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BLUE WHALES FEEDING ON HIGH CONCENTRATIONS OF EUPHAUSIIDS AROUND MONTEREY SUBMARINE CANYON

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Abstract

An unusually high concentration of blue whales, *Balaenoptera musculus*, fed on euphausiids that were concentrated in deep scattering layers and daytime surface swarms in Monterey Bay, CA during fall 1986. Blue whales were closely associated with deep scattering layers which were elongated along the southeast edge of the Monterey Submarine Canyon throughout most of November 1986. These scattering layers contained euphausiids, primarily *Thysanoessa spinifera*, which accounted for 45.4% of the total biomass of zooplankton tows taken through deep scattering layers. Tows taken above or outside the layers consisted of only 4.0% euphausiids. The greatest concentrations of blue whales were observed in areas of thick scattering layers which contained high krill biomass. In addition, surface lunging blue whales fed on daytime surface swarms of *Thysanoessa spinifera* near the head of Monterey Submarine Canyon on 11 and 12 November 1986. Surface tows taken in whale feeding areas were dominated by *T. spinifera* which accounted for 64.4% of the total biomass, while surface tows taken outside whale areas consisted of only 0.3% euphausiids. Euphausiid densities in surface swarms were slightly higher and more variable than deep layers. *Thysanoessa spinifera* size frequency distributions showed that surface swarms may be similar to the deep layer in some areas, but may contain larger, sexually mature individuals in other areas. Blue whale fecal samples confirmed that the whales were feeding on euphausiids. The disappearance of the blue whales was accompanied by a decline in krill biomass along the southeast edge of the submarine canyon. This coincided with the cessation of a prolonged upwelling period which persisted in Monterey Bay throughout November 1986.

Introduction

Most baleen whales undergo seasonal feeding migrations in search of heavy concentrations of food organisms. Although this relationship has been established for many geographic areas, it is not well quantified. The whale/plankton link was initially supported by agreements between whale catch records and general euphausiid distributions in the Antarctic (Hardy and Gunther, 1935; Mackintosh, 1934). Stronger evidence of the whale/prey relationship was revealed when stomach contents and catch statistics of baleen whales in the North Pacific were compared to published plankton data (Nemoto, 1957; 1959; 1963).

More localized studies revealed that baleen whale distributions were closely associated with that of their prey. The distribution and movements of humpback whales off New England and Newfoundland were related to the distribution and movements of schooling fish (Payne, et al., 1985; Whitehead and Glass, 1985). Humpback whales in southeastern Alaska were concentrated only in areas of extensive prey concentrations, primarily deep layers of euphausiids (Krieger and Wing, 1986). Sonar scans and underwater camera footage revealed that humpback whales fed on dense patches of euphausiids in Frederick Sound, Alaska (Dolphin, 1987a). These studies give stronger evidence of the relationship between whales and their prey; however, they lack quantitative data on prey availability outside whale feeding areas.

A few recent studies have convincing prey data from both inside and outside whale feeding areas. Surface feeding right whales occurred in areas of extraordinarily dense *Calanus* concentrations in the Great South Channel off New England (Wishner, et al., in press). Bowhead whales fed in areas of thick copepod layers in the Eastern Alaskan Beaufort Sea (Richardson, 1987). In both studies, data from the feeding whale areas were limited to only a few days and lack quantified correlations between the number of whales and the quantity of available prey.

This study was intended to explore the relationship between blue whales which fed on euphausiids in deep scattering layers and surface swarms around Monterey Submarine Canyon. Euphausiids were found in large densities within whale feeding areas, orders of magnitude larger than densities observed outside the whale areas. The number of feeding blue whales was positively correlated with the density of euphausiids. The densest patches of both euphausiids and blue whales were associated with steep topographical features of the Monterey Submarine Canyon.

Study Area

Monterey Bay is located along the central California coast and contains one of the largest submarine canyons along the west coast of North America. This canyon, which extends very close to the shore, has a profound effect on the circulation in Monterey Bay. Submarine canyon topography acts like a funnel, channeling seasonal upwelling events onshore. Coastal upwelling occurs north and south of Monterey Bay between March and October, and upwelled waters from these areas may be advected into the Bay. This upwelling relaxes during late summer and fall and the Davidson Current has usually become established by early November (Breaker and Broenkow, in press). Changes in abundance and composition of phytoplankton (Bolin and Abbott, 1963; Garrison, 1979) and zooplankton (Barham, 1956) have been shown to be associated with these hydrographic periods.

The upwelling conditions in Monterey Bay may affect the distribution patterns of euphausiids. Dense accumulations of euphausiids are most likely to be found where turbulence or upwelling occurs (Eddie, 1977). Monterey Submarine Canyon provides channels for onshore, upward advection of deep nutrient-rich waters. It is during such upwelling periods that tremendous surface swarms of *Euphausia pacifica* (Barham, 1956) and *Thysanoessa spinifera* (Harvey, 1979) have been observed around Monterey Submarine Canyon.

In autumn, blue whales have been frequently observed in the outer portions of Monterey Bay and over the Monterey Submarine Canyon (Dohl, et al., 1983). The blue whales are presumably migrating south from their Alaskan feeding grounds during this time (Rice, 1974). Sears (1987) suggested that the blue whales sighted off California could be the same as those he observed in the Gulf of California. He recently matched photographs of two blue whales observed in the Gulf in a previous year with individuals seen in Monterey Bay during fall 1986 (pers. comm.).

Unusually large numbers of blue whales were present in Monterey Bay from August through most of November 1986. From the beginning of August, groups of up to 7-9 animals were reported by local charter boats (Shearwater Journeys) and research vessels (University of California, Santa Cruz and Monterey Bay Aquarium). In early October, while conducting a survey of marine birds and mammals, researchers from Moss Landing Marine Laboratories observed 14 blue whales in Monterey Bay. Large aggregations (of perhaps over 20 animals) were frequently concentrated along the southeast edge of the Monterey Submarine Canyon during October and November. On several occasions the whales were seen lunge feeding on surface swarms of euphausiids near the head of the Monterey Submarine Canyon.

Methods

From October 1986 through March 1987, field data were collected from cruises aboard the Moss Landing Marine Laboratories' 35-foot research vessel Ed Ricketts. The boat was equipped with a Gearmatic Model-5 utility winch, North Star 8000 LORAN, Lowrance X-15B recording depth sounder (operating at 192 kHz), Ross 800-B depth sounder (50 kHz operating frequency) and a 3-meter high observation platform. Distribution and abundance of krill were assessed by acoustical techniques and net tows. Since echo sounders operating at high acoustic frequencies (50-200 kHz) successfully record layers and patches of euphausiids (Eddie, 1977; Nemoto, 1983), the distribution of euphausiid biomass was estimated from echo records. Zooplankton biomass was further quantified using a 1-meter diameter, 505-micron mesh plankton net. While sitting on the platform, observers using binoculars independently recorded whale sightings.

Sampling efforts were primarily focused on the areas of greatest whale concentrations, most frequently along the southeast edge of the Monterey Submarine Canyon (Figure 1, rectangular box). Upon departing Moss Landing harbor, the vessel would generally follow the canyon edge south to this area until whales were sighted. The blows of blue whales were often visible for over 2 kilometers, which allowed an area well beyond the boat's actual course to be surveyed for the presence of whales. Whale observers on the platform recorded the number of whales, their distribution and behavior while the Lowrance depth sounder recorded prey concentrations (Table 1). In addition, researchers in the wheelhouse recorded the LORAN position, bottom depth and sea surface temperature.

On 16 and 18 November 1986, a series of transects, two kilometers apart, were run perpendicular to the southeast edge of the Monterey Submarine Canyon at a speed of 2 meters/second (4 knots). The length of each transect varied somewhat, from 2.3 to 4.6

km. However, all transects consistently extended from a 110 meter bottom depth nearshore to a bottom depth of greater than 375 meters (over the submarine canyon drop-off). The Lowrance depth sounder continuously recorded bottom depth and presence of scattering layers. Meanwhile, whale observers on the platform surveyed the area ahead of the boat and 90 degrees to either side. All whales observed within one kilometer of the boat were recorded; sightings were considered accurate in sea conditions up to a Beaufort scale 3.

Whales were identified as feeding or not feeding based primarily on surface behavior. Non-feeding whales followed a relatively straight-line path through the survey area, as indicated by body orientation during successive surfacings. In contrast, whales feeding below the surface dove and surfaced repeatedly within a localized area. Occasionally, whale feces (later found to contain krill remains) were observed in this area. Localized dive activity and presence of feces have been used as evidence of feeding at depth in other baleen whale studies (Dolphin, 1987b; Würsig et al., 1985). Whales which were surface feeding lunged rapidly through aggregations of euphausiids; often the distended throat pleats of the whales were observed during the lunge.

Deep scattering layers were quantified by echo records and plankton net tows. The depth to the scattering layer and thickness of the layer were measured from the echo traces. Plankton net tows were used to identify and quantify the abundance of krill and other zooplankton. While the boat was stationary, the net was lowered to a depth below the layer, allowed to settle for one minute and then raised vertically through the water column at an average rate of 0.6 meters/second (s.d.= 0.02 m/sec, n=26). If no layer was present, the net was towed vertically from 200 meters below the surface, the maximum depth from which the Lowrance sounder could detect a layer. On 9, 14 and 25 November, plankton tows were taken both within and outside of whale feeding areas.

