BEHAVIORAL RESPONSES OF SUMMERING HUMPBACK WHALES TO VESSEL TRAFFIC: EXPERIMENTAL AND OPPORTUNISTIC OBSERVATIONS

Technical Report NPS-NR-TRS-89-01

C. Scott Baker and Louis M. Herman

United States Department of the Interior
National Park Service

March 3, 1849

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C. Scott Baker[1] and Louis M. Herman
Kewalo Basin Marine Mammal Laboratory
University of Hawaii
1129 Ala Moana Blvd.
Honolulu, Hawaii 96814

June 1989

Final Report to the National Park Service,
Alaska Regional Office
Anchorage, Alaska

U.S. Department of the Interior
National Park Service
Alaska Regional Office
2525 Gambell Street, Room 107
Anchorage, Alaska 99503

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[1] Current address: Laboratory of Viral Carcinogenesis, Building 560, Room 21-105, National Cancer Institute, Frederick, Maryland 21701-1013

ABSTRACT

The behavior of humpback whales summering in southeastern Alaska was observed in the presence and absence of vessel traffic. During the first study year (1981), small- and medium-sized vessels were directed to operate within 400 m of whales according to an experimental plan. The second study year (1982) concentrated on observations of whales during the opportunistic passby of medium and large vessels at distances generally greater than 400 m. Whales showed predictable behavioral responses to vessels operating at distances of less than 4,000 m. Changes in whale behavior were correlated with the speed, size, distance, and numbers of vessels within this proximity. Changes in the whales' respiratory behavior and orientation were the most sensitive indicators of vessel disturbance. Whales responded to the close proximity of vessels by decreasing blow intervals, increasing dive times, and moving away from the vessels' path. Changes in group composition, aerial behaviors, and surface-feeding behaviors were, in general, too infrequent to be a reliable measure of disturbance. At a high density of vessels, however, occurrences of aerial behaviors were inversely correlated with vessel distance. Detailed case histories indicated that the repeated approach or passby of vessels could result in the temporary displacement of whales from preferred feeding areas. Overall, our observations indicate that humpback whales exhibit a considerable degree of short-term changes in their behavior in response to vessel traffic.

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GENERAL INTRODUCTION

The North Pacific humpback whale, *Megaptera novaeangliae*, is considered to be one of the most endangered of all baleen whale populations (Herman and Antinoja 1977; Johnson and Wolman 1984). Thought to have numbered between 15,000 and 20,000 animals prior to exploitation, intensive 20th-century whaling reduced this population to less than 1,000 individuals (Rice 1978). Since their international protection in 1967, humpback whales in the North Pacific have shown evidence of only a slow recovery. Current estimates of this population range from less than 1,200 to slightly more than 2,000 animals (Johnson and Wolman 1984; Baker et al. 1986; Darling and Morowitz 1986; Baker and Herman 1987).

Having survived near-extinction at the hands of the commercial whaling industry, humpback whales now face a new threat, the potential loss of their seasonal habitats to encroaching continental-shelf and near-shore development. Humpback whale feeding grounds in the Gulf of Alaska and the Bering Sea are presently leased or scheduled to be leased for petroleum exploration and exploitation. In the Hawaiian Islands, ongoing or planned projects that may impact humpback whale breeding and nursing areas include deep-water mining and ocean thermal energy conversion (OTEC) stations. As a result of growth in coastal development and the commercial whale-watching industry, humpback whales on both the feeding and wintering grounds have experienced a dramatic increase in exposure to commercial and private vessel traffic (Norris and Reeves 1978; Johnson and Wolman 1984; Anonymous 1984).

Concern for the recovery of North Pacific humpback whale is suggested by observations of a relatively low rate of reproduction in this population. Based on multiple observations of naturally marked individuals, Baker et al. (1987) reported that estimated interbirth interval of female humpback whales in southeastern Alaska was lower than expected given historical estimates of pregnancy rates from whaling records. They hypothesized that, among other possible factors, environmental contaminants or chronic human disturbance could be depressing reproductive rates in these whales.

Human disturbance has the potential to reduce an animal's biological fitness, defined as its relative reproductive contribution to subsequent generations, and thus inhibit the recovery of an endangered population. A reduction in fitness could occur from the cumulative effects of stress (Laws 1973; Herrenkohl 1979), the interruption of important behaviors such as courtship, mating, nursing, and feeding (Norris and Reeves 1978; Reeves 1977), or the displacement of whales from preferred habitats (Herman and Antinoja 1979; Herman et al. 1980; Anonymous 1984).

The apparent departure or displacement of humpback whales from areas of chronic human disturbance has been documented in several cases. Aerial surveys of Hawaiian waters show relatively low densities of whales in areas of the greatest human activity (Herman et al. 1980). Non-systematic, vessel-based surveys of humpback whales suggest a decline in the use by cow-calf pairs of near-shore waters adjacent to human development on the island of Maui (Glockner-Ferrari and Venus 1983). In southeastern Alaska, the abrupt departure of whales from Glacier Bay in the summer of 1978 was coincident with an exponential increase in vessel traffic during the five previous years (Jurasz and Palmer 1981a; Marine Mammal Commission 1980; Anonymous 1984). Concern for the welfare of humpback whales prompted the National Park Service, in consultation with the National Marine Fisheries Service, to institute regulations limiting the number of vessels entering the bay each summer and prohibited vessels from approaching closer than 0.25 nautical miles to a whale. Although whale use of Glacier Bay remained low during 1979 and 1980, subsequent surveys have shown a general increase in the number of whales using Glacier Bay and the adjacent waters of Icy Strait (Baker 1986; Baker et al. 1988). In addition, long-term sighting records of naturally marked individuals demonstrates that many of the individuals that summered in the Glacier Bay area during the early 1970's, have continued to visit this area throughout the 1980's (Baker et al. 1988).

Although sudden changes in the distribution of humpback whales in some areas suggests that human activity is a factor, the cause-effect relationship of this disturbance has not been clearly demonstrated. In addition, alternate explanations of changes in whale distribution have only recently received sufficient study (Wing and Krieger 1983; Krieger and Wing 1984; 1986). Here we present the results of studies designed to measure the behavioral response of humpback whales to vessel traffic on the southeastern Alaska feeding grounds. During the summer of 1981, we used an experimental design to determine the response of whales to different vessel sizes and activities at relatively close range, generally less than 400 m (Baker et al. 1982). During the summer of 1982, we observed and recorded the behavior of whales during opportunistic interactions with both high and low densities of vessel traffic (Baker et al. 1983). In both years, the behavior and movement of whales and vessels were recorded and monitored, primarily from elevated shore stations to insure that the observation platform was not, in itself, a source of disturbance to the whales. The combined two-year study suggests that the proximity of vessel traffic results in predictable patterns of short-term changes in the behavior of humpback whales.

GENERAL METHODS

Study Area

Southeastern Alaska, including the Alexander Archipelago and adjacent mainland between 50 and 60 degrees latitude north (Figure 1), is characterized by an intricate system of protected bays, channels, and inlets often referred to as the Inside Passage. Like other feeding grounds of humpback whales throughout the world, southeastern Alaska is an area of high seasonal productivity. Fish species thought to be taken by humpback whales in this region include the following (Krieger and Wing 1984; 1986): adult Pacific herring, *(Clupea harengus pallasi)*, capelin, *(Mallotus villosus)*, Pacific sand lance *(Ammodytes hexapterus)*, and juvenile walleye pollack *(Theragra chalcogramma)*. The primary invertebrate prey are thought to include at least four species of euphausiids: *Thysanoessa raschii, T. longipes, T. spinifera,* and *Euphausia pacifica* (Andrews 1909; Bryant et al. 1981; Wing and Krieger 1983).

Seasonal changes in the abundance and distribution of humpback whales in southeastern Alaska are complex. Whales probably begin returning in substantial numbers from low-latitude wintering grounds during May and June. The largest numbers of whales are generally found in late August and early September but the timing of seasonal influx and the patterns of regional occupancy change somewhat from year to year (Baker et. al. 1985). Capture-recapture analyses of photo-identification data indicate a summer population of 270 to 372 humpback whales in this feeding region (Baker et al. 1985).

The primary study areas within southeastern Alaska were Glacier Bay and the adjacent waters of Icy Strait (referred to as Glacier Bay in this text), and the confluence of Frederick Sound and Stephens Passage (referred to as Frederick Sound). Although separated by approximately 160 km, these two areas are not discrete. Individual whales are found in both areas in alternate years and at different times of the same summer season (Baker et al. 1983). Whales from Glacier Bay tend to move to Frederick Sound towards the end of the summer, possibly tracking seasonal changes in the abundance of prey (Perry et al. 1985; Baker 1985b; Baker 1986).

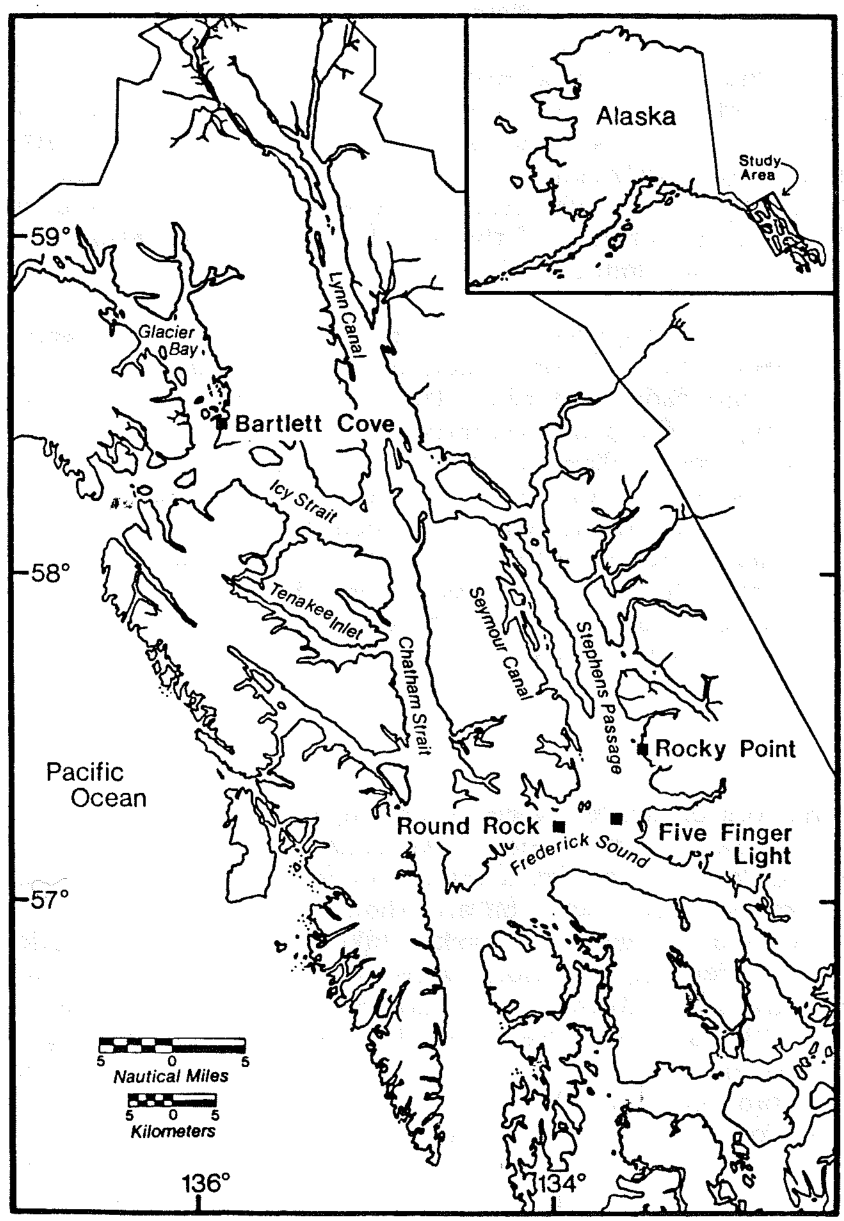


Figure 1. The southeastern Alaska study region and locations of shore observation platforms.

Data Collection

Observation Platforms

Whale behavior and movement were observed and recorded primarily from shore platforms in Frederick Sound and Glacier Bay (Figure 1). In both study years, a permanent shore station was established on the Coast Guard Five Finger Light Station in the center of Frederick Sound. The Five Finger Light Station platform was 17.2 m above mean high tide and offered a 340-degree view of the waters surrounding Five Finger Island. Shore stations at Round Rock and Rocky Point were used intermittently depending on changes in the local distribution of whales. Rocky Point, on the eastern coast of Frederick Sound, was 40.8 m above mean high tide and offered a 180-degree view of waters to the west. Round Rock was a small, treeless island with an elevation of 14.9 m above mean high tide and a 360-degree view of surrounding waters. In 1982, a single observation station was established on the shore of Bartlett Cove near the mouth of Glacier Bay. Although the elevation of this shore station was only 2.8 m above mean high tide, it was sufficient to track the activity of four humpback whales that remained within the confines of this small cove (approximately 2 km wide by 4 km in length) for much of the summer.

Operating a shore station required three personnel: a behavioral observer, a behavioral recorder, and a theodolite operator. When available, a fourth person contacted passing vessels with a marine radio and requested information on the vessel's size, engine speed, and engine type. The combined data collected from the shore station provided a complete real-time record of the behavior and movement of vessels and whales. During the 1981 season, about 25% of the behavioral observations were collected from a research vessel lying dead in the water between 400 and 1,000 m from the focal pod. The behavioral observer was positioned on an elevated platform, approximately 4 m above the water, and the recorder was stationed on the deck below the observer. Although it was not possible to operate a theodolite from the vessel, the distance to the focal pod was estimated with optical ranging devices.

Whale Behavior

The surface behaviors of whales were described by a single observer using 7 x 35 mm binoculars or a 10-power spotting scope. All behavioral events were assigned a numeric code and recorded in real-time on a microprocessor equipped with an internal clock. Behavioral descriptions were based on an ethogram developed during several years of research in Hawaii and southeastern Alaska (Baker et al. 1982). Additional descriptions and terminology for feeding behaviors were obtained from Jurasz and Jurasz (1979). Inclusion of a behavioral pattern in the ethogram followed the three criteria suggested by Slater (1978): 1) behavioral patterns were species typical; 2) component movements in a behavioral pattern occurred together, simultaneously or sequentially, with a high degree of predictability; and 3) behavioral patterns were discrete and repeatable recognizable. A fourth requirement was necessary for observations from the shore station: 4) behavioral patterns were clearly recognizable at relatively great distances (up to 4 km from the observer). The complete ethogram included more than 40 behavioral patterns classified into four major categories: respiratory, aerial, feeding, and social. Respiratory behaviors include the explosive "blow" marking a whale's respirations and behaviors which predict the onset of a prolonged submergence or "dive." In humpback whales, and other baleen whales, the onset of a dive is reliably predicted by the arching of the caudal stalk and raising of the tail or "flukes" (Gunter 1949). Aerial behaviors included five subcategories (Figure 2): leaps (breaches and head-slaps), flipper-slaps, fluke-slaps, peduncle-slaps, and head-rises. Feeding behaviors were restricted to the two subcategories observable at the surface (Jurasz and Jurasz 1979): lunge-feeding and bubble-netting. Social behaviors included only changes in the composition of a pod due to affiliation or disaffiliation of pod members.

