Social Behavior and Ecology of "Southern Resident" Killer Whales (*Orcinus orca*)

Jennifer Anne Marsh

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ProQuest LLC
789 E. Eisenhower Parkway
PO Box 1346
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Chair of the Supervisory Committee:

James C. Ha

Reading Committee:

James C. Ha

Joseph A. Sisneros

Samuel K. Wasser

Date: 3/14/08

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Date 5/2/08

University of Washington

Abstract

Jennifer Anne Marsh

Chair of the Supervisory Committee:
Associate Professor James C. Ha
Department of Psychology

The purpose of the current study was to examine factors that influence social behavior and behavior states in "southern resident" killer whales. Analyses of social behavior indicated that synchronous surfacing between whales was significantly affected by sockeye salmon, with less synchronous surfacing occurring when sockeye were more abundant, suggesting that when whales were foraging, they were spending less time swimming and breathing in synchrony. Furthermore, cartwheels and breaches were significantly affected by time of day, with more of these behaviors seen during mid-day, presumably because human activities are often at their peak during those hours, and whales may be using these behaviors as a warning signal to conspecifics or vessels. Physical contact and spyhops were found to be significantly affected by commercial vessels, as these behaviors increased in the presence of intensifying commercial vessel abundance. As spyhops and contact were posited to be information gathering and subsequent reassurance behaviors, commercial vessels may present a perceived threat to these animals in terms of both noise and size, and whales may therefore produce a higher quantity of these behaviors in their presence. In addition, analyses of behavior states indicated a significant relationship between year and slow travel, with significantly more slow travel seen in 2003 than in 2004 or 2005. Fast travel was found to be significantly different for J pod than for K and L pods, with J pod engaging in fast travel more often than the other two pods. As J pod is more often seen in this region of Washington, it was suggested that habitat familiarity may affect the speed with which J pod transits through the area. Furthermore, a significant relationship between pod and rest was also documented, with K pod found to engage in more resting behavior than J and L pods. In conclusion, complex subtleties emerged from this analysis indicating that killer whale social behaviors are indeed affected not only by multiple ecological variables including salmon abundance and the presence of commercial vessel traffic, but that some of these behaviors vary significantly among pod, time of day, and year.

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PREFACE

When I began this journey at the University of Washington, I set out to collect detailed behavioral data on "southern resident" killer whales in an attempt to elucidate the complex relationships between ecological factors, human impacts, and killer whale social behavior. I spent five full summers living on San Juan island, collecting pilot and dissertation data, and came out of this experience not only with a substantial amount of data, but a respect for these whales, and for their environment as well.

What follows are the five main chapters of this dissertation. Chapter 1 is a background literature review, including a general introduction to cetacean social behavior, killer whale social behavior, and more generally, the social ecology of cetaceans and other socially similar species. Chapter 2 includes an analysis of historical data on killer whale social affiliation patterns, and their relationship to vessel traffic and salmon abundance over the last 25 years. This chapter is intended as a stand-alone manuscript, as are Chapters 3 and 4, and each will be submitted as such in the near future. Chapter 3 is an analysis of the ecology of social behavior of killer whales using principal components analysis and general linear modeling techniques. Chapter 4 is an analysis of behavior states in these whales, examining the relationship between states and ecological variables. Lastly, Chapter 5 is a general conclusion and summary of this study.

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First and foremost I would like to thank Jim Ha for not only his support and mentoring during the past seven years, but for his friendship as well. The skills I have learned from you include not only research and data collection, but statistics and teaching. These skills have been invaluable to my development as a graduate student, and are even more essential as I transition to a professional position in academia. In addition, you have become an important part of Ryan's life, and a special part of our family. My gratitude is also extended to David Barash, who allowed me to explore the realm of evolutionary analysis with him. He taught me a great deal about teaching animal behavior to undergraduate students, and also allowed me to implement my own ideas and exercises in the process. I would like to thank Sam Wasser for his guidance and mentoring as a conservation biologist and committee member, and for his immeasurable time and input. To Robin Baird, fellow cetacean biologist and researcher, thank you for all of your time, effort, and mentoring not only in the domain of writing, but in data analysis and data collection. To Joe Sisneros and Patty Betrus, thank you for serving on my committee.

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I would like to thank my parents, Fred and Anne Lopez, who believed in me when I told them I wanted to study killer whales, and move thousands of miles away from California to do so. Most importantly, thank you for all your love and support during this long and arduous journey. To my sister Jamie, fellow animal-lover and friend, thank you for letting me use your boat for two years, and for always being there for me.

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Chapter 1: Literature Review of Mammalian and Cetacean Social Behavior and Ecology

A major research objective when studying mammalian societies is to understand the ways in which ecological forces and behavioral characteristics interact to shape the structure and dynamics of social systems. As an understanding of these interactions develops, it often becomes possible to discern how a society functions and to predict how changes in environmental characteristics may influence social relationships and population dynamics (Crook, Ellis, & Goss-Custard, 1976).

Purpose of Literature Review

The purpose of this literature review is to examine past research on social behavior and how it is linked to ecology in mammalian, and specifically in cetacean species including killer whales. In many cetacean species, and especially in fish-eating killer whales, there has been a minimal amount of research linking these two subjects, and my intention is to establish the importance of examining the relationship between social behavior and ecology, as well as show the intrinsic value of studying both social behavior and ecology in order to address conservation issues and implement effective policies.

Mammalian Social Behavior and Ecology

Mammalian societies are often complex systems, influenced by both behavioral and ecological variables. Ecological factors affecting social structure include dispersion and availability of food, type and quality of habitat, and predation pressure (Crook, Ellis, & Goss-Custard, 1976; Snaith & Chapman, 2007). Defining and quantifying ecological influences acting upon the social structure of a population is an important part of detailing its behavioral ecology.

The structure of mammalian societies is thought to be affected by many food-related variables, including: resource availability, temporal and spatial distribution of prey, food capture techniques, and foraging strategies (Caraco & Wolf, 1975). For example, when food is widely dispersed and randomly located over an area, individuals may group into flocks or herds (Altman, 1974; Cody, 1974). Cody argued that by feeding in flocks, group members were more efficient at food exploitation, as also seen among East African ungulates (Clutton-Brock, 1974; Jarman, 1974). Most plains-dwelling, grazing species (*Alcelaphinae*), whose food supply tends to be clumped and relatively unpredictable, aggregate in large, widely ranging herds. Similarly, several primate species, including chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles spp.*), rely almost entirely on patchy food resources, and show short-term variation in group size reflecting the availability of this resource (Snaith & Chapman, 2007). In contrast, most browsing species of ungulate (*Neotraginae*), whose food supply tends to be more uniform and stable, live alone or in small groups, and occupy small ranges (Clutton-Brock; Jarman).

Foraging strategies may also influence the degree of sociality in marine mammals. Mammal-eating killer whales (*Orcinus orca*) also use cooperative hunting strategies which may influence social structure. Baird and Dill (1996) suggested that large groups of mammal-eating killer whales may be important for increasing success rates for mammalian prey that are difficult to capture such as Dall's porpoise (*Phocoenoides dalli*), and whose capture involves risk of injury, such as sea lions (*Otariidae*).

Predation pressure plays a role in the structure of mammalian societies by promoting protective behaviors. Being a member of a large group of individuals may provide several benefits, including increased efficiency of predator detection, a "confusion effect" on predators, deterring the predator, and cooperative defense (Miller, 1922; Altman, 1974; Bertram, 1978). Altman suggested that living in large groups may provide greater sensory ability, allowing for more efficient surveillance and detection of predators. For example, in baboons, any member of a group that sees a predator gives an alarm call to alert other group members of potential danger. Thus, each individual benefits from the collective predator-detecting ability of the group (Altman). Another benefit of group living in relation to predator avoidance is the "confusion effect." Miller suggested that a flock of bush tits (*Psaltriparus minimus*), engaged in uniform behavior, tended to confuse an approaching predator by dividing its attention among a number of individuals. Lastly, large groups may provide increased cover for individuals, and aid in cooperative defense (Norris & Dohl, 1980). In dolphins, for example, younger, more vulnerable animals are sometimes contained in the center of a group, which allows larger, more experienced animals to occupy the perimeter of the group for defense (Norris & Dohl).

Habitat type, whether terrestrial or aquatic, plays an important role in structuring mammalian societies, and can be broadly classified as open or complex. Open habitats include desert or plains in the terrestrial environment, and sandy bottom in the aquatic environment. Complex habitats include forests and heavy bush or woodland, and nearshore reefs and kelp forests.

Habitat type may affect the strategy employed by a species to locate and gather food items, and can therefore have substantial influence on the expressed social structure of a population. A good example of habitat effects on social structure is seen in delphinids. In open water, some dolphins usually search for food in broad ranks up to a hundred meters wide, presumably to increase the chances of finding prey (Würsig, 1986). Dolphins near shore often find food in a less cooperative manner, with individual dolphins seeking out prey (Würsig). Similarly, predator avoidance behaviors may also be affected by habitat type. For example, antelope living in complex habitats such as thicket or relatively dense woodland remain motionless to avoid detection, but quickly flee once detected. In comparison, antelope in open habitats slowly move away from predators, while keeping them in sight (Jarman, 1974).

Van Schaik (1983) suggested that for primates, the risk of predation is greater for terrestrial species in open habitats than for forest-dwelling species. Refuges are scarce in open habitats and thus predators must be detected at large distances to allow for safe retreat or organization of defense strategies. Therefore, primates in open habitats would be expected to live in larger groups than their forest-dwelling counterparts (Jorde & Spuhler 1974; Clutton-Brock & Harvey, 1977; Van Schaik). A similar pattern is also seen in some cetacean species. Riverine species such as the Ganges River dolphin (*Platanista gangetica*), and Amazon River dolphin (*Inia geoffrensis*) are typically found alone or in pairs, whereas pelagic species such as common dolphins (*Delphinus delphis*) commonly form groups numbering in the hundreds or even thousands (Norris & Dohl, 1980). This too may be a function of predation pressure, where the risk is greater for those cetaceans inhabiting open ocean habitats.

Social Behavior and Ecology of Cetaceans

Social behavior and ecology have likewise been examined in multiple cetacean species, and are also believed to be affected not only by food related variables and habitat type, but by predation pressure as well. For example, foraging strategies and prey abundance have been found to affect behavior in several cetacean species, including dusky dolphins (Würsig & Würsig, 1980). The behavior and ecology of dusky dolphins was investigated off Argentina by Würsig and Würsig in the early 1970s, and the authors found dolphin group sizes to increase during feeding behavior, primarily as other groups joined feeding activities.

The effect of habitat on social behavior has been explored in many studies, and across several species, including bottlenose (Quintana-Rizzo & Wells, 2001; Grigg & Markowitz, 1997) and dusky dolphins (Garaffo, Dans, Pedraza, Crespo, & Degrati, 2007). In Cedar Keys, Florida, Quintana-Rizzo and Wells conducted photo-identification surveys from June 1996 through May 1997 in order to investigate the social structure of open estuary bottlenose dolphins. Researchers concluded that association patterns of dolphins seen more than eight months of the year resembled the associations of resident bottlenose dolphins inhabiting closed estuarine bays, and that the selective pressures acting on association patterns may be the same in both aquatic systems. Similarly, in a study conducted between Fall 1995 and Spring 1996, bottlenose dolphins at Turneffe

Atoll, Belize were found to vary group size based on habitat type, and researchers concluded that some areas of the atoll were preferred by groups of particular sizes (Grigg & Markowitz). For example, dolphins were consistently sighted within two study sites associated with breaks in fringe reef. It was postulated by the authors that these areas provided feeding opportunities for dolphins. Habitat usage has also been addressed in dusky dolphins off the Patagonian coast, and researchers determined that mothers with calves and small groups were resting in shallow waters, and that travel occurred in the deepest areas (Garaffo, Dans, Pedraza, Crespo, & Degrati).

Predation pressure plays an substantial role in the social behavior of cetacean species, including bottlenose dolphins (Heithaus & Dill, 2002). Heithaus and Dill researched tiger shark predation in relation to food availability and group size in bottlenose dolphins in Shark Bay, Western Australia from 1997 to 1999. These authors found that dolphin groups were larger in more dangerous shallow habitats, an area where shark density was found to be highest.

Social Behavior and Ecology of Mammal-eating and Fish-eating Killer Whales

Fish-eating killer whales are one of three distinct killer whale ecotypes found in the inshore waters of Washington state, which also include mammal-eating, and offshore forms (Ford, Ellis & Balcomb, 2000). There are two communities of fish-eating killer whales found in this region, termed "northern resident" and "southern resident" killer whales. "Northern resident" killer whales utilize Johnstone and Queen Charlotte Straits as core areas during summer months, whereas "southern resident" killer whales frequent inshore waters between Southern Vancouver Island, British Columbia, Canada, and the

San Juan Island, Washington, USA (Osborne, 1999). Both of these fish-eating killer whale populations are characterized by their piscivorous diet, and are highly social mammals that live in stable subgroups of several related females and their young. Offspring of both sexes remain in their natal group for life, and groups are organized along matrilineal lines (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990).

Research on fish-eating killer whales began in the early 1970s in the inshore waters of British Columbia and Washington State. Formal study of these killer whale communities began in 1972, and continue to date (Balcomb, Boran, & Heimlich, 1982). Individual whales were identified each year from unique dorsal fin and saddle patch characteristics, and this method became a standard method for tracking killer whales annually (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990).

Two populations of killer whales, mammal-eating and fish-eating, were described by early research (Olesiuk, Bigg & Ellis, 1990; Morton, 1990). Mammal-eating killer whales were typically found to travel in groups of 2-5 individuals, and had erratic patterns of occurrence and movement. Their dorsal fins tend to be pointed at the tip, whereas fish-eating killer whales have a more rounded dorsal fin tip. Approximately 170 mammal-eating whales were identified in coastal waters, and were found to prey primarily on harbor seals. Typical groups consisted of an adult female and 1-2 offspring (Baird & Whitehead, 2000). Some offspring leave their natal group as adolescents, often following the birth of a younger sibling. Adult males occasionally travel alone, but at times join with other mammal-eating killer whales to form temporary foraging groups. Bulls seldom travel solely with other adult males (Baird & Whitehead).

In contrast, fish-eating killer whales are piscivores, eating mostly salmon. As of 1993, 305 whales had been photo-identified in the Washington and British Columbia regions, and found to live in stable subgroups of several related females and their young. Fish-eating killer whale society members can be assigned to a series of social units according to maternal genealogy. The bonds within social units get progressively weaker, and as such, relatedness between individuals is strongest in matrilineal groups, and decreases incrementally for subpods, pods, clans, and communities (Bigg, Olesuik, Ellis, Ford, & Balcomb, 1990).

Matrilineal groups are the basic social unit of fish-eating killer whales, composed of mothers and their offspring. Matrilineal groups usually contain 2-9 individuals, and travel together and in close proximity to one another. A subpod is a social unit of one or more matrilineal groups that typically travel together at all times. Females within the matrilineal groups of a subpod are likely to be sisters, daughters, and cousins. Individual fish-eating killer whales appear to remain in the same subpods all of their lives. Subpods are composed of 1-11 matrilineal groups, although most contain two matrilineal groups (Bigg, Olesuik, Ellis, Ford, & Balcomb, 1990).

Pods are the next level of social unit and consist of subpods that tend to travel preferentially with each other. Each pod of fish-eating killer whales maintains a different vocal dialect, and placement of subpods into pods can be determined from long-term associations or dialects. It is not uncommon for subpods to leave the main pod for days, weeks, or even months. Pods usually consist of 1-3 subpods, and most pods contain between 10-20 whales (Bigg, Olesuik, Ellis, Ford, & Balcomb, 1990).

The organizational level above the pod is the clan. A clan of killer whales is comprised of pods that have similar vocal dialects and are therefore considered related (Ford, Ellis, & Balcomb, 2000). It is a term used to describe an acoustic group of pods, and not a social group as most pods demonstrate little preference for travelling with pods within their clan. Finally, a community is the broadest level of the social structure, and is made up of pods that associate with one another. Communities are usually composed of 1-3 clans (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990).