On 16 and 28 November, tows were taken above the scattering layer in addition to tows taken through the scattering layer. The tow rate was similar for these shallower tows (linear relationship between ascent time and tow depth).

Within the upper 10 meters of the water column, surface swarms of krill were recorded as distinctive "features" on the Lowrance depth sounder (Figure 2). Though incidental surface reverberations were continuously recorded in the upper 1 to 2 meters of the water column, scattering areas which extended to a depth of at least 3 meters were defined as distinctive features. Adjacent features were difficult to differentiate, but were conservatively recorded only if they were at least 10 meters apart. Surface scattering was continuously recorded in conjunction with LORAN positions, during transects run through whale feeding areas at a speed of 1 meter/sec (2 knots). On 12 November, similar transects were also run in two areas outside of whale feeding areas. The surface scattering records were later used to determine average width and maximum depth of the features for each area. These swarm characteristics from the two whale feeding areas were statistically compared to each other using the student's t-test (Zar, 1984). The plankton net was horizontally towed just below the surface for 1.5 minutes at an average speed of 0.6 meters/sec (1.2 knots), both inside and outside the whale feeding areas.

Plankton samples were brought to the laboratory where they were fixed in 10% formalin, then transferred to 40% isopropyl alcohol. They were split to an approximate 25-milliliter volume with a Folsum plankton splitter. Using a Bausch & Lomb dissecting microscope (10x to 40x), krill were sorted, identified to species using Boden et al. (1955) identification key and enumerated. Wet weights were determined using a Scientech Model 300 top loading balance. Larval krill, as defined by Brinton and Wyllie (1976), were sorted, counted and weighed but not identified to species. The remaining non-euphausiid zooplankton was also weighed.

Total krill biomass and other plankton biomass were statistically analyzed. Two-factor analyses of variance were used to compare deep tows taken inside and outside whale feeding areas on 9, 14 and 25 November and those taken through and above the deep scattering layer on 16 and 28 November (Zar, 1984). Due to lack of homogeneity of variances, surface tows taken inside and outside whale feeding areas were compared using a non-parametric Mann Whitney U-test, comparing pooled data from the two areas of feeding whales to the areas outside of feeding whales.

Total krill biomass and number of non-larval krill were standardized per cubic meter of water filtered. Areas outside surface swarms and outside or above deep layers were standardized assuming that the small amount of krill encountered were integrated throughout the water column. The krill biomass and numbers per tow were standardized by dividing by the total volume of water filtered (area of net mouth x tow distance). For a given day, the average biomass and number of krill per tow outside surface swarms or outside or above deep layers were subtracted from the tows done through surface swarms or deep layers on the same day. These numbers were then standardized to grams or numbers per cubic meter by dividing by area of net mouth x distance of tow (for surface tows) or by area of net mouth x thickness of scattering layer (for deep tows).

Total length (tip of rostrum to tip of telson) was measured to the nearest millimeter for all *Thysanoessa spinifera* sorted in the plankton splits from 15 and 16 November deep tows and 11 and 12 November surface tows. Fertilized females were distinguished by the presence of their distinctive brownish, barbell-shaped spermatophores. Size frequency distributions were generated from pooled data for each area and statistically compared using Kolmolgorov-Smirnov test for differences in relative cumulative frequency distributions.

Five blue whale fecal samples were retrieved by using a fine mesh net or a bucket. A 0.5 ml aliquot was taken from homogeneous mixtures and approximate volumetric percentages of prey items were estimated visually. The number of *Thysanoessa spinifera* molars and spermatophores were then enumerated from this aliquot.

Oceanographic data were indirectly assessed from daily satellite images, monthly coastal upwelling index anomalies and sea surface temperature anomalies for August 1986 through January 1987, in order to better understand what processes may have caused aggregations of whale prey in Monterey Submarine Canyon. Archived satellite images of the eastern North Pacific were studied at the National Weather Service in Redwood City, CA and images, that clearly depicted the oceanographic conditions in Monterey Bay, were processed by Scripps Institute of Oceanography Satellite Services. The coastal upwelling indices calculated for 36° N, 122°W were compared to the 20-year average reported by Bakun (1973). Sea surface temperatures measured at Granite Canyon were compared to a 12-year record for that area, calculated by Breaker (1983).

Results

Blue whales were closely associated with the deep scattering layer observed along the southeast edge of the Monterey Submarine Canyon (Figure 3). On both 16 and 18 November, over 75% of the whales observed were sighted directly over the scattering layer. The location of the scattering layer changed between days; it occurred slightly further offshore and in deeper water on 18 November. The thickness and depth of the layer varied, both between days and between transect lines on a given day (Figure 4). In general, the scattering layer was 1-2 km wide and elongated along the canyon edge with the thickest patches concentrated along the canyon drop-off at depths of 130-140 meters.

Later in the afternoon, the scattering layer often appeared in shallower water, concentrated just above the sea floor, at depths of 100-110 meters.

The greatest concentrations of blue whales were observed in areas of thick scattering layers and high krill biomass (Table 2). The number of whales observed within the 1-kilometer survey area was strongly associated with both thickness of scattering layer ($r=0.88$, $p<0.001$) and with krill biomass ($r=0.81$, $0.002<p<0.005$). Similarly, krill biomass was highly correlated with the thickness of the scattering layer ($r=0.77$, $0.005<p<0.01$), (Figure 5). Although the tow depth varied between days, there was no correlation between krill biomass and tow depth ($r=0.16$, $p>0.05$). Thus, krill biomass was more closely associated with the location of the scattering layer than with the tow depth.

Lunge-feeding blue whales were observed on 11 and 12 November over the Monterey Submarine Canyon mouth (Figure 1). Surface swarms of krill occurred within the surface-feeding areas, but not outside these areas. Krill swarms were characterized by an overall mean width of 39.4 meters (s.d.= 55.4 m, n=36) and maximum depth of 4.6 meters (s.d.= 1.6 m, n=36). There was no significant difference in feature width ($t=0.14$, $p>0.05$) or maximum depth ($t=0.22$, $p>0.05$) between the two whale areas (Table 3). The swarms appeared to be more concentrated in Area II (4.5 features/km) compared to Area I (2.7 features/km); however, the transects in Area II were more localized in the whale feeding area.

Euphausiids, primarily *Thysanoessa spinifera*, accounted for 31.5% (s.d.=15.3%, n=10) of the zooplankton biomass of the deep tows taken inside whale feeding areas, but contributed only 3.9% (s.d.=4.4%, n=10) to the total biomass outside the whale feeding areas (Table 4). Overall, *T. spinifera* accounted for 23.3% (s.d.=16.3%, n=10) of the total biomass in whale feeding areas on 9, 14 and 25

November; *Euphausia pacifica* accounted for an additional 16.1% (s.d.=2.2%, n=3) of the total biomass on 14 November, while *Nyctiphanes simplex* contributed another 4.9% (s.d.=5.5%, n=5) of the biomass on 25 November. Larval krill accounted for only 0.8% (s.d.=0.5%, n=10) of the biomass in whale feeding areas and a similar 0.9% (s.d.=0.5%, n=10) outside whale areas. Total krill biomass and other plankton biomass was significantly higher inside whale areas than outside whale areas (krill biomass: $F=22.09$, $p<0.001$; other plankton biomass: $F=7.03$, $p<0.05$) but not significantly different between days (krill biomass: $F=2.52$, $p>0.05$; other plankton biomass: $F=3.06$, $p>0.05$). There was no significant interaction between these two factors (krill biomass: $F=2.88$, $p>0.05$; other plankton biomass: $F=3.39$, $p>0.05$).

Krill biomass was not significantly associated with other plankton biomass ($r=0.13$, $p>0.05$). Nevertheless, of the 8 tows containing highest krill biomass, 7 of these had other plankton biomass lower than the median other plankton biomass (Figure 6).

Euphausiids accounted for 65.2% (s.d.=25.8%, n=7) of the total biomass from deep tows taken through the scattering layer, while tows taken above the layer consisted of only 5.4% (s.d.=3.4%, n=7) euphausiids (Table 5). On 16 November, *T. spinifera* dominated the catch, accounting for 77.6% (s.d.=3.2%, n=4) of the total biomass; while on 28 November, *E. pacifica* was the predominant krill species, contributing 40.1% (s.d.=20.1%, n=3) of the total biomass. Larval krill averaged only 1.1% (s.d.=0.9%, n=7) of the total biomass in tows through the scattering layer and 4.1% (s.d.=3.8%, n=7) for tows above the layer.

Total krill biomass was significantly higher in tows taken through the scattering layer, rather than above the layer ($F=151.16$, $p<0.001$). There was also a significant difference in krill biomass between the two days ($F=72.38$, $p<0.001$), as well as a significant interaction between these two factors (F=72.93, p<0.001). Other plankton biomass did not differ in tows taken through versus above the layer (F=1.08, p>0.05), but was significantly different between days (F=9.00, p<0.05). There was no significant interaction between these factors affecting other plankton biomass (F=1.24, p>0.05).

Surface tows taken in whale feeding areas were dominated by *T. spinifera* , which accounted for 64.4% (s.d.=38.9%, n=10) of the total biomass while surface tows taken outside whale areas consisted of only 0.3% (s.d.=0.3%, n=10) euphausiids (Table 6). Only trace amounts of other krill species were encountered in these surface tows. Larval krill accounted for only 0.1% of the total biomass in the whale areas (s.d.=0.2%, n=10), and 0.3% outside whale areas (s.d.=0.3%, n=10). Whale feeding areas had significantly higher krill biomass (U=100, p<0.001) than areas without feeding whales. However, biomass of plankton other than krill did not differ significantly inside and outside whale feeding areas (U=52, p>0.05).