Whale and Vessel Movement

The positions of whales and vessels were determined with the aid of a precision theodolite equipped with a 30-power spotting scope. The theodolite measured vertical and horizontal angles to a "target" on the surface of the water (Tyack 1981, 1982; Baker et al. 1983). The time and angles of each theodolite sighting were recorded by voice and later entered into a microcomputer. A computer program calculated the position of each whale and vessel by converting the theodolite angles to rectangular coordinates using the known elevation of the theodolite above sea level and a correction for changing tide height and the curvature of the earth. Based on the target positions and sighting times, the program then calculated the speed, direction, and distance between all whales and vessels in each observation. Measured horizontal and vertical angles of the theodolite were accurate to +/- 10 seconds of arc. Because the accuracy of the theodolite increases with the elevation of the instrument, measurements were most accurate from Rocky Point and progressively less accurate at Five Fingers, Round Rock, and Bartlett Cove. From the Five Finger shore platform (17.2 m above mean high tide), for example, positions of whales and vessels could be calculated with a precision of +/- 0.4% at a distance of 1 km, +/- 0.8% at 2 km, and +/- 1.6% at 4 km. Given the potential for theodolite and observer error at longer distances, all analyses were restricted to cases in which the whales were less than 4 km from the observation platform. Vessels presented a larger, more persistent theodolite target than whales and were tracked out to 8 km or to the limits of the horizon.

The Focal Pod and Observational Sessions

The social unit of interest for this study was the single whale or small pod of whales. A pod was defined as two or more individuals moving in the same direction, within two or three whale lengths of each other, and acting together in synchrony, particularly with respect to respiration, surfacing, and diving. Although we did not attempt to quantify spatial proximity or behavioral synchrony, pods were easy to distinguish by this criteria. For convenience, a single whale was also referred to as a pod. Since the majority of whales in southeastern Alaska are found alone or in small pods (Baker 1985a), our analyses focused on singles, pairs of whales, and cow-calf pairs. The emphasis on single whales and small pods was in keeping with the focal individual or focal group approach advocated by Altmann (1974). Focal pod sampling, in conjunction with randomly assigned experimental conditions (see Experimental Design) protects against the bias toward over-reporting dramatic or conspicuous behaviors that often results from scan-sampling or related techniques.

Focal pod observations were collected during hour-long observational "sessions." Each observational session was divided into three "trials" of approximately 20-min in duration. A observation trial began with a surface behavior and ended with the first surfacing behavior after the elapse of 20 minutes. The surface behavior that ended one trial simultaneously began the next trial in the sequence. For the experimental design used in the 1981 season the three trials in a session constituted the pre-test, test, and post-test of the vessel interaction (see Experimental Design). On a few occasions, an observational session included more than three trials. The 20-min sampling duration was chosen to insure that a trial was of sufficient duration to encompass a prolonged submergence but brief enough to assume that the behavior of the focal pod was relatively "stationary" (e.g. not subject to major shifts in motivational states).

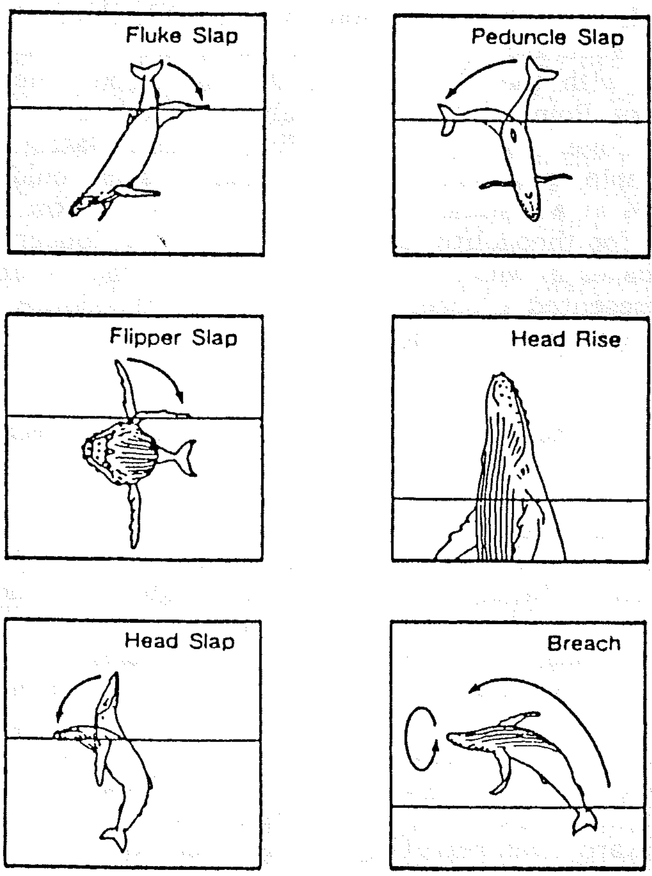


Figure 2. Characteristic aerial behaviors of humpback whales.

EXPERIMENTAL INTERACTIONS

During the 1981 study season, humpback whales were observed during interactions with vessels under the direction of the research team. These experimental interactions were designed to examine the responses of whales to different sizes and operational patterns of vessels operating within relatively close proximity (less than 400 m).

Methods

Experimental Design

Humpback whales were exposed to three conditions of vessel interaction: 1) Obtrusive, 2) Unobtrusive, and 3) Passby. Whales were also observed during a control condition in which they were presumably undisturbed by any vessel activity. During the Obtrusive condition, the experimental vessel was requested to rapidly approach and circle a whale while making abrupt changes in engine speed and engaging and disengaging gears. During an Unobtrusive condition, the vessel was directed to follow and approach a whale while operating as slowly and with as few changes in speed and gears as possible. During a Passby, the vessel was directed to travel past a whale without changing course, engine speed, or gear. The vessel was directed to approach to between 25 and 100 m of the focal pod during each experimental interaction.

Each experimental interaction was conducted using one of the two vessels operating under contract to the research team. The vessels were chosen to represent medium and small-sized fishing and pleasure craft that are common in southeastern Alaska. The medium-size vessel was a steel-reinforced, wooden-hulled schooner, 20 m in length at the waterline. The schooner was powered by a Caterpillar diesel engine (165 maximum shaft horsepower) and a single off-center propeller. The small vessel was a 4.2 m inflatable powered by a 25 hp outboard engine. The acoustic characteristics of these two vessels were very different from each other but similar to the classes of vessels they were chosen to represent (Malme et al. 1982). The inflatable, operating at full throttle or approximately 24 to 28 km/hr, showed a noise signature skewed towards the higher frequencies (Figure 3). The schooner, operating at 3/4 throttle or approximately 8 to 12 km/hr, was considerably louder overall and showed a noise signature skewed towards the lower frequencies.

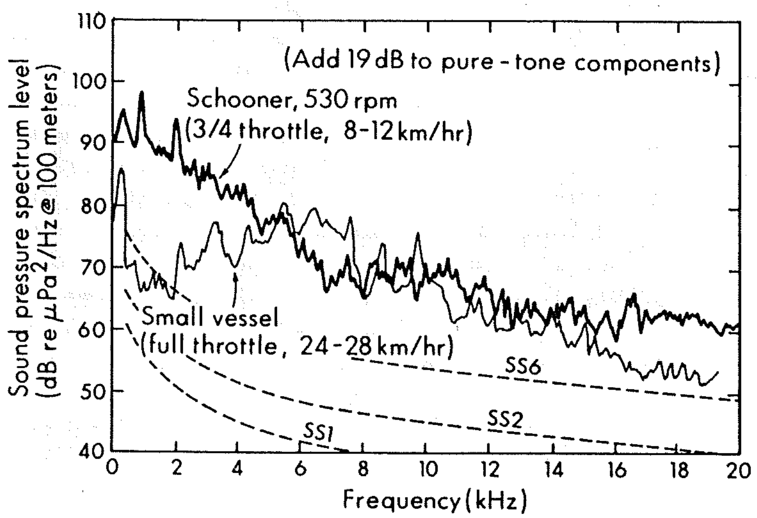


Figure 3. The noise profiles of the two experimental vessels (adapted from Malme et al. 1982).

A focal pod was exposed to an experimental condition according to a random, counterbalanced design. Because the assignment of a focal pod to a given experimental or control condition was random, the overall experiment qualifies as a "true experimental design" (Cook and Cambell 1979). A complete experimental condition consisted of three trials: 1) a pre-test during which no vessels were within 400 m of the pod and during which the focal pod was presumably undisturbed; 2) a test during which the experimental vessel approached, interacted with, and departed from the pod; and 3) a post-test following the departure of the vessel. Control observations were also divided into three pseudo-trials to help assure consistent methodology.

Results

Data Base

Over the course of the 1981 study, a total of 115 observation sessions were begun and completed through at least the end of the pre-test trial. Of these observations, 90 were completed through the test trial and 62 were completed through the post-test trial. An additional 16 trials were collected during attempts to perform repeated interactions. Of the 283 trials, 76 were collected from the vessel platform and consisted only of behavioral data. The remaining 207 trials were collected from the shore platforms and include data on the positions and movement of whales and vessels collected by theodolite in addition to behavioral data.

The final analysis was restricted to sessions that were completed satisfactorily through at least the test trial. Trials were also deleted from one or more of the analyses for the following reasons: 1) an inability to distinguish the focal animal or pod from other whales in the area; 2) the movement of the whale beyond 4 km from the observation platform; or 3) the approach of a vessel not under direction of the researchers. A preliminary analysis indicated that most behavioral categories changed significantly with pod size and the presence of a calf. To simplify the analysis and interpretation, the data were further restricted to observations of singletons unless otherwise noted.

Vessel Movement

To verify that the actual movement of vessels agreed with the experimental categories, theodolite data, when available, were used to describe vessel activity during the test trial of each experimental condition. As described earlier, the theodolite measures vertical and horizontal angles to a target on the surface of the water. Each pair of angles, referred to as a "sighting," was then used to calculate the rectangular coordinates of the target at a given time. Any two theodolite sightings defined a single "leg" of movement with a given length, direction, and speed. A single leg or series of legs were used to derive the following variables of vessel and whale movement for each 20-min trial of observation: 1) Straight-line velocity: the straight line distance from the first to the last sighting of a given vessel or whale in a trial, divided by the total time between sightings; 2) Total-length (TL) velocity: the sum of the length of each leg in a trial divided by the duration of each leg; 3) Linearity: the SL velocity divided by the TL velocity (ranging from 0 to 1); 4) Closest point of approach (CPA): the minimum distance between the path of a vessel and the path of a whale during a given trial. CPA was estimated by assuming a linear path and constant speed between sightings of whales and vessels.

The observed values of vessel movement variables showed good agreement with the prescribed activity of the two vessels during each condition (Table 1). TL velocity was highest and showed the greatest coefficient of variation during the Obtrusive and Unobtrusive conditions. Linearity was lowest during the Obtrusive condition and increased during the Unobtrusive and Passby conditions. The CPA's were similar for the Obtrusive and Unobtrusive conditions (about 75 m) but somewhat greater during the Passby.

Table 1. Summary of vessel movement during Experimental conditions.

	Experimental Condition					
	Obtrusive (n = 19)		Unobtrusive (n = 15)		Passbys (n = 16)	
	mean	SD	mean	SD	mean	SD
Total Velocity (km/hr)	9.3	8.8	7.1	7.5	9.4	3.1
Straight Line Velocity (km/hr)	7.3	7.9	6.3	7.7	8.4	3.4
Linearity (SLV/TV)	0.74	0.29	0.85	0.22	0.88	0.19
Closest Point of Approach (m)	75.7	48.9	70.0	74.8	139.0	101.0

Respiratory Behavior

The frequency distribution of respiratory interval for single whales showed considerable differences between the experimental and the control conditions (Figure 4). A respiratory interval was defined as the time between any two consecutive blows of a single whale. During the combined Obtrusive, Unobtrusive, and Passby conditions, the number of relatively short intervals increased and the number of medium length intervals decreased. While the mean respiratory interval showed only a slight decrease during the experimental interactions (85 sec) in comparison to the control (90 sec), the median interval of the experimental interaction (22 sec) was less than half as large as the control (51 sec). This decrease in the median respiratory interval was significant (Wilcoxon 2-sample test, Z = -6.82, p = 0.0001).

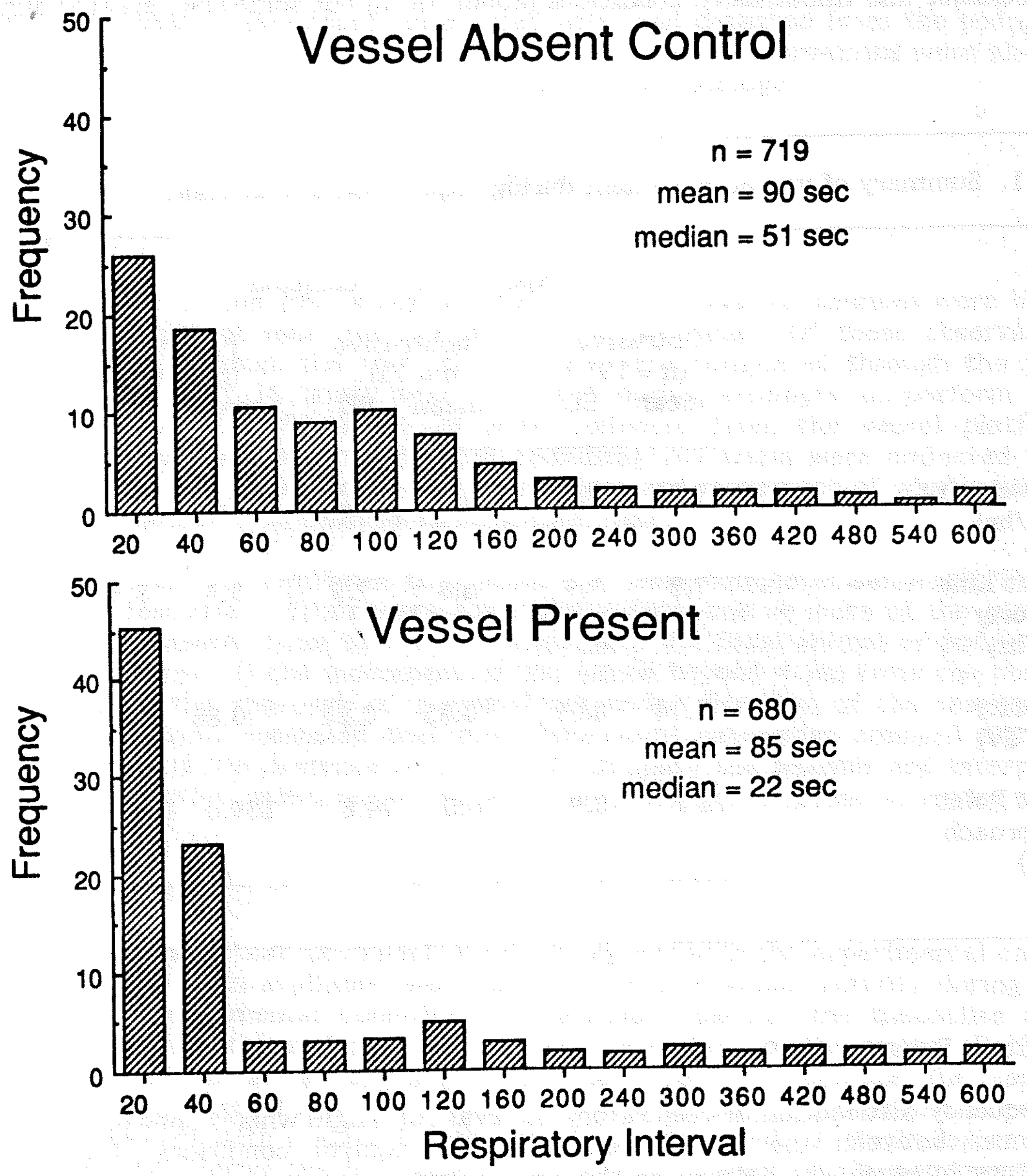


Figure 4. The frequency of respiratory intervals of single whales during Control and Experimental observations.

