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Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches

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Abstract

Johnstone Strait provides important summer habitat for the northern resident killer whales *Orcinus orca* of British Columbia. The site is also an active whale-watching area. A voluntary code of conduct requests that boats do not approach whales closer than 100 m to address perceived, rather than demonstrated, effects of boat traffic on killer whales. The purpose of the study was to test the relevance of this distance 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 spy-hopping were recorded. On average, 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 used 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 suggest 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 large sample size and extensive experimentation when assessing the impacts of human activity on killer whales.

Key words: whale, whale-watching, behaviour, canonical correlation, disturbance, *Orcinus orca*

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 coast of British Columbia were considered as recently as 1960 (Ford, Ellis & Balcomb, 1994). Today, such plans 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 (Johnstone Strait Killer Whale Committee (JSKWC), 1991; Kruse, 1991; Adimey, 1995; Trites, Hochachka & Carter, 1995).

Cetacean populations around the world are becoming targets for the growing ecotourism industry (Hoyt, 1997). In 1993, the International Whaling Commission (IWC) 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. 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 & Dearden, 1993). However, vessel traffic may carry costs for whales (IWC, 1995). A suitable management goal 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 four distinct populations of killer whales on the British Columbia coast that have

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overlapping ranges, but are socially and ecologically isolated (Ford *et al.*, 1994). Whale-watching tends to focus on the northern and southern populations of *resident* killer whales, the fish-eating types, since these whales are sighted more consistently than the *offshores* or the marine-mammal-eating *transients*. One of the most reliable places to see killer whales in the wild is Johnstone Strait, British Columbia, Canada (Fig. 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 funnelled through the narrow strait (Nichol & Shackleton, 1996). A similar core habitat for southern resident killer whales is found in Haro Strait between British Columbia and Washington State, where proximity to urban areas makes whale-watching a much larger industry than in Johnstone Strait. In 1995 and 1996, the core whale-watching fleet in Johnstone Strait consisted of three operators, with a total of four boats. Operators typically offered one or two tours daily from mid-June to early September. In contrast, the southern resident whale-watching industry employed 34 Canadian and American companies in 1995 and 40 in 1996, which represents a fleet of 47 (1995) and 54 (1996) vessels (Osborne & Otis, 2000). The southern resident whale-watching season is also longer and more variable, with companies operating one to six trips daily, based on demand, from May to September (Osborne & Otis, 2000).

Johnstone Strait is unique for reasons other than its designation as the core habitat for northern resident killer whales. It is an important area for commercial salmon fishing (JSKWC, 1991). It is also home to people who have been successful in encouraging the provincial government to protect Robson Bight as a critical habitat for killer whales, and who have established voluntarily a code of conduct to self-regulate behaviour around whales (JSKWC, 1996). In 1990, British Columbia Parks initiated a warden and monitoring programme of boat and whale usage of the Robson Bight–Michael Bigg Ecological Reserve, and the waters immediately adjacent to it. Analysis of data from 1990–94 by Trites *et al.* (1995) found that the likelihood of whales leaving the Ecological Reserve increased as increasing numbers of boats entered it. 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. Current self-imposed whale-watching guidelines request that boats remain 100 m from whales, but this may be based more on aesthetics than biological relevance. 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 boats are not disturbing whales, provided that they follow some groundless rules.

The primary goal of our study was to test whether a vessel following whale-watching guidelines affected the behaviour of northern resident killer whales during summer in Johnstone Strait. A whale might respond to boats by varying the duration of its 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 the attention span of a whale-watcher. Whales may also display agonistic behaviours, such as slapping flukes or pectoral fins on the surface of the water.

Our secondary goal was to describe how whale behaviour varied across the range of traffic conditions seen 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 difficult 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.

MATERIALS AND 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; Fig. 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). The shore-based nature of the study allowed observation of vessel activity without contributing to potential vessel effects.

Data were collected using an electronic theodolite (Pentax ETH-10D with a precision of ±10″ of arc) connected to a laptop computer equipped with custom software (THEOPROG: available from D. E. Bain). Cliff height was measured by stretching a rope of known length at the water's edge on a beach below the cliff and by using the theodolite to obtain horizontal and vertical angle coordinates for both ends (Williams, 1999). Height was then calculated using trigonometric relationships described by Davis *et al.* (1981) and Würsig, Cipriano & Würsig (1991). The theodolite was located *c.* 50 m a.s.l.

Reliability of the theodolite–computer apparatus was measured by stretching a rope of known length along the water's edge on a beach across the strait from the cliff. At a distance of 3.79 km, our mean estimate of the length of a 30 m rope as measured by the theodolite–computer apparatus was 28.93 m ($n = 20$, SE = 0.18). This translates to a measurement error of *c.* 3.5% in terms of accuracy, and < 1% in terms of precision. Per cent errors in measuring cliff height, distance travelled and speed tend to be approximately equal (Würsig *et al.*, 1991).

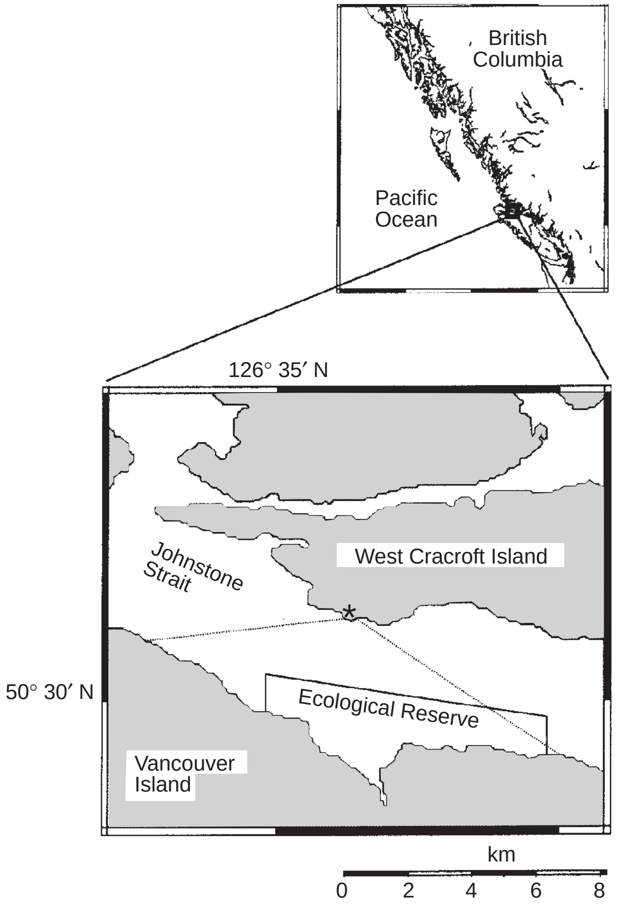

Fig. 1. Study area in Johnstone Strait, BC, Canada, showing lines of sight (- - -), position of theodolite (*), and boundaries of Robson Bight–Michael Bigg Ecological Reserve.

