

BEHAVIOURAL RESPONSES OF KILLER WHALES TO WHALE-WATCHING: OPPORTUNISTIC OBSERVATIONS AND EXPERIMENTAL APPROACHES

by

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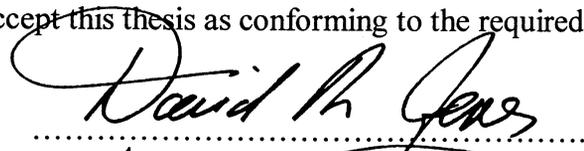
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Abstract

Johnstone Strait provides important summer habitat for British Columbia's northern resident killer whales (*Orcinus orca*). The site is also an active whale-watching area. A voluntary code of conduct recommends that boaters do not approach whales closer than 100 m to address perceived, rather than demonstrated, effects of boat traffic on killer whales. The purpose of my study was to test the relevance of this guideline. Relationships between boat traffic and whale behaviour were studied in 1995 and 1996 by shore-based theodolite tracking of 25 identifiable focal animals from the population of 209 whales. Individual killer whales were repeatedly tracked in the absence of boats and during approaches by a 5.2 m motorboat that paralleled each whale at 100 m. In addition, whales were tracked opportunistically, when no effort was made to manipulate boat traffic. Dive times, swim speeds, and surface active behaviours such as breaching and spyhopping were recorded.

Male killer whales swam significantly faster than females. Whales responded to experimental approaches by adopting a less predictable path than observed during the preceding, no-boat period, although males and females employed subtly different avoidance tactics. Females responded by swimming faster and increasing the angle between successive dives, whereas males maintained their speed and chose a smooth, but less direct, path. Canonical correlations between whale behaviour and vessel proximity are consistent with these conclusions, which suggests that weakening whale-watching guidelines, or not enforcing them, would result in higher levels of disturbance. High variability in whale behaviour underscores the importance of experimental studies when assessing behavioural impacts of human activity on killer whales.

Table of contents

Abstract	ii
Table of contents	iii
List of tables	v
List of figures	v
Acknowledgements	vi
Introduction	1
Methods	5
Study area	5
Selection of focal animals	7
Tracking	9
i. <i>Tracking whales</i>	9
ii. <i>Tracking boats</i>	10
iii. <i>Track types</i>	10
1. Control	10
2. Treatment	11
3. Opportunistic	11
Data compilation	11
i. <i>Calculating predictor variables</i>	11
1. Temporal and biological variables	11
2. Traffic variables	13
ii. <i>Calculating response variables</i>	14
Data analysis	16
i. <i>Gender and age effects</i>	16
ii. <i>Experimental approaches</i>	17
iii. <i>Opportunistic observations</i>	17

Results	19
Sample size	19
Gender and age effects	19
Experimental approaches	20
i. <i>Male response</i>	25
ii. <i>Female response</i>	26
Opportunistic observations	26
i. <i>Male behaviour</i>	27
ii. <i>Female behaviour</i>	32
Discussion	34
Horizontal avoidance tactics	34
Effect size	40
Repeating patterns	46
Recommendations	48
Literature Cited	51
Appendices	
1. JSKWC whale-watching guidelines	60
2. GAWK program for calculating angle between surfacings	61

List of Tables

Table 1: Sample size, listed by gender and traffic conditions	19
Table 2: Correlations, canonical correlations, percents of variance extracted and redundancies between explanatory and behavioural variables and their corresponding canonical variates	30

List of Figures

Figure 1. Study area	3
Figure 2. Sample track	12
Figure 3. Two measures of path predictability	15
Figure 4. Relationship of gender and relative age to whale behaviour	21
Figure 5. Sample tracks of male whales with the experimental boat	22
Figure 6. Sample tracks of female whales with the experimental boat	23
Figure 7. Behavioural responses to experimental approaches	24
Figure 8. Scatterplot matrix of explanatory and behavioural variables for male whales	28
Figure 9. Scatterplot matrix of explanatory and behavioural variables for female whales	29
Figure 10. Schematic representation of avoidance responses	36

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Introduction

In recent decades, a dramatic shift has occurred in the way that people relate to killer whales (*Orcinus orca*). Plans to ‘cull’ killer whale populations on the BC coast were considered as recently as 1960 (Ford *et al.* 1994). At that time, the Federal Department of Fisheries and Oceans mounted a machine gun at Seymour Narrows to address the species’ reputation as unfair competitors for salmon. Today, such an action would be unthinkable. In fact, many people are concerned that the killer whale is now too popular in British Columbia, and may be suffering from too much attention (JSKWC 1991; Kruse 1991; Trites *et al.* 1995).

Cetacean populations around the world are becoming targets for the growing ecotourism industry (Hoyt 1997). In 1993, the International Whaling Commission adopted a resolution that declared its desire “to encourage the further development of whale watching as a sustainable use of cetacean resources” (IWC 1994). The economic benefits of this industry are undeniable. Revenues from whale-watching and associated tourist activities play a critical role in the economies of many communities. The whale-watching industry has exposed millions of urban-dwellers to animals in their natural environment, which may change attitudes toward protecting critical habitat and threatened populations (Barstow 1986, Duffus and Dearden 1993). However, vessel traffic may carry costs for whales (IWC 1995). A suitable management goal, then, might be to ensure that the economic and conservation value of whale-watching does not come at the price of excessive stress to individual whales or their populations.

Researchers have identified three distinct populations of killer whales on the British Columbia coast that have overlapping ranges, but are socially and ecologically isolated (Ford *et al.* 1994). Whale-watching has tended to focus on *resident* killer whales, the fish-eating type, since these whales are sighted more predictably than the *offshores* or the marine-mammal-eating *transients*. British Columbia's resident killer whales are composed of the northern and southern resident communities. One of the most reliable places to see these whales in the wild is Johnstone Strait, BC, Canada (Figure 1). Northern resident killer whales return here each summer to socialize, to rub their bodies on smooth pebble beaches, and to prey on migrating salmon as they are funneled through the narrow strait (Nichol and Shackleton 1996).

Johnstone Strait is unique for reasons other than its designation as core killer whale habitat. It is an important area for commercial fishing (JSKWC 1991). It is also home to people who have been monitoring resident killer whales for two decades. Members of the local community were successful in encouraging the province of British Columbia to protect Robson Bight as critical killer whale habitat. Local people have also supported visitor education programs, and have voluntarily established a code of conduct to self-regulate behaviour around whales (JSKWC 1996, Appendix 1). In 1990, BC Parks initiated a monitoring program of boat and whale usage of the Robson Bight – Michael Bigg Ecological Reserve, and the waters immediately adjacent to it. Analysis of data from 1990-1994 by Trites *et al.* (1995) found no significant relationship between boat presence and number of whales using the Reserve, but did reveal an effect of boats on whale movements. Their study found the likelihood of whales leaving the Ecological Reserve increased as increasing numbers of boats entered it.

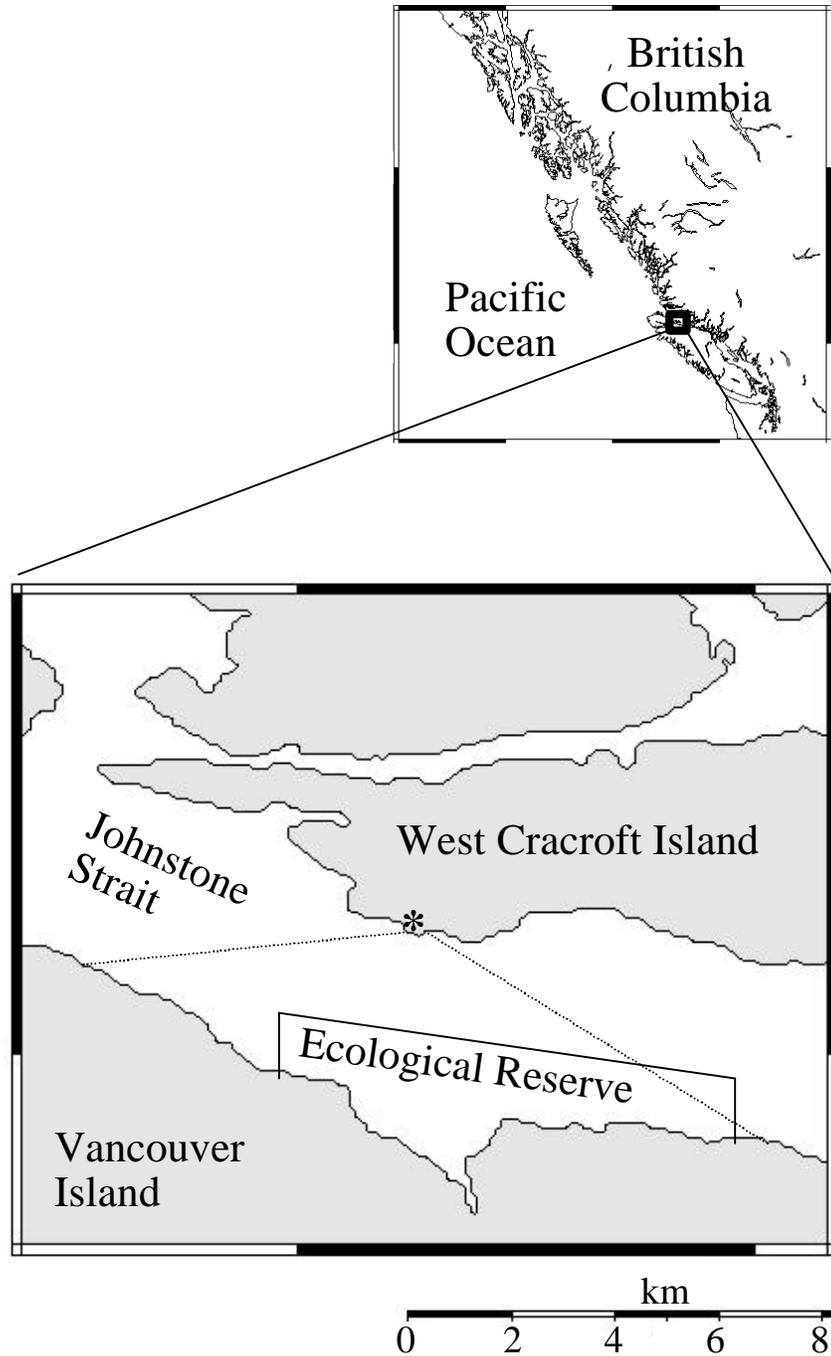


Figure 1. Study area in Johnstone Strait, BC, Canada, showing lines of sight (- - -), position of theodolite (*), and Robson Bight - Michael Bigg Ecological Reserve.

Unfortunately, studies that compare whale behaviour in the presence and absence of boats are of limited use for the management of whale-watching activity, since the presence of boats is unavoidable in this busy section of the Inside Passage. Descriptions of how these whales behave in the presence of boats (Adimey 1995, Kruse 1991, Trites *et al.* 1995) certainly underscore the importance of providing a requiem reserve at Robson Bight. However, sound scientific management of whale-watching must involve more than simply closing critical habitat to boats: it must also define and promote responsible whale-watching activities outside the Reserve. Studies that test for responses to vessel activity will assist resource managers in their efforts to identify types of whale-watching that minimize disturbance. Meaningful guidelines will balance people's desire to see whales in the wild with the habitat needs of the animals themselves.

There is clear evidence for short-term behavioural responses of resident killer whales to the presence of boats (Adimey 1995, Briggs 1991, Kruse 1991, Trites *et al.* 1995). Current self-imposed whale-watching guidelines (i.e. the 100 m 'rule') attempt to address some of these concerns, but may be based more on aesthetics than biological relevance. [It seems that the choice of this distance guideline was influenced by US regulations, which were also chosen arbitrarily (J. Ford, pers. comm.).] Furthermore, Duffus and Dearden (1992) question the value of any study of boat-whale interactions that rely solely on opportunistic observations. Guidelines should be based on actual impacts of human activity on whale behaviour, rather than perceived effects. Otherwise, token guidelines may give the false sense that boaters are not disturbing whales, provided that they follow some groundless rules.

The primary goal of my study was to test whether a vessel following whale-watching guidelines affects the behaviour of northern resident killer whales that summer in Johnstone Strait. Field observations suggest that a whale might respond to boats by varying the duration of their dives [vertical avoidance], or by swimming faster or altering the direction of swimming [horizontal avoidance]. Longer dives can be considered vertical avoidance, if the whale holds its breath longer than a whale-watcher's attention span. When killer whales were chased during live-capture attempts, animals were said to adopt erratic surfacing patterns (Spencer *et al.* 1966), which is a form of horizontal avoidance. Killer whales may also display agonistic behaviours, such as slapping flukes or pectoral fins on the surface of the water. Responses may vary among individuals, or they may be related to age and gender (Adimey 1991, Bauer and Herman 1986).

My secondary goal was to describe how whale behaviour varied across the range of traffic conditions that exist in Johnstone Strait in summer. Observing whales opportunistically, when many boats were present, and when boats approached animals closely, allowed insights into killer whale behaviour under traffic conditions that would have been logistically difficult, or unethical, to replicate experimentally. This dual nature of data collection allowed the causal relationships identified by experimental approaches to be compared with trends in whale behaviour across a wide range of traffic conditions.