Four subcategories of respiratory behavior were derived for further, more detailed, analyses: 1) "Blow intervals," the duration of the relatively brief intervals between respirations when a whale was at or near the surface; 2) "Dive times," the duration of the prolonged submergences predicted by arching of the peduncle followed by a fluke-up or fluke-down dive; 3) "Maximum intervals," the longest respiratory interval during a trial, regardless of the occurrence of fluke-up or fluke-down dive; 4) "Blow rates," the number of blows per minute during a trial.

To help assure a parametric distribution of the dependent variables, blow intervals were converted to a logarithmic measure; and both dive times and blow intervals were averaged across each 20-min trial to reduce variability. A repeated-measures analysis of variance (ANOVA) was used for each variable. This allowed the variance of each dependent variable to be partitioned hierarchically according to the effects of the experimental conditions, the vessel classes, the individual whales, the trials, and the interactions of these variables (Pedhauzur 1978). The Tukey test was used for pair-wise comparisons between the means of each condition and for each vessel class ($p < 0.05$ level of significance).

The main effects of the experimental conditions or the vessel classes, or both, were significant for each of the four respiratory variables (Table 2). The amount of variance explained by the experimental conditions and the vessel classes combined ranged from 13% to 31%. Individual variation was large, accounting for 38% to 53% of the variation in each analysis. There were no significant differences across trials and no significant interactions between the independent variables.

Blow rates averaged 0.66/min during the control conditions and increased variably during each of the experimental interactions (Figure 5). Differences in blow rates across conditions were not significant. Only the blow rates during exposure to the small-vessel, averaged across experimental conditions, were significantly greater than the control and significantly greater than the blow rates during exposure to the schooner.

Blow intervals averaged 36 sec in length during the control conditions and decreased to 24 sec, 22 sec, and 14 sec during the Passby, Unobtrusive and Obtrusive conditions, respectively (Figure 5). The decrease in blow intervals was significant for the Obtrusive and Unobtrusive conditions and in response to each vessel as averaged across all conditions. Differences between the two vessel classes were not significant.

Maximum intervals averaged 390 sec in length during the control observations and increased significantly during the Obtrusive interaction (Figure 5). Slight increases in maximum intervals during the Unobtrusive and Passby conditions were not significant. The effect of vessel class was also significant but only the response to the schooner, averaged across all conditions, was significantly different from the control.

Finally, dive times averaged 340 sec in length during the control condition and did not change significantly across the three experimental interactions (Figure 5). However, dive times during exposure to the schooner were significantly longer than during the control or during exposure to the small vessel.

Table 2. Summary of repeated–measures analysis of the respiratory behavior of single whales from Frederick Sound during Control and Experimental conditions (1981).

Source	Sum of squares	df	r–square	F	p <
		Blow Intervals			
MODEL	6.47	58	0.875	5.08	0.001
Condition*	2.00	3	0.273	7.50	0.001
Vessel	0.02	1	0.002	0.17	0.682
Condition x Vessel	0.24	2	0.032	0.27	0.269
Subjects	3.74	42	0.510	4.06	0.001
Trials	0.14	2	0.019	3.11	0.055
Trials x Condition	0.27	6	0.037	2.01	0.086
Trials x Vessels	0.07	2	0.009	1.50	0.234
ERROR	0.92	42			
TOTAL	7.33	100			
		Dive Times			
MODEL	2280639	51	0.845	3.46	0.001
Condition	170929	3	0.063	1.45	0.245
Vessel*	455448	1	0.167	11.58	0.002
Condition x Vessel	56835	2	0.021	0.72	0.493
Subjects	1377090	35	0.504	3.05	0.001
Trials	4370	2	0.002	0.17	0.845
Trials x Condition	127528	6	0.047	1.64	0.164
Trials x Vessels	88437	2	0.032	3.42	0.054
ERROR	452019	35			
TOTAL	2732656	86			
		Maximum Interval			
MODEL	3060890	58	0.741	2.22	0.003
Condition*	593356	3	0.144	5.23	0.004
Vessel*	470191	1	0.114	12.44	0.001
Condition x Vessel	104543	2	0.025	1.38	0.262
Subjects	1587514	42	0.384	1.59	0.064
Trials	19853	2	0.005	0.42	0.661
Trials x Condition	224623	6	0.054	1.58	0.176
Trials x Vessels	60807	2	0.014	1.28	0.288
ERROR	1068941	45			
TOTAL	4129826	103			

(continued)

Table 2 (continued)

Source	Sum of squares	df	r–square	F	p <
			Blow Rates		
MODEL	15.17	62	0.710	2.29	0.001
Condition	0.53	3	0.025	0.72	0.542
Vessel*	1.26	1	0.059	5.14	0.028
Condition x Vessel	0.97	2	0.045	1.81	0.150
Subjects	11.26	46	0.527	1.94	0.002
Trials	0.08	2	0.004	0.28	0.659
Trials x Condition	1.05	6	0.049	1.27	0.153
Trials x Vessels	0.00	2	0.000	0.02	0.978
ERROR	6.21	58			
TOTAL	21.38	120			

* Significant values of interest.

Whale Movement

The movement of a focal pod was described by its total–length (TL) velocity and its linearity during each 20–min trial (see description of variables in Vessel Movement). Straight–line velocity was not evaluated since it was a direct function of the other two movement variables. An analysis of pod composition showed no significant differences between singles, pairs, and cow–calf pairs for either TL velocity or linearity (Repeated–measures ANOVA for TL velocity: F [2/52]] = 0.13, p = 0.87; linearity: F [2/52]] = 1.93, p = 0.155). Consequently, subsequent data were accordingly based on the combined data for all pod compositions to increase the sample size.

For the three pod composition combined, TL velocity averaged 3.31 km/hr and linearity averaged 0.75 during the control conditions. The ANOVA showed no significant changes across conditions, vessel classes, or trials (Table 3).

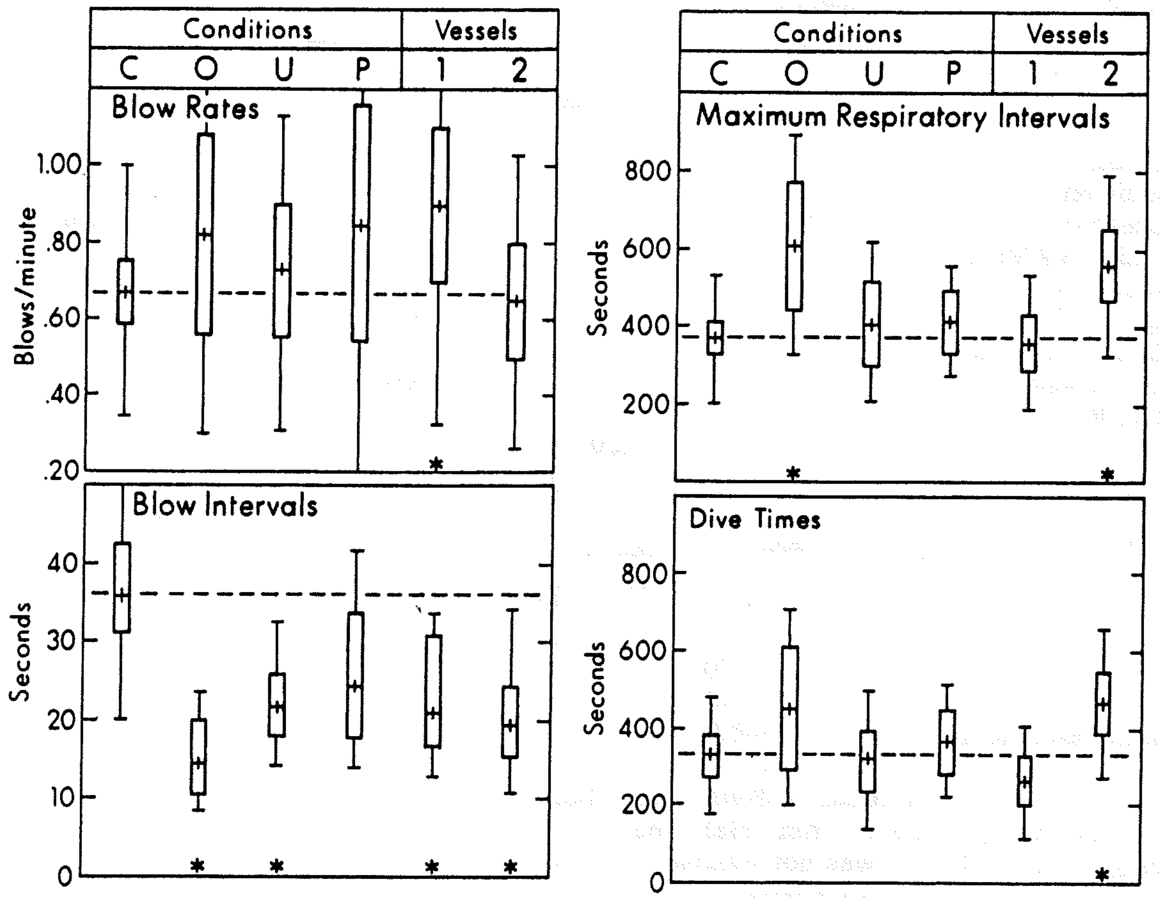


Figure 5. The means (+), SD (bars) and the 95% confidence intervals of each mean (boxes), adjusted for Tukey's multiple comparison test, for subcategories of respiratory behavior during Control (C), Obtrusive (O), Unobtrusive (U), and Passbys (P) for both vessels combined and for vessels one and two across all experimental conditions. Dashed-line shows the control baseline. Asterisks (*) indicate Experimental conditions that differed significantly from the Control (Tukey's multiple comparison test, $p < 0.05$).

Table 3. Summary of repeated-measures analysis of pod (singles, pairs, and cow-calfpairs) movement during control and experimental conditions in Frederick Sound, 1981.

Source	Sum of squares	df	r-square	F	p <
			Pod Speed		
MODEL	194.37	65	0.667	1.67	0.028
Condition	11.76	3	0.041	1.20	0.321
Vessel	4.81	1	0.016	0.73	0.485
Condition x Vessel	3.21	2	0.011	0.98	0.327
Subjects	157.22	48	0.540	1.82	0.016
Trials	6.05	2	0.021	1.69	0.195
Trials x Condition	10.91	6	0.037	1.01	0.427
Trials x Vessels	0.39	2	0.000	0.07	0.969
ERROR	96.92	54			
TOTAL	291.30	119			
			Linearity		
MODEL	5.93	65	0.714	2.11	0.003
Condition	0.28	3	0.034	0.83	0.483
Vessel	0.14	1	0.017	0.65	0.527
Condition x Vessel	0.00	2	0.000	0.01	0.937
Subjects	5.30	48	0.638	2.55	0.001
Trials	0.03	2	0.004	0.36	0.700
Trials x Condition	0.15	6	0.018	0.59	0.738
Trials x Vessels	0.03	2	0.004	0.21	0.887
ERROR	2.38	55			
TOTAL	8.31	120			

Aerial, Feeding, and Social Behavior

Across all pod sizes and observational conditions combined, the occurrences of aerial behavior, surface feeding, and changes in pod composition were infrequent and highly variable (Table 4). If occurrences of these behavioral events were randomly distributed in time, the number of events in a trial should approximate a time-homogeneous Poisson process, with a resulting coefficient of variation (CV) near one (Fagen and Young 1978; Snedecor and Cochran 1967). Instead, the CV for each behavioral category ranged between three and five, indicating a very clumped distribution in time.

Table 4. The frequencies and percent occurrences of aerial, social, and surface-feeding behavior of single, pairs, and cow/calf pairs during the combined Control and Experimental trials (n = 262) in Frederick Sound (1981).

	Occurrence	Mean	SD	CV	Maximum
Aerial					
Head rises	5.3%	0.10	0.72	7.3	11
Leaps	5.7%	0.27	1.63	6.0	15
Flipper-slaps	7.6%	1.18	9.89	8.4	123
Fluke-slaps	3.4%	0.26	2.00	7.6	22
Peduncle-slaps	3.4%	0.24	2.39	10.1	33
Social					
Affiliations	9.1%	0.10	0.31	3.2	2
Disaffiliations	6.5%	0.06	0.25	3.8	1
Surface-feeding					
Lunge-feeding	7.3%	0.42	2.64	6.3	27
Bubble-netting	3.1%	0.10	0.70	7.3	8

We attempted to reduce the variability of these measures by examining only the presence or absence of a given behavioral event in each trial. Referred to as zero-one sampling (Altmann 1974), the resulting averages for the control and experimental conditions reflected the probability of observing one or more occurrences of a given behavioral event during a single 20-min trial. An analysis of the zero-one probabilities indicated significant correlations between subcategories of behavioral events within the three major categories (Contingency coefficient > 0.25; Fischer's exact two-tailed test, $p < 0.05$). Among aerial behaviors, for example, the occurrence of a leap was significantly correlated with the occurrence of a fluke-slap, a flipper-slap, a peduncle-slap, and a head-rise. Because of this intercorrelation, subcategories of behavioral events were in turn combined with the major categories. Further analyses of aerial behavior were also restricted to single whales to simplify interpretation of behavioral rates.

Even given the collapsed categories and the zero-one sampling conversion, the occurrences of aerial, social, and surface-feeding behaviors were infrequent. During control observations of single whales, aerial and surface-feeding behaviors occurred during only 11% of the trials and social behavior (e.g. changes in pod composition) occurred during only 16%. Although the probability of observing an aerial behavior or a change in pod composition approximately doubled during the Obtrusive condition, a Chi-square Test of Independence did not indicate significant differences across the experimental and control conditions for any of the three behavioral categories (Table 5).

Table 5. The occurrences of aerial, social, and surface-feeding behaviors by single whales during Control and Experimental trials in Frederick Sound (1981).

Condition	Aerial 0	Aerial 1	Social 0	Social 1	Feeding 0	Feeding 1
Control	57 (89%)	7 (11%)	54 (85%)	10 (15%)	57 (89%)	7 (11%)
Obtrusive	15 (79%)	4 (21%)	13 (68%)	6 (32%)	17 (89%)	2 (11%)
Unobtrusive	24 (96%)	1 (4%)	23 (92%)	2 (8%)	11 (85%)	2 (15%)
Passby	12 (92%)	1 (8%)	12 (92%)	1 (5%)	25 (100%)	0 (0%)
Total	108 (89%)	13 (11%)	102 (84%)	19 (16%)	110 (91%)	11 (9%)
Chi-square	3.42		5.37		3.45	
df	3		3		3	
P =	0.17		0.14		0.32	

Discussion

Overall, respiratory behaviors were the most sensitive indicators of a response to vessel traffic during the experimental conditions. As compared to the control observations, the Obtrusive condition produced a striking decrease in the duration of intervals between blows when the whale was near the surface and an increase in the longest submergence observed during an experimental trial. These effects declined considerably as the activity of the vessel moderated during the Unobtrusive and Passby conditions.

