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# Acoustic observations of finescale zooplankton distributions in the Oregon upwelling region

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#### Abstract

We collected data on two GLOBEC cruises to investigate the ubiquity and character of small and finescale phytoplankton and zooplankton vertical distributions in continental shelf waters. Coincident data from a four-frequency echosounding system (38, 120, 200, and 420 kHz), CTD, 150 kHz ADCP, and a suite of high-resolution bio-optical instruments were collected at three continental shelf stations off the coast of Oregon in June and August of 2000. Temporally and spatially coherent finescale features were identified in the acoustic record at all sites throughout the upper water column and the dominant characteristics were observed. There was evidence of an association between the vertical structure of horizontal velocity and the finescale structure seen in the acoustic data. These observations support the hypothesis that discrete, finescale vertical distributions of phytoplankton and zooplankton may be common in productive upwelling areas and indicate that additional concurrent physical and biological measurements, at appropriate temporal and spatial scales, must be made to further characterize the ecological significance of these finescale distributions.

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## 1. Introduction

The Oregon coastal ocean is physically dynamic due to wind-driven upwelling during spring and summer (Smith, 1968; Small and Menzies, 1981; Huyer, 1983). The region supports high primary and secondary production, making it an important nursery ground for many invertebrate and fish stocks. Fluctuations in coastal salmon stocks over the last decade, which appear to coincide with changes in climate ocean conditions (McFarlane et al., 2000), have inspired research efforts to assess the conditions juvenile salmon encounter in their early oceanic phase (Brodeur et al., 2003). Characterizing the physical environment and determining the abundance and distribution of zooplankton prey for these fish are important components of these assessments.

Knowledge of the abundance and distribution of plankton is important for understanding pelagic food web interactions, population dynamics,

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community stability, and elemental cycling (Steele, 1974; Levin, 1992). Plankton distributions are known to be patchy at the scales of centimeters to meters (Cassie, 1963; Owen, 1989). The importance of finescale (less than 10 m) vertical features depends upon how common, intense, and persistent they are. Many critical biological processes (feeding, mate location, etc.) occur on spatial scales of meters or less. Thus, high spatial resolution sampling may be necessary to properly characterize the distributional patterns and variability in plankton populations and to detect significant population changes.

Detailed mapping of vertical zooplankton distributions on scales less than 10 m is difficult, and in many cases impossible, with traditional sampling equipment such as nets. The relatively coarse sampling resolution of these systems combined with ship motion and internal wave activity makes it extremely difficult to resolve features. Multifrequency acoustics finescale have emerged as a powerful tool for investigating zooplankton patchiness on small vertical and horizontal scales in a variety of environments (lakes, protected inlets, coastal and open ocean) (Holliday et al., 1998, 2003). Towed multifrequency acoustic systems have the advantage of being capable of rapidly surveying a large area and mapping scattering distributions on vertical scales of a few meters (Wiebe et al. 1996).

Characterizing the temporal and spatial scales of distributional patterns of zooplankton is essential to understand zooplankton population dynamics. The next step, and probably most difficult one, is determining the mechanisms that control these distributions. Some studies have found a correlation between plankton distributions and physical factors, such as density discontinuities and currents (Boyd, 1973; Mackas et al., 1985, 1997; Haury et al., 1990; Roman et al., 2001). Most of these studies focused on patches on the scale of tens of meters. More recent work has focused on small to finescale vertical layers (Holliday et al., 1998; Osborn, 1998; Dekshenieks et al., 2001; McManus et al., 2003). The results of these studies show that there is often an association between the location of layers of plankton and water column stability, density discontinuities, and vertical shear.

There is evidence of persistent finescale phytoplankton distributions in the Oregon coastal upwelling region. Thin layers of phytoplankton were observed over the continental shelf within narrow density intervals (+0.003 sigma-t units)(Cowles et al., 1998). These layers were continuously observed for at least 4-6 h, a time period in which significant grazing activity can occur and potentially enhance secondary production (Mackas and Burns, 1986). Chlorophyll concentrations were greatly enhanced in these layers compared to the rest of the water column (four to five times higher), so this phenomenon could have important implications for zooplankton distributions. Additionally, the association of these thin layers with physical parameters suggests that with more observations, we may be able to determine the range of conditions over which layers occur, and perhaps ultimately predict distribution patterns associated with measured physical factors.

