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The spatial distribution of euphausiid aggregations in the Northern California Current during August 2000

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Abstract

The location and size of euphausiid aggregations (patches) were identified using acoustic volume backscattering strength at 38 and 120 kHz and vertically stratified MOCNESS sampling during a US GLOBEC cruise off southern Oregon and northern California in August 2000. Euphausiid patches were clustered inshore of Heceta Bank (44.0°N) and off Cape Blanco (42.8°N), but were not common elsewhere. The distribution of euphausiid patches throughout the study area was correlated with that of near-surface chlorophyll. We suggest that Heceta Bank and Cape Blanco were zones of plankton retention and concentration along the shelf and slope, and also that large offshore meanders in the equatorward upwelling jet carried upwelled water, chlorophyll, and euphausiids offshore. In particular, the complex interaction of mesoscale physical features, shoaling bottom topography, and diel vertical migration created large patches of euphausiids. These euphausiid patches, probably persisting on timescales of days to weeks, could function as relatively large and persistent resources for euphausiid predators.

1. Introduction

Euphausiids are a key energetic link between plankton stocks and higher-trophic-level animals in the northeast Pacific Ocean (Brodeur and Pearcy, 1992; Robinson, 2000; Tanasichuk, 2002). The dominant euphausiids in this region are *Euphausia pacifica* and *Thysanoessa spinifera* (Gómez-Gutiérrez et al., 2005), which are major food items for important large marine predators in this ecosystem, including juvenile and adult salmonids (Brodeur and Pearcy, 1992), spiny

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dogfish (Tanasichuk et al., 1991), rockfishes (Brodeur and Pearcy, 1984), Pacific hake (Livingston, 1983; Brodeur and Pearcy, 1992; Buckley and Livingston, 1997), seabirds (Ainley et al., 1996), and marine mammals (Schoenherr, 1991). The interaction of water circulation, bottom topography, and euphausiid behavior can lead to retention of euphausiids and the formation of large aggregations or patches, which may be in turn be exploited by upper trophic-level predators (Brodeur and Pearcy, 1984; Simard et al., 1986; Simard and Mackas, 1989; Barange and Pillar, 1992; Coyle et al., 1992; Mackas et al., 1997). Mauchline (1980) used the term "patches" to refer to aggregations of euphausiids due to physical or chemical factors, particularly along bottom topography; we use this terminology here.

The Pacific continental margin off Washington, Oregon, and northern California is a productive, temperate ecosystem, known regionally as the northern California Current System (CCS). Upwelling driven by predominately southward winds between April and September results in cool, nutrient-rich surface waters along the coast during those months, while downwelling-favorable winds occur during the remainder of the year (Hickey, 1989). Annual primary production is correspondingly seasonal with the highest rates occurring in the spring, averaging 646 g $\mathrm{C\,m^{-2}\,y^{-1}}$ on the shelf, 294 g $\mathrm{C\,m^{-2}\,y^{-1}}$ on the slope, and 229 g $\mathrm{C\,m^{-2}\,y^{-1}}$ in oceanic waters off the coast of Washington (Perry et al., 1989). Geographic features (Fig. 1) such as Cape Blanco (a coastal promontory at 42.8°N, 124.6°W) and Heceta Bank (a large, submerged rocky reef on the edge of the continental shelf at 44.0°N, 124.8W, off Heceta Head) appear to influence both circulation patterns and biological productivity (Batchelder et al., 2002a). In particular, Heceta Bank is thought to provide key habitat for a diverse assemblage of fish and invertebrates, including commercially important groundfish (Hixon et al., 1991; Nasby-Lucas et al., 2002).

Batchelder et al. (2002a) and Barth et al. (2005) report complex temperature and chlorophyll distributions at the mesoscale (20–200 km) during August 2000, with cold, recently upwelled water offshore as well as along the coast. Phytoplankton stocks were patchy, with highest concentrations inshore of Heceta Bank and near Cape Blanco. Copepod biomass varied spatially both cross-shelf and along-shelf, and tended to track chlorophyll concentrations; large medusae (Suchman and Brodeur, 2005), seabirds and marine mammals were concentrated near shore in areas of high chlorophyll as well (Batchelder et al., 2002a; Ainley et al., 2005; Tynan et al., 2005). Upper trophic level predators that forage upon zooplankton stocks in both the southern CCS (Schoenherr, 1991; Ainley et al., 1996) and elsewhere (McClatchie et al., 1989; Macaulay et al., 1995) may be distributed patchily, as they seek and utilize persistent concentrations of prey resources.

A meandering upwelling jet with cyclonic and anticyclonic eddies and offshore extending filaments is common in the CCS during summer and fall (Huyer et al., 1998; Barth et al. 2000b; Strub and James, 2000). One of the main goals of the US Global Ocean Ecosystem Dynamics (GLOBEC) Northeast Pacific program is to understand how mesoscale features and processes influence the distributions of phytoplankton, zooplankton, and nekton (see Batchelder et al., 2002a), and how complex bottom topography in shelf regions may influence mesoscale variability. During a GLOBEC research cruise in August 2000, two mesoscale biological "hot spots" were encountered, one inshore of Heceta Bank and the other near Cape Blanco. In these areas, surface chlorophyll was locally enriched, copepod biomass was high, juvenile coho and chinook salmon were more abundant, humpback whales were more frequently sighted, and seabird biomass was elevated (Batchelder et al., 2002a). In this paper, we use multifrequency acoustic backscatter measurements and vertically stratified net samples gathered on that cruise to show that areas near Heceta Bank and Cape Blanco were also "hot spots" in terms of euphausiid patches.

2. Methods

From 30 July to 17 August 2000, the R.V. *Wecoma* made a total of 36 east–west transects

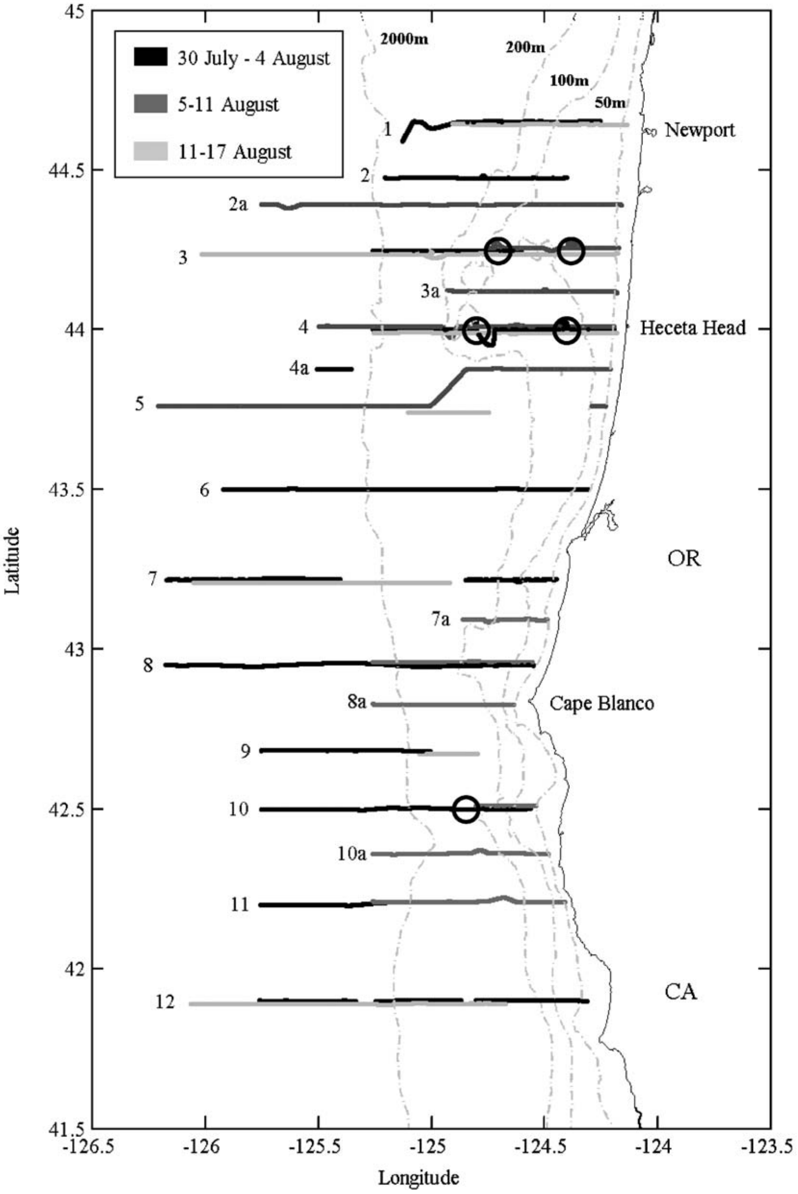

Fig. 1. Of 36 east west transects made, 35 separate daytime transect segments were analyzed. Repeat passes of the same daytime segment are offset slightly for clarity; the grayscale legend in the top left corner of the figure indicates the time period when the segment was completed. The transect line number is indicated to the left of each transect. Bottom contours at 2000, 200, 100, and 50 m are shown as gray dash-dot lines. The locations of five MOCNESS tows used for direct comparison with acoustic data are shown as black circles.

