Feeding Ecology of "Southern Resident" Killer Whales (*Orcinus orca*): Benthic Habitat and Spatial Distribution

by

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Abstract

Feeding Ecology of “Southern Resident” Killer Whales (*Orcinus orca*): Benthic Habitat and Spatial Distribution

Jeremy Lucas

Though among the most geographically distributed mammals on earth, there are separate, distinct populations of killer whales (*Orcinus orca*) occupying specific geographic areas. In the coastal temperate northeast Pacific Ocean, one such population, the so-called “southern resident” killer whales (SRKWs), found in the inland waters of Washington State and southern British Columbia, have been listed as endangered by the governments of the United States and Canada. Possible reasons for their population decline include contamination as a result of decades of pollution, a decline in the numbers and density of their preferred prey, Pacific salmon (*Oncorhynchus* spp.), and the impaired ability to find prey or perform other biologically important functions due to excessive ambient noise in their environment. This study examines the potential of classifying critical habitat for these killer whales based on benthic topography and spatial distribution. From 2004-2007, field data were collected in the San Juan Islands and Puget Sound of Washington State to ascertain 1) if there are any differences between where killer whales feed versus where they do not feed and 2) if there are any spatial density patterns that describe where these animals are found. A Kruskal-Wallis and chi-squared test revealed that there were no significant differences between where killer whales were thought to feed versus where they were not. Additionally, a chi-squared test found that there were no differences in the geographic location of feeding areas versus non-foraging areas. A density analysis did reveal that all areas of highest killer whale density were found in the Haro Strait, which is one of the deepest areas within the archipelago’s marine habitat. This thesis’ findings support previous studies that the Haro Strait is important habitat for SRKWs but does not provide evidence that killer whales select for benthic characteristics when feeding.

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Introduction

There are few animals as easily recognizable as killer whales (*Orcinus orca*). Fewer animals seem to be a part of human culture. Until the mid 1970's, killer whales were thought to be a predator of humans (Ford et al 2000). Even now, some fishermen may feel animosity for killer whales, and other marine mammal species, that compete for dwindling fish populations.

Combined with their interesting (some might say "clown-like") coloration pattern, their public display in aquariums such as Sea World and featured in popular movies like the Free Willy series makes killer whales known to children and adults alike. Killer whales are the largest member of the family *Delphinidae*, the ocean dolphins. Males can grow up to 9.8m in length and weight 10,000kg and females can grow up to 8.5m long and weigh 7,500kg (Jefferson et al 2008). Their towering dorsal fins and coloration make them relatively easy to spot and identify in the wild. As the ocean's top predator, killer whales serve an important ecological role in the marine ecosystem.

Globally, killer whales are second only to humans as the most geographically distributed mammal on earth (Jefferson et al 2008). There are, however, areas of higher-than-expected concentrations, such as the waters off of Washington State, British Columbia, Alaska, Japan, Antarctica, Norway and Iceland (Ford et al 2000). Food preferences and feeding strategies differ among populations, even in sympatric populations (Ford and Ellis 1999; Ford et al 2000; Baird 2001). Off the Patagonian coast of Argentina, killer whales frequently beach themselves to capture southern elephant seals (*Mirounga leonina*) and southern sea lions (*Otaria flavescens*) and drag them into deeper water (Lopez and Lopez 1985; Hoelzel 1991). Feeding strategies in Norway are distinctly different as killer whales "herd" schools of herring (*Clupea harengus)* into increasingly tight balls, use their flukes to swat at these herring balls, thereby stunning and then consuming the affected individuals (Nottestad et al 2002).

In the coastal temperate northeast Pacific Ocean, there are three distinctly different ecotypes of killer whales (Ford et al 2000). These populations have been termed "residents", "transients" and "offshore" killer whales. Though it is also hypothesized that offshore killer whales are not a distinct ecotype but rather are another population of the resident ecotype since their life histories are very similar (Robin Baird pers. comm.).

Resident killer whales are primarily fish-eaters. During predation studies conducted on the resident killer whale populations in the Kenai Fjords and Prince William Sound, Alaska, researchers found that 95% of the prey remains came from coho salmon (*Oncorhynchus kisutch*) (Matkin et al 1999; Saulitis et al 2000). Further south, northern resident killer whales (NRKWs), which occupy the waters of Johnstone Strait and northern Vancouver Island, and southern resident killer whales (SRKWs), whose core summer habitat is the waters surrounding the San Juan/Gulf Island chain of Washington State and southern British Columbia, diet preferences are distinctly different. Ford and Ellis (2006) found that 96% of southern and northern resident killer whale prey was salmon, where 71.5% of all salmonid kills were Chinook (*O. tshawytscha*), 22.7% were chum (*O. keta*) and a combination of coho, sockeye (*O. nerka*), pink (*O. gorbuscha*) and steelhead (*O. mykiss*) represented the remaining 6% of salmonid kills. It should be noted that there was a large bias towards NRKWs; 87.5% of observations involved northern residents whereas only 12.5% involved southern residents. Similar results have been found for southern resident killer whales in a study that was independent of any northern resident individuals (Hanson et al in prep).

Even though transient killer whales are sympatric with both resident populations of Washington State and British Columbia, they exhibit very different feeding preferences. Unlike their fish-eating relatives, transients feed primarily on marine mammals and, on rare occasions, seabirds (Baird and Dill 1995; Ford and Ellis 1999; and Saulitis et al 2000). Despite overlapping ranges, evidence suggests that transients are genetically isolated from residents—they do not interbreed (Hoelzel et al 1998; Barrett-Lennard 2000). In fact, when in the vicinity of resident populations, transients will change their route to avoid the fish-eating animals (Baird and Dill 1995), while residents, on the other hand, do not seem to alter their path.

Killer whale ecotype variations are not limited to the waters of Washington State and British Columbia. Matkin et al (2007) found three similar ecotype populations in the eastern Aleutian Islands of Alaska. Though not as intensively studied, there appears to be a distinct difference in mammal-eating and fish-eating populations in Antarctica as well (Berzin and Vladimirov 1982). In Antarctic waters, Type A and B are primarily marine mammal eaters (Smith et al 1981; Berzin and Vladimirov 1983) while Type C are fish-eaters (Berzin and Vladimirov 1983). All three types of Antarctic killer whales are morphologically different (Pitman and Ensor 2003).

There are numerous studies on resident populations that ascertain foraging behavior. Current studies (Hoelzel 1993; Baird and Hanson 2004; and Ford and Ellis 2006) have found that resident killer whales possibly exhibit certain behavioral patterns when foraging. A study on SRKWs revealed that a series of surface activity, including rolls and turns, was common when foraging (Hoelzel 1993). Baird and Hanson (2004) and Ford and Ellis (2006) found a suite of subtle behavioral cues that could indicate hunting or successful capture of a fish. Ford and Ellis (2006) studied both northern and southern resident communities and found that, when foraging, killer whales often swam in zig-zag patterns rather than straight lines. Directional and non-directional chases, long dives, and convergence of whales were also indicators of foraging behavior. Baird and Hanson (2004) studied southern residents in the summer of 2004 and recorded twenty-seven behavioral cues, which included thirteen fast non-directional surfacings and eight moderate non-directional surfacings. Ten of these twenty-seven cues yielded evidence of predation (fish scales and/or bits in the water).

Due to their cosmopolitan distribution, assessing killer whale conservation status on a global scale rather than localized is very challenging. In 2008, their global status was not determined because data were deficient (International Union for Conservation of Nature and Natural Resources 2008). However, when tracking the status of stocks, or meta-populations, the task can be more manageable. Since 1976, The Center for Whale Research has conducted a long-term population assessment on southern resident killer whales (Center for Whale Research 2008). At the time this thesis was written, there were eighty-seven individuals in the southern resident community divided into three pods, J-pod (n=25), K-pod (n=20), and L-pod (n=42). Though this number is up by eleven individuals from when surveys first started, it is one of the lowest population estimate numbers since 2002 and reflects a declining population trend since the mid- and late 1990s when the population was as high as ninety-seven (Center for Whale Research 2008). As a result of these troubling trends, the southern resident killer whale community was listed as endangered under the Canadian Species at Risk Act (SARA) in 2002 and the United States Endangered Species Act (ESA) in 2005. The challenges they face on the road to recovery are discussed below.

Live Capture

The coastal temperate northeast Pacific population of killer whales was an intensively used resource for the “live-capture” industry for marine-theme parks such as Marineland, the Vancouver Aquarium, and the Seattle Aquarium (Center for Whale Research 2008). The first animal was taken in 1961 and the “fishery” was closed in 1976 (Asper and Cornell 1977; Hoyt 1990; and Center for Whale Research 2008). As many as 303 individuals were captured from the waters of Washington, British Columbia and California with fifty-six kept (Asper and Cornell 1977). Many of the 303 animals captured were repeated captures of the same individuals (Robin Baird pers. comm.). There were individual mortalities associated with these capture attempts as well, which were as high as ten (Asper and Cornell 1997) or eleven (Hoyt 1990). As many as sixteen individuals were reported to have died within their first year of captivity (Hoyt 1990). Community membership (i.e. a NRKW individual or a SRKW individual) was poorly understood during the years of harvest. However, based on what is now known about the range of each killer whale population, it can be safely assumed that a substantial number of killer whales taken were from the southern resident community.

The decline of the SRKW population in the 1980s can most likely be attributed to the intensive live-capture industry of the previous two decades (Baird 2001). However, given that the population rebounded in the mid- and late-1990s it seems unlikely that the history of the live-capture industry continues to have an impact on the southern resident killer whale community.

Salmon

As previously mentioned, salmon are the preferred prey of the southern resident killer whales. Population numbers of all salmon species have declined in many areas in Washington State and British Columbia (Augerot et al 2005). Understanding the reasons for these declines is as complex as it is perilous and to provide an exhaustive description is beyond the scope of this thesis. However, a few of the most widely-accepted reasons as to the current state of Pacific salmon (*Oncorhynchus* spp.), known as the "4 H's"; Harvest (overfishing), Hydro (damming of rivers), Hatcheries (artificial propagation), and Habitat (loss of habitat) (Lichatowich et al 1999) are discussed below.

Of the "4 H's", Harvest is the most complex and dynamic. There are many rules and regulations that allocate certain percentages of the quota to native and subsistence fishermen and to recreational and commercial fishermen, time of year salmon can be fished, who can fish, and who manages the fish (National Marine Fisheries Service 2007). Equally complex is understanding the toll overfishing takes on the salmon population as a whole. While it is generally thought that overfishing is of lesser importance than habitat loss (National Marine Fisheries Service 2007), it has also been found that overharvesting is linked to population trends of Chinook salmon in both the large scale area of the Pacific Northwest and the small scale area of Puget Sound (Hoekstra et al 2007).

The intensive commercial salmon fishery began in 1866 (Lichatowich et al 1999) and was so efficient that specific river runs were closed by 1915 (National Marine Fisheries Service 2007). In British Columbia, total tonnes of all salmon species caught by the commercial fishery declined by 62% from 1952 to 2004, declines were seen in all species individually except chum salmon from the same time period (Irvine et al 2005). In the Columbia River, total catch of all species declined drastically from 1866 to 1993 (Lichatowich 1999). Between 1976 and 2000, Chinook salmon catch in Washington State declined by 84% (National Marine Fisheries Service 2007). In addition to the large number of individuals being removed from the population, there are evolutionary ramifications to intensively fished salmon populations. Although still under debate, selection for salmon size as well as timing of fisheries could be causing a shift to smaller salmon in general and a shift in timing for the migration back to native rivers to spawn (Hard et al 2008).

The damming of rivers has also led to the decline of Pacific salmon. By the 1930s, dams designed to either generate hydroelectricity, divert water for irrigation, or to create reservoirs for stored drinking water were being constructed throughout the Pacific Northwest (Lichatowich et al 1999). Dams alter the characteristics of a natural river system by decreasing flow velocity and changing water temperature, as well as impact water quality by draining irrigated areas of water full of sediment and agricultural contaminants (Waples et al 2007). Additionally, Waples et al (2007) reported that river migration routes, especially for juvenile salmon migrating to estuaries, have been severely impacted by dams.

The mitigation tactic of barging fish around these dams has been undertaken. However, in a Columbia River case study (Keefer et al 2008), this process has been shown to alter the return migration of both Chinook salmon and steelhead. Both species are known for their homing ability (finding their way back to the stream in which they were spawned) with some “not finding their way home” and returning to a different river to spawn (straying). It is theorized that salmon collect information about their home stream and their spawning grounds while swimming downstream (Quinn 2005), which is how they locate their native rivers. Keefer et al (2008) found that juvenile Chinook salmon and steelhead that had been barged around dams were more likely to stray as adults. The Columbia River is one of the most hydroelectrically-developed river systems in the world (Pacific States Marine Fisheries Commission 1997; Augerot et al 2005) and many of its dams are impassable. Those that are passable are treacherous as they are thought to kill 70-96% of salmon juveniles swimming downstream (Pacific States Marine fisheries Commission 1997). In Puget Sound, of the “4 H’s”, dams may have the largest impact on salmon density (Hoekstra et al 2007).