Methods

Study area

Data were collected between 1 July and 31 August, 1995, and between 16 July and 10 September, 1996, from a land-based observation site on the south shore of West

Cracroft Island in Johnstone Strait (50° 30' N, 126° 30' W; Figure 1). This cliff-top site is an ideal vantage point to view whales in the Reserve (with relatively little whale-oriented boat traffic), and adjacent to the Reserve (where whale-watching vessels often congregate). This shore-based platform also allowed for the measurement of vessel impact without contributing to potential vessel effects.

Data collection was accomplished using an electronic theodolite (a Pentax ETH-10D with a precision of ± 10 seconds of arc) connected to a laptop computer equipped with custom software (THEOPROG: written by Dr. David Bain of University of Washington and Marine World Foundation). The height of the cliff was measured by stretching a rope of known length at the water's edge on a beach immediately below the cliff and using the theodolite to obtain horizontal and vertical angle coordinates for both ends. Cliff height was thus calculated by knowing the distance between rope ends and the position of the tide on our scale, using the trigonometric relationships described by Davis *et al.* (1981) and Würsig *et al.* (1991).

Cliff height was measured at least 10 times at the beginning, middle and end of each season to ensure that the position of the theodolite tripod had not shifted during the study. At no point in the study did the mean measurement of cliff height fall outside the range of measurements recorded during that season's setup period. The apparatus was 46.99 ± 0.05 m (mean \pm SEM) above a fixed, zero point marked on a rock wall below the cliff. In 1996, the theodolite tripod height was 46.85 ± 0.03 m above that same zero mark. Below this reference was a scale marked at 10 cm intervals. Tide height during tracking sessions ranged from 1.1 to 5.4 m below the zero mark, with a mean value of 2.9 m below zero. The theodolite was thus located approximately 50 m above mean sea level.

Accuracy of the tracking equipment was tested by stretching a rope of known length along the water's edge on a beach across the Strait from the cliff (Figure 1). At a distance of 3.79 km from the cliff, the mean estimate of the 30 m rope's length as measured by the theodolite-computer apparatus was 28.93 ± 0.18 m. Small standard errors in cliff height and 3.5% error in estimating distance at an extreme range are encouraging, since percent errors in measuring cliff height, distance traveled and speed tend to be approximately equal (Würsig *et al.* 1991). Observations were made between 08h00 and 20h00 in 1995. In 1996, a camp was set up nearer the theodolite so that observations could be made from dawn to dusk, with tracks recorded from 06h30 to 22h00.

Selection of focal animals

Northern resident killer whales entered the study area (Figure 1) in matrifocal social units called subpods (Ford *et al.* 1994, Olesiuk *et al.* 1990). Temporary groupings of subpods ranged in size from 2 to 120 individuals. Careful selection of a focal animal was chosen over random selection to ensure representative sampling of the population during the study and reliability of resighting an individual within a tracking session. Selecting a focal animal to observe was based on criteria of 'trackability' and 'desirability'. A trackable animal was one that would not be easily confused with other members of the group at a distance and was likely to be consistently re-sighted. It typically had a distinctive dorsal fin and saddle patch, was swimming apart from, or was easily distinguished from, the other whales in the group. Focal whales were usually within a few hundred metres, and always within acoustic range, of the rest of the group (Ford *et al.* 1994).

The position of the whale relative to the theodolite influenced focal animal selection. Whales swimming mid-Strait were preferable to those swimming along the Vancouver Island shore since the accuracy of a reading diminishes with distance from the theodolite (Würsig 1991).

Another consideration for choosing the most trackable subject was its position relative to other members of the group. Although individuals are uniquely identifiable, some whales bear more distinct markings than others. Generic-looking whales may be misidentified, especially when a surfacing is not broadside. In 1995, only males were tracked, however in 1996, the team was able to consistently re-sight distinctive females.

One of the criteria for desirability was whether an animal was likely to be visible for a minimum of 15 minutes, since earlier work has shown that tracks shorter than 1000 s tend to bias estimates of respiration rate (Kriete 1995). A second desirability criterion considered individual variability and the frequency of visits to Johnstone Strait, to ensure that as many different individuals as possible were tracked under a wide range of traffic conditions. Given that family groups have an unequal probability of being sighted in the study area, desirability was inversely related to its subpod's frequency of visits to the Strait as reported by Trites *et al.* (1995). Thus, every opportunity was taken to track rare visitors, to ensure that data were obtained from both rare and frequent visitors. Similarly, a desire to see how individuals behave under a variety of traffic conditions necessitated prioritizing whales for whom the fewest tracks had been made.

Finally, focal animals were selected only when engaged in typical foraging behaviour. This activity is the most commonly observed activity of killer whales in summer in Johnstone Strait (Nichol and Shackleton 1996), and is recognized when

groups are spread out and all animals are swimming essentially in the same direction (Ford *et al.* 1994). This study did not attempt to confirm reports that whales are particularly vulnerable to disturbance while resting (Ford *et al.* 1994) or rubbing (Briggs 1991; Trites *et al.* 1995). Whales that were socializing with members of other subpods were not chosen as focal animals, due to increased potential to misidentify the focal whale. This consistency in tracking only foraging animals prevented the effect of a whale's activity state on respiration rate and swim speed from masking potential effects of boat traffic.

Tracking

i. Tracking whales

The three-member tracking team consisted of a spotter, a theodolite operator and a computer operator. The spotter scanned for boats near the whale and announced each time a focal animal surfaced to breathe or displayed surface active behaviour. The theodolite operator located the position of the whale in the crosshairs. Behaviours recorded by the computer operator using codes included: breath, breach, fluke slap, pectoral fin slap, dorsal fin slap, unidentified splash, porpoising and spy-hop (see Ford *et al.* 1994). A computer was linked to the theodolite to record the time that horizontal and vertical angle coordinates of the whale's position were retrieved. This arrangement eliminated transcription error. Water level was noted every 15 min to determine the height of the theodolite above sea level over changing tides.

Accuracy of each x-y coordinate of a whale was confirmed by plotting positions on the computer screen as they were collected. Deviation from a smooth path, or atypical

spacing between surfacings, prompted discussion between the computer operator and the theodolite operator. Thus, each position was scrutinized as it was collected.

ii. *Tracking boats*

During the whale's long dives, the position of each associated boat was recorded along with information about vessel type, whale-watching status (ignoring, passive, active or chasing the whale), orientation relative to the whale, estimated distance from the whale, and its direction of travel. The position of every boat within 3 km of the whale was recorded. This distance was chosen as a reasonable estimate of the area that the team could reliably cover, without missing a passing boat.

A vessel was deemed to be ignoring the whale if it made no direction change toward the whale, continued out of the study area, or if it was engaged in a non-whale-oriented activity such as fishing. For analysis, all vessel traffic was categorized as either whale-oriented or non-whale-oriented. Every attempt was made to record when a vessel's whale-watching activity changed within a tracking session.

iii. *Track types*

Whales were tracked under three traffic conditions:

1. *Control.* Control tracks occurred when no boats were within 3 km of the focal animal. During the 1996 season, local charter operators and the Reserve wardens were in radio contact with the tracking team, and agreed to stay away from the focal whale while the crew tracked its movements, thereby increasing the number of control tracks.

2. *Treatment.* During the 1996 season, an experimental boat was available to parallel the focal animal at approximately 100 m for a minimum of 20 minutes, usually following 20 minutes of observation under control conditions (Figure 2). The vessel was a 5.2 m Hourston fibreglass motorboat with a 90 hp Yamaha outboard engine. The operator attempted to follow whale-watching guidelines as closely as possible, by approaching the focal whale slowly from the side. No sudden direction changes were made, and the operator was instructed never to place the boat in the path of the whale (an activity referred to as ‘leapfrogging’). The operator attempted to maintain constant speed, and was in VHF radio contact with the cliff-based crew to ensure that the boat stayed approximately 100 m from the whale.
3. *Opportunistic.* Opportunistic tracks occurred when at least one boat was present within 3 km of the focal whale, and no effort was made to manipulate traffic around the focal animal. These included a wide range of traffic conditions and vessel types.

Data compilation

- i. *Calculating predictor variables*
 1. Temporal and biological variables

Whales were defined as either young or old, based on life history information for individuals in this population (Olesiuk *et al.* 1990). A female was classified as old if her presumed age was at least 40 years, which is the average age for the onset of reproductive senescence. A male was considered old if his presumed age was at least 30 years (the

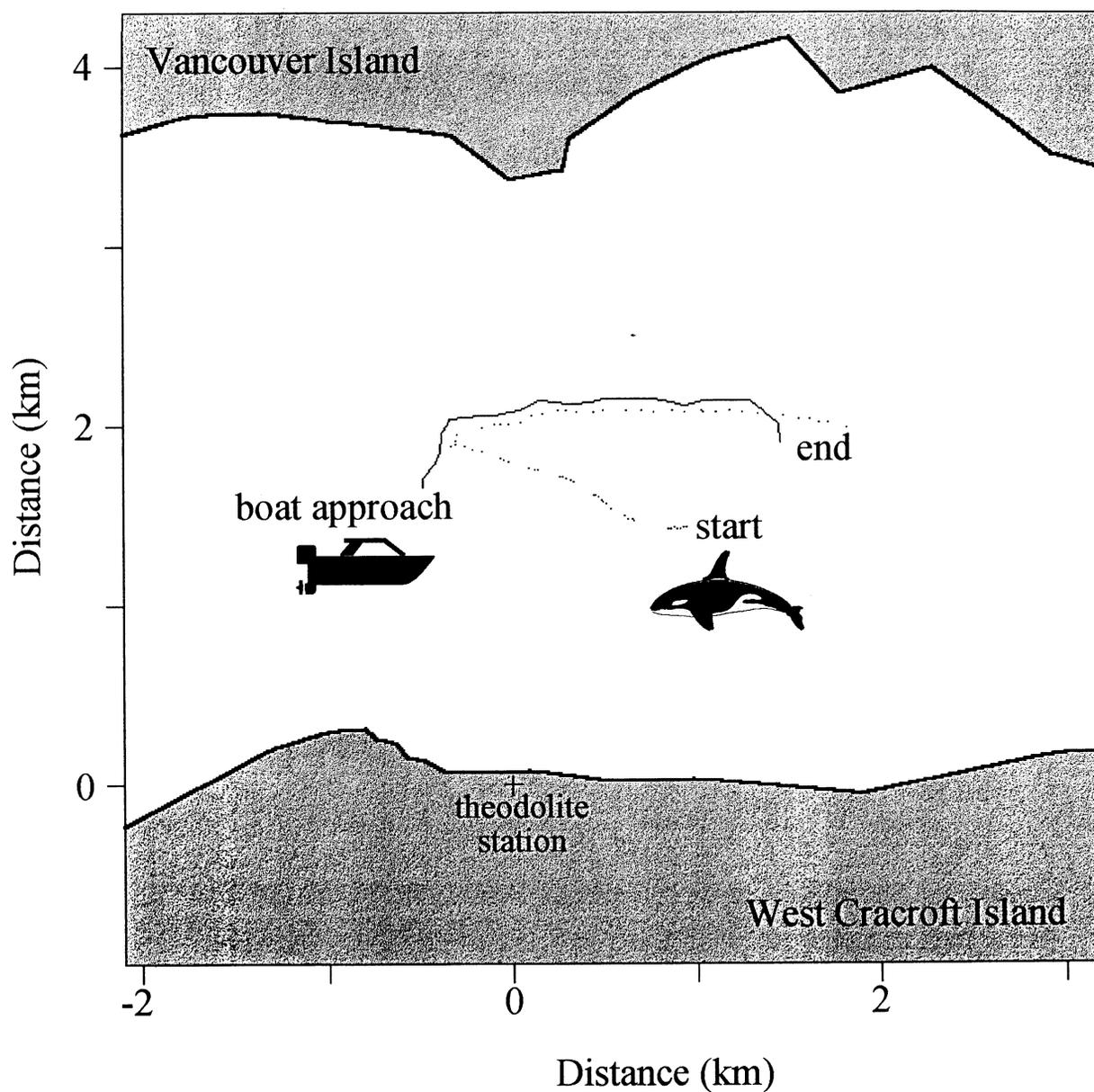


Figure 2. Sample track showing position of theodolite station (+), path of the male focal whale (···), and path of experimental boat (—).

average life expectancy for male northern resident killer whales) (Olesiuk *et al.* 1990). Since individuals in this population have been photographed annually since the mid-1970's, age estimates for young whales are more reliable than those of old whales (Ford *et al.* 1994).

2. Traffic variables

THEOPROG was used to sort and transform the series of angles, times and codes into x-y coordinates and speeds. Boats were recorded less frequently than the focal animal, and were assumed to travel at constant speed between marks. The position of each boat was interpolated to determine where it was every time the whale surfaced. When boats arrived during a tracking session, positions were extrapolated to determine its approximate location at the beginning of the track. Distance between the whale and every boat was calculated for each surfacing in a track using the actual position of the whale and the interpolated or extrapolated position of each boat.

