Contrasting fine-scale distributional patterns of zooplankton driven by the formation of a diatom-dominated thin layer

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Abstract

Although plankton thin layers have been described and modeled in a variety of environments, the physical structure surrounding the layer, associated biological rates, and distributions of multiple trophic levels are rarely examined simultaneously. Similar combinations of measurements, such as growth, mortality, and spatial relationships among plankton, are key to understanding how physical processes generating thin layers can influence abundances, composition, and predator-prey interactions. An in situ imaging system was deployed along a southward-oriented transect to describe the full ~2.3-km extent of a thin layer arching from 8 to 4 m deep, with Chlorophyll a enhanced by an order of magnitude inside the layer (23.9 mg m$^{-3}$ peak concentration). Physical oceanographic measurements, distributions of different plankton groups, and output from a high-resolution model indicated that surface convergence and vertical shear drove the formation of the layer, which was dominated by Odontella sp. diatoms that were relatively scarce in the broader study region. Phytoplankton apparent growth (0.64 d$^{-1}$) balanced microzooplankton grazing rates (0.52 d$^{-1}$) within the layer, whereas grazing mortality (2.23 d$^{-1}$) greatly exceeded phytoplankton growth ($-0.39$ d$^{-1}$) outside the thin layer. Mesozooplankton had starkly differing distributions; copepods aggregated south of the layer near the surface, and doliolids followed the thin layer trajectory. A physical oceanographic model run over a 1-month time period, including the time of sampling, indicated that similar surface convergences occurred frequently. Thin layers driven by convergence and shear may be common, with behavioral and buoyancy differences among plankton likely contributing to community structure and modification of trophic transfer.

Continental shelf seas are often characterized by strong vertical and horizontal gradients in oceanographic properties, such as temperature, salinity, and light—all of which influence plankton abundances and biological processes (Denman and Powell 1984; Mackas et al. 1985; Barry and Dayton 1991). Although the physical dynamics driving these gradients are well described on relatively large spatial scales, the corresponding biological structure is often complex, with small scale variability that may elicit different zooplankton behavioral responses. (Widder et al. 1999; Möller et al. 2012; Cowles 2016). Plankton behavior and oceanographic details reveal individual-scale (centimeters to meters) cues that influence overall biological production, yet responses to this patchiness remain poorly resolved for a variety of abundant taxa. Biophysical coupling is difficult to measure because plankton are not passive tracers of the water column, and their populations respond to ocean conditions with various time lags dependent on swimming behaviors, diets, fecundity, and the temporal duration and survival rates of early life stages (Hooff and Peterson 2006; Auth et al. 2011; Litchman et al. 2013).

The plankton community encompasses multiple interacting autotrophic and heterotrophic groups (or a combination, i.e., mixotrophy) that are often described with bulk measurements both in the field (e.g., Chlorophyll fluorescence, total zooplankton abundance, and phytoplankton biovolume) and in ecosystem models (e.g., biomass within discrete size classes).
Because these measurements aggregate complex ecological processes within plankton communities into a single metric, they have limited utility for predicting responses to changing environmental conditions (Pugh 1978). More fundamentally, these bulk measurements are decoupled from the important biological processes driving the transfer of energy throughout the food web (e.g., predator-prey dynamics for multiple species or functional groups). Predator-prey interactions occur among individuals with differing functional traits that have tradeoffs under different oceanographic conditions (Kiorboe et al. 2018). Nevertheless, plankton ecologists are perpetually faced with the challenge of sampling multiple components of the plankton community that all have differing “catchability” depending on the type of sampling gear used, as well as different ecological traits that influence their spatiotemporal distributions and responses in controlled experiments. Advances in sampling technology, however, are leading to new discoveries about the abundances and distribution of different planktonic taxa that have been difficult or impossible to sample with conventional methods (Davis and McGillicuddy Jr. 2006; Greer et al. 2013; Luo et al. 2014; Biard et al. 2016). Comparison of distributions of multiple taxa with differing life histories and behaviors can provide indirect evidence of population level responses to oceanographic conditions.

Widespread deployment of high-resolution sampling platforms, such as optical profilers, in situ imagers, and acoustics, have led to the detection of fine-scale oceanographic features that influence organism distributions and likely overall biological productivity (Benoit-Bird and McManus 2012; Luo et al. 2014; Benoit-Bird and Lawson 2016; Greer and Woodson 2016; Briseño-Avena et al. 2018). Thin layers are one such feature, defined as dense aggregations of phytoplankton or zooplankton spanning less than 5 m in the vertical dimension, extending several kilometers in the horizontal (Dekshenieks et al. 2001; Alldredge et al. 2002; Rines et al. 2002), and persisting for hours to days (McManus et al. 2003). These layers are “trophic hot spots” that are found in a variety of coastal and open ocean environments (Cowles et al. 1998; Alldredge et al. 2002; Churnside and Donaghy 2009; Sullivan et al. 2010; Menden-Deuer 2012). Field measurements within and around thin layers have shown enhanced rates of phytoplankton growth and microzooplankton herbivory (Menden-Deuer and Fredrickson 2010; Calbet et al. 2015), phytoplankton reproduction (Sullivan et al. 2010), nutrient uptake and recycling (Rines et al. 2010), toxin production (Donaghy and Osborn 1997; Timmerman et al. 2014), and predator-prey encounters (Tisellius 1992; Sullivan et al. 2010; Greer et al. 2013). Because thin layers are ephemeral and occur on fine spatial scales, quantifying their contribution to trophic transfer and community structure remains a challenge (Benoit-Bird et al. 2013; Greer and Woodson 2016).

Thin layers can form via several different mechanisms that depend on the dominant physical forcing agents and common plankton types in a particular region. For example, in areas of abundant marine aggregates or diatom-dominated phytoplankton communities, thin layers are often formed via vertical temperature or salinity stratification and differential settling of plankton or particles at the interface (Alldredge et al. 2002; McManus et al. 2005; Benoit-Bird et al. 2008; Greer et al. 2013; Prairie et al. 2013). However, some plankton layers can form independently of physical oceanographic structure due to a combination of growth and grazing (Calbet et al. 2015), and layer shape can be modified by trophic interactions (Benoit-Bird et al. 2009). In more physically dynamic oceanographic conditions, convergence and vertical shear stimulate layer formation (Franks 1995; Ryan et al. 2008). The difference between shear-induced layer formation and a simple deepening of a plankton patch can depend on phytoplankton swimming and fine-scale details of thin layer geometry (Shaw and Stastna 2017). Simultaneous measurements of thin layer structure and plankton abundances from multiple trophic levels (e.g., Benoit-Bird and McManus 2012; Greer et al. 2013), along with biological rate measurements (Sutor and Dagg 2008), are rarely obtained due to technological or logistical constraints. These detailed observations, when placed in the context of an appropriately-scaled physical circulation model (Donaghy and Osborn 1997), are critical for understanding the relative importance of biological and physical processes structuring the patterns surrounding thin layers.

