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NOTE

Observations of Thin Layers in Coastal Hawaiian Waters

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Abstract Thin layers of plankton have been documented in a wide variety of environments. The growing body of observations indicates that these features are a critical component of marine ecosystem dynamics and functioning. In the past two decades, much of the research on thin layers was undertaken in temperate coastal waters. Here, we report the first known observations of thin layers of phytoplankton in tropical Hawaiian waters. We conducted an overnight shipboard study during which time we made high-resolution observations of physical and optical structure in the water column. During the overnight cruise, we observed the greatest number of thin layers in the early evening hours when thermal stratification was strongest and most persistent due to a combination of warm air and surface water, as well as light winds. A comparison of these observations with those from temperate regions leads us to hypothesize that the nature and persistence of the physical structure is very important in determining the persistence of thin layered structures. Because plankton biomass is generally lower in tropical regions, the heterogeneous aggregation of food in thin subsurface layers may be more critical to the marine ecosystem than it is in temperate regions where plankton are generally more abundant.

Keywords Thin layer · Physical processes · Hawaii

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Introduction

Within the ocean, organisms and particles can accumulate in discrete, vertically thin patches, <5 m in vertical extent. These features, referred to as "thin layers," are common in stratified coastal oceans; however, they often go unobserved due to the coarse resolution of traditional sampling techniques (e.g., Donaghay et al. 1992; Cowles and Desiderio 1993; Holliday et al. 1998, 2003). Despite being only a few centimeters to a few meters in thickness, these fine-scale features can occur over large horizontal scales, from hundreds of meters to several kilometers (Cheriton et al. 2010; Moline et al. 2010; Ryan et al. 2010), and can persist for days (McManus et al. 2008). Thin layers can be composed of a variety of living and non-living material, including phytoplankton, zooplankton, fish and barnacle larvae, bioluminescent organisms, detritus, as well as bacteria (Donaghay et al. 1992; Alldredge et al. 2002; McManus et al. 2003). In this contribution, we will focus specifically on thin layers of phytoplankton. Though the traditional definition of a thin layer includes any dense, continuous patch of organisms or particles <5 m in vertical extent (Dekshenieks et al. 2001), the majority of observed thin phytoplankton layers have a vertical thickness <3.6 m (e.g., Dekshenieks et al. 2001; Ryan et al. 2008, 2010; Benoit-Bird 2009; Churnside and Donaghay 2009; Sullivan et al. 2010a), indicating a clear separation in scale from the commonly recognized "subsurface" or "deep" chlorophyll maximum.

The formation, maintenance, and dissipation of thin planktonic layers can be controlled by a variety of physical and biological processes (Donaghay and Osborn 1997; Sullivan et al. 2010a). Organisms can accumulate on density interfaces (Dekshenieks et al. 2001), facilitated by either the buoyancy of the organisms (Franks 1992) or turbulence patterns (Steinbuck et al. 2009). It has been suggested that large patches can be thinned by horizontal current shear (Eckhart 1948; Kullenberg 1974; Franks 1995; Stacey et al. 2007; Ryan et al. 2008) or entrained in horizontal intrusions (Steinbuck et al. 2009; Cheriton et al. 2010; Ryan et al. 2010). Franks (1995) also proposed a mechanism by which horizontal biomass gradients could be turned into thin layers through interactions with internal waves. In addition, thin layers can be formed through the swimming patterns of plankton, as has been observed for dinoflagellates migrating to the nutricline at night (Hanson and Donaghay 1998; Sullivan et al. 2010b).

The growing body of knowledge on thin layers indicates that these features are a critical component of marine ecosystem dynamics and functioning. The density of organisms in thin layers can greatly exceed that in the rest of the water column (Holliday et al. 2010; Sullivan et al. 2010b) suggesting that these features may be "hot spots" for a variety of biological processes, including growth, productivity, predation, mortality, and reproduction. In addition, these features may act to physically partition biological communities within an otherwise relatively homogenous environment; indeed, multiple thin layers composed of different species structures have been observed in the water column simultaneously (Alldredge et al. 2002; McManus et al. 2003; Benoit-Bird 2009). In addition, harmful algal bloom (HAB) species are often observed in thin layer structures (McManus et al. 2008; Velo-Suárez et al. 2008). Thus, the frequency of thin layer occurrence may have important implications for coastal HAB detection and monitoring.