Hatcheries present an interesting paradox as they were originally designed to address the problem of declining salmon stocks (Lichatowich 1999). Hatchery-reared fish are those fish raised in human-controlled environments (hatchery facilities or hatcheries) with the purpose of increasing the number of salmon in the fishery. Hatchery-reared salmon are raised in very high densities with specialized diets and conditions designed for increased survival of juvenile fish. The success of hatcheries has been far from what was expected, however. The program as a whole has shown little, if any, positive results (Lichatowich et al 1999) and over-shadows the true issue of declining wild salmon runs in the northwest (Larry Dominguez pers. comm.) potentially increasing the declining rate of wild fish (Quinn 2005). Though interactions are complex, there is evidence to suggest that hatchery fish may hinder the ability of wild fish populations to recover (Levin et al 2001). Although some studies have shown evidence to the contrary, it is generally shown that hatchery-reared salmon are more aggressive and larger than wild salmon within the same stream (Weber and Fausch 2003) creating a population of salmon capable of out-competing the native population for resources. The sheer number of hatchery fish placed into a river may overwhelm native fish. Broodstock used by a given hatchery may not be from that specific watershed thus potentially altering of the gene pool (Weber and Fausch 2003; Goodman 2005). Additionally, hatchery-reared salmon suffer higher mortality rates than wild salmon because hatchery fish do not have well-developed predator-avoidance behavior (Olla et al 1994; 1998). There is also evidence to suggest that hatchery salmon may be less fit to survive in the wild due to artificially controlled "favorable" conditions in hatcheries (Araki et al 2008). Araki et al (2008) also summarized studies showing that hatchery environments substantially increase the survival rate during the egg-to-smolt part of the salmon life cycle, therefore unfavorable genes expressed by individuals that would otherwise be filtered out via natural selection by the environment are now surviving past the smolt stage, introducing these genes into the gene pool. The effectiveness of hatcheries is still in question but there are a number of concerns about their impacts on wild salmon.

The last of the "4 H's", and perhaps the most important in terms of its impact on salmon, is loss of habitat. Salmon are anadromous, meaning they utilize a wide variety of freshwater, estuarine, and oceanic habitat for different parts of their life cycle. In the freshwater environment, there are numerous factors related to salmon survival, but two of the most well-known are gravel size and flow regimes. In general, the finer the gravel, the lesser of value it serves as salmon spawning habitat. Fine gravel blocks the exchange of good quality water into the salmon redds ("nests") and can rob developing salmon alevins in the gravel of water rich in oxygen (Quinn 2005). Development of land within a given watershed can also have impacts on the distribution of salmon within that watershed, causing salmon to shift to areas of less development and away from areas of high development (Burnett et al 2007; Bilby and Mollot 2008).

As salmon begin to acclimate to the marine environment, they rely on estuarine habitats to complete their physiological changes (known as smolting). These valuable nearshore habitats have undergone tremendous anthropogenic changes. Estuarine wetlands, which provide juvenile salmon areas for foraging and hiding from predators, have been reduced to a fraction of their historic Puget Sound distribution (Tanner et al 2002; Puget Sound Action Team 2007). In the Fraser River delta of southern British Columbia, less than 1% of valuable wetland habitat remains from historic times (Environment Canada-British Columbia Ministry of Environment, Lands and Parks 1992). Altering shoreline habitat could also alter the behavior and the distribution of salmon (Toft et al 2007).

It is unclear how southern resident killer whales will respond as food resources continue to dwindle. Currently, there is no reason to suspect that they would switch to another salmonid species. Chinook salmon are already the least abundant of salmon species found in SRKW habitat (Quinn 2005) and although other salmon are readily available, they are rarely taken. Puget Sound Chinook salmon populations are at only a fraction of what their historical levels were (National Marine Fisheries Service 2007), and the lack of their population restoration is undoubtedly hindering the recovery of southern resident killer whales.

Pollution

Puget Sound has a long, rich history of human-introduced contaminants into its waters. The Puget Sound Action Team (2007) noted that degraded sediments, high levels of polychlorinated biphenyls (PCBs), polybrominated diphenyl ethers (PBDEs), polycyclic aromatic hydrocarbons (PAHs), and other persistent organic pollutants (POPs) are impacting the ecosystem. Many of these toxins are capable of accumulating in the tissue of living organisms and increase in levels and magnify in effects as they move up the food chain (Puget Sound Action Team 2005), a process known as bioaccumulation.

Understanding the complexity of pollution inputs into the food web used by southern resident killer whales is no easy task. The Puget Sound/Georgia Strait basin surrounding the prime summer habitat of these whales is heavily populated by humans and is projected to keep growing. In 2000, 7 million people lived in basin, and over 9 million are expected to reside in the area by 2020 (Fraser et al 2006). The increasing population is going to call for more development of land. Nutrients, metals, toxic chemicals and other contaminants are finding their way into the Sound via storm runoff that is unable to penetrate and soak into the ground where development has occurred (Washington State Department of Ecology 2009a). This has been cited as the number one cause of pollution in Puget Sound (Puget Sound Partnership 2008). PCBs and PBDEs, both suspected to have impacts on the health of the southern resident killer whales, were developed primarily as electrical insulators and flame retardants, respectively (Ross 2006). Despite having been banned in the United States and Canada in 1977, PCBs are still present in the environment (Ross et al 2000; Missildine et al 2005; Ross 2006; Krahn et al 2007; and Cullon et al 2009). In 2007, Washington State became the first American state to ban PBDEs, however, unfortunately due to their persistent nature similar to PCBs, they will most likely be found in the ecosystem for decades to come. In fact, PBDEs are doubling every four years and by 2020 will surpass PCB levels in many species, making it the most "important" contaminant in the habitat used by southern resident killer whales (Puget Sound Action Team 2007).

In addition to causing cancer in animals, the Environmental Protection Agency (EPA) reported that PCBs damage the immune, endocrine, reproductive, and nervous systems (2008). PBDEs are not as well understood but animal studies show that PBDEs impact brain development and impact an animal's ability to learn (Washington State Department of Health 2009). With chemical structure comparable to PCBs, long-term studies may reveal that these two compounds may have similar impacts on organisms.

Due to their industrial nature, these pollutants are found at much higher levels in aquatic environments in close proximity to urban areas. Missildine et al (2005) reported that Chinook salmon returning to hatcheries within the highly urbanized Puget Sound had almost 2.5 times the PCB concentrations than Chinook salmon returning to hatcheries along the sparsely populated Washington coast. Chinook salmon in the relatively pristine Johnstone Strait of northern British Columbia had lower levels of PCBs than Chinook found in the lower Fraser River (Vancouver, BC), Duwamish River (Seattle, WA) and the Deschutes River (Olympia, WA) (Cullon et al 2009). PBDE concentrations in English sole, herring, and harbor seals located within Puget Sound were much higher than those species populations found within the Georgia Strait (Puget Sound Action Team 2007).

The persistence of these chemicals is reflected in southern resident killer whales. PCB and PBDE burdens in southern resident killer whales are three and five times higher, respectively, than northern resident killer whales (Ross 2006). Unlike southern residents, northern resident killer whale habitat is sparsely populated and has been spared the habitat degradation experienced by the southern population. It should be noted that transient killer whales have approximately 60% higher concentrations of PCBs (but no real difference in PBDE concentrations) (Ross 2006). This probably reflects the fact that transients feed on other marine mammals, which are higher up the food chain, increasing the likelihood of higher PCB concentrations due to bioaccumulation. PCB concentrations increase with age in males from both northern resident (Ross et al 2000) and southern resident killer whales (Krahn et al 2007). There is no evidence that PCB concentration increases over the lifespan of females until post-reproductive stage (Ross et al 2000). Since PCBs and PBDEs are lipid-soluble, these toxins are passed from mother to offspring via milk, thus females offload a lot of their toxic burden to their offspring. Therefore, it makes sense that J1, the oldest male in the southern resident community would logically have the highest burden of PCB contaminants in the population (Krahn et al 2007). PCB concentrations in sampled southern resident killer whales are significantly higher than health effect thresholds (Ross et al 2000; Ross 2006; and Krahn et al 2007). PBDEs were not age specific, which could reflect their continued use and introduction into the environment long after the PCB ban. In Washington State, a law was passed that calls for the gradual phasing out and banning of PBDEs (Washington State Department of Ecology 2009b). Given that PBDEs are in many products consumed in the northwest, the absence of a law banning PBDEs in British Columbia, and their persistence in the aquatic environment, it is unclear what success the Washington State ban will have in reducing PBDEs in the environment.

Despite no real difference in PBDE concentrations between southern residents and transients, there does seem to be evidence that SRKW concentrations are higher than northern residents (Rayne et al 2004). The pristine conditions of the northern resident population habitat when compared to the southern resident's is the most likely explanatory variable for differences in contamination since they both feed at the same level on the food chain. More troubling is as the human population increases in the Puget Sound/Georgia Strait basin, forward planning and management for habitat restoration will be challenging at best.

Effects from Boats

Southern resident killer whales' core summer habitat is surrounded by a high number and density of people. As a result, many large commercial shipping vessels frequent the waters carrying goods to the millions of people living in the Puget Sound/Georgia Strait region. Additionally, killer whales are charismatic megafauna, therefore enthusiastic whale watchers congregate on commercially operated and recreational private vessels, making southern residents easily accessible to a large number of people.

Globally, whale watching has been a very profitable industry. From 1994 to 1998, the total number of whale watchers increased from 5.4 million to 9 million, with an expenditure increase from $504 million to $1.049 million (Hoyt 2001). The whale watch operations focused on southern resident killer whales has also experienced an increase in the number of paying customers. From 1990 to 2000, the number of whale watching vessels increased fivefold (Foote et al 2004). In 2005, there were a total of 74 commercially operated boats from various Canadian and American ports that carried more than 250,000 people to view southern resident killer whales (Koski 2005).

The potential impacts of whale watching on killer whales are one of the more recently studied phenomena. A study on northern resident killer whales in the Johnstone Strait revealed that killer whales swam away from shore and out towards open water when boats were present, but did not alter their speed or spacing (Jelinski et al 2002). It was also observed that vessels violated both a motorized vessel-restricted area and recommended distance buffer from the whales. A study of southern resident killer whales revealed that boat presence within 400 meters significantly decreased the time the animals spent foraging and significantly increased the time the animals spent traveling when compared to boat absence (Lusseau et al 2009). An increase in the number of boats also led to a decrease in the amount of time between breaths, altered dive durations, and increased swim speed (Williams et al 2009). Whales being cut off by boats alter the direction of their migration path (Willams et al 2002).

Foote et al (2004) found that southern resident killer whales may adjust their vocal calls in response to anthropogenic noise. From 2001 to 2003, they found that killer whale call duration increased in the presence of boats. Although they did not find a significant increase in call duration when exposed to vessel noise, Holt et al (2008) did report that killer whales increase their vocal amplitude when exposed to higher levels of ambient noise. The energy expended by killer whales in the presence of vessel noise could also be higher than in the absence of boats (Williams et al 2006). Williams and Ashe (2007) hypothesized that killer whale evasive tactics in the presence of boats mimics evasive tactics used by other animals when being pursued by predators. Considering all of this, the importance of whale-watching should not be understated. In addition to providing valuable economic opportunities, they also provide conservation opportunities and give people a chance to see killer whales in their natural habitat.

The risk factors mentioned above are among the most common reasons as to why the population of southern resident killer whales has declined and its lack of recovery. These risk factors must be addressed if the recovery of the Puget Sound/Georgia Strait population of this iconic species is to be achieved. The purpose of this thesis, however, is to examine feeding habitat. Many cetacean habitat studies focus, at least in part, on benthic characteristics, and/or spatial distribution in defining habitat characteristics for a given population (for reviews of some of these studies please see the discussion section). This thesis will use both benthic characteristics and spatial distribution to determine differences between where killer whales were successful and where they were not. From 2004-2007 southern resident killer whales were studied in their core summer habitat around the San Juan Islands, and to a lesser extent in Puget Sound proper. Types of killer whale observed behaviors were numerous but were generally defined as feeding (evidence of successful predation event), possibly feeding (no evidence of successful predation event but behaviors that are thought to be signs of foraging (Baird and Hanson 2004; and Ford and Ellis 2006)) and probably not feeding (no evidence of successful predation event and no behavioral cues). The primary purpose of this study was to:

- Examine benthic habitat and spatial distribution of each of these killer whale follow types and test for differences in benthic depth, benthic slope, benthic aspect and distance to shore (habitat variables).

Additionally, areas of high killer whale densities were identified during this study. A secondary question to this thesis became:

- Are there any benthic habitat characteristics guiding killer whale occurrence densities?

Since it is logical to assume that predator foraging habitat is guided by prey distribution, the results may provide as much insight into salmon habitat preference as much as it does killer whale foraging habitat preference. As the Chinook salmon population continues to decline, understanding where killer whales hunt for these fish is crucial if SRKW conservation and restoration is to be achieved. This thesis will attempt to identify critical killer whale feeding habitat.

Understanding how southern resident killer whales use habitat for feeding could potentially have implications for their recovery. There are numerous studies (e.g. Heimlich-Boran 1988; Hoelzel 1993; and Hauser 2006) that identify the Haro Strait as important habitat for these killer whales, but to-date, no studies quantify feeding habitat. Learning more about where this population feeds could, for example, identify patches of marine protected areas that would guide management regimes. Quantifying SRKW feeding habitat could create buffers of “no-take” zones protecting Chinook and other salmon species, reserving those resources in these newly-created areas for killer whales. In addition, boater restriction zones or areas of increased boater regulation could be implemented.

Methods

Field Methods

Fieldwork was conducted during spring, summer and fall months during 2004-2007 (Table 1).

Table 1. Days Where Killer Whale Follows Occurred.

