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Thomas R. Kieckhefer
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**Feeding ecology of humpback whales in continental shelf waters
near Cordell Bank, California**

Kieckhefer, Thomas Ridgway, M.S.

San Jose State University, 1992

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Ann Arbor, MI 48106

**FEEDING ECOLOGY OF HUMPBACK WHALES
IN CONTINENTAL SHELF WATERS NEAR
CORDELL BANK, CALIFORNIA**

A Thesis

Presented to

The Faculty of the Department of Moss Landing Marine Laboratories

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

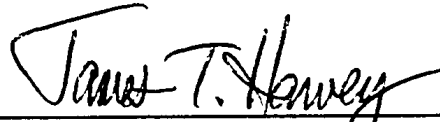
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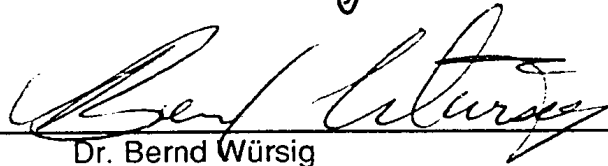
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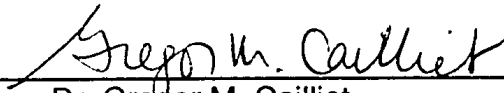
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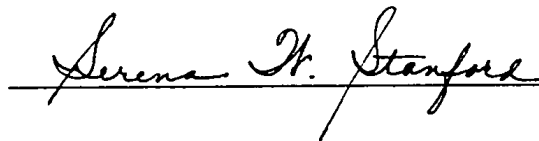


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ABSTRACT

Daytime feeding behavior of humpback whales (*Megaptera novaeangliae*) in Gulf of the Farallones, California, and adjacent waters was observed during autumn of 1988 to 1990. Bodega Canyon, Cordell Bank, and the Farallon Islands were the primary sites of feeding activity. Fecal samples of whales and zooplankton tows contained euphausiids exclusively, dominated by *Thysanoessa spinifera* (79%), with lesser amounts of *Euphausia pacifica* (14%), *Nyctiphanes simplex* (4%), and *Nematoscelis difficilis* (3%). In 1988 and 1990, whales also were infrequently observed feeding on small schooling fish, presumably Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), and juvenile rockfish (*Sebastes spp.*).

Feeding was the most common behavior observed (52%), and less frequently traveling (23%), milling (21%), and resting (4%). Whales used different methods to consume euphausiid prey at the surface (0-10 m), in shallow water (11-60 m), and deep water (61-140 m). Humpback whales fed at the surface 56% of time in 1988 and 32% of time in 1990, using primarily lateral lunges to capture swarms of euphausiids. In 1989, no surface feeding was observed; however, deep, long-duration dives were followed by extended surface intervals with many respirations. These 1989 observations coincided with increased prey depth as indicated by depth sounder records of diving whales and prey scattering layers.

In 1989, increased prey depth and associated feeding behaviors were strongly associated with unusually high surface temperatures, calm seas, and changes in water circulation. Environmental conditions in 1989 triggered the most intense and wide-spread occurrence of red tide in this region since 1980. Red tide samples collected throughout this period contained *Alexandrium (=Gonyaulax) catenella* and *Noctiluca scintillans*. Surface feeding was observed only in 1988 and 1990, when surface prey were available and red tides were very limited in extent, duration, and intensity. Annual variations in humpback whale feeding behavior were related to prey availability which is affected by corresponding environmental conditions.

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INTRODUCTION

Most humpback whales (*Megaptera novaeangliae*) in the northeast Pacific feed in Alaskan waters in summer and breed in waters surrounding Hawaii and Mexico during winter. Each autumn, 100 to 200 individuals, primarily adults from the Mexican group, migrate to the Gulf of the Farallones, California, and adjacent waters to feed (Dohl et al. 1983; Webber and Cooper 1983; Calambokidis et al. 1989a, 1990, 1991a). This central California assemblage of humpback whales was severely depleted during commercial whaling from 1956 to 1965 (Rice 1963, 1971, 1978). Gulf of the Farallones surveys from 1980 to 1982 indicated that numbers of humpback whales were increasing (Dohl 1983; Dohl et al. 1983). However, recent surveys conducted by Cascadia Research Collective from 1986 to 1988 found that the numbers of humpback whales were less than reported in 1982, and no current evidence suggests their recovery (Calambokidis et al. 1989a, 1990, 1991a,b; Steiger et al. 1989). Annual variations in their numbers and distribution were great, which possibly related to the distribution and availability of prey (Calambokidis et al. 1990, 1991b).

Aside from observations of humpback whales feeding in and around the Gulf of the Farallones, little is known about their behavior in these waters. Several studies have quantitatively linked feeding behavior of whales to availability and type of prey (Würsig et al. 1984, 1986; Dolphin 1987a,b,c,d; Hamner et al. 1988; Guerrero 1989). Würsig et al. (1984) found that blow rates of bowhead whales (*Balaena mysticetus*) feeding in the Arctic decreased when they fed in the water column versus when they were skim feeding at the surface.

Likewise, Hamner et al. (1988) reported southern right whales (*B. australis*) slowly moving at the surface and hyperventilating before long dives to feed on sub-surface Antarctic krill (*Euphausia superba*). Guerrero (1989) found that surface behaviors of gray whales (*Eschrichtius robustus*) were different when they were feeding on mysid swarms compared with feeding on infaunal amphipods. Dolphin (1987a,b,c,d) found that respiration rates of humpback whales in southeast Alaska were positively correlated with depth of feeding.

Observations of humpback whale surface feeding have confirmed that they have a diverse repertoire of behaviors, such as lunge feeding and "bubble-netting" (Ingebrigsten 1929; Jurasz and Jurasz 1979; Watkins and Schevill 1979; Hain et al. 1982; Baker 1985; D'Vincent et al. 1985). Various prey species or densities may affect these different feeding methods (Jurasz and Jurasz 1979; Watkins and Schevill 1979; Hain et al. 1982; Baker 1985). In lunge feeding, whales display several different behaviors, with variations occurring in their body postures and angles of trajectory from the water's surface. Jurasz and Jurasz (1979) reported lunge angles of 30° and 90°, which described a lateral and vertical lunge. In addition, diagonal (45°) lunges, with bodies upright and oblique to the water's surface, were used when whales fed on fast, schooling prey (Kieckhefer pers. obs. S.E. Alaska 1982). During bubble-net feeding, a whale forms a circular or cylindrical-shaped screen of bubbles by a series of underwater exhalations, apparently to herd and concentrate prey at the surface (Jurasz and Jurasz 1979). Following the completion of a bubble-net, a vertical lunge is often executed in the center.

In southeast Alaska, apparent cooperative feeding of humpback whales (e.g. 8-11 whales synchronously lunging at the surface capturing herring) have

been described, and vocalizations may have assisted in corralling fish prey or coordinating whale efforts (Baker 1985; D'Vincent et al. 1985). In the same area, two to four whales eschelon feeding or surface lunge-feeding in staggered formation has been observed (Jurasz and Jurasz 1979; Baker 1985). Eschelon formations have also been reported in skim-feeding bowhead whales (*B. mysticetus*; Würsig et al. 1984; Würsig 1988).

Prey of humpback whales in the North Pacific were identified in samples obtained during whale feeding (Jurasz and Jurasz 1979; Wing and Krieger 1983; Krieger and Wing 1984; D'Vincent et al. 1985; Baker 1984; Dolphin 1987a,b; Krieger 1988) and in stomach contents of stranded animals and carcasses examined at whaling stations (Mathews 1937; Rice 1963, 1977; Nemoto 1970; Calambokidis et al. 1989a). Humpback whales, in southeast Alaska, fed mainly on euphausiids, especially *Thysanoessa rashii*, and less on *Euphausia pacifica*, *Thysanoessa longipes*, and *Thysanoessa spinifera* (Wing and Krieger 1983; Krieger and Wing 1984; Dolphin 1987a,b). Their diet also includes schooling fishes, such as Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and walleye pollock (*Theragra chalcogramma*; Wing and Krieger 1983; Krieger and Wing 1984). During 1956-65, commercially killed whales from the Cordell Bank/Gulf of the Farallones area contained anchovies and euphausiids. Stomach contents contained roughly 60% northern anchovy (*Engraulis mordax*) and 40% *Euphausia pacifica*, with only trace amounts (< 0.5%) of Pacific herring, *Thysanoessa spinifera*, shrimp, and rockfish (*Sebastes spp.*; Rice 1977; Calambokidis et al. 1989a). Distribution and abundance of prey changed annually.

Seasonally, there is an abundant supply of juvenile schooling rockfish,

especially shortbelly (*Sebastes jordani*), chilipepper (*S. goodei*), bocaccio (*S. paucispinis*), and yellowtail rockfish (*S. flavidus*) in the Cordell Bank/Gulf of the Farallones area, which are potential prey items for humpback whales (Larson 1987; D. Pearson pers. comm. 1988; Hobson and Howard 1989). In addition, Smith and Adams (1988) found abundant surface swarms of *T. spinifera* off the Farallon Islands.

Combined with concurrent studies of whale distribution, movements, and population size, this study proposes to accurately describe the importance of this region as a food resource to this remnant group of humpback whales. To investigate the feeding ecology of humpback whales near Cordell Bank/ Gulf of the Farallones, five objectives were pursued: (1) assess percentage of time spent feeding compared with other behavioral states of rest, slow travel, fast travel, and mill/search; (2) quantify respirations and surface behaviors associated with feeding (surface and sub-surface) and non-feeding; (3) characterize feeding behavior for different types of prey (e.g. euphausiids vs. fish, shallow vs. deep prey); (4) identify prey species and determine their depth in the water column; and (5) relate the distribution of prey to topographic features and annual variations of environmental factors.

METHODS

Surveys

From 21 August to 5 November 1988, 26 August to 3 December 1989, and 29 August to 12 December 1990, data were collected in and around Cordell Bank and the Gulf of the Farallones (Fig. 1). In 1988, a 4.9-m Mark III Zodiac with a 25 HP outboard motor was used, and in 1989 and 1990 a 6.7 m Boston Whaler with a main 175 HP outboard engine and a 30 HP auxiliary engine was used. Both vessels were docked in Bodega Bay, and equipped with a VHF radio, LORAN, and Lowrance X-16 depth sounder (192 kHz, 20° cone angle). Mean scattering layer depths were visually estimated from the thickness of the echo traces and measured to the nearest meter in the water column. A portable time/event recorder (Tandy 102-32K) was interfaced with the vessel's LORAN and an external portable hard drive. During surveys, the vessels' speed, direction, and location were automatically recorded every 10 min into the time/event recorder and the external portable disk drive provided unlimited storage space. Other information consistently recorded during surveys included: number and species of birds present within 300 m; scattering layer depth (± 1.0 m); and bottom depth (± 1.0 m); and environmental data (discussed later).

Aerial surveys of the study area were conducted opportunistically to document whale distribution, abundance, and movement patterns (Calambokidis et al. 1989a, 1991a). In addition, Oceanic Society Expeditions reported whale sightings near the Farallon Islands, and local commercial fishermen and party-boat skippers reported sightings around Cordell Bank and along the coast.

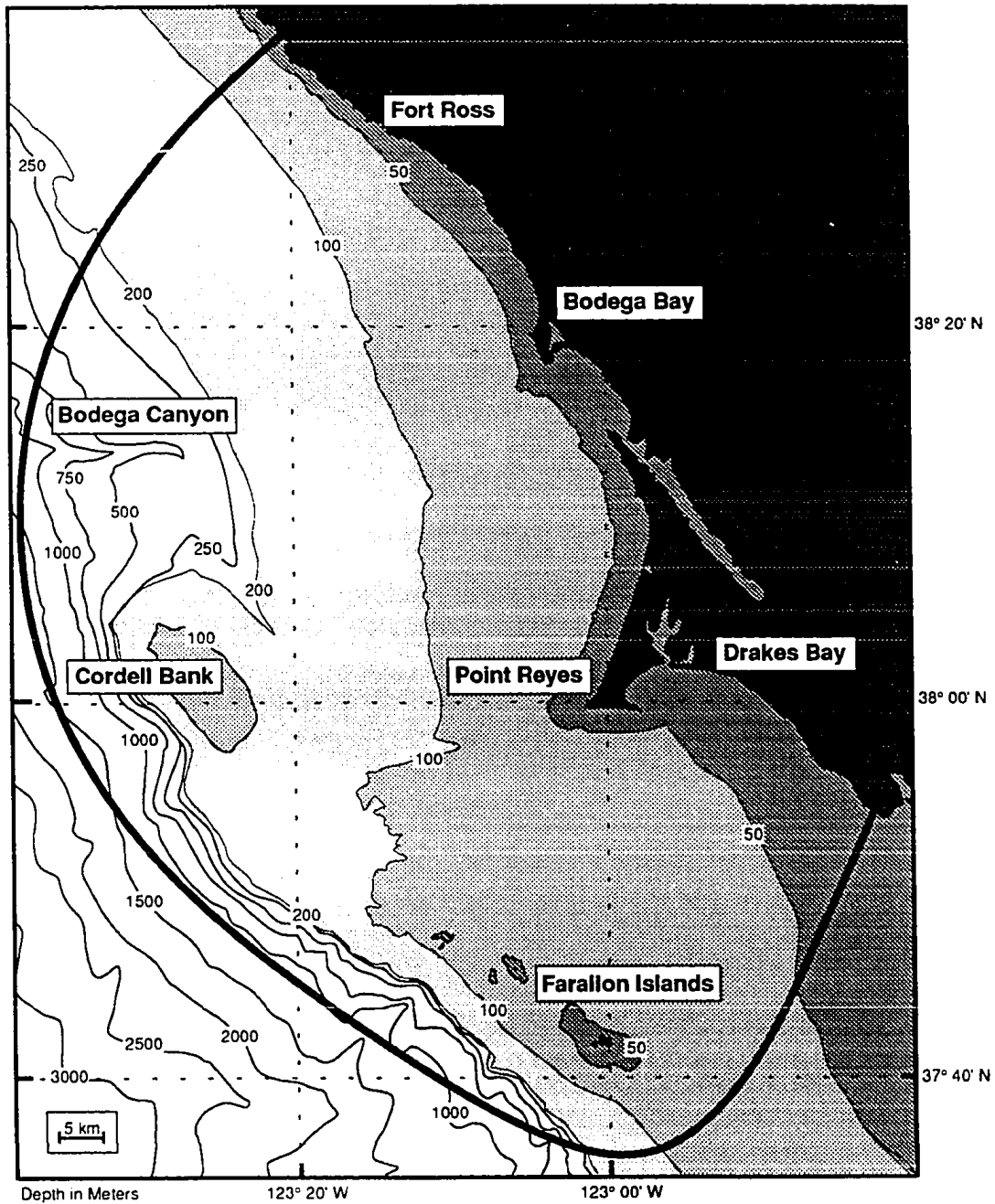


Figure 1. Humpback whale study area off central California (outlined) and geographical regions, Bodega Canyon, Cordell Bank, and the Farallon Islands referred to throughout the text as the primary sites of feeding activity. The study area was approximately 2600 km², which included Cordell Bank and the Gulf of the Farallones National Marine Sanctuaries.

Sampling effort usually occurred in areas of greatest whale concentrations, most frequently along Bodega Canyon, Cordell Bank, and the Farallon Islands (Fig. 2). Daily reports of the locations of whales determined our vessel course each day. Individual whales were tracked for approximately 30 minutes, during which time their location and behavioral states were recorded. To minimize disturbance of whales during behavioral observations, the boat remained > 100 m from whales, which is a National Marine Fisheries Service guideline (*Federal Register* 1979). In addition, the smaller engine was used approximately 20 min before and during the observation period. The motor was run at a constant speed to avoid noise associated with throttle shift, which causes a ratchet-like sound underwater and changes in pitch (Baker et al. 1983; Kieckhefer pers. obs. 1985; Bauer 1986; Watkins 1986; Dolphin 1987a,b,c,d; Whitehead and Carlson 1988). Work was conducted under permits obtained by National Marine Fisheries Service (no. 579, 1988 and 1989 and no. 703, 1990) and the Department of Fish and Game (no. 2253, 2153, and 7022, respective years).

Whale Observations

Two to four boat crew described individual whale behaviors and respiration patterns, and entered behavioral codes and comments into the time/event recorder. At the start and end of each whale observation the following data were recorded: time, date, position, sighting number for the day, group size, number of calves, number of boats and ships present within 2 km, number and species of birds present within 300 m, mean scattering layer depth, bottom depth, and environmental and sea conditions.

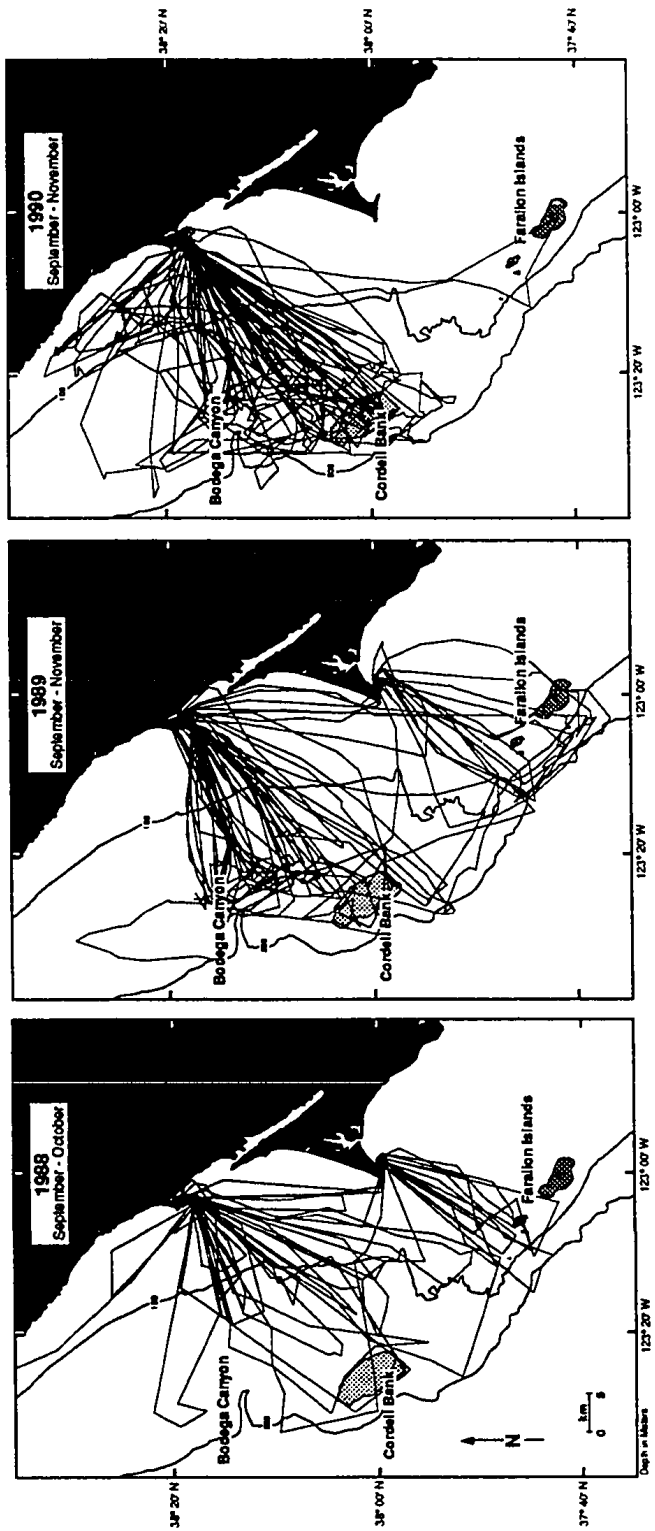


Figure 2. Track lines of vessel surveys from September to November in 1988, and from September to December in 1989 and 1990.

A group was defined as whales within five body lengths of each other (Würsig et al. 1986). Whale behaviors were categorized into 7 different states: rest, slow travel, fast travel, mill/search, surface feed, shallow feed, and deep feed (Appendix A). Behavioral categories were recorded throughout the observation period. Surface (0-10 m depth) feeding was the most obvious with behaviors such as, lateral, diagonal, and vertical lunging. Shallow (11-60 m) and deep (61-140 m) feeding depths of whales were indirectly determined from the occurrence of the scattering layer and echo traces of swimming whales.

Unique whales (ones with distinctive dorsal fin shapes or pigmentation) of groups were identified and tracked with 7 x 50 binoculars (Fujinon). All surfacings, respirations, dives, and aerial behaviors were systematically entered into the portable time/event recorder (Baker et al. 1983; Würsig et al. 1984, 1986; Bauer 1986; Appendix B). Five respiratory variables were recorded: blow interval, number of respirations (blows) per surface duration, duration at surface, dive duration, and blow rate (Würsig et al. 1984, 1986; Dolphin 1987a; Appendix C). Duration at the surface included whales near the surface and blow intervals less than 90 seconds. Duration of dive was the period of time spent diving below the near-surface waters (approx. 5 m depth) and was distinguished by blow intervals greater than 90 sec or by posturing of tail stock (arched peduncle or raised flukes). All feeding behaviors (i.e. lateral lunging, diagonal lunging, and shallow vs. deep dives) were quantitatively documented.

Opportunistic recordings of whale vocalizations were made on Marantz PMD-430 tape recording with a sonobuoy hydrophone and preamplifier. Sounds were categorized as feeding (uniform; D'Vincent et al. 1985), social

(unpatterned; Silber 1986), and songs (patterned; Payne and McVay 1971). All recording levels were constant throughout the study. Whale distance was estimated by volume level of recordings. After behavioral observations were concluded, all whales were approached slowly from behind, within 100 m when possible, photographed and identified by differences in dorsal fin shapes and pigmentation patterns on the ventral surface of their flukes (Katona et al. 1979). Various feeding behaviors also were photographically documented at this time. After photographs were taken, a new group of humpback whales would be located for observation.

Because successive respiration variables of whales were not independent data points, this "standard" approach (e.g. Dolphin 1987b,c ; Guerrero 1989; Harvey and Mate, 1984; Würsig et al. 1984,1986) was not used in the statistical analyses. For comparative purposes to other studies using the standardized approach see Appendix D.

