

A critical scale in plankton aggregations across coastal ecosystems

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[1] We examined the characteristics of biological patches at four different locations to assess the relationship of patch vertical scale, amplitude, and persistence. In contrast to patches of larger animals, we found that the majority of coherent aggregations of plankton at each site were vertically compressed, with most smaller than 5 m vertically. A subset of these layers, often referred to as “thin layers” in the literature, was distinguished by high intensity and greater persistence but not thickness. Our results suggest that ~5 m is a critical vertical scale below which aggregations of plankton frequently occur, pointing toward a controlling characteristic or a process common to a variety of regions and organism types. Given the commonality of this scale, insights into physical-biological dynamics gleaned from previous studies of the most intense and persistent of these patches may be applied more generally, leading to a better understanding of the ecosystem effects of heterogeneous plankton distributions. **Citation:** Benoit-Bird, K. J., E. L. Shroyer, and M. A. McManus (2013), A critical scale in plankton aggregations across coastal ecosystems, *Geophys. Res. Lett.*, 40, 3968–3974, doi:10.1002/grl.50747.

1. Introduction

[2] Highly concentrated, vertically compressed but horizontally coherent patches of oceanic organisms, referred to as “thin layers,” have been identified in a variety of coastal [Cheriton *et al.*, 2007] and oceanic [Churnside and Donaghay, 2009; Hodges and Fratantoni, 2009] ecosystems as new sampling capabilities have developed over the past several decades [Deksheniaks *et al.*, 2001; Sullivan *et al.*, 2010b]. This fine-scale patchiness of marine organisms is increasingly recognized as a signature of physical, chemical, and biological processes in the environment [Valiela, 1995]. Accordingly, these thin layers of planktonic organisms have motivated many studies that focus on the interaction between small-scale physical and biological processes (see a review in Durham and Stocker [2012]).

[3] There is increasing evidence that thin layers of plankton have significant impacts on organisms located within and outside of layers. Thin layers provide one solution to the survival paradox predicted for ocean predators based on averaged food concentrations [Lasker, 1975], altering behavior [Benoit-Bird, 2009; Clay *et al.*, 2004], foraging interactions [Benoit-Bird *et al.*, 2010; Benoit-Bird *et al.*, 2009],

and even the way pelagic ecosystems are structured [Benoit-Bird and McManus, 2012]. However, despite the ubiquity of these intense layered features, determining their role in the ecosystem is challenging. One step toward understanding their role in ecosystem processes is to assess the relationship of these features to plankton aggregations more generally. Using data acquired during independent studies designed to look at small-scale physical and/or biological phenomena in four different coastal habitats, we sought to determine how thin layers are distinguished from plankton aggregations more generally. Previous studies use a variety of criteria to identify thin layers; most require that a thin layer (1) persists over time or space, (2) be thinner than some maximum, and (3) exhibits a concentration above a set value relative to the background [Deksheniaks *et al.*, 2001; Sullivan *et al.*, 2010b]. Here we relaxed restrictions on the intensity and thickness (i.e., the vertical extent) of detected layers to understand if and how coherent plankton layers differ from thin layers.

