

**FROM WIND TO WHALES:
TROPIC LINKS IN A COASTAL UPWELLING SYSTEM**

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ABSTRACT

Due to their large body size and high mammalian metabolic rate, blue whales (*Balaenoptera musculus*) have the highest average daily total energy requirement of any species. Blue whales meet this energy demand by feeding exclusively upon dense but patchy schools of euphausiids. We used an integrated approach to determine whether a unique combination of seasonally high primary production supported by coastal upwelling works in concert with topographic breaks in the continental shelf off California to collect and maintain large concentrations of euphausiids that are exploited by foraging whales. Specifically we used concurrent ship- and mooring-based oceanographic, hydroacoustic, and net sampling, opportunistic whale sighting records, systematic visual surveys, and time-depth recorder deployment to: 1) define prey patches and whale foraging behavior within patches, 2) determine spatial and temporal patterns in the distribution and abundance of whale prey patches, and 3) examine the biotic and abiotic factors important in creating whale foraging patches in the seasonal upwelling context of Monterey Bay, California between 1992-1996.

Blue whales fed exclusively upon epipelagic euphausiids (*Thysanoessa spinifera* and *Euphausia pacifica*) that were larger and in proportions from that generally available in the Bay. Foraging blue whales targeted schools of adult *T. spinifera*, diving repeatedly to extremely dense patches aggregated between 150 and 200m on the edge of the Monterey Bay Submarine Canyon. These patches averaged 145 g m^{-3} , approximately two orders of magnitude greater than the densities generally available in the Bay (1.3 g m^{-3}). High euphausiid densities are supported by a combination of high primary production between April and August (average peak production $249 \text{ mg-C m}^{-3} \text{ day}^{-1}$) and the presence of a deep canyon that provided deep water downstream from the Davenport/Año Nuevo coastal upwelling center. Peak euphausiid densities occur in late summer/early fall, lagging the seasonal increase in primary production by 3-4 months. This lag likely

results from both the temporal development of euphausiids spawned around the seasonal increase in primary production in the spring and the shoreward collapse of productivity due to decreased intensity of coastal upwelling in the late summer. The annual migratory movements of the California blue whale likely reflect seasonal patterns in productivity in other foraging areas similar to those we have described for Monterey Bay.

INTRODUCTION

A fundamental goal in ecology is to understand the factors that determine the distribution and abundance of organisms. While a vast literature exists relating factors important in determining the distribution and movement patterns of terrestrial and near-shore predators to spatial and temporal patterns in the distribution of their food resources, similar studies for pelagic marine species are rare. This largely stems from the expense and difficulty of simultaneously measuring the distribution and abundance of predators, prey, and related environmental factors in the open ocean over the larger temporal and spatial scales they forage. As a result, most studies correlate distribution and abundance patterns of oceanic predators to direct or indirect indices of prey abundance and environmental parameters over small spatial scales and short time periods. This is particularly true for studies of the foraging ecology of large predators.

The blue whale (*Balaenoptera musculus*) is the largest organism that has ever existed. This combined with its mammalian metabolic rate, leads to the highest average daily total energy requirements of any species. Blue whales feed almost exclusively on euphausiids, at rates of up to 2 metric tons per day (Rice 1978). They satisfy this high energy demand by feeding in patchily distributed seasonal but ephemeral aggregations where euphausiids are found at high densities (Tomilin 1967, Yochem and Leatherwood 1985, Schoenherr 1991, Tershy 1992, Croll et al. 1998, Fiedler et al. 1998). Thus, blue whale foraging appears to only occur in regions of exceptionally high productivity. Traditionally, it has been speculated that blue whale distribution and movement patterns consist of a seasonal migration from high latitudes where foraging takes place to low latitudes where they mate and give birth (e.g. Mackintosh 1965; Lockyer 1981). However, data from the Pacific indicate that feeding also takes place at low latitude, “upwelling-modified” waters (Reilly and Thayer 1990, Fiedler et al. 1998, Croll et al.

1998), and data from both the Pacific and Indian Oceans indicate that some individuals remain at low latitudes year-round (Yochem and Leatherwood 1985).

Detailed information on the movement patterns of blue whales off California is not available, but they are believed to migrate annually between foraging areas in Central/Southern California (May-September), the west coast of Baja California (September-December) and the Gulf of California (January-April) (Calambokidis 1995). A number of studies have found that blue whales off California seasonally forage upon dense euphausiid schools in highly productive coastal upwelling regions (Schoenherr 1991, Croll et al. 1998, Forney and Barlow 1998, Fiedler et al. 1998). Croll et al. (1998) proposed that: 1) the distribution of blue whales in the coastal California current region is defined by their attraction to areas of predictably high prey density; 2) the preferred prey of these whales are several species of euphausiids (*Euphausia pacifica*, *Thysanoessa spinifera*, and *Nyctiphanes simplex*) that are abundant in the California Current region; 3) blue whale foraging efforts are concentrated on dense aggregations found at discrete depths in the water column; 4) these localized areas of high euphausiid densities are predictable and sustained by upwelling regions of seasonally high primary production; 5) topographic breaks in the continental shelf located downstream from these regions work in concert with euphausiid behavior to collect and maintain large concentrations of euphausiid swarms; and 6) despite seasonal and inter-annual variability, these processes are sufficiently consistent that the distribution of *Balaenoptera* whales can be predicted. In this study, we test these predictions for California blue whales feeding in a well-defined foraging area (Monterey Bay, California) over several years.

Since at least 1986 blue whales have been reported seasonally foraging in Monterey Bay on dense aggregations of euphausiids (*T. spinifera*, *E. pacifica*) (Schoenherr 1991, Calimbokidis 1995). Due to their high prey demands, we hypothesized that blue whales in Monterey Bay forage on dense aggregations of euphausiids that result from the processes we proposed above. To test this hypothesis, we used a combination of

concurrent ship- and mooring-based oceanographic sampling, hydroacoustic sampling, net sampling, opportunistic cetacean sighting records, visual surveys, and time-depth recorder deployments to describe the foraging ecology of whales within the seasonal upwelling context of Monterey Bay between 1992-1996. Specifically, we: 1) define prey patches and whale foraging behavior within prey patches, 2) determine spatial and temporal patterns in the distribution and abundance of whale prey patches, and 3) examine physical and biological factors important in creating whale foraging patches.

MATERIALS AND METHODS

Study Area

Monterey Bay, located on the central coast of California (36°45'N, 122° 00'W) (Fig. 1), is the largest bay (approximately 1,200 km²) on the West Coast with unrestricted access to the open ocean. It is further distinguished by the presence of the Monterey Submarine Canyon, a canyon of similar dimensions as the Grand Canyon (Shepard 1973).

Whale Distribution and Abundance – Opportunistic Surveys

General patterns in the distribution and abundance of blue whales in Monterey Bay was assessed using data gathered opportunistically between 1992-1996 in regular commercial whale-watching trips. Trips departed from Monterey and were usually 4-5 hours in duration. Typical cruises included 60-120 min in areas where whales, if present in the Bay, were generally found. Whale watches usually emphasized the southern regions of Monterey Bay. Experienced observers recorded the location, number, and species of all cetaceans sighted. Bi-monthly averages of the number of blue whales sighted trip⁻¹ were calculated for comparison with systematic survey data. For seasonal patterns in whale abundance, monthly averages of number of blue whales sighted trip⁻¹ were calculated for all trips between 1992-1996.

Whale Distribution and Abundance – Systematic Surveys

Between August-November 1996, a total of five systematic whale surveys were conducted for comparison with relative abundance estimates from whale-watching trips. Seven random-systematic track lines 10 to 25 km in length and separated by 5.6 km were run at a ship speed of 18.5 km hour⁻¹ (10 knots) (Fig. 1). Surveys were conducted using standard line transect methods for marine mammals developed by the U.S. National

Marine Fisheries Service (Barlow 1994). Three marine mammal observers recorded the location and number of all blue whales encountered from the track line out 90° abeam using 7X50 reticle binoculars from the flying bridge (5 m above sea level). Species, number of individuals, sighting cue, behavior, location, time, and weather conditions were recorded at the time of each marine mammal sighting. In addition, ship position along the track line was recorded every 10 minutes. Because all surveys were conducted in similar sea states, no adjustments were made for sea state. Whale density estimates were calculated using standard marine mammal line transect methods (Burnham et al. 1980, Buckland et al. 1993, Barlow 1994).