To statistically test data correctly with observations independent of the mean, the mean of each individual whale was calculated and analyzed (Zar 1984; Hoeskstra and Jansen 1986). Nonparametric statistics were used on all respiration variables analyzed due to their skewed distributions. Comparisons among years of mean surface duration, number of blows per surfacing, dive duration, and blow rate within each behavior category were tested using a Kruskal-Wallis test (3 group) and Mann-Whitney U-test (2 group) at the $P \leq 0.05$ significance level. Means of respiration variables were calculated for each behavior category except for rest, which was rarely observed. A nonparametric Tukey-type multiple comparison test (with unequal sample sizes) was used to determine between year differences. All behavioral observations were of

unique adults and whales older than two years under "undisturbed" conditions (other vessels > 2 km away). Statistical methods followed Zar (1984).

Prey Collections and Documentation

Prey information (samples, depth records) was collected only after observing a focal whale for at least 30 min. Presence (or absence) of scattering layers, and their mean depth in the water column, were continuously recorded while passing through areas where whales were feeding. Prey were captured with a dip net, horizontal tows with a plankton net (0.75 m diameter, 505 μ m mesh), or jigging with hook and line.

For surface (0-10 m) plankton tows, the net was towed horizontally at the corresponding prey depth obtained from the depth sounder for 10 to 20 min at an average boat speed of 4-6 km/h. Indirect methods of identifying deep prey layers were used in 1988 and 1989 (e.g. stomach content analysis of local salmon and rockfish caught in areas where whales were feeding). Shallow (11-60 m) and deep (61-140 m) zooplankton net tows in 1990 were used to quantify the relative percentage of euphausiids and other zooplankton in areas where whales were feeding. Once mean depth of prey was determined on the depth sounder, a 12 kg lead ball was attached to the net's stainless steel hoop and the appropriate amount of line released. A wire angle was used to determine the amount of line required (hypotenuse) to sample within the targeted scattering layer. The net was towed at a constant speed (approx. 4-6 km/h) and course for 10 to 20 min.

Laboratory Analyses

Plankton samples were fixed in 10% formalin within 8 hrs of collection, and later transferred to 40% ethanol before analyses. Samples were split into approximately 50 ml volumes with a Folsom plankton splitter. Using an Olympus dissecting microscope (10x to 40x), euphausiids were sorted, identified to species (Kathman et al. 1986), and counted.

Standard body length (tip of rostrum to tip of telson) was measured to the nearest millimeter for all *Thysanoessa spinifera* and *Euphausia pacifica* (Appendix E). Length comparisons of *T. spinifera* and *E. pacifica* were completed for 1990 only, because the previous years' towing gear did not provide adequate means of sampling deep-dwelling *E. pacifica*. Fertilized females of *T. spinifera* were distinguished by the presence of brownish, barbell-shaped spermatophores. Size-frequency distributions were generated for pooled data for each year. Distributions of *T. spinifera* and *E. pacifica* for 1990 and distributions of *T. spinifera* for 1988, 1989, and 1990 were statistically compared using Kolmogorov-Smirnov tests for difference in relative cumulative frequency distributions.

Humpback whale fecal samples were collected opportunistically using a 1 mm mesh net, bailing bucket, plastic bag, or nylon stocking. Samples were divided and preserved in 10% formalin and 40% ethanol (the latter was used due to a concern that 10% formalin might dissolve fish otoliths). All fish otoliths, and euphausiid right mandibles (Appendix F) and spermatophores were identified to species and counted from 5-ml aliquots of each sample.

Total body length of *T. spinifera* and *E. pacifica* were estimated from a regression equation applied to lengths of mandibles found in fecal samples.

Total body length classes of 10 mm, 15 mm, and 20 mm for *T. spinifera* (n = 169) and *E. pacifica* (n = 144) taken from plankton samples were equally selected and measured to the nearest millimeter. Right mandibles were removed and measured (tip of incisors to tip of mandibular insertion) to ± 0.1 mm with an Olympus Image Analyzer (Appendix E, F). Regression functions of total body length and total mandible length were calculated for both *T. spinifera* and *E. pacifica*.

Environmental Data

Environmental data were entered into the time/event recorder every survey hour or new whale sighting, and were updated as necessary every 10 min. Data included: sky condition and sea state (Appendix G), swell height (± 0.5 m), secchi depth (± 0.1 m), sea surface temperature ($\pm 0.2^\circ\text{C}$), along with bottom depth and mean scattering layer depth. Secchi depths were collected with a circular white-vinyl disk of 27-cm diameter and measured as described in Preisendorfer (1986). Sea surface temperature data were collected with a calibrated Micronta digital thermometer

Throughout each survey, a separate computer (LI-COR DataLogger) was programmed to continually record average surface light levels every 10 min from a fixed directional light meter (Quantum 2700). Light levels were measured in $\mu\text{E m}^{-2} \text{s}^{-1}$, where $2000 \mu\text{E m}^{-2} \text{s}^{-1}$ was equivalent to a clear and sunny sky at 12 noon. Total light energy was restricted to the wavelengths between 300 and 720 nm or photosynthetically available radiation (PAR). Average light levels were measured instead of instantaneous levels due to rough sea conditions and continual pitch and roll of the research vessel. Light penetrating the water

to a depth of 10 m was calculated from secchi depth using the vertical extinction coefficient as described in Parsons et al. (1984).

Other indicators of changing environmental conditions such as occurrence of red tide blooms, sea birds, fish, and turtles in the study area were noted and their positions recorded. Red tide samples were collected (via 303 μm mesh net or wide-mouth sample jar) and brought to the laboratory for identification.

Polynomial curves (2-degree) were fitted to daily mean scattering layer depth, sea surface temperature, Secchi depth, Beaufort state, and bottom depth for all whale sightings collected in 1989 and 1990. To determine if an environmental variable(s) had a significant effect on the vertical distribution of the scattering layer during 1989 and 1990, a stepwise regression at the $P \leq 0.05$ significance level was applied. Daily mean light measurements and corresponding scattering layer depths were analyzed separately.

Monthly coastal upwelling indices at 39°N, 125°W and sea surface temperature at NOAA buoy 46013 (38.2°N, 123.3°W) were compared from July through December 1989-90. In addition, archived satellite images of sea surface temperature (SST) were studied and images that clearly show the oceanographic conditions in the study area from July through December 1989-90, were processed at the Naval Postgraduate School in Monterey, California.

RESULTS

Whale Sightings

Humpback whale groups were observed for 232 hours during autumn of 1988, 1989 and 1990. Whale behavior was recorded on 26 groups (27 h) during 31 days at sea in 1988, 99 groups (96 h) during 53 days in 1989, and 146 groups (109 h) during 56 days in 1990. During these periods, mean group size was 2.1 to 3.0 individuals (1988: 2.5 ± 1.38 SD, range = 1-6; 1989: 3.0 ± 1.73 SD, range = 1-12; 1990: 2.1 ± 1.29 SD, range = 1-12). Detailed observations of respiration patterns and other surface activity were made on 138 different individuals: 23 in 1988 (12.5 total hours), 51 in 1989 (25.8 hours), and 64 in 1990 (25.0 hours).

Locations of humpback whale observations varied among years. In 1988, humpback whales and prey were dispersed and did not feed for long periods of time at one location. In 1989, concentrations of whales were located west of the Farallon Islands in September and near Cordell Bank and Bodega Canyon in mid-October and November. In mid-September 1990, whales were found in shallow waters near Fort Ross, whereas in October and November concentrations of whales occurred around Bodega Canyon and Cordell Bank (Fig. 3).

Mother-calf pairs were observed infrequently in all 3 years. In 1988, two sightings were made near North Farallon Island. Two sightings occurred near southeast Farallon Island in 1989, and eight sightings near Bodega Canyon and Cordell Bank were recorded in 1990.

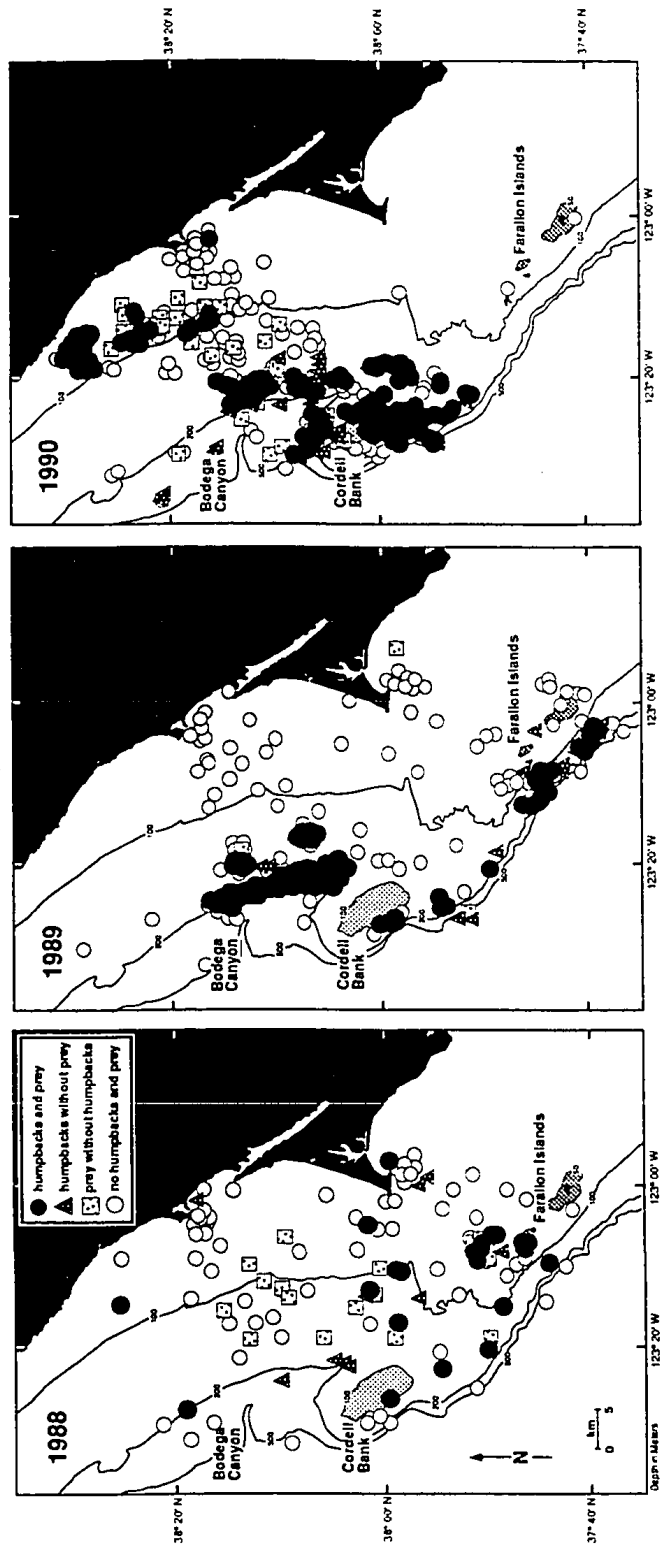


Figure 3. Locations of humpback whales and prey, humpbacks without prey, prey without humpbacks, and no humpbacks and no prey from vessel surveys during the fall of 1988, 1989, and 1990. The presence or absence of prey was primarily based on depth sounder recordings.

Whale Behavior

Feeding was the most prevalent activity observed in all three years, comprising about half the total percent frequency of occurrence (mean = 51.4% \pm 4.94 SD; Fig. 4). Mill/search behavior and slow travel occurred less often than feeding, and were seen with comparable frequency throughout the study (mean = 21.5 \pm 2.04 SD and 16.4 \pm 1.07 SD, respectively). Fast travel and rest occurred infrequently (mean = 6.5 \pm 1.87 SD and 4.2 \pm 4.08 SD, respectively) in all three years (Fig. 4).

Feeding depth varied significantly among years according to changes in depth of prey ($X^2 = 115.5$, $df = 4$, $P < 0.001$; Fig. 5). Surface feeding (0-10 m prey depth) was observed in 1988 and 1990, but was not seen in 1989. Deep sub-surface feeding (61-140 m prey depth) occurred mainly in 1989, less frequently in 1990, and was not observed in 1988. Shallow sub-surface feeding (11-60 m prey depth) occurred in all years.

Respiration variables were recorded for each behavior category except for rest, which was rarely observed (Table 1). Among-year differences in mean blow rate were significant only for feeding and milling behaviors ($H = 7.95$, $P < 0.01$ and $H = 6.53$, $P < 0.05$; $df = 2$; Fig. 6). When feeding, blow rate was less in 1989 than either 1988 or 1990; however, mean blow rates were statistically different only when 1988 and 1989 were compared (1.7 vs. 1.1; $Q=2.80$, $df = 3$, $P < 0.01$). There was no difference in mean blow rate among years when whales were engaged in slow travel and fast travel.

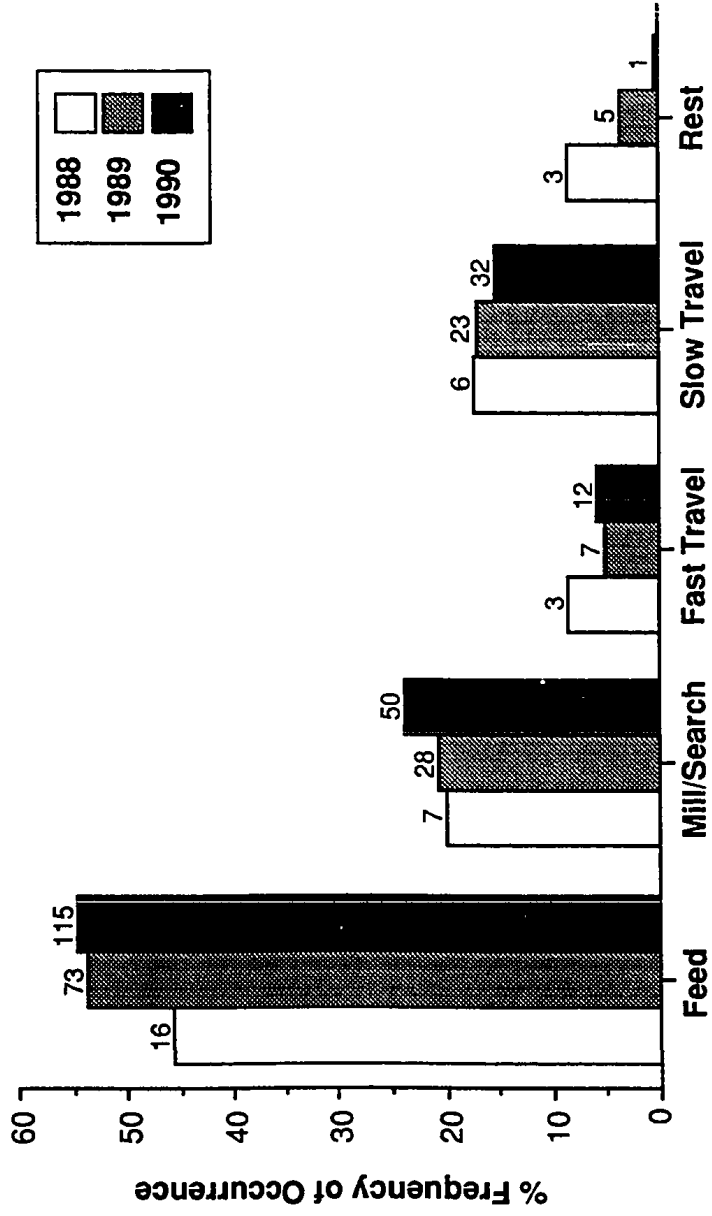


Figure 4. Percent frequency of humpback whale behaviors observed in 1988-1990. Sample sizes are above bars.

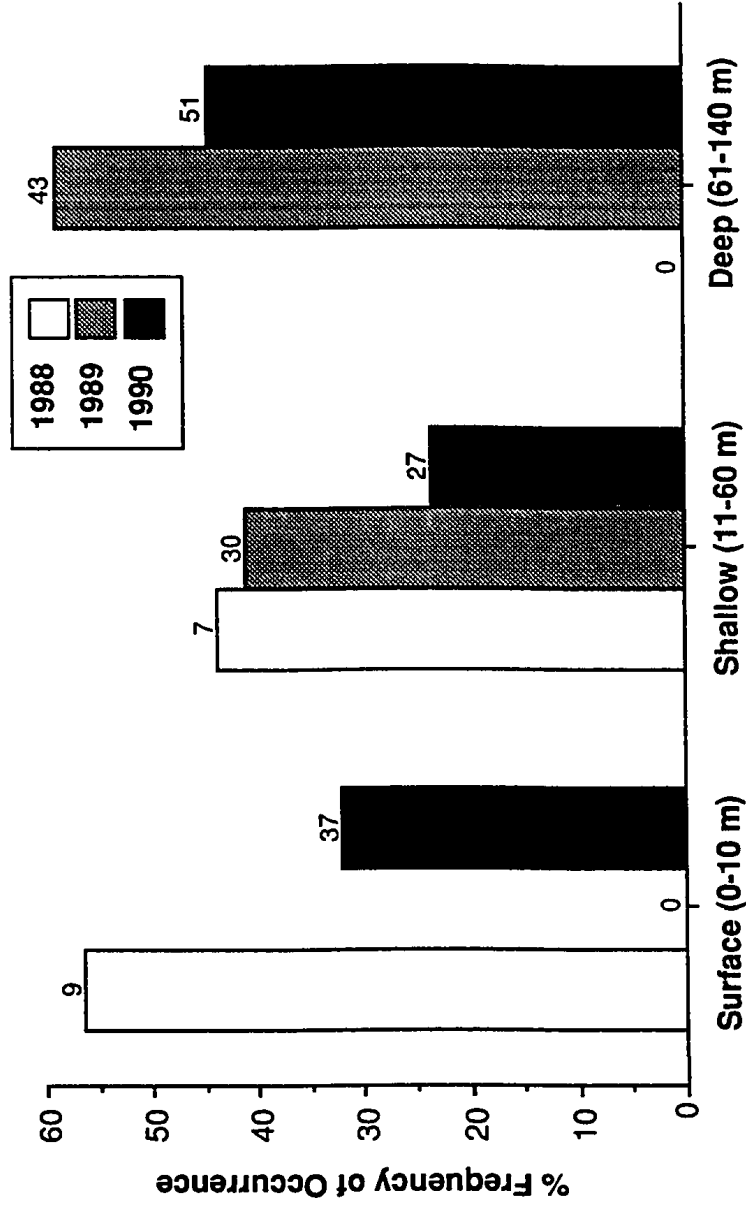


Figure 5. Percent frequency of surface, shallow, and deep feeding. Sample sizes are above bars.

Table 1. Respiration variables by behavioral categories of feeding, milling, and traveling humpback whales. Independent sampled means were calculated from the mean of individual whales (**bold**) for each year. Total number of sampled means are shown in parentheses. Among years significance levels from Kruskal-Wallis test are coded as follows: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, *ns* = not significant.

RESPIRATION VARIABLE	BEHAVIOR CATEGORY												
	Feeding			Mill/Search			Fast Travel			Slow Travel			
	88	89	90	88	89	90	88	89	90	88	89	90	
Duration at Surface mean (min)	0.9	3.4	1.7	0.9	3.0	2.0	1.0	1.8	1.1	<i>ns</i>	1.3	1.8	1.3
SD	0.52	1.54	0.88	0.51	1.29	1.33	0.38	1.66	0.36	0.72	1.17	1.01	0.47
95% CL	0.37	0.53	0.27	0.53	0.78	0.56	0.29	2.06	0.37	0.67	0.68	0.47	0.20
n	10	35	42	6	13	24	9	5	6	7	14	20	(53)
(n)	(132)	(120)	(299)	(27)	(36)	(59)	(55)	(32)	(23)	(21)	(46)	(53)	
No. Blows/Surface Duration mean	3.3	11.8	5.8	3.1	10.3	6.7	3.8	5.6	3.5	<i>ns</i>	4.7	6.3	4.3
SD	1.79	4.62	3.11	0.70	4.57	4.00	1.14	4.32	1.16	1.26	3.97	2.47	1.15
95% CL	1.28	1.59	0.97	0.73	2.76	1.69	0.88	5.37	1.21	1.17	2.29	1.15	0.20
n	10	35	42	6	13	24	9	5	6	7	14	20	(53)
(n)	(132)	(120)	(299)	(27)	(36)	(59)	(55)	(32)	(23)	(21)	(46)	(53)	
Duration of Dive mean (min)	1.4	6.7	3.4	0.7	5.5	4.9	1.8	4.1	1.6	<i>ns</i>	2.5	4.4	2.6
SD	0.91	2.67	2.80	0.40	2.12	3.04	1.28	2.12	1.08	0.84	2.37	1.76	0.90
95% CL	0.65	1.06	0.95	0.50	1.51	1.35	1.19	2.64	1.13	0.89	1.43	0.90	0.20
n	10	27	36	5	10	22	7	5	6	6	13	17	(48)
(n)	(125)	(105)	(290)	(19)	(32)	(58)	(48)	(33)	(22)	(18)	(46)	(48)	
Blow Interval mean (sec)	19.5	18.2	21.0	20.2	19.1	20.5	19.2	20.4	22.8	<i>ns</i>	18.7	18.9	21.4
SD	7.64	3.23	8.86	7.94	2.76	8.39	3.65	2.21	8.16	6.34	3.74	8.85	4.03
95% CL	5.47	1.06	2.73	8.33	1.60	3.46	2.46	2.32	6.82	5.87	2.16	4.03	0.21
n	10	38	43	6	14	25	11	6	8	7	14	21	(147)
(n)	(197)	(1279)	(954)	(54)	(251)	(331)	(162)	(118)	(72)	(70)	(223)	(147)	
Blow Rate mean (no. blows/min)	1.7	1.1	1.3	2.1	1.2	1.2	2.0	1.2	1.3	<i>ns</i>	1.2	1.2	1.3
SD	0.92	0.19	0.47	0.57	0.57	0.65	0.76	0.87	0.35	0.17	0.70	0.66	0.37
95% CL	0.66	0.08	0.17	0.71	0.40	0.30	0.70	1.08	0.37	0.18	0.42	0.37	0.15
n	10	24	34	5	10	20	7	5	6	6	13	15	(42)
(n)	(123)	(84)	(254)	(18)	(26)	(46)	(46)	(31)	(20)	(18)	(40)	(42)	

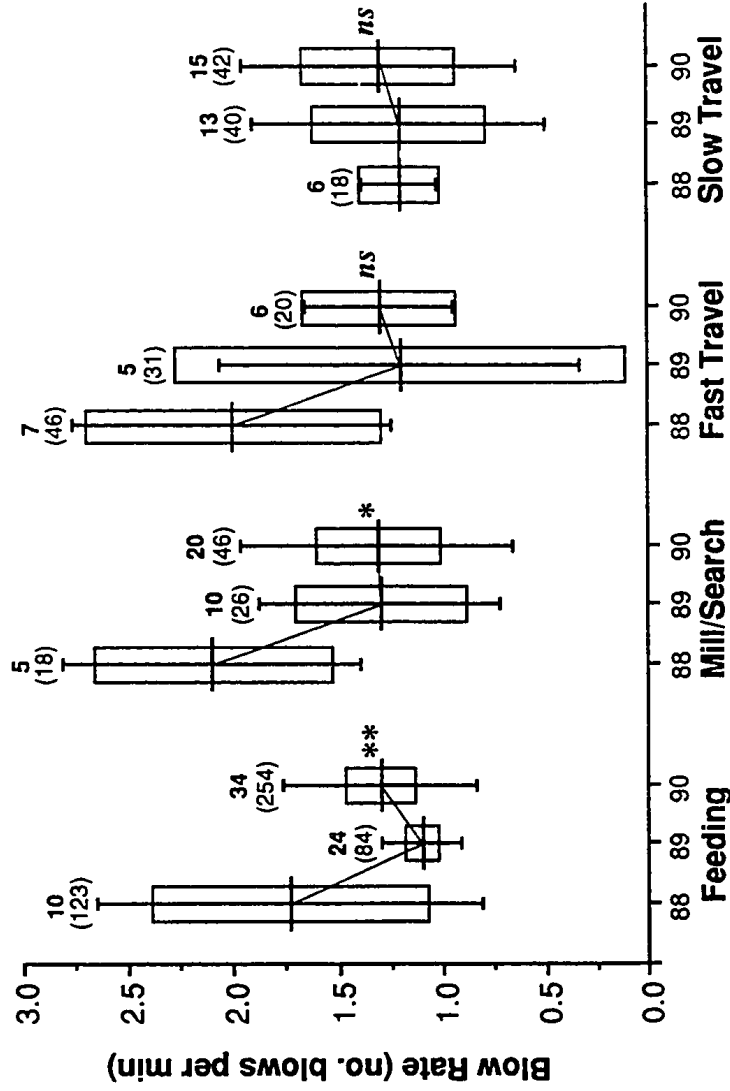


Figure 6. Mean blow rate of feeding, milling, and traveling humpback whales in 1988, 1989, and 1990. Mean (horizontal bar), ± 1 standard deviation (vertical line), $\pm 95\%$ confidence limits (box), number of whales (bold), and successive sample size (in parentheses) are shown. Between year significance levels from Kruskal-Wallis test are coded as follows: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant.