The Mississippi Bight region of the northern Gulf of Mexico (nGOM) is physically complex and biologically productive due to high amounts of nutrient-laden river discharge. During the summer, highly stratified conditions are favorable for mid-water thin layer formation of marine aggregates, also known as “marine snow” (Dzwonkowski et al. 2018b; Greer et al. 2018a). The spatial and temporal oceanographic variability in the nGOM system is driven primarily by winds and freshwater discharge plumes (Ohmann and Niiler 2005; Walker et al. 2005). The Mississippi Bight, although primarily influenced by Mobile Bay outflow and numerous small rivers, occasionally receives pulses of Mississippi River water (Sanial et al. 2019). Shelf waters can also become highly stratified due to the influence of buoyant freshwater discharge, and this, along with wind forcing, often drives circulation along coastal margins (Sanders and Garvine 2001; Whitney and Garvine 2005; Dzwonkowski and Park 2010).

Despite conditions favorable for strong stratification, and the summer phenomenon of bottom-water hypoxia (dissolved O₂ < 2.0 mg L⁻¹, Diaz and Rosenberg 2008; Dzwonkowski et al. 2018b), little is known about the ecological consequences of thin layers in the nGOM. If frequently occurring and generating overlapping high abundances among multiple trophic levels (Benoit-Bird and McManus 2012; Greer and Woodson 2016), these layers may contribute to the productive fisheries in this region (Grimes 2001). When containing flocs of marine snow entraining pollutants such as oil (Passow and Ziervogel 2016), thin layers could increase predicted exposure.
rates and transmission into marine food webs (Graham et al. 2010; Greer et al. 2018a)

The factors influencing the distributions of plankton can be inferred through a combination of high-resolution vertical distributions, including shape characteristics and life stage, as well as behaviors and a detailed description of the physical processes dominating the layer formation and persistence. The main objectives of this study were to (1) characterize the taxonomic composition and growth parameters of the phytoplankton associated with a thin layer, (2) assess how plankton behaviors and ecological strategies may influence their distributions, and (3) determine the physical mechanism(s) driving the thin layer formation and persistence. This approach combining field descriptions and modeling is a necessary step toward understanding the contribution of thin layers to biological productivity in shelf ecosystems.

Materials and methods

Study area and general sampling plan

This study was conducted as part of an intensive field sampling campaign undertaken by the CONsortium for oil exposure pathways in COastal River-Dominated Ecosystems (CONCORDE; Greer et al. 2018a). A component of the sampling was aimed toward investigating seasonal differences in the fine-scale processes operating in the nGOM, from which a subset of the summer 2016 survey was utilized in this study. There was clear evidence of a thin layer located near the 25 m isobath along the western margin of the Mississippi Bight (Fig. 1). This ~ 14-km transect was first sampled with the In Situ Ichthyoplankton Imaging System (ISIIS, Cowen and Guigand 2008), which undulated between the surface and ~ 2 m above the bottom, producing a live feed of plankton images and oceanographic data. After the transect was completed, water samples were collected at two stations (one inside and another adjacent to the thin layer within the Chlorophyll a (Chl a) maximum) to determine phytoplankton biomass (i.e., Chl a), microplankton community composition, and to perform seawater dilution experiments quantifying protistan growth and grazing mortality. A high-resolution physical model for the Mississippi Bight provided the broader spatiotemporal context and indications of forcing mechanisms.

In situ imaging system sampling and analysis

The ISIIS is a towed shadowgraph imaging system that simultaneously measures fine-scale oceanographic properties, including temperature, salinity (SBE 49, Sea-Bird Electronics), Chl a fluorescence (ECO FL-RT, Wetlabs), dissolved oxygen (SBE 43, Sea-Bird Electronics), and photosynthetically active radiation (PAR, QCP2300). The imaging component of the ISIIS is equipped with two shadowgraph lighting setups and line-scan cameras (DALSA) with differing lengths for the optical depth of field and field of view. The larger, higher depth of field unit is intended to capture rare, large plankton, such as larval fishes. The smaller camera unit is more useful for

Fig. 1. Map of the Mississippi Bight showing the portion of the transect where zooplankton and environmental data were collected with the ISIIS. The black portion shows the horizontal extent of the thin layer, and the stars show discrete water samples were collected.
abundant plankton that do not require imaging large volumes of water to obtain a quantitative sample.

The PAR data from the ISIIS were used to calculate the light attenuation coefficient following the equation:

$$K_d = \frac{\ln(\text{PAR (ref)})}{\Delta \text{Depth}} \quad (1)$$

where PAR (ref) is a reference PAR value near the surface, and \(\Delta \text{Depth}\) is the difference in depth between the reference and the in situ PAR value. These values (\(m^{-1}\)) were then used to estimate euphotic depth (location of 99% light attenuation) for each “profile” (up or down cast) of the ISIIS by dividing the mean water column \(K_d\) by 4.6 (Kirk 1996).

For this study, only the ISIIS small camera was used (4.3 cm field of view and 8.9 cm depth of field, ~ 42 \(\mu m\) pixel resolution) due to the high concentrations of plankton and marine snow aggregates in the sampling area. Images from the transect were extracted between 14:00:11 h and 15:31:22 h (local time, CDT), encompassing the time period leading up to and including sampling the thin layer on 24 July 2016. These images were first processed using a “flat-fielding” procedure implemented in ImageJ (Schneider et al. 2012), which evened out the background gray level and removed the small vertical lines typically found in images produced by a line-scan camera. Next, images were converted to black and white with a threshold gray-level value of 170, and contiguous black objects \(\geq 900\) pixels (including enclosed white areas, 1.4 mm equivalent spherical diameter (ESD), the diameter of a circle with equivalent area) were extracted automatically. The resulting 88,692 image segments were then classified into one of 10 different categories, including doliolids, chaetognaths, larval fishes, diatoms, marine snow, hydromedusae, siphonophores, shrimp, other, and unknown. For the doliolids, 28,330 individuals were further identified to life stage, which included gonoozooid/phorozooid (unable to distinguish in the image), gonoozooid (sexually reproducing phase), nurse, oozooid, phorozooid with gonoozooids, multiple individuals, and unknown stage. Organism identifications were merged to the environmental data using the image time stamp, producing a data set of the exact physical environment corresponding to each individual organism. For abundant zooplankton, such as copepods, seven sequential profiles (near-bottom to surface) spanning the full extent of the thin layer were examined (out of the 27 total undulations along the transect), and the images from these profiles were subsampled by viewing one-fourth of the image (randomly selected) and counting these smaller plankton in every fifth frame. The organism counts were then allocated into 0.2 m vertical bins, and the time the ISIIS sampled within each bin was used to calculate the volume sampled and concentration of each zooplankton type (volume imaged rate of 0.00957 m\(^3\) s\(^{-1}\)).

Physical and biological data visualization and analyses were performed in R (R Core Team, v3.2.2). The organism location data were binned to produce abundances per m\(^3\). A bin size of 8.71 m horizontal distance (0.033 m\(^3\)) was used because plankton were highly concentrated, and fine vertical resolution of abundances (~ 0.7 m bins) was needed to describe zooplankton responses to the thin layer. When plankton abundances were anomalously high, multiple individual organisms sometimes overlapped within one image segment. This happened predominantly with doliolids and diatoms, the two most abundant plankton groups found in the images. For diatoms, it is often not possible to determine the number of chains overlapping, so no further processing was performed for this group. For doliolids, however, all segments with multiple individuals were extracted and manually counted to ensure the accuracy of the concentrations derived from the images. The corrected organism counts per bin were then multiplied by 30 to give an estimated concentration for each m\(^3\) of sampled water. The organism concentrations and physical data were linearly interpolated using the R package “akima” (Akima and Gebhardt 2016), and the plankton concentrations were plotted with the R package “ggplot2” (Wickham 2016) to examine the changes in plankton distribution in relation to the physical environment associated with the thin layer. This interpolation scheme did not resolve variability on scales less than the chosen horizontal bin size (8.71 m), so microscale variation in abundance was not quantified because it did not fit with the goals of the study. With the ISIIS data, however, further investigations could resolve microscale patchiness, revealing detailed biophysical dynamics that we did not examine.

