# EFFECTS OF VESSELS ON BEHAVIOR OF SOUTHERN RESIDENT KILLER WHALES (ORCINUS SPP.) 2003-2005 

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#### Abstract

Vessel traffic may have contributed to Southern Resident Killer Whales becoming endangered. To determine the importance of this threat, we measured behavior of Southern Residents in the presence and absence of vessels in 2003-2005 at two different sites along San Juan Island. Data collected include: theodolite tracks of focal individuals, along with observations of their behavior; and scan sampling of activity states of subgroups, along with counts of vessels at various distances from each subgroup. Theodolite tracks were summarized in terms of directness and deviation indices, and travel speed. Rates of respiration and display behaviors were also determined for each focal sample. Vessel number and distance were used as candidate explanatory variables for differences in track indices and other behavior, along with natural factors such as sex, age, pod membership, time of day, time of year, geographic location, current and tide height. As with Northern Residents, directness index decreased significantly in the presence of vessels, and varied with number of vessels and distance to vessels. This increase in distance traveled in the presence of vessels would result in increased energy expenditure relative to whales that can rest while waiting for affected whales to catch up. The likelihood of surface active behavior increased significantly in the presence of vessels, and both rates and likelihood varied with number of vessels. Respiratory intervals increased significantly in the presence of vessels, and varied with number of vessels. Deviation index varied with number of vessels and distance to the nearest vessel. Swimming speed varied with number of vessels. Transitions between activity states were significantly affected by vessel traffic, indicating a reduction in time spent foraging as was observed in Northern Residents. If reduced foraging effort results in reduced prey capture, this would result in decreased energy acquisition. Each subgroup was within 400 m of a vessel most of the time during daylight hours from May through September. The high proportion of time Southern Resident Killer Whales spend in proximity to vessels raises the possibility that the short-term behavioral changes reported here may lead to biologically significant consequences.


## INTRODUCTION

The Eastern North Pacific Southern Resident Stock of killer whales declined to fewer than 80 individuals in 2001, resulting in their listing as "Depleted" under the Marine Mammal Protection Act and "Endangered" under the U. S. and Washington State Endangered Species Acts, and Canada's Species at Risk Act. The causes of this decline are uncertain, but many scientists consider a combination of reduction in prey resources, toxic chemicals, disturbance from vessel traffic, and other factors to have contributed (Bain et al. 2002, Wiles 2004, Krahn et al. 2002 and 2004, Federal Register 2004 and 2005, Killer Whale Recovery Team 2005).

Krahn et al. (2004) noted that the Southern Resident killer whale population increased at a normal rate in the late 1980's ( $\sim 3 \%$ / year). Growth began to slow in the early 1990's and was followed by a decline of $20 \%$ from 1996 to 2001. J and K pods exhibited little change in number during this period, in contrast to the expected growth. L Pod not only failed to grow, but it
declined and this decline resulted in the decline in number of the entire population. Factors in the inshore waters of Washington and British Columbia, such as declines in prey abundance, toxins and vessel traffic may be responsible for the lack of growth in all three pods. Differences in usage patterns of the inshore waters among the different pods (Bigg et. al 1990, Olesiuk et al. 1990, Osborne 1999, Hauser et al. 2005 and 2006) may account for some of the additional decline experienced by L Pod alone, but factors external to these waters (regional differences in prey abundance [Protected Resources Division 2004], and perhaps entanglement, exposure to oil, etc.) are likely to be of similar importance to factors in inshore waters.

Vessel traffic may have contributed to the decline through a variety of mechanisms. Collisions between vessels and killer whales occur occasionally in residents and other killer whales and result in injury or death (Visser 1999, Ford et al. 2000, G. M. Ellis pers. comm.). One collision was observed in Southern Residents in 2005 that resulted in injury (K. C. Balcomb pers. comm.). Chemicals such as unburned fuel and exhaust may contribute to toxin load. The presence of noise from vessels may contribute to stress (Romano et al. 2004). Noise from vessel traffic may mask echolocation signals (Bain and Dahlheim 1994) reducing foraging efficiency. Behavioral responses may result in increased energy expenditure, or disrupt feeding activity, which may reduce energy acquisition (Bain 2002, Bain et al. unpublished ms). Energetic mechanisms for impact are of particular concern, since Southern Resident Killer Whales may be food limited (Ford et al. 2005).

It stands to reason that repeated disturbance of wild animals could be implicated as a factor reducing the quality of life, foraging efficiency, fitness, or reproductive success of individual animals. Examples in the wildlife literature link anthropogenic disturbance to changes in foraging behavior (e.g., Galicia and Baldassarre 1997), reproductive success (e.g., Safina and Burger 1983), and mating system and social structure (e.g., Lacy and Martins 2003). These in turn, either singly or synergistically, could influence population dynamics (Bain et al. unpublished ms.).

Effects of vessel traffic have been studied in a range of cetacean species, including Cephalorhynchus: Bejder et al. (1999); Delphinus: Constantine (1997); Eschrichtius: Jones (1988), Duffus et al. (1998); Globicephala: Heimlich-Boran (1993), Heimlich-Boran et al. (1994); Megaptera: Corkeron (1995); Orcinus: Kruse (1991), Williams et al. (2002ab), Foote et al. (2004); Physeter: Fleming and Sarvas (1999); Sousa:Van Parijs and Corkeron (2001); Stenella: Angradi et al. (1993), Ritter (2003); Tursiops: Janik (1996), Allen and Read (2000), Nowacek et al. (2001), Constantine (2001), Yazdi (2005), Bejder et al. (in press); and Ziphius: Ritter (2003). Effects vary within and between species, and included changes in respiration patterns, surface active behaviors, swimming velocity, vocal behavior, activity state, interindividual spacing, wake riding, approach and avoidance, and displacement from habitat. Collisions may result in injury or death (Wells and Scott 1997, Laist et al. 2001). More detailed reviews of vessel effects can be found in Lien (2001) and Ritter (2003).

Kruse (1991) and Williams et al. (2002ab) demonstrated short-term behavioral changes in Northern Resident killer whales associated with vessel traffic. Kruse (1991) found Northern Residents increased swimming speed as vessel number increased. Nowacek et al. (2001) found Tursiops also increased swimming speed in the presence of vessels. Williams et al. (2002ab) found Northern Residents swam in less predictable paths in the presence of vessels, and Tursiops exhibit similar behavior (Nowacek et al. 2001). Williams et al. (2006) found Northern Residents
were less likely to forage in the presence vessels, and Tursiops exhibit the same change in parts of their range (Allen and Read 2000). Adimey (1995) found percussive behavior of Northern Residents was inhibited in the presence of vessels, though Williams et al. (2002ab) found no significant differences. However, for Southern Resident killer whales in the waters of Washington and British Columbia, even subtle behavioral responses to boats have not been reported in the primary literature. This is a critical area of study because the San Juan and Gulf Islands are a region with high vessel traffic.

In this region, the commercial whale watching day runs from about 0900-2100 in summer, and until sunset in spring and early fall. In addition to commercial whale watching vessels, other vessels are also in contact with whales throughout the day. Early in the morning (sunrise), whales are approached by recreational vessels transiting the area, scientific research vessels, and sport fishing vessels. For part of the season, seiners and gill netters are also present. In the middle of the day, these boats are joined by the commercial whale watching fleet, and a few of these commercial whale watching vessels remain with whales until near sunset.
Homeland security vessels are on the water much of the day, and sometimes approach whales or vessels near whales (pers. obs.). Further, commercial freight traffic is intermittently present 24 hours a day. Due to the variety of vessels observed in the presence of whales, the term whale watching as used in this paper refers to all whale-oriented vessel traffic, regardless of whether the vessels are commercial whale watching vessels or not. Because these whales are in the presence of vessels, including those not focused on whale watching, during much of the day, the potential for cumulative effects makes it important to investigate whether the behavior of killer whales is altered in the presence of vessels (Bain et al. 2006). This study addresses relationships between vessel activity and Southern Resident killer whale behavior.

## METHODS

## Study areas

From 28 July to 30 September 2003, 1 May to 31 August 2004, and 15 May to 31 July 2005, a land-based team of observers monitored behavior of whales and activity of boats from two study sites (Figure 1). One site (hereafter referred to as the North Site) was located at $48^{\circ} 30.561^{\prime} \mathrm{N}, 123^{\circ} 8.494^{\prime} \mathrm{W}$ at an altitude of approximately 99 m above mean lower low water. This site was chosen because its height offered an expansive and unobstructed view of the central and southwestern portions of Haro Strait, whales were known to pass it frequently while traveling close to shore, and it was located adjacent to the voluntary no-boat zone at Lime Kiln State Park.

The other (South) site was located at Mt. Finlayson, near the southeast tip of San Juan Island. The South site was located at Mt. Finlayson ( $48^{\circ} 27.421^{\prime} \mathrm{N}, 122^{\circ} 59.401^{\prime} \mathrm{W}$ ) at a height of 72 m and the view of the eastern portion of Juan de Fuca Strait was unobstructed. Further, whales have been reported to use this area heavily for foraging, whereas the North site appeared to be used primarily for travel and socializing (Felleman et al. 1991, Hoelzel 1993, HeimlichBoran 1988). Together, these sites were chosen to maximize sample size and to allow the behavioral observations to include the entire repertoire of the population.


Figure 1. The study area, with the North and South theodolite sites marked with stars.

## Research Teams

The team worked for 60 of 64 days in the summer of 2003. In total, 412 hours were spent searching for whales, or monitoring their behavior. Of these 60 days of research effort, whales were present on 38 days and absent on 22 days, or data were lost due to inclement weather (rain, fog, or Beaufort sea state 3 while whales were present). The team worked 6 days a week in May of 2004. From June through August 2004, the group divided into two teams to allow data collection every day. However, effort varied with 8 hours a day effort on three days of the week, 12 hours a day two days a week, and 14 hours a day the other two days a week. Data were obtained on 60 of 118 days in 2004. The team worked on 60 of 78 days in 2005 and obtained data on 30 days. For the three seasons combined, data were obtained on 128 days over approximately nine months in the field.

The study design involved two simultaneous data collection protocols. One observer collected broad-scale samples of the activities of all whales in the study area at 15 -minute intervals. The rest of the team collected fine-scale, continuous, observations of a focal animal. The two methods will be referred to subsequently as scan-sampling and theodolite tracking respectively, and are described in greater detail below. In 2003 and 2005, the team worked from 6 a.m. until 10 a.m., and then worked on an on-call basis daily until approximately 6 p.m. The exact timing of the research schedule was modified on an ad hoc basis from one day to the next, based on a combination of reports from monitoring of VHF commercial traffic and the local sighting network and weather conditions, in order to maximize time spent observing whales in the absence of boats. In 2004, the research day was extended from 6 a.m. until 8 p.m., although the number of individuals working varied from three to six, and not all hours were covered every day.

## Collection of scan-sampling data from focal groups

Scan sampling was conducted at 15 minute intervals to characterize subgroup size (ranging from one to the size of the school in the study area), activity state, and the number of vessels within 100, 400 and 1000 meters. Vessels were counted separately depending on whether or not they were engaged in whale watching, although commercial and recreational whale watching boats were not distinguished in scan sample counts. Distances were estimated by eye, and checked against measurements with a theodolite when possible to improve observer reliability with experience. Sequential observation of focal groups allows modeling the probability of animals' switching from one coarse activity state to another as a function of vessel traffic. This aspect of the study complements the fine-scale focal animal studies by including all age-sex classes, and all activity states.

A scanned group was defined as animals within 10 body lengths of one another at the time of a scan-sample observation, using a chain rule. That is, each individual was within 10 body lengths (approximately $80-100 \mathrm{~m}$ ) of another individual in the group, but large groups could extend over 100 's of meters. Thus, our subsequent use of the terms group or school implies nothing about the relatedness of animals within a group and whether all group members were engaged in the same behavior. Similarly, scanned groups could be of size one. Group membership was recorded for each identifiable individual. When individuals were too far away to be identified, their identity was assigned to categories based on size (e.g., calf, juvenile, medium sized whales [large juveniles or adult females], subadult male, adult male). When group composition remained unambiguous over time, but individual identity was unknown within the group, groups were given arbitrary labels ( $\mathrm{a}, \mathrm{b}, \mathrm{c} \ldots$ ) in order to track their activity over time.

The activity of the scanned group was recorded every 15 minutes using the following definitions: The sub-categories (1-9) could be combined to either match the categories described by Ford et al. (2000) as was done here, or those of Smith and Bain (2002) and Waite (1988).

Rest: characterized by prolonged surfacing in contrast to the rolling motion typically observed during travel

1. Deep rest, hanging, logging: whales do not progress through the water
2. Resting travel, slow travel: whales progress through the water, although they may not make forward progress over the ground.

Travel: characterized by a rolling motion at the surface, progress through the water, and membership in a subgroup of more than four individuals
3. Moderate travel, medium travel: travel in which whales do not porpoise
4. Fast travel: travel which includes porpoising

Forage: characterized by progress through the water by lone individuals or while a member of a subgroup of four or fewer individuals
5. Dispersed travel: foraging in a directional manner
6. Milling, feeding, pursuit of prey: foraging involving changes in direction

Socialize: interaction with other whales, or other species in a non predator-prey context
7. Tactile interactions: socializing that involves touching another whale, such as petting or nudging
8. Display: socializing that does not involve touching, but may include behaviors such as spy hops, tail slaps and breaches

Object play: tactile interaction with an object such as kelp, wood or fish (in a manner not related to feeding)
9. Kelping, object play: (when kelping also involved tactile interaction, it was counted as tactile interaction rather than object play.)

These definitions are shown in "dimensional" format (Ha 2004) in Table 1. A subgroup size dimension was added, as it formed part of the operational distinction between states 3 and 5 . These definitions are the product of a workshop attended by experienced killer whale observers and are intended to standardize definitions and allow comparison between studies. Workshop participants recognized that observers may not be able to record all aspects of behavior. Thus some dimensions of behavior are not listed in the table and data on those aspects of behavior were not recorded (e.g., orientation, acoustics), while other aspects of behavior were recorded, although they did not distinguish among behavior states (e.g., respiration). While the relationship between respiration rate and activity states were not analyzed for this report, the data could be applied to energetic studies addressing activity state, respiration rate, and swimming speed (e.g., Kriete 1995), and the table helps identify the suitability of the data for other purposes. Further, studies focusing on other events (e.g., prey capture, Hanson et al. 2006) could be used to assess the appropriateness of the definitions used here (e.g., for foraging).

