Turbulent mixing in fine-scale phytoplankton layers: Observations and inferences of layer dynamics

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Turbulence measurements in fine-scale phytoplankton layers (~1 to ~10 m) in the Gulf of Aqaba (Red Sea) were used to evaluate mechanisms of layer formation, maintenance, and breakdown. Simultaneous profiles of chlorophyll a (Chl a) fluorescence and temperature microstructure were measured in the upper 40 m of a 430 m water column over a 16-d period, using a Self Contained Autonomous MicroProfiler (SCAMP). Layers of concentrated phytoplankton were identified in 95 of the 456 profiles. The layers were situated in density stratiﬁed regions between 15 and 38 m depth and were characterized by intensities of 0.1 to 0.35 µg Chl a L−1 (as much as two times background concentrations) and an average thickness of 10 m. We show that turbulent mixing and isopycnal displacements associated with internal waves modulated the thickness of the layers. Variations in mixing rates within layers were connected to the vertical structure of the stratiﬁed turbulence and the stage of layer development. The breakdown of a persistent phytoplankton layer was tied to strong turbulent mixing at the base of the surface mixed layer, which encroached on the layer from above. Hydrographic observations and scaling analysis suggest that the layers most likely formed in horizontal intrusions from the adjacent coastal region. The cross-shore propagation of phytoplankton-rich intrusions may have important implications for the trophic state of offshore planktonic communities.

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1. Introduction

There has been a recent surge of interest in planktonic layers in the coastal ocean with vertical scales ranging from the fine-scale (~1 to ~10 m) to the microscale (< ~1 m). These features have anomalously high concentrations of plankton compared to vertically adjacent portions of the water column and may span kilometers in the horizontal (Dekshenieks et al., 2001). This small-scale vertical organization of plankton may have important ecological implications, including effects on behavior, reproduction, growth, predation, remineralization, and community composition (Cowles et al., 1998; McManus et al., 2003). Technological advancements in ocean optics and acoustics have permitted detailed descriptions of thin planktonic layers (Cowles et al., 1993; Holliday et al., 2003; Twardowski et al., 1999).

Several physical and biological processes have been proposed to explain the formation of fine- and microscale plankton layers (sometimes described as thin layers). Nielsen et al. (1990) documented the role of in situ growth in the development of a thin, mid-column phytoplankton layer. Sullivan et al. (2010) observed phytoplankton thin layers form via diurnal vertical migration. Kononen et al. (2003) found both migratory behavior and growth to be important in explaining relatively thin deep chlorophyll maximum (DCM) layers. Alldredge et al. (2002) observed a thin layer of marine snow form via particle settling at a depth of neutral density. Franks (1995) proposed a shear-induced straining mechanism for phytoplankton thin layer formation, further developed by Stacey et al. (2007) and Birch et al. (2008) and supported in field observations (Ryan et al., 2008). Bo Pederson (1994) linked observations of phytoplankton layers to intrusions generated by boundary mixing in shallow tidal flows.

The vertical structure and development of planktonic layers are also affected by the interplay of turbulence and density stratification. Dekshenieks et al. (2001) found phytoplankton thin layers only in regions of the water column with Richardson numbers, Ri, greater than the critical value of 1/4, suggesting that the stratification was sufficiently strong to suppress shear...
instabilities. McManus et al. (2003) observed a thin layer associated with buoyancy Reynolds numbers, \( \Re_b \), typically less than 15, indicating that the turbulence was dominated by stratification and likely insufficient to diffuse the layer through vertical mixing. Using scaling analysis, Stacey et al. (2007) showed that straining or particle buoyancy might have maintained thin layers of phytoplankton in the presence of turbulent diffusion in East Sound, Washington.

In this paper, we present observations of turbulence in fine-scale phytoplankton layers that occur in the upper 40 m of the Gulf of Aqaba, Red Sea. Scaling analysis and hydrographic observations suggest that the layers most likely formed in horizontal intrusions from the adjacent coastal region. The detailed physical measurements highlight the role played by stratified turbulence, advection, and internal waves in regulating layer dynamics and development.

2. Methods

2.1. Study site

The Gulf of Aqaba is a desert-bordered, semi-enclosed gulf located at the northeast end of the Red Sea. The gulf is approximately 180 km long, 6–25 km wide, and has a maximum depth of 1820 m. The sampling station (29.492°N, 34.929°E) was located approximately 1.6 km offshore of the Steinitz Marine Laboratory at the northern end of the gulf and had a local depth of approximately 430 m (Fig. 1). The temperature and salinity of summer surface waters are near 27 °C and 41 psu, respectively (Paldor and Anati, 1979; Reiss and Hottinger, 1984). Semi-diurnal tides, buoyancy, and wind stress are primary forcing mechanisms for the near-surface currents, which are typically in the range of 5–30 cm s\(^{-1}\) (Berman et al., 2000, 2003; Genin and Paldor, 1998; Monismith and Genin, 2004; Monismith et al., 2006). The Gulf of Aqaba is an oligotrophic marine system (Reiss and Hottinger, 1984). Chlorophyll \( \alpha \) (Chl \( \alpha \)) concentrations are typically between 0.02 and 0.8 \( \mu g L^{-1} \) (Berninger and Wickham, 2005) and the summer phytoplankton community is comprised primarily of Prochlorococcus and Synechococcus spp. (e.g. Al-Najjar et al., 2006; Lindell and Post, 1995; Fuller et al., 2005).

2.2. Sampling overview

The vertical structure of Chl \( \alpha \) and relevant physical variables were measured 12 August to 2 September 2007, in the upper water column. A Self Contained Autonomous MicroProfiler (SCAMP, made by Precision Measurement Engineering, Carlsbad, California, USA; Carter and Imberger, 1986) was deployed on 10 separate occasions from a small, anchored research vessel (456 profiles in total, with each deployment consisting of 10–96 profiles and ranging from 2.3 to 26.3 h in duration). The SCAMP sampled temperature, salinity, pressure, and in vivo fluorescence at 100 Hz while free falling at \( \sim 10 \text{ cm s}^{-1} \). During deployment, SCAMP profiles were performed every 15 min to a depth of approximately 40 m. Meteorological variables (including wind speed) were sampled concurrent with SCAMP profiles from the small research vessel. Water samples were collected coincidentally with SCAMP profiling from a second small research vessel for 1 week of the study period (16–23 August). Ten water samplers positioned from 22 to 40 m depth (2 m vertical resolution) were deployed 34 times. Extracted Chl \( \alpha \) was measured for each sample and later used to calibrate the SCAMP fluorometer and infer Chl \( \alpha \) from all of the fluorescence measurements using a linear fit that accounted for day–night differences in fluorescence intensity (\( n=201, r^2=0.63 \)). The Israel National Monitoring Program (NMP, http://www.iie-ielat.ac.il/NMP/Default.aspx) also provided measurements of extracted Chl \( \alpha \) from the Steinitz Marine Laboratory pier and water property data near the study site (Fig. 1).

