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Key Points:

- Time-series observations revealed varying phytoplankton responses to internal waves in euphotic layers of the South China Sea (SCS)
- Nutrient-replete and nutrient-depleted layers exhibited contrasting phytoplankton dynamics under internal wave influence
- Three-layer structure highlighted the complex interplay between internal waves, nutrients, light, and grazing in this oligotrophic system

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Responses of Phytoplankton Communities to Internal Waves in Oligotrophic Oceans

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Abstract Understanding the potential impacts of internal waves on phytoplankton communities in oligotrophic oceans remains an important research challenge. In this study, we elucidated the impact of internal waves on phytoplankton communities through a comprehensive 154-hr time-series of observations in the South China Sea (SCS). We identified distinctive variations in phytoplankton pigment biomass and composition across the upper, middle, and lower layers of the euphotic zone, which we attributed to the perturbations triggered by internal waves. Phytoplankton other than Prochlorococcus in the lower, nutrient-replete layer likely benefitted from allochthonous nutrients introduced by internal waves, but their growth rates were constrained by light limitation, and their pigment biomass was held in check by microzooplankton grazing. In contrast, in the upper, nutrient-depleted layer, the relative abundance of *Prochlorococcus* increased, likely because of the ammonium regenerated by zooplankton. The middle layer, characterized as the deep chlorophyll maximum layer, exhibited a dynamic equilibrium characterized by nutrient and light co-limitation. This equilibrium resulted in high nitrate assimilation and growth by phytoplankton. The balancing of those rates by significant grazing losses maintained total chlorophyll a concentrations at a high level. Based on these findings, we proposed a three-layer euphotic zone structure characterized by distinct physiological conditions, nutrient-light dynamics, grazing pressure, and phytoplankton responses to internal waves. This three-layer paradigm elucidated the intricate interplay between internal waves and phytoplankton communities and provided insights into the mechanisms that govern primary production and carbon cycling in oligotrophic oceanic ecosystems.

Plain Language Summary Internal waves, a common occurrence in stratified oceans, play a crucial role in oligotrophic oceans by delivering nutrients to the euphotic zone. The enhancement of phytoplankton growth and primary productivity by this nutrient supply impacts the phytoplankton community composition. However, the specific mechanisms behind these changes remain uncertain. Our study, conducted at the SouthEast Asia Time-series Study station, located at 116°E, 18°N in the northern South China Sea, provided valuable insights. Through satellite imagery, 154-hr time series observations, and barotropic tide data, we firmly established the presence of internal wave activity in this region. Our observations revealed distinct variations in phytoplankton communities across different layers of the euphotic zone, driven by internal wave-induced perturbations. We introduced a three-layer structure within the euphotic zone, shedding light on the complex interplay between internal waves and phytoplankton communities. This understanding advances marine primary production estimates and enriches our comprehension of the global carbon cycle.

1. Introduction

Internal waves, oscillatory disturbances within stratified fluids, are ubiquitous in stratified oceans and play an important role in promoting the movement of water masses and the exchange of nutrients and materials (Garwood et al., 2020; Whalen et al., 2020). These waves can significantly influence marine ecosystems, particularly phytoplankton (T.-Y. Chen et al., 2016; Li et al., 2018), which are photosynthetic microorganisms that require light and nutrients to grow and reproduce (Falkowski et al., 2003). The availability of these resources is often modulated by internal waves through several mechanisms, including the vertical displacement of phytoplankton into nutrient-rich layers (Orr & Mignerey, 2003), enhancement of vertical mixing and nutrient supplies (Pan

et al., 2012), and alterations of the light environment (Evans et al., 2008). As a result, internal waves can directly and indirectly affect the distribution, abundance, and community composition of phytoplankton, which in turn influence higher trophic levels and biogeochemical processes in marine ecosystems because phytoplankton form the base of marine food webs and contribute to biogeochemical cycling (Behrenfeld & Boss, 2014).

The effect of internal waves on phytoplankton community composition and distribution has been observed in different oceanic environments, including coastal (Margaret et al., 2001; Omand et al., 2011; Villamaña et al., 2019), shelf (Sharples et al., 2007), and upwelling regions (Ma et al., 2021; Villamaña et al., 2017), where nutrient availability is generally high. In these regions, phytoplankton responses to internal waves vary as a function of the local physical, chemical, and biological conditions, as well as the specific characteristics of the internal waves themselves, such as their frequency, amplitude, and direction of propagation. Oligotrophic oceans, characterized by low nutrient concentrations, cover vast areas of the global ocean and play a crucial role in biogeochemical cycling and climate regulation (C. M. Moore et al., 2013). In these oligotrophic oceans, mixing driven by internal waves can dominate the supply of nutrients to the euphotic zone (Tuerena et al., 2019) and thereby stimulate phytoplankton primary productivity (Li et al., 2018; Lucas et al., 2011). Investigating the processes and mechanisms by which internal waves drive phytoplankton community dynamics in oligotrophic oceans is crucial for understanding the complex interactions between physical processes and biological communities in these globally significant regions. However, our nascent understanding of how internal waves influence phytoplankton communities in oligotrophic oceans warrants further exploration.

Several methodologies including microscopy (Utermöhl, 1958), chemical biomarkers (Mackey et al., 1996), flow cytometry (Sieracki et al., 1998), and phylogenetic techniques (Saldarriaga et al., 2001) have been used to delineate phytoplankton community composition. Of these methods, pigment-based chemotaxonomic identification of phytoplankton groups has emerged as a particularly valuable tool at present (Mackey et al., 1996). This method is characterized by its capacity to simultaneously quantify the composition of the entire phytoplankton community, ranging from picoplankton to large colonies. However, the information this technique yields is typically restricted to taxonomic levels above the class level (L. Wang et al., 2015). Despite these limitations, pigment-based chemotaxonomy is the best method for acquiring high-resolution data on phytoplankton community composition (Poulton et al., 2006; Zapata et al., 2000) and can provide a robust framework for investigating the responses of phytoplankton to internal wave dynamics.