Studies on killer whale social behavior and ecology have been conducted on mammal-eating as well fish-eating killer whales. Baird and Whitehead (2000) used data collected from 1985–1996 to describe association patterns between mammal-eating killer whales around Vancouver Island, British Columbia, and to relate differences in association patterns between fish-eating and mammal-eating killer whales to ecological differences. Associations between these mammal-eating whales were found to be both strong and long-term, with nine discrete pods identified. Some males were found to disperse from the maternal pod, with others spending time alone, occasionally associating with groups containing potentially reproductive females. Females that disperse from their maternal pod were found to be highly gregarious, but with low maximum association rates. The authors suggested that differences in social organization between fish-eating and mammal-eating killer whales are due to foraging ecology, with mammal-eating whales maximizing their per capita energy intake by foraging in groups of three, with no such relationship documented in fish-eating killer whales (Baird & Whitehead).

Research on social behavior and ecology in fish-eating killer whales was conducted in a study by Nichol and Shackleton (1996). Utilizing observations from 1984 to 1988, the authors found "northern resident" killer whales most abundant in Johnstone Strait study area between July and October, a time when salmon are simultaneously migrating though this area. In addition, the occurrence of six killer whale pods was significantly associated with chum salmon.

The behavioral ecology of "southern resident" killer whales was examined by Heimlich-Boran (1988). Using observations from 1976–1983, the author determined that killer whales were using different portions of their habitat in divergent ways. Killer whales were found to feed in areas of high relief along the migration routes of salmon. Heimlich-Boran also found whales to travel across deeper waters while moving between feeding areas, and play in areas of open water or directly bordering feeding locales. He concluded that prey resources and prey capture areas were the most important factors in the behavioral ecology of this fish-eating population.

Social and foraging behavior of "southern resident" killer whales were investigated by Hoelzel (1993) during two consecutive field seasons from 1986-1987. Hoelzel found that fast, non-directional behavior, indicative of pursuing fish at the surface, correlated with slow speeds, decreased distance between subgroups, and travelling in smaller groups. In contrast to the study by Heimlich-Boran (1988), killer whale behavior was not found to be correlated with bottom topography or specific locations within the study area. Possible reasons for this discrepancy include disparity in data collection methodology, including utilization of a wider geographical area divided into four distinct ranges, as well as the use of more specific bottom-topography classifications. Based on the his overall findings, Hoelzel suggested that this population of killer whales may benefit from cooperative food searching, but not from cooperative food capture.

Why Investigate Social Behavior and Ecology in "Southern Resident" Killer Whales?

The "southern resident" killer whale population off Western North America, consists of three distinct pods, J, K, and L, and has declined from 98 individuals in 1995 to 78 whales in 2001, a decline of 20.4% (Biological Review Team, 2002), before returning to 82 in 2003, and increasing recently to 87 whales. In Canada, this population was listed as "threatened" in 1999 and "endangered" in 2001 by the Committee on the Status of Endangered Wildlife in Canada (Baird, 2001). More recently, NOAA Fisheries announced in November 2006 the listing of the "southern resident" killer whales as endangered under the Endangered Species Act (ESA), the highest level of protection possible by the United States federal government.

With the decline of this killer whale population and their formal endangered status, research on social behavior linked to ecology is crucial to the future protection of these marine mammals. The focus of the current study was the social behavior and ecology of "southern resident" killer whales. Since these whales are highly cognitive and display an extremely cohesive social structure, fluctuations in social behavior among killer whales may have important implications for the benefits of pod cohesion. If the relative amount of social behavior wanes over time due to ecological variables, killer whales may lose the group-living benefits of alloparental care, group foraging, sensory integration, and cultural trait transmission (Norris & Dohl, 1980).

As a measure of social behavior, percussive behaviors were examined in this study as they are considered communicative and may convey information to conspecifics (Pryor, 1986; Herzing, 2000). In previous studies on cetaceans, percussive behaviors have been defined as a behavior resulting in sound at the water surface, specifically as the result of a body part slapping the water (Ferrer, Cancho & Lusseau, 2006; Lusseau, 2006). Percussive behaviors have not only been considered communicative, but have also been suggested to function in foraging contexts as well (Würsig & Würsig, 1980).

Synchronous surfacing was also examined in this study, since surfacing together represents a social bond between two animals, and has previously been used to define the strength of affiliation among conspecifics in two species of bottlenose dolphins (*Tursiops truncatus*; Ballance, 1990; *Tursiops aduncus*; Connor, Smolker & Bejder, 2006). Surfacing in synchrony has been described in multiple studies on killer whales (Jacobsen, 1986; Heimlich-Boran, 1988; Similia, 1997), but not quantified. This study examined synchronous surfacing under multiple conditions and in varying behavioral contexts.

Cetacean behavior, including synchronous surfacing, has been examined in response to vessel traffic in multiple species, including bottlenose dolphins (*Tursiops truncates;* Janik & Thompson, 1996; Hastie, Wilson, Tufft, & Thompson, 2003; Lusseau, 2003; Constantine, Brunton, & Dennis, 2004; Mattson, Thomas & St. Aubin, 2005; Lemon, Lynch, Cato & Harcourt, 2006), Indo-Pacific humpback dolphins (*Sousa chinensis*; Ng & Leung, 2003; Stensland & Berggren, 2007), common dolphins

(*Delphinus sp.*; Stockin, Lusseau, Benedell, Wiseman, & Orams, 2008), and killer whales (Williams, Bain, Ford, & Trites, 2002; Williams, Lusseau, & Hammond, 2006; Williams & Ashe, 2007). In northern Scotland, Hastie *et al.* found that bottlenose dolphins increased breathing synchrony in response to vessel traffic, and in South Carolina, Mattson and her colleagues found that dolphins responded to vessel activity by changing behavior, group size, and direction of movement. In a recent study on common dolphins in New Zealand, Stockin and colleagues found foraging and resting periods to be disrupted by vessel interactions, as both the duration and overall time spend engaged in these activities decreased. Additionally, researchers found that foraging dolphins took longer returning to their initial behavior state when vessels were present, as well as an increased shift to social or milling behaviors after interactions with vessels (Stockin, Lusseau, Benedell, Wiseman, & Orams). For killer whales, Williams and co-authors reported that vessel presence was significantly linked to changes in the probability that a focal animal would switch activity states, and this led to significantly different activities when vessels were absent or present (Williams, Lusseau, & Hammond). Additionally, Williams and colleagues have found that higher levels of vessel traffic (few versus many vessels) had a significantly different effect on fish-eating killer whale behavior, with the swimming path of males in particular more sinuous when few boats approached, and straighter when many boats approached (Williams & Ashe).

Ecological variables that may influence social behavior, such as number of vessels present, salmon abundance, time of day, and pod identification were analyzed in this study. It has been shown that the behavior of fish-eating killer whales in Johnstone

Strait ("northern resident" killer whales) has been affected by vessel traffic (Williams, Lusseau & Hammond, 2006; Williams & Ashe, 2007), and in "southern resident" killer whales, time of day has been shown to have an effect on behavior as well (Baird, Hanson, & Dill, 2005). Additionally, it has also been found that in "northern resident" killer whales, percussive behavior rates differed by pod (Adimey, 1995).

In this study, it was hypothesized that social behavior would vary with whale-watching pressure, and specifically that percussive behavior would increase as whale watch pressure heightened due to the need to communicate at the surface, produce different sounds, and signal over long distances as underwater noise increased with increasing vessel traffic. It was specifically expected that breaches, which have been suggested to occur in response to disturbance or external stimuli such as boat noise (Pryor, 1986), would be observed more often in the presence of intensifying vessel pressure. Moreover, it was hypothesized that increased vessel pressure may directly affect the rate of synchronous surfacing in these fish-eating killer whales, as vessel pressure was expected to decrease the ability of whales to maintain spatial cohesion. It was additionally postulated that there would be a significant relationship between social behavior and prey abundance, with synchronous surfacing showing a marked decrease as prey abundance increased, since whales most likely would not be traveling in close proximity and maintaining social cohesion while foraging or capturing prey items. In contrast, it was expected that percussive behavior would increase as prey abundance increased, as these behaviors, including breaches and tail slaps, may be used by these killer whales in foraging contexts.

In my opinion, it is imperative that ecological variables be examined in relation to social behavior in an endangered species such as killer whales, and that results be applied to conservation efforts. As key killer whale habitats are determined, specific attention should be paid to areas where social behavior may be concentrated. This spatial-based approach to management may be the best way to protect this endangered population, and it is my hope that results from this study will contribute to such an approach. As social behavior is a biologically important aspect of killer whale life, studies of social behavior should not be ignored when making policies to protect these animals. It is only by conducting thorough, methodical, intensive research that useful information will be generated for practical use by policy-makers and scientists alike.

Chapter 2: Historical Analysis of Association Patterns in "Southern Resident" Killer Whales (*Orcinus orca*)

Introduction

"Resident" killer whales are one of three distinct killer whale ecotypes found in the inshore waters of Washington state, which also include "transient" and "offshore" forms (Ford, Ellis & Balcomb, 2000). There are two communities of "resident" killer whales, "northern" and "southern", and these killer whales are characterized by their piscivorous diet, and are highly social mammals that live in stable subgroups of several related females and their young. Offspring of both sexes remain in their natal group for life, and groups are organized along matrilineal lines (Bigg, Olesiuki, Ellis, Ford, & Balcomb, 1990). "Northern resident" killer whales utilize Johnstone and Queen Charlotte Straits as core areas during summer months, whereas "southern resident" killer whales frequent inshore waters between Southern Vancouver Island, British Columbia, Canada, and the San Juan Island, Washington, USA (Osborne, 1999).

The "southern resident" killer whale population off western North America, consists of three distinct pods, J, K, and L, and has declined from 98 individuals in 1995 to 78 whales in 2001, a decline of 20.4% (Biological Review Team, 2002), before returning to 82 in 2003, and increasing recently to 87 whales. In Canada, this population was listed as "threatened" in 1999 and "endangered" in 2001 by the Committee on the Status of Endangered Wildlife in Canada (Baird, 2001). More recently, NOAA Fisheries announced in November 2006 the listing of the "southern resident" killer whales as endangered under the Endangered Species Act (ESA), the highest level of protection possible by the United States federal government.

With the decline of the "southern resident" killer whale population and the establishment of their formal endangered status, behavioral research, and research on social behavior in particular, is crucial to the future protection of this whale population. Since these whales are highly cognitive and display an extremely cohesive social structure (Bigg, Olesiuki, Ellis, Ford, & Balcomb, 1990), fluctuations in social behavior among killer whales may have important implications for the benefits of pod cohesion. If the relative amount of social behavior wanes over time due to ecological or other variables, killer whales may lose the group-living benefits of alloparental care, group foraging, sensory integration, and cultural trait transmission (Baird, 2000; Ford & Ellis, 2006; Norris & Dohl, 1980).

Studies of social behavior in other aquatic species such as loggerhead sea turtles (Schofield, Katselidis, Diopoulos, Pantis & Hays, 2006) as well as terrestrial mammals like endangered Tehuantepec jackrabbits (Farias, Fuller, Cervantes & Lorenzo, 2006) have demonstrated the importance of behavioral research in the conservation of these species. For example, behavioral data collected on loggerhead turtles may be used to improve conservation policies in Greece, and in Mexico, basic information on social behavior in Tehuantepec jackrabbits has contributed to population analyses and models imperative to the conservation and management of this endangered species. Examining social behavior, and specifically reproductive ecology, has shown to be consequential in many species of fishes as well (Vincent & Sadovy, 1998).

Cetacean behavior has been examined in response to vessel traffic in multiple species, including common bottlenose dolphins (*Tursiops truncatus*; Janik & Thompson, 1996; Hastie, Wilson, Tufft, & Thompson, 2003; Lusseau, 2003; Constantine, Brunton, & Dennis, 2004; Mattson, Thomas & St. Aubin, 2005; Lemon, Lynch, Cato & Harcourt, 2006), Indo-Pacific humpback dolphins (*Sousa chinensis*; Ng & Leung, 2003; Stensland & Berggren, 2007), and killer whales (Williams, Bain, Ford, & Trites, 2002; Williams, Lusseau, and Hammond, 2006; Williams & Ashe, 2007). In northern Scotland, Hastie et al. found that common bottlenose dolphins increased breathing synchrony in response to vessel traffic, and in South Carolina, Mattson and her colleagues found that dolphins responded to vessel activity by changing behavior, group size, and direction of movement. In "northern resident" killer whales, Williams and co-authors reported that vessel presence was significantly linked to changes in the probability that a focal animal would switch activity states, and this led to significantly different activities when vessels were absent or present (Williams, Lusseau, & Hammond). Additionally, Williams and colleagues have found that higher levels of vessel traffic (few versus many vessels) had a significantly different effect on killer whale behavior, with the swimming path of males in particular more sinuous when few boats approached, and straighter when many boats approached (Williams & Ashe).

Ecological variables that may influence social behavior, such as number of vessels present as well as salmon abundance were analyzed in this study. This analysis utilized affiliation patterns in "southern resident" killer whales as a measure of social behavior, and for our purposes affiliation was defined as the mean frequency with which two individuals were present in the same social group at the same time. The frequency with which two individuals affiliate is basic to all other aspects of their social interactions. The objectives of this study were to quantify affiliation patterns within pods, to compare these values over years, and to quantify the effect of whale watching boats and salmon abundance on annual affiliation patterns for each pod.

Background on Affiliation Analysis

The use of social affiliation indices allows researchers to quantify and compare the strength or weakness of bonds among individuals and age/sex classes of animals within groups. There are several ways to quantify social affiliation patterns among mammals, including the half-weight, the twice-weight, and the simple indices (Ginsburg & Young, 1992).

The half-weight index, as developed by Dice (1945), has been used by many researchers to quantify social affiliation in terrestrial as well as aquatic mammals. Schaller (1972) used the half-weight index to quantify associations of lion prides in the Serengeti. A study of social affiliations among killer whales (Heimlich-Boran, 1986), and several studies on bottlenose dolphins (Wells, 1986; Wells, Scott, & Irvine 1987; Weller, 1991; Connor, Smolker, & Richards, 1992; Smolker, Richards, Connor, & Pepper, 1992; Bräger, Würsig, Acevedo, & Henningsen, 1994; Marsh, 2000) have used the half-weight index to quantify associations.

According to Cairns and Schwager (1987), the half-weight index is the least biased of the indices if animals are more likely to be sighted when separate than when together. Ginsberg and Young (1992) suggested that this index tends to overestimate associations since it averages individual sightings, thereby reducing the denominator. Bejder, Fletcher, and Bräger, (1998) chose the half-weight index to quantify associations among Hector's dolphins in order to examine whether associations were occurring more often than expected for a randomly associating population. This index was also used by Smolker and colleagues (1992) as well as Slooten, Dawson, and Whitehead (1993) because photographic identification studies are likely to underestimate the number of joint sightings. Weller (1991) and Marsh (2000) chose to use the half-weight index for their research on the social ecology of Pacific coast bottlenose dolphins, based on the hypothesis that California dolphins lived in a fluid society, and that two dolphins were more likely to be photographed apart than together.

The second index used to quantify association patterns is the twice-weight index. According to Ginsberg and Young (1992), the twice-weight index tends to underestimate associations since it double counts the samples in which members of the pair are located separately. Cairns and Schwager (1987) suggested that the twice-weight index is the least biased when sampling favors the sighting of individuals A and B together.

Finally, the simple index of association has been used by Heimlich-Boran (1993) to quantify associations among pilot whales (*Globicephala macrorhyncus*), by Dudzinski (1996) to examine associations among Atlantic spotted dolphins (*Stenella frontalis*), and by Slooten, Dawson, and Whitehead (1993) to investigate associations among Hector's dolphins. This index was considered by Ginsberg and Young (1992) to be the least biased of all the indices. They suggested that since it does not double the number of sightings in which both individuals are seen separately (*i.e.*, twice-weight index), and does not decrease the denominator by averaging the number of sightings of each individual (*i.e.*, half-weight index), that it is inherently the most accurate of the indices.

Half-Weight Index

Investigations in the Pacific Northwest were among the first to quantitatively examine patterns of social association for killer whales. Heimlich-Boran (1986) studied three "resident" pods of killer whales, and analyzed photographic and observational data collected over three years in order to assess the degree of association among known whales. Data for each year were analyzed separately using the half-weight index. Associations among age/sex classes of adults, mothers, barren adult females, adolescent calves, adolescent males, juveniles, and infants were examined. The most consistent associations were found among mothers and their offspring. Mothers and their calves had the highest association indices of all possible pair combinations. The associations among non-related females and calves tended to be between calves and their mother's primary associates from each year. Associations among calves showed the largest annual fluctuation, while associations among mothers and barren females showed the most stability over time. Barren females preferred mothers as affiliates, as opposed to other barren females, and mothers preferred barren females over other mothers. In all three years of the study, male pairs showed lower association indices than adult females or calves, and they also formed fewer associations in general (Heimlich-Boran). In the current study, the half-weight index of association was chosen in order to compare results to previous studies of affiliation in this population of "southern resident" killer whales.

