

Effects of Mesoscale Physical Processes on Thin Zooplankton Layers at Four Sites Along the West Coast of the U.S.

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ABSTRACT: Within the coastal marine environment, populations of phytoplankton, zooplankton, bacteria, viruses, and aggregations of marine snow are frequently concentrated beneath the surface in discrete, vertically thin layers. Thin layers range in vertical dimension from a few centimeters to three meters, and have been observed to extend horizontally for kilometers. They appear in the water column episodically and can persist for days. We present some of the results of an investigation of four coastal sites along the west coast of the United States to assess frequency of occurrence of thin layers of zooplankton. Our study sites included coastal sites near East Sound, Washington; Cape Perpetua, Oregon; Monterey Bay, California; and Santa Barbara, California. At each site, we collected several, weeks-long time series of hydrography, current velocity, and acoustic backscatter due to mesozooplankton. Our results show that thin layers were common features at all four sites. Across all study sites, a change in the predominant physical regime, usually precipitated by a change in the wind pattern, corresponded with an absence of thin zooplankton layers. In order to make a first-order prediction about when thin layers have the possibility of occurring in a coastal environment, we found it useful to examine regional wind and circulation patterns and to determine how they affect stratification in each local environment.

Introduction

For several decades, oceanographers have known that the water column is a heterogeneous environment for plankton distributions (Cassie 1963; Wiebe and Holland 1968; Haury et al. 1978), which can vary both horizontally and vertically across a range of temporal and spatial scales (Dekshenieks et al. 2001). Despite this awareness, the ability to resolve organism patchiness at small spatial and temporal scales was severely hindered by inadequate sampling design and capabilities (Denman and Mackas 1978; Haury et al. 1978; Donaghay et al. 1992; Holliday and Pieper 1995). There was a general suspicion that “variability in biomass at short time and space scales may have a greater impact on ecosystem structure and function than larger-scale variability (e.g., climate change)” (Haury et al. 1978, p. 280). Only recently have advances in acoustical and optical instrumentation and profiling technology enabled scientists to resolve the fine-scale structure of the biological communities in the water column (Donaghay et al. 1992; Holliday et al. 1998, 2003; McManus et al. 2003). Achieving reliable measurements of ocean physics at submeter

vertical scales is an accomplishment made in the past three decades, with substantial room remaining for future improvements (Osborn and Cox 1972; Gregg et al. 1973; Caldwell et al. 1985; Donaghay et al. 1992; Cowles et al. 1998).

We now know that within the coastal marine environment, populations of phytoplankton, zooplankton, bacteria, viruses, and marine snow frequently appear beneath the surface in discrete, vertically thin layers (Allredge et al. 2002; McManus et al. 2003). These features, referred to as thin layers, range in vertical dimension from a few centimeters to three meters, and have been observed to extend horizontally for kilometers (Rines et al. 2002). They appear in the water column frequently and can persist for days.

Many studies, both empirical and theoretical, have shown that the survival of larvae is dependent on two factors: whether larvae encounter high enough prey densities during the critical period of larvae development and whether the larvae are retained near their food in the marine environment (Hjort 1914; Sinclair 1987; Cushing 1990; Alexander and Roughgarden 1996; Cowen et al. 2000). The importance of larvae encountering food over yearly time scales is well documented (Sverdrup 1953; Cushing 1974; Cushing 1990). In addition to the requirement that larvae and their food overlap temporally, they must also overlap

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spatially. Lasker (1977, p. 136) stated that the “survival of larvae appears to be related to coincidence rather than abundance alone; that is, a patch of larvae will survive if it coincides with an adequate patch of food organisms and also if it does not coincide with a patch of predators adequate to destroy the larval patch.” Mullin and Brooks (1976) also found that the distributional heterogeneity of phytoplankton is important in determining the nutrition and survival of *Calanus pacificus* copepods. Thin layers of plankton are another mechanism by which food sources are vertically partitioned in the water column. Encountering a thin layer may make the difference between life and death for individual larvae.

Between 1998 and 2003, we undertook an investigation of multiple coastal sites along the west coast of the United States to determine the frequency of occurrence of thin layers of zooplankton. These sites included East Sound, Washington; Cape Perpetua, Oregon; Monterey Bay, California; and Santa Barbara, California. These locations consisted of a variety of environments, including shallow continental shelves, open bays, and fjords. At each of these sites, an assortment of instrumentation to detect thin layers and assess hydrography was deployed. The original objective for this study was simply to detect the presence or absence of thin high-frequency acoustical scattering layers and to obtain a first-order indication of their frequency of occurrence. The four sites discussed in this contribution were also sampled to assess the suitability of each site for a subsequent detailed process study on thin layers. As a consequence of our limited original objectives, only a few conventional net samples (e.g., oblique tows) were collected, and we were able to collect these net samples at only some of the sites. The purpose of the net samples was only to obtain a representative sample of the most abundant small zooplankton present and to determine their basic body shapes, for subsequent use in estimating biomass-size spectra from direct measurements of acoustical volume scattering spectral data.

Data collected from two sites, East Sound and Monterey Bay, were investigated and analyzed in some additional detail, resulting in several publications describing the phytoplankton and zooplankton layers themselves and the affects of physical processes across a range of temporal and spatial scales on those layers: Dekshenieks et al. (2001), Twardowski and Donaghay (2001), Alldredge et al. (2002), Rines et al. (2002), Holliday et al. (2003), McManus et al. (2003, 2005), and Stacey et al. (2007). The results from these individual studies revealed several findings. Work focusing on thin phytoplankton layers found that 71% of all these features are located at the base of or within the pycnocline. No thin phytoplankton layers were present in regions of the water column with

Richardson number < 0.23 (Dekshenieks et al. 2001).

The densities of organisms found within thin layers can be much greater than those above or below the layer (McManus et al. 2005). This suggests that thin layers likely play an important role in coastal marine ecosystems and many biological processes by altering local concentrations of nutrients, toxins, and organisms, and influencing interactions among conspecifics (e.g., competition, reproduction) or between species (e.g., competition, predation; Mason et al. 1993; Sieburth and Donaghay 1993; Johnson et al. 1995; Donaghay and Osborn 1997; Cowles et al. 1998). The thin zooplankton layers observed during the 2002 Monterey Bay study were located predominantly in regions of reduced flow or in the sheared layer of no motion between two oppositely moving water masses (McManus et al. 2005). As a consequence, populations within these thin layers are transported less distance by currents and have greater nearshore retention times than typical coastal waters. This relative lack of conveyance may have important implications for larval transport, as well as for the retention of harmful algal bloom species of phytoplankton, marine viruses, and bacteria (McManus et al. 2005).

Although the relationship between phytoplankton and zooplankton thin layers is not well understood, it has been suggested that zooplankton foraging behavior plays a role in the formation of zooplankton thin layers (McManus et al. 2003). Increases in zooplankton biomass have been observed on and around a thin layer of phytoplankton, suggesting that the zooplankton were forming layers in response to the presence of thin layers of phytoplankton (Holliday et al. 2003; McManus et al. 2003). Zooplankton can also exhibit avoidance, creating distinct vertical separations between different types of thin layers (Alldredge et al. 2002).

Because thin layers not only affect optical and acoustical signatures in the pelagic environment, but also have significant effects on the biological structure and dynamics of marine ecosystems, it is critical to refine our ability to observe these structures through continued development of new instrumentation. Ultimately, these advances may result in the capability to predict the spatial distribution and temporal occurrence of these structures. To this end, it is imperative to not only perform in-depth investigations of individual coastal sites, but to compare results across different sites. This type of research will foster a general understanding of fine-scale plankton distributions in the coastal environment by examining how thin layer responses to physical processes from the fine-scale to the mesoscale vary or remain consistent from one environment to another.