Respiratory patterns of feeding whales differed dramatically among years. The surface duration, number of blows per surface duration, and dive duration were significantly greater in 1989 than 1988 or 1990 ($H \geq 12.73$, $df = 2$, $P < 0.001$; Fig. 7). These same three respiration variables were greater in 1989 than 1988 and 1990 for shallow dives (Fig. 8), but there was no difference in these variables in 1988 and 1990. Surface duration and number of blows per surface duration during deep feeding were significantly greater in 1989 than 1990 ($Z = 2.81$ and 2.74 , $df = \infty$, $P < 0.01$). Mean dive duration, however, was not significantly different between 1989 (6.3 min \pm 2.91 SD) and 1990 (5.9 min \pm 2.31 SD). Within each year, increasing prey depth was strongly associated with increasing feeding dive duration, surface duration, and number of blows per surface duration. This relationship was best documented in 1990, the only year when feeding was recorded in all 3 depth categories ($H = 12.73$, $H = 25.57$, $H = 24.85$, respectively; $df = 2$; all $P < 0.001$; Fig. 9).

Surface feeding whales typically lunged to capture prey (92% total surfacings). They consistently performed lateral lunges (84% of surfacings) to capture prey more than other types of lunges (diagonal lunges 7%; vertical lunges 1%). Bubble-clouds were observed just before an executed diagonal and lateral lunge (Fig. 10). Due to variable sea conditions and observation distances exceeding 100 m most of the time, counts of bubble-clouds were not made consistently.

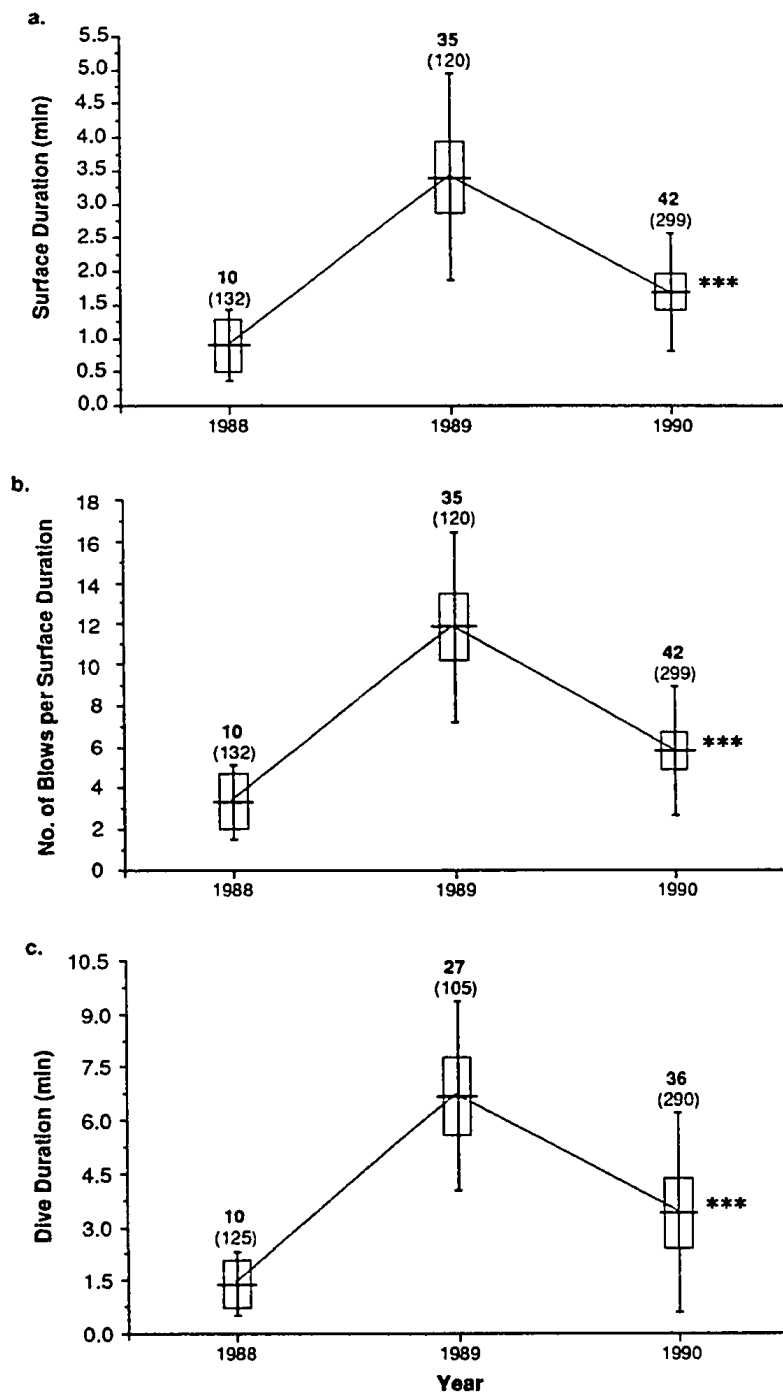


Figure 7. Surface duration, number of blows per surface duration, and dive duration in 1988, 1989, and 1990 for feeding at all depths (0-140 m). Presentation as in Figure 6.

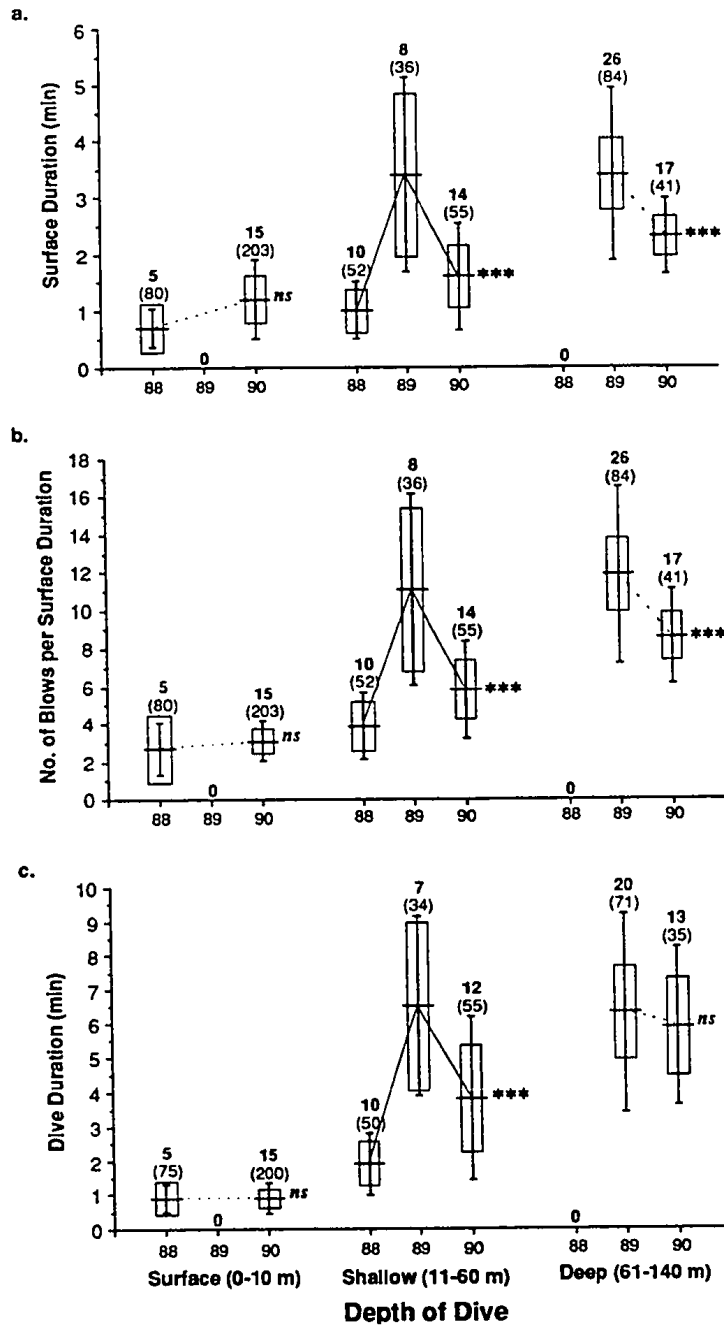


Figure 8. Surface duration, number of blows per surface duration, and dive duration of surface (0-10 m), shallow (11-60 m), deep (61-140 m) feeding, 1988-1990. Between year significance levels are from Kruskal-Wallis test (3 groups) and Mann-Whitney U-test (2 groups). Presentation as in Figure 6.

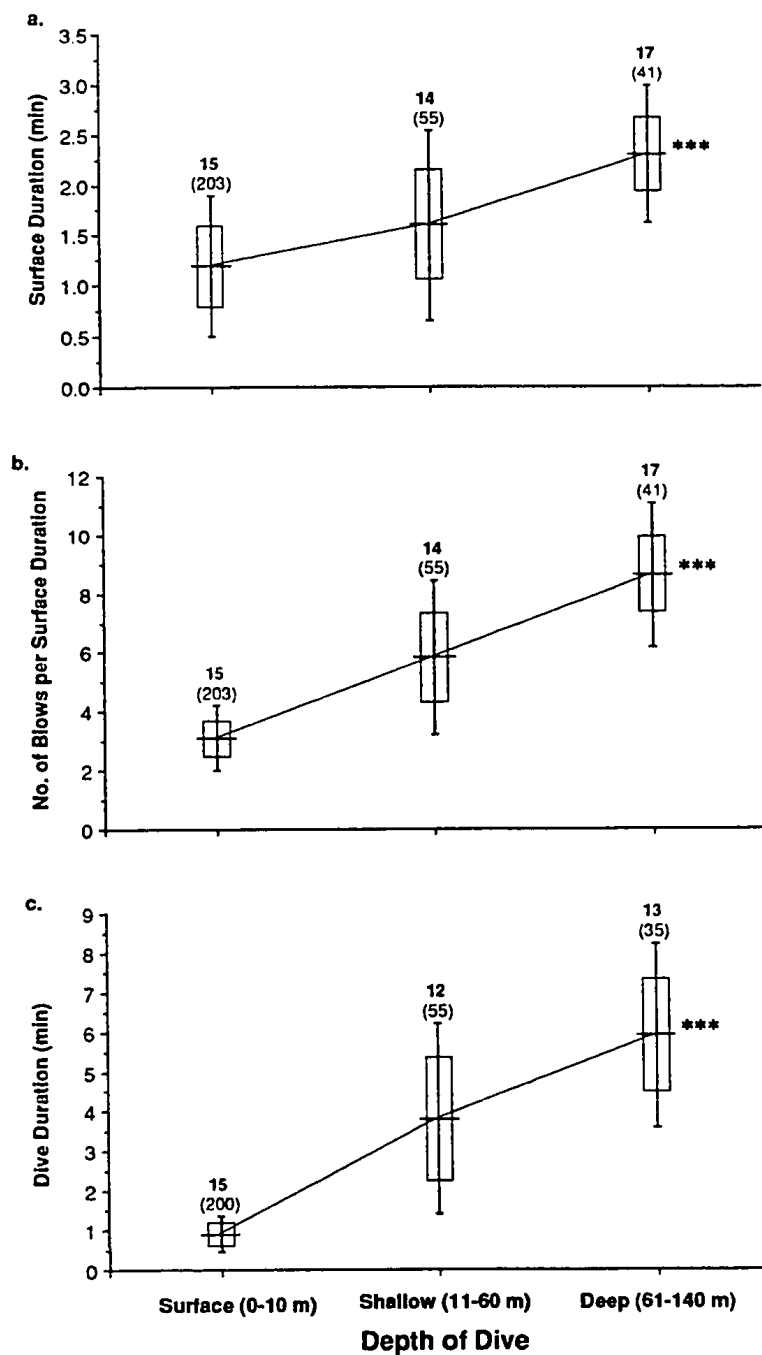


Figure 9. Surface duration, number of blows per surface duration, and dive duration of surface (0-10 m), shallow (11-60 m), deep (61-140 m) feeding for 1990. Between year significance levels are from Kruskal-Wallis test (3 groups). Presentation as in Figure 6.

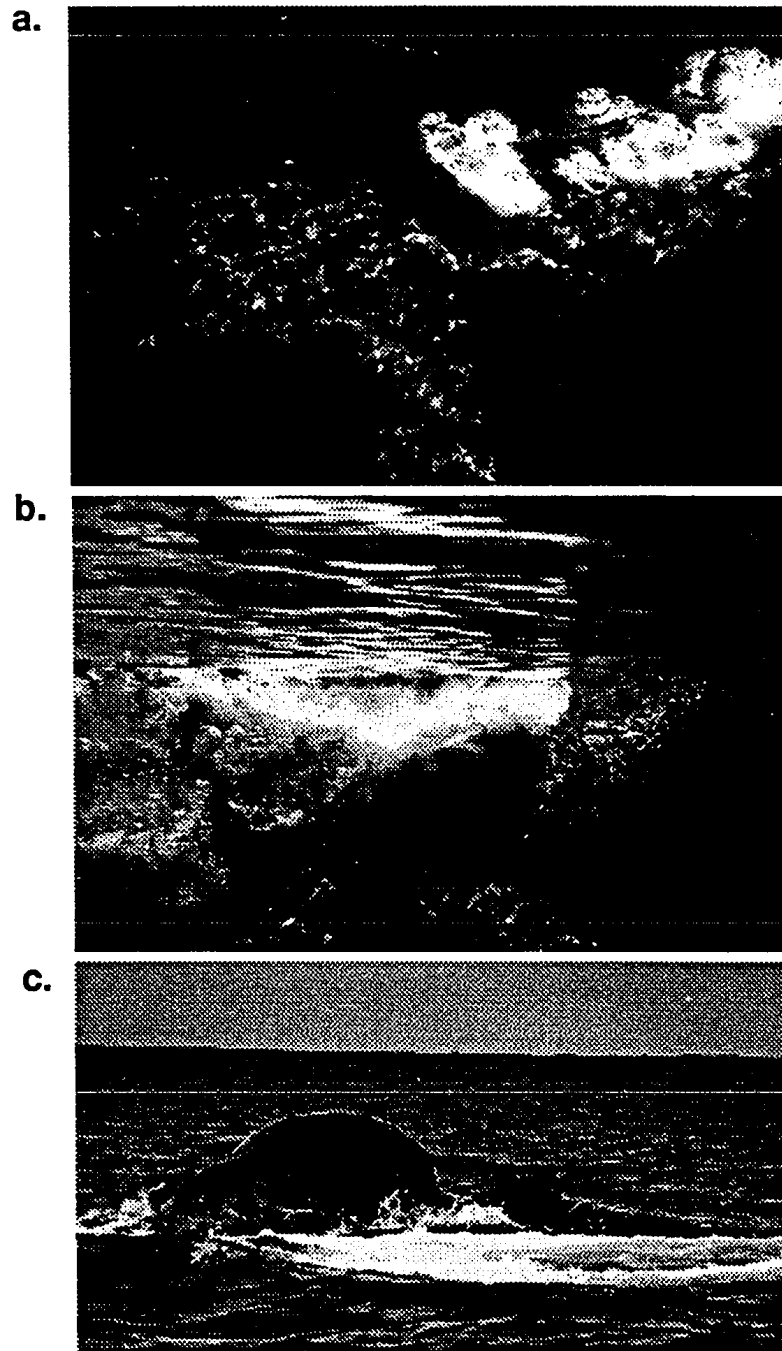


Figure 10. Humpback whale bubble-cloud formation: a) bubbles seen underwater coming out of a whale's mouth in Hawaii, 1982, b) bubbles breaking-down into fine mist (photos by author, courtesy of Kewalo Basin Marine Mammal Lab), and c) whale blowing a bubble-cloud just before a lateral lunge near Cordell Bank, California, 1990 (photo by Daniel E. Shapiro).

Fluke-down, fluke-up, and high fluke-up behaviors preceding feeding dives were strongly correlated to prey depth ($X^2 = 117.13$, $df = 4$, $P < 0.001$; Fig. 11). Fluke-down dives occurred most often during surface feeding (44% of total surface feeding dives). Fluke-up dives occurred most often during shallow feeding (67%); high fluke-up dives were seen most often during deep feeding (60%). Deep feeding dives were also typically preceded by a distinctive flex posture (i.e. a rolling concave stretch of the entire tail stock just before a high fluke-up dive). This flex posture preceded 77% of deep-feeding dives, and was never observed during surface or shallow feeding.

No attempt was made to record whale depth on the depth sounder. However, on seven occasions depth sounder records incidentally documented a fluke-down (30°), fluke-up (50°), and high fluke-up (80°) dive. On one occasion the entire descent (75° angle from surface) and ascent (60° angle to surface) of a whale travelling through a scattering layer at a mean depth of 100 m was recorded (Fig. 12). The duration of the dive was 4.2 min.

In 1988-90, 32 opportunistic hydrophone recordings were made of humpback whales engaged in feeding, mill/search, and traveling (Table 2). Recordings were 15 min to 45 min in duration, totaling 12.8 h of recording time for the 3-year period. Feeding sounds, social sounds, and songs were qualitatively distinguished for each behavior using characteristics identified by D'Vincent et al. (1985), Silber (1986), and Payne and McVay (1971). No feeding vocalizations were recorded. Whales were quiet during all modes of feeding, except for singers recorded during deep feeding on 24 September and 8 October, 1989.

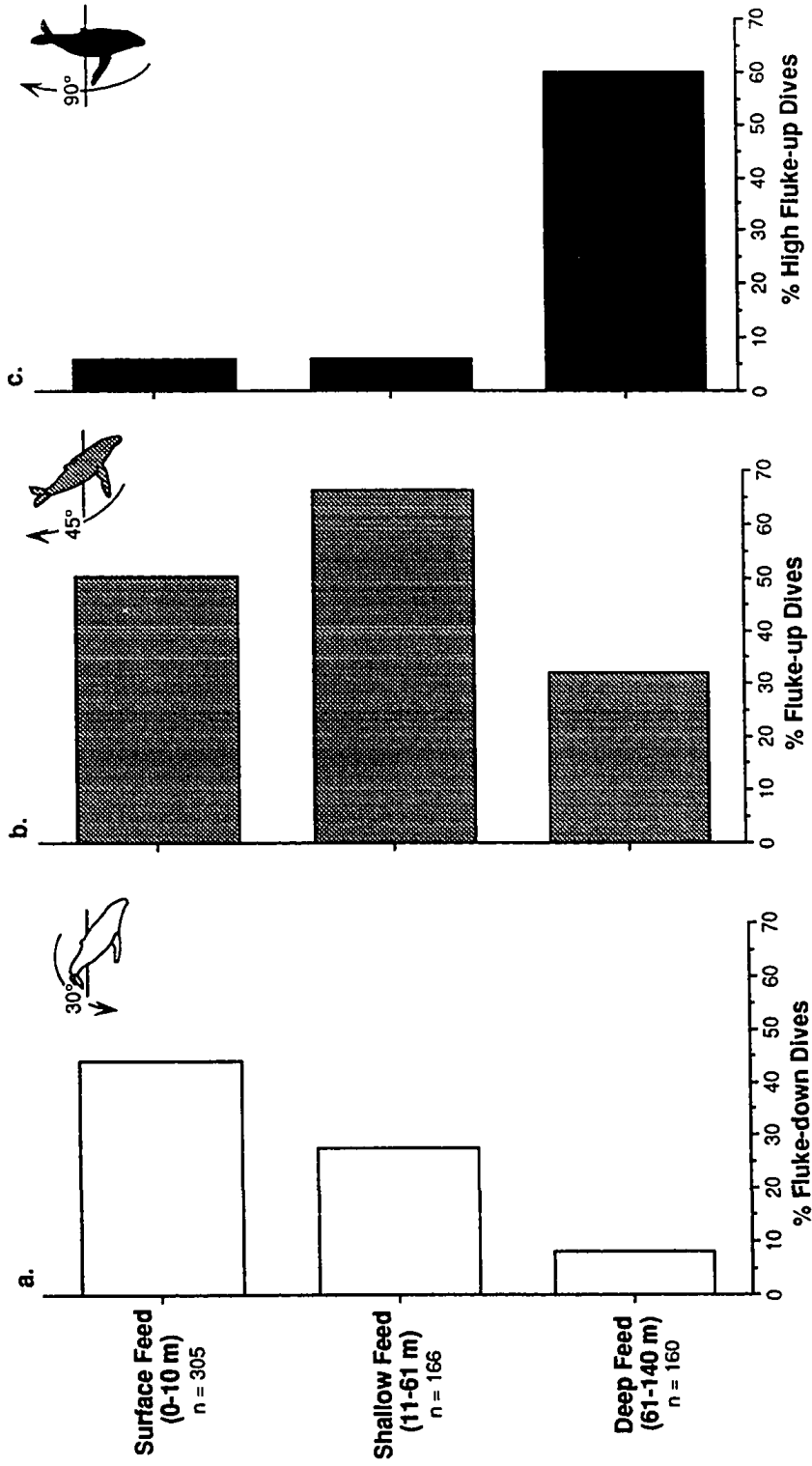


Figure 11. Percentage of fluke-down, fluke-up, and high fluke-up dives for surface (0-10 m), shallow (11-60 m), deep (61-140 m) feeding depths. Sample sizes (n) are shown.

