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

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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 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 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 $\leq$ 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 and 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**

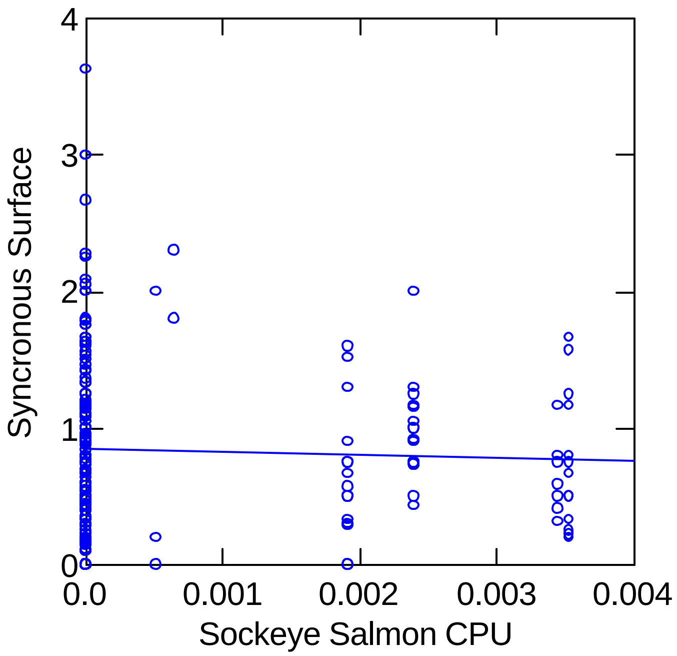

Figure 3.1. Relationship between synchronous surface behavior and sockeye salmon abundance in catch per unit effort. Units for synchronous surfacing is rate per individual whale.

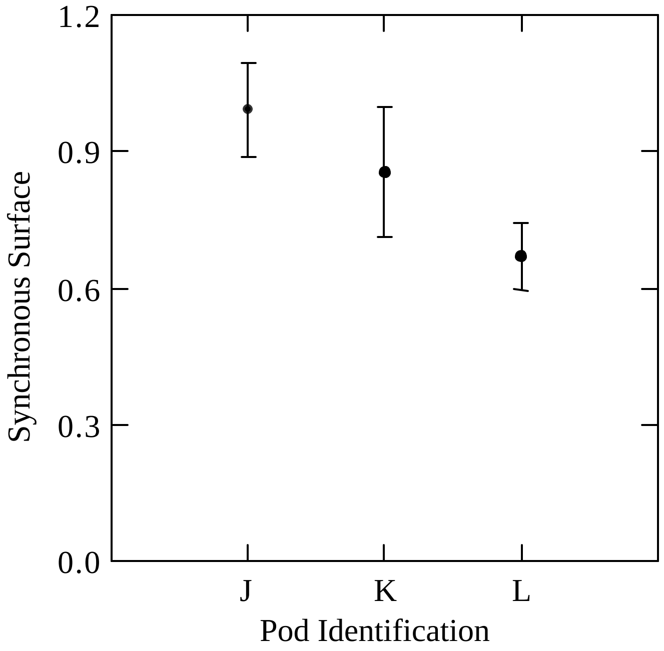

Figure 3.2. Relationship between synchronous surface behavior and pod. Units for synchronous surfacing is rate per individual whale.