Differences in respiratory variables were also attributable to vessel classes after accounting for differences due to the experimental conditions. Dive times and the duration of the longest submergence increased significantly only in response to the schooner. Blow rates, which showed no significant changes due to the experimental conditions, increased, overall, in response to the small vessel. These different responses could be attributed to the speed or maneuverability of the two vessels. Although we attempted to standardize the activity of the vessels during each condition, the schooner was far slower and far less maneuverable than the small vessel.

Differences in the noise of the vessels could also have contributed to the different reactions of whales. The noise of vessel traffic and industrial activity has often been suggested as a possible source of disturbance to baleen whales (Acoustic Society of America 1981; Richardson et al. 1983). Although little is known about the audition of baleen whales, they are presumably most sensitive to frequencies within the range of their own vocalizations (Myrberg 1978). For humpback whales, the frequency of vocalizations range from 40 Hz to over 8,000 Hz but are predominantly less than 2,000 Hz (Winn and Winn 1978). The diesel-powered schooner was much louder at equivalent speeds than the outboard-driven small vessel and its sound signature was shifted towards the lower frequencies (less than 2,000 Hz). Impulse sounds of the schooner, due to changes in gears and engine speed, were considerable and were not reflected in the steady-state noise signatures.

Pod movement and the occurrences of aerial, social, and surface-feeding behaviors were too variable or infrequent to indicate changes during the experimental conditions. The opportunistic observations and case histories discussed in the following sections, however, provide more conclusive evidence of changes in pod movement and aerial behavior during vessel interactions.

OPPORTUNISTIC INTERACTIONS

During the summer of 1982, whales were observed primarily during the opportunistic passby of vessels that were not under the direction of the research team. Of particular interest was the effect of vessels larger than, and at greater distances than, those examined in the previous experimental interactions. All observations were collected from shore stations in Frederick Sound or Bartlett Cove, Glacier Bay. Because of important differences in both whale and vessel usage, the analyses for each region were conducted separately.

Methods

Inferential Statistics and Independent Variables

Differences in the experimental design used in 1981 and the opportunistic design used in 1982 required some changes in the independent variables examined and the statistical methods used for their analysis. During 1981 the emphasis was on categorical differences in classes of vessels and their operation, as well as on comparisons to control observations. Differences in vessel speed and proximity to whales were subsumed under the experimental conditions. For this study of categorical independent variables, a factorial analysis (ANOVA) was appropriate.

In the opportunistic design used in 1982, the emphasis was on determining graded changes in the behavior of whales as a function of the wide range of vessel distances and speeds during passby conditions. For this purpose, a multiple-regression (MR) or "trend" analysis was more appropriate. In this model, vessel distance and vessel speed were measured as continuous independent variables. When more than a single vessel was within the observational arena, only the distance of the vessel nearest to the focal pod and the speed of the fastest vessel were included in the model. Graded changes in the behavior of whales (the dependent variables) during the observational sessions were then correlated with graded changes in the independent variables. The potential for curvilinear changes in response was examined by including the quadratic component of the vessel variables. As with the ANOVA model used in the 1981 study, the r-square of the MR model was used to assess the "fit" of the regression equation and the degree to which each independent variable contributed to explaining changes in the dependent variable.

Control conditions were defined as observation sessions during which no vessels approached within 8,000 m of the focal pod. Because the assignment of individual focal pods to control or passby conditions was not based on an experimental or randomized design, we did not generally attempt to test differences between the behavior of whales under these two conditions. Instead, the average values of dependent variables during the control sessions were used primarily for comparison to the graded changes observed during the opportunistic passbys. As with the previous experimental interactions, analysis was limited to focal pods within 4,000 m of the shore stations and within a 4,000 m "realm of influence" to the vessel activity.

Vessel-Whale Orientation

The orientation of pod movement with respect to a vessel's path was determined by calculating the heading of each leg of whale movement relative to the heading of the vessel. Knowing the adjusted pod heading, the speed of travel during each leg of movement, and whether the pod was traveling away from or toward the path of the vessel allowed us to calculate an "approach-avoidance" vector (Figure 6a). This vector reflected the orientation and speed of a pod in respect to the vessel's path regardless of whether the pod was to port, starboard, ahead, or behind the vessel at any given time. The approach-avoidance vectors were converted to rectangular coordinates in a circular distribution diagram scaled to km/hr (Figure 6b). When, on rare occasions, a leg of pod movement crossed the path of a vessel, pod orientation was determined at the time of the closest point of approach to the vessel during that leg.

In the example in Figure 6a, the five sightings of the whale provided four legs of travel. The four legs were converted to approach-avoidance vectors and plotted as a circular diagram (Figure 6b). In the first leg, the whale was traveling towards the path of the approaching vessel. During the second leg, the whale crossed the path of the vessel and continued moving away from the path at an angle of nearly 90 degrees. The CPA of this leg and of the overall session, occurred at 19:37. Since the whale crossed the vessel's path before the CPA, the second vector was judged to be away from the vessel. The whale continued moving away from the vessel's path during the third leg and turned back towards the vessel in the fourth. The whale's mean approach-avoidance vector (the X and Y shown in Figure 6b) for the session was 2 km/hr at an angle parallel and in the same direction as the vessel.

Circular distributions for selected legs of whale travel were tested for a preferred direction with the Hotelling's one-sample test, a parametric test similar to the t-test (Batschelet 1972, 1976). To interpret the results of the vectorial statistics, it is necessary to consider both the mean X and the mean Y, as well as the F test. A significant F value indicated that the vectorial mean differed from zero (i.e., there was a preferred orientation), but the mean X and Y determined the direction of the preferred orientation. In terms of the approach-avoidance vector, the mean X indicated the tendency of pods to move in the same or opposite direction of vessel travel along the axis parallel to the vessel's path. The mean Y indicated the tendency of pods to move towards or away from the vessel along the axis perpendicular to its path.

Aerial, Feeding and Social Behavior. Given their infrequency, it was not possible to examine changes in non-respiratory behavior as a function of graded changes in vessel distance or speed. Instead, subcategories of aerial, feeding, and social behavior were collapsed and reduced to a zero-one sampling strategy for each 20-min trial following the strategy described previously (Table 7). During control observations only 3.3% of the trials contained some aerial behavior, 13.3% contained some change in pod composition, and 10% contained some surface-feeding behavior. When vessels were within 4,000 m of the focal pod, the occurrences of aerial behaviors increased while changes in pod composition and feeding behavior decreased, but these changes were not significant.

Table 7. The percent occurrences and parametric statistics of aerial, social, and surface-feeding behavior during all observational trials (n = 129) in Frederick Sound (1982).

	Occurrence	Mean	SD	CV	Maximum
Aerial	3.1%	0.17	1.07	6.3	8
Social	6.2%	0.09	0.44	4.7	4
Feeding	4.6%	0.09	0.43	5.0	3

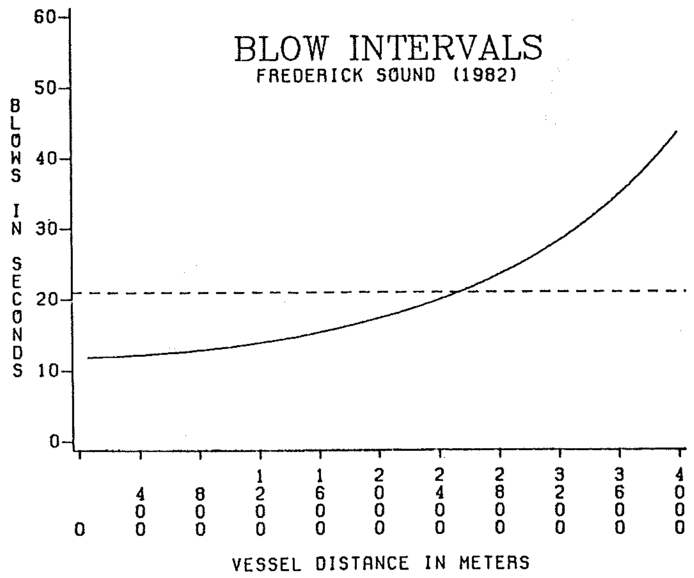


Figure 7. Changes in blow intervals of whales in Frederick Sound (1982) as a function of vessel distance. Dashed lines indicate average blow intervals during psuedo-control observations.

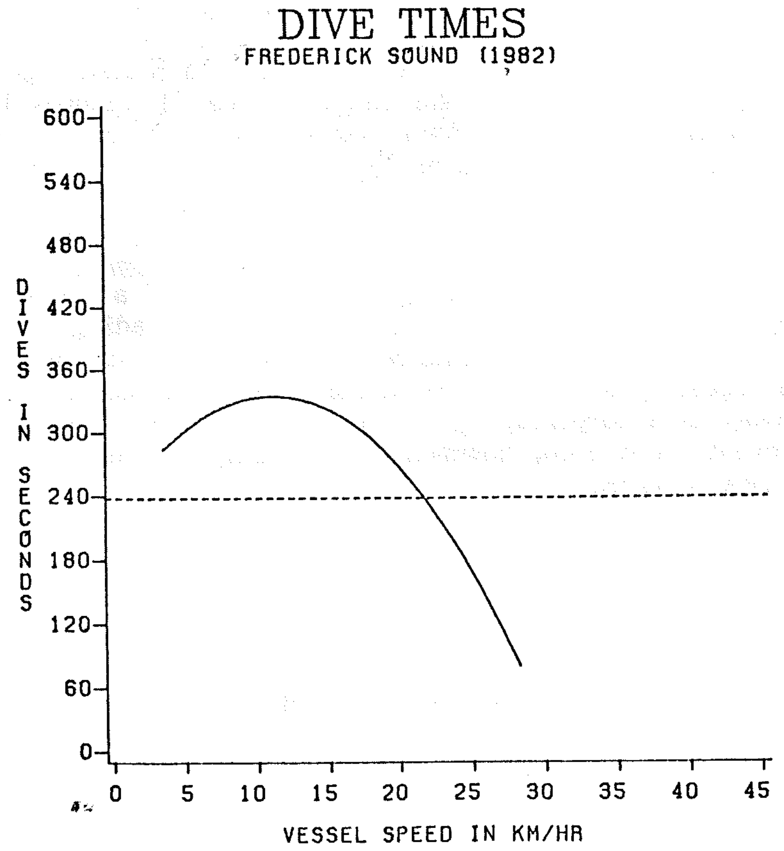


Figure 8. Changes in dive times of whales in Frederick Sound (1982) as a function of vessel speed. Dashed lines indicate average blow intervals during psuedo-control observations.

Pod Speed and Orientation. A preliminary analysis of pod movement showed no differences between pod sizes. Accordingly, subsequent analyses of whale movement and orientation included data from all observations of singles, pairs, and cow-calf pairs. A hierarchical analysis of vessel distance and speed accounted for 22.8% of the variation in pod speed (Table 6). Only the linear component of the two main effects was significant. To simplify the presentation of the MR model, vessel speed was dichotomized based on speed greater or less than 18.8 km/hr (10 knots). Dichotomizing this variable resulted in little loss in the fit of the model (r-square = 0.168, F[2/104]] = 10.48, P = 0.0001) and allowed the main effects to be plotted (Figure 9). In comparison to the average pod speed during the control condition, pod speed decreased linearly with decreasing vessel distance in the presence of both fast and slow vessels. In the presence of slow vessels, however, pod speeds were, overall, 1 km/hr slower than in the presence of faster moving vessels.

Focal pods showed a significant avoidance orientation when vessels were within 8,000 m of a pod (average CPA during all legs of pod movement = 3720 m). The angular component of the mean approach–avoidance vector indicated that pods oriented almost directly away from the path of a vessel and moved in that direction at an average speed of 0.26 km/hr (Figure 10a). Examining the mean approach–avoidance vectors of pods within 4,000, 2,000, and 1,000 m (inclusive) of a vessel indicated a graded increase in avoidance as the average distance to the vessel decreased (Figures 10 a,b,c, and d). When vessels were within 1,000 m, the focal pod, on average, moved directly away from the path of a vessel at a speed of 1.1 km/hr.

Further details of the whales' behavioral strategy were suggested by changes in the angular component of the approach–avoidance vector as a vessel approached and passed the position of a pod (Figure 11). During the approach of a vessel, pods were, on average, traveling in the same direction as the vessel's heading but at an angle 34 degrees away from its path. As the vessel reached its CPA, pods turned away from the vessel and in the opposite direction of its heading. After a vessel passed, pods turned almost directly away at a perpendicular to the vessel's path. The vectorial mean was significantly different from zero, however, only during the leg of pod movement in which the vessel CPA occurred.

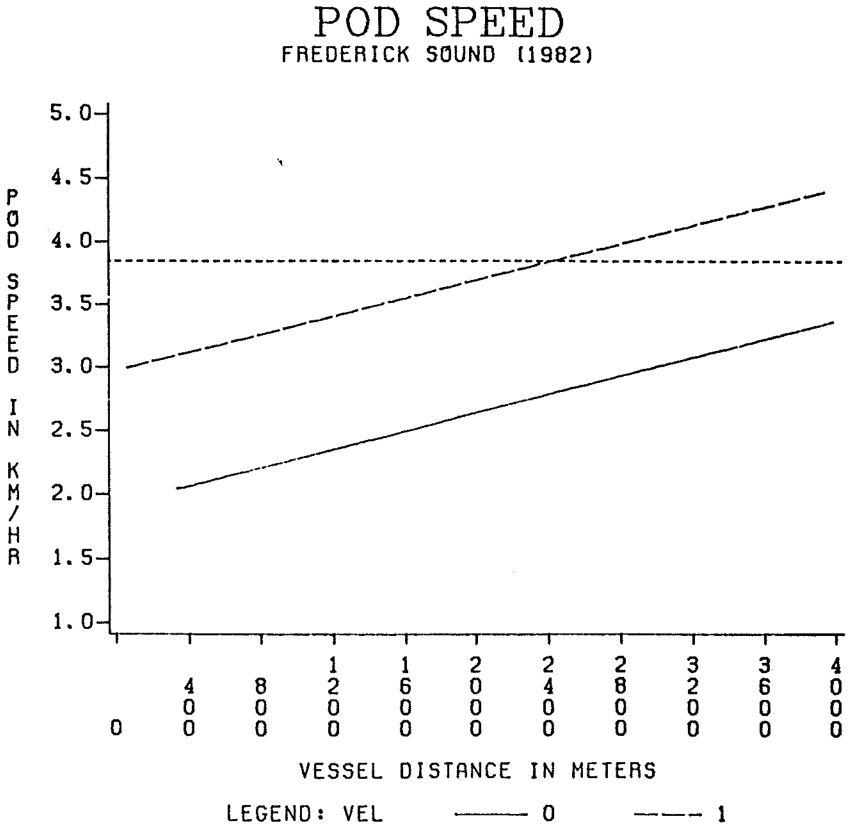


Figure 9. Changes in pod speed in Frederick Sound (1982) as a function of the distance of vessels operating at high (short dashed lines) or slow (solid line) speeds. Long dashed line indicate average blow intervals during psuedo–control observations.

