Layered organization in the coastal ocean: An introduction to planktonic thin layers and the LOCO project

1. Planktonic thin layers

In his seminal paper "The Paradox of the Plankton" G.E. Hutchinson (1961) asked: "How is it possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials?" Of course, we now know the oceans are anything but isotropic and unstructured. Heterogeneity in physical conditions and motions result in complex vertical and horizontal structures in the ocean, which, in turn, contribute to a similarly patchy and complex distribution of nutrients and plankton. This patchiness in physical, chemical and biological patterns spans all spatial scales, from millimeters to kilometers, in both vertical and horizontal dimensions. While much work has been done on elucidating pattern and structure at 10s of meters and larger scales (e.g. Cassie, 1963; Haury, 1976; Riley, 1976; Steele, 1978 (and references therein)), only recently have we begun to appreciate and quantify the ubiquity of fine-scale structures and thus, their full ecological importance.

Determining the *critical scales* at which measurements must be collected in order to effectively investigate particular phenomena is one of the most difficult and important aspects of observational oceanography. In comparison to large-scale processes, fine-scales processes may have an equal, if not greater influence on the distributions and abundances of marine organisms (Haury et al., 1978). Fine-scale patchiness is increasingly recognized as the signature of critical physical and biological processes in the environment (Valiela, 1995). And, thus, knowledge of fine-scale physical, chemical and biological patterns is requisite to understanding the dynamics of the marine environment as a whole. Despite the sustained scientific motivation to understand these fine-scale structures, the degree to which we can effectively investigate these scales has been highly dependent on available technology and sampling methodologies. Indeed, as sensor technologies and deployment methods continually improve, new phenomena are being discovered in the marine environment.

1.1. *Definition*

Owing to advances in vertical profiling technology and methodology, we now know that fine-scale, dense patches of organisms are ubiquitous features in the ocean. The term 'thin layer' is used to describe highly-concentrated patches of organisms, or particles, that have vertical extents on the order of centimeters to a few meters, yet can extend horizontally for many kilometers and persist for hours to weeks (e.g. Donaghay et al., 1992; Cowles et al., 1998; Dekshenieks et al., 2001; Holliday et al., 2003).

Several investigators have proposed sets of criteria to identify thin layer structures in specific environments. Such sets have been proposed for phytoplankton in East Sound, WA (Dekshenieks et al., 2001) and Monterey Bay, CA (Sullivan et al., this issue), as well as for acoustically measured zooplankton layers in Monterey Bay, CA (Cheriton et al., 2007; Benoit-Bird et al., 2009) as well as several other sites along the west coast of the US (Cheriton et al., 2007). Each of these definitions is distinct and customized to the type of organism in the layer, the particular instrument being used to detect the layer, and the region being studied. Consequently, there is currently no all-encompassing set of criteria for identifying thin layers.

While these sets of criteria differ in some ways, the features they have in common are: (1) The layer structure must persist over time and space; (2) the layer vertical thickness must be below some maximum, and there must be an objective, clearly-defined method for calculating the vertical thickness; and (3) the layer maxima must meet a minimum signal strength (e.g., 2 or 3 times greater than background values). The first criterion was established to ensure that the layers studied had some continuity in their spatial extent and temporal persistence, i.e. they were not ephemeral features. The second criterion was developed to differentiate thin layer structures from the larger vertical structures (e.g., deep chlorophyll maximums) that would not likely be missed by more coarse scale sampling practices (e.g. standard bottle sampling every 5 or 10 m). The third criterion was developed to indicate the degree of ecological relevance due to its magnitude. These three criteria have been honed during the evolution of thin layer research.

While over the years it has become apparent that one singular set of criteria to encompass all layer organisms, all instrument types, and all environments is not possible, we strongly emphasize the necessity of and importance of using the above framework to set clear guidelines for thin layer identification. Documenting how a thin layer is defined is critical to understanding differences between studies, as well as the ecological relevance of the structure.

1.2. *Detection methods*

Because of their small vertical scales, thin layers are notoriously difficult to detect and resolve in the marine environment.