2. Methods

[4] To examine the characteristics of plankton aggregations across a range of scales, we chose two common metrics that are useful as proxies of relative phytoplankton and animal (zooplankton and micronekton) concentrations, fluorescence and acoustic scattering, respectively. We examined data from four coastal sites to look for common traits across widely different habitats (Table 1). Data were collected during a number of independent field programs. In all cases, fluorescence data were collected using calibrated instruments mounted on a profiler that was lowered slowly through the water column using methods that decoupled the sampling platform from ship motion to provide a vertical sampling resolution of 2–10 cm. Acoustic backscattering data were collected from calibrated, shipboard, and scientific echo sounders. Fluorescence and multifrequency acoustic scattering data were collected synoptically during two of the studies: Monterey Bay as part of the 2005 Layered Organization in the Coastal Ocean experiment (detailed in Benoit-Bird *et al.* [2009]) and Oahu, Hawaii (methods in Benoit-Bird *et al.* [2008]). On the shelf and slope of New Jersey, fluorescence data were collected along with single-frequency acoustic scattering (tuned for the identification of zooplankton) as part of the Shallow Water 2006 experiment (detailed in Shroyer *et al.* [2011] and Tang *et al.* [2007]). This sampling overlapped in space and time with additional acoustic sampling from a separate vessel using multiple frequencies, which allowed the identification of both zooplankton and micronekton with identical sampling methods as those from Monterey Bay. Finally, off the Oregon coast (study described in Cheriton *et al.* [2007]), fluorescence (methods follow Cowles *et al.* [1998]) and multifrequency acoustic samplings (using the same methods

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Table 1. Summary of the Four Sites in the Study

| | New Jersey | Oregon | Monterey | Hawaii |
|---|---|---|--|--|
| Fieldwork methods | <i>Shroyer et al.</i> [2011]; <i>Tang et al.</i> [2007] | <i>Cheriton et al.</i> [2007]; <i>Cowles et al.</i> [1998] | <i>Benoit-Bird et al.</i> [2009] | <i>Benoit-Bird et al.</i> [2008] |
| Forcing processes identified in previous thin layer studies | No thin layer studies from this habitat have been published | Locally reduced mixing, high stratification ^{ab} | Shear ^c ; Grazing ^{de} ; Vertical migration ^f ; Mixing ^g | Thermal stratification ^h ; Advection of resources and organisms by internal tides ⁱ |
| Physical features during study | Sharp shelf break front modulated by winds and tides ^{j,k} | Upwelling driven coastal circulation ^l | Upwelling modulated by a wind shadow, low salinity intrusions, and the California Current ^m | Diurnal heating and winds and internal tides modulating a generally well mixed water column ^{h,i} |
| Site climate | Temperate | Temperate, variable productivity | Temperate, productive | Subtropical, oligotrophic |
| Topography of site | Wide continental shelf | Narrow continental shelf | Coastal embayment | Oceanic island with narrow shelf and steep slope |
| Water depth of measurements (m) | 25–500 | 25–500 | 20–200 | 20–200 |
| Mean/Median stratification (N, 1/s) | 0.021/0.012 | 0.018/0.015 | 0.013/0.011 | 0.007/0.006 |
| Amplitude of M2/K1 tide near shelf break ⁿ | 0.4 m/0.1 m | 0.8 m/0.4 m | 0.5 m/0.35 m | 0.1 m/0.15 m |
| Winds | Variable direction, average ~3 m/s, maximum 7 m/s | Northerly ~2.5 m/s | Northwesterly, ~5 m/s with relaxations every 10–14 days | Diurnal northeasterly trade winds averaging ~2.5 m/s |

^a*Cheriton et al.* [2007].

^b*Cowles et al.* [1998].

^c*Ryan et al.* [2008].

^d*Benoit-Bird* [2009].

^e*Benoit-Bird et al.* [2009].

^f*Sullivan et al.* [2010a].

^g*Steinback et al.* [2010].

^h*McManus et al.* [2012].

ⁱ*Sevadjian et al.* [2012].

^j*Lenz* [2008].

^k*Shroyer et al.* [2011].

^l*Hickey* [1998].

^m*Steinback et al.* [2010].

ⁿ*Egbert and Erofeeva* [2002].