Table 1. Activity state definitions using the dimensional system. All behavior states could consist of any orientation of individuals, degree of respiratory synchrony, acoustic behavior, and respiration rate, so these dimensions are not shown in the table. Distinctive characteristics of behavior states are highlighted with bold type.

| State | Directionality | Interindividual Distance | Speed | Events | Time | Subgroup Size |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | N/A | $>0$ | motionless | Respiration only | $\begin{aligned} & \hline>=1 \\ & \text { surfacing } \end{aligned}$ | Any |
| 2 | Directional | >0 | Slow | Respiration only | $\begin{aligned} & \hline>=1 \\ & \text { surfacing } \\ & \hline \end{aligned}$ | Any |
| 3 | Directional | $>0$ | Medium | Respiration only | $\begin{aligned} & \hline>=1 \\ & \text { surfacing } \end{aligned}$ | >4 |
| 4 | Directional | $>0$ | Fast, Porpoising | Respiration, porpoising | $\begin{aligned} & >=1 \\ & \text { surfacing } \end{aligned}$ | Any |
| 5 | Directional | $>0$ | Medium | Respiration only | $\begin{array}{\|l\|} \hline>=1 \\ \text { surfacing } \end{array}$ | < $=4$ |
| 6 | NonDirectional | $>0$ | Medium, Fast | Any | $>=2$ <br> surfacings | Any |
| 7 | Any | Contact | Any | Any | $\begin{aligned} & >=1 \\ & \text { surfacing } \end{aligned}$ | $>=2$ |
| 8 | Any | $>0$ | Any | At least Percussive, fluke displays, or spy hops, No objects | $\begin{aligned} & >=1 \\ & \text { surfacing } \end{aligned}$ | Any |
| 9 | Any | $>0$ | Any | At least contact with objects | $\begin{aligned} & \hline>=1 \\ & \text { surfacing } \end{aligned}$ | Any |

## Analysis of scan-sampling data from focal groups

We sampled behavior every 15 minutes, allowing us both to consider current behavior and how behavior changed over 15 minute intervals. This additional information is rarely tapped into, yet it lends itself very well to impact studies because it allows one to directly assess what the likelihood is for animals to go from one state to another depending on the occurrence of a potential impact between two samples. Understanding the recurrence of activity states allows one therefore to understand the likelihood that a state will be disrupted by, in our case, boat presence. The data were divided into a series of scan samples of a focal group which were treated as samples of activity state sequences. A sequence stopped when sampling stopped on a given day or when a focal group ceased to exist due to changes in group membership (through fission or fusion with other individuals), or because they left the study area. For the purposes of this study, we were only interested in understanding the change in the likelihood that when a group was in State A that they would be in State B 15 minutes later (i.e., at the next scan). These are called first-order transitions in activity. This sequence of discrete time samples could be treated as a Markov chain (Lusseau 2003, 2004) because it was ergodic. A time series is ergodic when transitions between all states are possible; in this study a group could transition from any state to another (there was no biological constraint preventing whales from switching between each state and the others). The other requirement for a time series to be ergodic is that there cannot be negative values for transition probabilities; since the sequence was bounded by time, sequences could only move in one way; that is forward in time, and therefore no negative values could be expected. Since we were scan sampling, it was possible for additional transitions to occur between scans, but such transitions went undocumented.

To understand the effect of boat interactions on the state transitions, the number of vessels in the field of view was counted, as these vessels may have contributed to ambient noise in the area (Bain, pers. obs.). The number of vessels within $100 \mathrm{~m}, 400 \mathrm{~m}$, and 1000 m of subgroups were also counted. In 2005, counts of vessels within 200 m were also recorded, but the sample from the single field season was too small for analysis. Distances were estimated visually as range rings around individuals or groups, but checked with a theodolite when possible. When the measured distance varied from the boundary distance (the boundaries marking the 100,400 or 1000 m range rings) by more than $10 \%$, observers consistently placed the vessel in the correct range ring. The numbers within specific distances were used as candidate explanatory covariates, to assess whether the probability of animals switching among activity states varied as a function of boat traffic.

We therefore constructed a transition matrix, representing the probabilities for whales to be observed in a State $i$ at time $t$ and subsequently in State $j$ at the next sampling event $(\mathrm{t}+15$ minutes):

$$
\mathrm{p}_{\mathrm{ij}}=\frac{\mathrm{e}_{\mathrm{ij}}}{\sum_{\mathrm{k}} \mathrm{e}_{\mathrm{ik}}} \text { where } \mathrm{e}_{\mathrm{ij}} \text { is the total number of times the transition was observed and } \sum_{\mathrm{k}} \mathrm{e}_{\mathrm{ik}} \text { is }
$$

the total number of time State $i$ was observed as the starting state.
This transition matrix is based on an ergodic time series which means that eigenanalysis of this matrix reveals several properties of activity states. Applying the Perron-Frobenius theorem
we show that the transition matrix long-term behavior, i.e., the amount of time that the whales spent in each activity state can be approximated by the left eigenvector of the dominant eigenvalue of the matrix (Lusseau 2003). Ultimately, this approach can be used to calculate stable, unbiased time-activity budgets. Further, reliance on transitions rather than individual scans helped control for possible effects of whale behavior on vessel behavior.

We were able to explore the effects of several parameters on the likelihood to go from one state to another (Lusseau 2003). We used log-linear analysis, LLA (SPSS algorithm), to test whether Site (North/South), Year (2003/2004/2005), Pod (J, K and L), or Vessel Traffic (boat present/absent within 100, 400 and 1000 m ) affected transitions in activity states, which was the likelihood that focal groups went from a preceding behavior (state at time $t$ ) to a succeeding behavior (state at time $t+15 \mathrm{~min}$.). Log-linear analyses can be thought of as generalized linear models for count data.

In a simple case in which we only have three independent variables (for example: Boat presence, Preceding behavior, and Succeeding behavior), we can assess the three-way effect by comparing the model containing all two-way effects (Preceding behavior by Succeeding behavior, Preceding behavior by Boat presence, Succeeding behavior by Boat presence) to the fully saturated model. This three-way interaction corresponds to the effect of boat presence on the state transition. In each case, the only difference between a candidate model and the fully saturated model is the effect we are trying to assess (the three-way interaction). An objective means of model selection is achieved by subtracting the maximum likelihood (approximated using $\mathrm{G}^{2}$ ) of the two-way model from the one of the fully saturated model and testing the significance of this difference. This technique is described in more detail in Lusseau (2003) and (2004).

We first tested the interactions between site and boat presence and their influences on behavioral transitions. We then tested whether the pod identity of the focal whales influenced the previous analysis. Due to sample size constraints, we only retained focal schools that were composed of only members of one pod. For the same reasons the latter analysis was carried out on only two behavioral states (foraging or not foraging) while the former was carried out on all states.

To assess whether distance to boats influenced the behavior of killer whales, we calculated the likelihood that whales that were foraging stayed foraging when boats interacted with them at 100,400 and 1000 m . We also looked at the effect of boat presence on the likelihood that whales that were foraging would stay foraging by comparing control situations (no boats within the given distance band) to impact ones. In all these analyses, foraging was selected because recent studies show that northern resident killer whales were more likely to switch activity states when boats approached foraging whales than when whales were engaged in other activity states. Furthermore, alteration to this state is likely to carry larger energetic consequences for killer whales, because it has the potential not only to increase energetic expenditure, but also to reduce acquisition (Williams et al. 2006).

We analyzed the scans containing distances between vessels and groups to determine mean and maximum vessel counts along with the proportion of time groups spent within 100,400 , or

1000 m of the nearest vessel (e.g., proportion of time within $100 \mathrm{~m}=$ the number of scans with boats within $100 \mathrm{~m} /$ the number of scans in which vessel distances were recorded).

## Theodolite tracking of focal individuals and boats

The theodolite tracking team consisted of three individuals who moved opportunistically between the two study sites to maximize sample size. The team recorded boat and whale positions and activity using a Pentax ETH-10D theodolite interfaced to a PC-compatible computer running Theoprog (Williams et al. 2002ab), a Bushnell 40x spotting scope, binoculars, and a mini-DV camera (see DeNardo et al. 2001).

As whales entered the field of view from a study site, a focal individual was selected. This individual was identified based on Ford et al. (2000) and more recent catalogs (van Ginneken et al. 2000 as updated annually by the Center for Whale Research) and tracked for at least 15 minutes. After a tracking session was completed, a new focal individual was selected, if possible. Individuals were selected haphazardly, but were drawn as evenly as practicable from all pods, age, and sex classes (that is if recent tracks had been of adult males, then subsequent selections were biased toward females and juveniles and vice versa, and whales from pods rarely present were selected over whales from a pod consistently present). We attempted to choose individuals that would not be confused with other individuals nearby, and that were sufficiently close to shore to be accurately identified (typically within 3 km , although this varied with lighting, fog, and individual distinctiveness). Since adult males are rare in this population, they were tracked more times per individual. Roughly $50 \%$ of the individuals in the population were sampled at least once during the three seasons. Approximately equal numbers of tracks of males and females were obtained in 2004, though we were less successful in balancing the sample in 2003 and 2005. The theodolite was used to record position of the focal individual at as many surfacings as possible, and the spotting scope and computer operators, who had a wider field of view, watched for surfacings missed by the theodolite operator, to ensure an accurate record of respiration rate and surface active behavior. We typically collected data only when it was not raining and the sea state was less than three, as whitecaps made tracking significantly more difficult, and rain typically impaired visibility to the point that it was impossible to identify individuals.

While the focal whale appeared to be down on a long dive, the theodolite operator recorded vessel positions. In some cases, a second theodolite tracked only vessels. Vessels were classified as commercial whale watching vessels, research and management vessels, commercial fishing vessels, recreational motor boats, sail boats, kayaks, or freight vessels. Estimated size and vessel type was also recorded (small $=$ under 20', medium $=20-40^{\prime}$, and large $=$ over 40', inflatable or hard-bottomed [rigid inflatable boats were counted as inflatables]).

In addition to recording positions of boats and whales, Theoprog was used to record activity states, behavioral events (e.g., respirations and surface active behaviors such as breaches) and other notes (Williams et al. 2002ab). Boat and whale data were summarized for each track, such that each track was represented only once in the analyses. Independent variables included those related to: Time (Year, Day of Year and Time of Day); Location (Site);

Focal Animal (Age, Sex); and Vessel Traffic (Point of Closest Approach, Overall Boat Count, Number of boats within 100, 400 and 1000 m of the focal whale, and Number of boats observed within the observers' field of view during the track). Calculation of these candidate explanatory variables is described in greater detail in Williams et al. (2002ab).

The five dependent (i.e., whale response) variables included:

1. Inter-breath interval [RESP]: A mean time between breaths was calculated (in seconds) for each track. The mean inter-breath interval was defined as the number of intervals (one less than the number of breaths) divided by the time from the onset of the first breath to the onset of the last breath. Only tracks lasting more than 800 seconds were included in the analysis to ensure the data reliably reflected the ongoing breathing pattern (Bain 1986, Kriete 1995).
2. Swimming Speed [SPEED]: The average swimming speed of the whale was obtained by dividing the total distance travelled by the duration of the tracking session and reported in $\mathrm{km} / \mathrm{h}$. Note that this represents total surface distance covered over time, rather than the crow's flight, or progressive distance. Speed was not corrected for the vertical component or underwater meandering, as underwater behavior was generally unknown, nor was it corrected for current, which is highly variable spatially in the study areas, so tabulated current only serves as an approximation.

Two measures of path predictability were calculated: a directness index and a deviation index.
3. Directness Index [DI]: The directness index measures path predictability on the scale of a tracking session. It is generated by dividing the distance between end-points of a path (i.e., crow's flight distance) by the cumulative surface distance covered during all dives and multiplying by 100 . The directness index can be thought of as the ratio of the diameter of a path to its perimeter, and ranges from zero (a circular path) to 100 (a straight line).

4 Deviation Index [DEV]: The deviation index measures path predictability from one surfacing to the next. It is the mean of all angles between adjacent dives, and can be considered an inverse measure of a path's smoothness. For each surfacing in a track, we calculated the angle between the path taken by a dive and the straight-line path predicted by the dive before it. If an animal breathed twice in a row at the same location, the direction of travel was undefined. However, we replaced this undefined value with 0 change in direction for the purpose of calculating average deviation. The deviation index is the mean of the absolute value of each of these discrepancies, in degrees (potentially ranging from 0 to 180), during the entire track.
5. Surface-active Behavior [SAB]: We recorded each time that surface-active events such as spy-hopping, tail-slapping or breaching occurred.

## Analysis of theodolite data from focal individuals

Theodolite heights were measured using the Survey program in the Theoprog package (Williams et al. 2002ab). A 100' tape measure was stretched along the shoreline at sea level, and theodolite readings were taken of the end points. Typically, the full length of the tape was used. However, if the theodolite operator was unable to see the point at sea level $100^{\prime}$ away, or an intervening point of land or an offshore rock required the tape measure to go over or around it, a shorter length was used. A tide table was used to estimate tide height at the time of the measurement. The length of the tape measured, theodolite readings, and tide height were entered into Survey, which calculated the theodolite height above mean lower low water. This process was repeated ten times and the resulting heights averaged. In a previous study, this method was compared against a measurement by a professional surveyor using GPS technology, and produced agreement within 5 cm (Smith and Bain 2002 and see also Bailey and Lusseau 2004).

These heights were entered into Theoprog to convert theodolite readings to $\mathrm{X}-\mathrm{Y}$ coordinates. Theodolite height was corrected for tide using interpolations between tabulated values updated every ten minutes. The accuracy of the calculated heights and tidal corrections was verified by "tracking" the shoreline and other charted landmarks and plotting the resulting locations on a nautical chart.

For each track, the location of each surfacing by the focal individual was calculated. In addition, locations of vessels marked with the theodolite were calculated. The sequence of surfacing locations was used to calculate the distance and direction traveled between successive surfacings. The time between the first and last point in the theodolite track was the elapsed time. In turn, these values were used to calculate swimming speed (surface speed was the sum of the distances traveled between each pair of surfacings divided by elapsed time, while progressive speed was the distance between the first and last point divided by elapsed time), directness index, and deviation index. Breaths missed by the theodolite operator but observed by another member of the research team were added to breaths observed by the theodolite operator to determine the number of breaths during the track. One was subtracted from this number to determine the number of intervals, and divided by the elapsed time between the first and last point in the theodolite track to calculate the mean inter-breath-interval. Surface Active Behavioral events by the focal whale were counted and divided by the elapsed time to determine the mean rate (per hour) of this behavior.

The overall boat count for a track was the maximum of three types of values. First, the computer operator did boat counts when there were breaks in the tracking (e.g., at the start and end of a track, and occasionally during long dives if boats weren't being marked). Second, the scan sampler did boat counts every 15 minutes, so normally one of these took place during a track (sometimes more for longer tracks). These are both instantaneous counts. The third count was the number of different vessels actually tracked. This number was cumulative, so was potentially greater than the maximum present (from the researchers perspective, though not necessarily the whales perspective) at any given instant, but would be an undercount when not all vessels were tracked.

For number of vessels at specific distances (100, 400, 1000), only the scan sample count was used, so these were instantaneous counts that took place at a moment that was independent of the start and end times of the track and trends in vessel number.

Many vessels were present intermittently. For the instantaneous counts, if a vessel happened to be present when the count was made, it got counted. Otherwise, it did not. For the third count, whether the vessel got counted depended on whether the theodolite tracker marked it. That depended on how close to the focal it got, and how many other vessels were closer. We used a single value, the maximum, to represent the whole track--we did not try to analyze tracks based on whether vessel numbers were consistent or variable during the track.

A spreadsheet was then prepared containing candidate explanatory variables and the five response variables (plus progressive speed, although this is redundant once surface speed and directness have been calculated) for each track.

A preliminary analysis suggested only tracks lasting more than 800 seconds should be included in the analysis, so tracks shorter than 800 seconds were dropped from further analysis (Appendix 4b). If a whale was lost briefly (e.g., behind a boat or in glare, or was missed when first surfacing after a long dive), the track was used. Respiration rate was corrected for surfacings observed by members of the team other than the theodolite operator. No corrections were made to deviation and directness indices. As a result, tracks with missed breaths would have artificially low deviation and artificially high directness indices, but the error was small as long as the proportion of breaths missed was small (on the order of $33 \%$ or less). We tested for bias by comparing results with percentage marked to determine whether tracks with a higher percentage of missed breaths were suitable for use. If too many surfacings were missed, bad portions were eliminated from the record, and whether the track was used at all depended on whether there was an 800 second segment within the track that met the criteria for use.

These data did not lend themselves to straightforward analysis. We approached the analysis in phases. The first was a naive, preliminary, binary analysis. Values for each track were assigned to a vessel present or vessel absent condition. Tracks were considered to have vessels present if either of the following conditions were met: 1) the interpolated position of at least one vessel was within 1000 m of the focal whale at any time during the track, or 2 ) the scan sampler recorded at least one vessel within 1000 m of the focal individual. The binary analysis ignored the potential for factors other than vessel traffic to have influenced the values in the vessel present and vessel absent datasets, but since the sampling protocol was designed to be as representative as possible of real world conditions, these values provide a best estimate of average behavior in the presence and absence of vessels. That is, this analysis provides good descriptive statistics, but for reasons discussed below, the statistical significance of the binary analysis should be treated with extreme caution.