ranging from ~50 to 130 km in length between Crescent City, CA (41.9°N) and Newport, OR (44.7°N). From 30 July to 4 August, a series of transects covering the entire study area was run from south to north (Fig. 1; line 12 through line 1). Subsequently, some of these transects were repeated along with the addition of more finely spaced transects off Heceta Head, off Cape Blanco, and additional offshore sampling (see grayscale legend in Fig. 1; Barth et al., 2005).

Acoustic volume backscattering strength (S_v, dB) data were collected with a Hydroacoustics Technology, Incorporated (HTI) 244 digital echosounder with four frequencies (38, 120, 200, and 420 kHz). Only data collected with the 38 and 120 kHz split-beam transducers were used in this paper. The transducers were deployed on a towed body at approximately 4 m depth while the ship surveyed at speeds of about 15 km h^{-1} (8 knots). Raw data gathered at approximately 1 ping s^{-1} were integrated into 12-s averages (resulting in a horizontal distance of approximately 50 m between the centers of adjacent 12-s samples). The time, location, and distance from the transducer (in 1 m vertical bins) were recorded for each measurement. Acoustic data were analyzed from 4 m below the transducer (8 m depth) to a depth limit of 150 m. These data were analyzed using custom software routines written in Visual Basic and Matlab.

2.1. Acoustic backscatter measurements

S_v can be used to study patterns in the biomass of zooplankton and fish (Foote and Stanton, 2000). Acoustic scattering models and direct measurements of acoustic backscattering from tethered animals (e.g., Stanton et al., 1994) show that acoustic backscatter from small euphausiid-like zooplankton targets generally becomes greater as the transmitted acoustic frequency increases (and wavelength decreases). The frequency-dependence of S_v is the basis for methods that invert acoustical backscatter measurements into estimates of zooplankton sizes and concentrations by explicit use of zooplankton scattering models (e.g., Holliday and Pieper, 1995; Pierce et al., 2003). We employed a more qualitative approach that has proven effective in other studies, using the difference between S_v at 38 and 120 kHz to identify backscattering from euphausiids and exclude backscattering from fish (Madureira et al., 1993; McKelvey, 2000; Swartzman, 2001). Euphausiids scatter strongly at 120 kHz but weakly at 38 kHz, while fish scatter strongly at both of these frequencies.

2.2. Identification of euphausiid patches

Euphausiids generally exhibit diel vertical migration (Mauchline, 1980), which we observed in our data, ascending to surface waters at dusk to feed and descending to darker, deeper waters at dawn to avoid visual predators, thus maximizing energy gain and minimizing predation risk (De Robertis, 2002). The weighted mean depth of adult *E. pacifica* during the nighttime is less than 30 m from the surface, while during daytime, they are located below 50–100 m on the shelf and slope, and are found even deeper offshore, where their daytime depth is often coincident with the depth of the poleward California undercurrent (Vance et al., 2003; Swartzman et al., 2005). As other authors have found (Simard et al., 1986; Simard and Mackas, 1989; Coyle et al., 1992, Mackas et al., 1997, Robinson and Gómez-Gutiérrez, 1998; McKelvey, 2000, Swartzman, 2001, Romaine et al., 2002), adult euphausiids are most readily discernible acoustically when these organisms form daytime patches in deeper waters, typically 50 m or more from the surface. During nighttime, it was difficult to identify scattering from euphausiids due to the dispersion of these patches and from scattering from other co-located zooplankton and fish in surface waters. Thus, only acoustic backscatter data from daytime and crepuscular (twilight) portions of transects and from samples located between 50 and 150 m water depth (150 m was the maximum range of reliable 120 kHz data) were used in this analysis. These portions of each transect were determined by using ship-measured surface irradiance data to determine the approximate time of local nightfall and daybreak, and by visually examining the acoustic backscatter images for patterns of vertical migration at dusk and dawn.

Thresholding, frequency differencing, and image processing algorithms were used to identify and define patches of “euphausiids” in the acoustic data, in a manner similar to that used by Swartzman et al. (1999, 2005). Bottom and false bottom reflections were removed from the original backscatter images before patch identification. Patches were defined using the following methodology. First, the S_v of a pixel in a backscatter image had to exceed −66 dB at

120 kHz. We chose -66 dB after an examination of histograms of S_v values and backscatter images in order to select patches with a relatively dense concentration of sound scatterers. Miyashita et al. (1996) used measured swimming angles and a scattering model to calculate a maximum target strength of -74.7 dB at 120 kHz for *E. pacifica* 16.4 mm in body length; an S_v of -66 dB at 120 kHz corresponds to a density of at least 7 m^{-3} for animals of this size. Second, S_v in the pixel had to be $\geqslant 2$ dB greater at 120 kHz than 38 kHz. A 2 dB difference is a minimum of values used by other authors for this purpose (Madureira et al., 1993; McKelvey, 2000; Swartzman, 2001). The choices of an S_v threshold and minimum difference between S_v at 120 and 38 kHz are somewhat arbitrary and depend upon the goals of the study. Small changes to these two criteria (a few dB) would not substantially alter the results of our analysis. Third, pixels meeting these threshold and difference criteria were smoothed into patches using a "closing" followed by an "opening" with a 3 pixel horizontal × 3 pixel vertical square structuring element. These operations are analogous to the application of a low-pass filter, smoothing patterns in the image that are smaller than the size of the structuring element (here, 3×3 means 150 m horizontally by 3 m vertically). Closing and opening operations are described in greater detail by Haralick and Shapiro (1992), and their application to acoustic image processing is detailed by Swartzman et al. (1999). Finally, since the horizontal distance covered by each acoustic sample and the depth of the tow vehicle varied with ship speed, only data collected when the ship was steaming at survey speeds were used, resulting in a cross-sectional area of 50 m^2 (50 m long × 1 m deep) for each pixel in an acoustic image.[1]

In summary, to be included in euphausiid patches in this analysis, a pixel in an acoustic image had to meet the following criteria: (i) the data were collected during daytime or crepuscular time periods, (ii) the depth was deeper than 50 m but shallower than 150 m, and (iii) the S_v at 120 kHz exceeded -66 dB and was at least 2 dB greater than S_v at 38 kHz. An example of acoustic backscatter images at 38 and 120 kHz and the corresponding euphausiid patches is shown in Fig. 2.

2.3. *Analysis of patterns*

At each point along a transect, the number of pixels that had been identified as a member of a patch was summed and multiplied by 50 m^2 (the cross-sectional area of each pixel) to produce a summary measurement of patch area encountered anywhere in the water column. When a euphausiid patch was "thick" in the vertical (depth) dimension, this alongtrack patch area index had a large value. This summary measurement of patch area was used for analysis of spatial patterns. The transect segments were interpolated to an exact spacing of 50 m, filling relatively small gaps of missing data (e.g., due to shutdown of the acoustic system during a transect; the median length of gaps of this type was 0.6 km). If there was a very large gap in a data series (e.g., a long segment of nighttime transect with daytime data before and after), the gap was not filled, and the segments of transect were treated separately. A nonparametric runs test was used to test the data for a clumped versus even distribution of euphausiid patch area along transects (Zar, 1999).