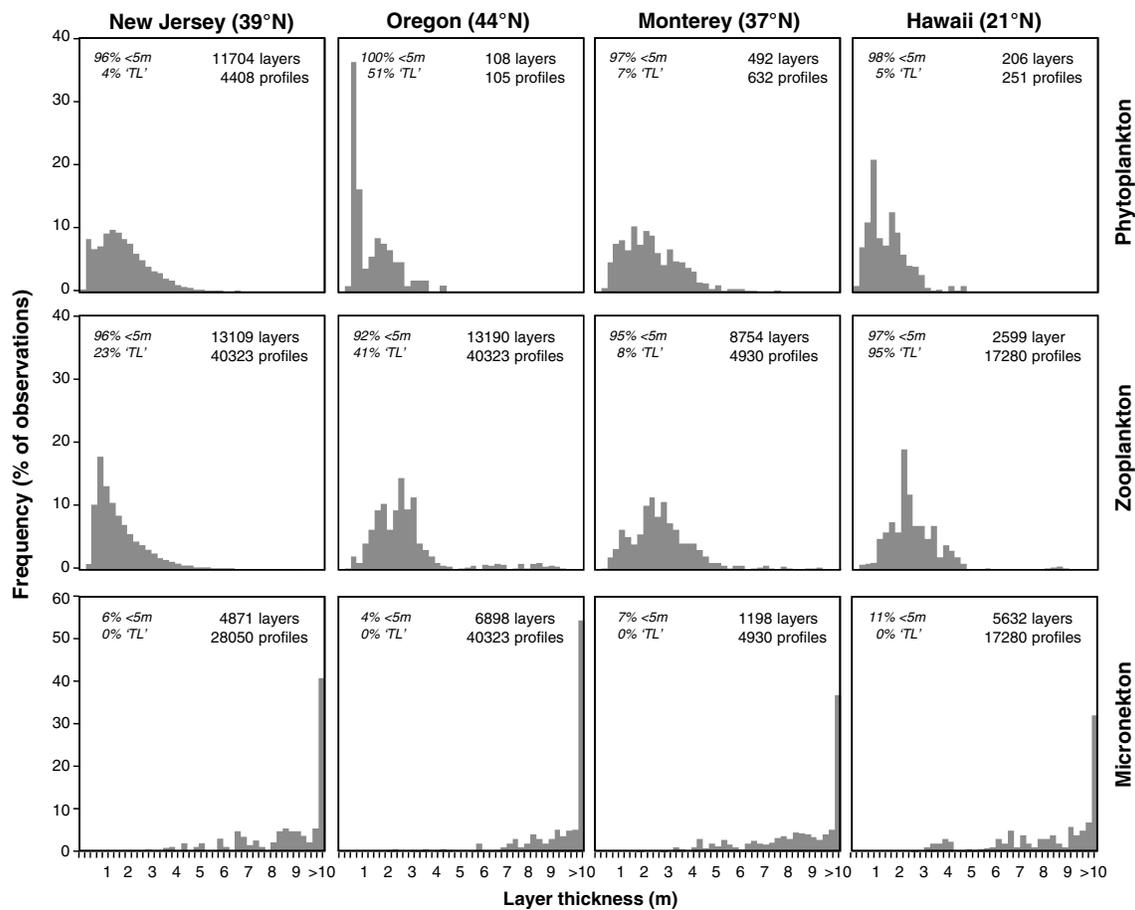


Figure 1. Distribution of layer thickness for each of three organism types measured at four sites. The number of profiles sampled at each of four sites and the number of layers of each type detected as well as the percentage of identified layers <5 m in thickness and those meeting the criteria for classification as thin layers [Dekshenieks *et al.*, 2001] are indicated in each panel.

used in Monterey Bay) were conducted as part of two independent programs in the same area separated by 5 years. Comparisons between layer types and locations should recognize differences in experimental designs and concurrence of measurements. However, utilizing a large and varied data set allows us to examine how layers composed of different types of organisms (phytoplankton, mesozooplankton, and micronekton) are related to one another within individual locations, as well as to identify commonalities between plankton aggregations.