In addition to characterizing phytoplankton community composition, it is crucial to investigate other physiological parameters to gain a comprehensive understanding of the impacts of internal waves on marine ecosystems. Measurements of nitrate assimilation rates, new production (NP), gross primary production (GPP), phytoplankton growth rates, and microzooplankton grazing rates are important in this context. Determination of nitrate assimilation rates provides information about potential shifts in phytoplankton community composition because there are distinct differences between some phytoplankton groups in their ability to use nitrate (Litchman et al., 2007). Quantifying NP based on nitrate assimilation enables estimation of the contribution of nitrate assimilation to the production of organic matter through photosynthesis (Dugdale & Goering, 1967). Comparing NP with observed changes of chlorophyll *a* concentrations enables assessment of the accumulation of phytoplankton biomass and provides insights into the sources and losses of chlorophyll *a* (Laws et al., 2000). Furthermore, measuring GPP allows identification of the potential influence of nutrient upwelling induced by internal waves on the overall primary productivity of a system (Boyd & Doney, 2002). These parameters collectively serve as crucial indicators of the impacts of internal waves on phytoplankton community dynamics. Assessments of phytoplankton growth rates and microzooplankton grazing rates via dilution experiments provide insights concerning trophic interactions within the phytoplankton community (Landry et al., 2008a, 2008b; Laws, 2013).

The northern South China Sea (SCS) basin is a typical oligotrophic ocean (Du et al., 2013, 2017). The Luzon Strait, which borders the SCS on the east, generates energetic internal waves that radiate both eastward and westward. The energy of these internal waves is concentrated mainly in internal tides (Lin et al., 2020), that is, internal waves of tidal frequency. In the SCS, the energy fluxes of semidiurnal internal tides propagate mainly toward the northwest (Zhao, 2014, 2020). These onshore, radiating, semidiurnal internal tides finally evolve into nonlinear internal solitary waves and dissipate on the continental shelf. In contrast, diurnal internal tides radiate toward the southwest and mainly affect the center of the SCS (Zhao, 2020). The northern SCS basin is therefore an area into which diurnal, internal waves from the Luzon Strait radiate. The SouthEast Asia Time-series Study (SEATS, 116°E, 18°N) station, located in the center of the northern SCS basin, is a site often used to study the

biogeochemical characteristics of oligotrophic oceans (Chou et al., 2006; Shih et al., 2021; Wong et al., 2007) and is an ideal region to study the influence of internal waves on phytoplankton communities in oligotrophic oceans.

In this study, we used 154 hr of data collected from the SEATS station during a cruise in the northern SCS during the summer of 2014. Our goal was to integrate assessments of phytoplankton community composition with measurements of nitrate assimilation rates, NP, GPP, phytoplankton growth rates, and microzooplankton grazing rates in different regions of the euphotic zone at SEATS to elucidate how internal waves influenced phytoplankton communities in the oligotrophic SCS basin. Our results revealed that the temporal variations of phytoplankton communities in the upper, middle, and lower layers of the euphotic zone differed and that the differences likely resulted from perturbations caused by internal waves. This conclusion suggested that the structure of the phytoplankton community at SEATS was best described by a three-layer system at steady state. The three-layer response of phytoplankton communities to the perturbations caused by internal waves helped to reveal that structure.

2. Data and Methods

2.1. Study Area and Sampling Procedures

Field observations were conducted onboard the R/V *Shiyan* 1 and lasted from 10:30 on 23 August 2014 to 20:30 on 29 August 2014 at SEATS. Water temperature, salinity, and pressure were recorded during each cast with a SeaBird model SBE9/11 conductivity-temperature-depth (CTD) recorder. A total of 40 CTD casts were conducted at different time intervals, including at least every 6 hr from 02:00 on 25 August to 22:00 on 27 August.

2.2. Identification of Internal Waves

The characteristics and influence of internal waves at SEATS were analyzed using the 26-year-coherent satellite altimeter results of Zhao (2020) based on a new mapping technique that combines plane wave analysis with 2-D band-pass filtering. The internal waves at SEATS are generated chiefly by the interplay between the tidal flow and topography in the Luzon Strait. To elucidate the genesis and propagation of these internal waves during our observation period, we analyzed barotropic tide data from August 2014 at both the Luzon Strait and SEATS. Tidal information was obtained from the regional tidal solution of the OSU TPXO Tide Models using Tide Model Driver (TMD) Matlab Toolbox (https://www.esr.org/research/polar-tide-models/tmd-software/). We also analyzed moderate-resolution imaging spectroradiometer (MODIS) true color images to confirm the presence of internal waves in our study area during our observational timeline.

2.3. Photosynthetically Active Radiation and the Maximum Quantum Yield of Photochemistry

Photosynthetically active radiation (PAR, 400–700 nm) and the maximum quantum yield of photochemistry (Fv/ Fm) were measured with a FastOcean Ambient Plus Dark fluorometer (Chelsea Technologies Group Ltd, UK). The fluorometer was lowered from the surface to a depth of 100–120 m. The instrument was lowered slowly (<0.4 m s⁻¹) and parked every 10 or 25 m to make a 30-s measurement. There was at least one valid profile every day, except for 27 August. We obtained a total of 12 valid PAR and Fv/Fm profiles.

2.4. Nutrient Concentrations

Seawater samples for nutrient analyses were collected from depths of 5, 25, 50, 75, and 100 m on the first cast. The concentrations of nitrate plus nitrite (NOx, μ mol L⁻¹) were measured with a QUAATRO nutrient analyzer. The detection limit was 0.03 μ mol L⁻¹.