Traditional oceanographic sampling techniques exhibit a number of shortfalls. Fine-scale structures can be smeared, undersampled, or missed completely by discrete bottle samples. Information on the true vertical structure of thin layers is lost by towed nets that integrate over depth, or by profiling systems influenced by ship motion. Effective measurement methods require platforms that are decoupled from ship motion, as well as sensors that can achieve vertical resolution on the order of centimeters. Such resolution is typically achieved from in-situ samplers through slow vertical profiling rates, high sampling rates, or a combination of the two; and in acoustic and optical systems through the choice of the outgoing signal coupled with a high sampling rate.

Because of the difficulty associated with resolving these features, thin layers research has been a catalyst for many recent innovations in oceanographic instrumentation and sampling methodologies (e.g. Donaghay et al., 1992; Sullivan et al., 2002, 2005; Holliday et al., 2003). As a result, there are now numerous sampling strategies and sensor configurations designed for the purpose of observing vertical fine-scale patterns, many of which are described in this issue. For example, within this issue, ship-based methods are detailed in Rines et al. and Sullivan et al.; acoustic methods are detailed in Benoit-Bird et al. and Holliday et al.; methods using moored autonomous profilers are described in Sullivan et al.; and methods using AUVs and gliders are described in Benoit-Bird et al., Moline et al., Ryan et al. and Wang and Goodman. In addition to the methods and instruments described in this issue, recently developed remote sensing techniques such as Light Detection and Ranging (LIDAR) are providing new information about the spatial extent and depth range of thin layers over large swaths of the upper ocean (Churnside and Donaghay, 2009), while mathematical theory and modeling has also played a major role in understanding thin layer dynamics (Franks, 1995; Osborn, 1998; Leising, 2001; Stacey et al., 2007; Durham, et al., 2009).

1.3. *Formation, maintenance and dissipation*

In order to understand the formation, maintenance and dissipation of a thin planktonic layer, one must consider the physical, chemical and biological mechanisms acting on a layer in concert. For thin layers to form and persist in the marine environment, divergent processes acting on the layer cannot exceed the convergent processes (e.g. Osborn, 1998; McManus et al., 2003; Stacey et al., 2007; Wang and Goodman, this issue). Turbulent mixing is a persistent divergence mechanism that, when present, will normally act to broaden the layer. Because of this effect, the majority of thin layers are found in stably stratified water columns, where turbulent mixing is reduced (but see Wang and Goodman, this issue). Recently, Stacey et al. (2007; Birch et al., 2008) presented a mathematical framework describing how the thickness of a phytoplankton layer is affected by processes acting to broaden the layer (i.e. divergence) and those acting to thin the layer (i.e. convergence). In this analysis, the divergent process was turbulent diffusion, which can be caused by a variety of physical processes ranging from regional winds, and convective overturns, to the passage of non-linear internal waves. The convergent process included the physical process of straining by shear (after Franks, 1995), the biological processes of passive settling of phytoplankton on a density surface (i.e. buoyancy), and active swimming or migration by phytoplankton.

While physical oceanographic processes, like turbulent mixing and shear, often provide the context for thin layer development, biological and chemical processes can play equal, if not more significant roles in the dynamics of thin layers. For example, non-motile or passive organisms/particles such as diatoms or marine snow may form thin layers by settling on or through strong density gradients (Alldredge et al., 2002), and motile organisms may actively aggregate into thin layers by responding to chemical and/or physical cues, seeking food, for sexual reproduction or for defense from predators (Dekshenieks et al., 2001; Leising, 2001; Holliday et al., 2003; McManus et al., 2003; Sullivan et al., this issue; Ryan et al., this issue). Other biological mechanisms such as in-situ growth, production, grazing and predation can also contribute to thin layer formation and persistence. For instance, if a thin layer of phytoplankton forms at a density surface that is within adequate light levels and co-located with a nutrient gradient, the population may experience higher growth rates, causing the layer to intensify. Furthermore, grazers such as zooplankton may form additional layers in response to this thin phytoplankton layer (McManus et al., 2003; Benoit-Bird et al.; Moline et al., this issue) which can feed back, causing the phytoplankton layer to become thinner and more distinct as a result of grazing pressure from zooplankton (Benoit-Bird et al., 2009). Physics, water column chemistry and biology can all interact to affect thin layer dynamics. For example, Ryan et al. (this issue) describe a doubling in the average intensity of phytoplankton thin layers in northern Monterey Bay corresponding with parallel increases in shallow stratification, light availability and nutrient concentrations in the thermocline. Environmental variability and the ecophysiology of a dominant phytoplankton species interacted to result in a thin-layer dominated bloom (Ryan et al., this issue).

