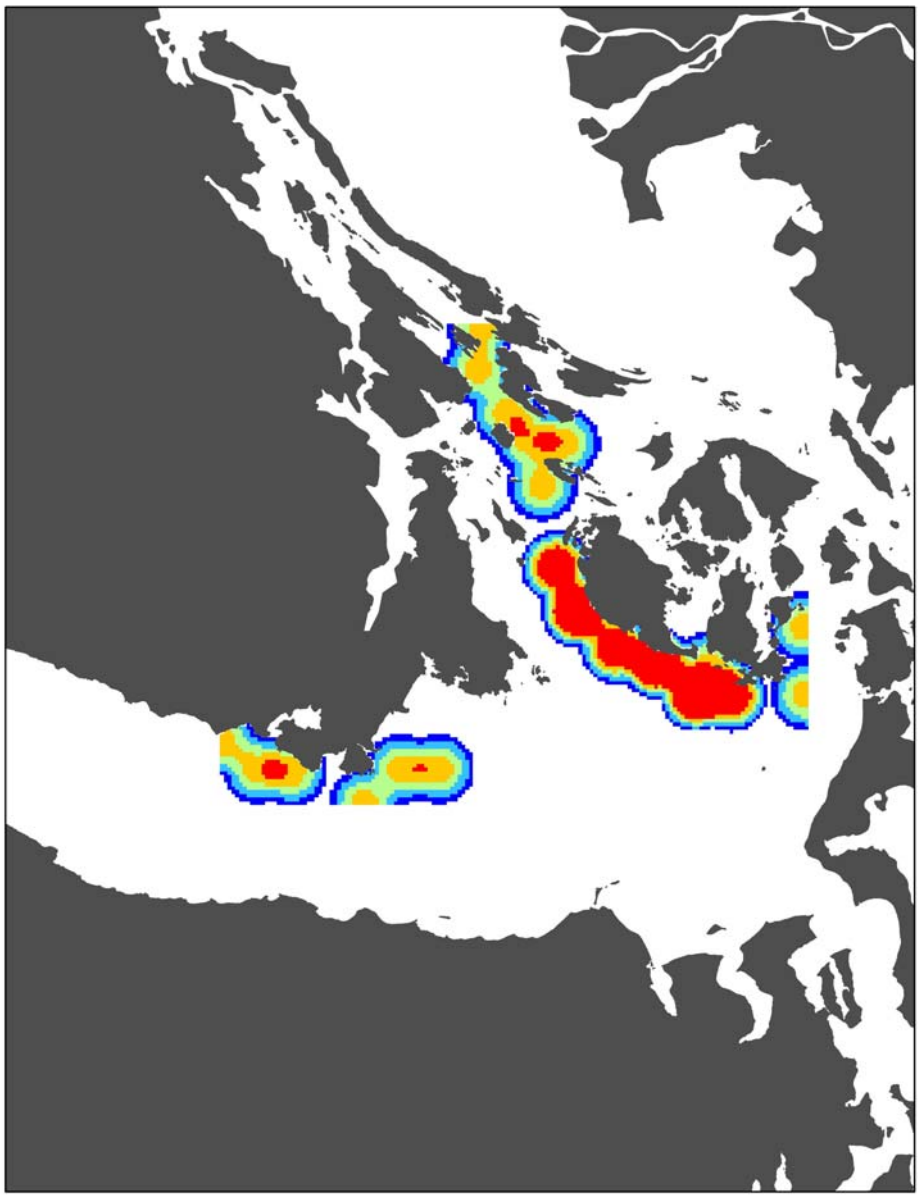

Figure C8. Week 29 of 1998 total space use by SRKW.

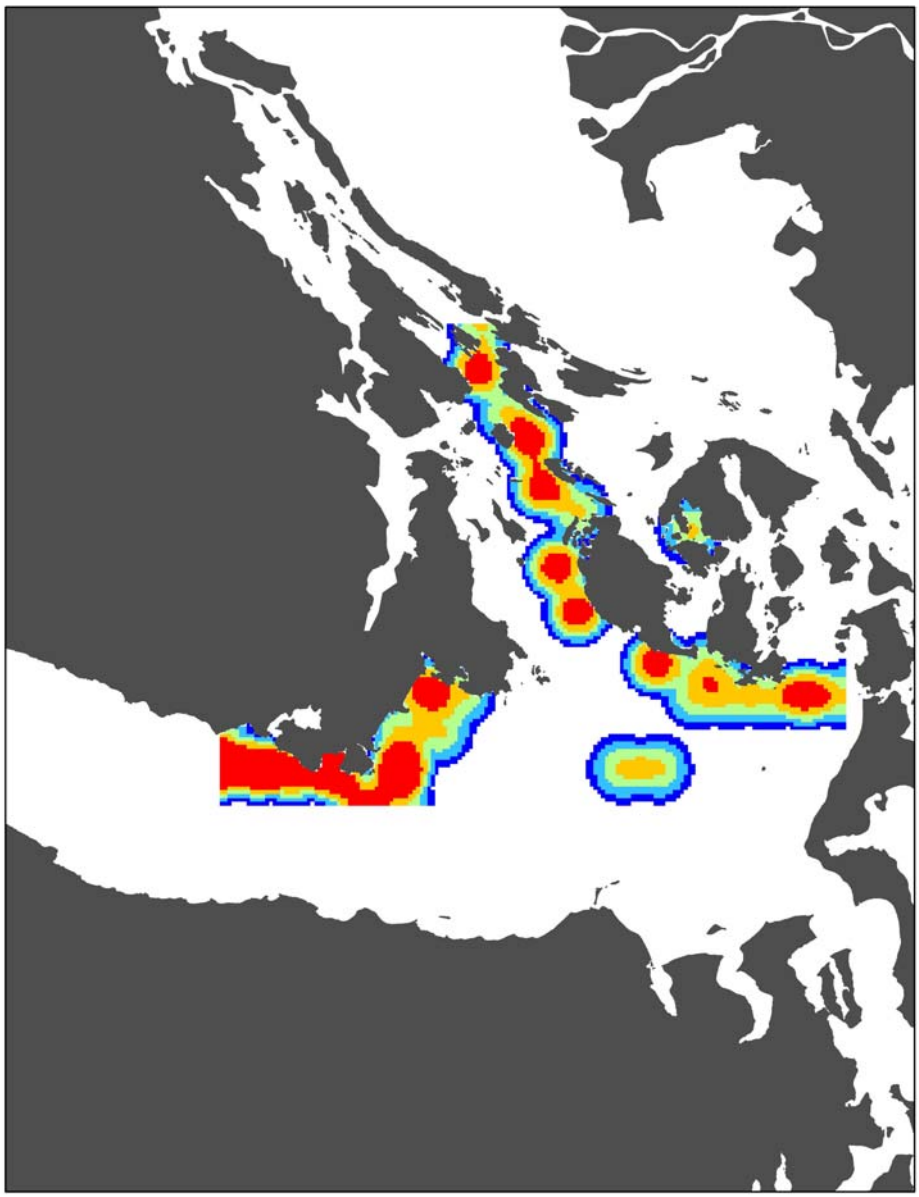

Figure C9. Week 30 of 1998 total space use by SRKW.

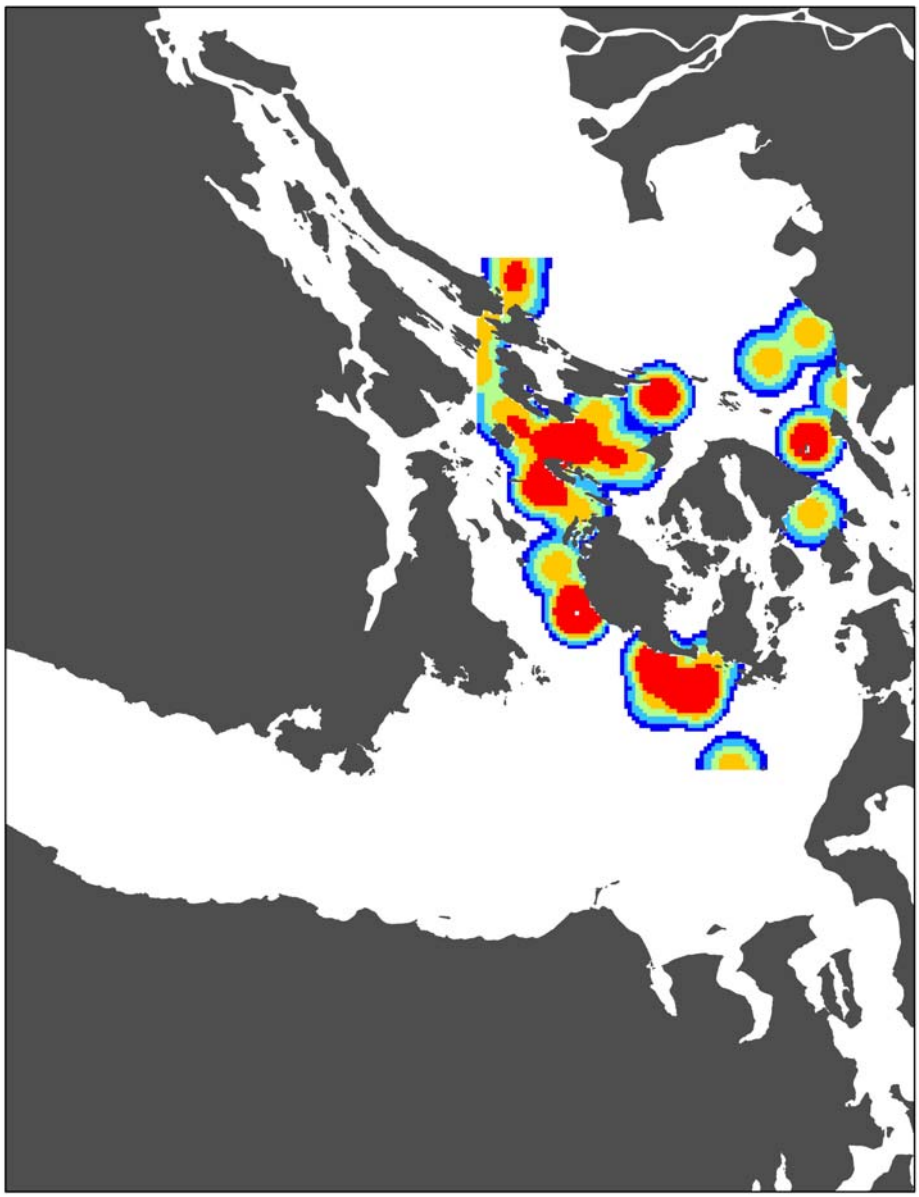

Figure C10. Week 31 (early August) of 1998 total space use by SRKW.