**Discrete water sampling**

Two discrete water samples, one within a plankton thin layer (29.5762°N, −88.6074°W) and one outside of the feature (29.5752°N, −88.6157°W) approximately 1 km to the west, were obtained after the ISIIS tow using a CTD rosette equipped with three horizontally-mounted 12-liter Niskin bottles. Both water samples were taken from the chlorophyll maximum, which occurred at 8.8 m and 7.3 m for the stations inside and outside of the thin layer, respectively. Vertical profiles of temperature, conductivity, density, and Chl \(a\) fluorescence were determined using a Sea-Bird SBE 911plus CTD equipped with a Wetlabs ECO FL fluorometer. Chl \(a\) fluorescence was used as an indicator of phytoplankton thin layers following the criteria outlined by Dekshenieks et al. (2001). A vertical profile of the water column was taken prior to collecting water for incubation experiments. The fluorometer was mounted adjacent to the bottle openings to ensure that sample water was collected at the correct depth within the layer. The CTD rosette system was lowered slowly (~ 0.5 m min\(^{-1}\)) to minimize disruption to the thin layer. Once the Chl \(a\) fluorescence maximum was determined, the rosette was held at that depth for 200 s to ensure the Niskin bottles were completely flushed from air bubbles and were sampling the water within the feature. The thin layer was sampled at 8.9 m, and once all three bottles were fired and pulled onto the ship, sample aliquots
were dispensed separately into acid-clean carboys and set aside for microzooplankton grazing incubations and microplankton imaging (FlowCAM, Sieracki et al. 1998). The second set of water samples (depth = 7.3 m, within the chlorophyll maximum) was conducted ~1 km to the west of the thin layer sampling station and was used to compare microplankton composition and phytoplankton growth/mortality to those found within the thin layer.

**Microplankton community composition and abundance**

Microplankton community composition and counts were evaluated using a B3 Benchtop Series FlowCAM fitted with 300-μm flow cell and 4x objective. A seawater volume of approximately 15 mL was analyzed at each station. Aliquots of 4.9 mL were run in triplicate in “trigger mode” to provide phytoplankton identification and particle characteristics (e.g., concentration and biovolume). Microplankton were identified visually to genus level, and particles (individual cells) were enumerated and biovolume. Microplankton were classified as the following shapes: diatoms as cylinders, microzooplankton and dinoflagellates as prolate spheroids, and small flagellates as spheres. Chl a (mg m$^{-3}$), a proxy for phytoplankton biomass, was determined using the methanol extraction technique (Welschmeyer 1994).

**Phytoplankton growth and mortality**

Instantaneous rates of phytoplankton growth ($\mu$) and mortality losses ($m$) due to microzooplankton grazing were investigated using the seawater dilution technique of Landry and Hassett (1982), modified to include a highly diluted treatment (Gallegos 1989). Niskin bottle samples were transferred via precleaned transfer tubing to experimental containers, following trace-metal clean protocols (Landry et al. 1995). All equipment was handled using clean Nitrile gloves. Sample aliquots from the Niskin bottles were dispensed immediately into a 30-liter carboy via acid-cleaned silicon tubing fitted with a 200-μm mesh to exclude larger macrozooplankton grazers. A fraction of the seawater was filtered through a clean, 0.2-μm polycap filter cartridge to produce the particle free seawater (PFSW) diluent, with the remaining unfiltered fraction serving as the natural or whole seawater (WSW) fraction. Each dilution experiment used 1.1-liter wide-mouthed clear polycarbonate bottles. Experiments were carried out in triplicate fractions with 0.05, 0.5, and 1.0 WSW with added nutrients (final concentrations of 5 μmol L$^{-1}$ nitrate and 0.5 μmol L$^{-1}$ phosphate). Three undiluted WSW bottles without nutrients were incubated as a natural seawater control. One bottle was filled with PFSW to serve as a control to account for organisms passing through the 0.2-μm filter capsule. All bottles were filled with PFSW and topped with WSS to the brim. The bottles were then covered with parafilm and secured with the screwcap lid. 24-h incubations were carried out on-deck in an acrylic open topped incubator that circulated surface seawater constantly. Bottles were gently inverted every ~2.5 h to mix the samples. Incubation bags consisted of black mesh screen at three different thicknesses ranging from 10% sunscreen to 55% sunscreen. To determine the amount of appropriate shading intensity, daytime PAR measurements using the CTD were conducted to identify approximate light intensity at that depth. Time zero Chl a was determined from triplicate 200 to 300 mL aliquots taken from sacrificial bottles. Each aliquot was filtered onto 2.5-cm Whatman GF/F filters, placed into cryotubes, and stored in liquid nitrogen until fluorometric analysis less than 1 month after collection. All bottles were terminated after 24 h incubations, following the same procedure for chlorophyll determination and storage. Protistan grazing impact on phytoplankton biomass, expressed as Chl a, was quantified using the following equation:

$$P_t = P_0 e^{(k-m)t}$$

(2)

where $P_t$ and $P_0$ are the initial and post-24 h incubation time ($t$, d$^{-1}$) phytoplankton biomass, respectively, $k$ ($d^{-1}$) is a measure of phytoplankton intrinsic growth rate in the absence of grazing, and $m$ ($d^{-1}$) is the phytoplankton mortality rate due to herbivory. Phytoplankton apparent growth rate ($d^{-1}$) is related to grazing and mortality by Eq. 2 at each dilution level, where $k$ and $m$ are the ordinal intercept and absolute value of slope, respectively, of the linear regression.

$$\left(\frac{1}{t}\right) \ln \left(\frac{P_t}{P_0}\right) = k - m$$

(3)

Phytoplankton instantaneous growth rates in the absence of added nutrients ($\mu_o$) and grazing were calculated as the sum of the intrinsic growth rate ($k$) plus grazing mortality ($m$); $\mu_o = k + m$. Grazing impact on phytoplankton biomass was estimated as the percentage of potential production grazed (d$^{-1}$) (Gifford 1988).

$$\left[\left(P_0 e^{d} - P_0 e^{k-m}\right)/P_0 e^{d}\right] \times 100$$

(4)

**Hydrodynamic model**

The high-resolution physical model of the nGOM provided the broader physical context for the oceanographic measurements surrounding the thin layer. The horizontal model resolution was 400 m, and the results in the vertical were interpolated on 30 vertical layers that changed size depending on bathymetry (coarser for deeper waters). At the location of the thin layer, the vertical resolution was 0.5 m at the surface and 1.46 m at the bottom, with a vertical resolution in the vicinity of the thin layer (5–10 m depth) ranging from 0.75 to 1.0 m. The model was run over the summer field sampling campaign and produced outputs of physical oceanographic variables (e.g., temperature, salinity, current velocity) every hour. Other parameters (e.g., density, convergence/divergence,
and shear) were calculated using the model output and visualized in two dimensions, both horizontally at the surface (to indicate surface convergence/divergence) and vertically along the field sampling transect (for vertical current structure). This high-resolution physical model has been shown to produce realistic circulation patterns when compared to field-deployed drifters (Greer et al. 2018a).