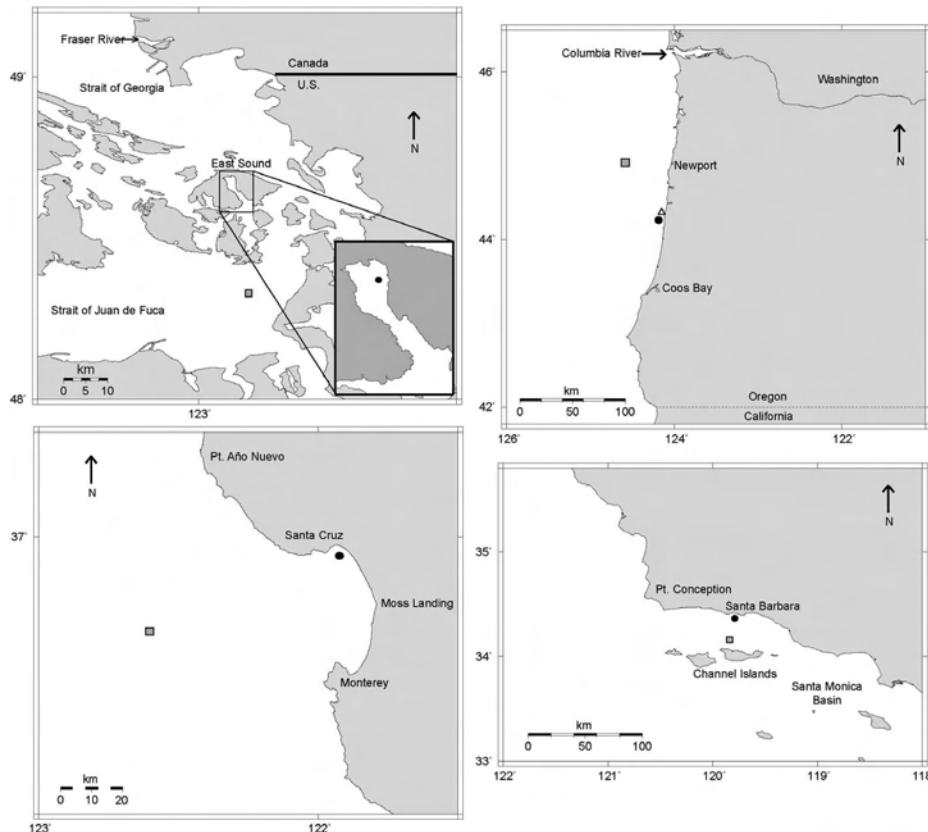


Fig. 1. Local maps of each survey site: East Sound, Washington; Cape Perpetua, Oregon; Monterey Bay, California; Santa Barbara, California. X-axis is longitude ($^{\circ}$ W), y-axis is latitude ($^{\circ}$ N). Black dots denote instrument deployment locations at each site; gray squares show location of NDBC buoy; the triangle in the Oregon panel denotes the location of the PISCO ADCP.

Materials and Methods

SITES

East Sound is a small fjord located at 48.682° N and 122.892° W in the San Juan Islands, Washington (Fig. 1). The average water depth is 30 m, and the Sound is approximately 13 km long and 2 km wide. A partial sill extends across the western side of the lower Sound at a depth of 12 m, while the eastern side of the lower Sound has a depth of ca. 40 m (McManus et al. 2003).

The Cape Perpetua site, at 44.250° N and 124.133° W, is located 3.3 km off the coast of Strawberry Hill, Oregon, 49 km south of Newport, Oregon, on a gently sloping shelf in 20 m of water (Fig. 1). The coastline here is fairly linear. From Newport to Florence, the continental shelf narrows from 27 to 10 km wide.

The Monterey Bay site was located at 36.937° N and 121.920° W. The Bay is an open embayment, measuring roughly 37 km along its north-south axis (i.e., across the mouth) and 19 km along its east-west axis (Breaker and Broenkow 1994). The Monterey Submarine Canyon, which runs along

the east-west axis, divides the Bay into northern and southern regions (Fig. 1).

The Santa Barbara study site was located in the Naples Reef region of the Santa Barbara Channel (SBC) at 34.405° N and 119.798° W, adjacent to the Pacific coast within the Southern California Bight (Fig. 1). The slope here is characterized by reefs, submarine canyons, and the SBC island complex.

INSTRUMENTATION

At each site at least one Tracor Acoustical Profiling Sensor (TAPS-6, BAE Systems) was deployed in an upward-looking mode. The TAPS-6 measures acoustical scattering at 6 frequencies: 265, 420, 700, 1,100, 1,800, and 3,000 kHz. These frequencies were selected because of their sensitivity to scattering from mesozooplankton (0.25 to 25 mm in length). The TAPS-6 collects profile with a vertical resolution of 12.5 cm (Holliday et al. 2003), and collects one profile every 1–3 min (see Table 1 for exact temporal resolution). The length of each TAPS deployment ranged from 1 to 10 wk.

In order to identify thin zooplankton layers from the TAPS data we developed a set of criteria to make

TABLE 1. Summary of instrumentation at the four survey sites.

	East Sound, Washington	Cape Perpetua, Oregon	Monterey Bay, California	Santa Barbara, California
Dates	June 5–August 12, 1998	August 23–September 2, 2002	August 6–September 6, 2002	May 6–May 28, 2003
Latitude, Longitude	48.650°N, 122.883°W	44.254°N, 124.127°W	36.934°N, 131.925°W	34.404°N, 119.785°W
Water depth (m)	21.5	20	20	20
Wind data source	NDBC SISW1	NDBC 46015	NDBC 46062	NDBC 46053
Tide data source	SeaBird Seagauge	Coos Bay tide predictor ¹	MBARI tide gauge ²	Santa Barbara tide predictor ¹
TAPS-6	3	1	1	1
Resolution	60 s, 12.5 cm	80 s, 12.5 cm	80 s, 12.5 cm	180 s, 12.5 cm
ADCP	RDI 300 kHz	RDI 600 kHz ³	Nortek 1,000 kHz	Nortek 1,000 kHz
Resolution	15 min, 1 m	2 min, 1 m	1 min, 0.5 m	2 min, 0.5 m
Thermistor chain	12 loggers	8 loggers	8 loggers	15 loggers
Height range	1.8–20.5 m	1.5–20 m	1.5–20 m	1–15 m
Sample rate	3 min ⁻¹	1 min ⁻¹	0.5 min ⁻¹	0.75 min ⁻¹

¹<http://tbone.biol.sc.edu/tide>²<http://www2.mbari.org/coletti/pagetide.cgi>³http://www.piscoweb.org/data/catalog/phys_ocean

our selection method objective and consistent. It is important to note that the application of these criteria is filtered through the spatial and temporal resolution of the TAPS data. The maximum scattering strength of the layer must exceed that of background levels by at least 7 dB. The thickness of the layer, defined as the difference between the maximum and minimum depths at which the layer scattering strength exceeds background levels by 5 dB, must be < 5 m (after Dekshenieks et al. 2001). This thin scattering feature must be continuous over time and vertical space, and must be present for at least 30 sequential profiles (the equivalent of 30 min). If the thin layer is absent for more than 10 sequential profiles (the equivalent of 10 min), we considered it disrupted.