2.5. Phytoplankton Pigment Analysis

Seawater samples for phytoplankton pigment analyses were collected from the same depths sampled for nutrient concentrations every 6 hr from 02:00 on 25 August to 22:00 on 27 August. Approximately 4–10 L of seawater was filtered through 25-mm-diameter Whatman GF/F filters under dim light conditions and pressure below 75 mm Hg. The filters were promptly frozen in liquid nitrogen and stored at -80° C. To extract the pigments, the frozen filters were soaked in 1 mL of *N*, *N*-dimethylformamide at -20° C for about 1 hr. The resulting solution containing

the pigments was filtered using 0.22 µm Millipore syringe filters to remove cell and filter debris. Afterward, the filtered solution was mixed with an equal volume of 1 mol L^{-1} ammonium acetate. High-performance liquid chromatography was used to measure the pigment concentrations following the modified method of Furuya et al. (2003). For analysis, 400 µL of the mixture was injected into a SHIMADZU LC 20A liquid chromatography system equipped with a 3.5-µm Eclipse XDB C8 column. Pigments were identified using chromatography with authentic standards and diode-array spectroscopy. The identified pigments included chlorophyll c2, chlorophyll c3, peridinin, 19'-butanoyloxyfucoxanthin, fucoxanthin, neoxanthin, prasinoxanthin, 19'-hexanoyloxyfucoxanthin, violaxanthin, diadinoxanthin, alloxanthin, diatoxanthin, zeaxanthin, lutein, chlorophyll a, chlorophyll b, divinyl chlorophyll a, α -carotene, and β -carotene. To determine the relative contributions of different phytoplankton groups to the total chlorophyll a (TChl a, chlorophyll a plus divinyl chlorophyll a), we used the CHEMTAX program (Mackey et al., 1996) with nine phytoplankton groups: dinoflagellates, diatoms, haptophytes_8 (typically Phaeocystis spp., Dicrateria spp., and Imantonia spp.), haptophytes_6 (mainly Emiliania huxleyi) (Zapata et al., 2004), chlorophytes, cryptophytes, Prochlorococcus, Synechococcus, and prasinophytes. Samples were categorized based on depth (L. Wang et al., 2015; Xiao et al., 2018), and the initial input ratios of diagnostic pigments to chlorophyll a were consistent across all groups. Successive runs were performed to achieve convergence between the input and output ratios following the CHEMTAX protocols described by Latasa (2007), which allows the data-driven determination of these ratios within each group.

2.6. Nitrate Assimilation Rate and Production

To determine the nitrate assimilation rate (ρ NO₃⁻), NP, and GPP, we collected water samples in acid-cleaned bottles from depths of 3, 17, 33, 55, and 110 m, corresponding to light intensities of about 88%, 50%, 25%, 10%, and 1% of the surface irradiance, respectively. We estimated the depth of the euphotic zone (110 m) and the diffuse attenuation coefficient (0.04 m⁻¹) based on the Secchi depth (31.4 m) measured after sunrise on the first day (10:30 on 23 August) (Lee et al., 2018). The rate of nitrate uptake (ρ NO₃⁻) was measured daily following the method of Dugdale and Wilkerson (1986). Incubation procedures and subsequent calculations of ρ NO₃⁻ have previously been reported in detail (Ma et al., 2021). In brief, each sample was spiked with a K¹⁵NO₃ tracer at a concentration one-tenth of the ambient nitrate concentration or 20 nmol L⁻¹ if the ambient concentration was less than 200 nmol L⁻¹. Neutral density screens were used to simulate irradiances at the sampling depths, and temperature control was achieved by flushing the incubators with near-surface seawater. Incubations began in the morning and lasted 2–4 hr. Analyses of particulate matter were conducted before and after incubations using GF/F filters, and concentrations of particulate organic nitrogen (PON) and ¹⁵N isotopic enrichment were determined with an elemental analyzer coupled to a mass spectrometer (EA-IRMS, Thermo Fisher Flash HT 2000-Delta V plus).

The nitrate assimilation rate (ρ NO₃⁻) was calculated using equations similar to those proposed by Kanda et al. (1985):

$$\rho \mathrm{NO}_3^- = \frac{P_f}{t} \times \frac{R_f - R_0}{R_s - R_0} \tag{1}$$

where P_f is the concentration of PON (µmol L⁻¹), *t* is the incubation time (hr), R_f is the atom% of ¹⁵N in the particulate nitrogen after incubation, R_0 is the atom% of ¹⁵N in the particulate nitrogen at the beginning of the incubation, and R_s is the atom% of ¹⁵N in the substrate after the addition of the tracer. To account for the overestimation of reaction rates caused by tracer addition in low-nutrient surface waters, we applied the Michaelis-Menten kinetic equation (Harrison et al., 1996; Kanda et al., 2003; Wan et al., 2018). The equation for nitrate uptake (ρ_{NO_T}) was as follows:

$$\rho_{\rm NO_3^-} = V_{\rm max} \frac{S}{K_m + S} \tag{2}$$

Here, V_{max} represents the maximum nitrate uptake rate (µmol L⁻¹ day⁻¹), K_m is the half-saturation constant for nitrate uptake (µmol L⁻¹), and S is the ambient nitrate concentration (µmol L⁻¹).

To estimate V_{max} and K_m , five different concentrations of ¹⁵N tracer were added to groups of bottles, resulting in final nitrate concentrations of $S + (0.04, 0.1, 0.2, 0.4, \text{ and } 1) \, \mu\text{mol } \text{L}^{-1}$. The concentration-dependent nitrate assimilation rate was then calculated based on Equation 1. The estimated values of S, V_{max} , and K_m were used to determine ρNO_3^- using Equation 2 (Kanda et al., 2003; Shiozaki et al., 2011).

NP was determined based on the ρNO_3^- and assuming a C/N ratio of 6.625 by moles. The same method has been used to estimate NP in the SCS by previous studies (Y.-L. L. Chen, 2005; Y.-L. L. Chen et al., 2007; Li et al., 2018; Liu et al., 2002). Although this approach may not capture the actual NP in situ because the C/N ratio

of the phytoplankton may not be 6.625 by moles, it is widely recognized as a reasonable estimate when direct measurements are not available (Dugdale & Goering, 1967; Eppley & Peterson, 1979).