The intensity of boat traffic was measured in three ways:

1. Track type: control, treatment or opportunistic.
2. Vessel proximity. Distance between each boat and the whale was calculated for every surfacing to determine one value for minimum proximity within a track.
3. Number of vessels. The number of whale-oriented vessels (passive, active and chasing) and non-whale-oriented vessels (those apparently ignoring the whale) were calculated within 100 m, 400 m, and 1000 m radii of each surfacing. The 100 m radius was chosen from the whale-watching guidelines. The 400 m radius was chosen for comparison with an earlier study of the relationship between boat traffic

and the behaviour of these whales, at the beginning of the whale-watching industry in this area (Kruse 1991). The 1000 m radius was chosen as an arbitrary upper limit for potentially-interacting vessel traffic. The range for acoustic interaction, of course, could be much greater than this. The maximum number of vessels (whale-oriented and non-whale-oriented) within the three radii was calculated for each track. This summary identifies peak intensity of boat traffic as indicated by vessel number and whale-watching status, rather than proximity.

ii. *Calculating response variables*

Duration of each dive and a mean dive time were calculated for each track. The average swimming speed of the whale was obtained by dividing the total distance traveled by the duration of the tracking session.

Two measures of path predictability were calculated: a directness index and a deviation index (Figure 3). The directness index measures path predictability on the scale of an entire tracking session. It is generated by dividing the distance between end-points of a path by the cumulative surface distance covered by all dives. The directness index can be thought of as the ratio of the diameter of a path to its perimeter, and is equivalent to the milling index of Kruse (1991) and Tyack (1982). The directness index ranges from zero (a circular path) to 100 (a straight line).

The deviation index measures path predictability from one surfacing to the next (Figure 3). 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, I calculated the angle between the path taken by a dive and the straight-line path predicted by the dive

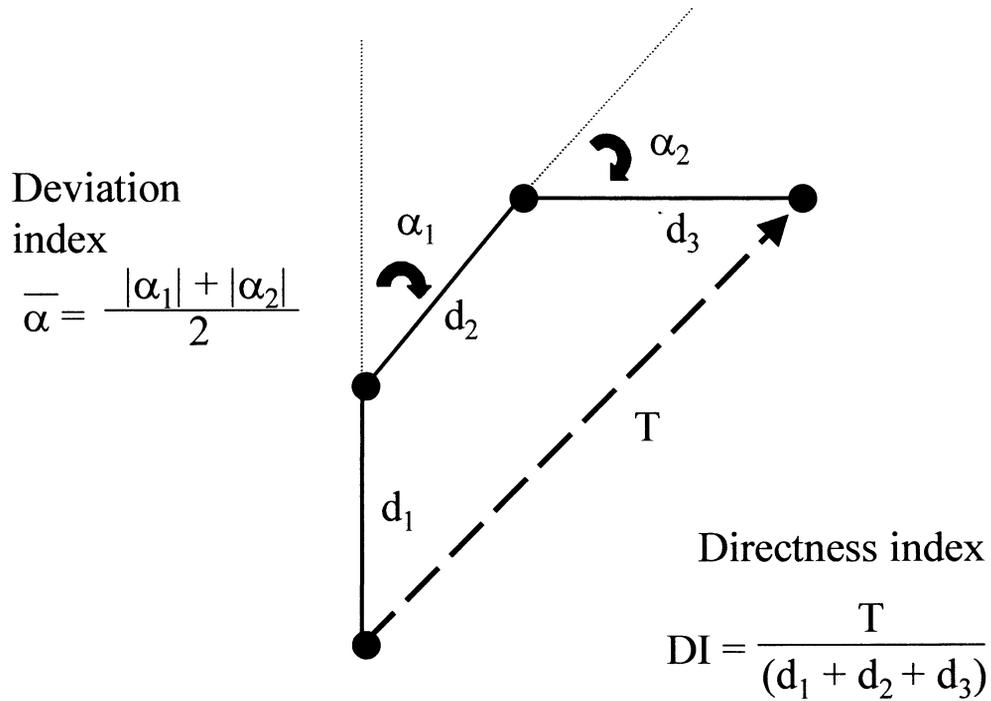


Figure 3. An example swimming path with four surfacings (●) and three dives (d_i), showing two measures of path predictability: deviation and directness. The deviation index is the mean of all angles between observed dives and the straight-line paths *predicted* (···) by preceding dives. The directness index is the ratio of the track diameter (T) to its perimeter.

before it (Appendix 2). The deviation index is the mean of the absolute value of each of these discrepancies, in degrees, during the entire track. A low deviation index implies a smooth path, while a high deviation index implies an erratic path. The procedure was repeated for each track. A track that shows high deviation and high directness is described as erratic, but directional, whereas a track with low deviation and low directness is smooth, but non-directional.

Since aerial displays by a focal animal were relatively uncommon, the various actions of spyhopping, breaching and slapping were pooled into a single category of surface active behaviour. The rate of surface active behaviour was standardized to the number of events expected by the focal animal in one hour, to account for varying track length in terms of track duration and number of surfacings.

Data analysis

i. Gender and age effects

Relationships among age, gender and whale behaviour were examined before considering effects of boat traffic on behaviour. One value for each dependent variable (mean dive time, mean swim speed, deviation index, directness index and rate of surface active behaviour) was calculated for each track. Mean values were averaged across all observations for an individual, regardless of traffic conditions. Means were then calculated for each gender and age class, such that each whale was represented only once in the analyses. Two-factor analyses of variance (ANOVA) were performed on each dependent variable.

ii. Experimental approaches

Variables recorded under control and experimental conditions were compared using two-tailed, paired t-tests. Comparisons were made only when 20 minutes of baseline, control observation were followed by an experimental approach of the same whale lasting at least 20 minutes. Separate analyses were performed on males and females to identify effects of the traffic treatment on each response variable (dive time, swim speed, deviation index, directness index and rate of surface active behaviour).

iii. Opportunistic observations

Whales' responses to experimental approaches were compared with whale behaviour across a continuous range of traffic conditions observed in Johnstone Strait. This description used canonical correlation (STATISTICA v. 5) to investigate how temporal, biological and traffic variables together related to whale behaviour. Canonical correlation analysis is a multivariate technique that is particularly well-suited to describe complex relationships between two sets of variables (Tabachnick and Fidell 1996). It has been used particularly well to reveal subtle trends in the highly variable datasets common to many cetacean studies (Bauer and Herman 1986, Whitehead et al. 1998). Canonical correlation allows exploration of simultaneous variance in predictor variable sets (e.g. boat traffic) and response variable sets (e.g. whale behaviour). The linear combinations (*variates*) that maximize correlation between predictor and response variable sets are selected (James and McCulloch 1990). The result is a canonical R^2 , which indicates the proportion of the variance in whale behaviour that is explained by variance in the

explanatory variable set. The maximum number of variates possible in canonical correlation is equal to the number of variables in the smaller set.

The contribution of a variable (e.g. distance to nearest boat) to its own (e.g. boat traffic) set is indicated by a standardized coefficient, the canonical *weight* (Milstein 1993). A canonical *loading* is a coefficient that reveals the contribution of a variable to its opposite set (whale behaviour). Canonical correlations are interpreted using the magnitude and direction of the weights and loadings, which allows some flexibility. Some authors have chosen 0.30 as an arbitrary minimum coefficient for interpretation (Tabachnick and Fidell 1996). Alternatively, inherent noise in cetacean behavioural data has been cited as a rationale for interpreting coefficients as low as ± 0.20 (Bauer and Herman 1986), which is the cutoff I used in my study.

Canonical correlations are interpreted based on the significance of the relationship between variates; the correlations between the original variables and the canonical variates; and the variance extracted (Tabachnick and Fidell 1996). A comprehensive analysis must reveal the proportion of variance in the original data that is extracted by: 1) the canonical correlation, 2) the variate of its own set, and 3) the variate of the opposite set, or *redundancy*.

Results

Sample size

Over two seasons, 1416 hours were spent observing boats and whales in the study area. This effort yielded 181 usable tracks of 25 individuals, in which 9863 respiratory intervals were timed. Focal animals were tracked continuously for 32.3 h in 1995 and 70.1 h in 1996. Sample size is listed by gender and traffic conditions in Table 1.

Table 1. Sample size, listed by gender and traffic conditions. Numbers in bold indicate number of tracks, whereas those in parentheses indicate number of individuals.

	Control	Treatment	Opportunistic	Total
Male	50 [12]	27 [11]	56 [15]	133 [16]
Female	27 [9]	13 [8]	8 [5]	48 [9]
Total	77 [21]	40 [19]	64 [20]	181 [25]

Gender and age effects

Mean values for each of the five dependent variables (dive time, swim speed, deviation and directness indices, and rate of surface active behaviour) were calculated for each of the 25 whales observed. The values for each variable were approximately normally distributed as indicated by Kolmogorov – Smirnov tests ($\alpha = 0.05$, Zar 1996). Age of focal whales ranged from 16 to 73 years for females, and from 15 to 39 years for males (Ford *et al.* 1994). The average age of female subjects, 43 years, was significantly greater than for males, 26 years (two-tailed $t_{23} = 3.24$, $p < 0.01$).

The 16 male northern resident killer whales swam approximately 34% faster than the 9 females when groups were engaged in typical foraging behaviour (Figure 4) ($F_{1,23} = 6.43$, $p=0.02$). Average swim speeds were 6.32 km/h for males and 4.71 km/h for females. No significant gender differences were observed in dive time (males 41.62 s, females 43.97 s; $F_{1,23} = 0.14$, $p=0.19$), deviation index (males 20.86, females 25.99; $F_{1,23} = 2.20$, $p=0.15$), or directness index (males 84.80, females 77.26; $F_{1,23} = 1.47$, $p=0.24$).

The most common surface active behaviour for all classes was tail-slapping, with spy-hops and pectoral fin-slaps accounting for most of the remaining activity. All surface active events were pooled to an expected rate of events per hour. No significant differences were found between the mean rates of surface active behaviour of males (0.84 h^{-1}) and females (1.17 h^{-1}) ($F_{1,23} = 0.20$, $p=0.66$). Similarly, no significant relationship was found between relative age and whale behaviour, nor were there any significant interactions between gender and relative age.

Experimental approaches

Whales were approached by the experimental boat on 40 occasions. Experimental approaches were preceded 32 times by at least 20 min of observation under control conditions. Examples of four experimental approaches of male and female whales are shown in Figures 5 and 6, respectively. Paired, two-tailed t-tests were performed on the 5 response variables for the control and treatment observations (Figure 7). Separate analyses were performed for experimental approaches of males and females, since

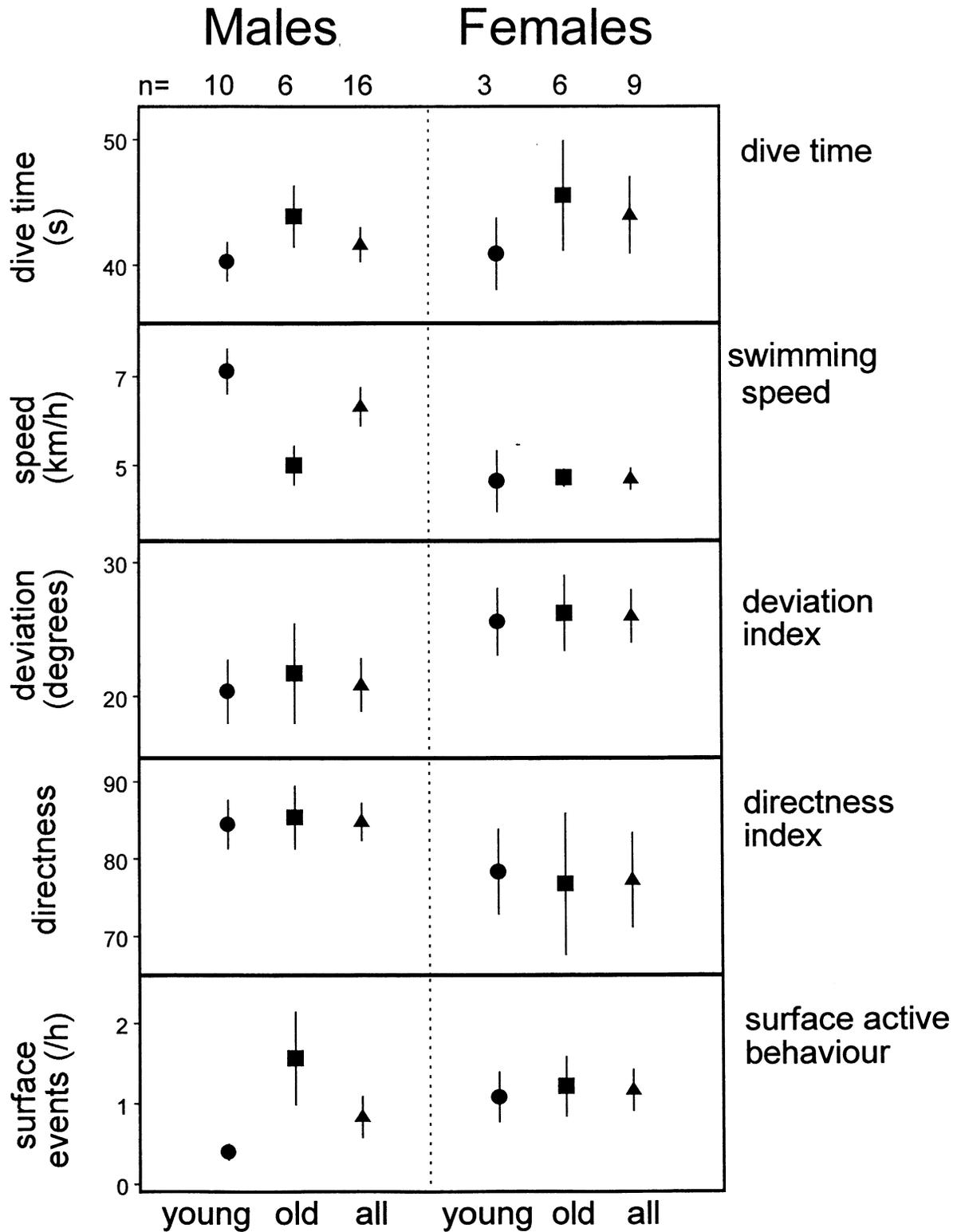


Figure 4. Relationship of gender and relative age to whale behaviour (mean \pm SEM), averaged across all traffic conditions. Each whale is represented only once.