In the past two decades, much of the research on thin plankton layers was undertaken in temperate coastal waters. These observations range from the fjords of the US Pacific Northwest (Holliday et al. 1998; Dekshenieks et al. 2001; Alldredge et al. 2002; McManus et al. 2003) to the coast of Oregon and California (Cowles et al. 1998; Sutor et al. 2005; McManus et al. 2005, 2008; Cheriton et al. 2007; Sullivan et al. 2010a), as well as the US East Coast (Holliday et al. 1989; Sieracki et al. 1998; Widder et al. 1999). In addition, thin layers have also been observed in the Baltic Sea (Bjornsen and Nielsen 1991; Carpenter et al. 1995) and the Irish Sea (Holliday 1993). The one published observation of zooplankton thin layers in Hawaiian waters came from a study of thin zooplankton layers on the south coast of the island of Oahu, Hawaii (Sevadjian et al. 2010). Here, we report the first known observations of thin layers of phytoplankton in tropical Hawaiian waters, indicating the ubiquity of these features and providing insight into potential mechanisms of layer formation and maintenance through the contrast in habitat.

Materials and Methods

Shipboard Study

We conducted a 24-h shipboard study off the northwestern, leeward coast of Oahu, Hawaii, anchored at (21.509° N, 158.238° W) in 25 m of water (Fig. 1). The purpose of the 24-h shipboard survey was to characterize the physical structure, physical processes, and optical properties of coastal Hawaiian waters in extremely high resolution. Instrumentation on a small (10 m) vessel (the *Alyce C*) included a high-resolution profiler and a 600-kHz acoustic Doppler current profiler (ADCP).

The high-resolution shipboard profiler was equipped with a number of instruments including a SBE-25 CTD (temperature, salinity, pressure), which samples at 8 Hz, and a WETLabs Inc. WETStar (chlorophyll *a* (chl-*a*) fluorescence, a standard proxy for phytoplankton concentration), which also samples at 8 Hz. A LI-192SA Underwater Quantum Sensor was also attached to the profiler. This sensor measured photosynthetically active radiation (PAR). The high-resolution shipboard profiler, which is designed to be slightly negatively buoyant and disconnected from ship movement, descends at an average rate of ~15 cm s^{-1}. Thus, the vertical resolution of data from the shipboard profiler was ~2 cm. Shipboard profiles were taken, on average, every ~4 min over the entire 24-h period. One downward-looking RD Instruments 600-kHz ADCP was attached to the side of the vessel using a custom bracket designed to fit over the vessel's gunwale. The ADCP measured current magnitude and direction each second, from near-surface to near-bottom with 0.5 m vertical resolution. The ADCP ran nearly continuously for the 24-h shipboard experiment.

Wind and Tide Measurements

Hourly wind and air temperature data were obtained from a weather station (21.529° N, 158.226° W) located approximately 2.5 km to the north–northeast of our anchor site, in the Makua Range along the coastline of Makua Valley, Oahu (Fig. 1; Horel et al. 2002). Tidal data were extracted from pressure data recorded by an upward-looking 300-kHz ADCP moored 100 m from the anchor site (21.509° N, 158.240° W) in 25-m water depth.