We tested the data for normality, but since they were not normally distributed, we ruled out the use of statistics that assume normality like a t-test. Due to the limited power of data sets with small sample sizes, we elected not to use non-parametric statistics, either. Therefore, we performed a Monte Carlo simulation (1000 iterations) to determine the probability, given the distribution in the vessel absent data (values were randomly selected with replacement from the
observed data), that a sample the size of the vessel present data would have means at least as divergent as those observed, if they had been drawn from the same distribution as the vessel absent data. This level of analysis simply determines whether the no-boat and boat data are drawn from the same population. A result indicating they are from the same population could be misleading, because effects could cancel out to give the appearance of no effects. Similarly, since Williams et al. (2002b) found a variety of variables other than vessel traffic influenced behavior, if all other things are not equal, a factor other than vessel traffic could be responsible for differences between the two datasets.

Thus we performed a more detailed analysis to test whether potentially confounding variables provided a better explanation for differences between the two datasets than vessel presence did. Each track was considered an independent sample of animal behavior. It is unlikely that repeated observations of the same individual under different traffic conditions are statistically independent in the strictest sense. However in a small, endangered population, sample size will always be limiting. To that extent, we chose an analysis framework that accounted for as much of the individual variability as possible, holding these natural covariates constant while modeling effects of the variables of interest. We knew, a priori, that our modeling approach would have to be a flexible one. Candidate explanatory variables included: binary variables (Year, Site, Sex); factors with varying numbers of levels (Month, Day, Hour, Pod, Age, number of boats within 100 m ); continuous variables (Point of Closest Approach, Tide height, Current speed, and two measures of data quality--the Percentage of surfacings successfully located with the theodolite and the Duration of the track) and count data from the variable of interest (boat counts at the other spatio-temporal scales: the 400 m and 1000 m range rings and the overall boat count). Similarly, the five response variables were all bounded by zero. They included those that might be expected to have derived from: a Gamma or log-normal distribution (perhaps swimming speed and inter-breath intervals); a quasi-Poisson distribution (expected number of surface-active events per hour); and two artificially constructed variables whose theoretical underlying distribution is not intuitive (deviation and directness indices), but are known to be bounded (between 0 and $180^{\circ}$, and between 0 and 100, respectively). Many of these variables can be expected to have violated assumptions underlying traditional linear modeling, such as homoscedasticity and normality. Sample size will not be equal, given the unpredictability of the movements of both people and free-ranging cetaceans. Finally, there is no reason to assume that any relationships between human activity and whale behavior ought to be linear, but neither can one derive from first principles the predicted shape that these relationships ought to follow.

We attempted to address as many of these problems as possible by describing heterogeneity in whale behavior using generalized additive models, GAMs (Venables and Ripley 2002). Generalized additive models (GAMs) were fitted in package mgcv (multiple generalized cross-validation) for program R (Wood 2001). Unlike the GAM implementation in S-Plus, the mgcv approach uses thin-plate regression splines (Wood 2003) for the smooth terms of each explanatory variable, but each spline carries a penalty for excessive flexibility (Wood 2000). Flexibility is determined by the number of 'knots' (approximately one higher than the estimated degrees of freedom, edf) for each model term, between which the functional, or smoothed, relationship was modeled. Smoothing splines were fitted using multiple generalized crossvalidation (GCV). In other words, the amount of flexibility given to any model term was
determined in a maximum likelihood framework by minimizing the GCV score of the whole model (i.e., given the other terms in the model), rather than each component score. That is, models were penalized for being over-parameterized, and the degree of smoothing was automated for each model term simultaneously. This avoided the problem common to many step-wise procedures, whereby the order in which terms are presented to the model influences the apparent significance of subsequent terms.

The default smoothing value used for splines was the default value set by package mgcv, 10 knots in each spline, corresponding to 9 degrees of freedom (Wood, 2001). In practice, few biological relationships are expected to display this degree of complexity, but setting lower values can cause problems with model convergence. Histograms of the response variables were used to determine the appropriate family distribution and link function. Variables that approximated a normal distribution were modelled using the quasi family. Rates of surfaceactive behavior were expected to approximate a Poisson distribution, given that they derived from count data. A quasi family with a log link was chosen for this analysis, which allowed the dispersion parameter to be modelled from the data. All others were fitted using the quasilikelihood family with an identity link, which allows the underlying distribution to be modelled in a maximum-likelihood framework.

While determination of the optimal amount of smoothing is automated by mgcv, the decision whether to include or drop a model term is not, so the decision whether to do so was guided by a set of criteria described below. Potential explanatory variables considered for inclusion in the model were Year, Julian Day, Time, Tide, Current, Site, Pod, Age, Sex, Point of Closest Approach (PCA), number of boats within 100m (SUM100), number of boats within 400m (SUM400), number of boats within 1000m (SUM1000), overall boat count (BOATS). Factor variables were entered as linear or grouping terms. Continuous variables were entered as candidates for smoothing $(\mathrm{s}(x))$ by mgcv. SUM100 was treated as a factor variable, but the other boat counts were treated as continuous variables.

However, the above suite of candidates pushes the limit of the analysis given our sample size, so we analyzed the remaining three parameters separately. We examined the relationship between percentage of surfacings marked and the five behavioral parameters to determine which tracks had acceptable accuracy, and excluded tracks with fewer than $2 / 3$ of surfacings marked. We did not consider the percentage marked in subsequent analyses.

We performed a similar analysis based on track duration, and found no obvious trends in behavioral indices in tracks longer than 800 seconds, except in the case of surface active behavior (although we saw no effect on respiration or speed individually beyond 800 seconds, Kriete [1995] found an interaction between these two parameters up to 1000 seconds in her data). So, we excluded tracks shorter than 800 seconds. Also, we excluded duration from further consideration except in the analysis of surface active behavior. For SAB, we examined both rates per unit time, which was negatively correlated with track duration, and probability of occurrence (one-zero sampling) which was positively correlated with track duration. This is discussed further below.

A recurring problem with small datasets such as ours is the difficulty of, or statistical power necessary for, incorporating mixed effects (e.g., to account for repeated measures of individuals). We addressed this by including candidate covariates, such as Age and Sex that were likely to have made pseudoreplication an issue. However, the overwhelming advantage of the mgcv approach in R is that it assesses the contribution of each term to the model given the effects of the other terms simultaneously. We believe that avoiding the problem common to many step-wise procedures (i.e., conflating importance of each term with the order in which it enters the model) was important enough to justify using this technique.

The following summarizes our model specification procedure adopted for each of the five response variables, $y$, during this study, using the framework proposed by Wood (2001):

1. A fully saturated model was fitted to the data: $\{y \sim$ Year $+J D a y+$ Time $+\mathrm{s}($ Tide $)+$ $\mathrm{s}($ Current $)+$ Site + Pod $+\mathrm{s}($ Age $)+$ Sex $+\mathrm{s}($ PCA $)+\mathrm{s}($ BOATS $)+$ SUM100 $+\mathrm{s}($ SUM400 $)$ $+\mathrm{s}($ SUM1000 $)+$ Current with the default degree of smoothing ( 10 knots, 9 df ).
2. Model fit was assessed using the summary.gam and plot.gam functions in mgcv, which showed coefficients, GCV score, explanatory power (deviance explained and R-squared score) and fit (residual plots).
3. For each linear term, the parameter coefficient (slope) was examined to see if it was near 0 and the significance term to see if it was near 1 . If so, the term was removed to see if the GCV score decreased and the explanatory power of the model increased. If so, the term was dropped from the model. If no marked improvement was detected by removing the term, then it remained in the model.
4. For each smooth model term, the estimated number of degrees of freedom was examined to see if it was near 1. The $95 \%$ confidence intervals for that term were examined to see whether they included zero across the range of observations. If so, the term was dropped temporarily, to see whether the GCV score dropped and the explanatory power of the model increased.
5. A term was dropped from the final model if it satisfied all three of the conditions in step 4 (i.e., edf $\approx 1 ; 95 \%$ CI's include zero across range of $x$; and dropping the term decreased the GCV score and increased the values for R-squared and deviance explained). If the first criterion was met (edf $\approx 1$ ), but not the other two, then the smooth term was replaced by a linear term.

## RESULTS

## SCAN-SAMPLING OF FOCAL GROUPS

Over the three field seasons we observed 593 behavioral transitions (135 in 2003, 217 in 2004, and 251 in 2005 out of 373 , 1058, and 770 scans, respectively). Sample sizes broken down by site, year, and vessel presence are shown in Table 2. The difference between number of transitions and the number of scans is due to two factors. One, it takes two scans to obtain a transition. A transition consists of two observations of the same group 15 minutes apart, and
may or may not include changes in behavior state. Second, groups may cease to exist due to fission and fusion, or leaving the study area (either being so far away that they are no longer recognizable as the same group or being out of sight altogether).

Table 2. The number of activity state transitions observed in the presence/absence of boats within 100 m .

|  | 2003 | 2004 |  | 2005 |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| Site | No boat | Boat | No boat | Boat | No boat | Boat |
| North site | 49 | 30 | 121 | 30 | 111 | 52 |
| South site | 45 | 11 | 46 | 20 | 40 | 48 |

We assessed the effects of Year (2003/2004/2005), Site (North/South), and Vessel Traffic (no boat within 100 m , boat present within 100 m ) on behavioral transitions using a five-way loglinear analysis (LLA) (see Table 2 for sample size). Due to small sample size the full interaction of the three independent variables could not be quantified. Figure 2 is designed to present models going from the most simple one at the top (the null model), to the more complex ones at the bottom by increasing the number of parameters involved in the models as one moves away from the null model. Each model builds on a previous, simpler one by adding new effects to it. The effects added have been color coded: blue for a site effect, red for a boat effect, and green for a year effect. Interactions terms could also be added and those are represented by striped arrows (colors are the 2 effects interacting). This analysis reveals that three models provided more information on the data's variance (Figure 2). The null model (i.e. no effects from independent variables (PS, BYLP), the model considering a site effect (LPS, BYLP), and the model considering a boat effect (BPS, BYLP) all had lower Akaike Information Criteria (AIC) than the other models (Table 3) indicating that the null, site effect, and boat effect models were each plausible. In addition, adding a boat and site effect to the model provided significantly more explanation of the data variance (significant effects represented by stars on Figure 2, and see Table 3), the site effect being still significant after the year effect was taken into consideration. The significance of the terms being derived from the maximum likelihood estimates derived as described in the methods. From this analysis, we can conclude both that boat presence within 100 m from the focal whales affected their behavioral transitions and that the whales behaved differently between the two sites, in contrast to the null model which was not rejected when considering the AIC value alone.

Figure 2. (next page). Tests of boat presence within $100 \mathrm{~m}(B)$, site ( $L$ for location to avoid confusion in abbreviations), and year of sampling ( $Y$ ) effects on behavior transitions (PS) using log-linear analyses. Models and their respective goodness-of-fit $\mathrm{G}^{2}$ statistics, degrees of freedom, and AIC values are shown in the boxes (adapted from Caswell 2001). Terms added are color-coded. Blue arrows represent the addition of a site effect (LS, LPS terms added to the previous model), red arrows represent the addition of a boat effect (BS, BPS), and green arrows represent the addition of a year effect (YS, YPS). To those terms correspond an increment in $\mathrm{G}^{2}$ and degrees of freedom, which are used to test for the significance of the term addition. Arrows are marked with a star when the term addition is significant ( $\mathrm{p}<0.05$ ). The top left star indicates a significant boat effect, and the center and right stars indicate significant site effects. Year effects were non-significant.

Effects of Vessel Presence, Year, and Location on Activity State Transition Probabilities


To elucidate these differences, we calculated the activity budgets of the whales at both sites, as well as in the presence and absence of boats. Whales tended to spend significantly more time traveling and less time foraging when boats were present within 100 m than when they were absent within 100m (Figure 3, all data pooled with site effect ignored). The difference in activity budgets between both sites only involved socializing (Figure 4, all data pooled with boat effect ignored). Whales spent significantly more time socializing at the north site.


Figure 3. The proportion of time focal killer whales spent in each activity state (their activity budget) depending on the presence of boat within 100 m of them. Data from all three pods at both study sites are combined. Error bars are $95 \%$ confidence intervals. Black stars indicate differences that are significant at the 0.05 level.

Activity Budget as a Function of Study Site


Figure 4. The proportion of time focal killer whales spent in each activity state (their activity budget) depending on the site sampled. Data from all three pods are combined. Error bars are $95 \%$ confidence intervals. Black star indicates difference that is significant at the 0.05 level.

Table 3. Information theoretic approach used to select models, from Figure 2, providing the most parsimonious explanation for the variation in the scan-sample dataset. The selection is based on the Akaike Information criterion. The models are described in Figure 2. The difference between the best fitting model and the other models, $\triangle \mathrm{AIC}$, helps defining models that are less plausible (usually $\Delta \mathrm{AIC}>4$ to 8 ). The likelihood of the model given the data can be approximated using an exponential transformation of $\Delta \mathrm{AIC}: \ell\left(\operatorname{model}_{\mathrm{i}} \mid\right.$ data $)=\mathrm{e}^{\left(-0.5 \Delta \mathrm{AIC}_{\mathrm{i}}\right)}$. The weight of evidence provided by each model can be obtained by normalizing these likelihoods so that they sum to 1 .

| Model | AIC | $\boldsymbol{\Delta A I C}$ | weight |
| :--- | :--- | :--- | :--- |
| Null model | -109.8 | 0 | 0.507 |
| Boat | -109 | 0.8 | 0.340 |
| Site | -107.4 | 2.4 | 0.153 |
| Year | -93.5 | 16.3 | 0.0001 |
| Boat + site | -97.5 | 12.3 | 0.001 |
| Site + year | -93.1 | 16.7 | $<0.0001$ |
| Boat + year | -82.2 | 27.6 | $<0.0001$ |
| Boat + year + site | -81.4 | 28.4 | $<0.0001$ |
| Boat x site | -86.8 | 23 | $<0.0001$ |
| Boat x year | -65.6 | 44.2 | $<0.0001$ |
| Year x site | -69.1 | 40.7 | $<0.0001$ |
| Year + (boat x site) | -76.3 | 33.5 | $<0.0001$ |
| Site + (boat x year) | -66.9 | 42.9 | $<0.0001$ |
| Boat + (year x site) | -55.9 | 53.9 | $<0.0001$ |

The introduction of a boat effect explains significantly more variation in the dataset than the null model alone (as shown by the red star in Figure 2). We can therefore conclude that while intrinsic behavioral processes and data structure (the null model) as well as site are explaining some of the variation in the dataset, a boat effect cannot be excluded (because of the AIC weights) and should be included as well (because this parameter is providing significantly more information than the null model alone).

## The influence of pod identity

The southern resident community of killer whales is composed of three pods ( $\mathrm{J}, \mathrm{K}$, and L), which do not spend the same amount of time within Puget Sound. This may result in differences in the cumulative exposure of each pod to whale watching and therefore may lead to variation in the way these pods respond to boat presence. We therefore assessed whether the identity of the focal whales affected the behavioral response observed in relation with boat presence. To do so, we conducted a log-linear analysis including pod identity and boat presence within 100 m as independent variables. Sample size restricted the analysis because we only considered focal schools composed of members of only one pod (see Table 4 for sample size). So we coarse-grained the analysis and only considered two states (foraging and not foraging).

Table 4. Number of activity state transitions observed with and without boats present within 100 m of subgroups for each pod for both sites in all years (considering only schools composed solely of members of one pod).

| Pod | No boat present | Boat present |
| :--- | :---: | :---: |
| J | 158 | 35 |
| K | 21 | 21 |
| L | 99 | 47 |

The log-linear analysis showed that there does not appear to be any variation in the way that whales responded to boat presence depending on their pod (Table 5) because there was no interaction between the pod and boat effect (Table 5). The analysis shows that while the best model was the null model, both pod effect and boat effect could not be discounted (Table 5, $\Delta \mathrm{AIC}<2$ ). This highlights that potentially the site effect we observed in the previous analysis (Figure 2) may just be a reflection of the difference in use of the two sites by the three pods (Figure $5 \& 6$ ). J pod seemed to be the pod most likely to be foraging and interestingly they seemed to be more likely to be foraging at the south site while K and L were equally likely to forage at both sites (Figure 6).