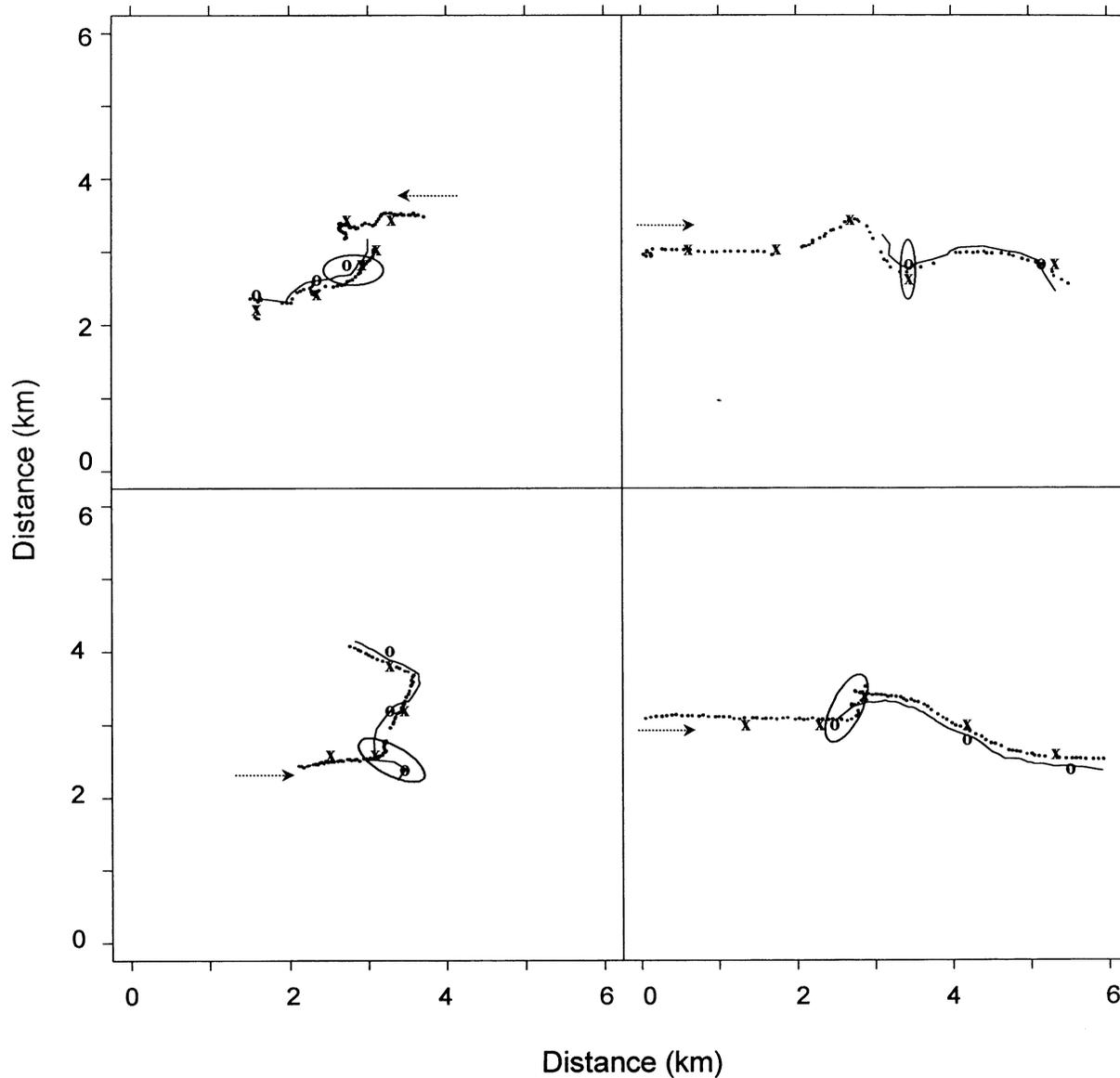


Figure 5. Four examples of paths taken by *male* focal whales (...) when approached by the experimental boat (-). Each dot represents a surfacing by the whale. The arrow indicates the whale's original heading. Letters are placed at 10-minute intervals: "x" indicates the interpolated position of the whale, and "o" indicates the interpolated position of the boat. The first synchronous pair of boat and whale positions is joined by an oval. In general, paths of male whales during experimental approaches were smooth, but less directional.

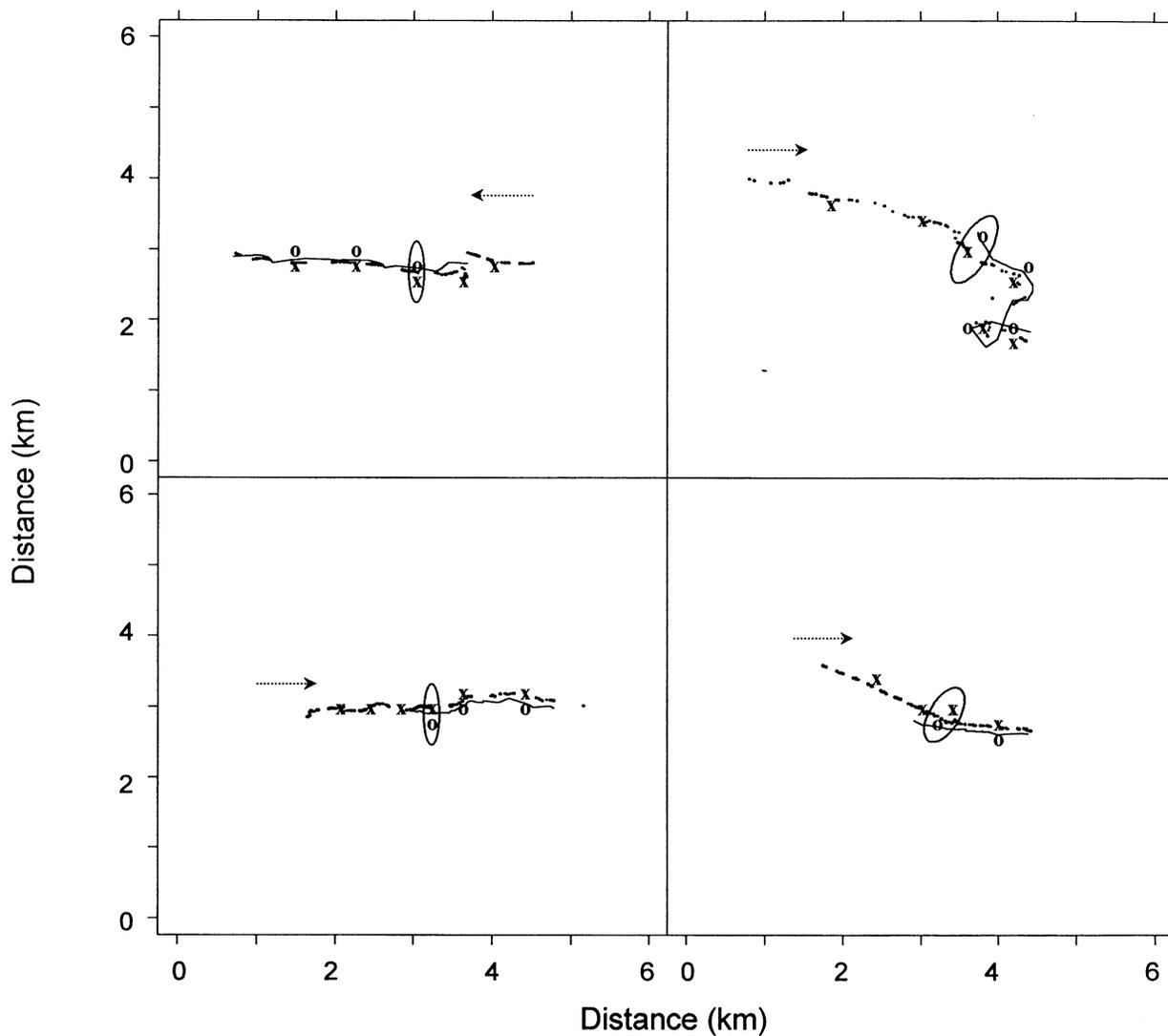


Figure 6. Four examples of paths taken by *female* focal whales (· · ·) when approached by the experimental boat (—). Each dot represents a surfacing by the whale. The arrow indicates the whale's original heading. Letters are placed at 10-minute intervals: "x" marks the interpolated position of the whale, and "o" indicates the interpolated position of the boat. The first synchronous pair of boat and whale positions is joined by an oval. In general, the path adopted by female whales during experimental approach was erratic, but directional.

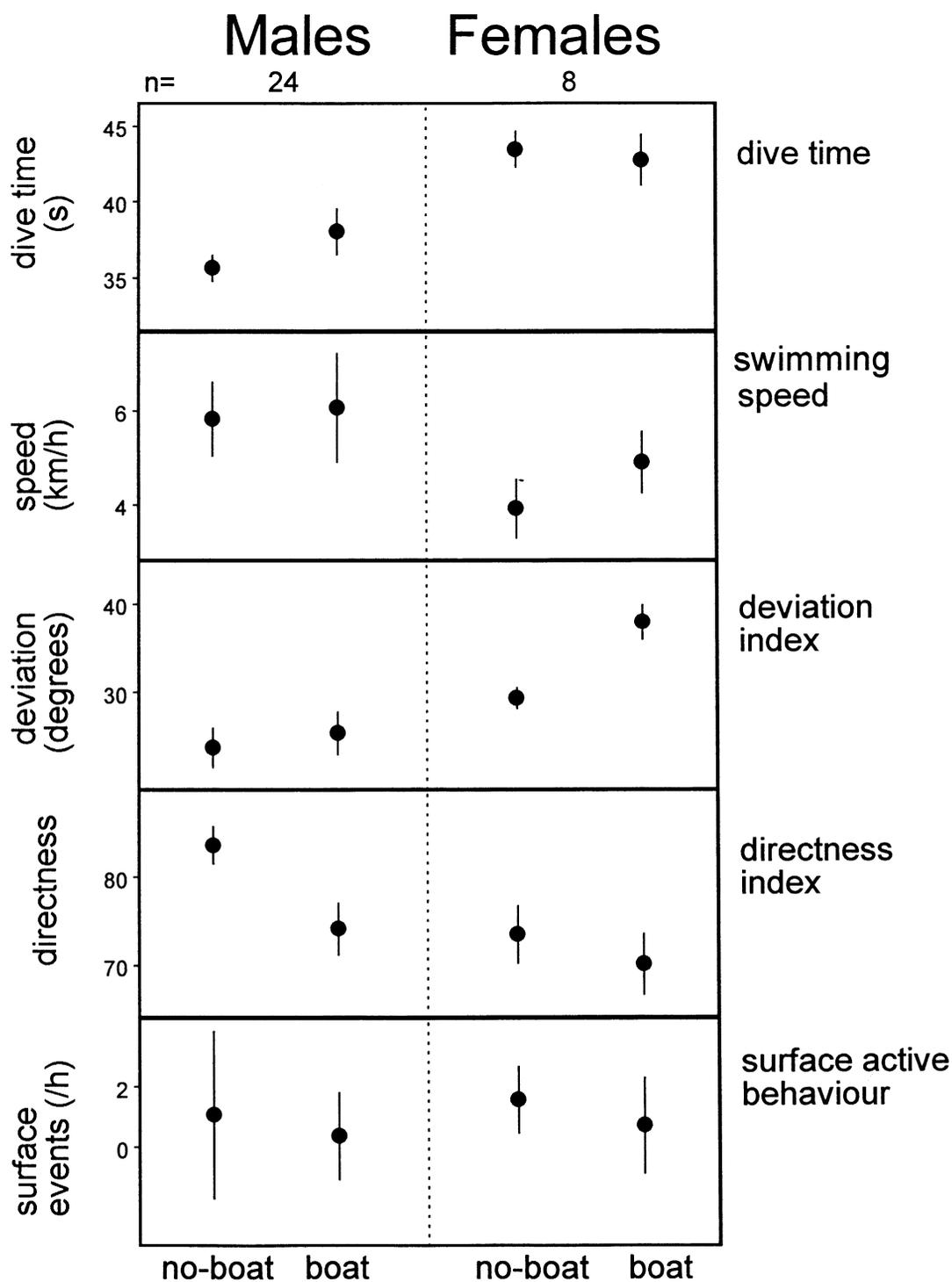


Figure 7. Behavioural responses (mean \pm SEM) of whales to experimental approach by one boat paralleling the whale at 100 m for 20 minutes. Some whales are represented more than once in these paired observations.

gender-based differences in swim speed (Figure 4) indicated potential for different responses to boat traffic.

