

Physically modulated phytoplankton production and export at submesoscales in the oligotrophic South China Sea Basin

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Abstract Oceanic submesoscales can significantly influence phytoplankton production and export owing to their similar timescales of days. Based on two-year Biogeochemical Argo (BGC-Argo) observations, this study investigated the development of submesoscale instabilities, particularly symmetric and mixed-layer baroclinic instabilities, and their impacts on biological production and export in the oligotrophic South China Sea basin. In the northern basin, near-surface winter blooms consistently cooccurred with seasonally deepened mixed layers. However, significantly stronger and weaker winter blooms were observed over two consecutive winters within the BGC-Argo observation period. During the first winter, symmetric-instability-induced upward nutrient entrainment played a crucial role in initiating the strong winter bloom in early December, when the mixed layer was approximately 20–30 m shallower than the nutricline. This bloom occurred approximately 20–30 days earlier than that anticipated owing to the contact between the seasonally deepened mixed layer and mesoscale-cyclone-induced uplifted nutricline. The symmetric instability also facilitated the export of fixed phytoplankton carbon from the surface to deeper layers. Conversely, during the second winter, remarkably intense mixed-layer baroclinic instability associated with an intense mesoscale anticyclone led to more significant shoaling of the mixed layer compared to the nutricline, thus increasing the vertical distance between the two layers. Under this condition, upward nutrient injection, phytoplankton bloom, and carbon export were suppressed. In contrast, the BGC-Argo float in the central basin revealed significantly inhibited seasonality of phytoplankton biomass and submesoscale instabilities compared to those in the northern basin, primarily owing to the significantly shallower winter mixed layer.

Keywords Submesoscale instability, Phytoplankton, Nutrient transport, BGC-Argo, South China Sea

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1. Introduction

The oceanic mixed layer (ML) features vertical homogeneity

owing to upright turbulent mixing while simultaneously hosting strong lateral density (buoyancy) fronts. These fronts serve as kinetic and potential energy reservoirs and can catalyze various instabilities within a typical spatial scale of 1–100 km and a synoptic timescale of 1–10 days, known as

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the submesoscale (McWilliams, 2016; Taylor and Thompson, 2023). Marine phytoplankton account for over half of the global primary production (Field et al., 1998), thus profoundly impacting the global carbon cycle and climate change (Sabine et al., 2004). Phytoplankton blooms consistently occur on the synoptic timescale of days, similar to the evolution timescale of submesoscale dynamics. Therefore, by modulating the availability of light and nutrients to phytoplankton, submesoscale processes can substantially impact upper-ocean photosynthetic carbon fixation and carbon export to deep oceans (Mahadevan, 2016; Lévy et al., 2018).

Submesoscale instabilities typically evolve within a dynamic regime wherein the Rossby number approaches or exceeds $O(1)$ and the Richardson number (Ri) is less than or close to $O(1)$, thus presenting both geostrophic and ageostrophic components (McWilliams, 2016; Taylor and Thompson, 2023). These submesoscale instabilities also follow distinct seasonal cycles, developing vigorously during winters when atmospheric forcing is the strongest (Calies et al., 2015). Directly driven by this atmospheric forcing, gravitational instabilities (GIs) occur under negative vertical stratification, inducing strong vertical convections near the ocean surface (Haine and Marshall, 1998). Symmetric instabilities (SIs) consistently emerge near sharp submesoscale fronts, where strong lateral buoyancy gradients lead to negative Ertel potential vorticity (PV , Thomas et al., 2013). SIs typically extract energy from thermal wind shear and trigger strong slantwise convections along tilted isopycnals (hence, SIs are also referred to as slantwise instabilities). Consequently, SIs not only facilitate nutrient transport from depths into the euphotic layer and promote blooms (Brannigan, 2016) but also export phytoplankton carbon from upper ocean blooms (Erickson and Thompson, 2018). Submesoscale baroclinic instabilities (often known as mixed-layer instabilities, MLIs) also manifest near submesoscale fronts, fueled by the available potential energy (APE) stored in lateral buoyancy gradients. MLIs can drive intense secondary overturning circulations, which are capable of re-stratifying the upper-ocean water column by releasing the APE stored within submesoscale fronts (Boccaletti et al., 2007). With ample nutrient supply, such restratification can confine phytoplankton cells to the euphotic zone, increasing mean light exposure and triggering blooms (Mahadevan et al., 2012; Mignot et al., 2018; Zhao et al., 2022).

The South China Sea (SCS) is among the largest marginal seas in the western North Pacific, situated within the East Asian Monsoon regime (Figure 1). The SCS holds dynamic significance as it harbors abundant and intricate processes at various spatiotemporal scales, including the seasonal large-scale circulation (Su, 2004), western boundary current (Fang et al., 2012), Kuroshio intrusion (Xue et al., 2004), upwellings (Hu and Wang, 2016), mesoscale eddies (He et al.,

2018), and internal waves (Park and Farmer, 2013), facilitating the development of active submesoscale processes (Lin et al., 2020). High-resolution satellite images and surface drifters have revealed that submesoscale eddies within the SCS exhibit a typical radius of 13 ± 5 km (Ni et al., 2021) and a typical timescale of 2–7 days (Qiu et al., 2022). These features strongly regulate the spatiotemporal variabilities of phytoplankton biomass (Ni et al., 2021), as evidenced by the patchy distribution patterns of chlorophyll-a (Chl-a) displayed in Figure 1b.

In situ experiments demonstrated that nutrient availability primarily constraints phytoplankton growth in the oligotrophic SCS, rather than light intensity and zooplankton grazing (Chen and Chen, 2006; Chen et al., 2004). Moreover, satellite observations reveal distinct seasonal patterns in surface phytoplankton biomass, with lower productions in summers and higher productions in winters (Fang et al., 2015; Tang et al., 2014). Based on the data from two Biogeochemical Argo (BGC-Argo) floats deployed in the northern and central SCS basins, Zhang et al. (2016) further noted that this seasonal pattern was pronounced in the northern basin but considerably diminished in the central basin. They identified a correlation between the observed heightened winter production and vertical nutrient transport driven by strong turbulent mixing within the deep ML in the northern basin. Similarly, using data from the two BGC-Argo floats, Geng et al. (2019) further evaluated the effects of wind- and cooling-induced mixing on winter nutrient transport in the northern and central SCS basins. Their analysis revealed that cooling-induced mixing played a dominant role in the northern SCS basin, while a combination of the two mixing processes governed the dynamics of the central SCS basin, albeit with considerably lower intensity. Furthermore, submesoscale processes are also known to significantly impact vertical nutrient transport and phytoplankton growth within the SCS basin; however, no studies have investigated this aspect yet.

To date, studies investigating the effects of submesoscale instabilities on phytoplankton production have predominantly focused on high-latitude oceans, which tend to be relatively eutrophic and low-light environments (e.g., North Atlantic, Erickson and Thompson, 2018; Mahadevan et al., 2012). However, similar studies focusing on oligotrophic and high-light low-latitude oceans are scarce. Moreover, investigations on the spatiotemporal characteristics of submesoscale instabilities and their biological responses within the SCS basin are still in their nascent stages and primarily rely on remote sensing (Ni et al., 2021) and numerical simulation data (Lin et al., 2020). Therefore, using high-resolution observational data from the two BGC-Argo floats deployed in the SCS basin, this study examines the spatiotemporal variabilities of the submesoscale instabilities (GI, SI, and MLI) and evaluates their impacts on phyto-