The NP was further used to estimate the accumulation of phytoplankton biomass in terms of chlorophyll *a* based on the ratios of carbon to chlorophyll *a* (C/Chl) at different light levels reported by Landry, Selph, Taylor, et al. (2011) in the HNLC equatorial Pacific, with an adjustment of 30% given that the ratios are at least 30% lower in the SCS than in the equatorial Pacific according to model simulations (Arteaga et al., 2016; Behrenfeld et al., 2016). Although there are uncertainties associated with using reference data and model simulations to adjust C/Chl ratios, this is a well-grounded approach that provides a practicable estimate in the absence of direct, in situ measurements (Cloern et al., 1995; Laws et al., 2000).

GPP was determined daily based on the difference of dissolved oxygen concentrations in light and dark bottles over a 24-hr incubation period following the procedure of Pablo et al. (1999). To maintain consistency with the NP estimate, the GPP estimated in terms of oxygen production was converted into carbon assimilation by assuming a photosynthetic quotient (O/C ratio) of $1.14 \text{ mol mol}^{-1}$ (Y.-L. L. Chen, 2005; Huang et al., 2021).

2.7. Phytoplankton Growth Rates and Microzooplankton Grazing Rates

We conducted two-point dilution experiments on 24 August to assess the growth rates (μ) of phytoplankton and the grazing rates (m) of microzooplankton at various depths using the methodology outlined in previous studies (Guo et al., 2014; Landry et al., 2008b). Seawater samples of 10 L were collected from depths of 5, 25, 50, 75, and 110 m. These samples were filtered through a 200- μ m mesh to exclude larger grazers and subsequently filtered through a 0.2- μ m filter capsule into clear polycarbonate bottles with a volume of 2.4 L. Two sets of samples were incubated at each depth: one with 100% unfiltered seawater and another with 25% unfiltered seawater diluted with 0.2- μ m filtered seawater. This experimental setup was replicated twice.

The incubation period lasted for 24 hr in an on-deck incubator cooled by continuously flowing surface seawater, maintaining ambient light conditions. Samples were collected before and after the incubation period, and chlorophyll *a* analysis was conducted by concentrating 0.6–1.0 L of seawater onto 25-mm Whatman GF/F filters. To account for the grazing mortality, which exhibited a linear decline with dilution as validated in previous studies in the region (B. Chen et al., 2013), we derived the net rate of change (*k*) based on the change of chlorophyll *a*. In undiluted bottles, *k* was equated to $\mu - m$, where μ is the phytoplankton growth rate and *m* is the mortality rate due to grazing. In the diluted bottles, the net rate of change (*k*_d) equaled $\mu - 0.25$ m. Therefore $\mu = (4k_d + k)/3$ and $m = 4(k_d - k)/3$.

2.8. Statistical Analyses

Generalized additive models (GAMs) were used to describe the nitrate assimilation rate, NP, and GPP as functions of depth according to the following formulation:

$$Y = \alpha + s(X) + \varepsilon, \tag{3}$$

where Y represents either the nitrate assimilation rate, NP, or GPP. The term s(X) represents a smoother function of depth and is based on one-dimensional nonlinear functions (Wood, 2007). To avoid over-fitting, the maximum number of basis functions was limited to five. The terms α and ε are the intercept and residual, respectively. The GAMs were evaluated using the function "gam" in the R package "mgcv."

3. Results

3.1. Meteorological Conditions and Ocean Currents

During the 7-day observation period, conditions were sunny on all days except 26 and 27 August. It rained for a short time on both 26 and 27 August. The water temperature and ocean currents at 100 m revealed by a global ocean eddy-resolving reanalysis data set indicated that SEATS was located at the center of an anticyclonic eddy (warm eddy) that persisted throughout the entire month of August 2014 (Figure 1).

3.2. Evidence of Internal Tides

The influence of internal waves at SEATS was revealed by satellite and field observations, as well as results of barotropic tide data (Figure 2). The 26-year-coherent satellite altimeter results indicated that internal waves at



Journal of Geophysical Research: Oceans



Figure 1. Water temperature and ocean currents at 100 m showing existence of an anticyclonic eddy throughout the entire month of August 2014. The asterisk indicates the location of SouthEast Asia Time-series Study. Data were collected from a global ocean eddy-resolving (1/12° horizontal resolution, 50 vertical levels) reanalysis data set (https://data.marine. copernicus.eu/product/GLOBAL_MULTIYEAR_PHY_001_030/).

SEATS were mainly diurnal internal tides. After their generation in the Luzon Strait, the diurnal, internal tides propagated southwestward, as shown by the energy fluxes and phases of the internal tides in Figure 2a. It took about 1.5–2 days for these waves to reach SEATS from the Luzon Strait. The fact that the barotropic tides in the Luzon Strait and at SEATS were basically in phase during August 2014 confirmed that SEATS experienced primarily diurnal tides during spring tide periods and showed that our observations covered the period from the spring tide before 25 August to the neap tide on 27 August (Figure 2b).

We analyzed MODIS true color images to identify whether there were internal waves at our study area during our observation period. Despite the challenge of detecting internal wave signals in the deep basin area through MODIS imagery, a MODIS true color image obtained at 05:25 on 28 August 2014 (Figure 2c) provided direct evidence of the presence of internal waves during our field observations. In this image, which had a spatial resolution of 250 m, surface imprints of internal waves were apparent near the Dongsha Atoll (117° E, 20.6°N). The signature was clear because of the nonlinear steepening of the internal wave during shoaling. The spatial distribution of the fronts of these internal waves were present and were influencing our field measurements. Moreover, temporal hydrographic variations revealed synchronous, diurnal fluctuations in the time-series of temperature, salinity, and density profiles as well as the depth of the maximum buoyancy frequency (N^2) (Figure 2d). This synchrony provided further support that diurnal internal tides were impacting conditions at SEATS during our observation period.