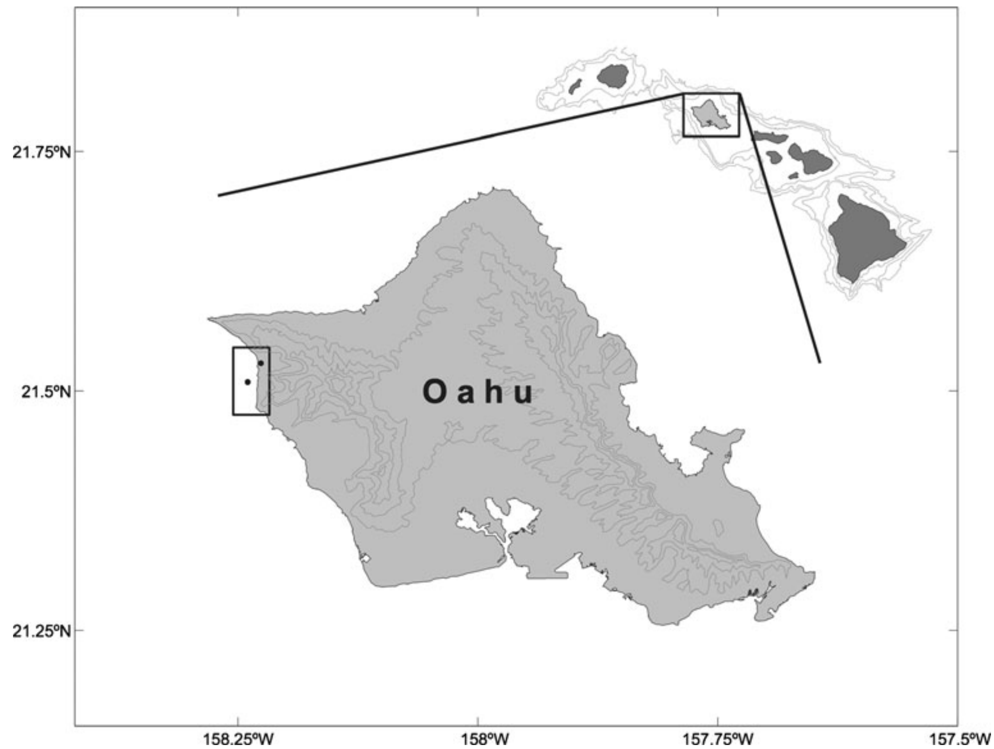

Fig. 1 Map of Oahu showing its location in the Hawaiian Island chain and the study area. *Filled circle* in the coastal ocean is the anchor site. *Filled circle* on land is the meteorological station. Elevation contours are 200 m. Bathymetric contours are 1,000 m

Identification of Thin Layers

As summarized in Sullivan et al. (2010a), several investigators have proposed sets of criteria to identify thin layer structures in specific environments. Each of these definitions is distinct and customized to the type of organism in the layer, the particular instruments being used, and the ocean area being studied. Consequently, there is no single all-encompassing set of criteria for identifying thin layers in all regions. Following the lead of Dekshenieks et al. (2001), we defined specific criteria to classify these identified optical structures as a thin layer.

First, the feature must be present in two or more subsequent profiles with the high-resolution profiler. This helps eliminate random or isolated accumulations of phytoplankton that lack spatial coherence. An example of thin layers of fluorescence from our study site is given in Fig. 2. In this figure, gray shaded boxes denote thin layers. The layer at 12 m in the 18:27 profile is not considered a thin layer because it is a single observation and did not pass the first criterion. Second, the vertical thickness of the feature (measured where the optical signal is halfway between the background level and the peak) must be ≤3.6 m. We chose a scale of 3.6 m based upon the findings of several researchers who initially used a scale <5 m, but found that most observed thin layers were actually <3.6 m (Dekshenieks et al. 2001; Ryan et al. 2008, 2009; Churnside and Donaghay 2009; Sullivan et al. 2010b). Third, the optical signal must be 30 % greater than the background (e.g., Fig. 2, panel 1, dashed vertical lines). Background levels were calculated following the method of Sullivan et al. (2010b). In East Sound, Washington, a highly stratified, highly productive system, Dekshenieks et al. (2001) used a criterion with an optical signal three times greater than the background value to define thin layer structures. In Monterey Bay, California, a highly stratified, seasonally productive system, Sullivan et al. (2010b) used a criterion with an optical signal two times greater than the background to define thin layer structures, while in the same study Benoit-Bird et al. (2010) used a criterion 1.2 times (20 %) greater than the background to define an optical thin layer structure. For tropical waters with comparatively lower biomass, we have chosen a criterion with a layer optical signal 1.3 times (30 %) greater than the background to define a layer structure. We find that, in combination with finding features in two or more subsequent profiles, this ratio consistently identifies layers in this tropical system. The conservative criterion that we have identified for tropical Hawaiian waters effectively eliminates ephemeral features.

Although we profiled continuously with the high-resolution shipboard profiler for 24 h during the survey, we only discuss layers occurring between 1800 hours on 2 May and 0700 hours on 3 May. During these evening and early morning hours, the average PAR in the upper 5 m of the water column was extremely low (<200 μE m^{-2} s^{-1}); thus, we avoid non-photochemical quenching of fluorescence. For comparison, the maximum PAR was 1,469 μE m^{-2} s^{-1} at 1230 hours on 3 May.