Methods

Analysis was conducted using archival data provided by Ken Balcomb and the Center for Whale Research. Killer whales were individually identified from unique markings on their dorsal fin and the gray saddle patch at the base of the fin. The markings on the dorsal fin and saddle patch were documented by high-quality black-and-white photographs, normally of the left side of the whale. This recognition process for killer whales was developed over approximately 10 years, and is now relatively streamlined. Even though researchers can distinguish many individuals by sight, we still rely on photographs for identification, especially for whales with indistinct markings.

Using photo-identification records from the Center for Whale Research, mean coefficient of association values were calculated for whales photographically identified in the same group on a particular day. Associations were calculated using the half-weight index: $x/0.5(Y_a + Y_b)$, where x is the number of joint sightings scored once for each occurrence of whales A and B together, and Y_a and Y_b are the total number of individual sightings for each animal. Coefficients of association range from 0.0 for two whales never sighted together, to 1.0 for two whales always seen together. Yearly patterns of coefficient of association values were compared using a one-way analysis of variance, and Tukey's post hoc test. Association values were calculated for all whales greater than eight years of age to control for age class transitions over the 15-year period of analysis. Data were also grouped into 3-year periods in order to control for temporal variation in bond strength from year to year. Annual number of whale watch boats was calculated as the mean number of whale watching boats off Limekiln Lighthouse in the immediate vicinity of the whales between May and August each year (Osborne, Koski, & Otis, 2002). These data served as an index of whale watching pressure on this population of whales. Chinook salmon estimates were generated from Puget Sound Catch and

Escapement stock strength calculation summaries from the Washington State Department of Fisheries. Annual abundance of chinook salmon were taken from catch-escapement run size calculation summaries, and these data were used in subsequent analyses.

Statistical Analysis

All statistical analyses were performed using Systat 7 (Wilkinson, Blank, & Gruber, 1996), and a probability of 0.05 was used as the criterion for rejection of the null hypotheses. General linear modeling was used for analyses of coefficient of association values for each pod, and independent variables included mean annual number of boats and chinook salmon abundance.

Results

Photo-identification records of individual whales from 1987 – 2001 (n = 11602) were used in analyses, and yielded 638 groups of killer whales. As stated previously, data were grouped into 3-year periods in order to control for temporal variation in bond strength from year to year. Mean sample size per year was found to be 2320.4 (s.d. = 687.79; 1987-1989 n = 1350; 1990-1992 n = 2262; 1993-1995 n = 2432; 1996 – 1998 n = 3286; 1999-2001 n = 2272). Mean whale watch boat number for the 15-year period was 13.42 (s.d. = 7.97), and the mean chinook salmon abundance estimate was found to be 178840 (s.d. = 48773.13) for this period as well.

In general, association patterns between whales showed a decrease over the 15-year period in all three pods. In J pod, there was a significant difference in mean values of association between the five time periods ($F_{4,79} = 12.75$, $P < 0.001$; Figure 2.1). For K pod, the mean coefficient of association during the last four periods were found to be significantly lower than the first period from 1987 – 1989 ($F_{4,64} = 6.88$, $P < 0.001$; Figure 2.2). In L pod mean coefficient of association values were significantly lower during the last two periods than the first three ($F_{4,208} = 68.00$, $P < 0.001$; Figure 2.3). When L pod was broken down into separate subpods, association values showed a similar trend. In the L12 subpod, coefficient of association values were significantly lower during the last three periods than the first two ($F_{4,48} = 32.43$; $P < 0.001$; Figure 2.4). Similarly, in the L25 subpod, association values were significantly lower during the last three periods than the first two ($F_{4,140} = 81.53$; $P < 0.001$; Figure 2.5).

The relationship between mean annual coefficient of association value and mean number of whale watch boats was also examined among pods. In all three pods, we found a significant negative relationship between number of whale watch boats and the degree of affiliation within the pod (J pod: $r^2 = 0.381$, $F = 8.001$, $P = 0.014$; K pod: $r^2 = 0.644$, $F = 23.472$, $P < 0.001$; L pod: $r^2 = 0.468$, $F = 11.413$, $P = 0.005$). However, the slope of these data was much shallower for J and K pod than for L pod (Figure 2.6). In addition, the relationship between mean coefficient of association and chinook salmon abundance was also significant, but only for L pod (L pod: $r^2 = 0.322$, $F = 6.185$, $P = 0.0274$; Figure 2.7).

Discussion

Mean coefficient of association patterns between whales showed a decrease over the 15-year period in all three pods. This decrease may be related to the increase in vessel activity observed off Limekiln Lighthouse during this period (Osborne, Koski, & Otis, 2002), as illustrated in subsequent analyses. More specifically, in all three pods, a significant relationship was revealed between number of whale watch boats and the degree of affiliation within the pod. However, the slope of the data was much shallower for J and K pod than for L pod, indicating that L pod may indeed be more sensitive than J or K pods to increased vessel traffic. Since L pod has a more extended range, often travelling west out to the Pacific Ocean through Juan de Fuca Strait (Osborne, 1999), these whales may be less adapted to vessel activity, and may therefore be more sensitive to their increasing presence. An alternative explanation for this observed relationship between L pod and vessel activity may be related to the number of L pod whales that have gone missing or died in the last decade (Center for Whale Research, 2008). L pod in particular has seen a decrease of approximately 47% of its pod members in the last 10 years, 14 of which were 20 years or older. Consequently, L pod has lost more mature pod members, which may have played a key role in the fracturing of L pod into two distinct subpod components (Bigg, Olesiuk, Ellis, Ford, & Balcomb, 1990), as is also reflected in the association indices calculated for this pod. Additional ramifications from the loss of older, more experienced whales may include loss of knowledge and experience maneuvering around and behaving in the presence of vessel traffic. If this information about behaving in the presence of increasing vessel traffic has indeed been lost, these whales may be losing the benefit of cultural trait transmission that may come from a cohesive social structure (Norris & Dohl, 1980).

In addition, the relationship between mean coefficient of association and salmon abundance was also significant, but only for L pod. L pod may be using different foraging techniques than J or K pod in the presence of chinook salmon, as the observed positive relationship with mean coefficient of association may reflect a preference to cooperatively forage. Since L pod is not consistently observed in the inland waters of Washington State and surrounding areas (Osborne, 1999), less is known about their foraging techniques, and behavior in general, especially during approximately nine months of the year that they are absent from this area (Baird, Hanson, & Dill, 2005).

In conclusion, association patterns between whales showed a decrease over the 15-year period in all three pods. Subsequently, association levels were found to be significantly related to numbers of whale watching boats for all pods over from 1987 - 2001. It was also found that for L pod, mean coefficient of association values increased as chinook salmon abundance increased. Although the study described above offered insights into the factors affecting killer whale social structure, archival data yielded relatively low resolution results. Data collected specifically for social affiliation analysis is needed in order to obtain higher resolution results and clearer conclusions.

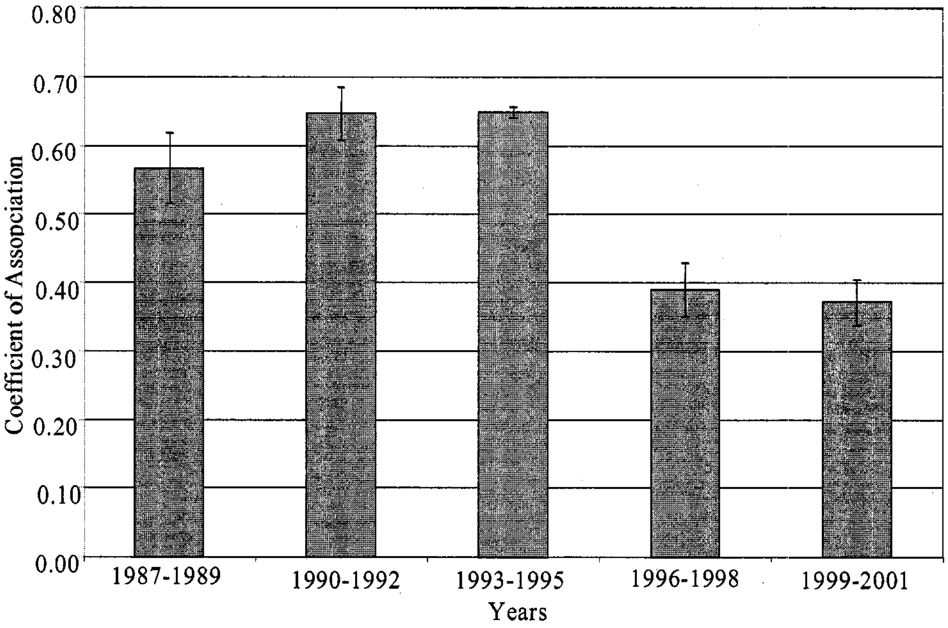

Figure 2.1. Mean coefficient of association (± SE) for J pod, in 3-year intervals.

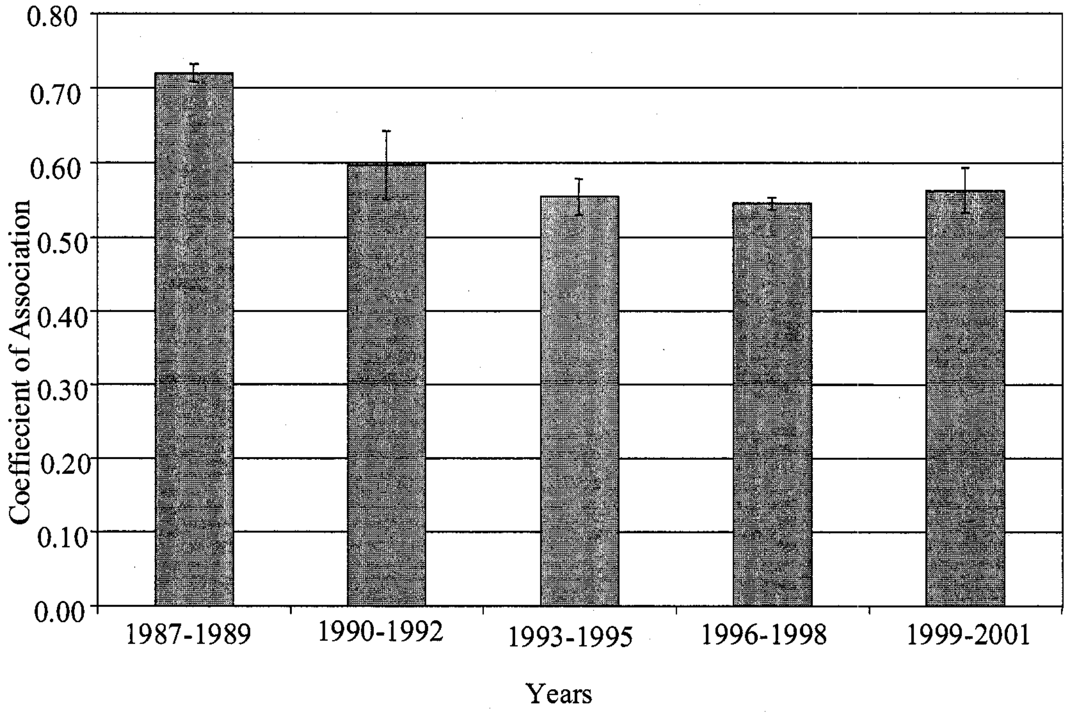

Figure 2.2. Mean coefficient of association (± SE) for K pod, in 3-year intervals.

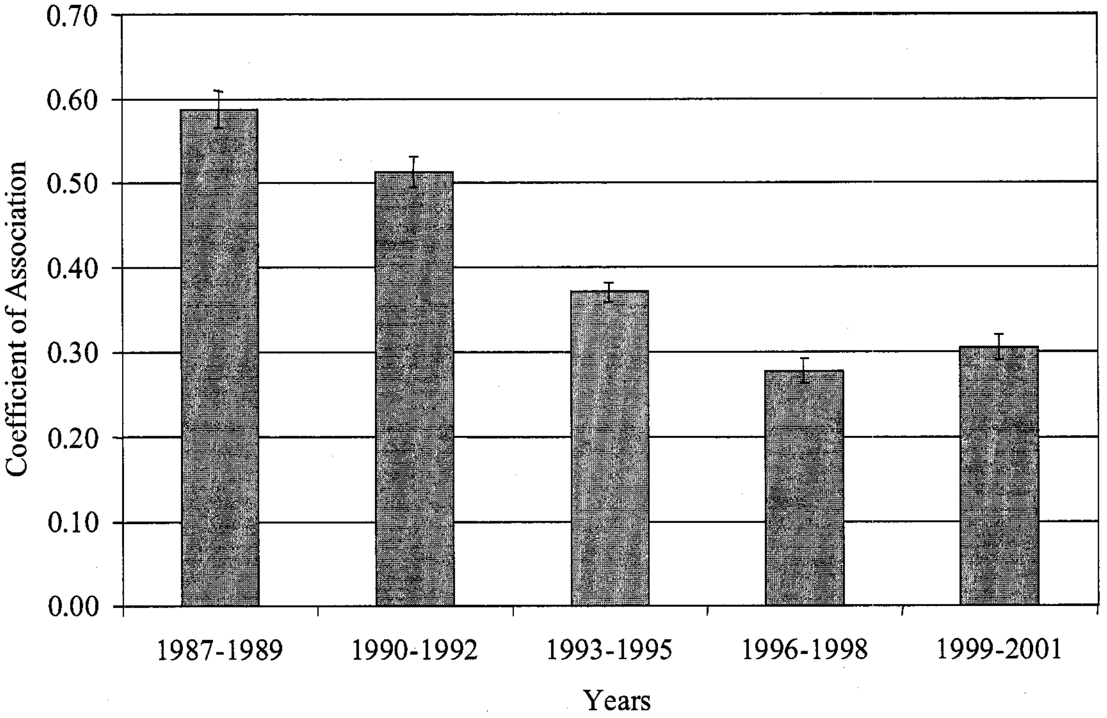

Figure 2.3. Mean coefficient of association (±SE) for L pod, in 3-year intervals.

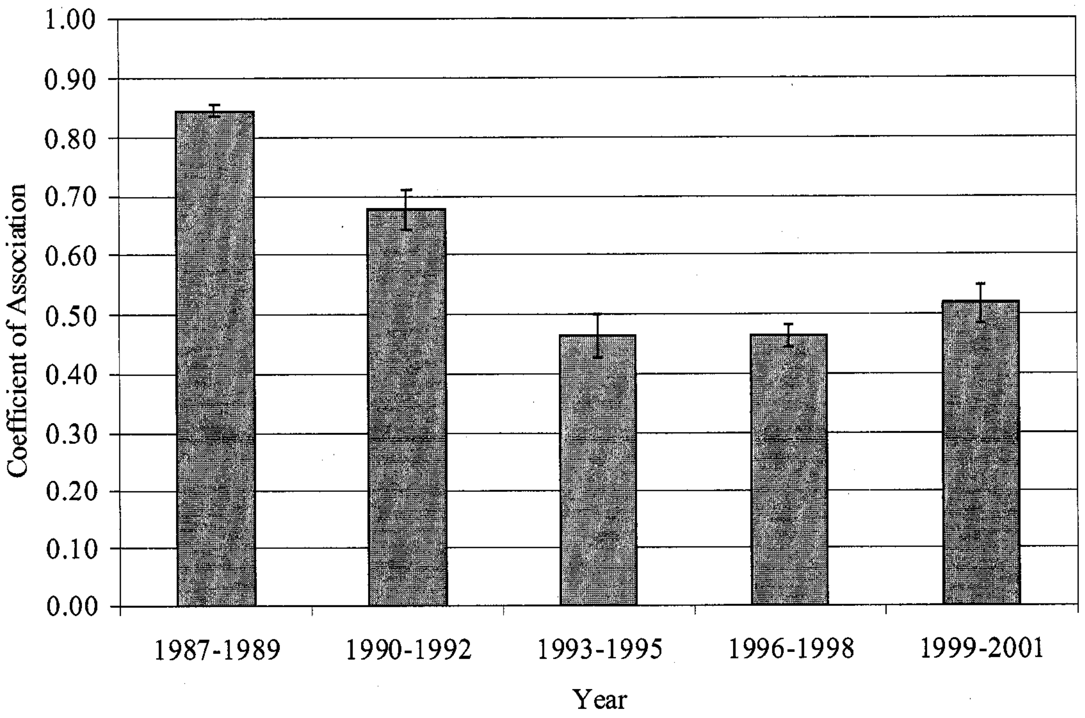

Figure 2.4. Mean coefficient of association (+SE) for L12 subpod, in 3-year intervals.