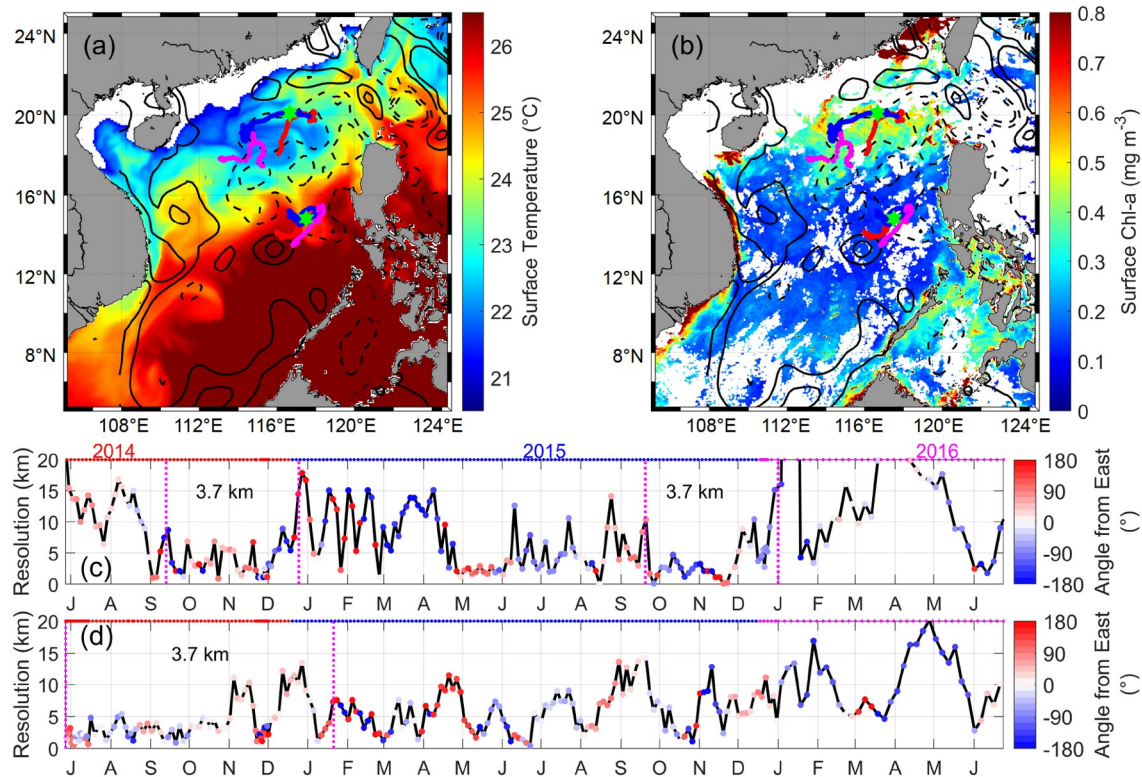


Figure 1 Sea-surface temperature ((a), CMEMS) and Chl-a ((b), OC-CCI) distributions averaged from 11–15 February, 2015, and along-track time-series plot of the BGC-Argo lateral resolution (black solid line) and orientation relative to the eastward direction (colors) in the northern (c) and central (d) SCS basins over the complete two-year period. (a), (b) Black contours represent the corresponding AVISO SLA, with solid and dashed lines denoting mesoscale cyclones and anticyclones, respectively. Green stars denote the corresponding locations of the BGC-Argo floats. Red, blue, and magenta dotted lines denote the BGC-Argo tracks in 2014, 2015, and 2016, respectively. (c), (d) BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively. Labeled months denote the middle of each month from July 2014 to June 2016. Magenta dashed lines denote the high-resolution observational periods (averaged resolution of approximately 3.7 km).

plankton production and export. Overall, the study aims at distinguishing the distinct effects of submesoscale instabilities on phytoplankton production and export in high- and low-latitude oceans.

2. Materials and methods

2.1 BGC-Argo observations

Two BGC-Argo floats were deployed in the northern and central basins of the SCS to conduct continuous and synchronous physical-biological observations in these regions over a two-year period from July 2014 to June 2016. The observational data could be obtained from Xiamen University (https://odc.xmu.edu.cn/BioArgo/DataBin/0347_dataabin.txt and https://odc.xmu.edu.cn/BioArgo/DataBin/0348_dataabin.txt). Equipped with an SBE 41CP CTD, a WET Labs ECO-MCOMS fluorometer, and an SBE 63 Optical Dissolved Oxygen Sensor, the floats recorded vertical profiles of *in situ* variables such as temperature, salinity, fluorescent Chl-a content, the particulate backscattering coefficient at 700 nm (*BBP*), and dissolved oxygen (*DO*)

levels approximately every 3 days (sometimes every 1–2 days). Each profile had vertical resolutions of roughly 2 m from approximately 4–1000 m and 50 m beyond the 1000 m depth. The lateral resolution between profiles varied from less than 1 km to more than 20 km, reaching approximately 3.7 km in certain periods, specifically from mid-autumn to early winter in 2014–2015 and 2015–2016 in the northern SCS basin (Figure 1c) and from summer to winter in 2014–2015 in the central basin (Figure 1d). These periods represent the primary focus of this study and will be hereinafter referred to as high-resolution observational periods. The high-resolution BGC-Argo observations could reasonably resolve submesoscale eddies in the SCS with a typical radius of 13 ± 5 km (Ni et al., 2021) and a typical timescale of 2–7 days (Qiu et al., 2022). Additionally, water samples were collected for *in situ* calibrations of the Chl-a fluorometer through high-performance liquid chromatography (Bidigare et al., 1985) and the *DO* sensor through the Winkler wet-chemical method. Further descriptions of the BGC-Argo floats can be found in papers authored by Zhang et al. (2016) and Xing et al. (2019).

Potential density was calculated based on *in situ* mea-

measurements of pressure, temperature, and salinity. The mixed-layer depth (MLD) was subsequently estimated as the depth at which the potential density exceeded the near-surface density at 10 m by 0.06 mg m^{-3} (Zhang et al., 2016). Additionally, the 22°C isotherm was used as a proxy for the nutricline depth (Xing et al., 2019; Zhang et al., 2016), as it closely aligned with the depth of the subsurface Chl-a maximum throughout the two-year observational period (Figure 2 and Appendix Figure S1, <http://earthcn.scichina.com>).

2.2 Ancillary data

We used the following data for our analysis: daily satellite sea-surface Chl-a data obtained from the Ocean Color Climate Change Initiative (OC-CCI) project of the European Space Agency (available at <https://esa-oceancolour-cci.org>); daily sea-surface temperature and sea-surface salinity data of the Global Ocean Physics Reanalysis product (GLORYS12V1) from the Copernicus Marine Environmental Monitoring Service (CMEMS, available at https://data.marine.copernicus.eu/product/GLOBAL_MULTIYEAR_

PHY_001_030/services); 6-hourly sea-surface heat flux and wind data from the National Centers for Environmental Predictions (NCEP)-DOE Reanalysis 2 dataset (Kanamitsu et al., 2002) (available at <http://www.cpc.ncep.noaa.gov/products/wesley/reanalysis2>); and daily sea level anomaly (SLA) provided by Archiving, Validation and Interpretation of Satellite Oceanographic (AVISO, available at <ftp://ftp.aviso.altimetry.fr>).