Euphausiid densities were orders of magnitude greater within surface swarms and deep layers, compared to areas outside these patches. Surface swarms showed higher and more variable standardized krill biomass estimates (overall mean=3.3 g/cu. m, s.d.=5.6, n=10) compared to within the deep layer (overall mean=1.7 g/cu. m, s.d.=1.3, n=17). Conversely, the average number of krill were lower within surface swarms (overall mean=60.7/cu. m, s.d.=105.6, n=10) compared to numbers found within the deep layer (overall mean=70.6/cu. m, s.d.=45.0, n=17) (Table 7). Outside these dense areas, krill biomass averaged 0.001 g/cu. m (s.d.=0.001, n=10) in the surface waters and 0.005 g/cu. m (s.d.=0.004, n=17) throughout the upper 200 meters of the water column. Similarly, low numbers of krill were encountered outside the patches, with surface waters averaging 0.02 individual krill/cu. m (s.d.=0.03, n=10) and the water column averaging 0.5 individuals/cu. m (s.d.=0.9, n=17).

Size frequency distributions of *T. spinifera* showed that surface swarms may be similar to the deep layer in some areas but may contain larger, sexually mature individuals in other areas (Figure 7). Deep layer tows consisted mostly of unfertilized females and/or males with an average total length of 15 to 16 mm. Area I surface swarms exhibited a similar distribution ($D=0.05$, $p>0.05$); however, Area II surface swarms consisted mainly of larger, fertilized females. This size frequency distribution was significantly different from both the deep layer ($D=0.69$, $p<0.001$) and the Area I surface swarms ($D=0.73$, $p<0.001$).

Blue whale fecal samples confirmed that the whales were feeding exclusively on euphausiids (Table 8). The fecal samples retrieved from surface-feeding whales were less digested than those from deep-feeding whales, which allowed a greater percentage of the euphausiid remains to be identified from the samples. In both deep and surface samples, all identifiable euphausiid remains were of *T. spinifera*.

The cessation of an extended upwelling period that persisted throughout November 1986 coincided with a decline in krill biomass and the disappearance of the blue whales in Monterey Bay. Satellite images from Monterey Bay showed that upwelling persisted through November and the warm-water Davidson Current did not appear until December (Figure 8). Monthly coastal upwelling index anomalies and sea surface temperature anomalies confirmed higher than normal upwelling during November, followed by higher sea surface temperatures in December (Table 9). By the beginning of December, aggregations of blue whales and their prey had also disappeared in Monterey Bay (Table 1).

Discussion

Dense aggregations of prey around Monterey Submarine Canyon supported abnormally large concentrations of blue whales during fall 1986. The distribution of the euphausiids directly influenced the distribution of as many as 20 blue whales in Monterey Bay, as evidenced by strong associations between the whales and their abundant prey. Blue whales fed in areas of highest krill biomass, characterized by euphausiid densities that were orders of magnitude larger than densities found outside these whale feeding areas. The euphausiid patches were always in close association with the canyon, either concentrated in dense scattering layers along the canyon edge or in large surface swarms near the head of the canyon.

Upwelling may be a potentially important mechanism providing increased prey aggregations around Monterey Submarine Canyon. Submarine canyon topography promotes circulation that enhances mixing and may lead to increased productivity (Church, et al., 1984). Abundance and concentration of deep water forage items in shallower water areas adjacent to submarine canyons may also be increased. Periods of highly intense advective processes, especially in conjunction with abundance peaks of dominant canyon organisms, could account for the occurrence of dense concentrations of fishes, birds and marine mammals in the vicinity of submarine canyons and along the edges of banks (Kenney and Winn, 1987; Morejohn, et al., 1978; Payne et al., 1986).

Anomalous upwelling that persisted in Monterey Bay throughout November most likely increased productivity and plankton biomass in the area. Zooplankton, especially krill, are known to accumulate in areas of increased turbulence or upwelling (Eddie, 1977; Everson, 1977; Witek, et al., 1982). High densities of *Thysanoessa spinifera* are associated with upwelling centers in the North Pacific (Brinton, 1962). Beklemishev (1960) found that krill was more abundant and more blue and humpback whales prevailed in regions of the Antarctic where cyclones were more frequent. Fin whales near Iceland concentrated in a semipermanent area of upwelling, where zooplankton biomass was higher than in surrounding areas (Foerster and Thompson, 1985).

The anomolous upwelling may have been responsible for high concentrations of the euphausiids that in turn provided food for blue whales around Monterey Submarine Canyon. This parallels a similar anomaly reported by Latyshkevich, et al. (summarized in McWhinnie, et al., 1981) in which increased advection resulted in higher krill concentrations in the Scotia Sea region of the Antarctic. Greater aggregations of fin and sei whales resulted in a particularly good year for Scotia Sea whaling.

Deep scattering layers were often variable in terms of thickness, depth in the water column and general patchiness but were always most dense along the canyon edge. The euphausiid patches were elongated along the canyon edge and were usually dispersed at the head of the canyon, perhaps as a result of increased vertical mixing. Simard et al. (1986a) found similar aggregations of euphausiids, distributed in a long, narrow patch along the edge of the Laurentian Channel, St. Lawrence estuary. Pieper (1979) also showed significant horizontal patchiness in the distribution of euphausiids as well as variable depths in the water column. Physical processes such as upwelling, circulation, semidiurnal internal tides, turbulence and tidal influences (Breaker and Broenkow, in press; Sameoto, 1983; Shea and Broenkow, 1982), and biological processes such as euphausiid behavior (Hamner, et al., 1983; Simard, et al., 1986a) could be acting as concentrating mechanisms.

Acoustical prey data provide indirect evidence for the depth of blue whale dives. Since blue whales were found over prey which was sometimes as deep as 165 meters, it can be inferred that these whales fed at this range. The maximum feeding depth of blue whales is not known; however, it is assumed that the normal range of baleen whales does not exceed 300 meters in depth (Nemoto, 1963). In the North Atlantic, Whitehead (1983) obtained depth sounder traces representing humpback whales in depths down to 195 meters, while Dolphin (1987a) found that humpbacks restricted their foraging to the upper 120 meters of the water column in nearshore feeding areas of south Alaska. More direct evidence, such as time-depth records or sonar traces, is needed to confirm the actual feeding range of blue whales.

Baleen whales must feed selectively in areas of concentrated prey. Euphausiids were consistently concentrated in the scattering layer and not integrated throughout the water column. Biomass measurements of euphausiids have been made in widely diverse areas; they usually constitute 5-10% of the total biomass of plankton (Mauchline, 1980). Vertical tows taken where there was no evidence of scattering layers or taken above scattering layers had similarly low euphausiid percentages (3.9% and 5.4%, respectively); however, those tows taken through scattering layers had significantly higher percentages of euphausiids (accounting for up to 88% of the total biomass). In general, zooplankton concentrations are orders of magnitude higher within the scattering layer than outside (Simard, et al., 1986b). Sameoto (1976; 1980) found that samples taken in the scattering layer always contained large numbers of euphausiids, while few or no euphausiids were found in samples taken above or in areas where there was no scattering layer.

The swarming behavior of euphausiids makes them an important prey item for many species of whales. The extensive surface swarms of *Thysanoessa spinifera* that attracted many blue whales to the head of the Monterey Submarine Canyon were an unusual occurrence this late in the year. Surface swarms have been reported in Monterey Bay (Barham, 1956; Harvey, 1979) and the Gulf of the Farallones (Smith and Adams, 1988) but only during spring and summer months, the time when upwelling events are most frequent and intense along the central California coast (Bakun, 1975). Efforts have been made to discover the environmental and biological conditions which govern these sporadic events; however, no single satisfactory explanation has been found (Komaki, 1967).

Size frequency distributions gave no evidence that swarms were only related to some reproductive phenomenon. Individuals taken on 12 November 1986 were mostly fertilized females, suggesting that swarming might be related to reproduction. Many euphausiid swarms have been characterized by distinctive sex ratios and reproductive states (Brinton and Wyllie, 1976; Endo, 1984; Nicol, 1984; O'Brien et al., 1986; Smith and Adams, 1988). However, the 11 November 1986 surface swarms suggest that some other process brought the euphausiids to the surface. There have also been reports of cases in which swarming was not apparently related to reproduction (Brinton and Wyllie, 1976; Brown, et al., 1979; Marr, 1962; Nicol, et al., 1987). Brinton and Wyllie (1976) suggested that principal reproductive areas tend to occur where differential transport is relatively efficient; Monterey Submarine Canyon may provide such a favorable environment for euphausiid reproduction.

Small patches of surface swarms utilized by blue whales had larger maximum euphausiid biomass than deep layers (15 g/cu. m compared to 4.5 g/cu. m). The high variability obtained in surface tows suggests that the swarms were more patchy than the deep layers. Nemoto (1983) suggested that euphausiid densities are generally higher in swarms than layers. Marr (1962) commented that "one is struck by the frequency with which the surface nets produce enormously larger samples than are produced by oblique nets fished at subsurface levels." Conversely, Sameoto (1983) proposed that high densities and biomasses reported at the surface may occur deeper in the water column as well.