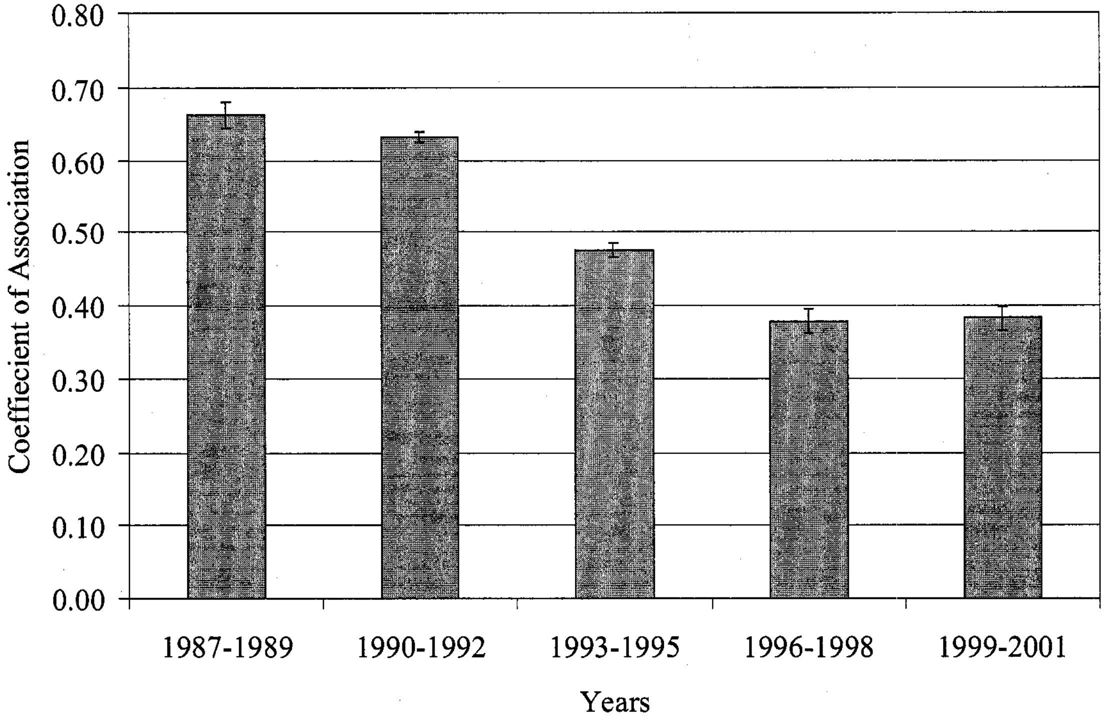

Figure 2.5. Mean coefficient of association (+SE) for L25 subpod, in 3-year intervals.

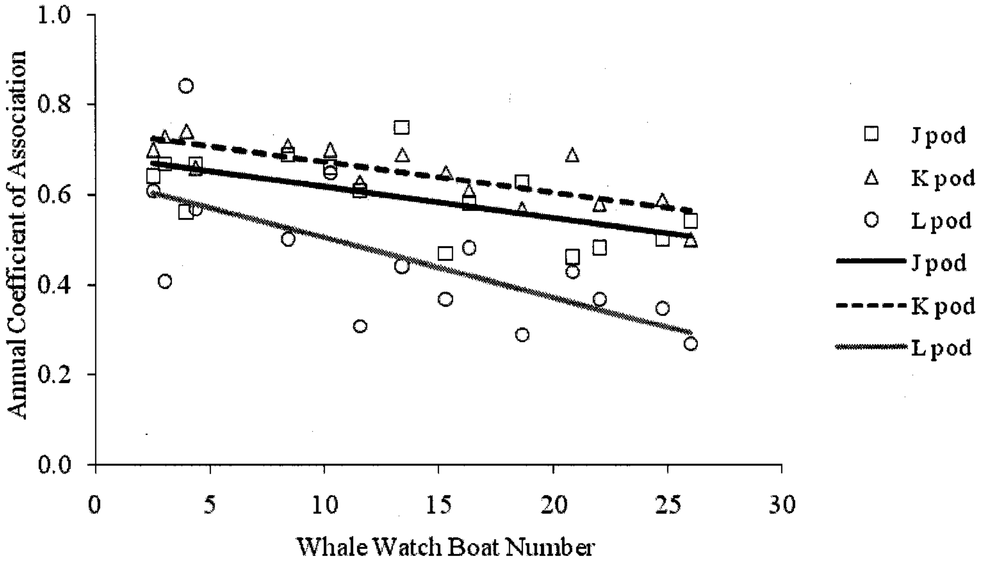

Figure 2.6. Relationship between annual mean whale watch boat number and annual coefficient of association (COA) for each pod.

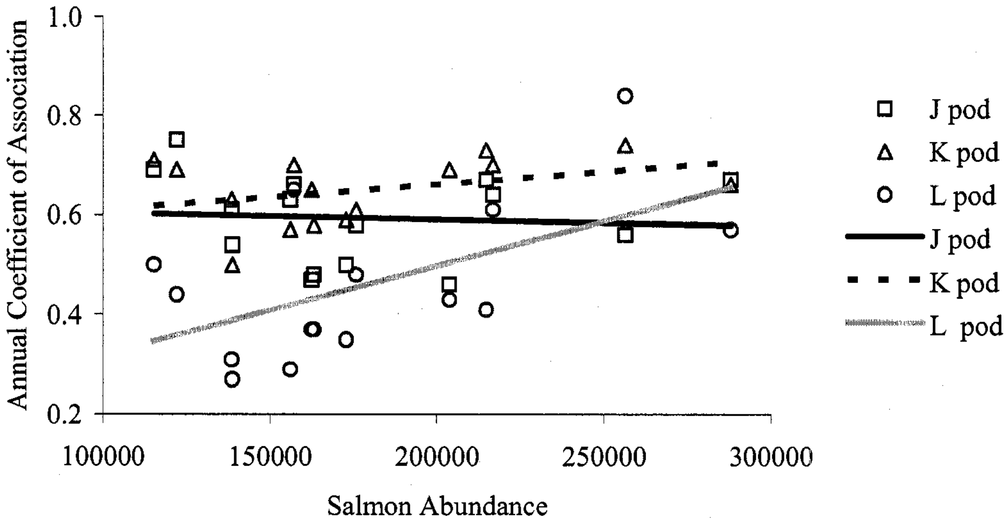

Figure 2.7. Relationship between chinook salmon abundance and annual coefficient of association (COA) for each pod.

Chapter 3: The Ecology of Social Behavior in "Southern Resident" Killer Whales (*Orcinus orca*)

Introduction

A major research objective when studying mammalian societies is to understand the ways in which ecological forces and behavioral characteristics interact to shape the structure and dynamics of social systems. As an understanding of these interactions develops, it often becomes possible to discern how a society functions and to predict how changes in environmental characteristics may influence social relationships and population dynamics (Crook, Ellis, & Goss-Custard, 1976).

The focus of the current study was the social behavior of "southern resident" killer whales in Washington State. Since these whales are highly cognitive and display an extremely cohesive social structure (Bigg, Olesiuki, Ellis, Ford, & Balcomb, 1990), fluctuations in social behavior among killer whales have important implications for the benefits of pod cohesion.

"Resident" killer whales are one of three distinct killer whale ecotypes found in the inshore waters of Washington state, which also include "transient" and "offshore" forms (Ford, Ellis & Balcomb, 2000). There are two communities of "resident" killer whales, "northern" and "southern", and these killer whales are characterized by their piscivorous diet, and are highly social mammals that live in stable subgroups of several related females and their young. Offspring of both sexes remain in their natal group for life, and groups are organized along matrilineal lines (Bigg, Olesiuki, Ellis, Ford, & Balcomb, 1990). "Northern resident" killer whales utilize Johnstone and Queen Charlotte Straits as core areas during summer months, whereas "southern resident" killer whales frequent inshore waters between Southern Vancouver Island, British Columbia, Canada, and the San Juan Island, Washington, USA (Baird, Hanson, & Dill, 2005).

The "southern resident" killer whale population in North America, consists of three distinct pods, J, K, and L, and has declined from 98 individuals in 1995 to 78 whales in 2001, a decline of 20.4% (Biological Review Team, 2002), before returning to 82 in 2003, and increasing recently to 87 whales. In Canada, this population was listed as "threatened" in 1999 and "endangered" in 2001 by the Committee on the Status of Endangered Wildlife in Canada (Baird, 2001). More recently, NOAA Fisheries announced in November 2006 the listing of the "southern resident" killer whales as endangered under the Endangered Species Act (ESA), the highest level of protection possible by the United States federal government.

With the decline of the "southern resident" killer whale population and the establishment of their formal endangered status, behavioral research, and especially social behavior research on this population is crucial to the future protection of these marine mammals. Studies of social behavior in other aquatic species such as loggerhead sea turtles (Schofield, Katselidis, Diopoulos, Pantis & Hays, 2006) as well as terrestrial mammals like endangered Tehuantepec jackrabbits (Farias, Fuller, Cervantes & Lorenzo, 2006) have demonstrated the importance of behavioral research in the conservation of these species. For example, behavioral data collected on loggerhead turtles may be used to improve conservation policies in Greece, and in Mexico, basic information on social behavior in Tehuantepec jackrabbits has contributed to population analyses and models imperative to the conservation and management of this endangered species. Examining social behavior, and specifically reproductive ecology, has shown to be consequential in many species of fishes as well (Vincent & Sadovy, 1998). In killer whales, if the relative amount of social behavior wanes over time due to ecological pressures, these animals may lose the group-living benefits of alloparental care, group foraging, sensory integration, and cultural trait transmission (Norris & Dohl, 1980), which will have important implications for conservation of this species.

As a measure of social behavior, percussive behaviors were examined in this study as they are considered communicative and may convey information to conspecifics (Pryor, 1986; Herzing, 2000). In previous studies on cetaceans, percussive behaviors have been defined as a behavior resulting in sound at the water surface, specifically as the result of a body part slapping the water (Ferrer, Cancho & Lusseau, 2006; Lusseau, 2006). Percussive behaviors have not only been considered communicative, but have also been suggested to function in foraging contexts as well (Würsig & Würsig, 1980).

Synchronous surfacing was also examined in this study, since surfacing together represents a social bond between two animals, and has previously been used to define the strength of affiliation among conspecifics in two species of bottlenose dolphins (*Tursiops truncates*; Ballance, 1990; *Tursiops aduncus*; Connor, Smolker & Bejder, 2006). Surfacing in synchrony has been described in multiple studies on killer whales (Jacobsen, 1986; Heimlich-Boran, 1988; Similia, 1997), but not quantified. This study examined synchronous surfacing under multiple conditions and in varying behavioral contexts.

Cetacean behavior, including synchronous surfacing, has been examined in response to vessel traffic in multiple species, including bottlenose dolphins (*Tursiops* *truncatus*; Janik & Thompson, 1996; Hastie, Wilson, Tufft, & Thompson, 2003; Lusseau, 2003; Constantine, Brunton, & Dennis, 2004; Mattson, Thomas & St. Aubin, 2005; Lemon, Lynch, Cato & Harcourt, 2006), Indo-Pacific humpback dolphins (*Sousa chinensis*; Ng & Leung, 2003; Stensland & Berggren, 2007), and killer whales (Williams, Bain, Ford, & Trites, 2002; Williams, Lusseau, and Hammond, 2006; Williams & Ashe, 2007). In northern Scotland, Hastie *et al.* found that bottlenose dolphins increased breathing synchrony in response to vessel traffic, and in South Carolina, Mattson and her colleagues found that dolphins responded to vessel activity by changing behavior, group size, and direction of movement. In killer whales, Williams and co-authors reported that vessel presence was significantly linked to changes in the probability that a focal animal would switch activity states, and this led to significantly different activities when vessels were absent or present (Williams, Lusseau, & Hammond). Additionally, Williams and colleagues have found that higher levels of vessel traffic (few versus many vessels) had a significantly different effect on killer whale behavior, with the swimming path of males in particular more sinuous when few boats approached, and straighter when many boats approached (Williams & Ashe).

Ecological variables that may influence social behavior, such as number of vessels present, salmon abundance, time of day, and pod identification were analyzed in this study. It has been shown that killer whale behavior in Johnstone Strait ("northern resident" killer whales) has been affected by vessel traffic (Williams, Lusseau & Hammond, 2006; Williams & Ashe, 2007), and in "southern resident" killer whales, time of day has been shown to have an effect on behavior as well (Baird, Hanson, & Dill, 2005). Additionally, it has also been found that in "northern resident" killer whales, percussive behavior rates differed by pod (Adimey, 1995).

In this study, it was hypothesized that social behavior would vary with whale-watching pressure, and specifically that percussive behavior would increase as whale watch pressure heightened due to the need to communicate at the surface, produce different sounds, and signal over long distances as underwater noise increased with increasing vessel traffic. It was specifically expected that breaches, which have been suggested to occur in response to disturbance or external stimuli such as boat noise (Pryor, 1986), would be observed more often in the presence of intensifying vessel pressure. Moreover, it was hypothesized that increased vessel pressure may directly decrease the rate of synchronous surfacing in these killer whales, as vessel pressure was expected to affect the ability of whales to maintain spatial cohesion. It was additionally postulated that there would be a significant relationship between social behavior and prey abundance, with synchronous surfacing showing a marked decrease as prey abundance increased, since whales most likely would not be traveling in close proximity and maintaining social cohesion while foraging or capturing prey items. In contrast, it was expected that percussive behavior would increase as prey abundance increased, as these behaviors, including breaches and tail slaps, may be used by these killer whales in foraging contexts.

Methods

Research was carried out in the inshore waters of Washington State. Data collection for the analyses presented here was conducted from June 2 through September 17 2003, June 1 through September 17 2004, and June 1 through August 31 2005.

Data Collection Procedure

For 2003 and 2004, a 5.6 meter Bayliner power boat with a 90 hp two-stroke outboard motor was used to collect data in the study area. For 2005, data were collected from the R/V Noctiluca, a 7.92 meter Pacific power boat with a 225 hp four-stroke outboard motor provided by the National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center. The research vessel departed from San Juan Island each morning at approximately 0600, weather permitting. All data collection was conducted in Beaufort sea state ≤ 3 and under visibility conditions adequate for locating and following killer whales. The general research method was to locate killer whales by boat each morning by searching frequent foraging locales, and also by monitoring VHF radio. When whales were located, the boat approached to within approximately 100m to allow for positive identification of individuals by sight, and then retreated to > 100m for subsequent behavioral observations. Multiple observers, including trained undergraduates from the University of Washington, assisted in behavioral data collection during 10-minute periods.

Data were collected using Event 3.0 software created by J. Ha on a PalmIII*xe*. Prior to each 10 minute period, pod identification, focal group size, and number of boats present were recorded. Focal group size was defined as whales that were behaving in a similar manner, and within the visual range of the researcher (Baird & Dill, 1996). Boats were categorized as private vessel, commercial whale watch vessel, or kayak within visual range of the researcher, and within approximately 0.5 miles of the whales.

All-occurrence sampling occurred for specific behaviors including breach, half breach, tail slap, inverted tail slap, pectoral fin slap, spy hop, physical contact, cartwheel, and synchronous surfacing. Using the ethogram developed by Jacobsen (1986), each of the behaviors was defined as in Table 3.1. Time of day was categorized as 0600 – 1000 (morning), 1000 – 1400 (midday), or 1400 – 1600 (afternoon).