[5] We used chlorophyll fluorescence as a proxy for relative phytoplankton concentration. Acoustic scattering was used as a proxy for relative animal concentrations. When multifrequency acoustic data were available, they were used to classify targets likely to be zooplankton from those likely to be fish using the observed frequency response in volume backscatter after removing resolvable single targets following *Benoit-Bird et al.* [2009]. Once classified, 120 kHz acoustic scattering was used as a proxy for zooplankton concentration and 38 kHz acoustic scattering as a proxy for micronektonic fish. When only 120 kHz acoustic scattering was available, it was visually scrutinized for features likely to be fish before integration for use as a proxy for zooplankton.

[6] Fluorometer data were averaged into 10 cm depth bins and acoustic data were integrated into 20 cm depth by 30 s

time bins before detection of layers. For each of these averaged “profiles” of acoustic or fluorometric data, a running 15 m median was calculated to define the background. This limited layer detection to 5 m from the surface to 5 m above the bottom of the profile. After removal of the background, “peaks” in fluorescence or acoustic scattering were identified using three criteria: Each peak (1) was made up of at least three values exceeding 1.1 times the 10% trimmed mean of the entire water column, (2) was a local maxima, adjacent to lower values (i.e., a negative/positive slope on the upper/lower edge), and (3) had a maximum intensity at least 1.5 times the standard deviation of the measure in the surrounding 5 m. No more than one peak was allowed per meter; in the event of multiple peaks, the highest value was selected for further scrutiny. These parameters were intended to identify coherent features with as lenient an amplitude criterion as possible. Our detection approach resulted in an average of 1%–2% of all data points being classified as peaks. To be classified as a “detected layer,” a category that encompasses all layers, including thin layers, peaks must be identified in at least two profiles with no more than a depth of 3 m separating peaks; just under 1% of all data points were identified as “layers.” We explored the effects of our selection criteria on the identified vertical scale of identified layers by changing the maximum intensity criteria (1.25 \times , 1.5 \times , 2 \times , 3 \times) and the width of the standard