Year	Day	Year	Day
2004		2006	
	29-Aug		16-May
	30-Aug		18-May
	31-Aug		19-May
	1-Sep		21-May
2005			22-May
	6-Jun		23-May
	7-Jun		24-May
	8-Jun		13-Jun
	9-Jun		14-Jun
	10-Jun		15-Jun
	12-Jun		16-Jun
	13-Jun		17-Jul
	6-Jul		18-Jul
	7-Jul		19-Jul
	8-Jul		20-Jul
	9-Jul		19-Sep
	11-Jul	2007	
	12-Jul		7-Jun
	9-Aug		8-Jun
	11-Aug		10-Jun
	12-Aug		11-Jun
	13-Aug		12-Jun
	15-Aug		13-Jun
	26-Oct		14-Jun
	30-Oct		16-Jun
			17-Jun
			18-Jun
			19-Jun
			20-Jun
			6-Sep
			10-Sep
			11-Sep
			14-Sep
			15-Sep

The primary sampling locations were the waters of the San Juan Islands in Washington State (Fig. 1), with additional samples collected in Puget Sound (Fig. 2). The research boat used was a 6.3m vessel with a custom pulpit designed for better visibility and sample collection. Killer whale locations were generally known prior to the research vessel leaving port as their movements within the inland waters of Washington State are well observed and reported via citizen monitoring groups such as the Orca Network or the commercial whale-watch pager network which has been proven to be very accurate in locating killer whales (Hauser 2006). On a few occasions, the general location of the whales was unknown and the research vessel was launched in order to find the animals.

Figure 1. The San Juan Islands Study Area.

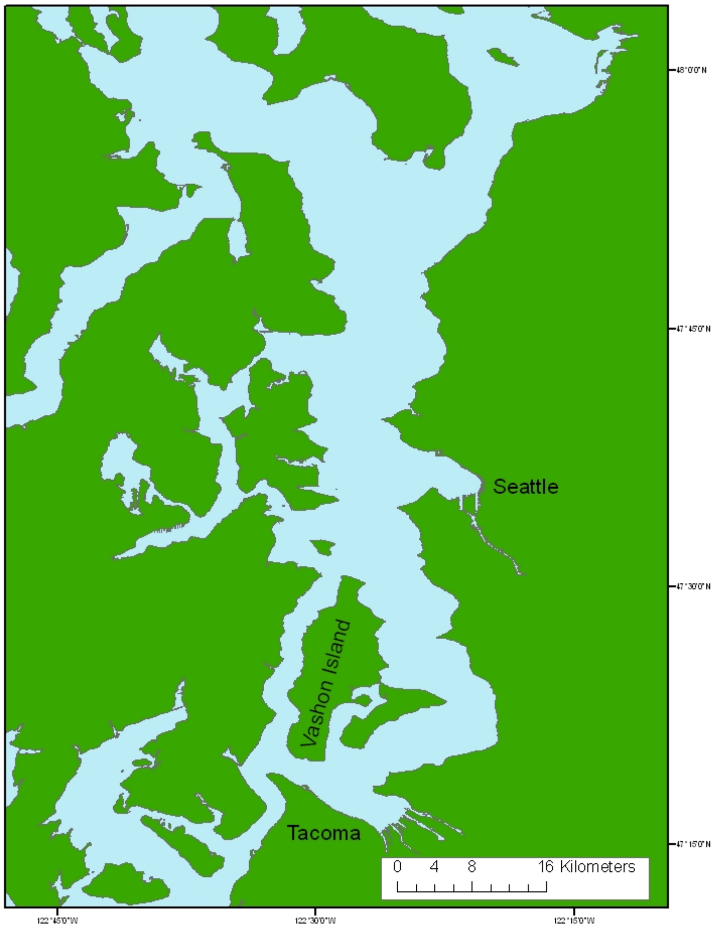

Figure 2. The Puget Sound Study Area.

While on the water, a Garmin GPS (various models) was used to automatically record the vessel location in five-minute increments (referred to as timestamps hereafter). General effort and survey information such as time of departure, weather and sea state conditions was also recorded. Sea state conditions were continuously monitored and updated.

Upon first observation of killer whales, the time of day, approximate number of animals, probable pod membership (J, K, L, or some combination), general direction of animal movement, and group envelope (geographic spread of group) was recorded. This was termed an encounter. Encounters lasted for as long as the vessel was generally close to the whales. Most days typically contained only one encounter and the conclusion of an encounter generally meant the sampling day was complete. There were a few days, however, that contained more than one encounter where the boat would leave the whales and re-establish contact later in the day. Once a group of whales was spotted, the research vessel would stay in the general geographic vicinity of that group until a smaller subset of the group became the target of more directed follows.

A follow was defined as when a whale or group of whales was being tracked in close proximity to the boat. To collect the data, the research vessel needed to follow one or multiple animals and record information on movements and behavior. Follows were classified as dedicated or opportunistic depending on how close the boat was and footprint or side depending on if the vessel was directly behind the animal(s) or on its/their side. When a follow started the exact time was recorded.

The number of animals and exact or probable identification of the whale were recorded at the beginning of each follow. If the whale(s) demonstrated behavioral cues (see Table 2 for a list) the type of cue and the exact time it occurred were recorded. Additionally, if any samples were collected from the water, such as scales and/or bit remains of fish (predation samples), fecal material from a whale, or other non-identifiable material, the time of these collections and location were also noted.

Table 2. Definitions of the Type of Behavioral Cues Associated with Foraging.

Behavioral Cue	**Brief Definition**
Long Dive	A longer than average time spent below the surface of the water
Fish in Water	A fish spotted in close proximity to a whale
Directional Surfacing (Moderate or Fast)	A surfacing that occurred with more velocity than average surfacing but in the same direction as previous surfacing
Directional Change	A sudden change in direction
Non-Directional Surfacing	A surfacing where the whale's direction changed by more than 45 degrees from previous surfacing
Chase	A whale pursuing prey
Convergence	A joining of two or more whales
Change in Speed	A whale or group of whales speeding up or slowing down
Fish in Mouth	A whale spotted with a fish in its mouth
Milling	A multi-directional slow movement

Follows ended for a number of reasons. If there was immigration or emigration from the group being followed, that follow would end and a new follow would immediately begin, reflecting a change in the group. A research permit was not available for Canadian waters; therefore, if the whales entered Canada, the follow (and the encounter) would end. Other reasons for ending a follow included a large number of whale-watching boats present, the animals getting too close to shore in areas with high human habitation or the determination that a desirable amount of data had been collected, and the vessel had the opportunity to follow a new whale or group of whales.

Data Organization and Spatial Analysis

The data collected from the field were transcribed into an Access database (Microsoft Corporation, Redmond, Washington). To better work with the data, spreadsheets were built using Microsoft Excel. All GPS timestamps and latitude/longitude were imported into Excel spreadsheets and grouped by study day. Encounters and follows were then added to the corresponding timestamp (it is important to note here that since timestamps were in five-minute intervals all data added to the spreadsheet were added to the appropriate timestamp and not to its exact time. For example if a follow began at 11:37 it is possible that the closest timestamp was 11:35 and thus does not reflect actual start time of the follow). Number of individuals followed, life history of the individual (individual name, matriline and pod memberships, and gender), behavioral cues, if any, and collections of samples from the water were also added to the spreadsheet in the same way.

Since the GPS recorded timestamps in five minute intervals starting from the moment the boat left the dock, recording location even when follows were not taking place, it was necessary to remove the timestamps that did not correspond to an actual follow, leaving only those timestamps corresponding to follows. These timestamps were imported as points into a GIS project using ArcView 9.2 (ESRI, Redlands, California) and overlayed with a 90 meter resolution digital elevation model (DEM) (NOAA's National Geophysical Data Center, Boulder, CO, http://www.ngdc.noaa.gov/mgg/coastal/coastal.html) that describes the depth of the seafloor surrounding the San Juan Islands and Puget Sound. The spatial Analyst extension was used to calculate both the slope of the seafloor (with the corrected z-factor value) and the aspect of the seafloor. Using Hawth's Tools (Hawthorne Beyer, www.spatialecology.com) the depth (meters), slope (degrees) and aspect (degrees) of the seafloor were extracted for each point. A polygon shapefile representing Washington State (Washington State Department of Ecology, Lacey, WA, http://www.ecy.wa.gov/services/gis/data/data.htm) was then added to the map project. Using the spatial join function, the distance to shore (meters) was calculated for each point. All of the GIS-derived variables were exported back into Microsoft Excel.

Benthic habitat points are highly correlated to one another, creating a problem for analysis because data are not independent. To address this, waypoints were not analyzed as raw data. Waypoints of corresponding follows had their depth, slope, aspect, and distance to shore data (hereafter referred to as habitat data) averaged to create one value for each habitat variable per follow. Though this does not remove all dependency it does minimize it. Follows then had to be divided based on definitely feeding, possibly foraging, and probably not feeding/foraging. Follows where predation samples were collected were said to have had evidence of feeding and were called "Feeding follows". Follows where there were no predation samples collected but there were behavioral cues generally associated with foraging were thought to be associated with possibly foraging whales were given the designation "Potentially Foraging follows". Follows where there were no predation sample collections and no behavioral cues observed to give any indication of feeding or foraging and were termed "Traveling follows". Because of their short duration, all follows less than five minutes (n=133) were removed from the analysis and will not be represented in the data from this point on.

In addition, Hawth's Tools were used to generate tracklines from the boat's 5-minute waypoints to generate general movement patterns of the boat during killer whale follows.

Follow Analysis

As mentioned above, to analyze the follows, waypoints of the same follows were averaged to generate one value for each of their habitat variables. Aspect values, which are directional data based on 0-360 degrees in order to quantify the cardinal directions, had to be converted to radians and have their sine and cosine values calculated to get the true average direction. For an example of this, consider two angles, 0 and 359 degrees, which are both quantitative representations of the direction north. A simple average of the two numbers generates a value of 179.5 degrees, which corresponds to an aspect of south. Since both observations correspond to north, the direction south cannot be the average but when calculating the average by first converting to radians, the value generated is 359.5, which is north.

Histograms for follow duration, benthic depth, benthic slope, and distance to shore were created. For the follow duration histogram, the bin range was 0.25 decimal hours. However, for each of the habitat variable histograms created, the bin range was calculated using a formula designed by Scott (1979) because he presents evidence that his formula provides the most accurate bin range for visually showing normality of data.

The next step was to evaluate differences in these variables between follows. Depth, slope, and distance to shore data were first imported into the statistical package R (http://www.r-project.org) and tested for normality using the Shapiro-Wilks test. When all three datasets failed, they were placed back into Microsoft Excel and a nonparametric Kruskal-Wallis test was used by leveraging the statistiXL package (Nedlands, Western Australia, http://www.statistixl.com).

Aspect values, which are directional in nature, were analyzed differently. Aspect values of each follow type were compared to a von Mises circular normal distribution by using a modified chi-square test (Greg Stewart pers. comm.).

Additionally, benthic depth, benthic slope, and distance to shore were pooled for Feeding follows and Potentially Foraging follows and compared to Traveling follows via Kruskal-Wallis test.

Habitat Analysis

To examine spatial distribution of these follows within Washington State inland waters, a grid system was created. Two grid coverages were created in GIS, one covered the San Juan Island Study Area (Fig. 3) and the other covered the Puget Sound Study Area (Fig. 4). Each cell was approximately 4.85km$^{2.}$ This cell size was determined to match a previous grid study (Heimlich-Boran 1988). Note that in the San Juan Islands, the study area and some of the cells are irregularly shaped. This is because the research was conducted in Canadian waters and the grid area was bounded by the international border.

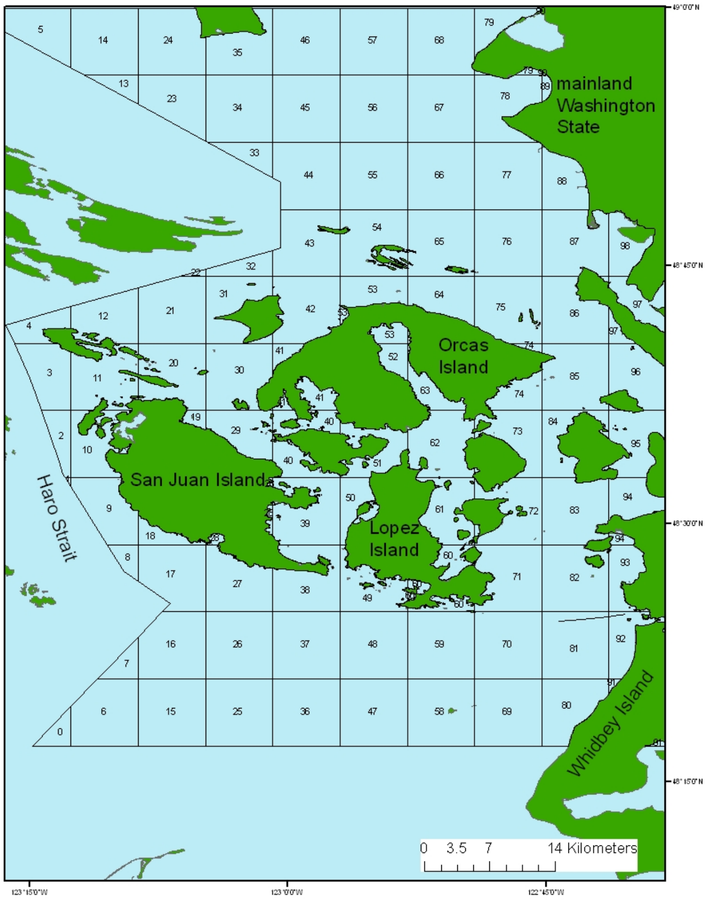

Figure 3. The Grid Coverage of the San Juan Islands Study Area.