Salmon abundance estimates were obtained from the Washington Department of Fish and Wildlife, Fish Division. These estimates were generated from data collected by recreational fisheries samplers with the Puget Sound Sampling Program. This program collects catch and effort data during angler interviews at boat ramps and docks across the Puget Sound region, with the objective of providing catch per unit effort data as well as species composition in the sport fishery (Washington Department of Fish & Wildlife, 2007). Only data from areas considered killer whale high use or home range areas were utilized in the analysis (Osborne, 1986). Catch Per Unit Effort (CPUE) was calculated for each salmon species by dividing the total number of salmon caught per week by the total number of anglers for the corresponding week.

Statistical Analysis

All statistical analyses were performed using Systat 7 (Wilkinson, Blank & Gruber, 1996), and a probability of 0.05 was used as the criterion for rejection of the null hypotheses. Principal components analysis (PCA) with varimax rotation was performed on all observed behaviors in order to establish behavioral intercorrelations (Joliffe, 2002; Sinn, Perrin, Mathier & Anderson, 2001; Notari & Goodwin, 2007; McBride & Wolf, 2007; Weiss, King & Perkins, 2006). Factor scores based on resulting latent variables were utilized during further analyses. PCA was also performed on salmon species including pink, coho, chinook, and sockeye in order to test for independence. Additionally, PCA was used to check for independence between vessel variables including commercial, private, and non-motor boat.

Backward stepwise general linear modeling was run on the five behavioral dependent variables created from the PCA (Tabachnick & Fidell, 2006). Independent variables included in all subsequent models were number of private and commercial boats, two PCA-generated salmon variables, year, time of day, pod identification, and focal group size, as well as all possible two-way interactions between boat and salmon.

Results

Sampling

In 2003, subjects were contacted and data were collected on 33 of 69 field days, yielding 333 samples, with a mean sampling rate of 10.09 ± 5.49 samples per contact day. In 2004, data were collected on 33 of 72 field days, resulting in 307 samples, and a mean sampling rate of 9.30 ± 6.62 samples per contact day. For 2005, data were collected on 28 of 53 field days, resulting in 362 samples, and a mean sampling rate of 12.93 ± 6.16 samples per contact day (total n = 1002).

Analyzing Covariance in Dependent and Independent Variables

Using varimax rotation, rotated loadings for each of five created factors are depicted in Table 3.2. Data were sorted on how heavily each was loaded on each dimension, with the value of 0.50 being the decided cut-off point for consideration. On these five dimensions alone, almost 75% of the total variance of the raw behavioral variables was explained. For Factor 1, inverted tail slap and pectoral fin slap loaded heavily, indicating that these behaviors were also often observed together. For Factor 2, breach and cartwheel covaried together. For Factor 3, contact and spyhop were seen to covary together. Lastly, for Factors 4 and 5, both synchronous surfacing and half breach were not seen to covary significantly with any of the other eight variables, and as such were considered separate variables. In the PCA analysis, tail slap was not seen to covary with any other behavior variable, and was subsequently considered an independent variable.

PCA was also conducted for catch per unit effort of salmon species on a weekly basis, and varimax rotation with rotated loadings produced two factors (Table 3.3). On Factor 1, pink and coho salmon covaried together, with chinook on the opposite end of the continuum, indicating that when large numbers of coho and pink salmon were caught, very few chinook were caught. Sockeye was identified as an independent variable, as it varied independently from pink, coho, and chinook species.

Finally, PCA was conducted for number of vessels observed during this study on a daily basis. Varimax rotation and rotated loadings yielded the independent factors

(Table 4). For each factor, there were no vessel types seen to covary significantly with any other vessel. Subsequent analyses incorporated these factor scores for vessel type.

Ecological Analysis of Surface Behaviors

While data were collected over a three year period, only behavioral data from 2004 and 2005 were utilized for general linear modeling due to changes in coding which would have affected the results. Additionally, only one sample per hour each day was randomly selected and utilized in these analyses as to ensure statistical independence of behavior samples. Non-motor vessels were also excluded from these analyses due to small sample size (n = 10).

General linear modeling indicated that synchronous surfacing between whales was significantly affected by not only sockeye salmon numbers (F = 3.994, df = 1,124, p = 0.048), but also by pod (F = 3.622, df = 2,124, p = 0.029; overall $r^2 = 0.132$). Specifically, synchronous surfacing was found to decrease as sockeye salmon abundance increased (Figure 3.1). Additionally, synchronous surfacing was found to be highest for J pod, moderate for K pod, and lowest for L pod (Figure 3.2).

Furthermore, cartwheels and breaches, which were found to covary significantly together in PCA analysis, were significantly affected by time of day, with more cartwheels and breaches observed during midday hours (F = 3.073, df = 2,124, p = 0.049; overall $r^2 = 0.092$, Figure 3.3).

Contact and spyhops, which were also found to covary significantly together in PCA, were found to be significantly affected by commercial boat presence (F = 7.922, df

= 1,124, $p = 0.0057$; overall $r^2 = 0.0921$), with contact and spyhops increasing with increasing numbers of commercial boats (Figure 3.4).

Half breaches were significantly affected by year ($F = 6.089$, df = 1,124, $p = 0.0149$; overall $r^2 = 0.115$), with more half-breaches seen during the 2004 data collection season (Figure 3.5).

Discussion

Principal Components Analysis of Surface Behaviors

Principal components analysis was performed on all surface behaviors observed during the study in order to determine how these behaviors related to each other. This type of analysis was important because a large number of behaviors were reduced to a smaller number of statistically independent categories, thus giving insight not only the function of the behaviors, but their contextual relevance as well.

The impetus for the relationship observed between surface behaviors may be related to function, reaction to a similar stimulus, or these behaviors may potentially be used to invoke group cohesion under varying circumstances. On Factor 1, inverted tail slaps and pectoral fin slaps covaried together, most likely because they both yield a similar sound at the surface. Both behaviors generate an audible slapping sound, and as such may be used to signal conspecifics. Jacobsen (1986) suggested that the function of a pectoral fin slap seemed to vary with context, and that the sound they produce may either act as a signal, or to flush out fish during foraging behavior. Similarly, Jacobsen suggested that inverted tail slaps seemed to function as a play behavior, or as a signal for herding fish. Given the similar sounds these slaps generate, it appears likely that inverted tail slaps and pectoral fin slaps may be used interchangeably by killer whales, and may either serve a communicative or foraging function.

For Factor 2, cartwheel and breach covaried, indicating that these behaviors are often observed together. The function of this pair of behaviors is most likely divergent from inverted tail slaps and pectoral fin slaps, and as such may occur in a completely different context. Cartwheels as well as breaches have both been considered foraging behaviors in past studies, and therefore may serve a function in either prey searching or capture by killer whales (Pryor, 1986; Jacobsen, 1986). Additionally, breaches have also been suggested to occur in response to a disturbance or external stimuli such as boat noise, or as a function of arousal (Pryor, 1986). It has also been suggested that breaches may be used to communicate position and/or to signal a threat or warning (Martinez & Klinghammer, 1978). Depending on context, cartwheel and breaching behavior may occur in a foraging context, and most likely were seen to covary due to this specific functionality. Breaches may also serve a communicative purpose in terms of threat or warning, and as such may not always occur in tandem with cartwheels.

On Factor 3, physical contact and spyhops covaried. Spyhops are considered an information-gathering behavior, as raising their eyes above the surface of the water provides visual information to whales (Martinez & Klinghammer, 1978). Physical contact on the other hand is clearly a social behavior, the function of which may involve reassurance and/or reconciliation (Noonan, 2007). Since these behaviors were found to covary significantly with each other, spyhops may serve to gather information, and subsequently lead to a reassuring behavior such as physical contact, especially if the type of information gathered included some sort of perceived physical threat or unknown object.

Tail slaps, unlike each of the other behaviors analyzed, were found to be independent of all other behaviors, and did not yield a factor score. As tail slaps are thought to be an effective predator behavior in killer whales feeding on herring, (Domenici, 2001), tail slaps may be used in these killer whales to drive salmon to other whales, or drive them to a desired location. Tail slaps occur at a speed that is faster than most prey items, making it an effective tool to control or affect salmon behavior. Tail slaps have also been suggested as a function of annoyance, and sometimes to signal a warning in small cetaceans (Pryor, 1986). As such, this behavior may occur in specific contexts including prey herding, or be used to signal warning or annoyance to conspecifics. In either case, this behavior was not found to covary with any other behavior measured in this study, and may therefore be unique in form, function, and context.

Lastly, synchronous surface and half-breach were both found to occur by themselves in PCA, indicating that these behaviors are independent and do not covary with any of the other behaviors examined. Synchronous surfacing is considered an indicator of social cohesion or organization (Jacobsen, 1986), and as such is most likely to appear as a separate factor when analyzed with a larger set of percussive behaviors. Half-breach on the other hand is a unique percussive behavior, and may simply be intended as a less aggressive or less intense breach, reflecting a lower signal strength or intensity. Since a half-breach may not be as intense as a breach, or generate as much energy or sound as another type of slap, it may be a separate behavior simply due to context.

Principal Components Analysis of Salmon and Vessel Abundance

PCA was also performed on salmon abundance data to test for statistical independence, and species were found to cluster into a smaller number of prey categories. Most notably, when coho and pink salmon were more abundant, lesser numbers of chinook salmon were observed. This was reflected in the correlation values obtained in the principal components analyses. Presumably, coho and pink salmon may either be adapted to similar conditions, or may return to the San Juan Island region at similar times. Although coho salmon are most closely related to chinook salmon in terms of genetics (Healey, 1991), coho and pink salmon species may behave more similarly, and therefore were seen to group together in terms of statistical analyses. Results of the salmon PCA also contributed to the interpretation of behavioral data, and provided additional insight into the function of killer whale social behavior. Lastly, PCA was performed on the three vessel categories, and analyses showed that commercial, private, and non-motor vessels did not covary, and were therefore considered statistically independent.

Interpretation of Ecological Influences on Surface Behaviors

Although found to be significantly related in PCA, inverted tail slap and pectoral fin slap were not found to be affected by any of the dependent variables examined in this study. Similarly, tail slaps were not affected by any of the variables included in analyses. One reason for this could be that these behaviors generalize to multiple contexts, and may therefore be used in varying situations and for multiple functions, particularly for communicative and foraging purposes (Jacobsen, 1986).

Synchronous surfacing was found to be significantly affected by sockeye salmon abundance as well as vary by pod. Although it has been found that the occurrence of several pods of "northern resident" killer whales was significantly positively associated with sockeye abundance in Johnstone Strait during summer months (Nichol & Shackleton, 1996), sockeye are not considered a substantial prey item for these "southern resident" killer whales (Ford & Ellis, 2006). As prey information for "southern resident" killer whales is currently considered preliminary (National Marine Fisheries Service, 2006), it is still possible that sockeye may be an occasional prey item for these whales, and as such any foraging behavior for sockeye would decrease synchronized surfacing between animals as they engaged in prey-capture related behaviors. In addition, all three pods behaved differently in terms of synchronous surfacing over the course of this study, with J pod engaging in this behavior the most, followed by K pod, and then L pod. The main reason for this pattern may be the stronger bonds in J pod and K pod relative to L pod, as L pod has almost twice as many pod members (National Marine Fisheries Service).

Cartwheels and breaches were found to be significantly affected by time of day. There appeared to be a significant increase in cartwheels and breaches during the mid-day period of 1000 – 1400. This may be a function of foraging behavior occurring more during these hours than during the morning and late afternoon, but this was not reflected in the model that included prey abundance. Since breaches in particular are often interpreted as a warning signal in whales (Pryor, 1986), they may serve a similar purpose in this context during the mid-day hours, when human and other water-related activities are usually at their peak.

Physical contact and spyhop behaviors were found to be significantly affected by commercial vessel presence only, and these behaviors showed a tendency to increase when vessel abundance increased. If spyhop and physical contact behaviors are used for information gathering and subsequent reassurance as posited earlier, these whales may be more sensitive to increasing numbers of these commercial vessels in their immediate vicinity.

Half-breaches were found to be significantly affected by year, with distinctly more half-breaches observed in 2004 as opposed to 2005. As previously suggested, half-breaches are a percussive behavior, and less intense than a full breach. As such, they may be a communicative or a warning behavior as has been suggested for breaches (Martinez & Klinghammer, 1978; Pryor, 1986), but seen viewed as a less intense gesture. In terms of the observed disparity in half-breach behavior between 2004 and 2005, this may be attributed to ecological conditions and/or extraneous variables such as shipping traffic and military activities, as these variables differ from year to year, and were not measured in this study.

In several cases, vessels were hypothesized to have a significant relationship with social behavior, but these hypotheses were not supported by subsequent analyses. First, percussive behavior, and breaches in particular, were hypothesized to show an increase with increasing vessel abundance, given that these whales may need to communicate at the surface and signal over long distances with amplifying noise levels. This hypothesis was not supported by this study; vessel abundance did not show a significant relationship with breaches or any other percussive behavior. A possible explanation for the lack of effect includes habituation by these whales to increasing vessel pressure. As this population of "southern resident" killer whales is the focus of a relatively large, multi-million dollar whale watch industry (Koski, 2004), these whales may have habituated to increasing vessel pressure in their immediate vicinity as the whale watch industry has expanded. Alternatively, it is possible that the percussive behaviors recorded in this study may not serve a communicative function for these whales, and therefore would not show an increase in the presence of intensifying vessel traffic. Percussive behavior may be a crude measure of communication in these animals, and future studies should focus on refining these measures before relating them to variables including vessel traffic.

Moreover, it was hypothesized in this study that increased vessel abundance would be directly related to a decrease in synchronous surfacing for these killer whales, as vessel pressure was expected to negatively affect the ability of whales to maintain spatial cohesion. This was not found to be true; vessel pressure was not significantly related to numbers of either vessel type. One explanation for this result could again be habituation by these whales to increasing amounts of vessel traffic. In the past 30 years, these whales have been exposed not only an expanding whale watch industry, but to shipping traffic, military vessel activity, commercial and private fishing vessels, as well as ferry and other vessel types (Koski, 2004). As such, these whales may have learned not only how to maneuver around such objects, but how to minimize the impacts of increasing vessel activity in their daily behaviors.

In this study, it was also expected that percussive behavior would increase as prey abundance increased, as these behaviors, including breaches and tail slaps, may be used by these killer whales in foraging contexts. Subsequent analyses failed to show a significant relationship between these behaviors and prey abundance, presumably because percussive behaviors may not play a key role in foraging contexts for these whales. Although breaches and tail slaps have previously been suggested as foraging behaviors in killer whales as well as other cetaceans (Jacobsen, 1986; Pryor, 1986; Domenici, 2001), it is possible that these whales may not regularly utilize these behaviors in a foraging context as they search for and capture salmonids.

Results from these analyses indicated that multiple behaviors were affected by ecological variables including salmon and vessel abundance, as well as time of day, pod, and year. Sockeye salmon abundance was found to be significantly related to synchronous surfacing in these whales, thus suggesting that when whales were foraging for sockeye, they spent less time swimming and breathing in synchrony. Moreover, commercial vessel abundance was found to be weakly, but significantly related to spyhop and physical contact behaviors, as these behaviors increased in the presence of intensifying commercial vessel abundance. Since the purpose of spyhop and contact behavior was posited to be information gathering and reassurance, commercial vessels may present a perceived threat to these animals in terms of both noise and size, and whales may therefore produce a higher quantity of these behaviors in their presence.

Conclusions

In this study, principal components analyses played an important role in reducing a large number of behaviors into a smaller number of statistically independent categories, which provided insight not only into the functionality of behaviors, but also into their contextual relevance as well. This type of analysis also provided unique insight into relationships among salmon species in the inshore waters of Washington State and British Columbia, and additionally served to demonstrate statistical independence between vessel categories. As analyses were completed, complex subtleties emerged from these behavioral data indicating that killer whale social behaviors are indeed affected not only by multiple ecological variables including salmon abundance and the presence of commercial vessel traffic, but that some of these behaviors vary significantly among pod, time of day, and year. Although several variables were found to have statistically significant effects on killer whale social behavior, these variables may not all be biologically significant, as these whales inhabit an environment that is fluid and continuously changing. Their capacity to adapt to this environment on a regular basis, be it daily, weekly, or yearly, speaks to their complex cognitive abilities.

Table 3.1. Ethogram of behaviors utilized in the current study.