Using this definition, we identified and manually traced each thin zooplankton layer using a 4-h long, time-depth visual rendering of the volume scattering strength from the 420 kHz frequency. This sampling frequency was chosen because, at all four sites, it best resolved the scattering by thin zooplankton layers against background scattering levels. Once a thin layer was identified using the criteria outlined above, the layer was digitally traced using MATLAB's *ginput* function, resulting in a time-and-depth vector pair that were subsequently concatenated for each entire thin layer. The mean thickness and height above seafloor for each layer was determined by averaging four equally spaced measurements of layer thickness and height, after McManus et al. (2005). It should be noted that because the near-surface acoustic data are often characterized by very high levels of scattering that may be due to waves and bubble injection, we did not include the high near-surface scattering region in our analyses.

We calculated the biovolume and sizes of the scatterers from volume scattering spectra measured

with the TAPS-6 using a nonnegative least squares inverse method and two forward scattering models: the truncated fluid sphere model and the Distorted-Wave, Born Approximation (DWBA) elongate model that used the shape of a mysid for its basic geometry. Biovolume is an analog of displacement volume, as used in conventional sampling with nets or pumps. The truncated fluid sphere model describes scattering due to small crustaceans (e.g., copepods; Costello et al. 1989), while the DWBA elongate model estimates the biovolume of elongate animals (e.g., mysids, euphausiids). The inverse code optimally apportions the energy in the acoustic scattering data for each selected time and depth interval into size classes chosen by the user (Holliday 1977; Medwin and Clay 1998; Holliday et al. 2003).

At each site we deployed a thermistor chain near the TAPS. These thermistor chains had varying number of loggers, with vertical separations that ranged from 1 to 2.5 m (Table 1). Current velocity measurements were obtained by bottom-mounted acoustic Doppler current profilers (ADCP) located near the TAPS at each site. For current velocity measurements at the Cape Perpetua site, we used ADCP data collected by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), a long-term ecological consortium funded by the David and Lucile Packard Foundation and the Gordon and Betty Moore Foundation.

For each site, hourly wind data were downloaded from the National Data Buoy Center (NDBC) website (<http://www.ndbc.noaa.gov>). A Seabird tide gauge collected tide data for East Sound. Monterey Bay tide data was downloaded from the Monterey Bay Aquarium Research Institute tide gauge at Moss Landing (<http://www2.mbari.org/coletti/pagetide.cgi>). Tide data for the Cape Perpetua and Santa Barbara sites were obtained from online tide predictors (Table 1).

TABLE 2. Thin zooplankton layer statistics.

Site	% Study days* layers were present	Average duration (h)	Average thickness (m)	Average height above seafloor (m)
East Sound, Washington	84	14.52	0.7	15.9
Cape Perpetua, Oregon	38	1.66	0.6	6.7
Monterey Bay, California	67	6.85	0.9	6.4
Santa Barbara, California	36	3.38	1.2	7.4

* Period's civil days (i.e., 24-h period, from midnight to midnight).

To examine water column stability relative to zooplankton thin layer structure, we calculated the Richardson number (Ri) for three of the four sites: Cape Perpetua, Monterey Bay, and Santa Barbara. Ri had already been calculated for our fourth site (East Sound) during June 10–26, 1998 using high resolution CTD profiles (McManus et al. 2003). A discussion of the McManus et al. (2003) Ri calculations, in relation to acoustic scattering from the East Sound data set is included in the discussion section.

Ri defines the relative importance of stabilization by vertical density stratification versus destabilization by vertical shear in horizontal velocity; it is generally accepted that regions of $Ri < 0.25$ are identified as mixing sites (Pinkel and Anderson 1997a,b). Ri was calculated as:

$$Ri = \frac{N^2}{S^2}$$

where N^2 is the squared Brunt Vaisala frequency, and S^2 is the squared shear calculated after Itsweire et al. (1989) where:

$$S^2 = \left(\frac{\partial U}{\partial z} \right)^2 + \left(\frac{\partial V}{\partial z} \right)^2$$

Density was computed by assuming a constant salinity at these three sites and using the equation of state (Pickard and Emery 2000). We specified a salinity value of 32.8 for the Cape Perpetua site (after Aguilar-Islas and Bruland 2006). The Columbia River outlet, located 110 km north of the study site, generally has low discharge in late summer-early fall (Neal 1972; Sherwood et al. 1990). At the latitude of the Cape Perpetua study site, the low-salinity Columbia River plume is found 50–100 km offshore (Landry et al. 1989). Based on values reported by Rosenfeld et al. (1994), we specified a constant salinity of 33.5 for Monterey Bay. Freshwater input into Monterey Bay during the summer and fall is minimal (Breaker and Broenkow 1994). Based on values reported by Dever (2001) a salinity value of 33.5 was specified for the Santa Barbara site. U.S. Geological Survey gauges on several rivers that flow into the SBC show that freshwater discharge into this

region was low (0–164 l s⁻¹; <http://waterdata.usgs.gov/>) during the study period.

Results

EAST SOUND

Thin layers of zooplankton were prominent and ubiquitous features throughout the 3-mo study at East Sound, with at least one thin layer present on 84% of the study period's civil days (i.e., 24-h periods, from midnight to midnight; Table 2 and Fig. 2). In total, 69 layers were observed. These layers were, on average, very thin (mean ~ 0.7 m) and had the longest duration of any layers observed at the four study sites, with the longest lasting layer persisting for 3 d, 20 h. On average, these thin layers were present in the upper mid-water column, but over the course of their duration they could exhibit significant variations in depth (between 5–10 m).

Over the 3-mo study period, winds were predominantly southerly, with periodic reversals that lasted 1–3 d (Fig. 2). Thin layers were present throughout the majority of the study, but there were seven instances when thin layers were absent from the upper water column for > 1 d. These layer absences followed southerly-to-northerly wind reversals and coincided with the resumption of strong (> 5 m s⁻¹) southerly winds. Five of the seven thin-layer gaps took place during spring tide, with tidal ranges > 4 m. These were also periods of enhanced current velocities along the north-south axis of the fjord during the periods of thin layer absence.

We used two forward models in an inverse calculation to compute biovolumes of scatterers over a range of size classes. The results of these calculations show that populations comprising the thin layers in East Sound were dominated by scatterers with the acoustical characteristics of a fluid sphere of ca. 10 mm, but occasionally a population of 10-mm elongate scatterers would also be present in the layer (Fig. 2). A large background biovolume of small (< 2 mm) fluid sphere scatterers was usually present throughout the water column, and a reduced biovolume of these same spherical scatterers was also sometimes present within the layer.