Whale Foraging Behavior

To examine whale diving behavior in relation to prey distribution, we attached microprocessor-controlled time-depth recorders (TDRs) to two blue whales foraging in the study area (Croll et al. 1998). Dive depth was sampled every 1 sec. Sampled depths were binned into 10 m bins and percent time at depth was calculated for each depth bin, excluding depths shallower than 20 m. Shallow depths were excluded as we assumed that time spent near the surface (≤ 20 m) is more likely associated with respiration than feeding. This is supported by the observation that no euphausiid swarms were observed in water ≤ 20 m. The diving behavior of foraging whales was correlated to the distribution and density of euphausiid prey schools by a series of small-area transects approximately 5.6 km long (3 nmi) covering an area of approximately 100 km², centered on the tagged, foraging whales (Croll et al. 1998).

Whale Diet

The species of prey taken by whales was determined through analysis of whale fecal samples collected opportunistically in the study region in August 1996. Samples were collected with a dip net and preserved in 70% ethanol. In the laboratory, an aliquot

was taken of a well-mixed sample and all right mandibles of euphausiids were removed and classified to species using methods developed by Kieckhefer (1992).

Euphausiid Distribution, Abundance, and Composition

The horizontal distribution of euphausiids was measured concurrent with a systematic whale abundance survey conducted August 13-14 1996. Acoustic backscatter was measured using a Simrad EY-500 echosounder operated at 200 kHz. The echosounder system was calibrated before and after the study using the standard sphere method (Johannesson and Mitson 1983). Detailed description of echosounder data analyses are presented in Croll et al. (1998) and Hewitt and Demer (1993). For plotting of prey distribution, backscattering area per 3.42 km² (1 nmi²) of sea surface integrated to 200m (s_A) was calculated from S_V values for every 0.9 km (0.5 nmi) of survey line.

From these large area surveys, we identified a region of high euphausiid and whale density. Within this region we conducted a series of small-area surveys to measure euphausiid density and vertical distribution between 19-22 August 1996 (Fig. 1). Twenty-three, 3.7 km (2 nmi) lines separated by 1.85 km (1 nmi) were run at a ship speed of 18.5 km hr⁻¹ (10 knots). Acoustic backscatter strength was measured as described above. The vertical distribution (10 m depth intervals) of euphausiid schools was measured using mean s_A values averaged over every 0.93 km (0.5 nmi) of survey trackline. Euphausiid school density in the whale foraging region was estimated using mean s_A values averaged over every 0.93 km of survey trackline and euphausiid size distribution from net samples (see below). These values were combined following Hewitt and Demer (1993), with adjustment made for transducer frequency (Greene et al. 1991).

Identification of euphausiid schools in echograms was confirmed by targeted plankton tows utilizing paired 0.7 m bongo nets fitted with 333 μ m mesh. Euphausiids were enumerated for the entire sample or a sub-split of the sample (minimum 200

individuals), identified to species and life history stage, and measured to the nearest mm.. Euphausiid species composition from net samples was compared with species composition from whale fecal samples. In addition to these targeted tows in August 1996, 200 m oblique net samples were taken in May, August, and September 1996 at the edge of the Monterey Submarine Canyon to examine seasonal changes in age composition of euphausiids.

Euphausiid size distribution from August net samples was used for hydroacoustic biomass estimates. Biomass estimates were calculated following the techniques described in Hewitt and Demer (1993), incorporating euphausiid size distributions measured in bongo net tows. Adjustment of biomass estimates for transducer frequency was made following Greene et al. (1991). Numerical densities of krill (individuals m⁻³) were estimated from acoustic estimates of biomass density using species composition and size distribution from net tows and the allometric conversion of standard length to euphausiid weight derived for *E. superba* (Hewitt and Demer 1993).

Seasonal Abundance of Zooplankton

The relative seasonal abundance of zooplankton in Monterey Bay was tracked using hourly averages of acoustic backscatter measured by a 75 kHz Acoustic Doppler Current Profiler (ADCP) permanently mounted on a mooring (located at 122°01' W, 36°36' N, Fig. 1), operating at 75 kHz. ADCP data have been used to provide relative estimates of zooplankton abundance through backscatter strength (e.g. Buchholz et al. 1995, Griffiths and Diaz 1996), but are not able to accurately provide quantitative estimates of zooplankton abundance (Brierly et al. 1998). Daily averages of 1996 ADCP volume backscatter were binned into 1 m bins and used to generate a seasonal comparison of zooplankton densities.

Oceanographic Sampling

Detailed methods for oceanographic sampling is described in detail elsewhere (Pennington and Chavez in press). Briefly, shipboard time-series data were collected twice monthly between 1992-1996 aboard the R/V Point Lobos on single-day cruises. In this paper we report results from two of the stations occupied in Monterey Bay (C1, M1; Fig. 1). Conductivity/temperature/depth (CTD) casts were made to at least 200m with a Sea-Bird 911 or 911+ CTD mounted in a General Oceanics 12-place rosette with 5-1 Niskin bottles (silicon o-rings). Conductivity and temperature sensors were calibrated annually. Downcast data were binned to 1 m depth intervals, and upcast data were averaged following each bottle trip.

Rosette Niskin bottles were filled at the surface, 5, 15, 30, 50, and 100 m. Water from these samples was used to calculate integrated Chlorophyll and primary production measurements. Chlorophyll *a* concentration (hereafter-termed 'chlorophyll', mg-chl m⁻³) was assayed with the standard fluorometric procedure of Holm-Hansen et al. (1965). This method was modified such that plant pigments were filtered onto 25 mm Whatmann G/FF filters and extracted in acetone in a freezer for 24-48 hr (Venrick and Hayward 1984, Chavez et al. 1991). Measurements were made on a Turner Model-10 fluorometer calibrated with commercial chlorophyll *a* (Parsons et al. 1984). Primary production was estimated as carbon fixation (hereafter-termed 'primary production', mg-C m⁻³ da⁻¹) for 100% light penetration depth (surface) using ¹⁴C uptake methods described in Pennington and Chavez (in press).

Upwelling indices for the study region during the study period were obtained from the Pacific Fisheries Environmental Laboratory/NOAA web site for 36°N 122°W (www.pfeg.noaa.gov). The indices are based on estimates of offshore Ekman transport driven by geostrophic wind stress derived from six-hourly synoptic surface atmospheric pressure fields (Bakun and Nelson 1991). Bi-monthly means of the daily upwelling indices were calculated.

Unless otherwise noted, means \pm S.D. are reported.

RESULTS

Whale Distribution and Abundance

Blue whale sightings from whale-watch trips between 1992-1996 were concentrated along the edge of the Monterey Submarine Canyon (Fig. 2), and were seasonally present in Monterey Bay between June and November (Fig. 3). Relative abundance estimates from whale-watch trips qualitatively tracked abundance estimates from systematic surveys (Fig. 4), and thus probably accurately reflect seasonal abundance of blue whales between 1992-1996. Systematic surveys revealed that blue whale density during the time period of peak abundance (August) was 0.034 whales km² (+0.056, -0.204 S.E.).

Whale Foraging and Diet

Two whales foraging during daylight hours (1100-1700) on the edge of Monterey Submarine Canyon were tagged with TDRs in 1996 (August 19 and 22, 1996). To account for short duration shallow dives associated with respiration, only dives that exceeded 2 min in duration and 30 m depth were included for analysis of foraging dives. This convention was supported by three observations: 1) all short duration shallow dives took place within a series of surface respirations, 2) no echo returns attributable to euphausiids were observed in water less than 30 m deep, and 3) zooplankton net hauls to less than 30 m did not contain euphausiids. Maximum foraging dive depth ranged from 144 to 176 m and 142 to 193 m in the two tagged whales, respectively. Mean maximum dive depth was 155 m (± 9.8) and 172 m (± 14.7), and mean dive durations were 8.8 min (± 0.8) and 8.3 min (± 1.4), respectively. Both whales showed a stereotypical pattern, diving consistently and directly down to the 150-200 m layer in the water column and performing a series of 1-4 20-30m vertical excursions on each dive (Fig. 5). Surface tracks of both whales remained within 5 km of the canyon edge throughout the tag deployment period, moving parallel to the canyon edge.

In August, 1996, blue whales fed exclusively upon euphausiids in proportions (percent by number) significantly different from the composition of euphausiids in net samples ($X^2=455.55$, $df=2$, $P<0.001$). Fecal sample analysis ($N=5$) revealed that blue whales in Monterey Bay fed primarily upon *Thysanoessa spinifera* ($80\% \pm 22.6\%$) and *Euphausia pacifica* ($13\% \pm 26.4\%$); other euphausiids accounted for $7\% (\pm 4.7\%)$ of diet. Euphausiid species composition within net samples collected during the same period consisted of $30.17\% (\pm 34.95\%)$ *T. spinifera*, $68.32\% (\pm 34.75\%)$ *E. pacifica*, and $1.51\% (\pm 2.56\%)$ other species. The mean size of *T. spinifera* and *E. pacifica* taken by whales was $19.3\text{ mm} (\pm 1.53, n=162)$, and $16.0\text{ mm} (\pm 2.05, n=82)$, respectively. This was significantly larger than the size of *T. spinifera* and *E. pacifica* taken in net samples ($16.3\text{ mm} \pm 3.71, n=100$ and $11.8\text{ mm} \pm 3.32, n=100$, respectively). T-test; *T. spinifera*: $t=9.12$, $d.f.=260$, $P<0.001$; *E. pacifica*: $t=9.99$, $d.f.=180$, $P<0.001$ (Fig. 6).