During the maintenance of a thin layer, one can presume that the divergences and convergences are in balance, or nearly so. During the formation stage, however, convergences must exceed divergences. In many cases, the processes responsible for maintaining the layer could also be responsible for forming it, but the timescale for layer development may dictate that other processes or conditions must be present during formation. An example was discussed in Steinbuck et al. (2009), in which it was found that a high dinoflagellate swimming speed was required during layer formation to overcome turbulent mixing and to match the observed formation time, but a reduced swimming speed was required to actually maintain the layer. Alternatively, variation in physical conditions (density, shear or turbulent mixing) may also allow layers to form more rapidly than would be expected based on conditions during the maintenance of the layer.

At the other end of the layer's lifetime, the dissipation of the layer is, of course, caused by layer divergence mechanisms exceeding the convergence mechanisms. Both organism behavior and turbulent mixing could be effective at dissipating a layer. Migration out of the layer could lead to a rapid and complete breakdown of the layer, while turbulence may have a more local effect on the layer, depending on the mechanism responsible for the increase in mixing. Large-scale changes in shear and stratification could lead to mixing that would dissipate an entire layer, whereas local mixing events, due to internal wave breaking or the passing of solitons, may only dissipate portions of the layer.

1.4. *Ecological importance*

The growing body of knowledge on thin layers indicates that these features may be a critical component to marine ecosystem dynamics and functioning. First, far from being unusual or rare, it is now clear that thin layers of plankton are common features and can be found in a wide variety of environments (Derenbach et al., 1979; Bjørnsen and Nielsen, 1991; Donaghay et al., 1992; Cowles and Desiderio, 1993; Carpenter et al., 1995; Holliday et al., 1998; Dekshenieks et al., 2001; McManus et al., 2003; Ryan et al., 2008). As thin plankton layers can often contain 50–75% (or more) of the total biomass in the water column (Holliday et al., 1998; Cowles et al., 1998; Sullivan et al., this issue), thin layers are likely to be concentrated areas of intense biological activity, likely playing a critical role in the life histories and evolutionary trajectories of many species that are found in or interact with thin layers. For example, it has been shown that fish feed preferentially on intense zooplankton thin layers, affecting the depth distribution and behavior of fish in Monterey Bay (Benoit-Bird, in review). While interactions within thin layers are just beginning to be investigated, thin layers are likely to be important for a variety of biological processes, including growth rates, reproductive success, grazing, predator–prey encounters, nutrient uptake and cycling rates, as well as toxin production (Lasker, 1975; Mullin and Brooks, 1976; Sieburth and Donaghay, 1993; Donaghay and Osborn, 1997; Cowles et al., 1998; Hanson and Donaghay, 1998; Dekshenieks et al., 2001; Rines et al., 2002; McManus et al., 2008). In addition, the layering of the ocean and its plankton species into persistent thin structures acts to diversify and expand available ecological niche space. To exploit these niches, species may exhibit more specialization and adaptations, which has likely been an important factor leading to the great species diversity of the plankton noted by Hutchinson (1961).