To determine the frequency of conditions favorable for thin layer formation, the model was run for 1 month in the summer (15 July 2016 until 15 August 2016). Surface divergence across the entire model domain and variation of vertical shear in the water column were computed using hourly output of modeled velocities. Temporal changes were visualized for the location where the thin layer was measured in the field study (−88.6075°W, 29.5801°N).

**Results**

**Ambient shelf conditions**

The broad-scale shelf characteristics of the Mississippi Bight during the thin layer event were typical for summer conditions in the nGOM (for a more detailed description, see

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**Fig. 2.** Physical oceanographic data collected with the ISIIS along the sampling transect: (a) salinity, (b) sigma-t, (c) temperature, (d) dissolved oxygen, and (e) Chl a fluorescence. Black lines in panel (d) show the portions of the transect enumerated for copepods, with numbers corresponding to panels in Figs. 3 and 9.
Dzwonkowski et al. 2018b; Greer et al. 2018a). While the summer season is dominated by upwelling favorable winds (i.e., south/southwest winds), this wind pattern is intermittently reversed by downwelling events (east/north winds) — the conditions under which this field survey was conducted. The regional circulation pattern during the study had westward and southward flowing currents following the Alabama/Mississippi and Louisiana coastlines, respectively. The nearshore portions of the Mississippi Bight clearly showed downwelling pycnocline consistent with this circulation pattern, while the broad shelf area was highly stratified (Dzwonkowski et al. 2018b). Furthermore, MODIS satellite imagery of Chl $a$, a proxy for salinity, showed intense gradients on the shelf due to the interaction of the Mississippi River plume and open ocean water masses (Dzwonkowski et al. 2018b).

**Physical conditions near the thin layer**

A phytoplankton-dominated thin layer, extending from 29.5771°N, −88.6074°W to 29.5970°N, −88.6074°W (~2.3 km), was found on 24 July 2016 during a north to south ISIIS transect beginning at ~ 10:00 CDT (Fig. 1). The conditions near the thin layer were generally stratified (buoyancy frequency $N ~ 0.015$ s$^{-1}$, Dzwonkowski et al. 2018b), although not more so than the areas of the transect where the thin layer was not present. Salinity was the main driver of the density stratification and became slightly more vertically homogenous at ~ 7000 m along the transect (Fig. 2a,b). In this area, there was a shift in the temperature distribution, with intermediate values occupying a broader section of the water column, which continued until the end of the transect (Fig. 2c). The thin layer, which was detected from Chl $a$ fluorescence, was also apparent in the distribution of dissolved oxygen, which formed a mid-water column oxygen maximum (Fig. 2d). Directly underneath the layer was a local oxygen minimum, with higher oxygen underneath, and the lowest dissolved oxygen concentrations at depth. The Chl $a$ fluorescence layer was ~ 0.5 m thick (at half maximum intensity) and extended ~ 2.3 km horizontally, gradually rising from 8 to 4 m depth toward the southern end of the transect (Fig. 2e). The southern end of the thin layer coincided with a temperature inversion, potentially indicating strong surface convergence and vertical shear.

The thin layer formation and extent altered the light environment for sequential “profiles” (up and down casts) with the ISIIS. At profile 5, a small increase in the attenuation coefficient ($K_d$) occurred at ~ 9 m depth. With each sequential profile, this feature became shallower, and by profile 13, it was found at ~ 5 m depth. When the light attenuation became strongest near the surface, there was a corresponding decrease in the euphotic depth in profiles 10–14 (Fig. 3). The trajectory of this light-attenuating feature closely matched the layer of Chl $a$ fluorescence (Fig. 2e).

Projections of the model output throughout the sampling region (nGOM) revealed distinct physical dynamics in the vicinity of the subsurface thin layer. The salinity range was similar to the field data (Fig. 4), and the near surface low salinity area showed some depth variation spatially. The depth expansion of low salinity surface water moved toward the north in the model output from 2 h later (Fig. 4). The temperature distribution closely followed the salinity changes, but the model temperature range was not as large compared to field collected data. The minimum temperature value was ~ 24°C and ~ 27°C for field and model data sets, respectively. Although there was a vertical expansion of high temperature waters on the southern side of the model domain near the surface convergence, the model did not capture the temperature inversion that was apparent just south of the thin layer in the field-collected CTD data. This may have been due to the...
model not matching the field-collected temperature range between surface and bottom waters, or model resolution may not have been adequate to exactly reproduce this feature. However, the overall hydrographic structure during the thin layer event appeared to be representative in that there was a two-layer oceanographic system with a vertical displacement of the pycnocline corresponding to the time when the thin layer was detected.

Meridional velocities showed a general southward movement of surface waters during the northward movement of the surface convergence feature. Velocities tended to accelerate toward the south until reaching the convergence zone (maximum of 0.6 m s\(^{-1}\)) where waters were advected toward the benthos at a maximum vertical velocity of ~1 cm s\(^{-1}\). In waters underneath the southward directed surface currents, a patch of near bottom water had a northward trajectory, generating shear between these two water masses on either side of the pycnocline (Fig. 4e,f). When viewed from the surface, the model showed numerous surface convergences in the western Mississippi Bight on 24 July—one of which passed over the sampling area (black diamond) at the time the thin layer was detected (Fig. 5).

**Phytoplankton community structure and growth/grazing rates**

A spatially structured community of phytoplankton, zooplankton, and marine snow was associated with the thin layer. The most obvious indicator of thin layer presence came from the ISIIS images, which showed a community dominated by...
diatom chains (> 1–2 cm in length), reaching such high concentrations as to almost occlude the 8.9 cm light path for the ISIIS small camera (Fig. 6, images from the ISIIS small camera). A variety of zooplankton and marine snow aggregates were also found within and around the thin layer (see Fig. 7 for examples).

Phytoplankton biomass, as measured by Chl $a$, was more than an order of magnitude greater within the thin layer (23.9 mg m$^{-3}$) relative to the Chl $a$ maximum at the station outside of the layer (2.2 mg m$^{-3}$). Total particle abundance, as measured by the FlowCAM, was more than five times greater within the thin layer. The phytoplankton community was dominated by large Odontella sp. and Rhizosolenia sp. diatoms, with Odontella sp. completely absent at the station outside the layer (Fig. 8a) where the phytoplankton cells were comprised predominantly of small unidentified diatoms (mean ESD [± standard deviation] = 35.3 [± 3.1] μm) and Rhizosolenia sp. The particle sizes were similar for Rhizosolenia sp. (259.8 [± 45.7] μm) and Odontella sp. (243.8 [± 16.0] μm, data not shown). Odontella sp., however, was the most abundant group and dominated the biovolume inside the layer due to large cell sizes. Chaetoceros sp., although well represented in terms of cell concentration, was not a major component of the biovolume because cell sizes were much smaller relative to Rhizosolenia sp. and Odontella sp. (Fig. 8a).