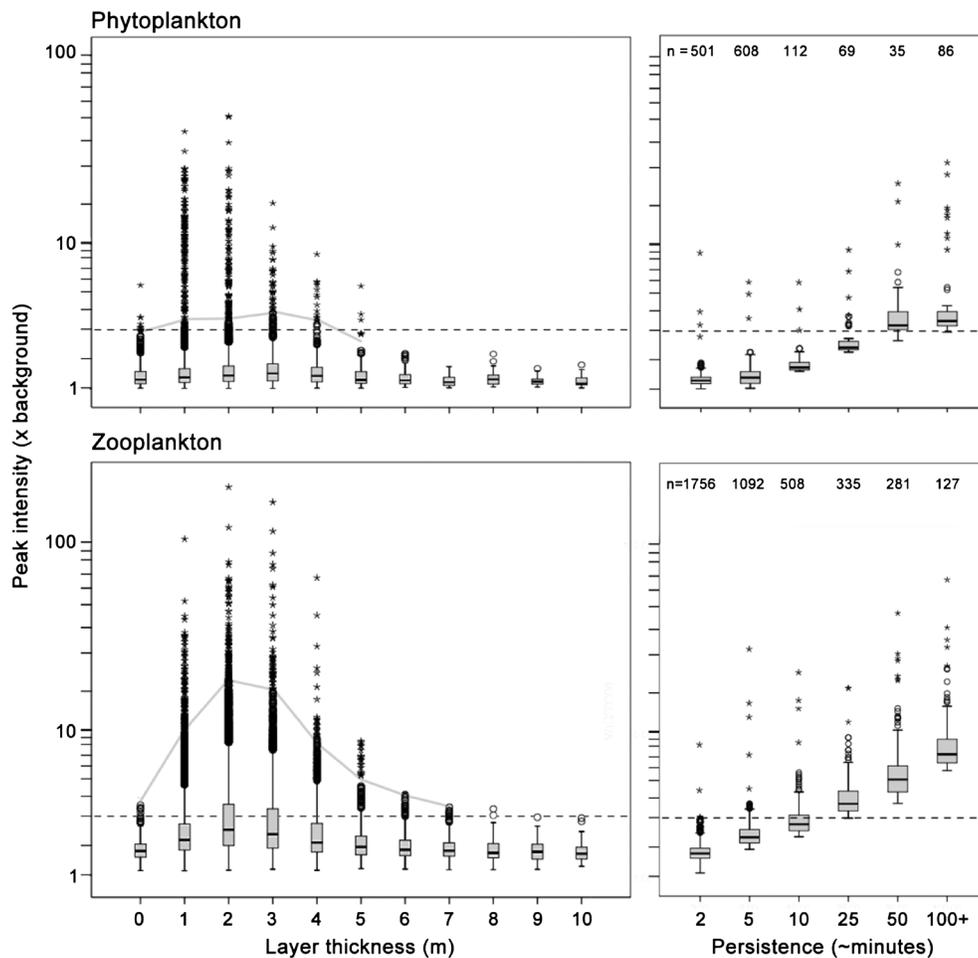


Figure 2. Layer peak intensity as a function of (left) layer thickness and (right) layer persistence for (top) phytoplankton and (bottom) zooplankton over the New Jersey shelf and slope. For each box, the dark line shows the median intensity value, the box one interquartile range, and the whiskers the 95% confidence interval. Outliers, those that are more than 1.5 times the interquartile range from the 75th percentile, are shown as circles, while asterisks show extreme values, those that are at least 3 times the interquartile range from the 75th percentile. The gray curve marks the intensity of the first extreme value in the left-hand plots. The dashed line in each plot indicates the 3 times background intensity value often used to define thin plankton layers.

deviation calculation (3, 5, and 10 m) in all possible combinations. The distribution of layer vertical scales was assessed for fit to hypothesized distribution patterns using a maximum likelihood approach implemented in EasyFit 5.5 (MathWave Technologies).

[7] For each identified layer, the depth of the peak defined its location in the water column. The locations of all identified layers were visually scrutinized in the raw data to confirm appropriate selection. The vertical scale of the layer was defined by measuring the thickness of the layer at half of the peak value without including the background (following the general approach of *Dekshenieks et al.* [2001]). To calculate the relative amplitude of each layer, the amplitude of the peak was divided by the background. Because in situ validation of fluorescence and backscattering varied from experiment to experiment, we did not attempt to convert measures to biologically relevant units. Rather, our goal was to identify patterns in the relative intensity of each proxy that indicated the presence of an aggregation and scaled these measures to the local background.

[8] Once all layers were detected, subset layers were identified as thin layers based on both their thickness (<5 m) and intensity ($3\times$ background) using criteria commonly cited in

other studies [*Dekshenieks et al.*, 2001]. The effects of time of day and category on detected and thin layer thickness and intensity were examined. An assessment of the temporal-horizontal persistence of fluorescent and acoustical scattering layers was also possible off New Jersey due to the regularity of profiling (one roughly every 60–80 s equating to a horizontal spacing of ~ 30 – 40 m). The number of contiguous profiles in which each detected layer was identified, or persistence, was examined as a function of the intensity and thickness of the layer averaged over the time period it was detected. The persistence of layers classified as thin layers was compared against the persistence of all detected layers. Note that persistence, as used here, is indistinguishable from patch size due to advection through our reference frame.

3. Results

[9] We examined a large number of fluorescence and acoustic profiles from four different coastal locations. Across the four locations, 92%–100% of plankton features were thinner than 5 m (Figure 1). Thickness distributions