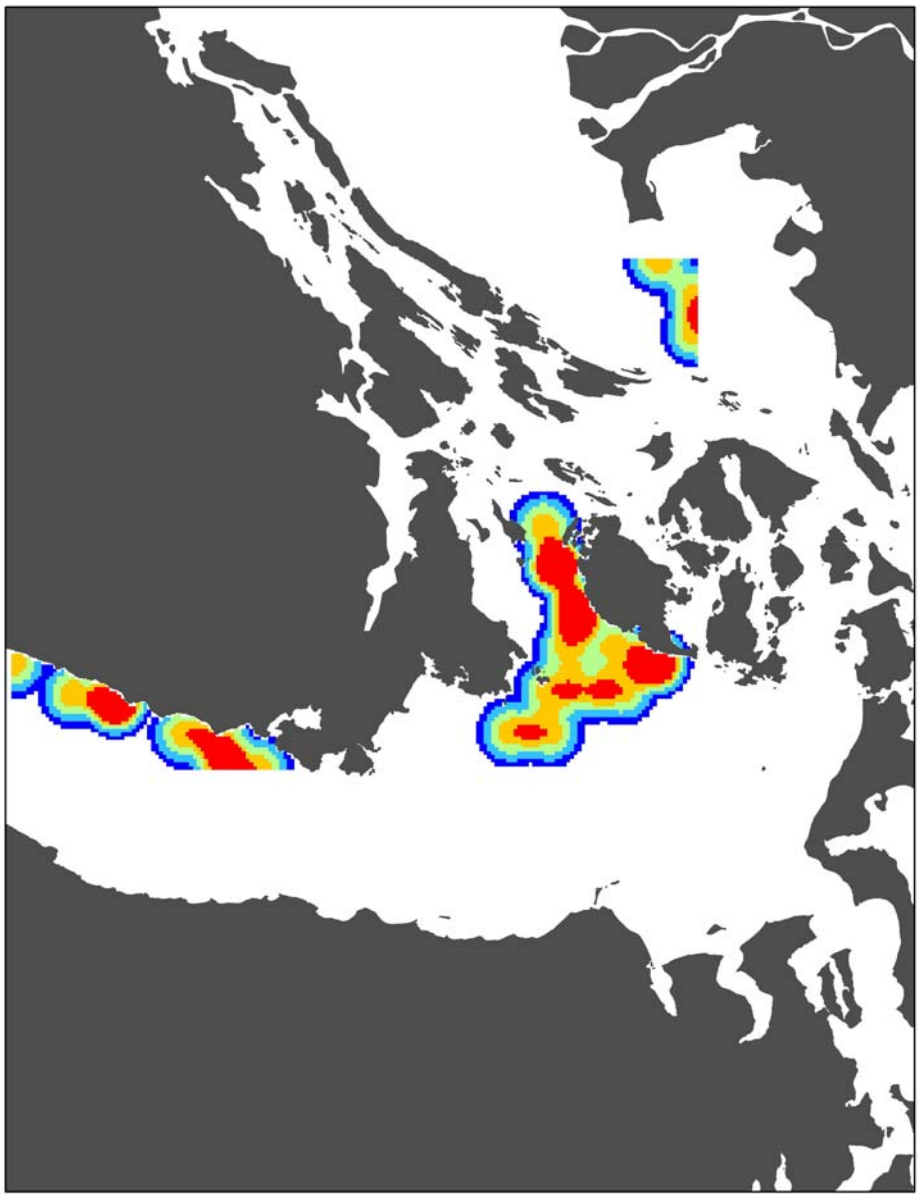

Figure C11. Week 32 of 1998 total space use by SRKW.

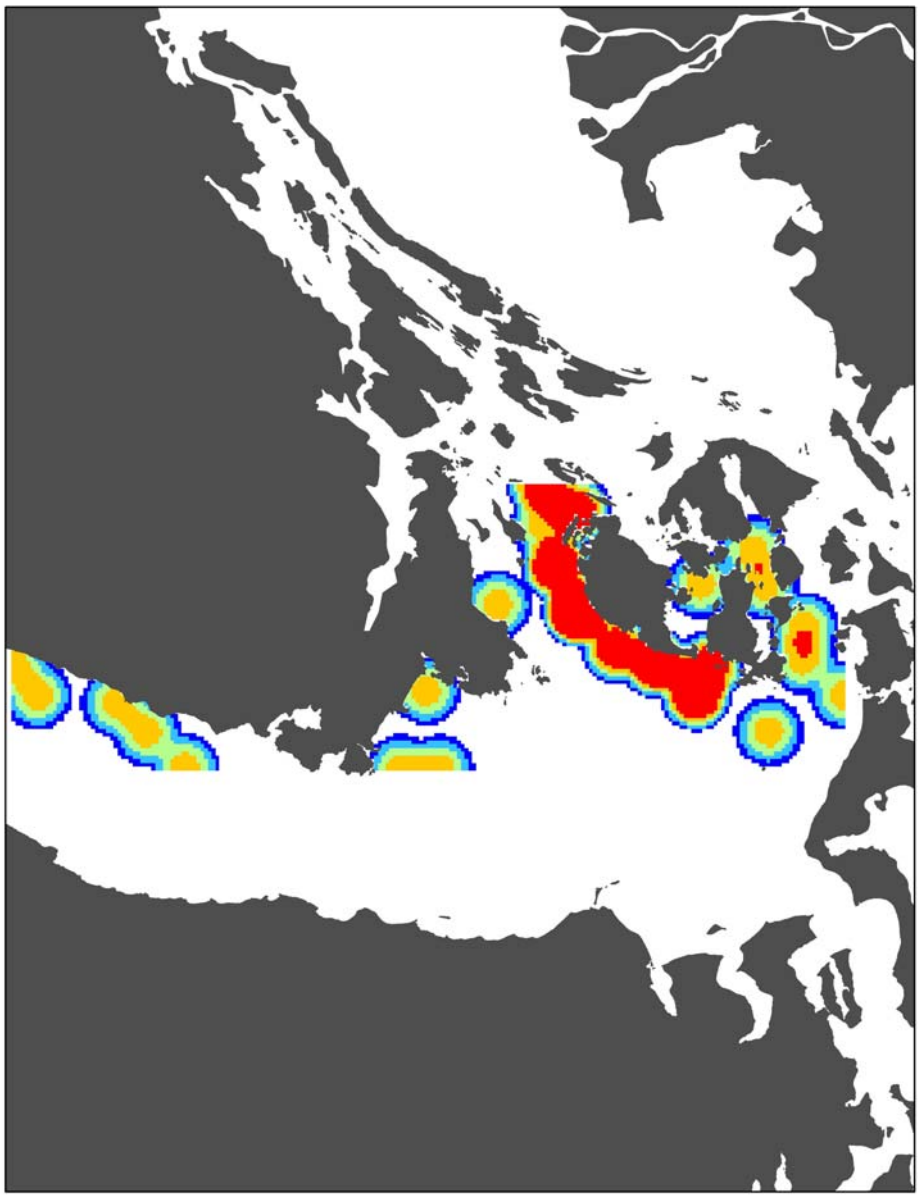

Figure C12. Week 33 of 1998 total space use by SRKW.