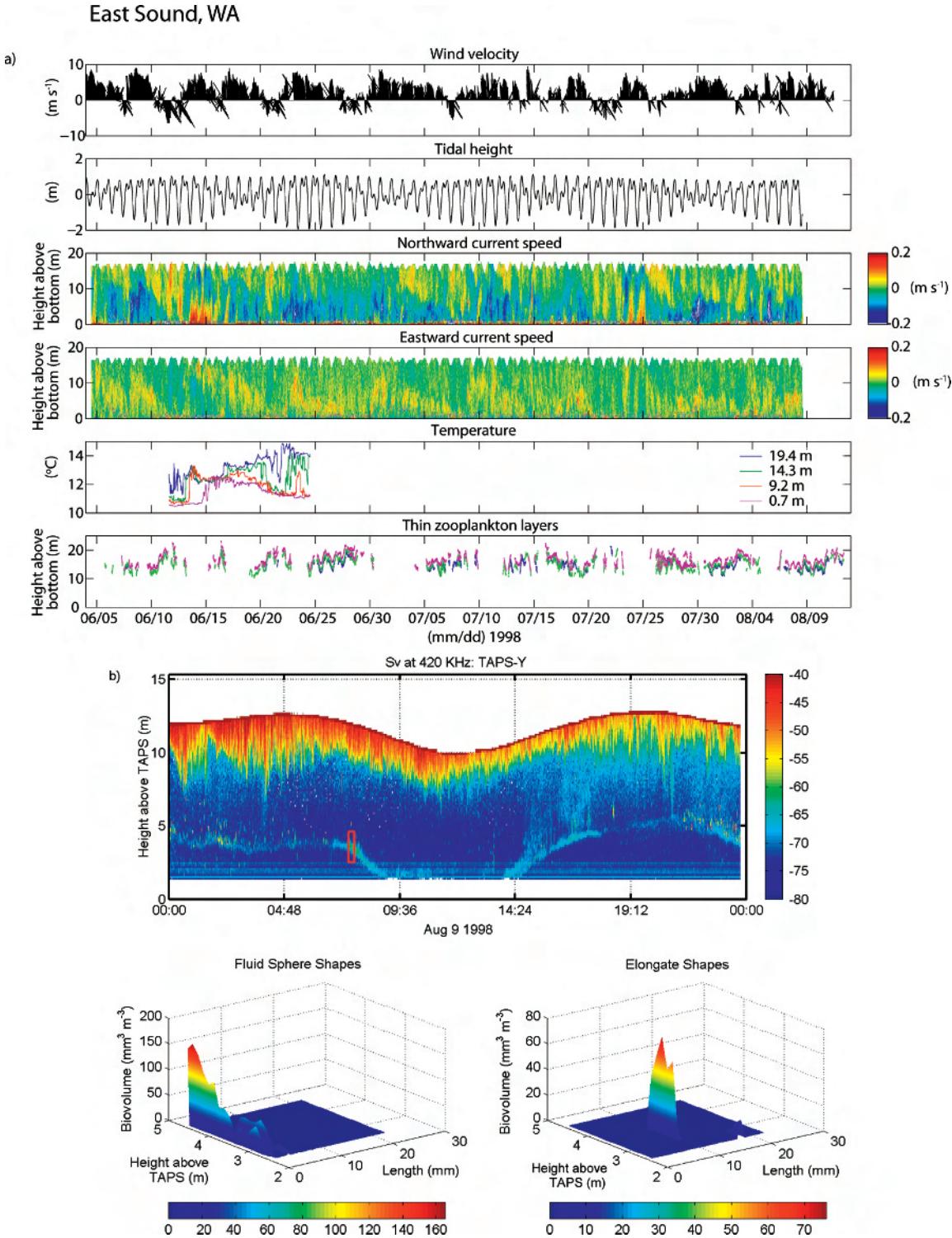


Fig. 2. East Sound, WA: a) time series of (i) wind velocity (m s^{-1}); (ii) tide height (m); (iii) and (iv) components of current velocity (m s^{-1}); (v) temperature ($^{\circ}\text{C}$) at certain heights above the bottom; (vi) thin zooplankton layers (blue = TAPS-X, green = TAPS-Y, pink = TAPS-Z) and regions where $\text{Ri} > 0.25$ (gray squares). b) Biovolume calculations with (i) acoustic profile from Tracor Acoustical Profiling Sensor where x-axis is time (hh:mm), y-axis is height above sensor (m) and colorbar indicates strength of scattering (dB; red is high scattering and blue is low scattering); box outlines the region of data used in the inverse calculations. Results from (ii) fluid sphere and (iii) elongate inverse model for a range of size classes. Please note the different scales of the z-axis.

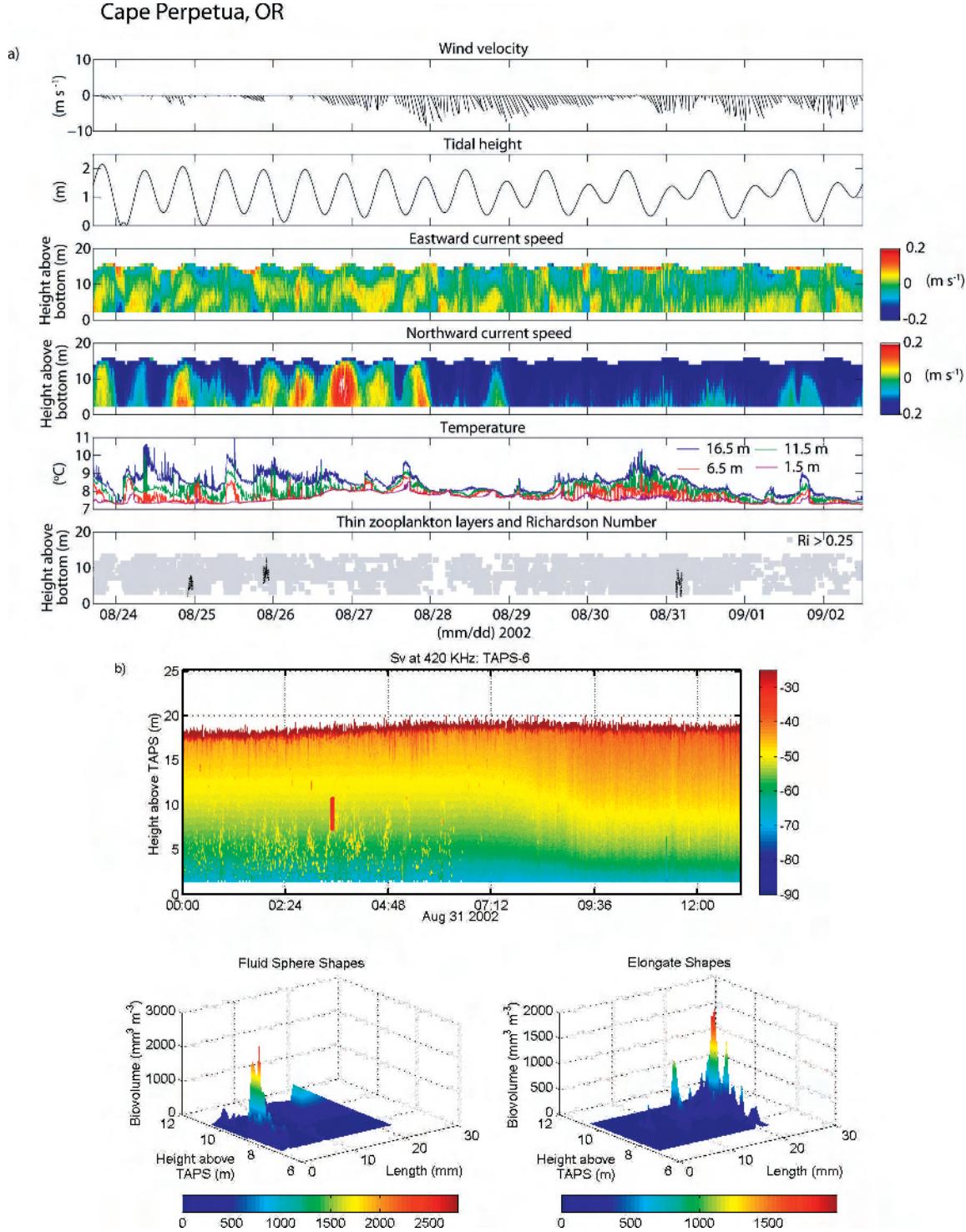


Fig. 3. As for Fig. 2, but for Cape Perpetua, OR. In a) (vi) thin zooplankton layers are indicated with black dots.

CAPE PERPETUA

During the Cape Perpetua study, thin layers were present on 38% of the study period's civil days

(Table 2). Three thin zooplankton layers were observed over the 8-d study period (Fig. 3). All three layers were exceptionally thin (average thickness ~ 0.6 m) and short-lived (< 2 h) (Table 2).