Current velocities were measured with a shipboard 153 kHz narrowband RD Instruments acoustic Doppler current profiler (ADCP), using 2.5 min ensembles and 8 m vertical bins (see Barth et al., 2005, for details). Barotropic tidal currents were predicted and removed using the 1 km Oregon State University Tidal Data Inverse Model, solving for the four constituents M2, S2, K1, and O1 (Erofeeva et al., 2003). Alongtrack chlorophyll concentrations converted from measured fluorescence at 5 m depth (see Barth et al. (2005), for details of undulating Seasoar tow

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[1] The distance between the centers of adjacent 12-s averages is 50 m at all depths. Our use of a constant pixel area is a simplification, however, because an acoustic beam becomes wider as the distance from the transducer increases. Here, the width of a 12-s average is about 56 m at 50 m depth and 68 m at 150 m depth. This difference is probably not important to our study, since the scale at which we are interpreting the euphausiid patterns is larger than both the width of the beam and the averaging interval. If a systematic beam-width bias were present in our study, patches at greater depth would appear longer than shallower patches, but there is no evidence to suggest that this is the case.

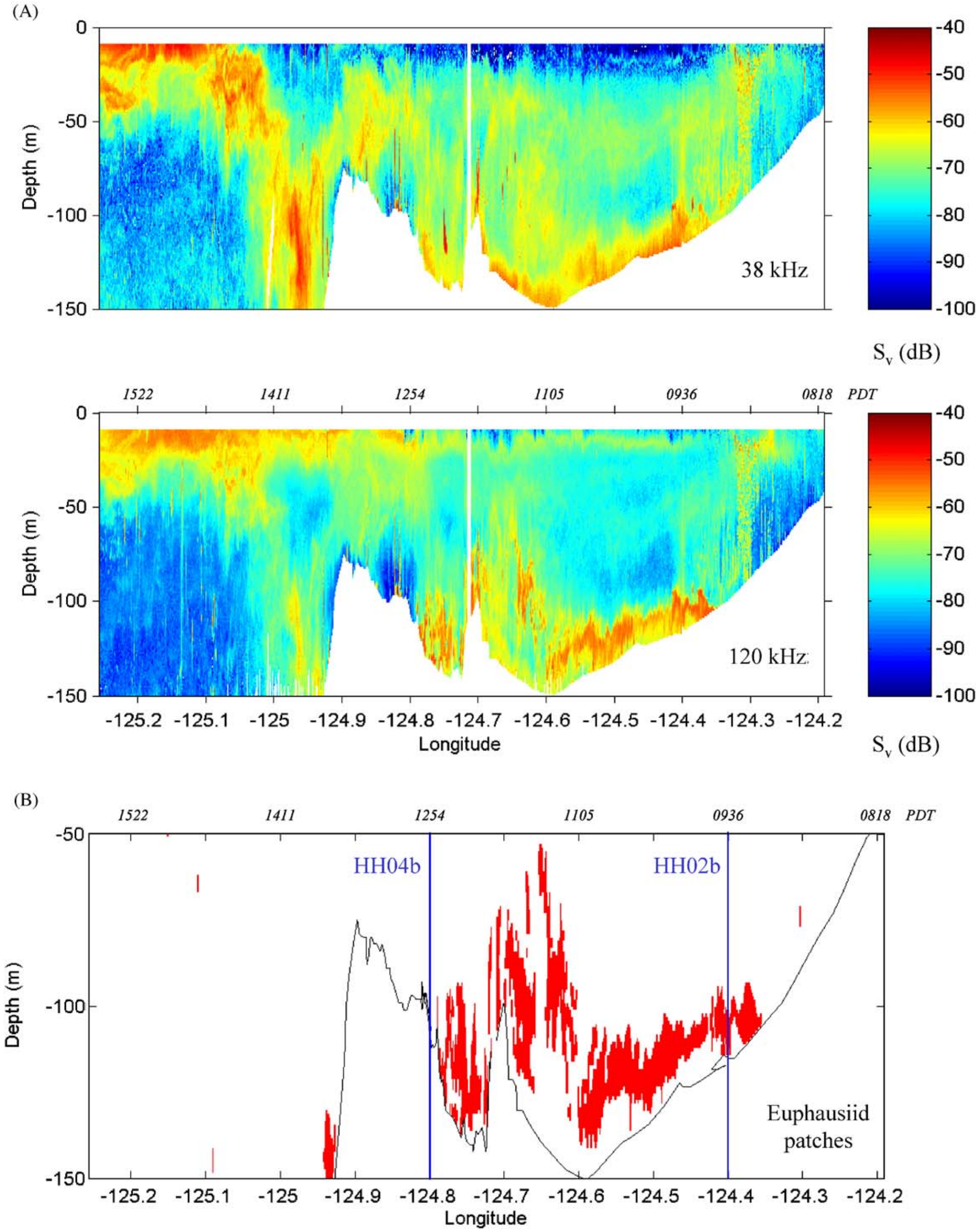

Fig. 2. An example of acoustic backscatter images at 38 and 120 kHz and the corresponding euphausiid patches. Panel A: Acoustic backscatter at 38 and 120 kHz on the HH line (line 4), 3 August 2000. Local time is given along the top of 120 kHz plot (both time and location are changing along the abscissa). Panel B: Euphausiid patches on this line at daytime depths, defined using acoustic backscatter at these two frequencies. Local time is given along the top of the plot, as in panel A. The positions of two concurrent MOCNESS stations (HH02b and HH04b) are indicated by labeled vertical lines.

vehicle data collection and further description of these data) at between 1 and 3 km spacing were linearly interpolated to match each alongtrack measurement of patch area. There were a few locations (about 2% of the acoustic samples) for which no Seasoar chlorophyll data were available. Finally, for each measurement of euphausiid patch area, a matching seafloor depth was interpolated from a database of bathymetry data.

Euphausiid patch area, chlorophyll, and seafloor depth were compared statistically in the following manner. The alongtrack acoustic averages ($n = 48,106$) are serially correlated, thus standard significance tests of simple correlations that assume independence among samples cannot be used (Legendre and Legendre, 1998). An alternative is to use partial Mantel correlations to test for relationships among variables in the presence of spatial autocorrelation (Legendre and Troussellier, 1988; Legendre and Legendre, 1998). This statistic compares the pairwise distances among objects for each variable (i.e. Euclidean distances among pairs of sample values) under the null hypothesis of no relationship. The Mantel statistic will be positive if samples have a similar distance score on each variable. In this case, partial Mantel correlations were calculated between euphausiid patch area and chlorophyll concentration at 5 m, and between euphausiid patch area and seafloor depth, while controlling for the influence of geographic distance among samples. Since the data were not normally distributed, the Mantel correlations were calculated on the ranks of the pairwise distances (Dietz, 1983). The significance of the correlations was estimated using randomization (Legendre and Legendre, 1998; 10,000 iterations). To reduce the time required for randomizing these relatively large data matrices, 1-km averages of the alongtrack data were used in calculating the statistics.

2.4. Net sampling

A 1 m^2 mouth area, 0.335-mm mesh Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS; Wiebe et al., 1985) equipped with 10 nets was deployed from a second vessel, the R.V. *New Horizon,* sampling the same transects. On five daytime occasions (see tow locations shown on Fig. 1), acoustic data were collected concurrently with a deployment of the MOCNESS, with the two vessels separated by less than about 1.85 km (1 nm). These occasions provide the best opportunity to compare the acoustic data with net samples. Each MOCNESS net sample typically filtered 100–300 m^3 of water, with a profile from bottom to surface requiring about 15–30 min at a ship speed of approximately 4.6 $km\,h^{-1}$ (2.5 knots). Samples were preserved in 5% buffered formalin. Subsampling was performed with a Folsom splitter to efficiently represent all species and size classes. Splits were made until there were approximately 50 euphausiids present. If there were multiple groups of species or life stages present, reducing the number of individuals in any important group to an inadequate level, other splits were processed so that all subsets were represented. All organisms >5 mm in body length in the subsample(s) were identified and measured. In this paper, we report only the numbers of adults, which comprise the size fraction (approximately 10 mm in body length and larger) most likely to dominate acoustic backscattering from euphausiids.[2]

For comparison with concurrent MOCNESS collections, summed euphausiid patch area was averaged over 1.85 km of distance along the east–west transect, with the start longitude of the MOCNESS tow as the center of this spatial average. This value was then compared to the integrated density of adult euphausiids from all nets sampling the 50–150 m depth interval (between 2 and 4 different nets) during the concurrent tow. Integrated adult euphausiid densities (number per m^{-2}) were calculated by first multiplying the density of adult euphausiids for each net (number m^{-3}) by the thickness of the depth interval sampled by that net (m), and then summing those values for all of the nets in a particular tow. The relationship between patch area and integrated density was evaluated statistically using the Spearman rank correlation.