The vertical structure of velocity and temperature were measured with ADCPs and thermistors positioned on two moorings located within approximately 200 m of the anchored vessel from which SCAMP was deployed. The velocity was measured over 2–85 m depth, using two moored ADCPs positioned at approximately 20 m depth: one upward-looking 600 kHz RD Instruments (2–20 m depth, 0.5 m vertical resolution, 4 pings averaged and recorded every 1.5 s); one downward-looking 300 kHz RD Instruments (20–85 m depth, 2 m vertical resolution, 1 ping recorded every 1.5 s). Temperature was recorded over 0–46 m, using 25 SeaBird Thermisters separated by 2 m in the vertical (1 m separation in the upper 2 m of the water column) that sampled on 15 s intervals.

2.3. Data processing

Phytoplankton layers were identified from the Chl \( \alpha \) profiles inferred from SCAMP fluorescence. The upper edge of a layer was identified as the highest point in the profile in which the vertical gradient in Chl \( \alpha \) exceeded the background vertical gradient by a tolerance. Similarly, the lower edge of a layer was identified as the lowest point in the profile in which the vertical gradient in Chl \( \alpha \) fell below the background gradient by the same tolerance. The background gradient was estimated from the water column above the layers (i.e., between the surface and 15 m depth). The gradient tolerance was tuned to approximately \( 5 \times 10^{-3} \mu g L^{-1} \text{ m}^{-1} \) so that the low intensity shoulders of the layer were included in the layer, as the dynamics at the layer edges are important to layer development. Profiles with both upper and lower layer edges meeting the criteria above were marked as containing a layer and the layer thickness was defined as the vertical distance between the upper and lower edges. Note, this procedure yields

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**Fig. 1.** Map of the study site with regional geography inset. The primary sampling station is marked with a ‘+’ symbol at 29.492°N, 34.929°E and the Israel NMP station is marked with a ‘+’ symbol at 29.465°N, 34.929°E. Figure adapted from Shellenbarger et al. (2006).
higher estimates of layer thickness than the full-width, half-maximum approach (Dekcheniak et al., 2001).

The layers were analyzed in the context of relevant physical parameters. The measured temperature and salinity profiles from SCAMP were used to estimate the strength of stratification via the squared buoyancy frequency, $N^2 = -\frac{g}{\rho_0} \frac{\partial \rho}{\partial z}$ (where $g$ is the gravitational acceleration, $\rho_0$ is a mean density, and $\rho$ is the local density), in 50% overlapping 256 sample (~26 cm) data segments. The ADCP-measured velocities were transformed into along- and across-shore components (oriented 45 degrees clockwise of north and east, respectively). Estimates of the squared shear, $S^2 = \frac{\partial U}{\partial z}^2 + \frac{\partial V}{\partial z}^2$, were computed by analytically differentiating cubic spline fits to 10-min mean horizontal velocities ($U$, $V$) from the ADCPs. The competition between the stabilizing density stratification and destabilizing shear field was evaluated in terms of the gradient Richardson number, $Ri = \frac{N^2}{S^2}$, where the last term includes a scaling relation for the velocity in terms of the layer thickness and vertical shear, $U \approx \frac{\partial u}{\partial z}$, and where $l_h$ is the horizontal lengthscale of the initial planktonic patch. For a straining-diffusion balance ($-\frac{\partial l}{\partial t_{strat}} \sim -\frac{\partial l}{\partial t_{turb}}$) with constant shear and diffusivity, the horizontal dimension of the initial planktonic patch should scale as

$$l_h \approx \frac{\rho_0 c_{24} \langle u \rangle}{K}$$  \hspace{1cm} (4)

Considering convergent swimming towards the layer centerline, the rate of layer contraction scales with the vertical swim speed of the cells in and around the layer

$$\frac{\partial l}{\partial t_{swim}} \sim -w_s$$ \hspace{1cm} (5)

For a swimming-diffusion balance ($-\frac{\partial l}{\partial t_{swim}} \sim -\frac{\partial l}{\partial t_{turb}}$), the required swim speed scales as

$$w_{bal} \sim \frac{K}{T}$$ \hspace{1cm} (6)

Similarly, cell settling to a layer of neutral density results in a layer contraction rate that scales with the velocity of the cells in and around the layer. For a low particle Reynolds number ($Re_p \ll 1$), Stokes’ law for the terminal settling velocity can be used to develop a scaling estimate for the rate of layer thinning

$$\frac{\partial l}{\partial t_{buoy}} \sim \frac{N^2 D^2}{18 \nu}$$ \hspace{1cm} (7)

where $N$ is the local buoyancy frequency, $D$ is the particle diameter, and $\nu$ is the viscosity. Neutral buoyancy within the layer is assumed, as the convergence associated with sinking cells passing through a pycnocline is unlikely to produce the observed layers. The spherical shape considered here is a good approximation for the most abundant phytoplankton, Prochlorococcus and Synechococcus spp. For a settling-diffusion balance ($-\frac{\partial l}{\partial t_{buoy}} \sim -\frac{\partial l}{\partial t_{turb}}$), a scale estimate for the required planktonic particle diameter is given by

$$D_{bal} \sim \sqrt{\frac{18 K}{N^2 \nu}}$$ \hspace{1cm} (8)

In the case of symmetric (two-sided) settling or swimming centered about the layer, the above scaling relations above should still be appropriate, with an implicit $O(1)$ factor of two (representing the additive effect of the two convergence rates) being absorbed.