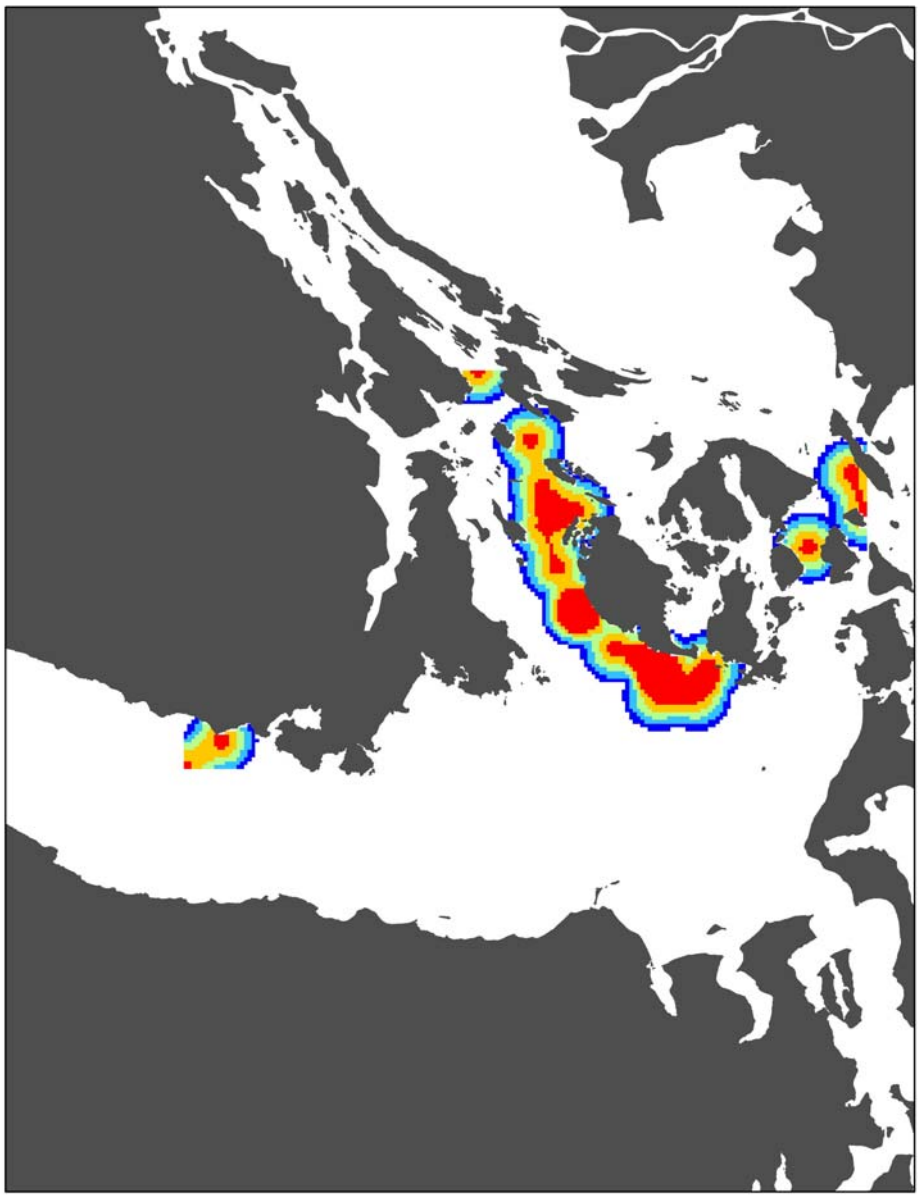

Figure C13. Week 34 of 1998 total space use by SRKW.

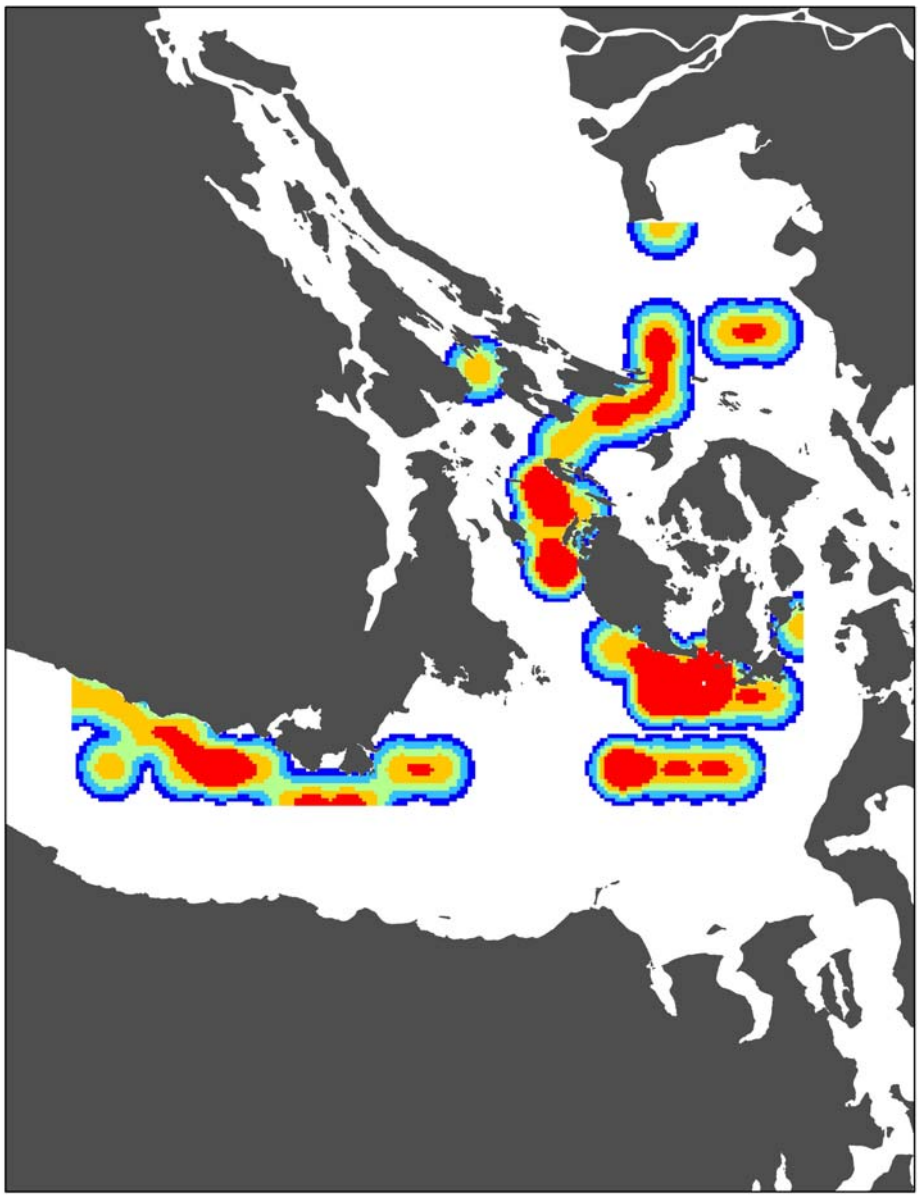

Figure C14. Week 35 of 1998 total space use by SRKW.

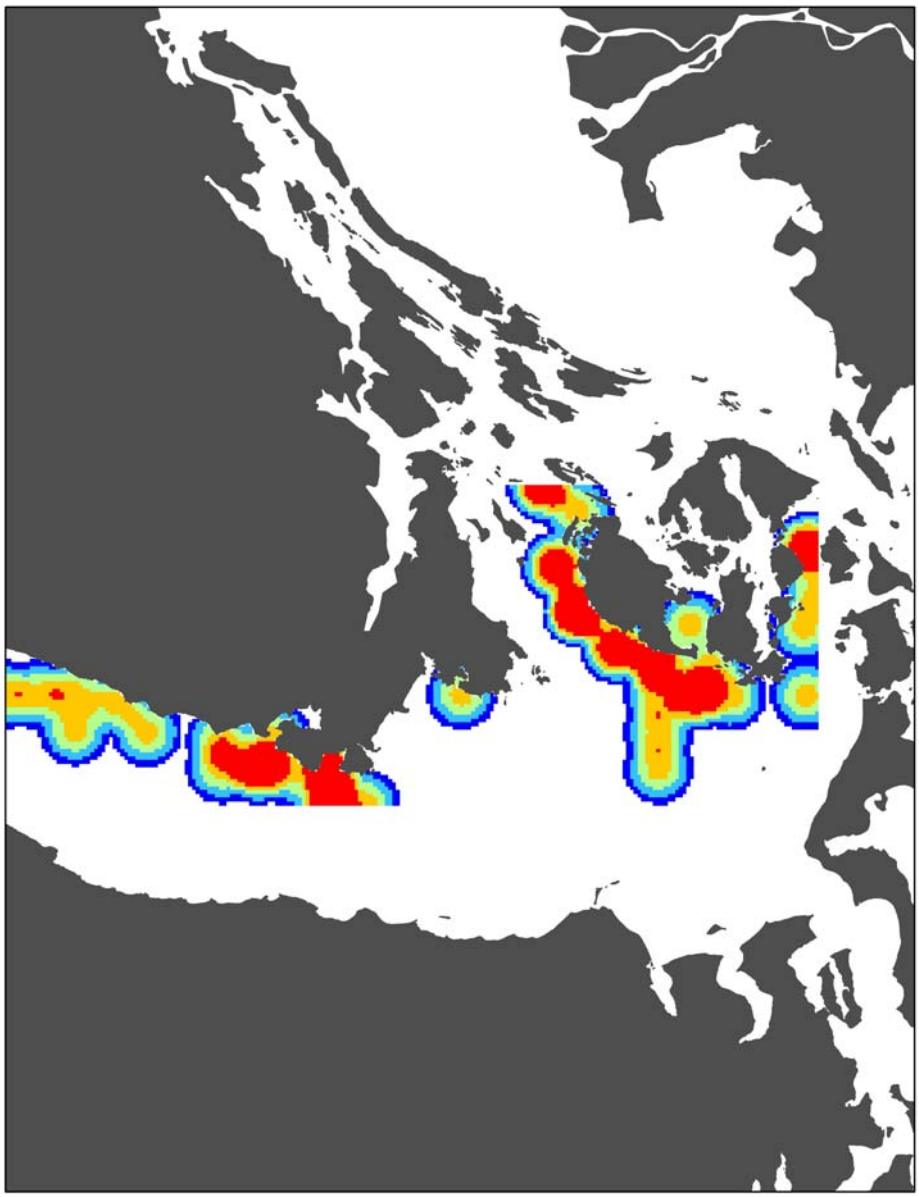

Figure C15. Week 36 (early September) of 1998 total space use by SRKW.