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[2] Body length for a euphausiid is the length of the body, not including the telson.

There were other MOCNESS collections during the cruise that were not done concurrently with the acoustic data collection. Some of these samples have been processed as described above, and the integrated densities of adult euphausiids from these tows are included for comparison with the spatial distribution of acoustically detected patches. Although the remaining MOCNESS tows from this cruise have not yet been enumerated, we do have semi-quantitative information on euphausiid abundances in these tows because we record at sea the taxa captured in each MOCNESS net. For adult euphausiids, each tow was assigned a logarithmic score (see below) by an experienced zooplankton analyst, based upon a visual estimate of the total number of adult euphausiids in the tow at the time of sample collection:

Score	Number of adult euphausiids
0	0–9
1	10–99
2	100–999
3	1000–9999
4	10,000–99,999

These scores were compared with the integrated adult densities for those MOCNESS samples that were completely enumerated and with the spatial patterns in the acoustic data.

3. Results

3.1. Acoustically defined patches of euphausiids and concurrent mocness data

Acoustic observations on east–west survey lines indicated large patches of euphausiids near the seafloor on the shelf off Heceta Head (line 4), particularly between longitudes 124.35°W and 124.75°W (Fig. 2). These large patches were observed in repeated transects through this area between 3 and 6 August (Figs. 3B and C), and were diminished but still present by 11 August (Fig. 3D). Daytime euphausiid patches in other parts of the study area appeared smaller and less contiguous than those on the shelf between Heceta Head and Heceta Bank. Relatively few euphausiid patches were observed between Heceta Bank and Cape Blanco. On line 6 (Fig. 3E), euphausiid patches were seldom encountered. Further south on line 8, near Cape Blanco, substantial daytime euphausiid patches were present, particularly along the shelf. However, with increasing distance offshore, the patches of euphausiids may have been deeper than 150 m (Fig. 3F). Data from line 9 support this contention, with euphausiid patches appearing in the 50–150 m depth range during the crepuscular period, migrating from below (Fig. 3G; local sunset was approximately 2040 PDT for this date and location). On line 10 (off the Rogue River), patches of euphausiids were observed in the acoustic data (from approximately 124.65°W to 125°W; Fig. 3(H), but these patches appeared smaller and less contiguous than those patches on lines 1–4 to the north (Figs. 3A–C).

At the five daytime opportunities for a matched comparison between MOCNESS and acoustics (locations shown in Fig. 1), patch area was a good relative proxy for the presence of euphausiids (Fig. 4). MOCNESS sampling on line 4 at approximately longitude 124.4°W (HH02b), done concurrently with the acoustic data collection, confirmed that the acoustic patches there (Fig. 2B) contained adult euphausiids (mostly *E. pacifica*) at densities averaging 3.37 m^{-3}. The large zooplankton in the nets sampling these patches were numerically dominated by adult euphausiids. Conversely, further seaward at longitude 124.8°W (HH04b), where no patches of euphausiids were identified, concurrent net sampling found no adult euphausiids in this depth range. Integrated densities (individuals per m^2) from net collections between 50 and 150 m were positively correlated with summed patch area averaged over 1.85 km around each tow location (Fig. 4; Spearman rho = 0.97, $P<0.05$). Error bars in Fig. 4 indicate the magnitude of alongtrack variation in the average of summed patch area. Despite potential sampling variability in both of these quantities, due to both vertical and horizontal patchiness of euphausiids at small scales, the available data indicate that when more patch area was detected, more adult euphausiids were caught by the MOCNESS in the 50–150 m depth range.

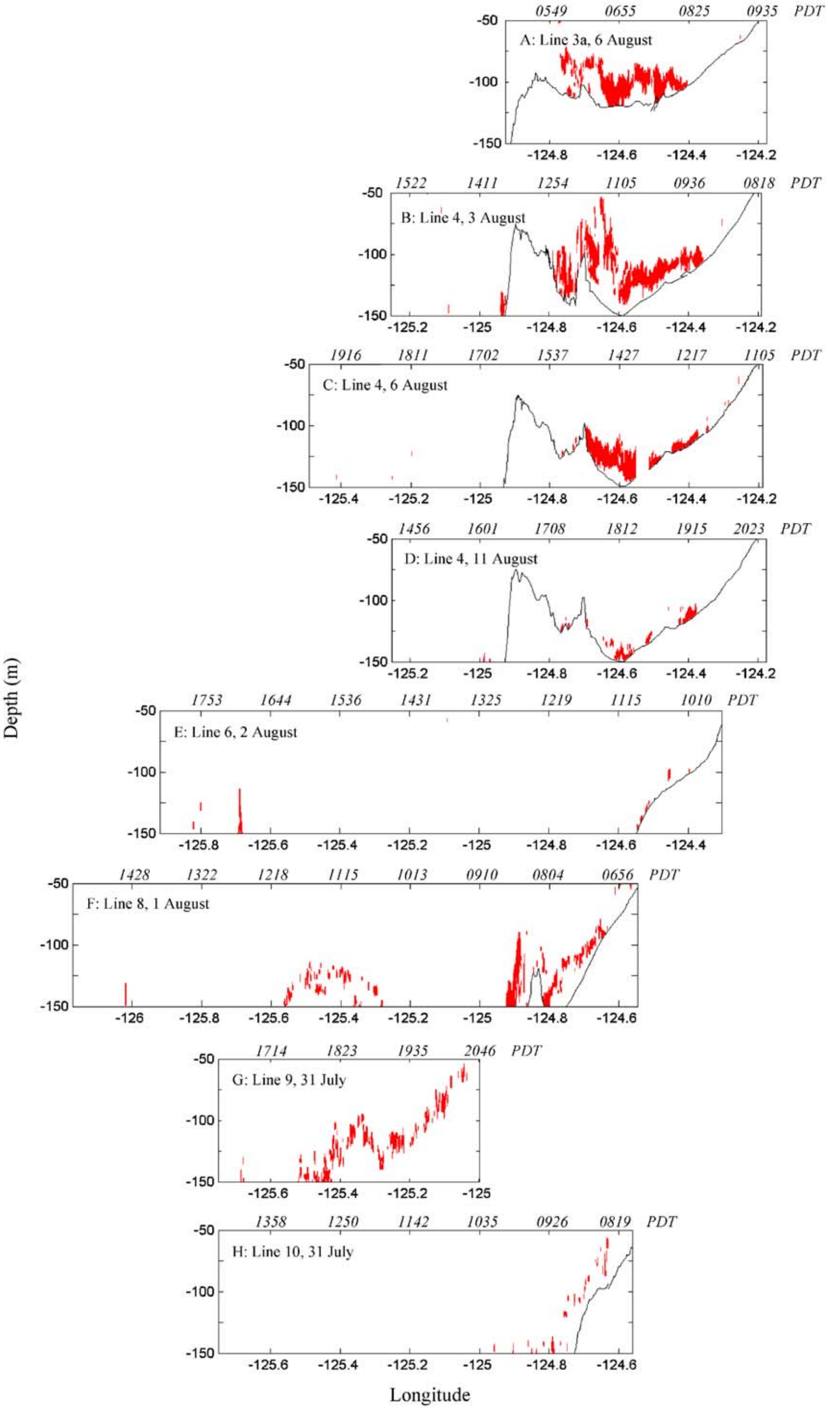

Fig. 3. Acoustically defined euphausiid patches identified on daytime portions of selected transects. The transect number and date are indicated on each plot, with local time given along the top of the panel (both time and location are changing along the abscissa). The plots are aligned by longitude; note that the longitude range is different in each panel. From top to bottom of the figure, the panels are ordered from north to south, with repeat passes of line 4 (panels B–D) in chronological order.