The organisms or particles comprising a thin layer can be widely diverse. Some of the organisms that have been found in thin layer structures include bacteria (McManus et al., 2003), phytoplankton (Rines et al., 2002), zooplankton (Holliday et al., 2003), bioluminescent organisms (Sullivan et al., 2003; Benoit-Bird et al.; Moline et al., this issue) as well as marine snow and detritus particles (Alldredge et al., 2002). While thin layers can contain mixed species assemblages and trophic levels (Rines et al., 2002, McManus et al., 2003), phytoplankton thin layers are often dominated by high concentrations of a single species (e.g. Nishitani et al., 1985; Richardson and Kullenberg, 1987; Nielsen et al., 1990; Dahl and Tangen, 1993; Bjørnsen and Nielsen, 1991; Carpenter et al., 1995; Gentien et al., 1995; Gisselson et al., 2002; Rines et al., 2002; Sullivan et al., 2003, 2005, this issue; Velo-Suárez et al., 2008). Interestingly, a large number of harmful algal species have been observed in thin layers (Rines et al., 2002, this issue; Sullivan et al., 2003, 2005, this issue; McManus et al., 2008), indicating that understanding thin layers could be critical to harmful algal bloom research.

1.5. *Ramifications for ocean sensing*

Thin layers can significantly affect underwater visibility, imaging, vulnerability, optical communication and optical remote sensing (e.g. Zaneveld and Pegau, 1998; Petrenko et al., 1998; Sullivan et al., 2005, this issue; Churnside and Donaghay, 2009). As phytoplankton thin layers typically contain a significant percentage of the total water column chlorophyll, a large percentage of the absorption (a) and scattering of light can occur within the thin layers (Sullivan et al., 2005, this issue). Thin layers composed of different phytoplankton species and particles may have very different effects on the Inherent Optical Properties (IOPs) of the water column. For example, a thin layer composed primarily of phytoplankton may have higher absorption and scattering than a thin layer composed primarily of marine snow or detritus, but much lower backscattering (b_b) and reflectance ($\sim b_b/a$), thus thin layers can increase or decrease the reflectance of the water column dependent on their optical properties. The thicker the thin layer, the shallower it occurs and the greater the layer's reflectance deviates from the surrounding waters, the larger the influence on the surface reflectance (Petrenko et al., 1998). Deep thin layers would be invisible to satellite remote sensing and could represent an underestimation in satellite derived coastal productivity and carbon estimates. As well as affecting in-situ IOPs, a thin layer of bioluminescent organisms may represent a large source of underwater light.

Thin layers not only impact oceanic optical properties and remote sensing, they can also affect acoustic propagation and sensing. While light is quickly attenuated in seawater, sound can be transmitted over great distances. As a result, sound is used in the ocean by humans and many other animals for sensing the environment, transmitting information, and navigating. Sound is lost in the ocean due to spreading, absorption, and scattering. Particles like zooplankton are important sources of acoustic scattering. Dense thin layers of zooplankton and ichthyoplankton can have significant impacts on the transmission and scattering of sound and thus how sound can be used in environments containing these layers. For example, an intense thin layer can affect the transmission of sonar signals through the water, backscattering so strongly that the sound cannot penetrate the layer, which can result in the layer being mistaken for the seafloor. This effect, however, varies with the composition of the layer because scattering is affected by the size, shape, and identity of the zooplankton in an assemblage (Holliday and Pieper, 1980). A layer made up primarily of copepods would likely not be detected by a low-frequency shipboard echosounder, but would be detectable by a bottlenose dolphin echolocating through the layer because of the higher frequency of its signal (Au, 1993). However, a layer of ichthyoplankton with gas filled swim bladders would be problematic for both the dolphin and for echosounders at all frequencies. Because sound is difficult to transmit through a strong acoustic scattering layer and the signal can be distorted by the scatterers, the presence of a zooplankton thin layer also has implications for underwater acoustic communications across the layer (Catipovic, 1990). While the effects of acoustic scatterers on signal transmission have been examined mostly for human communications systems, the effects are likely to be similar for a fish sending a mating call or a dolphin whistling to a companion. As a result, plankton thin layers have impacts both on the utilization of sound by humans and the behavior and ecology of acoustic species in the ocean.