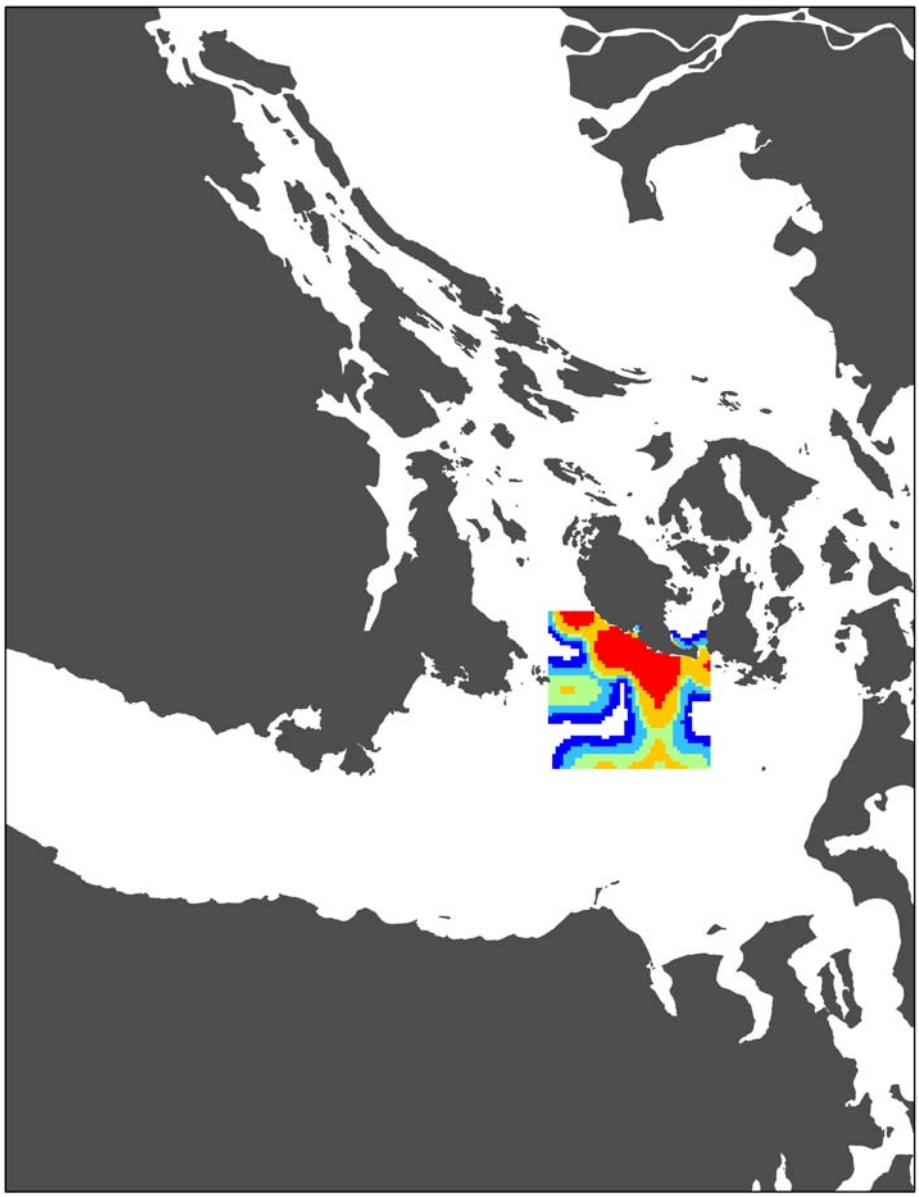

Figure C16. Week 37 of 1998 total space use by SRKW.

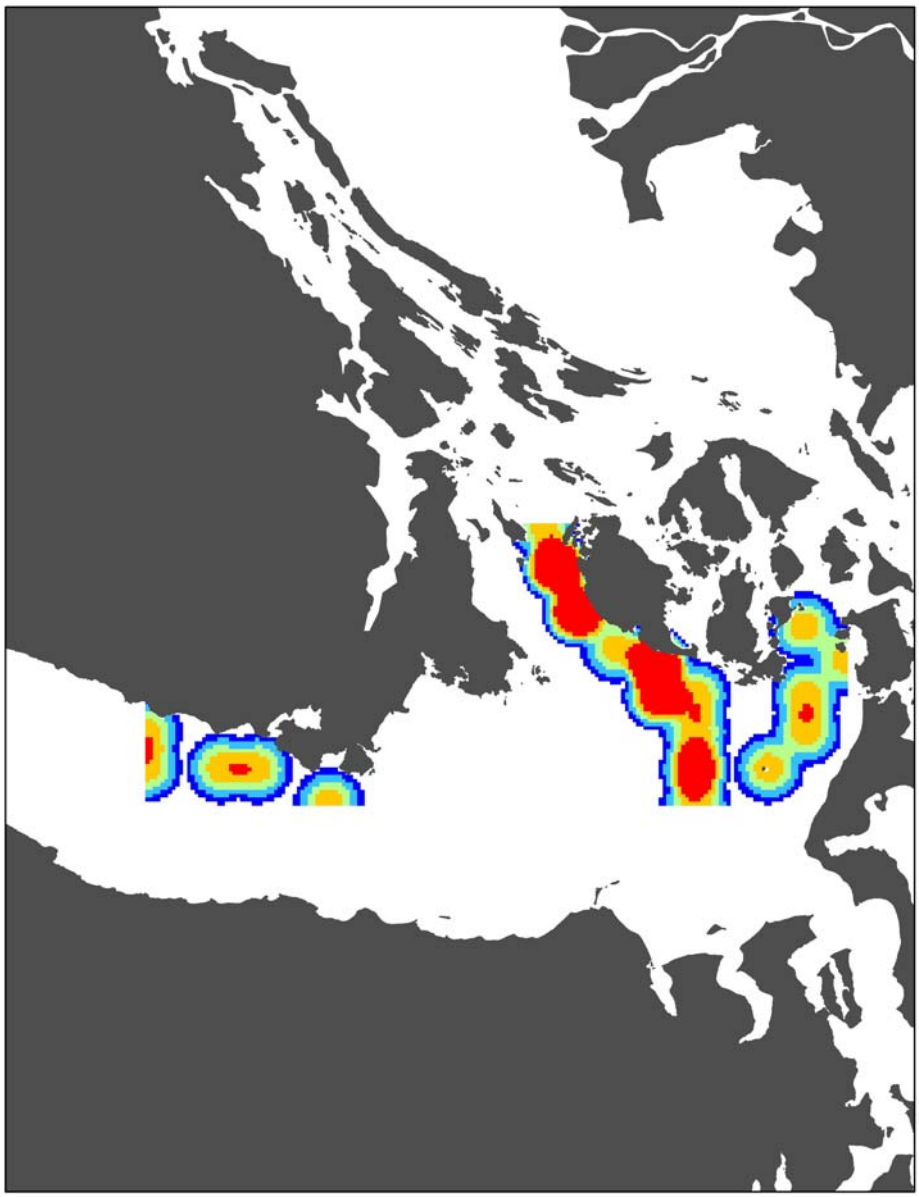

Figure C17. Week 38 of 1998 total space use by SRKW.

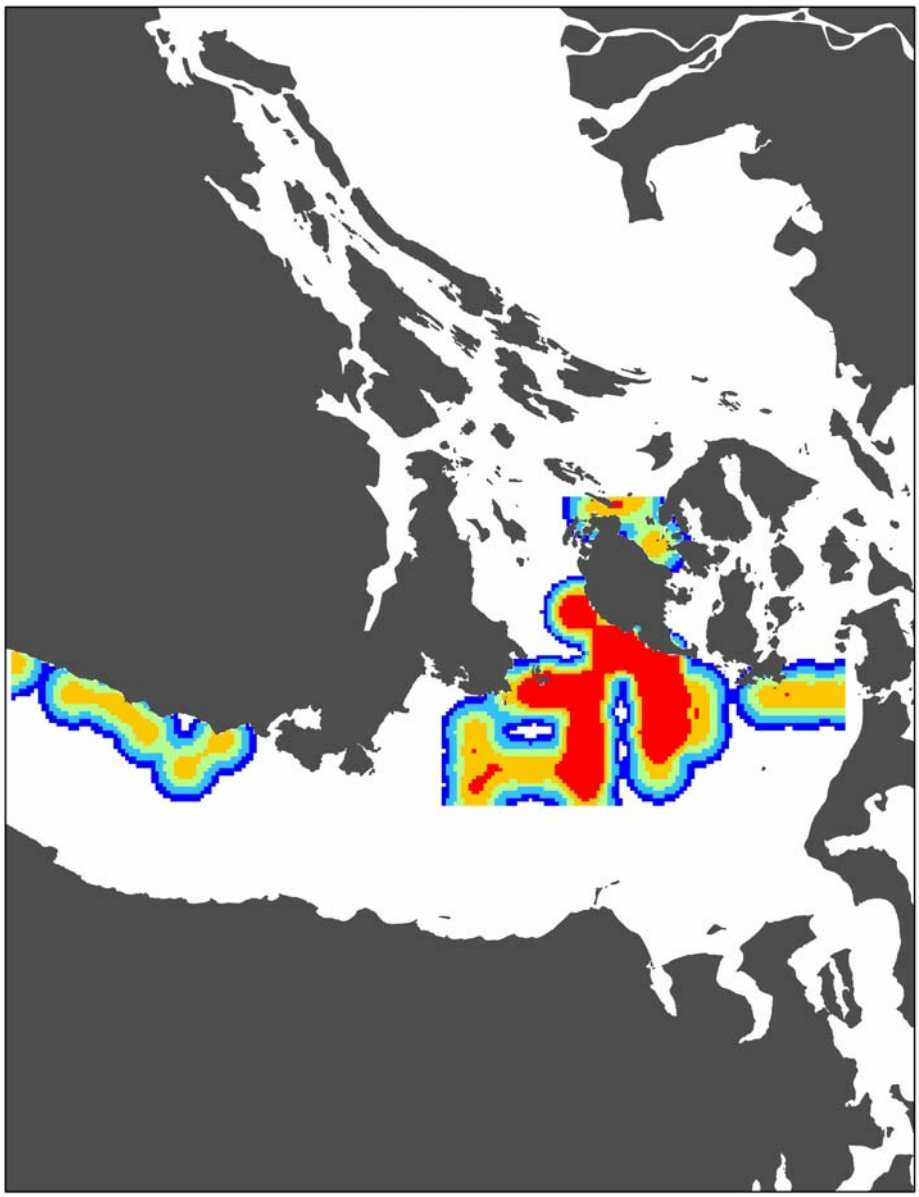

Figure C18. Week 39 of 1998 total space use by SRKW.