The high euphausiid concentrations found in whale feeding areas were similar to deep scattering layer densities reported in other studies (Table 10). Compared to reports for other species, surface swarms of *Thysanoessa spinifera* in Monterey Bay were lower in density; however, they served as a concentrated food source for over 15 blue whales. Euphausiid abundance is difficult to assess with ordinary plankton nets. Net catches are comprised of an undetermined number of patches; therefore, they provide estimates of average densities, not the maximum concentration within the swarm (Nemoto, 1983; Watkins, et al., 1986). Additional variables such as net avoidance (Brinton and Wyllie, 1976; Moore, 1950; Wiebe, et al., 1982), euphausiid population density and size (Brinton, et al., 1987) and swarming behavior (Hamner, et al., 1983) also affect euphausiid abundance measurements.

The fact that large numbers of blue whales occurred over euphausiid-rich areas for over a month strongly implies that the density of euphausiids was sufficient to support feeding blue whales. Brodie et al. (1978) estimated that a fin whale must feed on euphausiid concentrations of at least 17.5 g/cu. m to obtain its daily food requirements. Average euphausiid densities in areas of feeding blue whales were much lower than this estimate, perhaps due to sampling biases. It is likely that this discrepancy will be resolved by comparisons of *in situ* krill densities to densities determined from tow samples. For example, Dolphin (1987a) estimated densities of euphausiid layers to be 910/cu. m from underwater photographs, compared to maximum densities of 23.5/cu. m obtained from net tows. He determined the minimum euphausiid patch density upon which humpback whales fed was 50 krill/cu. m (but gave no estimate in terms of biomass).

Blue whales utilized highly concentrated, dense patches of prey in large, extensive deep scattering layers or localized surface swarms. Baleen whales feed preferentially in areas of higher than average zooplankton biomass and whenever they encounter areas where large but local food stocks are available, they undoubtedly prey upon them (Kawamura, 1980). There have been reports of blue whales feeding on large concentrations of krill (Sears, 1987) and possibly on shoals of pelagic red crabs (Rice, 1974) outside their summer feeding grounds. These sporadic feeding sessions may make a small contribution to the annual energy requirement of the whales.

High numbers of blue whales observed in the fall 1986 were exploiting locally abundant euphausiids in Monterey Bay. Important biological and hydrographic processes occurring in the Monterey Submarine Canyon may have increased the supply of these oceanic plankton. A better knowledge of these processes is necessary to determine the causes of euphausiid aggregations dense enough to support feeding blue whales.

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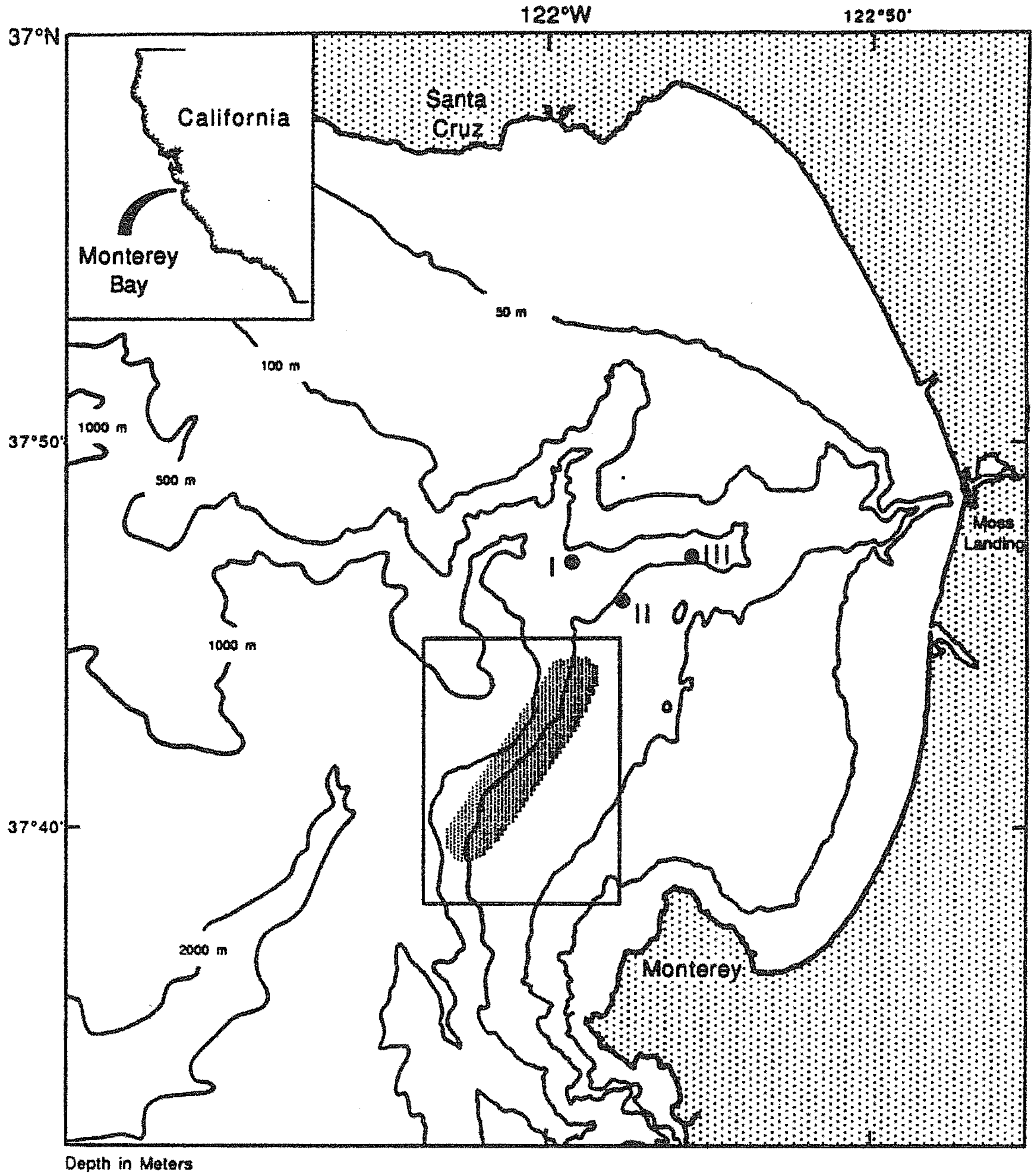

Figure 1. Bathymetry map of Monterey Bay, California (depth soundings in meters). Boat transect area along southeast edge of Monterey Submarine Canyon is depicted by rectangular box, with location of greatest blue whale and euphausiid concentrations noted (stipled area). Blue whales were observed feeding on daytime surface swarms of *Thysanoessa spinifera* in area I on 11 November 1986 and in area II on 12 November 1986. Additional surface sampling was conducted outside the whale concentration on 12 November 1986, in areas I and III.

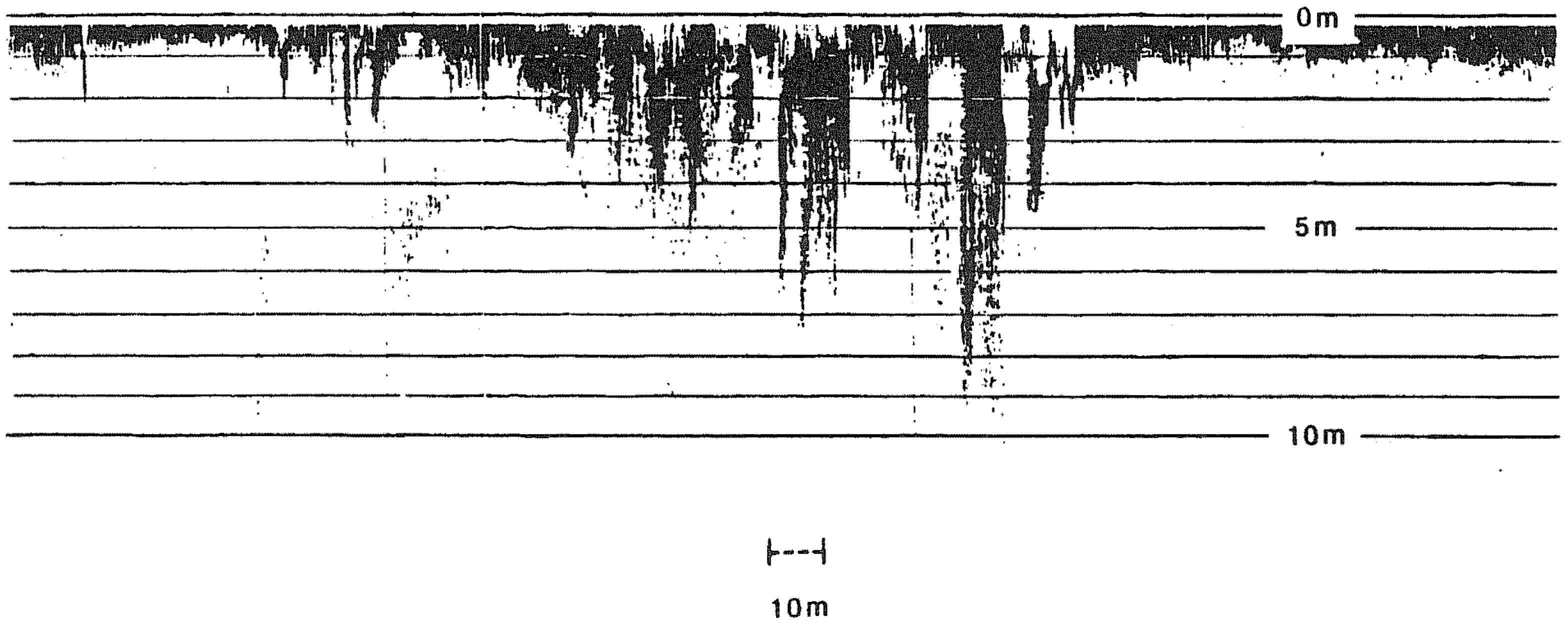

Figure 2. Surface scatter recorded by Lowrance depth sounder in area of surface feeding blue whales on 12 November 1986. (Characteristics of these surface features are given in Table 2).