Table 5. Information theoretic approach used to select models, from the log-linear analysis considering pod identity, site, and boat presence, providing the most parsimonious explanation for the variation in the scan-sample dataset. The difference between the best fitting model and the other models, $\Delta \mathrm{AIC}$, helps defining models that are less plausible (usually $\Delta \mathrm{AIC}>4$ to 8 ). The likelihood of the model given the data can be approximated using an exponential transformation of $\Delta A I C: \ell\left(\operatorname{model}_{i} \mid\right.$ data $)=e^{\left(-0.5 \Delta \mathrm{AIC}_{\mathrm{i}}\right)}$. The weight of evidence provided by each model can be obtained by normalizing these likelihoods so that they sum to 1 .

| Model | mle | Df | AIC | $\boldsymbol{\Delta}$ AIC | Weight |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Null | 21.43 | 22 | -22.57 | 0 | 0.378 |
| Pod | 14.43 | 18 | -21.57 | 1 | 0.229 |
| Boat | 19.22 | 20 | -20.78 | 1.79 | 0.154 |
| Site | 20.97 | 20 | -19.03 | 3.54 | 0.064 |
| Boat + site | 18.89 | 18 | -17.11 | 5.46 | 0.025 |
| Boat + pod | 13.42 | 16 | -18.58 | 3.99 | 0.051 |
| Site + pod | 12.44 | 16 | -19.56 | 3.01 | 0.084 |
| Site x pod | 8.66 | 12 | -15.34 | 7.23 | 0.010 |
| Site x boat | 18.21 | 16 | -13.79 | 8.78 | 0.005 |
| Boat x pod | 48.79 | 12 | 24.79 | 47.36 | $<0.0001$ |
| Boat x pod x site | 0 | 0 | 0 | 22.57 | $<0.001$ |

Activity Budget of Each Pod


Figure 5. The proportion of time focal killer whales spent in each activity state (their activity budget) depending on the pod membership of the focal school. Data from both sites are combined. Error bars are $95 \%$ confidence intervals. Black stars indicate differences that are significant at the 0.05 level.


Figure 6. The proportion of time focal killer whales spent foraging depending on the pod membership of the focal school and the site at which they were observed. Error bars are $95 \%$ confidence intervals. Black star indicates difference that is significant at the 0.05 level.

## The influence of the distance between the focal school and boats

While an effect of boat presence was apparent when boats were within 100 m of the focal schools, we wanted to assess whether more distant boats also influenced the activity states of the schools. Control samples are more difficult to obtain when considering boat presence at distances of 400 m and 1000 m , because boat traffic around the two sampling sites is consistently high. For this reason the current samples available did not allow us to assess the site effect in relation to boat presence within 400 m of the whales. Similarly, we could not assess the effects of boats within 1000 m of the whales because of the lack of a minimum amount of control samples. Therefore, we present only the results of the log-linear analysis assessing the effects of boat presence within 400 m of the whales without considering the other potential effects (i.e., merging samples obtained during all years and at both sites). Given that the site effect (or potentially the pod effect) was found to affect the activity budget in previous analyses, the following results need to be interpreted with caution.

As in previous models, we compared the model, obtained from log-linear analyses, containing all two-way interactions (Boat presence by Preceding behavior, Boat presence by Succeeding behavior, Preceding behavior by Succeeding behavior) to the fully saturated model (Boat presence x Preceding behavior x Succeeding behavior) to assess the effect of boat presence on behavioral transitions (Lusseau 2003). This comparison, based on the difference in maximum likelihood estimates of both models using $\mathrm{G}^{2}$ statistics, did not reveal an effect of boat presence within 400 m on behavioral transitions $\left(\Delta G^{2}=11.0, \Delta d f=9, p=0.28\right)$. However, trends in behavioral budgets depending on boat presence within 400 m were in the same direction as those when boats were within 100 m (Figure 3 and Figure 7), with whales spending significantly more time traveling and significantly less time foraging.

## Activity Budget as a Function of Vessel Presence Within 400 Meters



Figure 7. The proportion of time focal killer whales spent in each activity state (activity budget) depending on the presence of boat within 400 m of them, pooling across years and sites. Error bars are $95 \%$ confidence intervals. Black stars indicate differences that are significant at the 0.05 level.

We then assessed the effect of boat presence within 100, 400 and 1000 m on the probability to stay foraging when foraging. The effect size of boat presence, i.e. the difference in the likelihood to stay foraging when foraging between control and impact situation (vessels present within the specified distance), decreased with the distance to boat present increasing (Figure 8). The effect of boat presence appeared to be only significant when boats were within 100 m and 400 m (Figure 8, note the star and the confidence intervals), yet sample size might be preventing the detection of smaller effect size for the other treatment (Figure 8, 1000m). In addition, the likelihood to stay foraging when foraging increased as the distance between the focal group and boats present in the study area increased but not significantly (Figure 9).

## Difference in Likelihood to Remain Foraging as a Function of Distance to Nearest Vessel



Figure 8. Difference in the likelihood to stay foraging when foraging ( $\mathrm{p}_{\mathrm{F} \rightarrow \mathrm{F}}$ ) between control and impact situations ( $\mathrm{p}_{\text {control }}-\mathrm{p}_{\text {impact }}$ ), i.e. effect size, depending whether some boats were present within $100 \mathrm{~m}, 400 \mathrm{~m}$, or 1000 m of the focal whales. The diagram describes these three treatments in which the focal group is at the centre of the concentric doughnuts $(100 \mathrm{~m}, 400 \mathrm{~m}$, and 1000 m radii) and the boat exposure is represented in black. In order to test the effect of distance to boats, this analysis only takes into consideration samples when there were boats present only at the given distance. Error bars are $95 \%$ confidence intervals for the difference. If the interval includes 0 , the difference is not significant at the conventional ( $\mathrm{p}<0.05$ ) level (indicated by a star). The number of transitions observed is given above each bar ( $\mathrm{n}_{\text {control }}, \mathrm{n}_{\text {impact }}$ ).

Probability of Whales Remaining Foraging as a Function of Distance to Nearest Vessel


Figure 9. Likelihood that whales stay foraging when foraging, $p(F-F)$, when there is no boat present within $100 \mathrm{~m}, 400 \mathrm{~m}$, or 1000 m of the focal school. The diagram describes these three treatments in which the focal group is at the centre of the concentric doughnuts $(100 \mathrm{~m}, 400 \mathrm{~m}$, and 1000 m radii) and the boat exposure is represented in black. Error bars are $95 \%$ confidence intervals, and none of the conditions differ significantly from each other. The number of transitions observed is given above each bar.

## THEODOLITE TRACKING OF FOCAL INDIVIDUALS

We collected 42 tracks in 2003, 77 tracks in 2004, and 67 in 2005 that were of sufficient quality to use in the analysis. Whales were tracked for an average of 25.2 minutes over 2.6 km . Behavioral indices derived from theodolite tracks are summarized in Table 6. More details on track characteristics (e.g., breakdowns by individual, pod, location, vessel presence, etc.) are
shown in Appendices 1-3. Note that only two tracks in 2003 met the criteria for good boatsabsent tracks.

The relationship between percentage of surfacings marked and directness index shows no bias, supporting inclusion of all these tracks except the one in which fewer than $66 \%$ of surfacings were marked with the theodolite (an outlier both in terms of proportion marked and biased in the direction expected when surfacings are missed so it was excluded from the analysis, see Appendix 4a). Duration was similarly analyzed, and two tracks shorter than 800 seconds were dropped from further analysis (see Appendix 4b).

Whale behavior did vary with track duration in the case of surface active behavior, and our method for addressing that is described in the section on that response variable. DURATION was dropped from the list of candidate covariates in the case of the other four response variables, in order to assist model convergence, but retained for analysis of SAB (see Appendix 4b).

Example tracks are shown in Appendix 5.

## Results of binary (baseline/exposure) analyses

The mean values of the behavioral indices employed in this study and the probability of the with-boat and without-boat data being drawn from the same distribution based on the Monte Carlo simulation are shown in Table 6.

Table 6. Behavioral indices for Southern Residents in the absence (distance to nearest vessel $>$ 1000 m ) and presence of vessels (significance based on Monte Carlo simulation).

| Behavior | Value |  | Significance |
| :--- | ---: | ---: | :---: |
| Vessel presence: | Without Boats <br> $\mathbf{N = 2 5}$ | With Boats <br> $\mathbf{N}=\mathbf{1 6 1}$ |  |
| Directness Index | 80.40 | 74.16 | $\mathbf{p}<. \mathbf{0 0 1}$ |
| Deviation Index | 27.99 | 28.86 | $\mathrm{p}>.25$ |
| Respiratory Interval (sec) | 43.74 | 48.03 | $\mathbf{p}<.001$ |
| Surface Active (/hr) | 1.76 | 2.43 | $\mathrm{p}>.09$ |
| Surface Speed (m/hr) | 6309 | 6253 | $\mathrm{p}>.5$ |

Directness Index. Whales traveled in more direct paths when vessels were absent than when they were present. The magnitude of this effect was $8 \%$.

Deviation Index. Whales made insignificantly larger course changes when vessels were present than when vessels were absent. The magnitude of this effect was $3 \%$.

Breathing Patterns. The average time between breaths was significantly longer in the presence of boats than in their absence. The magnitude of this effect was $10 \%$

Surface Active Behavior. Surface active behavior was significantly more likely to occur but was insignificantly more frequent in the presence of vessels than in its absence. This was due to surface active behavior being 1.9 times more likely to occur in the presence of vessels ( $\mathrm{p}<.001$ ), and $38 \%$ more events occurring given that at least one occurred when vessels were present.

Swimming Speed. There was no significant difference in swimming speed due to vessel traffic found in the binary analysis (the difference in mean speed was less than $1 \%$ ).

Vessel Proximity. The proportions of subgroups scanned in proximity of vessels are shown in Table 7. The primary component of the reduction in scans with boats within 400 and 1000 m of whales in 2004 and 2005 is probably due to extending the field season prior to the opening of salmon fishing season. Trends in mean and maximum counts probably reflect the end date of each field season and the tendency of vessel numbers to increase later in the year. That is, these numbers should not be used to infer inter-annual trends in vessel numbers.

Table 7. Percentage of scan samples with at least one vessel within the distances shown of the subgroup in Southern Residents in 2003-5. WOT $=$ Whale Oriented Traffic, NOT $=$ Not whale Oriented Traffic, and ANY refers to the presence of at least one of either type of vessel.

| Year | Within <br> $\mathbf{1 0 0} \mathbf{m}$ |  |  | Within <br> $\mathbf{4 0 0} \mathbf{~ m}$ |  |  | Within <br> $\mathbf{1 0 0 0} \mathbf{~ m}$ |  |  | Field of <br> View |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ANY | WOT | NOT | ANY | WOT | NOT | ANY | WOT | NOT | ANY |
| 2003 | 23.3 | 22.5 | 0.8 | 81.0 | 75.6 | 9.7 | 90.1 | 84.2 | 19.0 | 99.5 |
| 2004 | 28.8 | 26.7 | 4.9 | 56.7 | 51.6 | 11.2 | 75.7 | 69.4 | 21.5 | 98.5 |
| 2005 | 28.5 | 26.9 | 2.6 | 58.7 | 55.3 | 8.9 | 79.5 | 74.1 | 21.4 | 97.5 |

Table 8. Maximum number of vessels in scan samples within the distances shown of the subgroup in Southern Residents in 2003-5. WOT = Whale Oriented Traffic, NOT = Not whale Oriented Traffic, and ANY refers to the sum of both types of vessels.

| Year | Within <br> $\mathbf{1 0 0} \mathbf{m}$ |  |  | Within <br> $\mathbf{4 0 0} \mathbf{m}$ |  |  | Within <br> $\mathbf{1 0 0 0} \mathbf{m}$ |  |  | Field of <br> View |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ANY | WOT | NOT | ANY | WOT | NOT | ANY | WOT | NOT | ANY |
| 2003 | 7 | 7 | 1 | 19 | 19 | 5 | 36 | 23 | 15 | 109 |
| 2004 | 9 | 8 | 3 | 16 | 14 | 6 | 42 | 40 | 13 | 78 |
| 2005 | 17 | 17 | 5 | 31 | 31 | 14 | 35 | 35 | 14 | 57 |

Table 9. Mean number of vessels in scan samples within the distances shown of the subgroup in Southern Residents in 2003-5. WOT = Whale Oriented Traffic, NOT = Not whale Oriented Traffic, and ANY refers to the average of both types of vessels combined.

| Year | Within <br> $\mathbf{1 0 0} \mathbf{m}$ |  |  | Within <br> $\mathbf{4 0 0} \mathbf{m}$ |  |  | Within <br> $\mathbf{1 0 0 0} \mathbf{m}$ |  |  | Field of <br> View |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | ANY | WOT | NOT | ANY | WOT | NOT | ANY | WOT | NOT | ANY |
| 2003 | 0.35 | 0.34 | 0.01 | 3.08 | 2.91 | 0.17 | 7.09 | 6.54 | 0.55 | 42.26 |
| 2004 | 0.58 | 0.52 | 0.06 | 2.88 | 2.58 | 0.31 | 10.18 | 9.18 | 1.00 | 25.05 |
| 2005 | 0.57 | 0.52 | 0.04 | 4.14 | 3.79 | 0.35 | 10.48 | 9.55 | 0.93 | 19.38 |

## Results of GAM-based analyses of focal animal behavior

Respiration analysis. The model that fitted the respiration data best included only three vessel traffic variables, but no whale related variables (age, sex and pod) or temporal variables (time of day and month of year, Table 10). The model described the variation in mean respiratory interval modestly, in that it was able to account for $13 \%$ of the deviance (note that the R-squared estimate is a less informative metric than the deviance explained for models based on anything other than normal error distribution). Two of the traffic variables (BOATS and SUM100) entered the model as linear terms, while the last variable (SUM400) entered the model as a smooth term.

As number of boats (the maximum of the total number of vessels identified by the theodolite operator, instantaneous counts by the theodolite and computer operators, and counts by the scan sampler within 1000 m ) increased, the inter-breath interval showed a small but significant tendency to decrease. The relationship between inter-breath interval and number of boats within 100 m , though, showed the opposite slope.

The smooth term describing covariation of SUM400 and inter-breath interval indicates that the relationship is not as straight-forward as suggested by the linear terms above. Dive times tended to be shorter when no boats were present within 400 m of the focal whale, and increased as number of boats increased to approximately 5 boats. When many more boats were present within this range, mean inter-breath interval declined, but this relationship became nonsignificant (i.e., the confidence intervals comfortably spanned zero).

Table 10. Summary of selected model describing heterogeneity in mean respiration rate as linear (top) and smooth (non-linear, bottom) functions of covariates selected by mgev.

Family: quasi
Link function: $\log$
Formula:
RESP $\sim$ BOATS + SUM100 + s(SUM400)
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|\mathrm{t}\|)$ |
| :---: | :---: | :--- | :--- | :--- |
| (Intercept) | 3.9333 | 0.05139 | 76.54 | $<2.22 \mathrm{e}-16$ |
| BOATS | -0.01078 | 0.004336 | -2.486 | 0.014022 |
| SUM100 | 0.06347 | 0.04384 | 1.448 | 0.14978 |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |
| :--- | :--- | :--- | :--- |
| s(SUM400) | 2.274 | 8.4529 | 0.021756 |

R-sq.(adj) $=0.0923$ Deviance explained $=13 \%$
GCV score $=6.0782 \quad$ Scale est. $=5.8687 \quad n=153$

Figure 10 shows the smooth spline relating mean time between breaths to the maximum number of boats counted within 400 m of the whale, the linear terms relating mean time between breaths to two boat count variables, and the residuals of the fitted GAM.