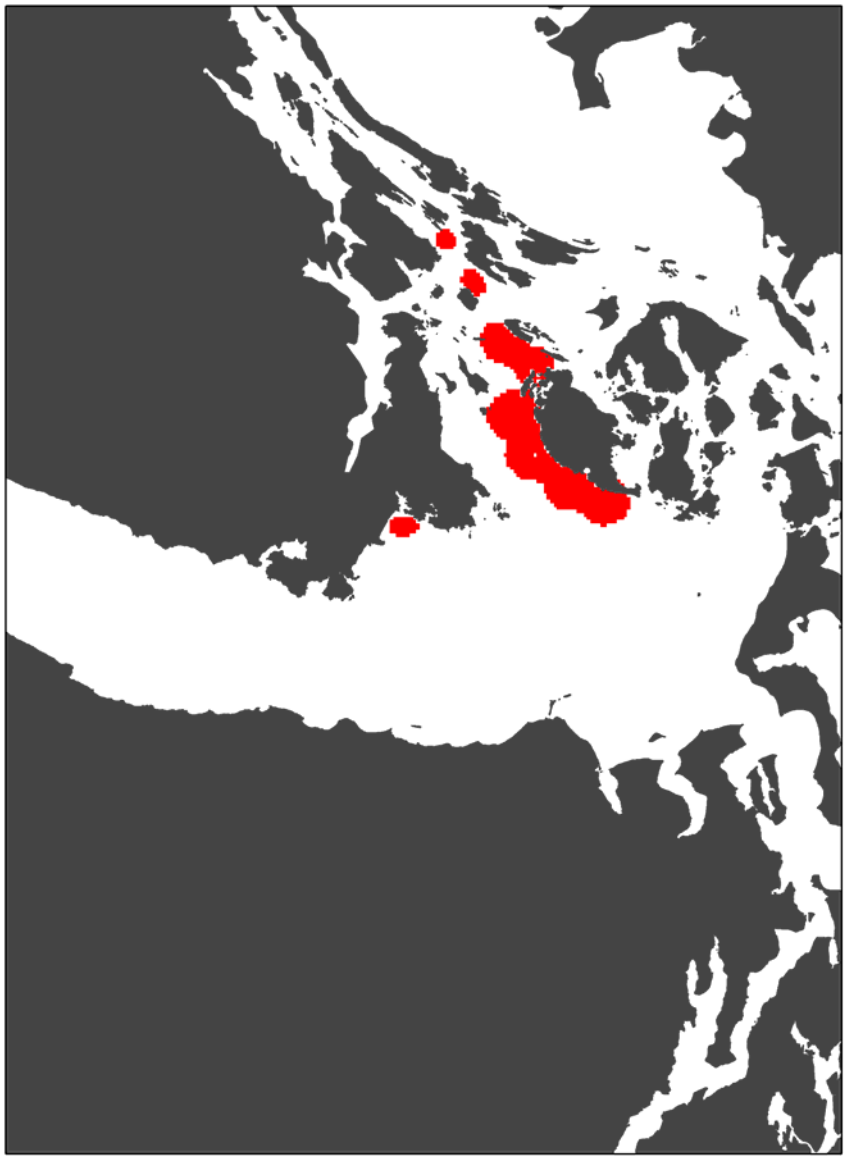

Figure C19. May core area in 1998 for SRKW.

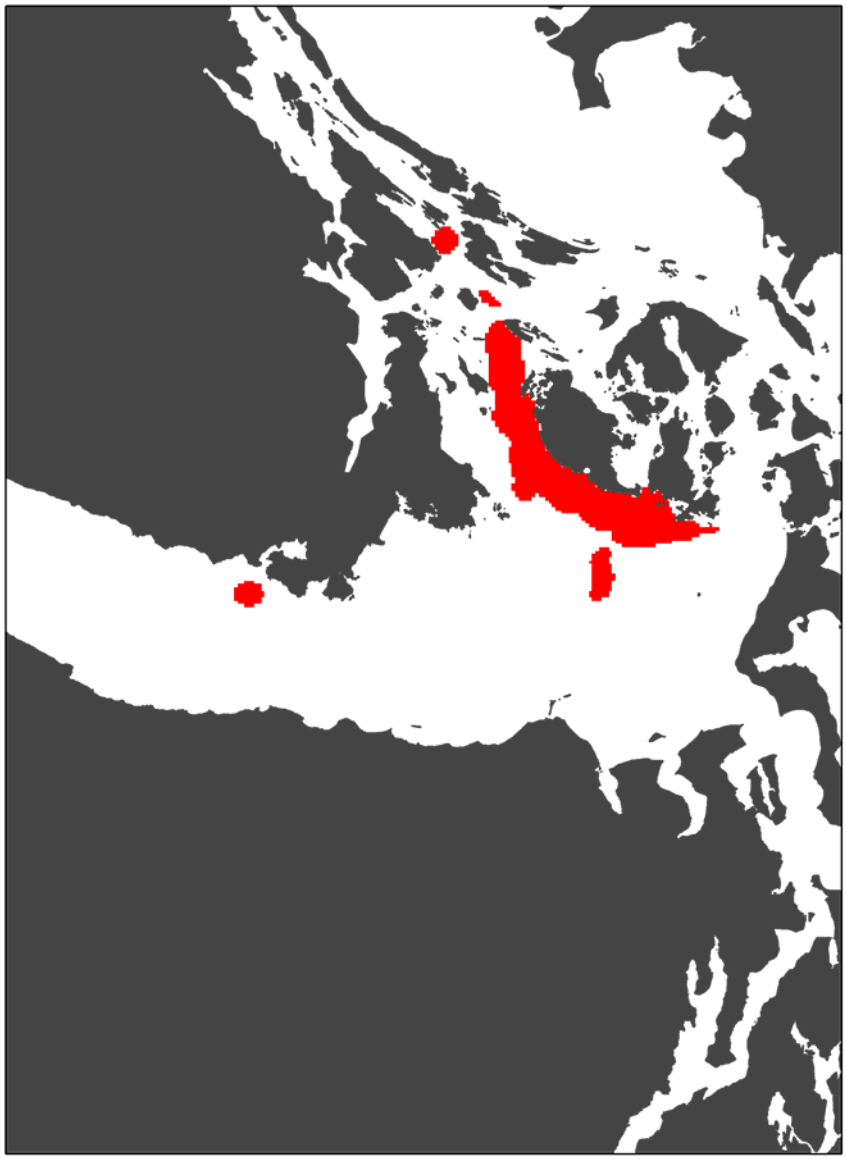

Figure C20. June core area in 1998 for SRKW.

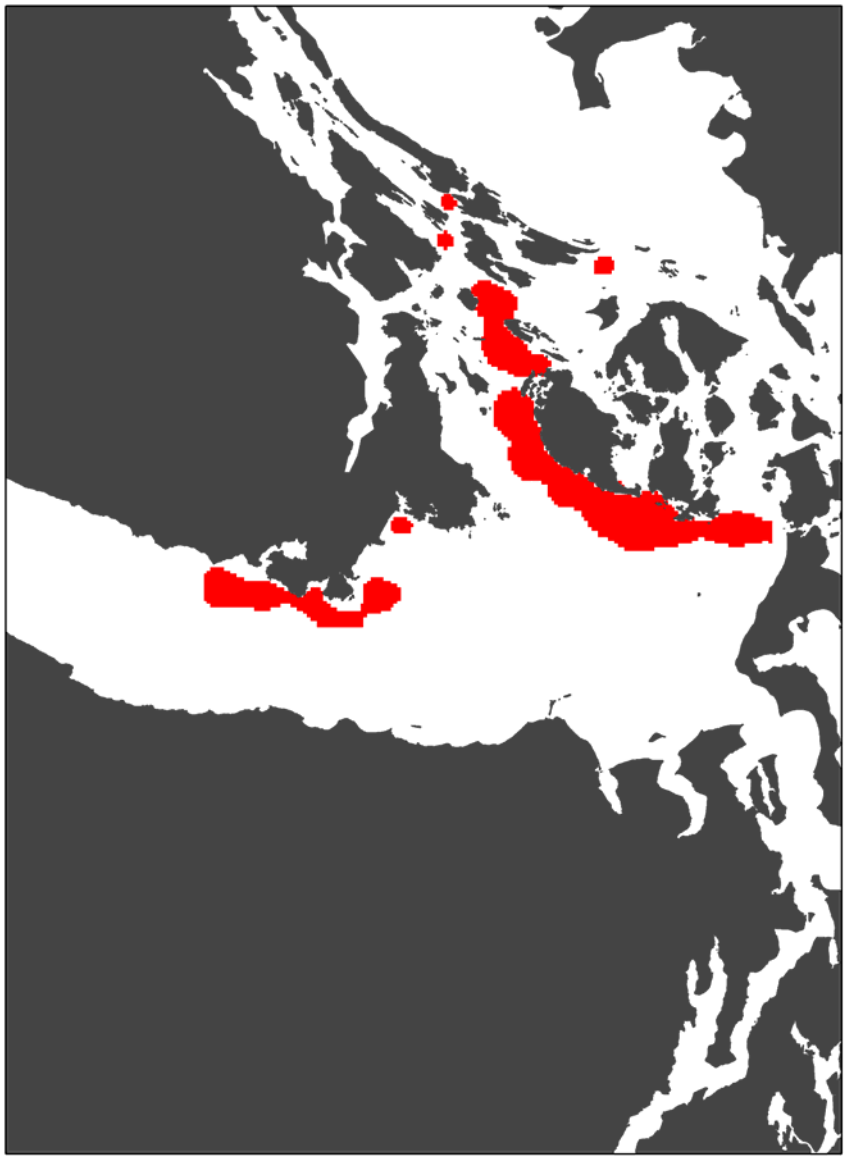

Figure C21. July core area in 1998 for SRKW.