3.3. Light Intensity and Fv/Fm

There were no available FastOcean data on 27 August, but the available data showed that the light intensity was significantly lower on 26 August than on the other 5 days (*t*-test, p < 0.01) (Figure 3a) precisely because of the cloudy conditions during the deployment of FastOcean. The Fv/Fm increased from the surface to depths of 75 and 100 m and then decreased with depth (Figure 3b). The Fv/Fm results did not differ significantly between





Figure 2. Satellite, tidal, and hydrographic characteristics showing evidence of internal waves in the SouthEast Asia Time-series Study (SEATS) station in summer 2014. (a) Blue arrows show depth-integrated energy fluxes, and black contours show propagating time of the K₁ internal tide from the Luzon Strait, based on the results of Zhao (2020). (b) Sea surface height (η) due to tides in the Luzon Strait and the SEATS station in August 2014. Black and red lines indicate the full tides (Full) and diurnal tides (D1), respectively. (c) Moderate-resolution imaging spectroradiometer true color image taken at 05:25 on 28 August 2014, with the propagating time of K₁ internal tide from the Luzon Strait. (d) Temporal variations of hydrographic parameters at SEATS, where N^2 is the squared buoyancy frequency, and the red solid line indicates the depth of maximum N^2 .

days, except on 26 August. In the upper 50 m, the Fv/Fm was significantly higher on 26 August than on the other five observation days (*t*-test, p < 0.01) (Figure 3b).

3.4. Vertical and Temporal Distributions of Phytoplankton Biomass and Community Composition

The TChl *a* concentration initially increased and then decreased with depth, and the deep chlorophyll maximum layer (DCML) appeared at 75 m (Figure 4). The dominant phytoplankton groups were mainly *Prochlorococ*-



Figure 3. Vertical profiles of (a) light and (b) Fv/Fm obtained from FastOcean.

cus and *Synechococcus* above the DCML and *Prochlorococcus* and Haptophytes_8 below the DCML. The total contribution of the five other groups to TChl *a* was less than 10% throughout the water column during our observation period (Figure 4). The relative abundance of *Prochlorococcus* exceeded 40% at each depth we sampled in the upper 100 m; it exceeded 60% at 25 and 50 m and was highest at 25 m. The relative abundance of *Synechococcus* was close to 40% at the surface, but it dropped to less than 20% at depths below 25 m. The relative abundance of haptophytes_8 was less than 15% in the upper 50 m, but it increased substantially to nearly 40% at 100 m (Figure 4).

During the 3-day observation period, there were significant changes of the concentrations of TChl a and the relative abundances of the main phytoplankton groups. The patterns of change varied between depths (Figure 5). The concentration of TChl a in the upper 50 m increased significantly over time (Figure 5a), but there was no obvious temporal trend at 75 and 100 m (Figures 5b and 5c). The changes of the phytoplankton community were attributable mainly to significant changes in the relative abundances





Figure 4. Vertical profiles of phytoplankton total chlorophyll *a* and contributions of nine phytoplankton groups. All data during the observation period have been averaged by depth.

of *Prochlorococcus* and *Synechococcus* during the observation period. The relative abundance of *Prochlorococcus* (quantified by the ratio of its marker pigment divinyl chlorophyll *a* to TChl *a*, i.e., Dv-Chl/TChl) increased significantly in the upper 50 m (Figure 5d) and decreased significantly at 100 m (Figures 5d and 5e), but there was no obvious change at 75 m (Figure 5f). The relative abundance of *Synechococcus* (represented by the ratio of its marker pigment zeaxanthin to TChl *a*, Zea/TChl) decreased significantly in the upper 50 m (Figure 5g), but there was no obvious trend at 75 and 100 m (Figures 5h and 5i). The relative abundances of other groups did not show regular changes during the observation period.

3.5. Nitrate Assimilation Rate and Production

The ρ NO₃⁻ underwent obvious changes during the 7-day observation period. High values at 55 and 110 m were particularly noteworthy on 24 and 25 August (Figure 6a), which corresponded to the time when the thermocline, halocline, and pycnocline were uplifted (Figure 2d). The value of ρ NO₃⁻ was highest at 55 m, extremely low in the upper 33 m, and intermediate at 110 m (Figure 6b). The ρ NO₃⁻ estimated with the GAM model reached a maximum at a depth of about 75 m (Figure 6b). The NP estimated from the ρ NO₃⁻ was significantly lower than GPP above 75 m, but the gap gradually narrowed at greater depths (Figure 6c). The theoretical accumulation of chlorophyll *a* estimated from the NP was significantly lower than the observed maximum



Figure 5. Temporal variations of phytoplankton biomass and community composition in different layers at SouthEast Asia Time-series Study. (a–c) TChl *a*; (d–f) The relative abundance of *Prochlorococcus* (represented by the ratio of its marker pigment divinyl chlorophyll *a* to TChl *a*, Dv-Chl/TChl); (g–i) The relative abundance of *Synechococcus* (represented by the ratio of its marker pigment zeaxanthin to TChl *a*, Zea/TChl).



Journal of Geophysical Research: Oceans



Figure 6. Temporal and vertical variations of nitrate assimilation rate and production at SouthEast Asia Time-series Study during our observation period. (a) Temporal variations of nitrate assimilation rate; (b) The vertical profile of nitrate assimilation rate was fitted by generalized additive models (GAMs); (c) GAM simulations of new production (NP) and gross primary production (GPP); (d) Comparison of chlorophyll *a* accumulation estimated from nitrate assimilation and maximum changes of observed chlorophyll *a*, where the black solid line is the variation of chlorophyll accumulation with depth or light level fitted by the GAMs, and the blue scattered points represent the maximum measured changes of chlorophyll *a*. For all GAM simulations, the dashed lines are the 95% confidence intervals.



Figure 7. Vertical profiles of phytoplankton growth rate, microzooplankton grazing rate, and grazing pressure, where solid dots and lines were results obtained in this study and boxes were results obtained from B. Chen et al. (2013) for surface and deep chlorophyll maximum layers, aligned with our observed data at corresponding depth ranges.

change of chlorophyll a in the upper 50 m. The opposite was true at 100 m, and at the DCML the two values were basically the same (Figure 6d).