## Terms in the Selected Model Describing Variability in Mean Time Between Breaths



Figure 10. Relationships between smoothed component (solid line; UPPER LEFT) of the explanatory variables ( x -axis) used in the fitted GAM (after accounting for the linear effects of BOATS and SUM100; UPPER RIGHT and LOWER LEFT, respectively) and the response variable, mean time between breaths. The explanatory variable in the smooth term, SUM400, represents the maximum number of boats ever observed within 400 m of the whale. SUM400 was allowed up to 9 d.f. in model selection, and the degree of smoothing was automated by mgcv. The x -axis contains a rugplot, in which small ticks mark locations of observations. Zero on the y axis corresponds to no effect of the covariate on the estimated response (here, inter-breath interval). Values above zero on the y-axis indicate positive correlation, i.e., long inter-breath intervals. The $y$-axis is labeled s(covariate name, estimated degrees of freedom) indicating the curve is smoothed. The dashed lines represent $\pm 2$ standard errors, or roughly $95 \%$ confidence intervals.

The last plot (BOTTOM RIGHT) shows the residuals of the fitted model. The slight positive skew (asymmetry about zero on the y axis) suggests that some over-dispersion in respiration rate remained unmodeled by the selected GAM, but that the model provided a reasonably good fit to the data overall.

Swimming speed. The selected model included the maximum number of boats scanned within 100 m and 400 m of the focal animal, as well as the site from which the data were collected (Table 11). Model fit was improved by dropping the intercept term. The model described variation in swimming speed quite well, in that it was able to account for $92.9 \%$ of the deviance (which is a better metric for quasi-family models than the adjusted R -squared value of 0.06 ). The linear relationship between boat count within 100 m and swimming speed was negative (i.e., whale swimming speed tended to decrease as number of boats within 100 m of the whale increased). The non-linear relationship between swimming speed and MAX400 mirrored this relationship, with the relationship being fairly flat until the number of boats within 400 m reached approximately 6 boats, at which point swimming speed increased dramatically.

Table 11. Summary of selected model describing heterogeneity in mean swimming speed as linear (top) functions of covariates selected by mgev.

## Family: quasi

Link function: $\log$
Formula:
SPEED $\sim$ SITE + SUM100 $+\mathrm{s}($ SUM400 $)-1$
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|t\|)$ |
| :---: | :--- | :--- | :--- | :--- |
| SITENORTH | 1.842 | 0.04349 | 42.35 | $<2.22 \mathrm{e}-16$ |
| SITESOUTH | 1.9573 | 0.06542 | 29.92 | $<2.22 \mathrm{e}-16$ |
| SUM100 | -0.086536 | 0.05863 | -1.476 | 0.14211 |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |
| :--- | :--- | :--- | :--- |
| s(SUM400) | 5.375 | 11.13 | 0.06751 |

R-sq. $(\mathrm{adj})=0.0601 \quad$ Deviance explained $=92.9 \%$
GCV score $=1.1132 \quad$ Scale est. $=1.0523 \quad n=153$
Figure 11 shows the smooth spline relating swimming speed to the maximum number of boats scanned within 400 m of the whale, the linear terms, and the residuals of the fitted GAM.

## Terms In The Selected Model Describing Variability In Whale Swimming Speed



Figure 11. TOP LEFT - the smooth spline relating swimming speed to the maximum number of boats scanned within 400 m of the whale suggests that whales tended to swim slowly when a few boats were observed within 400 m , and then swimming speed tended to increase as boat number increased. TOP RIGHT and BOTTOM LEFT - the linear terms that entered the model. All other things being equal, whales tended to swim faster at the South Site than the North Site. Whales generally slowed down as number of boats within 100 m increased. BOTTOM RIGHT- the residuals of the fitted GAM after accounting for the linear effects of Site, and maximum number of boats within 100 m , and a smooth spline of the maximum number of boats within 400 m of the whale. No pattern is evident in the residuals, indicating that the model fitted the data well, and that the maximum likelihood approach was able to account for the overdispersion in the response data.

Deviation index. The model that fitted the path deviation index data best included two boat count variables (BOATS and PCA), two whale-related variables (AGE and POD), and three ancillary variables (SITE, CURRENT and TIDE; Table 12). Model fit was improved by dropping the intercept term. The model demonstrated good power to describe variation in deviation index, accounting for $83.5 \%$ of the deviance explained, with an adjusted R-squared value of 0.188 .

Term-wise parameter estimates indicate that whales adopted smoother paths (i.e., lower deviation index) at the South site than at the North site. The maximum number of boats recorded by the theodolite operator (BOATS) entered the model as a linear term with negative slope, indicating that whales exhibited relatively smooth paths when few boats were observed close to the whale and more erratic paths when many boats were present (Table 10). The strong confounding effects of TIDE and CURRENT suggest that there may be something of biological importance, perhaps foraging activity, reflected in these data, and warrants further attention.

Table 12. Summary of selected model describing heterogeneity in path deviation index as linear (top) and smooth (i.e., non-linear, bottom) functions of covariates selected by mgev.

Family: quasi
Link function: $\log$
Formula:
DEV $\sim$ SITE + POD $+s($ AGE $)+s($ PCA $)+$ BOATS + CURRENT + TIDE -1
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|\mathrm{t}\|)$ |
| :--- | :--- | :--- | :--- | :--- |
| SITENORTH | 3.8345 | 0.1368 | 28.02 | $<2.22 \mathrm{e}-16$ |
| SITESOUTH | 3.7238 | 0.1459 | 25.52 | $<2.22 \mathrm{e}-16$ |
| PODK | -0.4178 | 0.1456 | -2.869 | 0.0047283 |
| PODL | -0.017296 | 0.1029 | -0.1681 | 0.86677 |
| BOATS | -0.015458 | 0.005596 | -2.762 | 0.0064791 |
| CURRENT | 0.12404 | 0.06914 | 1.794 | 0.074881 |
| TIDE | -0.002979 | 0.0009788 | -3.044 | 0.0027730 |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |  |
| :--- | :--- | :---: | :--- | :---: |
| s(AGE) | 5.202 | 15.052 | 0.014762 |  |
| s(PCA) | 5.523 | 14.487 | 0.022309 |  |
|  |  |  |  |  |
| R-sq. (adj) $=0.188$ | Deviance explained $=83.5 \%$ |  |  |  |
| GCV score $=202.28$ | Scale est. $=180.42$ |  | $\mathrm{n}=164$ |  |

The smooth term relating deviation index to PCA (Point of Closest Approach) in the selected model is shown in Figure 12. The spline shows weak evidence that swimming paths showed a non-linear relationship with point of closest approach, however the confidence intervals span zero across a wide range of X. Secondly, the rugplot reveals that the observations were not
uniformly spread across X . In other words, few observations were made when boats approached no closer than $500-1000 \mathrm{~m}$ of the whale. There seems to be a confounding effect of age.

Terms in the Selected Model Describing Variability in Whale Path Deviation


Figure 12. TOP LEFT, and TOP CENTER -- Relationship between smoothed component (solid line) of the two non-linear explanatory variables (AGE and PCA) selected in the fitted GAM (after accounting for the effects of the other terms), and the response variable, path deviation index. The explanatory variable, maximum number of boats observed within 1000 m , was allowed up to 9 d.f. and the degree of smoothing ( $\approx 1.48$ d.f.) was automated by mgev. The xaxis contains a rugplot, in which small ticks mark locations of observations. Zero on the y-axis corresponds to no effect of the covariate on the estimated response (deviation index). Values above zero on the $y$-axis indicate positive correlation, i.e., an erratic, or above-average, path deviation index. The y-axis is labeled s(covariate name, estimated degrees of freedom). The dashed lines represent $\pm 2$ standard errors, or roughly $95 \%$ confidence intervals. NEXT FIVE PLOTS (top right, middle row, bottom left) - The linear terms that entered the model. BOTTOM RIGHT - This plot shows the residuals of the fitted model. No pattern is evident, indicating that the model fitted the data well, and that the maximum likelihood approach was able to account for any overdispersion in the response data.

Directness index. The model that fitted the path directness index data best included two vessel traffic variables (PCA and BOATS), as well as YEAR, POD, and AGE (Table 13). Model fit was improved by dropping the intercept term. The model demonstrated some power to describe variation in directness index, accounting for $53.3 \%$ of the deviance (which is a better metric for quasi-family models than the adjusted R-squared value of 0.0326 ). The variables YEAR, POD and PCA entered the model as linear terms.

Table 13: Summary of selected model describing heterogeneity in path directness index as functions of covariates selected by mgcv.

Family: quasi
Link function: log
Formula:
$\mathrm{DI} \sim$ YEAR $+\mathrm{POD}+\mathrm{s}(\mathrm{AGE})+\mathrm{PCA}+\mathrm{s}($ BOATS $)-1$
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|\mathrm{t}\|)$ |
| :--- | :--- | :--- | :--- | :--- |
| YEAR | -0.00014202 | $1.553 \mathrm{e}-05$ | -9.145 | $2.9417 \mathrm{e}-16$ |
| PODJ | -0.040724 | 0.03777 | -1.078 | 0.28262 |
| PODK | 0.090947 | 0.04594 | 1.98 | 0.049479 |
| PODL | -0.050198 | 0.0372 | -1.349 | 0.17916 |
| PCA | $3.4896 \mathrm{e}-05$ | $1.596 \mathrm{e}-05$ | 2.186 | 0.030307 |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |
| :---: | :--- | :--- | :--- |
| S(AGE) | 1.967 | 4.6553 | 0.098005 |
| s(BOATS) | 1 | 5.4682 | 0.020626 |

R-sq. $(\mathrm{adj})=0.0544 \quad$ Deviance explained $=53.3 \%$
GCV score $=0.060885 \quad$ Scale est. $=0.058298 \quad \mathrm{n}=164$

Figure 13 shows the linear and non-linear terms that entered the model and the residuals of the fitted GAM. While there is no dramatic evidence of a pattern in the residuals, there is some suggestion of asymmetry about zero. Recall that directness index was bounded between 0 and 1 , but that direct paths (i.e., those near 1 ) were much more common than those near 0 . We found that the best model specification was the quasi-likelihood framework approach with a log link function. However, model fit and convergence may have been constrained by the asymmetry of this response variable.

## Terms in the Selected Model Describing Variability in Whale Path Directness



Figure 13. TOP-- Relationships between smoothed component (solid line) of the smoothed explanatory variables (AGE and BOATS) selected in the fitted GAM, and the response variable, path directness index. The explanatory variables, age and maximum number of boats recorded by the theodolite operator, was allowed up to 9 d.f. and the degree of smoothing was automated by mgev. The x-axis contains a rugplot, in which small ticks mark locations of observations. Zero on the $y$-axis corresponds to no effect of the covariate on the estimated response (deviation index). Values above zero on the $y$-axis indicate positive correlation, i.e., a more direct path. The y -axis is labeled s (covariate name, estimated degrees of freedom). The dashed lines represent $\pm 2$ standard errors, or roughly $95 \%$ confidence intervals. Overall, these plots suggest that young and old animals tended to mill in the study areas more than middle-aged whales (ca. 40a). The boat traffic plot suggests that when fewer than 10 boats were in the study area with the whale, paths tended to be less direct than when more than 10 boats were in the area. NEXT THREE PLOTS Relationships between the three linear terms (YEAR, POD and PCA) and the response variable. Note that YEAR and PCA explained negligible components of the variance, but their retention improved overall model fit. BOTTOM RIGHT -- Residuals of the fitted model. The model fitted the data reasonably well, and the maximum likelihood approach (with a constant variance term) was able to account for overdispersion in the response data. Some evidence of asymmetry about zero in the y-axis remains, suggesting that some heterogeneity remains in the fitted model. [Note that while approximately half of the values are positive, and half negative, the largest negative values are larger than the largest positive values - this reflects the boundaries of the original scale, which was bounded by 0 and 1 , but values of DI tended to be nearer 1 than 0 .]

Surface active behavior Surface active behavior tended to occur in bouts widely separated in time. As a result, many tracks had no surface active behavior. Those that did have any at all, tended to have at least a few events and could have many. We normalized the rate of SAB to number of events per hour, but found the model was unable to fit high rates of SAB , perhaps due to disproportionately large corrections in short tracks (i.e., if the interval between bouts is large compared to the sampling period, the correction for sample period would bias the data). Then we tried to treat SAB as either present (1) or absent (0) during a track (SAB.1.0). We found this value was positively correlated with track duration, as expected, but the GAM analysis could correct for this when considering other parameters. As a result, we analyzed both SAB and SAB.1.0, in hopes that asking two variations on a common question with opposite bias would elucidate underlying trends.

The results for SAB are shown in Table 14 and Figure 14. The results for SAB 1.0 are shown in Table 15 and Figure 15.

The model that fitted the SAB data best included only one vessel traffic variable (SUM100), but also POD and AGE (Table 14). Model fit was improved by dropping the intercept term. The analysis of SAB suggests that young animals were highly active, but this rate slowed as animals reach sexual and physical maturity, and by senescence, SAB was rare, although the trend was insignificant at most ages (Figure 14, UPPER LEFT). Rates of surface active behavior were higher in members of K pod than the other two pods (Figure 14, UPPER RIGHT). The effect of boats (SUM100, Figure 14, LOWER LEFT) was linear; SAB was highest when boats were absent, and lowest when number of boats within 100 m of the whale approached 4.

The model that fitted the SAB.1.0 data best included only one vessel traffic variable (SUM400) (Table 15). The analysis of SAB.1.0 suggests SAB was most likely to occur when the number of boats within 400 m of the whale was small (1-3 boats; Figure 15).

The consistent trend for both SAB and SAB. 1.0 to be maximized when the number of boats was small and they were in close proximity suggests that bias from sample duration was overcome in this aspect of the analysis.

Age was not a factor in SAB.1.0, perhaps suggesting that the probability of engaging in SAB is equal for all age classes, but that younger animals tend to do more once they get started. Similarly, pods may be equal in their probability of initiating SAB , but differ in the number of events once it is initiated.

Table 14. Summary of selected model describing heterogeneity in rates of surface active behavior as linear (top) and smooth (bottom, i.e., non-linear) functions of covariates selected by mgev.

Family: quasi
Link function: log
Formula:
SAB ~ POD $+\mathrm{s}(\mathrm{AGE})+$ SUM100-1
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|\mathrm{t}\|)$ |
| :---: | :--- | :--- | :--- | :--- |
| PODJ | 0.52211 | 0.394 | 1.325 | 0.18751 |
| PODK | 1.6992 | 0.4161 | 4.084 | $7.7327 \mathrm{e}-05$ |
| PODL | 1.1554 | 0.308 | 3.751 | 0.00026512 |
| SUM100 | -0.64357 | 0.4003 | -1.608 | 0.11034 |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |
| :--- | :--- | :--- | :--- |
| s (AGE) | 4.154 | 5.755 | 0.24128 |

R-sq.(adj) $=0.0582$ Deviance explained $=29.9 \%$
GCV score $=13.705 \quad$ Scale est. $=12.889 \quad n=137$


Figure 14. TOP - Relationship between smoothed component (solid line) of the explanatory variables (AGE, POD and SUM100) selected in the fitted GAM, and the response variable, rate of surface active behavior (average number of events per hour). The explanatory variables were allowed up to 9 d.f. and the degree of smoothing was automated by mgev, but only AGE was selected as a smoothed term. POD and SUM100 entered the model as linear terms. The x-axis contains a rugplot, in which small ticks mark locations of observations. Zero on the y-axis corresponds to no effect of the covariate on the estimated response (rate of surface active behavior). Values above zero on the $y$-axis indicate positive correlation, i.e., higher rates of surface active behavior. The $y$-axis is labeled s(covariate name, estimated degrees of freedom). The dashed lines represent $\pm 2$ standard errors, or roughly $95 \%$ confidence intervals. BOTTOM RIGHT - Residuals of the fitted model. The plot of residuals indicates poor ability to explain high rates of SAB.