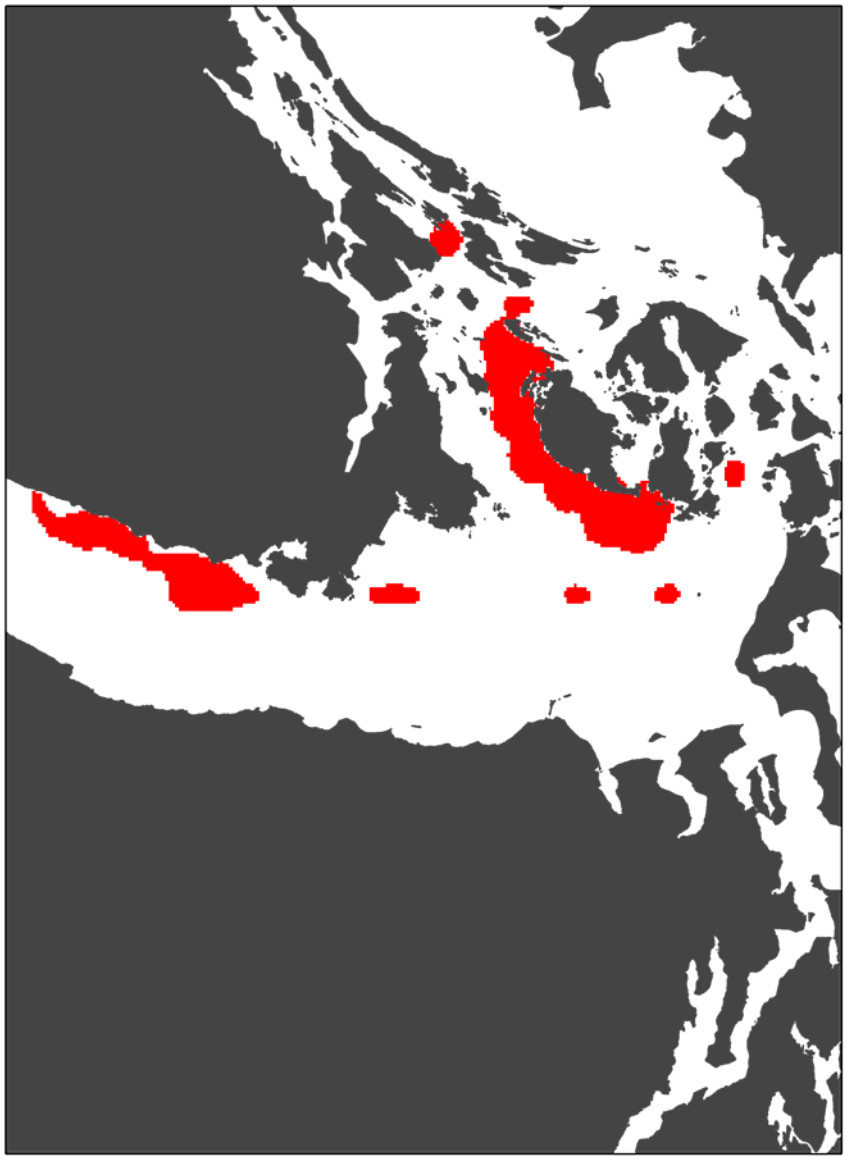

Figure C22. August core area in 1998 for SRKW.

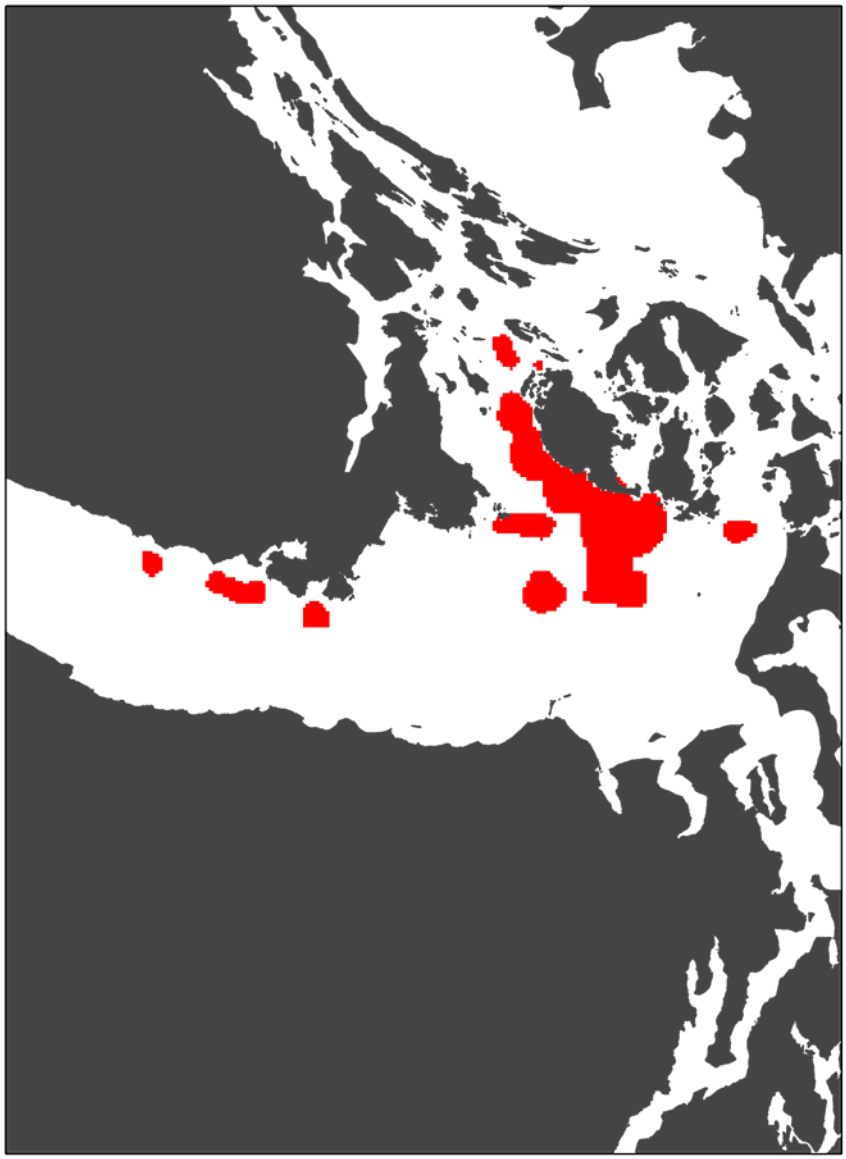

Figure C23. September core area in 1998 for SRKW.