2.3 Diagnostic methods

2.3.1 Instability classifications

Generally, several types of instabilities can develop when the Ertel PV has a sign opposite to the planetary vorticity (f) (Hoskins, 1974), i.e., negative, in the northern hemisphere. PV is formulated as follows:

$$PV = \zeta_a \cdot \nabla b, \quad (1)$$

where $\zeta_a = (f\bar{k} + \nabla \times \bar{u})$ denotes the absolute vorticity; $\bar{k}$ represents a unit vector along the vertical direction; ∇ denotes the three-dimensional Hamiltonian operator; $\bar{u} = (u, v, w)$ represents the three-dimensional velocity along the positive

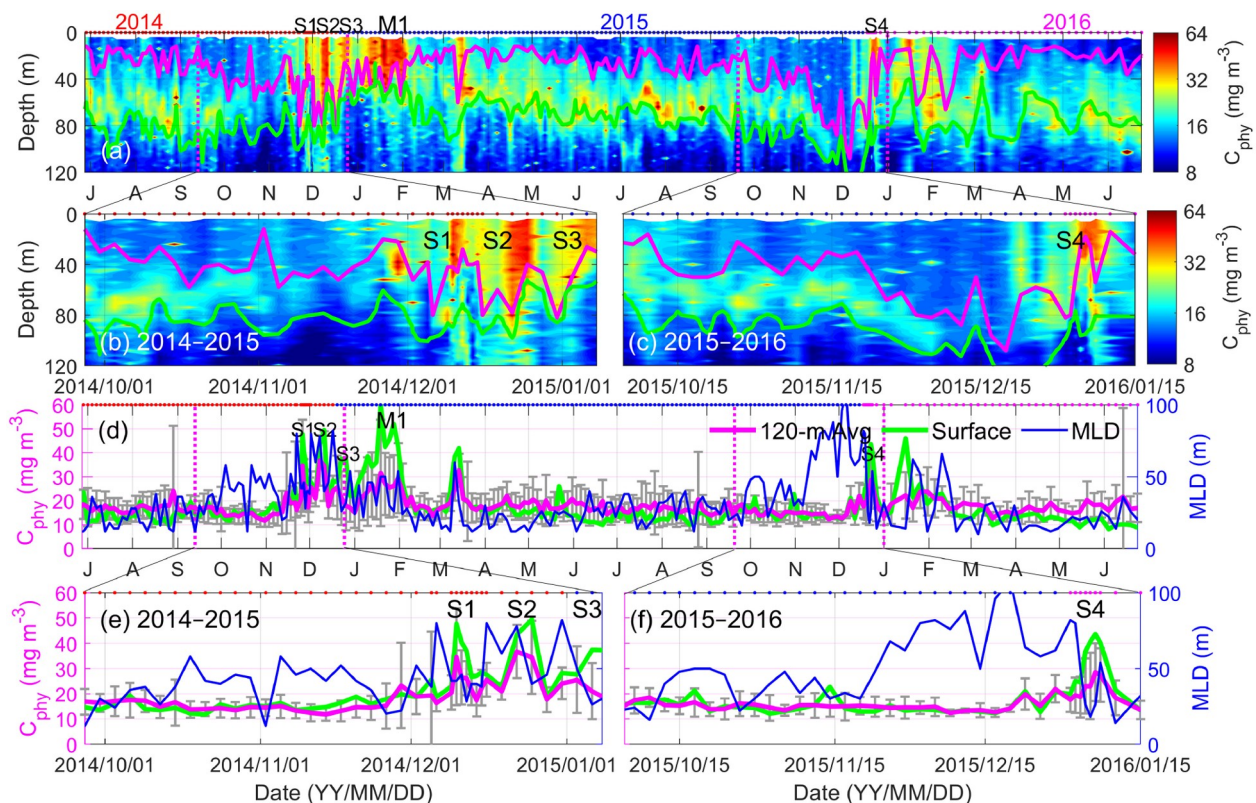


Figure 2 Along-track depth-time plot of the phytoplankton carbon concentration C_{phy} ((a)–(c)) and time-series plot of the surface layer (green line) and upper 120-m averaged (magenta line) C_{phy} derived from the BGC-Argo data in the northern SCS basin ((d)–(f)). (a), (d) The complete two-year period. (b), (e) The high-resolution observational period in 2014–2015. (c), (f) The high-resolution observational period in 2015–2016. (a)–(c) Magenta and green solid lines denote the MLD and nutricline depth, respectively. (d)–(f) Blue line denotes the MLD. The observed synoptic blooms are designated as S1–S4, and the month-long bloom is denoted as M1. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively. Months labeled in (a) and (d) denote the middle of each month from July 2014 to June 2016.

directions of x , y , and z ; and ∇b denotes the spatial derivative of buoyancy $b = -g\rho/\rho_0$, where g represents the acceleration due to gravity (9.8 m s^{-2}), ρ denotes the potential density, and ρ_0 represents the reference density (1025 kg m^{-3}). Notably, PV can be decomposed into two terms:

$$PV = PV_{bt} + PV_{bc} = \frac{PV_{bt}}{\zeta_g N^2} + \frac{PV_{bc}}{[(w_y - v_z)b_x + (u_z - w_x)b_y]}, \quad (2)$$

where PV_{bt} denotes the barotropic component associated with vertical vorticity $\zeta_g = f + (v_x - u_y)$ and vertical stratification $N^2 = b_z$, while PV_{bc} denotes the baroclinic component related to the horizontal vorticity and horizontal buoyancy gradients. Note that the subscripts “ x ,” “ y ,” and “ z ” denote partial differentiations.

As stated, this study focuses on submesoscale instabilities occurring within the open SCS basin, far from intense oceanic frontal jets such as the Kuroshio jet occurring near the Luzon Strait and the Vietnam offshore jet occurring during summertime. Therefore, submesoscale flows within the SCS basin are relatively diminished with weak ageostrophic components. Hence, we can disregard the vertical velocity, w , and posit that the flows are to leading order in thermal wind balance that is,

$$(u_z, v_z) = f^{-1}(-b_y, b_x). \quad (3)$$

Hence, PV_{bc} can be expressed as follows:

$$PV_{bc} = -f^{-1}|\nabla_h b|^2 = -f^{-1}M^4, \quad (4)$$

where ∇_h denotes the two-dimensional Hamiltonian operator along the horizontal direction. The intensity of the lateral buoyancy gradient $|\nabla_h b|$ is always denoted as M^2 .

As noted by Thomas et al. (2013), various instabilities can be categorized depending on the causes of negative PV s in the northern hemisphere. For barotropic flows, inertial or centrifugal instabilities develop when a negative PV_{bt} induces a negative PV with positive N^2 . Whereas GIs develop when a negative N^2 leads to a negative PV . For baroclinic flows, the baroclinicity of the fluid consistently reduces PV (eq. (4)). Hence, SIs develop when $|PV_{bc}| > PV_{bt}$ with $PV_{bt} > 0$. Moreover, states prone to SIs are also prone to MLIs, which can exist even when $PV > 0$ (Boccaletti et al., 2007).

Additionally, the balanced Ri (Ri_b) and associated angle (Φ_{Ri_b}) can be employed as alternative criteria for the development of instabilities, and these can be expressed as follows:

$$Ri_b = f^2 N^2 / M^4, \quad (5)$$

$$\Phi_{Ri_b} = \tan^{-1}(-Ri_b^{-1}). \quad (6)$$

Introducing the balanced Richardson angle, Thomas et al. (2013) summarized that a GI, a hybrid GI/SI, and an SI developed with angle ranges of $-\pi < \Phi_{Ri_b} < -3\pi/4$ ($Ri_b < -1$), $-3\pi/4 < \Phi_{Ri_b} < -\pi/2$ ($-1 < Ri_b < 0$), and $-\pi/2 < \Phi_{Ri_b} < \Phi_c$ ($0 < Ri_b < f/\zeta_g$), respectively. Here, the critical angle Φ_c is related to the vertical vorticity ζ_g as follows:

$$\Phi_c = \tan^{-1}(-\zeta_g/f). \quad (7)$$

Notably, $Ri_b < f/\zeta_g$ is a parallel condition as $PV < 0$, while $PV < 0$ is a relatively more stringent criterion for SI development (Bachman et al., 2017). Generally, SIs work toward restoring the fluid back to a marginally stable state with $Ri_b = 1$ (or $PV = 0$), and this state is always prone to MLIs.