Selection of focal animals

Northern resident killer whales entered the study area in matrifocal social units called subpods (Olesiuk, Bigg & Ellis, 1990; Ford *et al.*, 1994). 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 and reliability of re-sighting an individual within a tracking session. We chose focal animals that would not be confused easily with other members of the group and that were likely to be consistently re-sighted. A focal animal typically had a distinctive dorsal fin and saddle patch (Ford *et al.*, 1994). Focal whales were usually within a few hundred metres of other members of the group. Whales swimming mid-strait were chosen over those swimming along the Vancouver Island shore, since accuracy of a reading diminishes with distance from the theodolite (Würsig *et al.*, 1991). In 1995, only males were tracked (since their dorsal fins can reach twice the height of the those of adult females). However, in 1996, we were able to consistently re-sight distinctive females.

Animals were selected that were likely to be visible for a minimum of 15 min, because earlier work has shown that tracks shorter than 1000 s tend to bias estimates of respiration rate (Kriete, 1995). Animals were tracked only when displaying typical foraging behaviour. This activity is the most commonly observed activity of resident killer whales in summer in Johnstone Strait (Nichol & 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 consistency in tracking only foraging animals prevented any effect of activity state on respiration rate and swim speed from masking effects of boat traffic.

Tracking

Tracking whales

The tracking team consisted of a spotter, a theodolite operator and a computer operator. The spotter announced each time that a focal animal surfaced to breathe or display surface-active behaviour. The theodolite operator located the position of the whale. Behaviours recorded by the computer operator included: breath, breach, fluke slap, pectoral fin slap, dorsal fin slap, unidentified splash, porpoising, and spy-hop (Ford *et al.*, 1994). The computer was linked to the theodolite to record the time that it retrieved the horizontal and vertical angle coordinates of a whale's position. A scale, marked at 10 cm intervals, was painted on a rock wall below the cliff. Water level was noted every 15 min to determine the height of the theodolite above sea level over changing tides.

Tracking boats

During the whale's long dives, boat positions were recorded along with information about vessel type, whale-watching status, orientation relative to the whale, estimated distance from the whale, and direction of travel. The tracking team recorded the position of every boat within 3 km of the whale, as often as possible without losing track of the whale's position. 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. All others were deemed to be whale-oriented traffic. Every attempt was made to record when a vessel's status changed within a tracking session.

Track types

Whales and boats were tracked under 3 traffic conditions:

(1) *No-boat*. 'No-boat' tracks were defined as ones when no boats were seen within 3 km of the focal animal. During the 1996 season, local charter operators agreed to stay away from the focal whale while its

movements were tracked, thereby increasing the number of no-boat tracks.

(2) *Treatment*. In 1996, an experimental boat (a 5.2 m Hourston motorboat with a 90 hp Yamaha 2-stroke outboard engine) was available to approach focal animals. The boat operator followed local whale-watching guidelines by paralleling the whale at 100 m for a minimum of 20 min, after 20 min of observation under control (no-boat) conditions. No sudden direction changes were made, and the operator was instructed not to place the boat in the path of the whale (an activity referred to as 'leapfrogging'). The experimental boat operator was in constant VHF radio contact with cliff-based observers, who kept the boat 100 m from the whale by informing the operator periodically of the distance between boat and whale as measured by the theodolite.

(3) *Opportunistic*. Opportunistic tracks occurred when at least 1 boat was present within 3 km of the focal whale, and no effort was made to manipulate traffic around the focal animal.

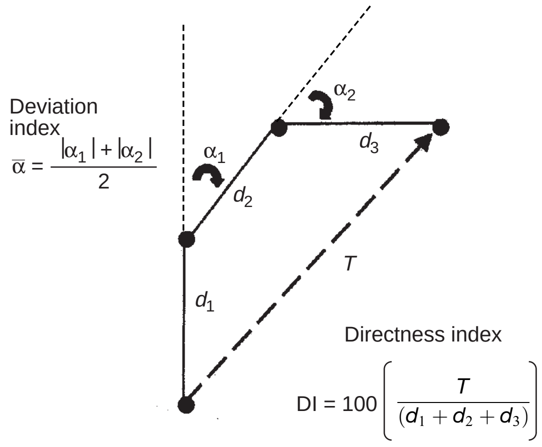

Fig. 2. A sample swimming path with four surfacings (●) and three dives (d_i), showing two measures of path predictability: deviation and directness. The deviation index is the mean of all angles between observed dives and the straight-line paths *predicted* (···) by preceding dives. The directness index is the ratio of the track diameter (T) to its perimeter.

Data compilation

Calculating predictor variables

Temporal and biological variables. Whales were classified as either young or old, based on life history information available 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 average life expectancy for male northern resident killer whales) (Olesiuk *et al.*, 1990). Age estimates of young whales are more reliable than those of old whales in this population, since annual photo-identification of most individuals began in the mid-1970s (Ford *et al.*, 1994).

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. This is a safe assumption in the Robson Bight area, where community pressure discourages boats from leapfrogging. The approximate location of each boat was interpolated in order to determine where it was every time the whale surfaced. Distance between whale and boat was calculated for every surfacing in a track using the actual position of the whale and the interpolated or extrapolated position of each boat.