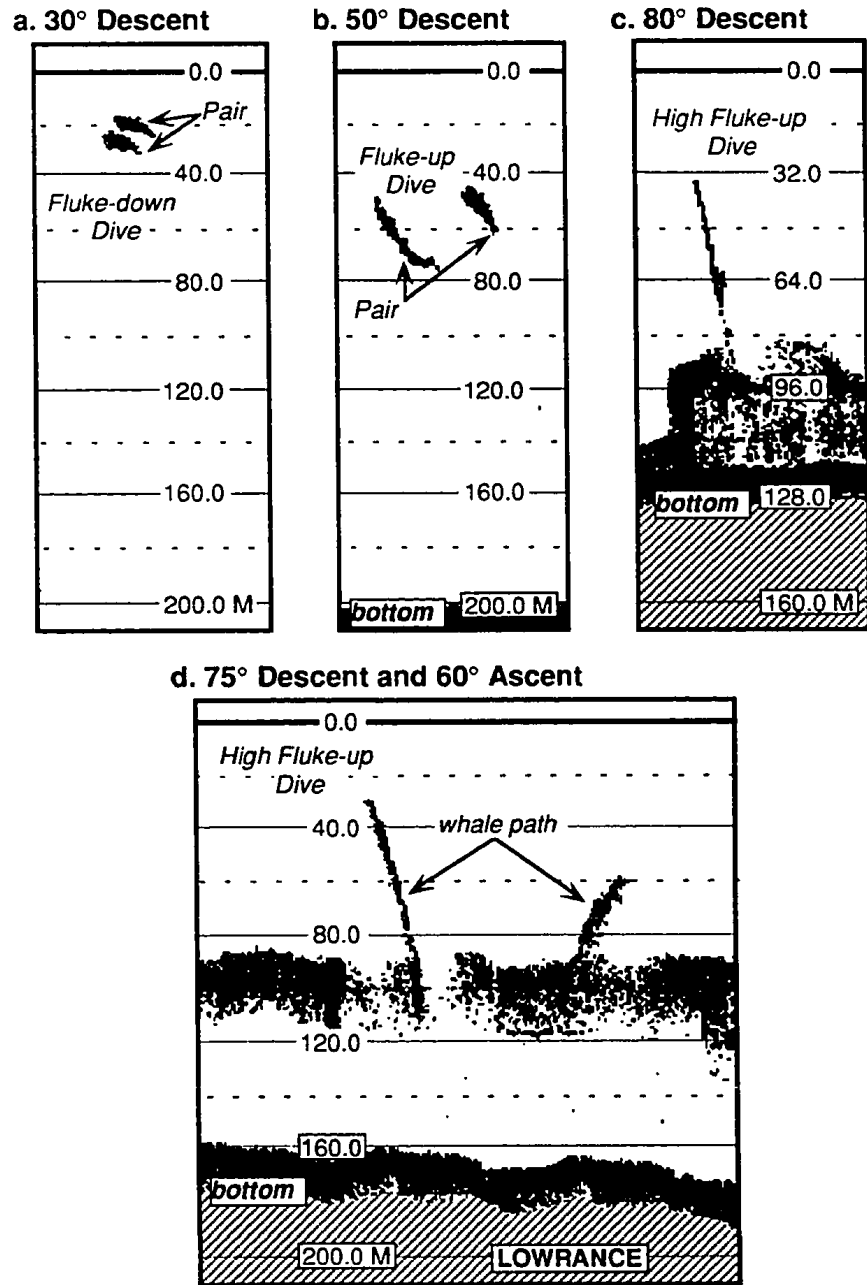


Figure 12. Depth sounder records of whales diving at (a) 30° fluke-down, (b) 50° fluke-up, and (c) 80° high fluke-up. Bottom chart recording (d) documents an entire descent (75° angle from surface) and ascent (60° angle to surface) of a whale swimming through a deep scattering layer. Duration of dive was 4 min and 30 seconds.

Table 2. Opportunistic recordings of humpback whale sounds in the Cordell Bank/ Farallon Basin area during the fall of 1988 to 1990. Feeding depth categories of surface (0-10 m), shallow (11-60 m), and deep (61-140 m) in bold. Vocalizations are scored either yes (Y) or no (N) and described as feeding, social, and/or songs (after D'Vincent et al 1985; Silber 1986; Payne and McVay 1971)

Year	Date (m-d)	Location (lat. & long.)	Time (h:m)	Behavior Category	Group Size	Calve	Vocal (Y or N)	Description	Distant Vocal (Y or N)	
1988	Sep-01	37° 51'N, 123° 08'W	15:45	surface feed	4	0	N		N	
	Sep-02	37° 51'N, 123° 06'W	10:35	surface feed	4	0	N	singing	N	
	Sep-21	37° 57'N, 123° 12'W	14:51	slow travel	3	1	Y		Y	
	Oct-12	38° 02'N, 123° 13'W	17:14	surface feed	2	0	N	social	N	
	Oct-12	38° 00'N, 123° 25'W	18:36	slow travel	2	0	Y		Y	
	Oct-29	38° 20'N, 123° 28'W	14:43	mill/search	2	0	N	singing	N	
	Oct-30	38° 04'N, 123° 21'W	11:25	mill/search	4	0	Y	singing	Y	
	Oct-30	38° 04'N, 123° 22'W	12:19	slow travel	2	0	Y	singing	Y	
	1989	Sep-07	37° 41'N, 123° 04'W	15:00	slow travel	4	0	Y	social	N
		Sep-08	37° 45'N, 123° 10'W	15:47	mill/search	4	0	N		N
Sep-12		38° 09'N, 123° 18'W	12:45	deep feed	2	0	N		N	
Sep-13		37° 55'N, 123° 26'W	15:15	deep feed	3	0	N		N	
Sep-14		37° 45'N, 123° 04'W	16:15	mill/search	1	0	N		Y	
Sep-24		37° 46'N, 123° 13'W	11:30	deep feed	2	0	Y	singing	Y	
Oct-08		38° 17'N, 123° 25'W	14:45	deep feed	5	0	Y	singing	Y	
Oct-09		38° 14'N, 123° 25'W	13:00	deep feed	3	0	N		N	
Oct-09		38° 16'N, 123° 29'W	17:45	deep feed	2	0	N		N	
Oct-31		38° 10'N, 123° 27'W	14:13	shallow feed	2	0	N		Y	
Oct-31		38° 10'N, 123° 23'W	18:15	shallow feed	2	0	N		Y	
Nov-09		38° 08'N, 123° 23'W	15:35	shallow feed	2	0	N		Y	
1990		Sep-20	38° 24'N, 123° 12'W	16:03	shallow feed	12	1	N		N
		Sep-21	38° 30'N, 123° 17'W	18:15	surface feed	1	0	N		N
	Sep-25	38° 28'N, 123° 20'W	16:30	surface feed	1	0	N		N	
	Oct-25	38° 04'N, 123° 28'W	16:19	mill/search	3	0	N		Y	
	Oct-26	38° 06'N, 123° 28'W	15:59	mill/search	2	0	Y	singing	Y	
	Oct-27	38° 08'N, 123° 31'W	18:01	slow travel	1	0	Y	singing	Y	
	Nov-10	37° 58'N, 123° 26'W	13:00	deep feed	2	0	N		Y	
	Nov-11	38° 00'N, 123° 27'W	17:30	deep feed	2	0	N		Y	
	Nov-13	37° 56'N, 123° 28'W	11:51	mill/search	3	1	N		Y	
	Nov-17	37° 58'N, 123° 19'W	14:16	surface feed	2	0	N		Y	
	Nov-18	37° 58'N, 123° 21'W	12:15	surface feed	1	0	N		Y	
	Nov-18	37° 59'N, 123° 21'W	13:09	surface feed	2	0	N		Y	

Songs of seven humpback whales were recorded: one near Point Reyes (9/21/88) and the Farallon Islands (9/24/89), two near Cordell Bank (10/30/88), and three near Bodega Canyon (10/8/89, 10/26/90, 10/27/90). Distant vocalizations (social) comprised over half (56%) the recordings made in 1988-90. Songs of humpback whales were recorded earlier in 1988 (9/21) and 1989 (9/24) than in 1990 (10/26).

Prey Occurrence

In 1988 and 1990, humpback whales fed on euphausiids (primarily *T. spinifera*) and occasionally schooling fishes (primarily *C. pallasii*), whereas in 1989, whales were only observed feeding on euphausiids (primarily *T. spinifera* and *E. pacifica*). Prey of surface-feeding whales were occasionally visible from the observation boat. In 1988 and 1990, euphausiid swarms were repeatedly ($n=17$) seen near lunge-feeding whales. On five occasions, surface-feeding whales were observed feeding on schooling fish. These fish were tentatively identified as Pacific herring, *Clupea pallasii* in four feeding events and juvenile rockfish, *Sebastes spp.* during one feeding period. In Half Moon Bay, 40 km south of the study area, humpbacks were frequently reported feeding on northern anchovy (*E. mordax*) throughout this 3-year study (pers. comm. R. LaMar 1990).

Depth of scattering layers during September and October varied significantly among years. Prey were consistently shallower in September-October 1988 ($13.9 \text{ m} \pm 10.97 \text{ SD}$, $n = 31$) and 1990 ($27.5 \text{ m} \pm 29.63 \text{ SD}$, $n = 38$) than in 1989 ($115.2 \text{ m} \pm 41.10 \text{ SD}$, $n = 87$). A deep (61-140 m) scattering layer was never recorded in 1988, and only rarely (14%, $n = 12$) in

1990. In contrast, 82% of scattering layers recorded in 1989 (n=31) occurred below 60 m depth (Fig. 13).

Eleven fecal samples of humpback whales were opportunistically collected in 1987 (n=1; collected by Cascadia Research Collective), 1988 (n=2), 1989 (n=2), and 1990 (n=6). Fecal samples contained only euphausiid hard parts. Based on right mandible counts, samples were composed of 80.6% *Thysanoessa spinifera* (± 15.21 SD, n = 1848) and 8.3% *Euphausia pacifica* (± 16.41 SD, n = 291; Table 3). No evidence of fish prey (e.g. otoliths, vertebrae) were found in fecal material.

Plankton tows were consistently dominated by a single euphausiid species. In 1990, when vessel equipment allowed sampling of all three prey depths, *T. spinifera* comprised 98.1% of surface tows (0-10 m) and 87.6% of shallow tows (11-60 m). *Euphausia pacifica* comprised 99.6% of deep (61-140 m) tows. Small numbers of *Nyctiphanes simplex* (1.7% and 0.4%) and *Nematoscelis difficilis* (1.5%) were caught in surface and shallow tows, respectively. In 1990, *T. spinifera* were significantly larger (12.3 mm \pm 2.54 SD) than *E. pacifica* (11.4 mm \pm 2.05 SD; $D = 27.94$, $P < 0.001$; Fig. 14).

Mean lengths of *T. spinifera* decreased significantly from 1988 to 1990 ($D \geq 24.84$, $P < 0.001$). Individuals were largest in 1988 (15.9 mm \pm 2.52 SD), smaller in 1989 (12.8 mm \pm 1.34 SD) and smallest in 1990 (12.3 mm \pm 2.54 SD; Fig. 15).

Calculated standard body lengths of *T. spinifera* and *E. pacifica* in fecal samples were longer than those caught in tow samples. Calculations were based on linear regressions of body length to mandible length from tow samples (Fig. 16).

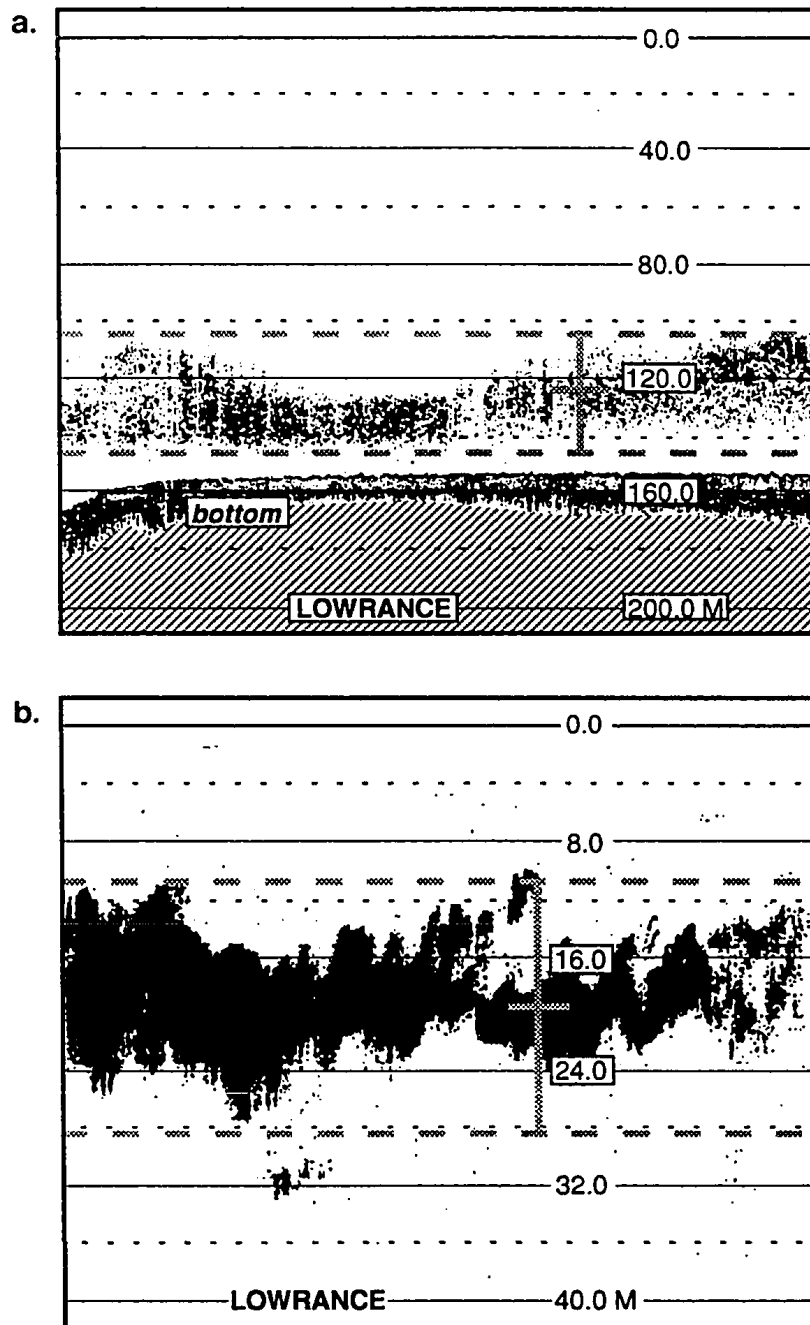


Figure 13. Depth sounder records documenting (a) deep scattering layer with a mean depth of 124 m on September 8, 1989 and (b) shallow scattering layer with a mean depth of 19 m on October 31, 1989, which only occurred later in the 1989 season.

Table 3. Humpback whale fecal samples (n = 11) collected in the study area during the fall of 1987 to 1990. Right mandibles and spermatophores were identified for each species and counted from a 10 ml aliquot. Sample sizes (in parentheses) and ± 1 standard deviations of the grand mean are shown.

Date	Percentage of Right Mandibles			No. of Spermatophores	
	<i>T. spinifera</i>	<i>E. pacifica</i>	Unknown?	<i>T. spinifera</i>	<i>E. pacifica</i>
1987					
Oct 7*	86% (63)	0% (0)	14% (10)	0	0
1988					
Oct 16*	89% (41)	0% (0)	11% (5)	2	0
Oct 16*	85% (79)	0% (0)	15% (14)	11	0
1989					
Sep 24	75% (162)	11% (22)	14% (31)	98	0
Dec 2	44% (86)	48% (93)	8% (15)	0	0
1990					
Aug 30	60% (326)	32% (176)	8% (43)	1	0
Oct 9	88% (144)	0% (0)	12% (20)	130	0
Oct 27*	89% (176)	0% (0)	11% (22)	0	0
Nov 12	89% (276)	0% (0)	11% (33)	2	0
Nov 12	87% (193)	0% (0)	13% (30)	5	0
Nov 13*	94% (302)	0% (0)	6% (19)	2	0
Grand Mean	80.6% ± 15.21 SD (1848)	8.3% ± 16.41 SD (291)	11.1% ± 3.00 SD (242)	23 ± 45.8 SD (251)	0
Other Prey Remains:					
Trace findings of copepods, fish eggs, ctenophores, and polychaetes.					
*Note: samples collected by Cascadia Research Collective.					

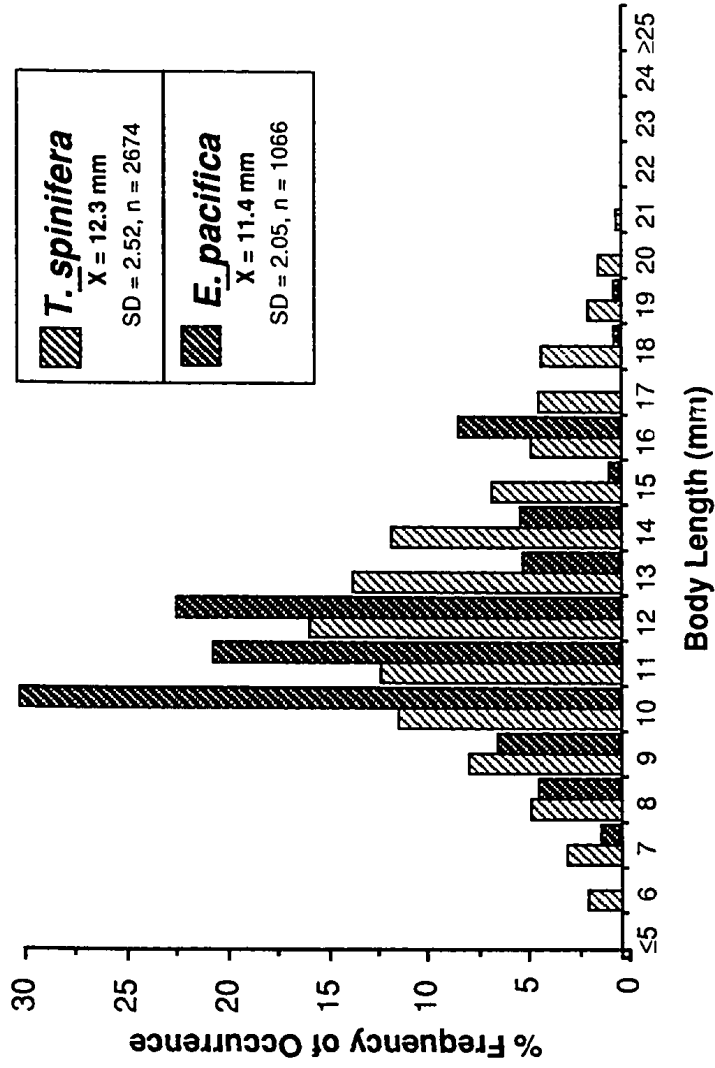


Figure 14. Length frequency histogram of 1990 tow samples, comparing the lengths of *Thysanoessa spinifera* to *Euphausia pacifica* (22 tows and 13 tows, respectively).