Euphausiid Distribution, Abundance, and Composition

The large-area survey conducted on 13-14 August 1996 revealed euphausiid schools were located close to the offshore edge of the submarine canyon (Fig. 1). Mean backscattering strength of euphausiids in this survey was $2,528\text{ m}^2\text{ nmi}^{-2}$ (± 461.7 S.E.), which is equivalent to a mean density of 1.3 g m^{-3} (± 6.35 S.E.), 39 individuals m^{-3} , or 260 g m^{-2} . Blue whales encountered during this survey were also located over or close to edge of the submarine canyon (Fig. 1). Small-area surveys revealed these canyon-edge euphausiid schools were concentrated between 80 and 180 m, averaged $15.1\text{ m} (\pm 8.38)$ in height ($N=226$, 0.5 nmi samples), with most euphausiid schools located between 120 and 160 m (Fig. 7). The mean integrated backscattering strength of these canyon-associated schools was $20,385\text{ m}^2\text{ nmi}^{-2}$ (± 1873 S.E.), which is equivalent to a mean density of 145.3 g m^{-3} (± 11.51 S.E.), $4,403$ individuals m^{-3} , or 2201 g m^{-2} (integrated over the mean 15.1 m school depth).

There was considerable variability between spatially distinct euphausiid schools both with respect to species composition and individual size structure. Percent composition and mean size for *T. spinifera* and *E. pacifica* within the seven targeted net samples conducted between August 14-21, 1996 are summarized in Table 1. The overall mean size for *T. spinifera* and *E. pacifica* individuals was $16.3 \text{ mm} \pm 3.71$, $n=100$ and $11.8 \text{ mm} \pm 3.32$, $n=100$, respectively, however, there were significant differences in the mean size of individuals between spatially distinct schools (Kruskal-Wallis *T. spinifera* $H = 89.91$ $p < 0.001$ $df = 2$, *E. pacifica* $H = 380.23$ $p < 0.001$ $df = 5$).

Net samples from May, August, and September, 1996 revealed strong seasonal recruitment and growth for both *T. spinifera* and *E. pacifica* populations within Monterey Bay (Fig 8). Juveniles made up the bulk of both populations in May of 1996, while adults became numerically dominant in August and September, though the persistent presence of juveniles within all samples indicated that recruitment was continuous throughout the summer.

Seasonal Abundance of Zooplankton

ADCP backscatter was averaged between 1992-96 to provide a seasonal climatology of zooplankton in Monterey Bay (Fig. 9). Early in the year (Jan-Feb) backscatter intensity is relatively high, with layers appearing near the surface and below 150m. By mid-March the deeper layer has disappeared and overall backscatter is at a minimum. Water column backscatter abruptly increases in July, and the deeper layer of zooplankton reappears. High levels of backscatter persist until mid-October when backscatter levels diminish, but the deeper layer persists.

Seasonal Patterns in Oceanography

Oceanographic climatology for Monterey Bay between 1992-1996 is summarized in Fig. 3. Upwelling-favorable winds lead to a shift in the upwelling index from negative

values (downwelling) to positive values (upwelling) in late February. Upwelling persists until late summer. This upwelling leads to a sharp decline in sea surface temperature, indicating cold nutrient-rich water has reached the surface by mid-March. This is linked to a mid-March increase in primary production, which is also reflected in surface chlorophyll-a values.

DISCUSSION

Whale Diet and Euphausiid Composition

Blue whales foraging in Monterey Bay fed exclusively upon epipelagic euphausiids (*T. spinifera* and *E. pacifica*), in proportions that were different from the overall composition in net samples. Schoenherr (1991) found that blue whales in Monterey Bay fed primarily upon *T. spinifera*, and while she did not report *E. pacifica* in the diet, it is likely that much of the unidentifiable material in her samples consisted of *E. pacifica*. This is supported by the observation that *E. pacifica* was the second most common euphausiid species she found in deep net tows. Because her study focussed upon surface feeding whales, and *T. spinifera* is found in the upper portion of the water column where it often forms surface swarms (Youngbluth 1976, Smith & Adams 1988), it is possible that the importance of this species was overemphasized in her study. Similar to our study, Fiedler et al. (1998) found that the dominant species in net tows in the vicinity of foraging blue whales and blue whale fecal samples near the Channel Islands, California were *T. spinifera* and *E. pacifica*.

Fiedler et al. (1998) speculated that foraging blue whales preferentially feed upon adult euphausiids. Comparison of our blue whale diet and net sample data in Monterey Bay support this hypothesis: euphausiids found in whale fecal samples were significantly larger than those taken in net samples. This observation may be due to several possibilities including bias towards less mobile euphausiids in net samples, escape of smaller euphausiids through the baleen of foraging whales, and/or preferential targeting of adult euphausiid schools by foraging whales. A number of observations support the hypothesis of preferential targeting of adult euphausiid schools: Individual size distributions for both species of euphausiids within whale fecal samples were similar to size distributions for adults collected within net tows, though in the case of *T. spinifera*,

there is some indication that whales were foraging on larger individuals (> 25 mm) that may have avoided capture in net tows (Fig 6). Furthermore, data on the species and size composition of euphausiid schools (Table 1) demonstrate that euphausiid schools are highly variable in species and size structure of fine spatial scales. Our direct measurement of the diving behavior of whales in Monterey Bay (Fig. 5) indicates that whales concentrate their foraging activity on deeper layers of euphausiids located between 150-200m. Several investigators (e.g. Lavaniegos 1996, Bollens et al. 1992) have found that later life history stages of euphausiids are found deeper in the water column. Wishner et al. (1995) also suggested that right whales select copepod aggregations with older lifestages.

Blue Whale Foraging

The distribution of blue whale sightings and euphausiid densities (Figs. 1 and 2), and the daytime vertical distribution of whale dives and euphausiids (Fig. 6) indicate that whale foraging effort is concentrated on dense euphausiid schools associated with the Monterey Submarine Canyon. Whales dove directly down to the densest aggregations of euphausiids between 150 and 200m on the canyon edge. Studies of blue whales foraging off the Channel Islands, California have reported similar behavior (Fiedler et al. 1998, Croll et al. 1998).

Whales sought patches that were approximately two orders of magnitude greater than the densities generally available in the Bay. Because our measurements were directed at patches where whales were observed foraging, we feel that this provides, for the first time, an estimate of the magnitude of prey densities for large rorquals. These densities are higher than both the mean ($6-73$ kg m⁻²) and maximum (154 kg m⁻²) densities estimated for *Thysanoessa raschi* and *Meganyctiphanes norvegica* by Simard and Lavoie (1999) using acoustics in the Gulf of St. Lawrence, an important blue whale foraging area. These values are also higher than mean values in other regions of high

euphausiid density: 2-102 g m⁻² for the Scotian Shelf, North Atlantic (*T. raschi*, *M. norvegica* and *T. inermis*) (Sameoto 1980, 1983, Cochrane and Sameoto 1991) and 30-61 kg m⁻² for Elephant Island, Antarctica (Hewitt and Demer 1993). Acoustic measurements from these other studies, however, were not directed at specific locations where large whales were concurrently foraging.

How do these densities compare with prey densities observed for other zooplanktivores? Brodie et al. (1978) estimated that fin whales (*Balaenoptera edeni*) required prey concentrations of at least 17.5 g m⁻³ to meet its daily energy requirements. Although mean euphausiid densities in Monterey Bay were much lower than this, such densities were readily available at the canyon edge. Dolphin (1987) estimated euphausiid densities where humpback whales were foraging at 910 individuals m⁻³ (compared to our finding of 4,403 individuals m⁻³), and that minimum required densities were about 50 individuals m⁻³. Wishner et al. (1995) found that zooplankton densities in regions where right whales foraged in the southwestern Gulf of Maine were approximately 3 times the mean densities in the region (whale feeding densities averaged 3.1-5.9 g m⁻³, compared to 1.1-3.6 g m⁻³ where whales were not foraging). In a related study, Macaulay et al. (1995), using hydroacoustic surveys, estimated zooplankton density where right whales were foraging at 18-25 g m⁻³ (compared to 1-5 g m⁻³ where whales were not foraging). Sims and Quayle (1998) found that basking sharks (another large filter-feeder) preferentially feed on the richest, most profitable zooplankton patches associated with fronts. In a related study, Sims (1999) found zooplankton densities in regions where sharks foraged where 3.2 times that of median zooplankton densities. They estimated the foraging threshold for these filter-feeding zooplanktivores at approximately 0.62 g m⁻³. Compared to these large zooplanktivores, blue whales are seeking extremely dense aggregations of zooplankton to meet their metabolic needs. Unlike blue whales, which lunge at discrete, dense concentrations of prey, right whales and basking sharks are skim feeders, filter feeding much larger volumes of water for prey in a less selective manner. Thus, they

should find patches of much lower prey density than those sought by blue whales profitable.