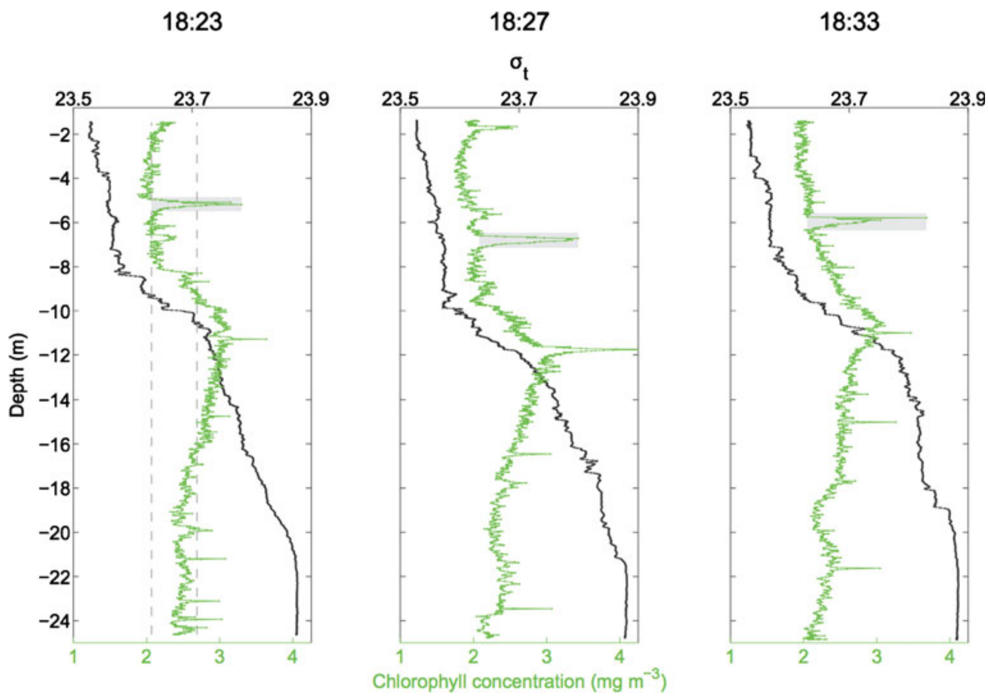

Fig. 2 Examples of individual profiles of chlorophyll fluorescence (*green*) and sigma-t (*black*) from the high-resolution profiler. *Dashed vertical lines* in *panel 1* represent background (*left*) and background+30 % (*right*) levels. Thin layers that met all three criteria are denoted by *gray-shaded boxes*

Calculation of Buoyancy Frequency

The buoyancy frequency (N^2) was calculated using data from the CTD on the high-resolution shipboard profiler:

$$N^2 = -\frac{g}{\rho_0}\left(\frac{\partial\sigma_t}{\partial z}\right) \tag{1}$$

where g is the gravitational acceleration, ρ_0 is the mean density, and $\sigma_t=\rho(s,\ t,\ p=0)-1{,}000$ (Pond and Pickard 1983).

Results

Winds

Under normal regional northeasterly trade wind conditions, our study area is in the wind shadow of the Makua Mountain Range. Due to local heating and cooling, the winds at our study site often have a clear diurnal signal with daytime wind from the northwest and nighttime winds from the south–southeast. During the transition periods between daytime and nighttime winds (at sunset and dawn), the winds are generally light and from the west. Measured early evening winds from 1800 to 2100 hours on 2 May were light, at an average of 1.95 ms^{-1} from the west (270°). Evening and nighttime winds, from 2200 hours on 2 May to 0700 hours on 3 May, averaged 2.48 ms^{-1} from the south–southeast (123°).

Air Temperatures

Air temperature from 1800 to 2000 hours on 2 May averaged 26.85°C. Air temperature began decreasing at 2000 hours, with a 1.93°C decrease in temperature between 2000 and 2100 hours and an additional 4.81°C decrease in temperature occurring between 2100 and 2200 hours.

Tides

Tides along the west coast of Oahu are generally mixed, semi-diurnal with two highs and two lows of unequal height each day. The 2–3 May study took place during a neap tide. The first low tide occurred at 1637 hours on 2 May (+0.16 m). The tide flooded from 1637 to 2302 hours on 2 May, with a range of 0.34 m. The first high tide occurred at 2302 hours (+0.50 m). The tide ebbed from 2302 hours on 2 May to 0608 hours on 3 May, with a range of 0.47 m. The second low tide occurred at 0608 hours on 3 May (+0.03 m; Fig. 3a).