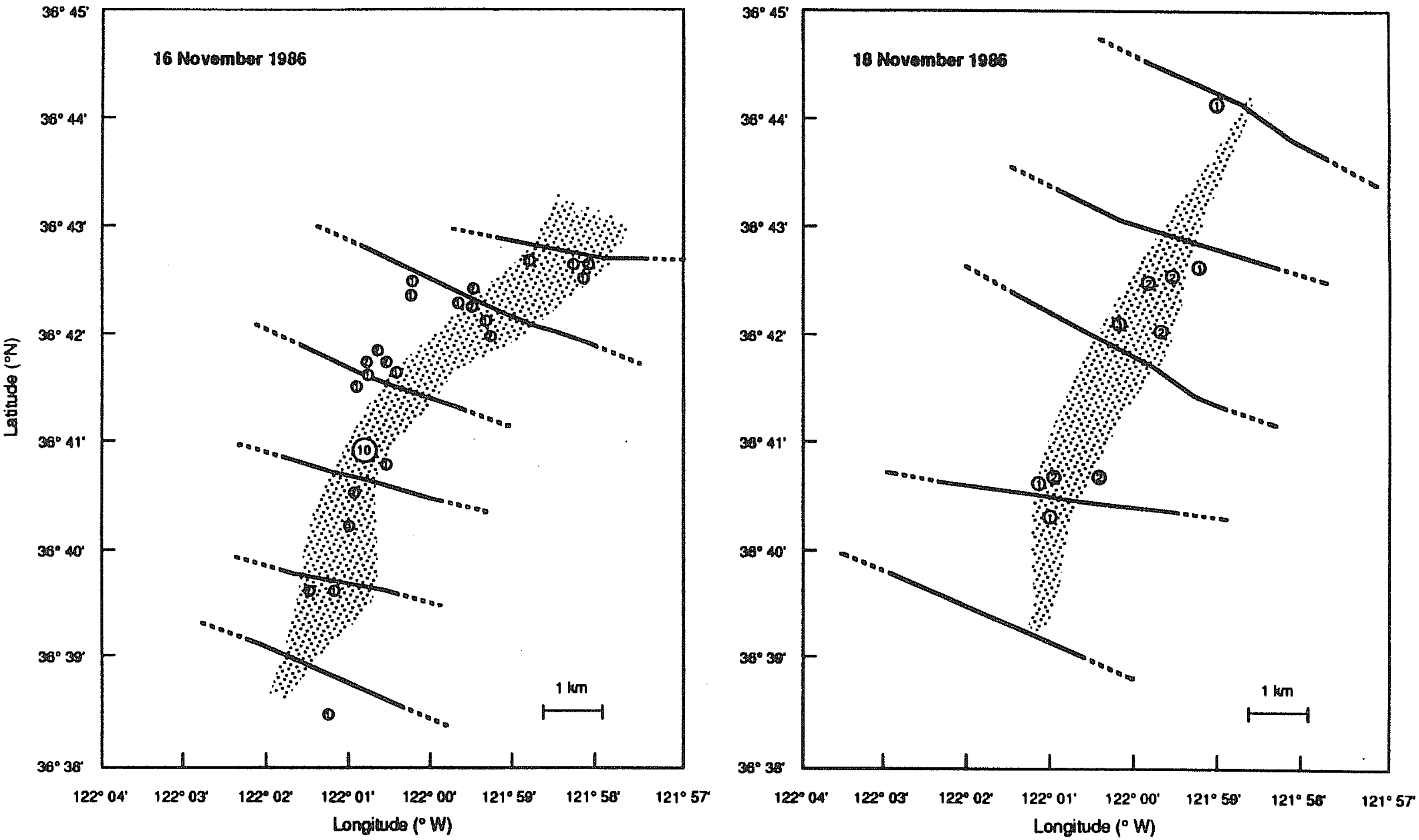

Figure 3. Blue whale sightings and deep scattering layer observations from boat surveys conducted on 16 and 18 November 1986. Solid lines show actual course of boat transects, while dotted lines show the extended area surveyed for the presence of whales. Presence of scattering layer is denoted by stipled area, while the number of blue whales and their positions are given in open circles.

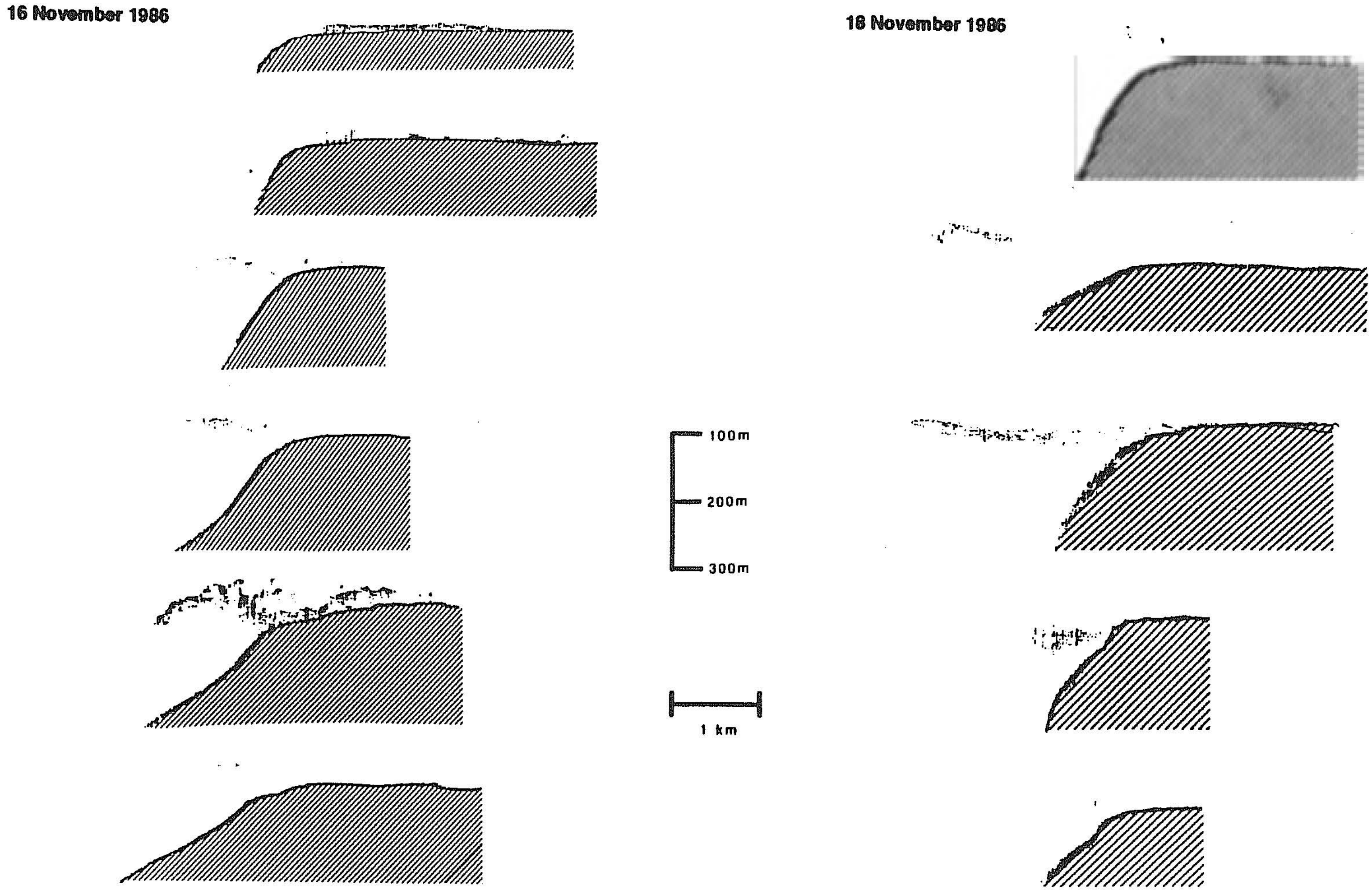

Figure 4. Deep scattering layers observed along southeast edge of Monterey Submarine Canyon during boat transects conducted on 16 and 18 November 1986 (as recorded by Lowrance depth sounder). Hatched area denotes bottom which leveled off in 100-110 meters of water.