We measured intensity of boat traffic in 3 ways:

(1) *track type*: control, treatment or opportunistic;

(2) *vessel proximity*: the distance between each boat and the whale was calculated for every surfacing to determine a minimum proximity within a track;

(3) *number of vessels*: the number of whale-oriented vessels (those that altered course toward whales) and non-whale-oriented vessels (those apparently ignoring the whale) was calculated within 100 m, 400 m, and 1000 m radii of each surfacing. The maximum number of vessels (whale-oriented and non-whale-oriented) observed within the 3 radii was then calculated for each track.

Calculating response variables

A mean dive time (i.e. average time between surfacings) was calculated for each track. The average swimming speed of the whale was obtained by dividing the total distance travelled by the duration of the tracking session. Two measures of path predictability were calculated: a *directness index* and a *deviation index* (Fig. 2).

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 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 the inverse of the milling index of Tyack (1982) and Kruse (1991). The directness index ranges from 0 (a circular path) to 100 (a straight line).

The deviation index measures path predictability from 1 surfacing to the next (Fig. 2). 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, the angle between the path taken by a dive and the straight-line path predicted by the dive before it was calculated (Williams, 1999). 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 indicates a smooth path, while a high deviation index indicates an erratic path. Indices of directness and deviation were calculated 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.

We recorded each time that surface-active events such as spy-hopping or breaching occurred. A bout of tail-slapping or fin-slapping was scored as 1 event if > 1 slap occurred on a surfacing.

Table 1. Number of tracks, by gender and traffic conditions. Bold numbers, number of observations; numerals in parentheses, number of subjects. For a further breakdown, see Williams (1999)

	No-boat	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)

Data analysis

Gender and age effects

Relationships among age class, 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, a deviation index, a directness index and a rate of surface-active behaviour) was calculated for each track. Scarcity of surface-active behaviour required us to pool all events into a single category of surface-active behaviour, which was standardized to the number of surface-active events/h. Mean values for each dependent variable 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. Two-factor analyses of variance (ANOVA) were performed on each dependent variable.

Experimental approaches

Variables recorded under control and experimental conditions were compared using two-tailed, paired *t*-tests. Comparisons were made only when at least 20 min of baseline, control observation was followed by an experimental approach of the same whale lasting at least 20 min.

Opportunistic observations

Whale responses to experimental approaches were compared with whale behaviour across a continuous range of boat traffic observed in Johnstone Strait. Canonical correlations (STATISTICA v. 5) enabled us to investigate how the combination of temporal, biological and traffic variables together related to whale behaviour. Canonical correlation analysis is a multivariate technique designed to describe complex relationships between 2 sets of variables (Tabachnick & Fidell, 1996). It has been used particularly well to reveal subtle trends in the highly variable datasets common to many cetacean studies (Bauer & 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 & 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 set (e.g. boat traffic) 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 (e.g. distance to nearest boat *vs* whale behaviour). Canonical correlations are interpreted using the magnitude and direction of the weights and loadings, which allows some flexibility in interpretation. Some authors have chosen 0.30 as an arbitrary minimum coefficient for interpretation (Tabachnick & Fidell, 1996). Alternatively, inherent noise in cetacean behavioural data has been cited as a rationale for interpreting coefficients as low as ± 0.20 (Bauer & Herman, 1986), which is the cut-off we used.

RESULTS

Sample size

Over two seasons, we spent 1416 h observing boats and whales in the study area. This effort yielded 181 usable tracks of 25 individuals, during 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.

Gender and age effects

Mean values for each of the five dependent variables were calculated for each of the 25 whales observed. The values were normally distributed as indicated by Kolmogorov–Smirnov tests ($P < 0.01$) (Zar, 1996). Recall that whales in this study were observed while the group was spread out, searching for food. Observations were pooled across all traffic conditions, since our goal was to describe variation within our sample in order to guide subsequent analyses.

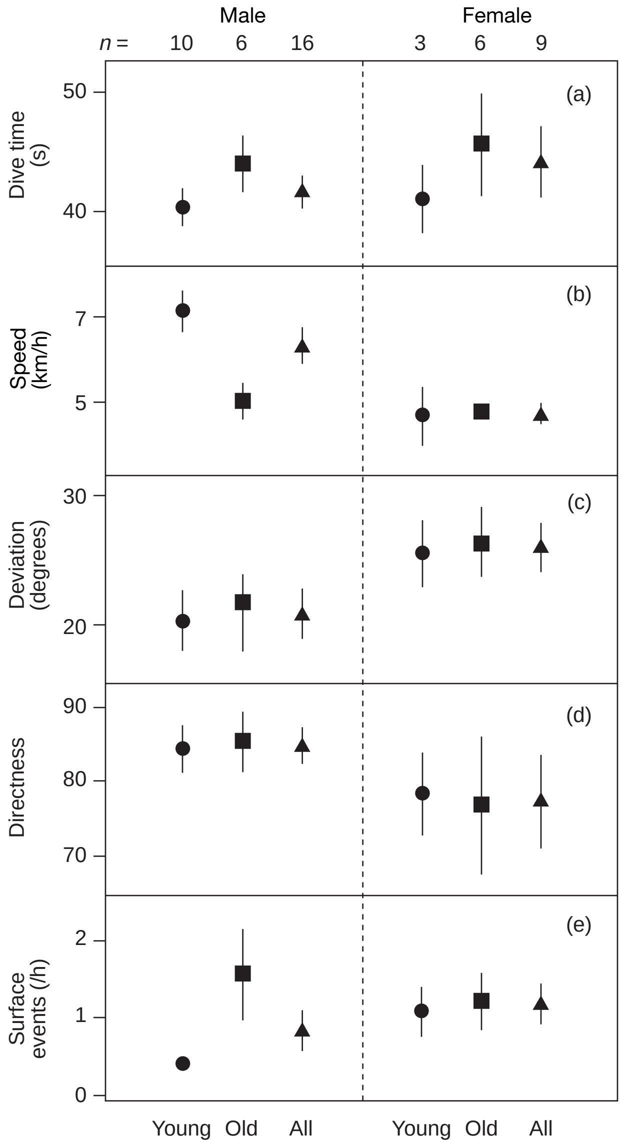

Fig. 3. Relationship of gender and age class to whale behaviour (mean ± se), averaged across all traffic conditions. Each whale is represented only once. (a) Dive time; (b) swimming speed; (c) deviation index; (d) directness index; (e) surface-active behaviour.