General Flow Patterns

In this region, the majority of currents are predominantly tidal and oriented alongshore (along-isobath; McManus et al. 2008). The surface tide propagates from north to south at the Hawaiian Islands; on the flood tide, the majority of the current flow in our study region is along isobath and to the south, while on the ebb tide the majority of the current flow is along isobath and to the north. During the 2–3 May overnight study, current velocities were oriented alongshore

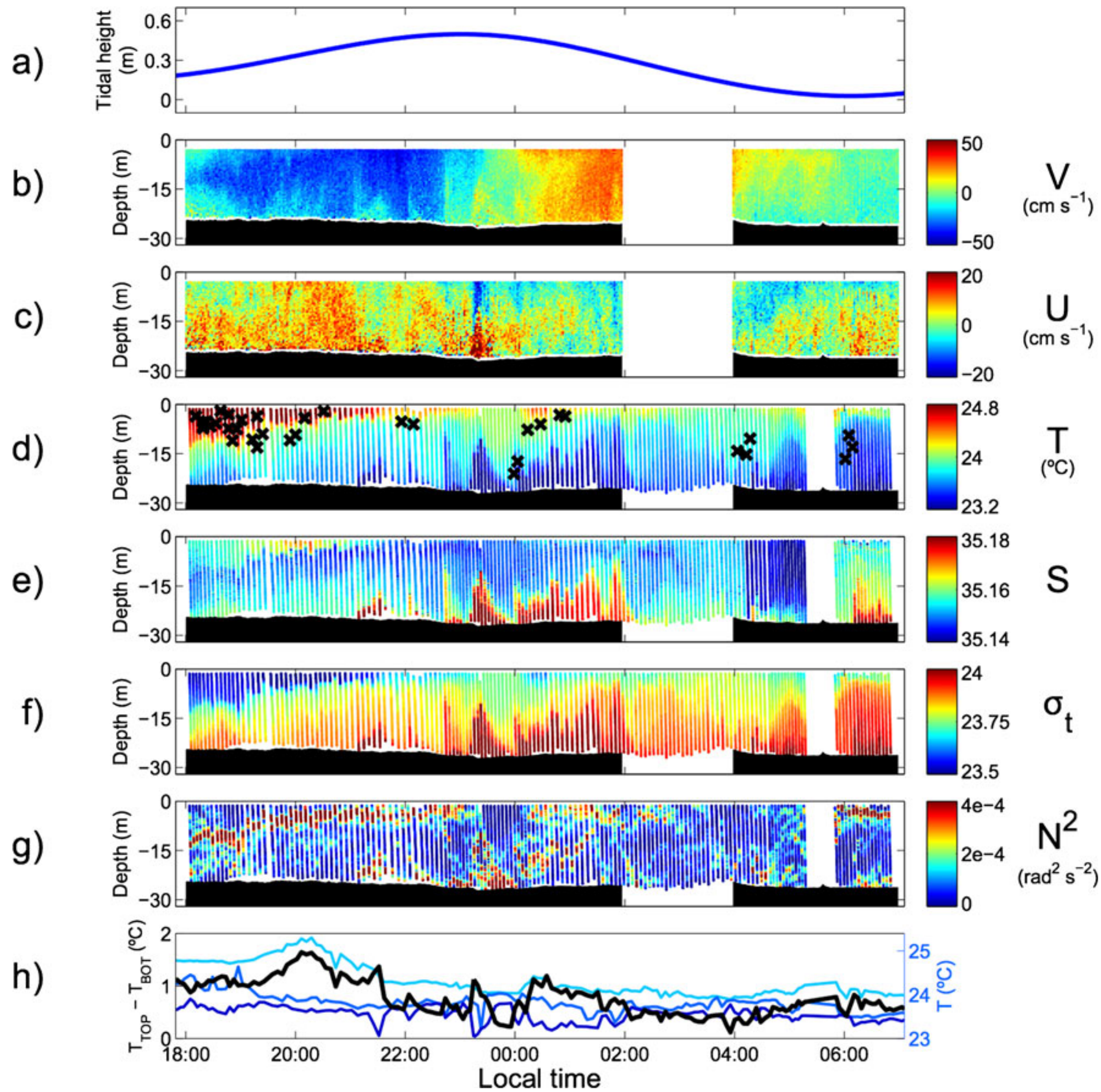

Fig. 3 Thirteen-hour time series data from 1800 hours 2 May to 0700 hours 3 May 2009. Tidal height from the 300-kHz ADCP 100 m from the anchor site (**a**); alongshore velocity (v) from the 600-kHz ADCP on shipboard +north, −south (**b**); across-shore velocity (u) from the 600-kHz ADCP on shipboard +east, −west (**c**); temperature from the high-resolution profiler on shipboard (*x mark* indicates the location of thin layer of fluorescence) (**d**); salinity from the high-resolution profiler on shipboard (**e**); sigma-t from the high-resolution profiler on shipboard (**f**); buoyancy frequency (N^2) calculated using data from the CTD on the high-resolution shipboard profiler (**g**); and temperature time series from the high-resolution profiler on shipboard. Surface temperature from 2.0 m, mid-water temperature from 11.0 m, near-bottom temperature from 20.0 m (*blue*), and temperature difference $\Delta T = T_{2.0} - T_{20.0}$ (*black*) (**h**)

(along isobath) 86.1 % of the time. During the flood tide, currents were to the south at an average of $-0.18\ \mathrm{m s^{-1}}$. Maximum flooding current velocities of $-0.33\ \mathrm{m s^{-1}}$ were observed just before 2200 hours (Fig. 3b)—no thin layers were observed when near-maximum current velocities were measured. During the ebb tide, currents were to the north at an average of $+0.03\ \mathrm{m s^{-1}}$. Maximum ebbing current velocities of $+0.27\ \mathrm{m s^{-1}}$ were observed just before 0200 hours (Fig. 3b); again, no thin layers were observed when near-maximum current velocities were measured. Unfortunately, there was some data loss between 0200 and 0400 hours on 3 May due to failure of an I/O adapter connected to the ADCP data cable.

There was also some across-shore (across-isobath) current activity. The across-shore currents were lower in velocity and display more shear with depth. Between 1800 hours on 2 May and 0700 hours on 3 May, when currents were directed onshore, the average onshore current velocity was $+0.05\ \mathrm{m s^{-1}}$ with maximum current velocities of $+0.11\ \mathrm{m s^{-1}}$. When currents were directed