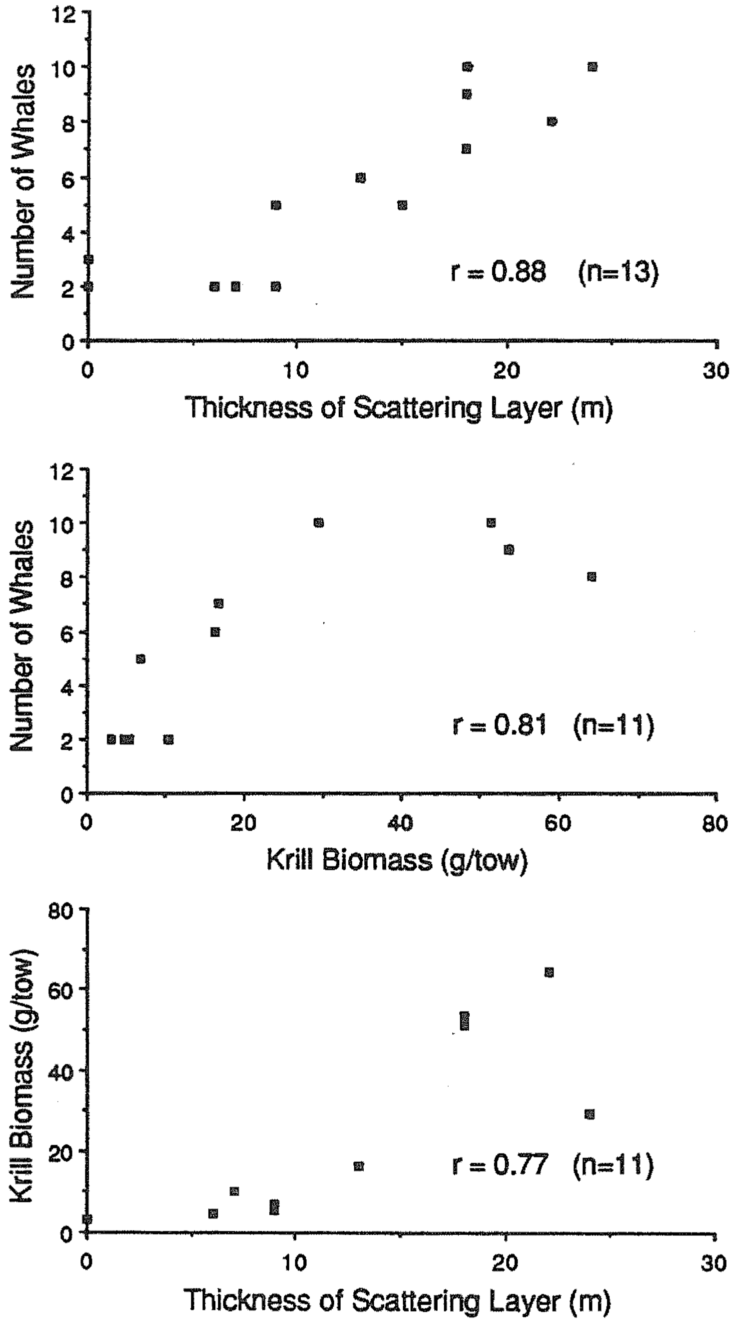

Figure 5. Relationship between number of whales, thickness of scattering layer and krill biomass from data listed in Table 1 (excluding "whales gone" category).

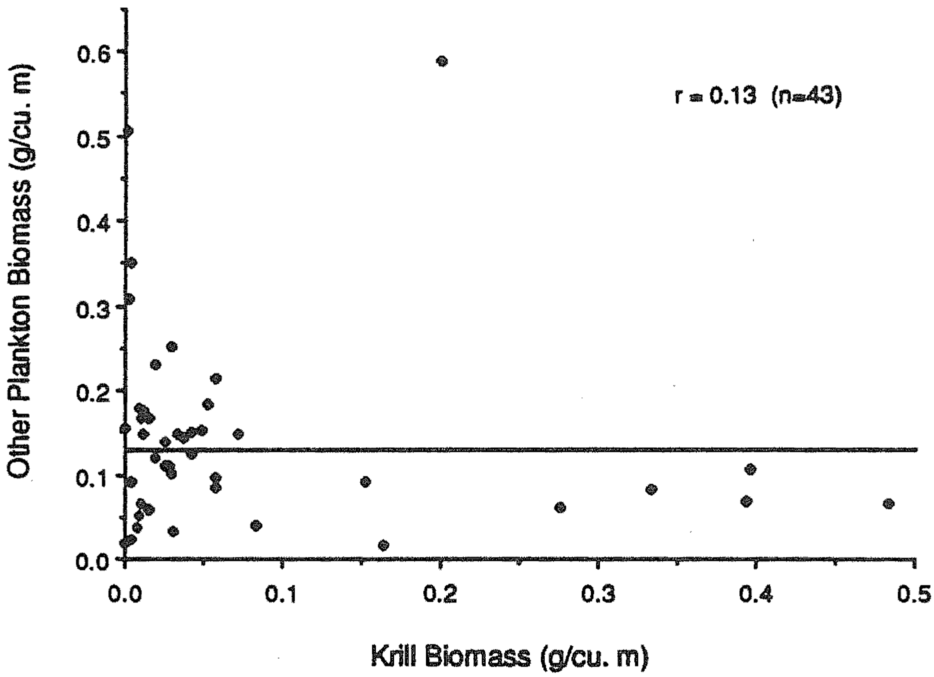

Figure 6. Relationship between krill biomass and other plankton biomass for deep tows taken along southeast edge of Monterey Submarine Canyon. Horizontal line represents median other plankton biomass.

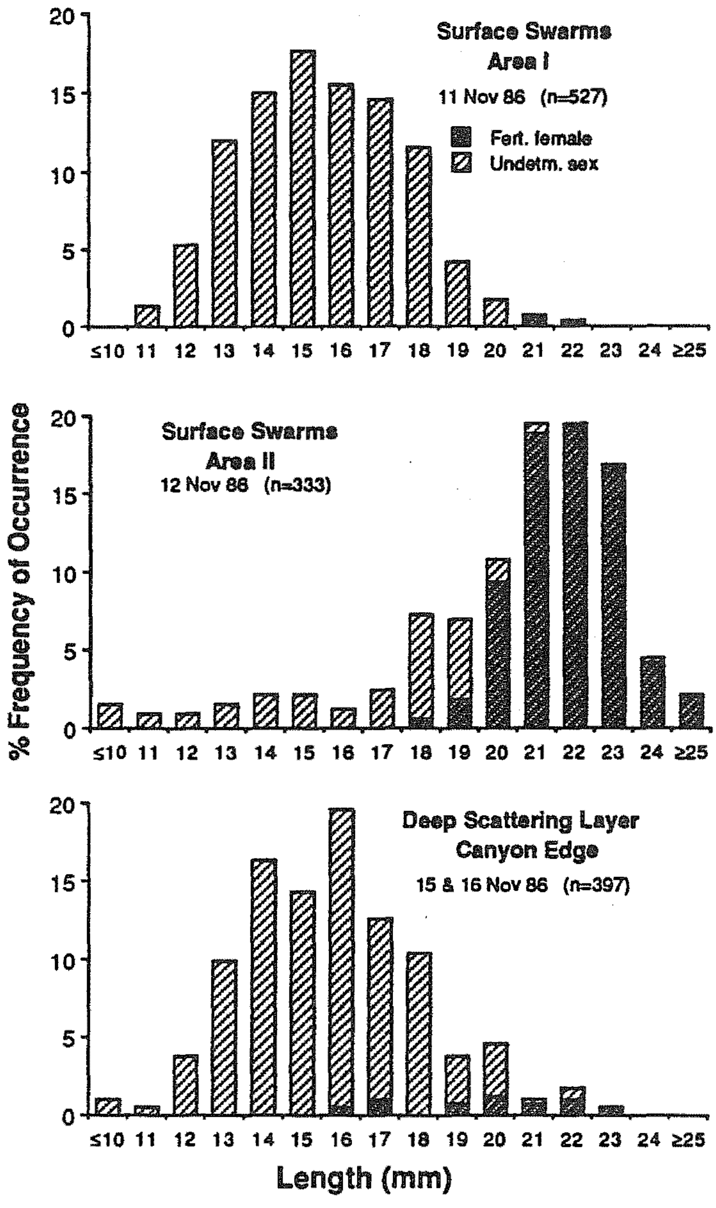

Figure 7. Size frequency histograms for *Thysanoessa spinifera* caught in surface tows on 11 and 12 November 1986 and deep tows on 15 and 16 November 1986. Fertilized females (dark hatches) were distinguished by the presence of transferred spermatophores.