In an effort to determine the extent to which planktonic distributions are defined by physical forcing factors, we collected optical, acoustical, and physical data over the Oregon continental shelf in the summer of 2000 as part of the Northeast Pacific Global Ocean Ecosystems Dynamics (NEP GLOBEC) program. Our objective was to evaluate the association among (1) finescale density structure, (2) horizontal velocity patterns, (3) finescale phytoplankton distributions, and (4) finescale acoustic backscatter features.

# 2. Methods

Density, horizontal current velocity, fluorescence, and acoustic volume backscatter ( $S_V$ ) data were collected on two cruises of the R/V *Wecoma* in June and August 2000 at three stations over the Oregon continental shelf (Fig. 1). Density data were collected with a Seabird 911 CTD, and fluorescence was measured with a Wetstar fluorometer. These instruments were mounted on a profiling frame that was slightly negatively buoyant and was allowed to drop slowly (15–30 cm s<sup>-1</sup>)



Fig. 1. Map of the study area off the coast of Oregon. Black squares mark the location of the three profiling stations and isobaths are in meters. Station 1 was sampled on 6 June 2000 during 17:38–23:13 PDT; Station 2 on 5 August, 2000 during 18:13–6 August 00:37 PDT; and Station 3 on 13 August 2000 during 17:29–19:59 PDT.

through the water column, independent of ship motion, to depths of approximately 90 m. The ship was allowed to drift during these profiles. The raw data (CTD, 24 Hz; Wetstar, analog response time 0.17 s) were processed according to standard CTD protocols and subjected to a seven point median filter, yielding a vertical resolution of approximately 3–5 cm.

Vertical profiles of horizontal current velocity data were obtained with the shipboard 150 kHz narrow-band RD Instruments acoustic Doppler current profiler (ADCP). The time-averaged data (2.5 min) have a vertical resolution of 8 m and the shallowest depth bin was at 17 m. Vertical shear was calculated from the depth bins of velocity data.

Acoustic backscatter data were collected with a four-frequency (38, 120, 200, and 420 kHz) scientific echosounder (Hydroacoustic Technologies Inc. 244) system (HTI). The transducers were oriented in a down-looking configuration in a fixed towbody that was deployed from the port side of the ship and held at a fixed depth of approximately 15 m. In this deployment, the effective depth of each frequency was 200 m (38 kHz), 150 m (120 and 200 kHz), and 100 m (420 kHz). The system returned an estimate of volume backscatter ( $S_V$ ) for each frequency.

$$S_V = 10 \log_{10}(s_V). \tag{1}$$

The volume scattering coefficient,  $s_V$ , at a single frequency is defined by Eq. 2. It is equal to the sum of the backscattering cross section ( $\sigma$ ) for each class of scatterers (represented by *j*) multiplied by the number of scatterers (*n*) in a fixed volume, usually 1 m<sup>3</sup>.

$$s_V = \sum_{j=1}^{j=n} \sigma_j n_j.$$
<sup>(2)</sup>

An increase in the abundance of a particular class of scatterer will result in an increase in the measured  $S_V$  at all frequencies (Medwin and Clay, 1998).

The HTI acoustic data have a vertical resolution of approximately 1 m. Volume backscatter measurements were corrected for changes in sound speed, which depends upon temperature, salinity, and pressure measured from the CTD profiles. The shallowest depth bin for the HTI data is 17 m.

Buoyancy frequency  $(N^2)$  was calculated from the density profiles and Richardson number (Ri)was calculated from the density profiles and the ADCP derived vertical shear profiles calculated from the ADCP data. The water column (or portion thereof) is considered stable if Ri is greater than 0.25 (Pickard and Emery, 1990). In this study, Ri was calculated over 8 m vertical intervals.

Individual vertical profiles of volume backscatter, current velocity, and vertical shear were constructed by taking 10 min. averages at the time of each CTD/Optics profile (each profile took approximately 10 min. to complete). Depth-lagged cross-correlation analysis was performed on these profiles to determine if volume backscatter was correlated with velocity, vertical shear, buoyancy frequency, or Ri.

# 3. Results

We observed a spatial relationship between the density structure of the water column and the distribution of phytoplankton. Fluorescence measurements show that phytoplankton were concentrated in horizontal layers located above 40 m at all the three stations (Fig. 2). The layers had sharp boundaries that were spatially correlated with steps in the density profile ( $\Delta \sigma_t = 0.102 \text{ m}^{-1}$ ). This relationship was strongest at Stations 1 and 3. These steps in density created local peaks in water-column stability, represented by  $N^2$ . The spatial

relationship between density steps, local peaks in  $N^2$ , and boundaries of fluorescence peaks are illustrated with an example profile (Fig. 3) typical of the 19 profiles collected (time of each profile is shown as a tick at the top of each panel in Fig. 4). The water column was very stable at Stations 2 and 3 with *Ri* values all above 0.25. At Station 1, *Ri* values ranged from 0.02 to 0.4 with all values between 40 and 60 m above 0.25.