Phytoplankton growth and grazing mortality rate estimates, measured in the bottle incubation experiments, were 0.64 d$^{-1}$ and 0.52 d$^{-1}$ within the thin layer and −0.39 d$^{-1}$ and 2.23 d$^{-1}$ outside the layer, respectively (Fig. 8b). Growth rate estimates in the absence of nutrients were not significantly different between nutrient-augmented treatments from within the thin layer (0.77 d$^{-1}$) but were significantly lower outside (−0.20 d$^{-1}$) the thin layer. Nutrient limitation was inferred by examining the ratio between growth rate estimates from undiluted treatments incubated without ($\mu_0$) and with ($\mu_n$) added nutrients (i.e., $\mu_0 : \mu_n$). The ratio from the thin layer

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**Fig. 5.** Surface divergence snapshots (m s$^{-1}$ deg$^{-1}$) from the physical oceanographic model for (a) 16:00 and (b) 20:00 UTC on 24 July and (c) 0:00 and (d) 12:00 UTC on 25 July (negative numbers indicate convergence). The thin layer was sampled closest to 20:00 UTC (15:00 CDT), and its location is encompassed by the black diamond.
experiment exceeded 1.0 ($\mu_0 : \mu_n = 1.20$), suggesting that nutrients in the non-nutrient amended treatments were sufficient to maintain growth. However, this ratio was significantly less than 1.0 at the station outside of the feature ($\mu_0 : \mu_n = 0.26$), indicating that nutrient addition may have had a stimulatory effect on phytoplankton growth. Overall, microzooplankton grazing losses accounted for only 41% of phytoplankton growth inside the thin layer, but 89% of phytoplankton growth was consumed outside of the feature.

### Plankton distributions and ecological characteristics around the thin layer

The two dominant phytoplankton macro-grazer taxa, copepods and doliolids, had differing spatial distributions in relation to the thin layer. Copepods, as measured from seven sequential upcasts with the ISIIS, were most abundant on the northern and southern edges of the thin layer (just outside of it), reaching a local maximum concentration of ~400,000 ind. m$^{-3}$ at 5 m depth just south of the layer. Inside of the layer, copepod abundances rarely exceeded 100,000 ind. m$^{-3}$ in any portion of the water column (Fig. 9). Throughout the transect, copepods were most abundant within the shallowest 5 m. Doliolids were imaged continuously (ISIIS upcasts and downcasts included) and showed strong spatial overlap with the thin layer (Fig. 10a). North of the thin layer, doliolids tended to be most abundant mid water column (4–8 m) and closely followed the distribution of dissolved oxygen, generally confined to waters with O$_2$ concentrations between 3 and 5 mg L$^{-1}$. Once inside of the layer, the abundance of doliolids increased by approximately an order of magnitude, with peak concentrations occurring near the high Chl $\alpha$ values on both the northern and southern ends of the layer (Fig. 10a). On the southern side of the layer, near the temperature inversion, the doliolids were shallower (~3.5 m) compared to any other portion of the transect.

The doliolid life stages were dominated by the phorozooids or gonozooids (74.6%, 21,123 individuals). The nurse stage, the terminal life stage for doliolids, made up only 0.9% of the individuals (Table 1). A total of 4469 individuals (15.8%) could not have their life stage identified with certainty because the image was blurry, precluding the ability to enumerate the muscle bands. However, these were likely also gonozooids or phorozooids because the nurse stage has a conspicuous tail of gastrozooids (i.e., feeding buds) that would be apparent even if the images were blurry.

The distribution of marine snow aggregates > 1.4 mm ESD (i.e., flocs of detritus), as detected by the ISIIS imagery, tended to follow the trajectory of the thin layer. The concentrations of these aggregates increased as the sampling moved toward the south and approached the thin layer. There was a local peak at ~9000 m distance and 5 m depth, and another peak, slightly deeper (~7 m), formed around the northern end of the thin layer. The highest

![Fig. 6. Vertical profile of Chl $\alpha$ and sigma-t from the station where rate measurements were taken for the microplankton community in the thin layer. Images captured with the ISIIS in the same area are shown for three different sections of the water column.](image-url)
concentrations occurred near the temperature inversion on the southern end of the layer around 5 m depth (Fig. 10b).

Other similarly-sized heterotrophic zooplankton groups were less abundant than the doliolids and copepods, and were distributed differently from one another. Hydromedusae, similar to the doliolids, were most abundant in the mid-water column north of the thin layer; however, once the layer appeared, the hydromedusae abruptly decreased in abundance and tended to aggregate in deeper waters underneath the layer (Fig. 10c). Chaetognaths were one of the only taxa found in the shallowest portion of the water column but were dispersed vertically, only avoiding the deeper waters with low dissolved oxygen concentrations. On the southern side of the thin layer, only 1–2 m below the Chl a maximum, chaetognaths were abundant, reaching peak concentrations of ~ 500 ind. m\(^{-3}\) (Fig. 10d). Siphonophores were more common in deeper waters underneath the thin layer (Fig. 10e). Finally, the distribution of shrimp tended to follow the thin layer trajectory, and there were peak abundances on the southern side of the thin layer but slightly deeper than the high concentrations of doliolids near the temperature inversion and within the layer (Fig. 10f).

Marine snow shapes, as determined by a fitted ellipse to each marine snow aggregate, indicated spatial changes in particle shape that could be connected to sinking. The marine snow aggregates within the layer tended to be more round—close to the average aggregate aspect ratio (1.949) along the entire transect. Immediately above and below the layer, the aggregates tended to be more elongated in shape (Fig. 11). For marine snow aggregates imaged north of the layer, most vertical bins showed below average aspect ratios (more round particles). This may indicate that marine snow aggregates were sinking faster in the vicinity of the layer compared to the aggregates found in other portions of the transect. Underneath the thin layer,

![Image](image.png)

Fig. 7. Example images from inside and around the thin layer: (a) *Odontella* sp. diatom, (b) several copepods from the surface just south end of the thin layer, (c) marine snow aggregate, (d) aggregation of diatoms within the thin layer that overlap and are segmented as one “particle,” (e) doliolid gonozoid or phorozoid, (f) doliolid nurse, (g) shrimp, (h) hydromedusa (*Clytia* sp.), (i) siphonophore (*Muggiaea* sp.), (j) hydromedusa (*Solmundella bitentaculata*), and (k) chaetognath.
marine snow aggregates tended to oblong in shape but also more variable compared to aggregates not associated with the thin layer (Fig. 11).

**Frequency of similar physical conditions**

The physical oceanographic model was run for 30 days from mid-July to mid-August 2016 to examine the frequency of occurrence of similar conditions associated with the thin layer. Throughout the month, the surface convergence eclipsed the $-20 \text{ m s}^{-1} \text{ deg}^{-1}$ threshold 11 times, similar to the conditions present when the thin layer was detected (Fig. 12a). There was also a consistent region of vertical shear between 2 and 5 m depth throughout the 30-day period (Fig. 12b), with strong shear reaching depths of 8–10 m for most of those high convergence conditions.

![Fig. 8](image)

**Fig. 8.** (a) Phytoplankton community composition at sampling stations inside and outside of the thin layer. (b) Phytoplankton apparent growth rates in response to changing fractions of unfiltered seawater inside and outside of the thin layer.