Increased possibility of Type I errors is a concern with these analyses. Concern about Type II error rates as well as other arguments given by Stewart-Oaten (1995) justified the avoidance of a multiple comparison technique at this stage of the analysis.

i. *Male response*

When approached by the experimental boat, the paths of male whales became less direct than during the preceding no-boat conditions ($t_{23} = 2.25$, $p = 0.03$). The reduction in directness from 83.6 to 74.1 can best be understood in terms of distance covered. A directness index of 83.6 equates to a whale swimming 119.6 m along a circuitous path to end up 100 m from his original position. That same whale, following a path with a directness index of 74.1, would cover 135 m to make 100 m headway. Thus, the average male responded to the experimental boat by covering 13% more distance along a circuitous path than it covered before the boat arrived.

No significant changes in dive time ($t_{23} = 1.55$, $p = 0.13$), swim speed ($t_{23} = 0.45$, $p = 0.66$), deviation index ($t_{23} = 0.56$, $p = 0.58$) or rate of surface active behaviour ($t_{23} = 1.17$, $p = 0.25$) were observed during experimental approaches.

ii. *Female response*

When approached by the experimental boat, female whales responded by swimming 25% faster ($t_7 = 3.29$, $p = 0.01$) and increasing the mean angle deviation between surfacings by 29% ($t_7 = 2.90$, $p = 0.02$). No significant changes in mean dive time ($t_7 = 0.29$, $p = 0.78$), directness index ($t_7 = 0.40$, $p = 0.70$) or rate of surface active behaviour ($t_7 = 1.34$, $p = 0.22$) were observed.

Opportunistic observations

Canonical correlation was performed between the set of whale behaviour variables and a set of explanatory variables. This allowed the binary results of experimental approaches to be compared with a multivariate description of trends in whale behaviour across a continuum of boat traffic. Separate canonical correlations were performed for males and females, since experimental tracks indicated potential for gender-based difference in boat tolerance (Figure 7). The whale behaviour variable set included dive time, swim speed, directness and deviation indices, and the rate of surface active behaviour.

Three traffic variables were included in the explanatory variable set: 1) the minimum distance in a track between any boat and the whale, 2) the maximum number of whale-oriented vessels within 1000 m of the whale, and 3) the maximum number of non-whale-oriented vessels within 1000 m of the whale. These allowed canonical correlations to consider effects of proximity, whale-watching status, and number of boats, on whale behaviour. The 1000 m radius was chosen since it most closely met the assumption of continuity of variables required for canonical correlation (Milstein 1993, Tabachnick and

Fidell 1996). The explanatory variables also included the day of the year, start time of each track, and the age of the subject. Additional traffic variables were eliminated to avoid concerns of multicollinearity (Tabachnick and Fidell 1996). No correlation within a variable set was greater than 0.5 after reducing the number of variables.

For illustrative purposes, Figures 8 and 9 show scatterplot matrices of relationships among the original variables included in canonical correlations for male and female whales, respectively. Table 2 shows how linear combinations of some of these relationships were synthesized in one multivariate description of male behaviour, and another description for females. Standardized correlation coefficients (weights) between the original variables and the first pair of canonical variates are also listed in Table 2, along with a significance level for the correlation with all five pairs of canonical variates included. This χ^2 test has $(k_x)(k_y)$ df, where k_x is the number of variables in the explanatory set, and k_y is the number of variables in the response set (Tabachnick and Fidell 1996).

i. *Male behaviour*

Using 133 tracks, a significant relationship was found between the set of explanatory variables and behaviour of male whales. The significant explanatory variables were the date and time of the observation, age, the maximum number of whale-oriented vessels within 1000 m, and the proximity of the nearest boat. Significant behavioural variables for male whales were swimming speed, directness index, and rate of surface active behaviour. The canonical correlation (r_c) for males was 0.44, indicating 19% overlapping variance between the two

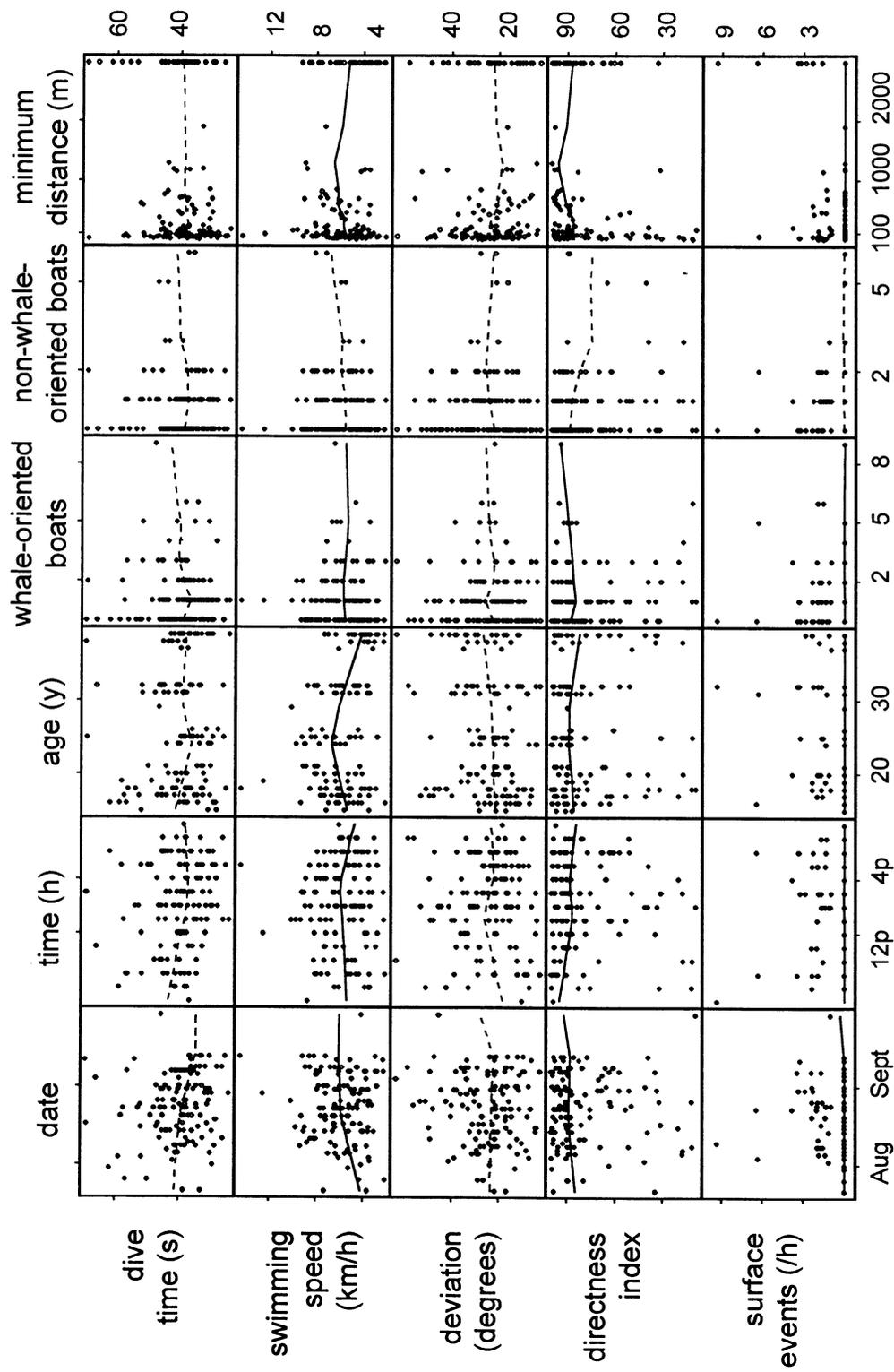


Figure 8. Scatterplot matrix showing relationships between the set of explanatory variables and behaviour of male whales ($n=133$). Each plot is smoothed with a lowess function. Relationships that were interpreted in the canonical correlation have a solid lowess line, while those that were not interpreted are given a dashed line.

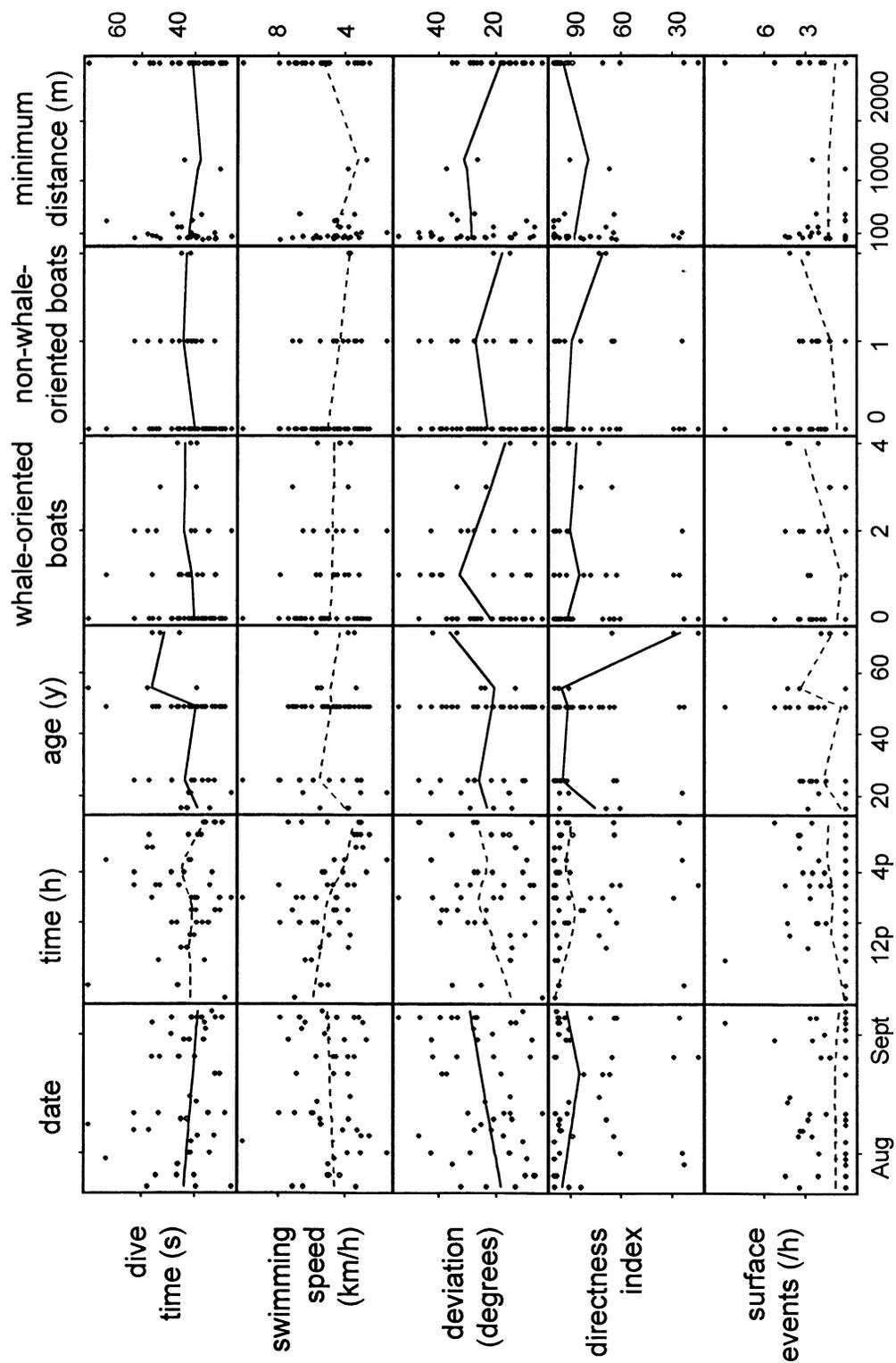


Figure 9. Scatterplot matrix showing relationships between the set of explanatory variables and behaviour of female whales ($n=48$). Each plot is smoothed with a lowess function. Relationships that were interpreted in the canonical correlation have a solid lowess line, while those that were not interpreted are given a dashed line.

Table 2. Correlations, canonical correlations, percents of variance extracted and redundancies, between explanatory and behavioural variables and corresponding canonical variates for 133 observations of males, and 48 observations of females. Numbers in bold face indicate variables that were interpreted.

	Standardized correlation coefficients between original variables and first canonical variates	
	MALE n=133	FEMALE n=48
<i>Explanatory set</i>		
DATE	-0.47	0.58
TIME	0.26	0.02
AGE	0.79	-0.40
WHALE-ORIENTED ¹	0.21	-0.35
NON-WHALE-ORIENTED ²	-0.15	-0.56
MINIMUM DISTANCE	0.47	-1.06
Percent of Variance	16%	10%
Redundancy	3%	5%
<i>Behavioural set</i>		
MEAN DIVE TIME	-0.19	-0.20
SWIMMING SPEED	-0.90	0.13
DEVIATION	-0.16	1.21
DIRECTNESS	0.36	0.65
SURFACE BEHAVIOUR	0.48	-0.05
Percent of Variance	20%	17%
Redundancy	4%	8%
Canonical correlation (r_c)	0.44	0.69
χ^2_{30} ^a (subsequent pairs of variates not significant)	50.121, p=0.012	49.744, p=0.013

¹ maximum number of whale-oriented boats within 1000 m of the whale.

² maximum number of non-whale oriented boats within 1000 m of the whale.