The acoustical data also showed that these layers were somewhat discontinuous over time (Fig. 3). All three thin layers exhibited large vertical depth changes (up to 3.5 m) and were located between the seafloor and mid-water depth.

The wind pattern at this site is predominantly northwesterly, with occasional wind reversals and cessations occurring every 5–14 d (Fig. 3). All three thin layers formed during low ($< 5 \text{ m s}^{-1}$) winds, increased thermal stratification, and coincided with the shift from ebb to flood tide. All three layers were in regions with $\text{Ri} > 0.25$. The temperature data show that the thin layers were associated with cold (7.5°C) bottom water, and even though large vertical displacements occurred in the isotherms when thin layers were present, there was generally no net change in their depth (i.e., isotherms were not tilted).

The first two layers occurred near the beginning of the study, separated only by 24 h (before midnight on August 24 and 25, respectively). They occurred during the transition from spring to neap tide (Fig. 3). During this time period, high ($> 0.15 \text{ m s}^{-1}$) northward current velocities were associated with the flood tide. August 24 and 25 were characterized by very low winds, noontime surface warming, and light ($2\text{--}3 \text{ m s}^{-1}$), northerly, afternoon sea breezes. The last thin layer observed (August 31) was separated from the first two layers by a 5-d period. This thin layer occurred during neap tide, a predominantly southward flow, and was also preceded by a day of very low (1 m s^{-1}) winds, elevated surface temperatures, and a more stable water column ($\text{Ri} > 0.25$). The 5-d period separating the third layer from the first two was characterized by increased wind velocities ($> 5 \text{ m s}^{-1}$), weak thermal stratification, and a less stable water column.

The inverse calculation results show that these three thin layers were composed of a variety of size classes and were both fluid sphere and elongate scatterers. All three layers contained elevated biovolumes of 6–8 mm fluid sphere scatterers and also 17 mm elongate scatters. Two of the layers also contained an elevated population of large, elongate (20 mm) and small, spherical (2 mm) scatterers (Fig. 3).

MONTEREY BAY

During the Monterey Bay study, thin layers were present on 67% of the study period's civil days (Table 2). Layers were generally long-lived (7 h) and on average 1 m thick. These thin layers exhibited rapid changes in depth (up to 7.3 m in 12.4 min), although their mean depth generally remained constant over their duration (Fig. 4).

Winds during this study were generally strong ($> 5 \text{ m s}^{-1}$) and northwesterly. There were two periods when the northwesterly winds reversed or lessened in strength (i.e., wind relaxation): August 11–17 and August 28–September 1. No acoustic data were collected during the first wind relaxation event due to a low battery. Ri values were > 0.25 throughout the entire study period (Fig. 4). All thin zooplankton layers were located in regions with $\text{Ri} > 0.25$.

At the start of this study, from August 6 to 9, there was a period during which numerous thin layers were present (Fig. 4). At least one thin layer was usually present, and occasionally two or more thin layers were evident simultaneously in the water column. These layers had very strong scattering intensities and exhibited large depth changes over short periods (up to 0.5 m min^{-1}). Over this same time period, it was spring tide, winds were strong ($7\text{--}10 \text{ m s}^{-1}$), thermal stratification increased, and along-shore current velocities were high ($> 0.1 \text{ m s}^{-1}$). This time interval was followed by neap tide and the first wind relaxation event, when wind velocities decreased to $< 3 \text{ m s}^{-1}$. On August 17, northwesterly wind velocities increased to $5\text{--}7 \text{ m s}^{-1}$ and the tide transitioned to the spring cycle, but thermal stratification was somewhat decreased. From August 17–28, winds steadily increased, the tide went from spring to neap, and thermal stratification decreased further. During this same time, thin zooplankton layers occurred approximately every other day at mid-water depths, and their formation usually coincided with the transition from ebb to flood tide. These layers were located in regions of reduced flow, between two oppositely moving water masses.

On August 28, the winds reversed from northwesterly to southerly (Fig. 4). This wind reversal was followed by a 2.5-d absence of thin layers. Starting August 30, as thermal stratification began to increase, thin layers began to form again. From August 30 to September 1, even though winds remained weak and southerly, several thin layers formed. These layers were generally deeper and exhibited less vertical displacement than the layers observed previously during this study.

The inverse calculation revealed that the thin layers were primarily composed of two size classes of elongate scatterers: 15 and 20 mm (Fig. 4). Occasionally the layers also contained populations of 17-mm, elongate scatterers. These layers were usually surrounded by a population of small (2 mm) fluid sphere scatterers. We also ran the inverse calculation on the August 30 layer, which formed during the second wind relaxation event, and found that this layer was composed of larger (22 mm) elongate scatterers and also larger fluid-sphere scatterers (10 mm), with both populations present in