The scaling estimates for $I_b$, $w_{bal}$, and $D_{bal}$ are later compared to known or inferred values to evaluate the viability of a particular dynamical balance. We note that the expansion and contraction of isopycnals due to internal waves may modulate the layer thickness scale, $l$ (by up to a factor of approximately two in the present study). However, given that we are interested in evaluating the order of magnitude of the scaling parameters, this effect should be relatively inconsequential for estimates of $w_{bal}$ and $D_{bal}$, which vary with $l^{-1}$. Since $l_b$ varies with $l^2$, the influence of internal waves is greater and the robustness of scaling estimates of $l_b$ benefits from averaging over different internal wave conditions.

3. Observations of layers

3.1. Hydrographic setting

Over the study period, the vertical structure of temperature, salinity, irradiance, nitrate, phosphate, and Chl $a$ were relatively stationary for the water column as a whole, as seen in profiles collected by the Israel NMP south of the study site (Fig. 2). This vertical structure is consistent with previous studies (e.g., Lindell and Post, 1995) and is similar to that observed at other NMP stations in the northern gulf over the same period. Typical of late summer conditions, the upper water column was strongly stratified.
upper 100 m, salinity and temperature both decreased with depth. The NMP profiles show that the deep chlorophyll maximum (DCM) was positioned at approximately 60–80 m depth, with a magnitude of 0.32–0.36 µg L\(^{-1}\). The DCM was approximately collocated with the top of the nitracline and phosphocline. Nitrate and phosphate varied from \(~10^{-2}\) µmol L\(^{-1}\) in the upper 60 m to values near 3 and 0.2 µmol L\(^{-1}\), respectively at the base of the nutricline (~250 m). In the study region ranging from the sea surface to approximately 40 m depth, the Chl \(a\) concentration was typically in the range of 0.1–0.25 µg L\(^{-1}\), with an increase in concentration with depth. For the two NMP profiles performed just after 11:00, irradiance was roughly 1200 µEin m\(^{-2}\) s\(^{-1}\) at 1 m depth and decayed to approximately 8% (100 µEin m\(^{-2}\) s\(^{-1}\)) at 40 m and 1% (12 µEin m\(^{-2}\) s\(^{-1}\)) at 80 m depth.

3.2. Layers and turbulence

Layers of enhanced Chl \(a\) were observed throughout the period of SCAMP profiling, 15–30 August 2007. Layers were identified with the gradient threshold technique in six of the 10 deployments of SCAMP. In one additional deployment, a layer structure was present, though the relatively weak Chl \(a\) gradients did not meet the gradient threshold criteria. In total, layers were identified in 20.8% of the profiles (95 of the 456 profiles) (Table 1). The layers were observed to persist for variable durations ranging from less than 1 h to approximately 17 h. Layers were observed at depths of 15–38 m and had vertical dimensions of approximately 4–21 m (Table 1). These layers were located 20–65 m above the DCM and the top of the primary nutricline.

The Chl \(a\) layers were observed in density stratified regions, below stratified or mixed surface layers and above a stratified interior (Fig. 3). The in-layer N\(^2\) values were primarily in the range 10\(^{-5}\) and 10\(^{-4}\) s\(^{-2}\). The layers were also found in regions of decreasing temperature and salinity with depth (Fig. 3). The Chl \(a\) content of the layers was elevated relative to the vertically adjacent waters, typically by 0.02–0.15 µg L\(^{-1}\) or by as much as a factor of two (Fig. 4). However, since there was often a background gradient in Chl \(a\) (increasing concentration with depth, Fig. 2), the concentrations within layers were sometimes comparable to concentrations at the base of the profiles, approximately 40 m depth (Fig. 3).

Within the Chl \(a\) layers, turbulence intensity and mixing rates were variable. Flows were typically stable to shear instabilities (\(Ri > 1/4\)) and \(\varepsilon\) was typically in the range of 10\(^{-10}\)–10\(^{-7}\) m\(^{2}\) s\(^{-3}\). The state of the stratified turbulence ranged from stratification-dominated (\(\text{Re}_b < 15\)) to turbulence-dominated (\(\text{Re}_b > 100\)) and \(K_z\) spanned five orders of magnitude, though near-molecular values (~10\(^{-7}\) m\(^{2}\) s\(^{-1}\)) were quite frequent (Fig. 4). The mixing conditions in the water column underlying layers were similar: typically \(Ri\) was above the critical value of 1/4; and the distributions of \(\text{Re}_b\) and \(K_z\) were similar, though with slightly more frequent occurrences of low \(\text{Re}_b\) and low \(K_z\) (Figs. 3, 4). In contrast, the mixing was more active in the overlying surface layer: the flows were typically susceptible to shear instabilities...
and the dissipation rates were primarily between $10^{-9}$ and $10^{-7}$ m$^2$ s$^{-3}$, with a large number of occurrences of $R_i < 1/4$ and $10^{-4} < K_z < 10^{-2}$ m$^2$ s$^{-1}$ (Figs. 3, 4). For periods in which a surface mixed layer (SML) and Chl $a$ layer were both present, the Chl $a$ layer was often positioned just beneath the SML (Fig. 3). In these cases, the top of the Chl $a$ layer was often collocated with a transition from $R_i < 1/4$ and high $K_z$ in the SML to $R_i > 1/4$ and low $K_z$ in the pycnocline (Fig. 3).

### 3.3. Development of a persistent layer

In this section, the maintenance and breakdown phases of layer development are examined for the most persistent phytoplankton layer, present on days 241 and 242. The layer was observed over a 17 h period in a 25 h record, between 15 and 35 m depth (Fig. 5). The 10-min mean in-layer velocities ranged from $\pm 20$ cm s$^{-1}$ in the alongshore direction and $+6$ and $-8$ cm s$^{-1}$ in the across-shore direction. Over the 17 h period, the layer appeared to translate 2 km, as determined by time integrating the in-layer velocities and assuming a horizontally homogeneous flow field. Thus, the layer was likely at least 2 km in horizontal extent. The observed lifetime of the layer may be separated into two stages: (stage 1) thick (roughly 10–20 m in vertical extent), intense, and persistent for the first 8.5 h (11:00–19:30); (stage 2) thin (~5 m), relatively less intense, and intermittently present for 8.5 h (19:30–04:00). In the final 8 h following stage 2, there was no distinct layer present.