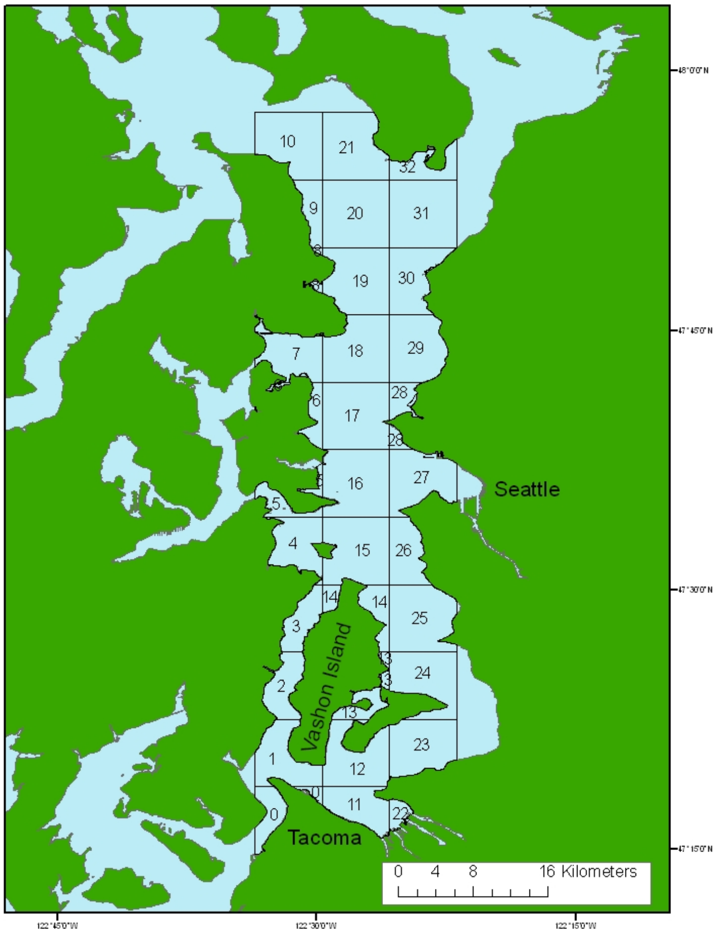

Figure 4. The Grid Coverage of the Puget Sound Study Area.

Within the cells, each follow is represented by one point. All follows were assigned to one cell, whether the follow stayed within that cell or not. If the follow stayed entirely within one cell, the point representing the follow corresponds with the first waypoint of the follow. If the follow spans two or more cells, the follow was assigned to the cell where the most number of waypoints for that follow were, and marked by the first waypoint within that cell. For follows that span two or more cells but have equal number of waypoints in each cell, the follow was assigned to the cell where the first waypoint was recorded.

The cell number for each follow was recorded. Follow duration for each follow was also recorded and used to calculate the amount of time per follow type in each cell, and the total amount of time spent in each cell. A chi-square test was to assess whether there were significant differences among follow type and follow type duration in each cell.

To determine areas of higher killer whale follows, Hawth's Tools were used to calculate spatial density for the follows within the San Juan Islands Study Area. This was not done in the Puget Sound Study Area because of the small number of follows in this portion of the study area (n=29) when compared to the San Juan Islands study area (n=443) and because there are only three clusters of points confined to the main Puget Sound channel between Point No Point and the city of Tacoma.

The kernel density calculations were then classified into 3 areas, areas with a high density of follows (0.04-0.07 follows per square kilometer), areas with low density of follows (0.002-0.04 follows per square kilometer), and areas with no follows. These areas were converted into a series of points and Hawth's Tools was used to extract depth, slope and aspect for each point. These data were used to find the average value per variable for each area.

Results

From 2004-2007 a total of approximately 170 hours of focal follows were conducted. Figures 5 and 6 show the tracklines of all follows for the San Juan and Puget Sound Study Areas respectively.

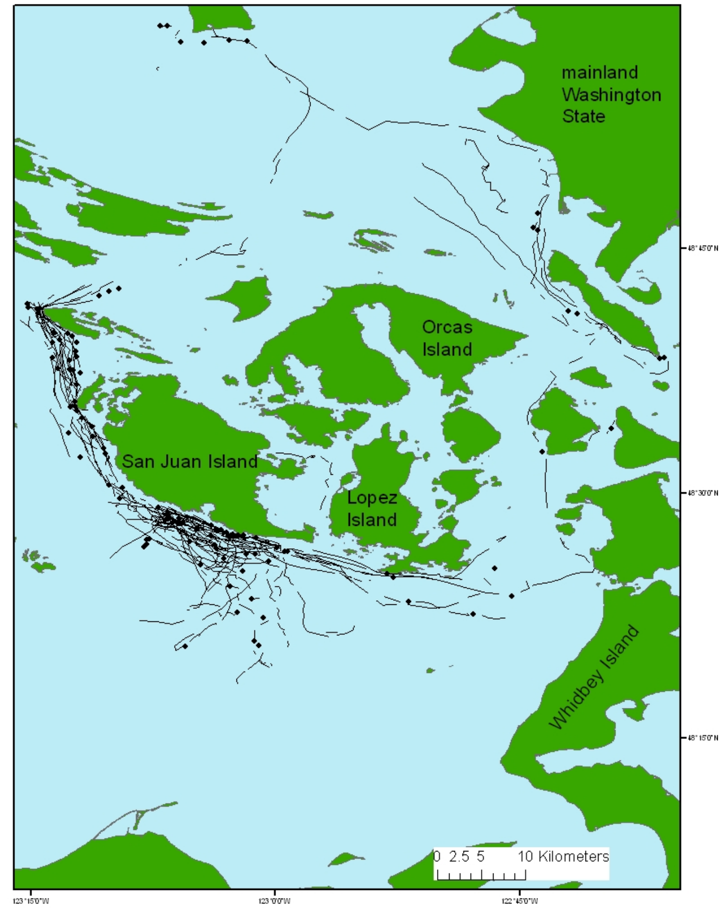

Figure 5. Killer Whale Follow Tracklines in the San Juan Islands Study Area. The lines indicate follows where there were at least two waypoints whereas the dots display follows where only one waypoint was recorded.

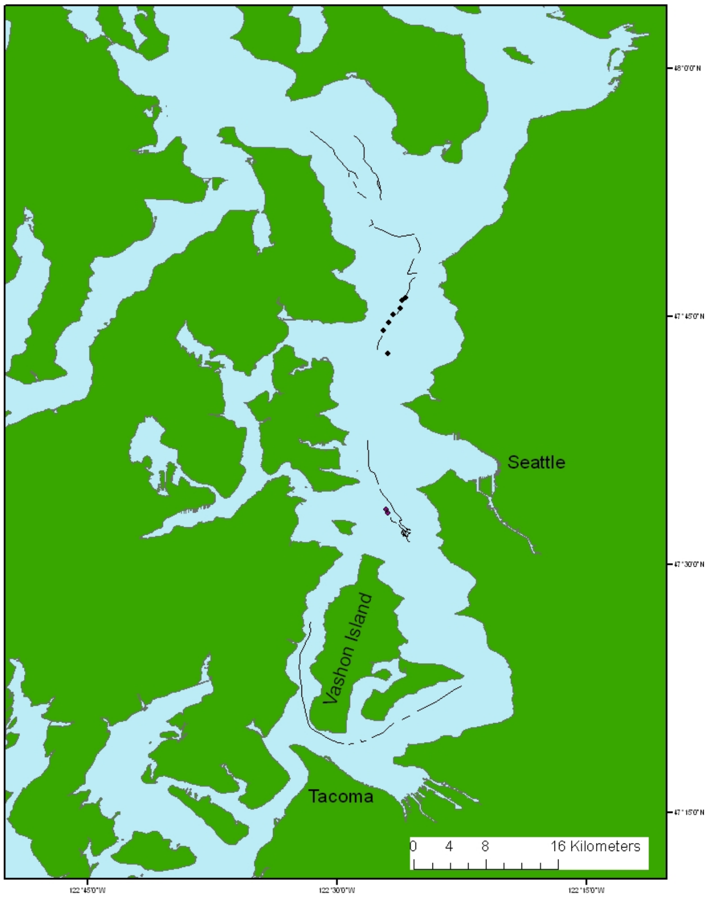

Figure 6. Killer whale Follow Tracklines in the Puget Sound Study Area. The lines indicate follows where there were at least two waypoints whereas the dots display follows where only one waypoint was recorded.

Follow Summaries

There were a total of 472 follows used in the analysis. Of those 472 follows, 16.74% were follows with confirmed successful predation events (Feeding Follows), 25.42% were follows with no confirmed predation events but probable foraging based on foraging behavior (Potentially Foraging Follows), and 57.84% were follows with no predation events and no foraging cues (Traveling Follows). The average follow lasted twenty-one minutes. Despite the fact that most follows were Traveling follows, Traveling follows had the lowest average follow duration with eighteen minutes whereas the average feeding and Potentially Foraging follows were twenty-six minutes and twenty-five minutes, respectively. The differences in follow durations were significant (H=22.75, df=2, p-value=.00001). Figure 7 shows the histogram of all follow durations, It should be noted that about 81% of all follows (n=381) fall within the first two bins, indicating that follows with longer durations are uncommon.

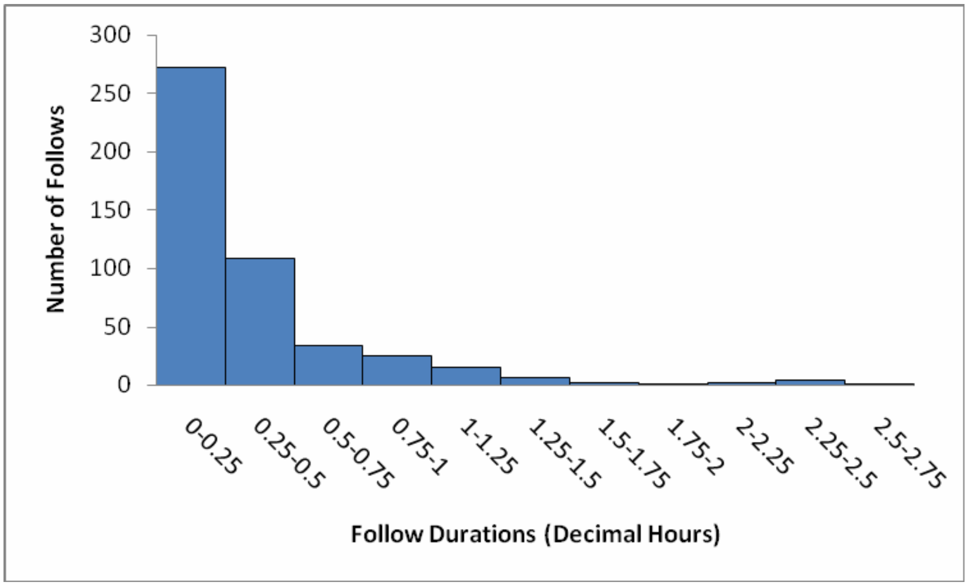

Figure 7. Histogram Showing the Duration of All Follows.

The average depth for all follows was about 156 meters (standard deviation approx 79). The average slope was 5 degrees (standard deviation approx. 8). The average distance to shore was 2 kilometers (standard deviation approx. 3). For a review of the distribution of these three variables see figures 8-10. Since aspects are directional values based on degrees of a circle, a histogram of a conventional distribution does not apply. Table 3 shows the number of follows for each cardinal direction, with their corresponding range of degrees. Of the nine possible directions, an aspect of southwest is the overwhelmingly favored direction, representing 28.6% of all aspect observations with an aspect of west in a distant second at 14.6%. A direction of "flat", which means there is no aspect because the slope at that point is zero, represents the smallest percentage of observations at 2.5.

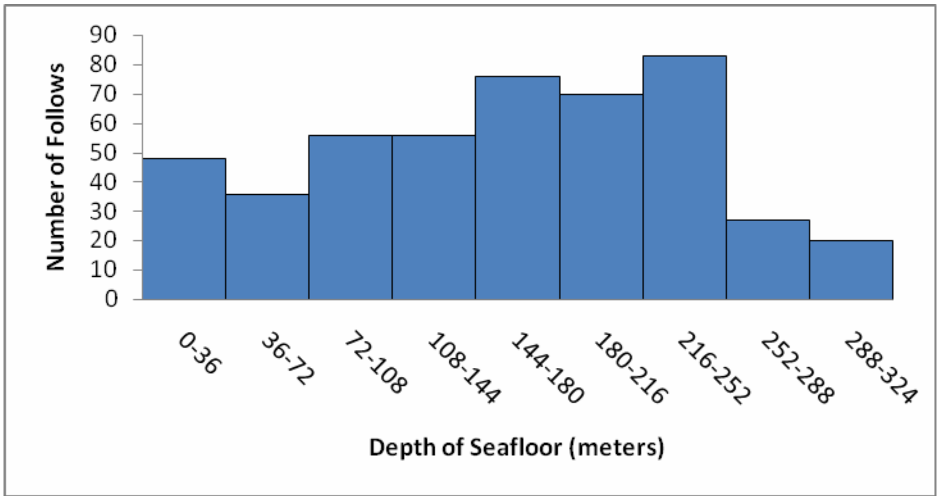

Figure 8. Histogram Showing the Distribution of Seafloor Depths for Each Follow.

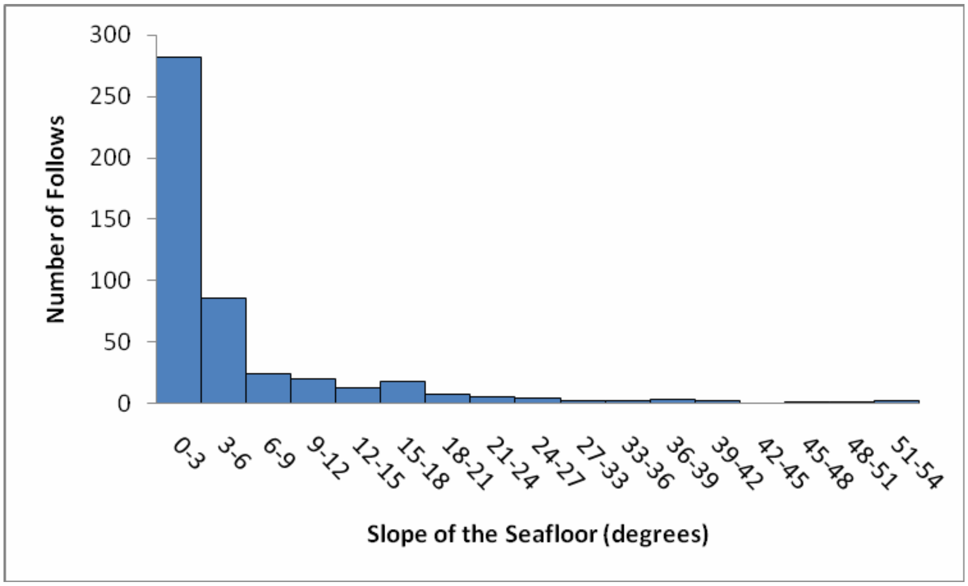

Figure 9. Histogram Showing the Distribution of the Seafloor Slopes for Each Follow.