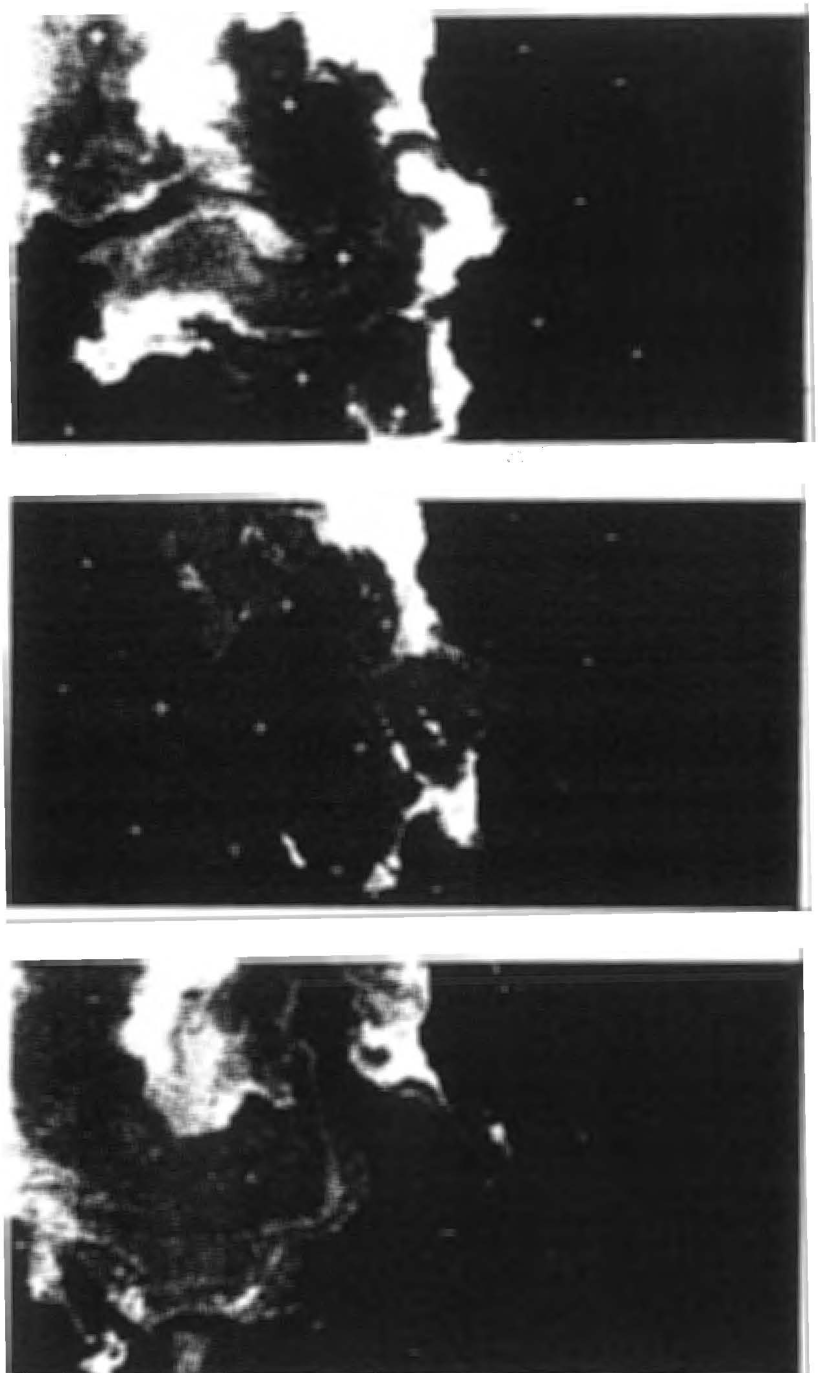

Figure 8. Satellite images indicating sea surface temperatures along central California coast during fall 1986. Cold upwelled water (white areas), which may be responsible for increased euphausiid concentrations, is clearly visible along most of the coast on 11 and 25 November. The warm-water Davidson Current (darker areas) entered the area on 07 December. These images were processed courtesy of Scripps Institute of Oceanography.

Table 1. Sampling effort summary of areas surveyed for presence of blue whales and/or their prey in the fall of 1986, Monterey Bay, California. An estimate of the number of whales around the Monterey Submarine Canyon, their general distribution and any records of their prey (from echo records) are listed.

Date	Survey Area	# Whales	Distribution of Whales	Prey	Whale Behavior*
01 Nov	SE Edge	12	Concentrated	Concentrated	Deep feeding
05 Nov	Canyon head & SE edge	>10	Dispersed	Not concentrated	Mixed
07 Nov**	Canyon head	3	Dispersed	No record	Not feeding
09 Nov-am	SE Edge	10	Dispersed	Not concentrated	Mixed
-pm	SE Edge	10	Concentrated	Concentrated	Deep feeding
11 Nov	SE Edge	3	Dispersed	Not concentrated	Not feeding
	Canyon head	>15	Concentrated	Concentrated	Lunge feeding
12 Nov	Canyon head	>15	Concentrated	Concentrated	Lunge feeding
14 Nov	SE Edge	7	Dispersed	Patchy	Deep feeding
15 Nov	SE Edge	>18	Concentrated	Concentrated	Deep feeding
16 Nov	SE Edge	>15	Concentrated	Concentrated	Deep feeding
18 Nov	SE Edge	10	Dispersed	Patchy	Deep feeding
21 Nov**	SE Edge	3	Dispersed	No record	Not feeding
22 Nov**	SE Edge & South	4	Dispersed	No record	Not feeding
23 Nov	SE Edge & South	5	Dispersed	Not concentrated	Not feeding
25 Nov	SE Edge	9	Dispersed	Concentrated	Deep feeding
26 Nov	SE Edge & North	8	Dispersed	Not concentrated	Not feeding
28 Nov	SE Edge	5	Dispersed	Patchy	Not feeding
30 Nov	SE Edge & North	3	Dispersed	Not concentrated	Not feeding
10 Dec	SE Edge	0		Not concentrated	
14 Dec	SE Edge	0		Not concentrated	
18 Jan	SE Edge	0		Not concentrated	
11 Mar	SE Edge	0		Not concentrated	

* Feeding behavior is defined in text; however, mixed behavior consisted of some fluke out dives and some surface activity, but no real lunging

** denotes days of rougher weather (Beaufort scale >3)

Table 2. Number of whales (within 1 km radius of boat), krill biomass (mean ± standard deviation for stated number of tows) and scattering layer characteristics (from echo soundings) along southeast edge of Monterey Submarine Canyon.

Feeding Whales Present

# Whales	Krill Biomass (g/tow)	Tow Depth (m)	Thickness of DSL (m)	Depth to DSL (m)	Date
10+	29.4 ± 10.5 (2)	170	24	119	15 Nov 86
10+	51.3* (1)	230	18	165	13 Oct 86
9	53.6 ± 8.2 (4)	170	18	128	16 Nov 86
8+	64.2 (1)	225	22	146	01 Nov 86
7	16.8 ± 14.3 (2)	225	18	137	09 Nov 86
6	16.2 ± 12.7 (2)	160	13	119	18 Nov 86
5	No Data	---	15	137	17 Nov 86
5	6.9 ± 2.3 (5)	200	9	150	25 Nov 86
2	5.3 ± 2.2 (3)	170	9	128	14 Nov 86

Whales Present But Not Feeding

# Whales	Krill Biomass (g/tow)	Tow Depth (m)	Thickness of DSL (m)	Depth to DSL (m)	Date
3	No Data	---	None	---	05 Nov 86
2	4.7 ± 0.9 (2)	200	6	165	26 Nov 86
2	10.3 ± 3.4 (3)	200	7	146	28 Nov 86
2	3.1 (1)	225	None	---	11 Nov 86

Whales Gone

# Whales	Krill Biomass (g/tow)	Tow Depth (m)	Thickness of DSL (m)	Depth to DSL (m)	Date
0	2.2 ± 2.1 (4)	200	None	---	30 Nov 86
0	1.9 ± 0.3 (4)	200	None	---	10 Dec 86
0	2.5 ± 1.4 (4)	200	None	---	14 Dec 86
0	0.8 ± 0.6 (4)	200	None	---	18 Jan 87
0	1.3 ± 1.9 (4)	200	None	---	11 Mar 87

* Tow taken with a 1 meter square net with 2 mm mesh.

Table 3. Scattering characteristics recorded inside and outside of surface feeding whale areas near Monterey Submarine Canyon head on 11 and 12 November 86. Daytime surface swarms of *Thysanoessa spinifera* were responsible for the surface scattering features. Mean width and depth ± one standard deviation are given for the stated number of features.

	Whales Present		No Whales Present	
	Area I	Area II	Area I	Area III
# features/km	2.7	4.5	0	0
Width (m)	38.2 ± 53.1 (n=20)	40.8 ± 58.1 (n=16)	---	---
Max. Depth (m)	4.6 ± 1.7 (n=20)	4.5 ± 1.5 (n=16)	---	---
Total transect length (km)	7.4	3.6	2.6	2.2

Table 4. Deep tows taken inside and outside whale feeding areas, along the southeast edge of the Monterey Submarine Canyon. Mean biomass and numbers ± one standard deviation are given for tows taken on 09, 14 and 25 November 1986.