Distribution of Whales and Euphausiids

Schoenherr (1991) first reported the association of blue whales with the steep topography of the Monterey Submarine Canyon, and our study confirms this observation. This association could result from whales directly responding to physical patterns in water temperature or currents in this region, or they may be associating indirectly via patterns in the distribution of biological resources that are directly responding to the canyon edge habitat. Water temperature and current patterns in the upper portion of the water column in Monterey Bay are most strongly influenced by upwelling north of the Bay than the canyon feature itself (Paduan and Rosenfeld 1996, Rosenfeld et al. 1994), so it is unlikely whales are directly associating with the canyon. Instead, both our study and Schoenherr's demonstrate that whales are aggregating on the canyon edge as they exploit dense schools of euphausiids associated with the canyon.

There are several factors that may lead to the association of euphausiids with the canyon edge. Euphausiids are generally found in regions of high primary productivity (Brinton 1962a, 1962b, Mauchline 1980). In most areas they have been studied, adult epipelagic euphausiids such as *E. pacifica* and *T. spinifera* undergo diel migrations to depths in excess of 100 m (e.g. Hovekamp 1989, Greenlaw 1979, Bollens et al. 1992). Along the central California coast, the continental shelf break occurs at a depth of around 100-150 m. Some of the most productive coastal waters along the California coast are found over inshore of the shelf break, downstream from upwelling centers (Reid et al. 1958, Wooster and Reid 1963, Rosenfeld et al. 1994, Pennington and Chavez in press). Topographic breaks in the shelf such as the Monterey Submarine Canyon bring water depths in excess of 1,000 m within 10 miles of shore, downstream from upwelling centers such as Pt. Ano Nuevo. These breaks provide euphausiids that aggregate in the canyon

the ability to undergo diel migrations in excess of 100 m (presumably to minimize predation in daylight hours) while remaining in the highly productive recently upwelled nearshore waters (Rosenfeld et al. 1994).

The current dynamics of the canyon may also help reduce energetic costs for swimming in euphausiids during the day. Below 100 m over the continental slope off central California, the dominant current is the northward-flowing California Undercurrent (Chelton 1984, Wickham et al. 1987, Chelton et al. 1988, Tisch et al. 1992). Ramp et al. (1997) found that northward currents at 100 m depth off Pt. Sur, California (approximately 60 km south, outside of Monterey Bay) averaged 9.5 cm s^{-1} . In contrast, currents at 100 m in the Monterey Submarine Canyon where euphausiids were aggregated averaged $<2 \text{ cm s}^{-1}$ (Chavez, unpub. Obs.). Thus, the Monterey Submarine Canyon habitat would provide: 1) the opportunity for high energy gain during nighttime surface feeding due to its location downstream from an upwelling center; 2) a refuge from daytime predation as euphausiids can migrate to depths in excess of 100 m in the canyon, and 3) reduced swimming energy output during daytime schooling at depth due to reduced canyon slope currents. Similar factors may be important in other blue whale foraging areas off the California and Baja California coasts where bottom topography provides deep water access downstream from coastal upwelling centers (e.g. Santa Barbara Channel, Cordell Bank, Gulf of the Farallons, Punta Eugenia, Bahia Loreto).

Seasonal Patterns in Oceanographic Processes and Whale Abundance

Coastal upwelling occurs seasonally along the coast of California (Reid et al. 1958, Wooster and Reid 1963, Bakun et al. 1974, Bakun 1990). Equatorward winds develop in the spring due to movements of the Aleutian low-pressure system and North Pacific high. These winds act in combination with the Coriolis force, leading to a positive curl in the wind stress that moves an Ekman layer of surface waters offshore. This draws cold, nutrient-rich deeper water to the surface that extends as a broad band of cool water 10's

of kilometers along the California coast (reviewed by Hickey 1979). In some regions fronts, plumes, and eddies can develop, extending >100 km offshore (Abbot and Zion 1985, Kelley 1985, Strub et al. 1991). This seasonal upwelling of nutrient-rich water supports high primary production and, in turn, higher trophic levels (Reid et al. 1958, Barber and Smith 1981, Hutchings et al. 1995).

In Monterey Bay, California, high levels of primary and zooplankton production are supported by springtime upwelling to the north of the Bay between Pt. Año Nuevo and Davenport (Rosenfeld et al. 1994, Service et al. 1998, Pennington and Chavez in press). Skogsberg (1938) defined three oceanographic periods in the Bay: 1) a spring/summer 'upwelling season'; 2) a summer/fall 'oceanic season', and 3) a winter 'Davidson Current season'. These periods have generally been accepted by subsequent studies (Barham 1957, Bolin and Abbot 1963, Pennington and Chavez in press). During the upwelling season, pulses of northwest wind lasting a few days generally develop around February, supporting pulses of high primary production which lag the initiation of upwelling by 6-10 days (Dugdale and Wilkerson 1989, Service et al. 1998). Depending on conditions, these pulses can sporadically occur into the oceanic season (Pennington and Chavez in press). Fewer studies have examined seasonal changes in secondary productivity, but Barham (1957) found that zooplankton abundance was highest in the late upwelling and early oceanic seasons.

Physical and biological oceanographic climatologies for Monterey Bay between 1992-1996 confirm these seasonal patterns and demonstrate linkages between physical forcing, sea surface temperature, and productivity in the Bay (Fig. ***). Increased wind forcing in February leads to decreases in sea surface temperature (upwelling) and increases in primary production and surface chlorophyll. However, it is less clear how these events are linked to seasonal patterns in zooplankton and blue whale abundance.

Moderate zooplankton abundance appear to persist through February, with distinct scattering layers near the surface and below 150 m (Fig. 9). However, by March,

zooplankton backscatter is considerably reduced, and the deeper backscatter layer is no longer present. It is not until July, several months after the seasonal increase in primary production (Fig. 3) and the initiation of the oceanic period, that zooplankton backscatter dramatically increases. At this time both the shallow and deeper backscatter layers reappear, persist through September and begin to taper off in October. The seasonal arrival of blue whales in Monterey Bay appears to be linked to this dramatic increase in zooplankton in July. In a long-term study of productivity off Pt. Conception, California, Hayward and Venrick (1998) similarly found close linkages between physical forcing and integrated chlorophyll values. They also found that while integrated chlorophyll peaked in spring, zooplankton biomass did not peak until one to four months later.

Two non-exclusive hypotheses may explain the July increase in zooplankton density and arrival of blue whales in Monterey Bay. First, ontogenetic development of euphausiid larvae, spawned from over-wintering adults between January-February, may lead to a July recruitment of adult euphausiids. This hypothesis is supported by the changes in euphausiid development from net samples in May (mostly larval euphausiids) into August and September (predominantly adult euphausiids) (Fig. 8). Second, a seasonal decrease in the intensity and frequency of upwelling-favorable winds leading to a shoreward collapse of offshore productivity towards the coast (Abbot and Barksdale 1991). This would lead to a seasonal peak in euphausiid density as euphausiids tracking this shoreward collapse arrive in Monterey Bay. Both of these factors would explain seasonally high densities of adult euphausiids in Monterey Bay, leading to the appearance of blue whales in the Bay in July.

An interesting parallel to our study is that of Robison et al. (1998). They examined the 1993-1995 seasonal abundance in Monterey Bay of *Nanomia bijuga*, a predatory siphonophore that feeds primarily upon the same euphausiid species as blue whales (Alvarino 1971, Mackie 1985). They found that daytime population densities were highest between 200 and 400 m, deeper than our ability to measure zooplankton

abundance with acoustics. Similar to our observation for blue whales, they found that siphonophore populations peaked in July, about 3-4 months after the seasonal peak in primary production. Unlike blue whales, which seasonally migrate to Monterey Bay, Robison et al. hypothesized the seasonal increase in *Nanomia* resulted either from onshore advection through the intrusion of offshore oceanic water due to decreased upwelling (essentially tracking the shoreward collapse of Euphausiids), or *in situ* population growth of siphonophores.

Prey Resources and Whale Migration Patterns

The annual migratory movements of the California blue whale likely reflect seasonal patterns in productivity in other foraging areas similar to those we have described for Monterey Bay. Regions with different seasonal upwelling patterns and euphausiid species with different life history traits will show temporal differences in peak euphausiid abundance. Due to their high total prey requirements, California blue whales likely migrate seasonally between dense, ephemeral euphausiids patches that appear in southern/central California in the summer and fall, the Gulf of California in the winter, and the central Baja California Pacific coast in the spring. Tershy (1992) hypothesized that such seasonal movement patterns by rorqual whales in response to ephemeral and patchy prey resources are similar to patterns described for terrestrial ungulates.