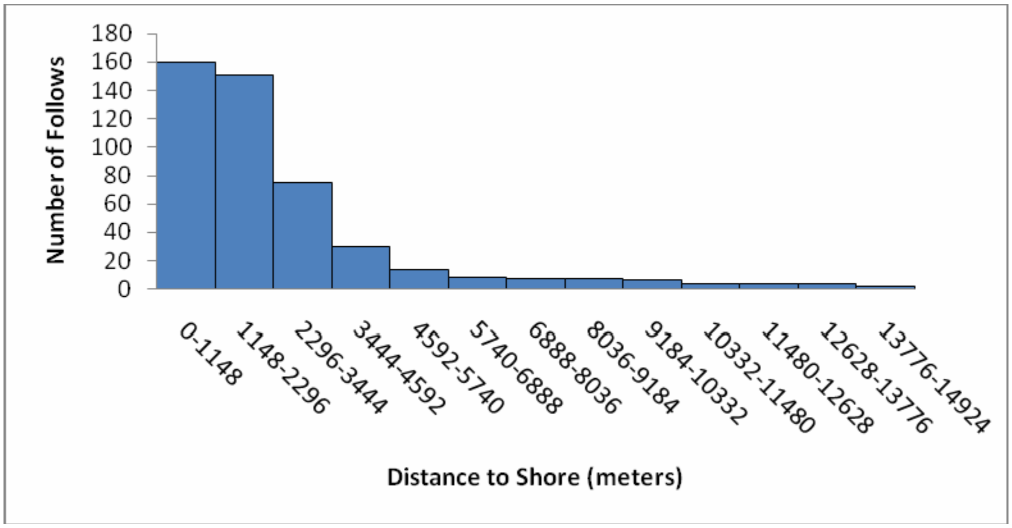

Figure 10. Histogram Showing the Distance to Shore for Each Follow.

Table 3. The Number of Observations for Each Aspect Direction.

Degrees	Cardinal Direction	Number of Follows
0-22.5, 337.5-360	North	53
22.5-67.5	Northeast	32
67.5-112.5	East	21
112.5-157.5	Southeast	37
157.5-202.5	South	59
202.5-247.5	Southwest	135
247.5-292.5	West	69
292.5-337.5	Northwest	54
-1	Flat	12

All of the above summary data were conducted on data where the follows were the unit of analysis. Each habitat variable for all waypoints within a follow were averaged together to create one value per variable per follow.

Follow Analysis

To compare the depth, slope, and aspect of the seafloor between all three follow types, a Kruskal-Wallis test was conducted. The test did not produce significant results for depth (H=1.57, df=2, p-value=0.456), slope (H=0.598, df=2, p-value=0.741) or distance to shore (H=0.877, df=2, p-value=0.645). A modified chi-square test was leveraged to compare the aspect values to a von-Mises circular distribution. The results show that each type of follow differs from a normal circular distribution (for Feeding; χ^2=37.1818, df=7, p-value<0.05, for Potentially Foraing; χ^2=29.5042, df=7, p-value<0.05, and for Traveling; χ^2=91.81818, df=7, p-value<0.05). Though these results do indicate there is a potential difference in observed aspect values compared to a normal distribution, there doesn't appear to be any differences between follow types as southwest makes up the majority of observations in each follow followed by west. This is most likely explained by the fact that west and southwest facing aspects are the most common in the study area (see below) and not by an actual selection for these habitat criteria. In all cases east make up the least observed true direction for the seafloor for each follow. A "flat" aspect is the least observed absolute value for all follow types but was removed from the analysis because it is not a true direction on a circular distribution.

For the analysis that compared the pooled Feeding and Potentially Foraging follows to the Traveling follows, no significant differences existed for depth (H=0.143, df=1, p-value=0.705), slope (H=0.544, df=1, p-value=0.461) or distance to shore (H=0.784, df=1, p-value=0.376).

Habitat Analysis

Figures 11 and 12 show the spatial distribution of the killer whale follows for the San Juan and Puget Sound gridded study areas respectively. Each point represents one follow.

A Chi-Squared analysis was conducted to examine differences in follow type duration per cell. Although there were two cells (one in each study area) that produced significant results, these cells only had Traveling follows. None of the other cells that had multiple follow types produced significant results and for the purposes of this study it will be assumed that there are no significant differences in follow type durations over the study areas as a whole. Individual Chi-Square values will not be reported separately in the text as there were too many cells examined and the vast majority was not significant. In the San Juan Islands Study Area, the types of follows were spread throughout the study area with the largest proportion of each follow type occurring in the waters off the west and southwest coast of San Juan Island. In Puget Sound, on the other hand, most of the Potentially Foraging and all of the Feeding follows were located between north Seattle and the northern extent of Puget Sound whereas follows between south Seattle and Tacoma were almost exclusively Traveling follows. Traveling follows were also abundant in the northern area of Puget Sound.

The above process was also repeated for the number of each follow type per cell. In this case, seven cells had significant differences. To the southwest of San Juan Island, cells 17 (χ^2=10.38, df=2, p-value=0.005) and 27 (χ^2=26.07, df=2, p-value=0.000002) had a significantly different number of follow types. Northwest of San Juan Island, cells 3 (χ^2=11.68, df=2, p-value=0.002), 4 (χ^2=14.8, df=2, p-value=0.0006), 10 (χ2=19.76, df=2, p-value=0.00005) and 12 (χ^2=14, df=2, p-value=0.0009) all had a significantly different number of follows. Southwest of Lopez Island, the number of follows per value type were significantly different in cell 49 (χ^2=10.75, df=2, p-value=0.004). In all cases, Traveling follows were observed as the most frequent follow type within these cells whereas Feeding follows were the least common in all but two cells.

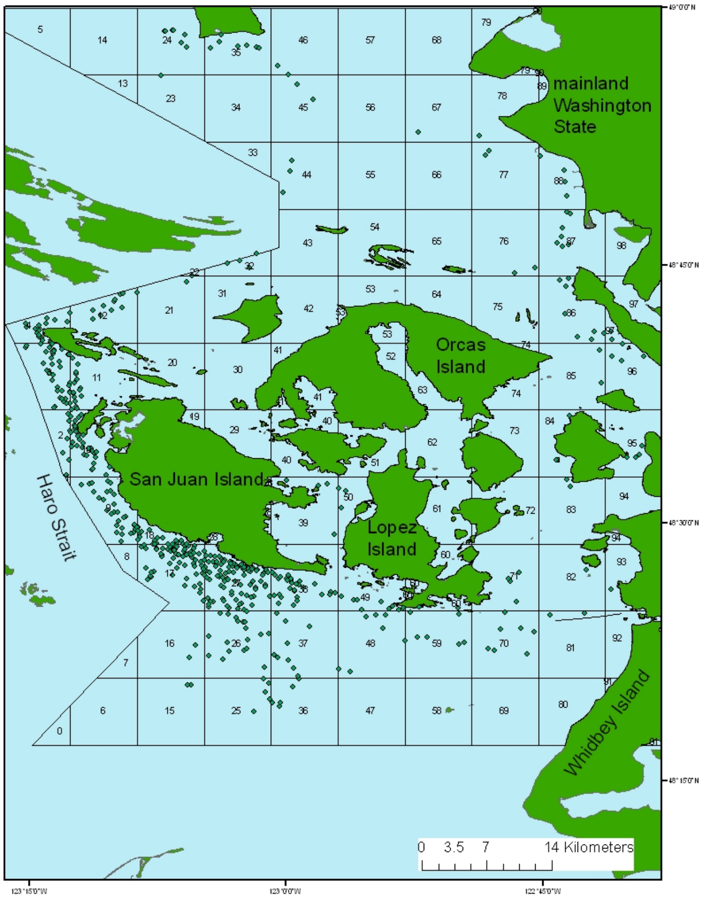

Figure 11. The Spatial Distribution of Follows within the San Juan Islands Study Area.

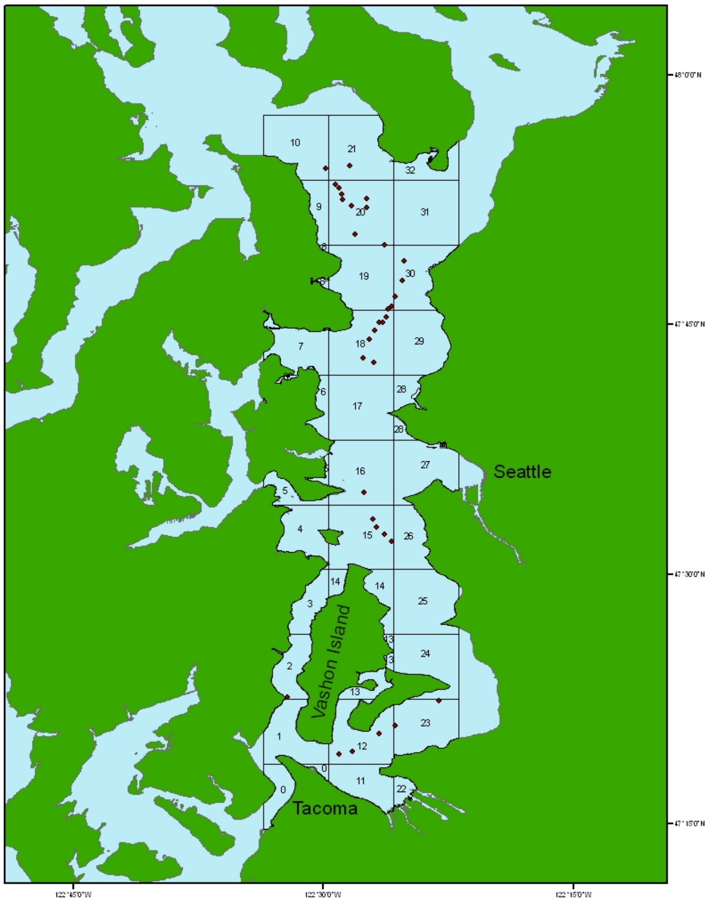

Figure 12. The Spatial Distribution of Follows within the Puget Sound Study Area.

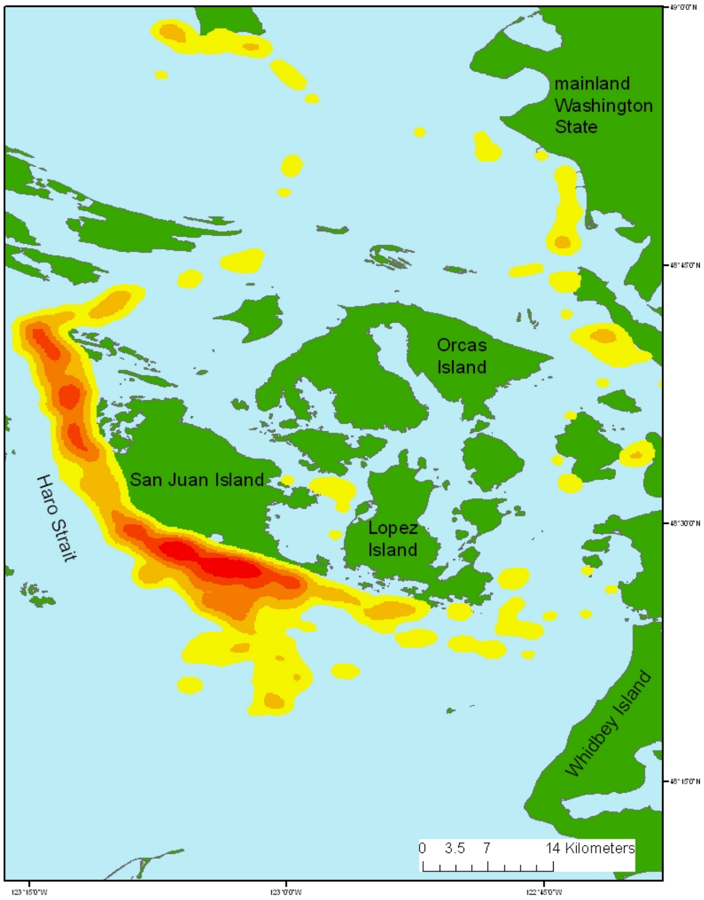

Figure 13. The Density of Follows within the San Juan Islands Study Area (higher densities shown in red).

Figure 13 shows the density of those follows in the San Juan Study Area. Note that the highest density of follows (shown in red) are in areas southwest of San Juan Island, and west of Henry and Stuart Islands, all located in the Haro Strait. These density areas were redefined into GIS shapefiles (figure 14) and compared to one another. High density areas, all located in the Haro Strait, averaged approximately 185 meters in depth (stdev approx. 81), a slope of approximately 6 degrees (stdev approx. 11) and an average aspect of west. Of the entire San Juan Island study area, high density areas made up 1.5% of the area. Low density areas were more spread across the study area though the majority of this area was also west or southwest of San Juan Island. Low density areas made up 16.2% of the entire study area and had an average depth of approximately 123 meters (stdev approx. 81), average slope of approximately 3 degrees (stdev approx. 7) and an average aspect of southwest. The rest of the area, making of 82.3% of the entire study area, had an average depth of approximately 71 meters (stdev aprrox. 55), average slope of approximately 2 degrees (stdev approx. 5) and an average aspect of southwest.