The 16 male northern resident killer whales that were tracked swam *c.* 34% faster than the nine females when engaged in typical foraging behaviour (Fig. 3) ($F_{1,23} = 6.43$, $P = 0.02$). 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; $F_{1,23} = 1.47$, $P = 0.24$). With males swimming faster than females, and with no difference seen in direction and deviation indices, it seems that males always outdistance females. Recall that whales were tracked only during foraging activity, when groups dispersed temporarily. Other activities, such as resting and socializing, require group cohesion, during which pods regroup.

The most common surface-active behaviour for both age and sex classes was tail-slapping, with spy-hops and pectoral fin-slaps accounting for most of the remaining activity. Rarity of surface-active events required us to pool observations to an expected rate of any surface-active event/h, even though these activities undoubtedly serve different purposes. No significant differences were found between 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 age class and whale behaviour, nor were there any significant interactions between gender and age class.

Experimental approaches

The experimental boat approached whales on 40 occasions. Of these, experimental approaches were preceded 32 times by at least 20 min of observation under control conditions. Paired, two-tailed *t*-tests were performed on the five response variables for the 32 paired observations (Fig. 3). Examples of four experimental approaches of male and female whales are shown in Fig. 4 and Fig. 5, respectively. Separate analyses were performed for experimental approaches of males and females, since gender-based differences in swim speed (Fig. 6) indicated potential for different responses to boat traffic.

Increased probability of Type I errors is a concern with these analyses. Greater 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.

Male response

When approached by the experimental boat, the paths of male whales became less direct than during the preceding control conditions ($t_{23} = 2.25$, $P = 0.03$). The reduction in directness can best be understood in terms of distance covered. A directness index of 83.6 (the average directness during control sessions) translates to a whale swimming 119.6 m along a circuitous path to end up 100 m from his original position. The same whale, following a path with a directness index of 74.1 (the average directness during treatment sessions), would need to 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.

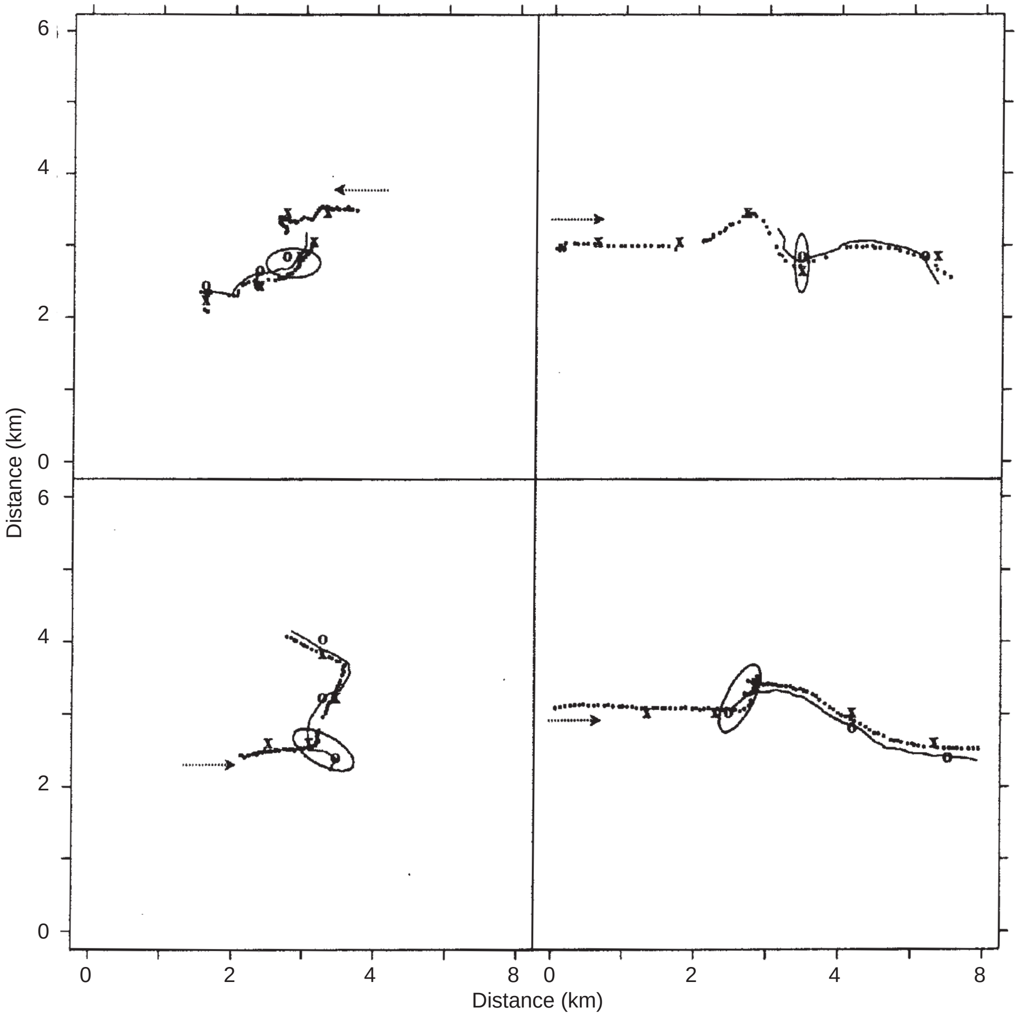

Fig. 4. Four examples of paths taken by male focal whales (···) when approached by the experimental boat (—). Each dot, a surfacing by the whale; arrow, the whale's original direction of travel. Letters are placed at 10-minute intervals: x, the position of the whale; o, the interpolated position of the 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 than during control conditions.

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 correlations were calculated between the set of whale behaviour variables and a set of explanatory variables. Separate canonical correlations were performed for males and females, since experimental tracks indicated potential for gender-based difference in boat tolerance (Fig. 6). 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; (3) the maximum number of non-whale-oriented vessels within 1000 m of the whale. The explanatory variables also included the day of year, start time of each track, and age in years. Additional traffic variables were eliminated to avoid concerns of multicollinearity (Tabachnick & Fidell, 1996). No correlation within a variable set was > 0.5 after reducing the number of variables.