Behavior	Definition
Breach	Whale accelerates rapidly under water, jumps out at an angle to the surface, and falls back into the water on its side, generating a large splash.
Half Breach	Less than half the body emerges from the water, and the whale falls on its ventral or side surface.
Tail Slap	When the whale raises and lowers its flukes, dorsal side up, while swimming at or just below the surface of the water. The tail slaps the surface of the water, generating a loud sound above the water surface.
Inverted Tail Slap	Similar to a tail slap, but with the whale's ventral side up.
Pectoral Fin Slap	Whale turns on its side and slaps the water with one pectoral fin.
Spyhop	Occurs when the whale rises vertically out of the water so that both eyes are exposed. Pectoral fins can be in or out of the water.
Physical Contact	Contact between two whales with any body part.
Cartwheel	A fluke throw performed vigorously so that most of the body is exposed, and travels in a semicircular arc before entering the water again with a large splash. This behavior is often carried out rapidly and repeatedly.
Synchronous Surface	Occurs when two or more whales surface at the same time, when next to each other.

Table 3.2. Rotated loadings for each of five created factors using varimax rotation in principal components analysis of behavior.

Behavior	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Inverted tail slap	**0.871**	0.047	0.084	0.009	0.039
Pectoral fin slap	**0.831**	0.171	0.027	0.011	0.079
Cartwheel	0.125	**0.853**	-0.013	-0.021	-0.156
Breach	-0.006	**0.708**	-0.042	0.026	0.419
Tail slap	0.411	0.521	0.206	0.103	0.166
Contact	-0.099	0.043	**0.864**	0.041	-0.002
Spyhop	0.363	-0.013	**0.672**	-0.063	0.002
Synchronous surfacing	0.025	0.029	-0.007	**0.994**	-.008
Half breach	0.118	0.074	0.006	-0.012	**0.937**
Variance (Eigenvalues)	**1.791**	**1.542**	**1.253**	**1.007**	**1.114**
% of the Total Variance Explained	**19.896**	**17.129**	**13.917**	**11.185**	**12.377**

Table 3.3. Rotated loadings for two factors using varimax rotation in principal components analysis of salmon species.

Salmon species	Factor 1	Factor 2
CPU chinook	-0.7760	-0.1353
CPU coho	**0.6294**	-0.5124
CPU pink	**0.6079**	0.0105
CPU sockeye	0.1237	**0.9193**
Variance (Eigenvalues)	**1.3831**	**1.1259**
% of the Total Variance Explained	**34.58%**	**28.15%**

Table 3.4. Rotated loadings for two factors using varimax rotation in principal components analysis of salmon species.

Vessel Type	Factor 1	Factor 2	Factor 3
Private vessel	**0.965**	0.086	0.244
Non-motor vessel	0.080	**0.993**	0.089
Commercial vessel	0.245	0.095	**0.965**
Variance (Eigenvalues)	**0.999**	**1.002**	**0.998**
% of the Total Variance Explained	**33.32%**	**33.40%**	**33.29**

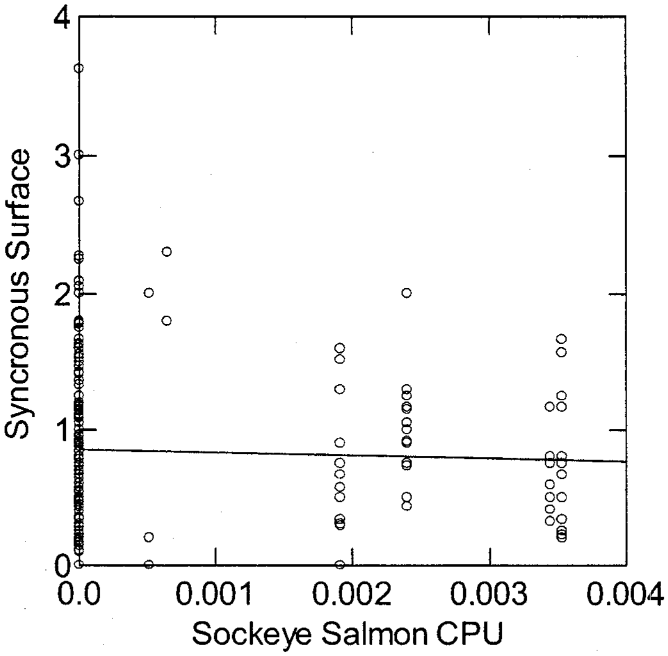

Figure 3.1. Relationship between synchronous surface behavior and sockeye salmon abundance in catch per unit effort. Units for synchronous surfacing is rate per individual whale.

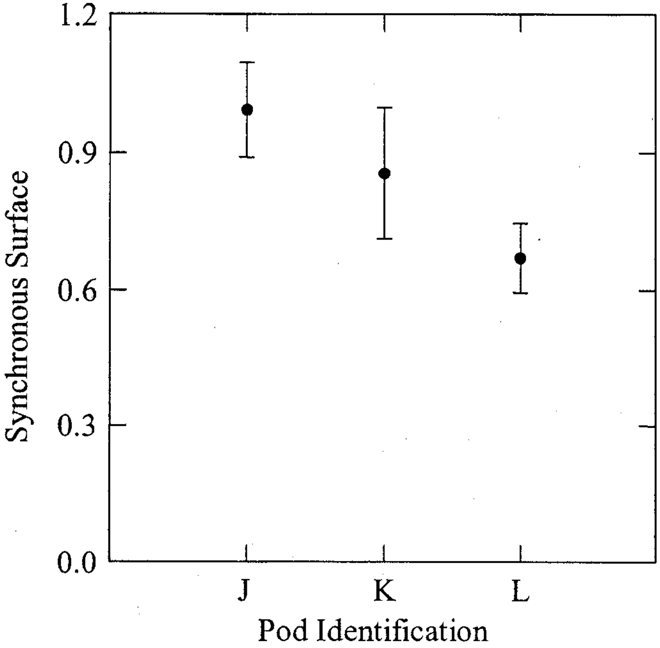

Figure 3.2. Relationship between synchronous surface behavior and pod. Units for synchronous surfacing is rate per individual whale.

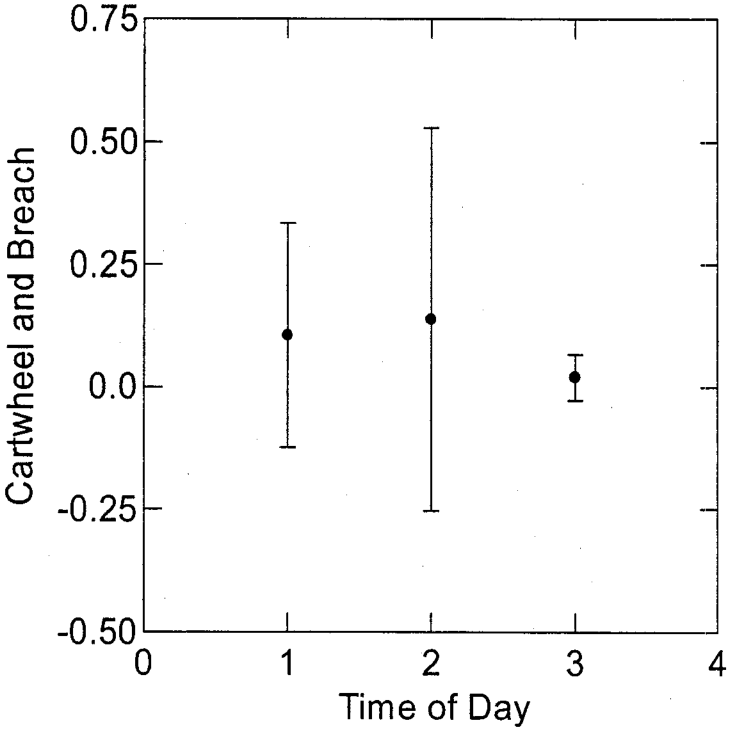

Figure 3.3. Relationship between cartwheel/breach and time of day. Units for cartwheels and breaches are rate per individual whale. Time of day was categorized as 0600 – 1000 (1), 1000 – 1400 (2), or 1400 – 1600 (3).

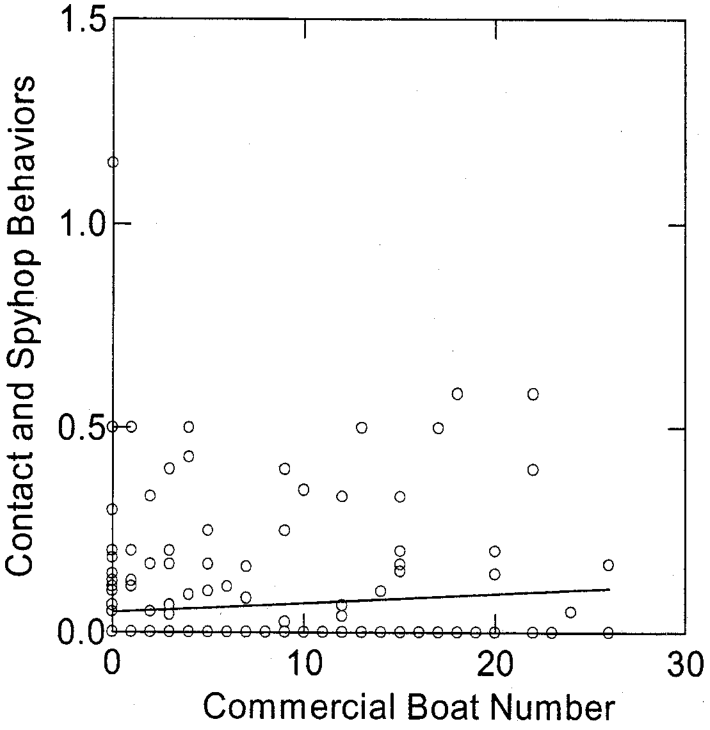

Figure 3.4. Relationship between commercial boats and contact and spyhop behaviors. Units for contact and spyhops are rate per individual whale.

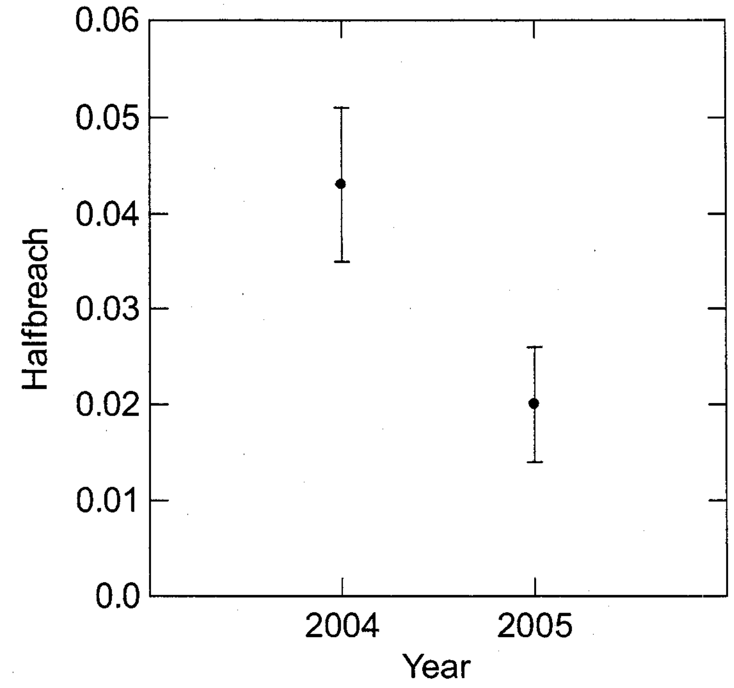

Figure 3.5. Relationship between half-breach and year. Units for half-breach is rate per individual whale.

Chapter 4: The Ecology of Behavior States in "Southern Resident" Killer Whales (*Orcinus orca*)

Introduction

The focus of the current study was the relationship between ecology and behavior states in "southern resident" killer whales in Washington state. "Resident", or fish-eating killer whales are one of three distinct killer whale ecotypes found in the inshore waters of Washington state, which also include "transient" and "offshore" forms (Ford, Ellis & Balcomb, 2000). There are two communities of "resident" killer whales, "northern", which utilize Johnstone and Queen Charlotte Straits as core areas during summer months, and "southern", which frequent the inshore waters between Southern Vancouver Island, British Columbia, Canada, and the San Juan Islands, Washington, USA (Baird, Hanson, & Dill, 2005). The "southern resident" killer whale population in North America, consists of three distinct pods, J, K, and L, and declined from 98 to 78 whales in the six years between 1995 and 2001, a decline of 20.4% (Biological Review Team, 2002), before returning to 82 in 2003, and increasing more recently to 87 whales. In Canada, this population was listed as "threatened" in 1999 and "endangered" in 2001 by the Committee on the Status of Endangered Wildlife in Canada (Baird, 2001). More recently, NOAA Fisheries announced in November 2006 the listing of the "southern resident" killer whales as endangered under the Endangered Species Act (ESA), the highest level of protection possible by the United States federal government.

In killer whales, if behavior is altered due to ecological pressures such as vessel traffic, these animals may need to increase energy intake in order to compensate for any additional energetic demands (Williams, Lusseau & Hammond, 2006). Past research on the effect of human activities on time budgets have contributed to conservation efforts in several mammalian and avian species, including desert bighorn sheep (*Ovis canadensis nelsoni*), woodland caribou (*Rangifer tarandus caribou*), and eastern bluebirds (*Sialia sialis*; Stockwell & Bateman, 1991; Tyler, 1991; Duschesne, Cote & Barette, 2000; Kight & Swaddle, 2007). For example, Stockwell and Bateman examined time budgets for bighorn sheep to ascertain the effect human activities may have on food intake. These authors found that bighorn sheep reduced foraging efficiency in the winter, but not spring, implying that bighorn sheep may be sensitive to human disturbance in winter, but not spring, when they had migrated to lower elevations and were further from human disturbance (Stockwell & Bateman). In Canada, Duchesne and colleagues found that the presence of ecotourists in winter affected time spent resting and foraging in caribou, and suggested that proper precautions be incorporated into ecotourist activities in order for these animals to tolerate such human activity (Duchesne, Cote & Barette).

The focus of the current study was the ecology of behavior states in “southern resident” killer whales. Ecological variables that may influence behavior state, such as salmon and vessel abundance, time of day, year, group size, and pod were analyzed. Cetacean behavior has been examined in response to vessel traffic in multiple species, including bottlenose dolphins (*Tursiops truncatus*; Janik & Thompson, 1996; Hastie, Wilson, Tufft, & Thompson, 2003; Lusseau, 2003; Constantine, Brunton, & Dennis, 2004; Matteson, Thomas & St. Aubin, 2005; Lemon, Lynch, Cato & Harcourt, 2006), Indo-Pacific humpback dolphins (*Sousa chinensis*; Ng & Leung, 2003; Stensland & Berggren, 2007), common dolphins (*Delphinus sp.*; Stockin, Lusseau, Binedell, Wiseman, & Orams, 2008), and killer whales (Williams, Bain, Ford, & Trites, 2002; Williams, Lusseau, and Hammond, 2006; Williams & Ashe, 2007). In South Carolina, Mattson and her colleagues found that bottlenose dolphins responded to vessel activity by changing behavior, group size, and direction of movement. Likewise, Lusseau found that social and resting states were disrupted by interactions with vessels in bottlenose dolphins, and that the duration and total amount of time spent in behavior states decreased. Researchers in the Bay of Islands, New Zealand, discovered that bottlenose dolphins decreased resting behavior as boat number increased, and that dolphins rested less and milled more in the presence of dolphin-watching (commercial) boats as opposed to non-permitted (private) boats (Constantine, Brunton, & Dennis). Analogously, researchers in Australia found that bottlenose dolphins were affected by experimental approaches by powerboats, and that these dolphins not only altered surface behavior while traveling, but also changed the direction of travel in response to a powerboat approach (Lemon, Lynch, Cato, & Harcourt). Lastly, in a recent study on common dolphins in New Zealand, Stockin and colleagues found foraging and resting periods to be disrupted by vessel interactions, as both the duration and overall time spend engaged in these activities decreased. Additionally, researchers found that foraging dolphins took longer returning to their initial behavior state when vessels were present, as well as an increased shift to social or milling behaviors after interactions with vessels (Stockin *et al.*).

In killer whales, it has been shown that activity state was affected by vessel traffic in northern residents, and specifically, that vessel presence was significantly related to switching from one activity state to another (Williams, Lusseau & Hammond, 2006). Additionally, Williams and colleagues found that in the presence of vessels, whales decreased the time spent feeding and rubbing, which thereby could have resulted in decreased energy intake.