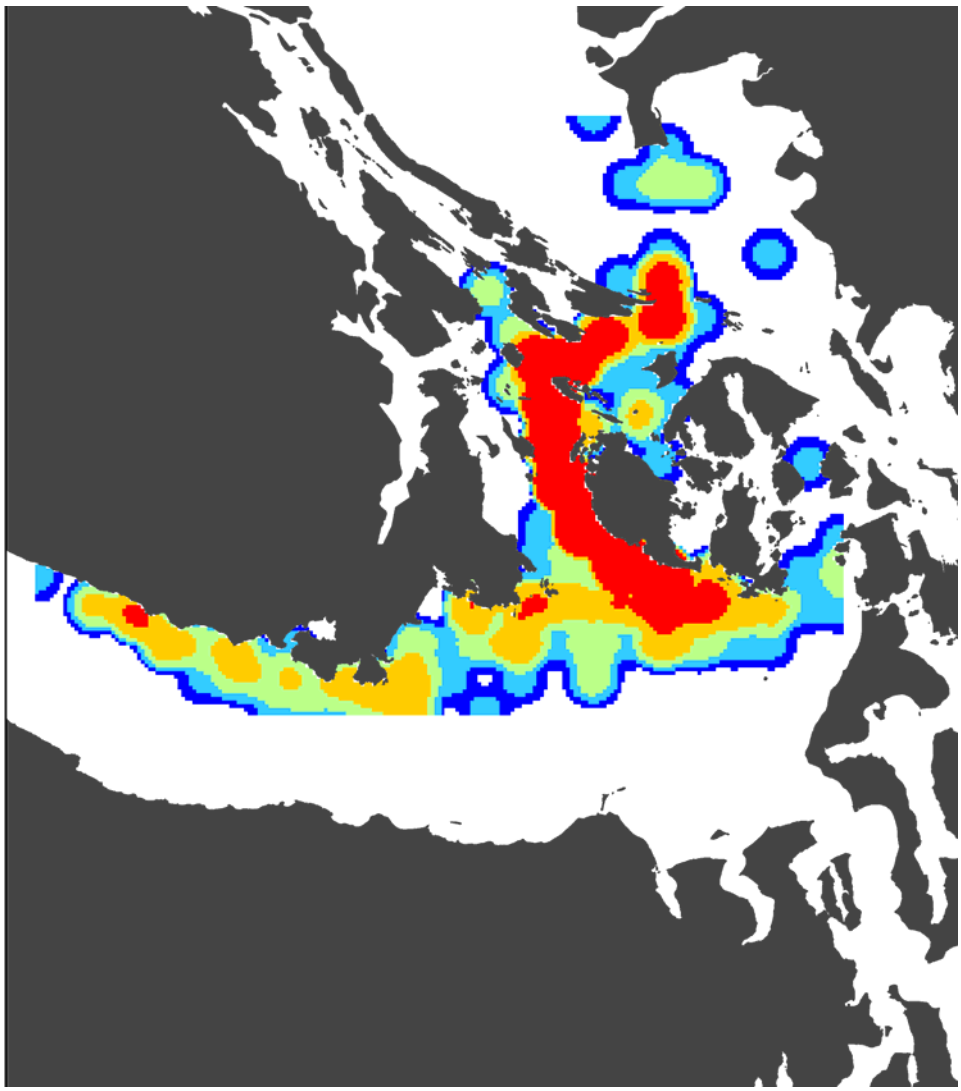

Figure C24. Total space used by SRKW over the 1996 summer season.

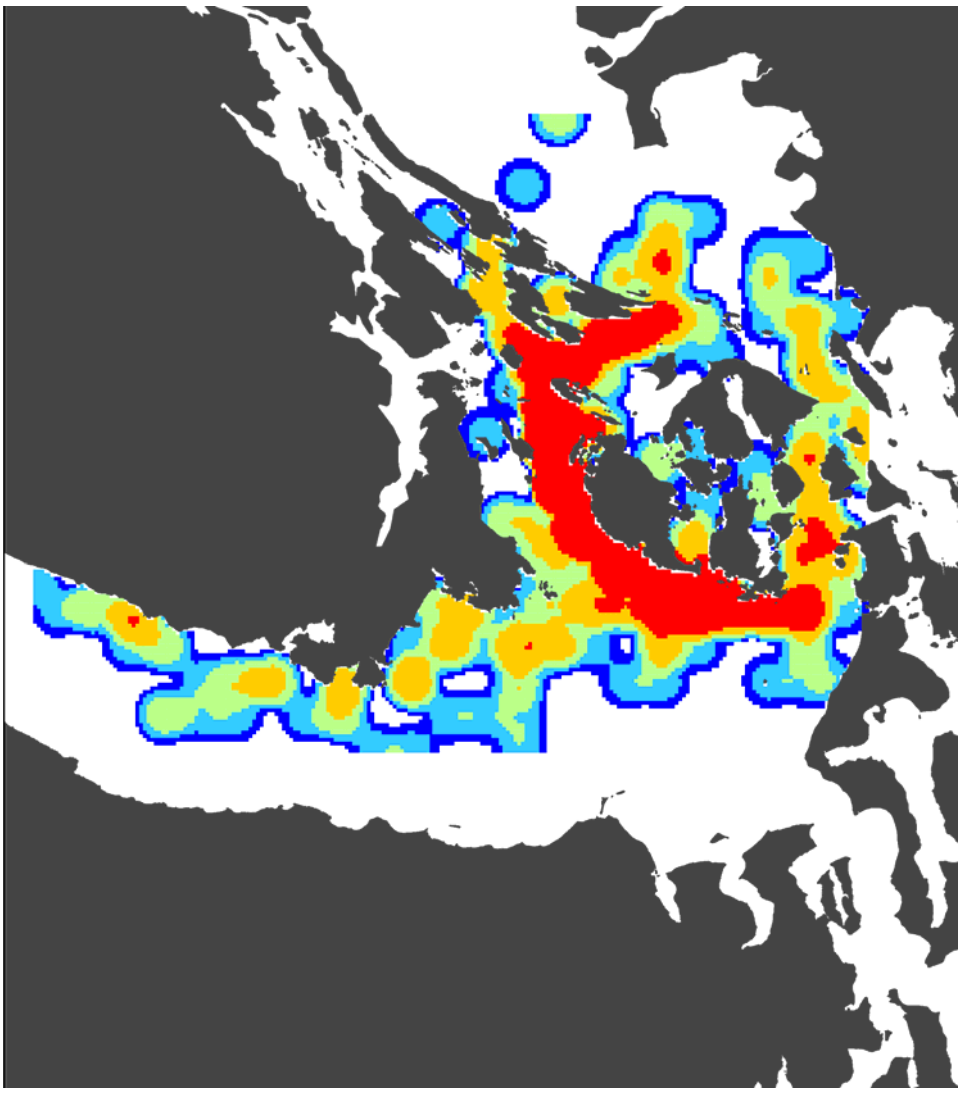

Figure C25. Total space used by SRKW over the 1997 summer season.

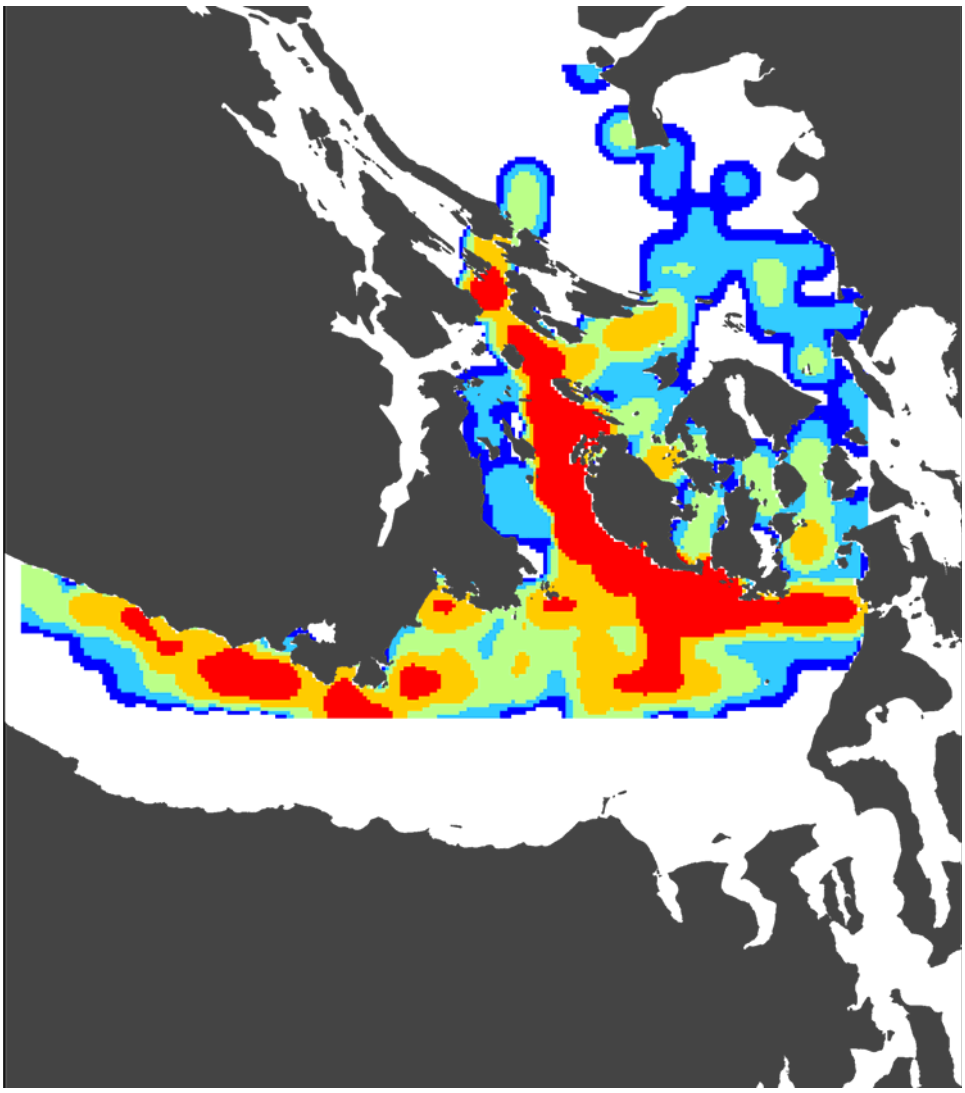

Figure C26. Total space used by SRKW over the 1998 summer season.