To analyze submesoscale instabilities using PV and Ri_b , this study employed BGC-Argo observational data with high lateral resolution of approximately 3.7 km (Figure 1c and 1d). Following the approach adopted by Thompson et al. (2016), the along-track and cross-track directions were considered as x and y , respectively, regardless of the orientation. As submesoscale flows occurring within the open SCS basin exhibit relatively weak ageostrophic components, the vertical relative vorticity can be reasonably neglected, and $Ri_b < 1$ emerges as a sufficient condition for SI development (Taylor and Ferrari, 2009; Taylor and Ferrari, 2010). Note that relative vorticity is primarily related to smaller-scale shear instabilities (e.g., inertial or centrifugal instability). Capturing these phenomena using floats is challenging, and they lie beyond the scope of the present study. Thus, the observational expression for the PV becomes

$$PV_{obs} = PV_{bt,obs} + PV_{bc,obs} = \frac{PV_{bt,obs}}{fN^2} - \frac{PV_{bc,obs}}{f^{-1}M^4}, \quad (8)$$

where $M^2 = b_x$ denotes the along-track horizontal buoyancy gradient. Additionally, the critical Richardson angle becomes $\Phi_c = \tan^{-1}(-1) = -\pi/4$, and SI develops with a balanced Richardson angle range of $-\pi/2 < \Phi_{Ri_b} < -\pi/4$ ($0 < Ri_b < 1$).

2.3.2 MLI parameterization

Lateral density gradients provide a reservoir of APE that can be released by MLI, even when the system becomes marginally stable for SI, i.e., $Ri_b = 1$. Fox-Kemper et al. (2008) provide a parameterization for the streamfunction of the secondary overturning circulation driven by MLI:

$$\psi_e = 0.06\mu(z)H^2b_x/f, \quad (9)$$

where $\mu(z)$ is a vertical structure function defined as follows:

$$\mu(z) = [1 - (1 + 2z/H)^2][1 + (5/21)(1 + 2z/H)^2], \quad (10)$$

where H denotes the MLD. The vertical and horizontal ve-

locities induced by MLI are thus expressed as follows:

$$w_e = -\partial\psi_e / \partial x, \quad (11)$$

$$u_e = \partial\psi_e / \partial z. \quad (12)$$

Energetically, the rate of conversion from APE to eddy kinetic energy by MLI (i.e., buoyancy flux; denoted as BuoFlux) can be parameterized as follows:

$$\overline{w'b'} = \psi_e b_x = 0.06\mu(z)H^2 b_x^2 / f. \quad (13)$$

Notably, the above parameterization only represents the potential effect of MLI that can slump the tilted isopycnals but not the dynamic process itself (Tang et al., 2023).

2.3.3 Temperature-salinity relations

Density (or buoyancy) fronts are always generated by lateral temperature and salinity gradients in the upper ocean. In particular, the contributions of these lateral temperature and salinity gradients to the lateral density gradient can be demonstrated using the density ratio (Barkan et al., 2017):

$$R = \alpha \Delta T / \beta \Delta S = \alpha T_x / \beta S_x, \quad (14)$$

where α and β denote the thermal expansion and saline contraction coefficients of the potential temperature T and salinity S , respectively, and T_x and S_x denote the temperature and salinity gradients over a lateral spatial interval that lies along the BGC-Argo float track. The value of R has an infinite range from $-\infty$ to $+\infty$. A positive R value indicates that the temperature and salinity gradients produce opposing effects on the density gradient, whereas a negative R value suggests that they reinforce the density gradient. Typically, salinity is dominated when $-1 < R < 1$, whereas temperature is dominated when $1 < |R| < +\infty$. T - S compensation occurs when the temperature and salinity gradients perfectly oppose each other, i.e., $R = 1$. Conversely, equipartition occurs when the temperature and salinity gradients make equal and reinforcing contributions to the density gradient, i.e., $R = -1$.

The turner angle (Tu) is expressed as follows:

$$Tu = \arctan(R). \quad (15)$$

It offers a better description of the above T - S relations because it has a finite range from $-\pi/2$ to $\pi/2$. The salinity-dominated region corresponds to $-\pi/4 < Tu < \pi/4$, whereas the temperature-dominated region corresponds to $|Tu| > \pi/4$. T - S compensation is accompanied with $Tu = \pi/4$, whereas equipartition is accompanied with $Tu = -\pi/4$.

The T - S covariance, C_{TS} , is expressed as follows:

$$C_{TS} = 2\alpha\beta T_x S_x / (\alpha^2 T_x^2 + \beta^2 S_x^2). \quad (16)$$

It represents the comparison between lateral density and spice gradients, which can also be used to interpret the evolution of T - S relations. Generally, C_{TS} is bounded between -1 and 1 . When C_{TS} is close to -1 , the magnitude of

the density gradient considerably exceeds that of the spice gradient (i.e., isopycnals are much steeper), indicating T - S equipartition ($Tu = -\pi/4$). Conversely, when C_{TS} is close to 1 , the magnitude of the density gradient is considerably smaller than that of the spice gradient (i.e., isopycnals are much shallower), suggesting T - S compensation ($Tu = \pi/4$). If C_{TS} is near zero, the magnitudes of the density and spice gradients are comparable. Thus, in this case, the temperature and salinity gradients neither oppose nor reinforce the density gradient.

Notably, high-resolution observations within the ML often reveal that the lateral temperature and salinity gradients tend to counterbalance their impacts on the density gradient at the submesoscale level (Rudnick and Ferrari, 1999), a phenomenon that can be attributed to the development of submesoscale instabilities in the ML. When the APE reserved in density fronts associated with the lateral temperature and salinity gradients is released by the MLI, the resulting secondary overturning circulation tends to not only eliminate any lateral buoyancy gradients with compensated temperature and salinity gradients but also drive near-surface restratification with slumped isopycnals. The effective buoyancy flux leading to T - S compensation (denoted as BuoFlux_{Comp}) scales as follows:

$$\overline{w'b'}_{comp} = \overline{w'b'} |C_{TS}| = 0.06\mu(z)H^2 b_x^2 |C_{TS}| / f. \quad (17)$$

2.3.4 Steric height

As the baroclinic component of the sea surface height, steric height (SH) originates from multi-scale processes such as mesoscales, submesoscales, and different types of internal gravity waves (Miao et al., 2021). The SH at level z referenced to level z_0 can be calculated as follows:

$$SH(z) = - \int_{z_0}^z (\rho - \rho_{ref}) / \rho_{ref} dz, \quad (18)$$

where ρ and ρ_{ref} denote the potential density and its temporal-mean value at each depth z throughout the two-year observational period, respectively. Owing to the coverage of the available BGC-Argo data, the vertical integral range extends from 4 m to 860 m (the shallowest z is 4 m, and z_0 is set to 860 m). Notably, this value of z_0 is sufficiently deep to serve as the reference depth. Moreover, with the predominantly three-day temporal resolution of the BGC-Argo measurements, they can only resolve mesoscale and submesoscale signals.

2.3.5 Phytoplankton carbon

As a better proxy for phytoplankton biomass and primary production, phytoplankton carbon (C_{phy}) can be estimated based on the observed BBP at 700 nm (Xing et al., 2021):

$$C_{phy} = 13000 \times [BBP \times (443 / 700)^{-1} - 0.00035]. \quad (19)$$

2.3.6 Apparent oxygen utilization

The apparent oxygen utilization (*AOU*) metric can be derived from the observed *DO* (Omand et al., 2015):

$$AOU = DO_{sat} - DO, \quad (20)$$

where DO_{sat} denotes the saturation oxygen at the measured temperature, salinity, and surface pressure. Ocean water obtains oxygen from both atmosphere and photosynthetic phytoplankton. Thus, *DO* levels are relatively elevated in the upper layer and diminished in the lower layer, leading to negative and positive *AOU* within the upper and lower layers, respectively.