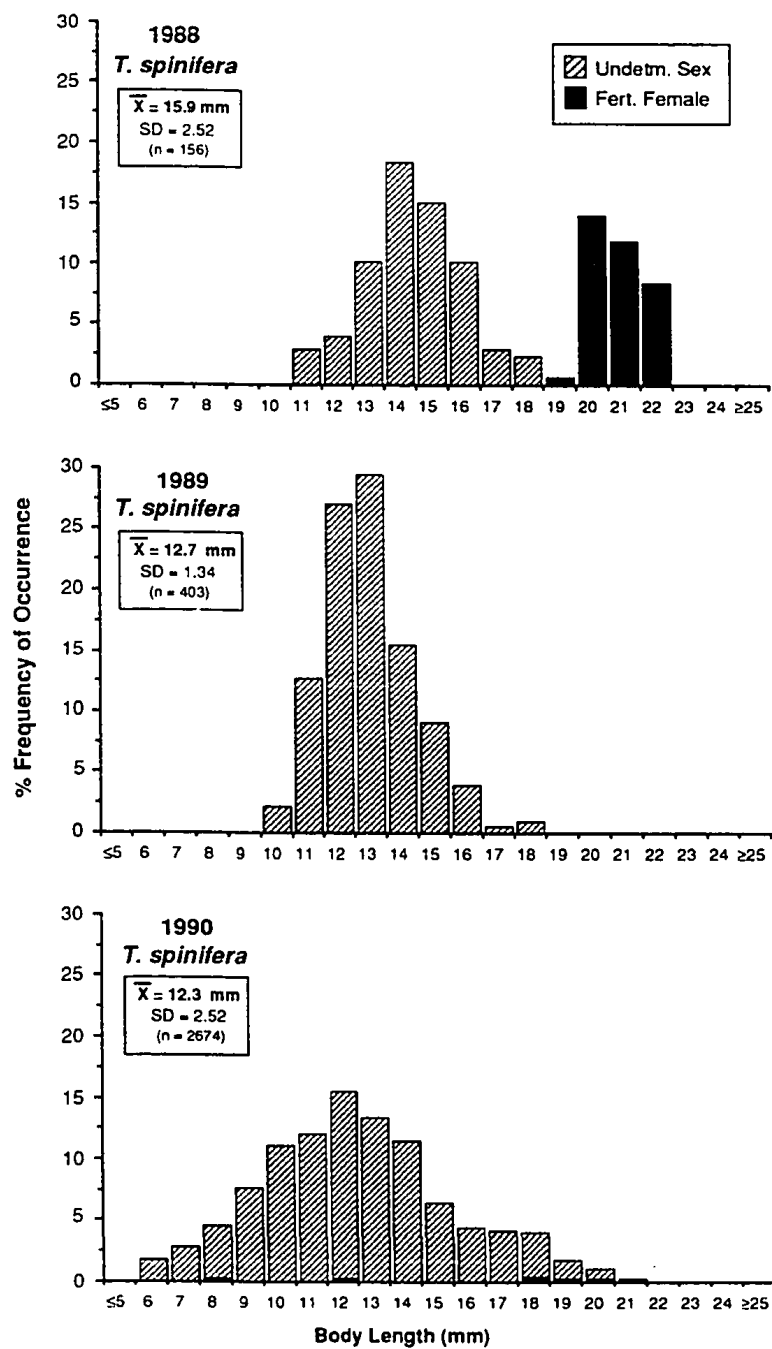
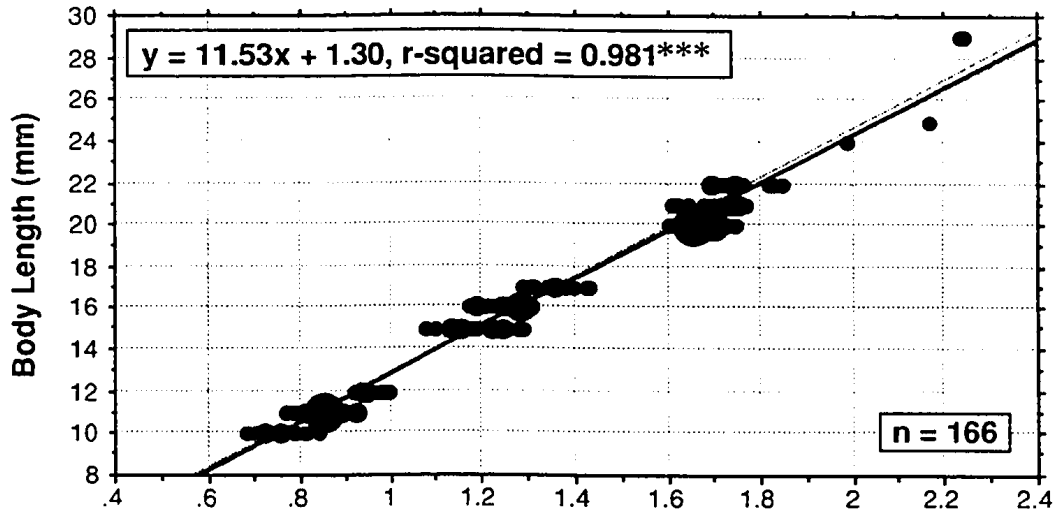


Figure 15. Length frequency of *Thysanoessa spinifera* caught in tows for 1988, 1989, and 1990 (4, 3, and 22 tows, respectively). Fertilized females (black) were distinguished by the presence of transferred spermatophore packets.

a. *Thysanoessa spinifera*



b. *Euphausia pacifica*

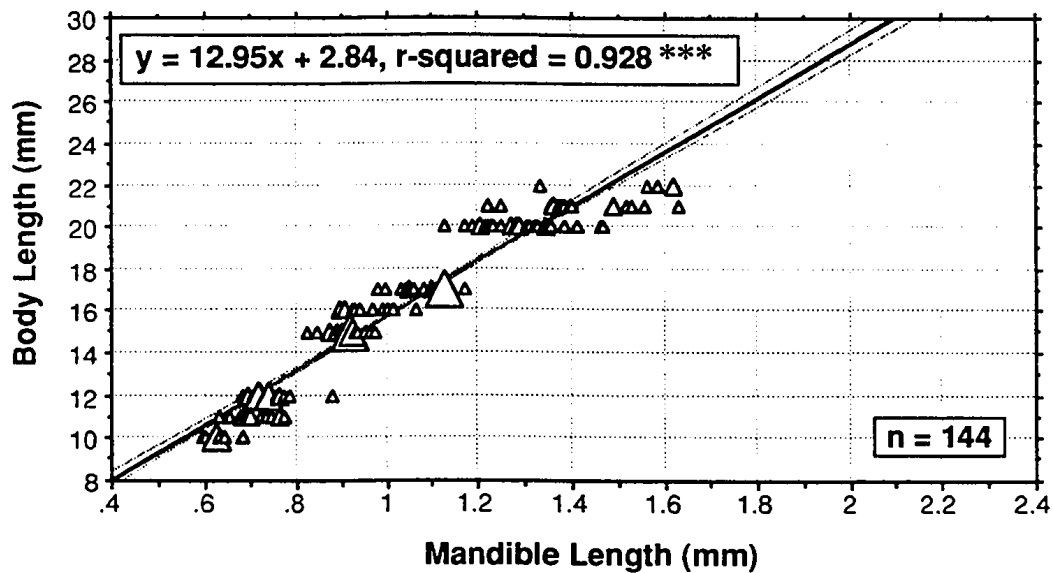


Figure 16. Linear regressions of standard body length versus right mandible length of *Thysanoessa spinifera* and *Euphausia pacifica*. Equations, 95% confidence limits for the slope of regression line, and significant levels of*** $P < 0.001$ are shown.

Mean body lengths (\pm SD) of *T. spinifera* in fecal samples were 16.0 mm (\pm 1.81) in 1988, 16.7 mm (\pm 2.19) in 1989, and 16.2 mm (\pm 1.88) in 1990. *Euphausia pacifica* had a mean body length of 16.1 mm (\pm 2.16) in 1989 and 16.0 mm (\pm 2.58) in 1990 (Fig. 17).

There was a greater percentage of fertilized female euphausiids in the plankton tows for 1988 (34.5%) than 1989 (0%) and 1990 (1.1%; Fig. 15).

Thysanoessa spinifera spermatophores were identified in fecal samples each year; the highest number occurred in 1989 (96 on 24 Sep) and 1990 (130 on 9 Oct; Table 3).

In 1990, *T. spinifera* were most of the biomass collected in surface and shallow plankton tows (grand mean = 92.8% \pm 7.35 SD), whereas *E. pacifica* accounted for 99.6% \pm 0.64 SD of the biomass in deep tows (Table 4).

Nyctiphanes simplex and *N. difficilis* occurred rarely and only in surface and shallow tows (grand mean = 1.1% \pm 0.92 SD and 0.8% \pm 1.06 SD, respectively).

The occurrence of 3 species of planktivores, Cassin's auklet (*Ptychoramphus aleuticus*), Red Phalaropes (*Phalaropus fulicaria*), and Red-necked Phalaropes (*P. lobatus*), were closely correlated with the presence of surface and near-surface scattering layers (Fig. 18).

Environmental Data & Red Tide

Daily mean scattering layer depths and corresponding environmental factors when whales were present were measured less frequently in 1989 than 1990 (18 and 32 days, respectively). For 1989 and 1990, the daily surface temperature, Secchi depth, Beaufort state, and bottom depth were highly variable compared to the distribution of scattering layer depths (Fig. 19).

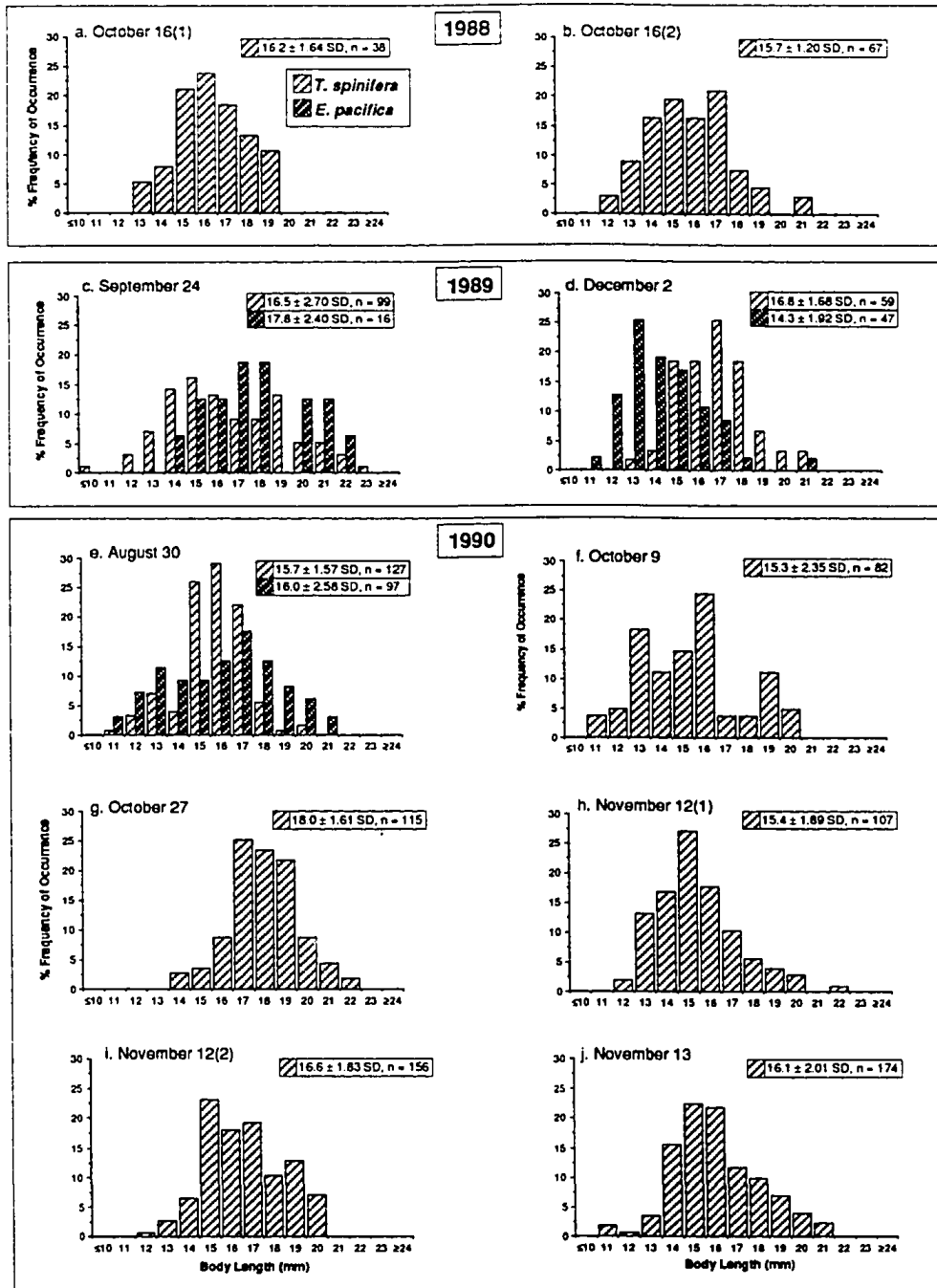


Figure 17. Calculated standard body length frequencies for *Thysanoessa spinifera* and *Euphausia pacifica* from right mandibles collected in humpback whale fecal samples, 1988-90. Mean, ± 1 standard deviation, and sample size (n) for each species and sample are shown.

Table 4. Percentage of euphausiid prey species caught in plankton tows in 1990 at the surface (0-10 m), shallow (11-60 m), and deep (61-140 m). Sample sizes (n), ± 1 standard deviations, and pooled sample sizes (in parentheses) are shown.

PLANKTON TOW DEPTHS	% EUPHAUSIID PREY SPECIES			
	<i>T. spinifera</i>	<i>E. pacifica</i>	<i>N. simplex</i>	<i>N. difficilis</i>
Surface (0-10 m) n = 9	98.0% ± 1.74 SD (1246)	0.7% ± 1.17 SD (4)	1.7% ± 1.85 SD (12)	0.0% ± 0.00 SD (0)
Shallow (11-60 m) n = 12	87.6% ± 22.39 SD (1424)	10.5% ± 17.86 SD (131)	0.4% ± 0.85 SD (7)	1.5% ± 5.25 SD (14)
Deep (61-140 m) n = 3	0.4% ± 0.64 SD (4)	99.6% ± 0.64 SD (931)	0.0% ± 0.00 SD (0)	0.0% ± 0.00 SD (0)

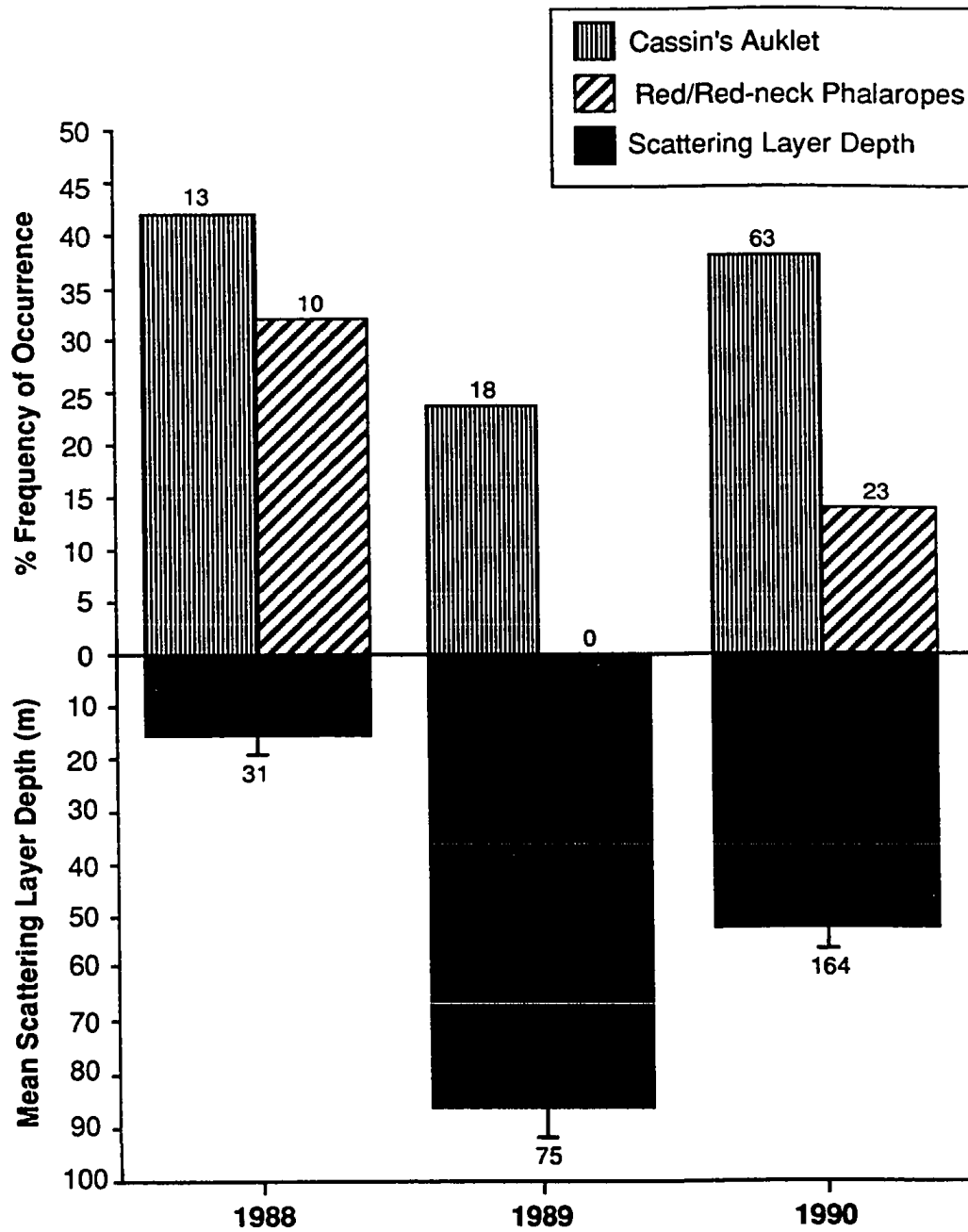


Figure 18. Percent frequency of occurrence of Cassin's auklet and Phalarope observed relative to mean prey depth for 1988, 1989, and 1990. Standard errors (lines below bars) and sample sizes are shown.

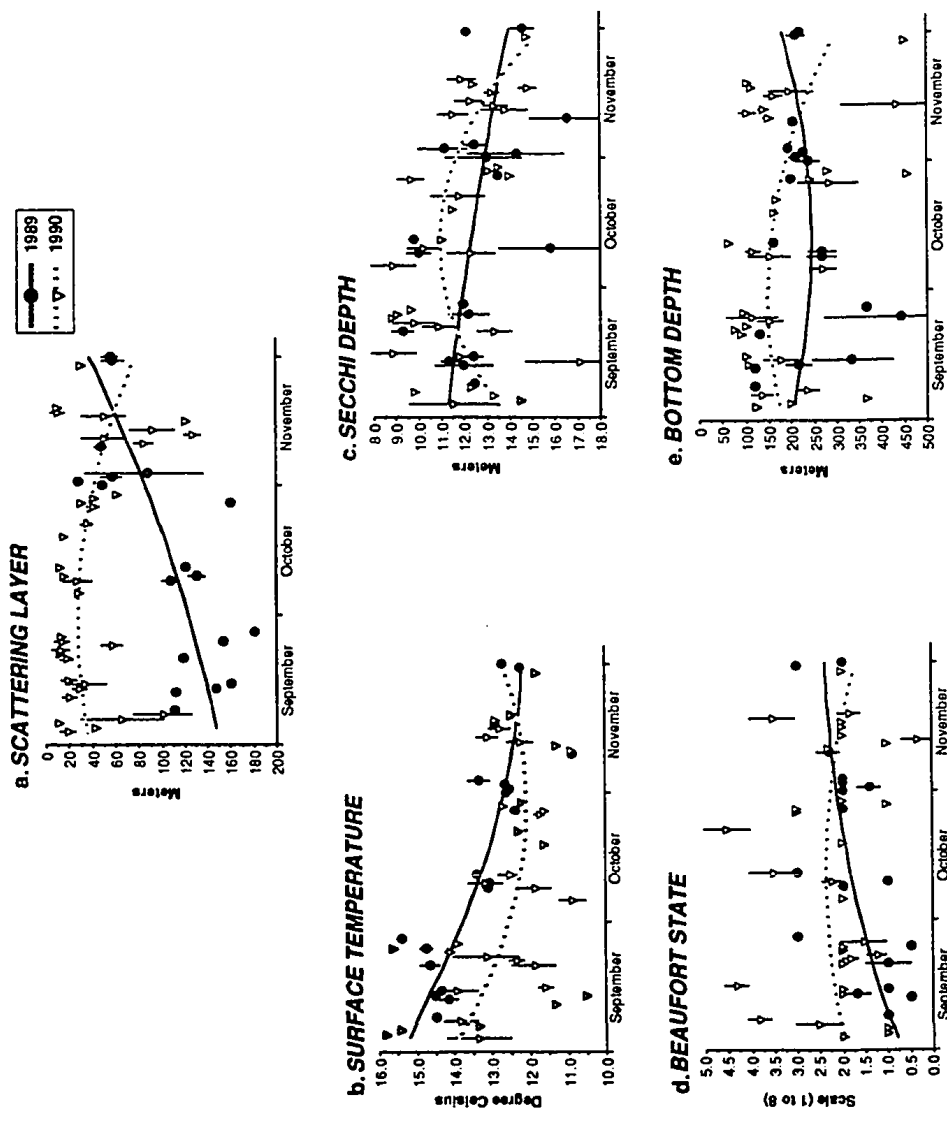


Figure 19. Fitted curves comparing mean daily prey depth, temperature, Secchi depth, Beaufort state, and bottom depth, for September, October, and November in 1989 and 1990. Standard errors (vertical lines) are shown.

In 1989, daily mean depth of the scattering layer was greater than in 1990 during September and October. In 1989 and 1990, surface temperatures declined throughout the study period. Secchi depth increased in 1989, and visibility improved during the 3-month study period. However, in 1990, water visibility fluctuated from relatively clear to turbid waters by mid-October and back to clearer waters again by the end of November. Beaufort state increased during the study period in 1989, but remained the same in 1990. Daily mean bottom depths where humpback whales fed were highly variable for both years, but fitted curves yielded equivalent depths throughout the study period ($t = 1.889$, $df = 48$, $P < 0.01$).

The greatest difference in depth of scattering layer between 1989 and 1990 occurred during September. During September, the mean surface temperature in 1989 ($14.6\text{ }^{\circ}\text{C} \pm 0.39\text{ SD}$) was greater than in 1990 ($13.3\text{ }^{\circ}\text{C} \pm 1.64\text{ SD}$), whereas Beaufort state ($1.5 \pm 0.71\text{ SD}$ and $2.3 \pm 1.21\text{ SD}$, respectively) and secchi depth ($11.7\text{ m} \pm 1.12\text{ SD}$ and $12.5\text{ m} \pm 3.83\text{ SD}$, respectively) were less.

In 1989, only surface temperature was significantly related with scattering layer depth (stepwise regression, $F = 17.5$, $df = 17$, $p < 0.001$), where greater surface temperatures corresponded closely to greater depths of the scattering layer ($r^2 = 0.52$; Fig. 20). Other variables were not related to prey depth in 1989 or 1990. However, in 1990, daily mean Beaufort states were greater and more variable than in 1989, resulting in more wind-induced mixing of subsurface waters. Lower mean surface temperature and secchi depths recorded during 1990 were a reflection of periodic upwelling events.