In this study, it was hypothesized that there would be a significant relationship between behavior state and vessel abundance, and specifically that rest, forage, and play would decrease as vessel pressure heightened due to the potential disruption in both acoustic and physical environments. Specifically, it was hypothesized that increased vessel pressure may be associated with a marked decrease of resting observed in these whales, as vessel pressure may affect the ability of whales to maintain spatial cohesion during a resting state. It was additionally postulated that there would be a significant relationship between behavior state and prey abundance, with rest and play showing a tangible decrease as prey abundance increased, since whales most likely would not be engaged in rest or play while foraging or capturing prey items. Furthermore, it was hypothesized that the Shannon-Weiner Index (H) would not show a relationship with behavior state, as these whales show strong bonds and social cohesion, and therefore should most often engage in the same behavior state. Effects of time of day, year, pod, and group size were hypothesized to show no significant relationship with behavior state.

Methods

Research was carried out in the inshore waters of Washington State. Data collection for the analyses presented here was conducted from June 2 through September 17 2003, June 1 through September 17 2004, and June 1 through August 31 2005.

Data Collection Procedure

For 2003 and 2004, a 5.6 meter Bayliner power boat with a 90 hp two-stroke outboard motor was used to collect data in the study area. For 2005, data were collected from the R/V Noctiluca, a 7.92 meter Pacific power boat with a 225 hp four-stroke outboard motor provided by the National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center. The research vessel departed from San Juan Island each morning at approximately 0600, weather permitting. All data collection was conducted in Beaufort sea state ≤ 3 and under visibility conditions adequate for locating and following killer whales. The general research method was to locate killer whales by boat each morning by searching frequent foraging locales, and also by monitoring VHF radio. When whales were located, the boat approached to within approximately 100m to allow for positive identification of individuals by sight, and then retreated to > 100m for subsequent behavioral observations. Multiple observers, including trained undergraduates from the University of Washington, assisted in behavioral data collection during 10-minute periods.

Data were collected using Event 3.0 software created by J. Ha on a PalmIII*xe*. Prior to each 10 minute period, pod identification, focal group size, and number of boats present were recorded. Focal group size was defined as whales that were behaving in a similar manner, and within the visual range of the researcher (Baird & Dill, 1996). Boats were categorized as private vessel, commercial whale watch vessel, or kayak within visual range of the researcher, and within approximately 0.5 miles of the whales.

During each 10 minute period, scan sampling occurred every two minutes to document the behavior state of each visible animal. When possible, age, sex, and/or individual identification was recorded for each animal as well. Behavior categories included those listed in Table 4.1. Time of day was categorized as 0600 – 1000 (morning), 1000 – 1400 (midday), or 1400 – 1600 (afternoon).

Salmon abundance estimates were obtained from the Washington Department of Fish and Wildlife, Fish Division. These estimates were generated from data collected by recreational fisheries samplers with the Puget Sound Sampling Program. This program collects catch and effort data during angler interviews at boat ramps and docks across the Puget Sound region, with the objective of providing catch per unit effort data as well as species composition in the sport fishery (Washington Department of Fish & Wildlife, 2007). Only data from areas considered killer whale high use or home range areas were utilized in the analysis (Osborne, 1986). Catch Per Unit Effort (CPUE) was calculated for each salmon species by dividing the total number of salmon caught per week by the total number of anglers for the corresponding week.

Statistical Analysis

All statistical analyses were performed using Systat 7 (Wilkinson, Blank & Gruber, 1996), and a probability of 0.05 was used as the criterion for rejection of the null hypotheses. Principal components analysis (PCA) with varimax rotation was performed on salmon species including pink, coho, chinook, and sockeye in order to test for independence (Joliffe, 2002; Sinn, Perrin, Mathier & Anderson, 2001; Notari & Goodwin, 2007; McBride & Wolf, 2007; Weiss, King & Perkins, 2006). Factor scores based on resulting latent variables were utilized during further analyses. Additionally, PCA was used to check for independence between vessel variables including commercial, private, and non-motor boat. The Shannon-Weiner Index, used in this study as a measure of behavioral diversity, was calculated by multiplying the behavior state proportion by the log of that proportion, and summing across all behaviors. The resultant value ranged from zero to infinity, with a value of 0 indicating all animals were engaged in single behavior state, and higher value indicative of a more extreme, uneven distribution of behaviors, for example, animals simultaneously engaging in two or three different states.

General linear modeling was utilized for analysis of four behavior states (Tabachnick & Fidell, 2006). Independent variables included in all models were number of private and commercial boats, two PCA-generated salmon variables, year, time of day, pod identification. In addition, the Shannon-Weiner Index (H), used as a measure of behavioral diversity, was analyzed in relation to all independent variables listed above.

Results

Sampling

In 2003, subjects were contacted and data were collected on 33 of 69 field days, yielding 333 samples, with a mean sampling rate of 10.09 ± 5.49 samples per contact day. In 2004, data were collected on 33 of 72 field days, resulting in 307 samples, and a mean sampling rate of 9.30 ± 6.62 samples per contact day. For 2005, data were collected on 28 of 53 field days, resulting in 362 samples, and a mean sampling rate of 12.93 ± 6.16 samples per contact day (Total n = 1002).

Analyzing Covariance in Independent Variables

PCA was conducted for catch per unit effort of salmon species on a weekly basis, and varimax rotation with rotated loadings produced two factors (Table 4.2). On Factor 1, pink and coho salmon covaried together, with chinook on the opposite end of the continuum, indicating that when large numbers of coho and pink salmon were caught, very few chinook were caught. Sockeye was identified as an independent variable, as it varied independently from pink, coho, and chinook species.

Finally, PCA was conducted for number of vessels observed during this study on a daily basis. Varimax rotation and rotated loadings yielded the independent factors (Table 4.3). For each factor, there were no vessel types seen to covary significantly with any other vessel. Subsequent analyses incorporated these factor scores for vessel type.

Ecological Analysis of Behavior States

In order to ensure statistical independence of behavior samples, only one sample per hour was utilized in these analyses. In addition, play behavior was excluded from these analyses due to small sample size.

Multiple General Linear Modeling revealed a significant relationship between year and slow travel ($F = 21.037$, df = 2,183, $P < 0.001$; Wilks' Lambda $F = 5.406$, df = 10,358, $P = 0.000$; Figure 4.1). Additionally, pod had a significant relationship between two behavior states, including fast travel ($F = 31.497$, df = 2,183, $P = 0.0452$; Figure 4.2), and rest ($F = 3.691$, df = 2,183, $P = 0.0268$; Wilks'Lambda $F = 2.094$, df = 10,358, $P = 0.0242$; Figure 4.3). Lastly, the Shannon-Weiner Index (H), showed a significant trend with both sockeye salmon abundance (F = 3.1628, df = 1,184, P = 0.076; Figure 4.4) and year (F = 2.8581, df = 1,184, P = 0.0599; Figure 4.5).

Discussion

Principal Components Analysis of Salmon and Vessel Abundance

PCA was performed on salmon abundance data to test for statistical independence, and species were found to cluster into a smaller number of prey categories. Most notably, when coho and pink salmon were more abundant, lesser numbers of chinook salmon were observed. This was reflected in the correlation values obtained in the principal components analyses. Presumably, coho and pink salmon may either be adapted to similar conditions, or may return to the San Juan Island region at similar times. Although coho salmon are most closely related to chinook salmon in terms of genetics (Healey, 1991), coho and pink salmon species may behave more similarly, and therefore were seen to group together in terms of statistical analyses. Results of the salmon PCA also contributed to the interpretation of behavioral data, and provided additional insight into the function of killer whale social behavior. PCA was also performed on the three vessel categories, and analyses showed that commercial, private, and non-motor vessels did not covary, and were therefore considered statistically independent.

Interpretation of Ecological Influences on Behavior States

Results from these analyses indicated that multiple behavior states demonstrated significant relationships with year and pod. In addition, a trend towards significance was found between the Shannon-Weiner Index and sockeye salmon abundance as well as year.

A significant relationship was elucidated between year and slow travel, with significantly more slow travel seen in 2003 than in 2004 or 2005. This observed decrease in slow travel may be attributed to ecological conditions and/or extraneous variables such as shipping traffic and military activities, as these variables differ from year to year, and were not measured in this study.

Additionally, pod was found to have a significant relationship with fast travel as well as rest. Fast travel was found to be significantly different for J pod than for K and L pods, with J pod engaging in this behavior state more than the other two pods. As J pod is more often seen in this region of Washington state , even during fall, winter, and spring seasons (National Marine Fisheries Service, 2006), they may well be more familiar with the habitat, and choose to transit through areas at a faster pace than K and L pod. K pod was found to display more resting behavior than J or L pods in this study, and this observed increase may be related to an energetic demand on this pod, either due to a paucity of prey items and subsequent decreased caloric intake, or even an increase in energy expenditure that may be required while searching for prey items.

Lastly, the Shannon-Weiner Index (H), showed a trend towards significance with both sockeye salmon abundance and year. These results indicated that behavioral diversity may increase in the expanding presence of sockeye salmon, meaning that while some animals engaged in foraging activities, others choose to travel or even rest. This may be a function of prey preference, as sockeye are not considered a substantial prey item for these whales (Ford & Ellis, 2006). As such, not all animals may choose to forage on sockeye, even as this prey item becomes more copious. As for year, the trend towards significance when measuring behavioral diversity may merely be attributed to non-measured, extraneous variables that vary year to year.

In this study, it was hypothesized that there would be a significant relationship between behavior state and vessel abundance, and specifically that rest, forage, and play would decrease as vessel pressure increased due to the potential disruption in both acoustic and physical environments. This hypothesis was not supported, as vessel abundance did not show any visible relationship to behavior state during the three year study. It appears that any effects that vessel abundance may have on this population may indeed be minimal relative to pod differences and annual variability in the environment.

It was additionally postulated that there would be a significant relationship between behavior state and prey abundance, with rest and play showing a tangible decrease as prey abundance increased, since whales most likely would not be engaged in rest or play while foraging or capturing prey items. Again, this hypothesis was not supported in this study, as prey abundance did not show an observable relationship with any behavior state in these killer whales. It is possible that behavior states, as measured at the surface, are a crude indicator of underwater activity in these whales, and as such may not reflect the actual behaviors of individual whales in this population. Another explanation for the lack of relationship between prey and behavior state observed in this study is the behavior of the salmon themselves, and the foraging tactics employed by these whales to catch them. While chinook salmon are considered the preferred prey item for "southern resident" killer whales, they are also one of the least abundant salmonids in the Pacific (Ford & Ellis, 2006), and as such, foraging for this prey item may not occur on a regular basis during data collection hours, or in locales where data collection occurred. It is likely that these killer whales forage on chinook opportunistically when they are available, and not necessarily only in core areas where behavioral data are collected. Furthermore, another plausible explanation for the lack of relationship between prey and behavior state observed in this study is the notion that these whales may not be food limited. Although strong correlations have been demonstrated between chinook salmon abundance and the observed population decline in "resident" killer whales (Ford, Ellis, & Olesiuk, 2005), this population of killer whales may currently have enough prey available to them to meet their energetic requirements, and as such we would not expect to see a relationship between chinook salmon abundance and behavior state.

Lastly, it was hypothesized that the Shannon-Weiner Index (H) would not show a relationship with behavior state, as these whales show strong bonds and social cohesion, and therefore should most often engage in the same behavior state. This hypothesis was supported in this study, although several significant trends were found, suggesting a relationship may exist between this index and sockeye salmon, as well as year. As explained previously, sockeye salmon is not considered a preferred prey item for these whales (Ford & Ellis, 2006), and as such not all whales may choose to forage on sockeye salmon, even if readily available. This discrepancy would yield a higher H value in the presence of sockeye salmon, and this was demonstrated in the significant trend found during this study. As for the trend towards significance found between year of study and H, this could be attributed to not only extraneous variables including military activity and shipping traffic, but possibly prey distribution and density, as well as yearly fluctuations in vessel and other human activities.

Conclusions

In this study, principal components analyses provided unique insight into relationships among salmon species in the inshore waters of Washington State, and additionally served to demonstrate statistical independence between vessel categories. Results from these analyses indicated that behavior states including slow and fast travel, as well as rest, showed significant relationships with variables including year and pod. In addition, a trend towards significance was found between the Shannon-Weiner Index and sockeye salmon abundance as well as year. Although found to be significant, the observed differences in behavior states among year and pod may not translate to biological significance for these animals, as they inhabit an environment that is fluid and continuously changing. Their capacity to adapt to this environment on a regular basis, be it daily, weekly, or yearly, speaks to their complex cognitive abilities. Future studies should address the significant differences in behavior state observed under different ecological conditions, and subsequently attempt to translate results into energetic requirements for this endangered species in order to inform conservation policies on this population.

Table 4.1. Definitions of behavior states utilized in the current study.

State	Definition
Rest	Swimming at speeds of less than approximately 2 knots, often with respiratory synchrony and tight associations (Rose, 1992).
Slow Travel	Movement at a slow pace of approximately ≤ 6 knots, often with coordination of entire group.
Fast Travel	Movement at a fast pace of approximately ≥ 7 knots, often with coordination of entire group.
Forage	Searching and/or locating food indicated by arch dives, non-directional swimming, and lunges at the surface.
Play	Interacting with objects including trailing the dorsal fin with kelp or riding the stern/bow wave of a boat.

Table 4.2. Rotated loadings for two factors using varimax rotation in principal components analysis of salmon species.

Salmon species	Factor 1	Factor 2
CPU chinook	-0.7760	-0.1353
CPU coho	**0.6294**	-0.5124
CPU pink	**0.6079**	0.0105
CPU sockeye	0.1237	**0.9193**
Variance (Eigenvalues)	**1.3831**	**1.1259**
% of the Total Variance Explained	**34.58%**	**28.15%**

Table 4.3. Rotated loadings for two factors using varimax rotation in principal components analysis of vessel type.

Vessel Type	Factor 1	Factor 2	Factor 3
Private vessel	**0.966**	0.086	0.242
Non-motor vessel	0.081	**0.992**	0.092
Commercial vessel	0.244	0.099	**0.965**
Variance (Eigenvalues)	**0.999**	**1.002**	**0.998**
% of the Total Variance Explained	**33.32%**	**33.41%**	**33.27**

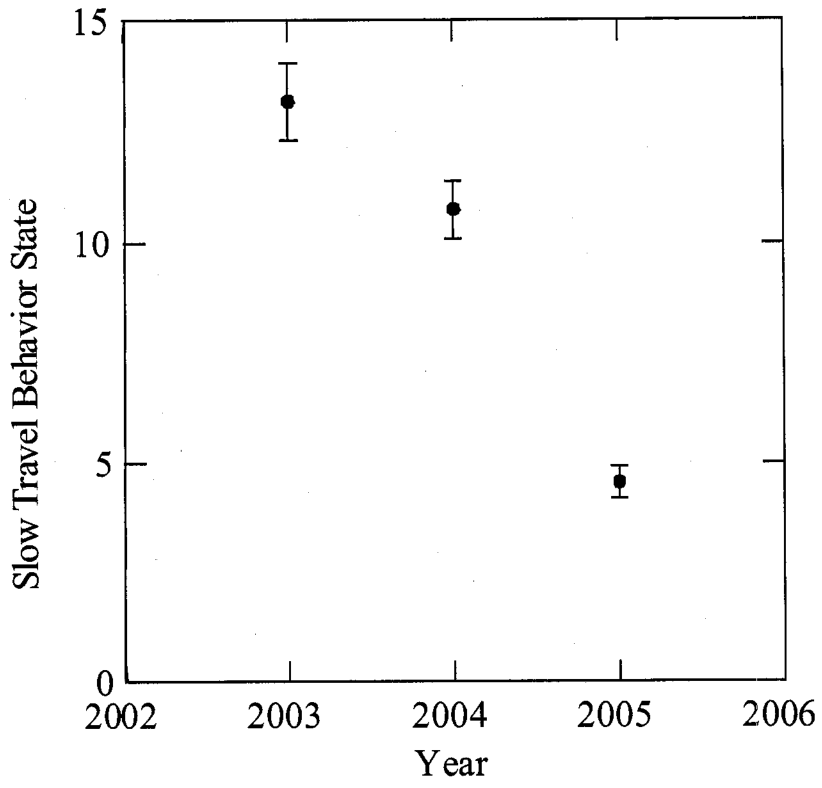

Figure 4.1. Relationship between year and slow travel behavior.