Figures 7 and 8 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

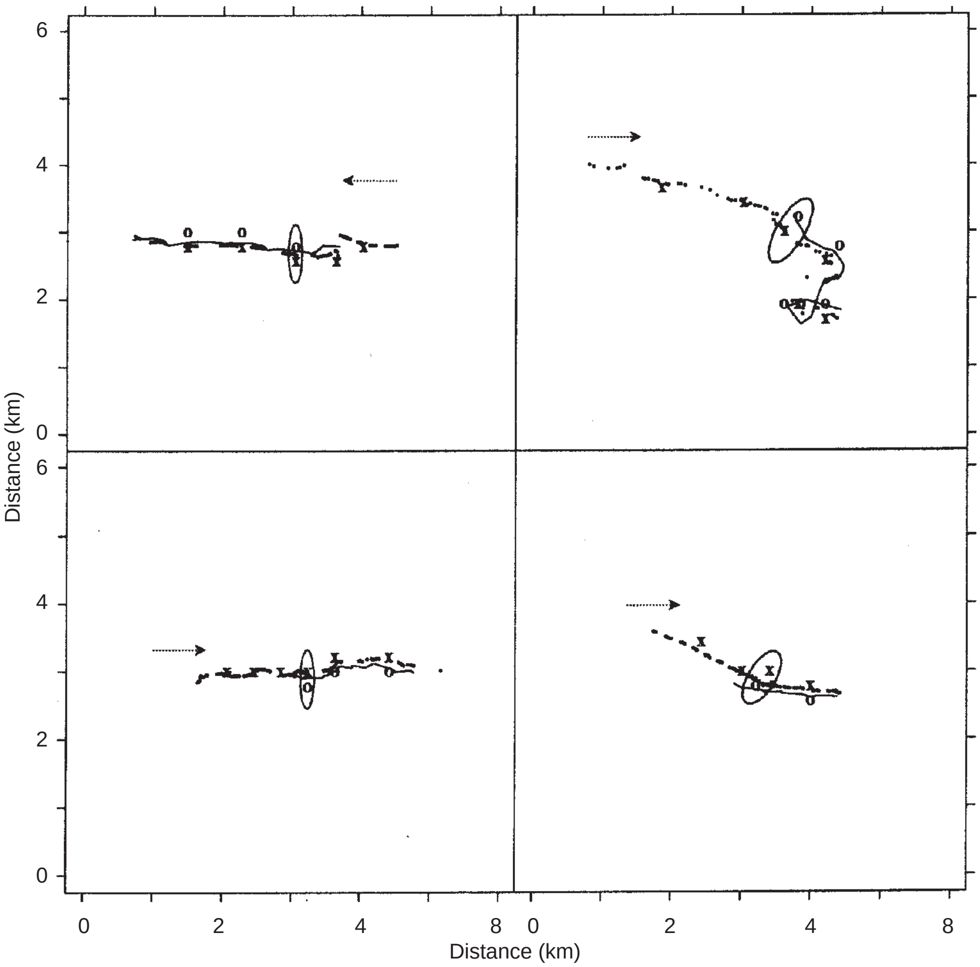

Fig. 5. Four examples of paths taken by female focal whales (···) when approached by the experimental boat (—). Each dot, a surfacing by the whale; arrow, the whale's original direction of travel. Letters are placed at 10-minute intervals: x, marks the interpolated position of the whale; o, the interpolated position of the boat. The first synchronous pair of boat and whale positions is joined by an oval. In general, when approached by an experimental boat, the path of female whales became more erratic while retaining directionality.

relationships were synthesized in one multivariate description of male behaviour, and another for females. Standardized correlation coefficients (weights) between the original variables and the first pair of canonical variates are 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 $(k_x)(k_y)$ degrees of freedom, where k_x is the number of variables in the explanatory set, and k_y the number of variables in the response set (Tabachnick & Fidell, 1996).

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: date and time of the observation; age; maximum number of whale-oriented vessels within 1000 m; 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 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 the original variables. 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 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 unknown whether the relationships presented here can be extrapolated

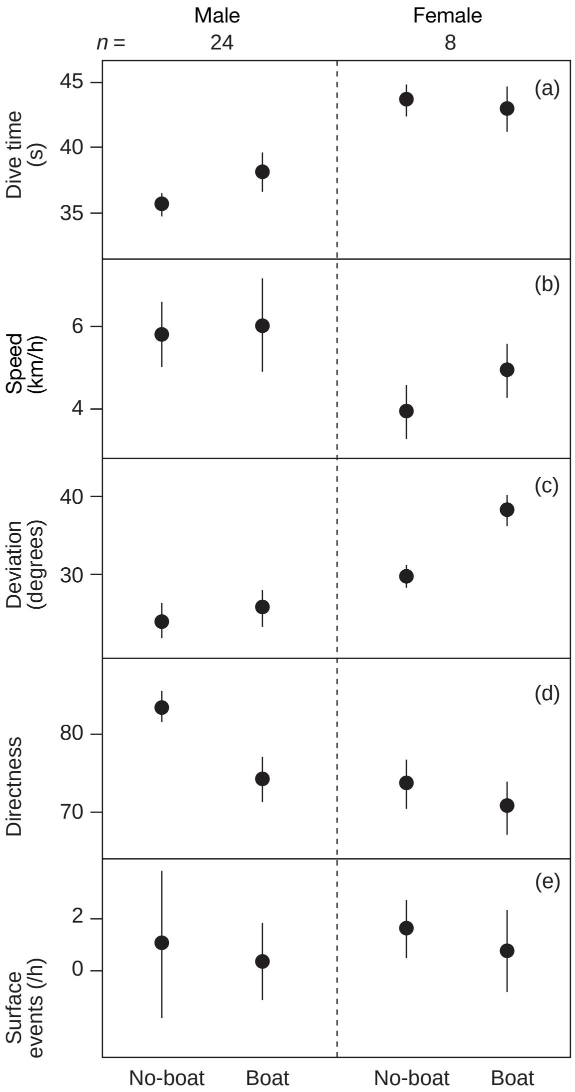

Fig. 6. Behavioural responses (mean ± se) of whales to experimental approach by one boat paralleling the whale at 100 m for 20 min. (a) Dive time; (b) swimming speed; (c) deviation index; (d) directness index; (e) surface-active behaviour.

directly to other regions, or seasons, or populations of killer whales.