Patterns in acoustic backscatter were characterized by layers and patches that were narrow in vertical extent (<10 m), persistent for the time period of the sampling (2.5–6 h), had intense scattering compared to the background, and had sharp boundaries ( $\Delta S_V / \Delta z > 10 \text{ dB m}^{-1}$ ) (Fig. 4, Layers 1A, 1B, 2A, 2B, 2C, 3A, and 3B). We show detailed data from 120 kHz for brevity; the features discussed have patterns at the other frequencies that are consistent with the 120 kHz.



Fig. 2. Wetstar fluorometer voltage with density ( $\sigma_t$ ) contours from CTD overlaid. Arrows on the top of each panel indicate the time of each CTD profile. The circled arrow is the profile shown in Fig. 3. The *x*-axes span the time range of acoustic sampling at each station. Local time is PDT.



Fig. 3. Example profile of (A) density, (B) buoyancy frequency ( $N^2$ ), and (C) fluorescence from Station 1. Arrows indicate boundaries of fluorescence peak (C), corresponding steps in density (A) and local peaks in  $N^2$  (B).

At Station 1, the pattern of acoustic backscatter was related to changes in the bathymetry that occurred as the vessel drifted during our observations. There was a layer of backscatter centered around 50 m (Layer 1A) located offshore of a submarine bank. At the edge of the bank, there was a break in this layer and it subsequently disappeared in the onshore direction over the bank. At Station 2, there was a layer of backscatter (Layer 2A) that appeared to rise off the bottom and ascend in the water column approximately 1 h after sunset (approximately 20:30 or 217.85 local time). Another scattering layer (Layer 2C) was observed after 23:00, local time, in the upper water column at the offshore edge of the bank.

The observed layers had distinct scattering spectra (Fig. 5). Layers 1A and 2A showed low scattering at 38 kHz, higher scattering at 120 and 200 kHz, and slightly lower scattering at 420 kHz. Layer 3A showed the same trend at 38, 120, and

200 kHz but because the depth of this layer was beyond the range of 420 kHz, there were no acoustic data at this frequency.

There were distinct vertical transitions in the horizontal flow field at all three stations (Fig. 6). At Station 1, the east-west component of horizontal flow showed that the lower portion of the water column, 20-30 m above the bottom, was flowing faster and to the east while the upper part of the water column was flowing slowly to the west. There was a layer of faster westward flow between 30 and 40 m. The north-south component of horizontal flow showed that there was a layer of northward flow between 50 and 60 m surrounded by slow, southward flow. Later in the time record there was a layer of increased southward flow above 50 m. At Station 2, the east-west and north-south components of horizontal flow show similar patterns. There was a layer of southwestward flow above 40 m and a layer of southeastward flow above 80 m later in the time record.



Fig. 4. Volume backscatter ( $S_v$ ) from 120 kHz. Layers of interest are labeled 1A, 1B, 2A, 2B, 2C, 3A, 3B. Arrows on the top of each panel indicate the time of each CTD profile. The circled arrow is the profile shown in Fig. 3. The *x*-axes span the time range of collection of acoustic data at each station. Local time is PDT.



Fig. 5. Average volume scattering spectra for layers 1A, 2A, and 3A at the four frequencies 38, 120, 200, and 420 kHz.

At Station 3, all of the water from 15-200 m was flowing to the west with an increase in velocity above 100 m. The north-south component of horizontal flow showed that there was a transition between northward and southward flow that bends upward from 160 m at the beginning of the time record to 120 m at the end of the time record.

Although there was some spatial correspondence visible in the plots of acoustic backscatter and current velocity, depth-lagged cross correlation analysis did not reveal any statistically significant relationships between volume backscatter, horizontal velocity, or vertical shear. The current velocity data had a much coarser vertical resolution than the acoustic data (8 m vs. 1 m) so it was difficult to accurately determine the relationship between gradients in current velocity and



Local Time (Decimal Year-Day)

Fig. 6. Horizontal velocity from shipboard 150 kHz ADCP. Sidelobe bottom reflection contaminates data within 10-30 m of the bottom and these data are not shown. The *x*-axes span the time range of collection of velocity data at each station. Local time is PDT.

scattering distributions. Despite the lack of statistically significant relationships, there were distinct qualitative correlations between patterns of horizontal current velocity and acoustic backscatter.