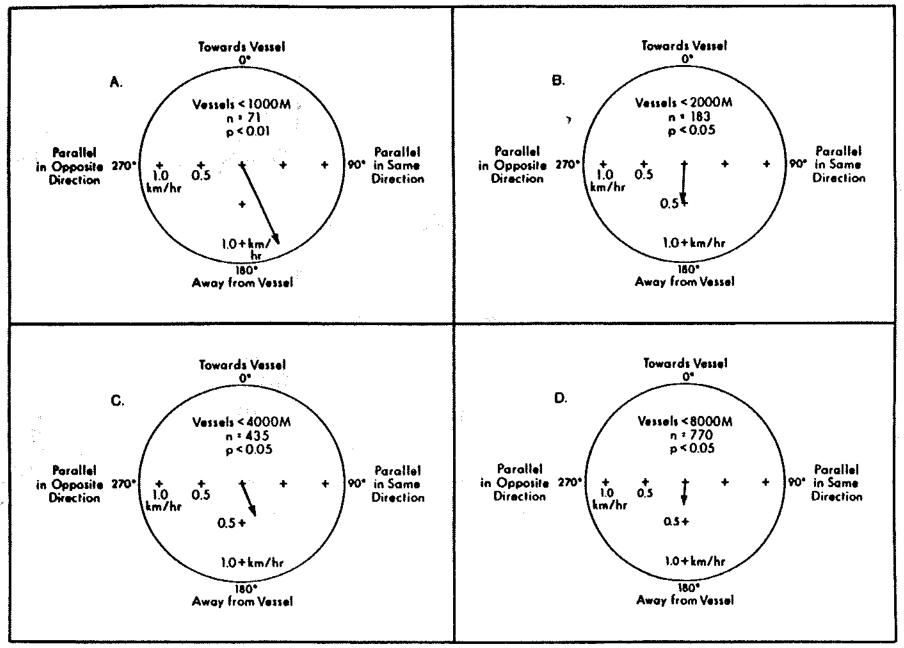


Figure 10. The mean approach–avoidance vector of focal pods within 1000, 2000, 4000, and 8000 m, inclusive, of vessels in Frederick Sound during 1982.

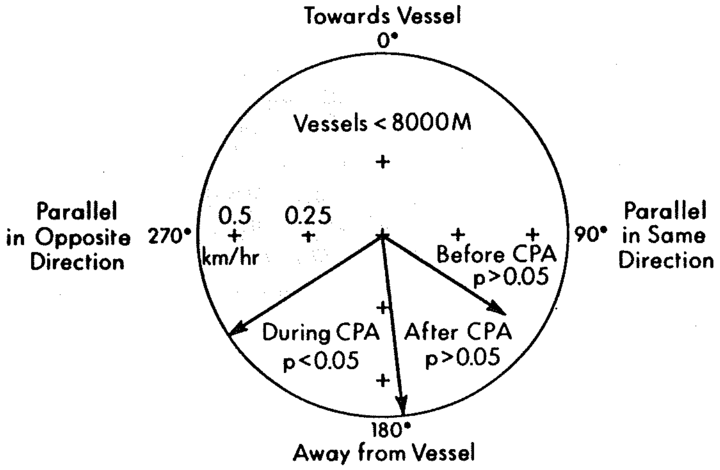


Figure 11. The mean approach–avoidance vector of focal pods before, during, and after the passby of vessels in Frederick Sound during 1982.

Bartlett Cove, Glacier Bay

Important differences between Frederick Sound and Bartlett Cove required some modification to the previous strategy for the analysis of whales' responses to vessel traffic. First, Park Service regulations limited vessels in Bartlett Cove and other parts of Glacier Bay to a mid-channel course and a speed of 18.2 km/hr or less (Anonymous 1984). Due to this restricted range of speed, vessel speed was not considered as an independent variable in the MR analysis. Second, Bartlett Cove is the location of the National Park Service dock and visitor concession. The departure of concession tour boats, charter fishing vessels, and private pleasure boats resulted in an average of 3.9 vessel passbys/hr during opportunistic observations and only one observation session did not involve at least one vessel passby. By comparison, the 25 opportunistic observations in Frederick Sound averaged only 1.9 passbys/hr. To examine the potential cumulative effects of vessel traffic in Bartlett Cove, we derived an index of vessel density based on the number of vessels operating within 4000 m of the focal pod. This index was included as an independent variable in the MR analysis of whale respiration and pod speed.

Third, Bartlett Cove was the site of personnel transfer from large cruise ships which visited Glacier Bay on an average of about two per day during the summer of 1982 (Anonymous 1984). Although these ships were generally travelling at slow speeds (4 to 8 km/hr) as they approached Bartlett Cove, changes in engine speed and propeller pitch during maneuvering sometimes produced more underwater noise than other closer or faster-moving vessels (see later section on Case Histories, as well as Malme et al. 1982; Miles and Malme 1983). Previous research (Jurasz and Jurasz 1981b; Dean et al. 1985) suggested that frequent passage of these large ships was an important variable influencing the behavior of humpback whales in Glacier Bay. To examine this possibility, we included a dichotomous variable representing the presence or absence of a large ship (e.g. greater than 100 tons of registry) during each observational session. This dichotomous variable, referred to as "large ships," was used along with vessel distance and the index of vessel density in the analysis of whale respiration and pod speed.

Finally, Bartlett Cove differed from Frederick Sound in the unique residency of a cow-calf pair and two adult whales throughout the 1982 study period (Baker et al. 1983). Because of the pod's proximity to the shore observation station and the unique characteristics of each resident's dorsal fin (Perry et al. 1985), it was possible to record the respiratory behavior of each adult separately. Recording the respiratory behavior of the calf was more difficult. The calf often respired without the visible plume of vapor associated with adult respiration and its surfacing were sometimes obscured by its proximity to the cow. Consequently, the respiratory behavior of the calf was omitted from the analysis. Determining the individual involved in aerial or surface feeding behavior was more problematic since these behaviors occurred so quickly. Consequently, aerial behavior, surface feeding, and social behavior reflected the activity of the pod as a whole.

Data Base. A total of 209 trials were collected during 77 observational sessions in Bartlett Cove. The focal pod in all sessions included one or more of the Bartlett Cove residents (average size of focal pod = 2.6 whales). Although other whales visited Bartlett Cove for relatively brief periods, the sample of behavioral data collected from these individuals was not large enough for analysis.

Respiratory Behavior. The relationship between vessel activity and the respiratory behavior of the Bartlett Cove adults was examined for cases in which vessels were less than 4,000 m from the focal pod. The main effects, quadratic components (where appropriate), and two-way interactions of the MR model were entered hierarchically in the following order: subjects (the three adults), vessel distance, presence of large ships, and vessel density.

Blow intervals were weakly correlated with vessel distance, large ships, and the quadratic component of vessel density. The amount of variance explained by these main effects, however, was too small ($p < 0.01$) to interpret meaningfully. Dive times, by comparison, were more strongly correlated with large vessels and vessel density, though not with vessel distance. To interpret these effects, the full MR model was reduced to only these two main effects. The new MR model accounted for nearly as much variance ($F[2/444]] = 35.57$, $p < 0.0001$, r -square = 0.138) as the full model. A plot of the simplified model indicated that dive times decreased as vessel density increased (Figure 12). In the absence of a large ship, dive times decreased from 330 sec to 200 sec as vessel density increased from one to six. In the presence of a large vessel, dive times were on average 60 sec shorter.

Pod Speed and Orientation. The relationship between pod speed and vessel activity was examined with the MR model used in the previous analysis of respiratory behavior (Table 8). The full model was significant but many of the main effects and interactions were not. A simplified model accounted for as much variation ($F[3/1188]] = 16.92$, $p < 0.0001$, r-square = 0.041) as the full model but included only the presence of large ships, vessel density, and their interactions. A plot of the regression equation indicated that, in the absence of a large ship, pod speed decreased by nearly 1 km/hr as the number of vessels increased from one to six (Figure 13). When a large ship was present, however, the direction of this correlation was reversed; pod speed increased as vessel density increased.

The average approach-avoidance vectors of the focal pod showed no significant orientation in response to vessels within 4,000, 2,000, and 1,000 m, inclusive. Changes in the pod's orientation as a vessel approached and passed their position, however, differed from changes observed in Frederick Sound whales (Figure 14). Within the 4,000 m realm of influence, Bartlett Cove residents showed no significant orientation during the approach and CPA of a vessel. Only after the vessel passed did the pod orient away from the vessel's path at a vectorial speed of 0.586 km/hr. When the analysis was restricted to a 1,000 m realm of influence, the vectorial speed at which the pod moved away from the path of vessels following CPA increased to 0.982 km/hr.

Aerial, Feeding, and Social Behavior. The Bartlett Cove residents engaged in a large number of aerial behaviors and changes in pod composition (Table 9). Aerial behaviors averaged 6.0 events per observational trial and changes in pod composition averaged 0.5 events, while surface feeding behavior averaged only 0.04 per trial. In some cases, episodes of aerial behaviors were extremely intense. We observed as many as 80 aerial behaviors during a single 20-min trial and as many as 176 during a single hour-long session.

Although the frequencies of aerial and social behavior in Bartlett Cove were great enough for parametric statistics to be meaningful, the data were converted to zero-one samples (i.e. the percentage of trials in which a behavioral type occurred) for comparison to Frederick Sound data and for further analyses (Table 9). The possible relationship between vessel traffic and the occurrences of aerial and social behavior was examined using the following measures of vessel activity (Table 10): 1) the closest point of approach of a vessel within 4,000 m of the focal pod during an observational trial; 2) the presence or absence of a large ship within an observational session; and 3) the maximum number of vessels operating within 4,000 m of the focal pod during a trial (vessel density). This analysis showed two significant correlations: changes in pod composition increased in the presence of a large ship (Fischer's Exact Test, p = 0.046); and, the probability of an occurrence of aerial behavior increased as the distance to vessels decreased (Spearman's correlation coefficient = −0.225, p = 0.012). Vessel density was not correlated with the occurrences of either aerial or social behavior.

Table 8. Multiple-regression analysis of whale respiration and pod swimming speed during opportunistic passby of vessels within 4000 m of focal pod in Bartlett Cove, Glacier Bay (1982).

Source	Sum of squares	df	r-square	F	p <
			Blow Intervals		
MODEL	5.74	14	0.048	6.56	0.001
Subjects	3.14	2	0.026	25.10	0.001
Vessel distance					
linear*	0.29	1	0.002	4.58	0.032
quadratic	0.00	1	0.000	0.39	0.827
Large ships*	0.30	1	0.002	4.73	0.030
Vessel density					
linear	0.02	1	0.000	0.39	0.532
quadratic*	0.81	1	0.007	13.04	0.001
Interactions	1.18	7	0.009		
ERROR	112.84	1804			
TOTAL	118.39	1818			
			Dive Times		
MODEL	1509441	14	0.222	8.81	0.001
Subjects	10289	2	0.002	0.42	0.658
Vessel distance					
linear	8598	1	0.001	0.70	0.402
quadratic	21049	1	0.003	1.72	0.190
Large ships*	482516	1	0.071	39.43	0.001
Vessel density					
linear*	455222	1	0.067	37.10	0.001
quadratic	2456	1	0.000	0.20	0.654
Interactions	529311	7	0.078		
ERROR	5313141	432			
TOTAL	6796488	446			

(continued)

Table 8. (continued)

Source	Sum of squares	df	r-square	F	p <
			Pod Speed		
MODEL	288.30	12	0.072	7.64	0.001
Vessel distance					
linear	15.85	1	0.004	5.04	0.025
quadratic	0.47	1	0.000	0.15	0.699
Large ships*	3.64	1	0.001	1.16	0.282
Vessel density					
linear*	35.26	1	0.009	11.21	0.001
quadratic	0.51	1	0.000	0.16	0.688
Interactions	232.56	7	0.058		
ERROR	3708.74	1179			
TOTAL	3997.04	1191			

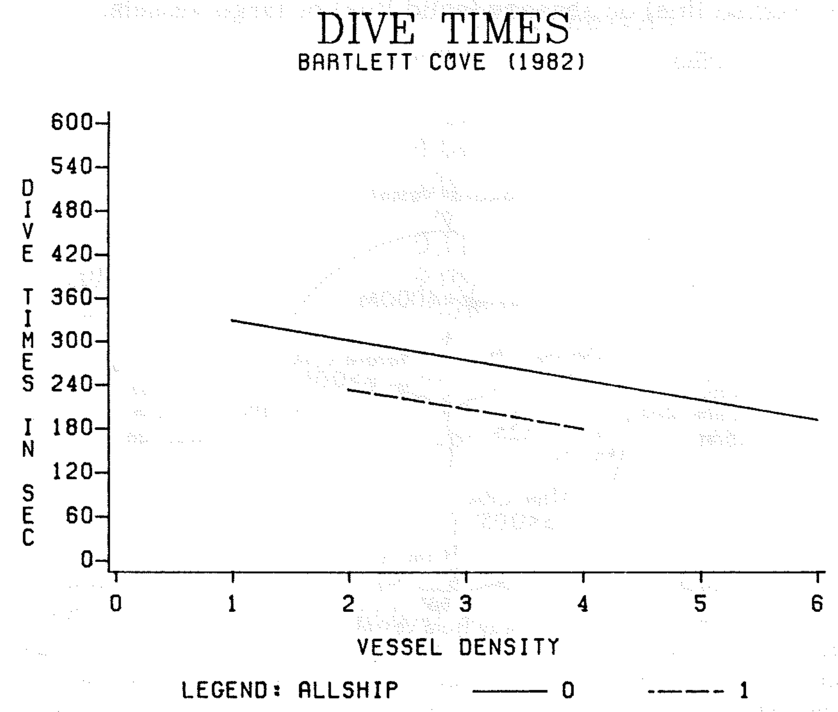


Figure 12. Changes in dive times of whales in Bartlett Cove (1982) as a function of vessel density and the presence (dashed line) or absence (solid line) of large vessels.

relationship between vessel traffic and the occurrences of aerial and social behavior was examined using the following measures of vessel activity (Table 10): 1) the closest point of approach of a vessel within 4,000 m of the focal pod during an observational trial; 2) the presence or absence of a large ship within an observational session; and 3) the maximum number of vessels operating within 4,000 m of the focal pod during a trial (vessel density). This analysis showed two significant correlations: changes in pod composition increased in the presence of a large ship (Fischer's Exact Test, p = 0.046); and, the probability of an occurrence of aerial behavior increased as the distance to vessels decreased (Spearman's correlation coefficient = -0.225, p = 0.012). Vessel density was not correlated with the occurrences of either aerial or social behavior.

Table 8. Multiple-regression analysis of whale respiration and pod swimming speed during opportunistic passby of vessels within 4000 m of focal pod in Bartlett Cove, Glacier Bay (1982).