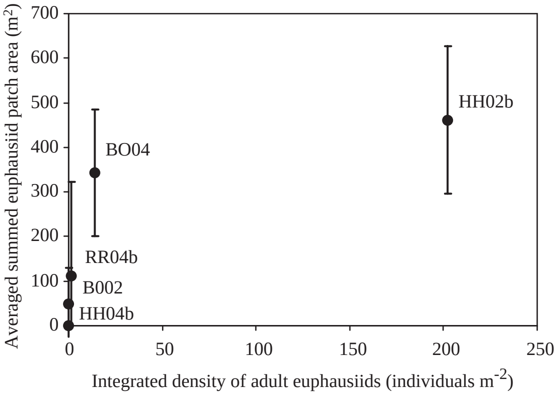

Fig. 4. Comparison between concurrent MOCNESS and acoustic data. Alongtrack summed euphausiid patch area values (m^2) were averaged over 1.85 km (1 nm) around each of the five MOCNESS station locations ($n = 5$ comparisons). These values are plotted on the ordinate, with error bars indicating + one sample standard deviation (truncated at zero on the ordinate). The integrated density (number m^{-2}) of adult euphausiids between 50 and 150 m are given on the abscissa.

This relationship is consistent with the assumption that patches identified using acoustic data can be used to locate patches of these animals.

3.2. Spatial patterns

A summary of integrated patch area on all transect segments analyzed is shown in Fig. 5. Overall, these patches were detected in about 17% of the 50 m alongtrack acoustic samples. Euphausiid patches were not evenly distributed along transects across the study area (runs test, $P \ll 0.05$), but appear clustered on the shelf off Heceta Head and off Cape Blanco. The amount of integrated patch area (height of the bars in Fig. 5) was relatively greater in these locations as well. Between Heceta Bank and Cape Blanco (e.g., lines 6 and 7), few patches of euphausiids were observed. Most of the euphausiid patches were observed along the continental shelf and upper slope, although some were observed in deeper water (portions of lines 5, 8, 8a, 9, seaward of about 124.75°W). Repeated sampling off Heceta Head and Cape Blanco (Fig. 5, where the grayscale indicates when different transects were completed; Figs. 3B and 3C–D) show that the presence of euphausiid patches in these places was spatially and temporally persistent throughout the cruise.

The net sampling data do not provide the same spatial resolution as the acoustics, but they do show the same general patterns. Densities of adult euphausiids integrated to the maximum depth of the tow (Fig. 6A; note that these data have been log-transformed) confirm the presence of substantial numbers of adult euphausiids inshore of Heceta Bank (on line 4, 44.0°N, 124.4°W), on the upper slope seaward of the bank (44.0°N, 125.0°W), and on the shelf and slope south of Cape Blanco (on line 10, 42.5°N, 124.5°–125.0°W). While not as valuable as the complete counts, the semi-quantitative scores for all MOCNESS tows (Fig. 6B) can augment the spatial coverage of the net sampling data we show here. These scores, which were well correlated with quantitative enumerations of adult euphausiids per m^2 (Fig. 6C), also indicate high densities on the shelf and slope near Heceta Bank and south of Cape Blanco. They also show high densities extending offshore across the shelf and slope west of Cape Blanco (42.8°N). Relatively high densities also were indicated further to the south, along the upper slope off of Crescent City, CA (41.9°N). Integrated adult densities were lower in the tows made far offshore (seaward of 125.5°W, approximately 42.9°–43.8° N), although there were clearly cases where the MOCNESS, which sampled as deep as 350 m in deeper water, collected euphausiids during the day that could not have been seen by the more range-limited acoustic sampling.

Euphausiid patches were concentrated off Heceta Head and Cape Blanco in areas of high near-surface chlorophyll, which exceeded 5–10 mg m^{-3} (Fig. 7A; Barth et al., 2005). The spatial distribution of euphausiid patches was associated with that of surface chlorophyll (Figs. 5 and 7). However, euphausiid patch area was not elevated in all areas of high chlorophyll, and a plot of euphausiid patch area as a function of chlorophyll concentration shows a great deal of scatter (Fig. 8A). The calculated Mantel correlation between euphausiid patch area and chlorophyll at 5 m controlling for spatial autocorrelation among samples was positive and significant

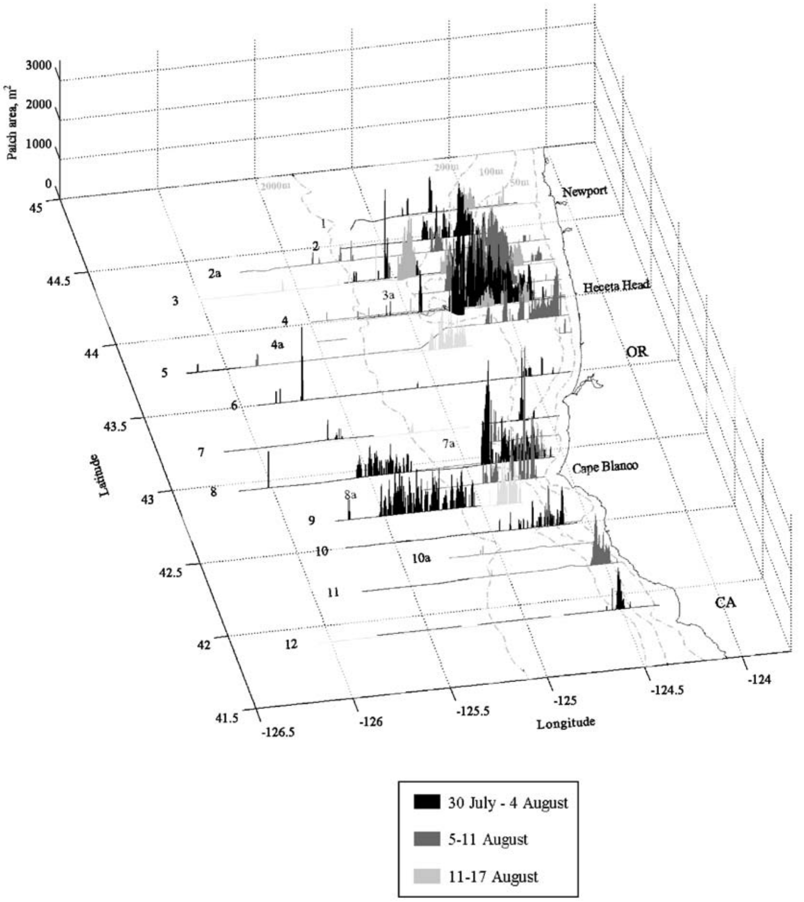

Fig. 5. Along-track sum of euphausiid patch area (m²) on all transects. Repeat passes of the same daytime segment are offset slightly for clarity; the grayscale legend in the lower left corner of the figure indicates the time period when the segment was completed. The transect number is indicated to the left of each transect. Bottom contours at 2000, 200, 100, and 50 m are shown as gray dash-dot lines.

($r_M = 0.2188$, $p = 0.0001$, $n = 2328$), indicating a tendency for sample locations with large patch area values also to have high values of chlorophyll. Many of the euphausiid patches were associated with the shelf and slope, although a substantial number were also found offshore (Fig. 8B). The Mantel correlation between euphausiid patch area and seafloor depth was negative but not statistically significant ($r_M = -0.0358$, $p = 1$, $n = 2391$), probably in part because the relationship between distance scores for patch area and depth was not monotonic. There was a tendency for euphausiid patches to be found in areas of elevated chlorophyll in both shallow and deep water.