At Station 1, Layer 1A coincided with a band of weak northerly flow between 50 and 60 m surrounded by slow, southerly flow (Figs. 4 and 7). Other scattering layers, labeled 1B, are located at a gradient in southward flow. Laver 2A at Station 2 was associated with a transition between northerly and southerly flow. Layer 2B appears to be affected by short wavelength internal waves and is located between the 0.08 and  $0.03 \,\mathrm{m \, s^{-1}}$  northward velocity gradients. There was some correspondence between the southeasterly flow in the upper 100 m of the water column late in the record (decimal year-day 218.0) and the patches of increased scattering above 30 m. At Station 3, Layer 3A tracked the boundary between northerly and southerly flow, and was located several meters

below this boundary in an area of weak southerly flow. A broad layer of increased scattering above 80 m (Layer 3B, Fig. 4) is located in an area of stronger northward flow (Figs. 6 and 7).

We observed one case in which a scattering feature was associated with the peak in fluorescence. At Station 3, there was a broad layer of increased fluorescence between 5 and 30 m (Fig. 2) that corresponded with the location of Layer 3B (Fig. 4). Layer 1A at Station 1 (Fig. 4) was clearly not collocated with the peak in fluorescence which was located between 10 and 30 m (Fig. 2), approximately 20 m above the scattering layer. At Station 2, the peak in fluorescence is above 15 m (Fig. 2) and so is above the shallowest depth bin of acoustic data, and the potential spatial relationship between scattering and fluorescence cannot be determined. Overall, there is no clear pattern to the spatial relationship between acoustic scattering and fluorescence features, but it is clear



Fig. 7. Northward velocity contours (m s<sup>-1</sup>) overlaid on 120 kHz  $S_v$ . Solid lines indicate contours of Northward flow and dashed lines indicate contours of Southward flow. The *x*-axes span the time range of collection of acoustic data at each station. Local time is PDT.

that scattering features are not always associated with peaks in fluorescence.

### 4. Discussion

The data from our three stations show that phytoplankton were distributed in discrete layers with sharp vertical gradients that often were associated with physical properties of the water column. These features were seen both nearshore (Stations 1 and 2) and offshore (Station 3) in June and August 2000, indicating that these distributional patterns may be common during upwelling off the Oregon coast.

Phytoplankton were concentrated in distinct, though not always thin, layers which were correlated to the density structure of the water column. Boundaries of fluorescence peaks were characterized by sharp vertical gradients that were associated with steps in the density profile and local peaks in  $N^2$ . The relationship between the location of fluorescence boundaries and the density structure was seen in all of the 19 CTD profiles taken at the three stations, showing that this is a potentially common relationship.

Our observations revealed considerable finescale pattern in acoustic volume backscatter over the Oregon continental shelf. Scattering features frequently took the form of horizontal layers with sharp vertical gradients that had intense volume backscatter levels relative to the background (>10 dB differences between adjacent 1 m vertical bins). These layers were often less than 10 m-thick and were persistent for intervals of 2.5–6 h. The observed scattering patterns sometimes corresponded with horizontal velocity patterns, but the relationship was not consistent. Other studies also have observed distinct scattering features with sharp vertical gradients (Holliday and Pieper, 1980; Greene and Wiebe, 1991; Batchelder et al., 1995; Wiebe et al., 1996; Hitchcock et al., 2002; Ressler and Jochens, 2003; Ressler et al., 2005). In some cases, the vertical boundaries of these features were associated with physical parameters such as the location of the pycnocline or temperature front (Hitchcock et al., 2002) and horizontal boundaries with the presence of mesoscale circulation features (Ressler and Jochens, 2003; Ressler et al., 2005). Wiebe et al. (1996) suggest that physical forcing mechanisms may have played an important role in the formation of the different types of scattering features they observed in a stratified versus well-mixed area. No specific comparisons were made between the location of scattering features and the vertical profile of horizontal velocity patterns, so we cannot compare this aspect of our results with those of other researchers.