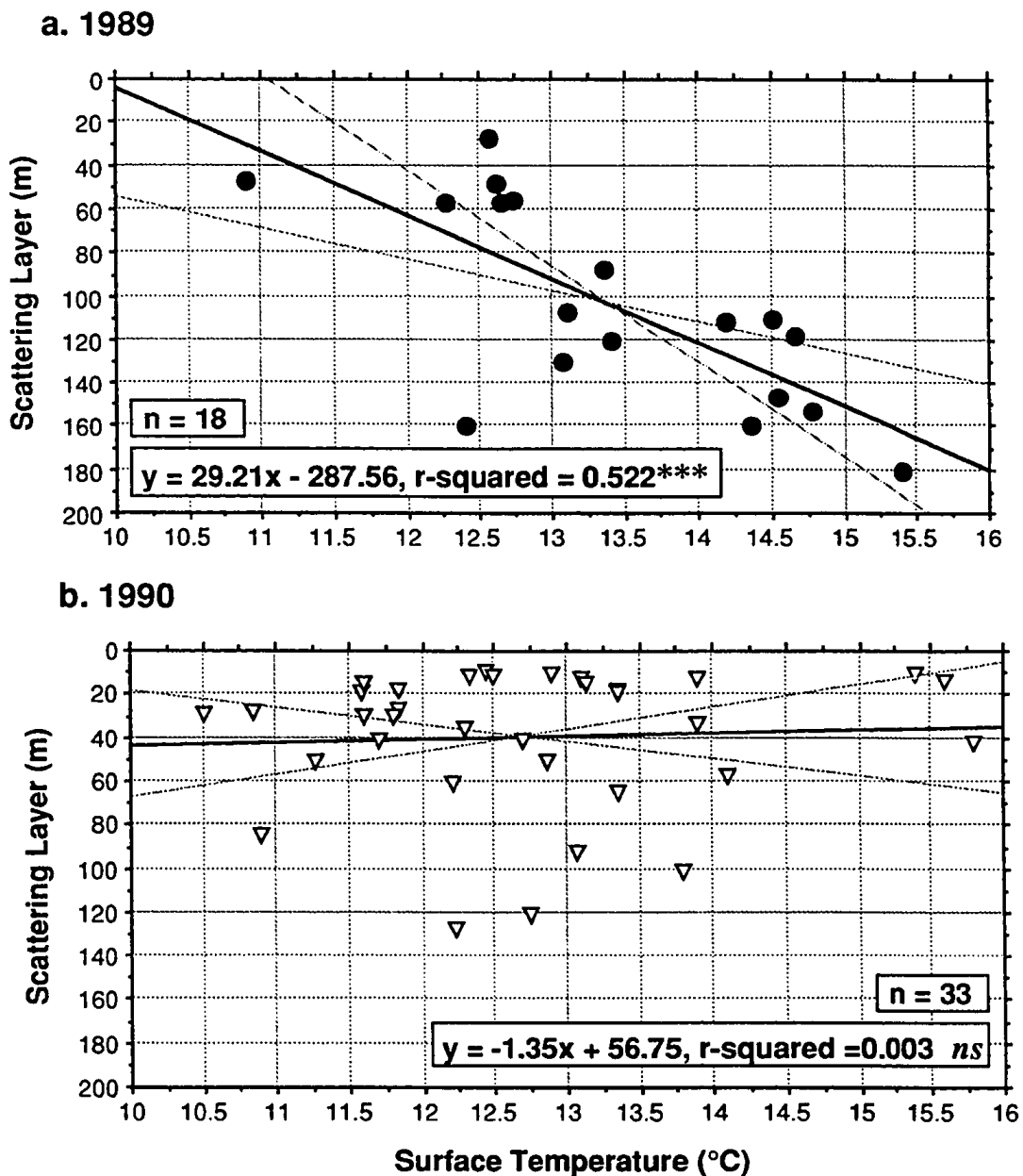


Figure 20. Linear regressions of prey depth versus surface temperature for 1989 and 1990. Equations, 95% confidence limits for the slope of regression line, and significance levels (***) $P < 0.001$ and *ns* = not significant) are shown.

Overall, irradiance (overcast vs sunny) was not significantly related to prey depth in 1989 or 1990. Mean irradiance was slightly greater in 1989 ($1031 \mu\text{E m}^{-2} \text{s}^{-1} \pm 439.3 \text{ SD}$, $n = 40$) than 1990 ($988 \mu\text{E m}^{-2} \text{s}^{-1} \pm 448.1 \text{ SD}$, $n = 158$). However, during September, irradiance in 1989 was significantly greater than 1990 ($1567 \mu\text{E m}^{-2} \text{s}^{-1} \pm 154.6 \text{ SD}$ vs. $1243 \mu\text{E m}^{-2} \text{s}^{-1} \pm 469.9$; $Z = 2.35$, $df = \infty$, $P < 0.05$). Light avoidance by euphausiid prey was not apparent in 1989 or 1990, but their orientation to daily fluctuations in light levels (phototaxis) was positive. In 1990, there was a slight vertical movement of the scattering layer (approx. 20 m) to increasing and decreasing light levels during the study period (Fig. 21).

In 1989, prey depth was positively correlated ($r = 0.96$, $P < 0.05$) with the monthly magnitude of red tide as determined by the Department of Health (Fig. 22). Red tide blooms varied in duration and extent during the three-year study period (Fig. 23). In late October 1988, a red tide bloom was observed around Bodega Bay. The red tide blooms in early October and late November 1990 were comparable, extending 16 km off Bodega Bay. The 1989 bloom persisted much longer, from September to mid-October, and its range extended much further out, approximately 32 km out from Bodega Bay to the Farallon Islands and Cordell Bank (Fig. 23).

Dinoflagellate species varied among years and locations. Red tide samples collected in the study area were composed of *Noctiluca scintillans* in all three years and were red/orange. In 1988 and 1990, brief outbreaks of brownish/red *Ceratium tripos* (red was *Noctiluca scintillans* intermixed) occurred in late October 1988, and were present in early October and late November in 1990.

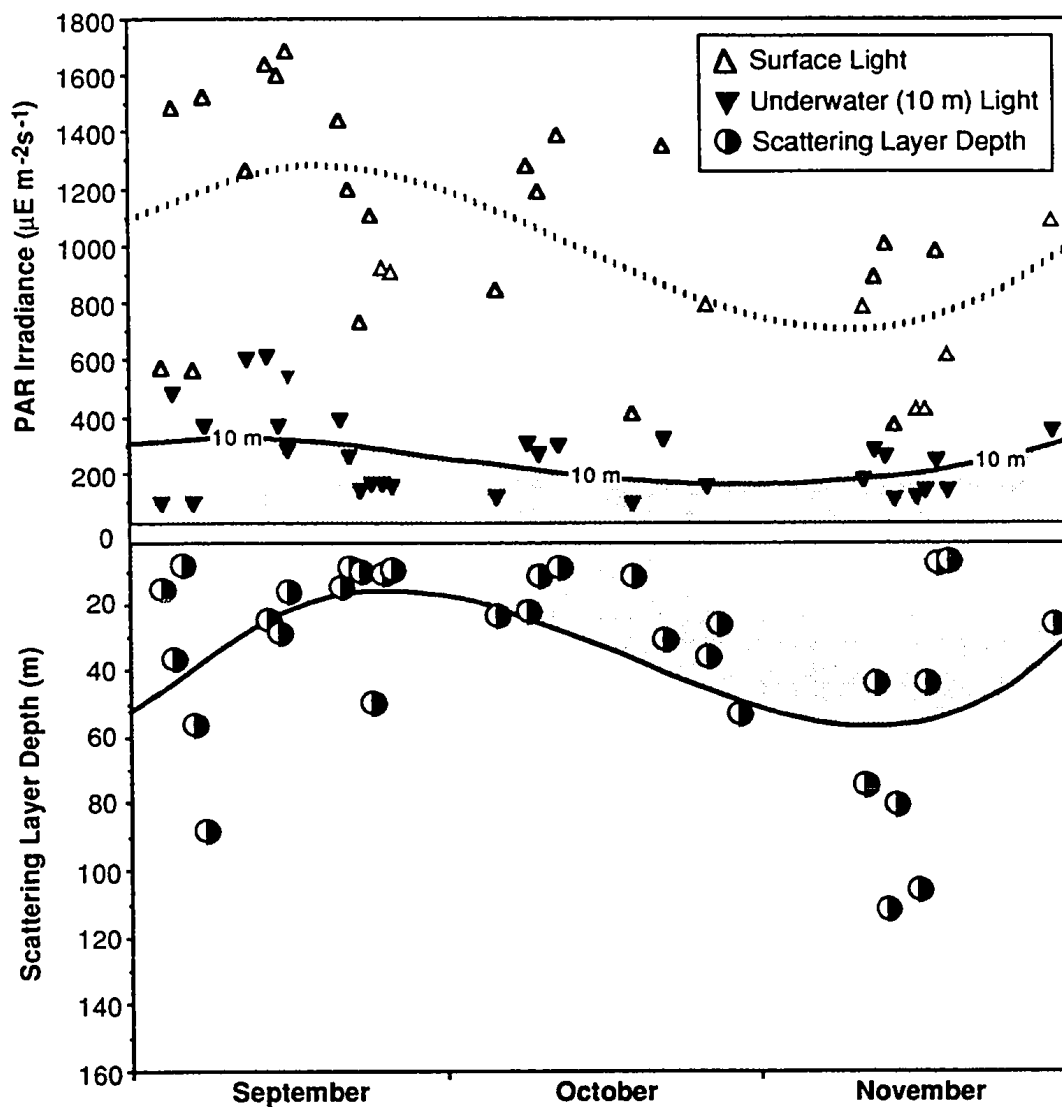


Figure 21. Fitted curves comparing mean daily surface light and underwater (10 m) light with scattering layer depths for the months of September, October, and November in 1990. Total light energy was restricted to the wavelengths between 300 and 720 nm or photosynthetically available radiation (PAR).

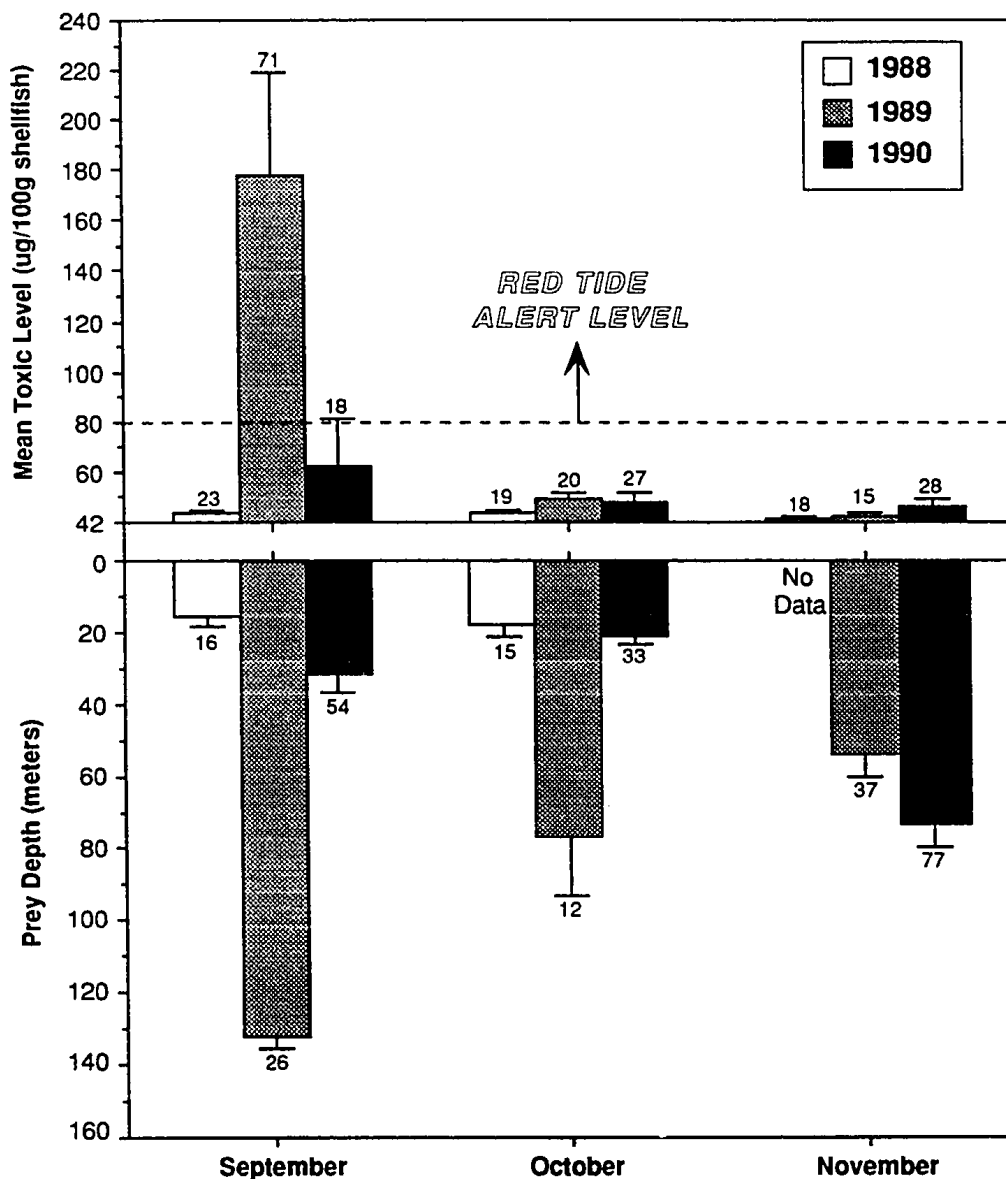


Figure 22. Monthly mean Paralytic Shellfish Poison (PSP) toxin levels for Marin County, California, and mean prey depth for the months of September, October, and November in 1988-90. Micrograms of toxin per 100 grams of intertidal mussel and oyster shellfish were analyzed. Levels below 42 are below the limits of detection, and levels of 80 or above are alert levels (PSP data are from the Department of Health Services, CA, PSP Final Reports). Monthly sample sizes (above and below bars) and standard errors (length of t-bars) are shown.

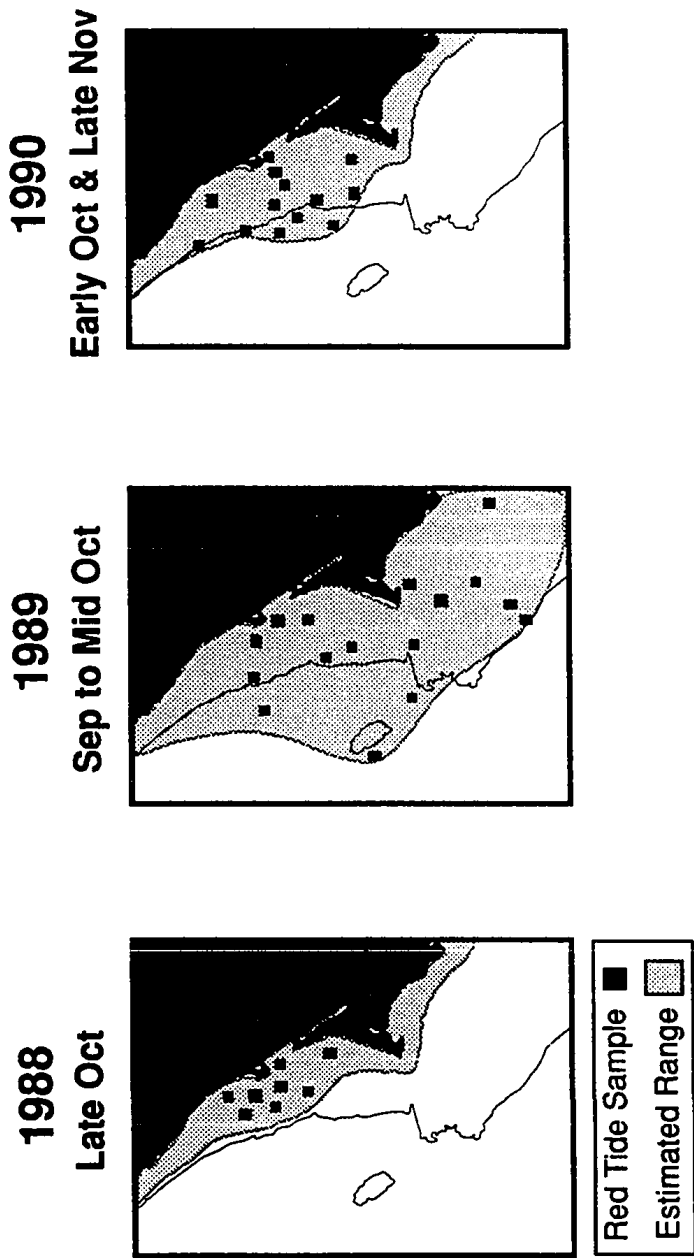


Figure 23. Locations of collected red tide samples in late October 1988, September to mid-October 1989, and early October and late November 1990. The range of red tides were estimated by visual confirmation, collected samples on vessel surveys, and PSP reports from the Department of Health Services.

In contrast, samples collected early during the extensive 1989 bloom contained the toxic dinoflagellate, *Alexandrium catenella* (previously named *Gonyaulax catenella*) and was succeeded in late September by a thick bloom of *Noctiluca scintillans*.

DISCUSSION

Foraging Behavior and Energetics

Humpback whale feeding behavior differed significantly in 1989 compared with 1988 and 1990, corresponding closely to differences in prey depth. Surface feeding was typically lateral lunging preceded by a fine-misted bubble-cloud emitted underwater and observed at the surface. Though it is not known how whales create this cloud, it is possible that they emit bubbles from their mouth, allowing their baleen to sieve a mist of fine bubbles which rise to the surface (Reidenberg and Laitman 1991; J. Reidenberg, pers. comm., 1991; Fig 10). In an aquarium, bubbles emitted from an air stone disoriented *T. spinifera*. Fine bubbles adhered to their feeding appendages and under their carapaces; this disrupted free swimming and immediately drove them to the surface (Komaki 1966; Kieckhefer pers. obs. 1990). Bubble-clouds produced by feeding whales may similarly incapacitate swimming euphausiids and concentrate them at the water's surface (Jurasz and Jurasz 1979; Hain et al. 1982; Baker 1985), making surface feeding more efficient. Other feeding behaviors using bubbles, like bubble-net feeding (Ingebrigsten 1929; Jurasz and Jurasz 1979; Hain et al. 1982), were not observed. Likewise, Dohl et al. (1983) from 1980 to 82 and Calambokidis et al. (1989a, 1991a) from 1986 to 1990 never observed humpback whales bubble-net feeding in the study area. There were a few unconfirmed reports of bubble-net feeding further south, off Pigeon Point and Half Moon Bay, possibly correlated with humpback whales feeding on northern anchovy (R. LaMar, pers. comm. 1990).

Surface-feeding groups were observed on four occasions in 1988 and

on eleven occasions in 1990, where two or three whales appeared to combine their efforts in capturing prey. On eight occasions, pairs of whales were repeatedly observed lateral lunging in tandem (approximately 4 m between individuals), whereas on four occasions, one whale would execute a lateral lunge immediately followed by a second following whale executing a diagonal lunge. On three occasions, whale trios were observed apparently feeding cooperatively. The two outside whales lateral lunged, while the center whale performed either a vertical or diagonal lunge. This feeding method, known as "echelon" feeding, was used by humpback whales feeding in southeast Alaska (Baker 1985) and by skim feeding bowhead whales in the Arctic (Würsig et al. 1984; Würsig 1988). It is possible that this configuration of whale feeding counteracts the classic escape response of schooling prey (e.g. fountaining or swimming around and behind the stimulus), because the trailing whale intercepts prey escaping from the lead whale (Pitcher and Wyche 1983; Hamner et al. 1983; Hamner 1984; Baker 1985; Hall et al. 1986; O'Brien 1987; Strand and Hamner 1990).

Nevertheless, cooperative surface feeding was rarely seen, compared with southeast Alaska. In southeast Alaska, larger groups (8-11) have been observed feeding on faster, more mobile prey, such as Pacific herring (Jurasz and Jurasz 1979; Baker 1985; D'Vincent et al. 1985). It is possible that feeding on euphausiids does not require a cooperative effort, because euphausiids are slower swimmers than fish.

Humpback whales feeding cooperatively on schooling fish vocalize before surface lunging in southeast Alaska (D'Vincent et al. 1985). In addition, it has been reported that humpback whales feeding in the same area, on

euphausiids and fish vocalize when they create bubble-nets (Payne 1979; Kieckhefer pers. obs. 1982). It has been suggested that the mechanical vibration created by humpback whale vocalizations may assist in corralling prey or coordinating group efforts (Baker 1985; D'Vincent et al. 1985). In contrast, humpback whales feeding near Cordell Bank were silent ($n = 18$, Table 2).

Songs of humpback whales were recorded several times in the Cordell Bank area. Though songs are generally produced in the breeding grounds (e.g. Schevill 1964; Winn and Winn 1978; Thompson et al. 1979), humpback songs have been reported in the feeding areas in the North Atlantic (Stellwagen Bank, Massachusetts; Mattila et al 1987) and North Pacific (Stephens Passage/Frederick Sound, Alaska; McSweeney et al. 1989). Mattila et al. (1987) suggested that singing in the feeding grounds may be related to (1) mixing of individuals from different regions or to (2) unknown factors that stimulate migration. Because humpback whales are often sighted in the study area from April through December with peak abundance in September (Dohl et al. 1983, Calambokidis et al. 1989a) and when songs were first recorded in this study (Table 2), it is more likely that the former theory, relating to mixing, would be true. In general, vocalizations of any nature produced in the feeding grounds could confer some feeding advantage. For example, they may inform other whales of a localized food source (Mobley et al. 1988).

Surface feeding was characterized by fast, short-duration dives, and rapid surface swim speeds compared with deep diving, thus possibly incurring higher oxygen demand (Costa 1991). In 1989 and 1990, blow rates of surface feeding whales were significantly greater than deep feeding whales in 1988 and 1990. It is likely that euphausiids at the surface avoided predators better in

deep than shallow water. Well illuminated, relatively warm surface water may enable them to detect shadows more easily, cooperate in more efficient evasive schooling responses, and move faster (O'Brien 1987; Strand and Hamner 1990). Cooperative surface feeding among humpback whales in this setting may greatly increase feeding success.