Jarman (1974) related the distribution of antelope species to gradients in food quality, patch size, and spatial/temporal distribution. He proposed that high quality food that is found in small and predictable patches is exploited by small, resident, territorial species with low total caloric requirements and high mass-specific metabolic rates. At the other extreme, low quality food that is found in large and unpredictable patches is exploited by large, migratory, non-territorial species with high total caloric requirements and low mass-specific metabolic rates. Similar patterns have been found in carnivorous, omnivorous, and frugivorous species (Bekoff et al. 1981, Clutton-Brock 1974, Fleming

1991, Jarman and Southwell 1986, Lovegrove and Wissel 1988). Our study of the relationship between the world's largest predator and the temporal and spatial distribution of its prey support Tershy's (1992) hypothesis.

We found that California blue whales foraging in the coastal upwelling zone sought extremely dense patches of euphausiids aggregated on the edge of the Monterey Bay Submarine Canyon. High euphausiid densities appear to result from the habitat provided by the proximity of the deep canyon to an upstream coastal upwelling center. Dense patches seasonally develop, lagging the seasonal increase in productivity by 3-4 months. This lag may result from the temporal development of euphausiids spawned around the seasonal peak in primary production and the tracking of the shoreward collapse of productivity with decreased coastal upwelling.

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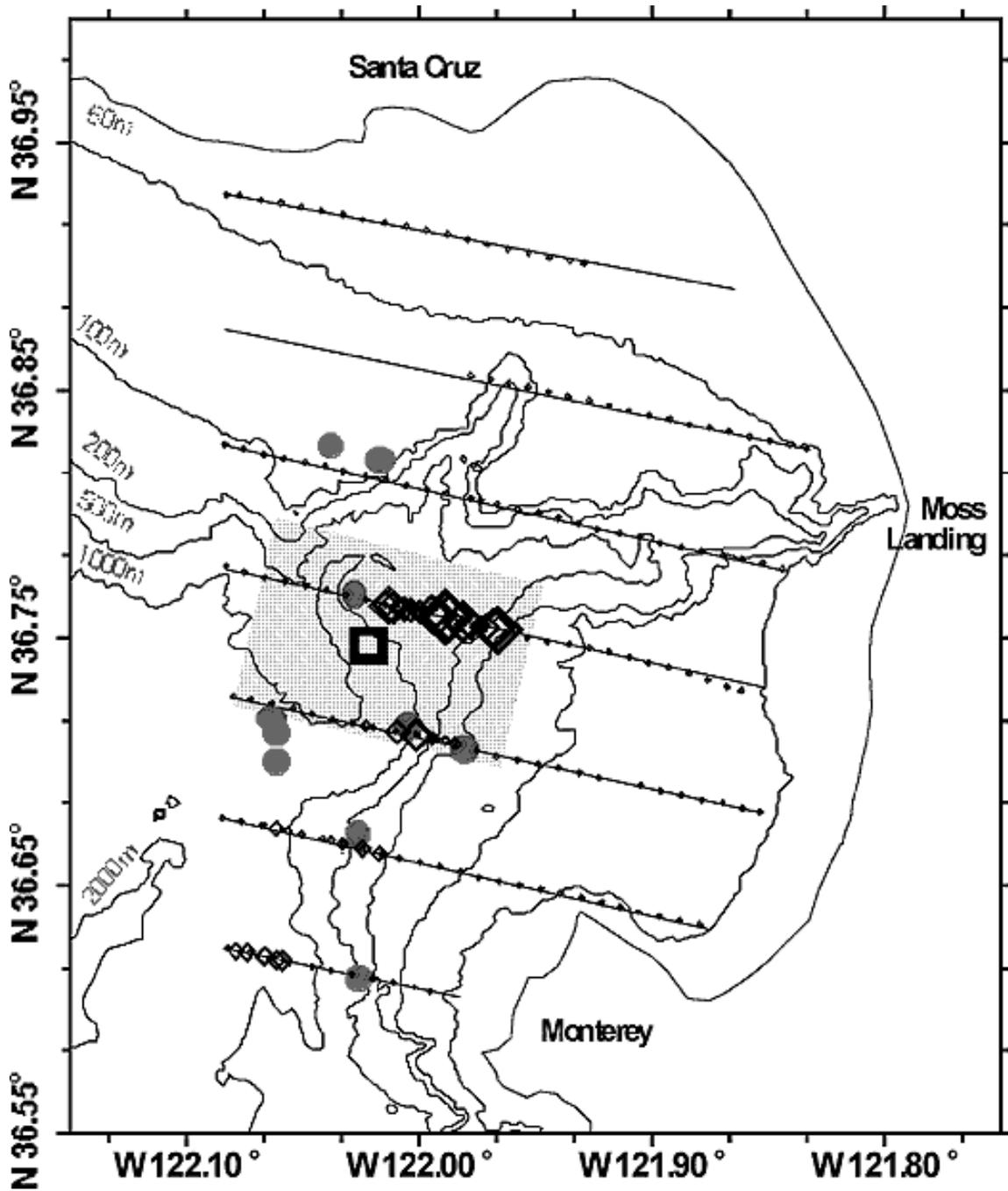


Figure 1. Monterey Bay, California study area. Systematic survey tracklines indicated. Euphausiid acoustic backscatter during August 13-14 survey shown as scaled diamonds, blue whale sightings shown as circles. Open square indicates location of oceanographic sampling station M1. Shaded area denotes small-area survey region.

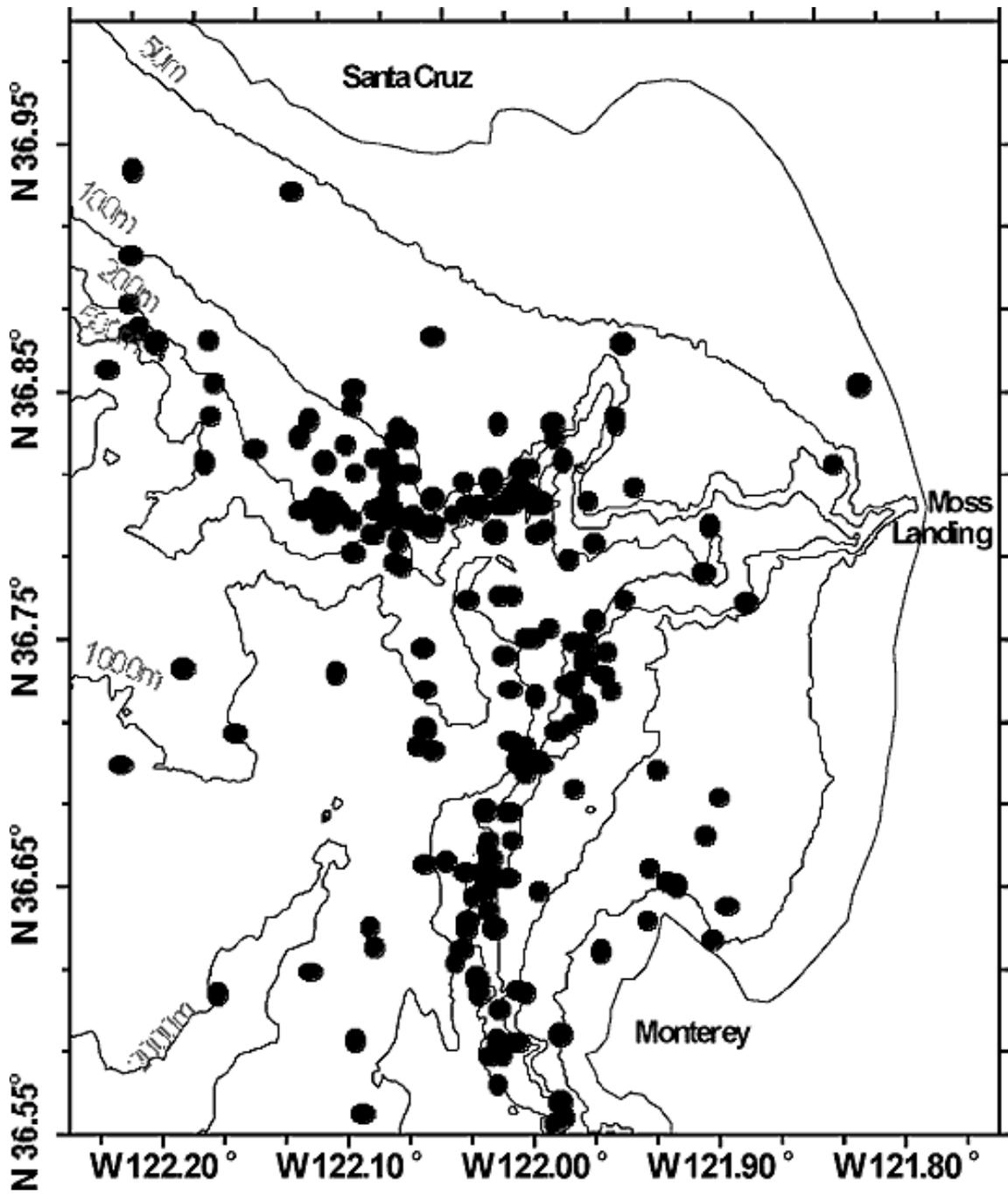


Figure 2. Location of blue whales sighted during opportunistic whale watch surveys between 1992-1996 in Monterey Bay, California.