All other things being equal, paths of male killer whales tended to be less direct as boats got closer (Table 2), just as the experimental tracks would predict (Fig. 6). 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 seems 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. These potential diurnal and seasonal effects are unlikely to have affected our experiment, since treatment observations immediately followed control observations, and thus, date and hour were constant.

Table 2. Correlations, canonical correlations, per cents 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, variables that were interpreted in the text

	Standardized correlation coefficients between original variables and first canonical variates	
	Male ($n = 133$)	Female ($n = 48$)
Explanatory set		
Date	**−0.47**	**0.58**
Time	**0.26**	0.02
Age	**0.79**	**−0.40**
Whale-oriented[a]	**0.21**	**−0.35**
Non-whale-oriented[b]	−0.15	**−0.56**
Minimum distance	**0.47**	**−1.06**
Per cent of variance	16	10
Redundancy (%)	3	5
Behavioural set		
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
Per cent of variance	20	17
Redundancy (%)	4	8
Canonical correlation (r_c)	**0.44**	**0.69**
χc^2_{30} (subsequent pairs of variates not significant)[c]	50.121, $P = 0.012$	49.744, $P = 0.013$

[a] Maximum number of whale-oriented boats within 1000 m of the whale.

[b] Maximum number of non-whale-oriented boats within 1000 m of the whale.

[c] degrees of freedom in chi-square refers to the product of the number of variables in each set, not number of observations.

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.

Female behaviour

Using 48 tracks, we found a significant relationship between the set of explanatory variables and behaviour

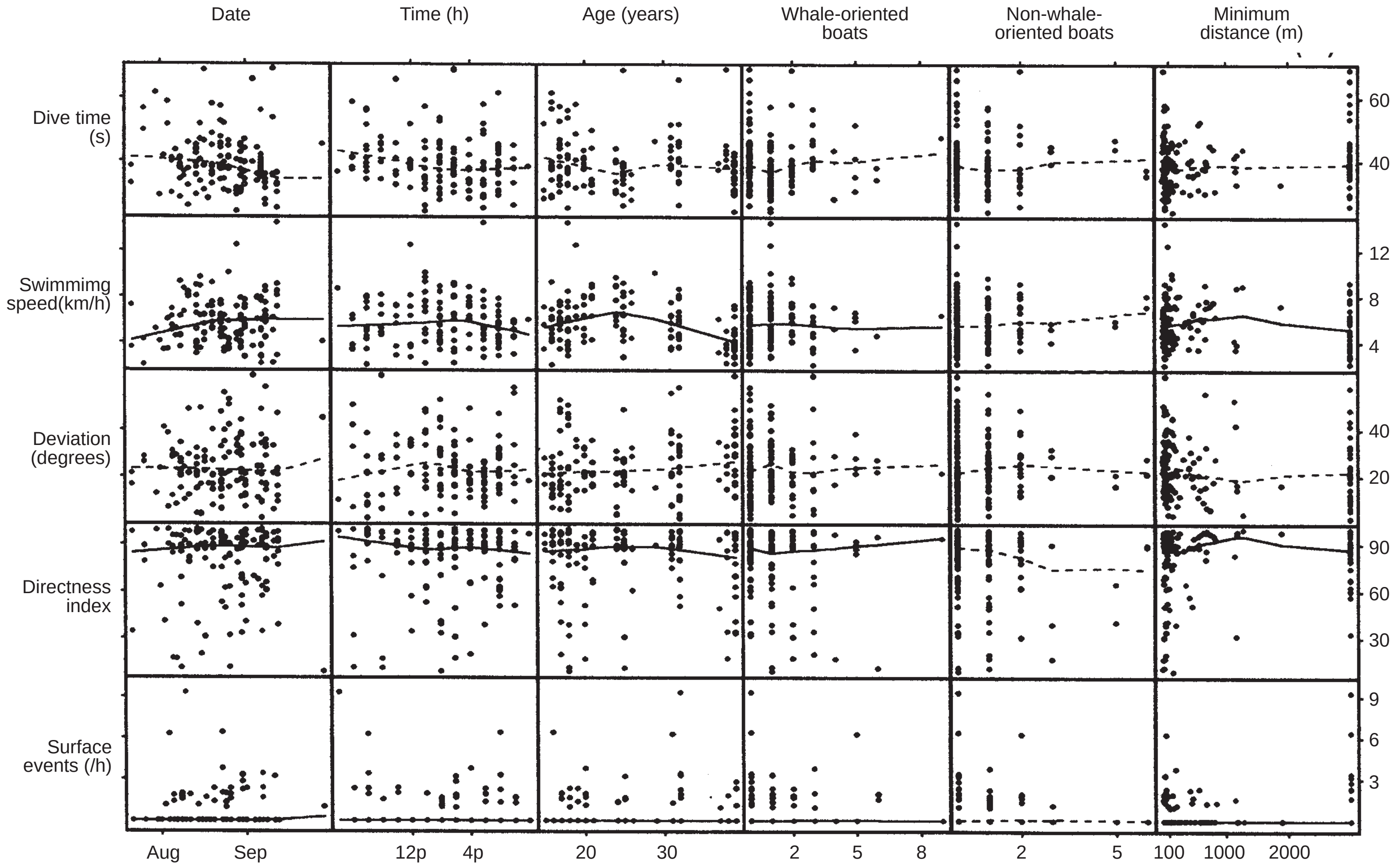

Fig. 7. Scatterplot matrix showing relationships between the set of explanatory variables and behaviour of male whales ($n = 133$). Each plot is smoothed with a lowess function. Solid lowess line, relationships that were interpreted in the canonical correlation; dashed line, relationships that were not interpreted.