^a degrees of freedom in chi-square refers to the product of the number of variables in each set, not the number of observations, N.

sets, with all five pairs of canonical variates included ($\chi^2_{30} = 50.121$, $p = 0.012$). After removing the first pair of canonical variates, subsequent χ^2 tests were not significant, therefore the first pair of canonical variates accounted for the significant canonical correlation between the two sets of variables.

Results of the canonical correlation should be interpreted with caution. The technique describes trends based on linear combinations of variables (variates), rather than on the original variables themselves. The correlation between the first pair of canonical variates is statistically significant, and suggests potentially-important relationships based on the strength of linear correlations. However, it does not imply causality of those relationships. The following statements about pairwise relationships simply describe trends that contributed most to the significant canonical correlation, rather than suggesting a statistically-significant relationship between any pair of variables. Similarly, it is unwise to assume that the relationships presented here can be extrapolated to other regions, or seasons, or populations of killer whales.

In general, the paths of male killer whales tended to be less direct as boats got closer to the whales (Table 2), just as the experimental tracks predicted (Figure 7). However, paths were more direct when the number of whale-oriented boats increased. Whales tended to swim faster as boats got closer, and to slow down as number of boats increased. Rates of surface active behaviour decreased as boats moved closer to the whales, but increased as the number of whale-oriented vessels increased.

These trends are confounded by the fact that older whales tended to swim more slowly, more directly and with more surface active behaviour than younger whales. Similarly, there appears to be a seasonal component to whale behaviour, since speeds increased during the study period as path directness and rates of surface active behaviour declined. Male whales tended to swim slower, more directly and with more surface active behaviour as the day progressed.

While the canonical correlation between the two sets is significant, the proportion of variance extracted by the first pair of variates is moderate. The first canonical variate of the explanatory set extracts 16% of the variance in its own set. In addition, it accounts for 4% of the variance in its opposite set of behavioural variables (the so-called *redundancy* of the behavioural set). The first canonical variate of the behavioural set extracts 20% of the variance of its own set, and 3% of the variance in the explanatory set.

ii. *Female behaviour*

Using 48 tracks, a significant relationship was found between the set of explanatory variables and behaviour of female killer whales. The significant explanatory variables were date, age, the maximum numbers of whale-oriented and non-whale-oriented vessels within 1000 m, and the proximity of the nearest boat. Significant behavioural variables for female whales were mean dive time, and the deviation and directness indices. The canonical correlation (r_c) was 0.687 for female whales, indicating 47% overlapping variance between the two sets, with all five pairs of canonical variates included ($\chi^2_{30} = 49.744$, $p = 0.013$). After

removing the first pair of canonical variates, subsequent tests were not significant, therefore the first pair of canonical variates accounted for the significant canonical correlation.

Once again, relationships are interpreted among those variables that weighed heavily on the significant pair of canonical variates. This does not imply that any one pair of variables shows a significant correlation. In addition, the 48 observations of female whales represents a ratio of only 8 cases for each explanatory variable, rather than the suggested 10 (Tabachnick and Fidell 1996). While the technique appears to be robust to such a minor violation (Tabachnick and Fidell 1996), the correlation between boat traffic and behaviour of male whales may be more reliable than for females.

As boats got closer to female whales, the deviation index tended to increase (Table 2). This is consistent with results from experimental tracks (Figure 7). Thus, as boats got closer, tracks tended to be erratic but directional, and dives tended to be shorter. Once again, however, the relationship between whale behaviour and proximity shows the opposite trends as the one between behaviour and boat number. As the number of boats (both whale-oriented and non-whale-oriented) increased, the deviation index decreased, dives got shorter and paths became less direct. Thus, with many boats, female whales tended to adopt a smooth, non-directional path. As the season and day progressed, dives tended to get shorter and paths tended to become more erratic (Table 2).

Discussion

This land-based study of killer whales, combining experimental approaches and opportunistic observations, has revealed a complex relationship between whale behaviour and vessel activity. It has shown that movement patterns of northern resident killer whales are affected by a single vessel following whale-watching guidelines. Furthermore, this study provides a useful description of how whale behaviour varied with the presence and activity of whale-watching vessels in Johnstone Strait.

The utility of this study can be judged in three ways. First, the study identified *how* the behaviour of focal animals changed when they were approached by the experimental boat. Thus, it defines the nature of the effect in this population at this time. Secondly, the study identifies *how much* the animals' behaviour changed during experimental approaches. This provides information about effect size at the treatment level of current whale-watching guidelines, with the present number and group of whale-watching operators. Finally, opportunistic observations suggest that effect size is related to proximity of vessels. Therefore, the study cautions that weakening guidelines, by allowing boats to approach whales closer than 100 m, will mean accepting higher levels of disturbance.

Horizontal avoidance tactics

The tendency for whales' paths to become less predictable when approached by the experimental boat is consistent with horizontal avoidance. This offers observers new information when interpreting behaviour of these animals, since the study also measured parameters, such as dive time and surface active events, that showed less consistent

variation with boat activity. Intriguingly, the trend toward less predictable paths was detected on two different scales. Female killer whales tended to reduce predictability from one surfacing to the next, while males reduced path predictability on the scale of an entire tracking session. Essentially, females tended to evade a pursuing boat by adopting an erratic but directional path, whereas males adopted a smooth, non-directional path (Figure 10). Swim speeds also increased as the experimental boat approached female whales (Figure 7) and as all boats got closer to male whales (Table 2). Although gender-based differences in vessel avoidance are interesting, the key point is that both males and females responded to experimental approaches by adopting less predictable paths.

Howland (1974) and Weihs and Webb (1984) described efforts to model optimal strategies for evading predators. In both models, successful escape is linked to the *simultaneous* variation of velocity and turning radius. In order for this simple form of horizontal avoidance to be successful, prey must vary their speed and the extent to which they turn away from the path of the predator. Prey may opt to compensate for a larger turning radius by increasing speed, or may increase maneuverability to compensate for slower movement. Thus, slower prey might escape from faster predators if prey are able to turn more sharply (Howland 1974).

The response of a killer whale to a boat that follows it may be considered loosely analogous to a predator-prey interaction. In fact, some tracks of killer whales and the experimental boat (Figures 5 and 6) are reminiscent of long-exposure photographs of moths evading bats (Roeder 1967). This resemblance creates an opportunity to compare behaviour of whales around a boat to the tactics that some prey use to escape predation. Of course, the analogy must be interpreted with the critical caveat that while a prey's life

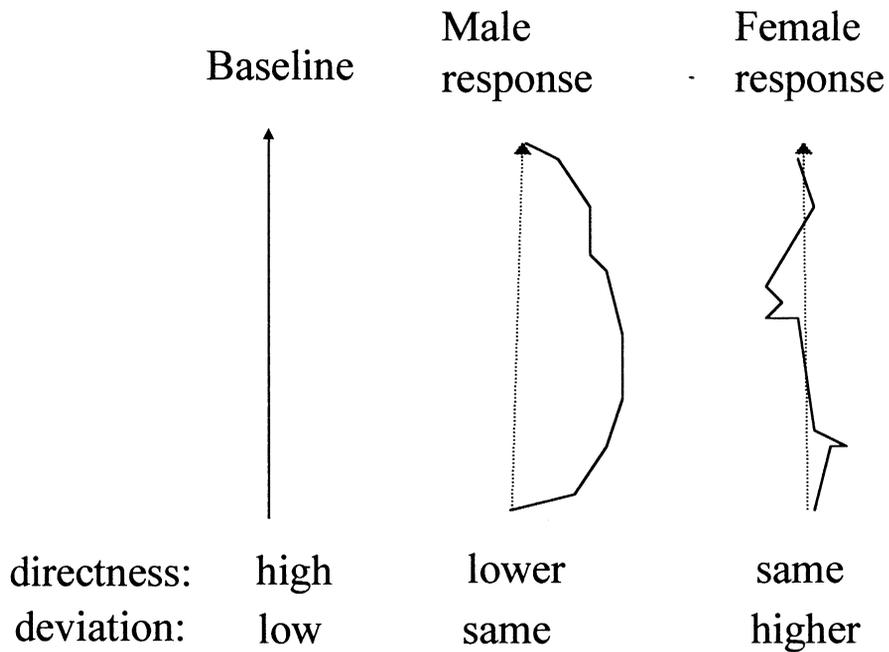


Figure 10. Schematic representation of male and female killer whale avoidance responses to close approach by a single boat. Males tended to adopt smooth, but less directional, paths compared to no-boat periods. Females tended to maintain fairly direct paths, but paths were more erratic than during no-boat periods. Solid lines indicate paths taken by each dive. Dashed lines indicate the cumulative distance covered from beginning to end of a tracking session.

depends on successful evasion, a killer whale's life does not. Therefore, while optimal predator-avoidance strategies can be used to better understand multivariate behavioural responses of killer whales to vessel traffic, I would expect killer whales to stop short of evasive maneuvers that carry high metabolic costs.

The analogy between a killer whale's boat response and a typical predator-avoidance strategy becomes apparent when one recalls that killer whales [prey] tended to increase both swim speed and deviation from a straight-line path as a boat [predator] approached closely. While gender-based differences in avoidance tactics are present, they are merely variations on a common theme of evading boats by adopting an irregular path. The difference in surfacing patterns seen between male and female killer whales may be accounted for by Howland's (1974) tradeoff paradigm: i.e., female killer whales may compensate for relatively slow swimming speeds (Figure 4) by increasing the 'escape angle' of Howland's model – the deviation index (Figure 7).

The suggestion that gender-based differences in avoidance strategies are linked to maneuverability and relative swim speeds may appear speculative. However, in an aquatic environment, acceleration performance and maneuverability are expected to decline with increasing size. This is "because a thrust that is proportional to surface area is used to maneuver a resistance that is proportional to volume" (Webb and de Buffr nil 1990), and male killer whales possess substantially greater body volume than females (Kriete 1995). Gender-based differences in speed and maneuverability may even play a role in killer whale societies. Jefferson *et al.* (1991) noted that male killer whales typically play a peripheral role in observed attacks on large baleen whales. Perhaps the

gender-based differences revealed in my study hint at underlying specialization of killer whales, with males adapted for speed and females for maneuverability.

The existence of subtle gender-based differences in boat tolerance is not altogether surprising. Matriarchs in this population are described as being more difficult than males to approach closely for photo-identification (G. Ellis, pers. comm.) and biopsy (Barrett-Lennard *et al.* 1996). Humpback whales demonstrate differential boat responses among age-sex classes when on the winter breeding and calving grounds off Hawaii (Bauer and Herman 1986).

The tendency for cetaceans to evade boats by speeding up or becoming less conspicuous has been described previously. Anecdotal evidence suggests that killer whales adopted erratic paths when chased during live-capture attempts (Spencer *et al.* 1966). Boat traffic has been correlated with increased swim speeds in killer whales (Kruse 1991), and with increased swim speeds and longer dives in fin whales (Notarbartolo di Sciara *et al.* 1996), bowhead whales (Fraker *et al.* 1982) and humpback whales (Bauer and Herman 1986, Green 1998). My study, though, quantified the extent to which killer whales use horizontal avoidance tactics to evade a boat following whale-watching guidelines; but the evidence of vertical avoidance in terms of increased dive time was weak. However, as number of boats increased, dive times of females tended to increase. Other researchers have been unable to detect use of increased dive time as an avoidance response in killer whales (D. Duffus, unpublished data), although the strategy appears to be common among baleen whales.

A final point regarding the nature of the effect of vessels on killer whales is that a predator-prey analogy also offers a plausible framework for context-specific avoidance

tactics. Whales would be expected to display a variety of responses to a variety of traffic scenarios, depending on the speed and maneuverability of the whale and vessel(s) involved. Certainly, the avoidance responses generated by the experimental boat are reaffirmed by canonical correlation between close boats and less predictable swim paths. However, as number of vessels increased, swim paths became more predictable (i.e., the paths of male whales tended to be more direct, and the paths of females tended to be less erratic).

The tradeoff between number and proximity of boats suggests either that whales were less disturbed by other boats than by the experimental boat, or that the avoidance tactic is abandoned when many boats approach. An irregular path may be a useful avoidance tactic with a single boat but ineffective with more than one. In a multiple-vessel scenario, a dive that takes a whale farther from one boat may bring it closer to another. Perhaps the positive correlation between vessel number and dive time seen in female whales (Table 2) suggests that these animals shifted from horizontal avoidance of a single boat, to vertical avoidance with many boats. This compromise deserves further attention in the form of a multiple-vessel experimental treatment.

An earlier study also found context-specific responses to vessel number and proximity. In 1992 and 1993, Adimey (1995) observed killer whales from a boat in Johnstone Strait and concluded that increased rates of surface active behaviour could indicate that a whale is disturbed by a vessel approaching too closely. However, surface active events were less common in Adimey's study when the number of boats was high. Alternatively, my study found that for males, rates of surface active behaviour declined as the nearest boat got closer, and became more common as number of whale-oriented

boats increased. The opposite findings of the current study with Adimey (1995) probably reflect a narrower range of traffic intensities in my study, but may also stem from the lack of control observations in Adimey's boat-based study. Our findings do agree on one issue, though: the response to close approaches is opposite to the response to many vessels. The discrepancy between our two studies illustrates the importance of experiments in assessing behavioural impacts. Similarly, the relationships among date, time and whale behaviour (Table 2) serve as a reminder that distribution of salmon is the most important determinant of whale position and activity in Johnstone Strait (Nichol and Shackleton 1996).