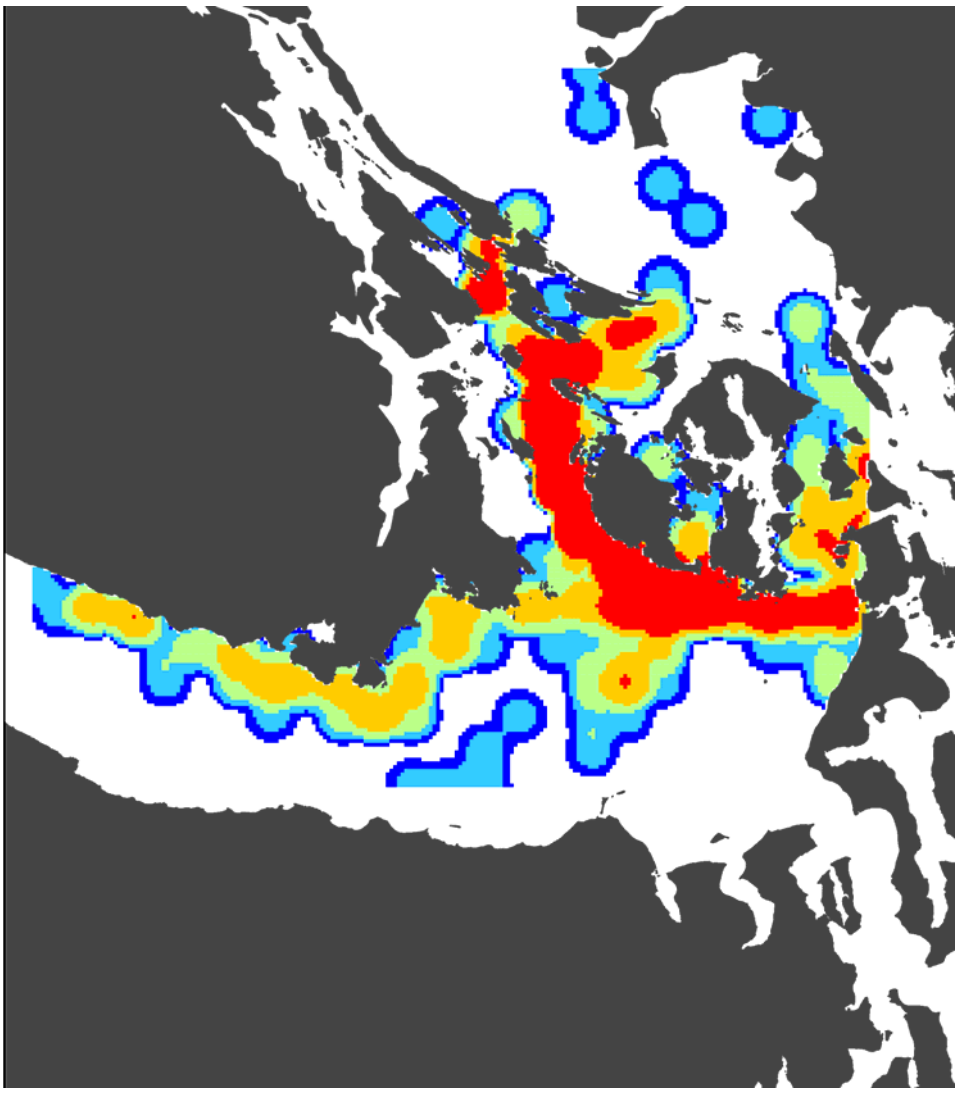

Figure C27. Total space used by SRKW over the 1999 summer season.

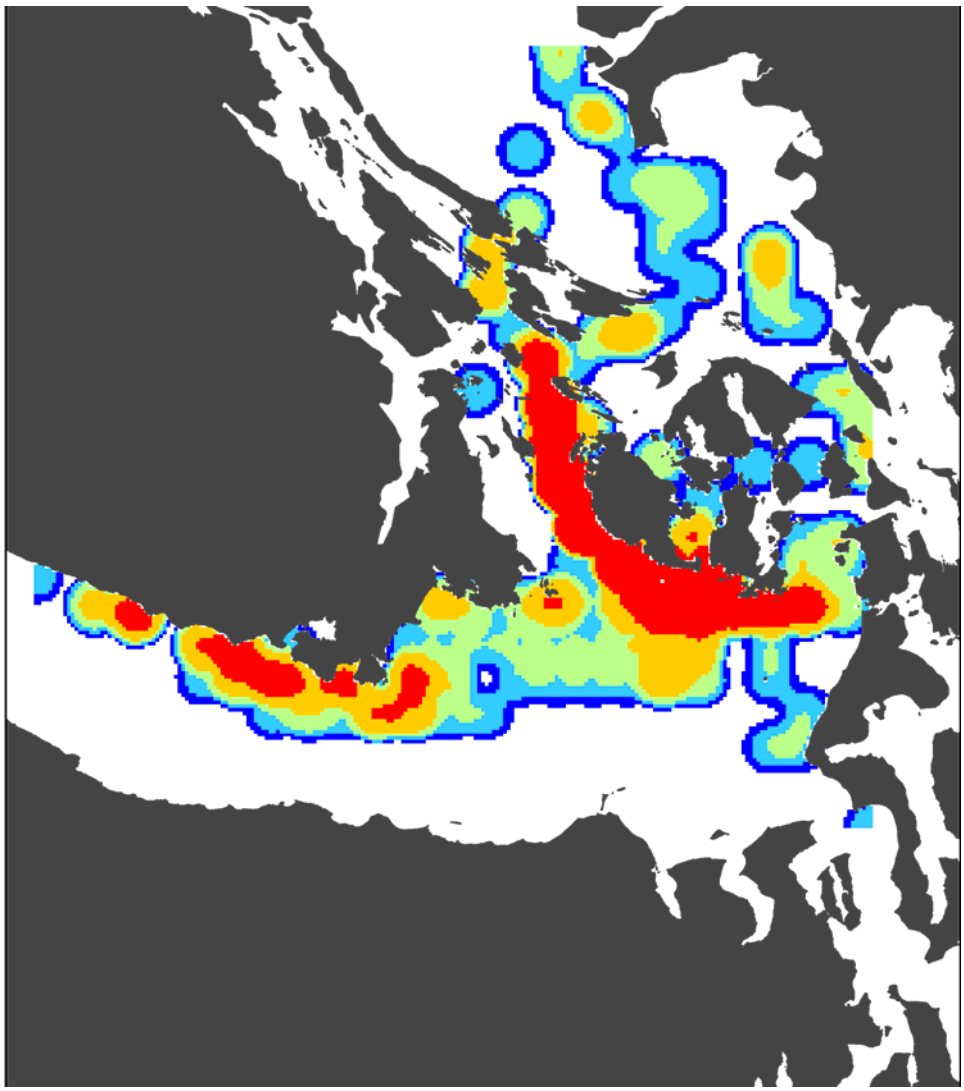

Figure C28. Total space used by SRKW over the 2000 summer season.

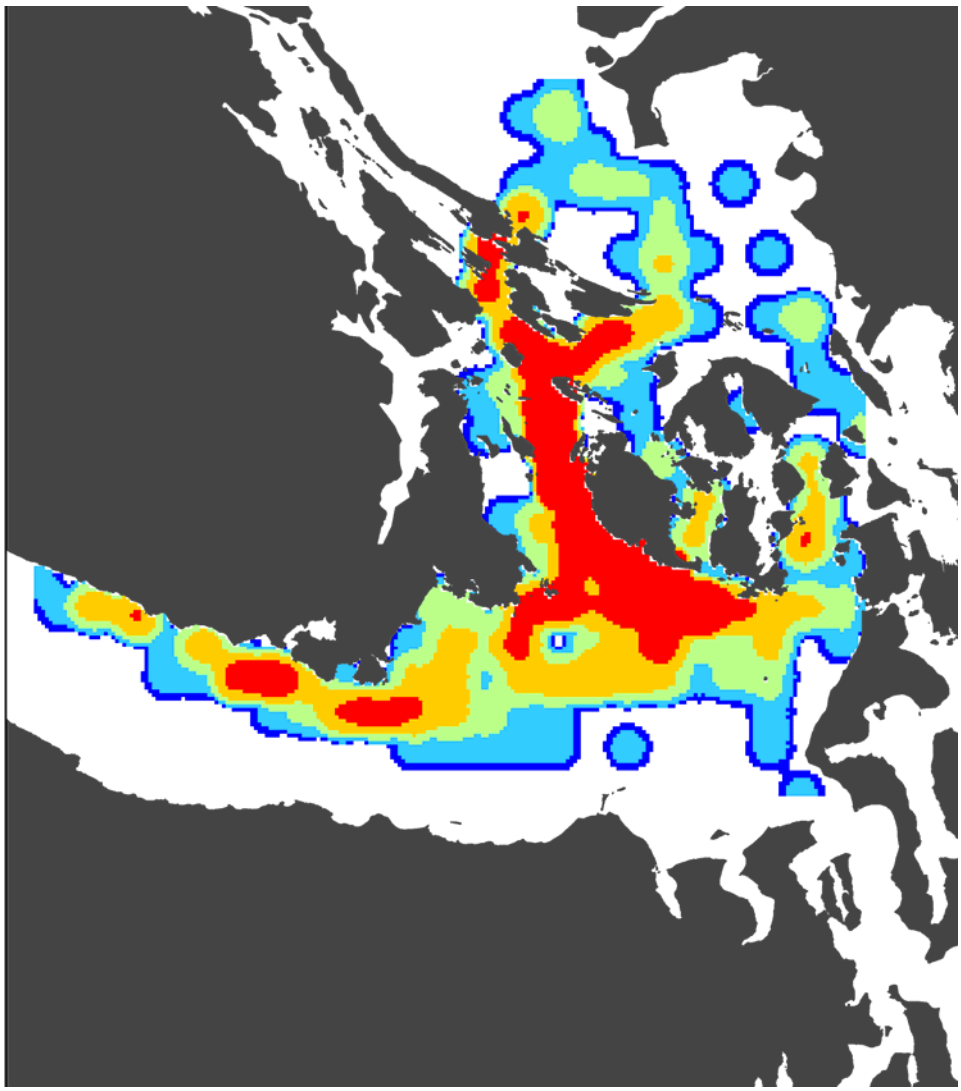

Figure C29. Total space used by SRKW over the 2001 summer season