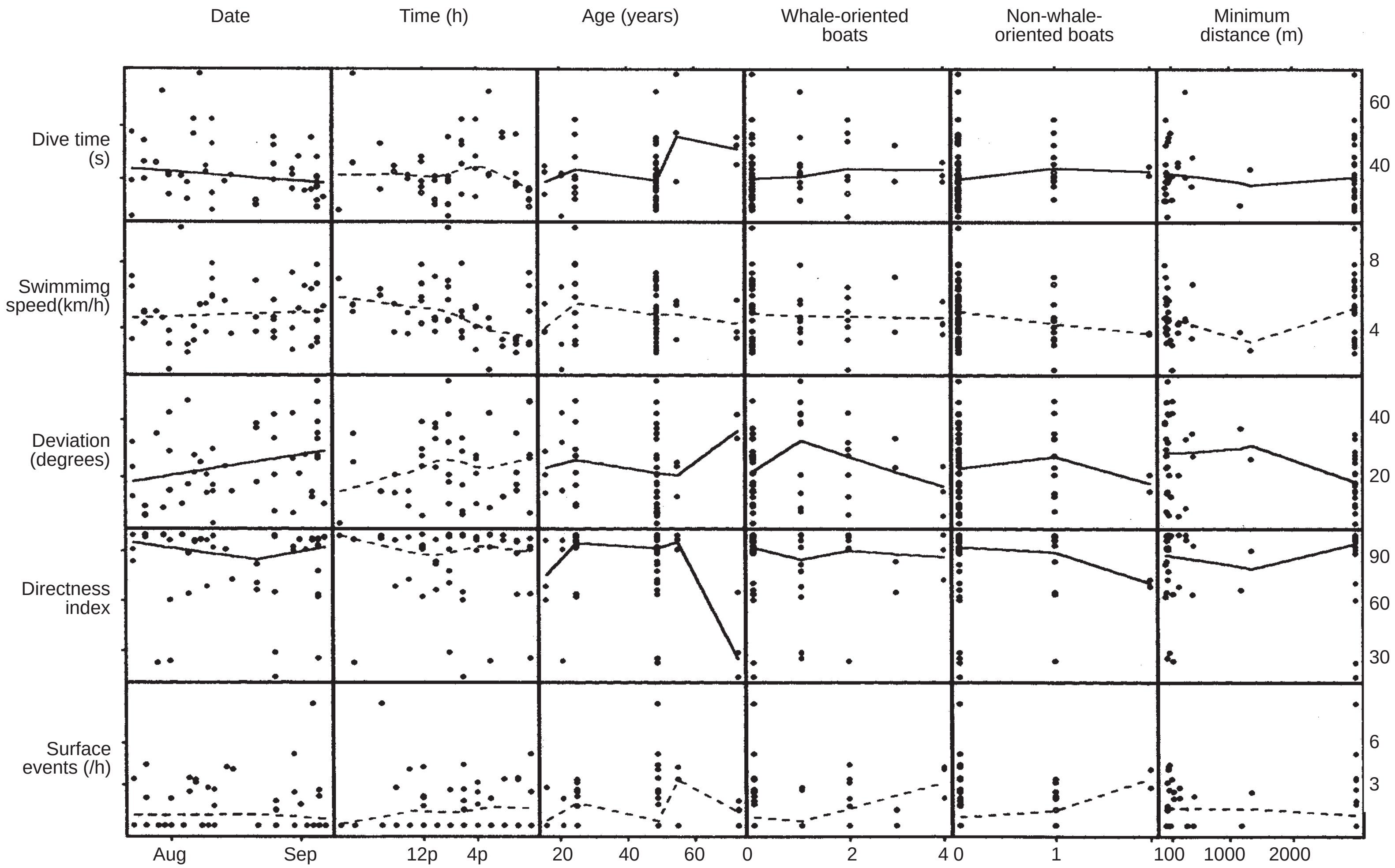

Fig. 8. Scatterplot matrix showing relationships between the set of explanatory variables and behaviour of female whales ($n = 48$). Each plot is smoothed with a lowess function. Solid lowess line, relationships that were interpreted in the canonical correlation; dashed line, relationships that were not interpreted.

of female killer whales. The significant explanatory variables were date, age, maximum numbers of whale-oriented and non-whale-oriented vessels within 1000 m, and proximity of the nearest boat. Significant behavioural variables for female whales were mean dive time, and 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.

As boats got closer to female whales, the deviation index tended to increase (Table 2). This is consistent with results from experimental tracks (Fig. 6). 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 ones 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

Our land-based study of killer whales, combining experimental approaches and opportunistic observations, reveals a complex relationship between whale behaviour and vessel activity. It has shown that a single vessel following whale-watching guidelines affects the movement patterns of northern resident killer whales. Furthermore, our study provides a useful description of how whale behaviour varied across a range of traffic conditions in Johnstone Strait.

The utility of our study can be judged in three ways. First, the study identifies *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. Second, 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 a given number and community 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 yield higher levels of disturbance. Of course, adopting more conservative distance guidelines would confer even greater benefit to the animals.

Horizontal avoidance tactics

The tendency for the paths of whales to become less predictable when approached by the experimental boat is consistent with horizontal avoidance patterns. This offers observers new information when interpreting the 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 spatial 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. Swim speeds also increased when the experimental boat approached female whales (Fig. 6) and as 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 & 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 vary their speed and the extent to which they turn away from the path of the predator. Prey may compensate for a larger turning radius by increasing their speed, or may increase manoeuvrability to compensate for slower movement. Thus, slower prey can escape 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 (Figs 4 & 5) 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.

The analogy between the response of a killer whale to a boat and a typical predator–avoidance strategy becomes more 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 males and females may be accounted for by Howland's (1974) trade-off paradigm. Perhaps female whales compensate for slower swimming speeds (Fig. 3) by increasing the 'escape angle' in Howland's model – the deviation index (Fig. 6). While there is no evidence that female killer whales cannot swim at the speeds observed for males in this study, female killer whales do seem to swim less efficiently at higher speeds than males (Kriete, 1995). The existence of gender-based differences in boat tolerance is not altogether surprising. Matriarchs in this population have been described as more difficult than males to approach closely for biopsy (Barrett–Lennard, Smith & Ellis, 1996) and humpback whales demonstrate differential boat responses among age–sex classes when on the winter breeding and calving grounds off Hawaii (Bauer & Herman, 1986).