2. The LOCO project

The Layered Organization in the Coastal Ocean (LOCO) project was a multi-investigator, multi-institutional, interdisciplinary program that undertook two, several weeklong field experiments in 2005 and 2006 to investigate thin plankton layers in Monterey Bay, CA. This project was a Department Research Initiative (DRI) funded by the Office of Naval Research (ONR) and involved 15 lead scientists, numerous graduate students, postdoctoral researchers and technical staff from 11 different institutions. The design and implementation of the LOCO experiment marked the culmination of over 10 years of previous thin layers research.

One of the paramount objectives for thin layers research is to understand both how thin layers are governed by the physical, chemical and biological environment and to evaluate the ecological importance of these fine-scale biological structures in the marine environment. To this aim, the objectives of the LOCO project were to further investigate the spatial and temporal scales of thin layers, to quantify the relationship between thin layers and biological phenomenon as well as physical processes (from the mesoscale to the microscale), and to investigate the relationship between nearshore and offshore layers.

2.1. *Preceding experiments*

Two early thin layers experiments took place in 1996 and 1998, both in East Sound, WA, a fjord of Orcas Island-part of the San Juan Island group. The purpose of these experiments was to utilize new optical and acoustical instrumentation in conjunction with high-resolution physical measurements and new deployment techniques to quantify the temporal and spatial scales of thin layers in the fjord. These experiments provided important insights into the physical, chemical and biological mechanisms contributing to thin layer dynamics (see Dekshenieks et al., 2001; Alldredge et al., 2002; Rines et al., 2002; McManus et al., 2003; Sullivan et al., 2003). In addition, these researchers found that, within the protected waters of East Sound, thin biological layers occurred frequently and could persist for days.

This engendered the question, how prevalent are thin layers in other coastal areas? To answer this question, from 1999 to 2003, the Coastal Ocean Exploration: Searching for Thin Layers (COESTL) project surveyed 7 US coastal ocean sites for the presence of thin optical and acoustical layers. Thin layers were detected at 6 of these 7 sites: Cape Perpetua, OR; Monterey Bay, CA; Santa Barbara, CA; Oceanside, CA; Charleston Harbor, SC; and Destin, FL. The results from this survey showed that thin layers can develop not only in coastal fjords such as East Sound, but also in a variety of coastal systems, such as open bays, estuaries, and unprotected continental shelf regions (Cheriton et al., 2007). Of the 7 sites monitored, Monterey Bay, CA and East Sound, WA were identified as sites with the most intense and the most persistent thin layers.

2.2. *Study site for LOCO*

Monterey Bay was chosen as the study site for the LOCO project for several reasons. First, thin plankton layers were found to be both common and persistent features over the inner bay shelf during COESTL. Secondly, being a large coastal embayment with an open connection to offshore waters, Monterey Bay provided strong contrast with East Sound, where extensive thin layer studies were previously conducted. Third, the dynamics of the California Current strongly influence the bay, affording the opportunity to study thin layer ecology under a variety of conditions and forcing processes. Last, Monterey Bay and adjacent waters have long-term mooring and ship time-series, which provided understanding of the regional and seasonal context and valuable environmental data during the LOCO field programs.

2.3. *LOCO field program*

The LOCO Monterey Bay thin layer studies took place in the summers of 2005 and 2006. Two other programs in Monterey Bay, directly related to LOCO, also provide critical information for this special issue: the COESTL program, which occurred in August 2002, and the Autonomous Ocean Sampling Network II program, which occurred in the summer of 2003.

A nested sampling strategy was used to investigate the physical, biological and chemical processes contributing to thin layer dynamics in northern Monterey Bay. This nested sampling strategy consisted of a central mooring array (1–2 km), small vessel surveys (1–9 km), and large vessel and autonomous underwater vehicle surveys (25–30 km).

Mooring array: The mooring array formed the ‘core’ of the program. Instruments to measure physical oceanographic structure and processes, nutrients, optics and acoustics were deployed in northern Monterey Bay in an array configuration. The center of the array (36°56.2′N, 121°55.8′W) was located in roughly 20 m of water, 2.5 km from shore. The configuration of the array differed slightly between 2005 and 2006. Details of the arrays are given in the papers included in this special issue.