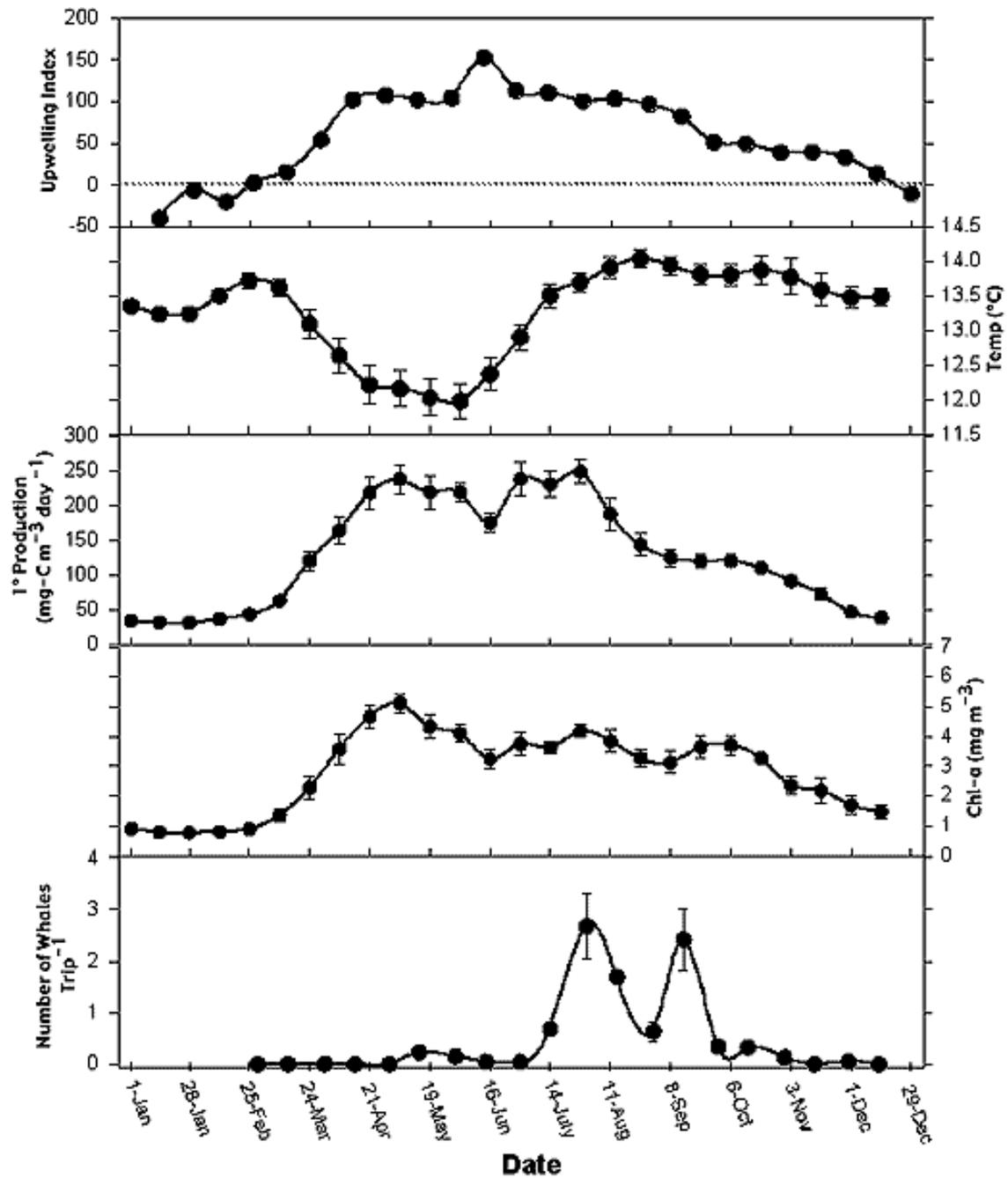


Figure 3. Oceanographic climatology (mean \pm S.D.) for Monterey Bay, California between 1992-1996. From upper to lower panels: Pacific Fisheries Environmental Laboratories/NOAA upwelling indices, sea surface temperature, primary production at 100% light levels, integrated chlorophyll-a, and number of whales per trip in opportunistic whale watch surveys.

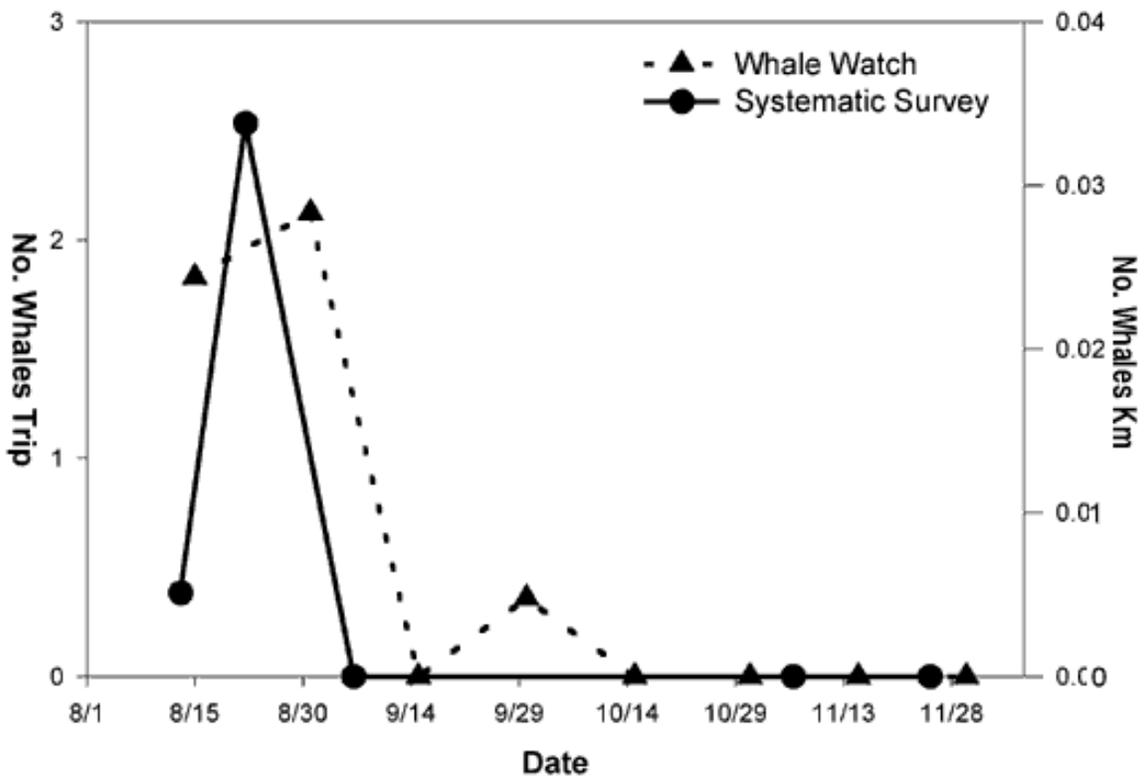


Figure 4. Comparison of results of opportunistic whale watch surveys (dashed line) and systematic marine mammal surveys conducted between August and November, 1996, Monterey Bay, California.