Since the low density areas are spread across the study area, it was determined to be valuable to compare the low density areas west and southwest of San Juan Island with the rest of the low density areas scattered across the archipelago. The low follow density areas west and southwest of San Juan Island had an average depth of approximately 155 meters (stdev approx. 81) and average slope of approximately 4 degrees (stdev approx. 8) compared to an average depth of approximately 71 meters (stdev approx. 48) and average slope of approximately 2 degrees (stdev approx. 4) for the scattered areas throughout the rest of the archipelago. Aspect was deemed not important since west and southwest facing slopes represent the majority of aspects throughout the entire study area.

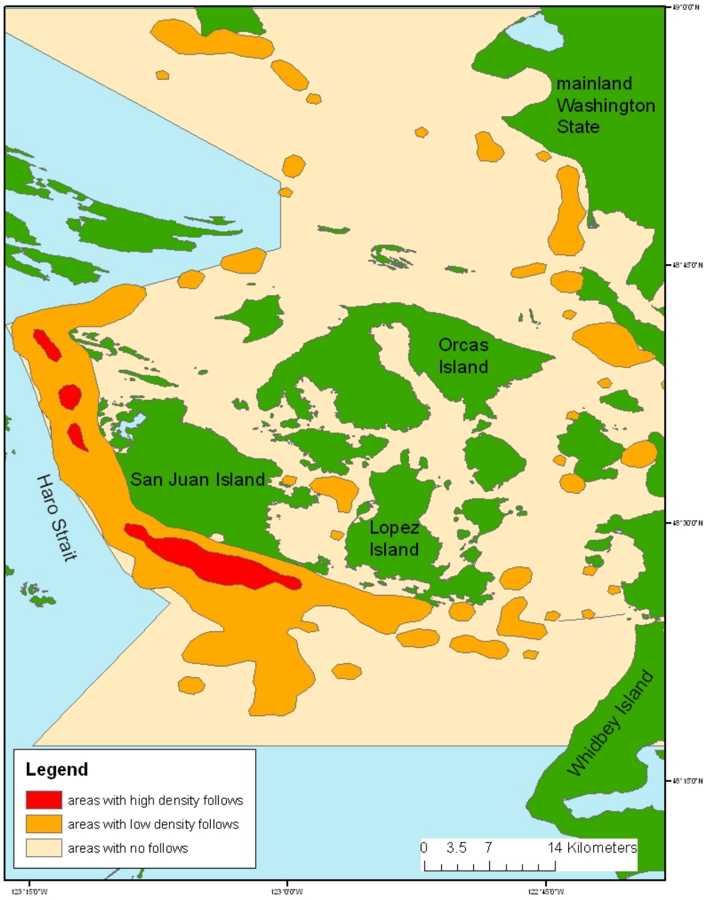

Figure 14. The Spatial Representation of Areas with High and Low Density Killer Whale Follows as well as Areas where No Follows Occurred.

To examine if there are differences in the frequency of follow type, each follow was tallied and assigned to a category based on the type of follow and in which spatial density it occurred (see Table 4). The results indicate that the frequencies of follow types do not differ between higher and lower densities, even though lower densities cover more area and higher densities have more tightly clustered follows.

Table 4: The Percentage of Follow Types per Density Areas

Follow Type	High Density Areas	Low Density Areas
Feeding	16.57%	17.16%
Potentially Foraging	29.71%	25.37%
Traveling	53.71%	57.46%

Discussion

Although most follows (57.84%) were Traveling follows (follows with no evidence of a successful predation event or foraging cues), they averaged only eighteen minutes in duration. Feeding and Potentially Foraging follows represented 16.74% and 25.42% respectively yet were generally longer follows averaging twenty-six and twenty-five minutes respectively. This may be explained by the priority that collecting prey remains had on the project. Since it was most important to collect prey remains, follows involving animals exhibiting traveling behavior were broken off in hopes of having better luck finding prey remains from actively foraging animals. The average duration of all follows was approximately twenty-one minutes. Follows ended for a variety of reasons. Southern resident killer whales attract a large number of commercial and recreational whale-watching vessels, with an average of 20 boats around groups of these whales (Koski 2005). To prevent a negative impact on commercial operations, and in order to continue to facilitate cooperative relationships with the industry, follows would occasionally be terminated when a large number of whale-watching boats were present and had interest in the individual(s) that were the focus of the follow. Follows were also ended if the followed individual(s) entered Canadian waters, traveled too close to shore in areas with high human population density, or if daylight was waning. The primary study objective was to collect any remains from a predation event, therefore, if the followed individual(s) appeared inactive, and another individual or group of individuals appeared to be exhibiting foraging cues we would switch the follow to potentially foraging whales, thereby reducing the potential for harassment due to extended follow duration. This could contribute to the longer duration of Feeding and Potentially Foraging follows; if whales appeared to be foraging or if evidence of foraging existed, follows may have been less likely to have been broken off, whereas non-foraging whale follows (Traveling) would be abandoned in favor of whales demonstrating potential predatory behavior.

Follow Type Comparison

Habitat variables were compared to examine the differences, if any, between the three follow types. Surprisingly, there were no significant differences in depth of the seafloor, slope of the seafloor, aspect, or distance to shore for any of the follow types. When the Feeding and Potentially Foraging follows were pooled to compare to the Traveling follows, no significant differences were found in depth, slope or aspect. Aspect was not tested in this pooled dataset because not only were the aspect values and the proportions they represented in the dataset virtually identical between follows but these values also reflect the available aspect in the study area. Thus aspect was deemed unimportant. These results indicate that southern resident killer whales may not pick certain areas, based on these criteria, to find salmon. It could, however, potentially indicate that salmon do not select for habitat based on these criteria either, logically assuming that the predator will selectively find food where its prey can be found.

Two problems exist with testing differences in environmental variables between follows in this fashion, both related to data dependency. Similar to an ANOVA, one of the assumptions of a Kruskal-Wallis test is that data are independent of one another. The waypoints collected that ultimately made up a follow were not independent. With bathymetry, each point is correlated (the depth at one point is related to surrounding areas and thus is not truly "free" to be any depth). To minimize the impact of bathymetric dependency, all waypoints for a given follow were averaged together to create one value for benthic depth, benthic slope, benthic aspect, and distance to shore for each follow instead of one value for every waypoint within a follow. The second problem was that the follows themselves were spatially correlated. In many cases when one follow ended, another would immediately begin, making the environmental features of both follows correlated to one another. Again the combining of waypoints to create one average for each of the four habitat variables for each follow was an attempt to minimize this.

There may be other limiting factors to killer whales foraging ecology not measured here. For New Zealand's Hector's dolphins (*Cephalorhynchus hectori*), water clarity and sea surface temperature (SST) were significantly important for habitat selection (Brager et al 2003). Physical and chemical data about the water were not recorded in this study. However, changes in the water and its effects on killer whale foraging would manifest itself in salmon distribution. Though it is clear that water variables influence salmon presence/absence on a large scale and their vertical migration (Quinn 2005) information about these factors' influence on salmon abundance at a fine scale are limited in coastal and estuarine waters. Hoelzel (1993) found no correlations between bathymetry and fast non-directional behaviors with southern resident killer whales. Though the current study does not test correlations in bathymetry and follow type, it does lend strength to Hoelzel's findings that bathymetry may not effect foraging. In addition to changes in the water, physical habitat differences could explain feeding vs. non-feeding follows. In areas of western Florida, foraging bottlenose dolphins (*Tursiops truncatus*) selected for dredged channel and spoil-Island habitats in one area and natural channels in the other (Allen et al 2001). There may be differences in the type of physical environmental features between these follows that were not measured here that could have influenced the distribution of salmon. This seems unlikely given that the greatest density of all three follow types occur west of San Juan Island in a relatively small area but should not be ruled out until properly investigated.

Another factor that could have impacted the results reported here is the issue of spatial scale. With all spatial studies, the issue of spatial scale could impact the results. The spatial scale chosen here was 90 meters, and this was chosen primarily because it was the smallest spatial scale available. Follow waypoints were pooled to create one value for each habitat variable per follow so increasing spatial scale was deemed inappropriate given that resolution was being decreased by this process. However changing the spatial scale would undoubtedly alter the habitat values for each waypoint, which in turn could cause results that indicate significant differences between follow types.

Habitat Analysis

A grid system containing cells roughly 4.85km^2 was created to closely match a previous study done by Heimlich-Boran (1988), though his study used 4.6km^2 cells. It was determined that 4.85km^2 were the dimensions to use because it could be easily created in GIS and still closely match the dimensions of the comparative study. Both time spent on each follow (duration per follow type) and number of observed follows per cell were analyzed.

For follow durations, only two cells, one from each study area, yielded significant results. Both of those cells, however, had only Traveling follows located within them. Given this, it seems that spatial location did not influence follow duration differences. In fact, the Haro Strait had the greatest number of all three follow types. This information does seem to reveal that although spatial location does not influence killer whale feeding, it does influence killer whale presence/absence.

Number of observed follows, on the other hand, revealed significant differences. In the San Juan Islands Study Area, two cells southwest and four cells northwest of San Juan Island had a significant different number of follows per follow type. In one cell southwest of Lopez Island, significant differences in number of follows per follow type were also observed. In all cells, Traveling follows were the most numerous follow type. In most cases, Potentially Foraging follows were the second most numerous while Feeding follows were the least observed follow type. Though differences were not tested between these cells and the study area as a whole, nor was the significance tested for the number of follow types for the entire study area, trends for these cells seem to match the entire four year sample, where Traveling follows were the most numerous and Feeding follows were the least numerous.

The sample size in Puget Sound is considered to be too small to draw any conclusions about fine-scale habitat use in that study area but what is known is that Puget Sound plays an important role in southern resident killer whale ecology. Orca Network (www.orcanetwork.org), which collects sighting data on many marine mammal species including both resident and transient killer whales, gray whales (*Eschrichtius robustus)*, and minke whales (*Balaenoptera acutorostrata*), has logged 102 days where resident killer whales were sighted within Puget Sound during 2004-2007. During this time period, there are very few days where resident killer whales were located south of the Tacoma Narrows (n=5). The majority of the sightings (n=38) where around Vashon Island. Other areas of higher number of sightings compiled by Orca Network were Kingston (n=18) and Bainbridge Island (n=11). The majority of these sightings are from recreational, non-professional whale watchers therefore positive species and pod/individual identifications have not been verified. It is possible that some of these animals could be mammal-eating transients. Another potential data bias could be found in a larger number of sightings occurring around higher density human populated areas. For instance, although Vashon Island itself is not heavily populated, it can be easily seen and accessed by boaters from Tacoma to Seattle, the two largest cities in the Puget Sound region. Bainbridge Island can be seen and accessed easily by boaters from Seattle and can be easily accessed by Bremerton and Port Orchard. Three of the areas with relatively few sightings, Cooper Point (n=2), Squaxin Island (n=2), and Fox Island (n=1) are all south of the Tacoma Narrows where the population is less dense than the Seattle-Tacoma metropolitan area. Regardless of these potential sighting biases, Puget Sound appears to be valuable habitat for the southern resident killer whales. More research in the Puget Sound basin is warranted.

Comparisons with Heimlich-Boran's (1988) work were considered valuable to examine trends in spatial-habitat use. It should be noted that Heimlich-Boran broke his observed behavioral patterns into four categories (feeding, travel, rest, and socializing) and sub-divided those categories further down. To compare his data with data presented here, some liberties must be taken in regards to the broader classifications used in this study. For example, he differentiates between "resting" and "traveling" whereas any follow that did not have any evidence of a predation event or foraging behavioral cues was classified as a Traveling, regardless of other behavior observed, not just whether they were resting or actively traveling.

Similar to the data here, Heimlich-Boran's study found a high density of killer whale encounters west and southwest of San Juan Island. In addition, he had a high number of encounters extending all the way into Canadian waters to the mouth of the

Fraser River. This study did not extend into Canadian waters therefore we cannot know if that pattern would be seen here also. Although the results are not identical, similar patterns do exist. Southwest of San Juan Island saw the longest Feeding follow durations. In Hemlich-Boran's paper, these were areas defined as locations that saw "increased feeding". Traveling northwest up the coast of the Island, less time was spent on Feeding follows and a greater proportion of time was spent on Traveling follows. In the comparison paper, it was observed that, this area was generally used for either traveling or resting. Though these results are not statistically significant, there does seem to be similarities in the two datasets. The only major differences in the datasets lie in the area around Point Roberts (figure 11, cells 24, 35, and 45; Heimlich-Boran calls this area central Georgia Strait). Hemlich-Boran (1988) identified this as an area of increased traveling behavior; however, this study found that Feeding follows were observed a majority of the time (66.3%).

Hauser (2006) also found that the Haro Strait is heavily used by southern resident killer whales during the summer months regardless of pod membership. She also found that depth had a significant relationship with southern resident killer whales; it was reported by Hauser that killer whales were found in greater density in deeper cells. Slope and distance to shore were also found to be important. Likewise, in the data presented here, killer whale density was also greatest in areas of deeper waters. However, killer whale density in this study was also greatest in the Haro Strait (west and southwest of San Juan Island), which is the deepest part of the waters around the San Juan Island archipelago. In Hoelzel's (1993) study, southern resident killer whales were also found more often over deep areas. It is possible that factors besides depth, such as its potential importance as a salmon migration route, could make the Haro Strait area important to killer whales. There are six areas within the Haro Strait that have been identified as "biological hotspots" (Bloch et al 2002), indicating that this area is ecologically productive.