offshore, the average offshore current velocity was $-0.03\ \mathrm{m s^{-1}}$, with maximum current velocities of $-0.06\ \mathrm{m s^{-1}}$. Many across-shore events off leeward Oahu are associated with “cold pulses” (McManus et al. 2008). One example of a cold pulse (with colder, higher salinity, and denser water) can be seen in Fig. 3 just after 2300 hours between the bottom and 14-m depth. The pulse is characterized by rapid onshore velocities (+east) in the lower water column, and offshore velocities (−west) in the upper water column, and is accompanied by increased buoyancy frequencies in the lower water column. These cold pulses were first noted by McManus et al. (2008) and are described in detail in Sevadjian et al. (Planktonic responses to episodic near-bottom water pulses in tropical waters, in review).

Stratification

During our study, periods of significant stratification were short-lived and intermittent, with the periods of most persistent stratification occurring during the late afternoon and early evening due to a combination of light winds from the west, warm air and surface sea surface temperatures, and low current velocities during a neap tidal phase.

There was no significant rainfall in May, nor are there significant land-based sources of freshwater in our study region. Thus, the observed salinities fall within a narrow range, and stratification was primarily influenced by temperature. Cold pulses can temporarily increase the density gradient near-bottom (Sevadjian et al. in review). Although these near-bottom intrusions are higher in salinity, overall, temperature remains the main determinant of the density of these inner-shelf tropical waters.

Thin Layers of Chl-*a* Fluorescence

Between 1800 hours on 2 May and 0700 hours on 3 May, we took one profile every ~4 min, resulting in 158 profiles over this 13-h period. Using the strict criteria set forward in “Materials and Methods,” 35 individual observations of thin layers were identified over the 13-h period. Thus, thin layers were found in 20.2 % of the shipboard profiles (Fig. 3d).

One of the criterion used to classify the layered structures as a thin layer was that the layer must be present in more than one profile. Of the 35 individual observations of thin chlorophyll peaks, we observed 12 continuous thin layers. The average length of time these layers persisted was 18.7 min; some layers persisted on time frames as short as 4.0 min (e.g., for only two profiles), while one layer lasted 59.0 min. Layers observed in the early evening hours of 2 May, when thermal stratification was strongest, persisted longer than layers observed at any other time.