The spectra of these backscatter features suggest that they may have been composed of zooplank-

ton. We can use multifrequency acoustic techniques to indicate whether observed patches and layers in the water column may have the same composition of scatterers. Assemblages which give different measures of  $S_v$  at different frequencies can be composed of either different types of scatterers, different numbers of scatterers, different sizes of scatterers, or a combination of these three (Greenlaw, 1979). Fig. 8 shows the theoretical volume scattering strength curves for several different individual organisms of a particular size derived from models created by Stanton (1998a, b). If the size of one of these organisms was decreased, the curve would retain the same shape, but would shift to the right, to higher frequencies, and the magnitude of scattering would decrease. The sizes of the individual zooplankton shown in Fig. 5 represent maximal sizes encountered in this area (Sutor, 2004). Therefore, we make the assumption that these curves represent the upper bound of expected scattering and that volume scattering spectra from representative zooplankton off the Oregon coast would most likely have curves



Fig. 8. Plot of theoretical target strengths at different frequencies for several different organisms (6 mm long copepod, 2 mm diameter shelled pteropod, 2.5 cm long euphausiids). These curves are based on the scattering models of Stanton et al. (1998a, b). Arrows mark the location of 38, 120, 200, and 420 kHz on the *x*-axis. (After Fig. 3 in A. Lavery et al., 2002).

that were shifted to the right and were lower in magnitude than the curves displayed. Assuming this, we can make some comparisons between the scattering spectra we measured and these theoretical curves. From this plot, we can see that organisms such as euphausiids, copepods, and pteropods have relatively low scattering at 38 kHz, higher scattering at 120 and 200 kHz. and are in the range of geometric scattering at 420 kHz. This means that measured scattering can show an increase or decrease from 200 to 420 kHz, depending upon the shape and size of the scatterer. Organisms such as fish with swimbladders and gas-bearing siphonophores have relatively high scattering at 38 kHz and show little change in scattering level at 120, 200 and 420 kHz. Additionally, other researchers have shown that the difference in scattering between 38 and 120 kHz can be used to distinguish patches of fish and euphausiids; euphausiids have low scattering at 38 kHz and high scattering at 120 kHz (Maduriera et al., 1993; Swarzman et al., 1999).

The average scattering spectra of the three scattering layers we observed (Fig. 5) show low scattering at 38 kHz, increased scattering at 120 and 200 kHz, and Layers 1A and 2A show decreased scattering at 420 kHz. The spectral curves for Layers 2A and 3A show the same shape, differing only in amplitude while Layer 1A shows a slightly different spectral curve with a lower average value of  $S_V$  at 200 kHz. Ressler et al. (2005) observed similar scattering features over the Oregon shelf in August 2000 with the same spectral characteristics. These scattering features were determined to be composed of euphausiids by net-tow data (Ressler et al., 2005). Given the observed spectra (lower scattering at 38 kHz and higher scattering at 120, 200 kHz), our empirical knowledge of scattering spectra shown in Fig. 5, the results of Maduriera et al. (1994) and Swartzman et al. (1999), and the supporting evidence from Ressler et al. (2005), we conclude that these layers are most likely composed of zooplankton without gas inclusions, keeping in mind that without knowledge of the size structure of the zooplankton in these layers, exact comparisons are not possible.

Physical phenomena, such as temperature and salinity microstructure also can cause scattering (Seim and Gregg, 1994; Stanton et al., 1994; Seim et al., 1995; Warren et al., 2003). Our highresolution temperature, salinity, and density profiles revealed no evidence of water-column overturns and so the presence of significant microstructure is unlikely.

It is not possible to draw definite conclusions about the correlation between phytoplankton and zooplankton distributions from these data. Only the scattering feature located above 30 m at Station 3 was associated with a peak in fluorescence. Because the acoustic instrument was held at a fixed depth of 15 m, the first effective acoustic data are from 18 m, which is below part (Stations 1 and 3, Fig. 4) or all (Station 2, Fig. 4) of the peak in fluorescence. However, many of the spatially discrete, intense, scattering features were observed in areas of the water column where the fluorescence was low, suggesting that the location of zooplankton may not be associated with the location of maximum phytoplankton abundance in many cases. This observation has been reported in other studies (Herman, 1983; Napp et al., 1988; Huntley et al., 1995; Jaffe et al., 1998).

The role of physical mechanisms of formation and maintenance of finescale scattering distributions is not clear from this study. The horizontal velocity data had coarse resolution (8m vertical bins) compared to the acoustic data (1 m vertical bins). To assess more carefully, the role of horizontal current velocities and shear in creating biological structure, we must obtain current data with the same spatial resolution as the acoustic data. In addition, it is possible that physical factors controlled the formation of the layers we observed but our sampling began after the formation event took place. For example, the deep scattering layer at Station 3 closely tracked the boundary between northern and southern flow, so the boundaries of this layer may have been associated with areas of increased vertical shear that could act to flatten and extend a thick layer or patch into the observed thin layer. This station is located at the southern edge of a mesoscale circulation feature (Barth et al., 2005, Fig. 2b) and the observed scattering distributions may be

potentially influenced by this feature. Unfortunately, the coarse vertical resolution of the horizontal velocity and shear data does not allow us to clearly determine the relationship between scattering features and shear. Sampling for longer time periods with higher spatial resolution velocity data would allow us to observe a sequence of events that may better explain the potential role of currents and shear in the formation and maintenance of scattering layers. We also cannot discount the role of behaviors such as aggregation on food sources or vertical migrations in forming the observed scattering patterns. The lack of consistent collocation of phytoplankton and zooplankton suggests that aggregation of zooplankton on layers of phytoplankton is not the only behavioral process accounting for the formation of zooplankton layers.