Source	Sum of squares	df	r-square	F	p <
			Blow Intervals		
MODEL	5.74	14	0.048	6.56	0.001
Subjects	3.14	2	0.026	25.10	0.001
Vessel distance					
linear*	0.29	1	0.002	4.58	0.032
quadratic	0.00	1	0.000	0.39	0.827
Large ships*	0.30	1	0.002	4.73	0.030
Vessel density					
linear	0.02	1	0.000	0.39	0.532
quadratic*	0.81	1	0.007	13.04	0.001
Interactions	1.18	7	0.009		
ERROR	112.84	1804			
TOTAL	118.39	1818			
			Dive Times		
MODEL	1509441	14	0.222	8.81	0.001
Subjects	10289	2	0.002	0.42	0.658
Vessel distance					
linear	8598	1	0.001	0.70	0.402
quadratic	21049	1	0.003	1.72	0.190
Large ships*	482516	1	0.071	39.43	0.001
Vessel density					
linear*	455222	1	0.067	37.10	0.001
quadratic	2456	1	0.000	0.20	0.654
Interactions	529311	7	0.078		
ERROR	5313141	432			
TOTAL	6796488	446			

(continued)

Table 8. (continued)

Source	Sum of squares	df	r-square	F	p <
			Pod Speed		
MODEL	288.30	12	0.072	7.64	0.001
Vessel distance					
linear	15.85	1	0.004	5.04	0.025
quadratic	0.47	1	0.000	0.15	0.699
Large ships*	3.64	1	0.001	1.16	0.282
Vessel density					
linear*	35.26	1	0.009	11.21	0.001
quadratic	0.51	1	0.000	0.16	0.688
Interactions	232.56	7	0.058		
ERROR	3708.74	1179			
TOTAL	3997.04	1191			

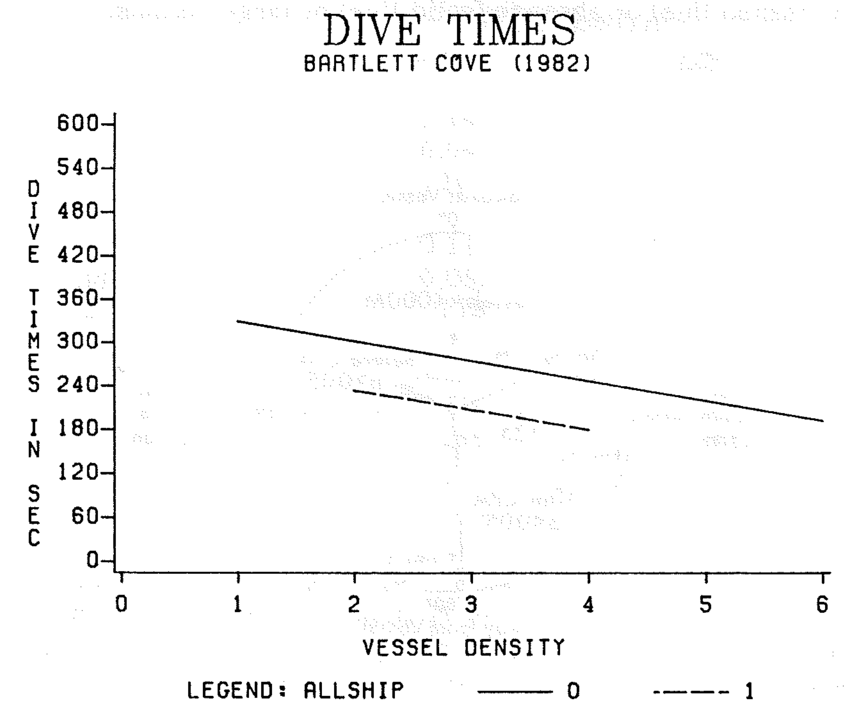


Figure 12. Changes in dive times of whales in Bartlett Cove (1982) as a function of vessel density and the presence (dashed line) or absence (solid line) of large vessels.

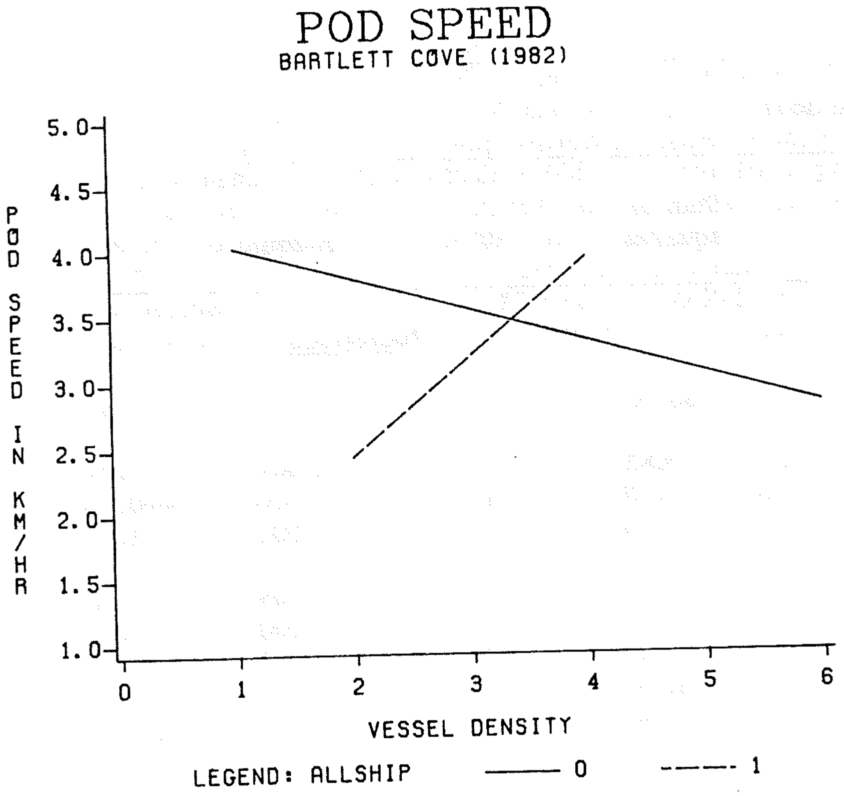


Figure 13. Changes in pod speed in Bartlett Cove (1982) as a function of vessel density and the presence (dashed line) or absence (solid line) of large vessels.

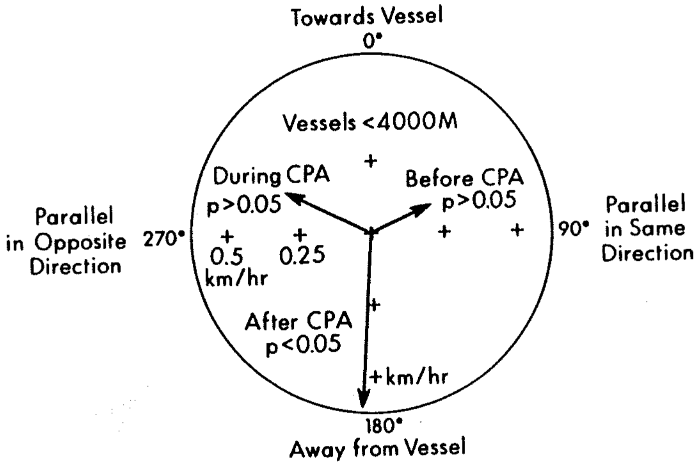


Figure 14. The mean approach-avoidance vector of the focal pod before, during, and after the passby of vessels in Bartlett Cove (1982).

Table 9. The percent occurrences and parametric statistics of aerial, social, and surface-feeding behavior during all observational trials (n = 209) in Bartlett Cove, Glacier Bay (1982).

	Occurrence	Mean	SD	CV	Maximum
Aerial	43.1%	6.06	13.40	2.2	80
Social	33.5%	0.53	0.88	1.6	5
Feeding	4.4%	0.04	0.23	4.9	2

Table 10. The correlation[1] of aerial and social behavior with vessel activity during opportunistic vessel passbys in Bartlett Cove, Glacier Bay (1982).

	Whale Behavior	
	Social	Aerial
Large ship (r)	0.149	0.012
(p)	0.047	0.866
(n)	197	197
Vessel proximity (r)	0.115	−0.225
(p)	0.061	0.012
(n)	178	178
Vessel density (r)	−0.038	0.093
(p)	0.625	0.227
(n)	168	168

[1] Aerial, social behavior, and large ships are expressed as dichotomous variables (e.g., occurrence or non-occurrence) for each 20-min observational trial. Vessel proximity and vessel density are continuous or scaled variables. The relationship between the behavior was tested with Fischer's exact test (two-tailed). The relationship of vessel density and vessel proximity with the occurrence of aerial or social behavior was tested with the Spearman rank-correlation coefficient. The following abbreviation were used: r = Spearman's correlation coefficient; p = the probability value for the appropriate test; n = number of 20-min observational trials.

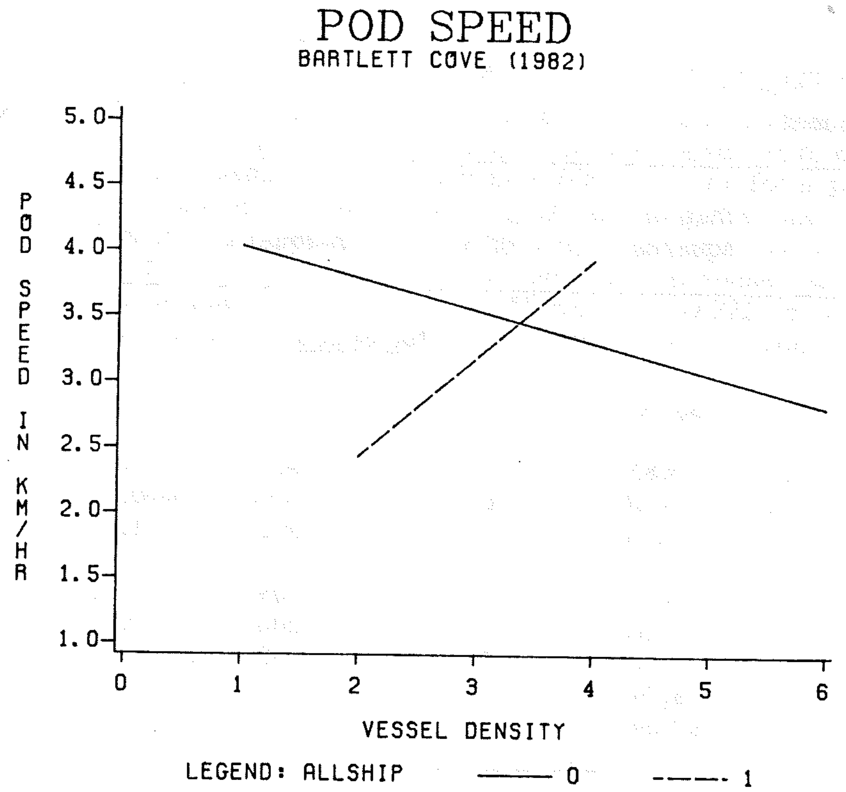
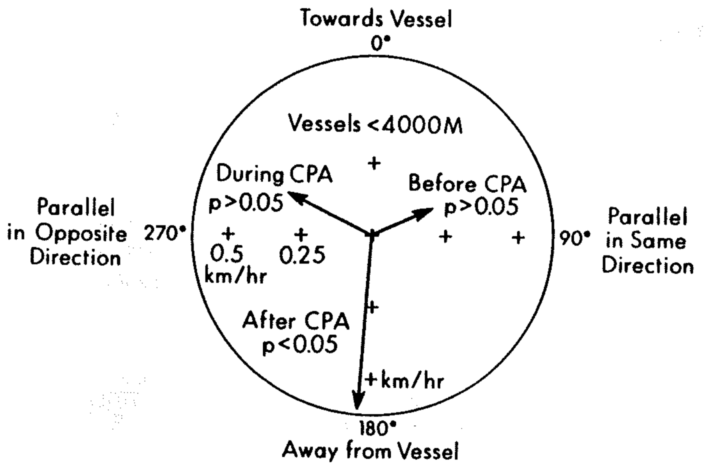


Figure 13. Changes in pod speed in Bartlett Cove (1982) as a function of vessel density and the presence (dashed line) or absence (solid line) of large vessels.



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occurred with a 50% probability when vessels approached within 478 m of the focal pod. The increased levels of aerial behavior and changes in pod composition could both be interpreted as indications of social disruption.

Although the simple residency of the focal pod in Bartlett Cove indicates a considerable tolerance for vessel traffic, the possibility cannot be excluded that these animals were simply "making the best of a bad situation". Hydroacoustic surveys of Bartlett Cove during the summer of 1982 indicated the residency of a large school of capelin (Wing and Krieger 1983). For the whales, the availability of this rich food source may have outweighed the disadvantages posed by the high level of vessel traffic in the cove. It is also probable that Park Service regulations controlling the speed and approach of vessels helped to mitigate the disturbance of whales in the cove.

CASE HISTORIES

Not all elements of the behavioral response of whales to vessel traffic were amenable to statistical analysis. The magnitude of some qualitative responses and the specific stimulus initiating a response were not described fully by simple measures of orientation or frequencies of behavioral events. Rather than fall victim to the "tyranny of the mean" we chose to present the details of a few vessel-whale interactions as complete case histories. These case histories, however, were not chosen at random to represent average or typical responses by whales to vessel traffic. Instead, they were selected to document infrequent but dramatic responses. Generalizations about "average" response of whales to vessel traffic are best drawn from statistical tests discussed earlier.

Response to Acoustic Stimuli

Underwater acoustic monitoring was conducted in parallel with some opportunistic observations of vessel-whale interactions during the 1982 season (Miles and Malme 1983). The following case history presents the most complete record available of humpback whale movement and behavior in relationship to vessel activity and underwater noise.

Case 1

On the morning of July 30 at 06:43, three of the Bartlett Cove residents (a cow-calf pair and accompanying adult) were swimming along the east shore at the mouth of the cove. A 177 m cruise ship was entering the mouth of Glacier Bay about 7 to 9 km away from the pod (Figure 16a). The focal pod moved northwards into the cove for about 16 min without any displays of aerial behavior. At 07:00 the cruise ship began decreasing her speed from 13 km/hr to 8.3 km/hr while changing the pitch of her propeller. By this time the ship had approached to within 2,500 m of the focal pod which continued moving north into the cove. As the cruise ship slowly turned at the mouth of the cove, the starboard engine and bow-thruster were engaged. Acoustic measurements indicated a slowly rising baseline of about 118 dB (estimated source level at the position of the whales) with transient peaks of about 6 dB at 07:00 and a steep rise of 12 dB beginning at 07:01 (Figure 16b). The 12 dB rise was followed within seconds by a series of three breaches and a headslap by the whales.

The closest point of approach between the cruise ship and the pod was 2,044 m and occurred at 07:04. Between 07:05 and 07:08, the cruise ship increased speed, added a port engine, and changed propeller pitch. The acoustic level showed an abrupt drop and return, from 134 dB to 118 dB and back to 134 dB, over a 50-second period. The rise back to 134 dB at 07:07 was followed immediately by a series of 11 breaches.

As the cruise ship approached the mouth of the cove, the focal pod moved rapidly into the cove and away from the ship. At 17:13, the accompanying adult disaffiliated from the cow-calf pair and continued deeper into the cove (indicated by the vector labeled "single adult" in Figure 16a). Aerial behavior by the cow and calf continued until 07:16, at which time the cruise ship was approximately 4,177 m away and moving up bay. No aerial behaviors were observed from 07:17 to 07:33 as the cow-calf pair moved slowly back toward their original location at the mouth of the cove. At 07:34, a 20-m-long tour boat left the Bartlett Cove dock and headed out of the cove at a speed of 18 km/hr. At 07:39, when the tour boat was about 1,000 m away from the cow-calf pair, the calf began a series of eight breaches that lasted until 07:43. The closest point of approach of the tour boat was 509 m and occurred at 07:42. The observational session was terminated at 07:45 because of fog.