3.3. Circulation patterns

Average current velocities between 50 and 150 m show that areas of high chlorophyll concentration and large euphausiid patches may have been regions of weak flow and retention (Fig. 7B; Barth et al., 2005). On lines 3 and 4, inshore of Heceta Bank at approximately 124.75°W longitude on the shelf, velocities were weak and directed onshelf. Further south, off Cape Blanco, there is also evidence of weak flow inshore along the shelf on lines 8 and 9, as well as flow directed upslope along the shelf break. It is interesting to note that the inshore end of line 8 crosses Coquille Bank (43.0°N, 124.8°W; Fig. 3F), a rocky outcrop

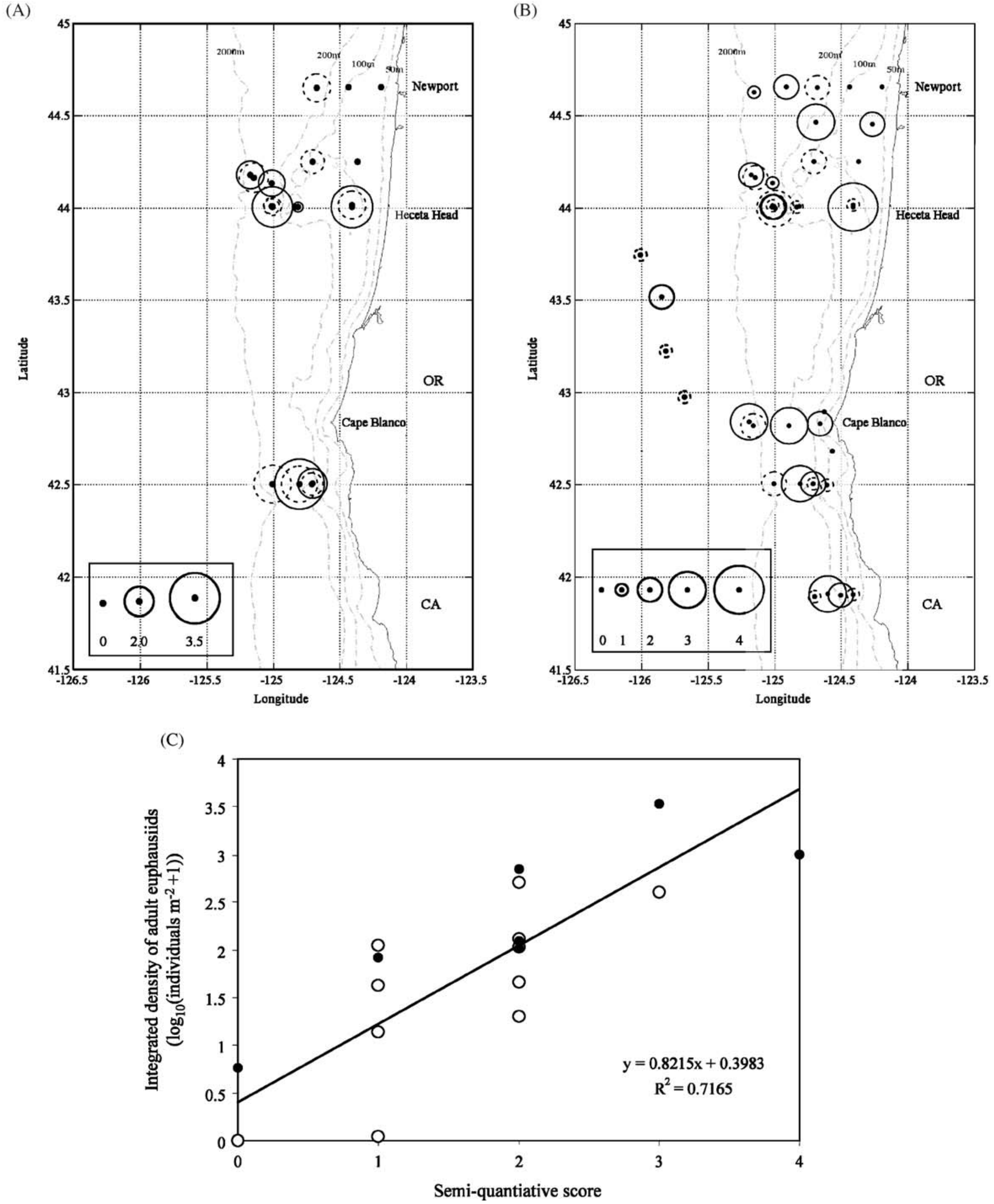

Fig. 6. Integrated adult euphausiid densities from MOCNESS tows. Panel A: Adult euphausiids ($\log_{10}$(number $m^{-2}+1$) are shown as bubbles at tow locations on the plot, for which a scale is provided. Dashed circles indicate daytime tows, while solid circles indicate nighttime tows. Panel B: Semi-quantitative index scores are shown as bubbles at tow locations on the plot, for which a scale is provided. Dashed circles indicate daytime tows, while solid circles indicate nighttime tows. Panel C: Relationship between semi-quantitative index scores and log-transformed integrated adult euphausiid densities. Daytime points are shown as open circles, and nighttime points as solid circles. The line, equation, and coefficient of determination for a linear fit to these data are shown.

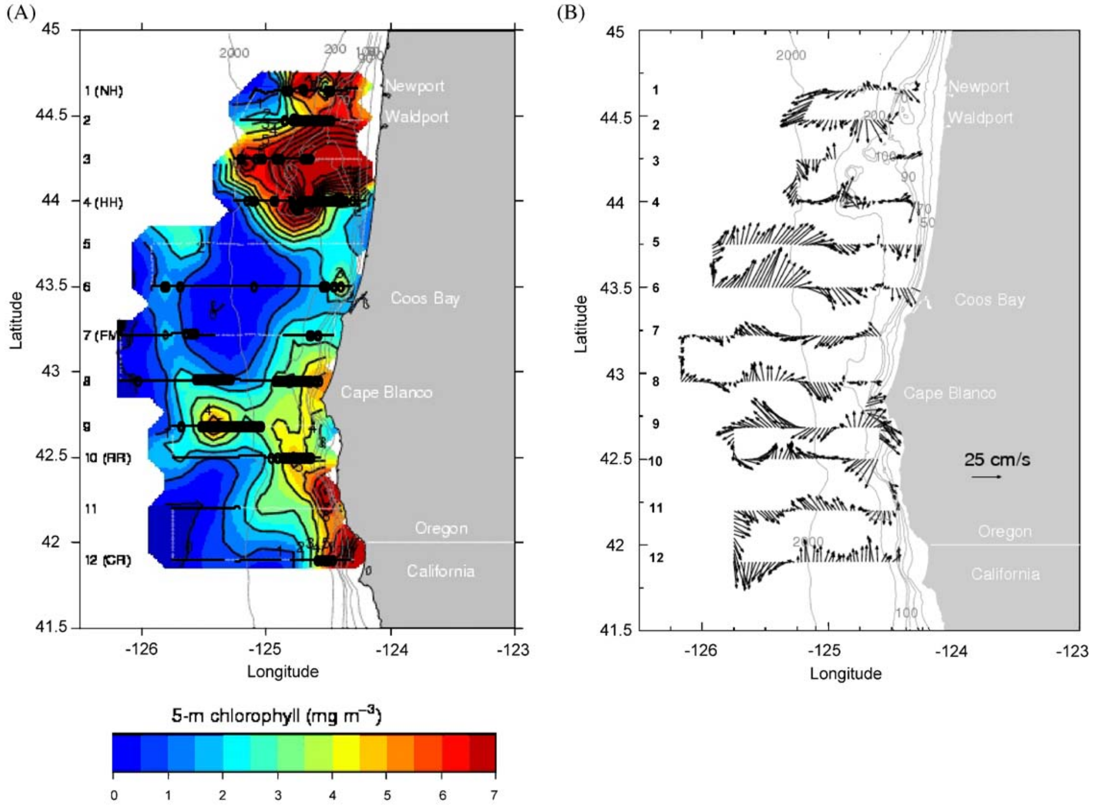

Fig. 7. Mesoscale data collected between 30 July and 4 August. The transect numbers for this part of the cruise are indicated to the left of the transects. Bottom contours at 2000, 200, 100, 90, 70, and 50 m are shown in gray. Panel A: Chlorophyll-*a* in mg m^{-3} calculated from fluorescence measured at 5 m depth (see Barth et al., 2005). The black circles on the plot show locations where euphausiids were detected, and the black east–west lines indicate daytime survey effort. Panel B: Average velocity between 50 and 150 m depth measured by an acoustic Doppler current profiler (ADCP; see Barth et al., 2005). Each vector points in the direction of flow, and the length of the vector is scaled to speed in cm s^{-1}. Barotropic tidal currents have been predicted and removed (see Section 2).

deeper and much smaller than Heceta Bank, but one that is also thought to be important fish and invertebrate habitat (Hixon et al., 1991) and may be a local influence on circulation.