The results of this study show that accurate assessment of the zooplankton biomass and distribution patterns in this system requires a vertical resolution of less than 10 m. The finescale scattering features observed on these cruises did not appear to be random or transient. Sampling must be conducted for longer periods at the appropriate spatial scales to better quantify the persistence of such features. The evidence from these data show that finescale aggregations are not so short lived that they can be treated as random when sampling.

Multifrequency acoustic measurements can identify patches of different composition and, when used in conjunction with theoretical scattering models, we can draw some broad conclusions about the most likely composition of observed scattering features. However, these measurements alone cannot give us quantitative numbers of animals or their identity. The only way to clearly determine the identity of the scatterers in each patch is to sample them directly or observe them with image-forming optical instruments. Density and identities of zooplankton are critical factors to assess along with distribution patterns to create a complete spatial picture of the zooplankton community.

We need a better understanding of how common and persistent finescale zooplankton distributions are in the Oregon shelf upwelling region. This knowledge will determine the type of sampling methods necessary to accurately assess zooplankton distribution and biomass and will illustrate the potential coupling between primary producers and grazers which has implications for particle flux and elemental cycling. Finer-scale current and shear data are necessary to determine the role of physical factors in the formation and maintenance of these finescale distributions. We also need sea-truthing data to determine the identity of the scatterers so that we can assess more accurately the biomass distributions and behavioral mechanisms controlling distributions. The timing of the ascent at Station 2 is consistent with diel vertical migration, but to correctly assess the importance of this and other behaviors, we must confirm the composition of these layers. Previous work utilizing the Video Plankton Recorder and MOCNESS has shown the utility of these technologies to provide seatruthing data for acoustics on various spatial scales (Benfield et al., 1998, 2003). Collecting coincident, finescale physical and biological data, which allow us to determine the distribution and identity of zooplankton, is critical to assessing the factors which control zooplankton distributions.

In summary, we found that zooplankton were distributed in finescale, intense, and persistent vertical layers. There was (1) a strong association between phytoplankton distributions and density structure but no apparent association between zooplankton distributions and density structure, (2) some association between zooplankton distributions and horizontal velocity patterns, and (3) no clear association between maximal phytoplankton and zooplankton distributions. These results indicate that plankton distributions of this kind may be common and physical mechanisms may play an important role in the formation and maintenance of these layers. With longer term sampling and higher vertical resolution velocity data, the relative importance of physical and biological mechanisms of layer formation can be assessed more clearly.

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#### References

- Barth, J.A., Cowles T.J., Pierce, S.D., 2005. Mesoscale structure and its seasonal evolution in the Northern California Current system. Deep-Sea Research II, this volume [doi:10.1016/j.dsr2.2004.09.026].
- Batchelder, H.P., VanKeuren, J.R., Vaillancourt, R., Swift, E., 1995. Spatial and temporal distributions of acoustically estimated zooplankton biomass near the Marine Light-Mixed Layers station (59°30'N, 21°00'W) in the North Atlantic in May 1991. Journal of Geophysical Research 100 (C4), 6549–6563.
- Benfield, M.C., Lavery, A., Wiebe, P.H., Greene, C.H., Stanton, T.K., Copley, N.J., 2003. Distributions of physonect siphonulae in the Gulf of Maine and their potential as important sources of acoustic scattering. Canadian Journal of Fisheries and Aquatic Sciences 60 (7), 759–772.
- Benfield, M.C., Wiebe, P.H., Stanton, T.K., Davis, C.S., Gallager, S.M., Greene, C.H., 1998. Estimating the spatial distribution of zooplankton biomass by combining Video Plankton Recorder and single-frequency acoustic data. Deep-Sea Research II 45, 1175–1199.
- Boyd, C.M., 1973. Small scale spatial patterns of marine zooplankton examined by an electronic in situ zooplankton detecting device. Netherlands Journal of Sea Research 7, 103–111.
- Brodeur, R.D., Fisher, J.P., Teel, D., Emmett, R.L., Casillas, E., Miller, T.B., 2003. Distribution, growth, condition, origin and environmental and species associations of juvenile salmonids in the Northern California Current. Fisheries Bulletin, US 102, 25–46.
- Cassie, R.M., 1963. Microdistribution of plankton. Oceanography Marine Biology Annual Review 1, 223–252.
- Cowles, T.J., Desiderio, R.A., Carr, M.E., 1998. Small-scale planktonic structure: persistence and trophic consequences. Oceanography 11 (1), 4–9.
- Dekshenieks, M.M., Donaghay, P.L., Sullivan, J.M., Rines, J.E.B., Osborn, T.R., Twardowski, M.S., 2001. Temporal and spatial occurrence of thin phytoplantkon layers in relation to physical processes. Marine Ecology Progress Series 223, 61–71.
- Greene, C.H., Wiebe, P.H., 1991. Probing the fine structure of the ocean sound-scattering layers with ROVERSE technology. Limnology and Oceanography 36 (1), 193–204.
- Greenlaw, C.F., 1979. Acoustical estimation of zooplankton populations. Limnology and Oceanography 24 (2), 226–242.