Table 15. Summary of selected model describing heterogeneity in likelihood of surface active behavior as linear (top) and smooth (bottom, i.e., non-linear) functions of covariates selected by mgev.

Family: binomial
Link function: logit
Formula:
SAB.1.0~s(SUM400)
Parametric coefficients:

|  | Estimate | std. err. | t ratio | $\operatorname{Pr}(>\|\mathrm{t}\|)$ |
| :--- | :--- | :--- | :--- | :--- |
| (Intercept) | -0.99329 | 0.1941 | -5.118 | $3.0939 \mathrm{e}-07$ |

Approximate significance of smooth terms:

|  | edf | chi.sq | p-value |
| :--- | :--- | :--- | :--- |
| $\mathrm{s}($ SUM400 $)$ | 3.214 | 7.0758 | 0.08098 |

$\begin{array}{lll}\text { R-sq. }(\mathrm{adj})=0.0389 & \text { Deviance explained }=5.97 \% & \\ \text { UBRE score }=-0.0097255 & \text { Scale est. }=1 & \mathrm{n}=153\end{array}$
Terms in the Selected Model Describing Variability in the Probability of Surface Active Behavior


Figure 15. LEFT - Relationship between smoothed component (solid line) of the explanatory variables (SUM400) selected in the fitted GAM, and the response variable, probability of surface active behavior occurring. The explanatory variables were allowed up to 9 df and the degree of smoothing was automated by mgev. The x -axis contains a rugplot, in which small ticks mark locations of observations. Zero on the $y$-axis corresponds to no effect of the covariate on the estimated response (likelihood of surface active behavior). The y-axis is labeled s(covariate name, estimated degrees of freedom). The dashed lines represent $\pm 2$ standard errors, or roughly $95 \%$ confidence intervals. RIGHT - Residuals of the fitted model. The plot of residuals indicates a good ability to classify samples into those with a high versus those with a low probability of having a surface active event occur.

## DISCUSSION

## COMMENTS ON GENERAL ANALYSIS APPROACH

Due to sample size constraints, it was not possible to use an ideal approach to data analysis. With 10 classes of independent variables (Year, day of season, time of day, site, age, sex, pod, individual, distance to boats, and number of boats), there would be over 1000 possible conditions, even if variables with large ranges like distances to boats, number of boats, day of season, and individual were placed into binary categories, as would only be appropriate for variables like site, or sex. Ideally there would be a sample of at least 10 observations in each cell (over 10,000 tracks). That is, even ignoring potentially important variables (e.g., behavior states during tracks, individual variation) and over-simplifying others (e.g., number of boats and distance), far more data would be needed than we were able to collect. Indeed, for some analyses, far more data would be required than there are whales to be studied in the population of interest.

We chose two different approaches to deal with these limitations. One was to reduce data to baseline and exposure conditions. While this ignored a great deal of potentially important information, the assumption made would be that the data were representative of overall conditions. That is, data were collected during five months of the year, 14 hours of the day, at two different sites, individuals ranging in age from new calves to the oldest individuals in the population, from both males and females, 45 individuals from all three pods (roughly $50 \%$ of the whales in the population), and with boat densities ranging from 0 to the highest in the area.

The other was to use Log-Linear Analysis and General Additive Models. These approaches look at the relative importance of various factors. "Importance" is a combination of magnitude of effect size and statistical significance. These approaches are implemented sequentially. That is, analysis begins anew after each important variable is identified. As a result, only one of a group of variables correlated with each other might be identified, even though another might be important in its own right. While such compromises limit the interpretations that can be drawn from the analysis, these techniques are suitable for a sparse data set such as ours.

Finally, we combined these two approaches to a limited degree. For example, site was found to be a significant factor. Therefore, we looked at data separately by site. Such results cannot be extrapolated to a large portion of the range, and such reanalysis needs to be pursued cautiously. As the number of analyses increases, the probability of obtaining spurious results increases.

## SCAN-SAMPLING OF FOCAL GROUPS

General conclusions. Behavioral sequences varied significantly between locations, as expected. They also differed significantly with the presence of vessels. It is possible that the observed differences between locations is actually related to pods using the two sites with different intensity and some differences in behavioral sequences existing between pods.

Southern resident killer whales behaved differently at the two study sites. In addition, the three pods used these two sites with different intensities; J pod was more likely to be observed at the North site while L pod was more likely to be at the South site. Similarly, schools composed of members of all three pods were more likely to be observed at the North site.

Boats interacting within close vicinity of the whales (within 100 m ) affected their activity budget in a similar fashion at both sites. Whales were significantly less likely to be foraging and significantly more likely to be traveling when boats were around. This finding is in agreement with previous studies undertaken with the northern resident population (Williams et al. 2006). This effect raises concerns about the implications of this short-term displacement for the ability of individuals to acquire prey and the potential for long-term repercussions at the level of the population; especially in the light of the level of whale-watching activities carried out with Southern Residents. Vessel activity is also believed to reduce foraging success in other species (Tursiops, Allen and Read 2000).

After controlling for effects of site and boats, there was no significant difference in the data between years. Additional years of study will be needed to determine whether the three years happened to be similar in factors that vary on an annual time scale (e.g., prey abundance), or if our results will be robust across a range of conditions.

This study shows whales are displaced short distances by the presence of vessels. Thus whales may be displaced from optimal foraging routes. Further, Bain and Dahlheim (1994 and see Bain et al. unpublished ms.) suggested noise would mask echolocation signals and reduce foraging efficiency. These data are also consistent with observations of Northern Residents (Williams 2003; Williams et al. 2006.). Thus we would encourage further study to determine how noise and proximity interact to reduce foraging effort.

The influence of pod identity. Boat interactions appear to have the same effect on all three pods, yet more sampling is required to fully understand the interaction between the composition of focal groups and the influence of boats on their activity state. Since pods appear to use certain areas preferentially (Hauser et al. 2005, 2006), and whales use both study sites differently, it was not surprising to see that the site effect observed earlier may actually relate to a pod effect. J pod, which spends the most time in the Sound, was more likely to be observed foraging than the two other pods. That pod was also significantly more likely to be foraging at the south site than at the north site, while the two other pods were equivocally foraging at both sites. This may relate to a better knowledge of the area.

The influence of the distance between the focal school and boats. Boats within 100m clearly have a significant effect on whale behavior. Boats between 100 m and 400 m also have a
significant effect, although we cannot say whether boats throughout this range cause effects, or the significance is due to effects of vessels just over 100m away. More spatial resolution in the data collection protocol would have been needed to address this issue (e.g., in 2005 we divided the 100-400 ring into a 100-200 ring and a 200-400 ring, but one year of data was insufficient for analysis). Similar but smaller differences were observed when the closest vessels were between 400 m and 1000 m away. However, the sample is such that the results in the $400-1000$ ring differ significantly neither from the larger effects when boats were closer than 400 m , nor from no effect at all. That is, a larger sample would be needed to determine whether effects extend beyond 400 m . These results suggest the zone of influence of vessels in this area exceeds the 100 m radius in current guidelines, and that more extensive guidelines such as those developed by the Whale Watch Operators Association NorthWest (2003), or those proposed by Orca Relief Citizens Alliance (2005) will be necessary to completely prevent behavioral changes caused by vessels, and more data will be needed to determine appropriate guidelines.

One potential explanation for these results is that noise impairs the ability to forage using echolocation (Soto et al. 2006). Previous studies have shown that the active acoustic foraging range of killer whales can be reduced or masked by boat noise (Erbe 2002; Bain and Dahlheim 1994, and see Bain et al. unpublished ms.). Since received noise levels typically decline with distance, the closer the boats are, the more echolocation range is reduced (Williams et al. 2002a), potentially leading to foraging disruption, as suspected here. To test this hypothesis, acoustic monitoring would be required, as noise produced varies with engine type, and the speed at which boats operate. These data were beyond the scope of this study. The changes in deviation and directness indices observed here and reported by Williams et al. (2002ab) reflect increases in non-directional movement that would make behavior tend to more closely resemble foraging, indicating movements to avoid vessels cannot account for a decrease in foraging.

## THEODOLITE TRACKING OF FOCAL INDIVIDUALS

General conclusions. In the binary analyses, there was little change in values for the vessel present condition due to the addition of the 2005 dataset to the 2003-4 dataset (compare with Bain et al. 2006). However vessel absent values did change, resulting in changes in the significance of some results, although the direction of differences did not change. The 2005 data constituted only $16 \%$ of the vessel absent data, but $39 \%$ of the vessel present data. This suggests that the sample for vessels present is large enough, but the no-boat sample is still too small to produce robust results. This suggests focusing future effort early in the season when vessel traffic is less ubiquitous and more no-boat data can be obtained.

Despite a model specification approach that penalized over-parameterization, all six models fitted the data better with boat variables included than when they were excluded. The models lend support for concluding that boats exerted a small but significant effect on behavior of southern resident killer whales in 2003-2005, but that the relationships were complex and often non-linear.

Williams (1999) suggested that vessel number and vessel proximity were different dimensions of vessel traffic, and that a whale's response to changes in vessel number is likely to
occur independently of its response to changes in proximity, and vice versa. As such, an increase in proximity need not have the same effect as an increase in number. This study supports his conclusion. Further, there are hints in our dataset that number and proximity may interact. That is, boat counts at different distances entered the models independently. In some cases the effects of changing boat numbers at different distances were similar (e.g., boat numbers within 100 m and 400 m both led to increases in respiratory interval with increasing boat number in the range of $0-4$ boats). In other cases, trends were different (e.g., respiratory interval increased with increasing boat number when the count only included boats within 100 m , but respiratory interval decreased with increasing boat number when all boats within about 2 km of the focal whale were included in the count).

We also observed non-linear effects. Qualitatively, sometimes it appeared there was a baseline distribution of behavior when boats were absent, a trend from 1 to about 3 vessels, and the opposite trend when the number of vessels was large ( $>10$ ). Intermediate numbers produced different trends than large or small numbers of vessels, though it is unclear whether intermediate numbers result in a distinct pattern of changes, or simply reflect the interactions of trends when vessel numbers are small with those when numbers are large. The result was sometimes a Ushaped pattern, and in other cases a linear pattern where the mean occurred at an intermediate number of boats. Similarly, non-linear trends with distance were observed.

The complexities described above may account for inconsistencies among studies, many of which simply compared a vessel present to a vessel absent condition. It is striking how well our results agree with those for Northern Residents (Williams and Ashe in press) when vessel number is taken into account.

Directness Index. The decrease in directness of travel with vessel traffic has appeared consistently in studies such as this one (Williams et al. 2002ab, Smith and Bain 2002). This pattern is consistent with whales making concerted efforts to evade boats. Including the 2005 data resulted in a slight reduction of effect size relative to 2003-4. The effect size $(8 \%)$ is of similar magnitude to that reported for one boat paralleling the path of Northern Resident killer whales (Williams et al. 2002b): in the presence of boats, Northern Residents adopted a swimming path that was $13 \%$ less direct than during preceding, no-boat conditions. The GAM analysis confirmed both vessel number and proximity were significant factors even after taking natural factors into account.

Deviation Index. The deviation index remained higher when boats were present, though inclusion of the 2005 data meant the result was no longer significant in the binary analysis (compare with Bain et al. 2006). This trend has been consistent across studies, but the significance has been variable. Experiments conducted on female Northern Residents in 1995-6 (Williams et al. 2002b) and male Northern Residents in 1998 (Williams et al. 2002a) produced significant differences in this index, although the differences were insignificant in males in 19956. However, the GAM analysis found both vessel number and proximity influenced the deviation index, suggesting the non-significant result in the binary analysis may be due to variability caused by natural factors.

The deviation index would be expected to be relatively high during socializing and foraging. Tide and current were natural factors correlated with deviation index. Felleman (1986) suggested that foraging strategies of whales should take into account current related movements of their salmonid prey. This relationship merits additional investigation.

Breathing Patterns. Breathing changes have been inconsistent from one study to another. However, the inclusion of 2005 data resulted in little change from results based on the previous two years. The binary analysis showed respiratory intervals were longer when vessels were present. The GAM analysis suggests that interbreath-interval increases with increasing vessel number when the number of vessels is small (from 1 to about 5 vessels), but decreases when the number of vessels is large. This "U-shaped" response pattern may account for the inconsistent results. There may be alternative tactics employed that vary depending on vessel number and proximity. Vessel proximity did not enter directly as a factor, although boat counts at different distances entered separately, suggesting distance has some relevance. Perhaps this index is more sensitive to distances throughout the track relative to momentary close approaches than other indices are. Additional data will be needed to confirm whether the result reported here is robust in a wider range of conditions.

Surface Active Behavior. Changes in surface active behavior have been significant in many studies, although the direction of the change varies from one study to another. Our results suggest the inconsistency may be due to differences in methodology. For example, our work, and that of Williams (1999) suggest that SAB is maximized when one or a small number of boats approach closely, but SAB may be inhibited by other configurations of vessels. Data collected when boats are primarily in an inhibitory configuration may find vessels reduce rates of SAB. Alternatively, studies that pool all configurations may find no effect.

The analysis is further complicated by the relationship between track duration and measured values. Analysis of rates may need to be limited to longer tracks than some of those used here. Longer tracks would also be helpful for one-zero sampling, as that would allow subdividing tracks into multiple short segments. There is potential for binary analyses to be confounded by track duration, and other variables to be obscured in the GAM analysis. An alternative analysis approach would have been to truncate tracks to a fixed duration, resulting in a decrease in bias at the expense of an increase in noise due to reduced sample sizes.

Further, inclusion of the 2005 results emphasizes the importance of sample size. Although SAB events occurred in only one no-boat track in 2005, rates during that track were so high it resulted in nearly a 3-fold increase in the mean rate compared to 2003-4 alone, and while the sign of the difference did not change, the difference became insignificant ( $\mathrm{p}>.09$ ). That is, after nearly nine months of effort, the sample is still small enough that results can be swayed by a single sample. However, the 1-0 sampling measure remained highly significant ( $\mathrm{p}<.001$ ).

Although environmental factors, such as time of day and time of year, appeared to influence rates of surface active behavior in the 2003-4 dataset, inclusion of the 2005 data prevented these factors from entering the model. The tendency of surface active behavior to occur in bouts, along with the fact that surface active behavior is a somewhat artificial class composed of behavior patterns with a wide-range of functions, make it difficult to address these
behavior patterns with statistical rigor. While an $8 \%$ difference in directness index was statistically significant, a $38 \%$ difference in rates of SAB was not in the binary analyses. Nonetheless, the increased probability of SAB occurring in the presence of vessels appears robust, as the effect is large and present in numerous datasets.

One could speculate that threat displays consisting of surface active behaviors such as breaches, slaps, and fluke lifts (Tavolga 1966, Norris et al. 1994, Bain, pers. obs., Lusseau in press ab ) increased when vessels were close but not close enough to trigger an escape response (see Hediger 1964 for a discussion of the concept of flight distance). At greater distances, surface active behavior could be reduced to avoid attracting the attention of vessel operators. Baseline rates would reflect the use of surface active behavior for purposes independent of vessels such as communication among whales, foraging, and non-communicative purposes such as self-grooming.

Threat displays are precursors to physical aggression (e.g., leaping onto the back of a whale attempting to breathe and using the peduncle to swat another whale) and give the observer the opportunity to change behavior before the agonistic interaction escalates. Since Surface Active Behavior includes agonistic displays, it may reflect stress. Therefore, it is important to gain a better understanding of this complicated index of behavior.