3. Results and analyses

3.1 Phytoplankton variability in the northern basin

The BGC-Argo floats provided along-track measurements of fluorescent Chl-a contents and *BBP* values. In the northern SCS basin, the *BBP*-derived phytoplankton carbon and fluorescent Chl-a concentrations presented consistent and strong seasonal variabilities (Figures 2 and S1). Specifically, from spring (MAM) through autumn (SON), when the ML was shallow (20–30 m, magenta line in Figure 2a), these variables presented a subsurface maximum near the nutricline depth at 60–80 m (green line in Figure 2a). Conversely, during wintertime (DJF), when the ML deepened significantly, the subsurface maximum ascended into the ML, forming a pronounced surface peak indicative of a winter bloom. The intensity and duration of this winter bloom presented evident interannual variability, with significantly stronger and weaker winter blooms observed during the first (2014–2015) and second (2015–2016) winters of the BGC-Argo observation period. As presented in Figures 2 and S1, in the first winter of 2014–2015, the strong winter bloom persisted from early December to mid-February, with significantly enhanced surface and vertically averaged phytoplankton carbon and Chl-a concentrations (green and magenta lines in Figure 2d and 2e). Conversely, in the second winter of 2015–2016, the winter bloom appeared considerably weaker, with limited and sporadic increments in the surface and vertically averaged phytoplankton carbon and Chl-a concentrations (green and magenta lines in Figure 2d and 2f).

Despite the consistency observed in the *BBP*-derived phytoplankton carbon and fluorescent Chl-a concentrations, notable differences persisted between the two parameters. Specifically, the *BBP*-derived phytoplankton carbon concentration was approximately 24 mg m^{-3} at the subsurface maximum, and it increased to approximately 60 mg m^{-3} at the winter surface peak (Figure 2a). Conversely, the fluorescent Chl-a concentration remained relatively constant at approximately 1.5 mg m^{-3} for both the subsurface maximum

and winter surface peak (Figure S1a). Additionally, the *BBP*-derived phytoplankton carbon concentration exhibited sporadic high values beneath the ML base, indicating the deposition of fixed carbon from the ML to deeper layers, a phenomenon not evident in the fluorescent Chl-a measurements (e.g., during the early winter of 2014–2015, Figures 2b and S1b). These differences were attributed to the photoacclimation effect of phytoplankton cells (Xing et al., 2019), which could influence the amounts of pigments (such as Chl-a) per unit phytoplankton biomass on a daily timescale. The photoacclimation effect can be demonstrated based on the Chl-a: C_{phy} ratio (Xing et al., 2021). As depicted in Figure 3, high values of the Chl-a: C_{phy} ratio appeared in the region of the phytoplankton subsurface maximum from spring through autumn, as well as the near-surface region during winter, suggesting that photoacclimation increased the Chl-a concentration in phytoplankton cells under low-light conditions.

In this study, we focused on the spatiotemporal variability in the *BBP*-derived phytoplankton carbon concentration to avoid the risk of misestimating the phytoplankton biomass based on the fluorescent Chl-a concentration owing to the photoacclimation effect, as suggested by Erickson and Thompson (2018). The primary aim of this study was to investigate the bio-physical mechanisms associated with submesoscale processes contributing to the significantly stronger and weaker winter blooms observed over the two consecutive years by the BGC-Argo float.

3.2 SI-related strong bloom in the first winter (2014–2015)

The BGC-Argo float deployed in the northern SCS basin captured a strong winter bloom from early December through mid-February in the year 2014–2015 (Figure 2a). In the early winter (i.e., early December to early January), relatively strong net surface cooling effect (approximately -300 W m^{-2} , blue line in Figure 4a) induced a relatively deep MLD with an average value of approximately 65 m (magenta lines in Figure 4b and 4c). However, the MLD was still approximately 20–30 m shallower than the nutricline depth (green lines in Figure 4b and 4c). Subsequently, in the late winter (i.e., from early January to mid-February), although the MLD decreased to approximately 40 m under relatively weaker net surface cooling (approximately -150 W m^{-2} , blue line in Figure 4a), it contacted the nutricline, which was uplifted by an intense mesoscale cyclone, as indicated by the large and negative *SH* and *SLA* values depicted in Figure 5a and 5d (also see Figure S2d). This contact between the ML and nutricline facilitated upward transport of deep-lying nutrients, resulting in a month-long phytoplankton bloom and a near-surface phytoplankton carbon concentration of over 50 mg m^{-3} (designated as M1, Figure 2a and 2d). Im-

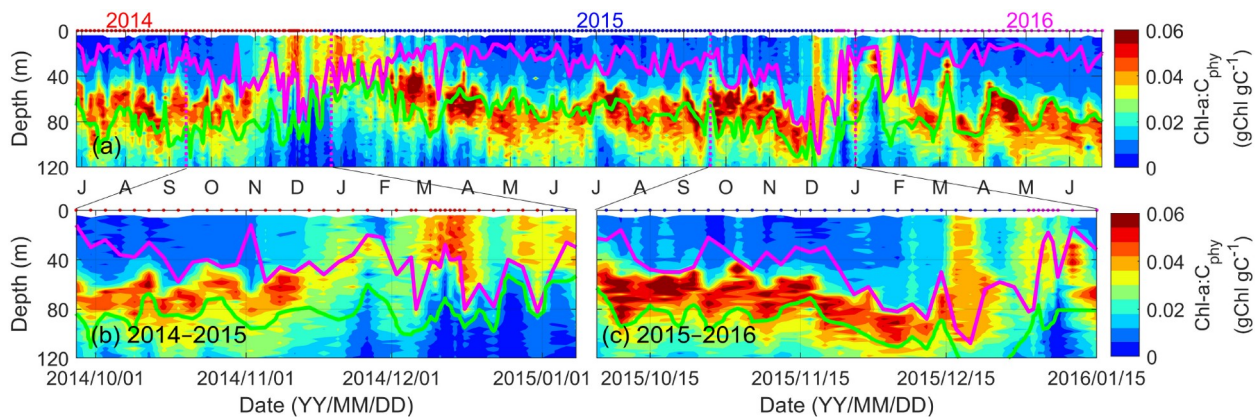


Figure 3 Along-track depth-time plot of the $\text{Chl-a:C}_{\text{phy}}$ ratio derived from the BGC-Argo data in the northern SCS basin. (a) The complete two-year period. (b), (c) The high-resolution observational periods in 2014–2015 (b) and 2015–2016 (c). Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements conducted in 2014, 2015, and 2016, respectively. Months labeled in (a) denote the middle of each month.