Costa (1991) asserted that the major factors influencing whether a predator will pursue prey at a specific depth are prey type, size and energy content, and behavior. At deeper depths, whales have no barriers, comparable to the air-water interface, against which to trap prey. Deeper prey depths require longer more demanding travel times. In 1989, whales made long-duration dives up to 17 min, and had extended durations of up to 9 min at the surface. At the surface, whales appeared to be hyperventilating, swimming slowly (0-1 kts) and breathing up to 23 times. In 1989, feeding humpback whales appeared extremely lethargic at the surface compared to the rapid, high-energy swimming of surface feeding whales in 1988 and 1990. Hamner et al. (1988) reported southern right whales (*B. australis*) slowly moving at the surface and hyperventilating before long dives to feed on sub-surface Antarctic krill (*Euphausia superba*). Because only deep-dwelling prey were available in 1989, whales apparently reduced their oxygen consumption by slowing down their swimming speed at the surface.

Time spent at the surface has been correlated positively with the duration of preceding dive of Weddell seals (*Leptonychotes weddelli*; Kooyman et al. 1980), bottlenose dolphin (*Tursiops truncatus*, Ridgway 1986, Ridgway et al. 1969), gray whales (*Eschrichtius robustus*, Harvey and Mate 1984; Würsig 1984; Würsig et al. 1986), southern right whales (*Eubalaena australis*, Hamner

et al 1988), sperm whales (*Physeter macrocephalus*, Lockyer 1977), and humpback whales (Baker 1985; Bauer 1986; Dolphin 1987a,b,c,d). The dive depth of humpback whales during feeding can be predicted with a high degree of confidence from their respirations and dive patterns (Dolphin 1987b).

Transit time to prey during deep dives was shortened by increasing the angle of descent. Humpback whales raise their posterior and flukes high into the air by braking forward momentum with their pectoral fins rotated forward, thus providing the initial downward thrust needed for sub-surface dives (Edel and Winn 1978; Kieckhefer pers. obs. 1983; Fig. 12). The angle of the body during a dive (30°, 45°, or 90°) was dependent on their swim speed and angle of their pectoral fins. In this study, fluke-up and high fluke-up dives were seen mostly during shallow and deep feeding. On seven occasions, depth sounder traces indicated humpback whales diving to deep scattering layers at an angle >70° after high fluke-up dives. In addition, whales were consistently observed flexing their tail stock before deep dives (77%). This behavior may enhance body circulation from consecutive deep diving periods, or generate enough momentum to reach a steep angle to descend more quickly to desired depths. These whales may have been diving as deep as 180 meters, based on depth of scattering layer (Fig. 19a). More direct evidence, such as time-depth records, are needed to confirm the actual feeding depth of humpback whales.

The maximum feeding depth of humpback whales is unknown; however, it is assumed that baleen whales do not exceed 300 meters in depth (Nemoto 1963). In the North Atlantic, Whitehead (1983) obtained depth sounder traces of humpback whales traveling to depths of 195 m (n = 104), whereas in southeast Alaska, Dolphin (1987a) found that humpback whales restricted their feeding to

the upper 120 m (n = 284) and only 8 dives (3%) exceeded 120 m. Dolphin (1987a) suggested that extended surface intervals and steady ventilations may be indications that these whales are exceeding their aerobic dive limit, revitalizing their oxygen debt after continuous deep dives. This suggestion was based primarily on anaerobic diving debts in seals, in which disproportionate increases in surface duration results (Kooyman et al. 1980). However, the slower swimming speed of humpback whales during deep, long duration dives may use oxygen more slowly, thus avoiding anaerobic diving (Kooyman 1989; Costa 1991).

Prey Distribution and Relative Abundance

Euphausiids represent a major fraction (5-10%) of the total biomass of plankton, and are a major food source for many marine birds, seals, and baleen whales (Mauchline 1980). However, it is not their numbers alone that make them so important in the food chain, but that they live in great concentrations. *Thysanoessa spinifera* are dominant in the neritic (coastal) environment, and *E. pacifica* is found further offshore along the northeast Pacific coast (Brinton 1962a; Hebard 1966; Youngbluth 1976). Extensive surface shoals of *T. spinifera* form along the California coast from Fort Ross to the Channel Islands (Barham 1956; Brinton 1962a; Harvey 1979; Smith and Adams 1988; Schoenherr 1991). Hebard (1966) found that *T. spinifera* was the most abundant species of euphausiid off Oregon from September through February. In the coastal areas of the Bering Sea, humpback whales fed largely on *T. spinifera* and its egg masses (Hollis 1939). During this study, humpback whale fecal samples and plankton tows confirmed that *T. spinifera* was the primary

euphausiid prey.

Plankton tows obtained during this study support Brinton's findings (1962b) that *T. spinifera* remains in the upper 100 m, whereas *E. pacifica* performs diurnal vertical migrations, with peak abundance at 200-400 m during daylight and at the surface at night. *Thysanoessa spinifera* was found predominantly in surface and shallow tows, whereas *E. pacifica* was 99.6% of the biomass in deep tows. The occurrence of *E. pacifica* in humpback whale fecal samples in 1989 may have been associated with whales feeding deep and further offshore along the continental shelf break.

Rice (1978) reported that stomach contents of humpback whales killed from 1956 to 1965, in the vicinity of Cordell Bank/Farallon Islands, contained roughly 60% northern anchovy and 40% *Euphausia pacifica*, with only trace amounts (<0.5%) of Pacific herring and *Thysanoessa spinifera*. Catcher boats operated 230 km from the Golden Gate Bridge, off the continental slope/edge in water depths of 2,700 to 4,000 meters (Rice 1963, 1971). Distance offshore may explain the high percentage of *E. pacifica* compared with *T. spinifera* in those humpback whales (Rice 1977; D. W. Rice. pers. comm. 1991). Five sub-samples of humpback whale stomachs from whales taken during the 1956-65 Cordell/Farallon whaling fishery (National Marine Mammal Laboratory, Seattle, WA) were examined. These samples contained mostly *E. pacifica* (>98%), which correlated with whales captured beyond the continental shelf in water depths of 2,200 to 3,700 meters (Table 5).

Table 5. Location and capture dates of humpback whales when stomach contents were collected during commercial whaling off Central California from 1960-64 (Sub-samples provided by D.W. Rice and A.A. Wolman, National Marine Mammal Laboratory, Seattle, WA).

Capture Date (d-m-y)	Location (lat. & long.)	Sex	Length (m)	Bottom Depth (m)	Prey Type*	Standard Body Length** (mean \pm SD, n)
30 Apr 60	37° 47'N, 123° 32'W	M	14.0	2561	<i>E. pacifica</i>	18.9 mm \pm 1.57 SD, n = 7
20 Aug 61	38° 00'N, 123° 42'W	F	11.0	2744	<i>E. pacifica</i>	19.3 mm \pm 1.24 SD, n = 19
24 Apr 62	37° 45'N, 123° 30'W	F	15.9	2195	<i>E. pacifica</i>	19.9 mm \pm 2.17 SD, n = 8
28 Apr 63	37° 50'N, 124° 02'W	F	10.7	3658	<i>E. pacifica</i>	19.0 mm \pm 1.07 SD, n = 15
29 Apr 63	37° 41'N, 124° 03'W	M	12.8	3567	<i>E. pacifica</i>	18.3 mm \pm 0.89 SD, n = 8

* Dominant prey item found in all sub-samples was >99%.

** Body lengths were derived from length measurements of right mandibles found in all sub-samples and calculated by appropriate standard body length/mandible length linear regression equation.

The formation of surface or subsurface swarms has been reported in 18 species of euphausiids living predominantly in higher latitudes (Omori and Hamner 1982). Euphausiids feed mainly on phytoplankton and/or small zooplankton, such as copepods. Daytime surface swarming of euphausiids is of interest, because they differ from normal vertical migrators. The factors that bring about the formation of daytime surface swarms are not clear and may be different for each species. Theories proposed to account for daytime surface swarms are: (1) predators driving euphausiids to the surface (Bigelow and Schroeder 1953; Komaki 1967; Brown et al. 1979; Endo 1984), (2) euphausiids congregating at the surface to feed (Mauchline and Fisher 1969; Brown et al. 1979; Hamner 1984), (3) maturation or reproduction occurring at surface (Endo 1984; Nicol 1984; Smith and Adams 1988), (4) passive transportation to the surface by currents or tides (Brinton 1962b; Forsyth and Jones 1966; Brown et al. 1979; Schoenherr 1991), or (5) a breakdown of an environmental barrier, such as a thermocline, which enables them to vertically migrate to the surface (Komaki 1967; Endo 1984).

Surface swarms of *E. pacifica* are rare along the California coast, whereas surface swarms of *T. spinifera* are common during summer (Brinton 1962b). Because *T. spinifera* remains in the upper 100 m both day and night, in contrast to *E. pacifica*'s diel vertical migrations, the California current's strong thermocline throughout most of the year may act as a barrier to *E. pacifica* occurrence at the surface. Endo (1984) found *E. pacifica* at the surface in spring off Sanriku, Japan. He suggested that the absence of a thermocline in early spring allowed *E. pacifica* to swarm at the surface. In the lower St. Lawrence estuary, Canada, *Thysanoessa raschi* and *M. norvegica*, however,

had no difficulty crossing the thermocline during their diel vertical migrations (Simard et al. 1986).

Smaller euphausiids caught in plankton tows than found in fecal samples was likely caused by net avoidance, especially by larger and faster swimming euphausiids. It has been suggested that euphausiids detect nets visually by seeing shadows during the daylight and bioluminescence at night (Wiebe et al. 1982), or acoustically by vibrational stimuli of the towing cable, harness, or approaching net (Fleminger and Clutter 1965; Hovekamp 1989). Although the fecal sample size was small ($n = 11$) for 1987-1990, the overall mean lengths of *T. spinifera* and *E. pacifica* in fecal samples were consistently larger than net samples, providing a more accurate estimate of size classes of euphausiids eaten by humpback whales.

Higher percentages of fertilized *T. spinifera* were collected in 1988 and 1990 than 1989. These undoubtedly comprise a richer food source for humpback whales, which may explain greater numbers of whales in 1988 and 1990 (Calambokidis et al. 1989a). The occurrence of fertilized euphausiid females likely reflects favorable oceanographic conditions that created more productive, nutrient-rich upwelled waters (Brinton 1962b).

Under-estimation of fish feeding was possible, because the digestive system of whales may completely dissolve fish otoliths and other calcium hard parts in its acidic solution before they are excreted (Jobling 1987). However, the coloration of all feces collected were red-brick, indicating euphausiid feeding; versus yellow-green, which indicate anchovy or saury feeding (Rice pers. comm. 1991). Yellow-green feces of humpback whales were frequently seen at the surface off Half Moon Bay and adjacent waters, during aerial surveys

(R. LaMar, pers. comm. 1990). This strongly suggested that humpback whales fed on fish south of the study area.

Oceanographic Conditions & Productivity

To understand fluctuations in prey availability in relationship to humpback whale distribution and abundance near Cordell Bank/Farallon Islands, it is essential to know something about the environment they both inhabit. The annual pattern of currents in the study area are divided into three variable, overlapping periods: (1) upwelling, from February through August; (2) oceanic, from September through October; and (3) Davidson, from November through January (reviewed by Sverdrup et al. 1942). This study focused on the peak feeding period of humpback whales, from September through November (Calambokidis et al. 1989a). During this time, the end of an upwelling period, the entire oceanic period, and the beginning of the Davidson Current were observed. In late summer and fall, the northwest winds subside, causing a reduction in the strength of the offshore California Current and reduction in cold, nutrient-rich coastal waters from upwelling. As a result, warm oceanic water and warm, nutrient-deficient waters from the northward-flowing counter-current (Davidson Current) moves coastward.

The interaction between wind stress and the California current appears to generate upwelling of cold, nutrient-rich water to the sea surface (e.g. Bakun and Parrish 1980; Parrish et al. 1981; Abbott and Barksdale 1991; Strub et al. 1991; Washburn et al. 1991). These seasonal surface conditions probably produce the large zooplankton biomass, which occurs in fall off central California (Abbot and Barksdale 1991; Smith et al. 1986). Topographic features,

like banks, sea mounts, canyons, and a wide range of continental shelf and slope widths, may have a significant influence on water circulation (Schwing et al. 1991). In this study, Bodega Canyon, Cordell Bank, and the Farallon Islands were the primary sites of feeding activity (Fig. 3). During upwelling periods, these topographic features create eddies, gyres, and fronts which may act as "trophic traps" concentrating and/or attracting prey for whales and other predators (Kenney and Winn 1986; Smith et al. 1986; Piatt et al. 1989; Schwing et al. 1991).

On 2 September 1990, a well-developed cyclonic gyre (Fig. 24 f), apparently generated in the south, deflected out of Bodega Canyon and around to the northeast of Cordell Bank (Ericksen 1991). Whale positions, 3 days before and after this image was taken, were consistently found along the north frontal edge of this gyre. However, if offshore flow is continuous or too strong, less motile organisms, such as phytoplankton and some zooplankton, will be dispersed rapidly offshore, creating relatively unproductive waters inshore (see Fig. 24 and 25, July and August 1989). On the other hand, if wind conditions are weak for long periods, it does not provide proper conditions to set-up of these boundaries between different water masses (Ramp et al. 1991). This was evident from September through December in 1989 (Fig. 24 and 25). Mean monthly upwelling indices for all three years indicated that 1989 had the most upwelling during the strong upwelling period of July and August, and upwelling dropped abruptly in the following months in conjunction with an increase in surface temperatures (Fig. 25). It is predicted that these environmental factors were instrumental in setting-up ideal conditions for red tide blooms (Franks et al. 1989).

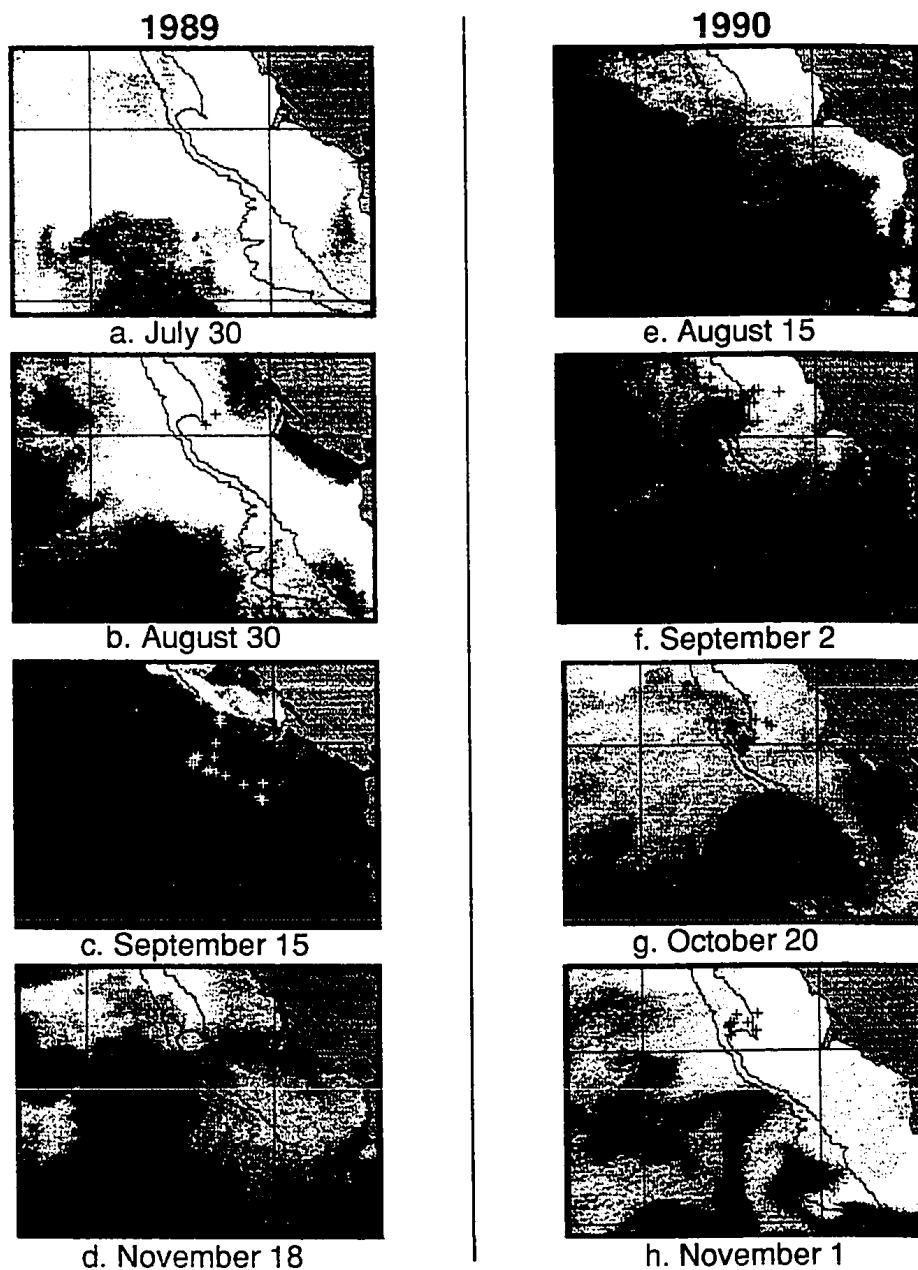


Figure 24. Satellite images (TIROS-N/NOAA) of sea surface temperature (SST) for the most cloud-free days found in 1989 and 1990. For all images the range of linear gray scale was set at 10-16° C. Lighter shades denote colder water. Plus symbols in b, c, f, g, and h denote whale positions 3 days before and after images were taken. The 200 and 1000 m depth contours are shown. (Images were provided by N. Garfield, Department of Oceanography/Naval Postgraduate School, Monterey, CA).

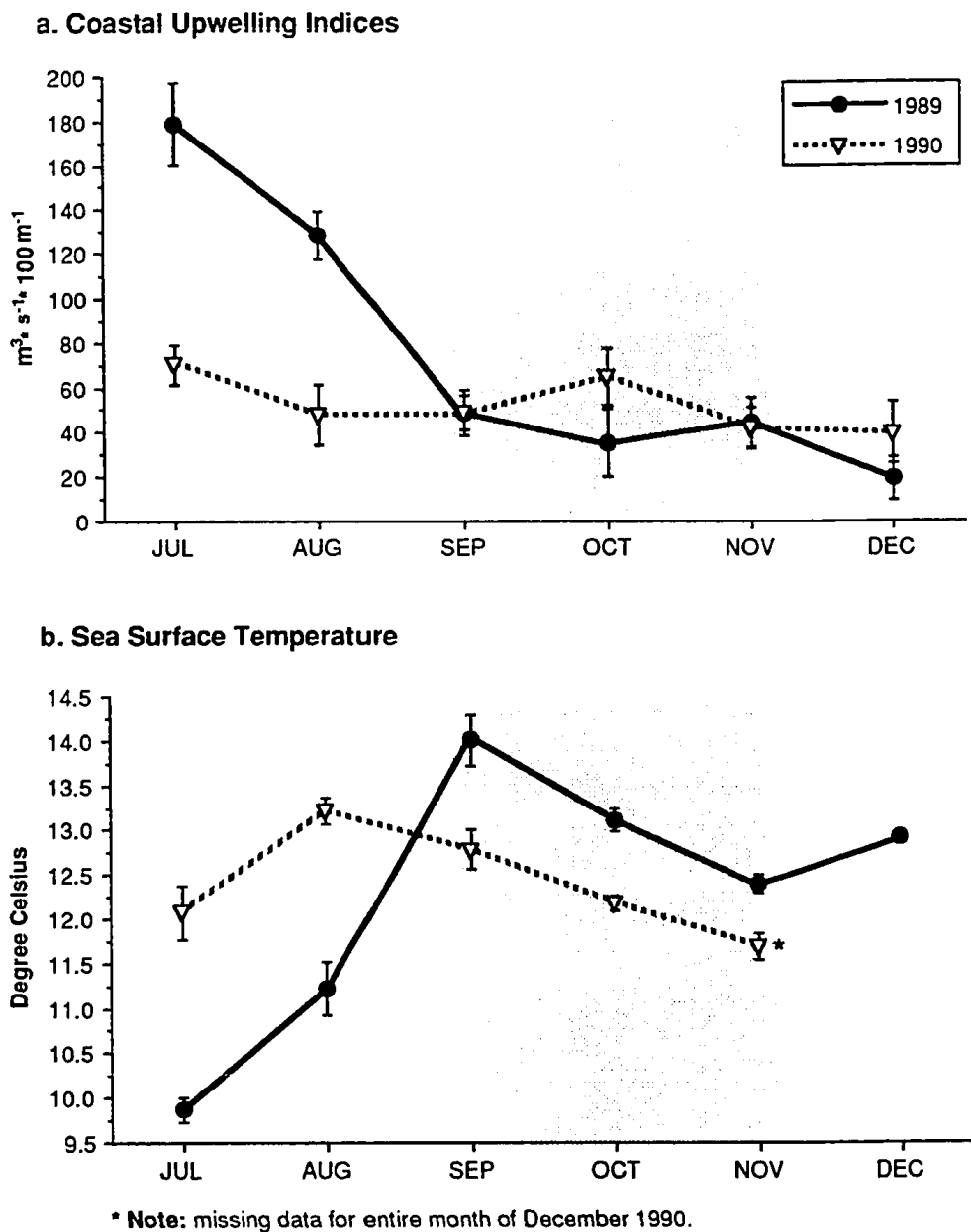


Figure 25. (a) Monthly coastal upwelling indices ($\text{m}^3 \cdot \text{s}^{-1} \cdot 100 \text{ m length of coastline}^{-1}$) at 39°N , 125°W and **(b)** sea surface temperature ($^\circ\text{C}$) at NOAA buoy 46013 (38.2°N , 123.3°W) for July-December 1989 and 1990. Note extremely high upwelling and low temperatures during July and August 1989 followed by a sharp decrease in upwelling and increase temperature in September. Study period (shaded area) and standard errors (vertical lines) are shown. (Data provided by D.M. Husby, Pacific Fisheries Environmental Group, Monterey, CA).

Correlations between Whale Behavior, Prey Occurrence, and Environmental Conditions

Altered environmental conditions, such as an increase in water temperature by a strong "El Niño," change prey availability for many sea bird populations near the Gulf of the Farallones (e.g. Ainley and Lewis 1974; Ainley et al. 1986; Kaza and Boekelheide 1984; Croll 1990), as well as around the world (review by Cairns 1987). More subtle changes in oceanographic conditions that trigger severe red tide (dinoflagellate) blooms, such as in 1989, may have physically displaced daytime surface swarming of *T. spinifera*, forcing them deeper in the water column (Boalch 1984, Potts and Edwards 1987, Ogata et al. 1989) or possibly killed them with their fatal toxins (Jenkinson 1989, White et al. 1989). Moreover, humpback whales may die from ingesting prey loaded with dinoflagellate toxins (Anderson 1988; Geraci 1989, Geraci et al. 1989).