3.6. Phytoplankton Growth Rate and Microzooplankton Grazing Rate

The phytoplankton growth rates and microzooplankton grazing rates agreed well with previous averages in the SCS (Figure 7). In general, the growth rates exceeded the grazing rates above the DCML, the two rates were similar at the DCML, and the grazing rates exceeded the growth rates below the DCML. The grazing pressure (the ratio of grazing rate to growth rate, m/μ) increased from the surface to 110 m (Figure 7).

4. Discussion

We found that the TChl a and the dominant phytoplankton groups at SEATS changed with time during our observation period from 02:00 on 25 August to 22:00 on 27 August (Figure 5). This pattern suggested that transient environmental shifts may have disturbed the system either during or preceding our study. Two noticeable environmental changes occurred. First, internal wave activity underwent a transition from spring tides (20–25 August) to

neap tides (27 post-August) (Figure 2b). Second, brief rainfall events were recorded on 26 and 27 August. Those were the days when the phytoplankton community changed (Figure 5). Although a mesoscale anticyclonic eddy influenced the study area throughout August 2014, that eddy did not change significantly during or prior to our observations (Figure 1). The implication was that its impact was part of the impact of the prevailing environmental conditions rather than that of a discrete disturbance. Because of the consistency of the anticyclonic eddy and the temporal alignment of our observations with the rainfall and internal wave activity, we hypothesize that these two factors were potential key players in influencing the system dynamics. We then asked what might have been responsible for the changes of the phytoplankton community structure at SEATS.

4.1. Assessing the Impact of Rainfall on the Phytoplankton Community

The rainy weather could have been associated with an increased flux of allochthonous nutrients from the atmosphere or a decrease in light intensity. We did not measure any parameter associated with atmospheric deposition, but a significant increase in the flux of nutrients from the atmosphere would have increased the nutrient concentrations in the upper water column and would inevitably have led to an increase of ρNO_3^- in the upper layers, which is typically *N*-limited in the SCS (Du et al., 2017). The increase of ρNO_3^- would inevitably have led to an increase in the upper layers of the biomass of phytoplankton groups with the ability to take up nitrate. However, the fact that ρNO_3^- at shallow depths did not change significantly during our 7-day observation period (Figure 6a) was inconsistent with the atmospheric deposition hypothesis. The main changes of the phytoplankton community in the upper 50 m were an increase in the relative abundance of *Prochlorococcus* and a decrease in the relative advantage if inorganic nitrogen were added in the form of nitrate to a nitrogen-limited system (Ahlgren & Rocap, 2006). The decrease in the relative abundance of *Synechococcus* was therefore inconsistent with an influx of nitrate from the atmosphere. The changes of both ρNO_3^- and the phytoplankton community structure were therefore unlikely to have resulted from an increase of atmospheric deposition.

Because of the rainy weather, the PAR at 13:00 was indeed significantly lower on 26 August than on other observation dates (Figure 3). However, the relative abundances of Synechococcus and Prochlorococcus were comparable at the surface (Figure 4). Even though the photosynthetic efficiency of Prochlorococcus may have increased because of a reduction of photoinhibition during cloudy conditions (Flombaum et al., 2013; Xiao et al., 2019; Xie et al., 2018), the photosynthetic efficiency of *Synechococcus* in the upper waters could have been reduced because of light limitation (Xiao et al., 2019). The compensating effects of the reduced photoinhibition of Prochlorococcus and the increased light limitation of Synechococcus could have resulted in no significant changes in the observed Fv/Fm. However, the Fv/Fm in the upper 50 m at noon was significantly higher on 26 August than on other measurement days (Figure 3). This result was also inconsistent with a reduction of light intensity. In addition, photoinhibition of *Prochlorococcus* has been observed only at the surface (Flombaum et al., 2013; Xiao et al., 2019; Xie et al., 2018). The effect of a decrease of light intensity on Procholorococcus would therefore have differed between the surface and subsurface. The fact that the changes of Procholorococcus abundance were almost the same at the surface and at 25 and 50 m was therefore inconsistent with the photoinhibition scenario (Figures 5d-5f). Hence the reduction of light intensity was unlikely to have been responsible for the changes in the phytoplankton community in the upper 50 m. Also, neither an increase of atmospheric deposition nor the decrease of light intensity could explain the decrease of the relative abundance of *Prochlorococcus* at 100 m (Figure 5f). We therefore concluded that the brief period of rainy weather was probably not the main factor that caused the changes of the phytoplankton community at SEATS.

4.2. Evaluating the Impact of Internal Waves on Phytoplankton Dynamics

The most likely causative mechanism was therefore internal waves. The impact of internal waves on phytoplankton is mainly the result of an increase in the supply of allochthonous nutrients (Garrett, 2003; Sharples et al., 2009). These nutrients would have been taken up by phytoplankton if there had been adequate light in the lower layers of the euphotic zone. The ρ NO₃⁻ in the lower euphotic zone (50–110 m) was higher during 23–25 August than afterward (Figure 6a), and 23–25 August was when the spring tides occurred (Figure 2d). The implication is that strong internal wave activity during the spring tides enhanced the influx of nutrients from the nutricline into the lower layers of the euphotic zone. One factor that might have contributed to the observed trends could have been diapycnal processes associated with internal waves. Although currently we have no direct evidence to support this hypothesis, Li et al. (2018) have estimated a significant nitrate diffusive flux of 635 µmol N m⁻² day⁻¹ triggered by internal waves in the northern SCS. Diapycnal mixing could cause some of the uplifted nutrients to remain in the upper layer after the passage of an internal wave and hence might have resulted in residual nutrient enrichment in these layers (Ledwell et al., 1993; St. Laurent & Nash, 2004).