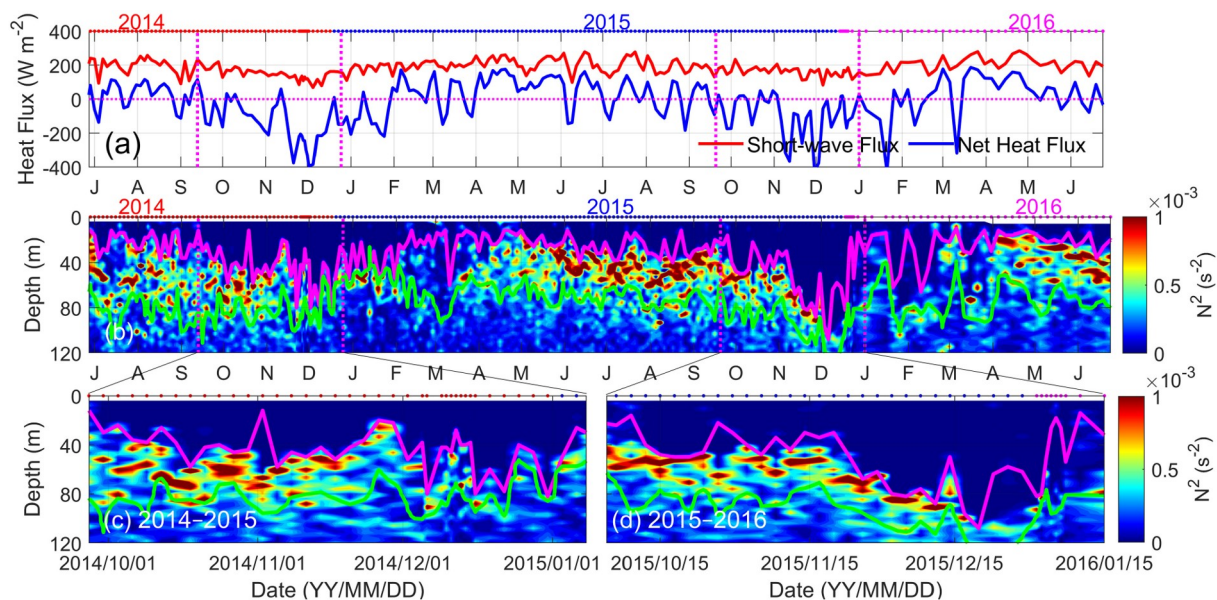


Figure 4 Along-track time-series plot of the NCEP surface heat flux (a), and depth-time plot of the vertical buoyancy gradient N^2 derived from the BGC-Argo data in the northern SCS basin ((b)–(d)). (a), (b) The complete two-year period. (c), (d) The high-resolution observational periods in 2014–2015 (c) and 2015–2016 (d). (a) Red and blue solid lines denote the short-wave radiation and net heat fluxes, respectively, with positive and negative values indicating warming and cooling, respectively. (b)–(d) Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively. Months labeled in (a) and (b) denote the middle of each month.

portantly, the entire winter bloom initiated in early December, approximately 20–30 days earlier than the month-long bloom, when the ML was shallower than the nutricline.

In the early winter, three synoptic blooms occurred around 10 December, 22 December, and 4 January, with the near-surface phytoplankton carbon concentration reaching 50 mg m^{-3} (designated as S1, S2, and S3, Figure 2b and 2e). This period is involved within the high-resolution observational period, enabling assessments of the contributions of submesoscale instabilities to synoptic blooms (Figure 1c). In this period, the impacts of mesoscale eddies were relatively

weak (Figures 5b and S2a–S2c). The strong surface cooling not only deepened the ML but also significantly eroded the stable pycnocline beneath the ML base (decreased N^2 , Figure 4c), leading to an MLD that was no longer well defined. Meanwhile, the lateral buoyancy gradients, M^2 , were relatively large in the upper ocean, particularly between the ML base (magenta line) and nutricline (green line), with a spatial scale of approximately 10 km and a synoptic timescale of several days (Figure 6a). The combined condition of large M^2 and low N^2 values led to low- Ri_b and low- PV waters both within and below the ML ($Ri_b < 1$ and $PV < 0$, Figure 6c and

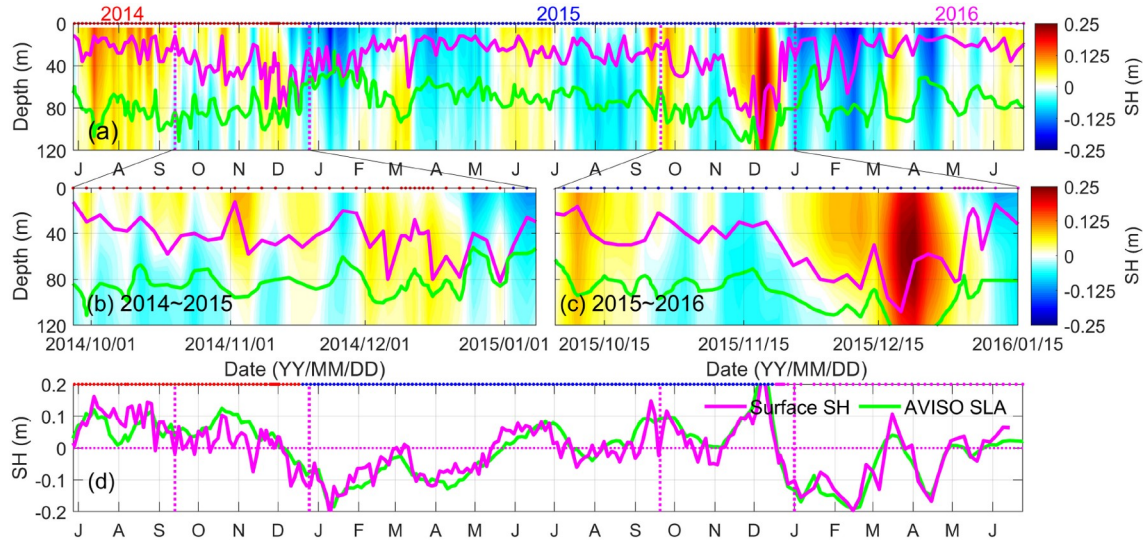


Figure 5 Along-track depth-time plot of the steric height SH derived from the BGC-Argo data ((a)–(c)), and time-series plot of the surface SH (magenta line) and corresponding SLA obtained from AVISO (green line) in the northern SCS basin. (a), (d) The complete two-year period. (b), (c) The high-resolution observational periods in 2014–2015 (b) and 2015–2016 (c). (a)–(c) Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively. Months labeled in (a) and (d) denote the middle of each month from July 2014 to June 2016.

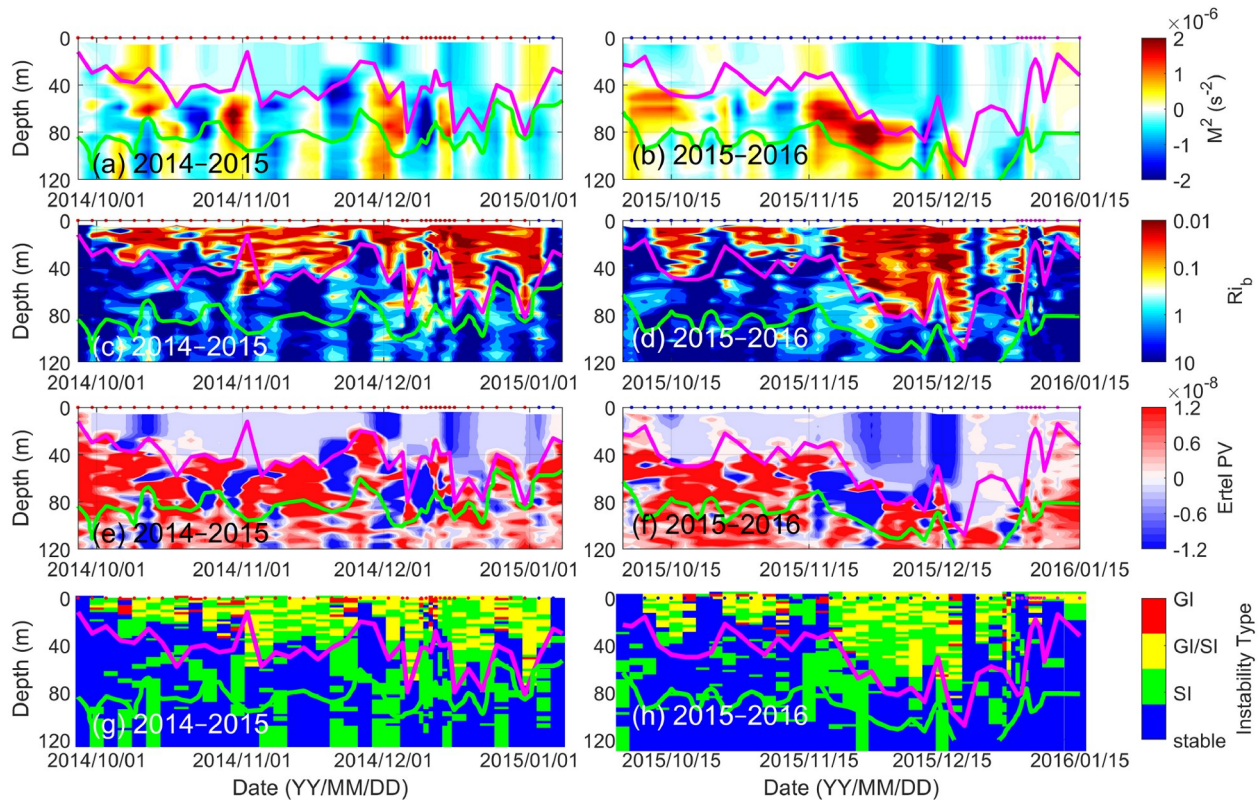


Figure 6 Along-track depth-time plot of the lateral buoyancy gradient M^2 ((a), (b)), Ri_b ((c), (d)), Ertel PV ((e), (f)), and instability type ((g), (h)) derived from the BGC-Argo data in the northern SCS basin over the high-resolution observational periods in 2014–2015 (left panels) and 2015–2016 (right panels). Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively.