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 manoeuvrability 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 trade-off between number and proximity of boats suggests either that whales were less disturbed by other boats than by the experimental boat, or that whales abandon this avoidance tactic 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 of many boats. This compromise deserves further attention in the form of a multiple-vessel experiment. Similarly, the relationships among date, time and behaviour (Table 2) serve as a reminder that distribution of salmon may be the best determinant of whale distribution and activity in Johnstone Strait (Nichol & Shackleton, 1996).

Effect – size

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, Geist & Johnston, 1982). It may be that after two decades of commercial whale-watching in Johnstone Strait, killer whales have reduced or altered their response 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 an increasing number of boats. In our 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 the number of boats increased. In fact, speeds of males were negatively correlated with the number of vessels. Does this apparent change in behaviour indicate habituation, or does it reflect differences in study design?

A gender-based sampling bias may have existed in Kruse's study. Mean speed of Kruse's 'undisturbed' whales (4.6 km/h) matches closely with that of female whales in our study (4.7 km/h), and speed of 'disturbed' whales (6.4 km/h) approximates that of male whales in our study (6.3 km/h). It is conceivable that no-boat tracks 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 avoidance being context-specific, the response could also change over time. Certainly, whales would have several incentives to abandon a fast-swimming avoidance tactic. As swim speed increases, breathing rate of grey 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 be simply an ineffective avoidance strategy around motorboats.

A more rigorous comparison of available data from the two periods is warranted. Our choice between these competing explanations, 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 & Baird, 1995). If the discrepancy between our study and Kruse's (1991) study indicates habituation to whale-watching, then this 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.

Boat noise can mask communication signals used by killer whales (Bain & Dahlheim, 1994). Bain & 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. They found that low-frequency components of calls, which are omnidirectional, were masked by noise, and that masking was strongest when the 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 & 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 & Webb, 1984) of increasing swim speed (Kruse, 1991; Green, 1998) and varying the time and/or position of surfacings (Bauer & Herman, 1986; Fraker, Richardson & Würsig, 1995; Notarbartolo di Sciara *et al.*, 1996). On a larger spatial 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, Vaughan & Andersen, 1996). Repeated disturbance in other taxa can force animals to be increasingly alert (MacArthur *et al.*, 1982; Weisenberger *et al.*, 1996), and may cost them foraging opportunities (Stephenson *et al.*, 1996; Burger & Gochfield, 1997; Galicia & Balassarre, 1997). Repeated disturbance can cause lowered immune function (Kraabel & Miller, 1997), abandonment of microhabitats (Eckstein *et al.*, 1979) and disruption of sleep patterns (Öhrström, Björkman & Rylander, 1990).

Currently, any proposed link between short-term response and long-term effects is tenuous. Although no study to date can address the underlying concern that short-term disruptions may have a cumulative, long-term effect that has not been measured yet, we do know that the whales continue to return each year, and that this 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.

Ultimately, though, managers must consider whether whale-watching traffic can influence reproductive success. Recently, there has been concern about whether whale-watching traffic may play a role in the recent decline of southern resident killer whales (Baird, 1999). We believe that it is unwise simply to assume that southern residents are disturbed to the same extent as northern residents by whale-watching traffic, particularly while the issue of habituation remains unresolved. Clearly, southern residents are exposed to more boat traffic, for a greater part of the year, than northern residents (Osborne & Otis, 2000). Our finding that focal male whales travel a more circuitous route when followed than when no boats are present certainly bears consideration in the context of southern resident killer whale conservation. If boat traffic generally forces animals to swim further to find food, then this undoubtedly carries a metabolic cost. However, additional studies should test the applicability of our findings to the southern resident community. In the meantime, we view boat traffic as one factor that can influence the 'cost of living' for whales. In other words, low levels of disturbance may not be problematic in a thriving population, but when coupled with reduced prey availability and increased contaminant load, short-term behavioural responses should not be dismissed lightly.

Recommendations

The northern resident killer whale population has served as a useful subject of many studies over the last 20 years. Long-term photo-identification studies of this population reveal no evidence of population decline (Ford *et al.*, 1994; Baird, 1999). Similar focus on sighting records will reveal whether these whales are using Johnstone Strait less today than in previous years. Careful comparison of our 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. This pattern has not been observed in northern resident killer whales (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.

Opportunistic tracking of boats and killer whales should continue. Initially, these tracks should target observations poorly represented in our dataset (Figs 7 & 8), namely those of females between 25 and 50 years of age, and of boat traffic between 500 and 3000 m. Similarly, experimental studies with a single boat should continue, in order to identify effects at closer and further distances than 100 m, in order to determine whether the relationship between boat proximity and whale avoidance is linear, as canonical correlation analyses assume. Ideally, these experiments should be conducted in parallel with studies on southern residents.

Our study measured behavioural responses of killer whales to a vessel that actually followed whale-watching guidelines. It is important to remember that distance is very difficult to judge at sea, so many boats may be violating whale-watching guidelines unintentionally.

Baird and Burkhart (2000) note, however, that humans have a tendency to underestimate distance. Thus, in a community where whale-watchers make a concerted effort to stay 100 m away from whales, they may be staying even further away than that.

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 & Dahlheim, 1994). Furthermore, placing a boat directly ahead of the whale's path puts the source of masking noise in the most disruptive position (Bain & Dahlheim, 1994). These factors may explain why avoidance responses to leapfrogging vessels seem to be more dramatic than to vessels travelling parallel to the whale (R. Williams, pers. obs.). In our predator-avoidance model, leapfrogging implies a fast, manoeuvrable, difficult-to-evade 'predator'. This suggests that a fight, rather than flight, response may be more effective, as indicated by increased rates of agonistic behaviour. This may be easier for us to detect subjectively against baseline than changes in travel patterns. Further studies of this type should also record group size during observation sessions. This will result in a clearer understanding of the relationship between boat traffic and rates of surface-active behaviour, which vary with group size in southern residents (Hoelzel, 1993).

The value of an experimental approach for detecting subtle behavioural responses cannot be overemphasized. The growing desire to see animals in their natural habitat is prompting enormous changes in how society values whales. Indeed, many identify whale-watching as a sustainable alternative to whaling (Barstow, 1986; IWC 1994; IFAW, Tethys Research Institute & Europe Conservation, 1995). However, such 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 sceptical 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 end up harming animals with our desire to appreciate them.

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