- Haury, L.R., Yamazaki, H., Itsweire, E.C., 1990. Effects of turbulent shear flow on zooplankton distribution. Deep-Sea Research I 37 (3), 447–461.
- Herman, A.W., 1983. Vertical distribution of patterns of copepods, chlorophyll, and production in north-eastern Baffin Bay. Limnology and Oceanography 28, 709–719.
- Hitchcock, G., Lane, P., Smith, S.L., Luo, J., Ortner, P.B., 2002. Zooplankton spatial distributions in coastal waters of the northern Arabian Sea, August, 1995. Deep-Sea Research II 49, 2403–2423.
- Holliday, D.V., Donaghay, P.L., Greenlaw, C.F., McGehee, D.E., McManus, M.A., Sullivan, J.M., Miksis, J.L., 2003. Advances in defining fine- and micro-scale pattern in plankton. Aquatic Living Resources 16 (3), 131–136.
- Holliday, D.V., Pieper, R.E., 1980. Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. Journal of the Acoustical Society of America 67 (1), 135–146.
- Holliday, D.V., Pieper, R.E., Greenlaw, C.F., Dawson, J.K., 1998. Acoustical sensing of small-scale vertical structures in zooplankton assemblages. Oceanography 11 (1), 18–23.
- Huntley, M.E., Zhou, M., Nordhausen, W., 1995. Mesoscale distribution of zooplankton in the California Current in late spring observed by the optical plankton counter. Journal of Marine Research 53 (4), 647–674.
- Huyer, A., 1983. Coastal upwelling in the California Current system. Progress in Oceanography 12, 259–284.
- Jaffe, J.S., Ohman, M.D., De Robertis, A., 1998. OASIS in the sea: measurement of the acoustic reflectivity of zooplankton with concurrent optical imaging. Deep-Sea Research II 45, 1239–1253.
- Lavery, A.C., Stanton, T.K., Wiebe, P.H., 2002. Variability in high frequency acoustic backscattering in the water column. In: Pace, N.G., Jensen, F.B. (Eds.), Impact of Littoral Environmental Variability on Acoustic Predictions and Sonar Performance, Kluwer Academic Publishers, pp. 63–70.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73 (6), 1943–1967.
- Mackas, D.L., Burns, K.E., 1986. Poststarvation feeding and swimming activity in *Calanus pacificus* and *Metridia pacifica*. Limnology and Oceanography 31, 383–392.
- Mackas, D.L., Denman, K.L., Abbott, M.R., 1985. Plankton patchiness: Biology in the physical vernacular. Bulletin of Marine Science 37 (2), 652–674.
- Mackas, D.L., Kieser, R., Saunders, M., Yelland, D.R., Brown, R.M., Moore, D.F., 1997. Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 54, 2080–2096.
- Maduriera, L.S., Everson, I., Murphy, E.J., 1993. Interpretation of acoustic data at two frequencies to discriminate between Antarctic krill (*Euphausia superba* Dana) and other scatterers. Journal of Plankton Research 15 (7), 787–802.
- McFarlane, G.A., King, J.R., Beamish, R.J., 2000. Have there been recent changes in climate? Ask the fish. Progress in Oceanography 47, 147–169.