Swimming Speed. The trend in swimming speed with respect to vessel traffic has been inconsistent from one study to another (e.g., contrast Kruse 1991 with Williams et al. 2002b). In this study, the binary analysis showed no difference. The GAM analysis suggested site and number of boats could be important. Given the potential for changes in swimming speed to carry energetic costs to whales, as well as reflecting their physical condition, the factors influencing swimming speed deserve more careful assessment.

Vessel Proximity. Killer whales had vessels in proximity for a large proportion of daylight hours. Even with stewardship programs in place, whales spent about $25 \%$ of their time (range 23.3 to $28.8 \%$ across the individual field seasons) with at least one vessel closer than the 100 meters allowed under current guidelines. Groups were within 400 m of vessels over $50 \%$ of the time (range 56.7-81.0\%). These vessels were close enough to cause behavioral changes. Groups were within 1000 m of vessels over $75 \%$ of the time (range $75.7-90.1 \%$ ). We were unable to determine whether or not vessels in the outer portion of this range affected behavior. Vessels were sighted on nearly $100 \%$ of scans (range $97.5-99.5 \%$ ), suggesting nearly continuous exposure to vessel noise.

## COMPARISONS WITH OTHER SPECIES

The results reported here exhibit similarities and differences with other species. Effects being stronger when vessels are within 100 m than when they are farther away is a common finding (e.g., Nowacek et al. 2001, Ritter 2003). A decrease in foraging behavior is also commonly found. Increases in travel and surface active behavior are also commonly found. Increases in horizontal avoidance and energy expenditure have also been reported in other species (e.g., Tursiops, Yazdi 2005).

In contrast, measures of swimming speed have varied among species and among studies within species, with some studies reporting increases (Orcinus sp.: Kruse 1991; Tursiops truncatus: Nowacek et al. 2001), some reporting no change (Orcinus sp.: this study; Globicephala macrorhynchus, Stenella coeruleoalba, Steno bredanensis: Ritter 2003), and some reporting both increases and decreases depending on vessel speed (Stenella frontalis, Tursiops truncatus: Ritter 2003). Some species show increased dive times as reported here (e.g., Eschrichtius, Sumich 1983), while other species shorten dives in the presence of boats. Some species are displaced from regions by vessels (e.g., Tursiops: Allen and Read 2000, Yazdi 2005, Bejder et al. in press), in contrast to resident killer whales who continued to use the same range in the presence of vessels.

## RECOMMENDATIONS FOR FUTURE RESEARCH

This study found evidence consistent with small changes in behavior in the presence of vessels. These effects support the development and enforcement of regulations for whale watchers, both recreational and commercial. Future research could address whether different approaches to whale watching have different degrees of impact (as paralleling and leap-frogging were compared by Williams et al. 2002ab). However, since it has proven difficult to demonstrate significant differences in behavioral responses to currently accepted practices and no disturbance, it could be expected to take carefully controlled experiments or many years of observation to compare the implications of proposed guidelines to current guidelines. Future research could also attempt further elucidation of age, sex, pod, and individual differences in responses to vessels.

It is possible that some may object to regulations and point to inconsistency of results among studies to question whether science adequately supports regulation. In that case, additional seasons of intensive effort such as those reported here could be justified. However, another approach to establishing which results are reproducible is to take advantage of existing data, such as those collected by Smith and Kriete (Smith and Bain 2002, Kriete 1995 and 2002). If new data are to be collected, we would point out that roughly $90 \%$ of our observations of whales without boats were obtained in May and June, despite extensive effort in July and August, and suggest that effort be focused early in the season. Given that variables like year and time of year are likely to be important, it would be valuable to mount an intensive effort so that changes through time do not confound the results. It may be valuable to add a third site (e.g., near the sites used by Kriete (2002) and Smith and Bain (2002), where the field of view is longer than at our North Site but whales tend to travel closer to shore than at the South Site. This site would be especially valuable for scan sampling work.

It is likely to be more productive to conduct research on impacts of vessel traffic through other mechanisms. Bain et al. (unpublished ms.) have suggested that the magnitude of impact through reduced foraging efficiency due to vessel noise is likely to be much larger than impact due to the increase in energy expenditure. Stress is a potential mechanism that has not been addressed. Similarly, Williams et al. (2006) suggested that for Northern Residents, reduction of energy acquisition for whales as vessels disrupt feeding activity has the potential to be 4-6 times greater than the increased energetic cost of avoiding boats. We urge additional analyses of this
and other datasets to place subtle, short-term behavioral changes in an energetic context. Any attempt to link vessel traffic to the decline of Southern Residents will require the synthesis of behavioral, acoustic, physiological and population dynamics studies in a quantitative modeling framework.

Studies on acoustic mechanisms could take several approaches. Noise could be measured with an acoustic tag placed on a whale. A less intrusive approach would be to measure noise with a hydrophone towed near whales. A third approach would be to incorporate noise monitoring into whale watch stewardship programs such as Soundwatch and M3. Shore-based hydrophones would allow monitoring changes in noise and behavior simultaneously. These data would complement source level and fixed-point ambient noise measurements already obtained. Data on how whales locate prey would also be needed, which might be accomplished through use of a Crittercam or imaging sonar (Ponganis et al. 2000, Hawks-Johnson 2003, Benoit-Bird et al. 2004).

Habituation to whale watching has been identified as a potential research area. The term habituation has been used both in the strict psychological sense, and a more general sense. Strictly, habituation is a lessening of a response to repetitive stimuli that is not due to fatigue. In discussions regarding habituation of killer whales to vessel traffic, it has also been used to refer to a lessening in response due to suites of related stimuli through a variety of mechanisms.

Whale watching does not lend itself to habituation in the strict sense. Boats are frequently changing the stimuli received by killer whales. Stimuli change as engines are turned on and off, engine speed changes, directions of travel change, distances between vessels and killer whales change, and spatial arrangements of multiple vessels change. Thus it is not surprising that after more than 30 years of exposure to whale-oriented vessel traffic, both Northern and Southern Residents still exhibit behavioral changes to vessel traffic.

Williams (1999) suggested killer whales adopted various tactics in the presence of vessels with various operating practices (speed, noise, distance, numbers, etc.). Thus it is possible for killer whales to optimize their selection of tactics in response to vessel practices, and the optimization process would correspond to habituation in the less strict sense. The similarity of the results for Southern Residents to those for Northern Residents, and the presence of significant effects in both Northern and Southern Residents after decades of intensive whale watching suggest that habituation in the strict sense is far from complete (for reasons mentioned above) and further habituation in the broad sense is unlikely to be substantial if these populations have, in fact, converged on optimal responses to vessels, given physiological and physical constraints.

Future research could focus on whether true habituation could be facilitated by limiting whale watching to a single vessel operating in a consistent manner (see Williams et al. 2002ab). Research to determine whether reduced time foraging is biologically significant, and whether noise reduces foraging success to the point that the optimal tactic is to avoid the energetic costs of foraging dives until the probability of successful prey detection becomes high enough would be valuable. The relationship between operating practices and noise (propulsion systems,
operating speeds, viewing distances) and foraging effort and success would also be valuable to determine.

Unfortunately, no data exist to address whether responses to vessels changed prior to Kruse's (1991) work in 1983 with Northern Residents or Kriete's (1995) work in 1987 with Southern Residents. Having said that, data from a NMFS-funded experimental study on Northern Residents in summer 2004 were collected to maximize sampling of individuals tracked in 1984, 1985, 1995-8, and 2002 (Williams and Ashe in press). This represents a time-series spanning 20 years, and would present a good opportunity to assess whether individuals changed their behavioral tactics around boats over time, versus alternative explanations for changing behavior, such as aging or changes in whalewatching practices.

Strong behavioral responses of animals to disturbance do not always indicate populationlevel effects. Indeed, inter-specific variability in site fidelity and availability of alternative suitable habitat make it difficult to infer population-level consequences from inter-specific variability in sensitivity to disturbance (Gill et al. 2001). Thus it will be important to develop the link between short-term behavioral effects and population dynamics (see Bain et al. unpublished ms .).

## SUMMARY AND CONCLUSIONS

As with Northern Residents, the presence of vessels inhibited foraging behavior. This may lead to a reduction in energy acquisition, and a priority research area would be to address directly through field studies whether prey capture actually is affected by vessel presence. In addition, modeling exercises should be carried out to identify potential mechanisms and the biological significance of any effects found.

Horizontal avoidance (evidenced by changes in Directness and Deviation indices) appears consistently across studies, although the statistical significance may depend on the sample size of the study and the pattern of vessel traffic experienced by the exposure group. This may lead to an increase in energy expenditure, and again, research designed to test this hypothesis should be pursued.

Surface active behavior often shows significant differences depending on vessel activity, although such results are inconsistent in their magnitude and direction. This indicates that surface active behavior can be triggered by vessels, in addition to its natural occurrence for other purposes. Surface active behavior is largely composed of threat displays, so a relationship to vessel traffic is not unexpected. Non-linear responses to changes in vessel proximity and number probably account for the inconsistent results. Since many surface active behaviors are threat displays, they may be indicative of stress, and we urge additional research on captive and free-ranging killer whales to assess potential linkages among anthropogenic activity, stress and rates of surface active behavior. Some surface active behaviors like breaching require increased energy expenditure, so should be considered when calculating cumulative effects.

Average inter-breath interval (IBI) and swimming speed do not show consistent changes across studies. However, when controlling for vessel number, our respiratory interval results agree well with those of Williams and Ashe (in press), so the inconsistencies may reflect inconsistency in sampling conditions, along with the importance of other factors in determining breathing patterns. This is not to say that other measures of breathing patterns might not vary more directly with vessel traffic. Alternatives to mean IBI, such as applying chaos theory to sequences of respiratory intervals (Bain 1995), have not been examined, to the best of our knowledge, but should be.

The behavior of Southern Residents in the presence of vessels is consistent with that observed in Northern Residents. This increases the confidence that can be placed in crosspopulation extrapolations, and in using individual Northern Residents as proxies for Southern Residents when conditions preclude experimentation on Southern Residents. Indeed, it is time for a meta-analysis of existing data from both populations, given the potential to increase statistical strength through the larger sample size to answer questions that small sample size precludes addressing through single studies alone.

Future research should focus on prey acquisition, and potential impact through other mechanisms such as noise and stress.

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## REFERENCES

Adimey, N. M. (1995). A descriptive study of the percussive behavior of orcas, Orcinus orca, in Johnstone Strait, British Columbia. MS. thesis, Nova Southeastern University, Fort Lauderdale, Florida.

Allen, M. C. and A. J. Read. 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Mar. Mamm. Sci. 16:815-824.

Angradi, A.M., Consiglio, C. \& Marini, L. 1993. Behaviour of striped dolphins (Stenella coeruleoalba) in the Central Tyrrhenian Sea in relation with commercial ships. Proc. 7th Ann. Conf. ECS, Inverness, Scotland. 77-79.

Bailey, H. and D. Lusseau. 2004. Increasing the precision of theodolite tracking: Modified technique to calculate the altitude of land-based observation sites. Mar. Mamm. Sci. 20:880-885.

Bain, D. E. 1986. Acoustic behavior of Orcinus: sequences, periodicity, behavioral correlates and an automated technique for call classification. In (B. C. Kirkevold and J. S. Lockard, eds.) Behavioral Biology of Killer Whales. Alan R. Liss. New York. 335-371.
Bain, D. E. 1995. Breathing patterns and health: a place for chaos theory? Poster presented to the International Marine Animal Trainers Association Conference. Las Vegas, NV.

Bain, D. E. 2002. A model linking energetic effects of whale watching to killer whale (Orcinus orca) population dynamics. Friday Harbor Laboratories, University of Washington, Friday Harbor, Washington.

Bain, D. E., W. Anderson, F. Felleman, M. Harris and P. Higgins. 2002. Orca Recovery Conference Report 2002. Earth Island Institute. 30 pp.

Bain, D. E. and M. E. Dahlheim. 1994. Effects of masking noise on detection thresholds of killer whales. Pages 243-256 in T. R. Loughlin, editor. Marine mammals and the Exxon Valdez. Academic Press, San Diego, California.

Bain, D. E., J. C. Smith, R. Williams and D. Lusseau. 2006. Effects of vessels on behavior of southern resident killer whales (Orcinus spp.). NMFS Contract Report No. AB133F03SE0959 and AB133F04CN0040. 61 pp.

Bain, D. E., R. Williams and A. W. Trites. Unpublished ms. Potential effects of whale watching on killer whale (Orcinus orca) population dynamics: insights from three models.

Bejder, L., S. M. Dawson and J. A. Harraway. 1999. Responses by Hector's dolphins to Boats and swimmers in Porpoise Bay, New Zealand. Marine Mammal Science. 15(3):738-750.

Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. Connor, M. Heithaus, J. WatsonCapps, C. Flaherty, and M. Krützen. In press. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology.

Benoit-Bird, K. J., B. Wursig and C. J. McFadden. 2004. Dusky dolphin (Lagenorhynchus obscurus) foraging in two different habitats: active acoustic detection of dolphins and their prey. Mar. Mamm. Sci. 20:215-231.

Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford and K. C. Balcomb III. 1990. Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. Rep. IWC Special Issue 12:383-405.

Caswell H. 2001. Matrix Population Models. Sinauer Associates, Boston, Massachusetts.
Constantine, R. 1997. Monitoring the commercial swim-with-dolphin operations in the Bay of Islands. Science for Conservation. Dept. of Conservation, New Zealand (56): 59pp.

Constantine, R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (Tursiops truncatus) due to long-term exposure to swim-with-dolphin tourism. Mar. Mamm. Sci. 17: 689-702.

Corkeron , P. 1995. Humpback whales (Megaptera novaeangliae) in Hervey Bay, Queensland. Behaviour and responses to whale watching vessels. Working paper for the Workshop on the Scientific Aspects of Managing Whale Watching, Montecastello Di Vibio, Italy, 30 March - 4 April, 1995. Canadian Journal of Zoology, 73:1290-1299

DeNardo, C., Dougherty, M., Hastie, G.D., Leaper, R., Wilson, B., and Thompson, P.M. 2001. A new technique for investigating variability in spatial relationships within groups of free ranging cetaceans. J. Appl. Ecol. 38: 888-895.

Duffus, D. A., J. Bass, J. S. Dunham and C. D. Malcolm. 1998. Ecology and recreational use of gray whales in Clayoquot Sound, Vancouver Island, Canada 1991-1997. Abstract submitted to the Whale watching Research Workshop: Biology, politics, esthetics and human attitudes. Monaco, January 18, 1998. Available at: http://office.geog.uvic.ca/dept/abstract.html

Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model. Mar. Mamm. Sci. 18:394-418.

Federal Register. 2004. Endangered and Threatened Wildlife and Plants: Proposed Threatened Status for Southern Resident Killer Whales. 69:76673-76682.

Federal Register. 2005. Endangered and Threatened Wildlife and Plants: Endangered Status for Southern Resident Killer Whales. 70:69903-69912.

Felleman, F. L. 1986. Feeding ecology of the killer whale (Orcinus orca). Master's thesis. University of Washington. 160 pp .

Felleman, F. L., J. R. Heimlich-Boran and R. W. Osborne. 1991. Feeding Ecology of the killer whale (Orcinus orca). In (K. W. Pryor and K. S. Norris, eds.) Dolphin Societies: Discoveries and Puzzles. University of California Press. Berkeley. 113-147.

Fleming, V. and T. H. Sarvas. 1999. Effects of whale watching on sperm whale (Physeter macrocephalus) behavior off Andoya, Norway. Proc. 13th Ann. Conf. ECS, Valencia, Spain. 103-107.

Foote, A.D., R.W. Osborne, and A.R. Hoezel. 2004. Whale-call response to masking boat noise. Nature 428(April 29): 910.

Ford, J.K.B., Ellis, G.M. and Balcomb, K.C. 2000. Killer Whales: The Natural History and Genealogy of Orcinus orca in British Columbia and Washington. 2nd Edn. UBC Press, Vancouver. 102pp.