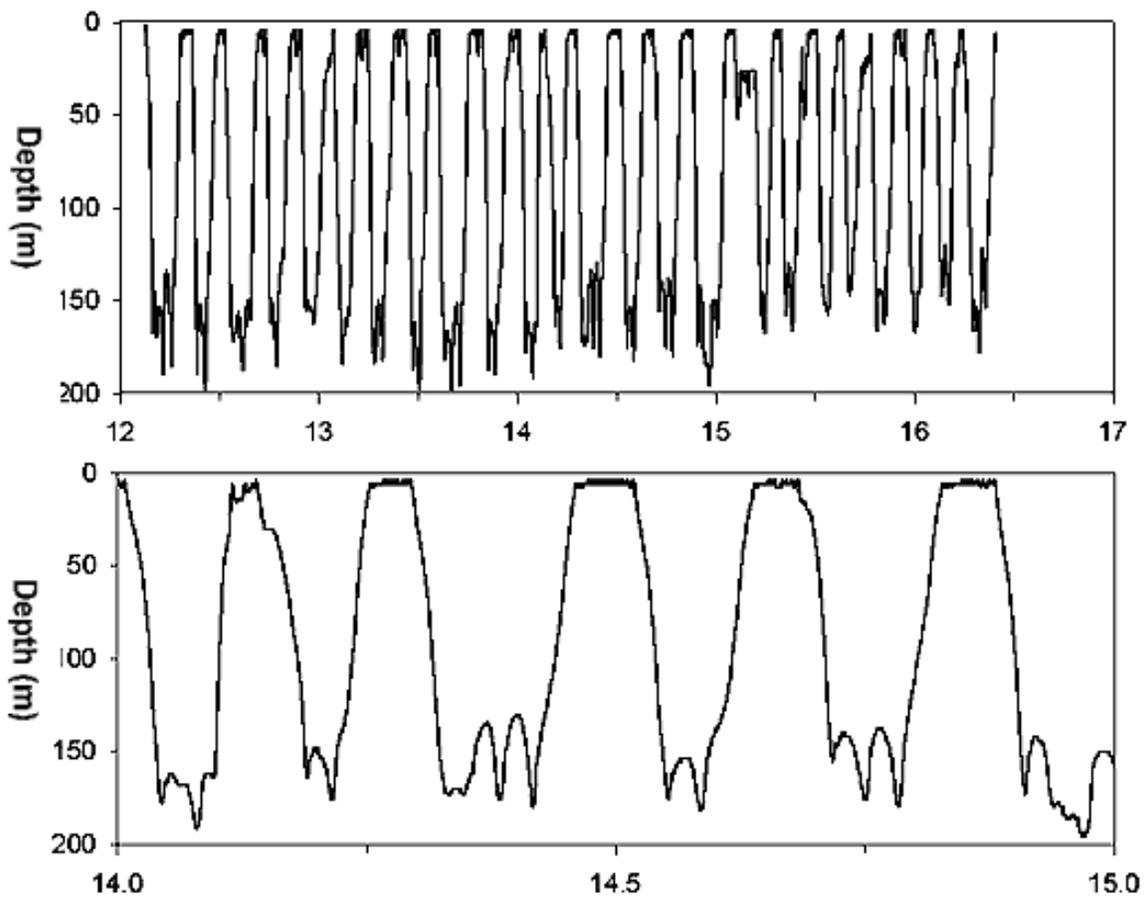


Figure 5. Diving behavior of blue whale tagged in the small area survey region on August 22, 1996, Monterey Bay, California.

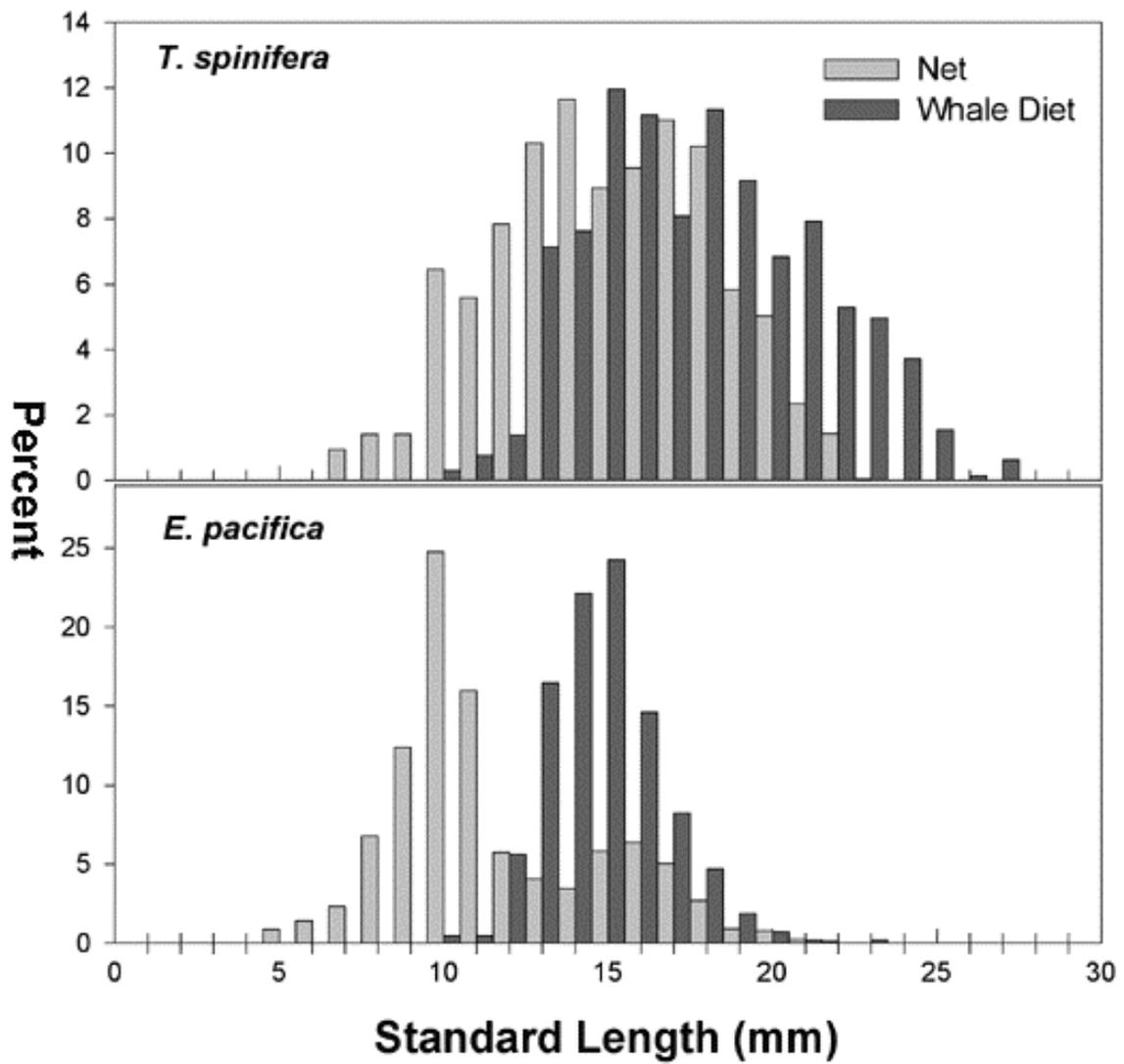


Figure 6. Comparison of length distribution of euphausiids captured in bongo net samples with those estimated from whale fecal samples collected in August, 1996 in Monterey Bay, California.