![Fig. 9](image)

**Fig. 9.** Vertical distributions of copepods for sequential upcasts from the ISIIS tow (exact location of each profile shown in black in Fig. 2d).
events. The two processes that appear to be necessary for thin layer formation in this region of the nGOM, patch generation from convergence followed by vertical shear, are summarized in Fig. 13.

**Discussion**

Different distributional patterns among similarly-sized zooplankton in relation to the diatom-dominated thin layer suggest that behavior (including buoyancy alteration by diatoms) is a major driver of their short time-scale (hours) responses to physical forcing. This is consistent with other observations.
from shelf ecosystems showing distinct vertical differences among zooplankton in relation to density stratification (Sutor and Dagg 2008; Greer et al. 2013, 2014). Unlike many previous studies of thin layer dynamics, however, we were able to quantify the abundances of multiple trophic levels of plankton, as well as growth/grazing rates, with little change in sampling resolution among groups. The surface convergence and northward propagation (during generally southward currents) likely caused a “piling up” of buoyant diatoms that were able to resist the associated downward vertical velocities of ~ 1 cm s\(^{-1}\). Surface-associated zooplankton tended to aggregate near the surface convergence, while slightly deeper (~ 8 m) gelatinous organisms accumulated on the northern side of the layer, ~ 3 km from the surface convergence (see Fig. 13 for conceptual summary). Model results from longer timescales (30 days) suggest that similar surface convergence and shear conditions are common in this region of the nGOM. These new insights into the biological processes and structure surrounding a thin layer have important implications for quantifying aspects of predator-prey interactions and plankton population dynamics on the nGOM shelf. In addition, quantifying the fine-scale interactions can improve estimates of potential exposure rates to pollutants, such as spilled oil.

**Model mechanism of thin layer formation**

Findings from only a few coastal systems have overwhelmingly contributed to our understanding of thin layer properties and formation mechanisms. In Monterey Bay and the coast of Washington, U.S.A., for example, the predominant formation mechanisms include the settling of phytoplankton along density interfaces with Richardson numbers > 0.25 (Alldredge et al. 2002; McManus et al. 2005; Cheriton et al. 2009) as well as straining of phytoplankton patches (Franks 1995; Birch et al. 2008; Ryan et al. 2008) often associated with frontal features and submesoscale currents (Lévy et al. 2018).

Synoptic observations of fine-scale biological and physical properties, along with high-resolution modeling for the latter

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**Fig. 11.** Vertical distribution of average marine snow aggregate shape (aspect ratio) for all aggregates pooled from ISIIS images captured within and around the thin layer (location indicated by the gray box) and north of the layer. Higher values indicate more elongated aggregate shape. Error bars represent 1.96 * standard error for the marine snow aspect ratio within each 0.5 m vertical bin. The vertical dotted line serves as a reference for the average marine snow aspect ratio for the entire transect.

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**Fig. 12.** Time series of model output from a point inside the thin layer from 15 July 2016 to 15 August 2016. The black vertical dotted line indicates the time when the thin layer was sampled in plots of (a) model surface divergence (m s\(^{-1}\) deg\(^{-1}\)) and (b) vertical shear (m s\(^{-1}\)).
component, allow for a deductive approach for identifying candidate forcing mechanisms. In this study, similar to other thin layer studies, direct measurements during formation of the thin layer were not captured, and the available in situ data have limitations. The physical model output, however, resolves submesoscale processes in the shelf environment and provides complementary insight into the conditions likely to be impacting the generation and evolution of the thin layer.

As summarized by Durham and Stocker (2012), the generation of thin layers has been attributed to physical (e.g., shear-flow straining and intrusions), biological (e.g., in situ growth, grazing, and vertical migration), and coupled biophysical interactions (e.g., settling along pycnoclines and gyrotactic trapping).

Most of the biological mechanisms (i.e., growth and grazing) appear to be limited contributors to the thin layer formation and persistence. The identification of the diatom *Odontella* sp. as the dominant phytoplankton genus eliminates mechanism that involve swimming (e.g., gyrotactic trapping), although buoyancy, which is augmented when nutrients are abundant, still plays a role (Richardson and Cullen 1995; Richardson et al. 1998; Kemp and Villareal 2018). The phytoplankton growth to grazing ratio in the layer (1.23) and the low background concentration of *Odontella* sp. in the study area suggest that neither in situ growth nor grazing down of an existing population would be sufficient to produce a thin layer. While there was strong stratification that might be conducive to buoyant settling in the pycnocline (Allredge et al. 2002; Prairie et al. 2013), the fact that the thin layer was observed to cross isopycnals is more indicative of a straining-induced generation mechanism (Hodges and Frantantoni 2009). This cross-isopycnal orientation also indicates that a water mass intrusion likely did not generate the thin layer, as this mechanism would be expected to form an aggregation traveling along a constant density interface.

If stratification and the settling of phytoplankton and marine snow were the dominant formation mechanism of this thin layer (Prairie et al. 2013), we would expect a continuous layer to form throughout the Mississippi Bight in the summer. This indeed does happen with respect to the distributions of marine snow, which mostly consist of large (> 2 mm) aggregates (Greer et al. 2018); however, the thin layer signature in the Chl *a* fluorescence (> 2x background concentration) was only detected in the southwestern corner of our sampling domain and contained diatoms as well as marine snow aggregates. This suggests a more complex mechanism driving its formation, rather than passive settlement, and highlights a bias in many studies toward fluorescent particles for thin layer detection (Graff and Menden-Deuer 2016).

For straining to be a feasible generation mechanism, an initial patch must form and subsequently undergo vertical shear. While neither patch formation or shear were directly observed, the model output can provide first order values for scaling methods (Stacey et al. 2007) to assess the whether the observed thin layer is consistent with theoretical expectations for generation via straining. To initialize such a thin layer, patch development is required and could arise through a biological bloom, physical aggregation, or a combination of the two. The divergence field for the model outputs did show a strong negative divergence feature (i.e., convergence) propagating northward in the vicinity of the thin layer. Given the transient nature of such features, an exact coupling of the convergence and the thin layer should not be expected, but
timing and proximity of this feature is certainly suggestive. This convergence is critically important, as it would provide a means of aggregating the diatoms whose background abundances were relatively low (D’Asaro et al. 2018; Taylor 2018). However, a patch of high diatom abundances cannot be created if there is no resistance to the net downward flow (i.e., plankton are passive tracers), which in this case, would come from the ability of diatoms to control their buoyancy (Richardson and Cullen 1995; Richardson et al. 1998; Kemp and Villareal 2018). There may be further augmentation of buoyancy by forming a “mat” of aggregated diatom chains, but the details of these particle dynamics are not well described. The piling up of diatoms at the convergence cannot occur indefinitely, and the patch eventually reaches a particular depth where it becomes subject to other physical processes occurring below the surface.