Increased light intensity in 1989 may have influenced deeper scattering layers compared with 1988 and 1990. However, direct response of light avoidance by euphausiid prey was not apparent. For example, in 1990, there was a slight vertical migration (approx. 20 m) of euphausiid prey to fluctuations of daily light over the study period; however, there was a positive phototaxis response (Fig. 21). In general, dinoflagellate blooms are primarily regulated by various environmental factors such as temperature, sea state (Beaufort), day length, light intensity, and quality and quantity of nutrients (Franks et al. 1989; Imai 1989). The combined environmental conditions in 1989 before the study period (July to August) may have triggered the most intense, wide-spread occurrence of red tide in this area since 1980 (Figs 23, 24, 25). When winds are

calm and temperatures peak shortly after a strong upwelling period, dormant cysts of dinoflagellates germinate and flourish near the surface waters. The depth of maximum cell concentration appears dependent primarily on light intensity. Passow (1991) hypothesized that dinoflagellates migrated upwards toward higher light intensities until a certain level of irradiance was reached, after which migration was directed downwards to avoid light intensities greater than threshold. Diel vertical migrations of concentrated shoals of dinoflagellates can exceed 40 m in depth (Passow 1991). During periods of wind, dinoflagellates are mixed deeper, to depths exceeding 40 m, and move near the surface to their threshold light levels during calm periods (Boalch 1984; Passow 1991).

In the Gulf of the Farallones and adjacent waters, seabirds, such as Red phalaropes (*Phalaropus fulicaria*), Red-necked phalaropes (*P. lobatus*), and Cassin's auklets (*Ptychoramphus aleuticus*), feed on surface and shallow sub-surface plankton. Phalaropes feed on copepods at the surface of fronts (Brown 1980; Briggs et al. 1984, Haney 1989). Cassin's auklets eat euphausiids primarily near the surface down to depths of 40 m (Burger and Powell 1990). The percentage decrease of observed Phalaropes (32% to 0%) in 1989 may have indicated the disappearance or displacement of copepods deeper in the water column (Fig. 18). Frequency of occurrence of Cassin's auklets also decreased in 1989 (42% to 24%), possibly because *T. spinifera* were less abundant (Mauchline 1967; Nemoto 1972). Mean depth of the scattering layer from September through November 1989, was 84.6 m \pm 46.30 SD, which exceeded the diving capabilities of Cassin's auklets (Burger and Powell 1990). In addition, large variation in Cassin's auklets' diet occurred in 1980,

T. spinifera was 68% of diet in 1979 and only 6% in 1980, whereas *E. pacifica* increased from 32% of diet to 75% (Ainley et al. 1990). This correlates with one of the largest red tide outbreaks in California, which began during the month of July 1980 (Price 1989; Price and Kizer 1990).

Potts and Edwards (1987), working off Plymouth Breakwater, England, observed the physical and toxic effects of the dinoflagellate, *Gyrodinium aurelum*, on larval, post-larval, and juvenile fish. Juvenile fish were not widely distributed throughout the water column, but were concentrated in a band 50 cm over the sea floor. Following the bloom there was a dramatic reduction in numbers of larval and post-larval fish. Boalch (1984) and Jenkinson (1989) reported concentrations of more than five million *G. aurelum* per liter of water during warm and stable sea conditions, which adversely displaced certain species deeper in the water column. Other less mobile species died, due to viscous, anoxic conditions created in the sea water and/or direct contact with the toxin. Kvitek et al. (1991) suggested that sea otters (*Enhydra lutris*) in southeast Alaska are displaced horizontally away from red tide blooms to the outer coast where toxic clams are rare.

There appears to be a fine balance between the optimal conditions of humpback whale feeding on surface swarming prey versus adverse conditions when prey are deep in the water column and less aggregated. Information on the demographic structure of the two primary euphausiid stocks, *Thysanoessa spinifera* and *Euphausia pacifica*, is needed for the survey area. It is also necessary that whale and prey data be integrated with CTDs, remotely sensed SSTs, and bathymetric data to examine correlations between their distribution and oceanographic features (Fairfield et al. 1991). Underlying hydrographic

processes occurring at this region were most likely missed by remotely sensed SSTs alone. More site-specific knowledge of hydrographic processes existing around the Farallon Islands, Cordell Bank, and Bodega Canyon may provide a better understanding of the physical and biological factors regulating the abundance and distribution of humpback whales and their prey.

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APPENDIX A

DEFINED BEHAVIOR CATEGORIES:

Behavioral states were categorized as:

1. **Rest:** indicated when a focal whale lies motionless near the surface for 5 min or more.
2. **Slow Travel:** consists of continuous, sustained swimming less than or equal to 6 km/h (3 knots), close to the surface with little change in direction.
3. **Fast Travel:** consists of continuous, sustained swimming greater than 6 km/h, close to the surface with little change in direction.
4. **Mill/Search:** erratic, non-oriented (zig-zagging) diving with changes in speed and direction as if searching for prey. No visible prey layer detected on the depth sounder.
5. **Surface Feed:** circling and diving over a localized area, often lunging with mouth open at the surface. Distinct prey layer visible within the upper 10 m.
6. **Shallow Feed:** circling and diving continually in the same area over a distinct prey layer detected between 10 and 60 m in the water column.
7. **Deep Feed:** circling and diving continually in the same area over a distinct prey layer detected below 60 m in the water column.

APPENDIX B

BEHAVIORAL ETHOGRAM:

RESPIRATION:

FS	= First Surface (with no blow)
F	= First Surface Blow
B	= Blow
M	= Missed Blow(s)?
N	= No Blow Rise
A	= Arch Back
D	= Fluke-DOWN Dive
U	= Fluke-UP Dive
H	= High Fluke-UP Dive
NF	= Not First Surfacing

BUBBLE & BLOW BEHAVIOR:

BH	= Bubbles at Blow Hole
BT	= Bubble Trail
BC	= Bubble Cloud
FB	= Fountain Blow
WB	= Wheeze Blow
TB	= Trumpet Blow

FEEDING BEHAVIOR:

BN	= Bubble Netting
LL	= Lateral Lunge
DL	= Diagonal Lunge
VL	= Vertical Lunge
UL	= Unidentified Lunge?

TAIL BEHAVIOR:

LT	= Lateral Tail Display
TS	= Tail Slap (belly-down)
LS	= Lateral Tail Slap
IT	= Inverted Tail Slap (belly-up)
TC	= Tail Clap (horizontal)
SW	= Tail Swish (side-to-side)
FL	= FLex (roll peduncle)

PECTORAL FIN BEHAVIOR:

PE	= Lateral Pec Extension
PS	= Lateral Pec Slap
VP	= Ventral Pec Slap (belly-up)
RP	= Roll back & forth Pec Slap
PD	= Pec Display

BODY BEHAVIOR:

HG	= HanGing (horizontal at surface)
UN	= UNdulation (bob up & down)
SS	= S-Shaped posture
ST	= Sharp Turn (erratic dir. change)

HEAD AND LEAPING BEHAVIOR:

BR	= BReach
SH	= Spy Hop
HL	= Head Lunge (not assoc. w/ feeding)
HS	= Head Slap
WC	= Whale Contact
HO	= Hits Object (other than whale)
AD	= Agonistic Display
BE	= BEached
SP	= Unidentified SPLash?

VOCALIZATIONS:

VV	= Vocalization cue for recordings.
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MISC. CODES:

Q	= QUESTION? (describe in comment)
MD	= Missed Data?
X	= Delete previous entry.
XX	= Delete last sequence of entries.

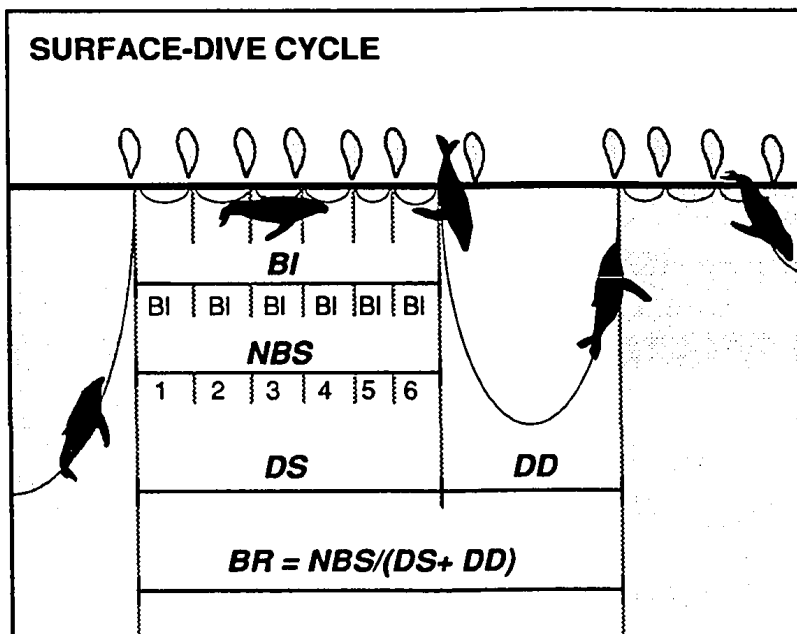
***Note:** Common humpback whale behaviors observed in Cordell Bank/Gulf of the Farallones region are in bold print.

APPENDIX C

DEFINED RESPIRATION VARIABLES:

Surface-dive cycles were used as primary means of quantifying differences in behavioral states. The following five variables of respiration were measured:

1. **Blow Interval (BI)** : time interval of 90 sec or less between exhalations at (or near) the surface.
2. **Number of Blows per Surface Duration (NBS)** : number of exhalations during a surface period.
3. **Duration at Surface (DS)** : period of time spent at (or near) the surface between successive dives. Surface duration was terminated by arching the peduncle or raising of the flukes above the water to initiate a dive, or by a submergence with blow interval exceeding 90 seconds.
4. **Duration of Dive (DD)** : period of time during a dive to first surfacing. First exhalation exceeding 90 sec in length usually marked the beginning of a surface duration.
5. **Blow Rate (BR)** : total number of exhalations divided by surface duration and dive duration from each complete surface-dive cycles.



APPENDIX D

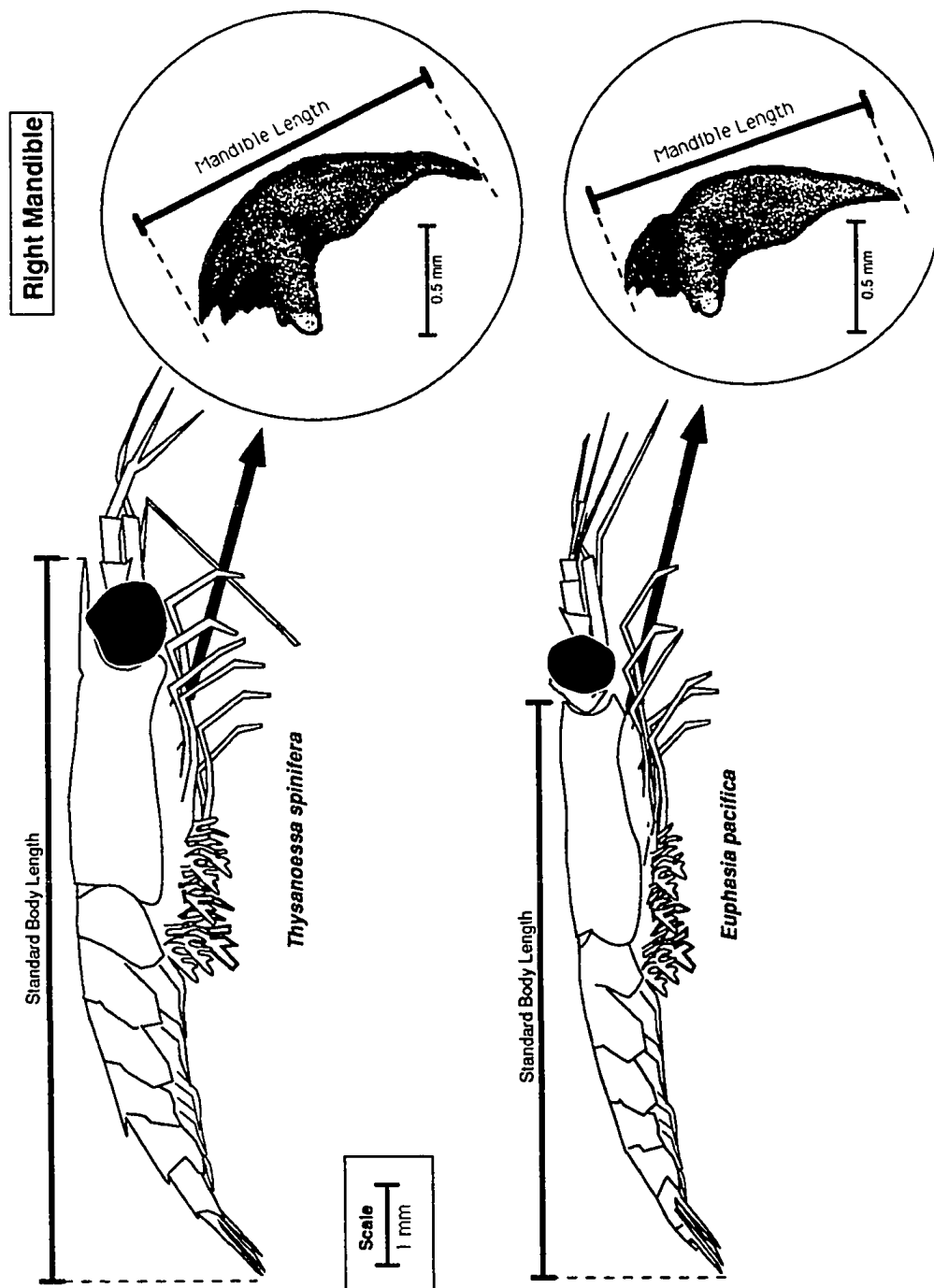
RESPIRATION VARIABLES/STANDARD APPROACH:

Table 1A. Respiration variables by behavior categories of feeding, milling, and traveling humpback whales. Dependent means and sample sizes (n) are shown.

RESPIRATION VARIABLE	BEHAVIOR CATEGORY											
	Feeding			Mill/Search			Fast Travel			Slow Travel		
	88	89	90	88	89	90	88	89	90	88	89	90
Duration at Surface mean (min) SD 95% CL (n)	0.7	3.1	1.3	0.8	2.3	1.8	1.0	1.2	0.9	1.1	1.7	1.1
	0.69	1.69	1.30	0.93	1.54	1.70	0.88	0.91	0.68	0.78	1.10	0.92
	0.12	0.31	0.15	0.37	0.52	0.44	0.24	0.33	0.29	0.35	0.33	0.25
	(132)	(120)	(299)	(27)	(36)	(59)	(55)	(32)	(23)	(21)	(46)	(53)
No. Blows/Surface Duration mean SD 95% CL (n)	2.5	10.5	3.9	3.0	7.4	6.1	3.7	4.3	3.0	4.1	5.7	3.6
	1.75	5.30	3.24	1.84	4.97	4.70	1.94	2.74	1.76	2.03	3.47	2.36
	0.30	0.96	0.37	0.73	1.68	1.22	0.53	0.99	0.76	0.92	1.03	0.65
	(132)	(120)	(299)	(27)	(36)	(59)	(55)	(32)	(23)	(21)	(46)	(53)
Duration of Dive mean (min) SD 95% CL (n)	1.3	6.2	1.8	0.9	5.4	4.5	1.9	3.7	1.6	2.5	4.3	2.5
	1.12	3.30	2.26	0.60	2.91	3.33	1.34	2.88	1.15	1.14	3.27	1.84
	0.20	0.64	0.26	0.29	1.05	0.87	0.39	1.02	0.51	0.57	0.97	0.53
	(125)	(105)	(290)	(19)	(32)	(58)	(48)	(33)	(22)	(18)	(46)	(48)
Blow Interval mean (sec) SD 95% CL (n)	23.1	18.7	22.5	19.6	19.5	19.3	20.5	19.6	23.1	18.4	19.7	23.3
	15.41	8.21	14.24	17.18	9.05	10.67	14.13	8.77	13.44	12.51	11.11	14.11
	2.17	0.45	0.91	4.69	1.13	1.15	2.19	1.60	3.16	1.50	1.47	2.30
	(197)	(1279)	(954)	(54)	(251)	(331)	(162)	(118)	(72)	(70)	(223)	(147)
Blow Rate mean (no. blows/min) SD 95% CL (n)	1.5	1.1	1.4	2.0	0.9	1.2	1.7	1.2	1.3	1.1	1.1	1.1
	0.74	0.45	0.65	0.92	0.53	0.75	1.21	1.07	0.41	0.50	0.59	0.58
	0.13	0.10	0.08	0.45	0.22	0.22	0.36	0.39	0.19	0.25	0.19	0.18
	(123)	(84)	(254)	(18)	(26)	(46)	(46)	(31)	(20)	(18)	(40)	(42)

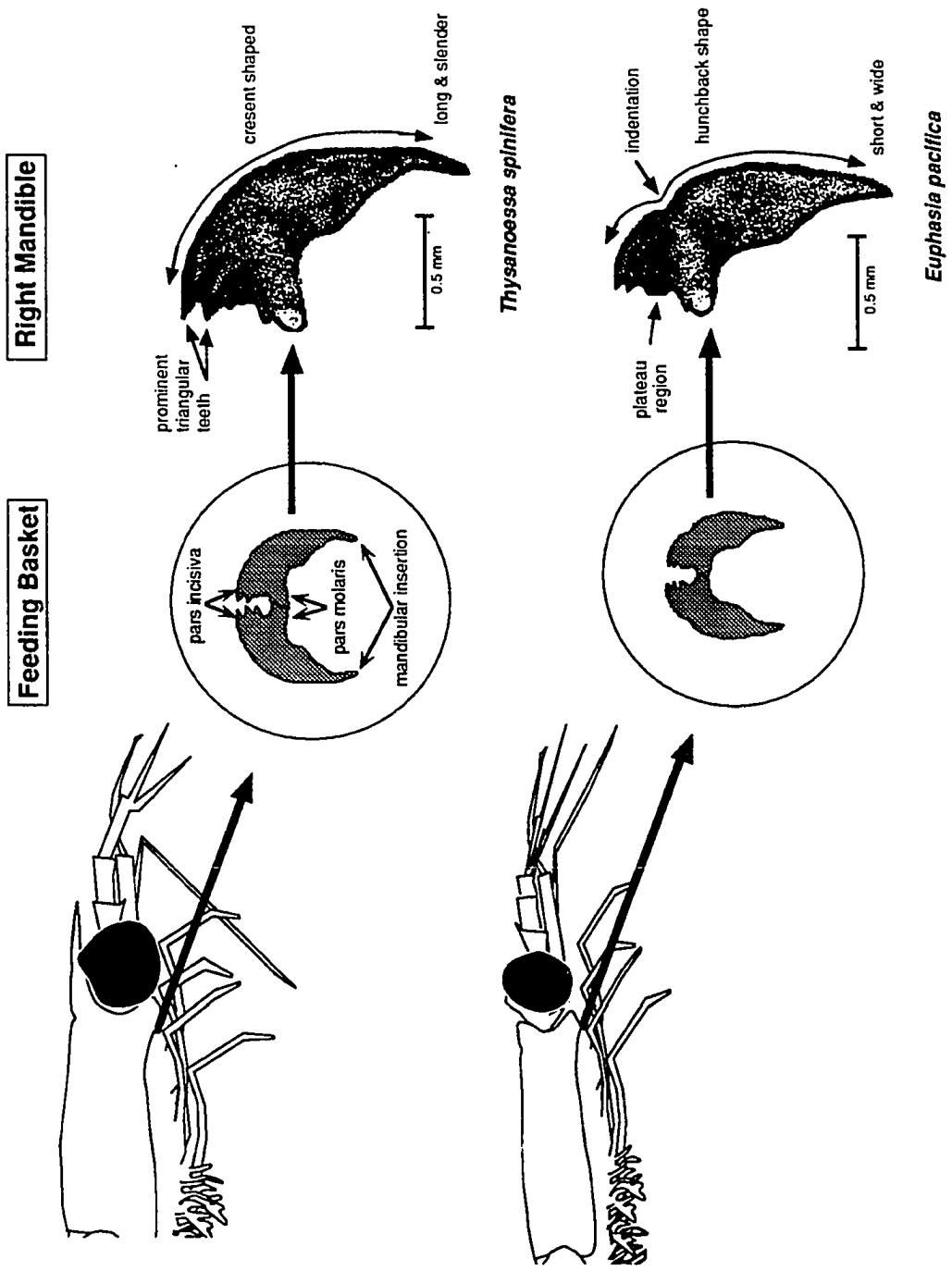
APPENDIX E

STANDARD BODY LENGTH & MANDIBLE MEASUREMENTS:



APPENDIX F

EUPHAUSIID RIGHT MANDIBLE IDENTIFICATION:



APPENDIX G

SKY CONDITION:

CODE NO.	DESCRIPTION
1	Clear
2	Partly cloudy
3	Cloudy
4	Overcast
5	Light rain or rain within 6 km
6	Heavy rain
7	Patchy fog or fog within 6 km
8	Serious fog
9	Rain and fog

SEA CONDITION (BEAUFORT):

BEAUF NO.	DESCRIPTION	WIND SPEED (km/h)	WAVE (m)
0	Smooth and mirror-like	Calm (0-2)	--
1	Light ripple	Light air (2-6)	0.3
2	Small wavelets, not breaking	Light Breeze (7-11)	0.6
3	Scattered whitecaps	Gentle Breeze (12-19)	1.2
4	Small waves, frequent whitecaps	Mod. breeze (20-30)	1.8
5	Moderate waves, many whitecaps	Fresh breeze (31-39)	2.0
6	All whitecaps, some spray	Strong breeze (40-50)	3.0
7	Breaking waves, spindrift begins	Near gale (51-61)	4.3
8	Medium high waves, foamy	Gale (62-74)	5.5

***Note:** Beaufort 6-8 not meaningful (time to go home!).