#### 3.3.1. Stage 1: Persistence and modulation by internal waves

In stage 1 (11:00–19:30), the layer was thick, intense, and persistent. The in-layer Chl $a$ concentration at times exceeded 0.3 µg L$^{-1}$, as much as two times that of the vertically adjacent water (Fig. 5A). The layer was sandwiched between two steps in both temperature and salinity, just below the SML and above the

### Table 1

Summary of Chl $a$ layer occurrences and properties from SCAMP deployments, using the gradient threshold criteria for layer identification. The layer detection algorithm did not identify layers for four deployments marked as "others." Mean layer depth and thickness are shown, as well as minimum and maximum values in square brackets.

<table>
<thead>
<tr>
<th></th>
<th>All days</th>
<th>227–228</th>
<th>231–232</th>
<th>233 day</th>
<th>233 night</th>
<th>234–235</th>
<th>241–242</th>
<th>Others</th>
</tr>
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<td>94</td>
<td>12</td>
<td>12</td>
<td>96</td>
<td>96</td>
<td>50</td>
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<tr>
<td>Profiles w/layers (#)</td>
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<td>10</td>
<td>5</td>
<td>9</td>
<td>1</td>
<td>26</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>Percentage w/ layers (%)</td>
<td>20.8</td>
<td>10.4</td>
<td>5.3</td>
<td>75</td>
<td>8.3</td>
<td>27.1</td>
<td>45.8</td>
<td>0</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>[15.0]</td>
<td>[24.7]</td>
<td>[16.3]</td>
<td>[23.0]</td>
<td>[25.5]</td>
<td>[15.0]</td>
<td>[16.3]</td>
<td>–</td>
</tr>
<tr>
<td>Thickness (m)</td>
<td>[3.9]</td>
<td>[4.1]</td>
<td>[4.6]</td>
<td>[9.0]</td>
<td>[9.8]</td>
<td>[3.9]</td>
<td>[4.3]</td>
<td>–</td>
</tr>
</tbody>
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![Fig. 3](image-url) (A) Profiles of Chl $a$, temperature, and salinity for a sample Chl $a$ layer. (B) Associated profiles of turbulent diffusivity, log$_{10}(K_z)$ (m$^2$ s$^{-1}$)), normalized Richardson number, log$_{10}(4R_i)$, and buoyancy Reynolds number, log$_{10}(Re_b)$. Chl $a$ layer edges are marked with solid horizontal lines at approximately 23 m and 29 m depth in both panels. In panel (B), a vertical dashed line marks log$_{10}(4R_i)$=0, corresponding to a critical $R_i=1/4$, and vertical dotted lines mark $Re_b=15$ and $Re_b=100$. The profile was taken from 03:00 of day 235.

(Ri < 1/4); and the dissipation rates $\varepsilon$ were primarily between $10^{-9}$ and $10^{-7}$ m$^2$ s$^{-3}$, with a large number of occurrences of $Re_b > 100$ and $10^{-4} < K_z < 10^{-2}$ m$^2$ s$^{-1}$ (Figs. 3, 4). For periods in which a surface mixed layer (SML) and Chl $a$ layer were both present, the Chl $a$ layer was often positioned just beneath the SML (Fig. 3). In these cases, the top of the Chl $a$ layer was often collocated with a transition from $R_i < 1/4$ and high $K_z$ in the SML to $R_i > 1/4$ and low $K_z$ in the pycnocline (Fig. 3).
stratification, strong temperature and salinity gradients and derived density region just within the defined layer edges) were collocated with stable to shear instabilities (top and bottom of the layer were situated in regions that were not independent: both depend on stratification and likely anisotropic. In this case, the intermediate 15–100 (Fig. 5F), indicating active turbulence that was affected by buoyancy Reynolds numbers were in the intermediate range of stability of the in-layer flow, quantified as Richardson number, log10(Reb), varied approximately 0.1 C, indicating the onset of nighttime surface cooling. Over the same period, the wind relaxed from approximately 7 to 3 m s\(^{-1}\) at 3.9 m above the sea surface, suggesting that wind stirring played a secondary role in the deepening process. This nighttime deepening was observed throughout the study period, likely due primarily to penetrative convection.

The deepening of the SML resulted in elevated turbulent mixing at the top of the layer, eroding the layer from above (Fig. 5G). As a result, the layer in stage 2 was thinned by vertically differential mixing (to \(\sim 5 \text{ m}\) in vertical extent) and weakened in intensity to approximately 0.2 \(\mu\)g L\(^{-1}\) (Fig. 5A). Relatively homogeneous distributions of temperature, salinity, and Chl a associated with the SML were observed at depths that the layer occupied during stage 1 (Fig. 5). Thus, the breakdown of the layer was strongly tied to enhanced mixing associated with the SML that encroached on the layer from above.

It is important to note that while the changes between stage 1 and stage 2 are likely due in part to temporal variations in the SML.

In stage 1, internal waves modulated layer thickness and vertical position (Fig. 5B). The layer was located approximately between the 27 and 27.4 C isotherms. With the passage of internal waves, isotherms (and isohalines) expanded, contracted, and migrated vertically. The edges of the layer tracked well with the variably positioned isotherms.

3.3.2. Stage 2: Intermittency and breakdown

In stage 2 (19:30–04:00), the layer was thin, less intense, and intermittently present (Fig. 5A). The SML deepened to 40 m depth over this period. Sea-surface temperature decreased by approximately 0.1 C, indicating the onset of nighttime surface cooling. Over the same period, the wind relaxed from approximately 7 to 3 m s\(^{-1}\) at 3.9 m above the sea surface, suggesting that wind stirring played a secondary role in the deepening process. This nighttime deepening was observed throughout the study period, likely due primarily to penetrative convection.

The deepening of the SML resulted in elevated turbulent mixing at the top of the layer, eroding the layer from above (Fig. 5G). As a result, the layer in stage 2 was thinned by vertically differential mixing (to \(\sim 5 \text{ m}\) in vertical extent) and weakened in intensity to approximately 0.2 \(\mu\)g L\(^{-1}\) (Fig. 5A). Relatively homogeneous distributions of temperature, salinity, and Chl a associated with the SML were observed at depths that the layer occupied during stage 1 (Fig. 5). Thus, the breakdown of the layer was strongly tied to enhanced mixing associated with the SML that encroached on the layer from above.
depth, advection should not be neglected. For example, the rapid reappearance of the layer (on the scale of \( \sim 15 \) min or less) after periods of absence in stage 2 suggests that the layer was likely advected back into the sampling site, not regenerated. From this perspective, layer absences may be interpreted as gaps in the layer, which may have formed in locations where the SML extended to the depths of the layer.