In addition to a convergence mechanism, the model output indicates that there was consistent vertical shear at the time and location of the thin layer. The model shear levels are consistent with previous regional observations (Dzwonkowski et al. 2018). Assuming the physical convergence in the model output is a key mechanism in producing the initial patch, the model shear is representative, and a reasonable turbulent diffusion coefficient can be determined. The scaling arguments of Stacey et al. (2007) for a straining-diffusion balanced thin layer can then be compared to observed properties in the ISIS data. Key characteristics can be estimated, such as the minimum layer thickness \(l_{\text{min}}\) and layer angle \(\theta_{\text{bal}}\) after incorporating time to achieve the balance \(t_{\text{bal}}\) which are:

\[
l_{\text{min}} = \left(\frac{KL_x}{\alpha}\right)^{1/3}
\]

\[
\theta_{\text{bal}} = \left(\frac{K}{\alpha L_x^2}\right)^{1/3}
\]

\[
t_{\text{bal}} = \left(\frac{L_x^2}{K\alpha^2}\right)^{1/3}
\]

where \(K\) is the turbulent diffusion coefficient, \(L_x\) is the initial width of the patch, and \(\alpha\) is the vertical shear (i.e., change in the horizontal velocities with depth).

While direct observations of these variables are not available, the model output can inform their estimation. The width of the convergence region in the model output is between 500 and 1000 m, so the initial width of the patch would not be expected to be larger than that feature, providing a value range for \(L_x\). The vertical shear \(\alpha\) in timeframe and location of the thin layer was 0.035 s\(^{-1}\). \(K\) is taken to be \(10^{-5}\) m\(^2\) s\(^{-1}\), similar to values determined by Stacey et al. (2007) and likely a reasonable order of magnitude for shelf environments beyond their study region. With these values, the resulting estimates are \(l_{\text{min}} = 0.5-0.7\) m, \(\theta_{\text{bal}} = 0.04-0.06\), and \(t_{\text{bal}} = 6-12\) h, which compare favorably to the thin layer width of 0.5 m and angle of 0.1°. A specific time scale for the observed thin layer could not be determined during the survey, but the estimated \(t_{\text{bal}}\) would allow common processes that are known to drive vertical shear at depth in the region (e.g., near-inertial oscillations) to strain the patch to its balance point. There are certainly several assumptions involved these estimates, but the lack of a biological mechanism in conjunction with the first order agreement with observed properties of the thin layer indicate the two-step process of surface convergence and vertical shear straining are the responsible formation mechanisms (Fig. 13).

**Issues with sampling thin layers and surface convergences**

Because surface convergence and shear likely generate these productive, fine-scale subsurface features, they may evade detection from conventional sampling protocols and remote sensing platforms (McManus et al. 2008; Chumsis and Donaghay 2009). If this mechanism is common in the biologically productive nGOM, it suggests that surface-level physics has a strong influence on subsurface ecological processes. The relatively ephemeral and nonstationary surface convergences are notoriously difficult to sample, yet multiple lines of evidence suggest they are important physical mediators of biological production (Woodson and Litvin 2015).

Researchers have highlighted that sampling of ocean fronts is biased toward ones that are deep and persistent, which are also often associated with anomalously high Chl \(a\) and biological productivity when described with remote sensing (Lévy et al. 2018). Interestingly, the results from modeling by Lévy et al. (2018) suggest that the feature we sampled would not contribute to productivity because the vertical currents associated with the convergence likely did not penetrate deep enough bring in new nutrients. While this is true for the feature we sampled, as nutrients on the nGOM shelf are predominantly supplied by riverine sources (Dagg and Breed 2003), the biological importance of a feature is not always directly related to its contribution to new production. This counterintuitive statement makes sense when considering alternative sources of higher trophic level productivity: namely, the fine-scale spatial overlap between predators and prey. If organisms experience much higher than average concentrations of prey, as they would at fronts and thin layers, this can result in high production of multiple trophic levels almost independent of nutrient supply (Benoit-Bird and McManus 2012; Woodson and Litvin 2015; Greer and Woodson 2016). Lévy et al. (2018) and other models of biophysical coupling also typically assume that all phytoplankton drift passively in response to currents; however, if phytoplankton buoyancy affects whether or not certain taxa stay within the sunlight portion of the water column, the downward-oriented currents can act as an ecological, short time scale (hours) selective agent for buoyant particles (D’Asaro et al. 2018), altering the phytoplankton photophysiology, community composition, and distribution, thus influencing the transfer of carbon within the food web.
In fact, as noted previously, the nonpassive behavior of phytoplankton is required to generate a patch for shear to later act upon for thin layer formation. Agent-based modeling of particles with differing sizes, potential grazers, and buoyancies could provide more insight into the role of vertical currents in structuring plankton and higher trophic level community dynamics. The surface currents within the model domain, other modeling studies (Jacobs et al. 2016), and observations in this region (D’Asaro et al. 2018) suggest that this area of the Mississippi Bight is a hotspot for surface convergence features. Therefore, any sampling transect spanning tens of kilometers should encounter several convergences and divergences, allowing for direct comparisons examining how these features shape plankton communities.

Grazer distribution and food-web dynamics

One biological property of the thin layer that follows from the generation mechanism may be the size composition of the diatom chains, which affects prey accessibility to grazers. Large phytoplankton cells are likely an adaptation to escape grazing (Kiørboe 1993), and modeling suggests that under nutrient replete conditions and absent of grazers, small phytoplankton cells should dominate (Cloern 2018). Because these conditions match those observed in this study, it suggests that smaller cells are being removed (either physically or through grazing pressure), promoting these large cell sizes, chains, and aggregations found in the thin layer.

The abundance of large cell sizes presents some challenges for interpreting incubations measuring growth and grazing. These diatom chains, which according to the in situ images, were ~ 100 μm thick and sometimes several centimeters in length, would have been removed or broken apart during the filtering process prior to incubations that measured grazing. Therefore, the protocols likely select for certain sizes and could produce results that do not reflect the actual conditions experienced by phytoplankton and grazers in the field, potentially biasing interpretations of grazing dynamics. Caveats with results derived from the dilution technique have been highlighted by others (Dolan et al. 2000; Nejstgaard et al. 2001; Calbet and Saiz 2013), and results can be particularly confounding during phytoplankton blooms or immediately after a bloom (Stoecker et al. 2015) due to the production of polyunsaturated aldehydes that inhibit grazing (Ribelat et al. 2014). The filtering step required in dilution experiments may be problematic in systems similar to the nGOM where phytoplankton communities are dominated by large diatom chains that are similar in size to mesozooplankton (and several times larger than microzooplankton).

Microzooplankton, the predominant grazers in the world’s oceans, were more abundant inside the thin layer relative to outside, although the fraction of phytoplankton grazed was significantly higher outside the layer. Microzooplankton grazing rates were also higher inside the layer, but peaks in macrograzer abundance (copepods, in particular) were horizontally offset from the layer. We did not obtain microzooplankton abundance or grazing rates on the same scale as the macrograzers, so it is unclear if the microzooplankton abundances followed similar patterns to the macrograzers. These nominal macrograzers are actually diverse consumers of phytoplankton and microzooplankton (Calbet and Saiz 2005), and their distributions and aggregations may reflect diet preferences or swimming behavior in response to convergence (Genin et al. 2005; Höfer et al. 2015) and straining that drove thin layer formation. Depending on the prey selectivity of macrograzers, the conditions described in this study could set up a planktonic trophic cascade whereby the predominant phytoplankton grazers (e.g., microzooplankton) are removed by copepods near the surface and by doliolids within the thin layer. Indeed, doliolid diets and prey availability measurements suggest doliolids selectively feed on larger size classes such as diatoms and a range of microzooplankton taxa (Walters et al. 2019). It is unknown whether these long (~ 1 cm) Odontella diatom chains experience grazing pressure from one or more of these groups, as diatoms in full length chain formation would be removed from the water prior to grazing experiments. Further resolution of the fine-scale conditions leading to diet shifts and a more precise description of prey morphology would help to resolve the ecological implications of these distributions.