There is usually a time lag between the uptake of nutrients and the increase of phytoplankton chlorophyll (Ma et al., 2021; Sharples et al., 2007; Y.-H. Wang et al., 2007). Changes of the phytoplankton community would therefore have become apparent after the spring tides. If nitrate were added at the base of the euphotic zone, Prochlorococcus would lose its competitive advantage because most Prochlorococcus ecotypes lack the ability to take up nitrate (Bouman et al., 2006), and other phytoplankton species with the ability to take up nitrate would benefit. This line of reasoning could well explain the significant decrease in the relative abundance of Prochlorococcus at 100 m (Figure 5f). However, we observed no noticeable increases in the relative abundances of other phytoplankton groups, and TChl a remained stable (Figure 5c). This unexpected result could be attributed to a combination of factors. First, the dominance of Prochlorococcus might have masked minor changes in the relative abundances of other groups. Second, the grazing pressure of microzooplankton on phytoplankton was relatively high at 100 m (Figure 7), consistent with previous observations (Landry, Selph, & Yang, 2011). The phytoplankton community in this water layer consisted primarily of groups of small cells, especially haptophytes_8 (Figure 4). Haptophytes_8, represented by species like Phaeocystis spp., Dicrateria spp., and Imantonia spp., are known to serve as ideal food sources for microzooplankton (Hansen et al., 1994; Kanayama et al., 2020; Verity, 2000) or larger zooplankton (e.g., krill) (Poulton et al., 2007). In addition, the growth of phytoplankton was severely light limited at that depth (Figure 7). The result was that the grazing of microzooplankton constrained the growth of other phytoplankton species, and hence there was no increase of these species and TChl a (Figure 5c).

In the DCML (75 m), the allochthonous nutrients supplied by internal waves led to high phytoplankton growth rates because the irradiances and nutrient concentrations enabled rapid growth, but the high rate of microzooplankton grazing balanced the high growth rates (Figure 7). Although there were diurnal fluctuations of the TChl a and the relative abundances of dominant groups in the DCML, there was hence no obvious trend in the composition or biomass of the phytoplankton community in the DCML during the 3 days of observations (Figures 5b, 5e, and 5h). The microzooplankton were likely consumed by mesozooplankton (Fonda Umani et al., 2005), which can move vertically (Hays, 2003), and their upward migrations might therefore have resulted in excretion of ammonium into the upper layers (King et al., 1987; Webb & Johannes, 1967). We did not directly determine ammonium concentrations and ammonium uptake rates, but the reduction of the NP/GPP ratio in the upper layers (Figure 6b) was an indication that recycled ammonium became relatively more important than nitrate as a source of inorganic nitrogen. The fact that most Prochlorococcus can use the ammonium excreted by zooplankton better than other phytoplankton such as Synechococcus (Berube et al., 2015; L. R. Moore et al., 2002) may explain why the growth of *Prochlorococcus* exceeded that of other phytoplankton in the upper 50 m (Figure 5d). The phytoplankton in the upper layers were not light-limited, and because the grazing pressure of microzooplankton was low (Figure 7), grazing could not constrain the accumulation of phytoplankton biomass. This line of reasoning could explain the increasing trend of TChl a in the upper 50 m (Figure 5a).

To further test the internal wave hypothesis, we assumed that all the nitrate taken up by phytoplankton within the 3 days (25-27 August) was converted into phytoplankton biomass. We then compared the theoretical accumulation of phytoplankton biomass in terms of chlorophyll a with the observed maximum change of chlorophyll within the 3 days to determine whether the biomass supported by nitrate equaled the change of total biomass. The observed changes of chlorophyll a consistently exceeded the changes estimated from nitrate uptake in the upper 50 m. The latter exceeded the former at a depth of 100 m, and the two were about the same in the DCML at a depth of 75 m (Figure 6d). The implication was that even if the phytoplankton biomass produced from nitrate uptake had accumulated monotonically during the 3 days, the estimated net accumulation would still have been significantly lower than the observed changes of chlorophyll in the upper 50 m. The implication was that nitrate was not the only source of nitrogen in the upper 50 m and underscored the importance of ammonium nitrogen in controlling the dynamics of the phytoplankton community in the upper 50 m. In contrast, the fact that the theoretical accumulation of chlorophyll a was significantly higher than the observed maximum change of chlorophyll a at 100 m implied that there was a large loss of phytoplankton biomass produced from nitrate uptake. This conclusion was consistent with the intense grazing pressure from microzooplankton at 110 m (Figure 7). The agreement between the theoretical and observed changes of chlorophyll a concentrations in the DCML suggested that any losses due to grazing by microzooplankton were balanced by uptake of autochthonous nitrogen (Figure 7).

Whereas our results support our hypothesis that internal waves were a significant contributor to the observed changes of the phytoplankton community, a decision to accept or reject this hypothesis must take into consideration the limitations of our methods and the complexity of oceanographic processes. For instance, our study relied primarily on correlations between different variables. We did not directly measure the impact of internal wave activity on nutrient fluxes. A more informed study would have involved direct monitoring of these complex and dynamic processes. Furthermore, whereas we observed a significant decrease in the relative abundance of Prochlorococcus at 100 m, we did not see a corresponding increase in other phytoplankton species. The apparent absence of an increase in the abundance of other species could have been due to high grazing pressure from microzooplankton at that depth coupled with the possibility that the great abundance of Prochlorococcus at 100 m masked minor changes in the relative abundances of other species. Testing these hypotheses would require further experiments. Moreover, although a mesoscale anticyclonic eddy was present throughout our observations, fully understanding the potential influence of such features on phytoplankton dynamics over longer timescales would require further investigations (Geng et al., 2021; Shih et al., 2020). We also recognize the importance of other physical mechanisms, such as fronts, on the distribution and composition of phytoplankton communities (Hales et al., 2009). Although significant fronts were absent during our study, their potential influence on phytoplankton dynamics in the SCS deserves attention in future studies. Lastly, we acknowledge the need for direct measurements of ammonium concentrations and uptake rates and a more comprehensive understanding of the complex interactions between different trophic levels to more accurately assess the dynamics of the phytoplankton community in the SCS.