4. Inferences of formation and maintenance

We now examine the formation and maintenance of all observed phytoplankton layers. The scaling approach of Stacey et al. (2007) is applied to assess the role of straining, swimming, and cell buoyancy. Horizontal intrusions and in-layer growth are evaluated subsequently.

Fig. 5. (A) Chl a (\( \mu g L^{-1} \)) of an intense and persistent layer observed during a 25 h SCAMP deployment on days 241 and 242. (B) Temperature contours from the same period (26.2–27.4 °C with 0.2 °C resolution). The 27 and 27.4 °C isotherms are labeled. (C) Squared buoyancy frequency, \( \log_{10}(N^2) \). (D) Squared vertical shear of horizontal velocities, \( \log_{10}(S^2) \). (E) Normalized Richardson number, \( \log_{10}(4Ri) \). (F) Buoyancy Reynolds number, \( Re_b \). (G) Vertical turbulent diffusivity, \( \log_{10}(K_z) \). Identified layer edges are overlaid with black circles in all panels. Note, shear estimates derived from the ADCPs in panel (D) extend to 85 m depth, while fields derived from SCAMP profiles are limited to the upper 40 m.
4.1. Straining, swimming, and cell buoyancy

For each profile containing a layer, the mean in-layer squared buoyancy frequency, squared shear, and diffusivity were computed (Fig. 6A, C, E). Using these values, the parameter scales associated with candidate dynamical balances were estimated: $l_b$ (straining–diffusion); $w_{bal}$ (swimming–diffusion); and $D_{bal}$ (buoyancy–diffusion) (Fig. 6B, D, F).

First, we consider the potential formation and maintenance of layers by the tilting and straining of horizontal patches of plankton by the shear field. For a straining–diffusion balance, the initial scale of the phytoplankton patch may be estimated, assuming constant shear and diffusivity over the lifetime of the layer. The median values of the horizontal scale of the patch are in the range of $10^2$–$10^4$ km for all layer events (Fig. 6B). This range of implied patch sizes is inconsistent with the patch sizes that could have likely been supported near the head of the gulf, on the order of $10^5$–$10^6$ km. The layers were also associated with moderate to weak shear (e.g., Fig. 5D) and appeared to track well with isotherms (e.g., Fig. 5B), rather than cross them as expected for the tilting mechanism (Franks, 1995). Thus, the tilting of a horizontal planktonic patch was not likely a primary mechanism for the formation and maintenance of these layers.

Second, we consider a swimming–diffusion balance. The median swim speeds required to maintain the layers in the presence of diffusion are in the range of $10^{-2}$–$10^{-1}$ km. However, there is some evidence that motile Clade III Synechococcus, the dominant Synechococcus clade in late summer and Clade III Synechococcus (the motile clade) appeared at much lower levels of hybridization and strains isolated from this clade were actually found to be non-motile. Still, there is some evidence that motile Clade III Synechococcus are found in the Gulf of Aqaba at some times of year (Table 1 in Fuller et al., 2003). Laboratory measurements have indicated a swim speed range for individual Synechococcus cells of $5$–$25$ μm s$^{-1}$ (Waterbury et al., 1985). This swim speed range (which converts to $0.4$–$2.2$ m d$^{-1}$) is sufficiently large to explain the swim speed scaling estimates from the swimming-diffusion balance (Fig. 6D). Thus, the potential role of motility in layer formation is examined further.

The timescale of layer formation, $t_{form}$, via swimming may be estimated from the ratio of the Chl $a$ anomaly of the layer and the net flux of Chl $a$ into the layer from swimming.

$$t_{form} = \frac{\Delta C_{anom}}{\Delta w_{swim} C_{ext}}$$

where $\Delta C_{anom}$ (mg m$^{-2}$) is the anomaly (above background) in vertically integrated Chl $a$ within the layer, $\Delta w_{swim}$ (μm s$^{-1}$) is the change in the population-average vertical swim velocity across the layer, and $C_{ext}$ (mg m$^{-3}$) is the Chl $a$ concentration outside (external to) the layer. The timescale estimate in Eq. (9) is a lower bound given that the effect of the turbulent fluxes are not incorporated and it is assumed that all of the ambient Chl $a$, $C_{ext}$, is

![Fig. 6](image-url)

(A) In-layer squared buoyancy frequency, $N^2$ (C) in-layer squared shear, $S^2$ (E) in-layer vertical diffusivity, $K_z$ for all layer events, along with steady-state scaling estimates for (B) the initial horizontal scale of the Chl $a$ patch, $l_b$, inferred from a straining–diffusion balance, (D) the required vertical swim speed towards the layer centerline, $w_{bal}$, inferred from a swimming–diffusion balance, and (F) the required planktonic particle diameter, $D_{bal}$, inferred from a buoyancy–diffusion balance. Median values of the distributions are shown with a circle, while vertical bars show the extent of the 25th and 75th percentiles of the distributions for each layer observed.
found in motile Synechococcus, while previous studies have shown that non-motile Prochlorococcus is actually more numerous at these depths. A broad range of $\Delta w_{\text{swim}}$ (0–10 $\mu$m s$^{-1}$) is considered, which is reduced from the range for individual Synechococcus cells (5–25 $\mu$m s$^{-1}$; Waterbury et al., 1985) to account for reorientation by small-scale shear and variably directed swimming.

For the smallest observed Chl $a$ anomaly of a layer (0.075 mg m$^{-2}$), only the highest $\Delta w_{\text{swim}}$ considered ($\sim 6 $ $\mu$m s$^{-1}$ and above) allow the layers to form within ~1 d or less. For the mean Chl $a$ anomaly of the observed layers (0.43 mg m$^{-2}$), the formation timescale via swimming ranges from a few days (for 10 $\mu$m s$^{-1}$ swim speed) to $\sim 200$ d for weaker swimming. For the largest Chl $a$ anomaly (1.47 mg m$^{-2}$), the formation timescale is 10s to 100s of days for all swim speeds considered. These results suggest that swimming by motile Synechococcus could explain only the formation of the smallest Chl $a$ anomalies (smallest observed layers) in a reasonable timescale (couple of days or less), given the intermittency of the layer observations. For the majority of the observed layers, another mechanism is required.