Effect size

While the most valuable aspect of this study may be its definition of the nature of the behavioural response, it is also important to attempt to describe the effect size at the treatment level of current whale-watching conditions in Johnstone Strait. Recall that International Whaling Commission guidelines caution against whale-watching practices that create "undue stress" for individual whales or populations (IWC 1995). There is evidence from other taxa that repeated disturbance can cause stress, which can have population-level repercussions. Degradation of whales' acoustic environment may have implications for their ability to find food, and each other. These processes may be creating serious consequences for the northern resident killer whale population; or they may be tempered by habituation. My study does indicate that whales attempted to avoid boats that approached too closely. Granted, in order to determine the extent to which this disturbance indicates stress for individuals and populations, more studies are needed.

However, current effect size can be assessed already in qualitative terms. Evidence for habituation is considered first. Plausible large-scale effects are considered next, with upper limits placed on any potential impact.

One characteristic of many interactions between humans and wildlife populations is that behavioural responses to human activity diminish over time. Habituation has been shown in chimpanzees exposed to long-term ecotourism ventures (Johns 1996). Bighorn sheep show reduced response to predictable human activity (MacArthur *et al.* 1982). It may be that after two decades of commercial whale-watching pressure in Johnstone Strait, killer whales have reduced their responsiveness to boat traffic. Indeed, perhaps the most intriguing aspect of these findings is the apparent change in avoidance strategies since these whales were tracked in 1983, near the beginning of commercial whale-watching in Johnstone Strait (Kruse 1991).

Kruse (1991) measured the swimming speeds of northern resident killer whales that were travelling singly or in small groups. She found that “milling indexes were about the same for both disturbed and undisturbed whales”. (Of the observations in Kruse’s “disturbed” category, 68% contained only one boat.) She also found a tendency for swimming speeds to increase with increasing number of associated boats. In my study, males (from canonical correlation) and females (from experimental approaches) tended to speed up as a vessel approached closely, but neither group swam faster as number of boats increased. In fact, speeds of males were negatively correlated with number of vessels. Does this apparent change in behaviour indicate habituation, or does it reflect differences in study design?

A sampling bias may have existed in Kruse's study. With their larger dorsal fins, male killer whales make a preferred photographic subject for some local whale-watchers (J. Borrowman, pers. comm.). Mean speed of Kruse's 'undisturbed' whales (4.55 km/h) matches closely with that of female whales in this study (4.71 km/h), and speed of 'disturbed' whales (6.37 km/h) approximates that of male whales in this study (6.32 km/h). It is conceivable that no-boat tracks of unidentified whales in the earlier study were biased toward females, with a disproportionate number of male tracks containing boats.

Habituation is the second explanation for the discrepancy. This would suggest that, in addition to whales' avoidance behaviour being context-specific, the response could also change over time. Certainly, killer whales would have several incentives to abandon the fast-swimming avoidance tactic. As swim speed increases, breathing rate of gray whales (Sumich 1983) and metabolic rate of killer whales (Kriete 1995) have been shown to increase exponentially. Thus, the shift away from Kruse's observed avoidance response may indicate that animals have shifted away from avoidance behaviour that carries relatively high energetic costs. In addition, the corresponding increase in surfacing rate (Sumich 1983) as whales swim faster may actually serve to make the animal more conspicuous. Finally, and most plausibly, swimming faster would simply be an ineffective avoidance strategy with most motorboats.

A more rigorous comparison of available data from the two periods is certainly warranted. This choice between competing explanations of sampling bias and habituation illustrates the key barrier to sound scientific management of whale-watching: uncertainty. In the context of ambiguous, and often apparently contradictory, findings,

managers are faced with a choice between maximizing immediate recreational benefits to humans and a precautionary approach that withholds interactions to mitigate perceived impacts on whales (Duffus and Baird 1995). If the discrepancy between my study and Kruse's study (1991) indicates habituation to whale-watching, it lends support to managing for human benefit. If, however, the apparent discrepancy simply reflects differences in sampling protocol, then it suggests that northern resident killer whales have yet to grow accustomed to sharing the Strait, even after a killer-whale-generation of commercial whale-watching activity. The evidence for habituation of northern resident killer whales to predictable boat traffic is equivocal at present. However, even if habituation should be demonstrated more convincingly, that does not eliminate the potential for larger-scale effects of repeated disturbance.

Repeated disturbances have been linked to long-term effects for terrestrial mammals, which have been better studied than those of cetaceans (IFAW 1995, Myrberg 1990). We may carefully use research on terrestrial animals to offer insight into possible effects, and to guide future cetacean studies. MacArthur *et al.* (1982) reported that human disturbance of bighorn sheep triggered heart rate to rise to a level consistent with sheep alert to possible predation risk. Elevated heart rate and increased alertness were also shown in both bighorn sheep and desert mule deer when exposed to jet aircraft noise (Weisenberger *et al.* 1996). Kraabel and Miller (1997) further report that simulated stress in bighorn sheep made the animals more susceptible to infection.

The tendency for terrestrial animals to become more vigilant when disturbed (MacArthur *et al.* 1982, Stephenson *et al.* 1996, Weisenberger *et al.* 1996) has also been linked to reduced foraging success (Stephenson *et al.* 1996). Human disturbance relating

to bird-watching in Florida has demonstrated a similar link between motorboat activity and increased alertness of birds (Galicía and Balassarre 1997). Presence of boats (Galicía and Balassarre 1997) and people (Burger and Gochfield 1997) have been shown to reduce feeding in several bird species. Even humans find traffic noise invasive, and the tendency for ambient noise to disrupt sleep is well-documented (e.g. Öhrström *et al.* 1990). The effects of unpredictable disturbances tend not to be tempered by habituation, so it is reasonable to be concerned that short-term responses to boat traffic may indicate larger-scale implications for killer whales exposed to whale-watching traffic.

We do know that boat noise can mask communication signals used by killer whales (Bain and Dahlheim 1994). Bain and Dahlheim (1994) tested the ability of captive killer whales to detect pure tones, discrete calls of conspecifics, and echolocation click trains under varying levels of background vessel noise. The authors found that low-frequency components of calls, which are omnidirectional, were masked by vessel noise, and that the masking effect was strongest when the noise source was placed directly in front of the whale. In addition, a higher level of boat noise elicited a stronger masking effect. This study has several implications for wild killer whales.

Bain and Dahlheim (1994) argue that the key consequence of masking is to reduce the distance over which killer whales can effectively search for food by masking the lateral, low-frequency components of calls. This hypothesis is critical for linking short-term behavioural responses to human activity and long-term implications for the health of individuals and populations. Such a link is difficult to establish, but examples from many disparate studies on a variety of taxa reveal some recurring themes.

Whales tend to respond to boat traffic with the stereotyped, short-term avoidance tactics (Howland 1974, Weihs and Webb 1984) of increasing swim speed (Green 1998, Kruse 1991) and varying the time and/or position of surfacings (Bauer and Herman 1986, Fraker *et al.* 1995, Notarbartolo di Sciara *et al.* 1996). On a larger scale, northern resident killer whales are more likely to leave Robson Bight as boat traffic enters that reserve (Trites *et al.* 1995), just as mule deer abandoned portions of their range when military activity intensified (Stephenson *et al.* 1996). Repeated disturbance in other species can force animals to be increasingly alert (MacArthur *et al.* 1982, Weisenberger *et al.* 1996), and may cost them foraging opportunities (Burger and Gochfield 1997, Galicia and Balassarre 1997, Stephenson *et al.* 1996). Repeated disturbance can cause lowered immune function (Kraabel and Miller 1997), abandonment of microhabitats (Eckstein *et al.* 1979) and disruption of sleep patterns (Öhrström *et al.* 1990).

Currently, any proposed link between short-term response and long-term effects is admittedly a tenuous one. Although no study to date can address the underlying concern that short-term disruptions may have a long-term, cumulative effect that has not yet been measured, we do know that these whales continue to return to Johnstone Strait each year, and the population continues to grow (Ford *et al.* 1994). Therefore, the only fair assessment of large-scale effects of boat traffic on northern resident killer whales is a qualitative one. The results presented here indicate that boat traffic can disrupt short-term behaviour of individuals, however there is no convincing evidence that human disturbance is adversely affecting northern resident killer whales on the level of the population. Similarly, it would be unwise to assume that these results typify the

behaviour of other populations, or even of the same population at other times or locations.

Repeating patterns

While binary analysis of results from experimental approaches revealed significant effects, additional information was gained from canonical correlation. These analyses showed that avoidance patterns of both male and female killer whales were correlated with the proximity of the nearest boat. This result indicates that weakening current whale-watching guidelines, or making no effort to enforce them, necessitates accepting a stronger disturbance effect than seen during experimental approaches.

The underlying concern prompting studies of behavioural impacts of human activities on whales is that repeated disturbance of individuals may have cumulative, adverse effects on the population. Granted, careful review of related studies does lend credibility to such fears. However, long-term monitoring of northern resident killer whales has demonstrated that the population is growing steadily (Ford *et al.* 1994). Perhaps the immediate threat is not related to conservation, but rather habitat usage.

Female killer whales responded to close boat approaches by choosing a path that was less predictable from one dive to the next. Thus, our ability to predict where a whale would surface after a dive declined as a boat got closer. This pattern was repeated for males, but was detected on a slightly larger scale. Males responded to close approach by adopting a path that was less predictable on the scale of an entire tracking session. That is to say, our ability to know where a whale would be at the end of a tracking session declined as a boat got closer. These results are reminiscent of the findings of Trites *et al.*

(1995), who noted that as the number of boats entering Robson Bight increased, the probability of whales leaving this reserve also increased. In other words, increased vessel traffic in the reserve reduced the predictability of whale distribution on the scale of a nine-kilometer section of coastline.

At this point, it becomes apparent that the relationship between boat traffic and path predictability in northern resident killer whales is repeated on different spatial scales. That is to say, three different analyses have revealed complex patterns on the scales of: one surfacing to the next; a tracking session; and the 9-km reserve at Robson Bight. Moreover, these patterns are self-similar, in that whales are using horizontal avoidance tactics at each scale. If these whales generally utilize horizontal avoidance tactics in response to intense whale-watching traffic, then there is reason to fear this pattern may be occurring on a larger scale as well.

Perhaps this is the real danger of human encroachment on killer whale habitat. The threat of disease and population decline is legitimate. However, before evidence of such impacts become apparent, I would expect to see less predictable usage of the portions of the whales' range that have the most human activity. Summer habitat usage is undoubtedly limited by the distribution of salmon and the availability of alternative habitat. However, it is the nature, rather than the extent, of the effect that concerns me. The whales responded to a disturbing stimulus by attempting to avoid it. If the pattern seen on three smaller scales is repeated on a larger one, the result will be less predictable seasonal movements of killer whales in Johnstone Strait. If this is so, then the ultimate impact will fall not only on the whales, but also on the people who benefit from the whales' continued usage of the area.

Recommendations

The northern resident killer whale population has served as a useful model for many studies over 20 years. The long-term photo-identification studies of this population have monitored population trends, and assuage some fears of large-scale impact, such as population decline (Ford *et al.* 1994). Similar focus on sighting records will reveal whether these whales are using Johnstone Strait less today than in previous years.

Careful comparison of my results to other datasets (e.g. Kruse 1991), where appropriate, could offer valuable insights into other processes, such as habituation, changes in habitat use, and disruption of foraging and resting activity. Bain (1986) found diurnal patterns in the behaviour of captive killer whales; a pattern that has not been observed in the wild (Ford *et al.* 1994). If circadian rhythms of killer whales can be changed in captivity, perhaps this can forge a link between short-term responses to boats and longer-term implications. Existing datasets should be examined to see whether the behaviour of northern resident killer whales has begun to reflect the diurnal patterns of whale-watching traffic.

The current study lends support for an iterative process in setting whale-watching guidelines. In this scenario, a community takes a precautionary approach (Duffus and Baird 1995) to whale-watching, tests for responses of whales to human activity, and continues to update guidelines as new information is acquired. Managers should decide on an acceptable magnitude of short-term disruption to set an appropriate distance guideline. The significant relationships between whale behaviour and boat numbers that have been demonstrated in this study and by Trites *et al.* (1995) have similar implications for a precautionary approach to managing whale-watching. This approach would place

whale-watchers on a few large vessels, rather than many small vessels, until the effects of multiple vessels on killer whales can be tested. While this precautionary approach does not address enforcement of a voluntary code of conduct, adherence to community-sanctioned guidelines in this region is laudable. In Johnstone Strait, biological relevance of whale-watching guidelines, rather than enforcement, appears to be the key concern.

The results of studies on masking sounds suggest that respectful whale-watching involves slow, parallel approaches. Leapfrogging may be inappropriate, since speeding up to overtake the whale increases the intensity of cavitation noise (Richardson *et al.* 1995). Increasing propeller rotation rate also shifts engine noise to higher frequencies (Richardson *et al.* 1995), which would have greater potential for masking killer whale communication signals (Bain and Dahlheim 1994). Furthermore, placing a boat directly ahead of the whale's path puts the source of the masking noise in the most disruptive position (Bain and Dahlheim 1994). These factors may explain why avoidance responses to leapfrogging vessels appear to be more dramatic than to vessels traveling parallel to the whale (R. Williams, unpublished data).