Thin layers ranged in vertical thickness from a minimum of 21 cm to a maximum of 129 cm. Of all 35 individual layer observations, the average vertical thickness was 67 cm. There was no significant trend in layer thickness over the study period. Estimated peak chlorophyll concentrations of the thin layers ranged in chlorophyll estimate from a minimum of 2.8 (mg m^{-3}) to a maximum of 4.2 (mg m^{-3}), with an average chlorophyll estimate of 3.6 (mg m^{-3}). Estimated background chlorophyll concentrations ranged in chlorophyll estimate from a minimum of 1.8 (mg m^{-3}) to a maximum of 3.1 (mg m^{-3}), with an average chlorophyll estimate of 2.2 (mg m^{-3}). When the estimated chlorophyll concentration is integrated across the water column, the average value was 43.9 (mg m^{-2}). When the estimated chlorophyll concentration is integrated within the depths of thin layers, values ranged from a minimum of 0.5 (mg m^{-2}) to a maximum of 5.1 (mg m^{-2}), with an average of 2.1 (mg m^{-2}). Thus, thin layer structures represent an average of 4.78 % (with a minimum of 1.14 % and a maximum of 11.62 %) of the total integrated chlorophyll.

Comparison of Physical Conditions and Thin Layers of Chl-*a* Fluorescence

Buoyancy frequency was calculated from physical measurements made at the exact depth interval of each thin layer. Buoyancy frequency indicates the strength of the vertical density gradient. Thin layers were located in regions of the water column where buoyancy frequency averaged 2.14×10^{-4} rad^2 s^{-2}, with a standard deviation of 2.77×10^{-4} rad^2 s^{-2}. Over the entire 13 h for all depths, the mean buoyancy frequency was 1.34×10^{-4} rad^2 s^{-2}, with a standard deviation of 1.79×10^{-4} rad^2 s^{-2} (Fig. 3g).

The layers ranged in depth from the near-surface (2.00 m) to near-bottom (21.25 m), with an average depth of 8.37 m. In the early evening hours of 2 May (1800–2230 hours), when the water column was thermally stratified, the layers were located in the upper region of the water column, with an average depth of 6.76 m and with low variance in depth. As the nighttime air cooled and, consequently, the water column cooled and convectively overturned, the layers were located deeper in the water column, with an average depth of 11.63 m and with increased variance in depth (Fig. 3d).

Sevadjian et al. (2010) found that over a 3-week period, depth-averaged N^2 was the lowest between 2200 and 1000 hours in Hawaiian coastal waters. Observations of cooling air temperatures after sunset and the low N^2 lead these investigators to conclude that convective overturn was occurring. At our study site, we found that depth-averaged N^2 decreased from 1800 to 2200 hours (Fig. 3g). This, combined with our observations of significant (−6.74°C) decreases in air temperature during the same time frame, leads us to conclude that the water column had the potential to convectively overturn after sunset.

Each of the 12 continuous thin layers we observed tended to lie along similar isopycnals (e.g., surfaces of constant density). In the early evening of 2 May, when the water column was thermally stratified, the layers were located on lighter isopycnals: σ_t averaged 23.63. As the nighttime air cooled and the surface waters convectively overturned, the layers were located on heavier isopycnals: σ_t averaged 23.83.

We were able to estimate the minimal horizontal spatial extent of each thin layer observed using the measured flow speed and the length of time we observed each layer. Shorter-lived layers measured ~0.2 km, while some longer-lived layers measured up to ~0.8 km in horizontal spatial extent. While this is not a definitive measure of spatial extent in the horizontal, it does provide some indication of the minimum size of these patches.

Discussion

Our observations are the first known observations of thin phytoplankton layers in tropical Hawaiian waters. A combination of an instrument platform, which is disassociated from ship movement, and high sampling rates made these fine-scale observations possible.

The greatest number of thin layers (68.6 %) was observed in the early evening hours (between 1800 and 2230 hours). Near-surface thermal stratification was stronger and more persistent during this period than any other period. This pronounced stratification was due to a combination of light winds from the west, warm air and sea surface temperatures, and low current velocities during a neap tidal phase. Between 2100 and 2200 hours, a combination of increased wind velocities from the south–southeast and a significant reduction in air temperatures led to decreased near-surface thermal stratification and, conversely, decreased buoyancy frequencies.