Whales Present

	9 Nov 86 (n=2 tows)		14 Nov 86 (n=3 tows)		25 Nov 86 (n=5 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	16.77 ± 14.38	604 ±413	2.62 ± 2.13	85 ± 65	5.17 ± 1.94	178 ± 64
E. pacifica	0.01 ± 0.02	8 ± 11	2.47 ± 0.97	201 ± 153	0	0
N. simplex	0	0	0	0	1.51 ± 1.89	211±268
T. longipes	0	0	0.01 ± 0.01	4 ± 5	0	0
N. difficilis	0	0	0	0	0	0
Larval Krill	0.04 ± 0.03	84 ± 51	0.16 ± 0.05	371 ± 130	0.25 ± 0.07	449± 109
Krill Total	16.81 ± 14.33	---	5.26 ± 2.15	---	6.93 ± 2.33	---
Other Plankton	20.78 ± 6.64	---	10.24 ± 5.11	---	21.71 ± 5.85	---
Total	37.59 ± 7.69	---	15.50 ± 6.45	---	28.64 ± 6.45	---

Whales Not Present

	9 Nov 86 (n=2 tows)		14 Nov 86 (n=3 tows)		25 Nov 86 (n=5 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	0.07 ± 0.01	24 ± 0	0.49 ± 0.39	13 ± 10	0	0
E. pacifica	0.06 ± 0.01	24 ± 11	0.19 ± 0.19	16 ± 11	0.02 ± 0.02	2 ± 2
N. simplex	0	0	0	0	0.06 ± 0.07	10 ± 12
T. longipes	0	0	0.02 ± 0.01	5 ± 2	0	0
N. difficilis	0	0	0	0	0.02 ± 0.03	3 ± 5
Larval Krill	0.06 ± 0.01	160 ± 22	0.13 ± 0.06	306 ±123	0.11 ± 0.05	207 ± 86
Krill Total	0.19 ± 0.02	---	0.82 ± 0.48	---	0.20 ± 0.07	---
Other Plankton	13.89 ± 2.80	---	11.02 ± 4.70	---	9.76 ± 2.67	---
Total	14.08 ± 2.78	---	11.84 ± 4.25	---	9.97 ± 2.67	---

Table 5. Deep tows taken through and above the deep scattering layer located along southeast edge of the Monterey Submarine Canyon. Mean biomass and numbers ± one standard deviation are given for tows taken on 16 and 28 November 1986. Scattering layer characteristics are listed in Table 2.

Through Scattering Layer

	16 Nov 86 170 m vertical tows (n=4 tows)		28 Nov 86 200 m vertical tows (n=3 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	50.02 ± 7.00	1624 ± 230	0.19 ± 0.32	5 ± 9
E. pacifica	2.07 ± 1.85	76 ± 40	10.02 ± 3.26	653 ± 264
N. simplex	0.39 ± 0.45	32 ± 37	0	0
T. longipes	0	0	0	0
N. difficilis	0	0	0.05 ± 0.09	5 ± 9
Larval Krill	1.13 ± 0.40	1268 ± 377	0.08 ± 0.02	147 ± 44
Krill Total	53.61 ± 8.20	—	10.33 ± 3.38	—
Other Plankton	10.79 ± 2.42	—	16.53 ± 8.91	—
Total	64.40 ± 7.27	—	26.86 ± 7.61	—

Above Scattering Layer

	16 Nov 86 110 m vertical tows (n=4 tows)		28 Nov 86 130 m vertical tows (n=3 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	0	0	0	0
E. pacifica	0	0	0.53 ± 0.24	229 ± 120
N. simplex	0	0	0	0
T. longipes	0	0	0	0
N. difficilis	0.03 ± 0.06	4 ± 8	0	0
Larval Krill	0.63 ± 0.19	960 ± 438	0.21 ± 0.12	341 ± 124
Krill Total	0.66 ± 0.23	—	0.75 ± 0.22	—
Other Plankton	10.56 ± 4.10	—	23.09 ± 6.75	—
Total	11.22 ± 3.90	—	23.84 ± 6.54	—

Table 6. Surface tows taken inside and outside whale feeding areas located near the head of Monterey Submarine Canyon. Mean biomass and numbers ± one standard deviation are given for tows taken on 11 and 12 November 1986.

Whales Present

	Area I 11 Nov 86 (n=5 tows)		Area II 12 Nov 86 (n=5 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	109.10 ± 221.96	2977 ± 5892	178.77 ± 282.80	2315 ± 3562
E. pacifica	0	0	0	0
N. simplex	0.02 ± 0.03	1 ± 2	0.02 ± 0.03	3 ± 4
T. longipes	0	0	0	0
N. difficilis	0	0	0	0
Larval Krill	0.02 ± 0.02	45 ± 68	0.01 ± 0.01	10 ± 9
Krill Total	109.14 ± 221.94	---	178.80 ± 282.78	---
Other Plankton	8.49 ± 11.22	---	9.54 ± 4.06	---
Total	117.63 ± 232.93	---	188.34 ± 279.75	---

Whales Not Present

	Area I 12 Nov 86 (n=5 tows)		Area III 12 Nov 86 (n=5 tows)	
	Biomass (g/tow)	Numbers	Biomass (g/tow)	Numbers
T. spinifera	0	0	0	0
E. pacifica	0	0	0	0
N. simplex	0	0	0	0
T. longipes	0	0	0.002 ± 0.003	2 ± 2
N. difficilis	0	0	0	0
Larval Krill	0.05 ± 0.06	57 ± 70	0.02 ± 0.03	57 ± 75
Krill Total	0.05 ± 0.06	---	0.02 ± 0.03	---
Other Plankton	16.79 ± 22.46	---	9.97 ± 9.21	---
Total	16.84 ± 22.49	---	9.99 ± 9.24	---

Table 7. Standardized krill biomass and number of non-larval krill from Monterey Bay, California during November 1986. Krill densities were orders of magnitude higher within deep layers and surface swarms.

	Krill Biomass (grams per cubic meter)		**Number of Krill** (number per cubic meter)	
	Mean ± Std. Dev.	Range	Mean ± Std. Dev.	Range
Within Deep Layers				
16 Nov 86 (n=4)	3.7 ± 0.6	3.1 - 4.5	127.4 ± 17.7	102.8 - 142.4
28 Nov 86 (n=3)	1.7 ± 0.6	1.1 - 2.2	79.2 ± 48.0	31.1 - 127.2
09 Nov 86 (n=2)	1.2 ± 1.0	0.5 - 1.9	39.9 ± 28.4	19.8 - 60.0
25 Nov 86 (n=5)	1.0 ± 0.3	0.4 - 1.2	53.2 ± 36.6	14.4 - 107.9
14 Nov 86 (n=3)	0.6 ± 0.3	0.4 - 1.0	36.0 ± 17.1	17.1 - 50.5
Within Surface Swarms				
12 Nov 86 (n=5)	4.1 ± 6.5	0.1 - 15.1	53.2 ± 81.7	0.3 - 189.4
11 Nov 86 (n=5)	2.5 ± 5.1	0.1 - 11.6	68.3 ± 135.1	1.6 - 309.7
Outside Deep Layers				
16 Nov 86 (n=4)	.008 ± .003	.004 - .011	.04 ± .09	0 - .18
28 Nov 86 (n=3)	.007 ± .002	.005 - .010	2.25 ± 1.18	1.10 - 2.25
09 Nov 86 (n=2)	.001 ± .001	.001 - .001	.28 ± .06	.23 - .32
25 Nov 86 (n=5)	.001 ± .001	.001 - .002	.09 ± .06	.02 - .18
14 Nov 86 (n=3)	.006 ± .004	.002 - .008	.25 ± .14	.09 - .34
Outside Surface Swarms				
12 Nov 86 (n=5)	.001 ± .001	.001 - .002	.03 ± .08	0 - .09
11 Nov 86 (n=5)	.001 ± .001	.001 - .003	0	0

Table 8. Blue whale fecal samples from Monterey Bay during fall 1986. Percent volume was estimated visually by Susan Smith at National Marine Fisheries Service, Tiburon Laboratory. The number of *T. spinifera* molars and spermatophores were enumerated from a 0.5 ml aliquot.

	Surface Feeding Whales		Deep Feeding Whales		
Prey Items	16 Oct	12 Nov	1 Nov	1 Nov	12 Nov
T. spinifera remains	75%	90%	15%	50%	20%
# molars/ml	445	819	138	243	112
# spermatophores/ml	0	36	2	5	2
Euphausiid remains (species unidentifiable)	20%	5%	65%	45%	70%
Probable Euphausiid remains	5%	5%	20%	5%	10%
Calanoid Copepods (*Acartia* sp.)	---	<1%	---	---	---
Other Prey remains	Trace	---	---	---	---
Sample Volume (ml)	7	63	88	354	110

Table 9. Monthly coastal upwelling index anomalies (cu. m/sec/100 m length of coast) at 36°N, 122°W and sea surface temperature anomalies (°C) at Granite Canyon for August 1986 through January 1987.

Month	Upwelling Index Anomaly (cu. m/sec/100m coast)	SST Anomaly (°C)
August	-2	+0.3
September	+1	+0.5
October	0	-0.4
November	+33	+0.1
December	-9	+1.8
January	-6	+0.5

Table 10. Euphausiid concentrations reported within deep scattering layers and daytime surface swarms.

Deep Scattering Layers

Max. density (no./cu m)	Max. biomass (g wet wt/cu m)	Species	Source
23.5		*T. raschii*	Dolphin, 1987a
280	4.5	*E. pacifica*	Bary, 1966
57	15	*T. raschii*	Simard, et al., 1986b
67	4.5	*M. norvegica*	Sameoto, 1976
122	10	*N. couchii*	Cushing & Richardson, 1956
	31	*T. raschii*	Kreiger & Wing, 1986
	8	*M. norvegica*	Brodie et al., 1978
138	4.5	*T. spinifera*	Present Study

Surface Swarms

Max. density (no./cu m)	Max. biomass (g wet wt/cu m)	Species	Source
49,000	60,000	*E. superba*	McWhinney, et al., 1981
30,000		*E. superba*	Hamner, et al., 1983
	5,000	*E. superba*	Brinton, et al., 1987
	500	*E. superba*	Macaulay, et al., 1984
1,000	200	*M. norvegica*	Brown, et al., 1979
1,500,000		*E. lucens*	Nicol, et al., 1987
5,123	157.7	*E. pacifica*	Terazaki, 1980
310	15	*T. spinifera*	Present study