It is worth noting that gut fluorescence in microzooplankton could have potentially contributed to the in vivo Chl $a$ signal of the layers. Microzooplankton ($< 100 \mu$m), including ciliates and unicellular zooplankton, reproduce extremely fast and are considered the major consumers of the ultraphytoplankton, making them a possible candidate for layer formation via swimming. Unfortunately, little is known about their density, migration or aggregation.

Third, we consider a buoyancy–diffusion balance. We find that the median diameter of particles required for the layer contraction rate to balance the expansion rate due to vertical turbulent diffusion is around $5 \times 10^3$–$4 \times 10^4$ $\mu$m (Fig. 6F). Yet, over 95% of the Chl $a$ is found in phytoplankton $< 5 \mu$m (Lindell and Post, 1995; Yahel et al., 1998). The settling rate of the abundant phytoplankton is insufficient to counter turbulent mixing. Thus, neither straining, swimming, nor cell buoyancy is a clear candidate for the formation of the layers and while swimming by motile Synechococcus is a plausible maintenance mechanism, this is highly unlikely given their rarity in previous years sampled.

4.2. Horizontal intrusions

We now consider the potential formation of the layers in horizontal intrusions. The temperature and salinity composition of the layers were distinct from the surrounding water column (Fig. 7). All layers were colder and less saline than the overlying water column and warmer and more saline than the underlying waters. Vertical mixing could explain such T–S structure, though not the embedded Chl $a$ layers. Horizontal intrusions could explain both the observed T-S structure and the Chl $a$ layers, as detailed below.

We investigate the origin of the layers by considering their horizontal position prior to arrival at the study site. Layer path lines were estimated by integrating the mean horizontal velocity at the depth of the layers (typically 20–35 m) backwards in time, starting from the first observations of the layers. Given that we integrated the velocity at the study site (not along the track of layer parcels), we assumed the flow field was horizontally homogeneous. We therefore interpret the path lines as rough approximations. The path lines indicate that the majority of the layers likely originated from the adjacent coastal region (Fig. 8A).

Two layers appeared to be transported alongshore to the sampling site, one from the northeast and one from the southwest. During deployments without layers, on the other hand, horizontal intrusions were observed in deployments without layers, but located at the same depths as layers.
advection was oriented from south to north, suggesting an offshore origin of these layer-devoid waters (Fig. 8B).

Given that the estimated path lines suggest that the layers were of coastal origin, we compare Chl \( a \) measurements made near the surface next to the Steinitz Marine Laboratory pier with near-surface and in-layer values at the sampling station 1.6 km offshore (Fig. 9). The comparison indicates that the nearshore surface values of Chl \( a \) were elevated by \( \sim 10^{-2} \) to \( \sim 10^{-1} \) \( \mu \text{g} \text{L}^{-1} \) relative to the surface values offshore, indicating a cross-shore gradient in Chl \( a \). Most interestingly, the Chl \( a \) values near the pier are comparable to the in-layer values offshore, suggesting that the nearshore waters were sufficiently rich in phytoplankton to be source waters for the offshore layers. It is also worth noting that the most intense and persistent layer (on days 241 and 242) was preceded by anomalously high Chl \( a \) at the pier, over 0.8 \( \mu \text{g} \text{L}^{-1} \) at its peak.

In these comparisons, we also consider the time of cross-shore transport. The time scale of intrusion propagation offshore is given by (Fischer et al., 1979)

\[
l_{\text{prop}} \sim \frac{L^2}{2K_H}
\]

where \( L \) is the distance offshore and \( K_H \) is a horizontal diffusion coefficient. In the presence of rotation, \( K_H \) may be estimated as \( K_H = Cg\rho^f \), with constant, \( C \), gravity anomaly, \( g \), intrusion thickness, \( h \), and coriolis parameter, \( f \) (Ivey, 1987). Using the results of Ivey (1987), we take \( C = 0.13 \) and \( g' = g'(0.14/2) \), where \( g' = g(0.14/2) \), and \( \rho_1 \) is the upper layer density (taken as the density at the top of the Chl \( a \) layers) and \( \rho_2 \) is a lower layer density (taken as the density at the base of the Chl \( a \) layers). For the distance \( L = 1.6 \) km to the sampling station and \( h = 3 \) set to the mean layer thickness for each layer event, \( l_{\text{prop}} \) ranges from approximately 5.0 to 19.5 h, which is comparable to the cross estimates from the path lines (Fig. 8A). Accounting for the time of offshore propagation, the pier and layer Chl \( a \) values remain comparable (Fig. 9).

We now consider whether an intrusion could persist as a fine-scale layer while propagating offshore in the presence of vertical mixing. For homogeneous turbulence, the vertical spreading of the layer scales as (Fischer et al., 1979)

\[
l' \sim \sqrt{2K_L l_{\text{prop}}}
\]

For the range of propagation timescales (5.0–19.5 h), we may expect a growth in layer thickness of 0.04–0.08 m (for \( K_L = 10^{-7} \) m\(^2\) s\(^{-1}\)).

\[
\Delta C_{\text{growth}} = \mu_{\text{net}} C_{\text{obs}} l_{\text{prop}}
\]

where \( \mu_{\text{net}} \) is the net production rate of Chl \( a \) (representing growth minus respiration and grazing across all taxa), \( C_{\text{obs}} \) is a background Chl \( a \) concentration (taken as the average concentration at the layer top and layer bottom), and \( l_{\text{prop}} \) is the timescale of intrusion propagation (Eq. (10)).