Although locations where killer whales were found in high density were in deeper areas of the San Juan Islands, killer whales were also found, albeit in lower densities, in shallower areas as well. All areas of high density follows were in Haro Strait. Most of the lower density follows were also observed in Haro Strait, however, there were other zones of lower density follows spread throughout the study region. However, when comparing the lower density follow areas in the Haro Strait to those scattered around the archipelago, the scattered areas were much shallower on average and are comparable to the average depth of water with no killer whale follows. In addition, prey remains have been collected in these shallower areas so thus importance of these areas should not be ignored. In fact, data here show that although there are areas where killer whales were found in higher densities (refer to Figure 14), the frequency of follow types observed do not differ between high and low density areas. On the surface, this indicates that areas where killer whales are less observed may be just as important in terms of foraging ecology. Note that the density values reported here reflect the spatial patterns of the follows that were conducted during the field surveys and not killer whale occurrence. These patterns may not necessarily reflect the density pattern of where the southern resident killer whale community can be found (even though spatial patterns reported in other studies report similar patterns).

Hauser (2006) also found that there could be a potential preference for steeper slopes by resident killer whales. As with the depth of the seafloor, there may be some preference for killer whales that were observed in this study to also select for areas with steeper slope. However, like depth, the Haro Strait has a steep slope gradient and thus could bias the data presented in this study.

As with depth, the low density areas were divided to compare the average slope of the low density areas within Haro Strait to the low density areas scattered around the rest of the study area. Unlike depth, however, the slope of the scattered areas did not match the slope of areas with no follows but rather was a mid-point between the Haro Strait data and the areas with no follows. Steeper slopes are more evenly distributed than depth across the study area, therefore it is possible that this is merely the byproduct of the spatial distribution of benthic slope rather than selection based on preference.

Finally, Hauser (2006) examined distance to shore and discovered that southern resident killer whales may prefer areas closer to shore. Although I examined distance to shore as a variable for comparing follow types, distance to shore was not examined when looking at presence/absence of killer whales within the study area. The research vessel, in general, avoided populated nearshore areas in favor of areas further off land or close to sparsely populated shorelines.

Aspect was also examined as a variable to determine killer whale density. A southwest aspect is the dominant value throughout the entire study area. In high density areas the dominant aspect was west. In low density areas and areas with no follows, southwest was the dominant sea floor aspect. Aspect was deemed not important in this study area as killer whale occurrence related to aspect does not differ from the average aspect found in the study area.

As with the Chi-Squared spatial analysis, the sample size within the Puget Sound study area was too small to draw any conclusions about benthic habitat variables and their influence on killer whale density. Therefore this analysis was not done in the Puget Sound area as the small sample size would not produce any meaningful results. It would be of value to examine densities of killer whale occurrence related to benthic habitat in Puget Sound in the future.

Understanding predator-prey interactions is important in ecological studies. As spatial habitat studies become more refined, new methods and findings will emerge.

For example, movement patterns of top predators such as killer whales, will be influenced, to some degree, by prey movements. In the Johnstone Strait of British Columbia, Canada, data were collected that support this hypothesis. The timing of northern resident killer whale occurrence and population increases coincide with occurrences and increases in the salmon population (Nichol and Shackleton 1996). Current research with southern resident killer whales reveals some interesting, and surprising results. McClusky (2006) found that although southern resident population fluctuations are correlated with population fluctuations of Chinook and chum salmon, SRKW spatial density did not match the density of salmon. Heimlich-Boran (1986) found different results; upon examination of all of the inland waters of Washington State (Puget Sound, Hood Canal, The San Juan Island archipelago and the Strait of Juan de Fuca), he found that there was a positive correlation between salmon distribution (based on catch data)and killer whale sightings in the study area as a whole. But more importantly, and contrary to McClusky (2006), there were positive correlations in salmon density and killer whale sightings in specific marine areas, such as the Strait of Juan de Fuca, the San Juan Islands as a whole, and the two northern management regions of Puget Sound stretching from Seattle to Point Wilson, WA.

A theme in ecology is that predators may maximize efficiency by matching their distribution to that of their prey's habitat and resources rather than actually following or randomly searching for prey (Flaxman and Lou 2009). This is known as the optimal foraging theory. As previously mentioned, Chinook salmon are the preferred prey item of southern resident killer whales. Though the influence of bathymetry on Chinook salmon is poorly understood, what is known is that Chinook salmon are found in deeper parts of the water column when compared to the other salmon species (Quinn 2005). Killer whales may be selecting for deeper areas in which to forage in response to the water column partitioning observed by the Pacific salmonids.

Depth is one of the most widely used variables when examining cetacean habitat. In the same study area as this study, it was discovered that harbor porpoise (*Phocoena phocoena*) sightings occurred over depths greater than 100 meters (Raum-Suryan and Harvey 1998). In the Bay of Fundy, Canada, two species were examined. Fin whales (*Balaenoptera physalus*) preferred waters less than 60 meters deep whereas minke whales preferred waters deeper than 60 meters (Ingram et al 2007). Even in other marine mammal species depth appeared to have some influence in distribution, as is the case with a harbor seal (*Phoca vitulina*) population in Scotland (Tolit et al 1998). This study found that harbor seals were generally found in depth ranges of 10-50 meters and would dive to the maximum depths within the foraging range.

A few studies revealed that depth was not important in determining distribution. One study, in Cook Inlet, Alaska, determined that bathymetry was not important in examining distribution of beluga whales (*Delphinapterus leucas*) (Goetz et al 2007). However for most cetacean studies, depth was important either as a primary explanatory variable or a secondary variable.

Slope is another widely examined and generally important variable in explaining cetacean habitat use. The Bay of Fundy study by Ingram et al (2007) determined that slope, specifically steeper slopes, was important to minke whales. In Scotland, grey seals (*Halichoerus grypus*) seemed to show a preference for areas with a greater variation in seabed slope (MacLeod et al 2007). Bottlenose dolphins along the west coast of Ireland showed a preference towards estuaries with a greater benthic slope (Ingram and Rogan 2002). The seabed gradient most likely has some affect on habitat characteristics. It is known that benthic slope is a major driver in benthic complexity, which in turn can create areas of biological “hotspots” (Ardron 2002). Habitat complexity is already known to have a positive impact on species diversity, such as pool-riffle habitat in river ecosystems. Benthic slope could also affect nutrient upwellings, which in turn could affect primary production.

Seabed aspect is not a commonly studied variable in marine mammal distribution. In one study involving Blainville’s beaked whales (*Mesoplodon densirostris*) around Great Abaco, The Bahamas, depth, slope, and aspect were examined (MacLeod and Zuur 2005). Although these whales showed preference for depth and slope ranges, aspect was discovered to be the most important variable describing distribution with a preference of a northeast facing aspect.

Variables not examined here are also used to explain cetacean distribution. A population of New Zealand dusky dolphins (*Lagenorhynchus obscures*) seemed to prefer areas with currents exceeding 12km/hr (Markowitz et al 2004). Interestingly, a dusky dolphin study conducted in Patagonia (Garaffo et al 2007) revealed that not only was sea floor depth important to dusky dolphins but that preference changed over a temporal scale from year to year. In many cases it is not one specific variable but a combination of two or more that are important to cetacean use. In the Cook Inlet beluga whale study, for example, proximity to mudflats and medium to high flow accumulations (river basin discharge) were important in determining habitat features (Goetz et al 2007). Chilean dolphins (*Cephalorhynchus eutropia*) in Yaldad Bay, southern Chilie did not use the bay uniformly but selected for areas close to shore with depths of 5-10 meters and in intermediate distances to rivers (Ribeiro et al 2007). In a study of Hector’s dolphins (*C. hectori*), which are endemic to New Zealand and endangered (Jefferson et al 2008), animals were frequently encountered in shallower, turbid waters with an SST of greater than 14 degrees Celsius (Brager et al 2003).

It is clear from over 30 years of field studies that the waters west and southwest of the San Juan Islands are important in killer whale ecology. This is one of the deepest part of the marine habitat surrounding the archipelago, as well as one of the areas with the highest slope. Its proximity to the Strait of Juan de Fuca, and salmon returning from the open ocean to their spawning grounds in Washington State and British Columbia may be an important factor for killer whale habitat preference. It is clear that the protection this area will play a vital role in the recovery of the southern resident killer whale population. The creation of the Orca Pass Stewardship Area as a marine protected area (MPA) has been one proposed method of protecting important biological hotspots (including important SRKW habitat) (Bloch et al 2002; Georgia Strait Alliance 2009). The degree to which MPAs provide protection is up to interpretation and debate based on implementation

Though the designs of MPAs are developed with best-available science and the best of intentions, in many cases the desired ecological benefit is not the outcome. In many cases, competing societal benefits can cause the size of the designated MPA to decrease from the design phase to their actual size and lack of fishing regulation can cause the productivity of these places to decrease (Le Quesne 2008). MPAs are more than just areas of high productivity identified by fishery managers, however. They are places that have ramifications on economics, politics, and tourism. As with any potential MPA (Charles and Wilson 2008), the area valued by southern resident killer whales will only be successfully protected if everyday citizens are actively involved in every stage in the development.

Conclusion

This thesis has added to the growing knowledge of habitat use by the endangered population of southern resident killer whales. A steady decline in the population since the mid-1990s, probably due to a decline in their favorite prey item, Chinook salmon, as well as other risk factors, has created concern for the long-term viability of this population. This paper focused on benthic and spatial habitat related to feeding and a secondary focus of benthic and spatial habitat related to density. The general findings were that, at least in the focal follows “collected” for this study, there are no habitat differences between three types of follows; follows where it was confirmed they were feeding (due to collections of prey remains), follows where it was thought that they were probably feeding (due to foraging cues displayed that have been previously linked to foraging), and follows where it was thought that they may not be foraging (no predation collections and no foraging cues). The lack of differences between follow type may be due to an error in parameters tested here. Sea surface temperate, turbidity, or proximity to marine benthic habitats (i.e. sea grass bed, river mouths, etc) may be the explanatory variables in follow type. Also, as with all spatial studies, the scale of data analysis could impact the results. Perhaps adjusting the spatial scale of the digital elevation model could lead to significant results. The spatial distribution of southern resident killer whale density matches what other studies have found; the areas of highest densities were in a part of the San Juan archipelago known as the Haro Strait. This area has already been identified as prime habitat for southern resident killer whales. Restoration of the salmon population in addition to protecting southern resident killer whale habitat will be needed if the goal is to restore the long-term viability of this species, especially in an area where population growth and subsequent human development will only increase in the coming years.