During an overnight study in Monterey Bay, Cheriton et al. (2009) used a similar instrument platform, the high-resolution profiler, with high sampling rates to quantify the physical structure and thin optical layers in the northeast corner of this bay in central California. During the Monterey Bay survey, a time series of 99 profiles was taken from 2130 hours on 26 August to 0600 hours on 27 August 2005, averaging one profile roughly every 5 min. This 8.5-h study, which covered an entire flood tide, was conducted at the transition from spring to neap tide, during a period of strong thermal stratification. Over the 8.5-h study, the temperature gradient between the surface (2 m) and the bottom measurement (16.5 m) averaged 4°C (Cheriton et al. 2009). It should be noted that similar to the west shore of Oahu, freshwater input into Monterey Bay during the summer and fall is minimal (Breaker and Broenkow 1994); thus, stratification in this region during the summer and fall is primarily due to temperature. A thin layer of particulate absorption at a wavelength of 440 nm was observed at the pycnocline over the entire 8.5-h period. While thin layers were evident in 97 of the 99 profiles (98 %), the feature broadened and increased in absorption over the survey period.

Throughout the Monterey Bay survey, the in-layer buoyancy frequency (N^2) remained fairly constant at 5.00×10^{-4} rad^2 s^{-2}. In the Hawaiian study, the in-layer buoyancy frequencies (N^2) averaged 2.14×10^{-4} rad^2 s^{-2}. This average value is less than one half of the value measured in Monterey Bay.

There is a striking difference in the persistence of the layers observed off the west shore of Oahu and the layer observed in the northeast corner of Monterey Bay by Cheriton et al. (2009). The thin layer observed by Cheriton et al. (2009) persisted for the entire 8.5-h sampling period. The thin layers observed off the west shore of Oahu persisted for a fraction of this time. The thin layers observed off the west shore of Oahu during the 2–3 May study persisted from a minimum time frame of 4 min (in other words, single layers observed in only two consecutive profiles) to a maximum of 59 min.

Thermal stratification (magnitude and persistence) of the Hawaii site was low relative to the Monterey Bay location. During the Hawaii study, when layers were observed, the temperature gradient (ΔT) between the surface (2 m) and the bottom (20 m) ranged from 0.4 to 1.5°C (Fig. 3h). In contrast, during the 8.5-h experiment in Monterey Bay, the temperature gradient between the surface (2 m) and the bottom measurement (16.5 m) averaged 4°C. Furthermore, the range of density sampled in the Monterey Bay overnight experiment was 24.5–25.5 ($\Delta1.0\sigma_t$), while the ranges of density between the surface and bottom measured during the Hawaii experiment was 24.02–23.52 ($\Delta0.5\sigma_t$). It follows that areas with stronger and more persistent periods of stratification would have layers that persist for longer periods of time.

Instances of significant stratification in Hawaii were short-lived; buoyancy frequencies where layers were observed in coastal Hawaiian waters were one half the values in Monterey, and most likely as a result, thin phytoplankton layers were shorter in duration. A similar pattern has been observed for thin zooplankton layers off the southern shore of Oahu by Sevadjian et al. (2010); the clear conclusion from both of these studies is that the nature and persistence of the physical structure is very important in determining the persistence of these layered structures.

Organism behavior may also play a role in the formation and maintenance of thin layers of phytoplankton. Cheriton et al. (2009) observed that the thin layer was populated by strong-swimming, vertically migrating dinoflagellates. These organisms spent daytime hours at the surface for photosynthesis and the nighttime hours at the persistent pycnocline uptaking nutrients. It is important to note that while biological processes contributed to the formation of the layer observed by Cheriton et al. (2009), it was the underlying physical environment that provided the critical behavioral cue leading to the layered aggregation of these organisms (Cheriton et al. 2009; Steinbuck et al. 2009). In a study in northern Monterey Bay, Benoit-Bird et al. (2010) found that trophic interactions were likely occurring between phytoplankton and zooplankton thin layers, but that phytoplankton thin layers were exploited by zooplankton only when phytoplankton thin layers represented a large fraction O[18–20 %] of the available phytoplankton in the water column. Because plankton biomass is generally lower in tropical regions, like Hawaiian coastal waters, the heterogeneous aggregation of phytoplankton into thin subsurface layers may even be more critical to the marine ecosystem than it is in temperate regions where plankton are generally more abundant (after Holliday et al. 2010).

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