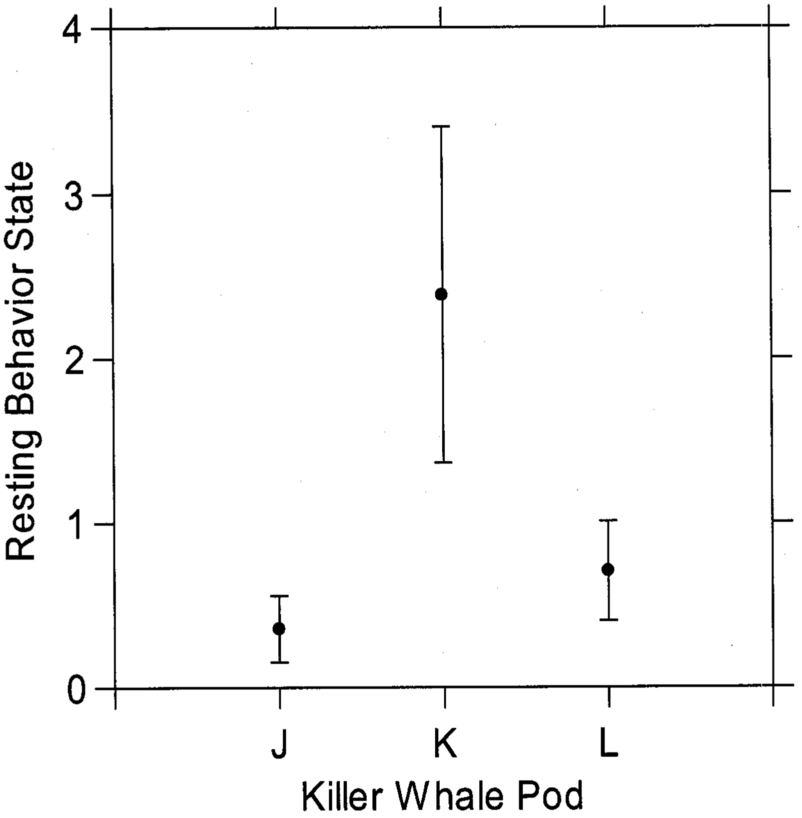

Figure 4.2. Relationship between killer whale pod and rest behavior.

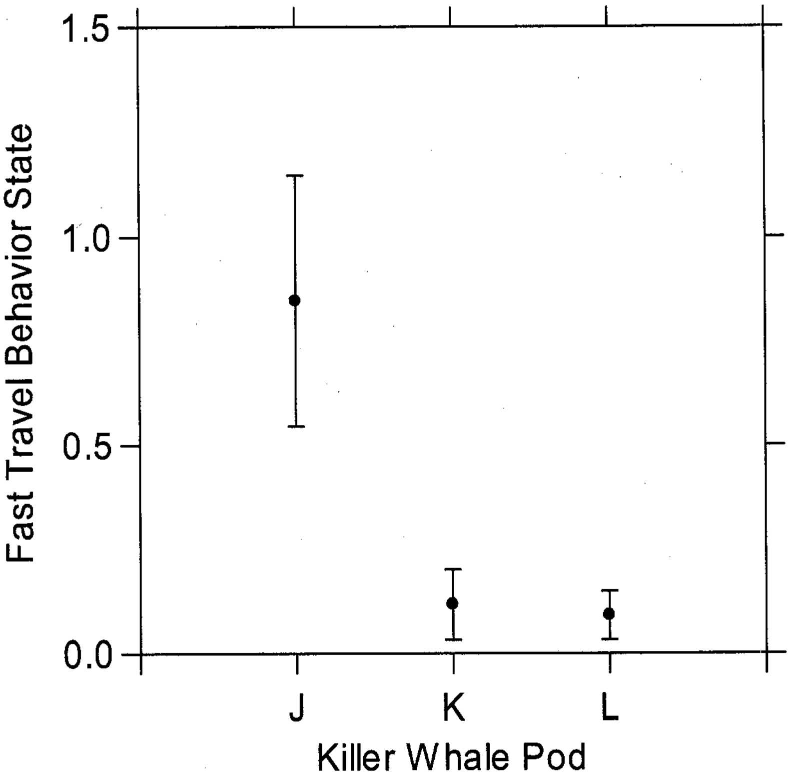

Figure 4.3. Relationship between killer whale pod and fast travel.

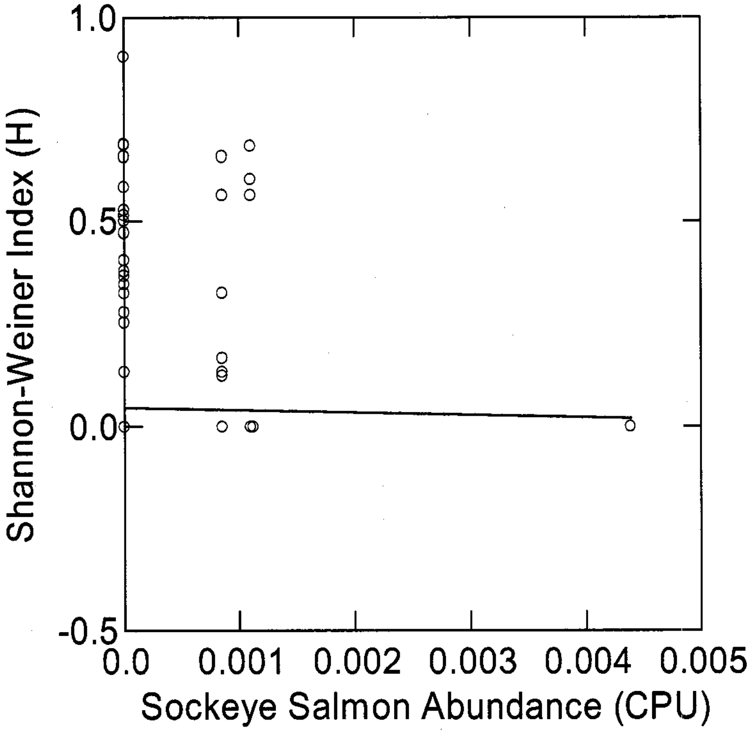

Figure 4.4. Relationship between sockeye salmon abundance and the Shannon-Weiner Index (H). Units for sockeye salmon abundance is catch per unit effort.

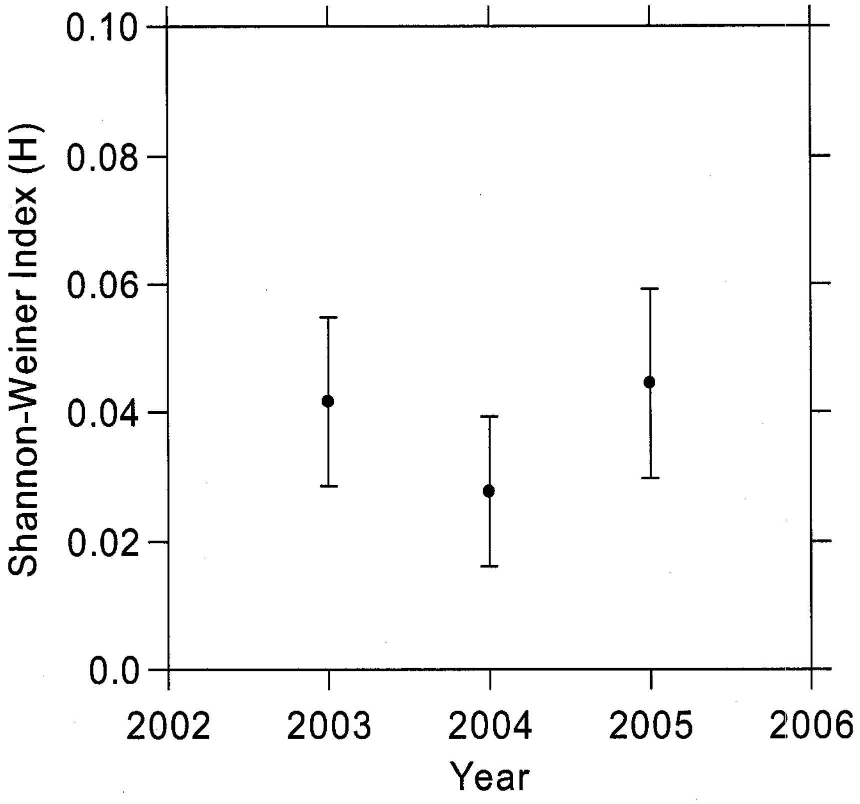

Figure 4.5. Relationship between year and the Shannon-Weiner Index (H).

Chapter 5: Summary and Conclusions

In this study, it was hypothesized that in “southern resident” killer whales, social behavior as well as behavior state would vary with whale-watching pressure, salmon abundance, and several additional ecological variables including time of day, year, pod identification, and group size. Hypotheses were generated not only by reviewing literature on social behavior, but from *ad libetum* sampling during field observations, and by analysis of historical patterns of behavior in these killer whales.

Preliminary analyses of association patterns between “southern resident” killer whales showed a decrease over a 15-year period from 1987 - 2001 in all three pods. These association levels were subsequently found to be significantly related to numbers of whale watching boats for all pods during that period, and it was also found that for L pod, mean coefficient of association values increased as chinook salmon abundance increased. This analysis offered insights into factors affecting killer whale social structure, and provided additional information from which more specific hypotheses were generated.

In the current study, ecological variables were examined in relation to social behavior and behavior states in “southern resident” killer whales over a three-year period. Research was conducted off the inshore waters of Washington State, and behavioral data were collected from a boat-based observation platform. Statistical methods, including principal components analysis, played an important role in reducing a large number of behaviors into a smaller number of statistically independent categories, which provided insight not only into the functionality of behaviors, but also into their contextual relevance as well. This type of analysis also provided unique insight into relationships among salmon species in the inshore waters of Washington State and British Columbia, and additionally served to demonstrate statistical independence between vessel categories. In examining social behaviors, analyses indicated that synchronous surfacing between whales was significantly affected by sockeye salmon, with less synchronous surfacing occurring when sockeye were more abundant, suggesting that when whales were foraging, they were spending less time swimming and breathing in synchrony. Furthermore, cartwheels and breaches were significantly affected by time of day, with more of these behaviors seen during mid-day, presumably because human activities are often at their peak during those hours, and whales may be using these behaviors as a warning signal to conspecifics or vessels. Physical contact and spyhops were found to be significantly affected by commercial vessels, as these behaviors increased in the presence of intensifying commercial vessel abundance. As spyhops and contact were posited to be information gathering and subsequent reassurance behaviors, commercial vessels may present a perceived threat to these animals in terms of both noise and size, and whales may therefore produce a higher quantity of these behaviors in their presence. As analyses were completed, complex subtleties emerged from these behavioral data indicating that killer whale social behaviors are indeed affected not only by multiple ecological variables including salmon abundance and the presence of commercial vessel traffic, but that some of these behaviors vary significantly among pod, time of day, and year.

Additionally, behavior states were also examined in this study over the three-year period from 2003-2005. Behavioral categories including rest, slow travel, fast travel, forage, and play were documented for each killer whale visible at the surface during a predetermined interval using scan sampling techniques. Analyses indicated a significant relationship between year and slow travel, with significantly more slow travel seen in 2003 than in 2004 or 2005. This observed decrease in slow travel was attributed to differing ecological conditions and/or extraneous variables such as shipping traffic and military activities, that were not measured in this study. Fast travel was found to be significantly different for J pod than for K and L pods, with J pod engaging in fast travel more often than the other two pods. As J pod is more often seen in this region of Washington, the authors suggested that habitat familiarity may affect the speed with which J pod transits through the area. Furthermore, a significant relationship between pod and rest was also documented, with K pod found to engage in more resting behavior than J and L pods. The greater amount of resting behavior observed in K pod may be related to an energetic demand on this pod, either due to a paucity of prey items and subsequent decreasing caloric intake, or increase in energy expenditure that may be required while searching for prey items. Results from this analysis indicated that multiple behavior states were divergent among pod and across year, and that behavioral diversity may differ across year and in the presence of prey as well. Contrary to predictions set forth by the authors prior to this study, vessel abundance did not show a relationship with behavior states. It appears that any effects that vessel abundance may have on this population may indeed be minimal relative to pod differences and annual variability in the environment. Future studies should address the significant differences in behavior state observed under different ecological conditions, and subsequently attempt to translate results into energetic requirements for this endangered species in order to inform conservation policies on this population.

In my opinion, it is imperative that ecological variables be examined in relation to social behavior in an endangered species such as this population of "southern resident" killer whales, and that results be applied to conservation efforts. As key "southern resident" killer whale habitats are determined, specific attention should be paid to areas where social behavior may be concentrated. This spatial-based approach to management may be the best way to protect this endangered population, and it is my hope that results from this study will contribute to such an approach. As social behavior is a biologically important aspect of killer whale life, studies of social behavior should not be ignored when making policies to protect these animals. It is only by conducting thorough, methodical, intensive research that useful information will be generated for practical use by policy-makers and scientists alike.

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CURRICULUM VITA

Jennifer Anne Marsh

ACADEMIC BACKGROUND

2001-2008	Doctor of Philosophy, Animal Behavior Area, Department of Psychology, University of Washington. Title: Social Behavior and Ecology of "Southern Resident" killer whales (*Orcinus orca*)
1997 – 2000	Master of Science, Interdisciplinary Studies, Animal Behavior, San Diego State University. Title: School characteristics and social affiliation patterns of California bottlenose dolphins (*Tursiops truncatus)*
1988–1992	Bachelor of Science, Biology, California Lutheran University

PROFESSIONAL EXPERIENCE

Fall 2001-Fall 2002	Teaching Assistant, Department of Psychology, University of Washington Courses: Fundamentals of Psychological Research (Psych 209), Animal Behavior (Psych 200)
Fall 2003	Teaching Assistant, Department of Psychology, University of Washington. Course: Fundamentals of Psychological Research (Psych 209)
Fall 2004	Teaching Assistant, Department of Psychology, University of Washington. Course: Fundamentals of Psychological Research (Psych 209)
Fall 2005-Winter 2006	Teaching Assistant, Department of Psychology, University of Washington. Course: Laboratory in Animal Behavior (Psych 330)
Fall 2006-Spring 2007	Teaching Assistant, Department of Psychology, University of Washington. Courses: Animal Behavior (Psych 300), Understanding Statistics in Psychology (Psych 315), Fundamentals of Psychology Research (Psych 209)
Spring 2008 (present)	Instructor, Department of Life and Physical Sciences, Allan Hancock College, Human Physiology

RESEARCH SKILLS

1997-2000	Photo-identification of bottlenose dolphins, land-based behavioral data collection, boat driving/handling, research team management
2002-2005	Photo-identification of killer whales, boat-based behavioral data collection using Palm III *xe*, boat driving/handling, research team management

HONORS, GRANTS AND AWARDS

1988	Presidential Scholarship, California Lutheran University
1990	Thouren Biological Scholarship, California Lutheran University
2001	Humane Society of the United States Research Grant ($500)
2002	Cetacean Society International Research Grant ($500)
	Ford Foundation Predoctoral Fellowship for Minorities ($48,000)
2003	Bolles Fund University of Washington ($800)
2003	National Marine Fisheries Service grant for "Social Behavior and Affiliation Patterns in Southern Resident Killer Whales (*Orcinus orca*)" ($16,000) Total award period covered: 07/17/03 – 08/30/03
2004	National Marine Fisheries Service grant for "Social Behavior and Affiliation Patterns in Southern Resident Killer Whales (*Orcinus orca*)": Year 2, Competitive Renewal ($35,000)
2004	Sigma Xi Grants in Aid of Research, University of Washington ($500)
2005	National Marine Fisheries Service grant for "Social Behavior and Affiliation Patterns in Southern Resident Killer Whales (*Orcinus orca*)" Year 3, Competitive Renewal ($35,000)
2007	Alcor Fellowship ($4,310)

PAPERS

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UNPUBLISHED PRESENTATIONS

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Marsh, J. A. & Ha, J.C. 2003. Historical patterns of affiliation in southern resident killer whales (*Orcinus orca*). Abstract submitted to the Animal Behavior Society Conference. Boise, ID.

AFFILIATIONS

Member, Animal Behavior Society
Member, American Cetacean Society
Member, Sigma Xi
Member, Society for Marine Mammalogy