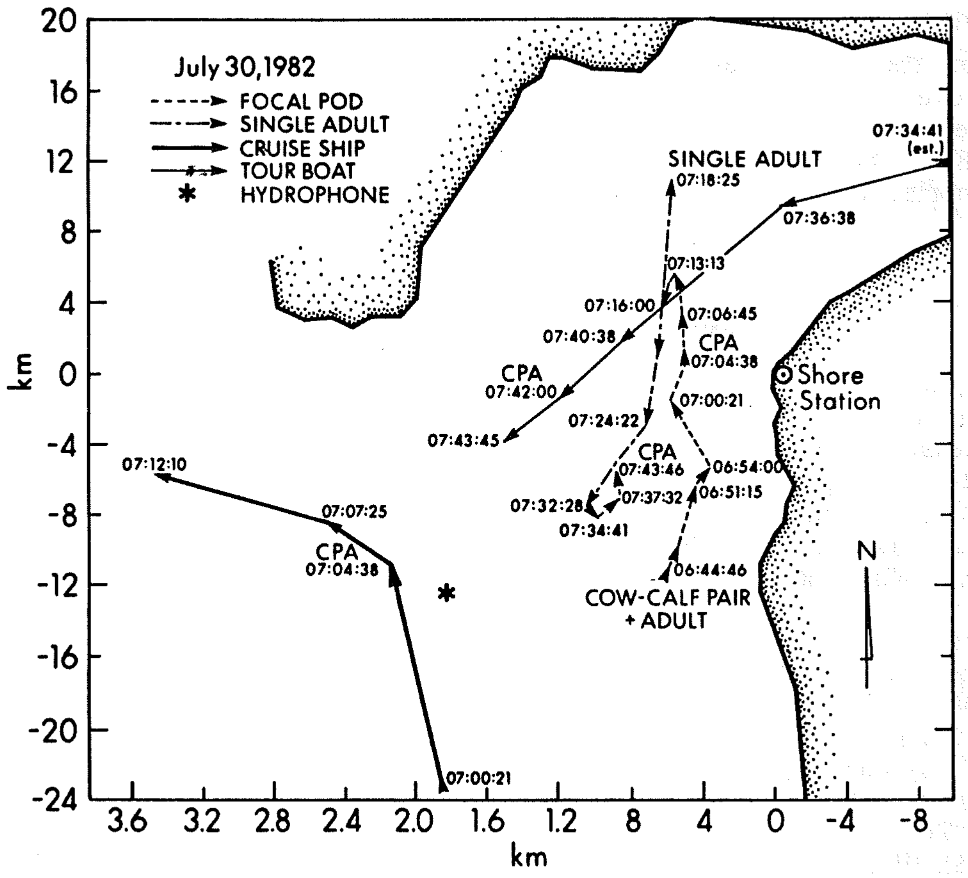

Figure 16a. The positions and movement of the focal pod, a 177-m cruise ship, and a 20-m tour boat in Bartlett Cove on July 30, 1982. The time of day is shown in hours:minutes:seconds.

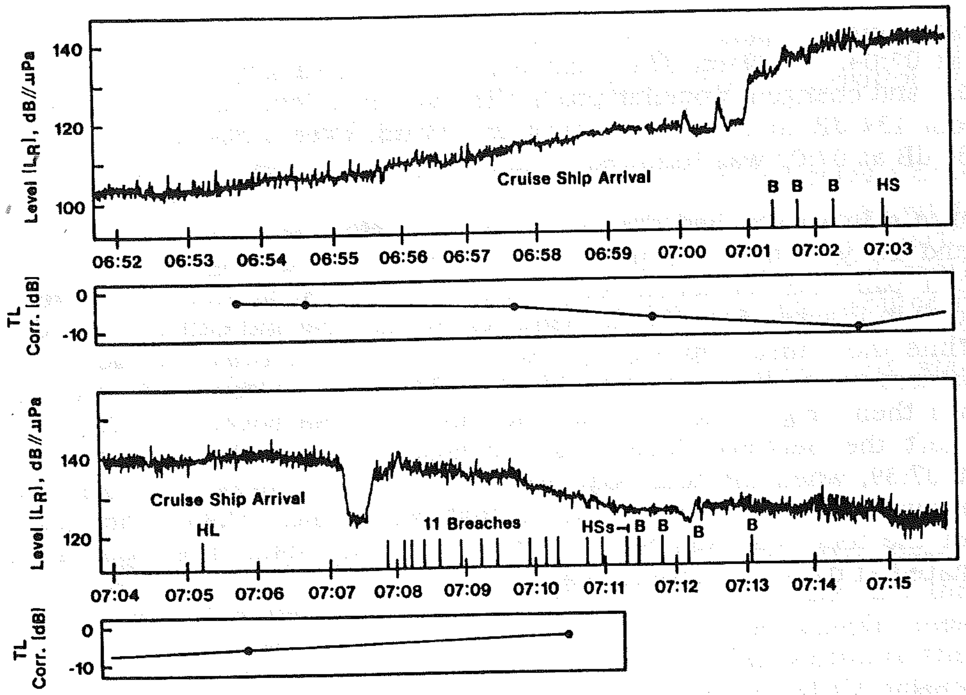

Figure 16b. The underwater sound level recorded during the passby of a 177–m cruise in Bartlett Cove on July 30, 1982. Transmission loss (TL) correction allows the estimation of the received levels of sound at the position of the focal pod (adapted from Miles and Malme 1982). The occurrence of aerial behavior by the focal pod is noted as tic marks along the horizontal axis of time (B = breach; HL = head–lunge; HS = head–slap).

Displacement from Preferred Feeding Site

The infrequency of surface–feeding behaviors during the study periods (see previous sections on Aerial, Social, and Feeding Behavior) prevented this variable from being a reliable measure of vessel disturbance. During the following case histories, however, it was possible to infer that animals were sub–surface feeding based on their diving patterns and non–directional movement (milling). This inference was supported by hydroacoustic assessment of humpback whale prey conducted in parallel with behavioral observations (Wing and Krieger 1982; Krieger and Wing 1984; Krieger and Wing 1986).

These case histories present details of observations documenting the interruption of feeding and the displacement of whales from preferred feeding sites. The first case involved whales feeding near the Frederick Sound shore station. Whales in this area generally did not establish specific preferred ranges (Baker et al. 1982; Baker et al. 1983). In this case, a preferred feeding site refers only to a short–term preference defined by the whales' movement during that observation. The second case involved one of the Point Adolphus "residents", animal #166 (Baker et al. 1982; Perry et al. 1985; Baker 1986). For a total of six summer seasons (1981 to 1986), animal #166 and five or six other whales established a preferred seasonal range in a small area within a few kilometers to either side of Point Adolphus in Icy Strait near the mouth of Glacier Bay (Baker 1985a; Perry et al. 1985). During the summer of 1982, animal #166 was radio–tagged and tracked intermittently, from July 24 until August 3, after which the

radio signal was lost (Baker et al. 1983). Photo–documentation showed that #166 was present before and after the tagging period from at least July 20 to August 15, 1982. With the single exception described in the following case history, animal #166 remained in the company of four or five other whales within a few kilometers of Point Adolphus throughout the study period. Hydroacoustic assessment showed that this area is rich in schooling fish which seemed to be the primary prey of the resident whales (Krieger and Wing 1984; Krieger and Wing 1986). In this case, the term "preferred" refers to a long–term preference for a specific feeding locale.

Case 2

On the evening of August 22, 1981, a pair of adult whales were slowly milling and presumably feeding about 1 km east of the Frederick Sound shore–station (Figure 17, time shown in hours and minutes from the start of the observation session at 17:10). As part of an experimental condition, the pod was observed during a 20–min pre–test trial during which there were no vessels within a 1–km radius of the whales (see previous description of Experimental Design). At the beginning of the test condition, the schooner (see previous description of experimental vessels) was directed to approach and pass by the pod at a target distance of 100 m while traveling at a speed of about 12 km/hr. Near the middle of the test trial (00:32) the schooner reached its CPA, passing within 24 m of the submerged whales' estimated position. The schooner continued past the whales at a constant speed and slowed to a stop about 2.6 km north of the pod. The pair of whales was not obviously disturbed by the passby and continued milling in the area throughout the post–test trial.

Following the end of the post–test trial (1:12), the schooner was directed to pass by the whales a second time at a similar distance and speed. The schooner reached her CPA at 1:28, passing within 233 m of the submerged whales' position, and continued heading south at 12 km/hr. As the schooner reached its second passby, the whales turned dead away from the vessel's path and moved rapidly (4–5 km/hr) west. One of the whales then flipper–slapped five times in quick succession and the pair disaffiliated while both continued moving in a west–southwesterly direction away from the area where they had been feeding previously.

Case 3

On July 31, at about 13:40, animal #166 and its companions were feeding within 500 m of the Point Adolphus coastline when a high–speed (approximately 26–32 km/hr), planing–hull vessel, approximately 8 m in length, passed within 100 m of the pod. After passing the pod, the vessel slowed, turned around, accelerated, and circled the pod before returning to its original course and leaving the area. Following the passby of the vessel, the pod dispersed and animal #166 began moving slowly across Icy Strait, reaching the southeastern shore of Pleasant Island at 17:18 (Figure 18). We followed #166 at a distance of about 1 km, using the signal from the radio tag to keep track of its position and surfacing intervals. For the next hour, #166 moved slowly along the southern shore of Pleasant Island. When the observation ended at 19:00:00, #166 was near a reef, about 2 km offshore of Pleasant Island. We were unable to return to Point Adolphus the following day; but by August 2, #166 had returned and rejoined its companions.

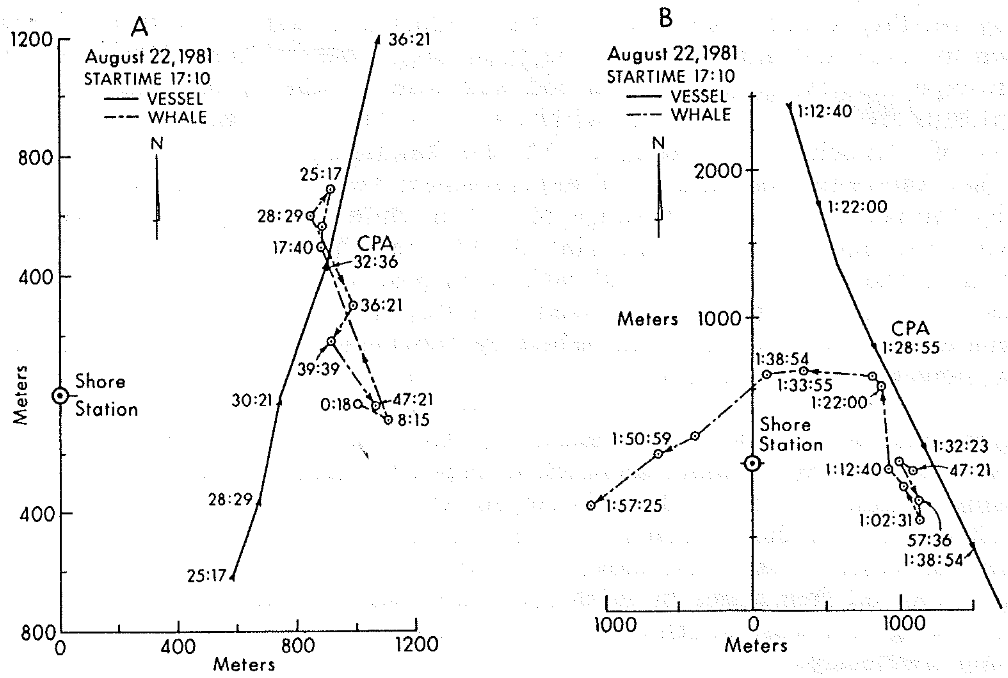

Figure 17. The position and movement of a pair of whales during the repeated passby of the experimental vessel (the schooner) on August 22, 1981. Time is shown in hours:minutes:seconds from the beginning of the observation.

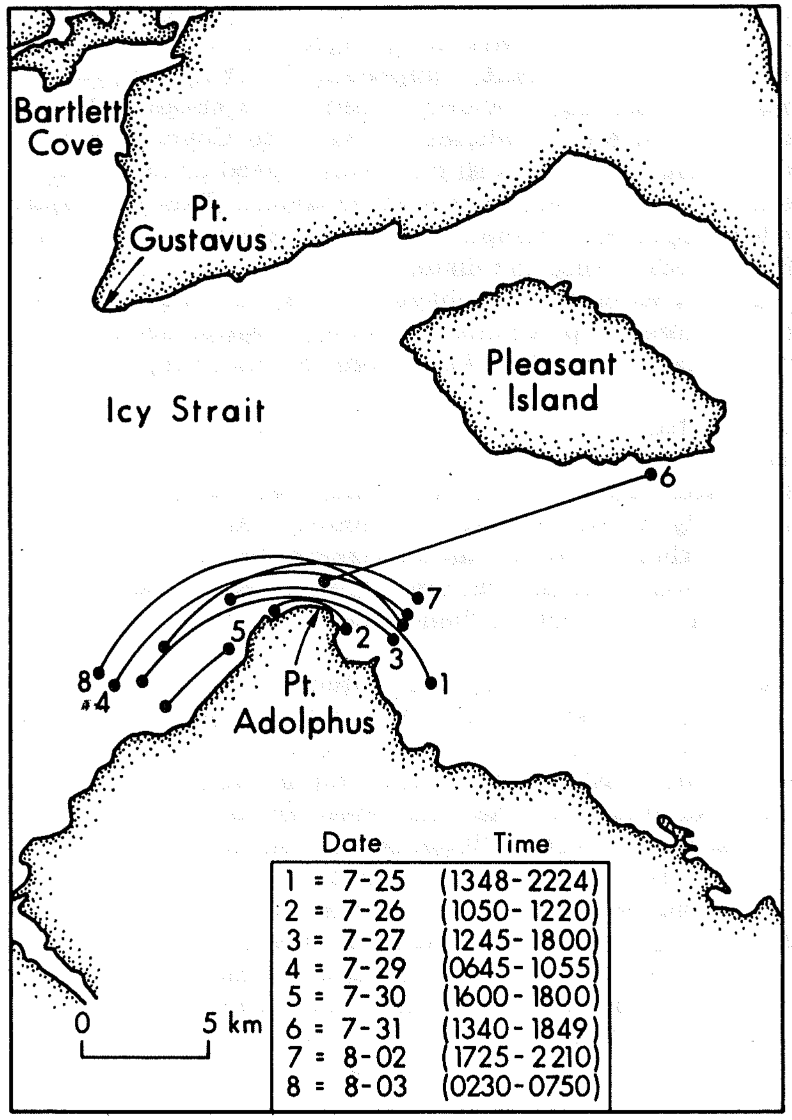

Figure 18. The range of daily movement of the radio-tagged animal, #166, from July 25 to August 3, 1982.

Discussion

Many of the behavioral trends indicated by the statistical analyses discussed earlier were evident in the response of the Bartlett Cove pod to the cruise ship (Case 1). The three whales appeared to avoid the path of the approaching ship by retreating into the cove. As they retreated, the whales engaged in a number of aerial behaviors. Following the ship's CPA, the adult companion disaffiliated from the cow-calf pair. Underwater acoustic monitoring provided considerable insight into the specific stimulus initiating the aerial behavior of whales in Bartlett Cove. Sudden changes in sound levels, as a result of changes in the ship's engine speed or propeller pitch, were closely correlated in time with the onset of aerial behavior. The propinquity of these events suggests a "startle" response accompanying the whales' movement away from the path of the vessel. It is worth noting the distance at which the acoustic stimulus exerted an influence. The first series of aerial behaviors began when the ship was over 2 km away and the noise of the cruise ship dominated the underwater acoustic environment even at relatively great distances (more than 4 km from the receiver).