4.3. Three-Layer Response of the Phytoplankton Community to Internal Waves in Oligotrophic Oceans

The euphotic zone of the SCS basin can be divided into a nutrient-depleted layer (NDL) above the nutricline and a light-limited layer or nutrient-replete layer (NRL) below the NDL (Du et al., 2017). However, the transition region between limitation by light or nutrients at SEATS was characterized by a clearly apparent DCML (Figure 4), where light and nutrients jointly limited photosynthetic rates and the rates of growth and loss of phytoplankton were in dynamic equilibrium (Figure 7). In the euphotic zone below the DCML, grazing exceeded phytoplankton growth (Figure 7). These scenarios were consistent with previous observations both in the SCS basin (B. Chen et al., 2013) and the equatorial Pacific (Landry, Selph, Taylor et al., 2011; Landry, Selph, & Yang, 2011). A similar three-layered structure has been observed in a cyclonic cold-core eddy (Cyclone Opal) in the lee of the Hawaiian Islands (Landry et al., 2008a). In this study, three distinct zones were identified, a surface mixed layer, an intermediate layer, and a deep zone dominated by large diatoms. This observed structure suggests that a three-layer model may enhance understanding of phytoplankton community dynamics under different nutrient and light conditions.

We therefore propose that the phytoplankton community in the euphotic zone of the oligotrophic SCS basin be characterized by a three-layer structure under steady state conditions: the upper portion of the NDL, where phytoplankton growth is strictly limited by nutrients; a middle layer, the DCML, where light and nutrients are co-limiting and phytoplankton gains and losses are in a dynamic equilibrium; and a light-limited region below the DCML, the NRL, where nutrients are abundant and the grazing pressure is greatest.

Figure 8 illustrates the implications of this proposed three-layer structure under different scenarios based on our key findings. This conceptual diagram serves as a visual tool to explain the dynamic interactions among the phytoplankton communities in each layer when subjected to internal wave-induced perturbations. The diagram suggested that if this system were perturbed by an influx of allochthonous nutrients from the bottom of the euphotic zone by internal waves, the differences between the physiological conditions of the phytoplankton in each layer would cause their responses to differ in ways that would clearly reveal the three-layer structure. More specifically, when there is a perturbation caused by internal waves, nitrate uplifted into the euphotic zone stimulates phytoplankton groups other than *Prochlorococcus* in the NRL, and because of light limitation, phytoplankton biomass is held in check by microzooplankton grazing. The result is a decreased relative abundance of *Prochlorococcus* and unchanged TChl *a*. In the DCML, weak co-limitation by nutrients and light results in high nitrate assimilation rates and high growth rates, but the increased phytoplankton growth rates are balanced by high grazing rates. The result is a stable, high TChl *a* concentration. In the NDL, *Prochlorococcus* benefits from ammonium regenerated by zooplankton that migrate from below. The result is an increased relative abundance of *Prochlorococcus* and increase of TChl *a*.

In the nutrient-rich upwelling region of the northern SCS, where diatoms contribute most of the phytoplankton biomass, internal waves cause an increase in diatom abundance within the euphotic zone, but there is no apparent three-layer structure (Ma et al., 2021). Conversely, at SEATS, diatoms contributed only a small fraction





Figure 8. The three-layer response of the phytoplankton community to internal waves in oligotrophic oceans.

of the phytoplankton biomass; the community was comprised predominantly of small phytoplankton, including *Prochlorococcus*, *Synechococcus*, and haptophytes_8 (Figure 6). Unlike the uniform distribution of diatoms throughout the euphotic zone of the upwelling region (Ma et al., 2021), the vertical distribution of the dominant phytoplankton groups at SEATS was very heterogeneous (Figure 4). This difference may be attributed to physical mixing throughout the euphotic zone of the upwelling region (Ma et al., 2021), whereas at SEATS, the phytoplankton communities in different layers are regulated by different mechanisms (Figure 8). Our analysis therefore emphasizes the distinct three-layer structure of the euphotic zone at SEATS, where each layer responds differently to internal waves. This structure reflects a dynamic equilibrium that evidences how phytoplankton communities adapt to variations of light, nutrients, and grazing pressure.

Although the mechanisms responsible for formation of DCMLs vary from place to place in the ocean (Cullen & Eppley, 1981), it has been a common assumption that the DCML is an ecologically important feature of stratified oceans since the seminal paper by Yentsch (1965). Primary production in the DCML accounts for 30%–70% of water column production, and this layer also accounts for the largest proportion of NP in the SCS (Cai et al., 2015; Y.-L. L. Chen et al., 2008). Production in the NRL is much lower because of severe light limitation (Figure 6), but its contribution to particle export flux can be high if grazing rates are high (Landry, Selph, & Yang, 2011). High grazing rates in the NRL and DCML combined with vertical migration by microzooplankton support high rates of autochthonous production in the NDL, which would enhance carbon export through the microbial carbon pump (Jiao et al., 2010). The concept of a three-layer euphotic zone may therefore facilitate estimates of marine primary production and enhance understanding of the carbon cycle in the upper water column of stratified marine systems.

5. Conclusions

We conclude that our observations of the responses of the phytoplankton community to internal waves in the oligotrophic SCS basin can be explained by a three-layer euphotic zone. The perturbations caused by internal waves brought an influx of allochthonous nutrients from the bottom of the euphotic zone that elicited distinct responses



from phytoplankton in each layer. In the NRL, internal waves stimulated the phytoplankton groups other than *Prochlorococcus*, but phytoplankton biomass was regulated by microzooplankton grazing because of light limitation. The DCML maintained stable, high chlorophyll *a* concentrations because of a balance between nutrient assimilation and grazing rates. *Prochlorococcus* in the NDL may have benefited from ammonium excreted by zooplankton that migrated from the NRL. The result was an increase of chlorophyll *a* in the NDL. This study provided significant insights into the complexity of the response of phytoplankton communities to variations in light, nutrients, and grazing pressure. We expect that theoretical consideration of the three-layer structure will enhance understanding of marine primary production and the global carbon cycle.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Physical-biochemical data collected onboard used in this study can be found in https://data.mendeley.com/ datasets/c5rknh37t5.

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