6e). These regions were thus prone to several types of instabilities (Figure 6g). Directly driven by the strong surface

cooling effect, GI was primarily distributed in the upper region of the ML (also known as the convective layer, re-

presented by the red and yellow shading in Figure 6g), leading to strong upright convections. Additionally, sub-mesoscale SI occurred deeper than GI, sporadically extending throughout the ML and even below the ML base and nutricline (yellow and green shading in Figure 6g). SI extracted energy from the thermal wind shear, driving strong slantwise convections and fluid parcel exchange along the tilted isopycnals. Moreover, submesoscale MLI occurred simultaneously with SI but was primarily constrained within the ML, as demonstrated by the MLI-induced secondary overturning cells in Figure 7a. MLI extracted energy from the APE of the strong lateral buoyancy gradients, leading to pronounced restratification and ML shoaling. Therefore, the restratification effect of MLI led to the relatively smaller M^2 value within the ML compared to that below the ML (Figure 6a).

Strong SI scenarios were observed near the three synoptic blooms S1–S3 in the early winter (approximately 2–3 days earlier, left panels in Figure 6). These strong SI events coincided with the synoptic deepening of the ML to a depth of approximately 80 m and extended deep below the ML base and nutricline (see the isolated pockets of low- Ri_b and low- PV waters). Near the first and second synoptic blooms, S1 and S2, SI was more prominent (see the lower Ri_b and PV in Figure 6c and 6e), which may be attributed to the relatively weak impact of the mesoscale anticyclone from early to mid-December (positive SH in Figure 5b; Figure S2a and S2b). Subsequently, near the third synoptic bloom S3, the SI became relatively weaker when the mesoscale cyclone (negative SH in Figure 5b; Figure S2c) began weakly influencing the BGC-Argo float from late December to early January. This variation in the intensity of the SI is consistent with that reported in previous studies, which suggest that mesoscale anticyclones are more favorable for the development of submesoscale instabilities (Brannigan et al., 2017). During blooms S1 and S2, the MLD was approximately 20–30 m

shallower than the nutricline. We anticipate that the slantwise convection induced by the strong SI transported deep-lying nutrients into the ML, triggering synoptic blooms. Whereas near bloom S3, although the SI became weaker, the nutricline was uplifted by approximately 10–20 m owing to the mesoscale cyclone, leading to a smaller vertical distance between the ML base and nutricline, which favored the upward nutrient entrainment facilitated by the weaker SI. Subsequently, when the month-long bloom M1 occurred in the late winter, the heightened impact of the mesoscale cyclone further uplifted the nutricline to contact the ML base (Figures 5a and S2d), leading to direct nutrient entrainment through upright mixing in the ML.

Additionally, the occurrence of synoptic blooms S1–S3 in the early winter led to relatively high phytoplankton carbon concentrations beneath the ML base (Figure 2b), indicating the transport of fixed carbon from near-surface blooms to the ocean interior. The phytoplankton subducted below the ML base appeared to concentrate in the isolated regions of low- Ri_b and low- PV waters. Meanwhile, this export signal was more prominent near blooms S1 and S2 when the SI was more active. Conversely, the signal was weaker near bloom S3 when the SI was weaker (left panels in Figure 6). This implied that the SI-induced slantwise convection could also facilitate the downward transport of fixed carbon into the ocean interior. However, during bloom M1 in the late winter, the lateral resolution of the BGC-Argo observation was inadequate to resolve submesoscale processes (approximately 10 km, Figure 1c), complicating the evaluations of the contributions of submesoscale instabilities to phytoplankton growth and export. The shallower MLD (approximately 40 m), as well as the much weaker signal of phytoplankton export compared to that in the early winter (Figure 2a and 2b), implied that the contributions of submesoscale processes were relatively weaker during this period.

The upward nutrient entrainment described above can be

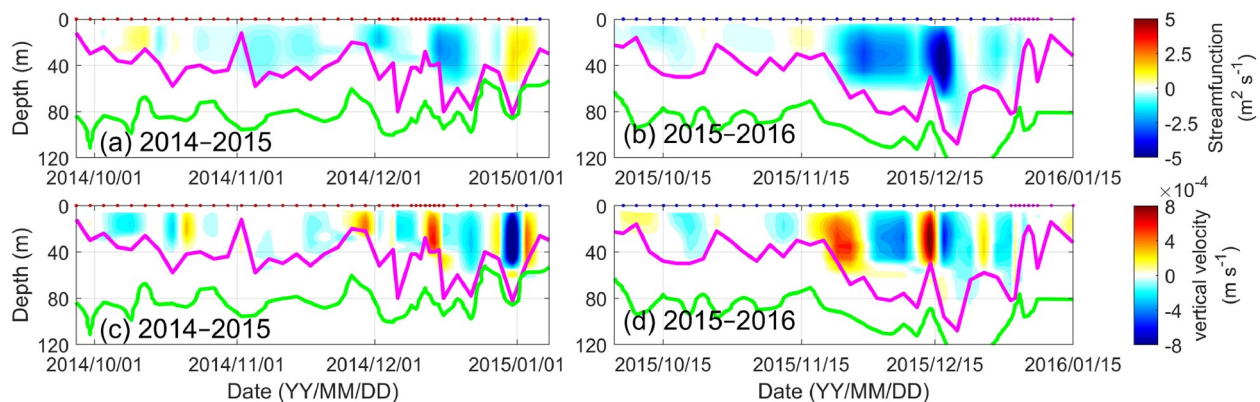


Figure 7 Along-track depth-time plot of the MLI-induced secondary circulation streamfunction ψ_e ((a), (b)) and vertical velocity w_e ((c), (d)) derived from the BGC-Argo data in the northern SCS basin over the high-resolution observational periods in 2014–2015 (left panels) and 2015–2016 (right panels). Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively.

tested using the BGC-Argo observations of the *AOU* (Figure 8, also see *DO* in Figure S3). Throughout the observation period, low *AOU* values (negative) were characteristic of waters above the nutricline. During the winter bloom in 2014–2015, the *AOU* increased from $-30 \mu\text{mol kg}^{-1}$ to nearly $0 \mu\text{mol kg}^{-1}$ within the ML. This indicated significant upward injection of high-*AOU* waters from below the ML and nutricline, as the *AOU* tended to decrease with enhanced photosynthesis during the strong winter bloom. In the early winter when blooms S1–S3 occurred, isolated pockets of high-*AOU* waters (approximately $80 \mu\text{mol kg}^{-1}$) were injected into the ML from below the nutricline (Figure 8b). These injection features aligned with the low- Ri_b and low- PV waters below the ML base (Figure 6c and 6e), highlighting the pivotal role played by the SI in the upward entrainment of nutrients and, thus, in the occurrence of synoptic blooms. Conversely, in the late winter when bloom M1 occurred, the high-*AOU* waters (over $80 \mu\text{mol kg}^{-1}$) continued to be injected into the ML base at a depth of approximately 40 m (Figure 8a). This was attributed to the eddy pumping effect of the intense mesoscale cyclone (negative SH in Figure 5a; Figure S2d).