Small vessel surveys: Several small vessels (<25 m) were used to make surveys of physical oceanographic structure and processes, nutrients, optics and acoustics in both 2005 and 2006. The availability of small vessels allowed researchers to make measurements throughout the water column both in and around the mooring array and most importantly, allowed direct sampling of the water column within the array. These samples were preserved onboard and later analyzed in the laboratory. The sampling undertaken by the small vessels covered a spatial scale extending from nearshore to as far as 9 km offshore.

Large vessel surveys: Two large vessels were used during the 2005 and 2006 experiments (the R/V *New Horizon* and the R/V *Thomas* G. Thompson, respectively) to conduct measurements of physical oceanographic structure and processes, nutrients, optics and acoustics in survey transects that extended from the vicinity of the mooring array to many kilometers both along and offshore of the array.

Autonomous vehicles: Autonomous underwater vehicles (AUVs) were deployed to measure physical oceanographic structure and processes, nutrients, optics and acoustics. These AUVs covered a larger spatial scale than the array and the small vessel surveys. Dorado and Slocum glider AUVs covered a spatial scale that ranged from the nearshore to more than 25 km offshore. REMUS AUVs covered a smaller spatial scale in the vicinity of the array.

Complimentary data: Monterey Bay was chosen for a site, in part due to the many complimentary Ocean Observing programs in the area. Data was also obtained from The Center for Integrated Marine Technology (CIMT), The Network for Environmental Observations of the Coastal Ocean (NEOCO), The Partnership for the Interdisciplinary Study of the Coastal Ocean (PISCO), The Monterey Bay Aquarium Research Institute (MBARI), and the National Data Buoy Center (NDBC). This complimentary data provided a longer time series and larger scale context of oceanographic data, which proved to be invaluable for the interpretation of the results of the study.

2.4. *LOCO special issue*

As noted above, the group of researchers that participated in the LOCO project used a diverse array of measurement platforms, methodologies and state-of-the-art instrumentation to examine the spatial–temporal characteristics and dynamics of thin layers in Monterey Bay. An overview of the methodologies and results from the studies presented in this issue is as follows: Ryan et al. integrated intensive water column surveys using the DORADO Autonomous Underwater Vehicle (AUV) with satellite and mooring data to examine the spatial–temporal scales and interacting processes of phytoplankton thin layer development over the inner and outer shelf areas of Monterey Bay. Sullivan et al. used hourly measurements from an array of moored autonomous profilers and small ship based sampling to examine the spatial–temporal dynamics (biological and optical) of phytoplankton thin layers over several weeks during 3 different years in Monterey Bay. Using a specialized REMUS AUV, Wang & Goodman made collocated spatial measurements of turbulence, physical fine structure and phytoplankton thin layers to examine if phytoplankton thin layers can exist in both weak and strong turbulent conditions. Benoit-Bird et al. combined measurements from multiple measurement platforms with acoustic instruments on both ships and moorings, and optical measurements on both ship based profilers and an AUV, to examine the interactions occurring between phytoplankton and zooplankton thin layers in vertical space. In a companion paper, Moline et al. used similar multiple measurement platforms to examine the horizontal length scales and interactions of phytoplankton and zooplankton thin layers. Cheriton et al. used towed vehicle surveys to examine the horizontal and vertical relationships of phytoplankton thin layers in the nearshore and offshore environments. Holliday et al. used a multi-frequency acoustic mooring array to examine the vertical fine-scale dynamics of zooplankton thin layers and Rines et al. used small ship based adaptive sampling to collect water samples from inside and outside phytoplankton thin layers to elucidate the role that species-specific properties play in their dynamics.

The papers in this special issue are but a subset of studies resulting from the LOCO project. Several LOCO investigators not represented in this issue nevertheless conducted important research that already has (or will be) published in other forums. Interested readers should search for studies by S. Bollens, T. Cowles, P. Donaghay, D. Fratantoni, A. Hanson, J. Steinbuck, and M. Sutor, while also searching for additional LOCO studies by the authors and co-authors included in this issue.

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