Most whale-oriented vessels observed in this study were commercial whale-watching vessels. It may be that whales are responding to the sound, rather than proximity or number, of boat engines, or have habituated to particular boats that they encounter often. Greene (1998) found that humpback whales in Hawaii showed stronger responses to boats with loud engines than to boats with quieter engines. The potential for different responses to different boats may indicate that the killer whales in the current study simply tended to avoid the experimental boat, but tolerated the predictable charter vessels whose distinctive engine sounds they recognized. This could account for some

unexplained variance in the canonical correlations, and underscores the need for an acoustic component to future studies. Most importantly, if whales avoided the experimental boat but not the charter boats due to differences in whale-watching technique, then guidelines should encourage recreational boaters to emulate their commercial counterparts. Future experiments are needed to test for effects of leapfrogging and multiple vessels on whale behaviour, and these experiments must incorporate an acoustic component.

The value of an experimental approach to detecting subtle behavioural responses can not be overemphasized. Although my study does not indicate alarming effects of boat traffic on the behaviour of this population of whales, which may already be habituated, it does caution against the currently unhindered expansion of boat-based whale-watching efforts. The recent trend toward viewing animals in their natural habitat has prompted enormous changes in the way that society values whales, and whale-watching has been identified as a sustainable alternative to whaling (Barstow 1986, IFAW *et al.* 1995, IWC 1994). However, such admirable efforts must be tempered by assurance that these encounters do not cost the health of individual whales or their populations (IWC 1995). If we do not remain skeptical of the apparently benign nature of ecotourism, we risk enforcing token whale-watching guidelines that may be counterproductive. Furthermore, if we do not test the biological relevance of these guidelines, we may also end up harming animals with our desire to appreciate them.

Literature cited

- Adimey, N.M. 1995. A descriptive study of the percussive behavior of orcas, *Orcinus orca*, in Johnstone Strait, British Columbia. M.S. thesis, Nova Southeastern University, Fort Lauderdale, Florida.
- Bain, D.E. 1986. Acoustic behavior of *Orcinus*: Sequences, periodicity, behavioral correlates and an automated technique for call classification. *In Behavioral biology of killer whales. Edited by B.C. Kirkevold and J.S. Lockard.* Alan R. Liss, New York. pp. 335-371.
- Bain, D.E. and Dahlheim, M.E. 1994. Effects of masking noise on detection thresholds of killer whales. *In Marine mammals and the Exxon Valdez. Edited by T.R. Loughlin.* Academic Press, San Diego. pp. 243-256.
- Barrett-Lennard, L.G., Smith, T.G. and Ellis, G.M. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. *Marine Mammal Science* **12**: 14-27.
- Barstow, R. 1986. Non-consumptive utilization of whales. *Ambio* **15**: 155-163.

- Bauer, G.B. and Herman, L.M. 1986. Effects of vessel traffic on the behavior of humpback whales in Hawaii. Report to National Marine Fisheries Service, Honolulu, Hawaii.
- Briggs, D. 1991. Impact of human activities on killer whales at the rubbing beaches in the Robson Bight Ecological Reserve and adjacent waters during the summers of 1987 and 1989. Report to BC Ministry of Environment, Land and Parks.
- Burger, J. and Gochfield, M. 1997. Effects of ecotourists on bird behavior at Loxahatchee National Wildlife Refuge, Florida. *Environmental Conservation* 25: 13-21.
- Davis, R.E., Foote, F.S., Anderson, J. and Mikhail, E. 1981. *Surveying theory and practice*. McGraw Hill, New York.
- Duffus, D.A. and Baird, R.W. 1995. Killer whales, whalewatching and management: a status report. *Whalewatcher*, pp. 14-17.
- Duffus, D.A. and Dearden, P. 1992. Whales, science and protected area management in British Columbia, Canada. Paper presented to World Congress on Parks and Protected Areas, Caracas, Venezuela, 10-21 February, 1992.

- Duffus, D.A. and Dearden, P. 1993. Recreational use, valuation, and management, of killer whales (*Orcinus orca*) on Canada's Pacific coast. *Environmental Conservation* 20: 149-156.
- Eckstein, R.G., O'Brien, T.F., Rongstad, O.J. and Bollinger, J.G. 1979. Snowmobile effects on movements of white-tailed deer: a case study. *Environmental Conservation* 6: 45-51.
- Ford, J.K.B., Ellis, G.M. and Balcomb, K.C. 1994. Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington State. UBC Press, Vancouver.
- Fraker, M.A., Richardson, W.J., and Würsig, B. 1982. Disturbance responses of bowheads. *In* Behavior, disturbance responses and feeding of bowhead whales *Balaena mysticetus* in the Beaufort Sea, 1980-1981. Unpublished report by LGL Ecological Research Associates, Inc., Bryan, TX, for U.S. Bureau of Land Management, Washington. pp. 145-248.
- Galicia, E. and Balassarre, G.A. 1997. Effects of motorized tourboats on the behavior of nonbreeding American flamingos in Yucatan, Mexico. *Conservation Biology* 11: 1159-1165.

- Green, M.L. 1998. The impact of vessels on the Hawaiian humpback whale (*Megaptera novaeangliae*): an experimental study. Report to National Marine Fisheries Service.
- Howland, H.C. 1974. Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* 47: 333-350.
- Hoyt, E. 1997. The potential of whale watching in Europe. Whale and Dolphin Conservation Society, Bath, UK, pp. 1-36.
- IFAW, Tethys Research Institute and Europe Conservation. 1995. Report of the workshop on the scientific aspects of managing whale watching. Montecastello di Vibio, Italy.
- International Whaling Commission (cited as IWC). 1994. Forty-fourth report of the International Whaling Commission. Cambridge.
- International Whaling Commission (cited as IWC). 1995. Forty-fifth report of the International Whaling Commission. Cambridge.
- James, F.C. and McCulloch, C.E. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box? *Annu. Rev. Ecol. Syst.* 21: 129-166.

Jefferson, T.A., Stacey, P.J. and Baird, R.W. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review* 21: 151-180.

Johns, B.G. 1996. Responses of chimpanzees to habituation and tourism in the Kibale Forest, Uganda. *Biological Conservation* 78: 257-262.

Johnstone Strait Killer Whale Committee (cited as JSKWC). 1991. Background report. BC Min. of Environment, Land and Parks and Dept. of Fisheries and Oceans.

Johnstone Strait Killer Whale Committee (cited as JSKWC). 1996. Johnstone Strait Whale Watching Guide. BC Min. of Environment, Land and Parks and Dept. of Fisheries and Oceans.

Kirkevold, B.C. and Lockard, M.E. 1986. Behavioral biology of killer whales. Alan R. Liss, New York.

Kraabel, B.J. and Miller, M.W. 1997. Effect of simulated stress on susceptibility of bighorn sheep neutrophils to *Pasteurella haemolytica* leukotoxin. *Journal of Wildlife Diseases* 33: 558-566.

Kriete, B. 1995. Bioenergetics in the killer whale, *Orcinus orca*. Ph.D. thesis, University of British Columbia, Vancouver.

- Kruse, S. 1991. The interactions between killer whales and boats in Johnstone Strait, B.C. *In Dolphin societies: discoveries and puzzles. Edited by K. Pryor and K.S. Norris.* University of California Press, Berkeley. pp. 149-159.
- Loughlin, T.R. 1994. Marine mammals and the *Exxon Valdez*. Academic Press, San Diego.
- MacArthur, R.A., Geist, V. and Johnston, R.H. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *J. Wildl. Manage.* 46: 351-358.
- Milstein, A. 1993. Factor and canonical correlation analyses: basic concepts, data requirements and recommended procedures. *In Multivariate methods in aquaculture research: case studies of tilapias in experimental and commercial systems. Edited by M. Prein, G. Hulata and D. Pauly.* ICLARM Stud. Rev. 20, pp. 24-31.
- Myrberg, A.A. 1990. The effects of man-made noise on the behavior of marine animals. *Environment International* 16: 575-586.

Nichol, L.M. and Shackleton, D.M. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. *Can. J. Zool.* 74: 983-991.

Notarbartolo di Sciara, G., Jahoda, M., Biassoni, N. and C. Lafortuna. 1996. Reactions of fin whales to approaching vessels assessed by means of a laser range finder. *In* Proceedings of the Tenth Annual Meeting of the European Cetacean Society, Lisbon, 11-13 March 1996.

Öhrström, E., Björkman, M. and Rylander, R. 1990. Effects of noise during sleep with reference to noise sensitivity and habituation. *Environment International* 16: 477-482.

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

Richardson, W.J., Greene, C.R., Malme, C.I. and Thomson, D.H. 1995. *Marine mammals and noise*. Academic Press, San Diego.

Roeder, K.D. 1967. *Nerve cells and insect behavior*. Harvard University Press, Cambridge.

- Spencer, M.P., Gornall, T.A. and Poulter, T.C. 1966. Respiratory and cardiac activity of killer whales. *J. Appl. Physiol.* 22: 974-981.
- Stephenson, T.R., Vaughan, M.R. and Andersen, D.E. 1996. Mule deer movements in response to military activity in southeast Colorado. *J. Wildl. Manage.* 60: 777-787.
- Stewart-Oaten, A. 1995. Rules and judgements in statistics: three examples. *Ecology* 76: 2001-2009.
- Sumich, J.L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. *Can. J. Zool.* 61: 647-652.
- Tabachnick, B.G. and Fidell, L.S. 1996. *Using Multivariate Statistics*. Harper and Row, New York.
- Trites, A.W., Hochachka, W. and Carter, S.K. 1995. Killer whales and vessel activity in Robson Bight from 1991 to 1994. Report to BC Ministry of Environment, Land and Parks.
- Tyack, P.L. 1982. Humpback whales respond to the sounds of their neighbors. Ph.D. thesis, Rockefeller University, New York.

- Webb, P.W. and de Buffrénil, V. 1990. Locomotion in the biology of large aquatic vertebrates. *Transactions of the American Fisheries Society* 119: 629-641.
- Weihs, D. and Webb, P.W. 1984. Optimal avoidance and evasion tactics in predator-prey interactions. *J. Theor. Biol.* 106: 189-206.
- Weisenberger, M.A., Krausman, P.R., Wallace, M.C., De Young, D.W. and Maughan, O.E. 1996. Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. *J. Wildl. Manage.* 60: 52-61.
- Whitehead, H., Dillon, M., Dufault, S., Weilgart, L. and Wright, J. Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. *Journal of Animal Ecology* 67: 253-262.
- Würsig, B., Cipriano, F. and Würsig, M. 1991. Dolphin movement patterns: information from radio and theodolite tracking studies. *In Dolphin societies: discoveries and puzzles. Edited by K. Pryor and K.S. Norris. University of California Press, Berkeley. pp. 79-111.*
- Zar, J.H. 1996. *Biostatistical analysis.* Prentice Hall, Upper Saddle River, NJ.

Appendix 1: Johnstone Strait Whale Watching Guidelines

1. Guidelines for a Single Vessel Watching Whales

Diving or swimming with whales constitutes a type of approach to killer whales and falls under the same guidelines and regulations.

It is illegal to hunt, chase, disperse, drive or herd pods or individual whales.

Approach no closer than **100 metres** (under review) and shift your motor into neutral or idle. Keep noise levels down – no horns, whistles, or racing of motors. Start your motor only after the whales are more than 100 metres from your vessel. Leave the area slowly, gradually accelerating when more than 300 metres from the whale(s).

Approach whales from the side, not from the front or the rear. Approach and depart slowly, avoiding sudden changes in speed or direction. Do not “leapfrog”. Avoid disturbing groups of resting whales.

Maintain low speeds and constant direction if travelling parallel to whales. When whales are travelling close to shore, avoid crowding them near shore or coming between whales and shore.

Limit the time spent with any group of whales to less than 30 minutes at a time when within **100 – 200 metres** of whales.

2. Guidelines for More than One Vessel at the Same Observation Site

Avoid any boat position that would result in encircling the whale(s).

Minimize the time spent and number of vessels with any one group of whales. Limit time to 30 minutes within 100 – 200 metres and then move out to allow other vessels access to good viewing positions. Coordinate activities by maintaining contact with other charter operators and ensure that all operators are aware of the whale watching guidelines.

Respect the same guidelines that apply when only one vessel is watching whales.

(from JSKWC 1996)

Appendix 2: GAWK program for calculating the angle between a dive and the straight-line path predicted by the dive before it

[Reads fields 1 and 2 as the x- and y-coord of a "track"

Computes the angle theta of the turn away from straight-ahead
Left and right are not calculated. © Alistair Blachford Nov'97]

```
NR==1{x1=$1;y1=$2;print $0,"NA";next}
NR==2{x2=$1;y2=$2;a1=x2-x1;b1=y2-y1;prev=$0;next}

{

a2=$1-x2; b2=$2-y2
x=(a1*a2 + b1*b2)/sqrt((a1*a1+b1*b1)*(a2*a2+b2*b2))
ninety=3.14159/2
theta=ninety - atan2(x,sqrt(1-x*x)) #arccos(x)
if(sqrt((a1+a2)^2 + (b1+b2)^2)>sqrt((a1-a2)^2 + (b1-b2)^2))
    {
        if(theta>ninety)theta=3.14159-theta
    }

else if(theta<ninety)theta=3.14159-theta
print prev, theta*180/3.14159
prev=$0
x1=x2;y1=y2;x2=$1;y2=$2;a1=a2;b1=b2

}

END{print prev,"NA"}
```