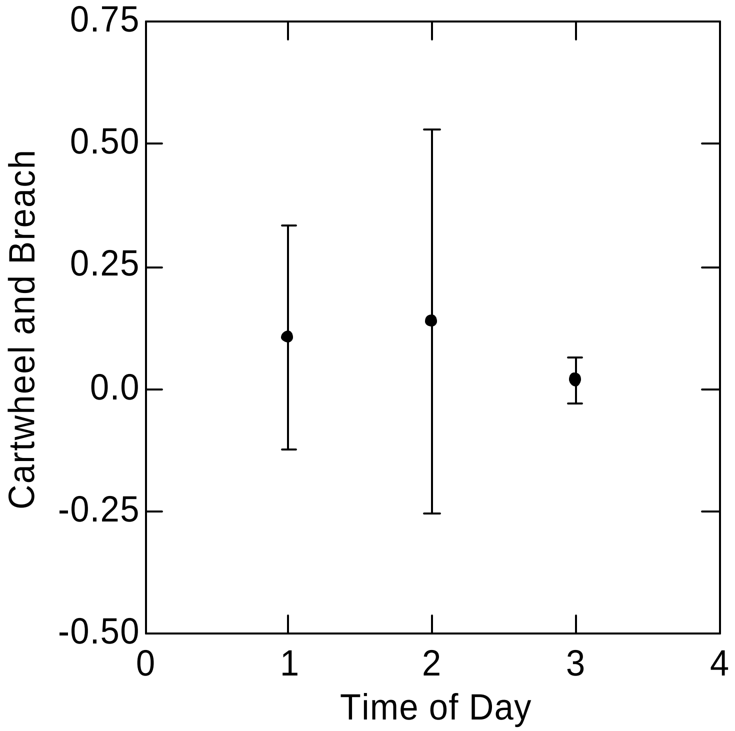

Figure 3.3. Relationship between cartwheel/breach and time of day. Units for cartwheels and breaches are rate per individual whale. Time of day was categorized as 0600 – 1000 (1), 1000 – 1400 (2), or 1400 – 1600 (3).

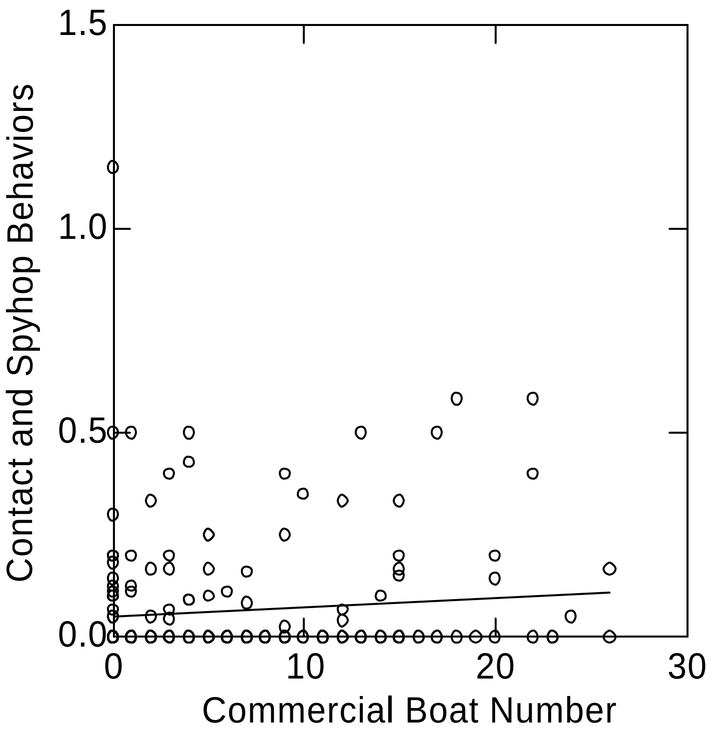

Figure 3.4. Relationship between commercial boats and contact and spyhop behaviors. Units for contact and spyhops are rate per individual whale.

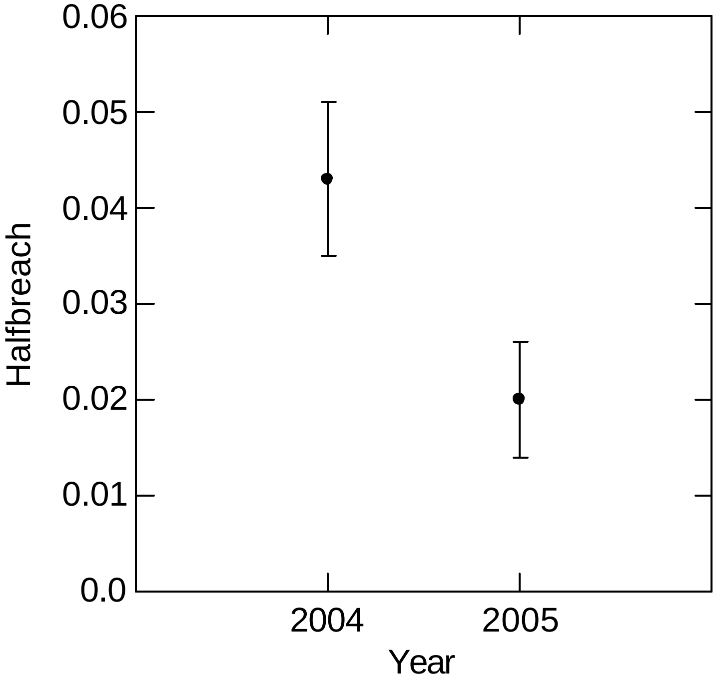

Figure 3.5. Relationship between half-breach and year. Units for half-breach is rate per individual whale.