Barth et al. (2005) define the location of the meandering equatorward upwelling jet that forms the offshore boundary of generally cool, salty, high-chlorophyll upwelled water. The areas of weak flow and retention along the upper shelf and slope identified above are inshore of this jet. Offshore of Cape Blanco, in what Barth et al. (2005) identify as a large offshore meander in the jet, the flow is stronger and directed to the north and west (Fig. 7B). This meander may have contributed to the presence of chlorophyll and euphausiids well offshore in deep water, to the west of Cape Blanco (lines 8–10 in Figs. 5 and 7).

4. Discussion

In the coastal upwelling system off Oregon and northern California, the distribution of euphausiid patches was not uniform or random. Rather, most of the euphausiid patches were clustered inshore of Heceta Bank and off Cape Blanco. The fraction of sampled transect on which euphausiids were detected (17%) does not reflect a probability of finding them, since the alongtrack samples are not independent, but it does imply that the dense

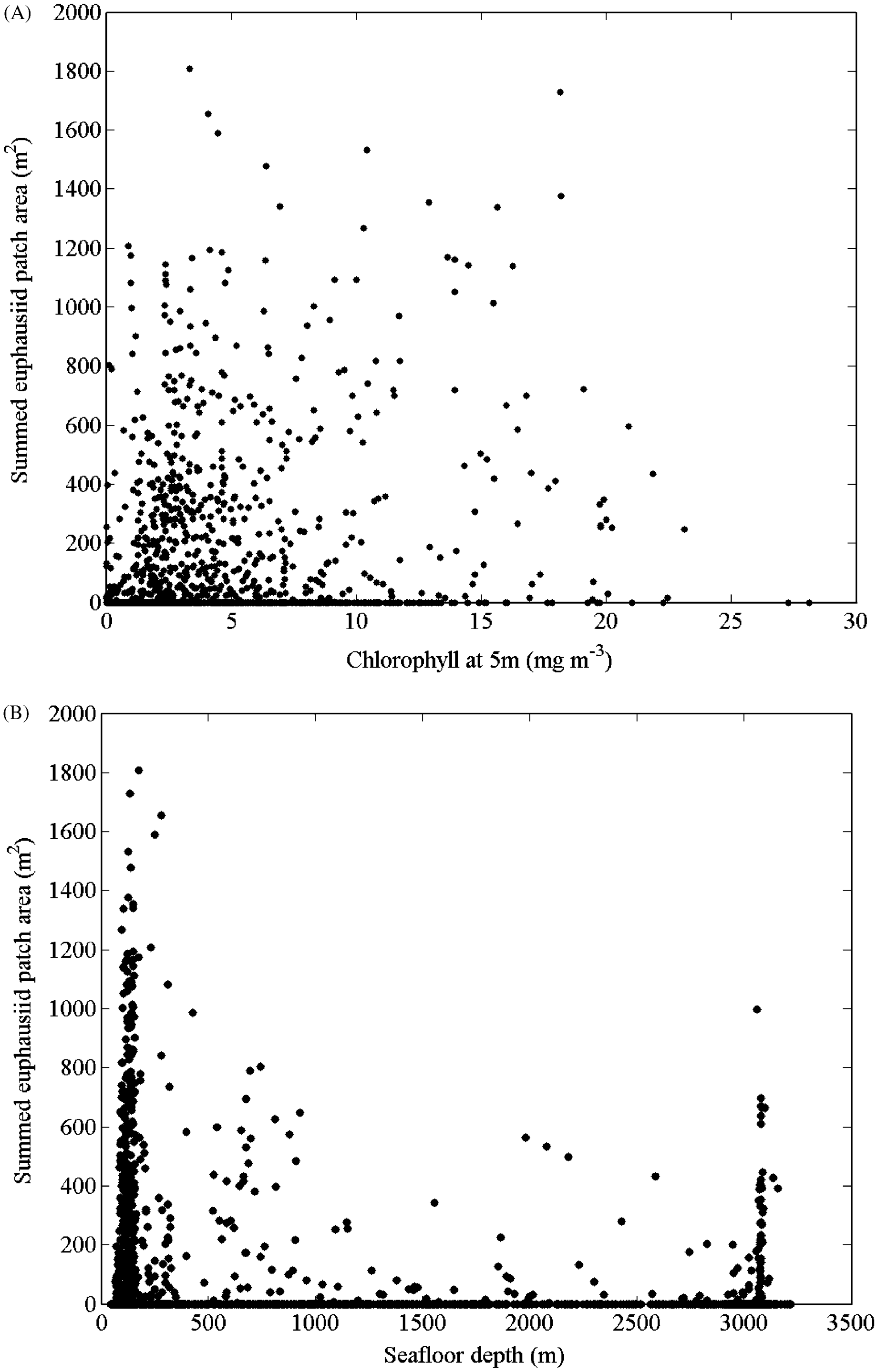

Fig. 8. Comparison between summed euphausiid patch area, chlorophyll concentration, and seafloor depth. Euphausiid patch area values (m^2) averaged every 1 km are plotted on the ordinate. Panel A: Chlorophyll concentrations at 5 m depth ($mg\,m^{-3}$), averaged every 1 km, are plotted on the abscissa. Panel B: Seafloor depths (m), averaged every 1 km, are plotted on the abscissa.

patches of euphausiids identified here occupy a relatively small portion of the total study area. This spatial distribution of these patches was similar to that of surface chlorophyll associated with the upwelled water inshore of the equatorward jet, water characterized by low temperature, high salinity, and high nutrients (Barth et al., 2005). Many of the euphausiid patches were found on the shelf and upper slope, but in deep water offshore of Cape Blanco, euphausiid patches also were observed where upwelled water was found far from the shelf break near 42.9°N, 125.4°W (part of the offshore meander described by Batchelder et al. (2002a) and Barth et al. (2005). In contrast, the area between Heceta Bank and Cape Blanco was predominately warm, low in chlorophyll, and had few euphausiid patches.

4.1. Heceta Bank

Though high chlorophyll over Heceta Bank and the adjacent shelf can be attributed to increased nutrient concentrations and high stratification, we suggest that retentive circulation patterns play a role as well (see also Barth et al., 2005), and that these same patterns may contribute to formation of euphausiid patches. Circulation patterns that in part drive euphausiid distribution—perhaps some of the same underlying physical processes leading to the elevation and concentration of chlorophyll stocks—may be coupled with bottom topography and euphausiid vertical migration, which could place the animals in different flow regimes by night and by day.

Batchelder et al. (2002a) noted an apparent return flow from offshore onto the shelf inshore of Heceta Bank (near 44.25°N, 124.42°W), a deflection of the southward flowing upwelling jet previously suggested by Barth et al. (2000b). Both Batchelder et al. (2002a) and Barth et al. (2005) note the presence of a pool of warm water on the shelf inshore of Heceta Bank, in the midst of otherwise much cooler temperatures. Barth et al. (2005) note, though, that surface salinity is consistently high everywhere on the bank, implying that this warm pool is upwelled water advected onshore and warmed by local surface heating. Barth et al. (2000a) argued that a low velocity region in the "lee" of Heceta Bank forms during periods of upwelling-favorable winds. The velocity data (Fig. 7B), hydrography, and the trajectories of surface drifters released at the northern end of the study (Barth et al., 2005) form compelling evidence for the presence of a low-velocity region inshore of Heceta Bank during August 2000, perhaps making the shelf there a zone of retention and concentration for phytoplankton and zooplankton advected from offshore, including euphausiids.