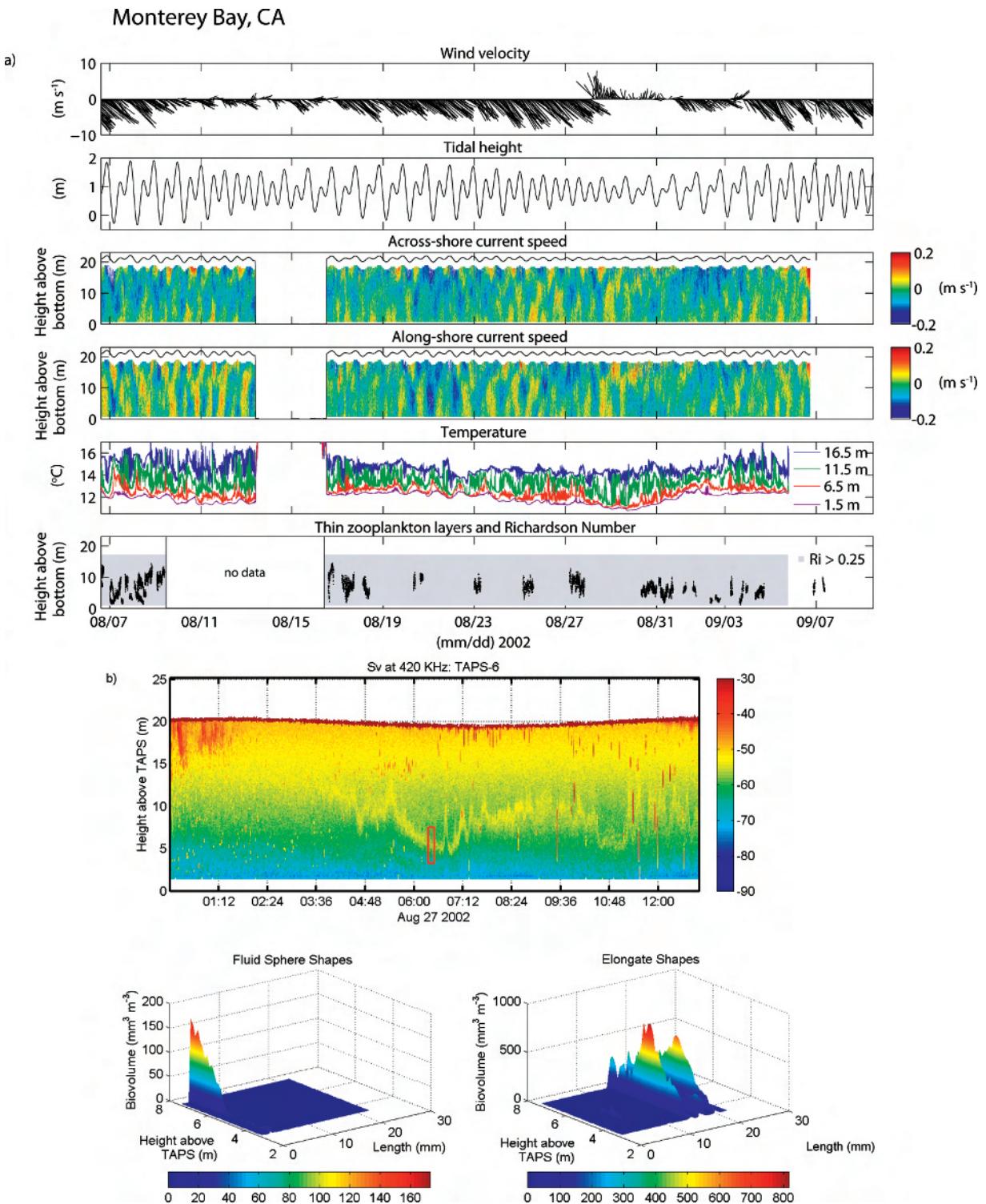


Fig. 4. As for Fig. 2, but for Monterey Bay, CA. For a): (iii) red = northeast (+), (iv) red = northwest (+); and in (vi) thin zooplankton layers are indicated with black dots.

relatively low biovolumes (170 and 20 mm³ m⁻³, respectively).

SANTA BARBARA

During the Santa Barbara study, thin layers were observed on 36% of the study period's civil days (Table 2). Over a 16-d period of predominantly strong ($> 10 \text{ m s}^{-1}$) northwesterly winds, 13 thin layers of zooplankton were observed at this site (Fig. 5). The majority of these layers were located between 3–10 m above the seafloor. Compared to the other survey sites, these layers were on average relatively short-lived (3.38 h) and thick (1.2 m; Table 2).

One thin layer was observed at the start of this study (May 7). On this day the water column was generally warm (12–15°C), stable ($\text{Ri} > 0.25$), and thermally stratified, with moderate ($< 0.1 \text{ m s}^{-1}$) tidally-driven currents (Fig. 5). No thin layers were present between May 8–13. During May 8–13, there were fewer regions of the water column with $\text{Ri} > 0.25$. On May 8, eastward current velocities throughout the water column increased to 0.2–0.25 m s⁻¹, and on May 9, a cold (9°C), less-thermally-stratified water mass was advected into the study area. On May 11, the alongshore velocity reversed to a westward flow. By May 13, surface waters began to warm, and thin layers formed towards the end of that day near the surface. Over the remainder of the study period, as the water column stratification increased, thin layers formed at greater depths. The thin zooplankton layers observed in the Santa Barbara region were primarily associated with the 12°C isotherm. The majority of layers formed at the transition between ebb and flood tide and dissipated before the start of the next ebb. Nearly all layers were located either in the layer of no motion or in regions of low current velocity, located just above a moderate (0.05 m s⁻¹) eastward bottom current. All thin zooplankton layers observed during the Santa Barbara study were in regions of the water column with $\text{Ri} > 0.25$.

The inverse calculation indicates that these layers were primarily composed of 17-mm, elongate scatterers, but occasionally also contained large, 22-mm elongate scatterers (Fig. 5). Only one layer contained fluid sphere scatterers (size $\sim 2 \text{ mm}$). The water column contained large biovolumes of 20-mm elongate scatterers, but these particular scatterers did not make up the thin layers. In fact, the scattering from the 20-mm elongates was usually at a minimum at the location of the layer.

Discussion

Thin layers of zooplankton were common features at all four sites in our survey. At each site there

were extended periods ($> 1 \text{ d}$) when thin zooplankton layers were absent from the water column. These absences coincided with a change in the predominant physical regime, usually precipitated by a change in the wind pattern.

At the East Sound site, the intermittent absences of thin zooplankton layers from the upper water column were most likely caused by influxes of low-density water into the fjord. Rines et al. (2002) observed the forcing of thin phytoplankton layers to greater depth after a northerly wind event caused the advection of a low-salinity lens into East Sound. Dekshenieks et al. (2001) also reported the deepening of thin layers of phytoplankton after a low-salinity plume moved into the fjord. These freshwater plumes originate from the Fraser River, located 20 km north of East Sound (Fig. 1).

Throughout the study in East Sound, southerly winds predominated (80% of the time); there were several wind reversals (Fig. 2). These reversals are known to enhance the advection of lower-salinity water from the Fraser River into the San Juan Islands region. At the end of each reversal, the resumption of southerly winds pushed the low-salinity water into the south-facing East Sound. Rines et al. (2002) reported that these freshwater influxes resulted in a depression of the pycnocline in the fjord. Five of the seven thin-layer gaps observed at this site took place during spring tides, with tidal ranges $> 4 \text{ m}$, which probably contributed even further to forcing the lower-density water into the fjord.

McManus et al. (2003) performed a focused analysis of both phytoplankton and zooplankton thin layers over a 48-h period during the East Sound study. Their investigation included observations of hydrographic conditions for the 2-wk period leading up to the 48-h study. The authors report that from June 13 to 15, a low-density water mass was advected into the fjord, causing a deepening of the pycnocline to within 3 m of the bottom. This low-density water mass exhibited intense vertical mixing and had a calculated $\text{Ri} < 0.25$ (McManus et al. 2003). The influx of this well-mixed water mass also coincided with an absence of thin zooplankton layers. After this event, the next long-lived ($> 24 \text{ h}$) zooplankton thin layer occurred from June 18 to 23. Over this same time period, McManus et al. (2003) reported a gradually strengthening and shoaling of the pycnocline and the persistence of a thin layer of phytoplankton in the northern part of the fjord.

The observations by McManus et al. (2003) support our hypothesis that the wind reversals in this region caused the advection of low density, well-mixed water into East Sound, which in turn resulted in an absence of thin zooplankton layers. It is unclear whether the thin zooplankton layers in East