In this section, the potential role of phytoplankton growth in layer formation is considered. The phytoplankton community structure in late summer and at the depths of the layers (15–38 m) is largely comprised of the high light-adapted Prochlorococcus spp. and Synechococcus spp. (Fuller et al., 2005). Although each has unique adaptations to the quantity and quality of light, it is not expected that either would produce such fine-scale layers in response to the vertical variations in the light field. Instead, in-layer growth would likely require an influx of nutrients (note, nitrogen and phosphorous were scarce in the upper 100 m; Fig. 2). Prochlorococcus cannot take up nitrate, although some low light-adapted strains can use nitrite and all strains can take up ammonium as well as a diversity of organic nutrients (Moore et al., 2002). Synechococcus utilizes a wide variety of nutrient sources, organic and inorganic (Moore et al., 2002). Both Synechococcus spp. and Prochlorococcus spp. utilize comparable phosphorus stores (Fuller et al., 2005). During the summer when nutrient levels are at the level of detection, Synechococcus spp. exhibit phosphorus stress whereas Prochlorococcus spp. do not (Fuller et al., 2005). Bottle experiments have shown that the phytoplankton community as a whole is co-limited by both nitrogen and phosphorus in summer (Al-Qutob et al., 2002; Mackey et al., 2007). Here, we consider two potential supplies of nitrogen and phosphorus to the near-surface: horizontal intrusions from the adjacent coastline and vertical turbulent fluxes.

We first consider whether intruding waters could have transported nutrients that subsequently stimulated in-layer phytoplankton growth offshore. The increase in Chl \( a \) concentration due to growth within an intrusion, \( \Delta C_{\text{growth}} \), during transport from shore to the offshore sampling station may be estimated from a discrete form of the growth term in the advection-diffusion equation (e.g., Sharples, 2008)

\[
\Delta C_{\text{growth}} = \mu_{\text{net}} C_{\text{obs}} l_{\text{prop}}
\]

where \( \mu_{\text{net}} \) is the net production rate of Chl \( a \) (representing growth minus respiration and grazing across all taxa), \( C_{\text{obs}} \) is a background Chl \( a \) concentration (taken as the average concentration at the layer top and layer bottom), and \( l_{\text{prop}} \) is the timescale of intrusion propagation (Eq. (10)).

To evaluate the viability of layer formation by growth within intrusions, we compare \( \Delta C_{\text{growth}} \) and the observed Chl \( a \) anomaly of the layers, \( \Delta C_{\text{obs}} \), which is taken as the concentration peak of the layer minus the background concentration \( C_{b} \) (Fig. 10). In the comparison, we consider a range of net growth rates for nutrient replete conditions from \( \mu_{\text{net}} = 0.004 \) to 0.016 h\(^{-1}\). These values of \( \mu_{\text{net}} \) represent maximum growth rates (measured in incubation studies with over-saturated nutrients) minus measured in situ grazing rates, both taken from studies in the Gulf of Aqaba in 2007 and 2008 (Genin et al. unpublished results). The resulting median values of \( \Delta C_{\text{growth}} \) are less than \( \Delta C_{\text{obs}} \) for all of the observed layers for \( \mu_{\text{net}} = 0.004 \) h\(^{-1}\) and for all but one layer (on day 231) for \( \mu_{\text{net}} = 0.016 \) h\(^{-1}\) (Fig. 10). This suggests that growth within intrusions cannot alone explain the formation of the layers (even for nutrient-replete conditions) and that the intrusions would have needed to be rich in phytoplankton prior to transport offshore.
A second possible mechanism for stimulating growth in the near-surface is via vertical turbulent fluxes of nutrients $F_{N} = -K_{z}\frac{\partial \nu}{\partial z}$, where $K_{z}$ is the vertical diffusivity and $\nu$ is the nutrient concentration. An upper bound estimate of $F_{N}$ at the depths of the layers was computed using a high (likely overestimated) value of $K_{z}$ at the base of the layer, $10^{-5}$ m$^2$ s$^{-1}$ (Fig. 4), and the vertical gradient in nitrate and phosphate estimated from a linear fit to the measurements in the upper 60 m from August and September (Fig. 2). Using this approach, the upward vertical flux of nitrate and phosphate is at most $\sim 2.5 \times 10^{-10}$ and $\sim 1.1 \times 10^{-9}$ µmol L$^{-1}$ m s$^{-1}$, respectively. The timescale required to supply the nutrients needed to support the growth of the layers may then be estimated as

$$T_{\text{supply}} = \frac{\Delta N_{\text{anom}}}{F_{N}}$$

where $\Delta N_{\text{anom}}$ (µmol L$^{-1}$ m) is the anomaly in the in-layer, vertically-integrated nutrients (nitrate or phosphate) required to support the observed Chl $a$ layers. The timescale $T_{\text{supply}}$ should be a lower bound, as Eq. (13) assumes that the nutrients entering the layer are completely taken up (i.e., the flux at the layer top is assumed to be zero). The values of $\Delta N_{\text{anom}}$ were calculated as follows. First, the Chl $a$ anomaly of the layers was computed by vertically integrating the Chl $a$ content of the observed layers and subtracting the background Chl $a$ content. Next, the amount of phytoplankton carbon was estimated from the Chl $a$. In recognition of the uncertainty in the ratio C:Chl $a$, a reasonable range of values were considered: 20, 50, 100 g g$^{-1}$ (Lefèvre et al., 2003). Then, the mass of phytoplankton carbon was converted to moles of nitrogen and phosphorus using the molar mass of carbon and molar ratios for C:N:P = 106:16:1 (Redfield, 1934) to the molar ratios specific to Prochlorococcus spp. and Synechococcus spp. for nutrient limited conditions, C:N = 7.5:1 and C:P = 779:1 (high end of range in Bertilsson et al., 2003).

As seen in Fig. 11, the resulting timescale required for the supply of nitrogen is on the order of $10^{3}$–$10^{4}$ d, clearly very long compared to the observed intermittency in layer occurrence (hours to days). For phosphorus, the timescale of supply is around $10^{5}$–$10^{6}$ d for one limit of the underlying assumptions

$$(C/\text{Chl}) = 20 \text{ g g}^{-1}, \ C(\text{P}) = 779/1$$

and is approximately in the range of $10^{3}$–$10^{4}$ d for the other assumptions on the elemental composition of the cells. Taken as a whole, the results suggest that the vertical fluxes of nutrients were likely inadequate to stimulate the growth of the layers. Further, it is not likely that vertical turbulent fluxes of nutrients in the upper 40 m (several tens of meters above the top of the nutricline) would result in such distinctly layered growth (Fig. 2).