The displacement of whales from a preferred feeding site or the interruption of feeding, including nursing of calves, during this short feeding season may be the most serious result of human disturbance. Since humpback whales fast on the winter breeding grounds, they have only a few months each summer and fall in which to gather enough food for a year. Although these animals must be able to tolerate occasional or intermittent interruption of their feeding, chronic disturbance will undoubtedly have a cumulative and deleterious effect on their fitness.

A factor common to all three of the case histories was the repeated passby of vessels during a relatively brief period of time. As indicated by the previous analysis of vessel density in Bartlett Cove, vessel traffic can have a cumulative or additive effect on the behavior of whales. The passby of the cruise ship in Bartlett Cove seemed to potentiate the whales to the later passby of the tour boat. In the first case of displacement, the initial passby of the schooner had little effect on the whales but the second passby resulted in an almost immediate displacement of the whales. In the second case of displacement, the passing vessel turned and circled the whales, resulting in three rapid passbys. Studies of gray whales, *Eschrichtius robustus,* and bowhead whales indicate that these animals may tolerate or habituate to fixed or slow-moving sources of continuous acoustic stimuli, such as drilling platforms or playback of industrial noise (Malme et al. 1983; Richardson et al. 1985). Erratic or rapidly moving stimuli, however, seem to have the opposite effect on humpback whales, resulting in a potentiation to respond.

SUMMARY AND CONCLUSIONS

Extent of Behavioral Disturbance

Ultimately, it would be valuable to estimate the direct energetic "cost" of human disturbance to humpback whales. This cost could then be compared with the whales' overall energy budget to determine the potential loss in long-term reproductive success as a result of disturbance. In other words, how much energy is expended or lost, as a result of disturbance, that might otherwise be devoted to reproduction? Although an exact measure of this loss is not available, each of the behavioral responses documented in our study have a known or suspected energetic cost. Locomotion, for example, is clearly an important component of the overall energy budget of baleen whales (Brodie 1975; Sumich 1983). A bout of repeated aerial behaviors must also require a considerable expenditure of energy (Whitehead 1985). Finally, changes in respiratory behavior, like changes in heart rate (MacArthur et al. 1979), are likely to be correlated with the overall energy expenditure of an animal.

If disturbance is defined as the measurable changes in whale behavior that are attributable to vessel activity, the relative extent of disturbance should be indicated by the r-square term of the parametric analyses of respiration and pod speed. As described previously, the r-square term indicates the proportion of change in a behavioral variable (i.e. blow intervals) that is explained by a given vessel variable (i.e. vessel distance). For the non-parametric analyses of aerial and social behavior, the analogous indices of disturbance are the square of the contingency coefficient or square of the Spearman correlation coefficient. For pod orientation, the percentage of average speed devoted to movement directly away from the path of vessels was used to indicate the extent of avoidance (for more details of this measure, see the Discussion section under Opportunistic Interactions). These indices of disturbance are summarized in Table 11.

In general, respiratory behaviors, particularly blow intervals and dive times, were the most sensitive indicators of disturbance from vessel activity. As much as 27% of the variance in these behaviors was accounted for by the presence and activity of vessels. Pod orientation was also a sensitive measure of disturbance and indicated that, on average, whales in the Frederick Sound area devoted 14.5% of their movement to avoiding vessels within a proximity of 4,000 m. Pod speed and linearity were less sensitive, though sometimes statistically significant, indicators of a response to vessel activity during the experimental interactions.

Aerial, social, and surface-feeding behaviors showed few predictable changes in response to vessel activity. In general, the infrequency and variability of these behaviors were an obstacle to statistical analysis. Only in Bartlett Cove, a confined area with a high density of vessels, was there a significant, though weak, correlation between vessel activity and aerial behavior. The selected case histories, however, demonstrated that, at times, whales interrupted their feeding behavior and engaged in dramatic episodes of aerial behavior in response to vessel activity.

Response to Acoustic Stimuli

The behavioral responses of humpback whales to vessel traffic were not uniform with regard to acoustic stimuli. Blow intervals, for example, were correlated only with vessel distance while dive times were correlated only with vessel speed. Since the received levels of sound at the position of the whales should increase as a result of both increasing speed and decreasing vessel distance, the response of the whales cannot be accounted for by a simple index of noise intensity. In addition, the potential for a variable startle response of whales to noise was demonstrated by the close correlation, in time, between episodes of aerial behavior and sudden increases or decreases in vessel noise (see Case History 1).

It seems likely that whales are basing their responses to vessels on considerable interpretation of acoustic stimuli. A whale's interpretation and subsequent response may be influenced by the perceived size of the vessel, its speed, its direction, the

Table 11. The relative extent[1] of disturbance to humpback whales behavior as a result of vessel traffic in southeastern Alaska.

Experimental Interactions in Frederick Sound: 400 m Realm of Influence

Whale Behavior	Vessel Condition	Vessel Class	Sum
Blow Intervals	27.3%	0.2%	27.5%
Dive Times	6.3%	16.7%	23.0%
Blow Rates	2.5%	5.9%	8.4%
Maximum Intervals	14.4%	11.5%	25.0%
Pod Speed	4.1%	1.6%	6.0%
Pod Linearity	3.4%	1.7%	5.1%
Aerial Behavior	---	---	ns
Social Behavior	---	---	ns
Surface Feeding	---	---	ns

Opportunistic Passbys in Frederick Sound: 4000 m Realm of Influence

Whale Behavior	Vessel Distance	Vessel Speed	Sum
		Frederick Sound	
Blow Intervals	29.4%	5.8%	35.2%
Dive Times	3.1%	19.4%	22.5%
Pod Speed	6.6%	10.7%	17.3%
Pod Orientation	---	---	14.5%
Aerial Behavior	---	---	ns
Social Behavior	---	---	ns
Surface Feeding	---	---	ns

---

[1] The relative extent of behavior disturbance is based on the r–square of the multiple regression model or related measures from each statistical analysis (see text for further details). Relative extent of disturbance is reported only for behavioral measures found to be statistically significant at the $p < 0.05$ level of probability. Non–significant measures are noted by the abbreviation "ns."

(continued)

Table 11 (continued)

Opportunistic Passbys in Bartlett Cove, Glacier Bay: 4000 m Realm of Influence

Whale Behavior	Vessel Distance	Large Ships	Vessel Density	Sum
Blow Intervals	2.8%	0.2%	0.7%	1.1%
Dive Times	0.4%	7.1%	6.7%	14.2%
Pod Speed	0.4%	0.1%	0.9%	1.4%
Pod Orientation	---	---	---	ns
Aerial Behavior	3.5	0.0%	0.9%	4.4%
Social Behavior	2.0%	2.2%	0.1%	4.3%
Surface Feeding	---	---	---	ns

predictability of its course, and the individual whale's past experience, as well as by the simple intensity of a vessel's noise signature.

Cumulative Effects of Vessel Traffic

The potential for a cumulative effect of vessel traffic on the behavior of humpback whales was suggested by the response of whales to the proximity, or repeated passbys, of more than one vessel. Although the resident whales of Bartlett Cove showed a considerable tolerance for vessel traffic, their behavioral responses did not suggest true habituation. Instead, several characteristics of the whales' behavior were correlated with an index of vessel density in the cove, suggesting a cumulative, though not simply additive, effect of vessel numbers.

A tendency for potentiation to vessel traffic was also suggested by the three case histories. In each case, a dramatic response by the whales was associated with the repeated passby of one or more vessels within a relatively short period of time (e.g. less than one hour).

The Question of "Abandonment"

During the summer of 1978, most of the whales that entered the bay abruptly departed soon after their entry. Two hypotheses were advanced to explain this sudden departure. The first asserted that the whales abandoned the bay because of an intolerable level of vessel traffic. The second hypothesis proposed that the whales' departure was the result of natural changes in the availability of their prey. In 1981 the National Park Service, with the consultation of the National Marine Fisheries Service, initiated a multi-disciplinary study of humpback whales to determine the probable causes of the whales' departure. Although a complete review and synthesis of these studies is beyond the level of this report, the resulting evidence supporting or refuting each of the two hypotheses can be summarized briefly.

Studies of humpback whales on their summering grounds, as summarized here, and on their wintering grounds, as summarized by Bauer (1986), clearly document a pattern of short-term behavioral disturbance in response to vessel traffic. Studies of other baleen whales, including the bowhead (Richardson et al. 1985) and gray whales (Malme et al. 1983), found similar patterns of disturbance in response to a variety of actual and simulated industrial activity. Some cases of local displacement of whales as a result of disturbance are reported for each of these three species. Although these studies have now established a cause and effect relationship between human activity and behavioral disturbance in baleen whales, this relationship is not conclusive evidence that large-scale displacement from a habitat could occur due to disturbance alone.

Studies of humpback whale prey availability and feeding behavior, on the other hand, demonstrate the influence of natural variations in prey on the local distribution of whales. During the study years (primarily 1981 to 1984), there was considerable within and between-year variability in the distribution and abundance of humpback whale prey in Glacier Bay and other areas of southeastern Alaska (Wing and Krieger 1983; Krieger and Wing 1984; 1986). Throughout the study region, prey densities and abundance were typically higher in areas in which whales were actively feeding than in areas in which whales were not found. In a small study area outside of Glacier Bay, the densities of euphausiids were paralleled by changes in the number of whales (Krieger and Wing 1986). In 1986, the influx of whales into Glacier Bay and their relatively sudden departure a few weeks later appeared to be associated with the availability of schooling fish in the lower bay (Baker 1986).

Marked differences in the reported feeding behavior of humpback whales in Glacier Bay before and after 1978 provide perhaps the most persuasive circumstantial evidence of a recent change in the primary prey species. In the years prior to 1978, bubble-netting and surface lunge-feeding on euphausiids were reported to be common modes of feeding by humpback whales (Jurasz and Jurasz 1979; Jurasz and Palmer 1981a). Although some feeding on schooling fish was reported, near-surface swarms of euphausiids were thought to be the primary prey in Glacier Bay (Earle 1979; Jurasz and Jurasz 1979). Since 1981, however, surface lunge-feeding has been infrequent and bubble-netting has not been observed at all in the bay (Baker et al. 1982; Baker et al. 1983; Wing and Krieger 1983; Krieger and Wing 1984; 1986). The primary prey of humpback whales has been small schooling fish, including capelin, sandlance, and juvenile pollack (Wing and Krieger 1982; Krieger and Wing 1984; 1986). Although euphausiids were found at some depths in the water column, they were not commonly found near the surface (Wing and Krieger 1982; Krieger and Wing 1984; 1986). Anecdotal evidence against a sudden change in the prey availability during 1978, however, comes from Jurasz and Palmer's (1981a) report that near-surface swarms of euphausiids were common throughout that summer.

In summary, the absence of quantitative information on prey availability prior to 1981 and the possibility that changes in the primary prey species in the bay occurred during the years 1979 or 1980 prohibits drawing a direct correlation between the whales' departure and a sudden decrease in prey abundance during 1978. Similarly, the establishment of a cause and effect relationship between human activity and behavioral disturbance cannot, in itself, prove that humpback whales were displaced from Glacier Bay. Future changes in whale abundance and prey availability could provide further insight into the abrupt departure of whales in 1978. For example, a sudden increase in the abundance of near-surface euphausiids followed by an increase in whale abundance and the frequency of surface feeding behavior would support the hypothesis that the 1978 change was due primarily to natural fluctuations in prey. Conversely, the sudden departure of whales from the bay following an increase in vessel traffic would indicate a tolerance threshold for vessel activity beyond which abandonment can occur (Anonymous 1984), if it could be established that no change in prey availability had taken place concurrently.

Implications for Management

Insuring that humpback whales are never disturbed by human activity would require unrealistic restrictions on vessel operations. In some cases, the distances at which whales responded to vessels was greater than the distance at which the whales would be obviously visible to the operator of that vessel. A management plan, in order to be effective, should seek to regulate vessel operations within the range of proximity that has the greatest potential for disturbance to whales.

The operational guidelines currently in effect for vessels in Glacier Bay National Park seem to provide a prudent compromise between conservation and enlightened access for human visitors. Although behavioral responses of whales to vessels can occur over greater distances, the summary of results in Table 11 suggests that vessels within 0.25 nm nautical mile (463 m, the current minimum limit for vessel proximity to whales in Glacier Bay) account for the majority of potential disturbance. Within the 400-m realm of influence in the experimental observations, for example, vessel operations account for 27.5% of the variance in the blow intervals of whales. Expanding the realm of vessel influence to 4,000 m in the opportunistic observations resulted in an increase of only 7.5% (to a total of 35.2%) in the r-square of the analysis. In other words, of the total variance in blow intervals attributable to vessels within a 4,000-m realm of influence, 78% was accounted for by those within the first 400 m, assuming relatively comparable conditions in the two observational situations. For dive times, there was no improvement in the explanation of disturbance when the realm of influence was increased from 400 m in the experimental observations to 4,000 m in the opportunistic observations. The potential for disturbance is further reduced by Park Service regulations prohibiting pursuit of a whale at distances less than 0.50 nautical mile (926 m) and limiting maximum vessel speed to 16 km/hr (10 knots) in the vicinity of whales.

The Park Service has also taken the important step of placing an upper limit on the number of vessels operating in Glacier Bay. This limit should help mitigate the potential for cumulative impact of vessel traffic, reduce the amount of time that whales are exposed to vessels, and decrease the probability of collisions between whales and vessels. However, the difficulties in determining experimentally the levels of disturbance that could result in the abandonment of a habitat by whales prevent any exact predictions about the number of vessels that would exceed such a tolerance threshold, if one exists.

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ACKNOWLEDGEMENTS

This final report was completed with the support of Cooperative Agreement No. CA-9700-3-8028 between the National Park Service, Alaska Regional Office and the University of Hawaii at Manoa. Additional financial or logistical support was provided by the following agencies: the National Park Service, Glacier Bay National Park and the Alaska Regional Office; the Auke Bay Laboratory, National Marine Fisheries Service (NMFS); the National Marine Mammal Laboratory, NMFS; and the University of Hawaii. This report contains original material of the authors. The opinions of the authors do not necessarily reflect the views of the National Park Service.

We are grateful to the following people for valuable technical assistance and logistical support during many of our research projects: Al Lovaas of the National Park Service, Alaska Regional Office; Don Chase and Gary Vequist of the Glacier Bay National Park and Preserve; Ken Krieger, George Snyder and Bruce Wing of the Auke Bay Laboratory; and Linda Jones, Sally Mizroch, Mary Nerini, Michael Tillman and the late James Johnson of the National Marine Mammal Laboratory. The collection of field observations would not have been possible without the following research assistants: Michael Aseltine, Brooks Bays, Pierre Dawson, Paul Forestell, Adam Frankel, Michael Herder, Thomas Kieckhefer, Jay Jaeckel, Frank Minogue, William Stifel, and Barbara Taylor. Finally, we wish to acknowledge the contributions of our associates Gordon B. Bauer and Anjanette Perry who assisted in all phases of this work.

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March 3, 1849

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NPS D-428 June 1989