could not be simply described by any of the distribution patterns tested (exponential, gamma, log-logistic, and lognormal; Kolmogorov-Smirnov statistics > 0.25 for all comparisons). There were no significant differences in the thickness distributions of plankton features between day and night (phytoplankton $\chi^2 = 0.86$, $p = 0.71$; zooplankton $\chi^2 = 2.05$, $p = 0.28$). The dominance of sub-5 m scale patches was insensitive to layer detection parameters used. Lowering the size of the window for standard deviation or decreasing the peak detection threshold increased the number of peaks detected dramatically, in some cases, by an order of magnitude, but changed the number of layers detected by no more than 3% as the consecutive peak rule became increasingly critical. Doubling the size of the window for the calculation of the standard deviation measure used in peak detection affected the detection of less than 10% of all layers, leaving the distributions of layer thickness unchanged (Wilcoxon signed ranks tests, all $p > 0.05$, $\beta > 0.68$). Increasing the threshold values used in peak detection decreased the fraction of data points identified as layers roughly proportionately (doubling the detection threshold reduced the number of identified layers by about half). Increasing the peak detection threshold significantly reduced the standard deviation layer thickness (analysis of variance: degrees of freedom (d.f.) = 3,12; $F = 9.31$; $p < 0.05$); however, the median of each distribution and the proportion of layers that were less than 5 m thick remained unchanged ($F = 1.59$, $p = 0.24$; $F = 0.48$, $p = 0.71$). These were results supported by paired t tests comparing the medians ($t = 0.37$; $p = 0.35$) and proportion of layers less than 5 m thick ($t = 0.18$; $p = 0.54$) detected with thresholds of $1.5\times$ and $3\times$. The parameters used picked the most features without detecting a large number of peaks outside of layers.

[10] Larger animals (micronekton) were only rarely found in sub-5 m thick layers using the same layer detection methods (micronekton were less likely to be detected in layers less than 5 m thick than plankton; contingency analysis; $p < 0.01$ for all locations) with layers detected up to the 15 m limit imposed by the layer detection algorithm (Figure 1).

[11] Features classified as thin layers based on both thickness and intensity criteria were not significantly different in thickness from all detected plankton layers (phytoplankton $\chi^2 = 1.13$, $p = 0.44$; zooplankton $\chi^2 = 1.72$, $p = 0.36$). Instead, intensity and persistence, but not thickness, were the characteristics that distinguished thin layers from other patches of plankton (Figure 2, left). Across the four sites, an average of 29% of plankton features was at least 3 times more intense than the background (Figure 1). Layer intensity tended to increase as thickness decreased. The variability of layer intensities generally decreased with increasing layer thickness above about 2 m. The distribution of layer intensities at all sites was significantly different between layers 5 m and thinner and other layers (phytoplankton $\chi^2 = 7.30$, $p = 0.01$; zooplankton $\chi^2 = 5.48$, $p = 0.01$). The relationship between the thickness and the relative intensity of plankton layers over the New Jersey shelf is shown in Figure 2. Only layers 5 m and thinner had extreme outliers in relative intensity. The transition to extreme outliers in phytoplankton layers generally matched the commonly used $3\times$ background definition for thin layers, while extreme outliers in zooplankton layers were $5\times$ to $10\times$ higher than the background.

[12] In the New Jersey data, where regular profiling made it possible to assess layer persistence, persistence of both

phytoplankton and zooplankton was related to intensity, such that more intense layers tended to be detected for long time periods (Figure 2, right). Similarly, layers that were thinner were also more persistent, underscoring the general relationship between thickness and intensity. Layers classified as thin layers were significantly more persistent than other features (phytoplankton $\chi^2 = 8.07$, $p = 0.01$; zooplankton $\chi^2 = 11.21$, $p = 0.01$).

4. Discussion

[13] Our goal was to quantitatively discern how thin layers of plankton, intense, vertically compressed plankton patches with large horizontal extents, relate to plankton aggregations in general. We found that the majority of coherent aggregations of fluorescent or acoustically scattering plankton in coastal waters were vertically compressed, in contrast to patches made up of larger animals (Figure 1). We anticipated that thin layers characterized by their thickness and intensity might be outliers from other plankton features due to their thickness, in part, because thickness was the characteristic that first limited their discovery [Donaghay *et al.*, 1992]. However, we found that most plankton patches ($> 90\%$ in all locations) were less than 5 m in vertical extent (thickness). This suggests that ~ 5 m is a critical vertical scale below which plankton aggregations are common regardless of patch intensity. It also highlights the subjectivity involved in separating thin layers from other plankton patches, potential biasing inquiry, and the resulting characterizations of ecosystems.