Doliolids were the most abundant of the mesozooplankton > 1.4 mm ESD and tended to follow the trajectory of the thin layer, which also overlapped strongly with marine snow aggregates. Recent evidence from doliolid diet studies has indicated that they selectively feed on diatoms and may rely on patches or layers of high concentrations of certain plankton types to feed (Walters et al. 2019). Our results suggest that the thin layer and the convergence zone would be areas of much higher than average concentrations of diatoms and marine snow, which may explain why the doliolid community was dominated by the phorozooid and gonozooid life stages, indicating this population was likely undergoing rapid growth via asexual reproduction (Paffenhöfer and Köster 2011). Indeed, doliolids and other pelagic tunicate populations can quickly increase or “bloom” in response to a nutrient pulse in shelf ecosystems (Paffenhöfer and Gibson 1999; Deibel and Paffenhöfer 2009) on time scales similar to thin layer persistence (days; Rines et al. 2002; McManus et al. 2003), and doliolids often overlap spatially with Chl α maxima (Paffenhöfer et al. 1991). Thin layers or similar physical processes generating patches of prey resources might represent an important mechanism of doliolid production in the nGOM, a region where nutrient input is dominated by river runoff rather than episodic upwelling events that are common in other shelf systems (Walters et al. 2019).

Zooplankton predator response

Chaetognaths, shrimp, and gelatinous zooplankton (not including doliolids) had differing distributions in relation to the thin layer, possibly due to mean depth preferences before the arrival of the surface convergence. Throughout the transect, hydromedusae displayed a peak concentration near midwater column (~ 8 m), with siphonophores even deeper
(~ 12 m), and both of these taxa were not common within the thin layer or near the surface convergence south of the layer. Chaetognaths, on the other hand, consistently aggregated near the surface and reached an abundance peak just south of the layer where copepods were also abundant. These slight vertical offsets appeared to have a strong influence on the location of the abundance maxima in relation to the surface convergence and thin layer—surface-oriented plankton peaked near the surface convergence, while deeper organisms were most abundant on the northern side of the thin layer. It is widely recognized that because current velocities change with depth, small vertical movements can dramatically influence the transport trajectory of plankton and passive constituents (Paris and Cowen 2004). These effects may be amplified in coastal river-dominated ecosystems because of the influence of wind and strong vertical gradients in oceanographic properties during spring and summer (Greer et al. 2018a). Other studies of thin layers have found intense shifts in abundance for different taxa surrounding the layer vertically (Benoit-Bird and McManus 2012; Greer et al. 2013), but this is the first study (to our knowledge) to resolve the different plankton taxa both vertically and horizontally surrounding a thin layer.

Taken together, the responses of the different zooplankton communities to the thin layer would generate patchiness that could lead to increased production of higher trophic levels (Greer and Woodson 2016). Further research into the gut fullness, diets, and feeding success of predators near these features (in contrast to areas outside the feature) would work toward establishing their importance in production of higher trophic levels (e.g., fisheries). For all groups measured in this study, there is a consistent theme of locally augmented food resources that cascade throughout the food web, but there may be other responses, such as behaviors or defenses (Almeda et al. 2017; van Someren Gréve et al. 2019), that we could not detect with our sampling approach and may alter trophic transfer rates.

**Thin layers in the nGOM**

Although the nGOM appears to have favorable conditions for thin layer formation (Dzvonkowski et al. 2018a), there are surprisingly few studies in this region and other coastal river-dominated ecosystems (but see Chumside and Donaghay 2009). The nGOM is known for high biological and overall fisheries production (Grimes 2001), which is generally attributed to the extensive riverine nutrient input fueling higher primary productivity relative to other marginal seas (> 300 g C m\(^{-2}\) yr\(^{-1}\); Heilman and Rabalais 2008; Lohrenz et al. 2014). Primary production can be even higher in diatom-dominated communities (Chakraborty et al. 2017), and aggregation of this production within a thin layer could augment the transfer to higher trophic levels, depending on its spatial coverage and temporal persistence.

Thin layers of large diatoms also alter the light environment on fine spatial scales and can cause light limitation immediately below the feature (Sullivan et al. 2010; Onitsuka et al. 2018), which may also shift ecological advantages for visual and contact predators (Eiane et al. 1999). In Monterey Bay, thin layer-derived light limitation may favor the proliferation of gelatinous contact predators below the layer (Greer et al. 2013). A similar pattern appears in the nGOM, where waters below the thin layer tended to have more siphonophores and hydromedusae, while fish larvae aggregated near the surface convergence (Greer et al. unpubl. data). The commonalities of thin layers altering the light environment and corresponding distributional shifts among contact vs. visual predators suggests that thin layers may be an important structuring mechanism for contrasting perception and feeding modes. Information on the metabolic condition of different planktonic groups near thin layers is a critical missing link toward understanding the ecological impacts of changes in light and spatial patchiness of predators and prey.

While there have been few studies of plankton thin layers and corresponding oceanographic influences in the nGOM, there is circumstantial evidence that subsurface chlorophyll maxima are common, particularly during the stratified summer season in areas without a surface freshwater plume (Qian et al. 2003). The summertime is also when the inner and mid-shelf areas experience a minimum in relative diatom abundance, while offshore waters have higher abundances of diatoms (Chakraborty and Lohrenz 2015). This suggests that northward propagating surface convergences, similar to the one described in this study, could concentrate diatoms in deeper waters and transport them onto the shelf.

**Conclusions**

The suite of oceanographic information obtained from imaging systems and coupled numerical models produces a clearer understanding of the biological implications of dynamic, fine-scale physical features. In this case, a surface convergence and vertical shear led to the formation of a diatom-dominated thin layer, with zooplankton responding in a manner likely dependent on their initial depth preferences and responsive swimming behaviors. These results support the notion that surface convergences can select for buoyant particles or organisms capable of swimming against the convergent flows (Genin et al. 2005; Höfer et al. 2015; D’Asaro et al. 2018), but there are more complex interactions below the surface. The disadvantage of the in situ image data is that they only provide a snapshot in time and space, and we have little understanding of how these distributions would change as the surface convergence propagates northward towards the shore and interacts with diel vertical migrations or predator-prey encounters (Greer et al. 2018b; Parra et al. 2019). Our incorporation of high-resolution modeling served as an attempt to expand the snapshot data towards larger spatiotemporal scales, elucidating biological and physical interactions within these (likely common) features in the nGOM.
Comparisons of these data to similar features at different times or places in the nGOM (or other river-dominated shelf systems) are needed to understand their influence on the ecology of different planktonic groups. In addition, sampling with a Lagrangian reference frame, along with improved descriptions of diets and feeding rates for different zooplankton groups, will help resolve the multiscale ecological impacts of these features in the nGOM and similar shelf ecosystems.

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Conflict of Interest

None declared.