The shallow bottom on the shelf provides a lower depth limit for vertically migrating euphausiids, meaning the euphausiid patches on the shelf were shallower in the water column relative to offshelf areas, where these animals might migrate to >200 m during the daytime. Three possible explanations for the large euphausiid patches inshore of Heceta Bank are that (i) the euphausiids were produced and developed there, (ii) they were advected onto the Bank as larvae or juveniles from an offshore source and then were retained on the Bank during development to adulthood, or (iii) they were advected onto the Bank at the offshore edge as adults at night during diel vertical migration and were carried onto the shelf. We think that the third explanation is most likely, given the probable age of an adult euphausiid (a minimum of 4.5–6 months for *E. pacifica*, from recent laboratory studies of northern CCS euphausiid growth rates; Leah Feinberg, Oregon State University, personal communication). The timescales of advection and retention due to circulation patterns inshore of Heceta Bank are relatively shorter, perhaps on the order of days to weeks, based on the timescale of upwelling-favorable wind events off Oregon (Huyer, 1983; Barth et al., 2000b). In either case, we know that the daytime depths of adult euphausiids in slope waters is greater than the depth of Heceta Bank (Simard and Mackas, 1989; Swartzman et al., 2005), leading us to suggest that the adult animals are trapped on the Bank and shelf both by circulation patterns and by the shallow bottom depths.

Finally, the role of diel vertical migration by adult euphausiids in the formation of patches along the shelf and upper slope should be emphasized. Modeling of the interaction of diel vertical migration by copepods with coastal upwelling circulation by Wroblewski (1982) and recently by Batchelder et al. (2002b) has shown that the coupling of these two processes is effective at retaining migrating animals nearshore. Batchelder et al. (2002b) also note that the same processes are probably important for vertically migrating euphausiids in upwelling systems. Observations of current velocities and adult euphausiid patches along the western coast of Vancouver Island reported by Mackas et al. (1997) are consistent with this hypothesis.

4.2. *Cape Blanco*

Few euphausiid patches were detected between Heceta Bank and Cape Blanco, either on the shelf or offshore. But just as on the shelf near Heceta Bank, upwelled, high-chlorophyll water is present near Cape Blanco, not only along the shelf break and to the south of the Cape but also extending far offshore into deep water. Barth et al. (2000b) described a deflection of the southward flowing upwelling jet in this location in 1995, similar to that seen off Heceta Bank. Unlike south of Heceta Bank, though, once the jet turns offshore here it "separates" from the coast and remains offshore, becoming an oceanic feature. In August 1995, this separation occurred south of the Cape Blanco, but in August 2000 it took place north of the Cape instead (Barth et al., 2005). Euphausiid patches were located along the upper slope, but particularly where weak flow and upslope flow was observed on the inshore end of line 8 (inshore of about 124.9°W; Figs. 3F, 5, and 7B), as well as further offshore on lines 8 and 9 in the meander, where the flow was stronger and directed offshore and to the north (near 125.4°W). On some occasions the daytime patches were below the useful range of the acoustics and were only seen during vertical migration (Fig. 3G), but on others they were observable above 150 m in the daytime (Fig. 3F), both offshore and along the slope and shelf near Coquille Bank. It is interesting to note that the data from net samples indicate high densities of adult euphausiids along the shelf and across the slope off Cape Blanco, but show a marked decrease much further offshore, seaward of the meandering equatorward jet (Fig. 6B, west of 125.5°W, approximately 42.9°–43.8°N). In summary, we suspect that the circulation near Cape Blanco concentrated euphausiids along the shelf and upper slope in a manner analogous to the flows inshore of Heceta Bank, but without the wide, shallow shelf and larger areas of weak flow, the patches of euphausiids were somewhat smaller and deeper in the water column. Offshore of the cape, we think euphausiids (along with chlorophyll) may have been swept to the west and north in the anticyclonic meander described by Barth et al. (2005), but high densities of animals remained mainly inshore of the equatorward jet.

4.3. *Temporal persistence*

Repeated portions of the survey revealed that these large-scale patterns were persistent over periods of several days to a week or more in time (Fig. 5). The areas offshore of Heceta Head and Cape Blanco were consistently higher in chlorophyll and cooler, saltier, and denser than surrounding waters, and these areas continued to contain most of the euphausiid patches identified using the acoustic data (Figs. 5 and 7A). However, there were some changes at a finer spatial scale with time. Euphausiid patches observed on line 4 (inshore of Heceta Bank) on 3 August and again on 6 August became smaller, deeper, and less spatially continuous by late in the cruise (11–12 August), when this transect was surveyed for a third time (Figs. 3B–D). Potentially, these changes could reflect recirculation around Heceta Bank due to the relaxation of upwelling favorable winds (Barth et al., 2000a, 2005), or the impact of euphausiid predators such as Pacific hake (Swartzman et al., 2005; Swartzman and Hickey, 2003; see hake distribution inshore of Heceta Bank in Guttormsen et al., 2003) upon these patches.

4.4. *Limitations*

The methods used here for detecting and characterizing the distribution of euphausiids are limited. Acoustic data do not provide taxonomic information, so net sampling is required to identify different euphausiid taxa and assess patterns in their distribution. However, many adult euphausiids are able to avoid plankton sampling gear such as the MOCNESS even at night (Coyle and Pinchuk, 2002); thus, their relative densities can only be approximated with the gear used. The limits on the detection of euphausiids using these methods (daytime within a limited depth range) restrict the spatial and temporal resolution of the survey, although with repeated transects, the impact of this problem was reduced because areas surveyed at nighttime during one pass were often surveyed in daytime during another. Euphausiids were rarely observed or were observed at very low densities in waters where the bottom depth was shallower than 50 m or within the upper 50 m during the daytime in net samples, suggesting that few euphausiid patches were missed by the upper depth range limit. However, vertical migrations seen in the acoustic data (e.g., Fig. 3G) and the contents of MOCNESS samples from below 150 m indicate that euphausiids were also present deeper than 150–200 m offshore during the daytime. These deeper patches may be associated with the upper boundary of poleward undercurrent flow (Swartzman et al., 2005). It is possible that the euphausiids were observed acoustically at shallower depths in offshore areas with high chlorophyll because of reduced light penetration (high chlorophyll in surface waters will result in more rapid attenuation of surface light), since the vertical migration of euphausiids is linked to in situ light intensity (e.g., Widder and Frank, 2001). Patterns in mesoscale circulation thus may not only act to transport and aggregate euphausiids, but may also indirectly affect their vertical distribution and accessibility to sampling gear.

4.5. *Ecological significance of patterns*

Even if some deep daytime euphausiid patches were missed, the distribution of euphausiid patches in the upper 150 m is still a useful operational and ecological measurement. Acoustic data can be used in an adaptive survey plan to identify areas for more intensive net sampling of euphausiids, and are useful in extending the information revealed by net samples at single locations. The spatial scale and distribution of patches is important in terms of foraging ecology as well as survey design. A shallower, larger, more accessible patch (e.g., those on lines 3a or 4) may be more favorable to euphausiid predators than deeper, smaller (albeit more numerous) patches (migrating patches on line 9, patches on line 10) or an area with very few, very small patches (lines 6 and 7) (Fig. 3). Brodeur and Pearcy (1984) speculated that daytime patches of euphausiids trapped over the continental shelf could be an important and temporally persistent food resource for rockfish (near-bottom predators that feed on pelagic organisms during the daytime) at the outer edge of Heceta Bank. Genin et al. (1988) hypothesized that predation on euphausiids by rockfishes occupying shallow banks may be so intense that it creates ‘gaps’ in the acoustic signal during the day. Simard and Mackas (1989) and Mackas et al. (1997) suggested that shelf break patches of euphausiids presented an advantageous feeding environment for Pacific hake and Pacific herring off the coast of Vancouver Island, Canada. Predictable prey patches driven by a complex interaction of flow, bathymetry, and prey behavior are found in many areas of the ocean (see review by Genin, 2004). Marine mammal and seabird observations gathered during this study (see Ainley et al., 2005; Tynan et al., 2005) showed that both the Heceta Bank and Cape Blanco areas were probably important foraging habitat. The distribution of accessible (shallow) daytime euphausiid patches, particularly those trapped along bottom topography, may be more important to potential euphausiid predators than is the distribution of all euphausiid patches in the area. If this truly reflects the distribution of high-density euphausiid forage in the study area, it implies that prey patches are concentrated in a relatively small fraction of the total habitat available. Finally, this analysis of acoustic data clearly demonstrates the importance of mesoscale circulation patterns and bottom topography to the distribution of an ecologically important group of zooplankton in the northern CCS, with Heceta Bank in particular standing out as a region of euphausiid aggregation and concentration.

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