[14] Much effort has been invested in identifying the diversity of physical, chemical, and biological processes that yield intense thin plankton layers. Proposed plankton layer formation mechanisms are physical, e.g., passive straining of patches by shear [Birch *et al.*, 2008; Stacey *et al.*, 2007], buoyancy settling [Alldredge *et al.*, 2002; Franks, 1992], the gyrotactic trapping of randomly swimming individuals [Durham *et al.*, 2009; Hoecker-Martinez and Smyth, 2012], and horizontal intrusions [Steinbuck *et al.*, 2010], as well as biological, e.g., convergent swimming of individuals in response to clines in resources [Benoit-Bird *et al.*, 2010; Sullivan *et al.*, 2010a] or physical properties [Grunbaum, 2009] and differential growth [Steinbuck *et al.*, 2010] or predation [Benoit-Bird *et al.*, 2009; Donaghay and Osborn, 1997]. The fact that the dominant vertical scale was sub-5 m regardless of location suggests that the processes leading to these features or the advantages of being in these structures are ubiquitous and share commonalities across systems and taxonomic groups. Previous efforts have emphasized thinning in examining what drives thin layers, while our results emphasize that the ecologically key processes in thin layer formation may instead be those leading to intensification and horizontal extension, both of which could disproportionately increase the ecological impacts of these layers.

[15] Thin layers and most other plankton patches in our four field sites occurred at scales that are difficult for traditional techniques like bottles, nets, and conventional profiled instruments to detect and enumerate, highlighting a potential gap in our understanding of these coastal systems. Techniques that undersample the plankton distribution can lead to substantial errors in depth-integrated measurements of abundance as well as measures of concentrations at a given depth [Strickland, 1968], resulting in patches that are smeared or missed altogether [Donaghay *et al.*, 1992].

[16] Because of their high signal-to-noise ratios, kilometer length scales [McManus *et al.*, 2003; Moline *et al.*, 2010], persistence over days [McManus *et al.*, 2007; Menden-Deuer and Fredrickson, 2010] to weeks [Bjornsen and Nielsen, 1991], and the intensification of biological processes observed within them, thin layers of plankton have proven to be valuable subjects for examination of plankton patchiness [Sullivan *et al.*, 2010b]. However, it has not been clear how thin layers fit into our understanding of plankton spatial structure more generally. Here we show that plankton are commonly aggregated at fine vertical scales (e.g., less than 5 m). Thin layers, while remarkable examples of heterogeneous distributions of organisms, are part of the spectrum of intensities of observed plankton patches—most of which occur at the same vertical scales. Studies of thin layers have facilitated insights into the processes involved in and resulting from fine-scale vertical patchiness. We now have evidence that fine-scale vertical patchiness is common in coastal plankton in a wide variety of habitats, yet we do not have a clear understanding of why this scale (sub-5 m) commonly dominates the vertical dimension of plankton aggregations. Perhaps, our gap in understanding is simply related to the emphasis of previous efforts to explain the spatial dimensions of plankton features rather than the intensification that separates thin layers from other heterogeneously distributed plankton. Regardless, the similarity in vertical scales among plankton across diverse environments points us toward looking for a universal biotic or abiotic process or a controlling characteristic common to a variety of regions and organism types. Our understanding that thin layers are part of a continuum of plankton patchiness points the way forward in studies of plankton patchiness. Our results suggest that insights gleaned from studying thin layers, relatively tractable plankton aggregations, may be applied more generally to plankton patches. Studies of thin layers of plankton can provide insights into physical-biological dynamics leading to plankton patchiness and the ecosystem effects of heterogeneous plankton distributions.

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