- McManus, M.A., Alldredge, A.L., Barnard, A.H., Boss, E., Case, J.F., Cowles, T.J., Donaghay, P.L., Eisner, L.B., Gifford, D.J., Greenlaw, C.F., Herren, C.M., Holliday, D.V., Johnson, D., MacIntyre, S., McGehee, D.E., Osborn, T.R., Perry, M.J., Pieper, R.E., Rines, J.E.B., Smith, D.C., Sullivan, J.M., Talbot, M.K., Twardowski, M.S., Weidemann, A., Zaneveld, R.V., 2003. Characteristics, distribution and persistence of thin layers over a 48 hour period. Marine Ecology Progress Series 261, 1–19.
- Medwin, H., Clay, C.S., 1998. Fundamentals of Acoustical Oceanography. Academic Press, Boston.
- Napp, J.M., Brooks, E.R., Matrai, P., Mullin, M.M., 1988. Vertical distribution of marine particles and grazers. II. Relation of grazer distribution to food quality and quantity. Marine Ecology Progress Series 50, 59–72.
- Osborn, T.R., 1998. Finestructure, microstructure, and thin layers. Oceanography 11 (1), 36–43.
- Owen, R.W., 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments. Journal of Marine Research 47, 197–240.
- Pickard, G.L., Emery, W.J., 1990. Descriptive Physical Oceanography: An Introduction. Butterworth Heinemann, Oxford.
- Ressler, P. H., Brodeur, R. D., Peterson, B., Pierce, S. D., Vance, P. M., Roestad, A., Barth, J. A., 2005. The spatial distribution of euphausiid aggregations in the Northern California Current in August 2000. Deep-Sea Research II, this volume [doi:10.1016/j.dsr2.2004.09.032].
- Ressler, P.H., Jochens, A.E., 2003. Hydrographic and acoustic evidence for enhanced plankton stocks in a small cyclone in the northeastern Gulf of Mexico. Continental Shelf Research 23, 41–61.
- Roman, M.R., Holliday, D.V., Sanford, L.P., 2001. Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maximum. Marine Ecology Progress Series 213, 215–227.
- Seim, H.E., Gregg, M.C., 1994. Detailed observations of naturally occurring shear instability. Journal of Geophysical Research 99 (C5), 10049–10073.
- Seim, H.E., Gregg, M.C., Miyamoto, R.T., 1995. Acoustic backscatter from turbulent microstructure. Journal of Atmospheric and Oceanic Technology 12 (2), 367–380.

- Small, L.F., Menzies, D.W., 1981. Patterns of primary productivity and biomass in a coastal upwelling region. Deep-Sea Research I 28 (A), 123–149.
- Smith, R.L., 1968. Upwelling. Oceanography and Marine Biology Annual Review 6, 11–46.
- Stanton, T.K., Chu, D., Wiebe, P.H., Martin Traykovski, L.V., Eastwood, R.L., 1998a. Sound scattering by several zooplankton goups. I. Experimental determination of dominant scattering mechanisms. Journal of the Acoustical Society of America 103 (1), 225–235.
- Stanton, T.K., Chu, D., Wiebe, P.H., 1998b. Sound scattering by several zooplankton groups. II. Scattering models. Journal of the Acoustical Society of America 103 (1), 236–253.
- Stanton, T.K., Wiebe, P.H., Chu, D., Goodman, L., 1994. Acoustic characterization and discrimination of marine zooplankton and turbulence. ICES Journal of Marine Science 51, 469–479.
- Steele, J., 1974. The Structure of Marine Ecosystems. Harvard University Press, Cambridge.
- Sutor, M., 2004. Finescale vertical distributions of zooplankton and their relationship to physical and biological factors: investigations using acoustical and optical technologies. Ph.D. Thesis, College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR.
- Swarzman, G., Brodeur, R.D., Napp, J.M., Walsh, D., Hewitt, R., Demer, D., Hunt, G., Logerwell, E., 1999. Relating spatial distributions of acoustically determined patches of fish and plankton: data viewing, image analysis, and spatial proximity. Canadian Journal of Fisheries and Aquatic Sciences 56 (Suppl. 1), 188–198.
- Warren, J.D., Stanton, T.K., Wiebe, P.H., Seim, H.E., 2003. Inference of biological and physical parameters in an internal wave using multiple-frequency, acousticscattering data. ICES Journal of Marine Science 60, 1033–1046.
- Wiebe, P.H., Mountain, D.G., Stanton, T.K., Greene, C.H., Lough, R.G., Kaartvedt, S., Dawson, J., Copley, N.J., 1996. Acoustical study of the spatial distribution of plankton on Georges Bank and the relationship between volume backscattering strength and the taxonomic composition of the plankton. Deep-Sea Research II 43 (7–8), 1971–2001.