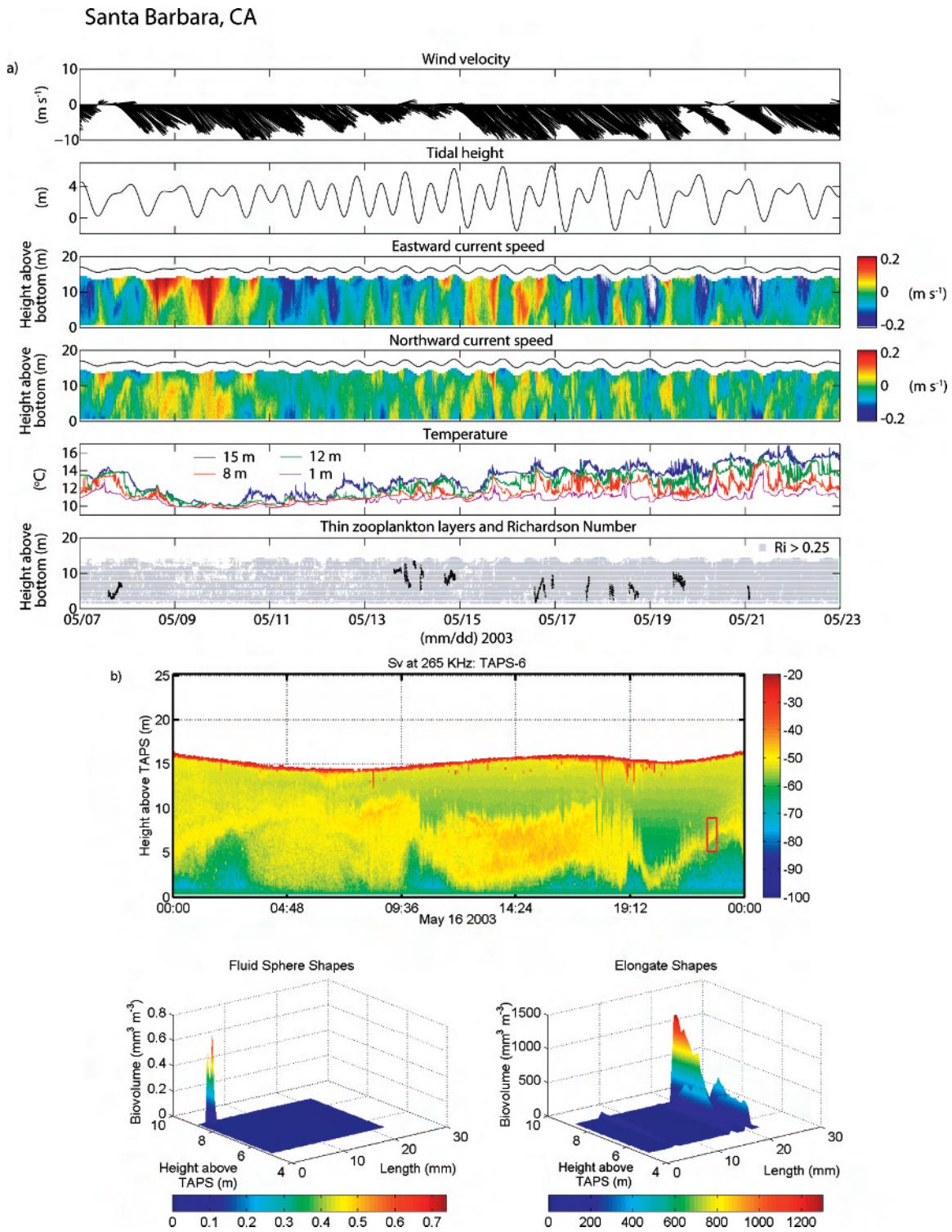


Fig. 5. As for Fig. 2, but for Santa Barbara, CA. In a) (vi) thin zooplankton layers are indicated with black dots.

Sound are responding to the physical forcing directly or to the displacement of phytoplankton layers by the vertical movement of the pycnocline.

At the Cape Perpetua site, increased upwelling of low-oxygen water likely played a key role in the decreased prevalence of thin zooplankton layers. Grantham et al. (2004) observed a low-oxygen event along the Oregon coast during July 9–September 7, 2002. This low-oxygen event resulted from the combination of strong nearshore stratification and the upwelling of water depleted in dissolved oxygen (concentrations between 0.21–1.57 ml l⁻¹) onto the continental shelf (Grantham et al. 2004). The outcome was a widespread hypoxia event that extended from 2 to 5 km offshore to within 700 m of the surf break (Grantham et al. 2004). This low-oxygen event caused massive mortalities of fish and invertebrates throughout the region.

The 3 thin zooplankton layers observed at the Cape Perpetua site (August 24, 25, and 31) occurred during decreased wind forcing, increased thermal stratification, and water column stability, and coincided with the shift from ebb to flood tide (Fig. 3). The absence of strong upwelling-favorable winds at this site may have reduced the influx of low-oxygen water onto the shelf, increased thermal stratification, and as a result, allowed formation of zooplankton thin layers.

At the transition from ebb to flood tide, strong tidal bores propagate onto the Oregon shelf (Stanton and Ostrovsky 1998). The shoreward propagation of these tidal bores is typically preceded by packets of nonlinear, internal solitons (Stanton and Ostrovsky 1998; Klymak and Moum 2003). During the shift from ebb to flood tide, temperature data indicate the presence of internal waves (Fig. 3). These onshore-moving internal waves were most likely at the leading edge of an internal tidal bore that has been shown to transport zooplankton across-isobath (Pineda 1999). The increased thermal stratification and isopycnal compression that characterized the water column during these periods created an environment suitable for the establishment of thin zooplankton layers. The first two thin layers, on August 24 and 25, were separated from the third by a 5-d period of increased upwelling-favorable winds. These winds likely enhanced the transport of hypoxic water onto the shelf, and that, combined with decreased thermal stratification, created an absence of thin zooplankton layers in the study region. The third layer formed on August 31, when the wind velocity decreased, changing from northwesterly to a mix of northerly and northeasterly, and thermal stratification increased.

Similar to the Oregon coast, the Monterey Bay region is also characterized as an upwelling-relaxation system that is driven by seasonal wind

patterns along the coast. Unlike the Oregon site, Monterey Bay is a semi-enclosed bay, and our sampling site here was located behind a headland, in an area sometimes classified as an upwelling shadow (Graham 1993; Graham and Largier 1997). When upwelling-favorable winds exist, cool, nutrient-rich water is upwelled to the surface near Point Año Nuevo (Fig. 1) and cyclonic circulation in the upper 25 m of the water column develops (Breaker and Broenkow 1994; Rosenfeld et al. 1994). The cool upwelled water moves equatorward and bifurcates, with one branch extending across the mouth of the bay and the other extending from the Point Año Nuevo upwelling center to Moss Landing (Fig. 1), creating a front between the cold, nutrient-rich water and the warmer inshore water (Rosenfeld et al. 1994). An upwelling shadow is formed in the northern part of the bay, approximately 6.5 km from shore, inshore from the front that separates the upwelled water from the warmer, nearshore waters by Santa Cruz (Graham 1993). Increased thermal input and longer residence times for the water in the region combine to make this a strongly stratified region during upwelling periods (Graham and Largier 1997).

When the upwelling winds reverse or weaken, offshore surface water is advected towards the coast, resulting in a general warming of the water column (Rosenfeld et al. 1994). The winds during our survey in Monterey Bay (August 6–September 8, 2002) were primarily upwelling favorable (northwesterly, > 5 m s⁻¹). On August 28, the winds reversed and remained weak and southerly until September 1. For 10 d prior to the wind reversal, thin layers were present at mid-water column depth approximately every other day. After the wind reversal on August 28, no thin layers were present for 2.5 d. As the relaxation event evolved, thermal stratification increased, and thin layers were able to form again on August 30, even though the winds were still relaxation-favorable. At no time was the water column ever unstable, as indicated by the calculated Ri values (cf., Fig. 4).

The northwesterly winds that dominate the coast of California detach from the coastline at Point Conception, where the coastline heads nearly due east-west, forming the northern boundary of the SBC, our fourth site (Fig. 1). The flow within the SBC is generally cyclonic, with westward flow along the northern boundary, where the Santa Barbara site was located. The winds inside the SBC are generally light and variable (Winant and Dorman 1997; Harms and Winant 1998; Oey et al. 2001), and as a result, flows inside the Channel tend to be governed by local gradients in sea level (Lentz and Winant 1986; Hickey 1993). This cyclonic flow pattern exists through a wide range of wind and

alongshore pressure gradient forcing combinations (Harms and Winant 1998). When the prevailing northwesterly winds north of Point Conception coincide with equator-ward winds inside and south of the SBC, unidirectional flow through the channel can result (Harms and Winant 1998; Oey et al. 2001; Winant et al. 2003). This scenario is most common during the spring months of March to May (Oey et al. 2001; Winant et al. 2003).