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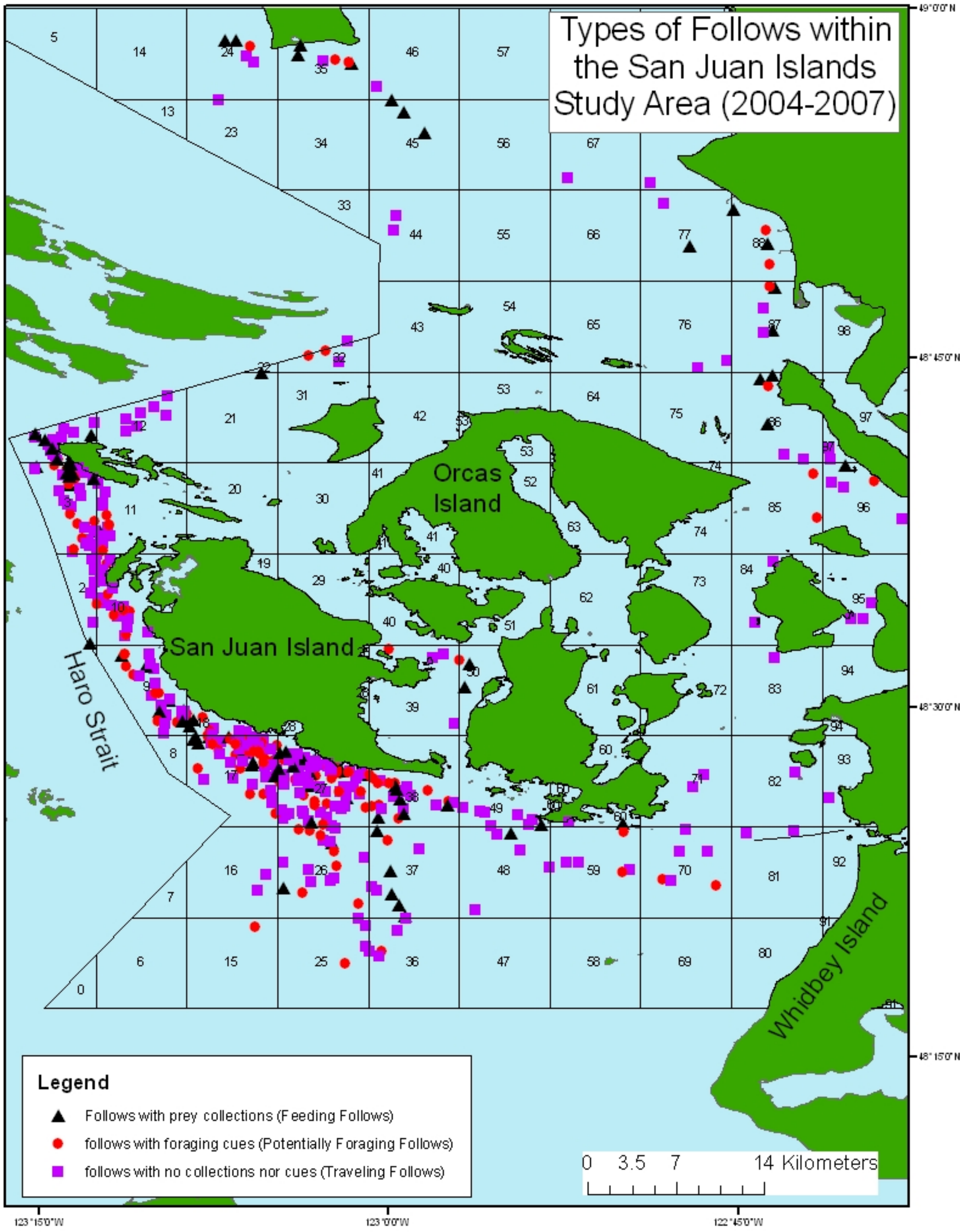
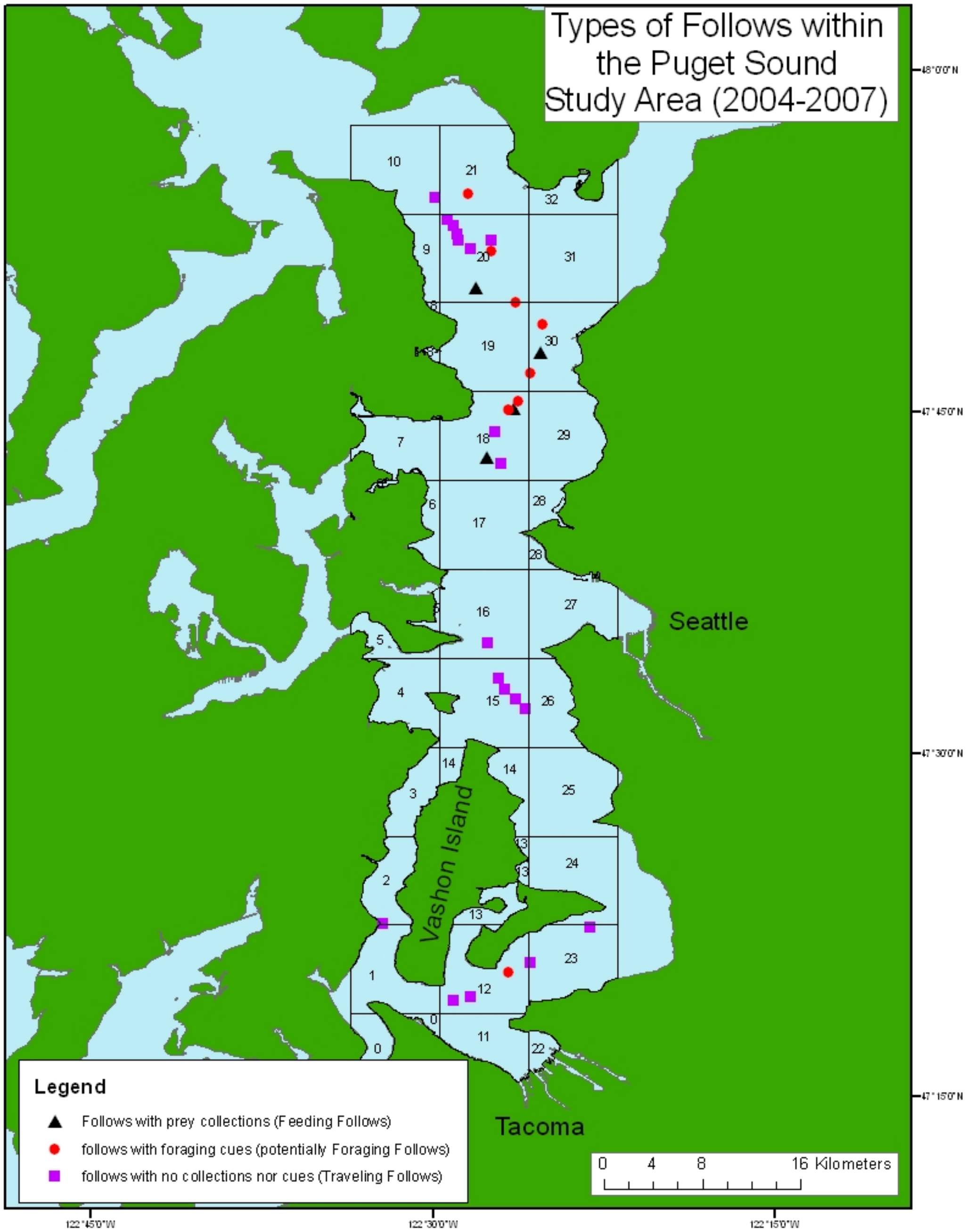
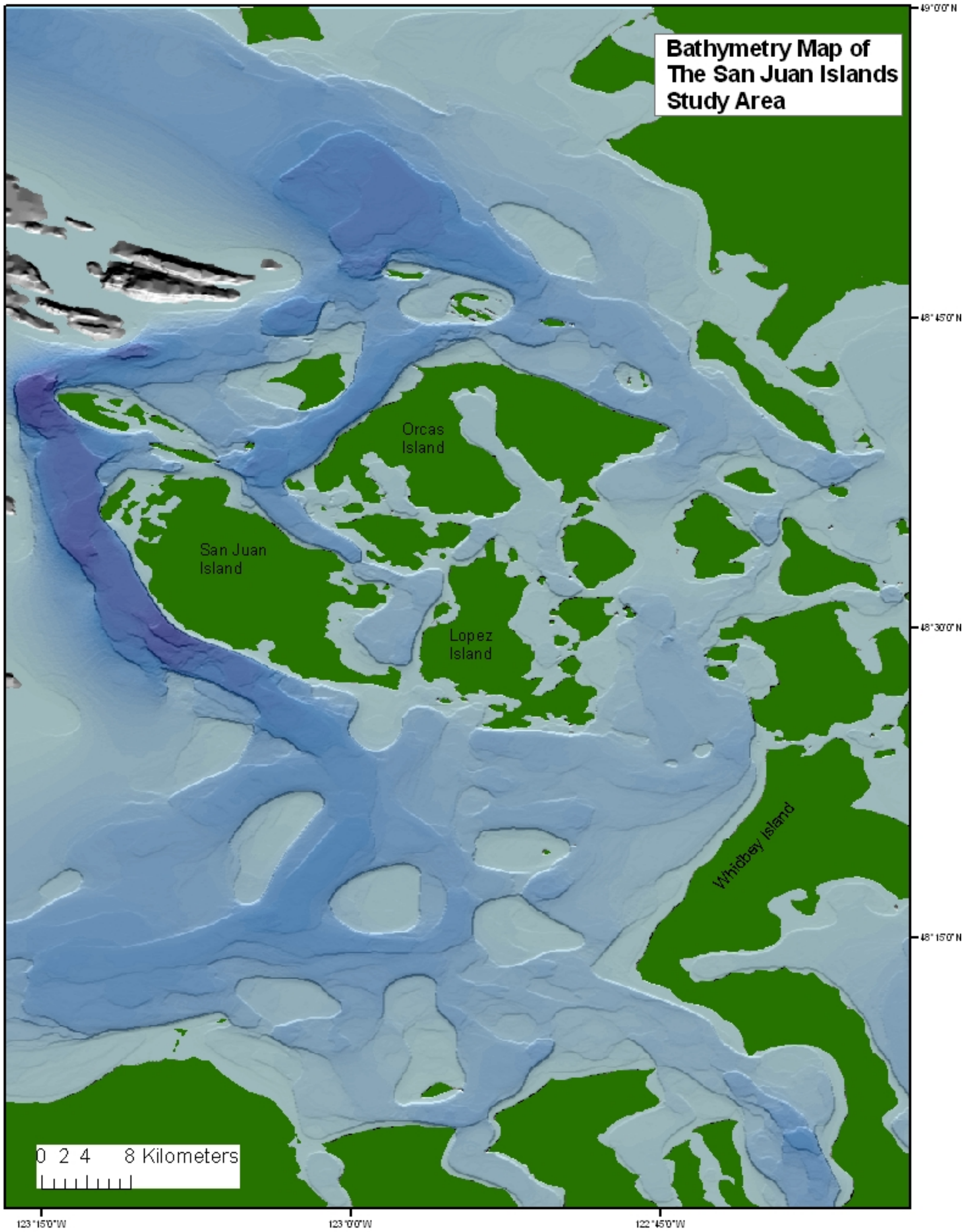
Appendix A


Types of Follows within the San Juan Islands Study Area (2004-2007)
Orcas Island
San Juan Island
Haro Strait
Whidbey Island
Legend
▲ Follows with prey collections (Feeding Follows)
● follows with foraging cues (Potentially Foraging Follows)
■ follows with no collections nor cues (Traveling Follows)
0 3.5 7 14 Kilometers
49°0'0"N
48°45'0"N
48°30'0"N
48°15'0"N
123°15'0"W
123°0'0"W
122°45'0"W

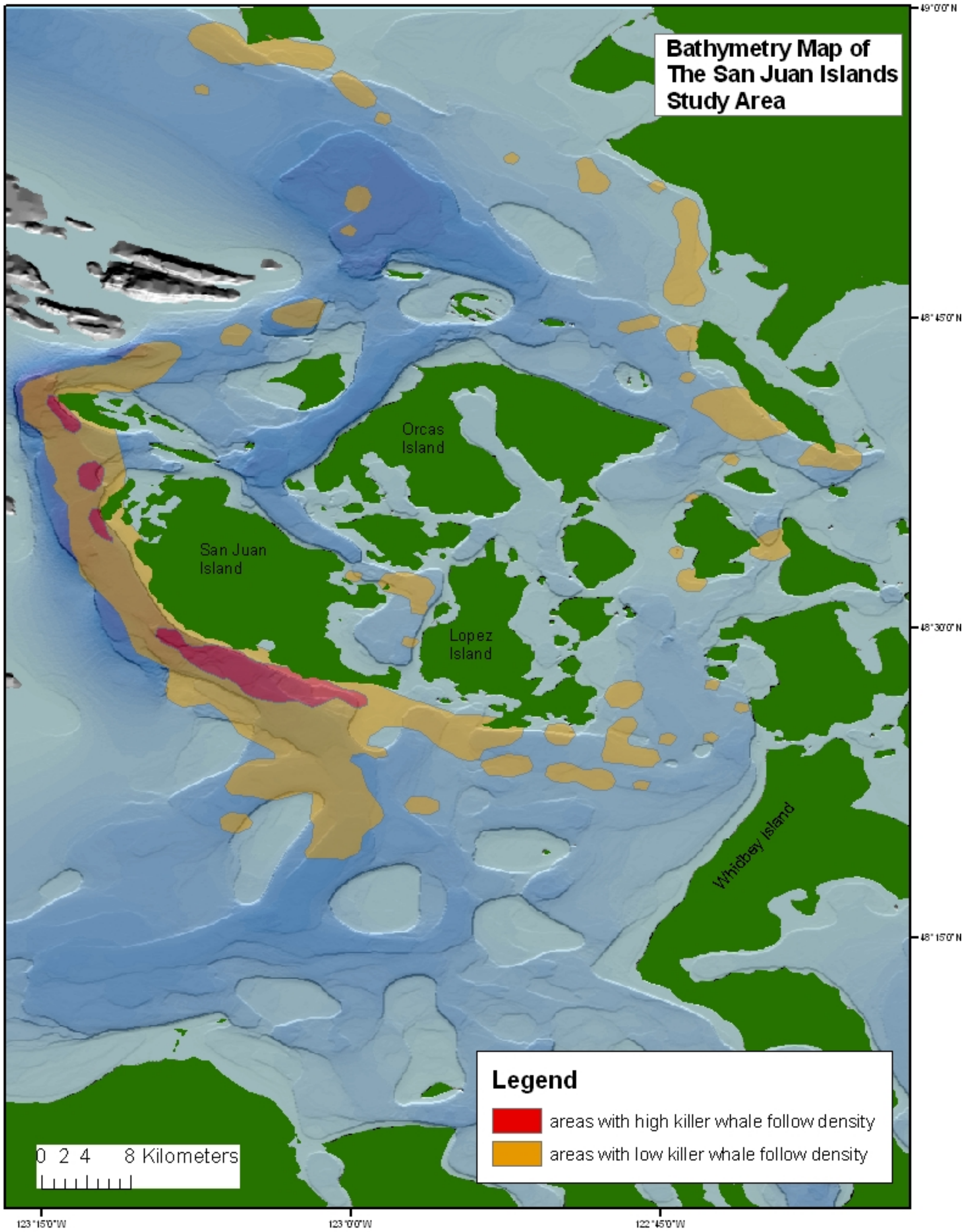
Appendix B


Types of Follows within the Puget Sound Study Area (2004-2007)
48°0'0"N
47°45'0"N
47°30'0"N
47°15'0"N
10
21
32
9
20
31
8
19
30
7
18
29
6
17
28
28
16
27
5
15
26
4
14
14
25
3
13
13
24
2
13
23
1
12
0
11
22
0
Vashon Island
Seattle
Tacoma
Legend
▲ Follows with prey collections (Feeding Follows)
● follows with foraging cues (potentially Foraging Follows)
■ follows with no collections nor cues (Traveling Follows)
0 4 8 16 Kilometers
122°45'0"W
122°30'0"W
122°15'0"W

Appendix C


Bathymetry Map of
The San Juan Islands
Study Area
Orcas
Island
San Juan
Island
Lopez
Island
Whidbey Island
0 2 4 8 Kilometers
49°0'0"N
48°45'0"N
48°30'0"N
48°15'0"N
123°15'0"W
123°0'0"W
122°45'0"W

Appendix D


Bathymetry Map of
The San Juan Islands
Study Area
Orcas Island
San Juan Island
Lopez Island
Whidbey Island
Legend
🟥 areas with high killer whale follow density
🟧 areas with low killer whale follow density
0 2 4 8 Kilometers
49°0'0"N
48°45'0"N
48°30'0"N
48°15'0"N
123°15'0"W
123°0'0"W
122°45'0"W