Ford, J. K. B., G. M. Ellis and P. F. Olesiuk. 2005. Linking prey and population dynamics: did food limitation cause recent declines of 'resident' killer whales (Orcinus orca) in British Columbia? Canadian Science Advisory Secretariat Research Document 2005/042. 31pp.

Galicia, E. and G. A. Baldassare. 1997. Effects of motorized tourboats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. Conservation Biology. 11:11591165.

Gill, J. A., Norris, K. and Sutherland, W. J. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265-268.

Ha, J. C. 2004. Southern resident killer whale behavior workshop final report. NMFS NWFSC. 5 pp .

Hanson, M. B., R. W. Baird and G. S. Schorr. 2006. Diet studies of "Southern Resident" killer whales in their summer and fall range: prey sampling and behavioral cues of predation. 2006 Symposium on Southern Resident Killer Whales.

Hauser, D. D., M. G. Logsdon, G. R. VanBlaricom, and E. E. Holmes. 2005. Southern resident killer whale (Orcinus orca) summer distribution patterns: effects of changing temporal scales. Paper presented at the $16^{\text {th }}$ Biennial Conf. Biol. Mar. Mammals. San Diego, CA. p. 124.

Hauser, D. D., M. G. Logsdon, E. E. Holmes G. R. VanBlaricom, and R. W. Osborne. 2006. Effects of environmental factors and temporal scale on pod-specific SRKW summer distribution patterns: implications for designating critical habitat. 2006 Symposium on Southern Resident Killer Whales. Abstract.

Hawks-Johnson, S. A. 2003. The power of prey : a quantitative analysis of surface and subsurface (echosounder) observations on the foraging behavior of the southern resident community killer whales (Orcinus orca). Master's Thesis. U. Washington.

Hediger, H. 1964. Wild animals in captivity. Dover. New York. 207 pp.
Heimlich-Boran, J. R. 1988. Behavioral ecology of killer whales (Orcinus orca ) in the Pacific Northwest. Can. J. Zool. 66:565-578.

Heimlich-Boran, J.R. 1993. Social organisation of the short-finned pilot whale, Globicephala macrorhynchus, with special reference to the comparative social ecology of delphinids. Ph.D.Thesis, Univ. of Cambridge. 132pp.

Heimlich-Boran, J.R., S. L. Heimlich-Boran, R. Montero, and V. Martin. 1994. An overview of whale-watching in the Canary Islands. Proc. 8th Ann. Conf. ECS, Montpellier, France. 37-39.

Hoelzel, A.R. 1993. Foraging behaviour and social group dynamics in Puget-Sound killer whales. Anim. Behav. 45:581-91.

Janik, V. M. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Mar. Mamm. Sci. 12: 597-602.

Jones, M. L. 1988. Response of gray whales to whale watching in San Ignacio Lagoon, Mexico. Page 16 in Proceedings of the Workshop to Review and Evaluate Whale Watching Programs and Management Needs. 14-16 Nov. 1988, Monterey, CA., Center for Marine Conservation, Washington, DC.

Killer Whale Recovery Team. 2005. Draft National Recovery Strategy for Northern and Southern Resident Killer Whales (Orcinus orca). Prepared for Public Consultations, Spring 2005, for Fisheries and Oceans Canada, on behalf of the Resident Killer Whale Recovery Team. 70 pp .

Krahn, M.M., M.J. Ford, W.F. Perrin, P.R. Wade, R.P. Angliss, M.B. Hanson, B.L. Taylor, G.M. Ylitalo, M.E. Dahlheim, J.E. Stein, and R.S. Waples. 2004. 2004 Status review of southern resident killer whales (Orcinus orca) under the Endangered Species Act. U.S. Dept. Commer., NOAA Tech. Memo. NMFSNWFSC-62, 73 p.

Krahn, M. M., P. R. Wade, S. T. Kalinowski, M. E. Dahlheim, B. L. Taylor, M. B. Hanson, G. M. Ylitalo, R. P. Angliss, J. E. Stein, and R. S. Waples. 2002. Status Review of Southern Resident killer whales (Orcinus orca) under the Endangered Species Act. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-54.

Kriete, B. 1995. Bioenergetics in the killer whale, Orcinus orca. Ph.D. Thesis, University of British Columbia, Vancouver, BC. 138pp.

Kriete, B. 2002. Bioenergetic changes from 1986 to 2001 in the southern resident killer whale population, Orcinus orca. Orca Relief Citizens’ Alliance. Friday Harbor, WA.

Kruse, S. 1991. The interactions between killer whales and boats in Johnstone Strait, B.C. pp. 149-59. In: K. Pryor and K.N. Norris (eds.) Dolphin Societies, Discoveries and Puzzles. University of California Press, Berkeley, California, USA. 397pp.

Lacy, K.E., and E.P. Martins. 2003. The effect of anthropogenic habitat usage on the social behavior of a vulnerable species, Cyclura nubila. Animal Conservation 6: 3-9.

Laist, D.W., A. R. Knowlton, J. G. Mead, A. S. Collet, and M. Podesta. 2001. Collisions between ships and whales. Mar. Mam. Sci. 17: 35-75.

Lien, J. 2001. The Conservation Basis for the Regulation of Whale Watching in Canada by the Department of Fisheries and Oceans: A Precautionary Approach. Can. Tech. Rep. Fish. Aquat. Sci. 2363: vi +38 p.

Lusseau, D. 2003. The effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology. 17: 1785-1793.

Lusseau, D. 2004. The hidden cost of tourism: Effects of interactions with tour boats on the behavioural budget of two populations of bottlenose dolphins in Fiordland, New Zealand. Ecology and Society 9: 2 [online] URL: http://www.ecologyandsociety.org/vol9/iss1/art2

Lusseau, D. in press a. Why do dolphins jump? Interpreting the behavioural repertoire of bottlenose dolphins in Doubtful Sound, New Zealand. Behavioural Processes.

Lusseau, D. in press b . The short-term behavioural reactions of bottlenose dolphins to interactions with boats in Doubtful Sound, New Zealand. Marine Mammal Science.

Norris, K. S., B. Wursig and R. S. Wells. 1994. Social Behavior. In (K. S. Norris, B. Wursig, R. S. Wells and M. Wursig, eds.). The Hawaiian Spinner Dolphin. University of California Press. Berkeley, CA. 103-121.

Nowacek, S.M., Wells, R.S. \& Solow, A.R. 2001. Short-term effects of boat traffic on bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida. Mar. Mam. Sci. 17: 673-688.

Olesiuk, P. F., M. A. Bigg and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. Rep. IWC Special Issue 12:209-243.

Orca Relief Citizens Alliance. 2005. The best view of our whales is from shore. Orca Relief Citizens Alliance. Friday Harbor, WA. 2 pp.

Osborne, R.W. 1999. A historical ecology of Salish Sea "resident" killer whales (Orcinus orca): with implications for management. Ph.D. Thesis, University of Victoria, Victoria, British Columbia.

Ponganis, P.J., R. P. Van Dam, G. Marshall, T. Knower And D. H. Levenson. 2000. Sub-ice foraging behavior of emperor penguins. J. Exp. Biol. 203, 3275-3278.

Protected Resources Division. 2004. Initial Assessment of NOAA Fisheries' Critical Habitat Analytical Review Teams For 13 Evolutionarily Significant Units of Pacific Salmon and O. mykiss. NOAA Fisheries Protected Resources Division. Portland, Oregon. 569 pp.

Ritter, F. 2003. Interactions of Cetaceans with Whale Watching Boats - Implications for the Management of Whale Watching Tourism. M.E.E.R. e.V., Berlin, Germany, 91 pp.

Romano, T. A., M. J. Keogh, C. Kelly, P. Feng, L. Berk, C. E. Schlundt, D. A. Carder and J. J. Finneran. 2004. Anthropogenic sound and marine mammal health: measures of the nervous and immune systems before and after intense sound exposure. Can. J. Fish. Aquat. Sci. 61:1124-1134.

Safina, C., and J. Burger. 1983. Effects of human disturbance on reproductive success in the black skimmer. Condor 85:164-171.

Smith, J. C. and D. E. Bain. 2002. Theodolite study of the effects of vessel traffic on killer whales (Orcinus orca) in the near-shore waters of Washington State: 2001 field season summary. Unpublished report.

Soto, N. A., M. Johnson, P. T. Madsen, P. L. Tyack, A. Bocconcelli and J. F. Borsani. 2006. Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (Ziphius cavirostris)? Marine Mammal Science. 22:690-699.

SPSS, Inc. 2003. Systat. www.systat.com.
Sumich, J., L. (1983): Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, Eschrichtius robustus. Canadian Journal of Zoology 61(3): 647-652.

Tavolga, M. C. 1966. Behavior of the bottlenose dolphin (Tursiops truncates): social interactions in a captive colony. In (K. S. Norris, ed.) Whales, Dolphins and Porpoises. University of California Press,. Berkeley, CA. 718-730.

Van Ginneken, A., D. Ellifrit, and K. C. Balcomb, III. 2000. Official orca survey field guide. Center for Whale Research, Friday Harbor, Washington.

Van Parijs, S.M. and P. J. Corkeron. 2001. Boat traffic affects the acoustic behaviour of Pacific humpback dolphins, Sousa chinensis. J. Mar. Biol. Assoc. U.K. 81: 533-538.

Venables, W.N. and Ripley, B.D. 2002. Modern Applied Statistics with S. New York: Springer.
Visser, I. N. 1999. Propeller scars on and known home range of two orca (Orcinus orca) in New Zealand waters. N. Z. J. Mar. Freshwat. Res.33:635-642.

Waite, J. M. 1988. Alloparental care in killer whales (Orcinus orca). Master's thesis. University of California at Santa Cruz.

Wells, R. S. and M. D. Scott. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, FL, Marine Mammal Science 13(3):475-480.

Whale Watch Operators Association Northwest. 2003. Best practices guidelines - 2003. [http://www.nwwhalewatchers.org/guidelines.html](http://www.nwwhalewatchers.org/guidelines.html)

Wiles, G.J. 2004. Washington State status report for the killer whale. Washington Department Fish and Wildlife, Olympia. 106 pp.

Williams, R. M. 1999. Behavioural responses of killer whales to whale-watching: opportunistic observations and experimental approaches. Master's thesis. University of British Columbia. 61 pp .

Williams, R. 2003. Cetacean studies using platforms of opportunity. Ph.D. thesis. St. Andrews University. St. Andrews, Scotland.

Williams, R. And E. Ashe. In press. Northern resident killer whale responses to vessels varied with number of boats. J. Zool. (Lond.).

Williams, R., D. E. Bain, J. K. B. Ford and A. W. Trites. 2002a. Behavioural responses of killer whales to a "leapfrogging" vessel. J. Cet. Res. Manage. 4:305-310.

Williams, R., D. Lusseau and P..S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). Biological Conservation. 133:301-311.

Williams, R., A. Trites and D. E. Bain. 2002b. Behavioural responses of killer whales (Orcinus orca) to whale-watching boats: opportunistic observations and experimental approaches. J. Zool. (Lond.). 256:255-270.

Wood, S. N. (2000). "Modelling and Smoothing Parameter Estimation with Multiple Quadratic Penalties." Journal of the Royal Statistical Society, Series B. 62: 413-428.

Wood, S. N. (2001). "mgcv: GAMs and Generalized Ridge Regression for R." R News 1(2): 20-25.

Wood, S. N. (2003). "Thin-plate regression splines." J. R. Statist. Soc. B 65(1): 95-114.
Yazdi, P. (2005): Einfluss der Tourismusboote auf das Verhalten und die Energetik der Großen Tümmler (Tursiops truncatus) vor der Insel Choros, Chile. Dissertation. Christian-Albrechts-Universität, Kiel. 198 pp. (In German with English summary).

## APPENDIX 1. Sample size information.

Relative frequencies of samples are broken down by year, month, time of day, and age.


APPENDIX 2. Sample sizes broken down by various parameters.

## Sample size (number of tracks)

| Study site | $\mathbf{2 0 0 3}$ | $\mathbf{2 0 0 4}$ | $\mathbf{2 0 0 5}$ | Total |
| :---: | ---: | ---: | ---: | ---: |
| North | 28 | 52 | 47 | 127 |
| South | 14 | 25 | 20 | 59 |
| Month |  |  |  |  |
| May | 0 | 33 | 14 | 47 |
| June | 0 | 13 | 27 | 40 |
| July | 4 | 19 | 26 | 49 |
| August | 16 | 12 | 0 | 28 |
| September | 22 | 0 | 0 | 22 |
|  |  |  |  |  |
| Track duration | 15 | 27 | 16 | 58 |
| 13.3-20 min | 27 | 50 | 51 | 128 |
| $>20$ min |  |  |  |  |
|  | 7 | 39 | 16 | 62 |
| Sex of focal animal | 27 | 38 | 41 | 106 |
| Female | 8 | 0 | 10 | 18 |
| Male |  |  |  |  |
| Unknown |  |  |  |  |
|  |  | 44 | 19 | 71 |
| Pod of focal animal | 9 | 9 | 11 | 24 |
| J K | 21 | 24 | 26 | 71 |
| K | 9 | 0 | 11 | 20 |

Traffic (number of unique boats in theodolite track)

| 0 | 2 | 19 | 4 | 25 |
| :--- | ---: | ---: | ---: | ---: |
| 1 | 2 | 2 | 10 | 14 |
| 2 | 0 | 4 | 2 | 6 |
| 3 | 3 | 6 | 3 | 12 |
| 4 | 1 | 6 | 2 | 9 |
| 5 | 6 | 2 | 2 | 10 |
| $6-10$ | 17 | 15 | 13 | 45 |
| $11-15$ | 6 | 11 | 16 | 33 |
| $16-20$ | 1 | 3 | 4 | 8 |
| $21-25$ | 2 | 2 | 9 | 13 |
| $26-30$ | 2 | 3 | 1 | 6 |
| $31-35$ | 0 | 1 | 0 | 1 |
| $36-40$ | 0 | 1 | 1 | 2 |
| $41-45$ | 0 | 2 | 0 | 2 |

Minimum number of focal individuals sampled (ignoring unknowns)

|  | 13 | 34 | 24 | 45 |
| :--- | :--- | :--- | :--- | :--- |
| Total | 42 | 77 | 67 | 186 |

Appendix 3. Theodolite track sample size by individual.


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Appendix 4a. Relationship of Directness Index to Percentage of Surfacings Marked. The leftmost point was identified as an outlier to be removed from the dataset.


Appendix 4b. Relationship of Directness Index to Track Duration (in seconds). The two leftmost points were identified as outliers to be removed from the dataset.


## Appendix 5 Sample Tracks Showing the Study Areas



Sample Track at the North Site. Lime Kiln Lighthouse is near the bottom of the chart. The red line is one-quarter mile from shore, and the blue line is one half mile from shore. +'s indicate whale positions and x's represent boat positions. Scale bars are $100 \mathrm{~m}, 400 \mathrm{~m}$, and 1000 m . Number in the upper right corner is a real-time report of the distance between the last two marks (useful for checking the distance between a vessel and a whale, or how far a whale traveled underwater, and to help train observers in distance estimation). Blue spot on the red triangle is the theodolite position. As can be seen, tracks sometimes extended off the chart, but this approximates the study area well, as visibility is restricted beyond Lime Kiln Point and Edwards Point (top of image).


Sample Track at the South Site. Cattle Point Lighthouse is near the top of the chart. The red line is one-quarter mile from shore, and the blue line is one half mile from shore. +'s indicate whale positions and x's represent boat positions. Scale bars are $100 \mathrm{~m}, 400 \mathrm{~m}$, and 1000 m . Number in the upper right corner is a real-time report of the distance between the last two marks (useful for checking the distance between a vessel and a whale, or how far a whale traveled underwater, and to help train observers in distance estimation). Blue spot on the green mark is the theodolite position. As can be seen, tracks sometimes extended off the chart, but this approximates the study area well, as visibility is restricted beyond Eagle Point and distance offshore becomes limiting.