At the Santa Barbara site, winds on May 7 were primarily strong and northwesterly. Sea-surface temperatures were 14°C, the water column had moderate thermal stratification and calculated Ri values > 0.25 (Fig. 5). On this same day, AVHRR satellite imagery from the National Oceanic and Atmospheric Administration CoastWatch revealed a cold (9°C) water mass present along the coast around and north of Point Conception (http://www.ndbc.noaa.gov/download_data.php?filename=46025h2003.txt.gz&dir=data/historical/stdmet/). This cold water was most likely upwelled by the strong northwesterly winds present along the central California coast during this time period. On May 8, wind data from the NDBC Santa Monica Buoy (#46025), located 57 km southeast of the SBC, showed an increase in the northwesterly wind magnitude (from 5 to $> 13 \text{ m s}^{-1}$; data not shown). On this same day, the satellite data showed that the cold water mass had entered the western edge of the Santa Barbara channel, and by May 9, it filled the entire region. The strong easterly currents associated with the advection of this cold water mass into the SBC were observed at the Santa Barbara study site (Fig. 5). The advection of this cold water mass into the channel, combined with very strong easterly currents, caused extensive cooling and breakdown of thermal stratification at the Santa Barbara study site. This cold water mass had decreased stability ($Ri < 0.25$). No thin zooplankton layers were observed during this period. By May 11, the NDBC Santa Monica winds had decreased in magnitude to $< 4 \text{ m s}^{-1}$. On this same day, winds at the study site were still very strong ($> 10 \text{ m s}^{-1}$) and out of the northwest, but presumably because the winds south of the SBC had returned to a weak, variable pattern, the eastward alongshore current velocity reversed, and by May 13, the water column began to thermally restratify, stabilize, and thin layers reappeared.

Three of the four sites, East Sound, Cape Perpetua, and Monterey Bay, showed evidence of internal waves modifying the depth of thin zooplankton layers. At the Cape Perpetua and Monterey Bay sites, even though these internal waves caused changes in depth layer of up to 8 m, at no time did these internal waves lead to the dispersion of the layers (McManus et al. 2005). For East Sound,

McManus et al. (2003) suggested a biological mechanism involving a spatially patchy migratory behavior bringing mysids to the pycnocline, resulting in a thin layer of acoustic scattering. The thin layers of mesozooplankton observed by McManus et al. (2003) were dispersed temporarily when current shear and turbulence were enhanced due to the passage of solitons (solitary internal waves). These dispersal events were brief and the thin mesozooplankton layers rapidly reformed due to behavior. This suggests that mesozooplankton swimming speeds in East Sound are high enough to overcome the average vertical mixing intensity in the water column (McManus et al. 2003). These mesozooplankton layers were temporarily diffused only when turbulence levels exceeded the speed of vertical migration (McManus et al. 2003).

Across all four of these study sites, a change in the predominant local physical regime, usually preceded by a change in the regional wind pattern, resulted in a change in the distribution of thin zooplankton layers. We speculate that at the Cape Perpetua and Santa Barbara sites, the change in wind patterns resulted in a breakdown in stratification and increased instabilities in the water column, which in turn caused an absence of thin zooplankton layers. While this phenomenon remained consistent between these two sites, evidence suggests that the sequence of events leading to the breakdown of thermal stratification varied. In the case of East Sound, the advection of a low-salinity lens of surface water into the fjord, forced by a change in wind patterns, caused a deepening of the pycnocline and, subsequently, an absence of thin zooplankton layers from the upper water column. At the Monterey Bay site, the wind reversal that coincided with a prolonged absence of thin zooplankton layers did not result in calculated Ri values < 0.25 . Even though the water column remained stable and well stratified, the transition between upwelling and relaxation conditions most likely resulted in the movement of warm, nutrient-poor offshore water into the inner bay. This in turn may have changed the distribution of zooplankton layers and the zooplankton assemblage in the nearshore waters.

In order to make a first-order prediction about the presence of thin layers in a coastal environment, we must first look at the regional wind patterns and determine how they affect local stratification and circulation. While this information may help us predict when thin layers of zooplankton will not be present, based on the results of this study we cannot yet definitively predict if thin layers will be present in an environment. We can evaluate whether local physical conditions are conducive to supporting thin-layer structures.

While our results indicate that there is a strong apparent relationship between thin layers of zooplankton and mesoscale, wind-driven physical processes, it is unclear from this data set whether this relationship is driven by the physical processes themselves or by how these wind-driven events affected the phytoplankton assemblage and its subsequent distribution. Past research established that there are strong statistical relationships between thin phytoplankton layers and physical properties of the water column; specifically, a stably stratified water column is required for these types of layers to form (Dekshenieks et al. 2001). McManus et al. (2003) suggested that the thin layers of zooplankton observed during the East Sound study were formed by a spatially patchy migratory behavior that resulted in zooplankton congregating at the pycnocline, where the greatest abundance of marine snow and phytoplankton occurred. A similar migratory behavior may have been responsible for the formation of the observed thin zooplankton layers at our four study sites. The wind driven events that resulted in a breakdown of thermal stratification at two of the four sites (Cape Perpetua and Santa Barbara) may have prevented the formation of thin phytoplankton layers, which in turn discouraged the migratory behavior responsible for zooplankton layer development. At East Sound the displacement of the thin phytoplankton layers may have also caused the migration of thin zooplankton layers out of the upper water column.

A wide range of zooplankton behaviors can be inferred from the acoustical scattering data. The zooplankton at all four sites exhibited diel migration patterns. At East Sound and Monterey Bay, thin layers would form throughout the day, while often at night a broad and intense scattering patch would form at mid depth. At the Cape Perpetua site, zooplankton appeared to come out of the seabed at night, after the strong daytime seabreeze had subsided. In the acoustical scattering data from Santa Barbara, there was not a well-defined diel pattern in zooplankton migration, but around midnight there was usually a distinct change in whatever type of zooplankton distribution was present in the water column. In addition to diel migration, there were many cases of vertical movement through the water column, usually by zooplankton patches and layers moving from near the seabed or surface to mid depth. The rates of these vertical migrations ranged between 0.02 and 1 cm s⁻¹. At the Monterey Bay site, when two or more thin layers of zooplankton were present simultaneously, sometimes these layers would converge and diverge, though it is not clear if the physical processes or the behavior of the zooplankton was driving these layer dynamics. Other studies

have also observed zooplankton responding to biological and chemical layers in the water column. Alldredge et al. (2002) reported zooplankton avoidance behavior in response to the presence of a dense thin layer of marine snow, and Holliday et al. (2003) observed a thin layer of zooplankton vertically bounded by the pycnocline below and an oxycline and phytoplankton layer above.

The inverse calculations reveal that the zooplankton comprising the thin layers at each of these four sites varied in shape and size. At East Sound, Monterey Bay, and Santa Barbara, thin zooplankton layers were generally composed of organisms of similar size classes. These layers were often surrounded by populations of smaller-sized scatterers that were noticeably absent from the thin layer region. The decreased biovolume of smaller scatterers from the layers may be due to grazing by the larger zooplankton within the layers or avoidance by the smaller scatterers. Cape Perpetua was the only site where both smaller-sized and larger-sized scatterers were simultaneously present in the thin layer. Because we were unable to collect a sufficient number of direct water samples, it is not possible for us to speculate on the species of these scatterers, but certain size classes in the two models can be attributed to different types of zooplankton and micronekton. In general, fluid sphere scatterers of 2 mm or less are copepods or nauplii, and fluid sphere scatterers in the 6–8 mm size class can be fish eggs, crab megalopae, or ostracods. Elongate scatterers in the 6–10 mm range are typically adult amphipods or adult krill. A variety of adult crustaceans (e.g., mysids and euphausiids) can account for elongate scatterers between 10–22 mm.

Thin layers of zooplankton were common features at all four sites in our survey, indicating that these structures are ubiquitous in the coastal ocean. A simultaneous understanding of local zooplankton and micronekton populations and physical processes across a range of scales is needed to determine which environments will support the formation of thin layers.

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