5. Discussion

5.1. Layer formation via intrusions

A number of previous studies have examined the role of coastal intrusions in supporting phytoplankton layers. For example, Simpson et al. (1982) developed a model of intrusion formation resulting from vertical mixing in the tidal flows around islands. The resulting nutrient-rich intrusions that may result was considered the result of boundary mixing (e.g., via shearing of tidal flows in the Celtic Sea. Bo Pederson (1994) developed a similar intrusion formation mechanism at tidal mixing fronts to explain the presence of phytoplankton layers in the North Sea and English Channel. Richardson et al. (2000) invoked the same mechanism to explain their observations of Chl $a$ peaks in the North Sea. The present study complements this previous work by further examining the dynamics and development of layers in the context of turbulent mixing processes offshore.

In the Gulf of Aqaba, coastal intrusions could possibly form as a result of boundary mixing (e.g., via shearing of tidal flows in the bottom boundary layer or by breaking internal waves; Bo Pederson, 1994; Ivey and Corcos, 1982; McPhee-Shaw et al., 2004; Simpson et al., 1982). Differential cooling is another possible mechanism for the formation of coastal intrusions. Monismith et al. (2006) observed cross-shore, subsurface flows developed in the Gulf of Aqaba in response to differential heating and cooling across-shore from surface heat fluxes. Neumann et al. (2004) observed a similar flow on the Jordanian side of the Gulf of Aqaba that transported phytoplankton-rich waters offshore at depth.
To further evaluate the plausibility of intrusion formation in the gulf, a cross-shore CTD transect was conducted immediately offshore of the Steinitz Marine Laboratory on 3 September 2008 (1 year after the study) using a Sea-Bird Electronics 19 CTD (Fig. 12). The thermocline and halocline both shoaled in the nearshore region (within ~0.3 km). The T–S signature of the inshore water was similar to deeper (~15 m deeper), stratified waters offshore, suggesting that deep waters were supplied to the shallow, nearshore environment perhaps by shoaling internal waves. Additionally, a cross-shore density (pressure) gradient was evident (Fig. 12C), which could produce an offshore flow. While this data cannot be linked to the layers in 2007, it does suggest that internal waves may play a role in mixing waters in the nearshore environment.

The cross-shore propagation of intrusions may be confined by rotation when the internal Rossby radius of deformation is small relative to the horizontal dimensions of the basin (Ivey, 1987). The Rossby radius is given by $L_D = Nh/f$, where $N$ is the buoyancy frequency, $h$ is the thickness of the intruding layer, and $f$ is the Coriolis parameter. For the Gulf of Aqaba, conditions of strong stratification offshore (maximum $N^2 \sim 10^{-3} \text{s}^{-2}$) and a typical layer thickness ($h=10\text{m}$; Table 1) imply an upper bound on $L_D$ of 4.4 km. We therefore expect the cross-shore extent of coastal intrusions to be bounded above by 4.4 km, or roughly half the width of the Gulf of Aqaba at the study site. Using a more typical strength of stratification in the pycnocline ($N^2 \sim 10^{-4} \text{s}^{-2}$), the Rossby radius, or implied horizontal extent of intrusion, is 1.4 km. The interplay of rotation and stratification will therefore be important to the cross-shore extent of intruding layers.

Cross-shore gradients in phytoplankton or nutrients coupled with cross-shore buoyancy-driven flows may represent a primary mechanism for fine-scale phytoplankton layer formation in the pycnocline of coastal environments and warrants further examination. The cross-shore flux of phytoplankton produced by such flows may also have important implications for the trophic state of offshore planktonic communities. For example, the presence of concentrated, fine-scale layers of phytoplankton would likely affect the transformation of carbon within the upper water column and alter the food web structure via interactions with zooplankton and virus communities (Cowles et al., 1998; Nagata...
In this study, fine-scale phytoplankton layer dynamics were considered in the context of turbulent mixing. The layers were observed at depths ranging from 15 to 38 m, in density-stratified regions with variable rates of turbulent mixing. Some of the variability in mixing rates within the layers was associated with the vertical structure of the stratified turbulence. The layers were often bounded below by a weakly turbulent, stratified interior and bounded above by a strongly turbulent surface mixed layer. There were also some occurrences of elevated mixing rates within the layer core as compared to layer edges.

The variability in mixing rates within layers was also tied to the stage of layer development. Analysis of a persistent layer on days 241 and 242 showed that initially, in stage 1, stratification insulated the layer from strong mixing in the SML above, allowing the layer to persist. The vertical structure and position of the layer during this period was strongly tied to vertical displacements associated with internal waves. Later, in stage 2, the layer breakdown was tied to a deepening SML that encroached on the layer from above. The process of layer breakdown by SML deepening may be relatively common. A number of recent studies have linked thin planktonic layers with the position of the pycnocline (Alldredge et al., 2002; Dekshenieks et al., 2001; McManus et al., 2003). The deepening of the SML by penetrative convection or wind stirring may then be a common mechanism for layer breakdown. For the case of penetrative convection, the deepening may be most pronounced at night or early morning and may therefore imply a timing and diel periodicity to layer breakdown.

The detailed turbulence measurements allowed for an evaluation of the role of various biological and physical processes in layer formation and maintenance. The scaling analysis shows that stratification, mixing, and cell buoyancy are not persuasive candidates for layer formation and maintenance. Only chemotaxis by Clade III Synechococcus appears to be a plausible maintenance mechanism, but this is still too weak to explain the observed intermittency in layer occurrence (hours to days). Instead, the results indicate that the layers may have formed from horizontal intrusions. While this hypothesis is not verified directly, it is consistent with several observations and inferences: (1) the layers had distinct T–S characteristics compared to vertically adjacent waters; (2) inferred layer parcel path lines suggest that the layers originated from the adjacent coastal region; and (3) nearshore waters sampled at the Steinitz Marine Laboratory pier had Chl a concentrations comparable to the offshore layers. In-layer growth stimulated by nutrient-rich intrusions or vertical turbulent fluxes of nutrients appears to have been inadequate to produce the observed Chl a anomalies. Instead, the results suggest that the intrusion source waters would have hosted elevated phytoplankton concentrations prior to offshore propagation. Intrusions could have persisted as vertically thin (~10 m) structures during transport 1.6 km offshore, given the in-layer mixing rates and the timescales of propagation.

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