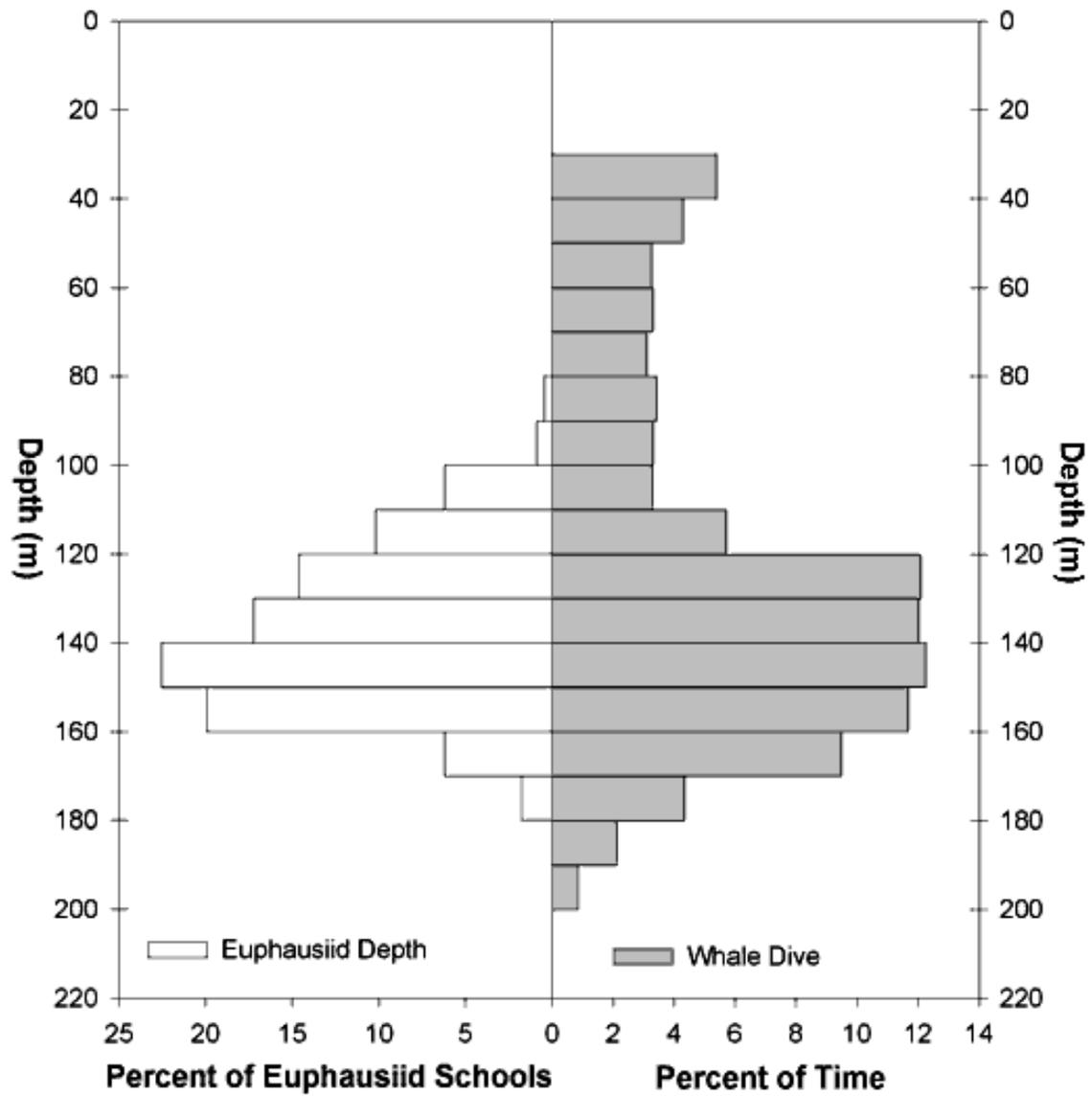


Figure 7. Comparison of the depth distribution of euphausiid schools encountered in small-area surveys in Monterey Bay, California with time spent at depth in two foraging whales tagged in the same area August, 1996.

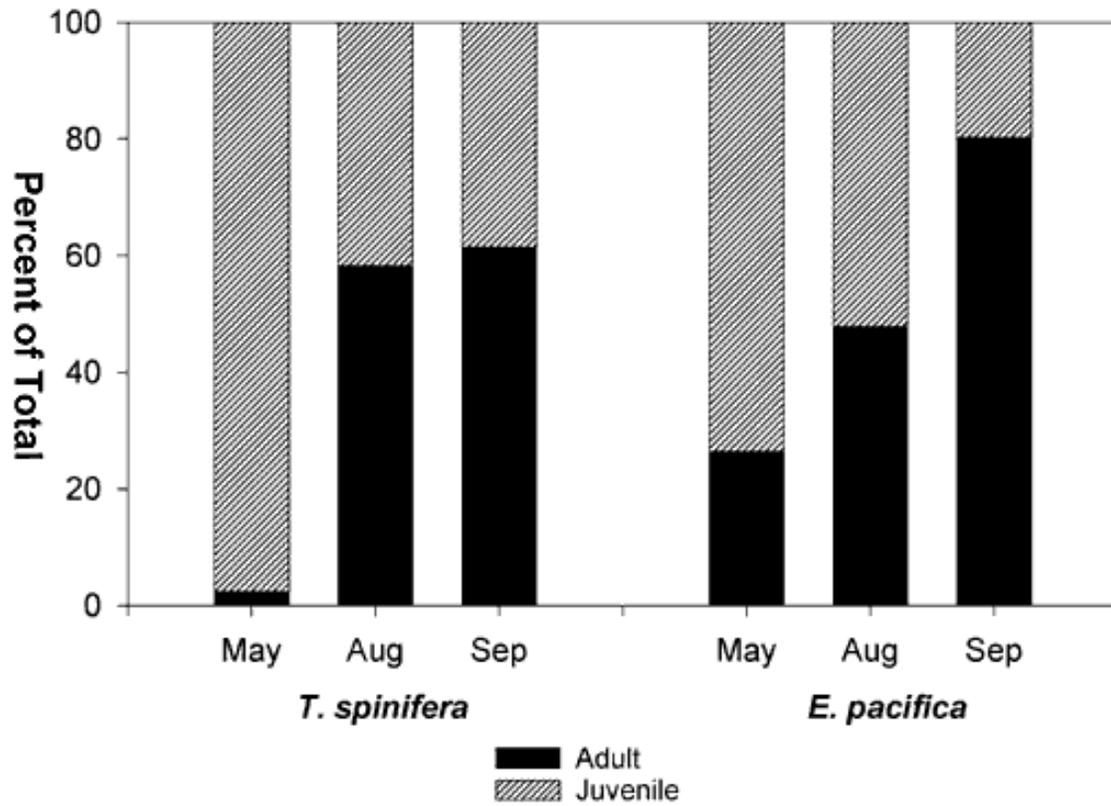


Figure 8. Age composition of euphausiids captured in bongo net samples in Monterey Bay, California, 1996. Juvenile euphausiids indicated by hatched bars, adults by solid bars.

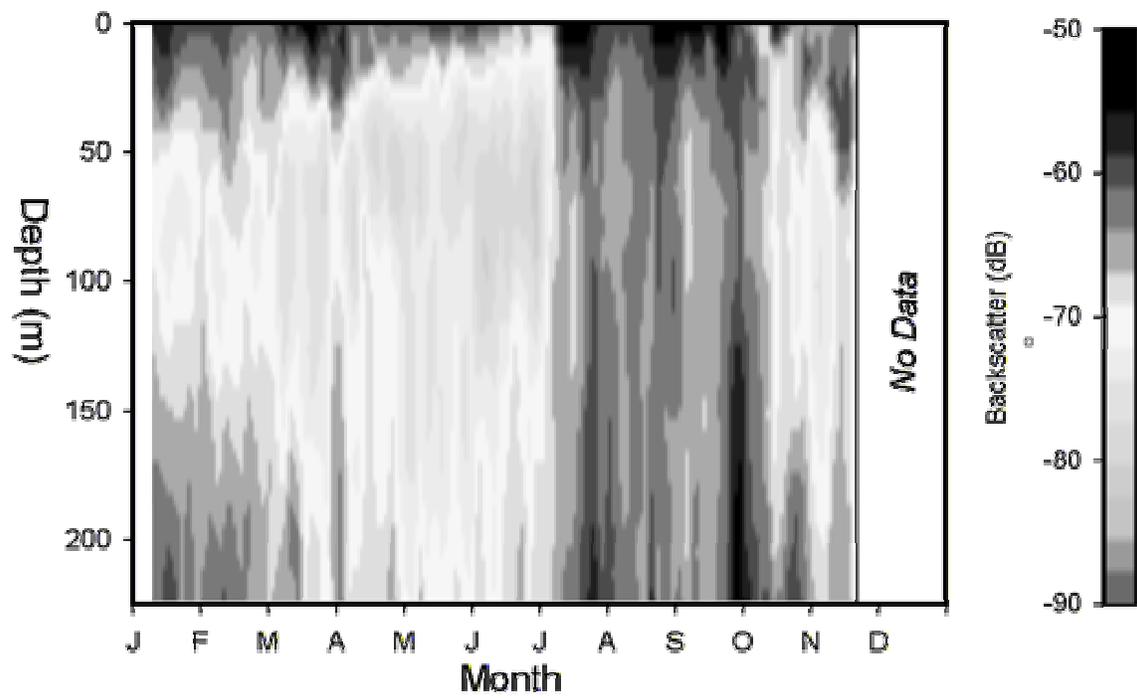


Figure 9. Seasonal density of zooplankton by depth averaged between 1992-1996 from acoustic doppler current profiler backscatter. ADCP located on mooring at station M1, Monterey Bay, California

Targeted Tow	<i>T. spinifera</i>: %; length(± s.d.)	<i>E. pacifica</i>: %; length (± s.d.)
A	0	99.53% 10.23 ± 3.07 mm (n=90)
B	0	100.00% 10.14 ± 1.58 mm (n=230)
C	11.53% 16.82 ± 3.51 mm (n=50)	81.07% 15.95 ± 1.98 mm (n=153)
D	29.44% 11.64 ± 3.34 mm (n=63)	70.56% 14.99 ± 3.48 mm (n=141)
E	2.51% 18.33 ± 2.26 mm (n=75)	97.49% 10.98 ± 3.30 mm (n=148)
F	40.08% 11.53 ± 2.09 mm (n=108)-	57.68% 12.04 ± 2.91mm (n=140)
G	98.56% 14.20 ± 2.88 mm (n=156)	0

Table 1: Percent composition and mean individual length ±s.d. of euphausiids collected in targeted net tows August 14-21, 1996 in Monterey Bay, CA