In addition to the SI, three synoptic scenarios of MLIs also occurred when the ML deepened to approximately 80 m in the early winter (see MLI-induced secondary overturning cells in Figure 7a), with the associated vertical velocity exceeding 50 m day^{-1} (approximately $6 \times 10^{-4} \text{ m s}^{-1}$, Figure 7c). However, the MLI-induced vertical velocity became zero at the base of the ML, according to the vertical structure function $\mu(z)$ in the parameterization proposed by Fox-Kemper et al. (2008) (eq. (10)). Therefore, the MLI minimally contributed to nutrient entrainment and phytoplankton subduction. Notably, the synoptic blooms S1–S3 occurred when the ML shoaled from approximately 80 m to 40 m (Figure 2b and 2e), which was expected to be attributed to the restratification effect of the MLI under persistent net surface cooling (Figure 4a). An analysis of the T - S relation revealed that the lateral density fronts were dominated by

temperature in the upper ocean (left panels in Figure 9). Three synoptic scenarios of the lateral temperature and salinity gradients evolving toward compensation accompanied the ML shoaling, with T_u and C_{TS} transiting toward $-\pi/4$ and -1 within the ML, respectively (Figure 9e and 9g). In terms of energetics, the MLI-related buoyancy fluxes ($\overline{w'b'}$ and $\overline{w'b'_{comp}}$) were positive and strong when the ML was deep. These values then decreased with ML shoaling (Figure 10a and 10c), suggesting that the MLI released the APE reserved in the tilted isopycnals of the ML, driving the synoptic T - S compensation and ML shoaling. According to previous studies, the MLI-induced ML shoaling could also contribute to synoptic phytoplankton growth by enhancing light exposure, under the precondition of the SI-induced upward nutrient entrainment. However, it was surmised that the contribution of the MLI was limited owing to the already intense solar radiation in the tropical SCS basin.

In summary, in the early winter of 2014–2015, when the MLD was approximately 20–30 m shallower than the nutricline, the SI-induced upward nutrient entrainment played a dominant role in initiating the stronger winter bloom, which was approximately 20–30 days earlier than that induced by the mesoscale eddies.

3.3 MLI-related weak bloom in the second winter (2015–2016)

The BGC-Argo float deployed in the northern SCS basin revealed that the winter bloom in 2015–2016 was considerably weaker than that in 2014–2015 (Figure 2). From late November to mid-December in the second winter, the MLD deepened significantly from approximately 30 m to 110 m (magenta lines in Figure 4b and 4d), driven by the increasing net surface cooling (approximately -250 W m^{-2} , blue line in Figure 4a), as well as an intense mesoscale anticyclone (positive SH in Figure 5c; Figure S4b–4d). However, the stable pycnocline below the ML base was not significantly eroded (Figure 4d), likely owing to the de-

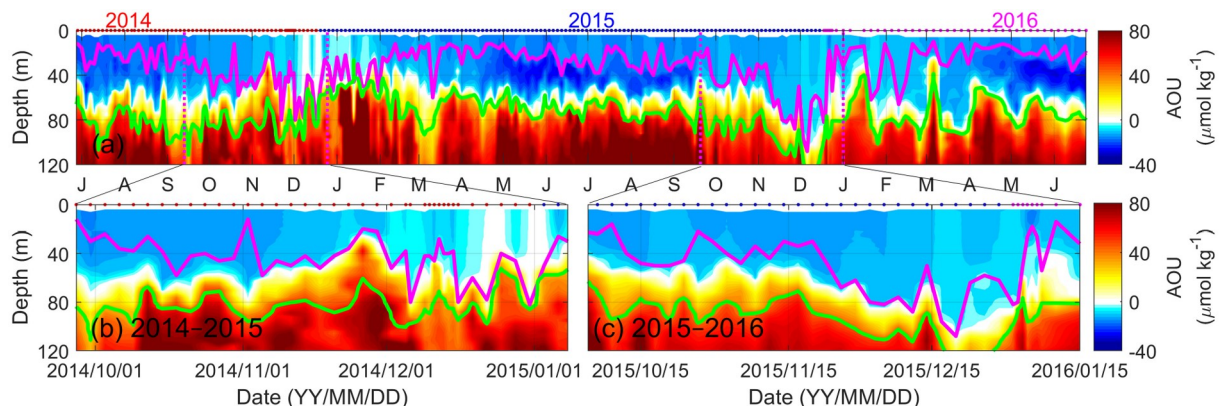


Figure 8 Same as Figure 3 but for *AOU*.

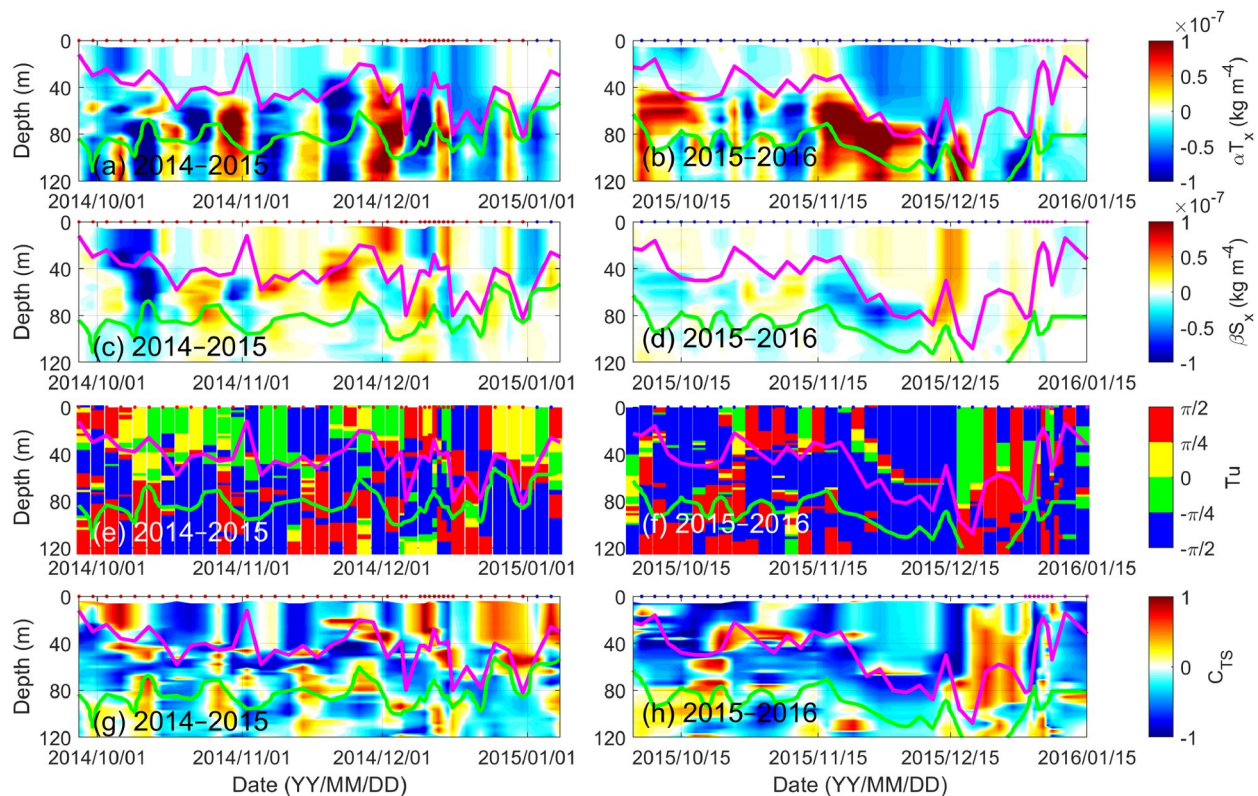


Figure 9 Along-track depth-time plots of the αT_x ((a), (b)), βS_x ((c), (d)), Turner angle Tu ((e), (f)), and T - S covariance C_{TS} ((g), (h)) derived from the BGC-Argo data in the northern SCS basin over the high-resolution observational periods in 2014–2015 (left panels) and 2015–2016 (right panels). Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively.

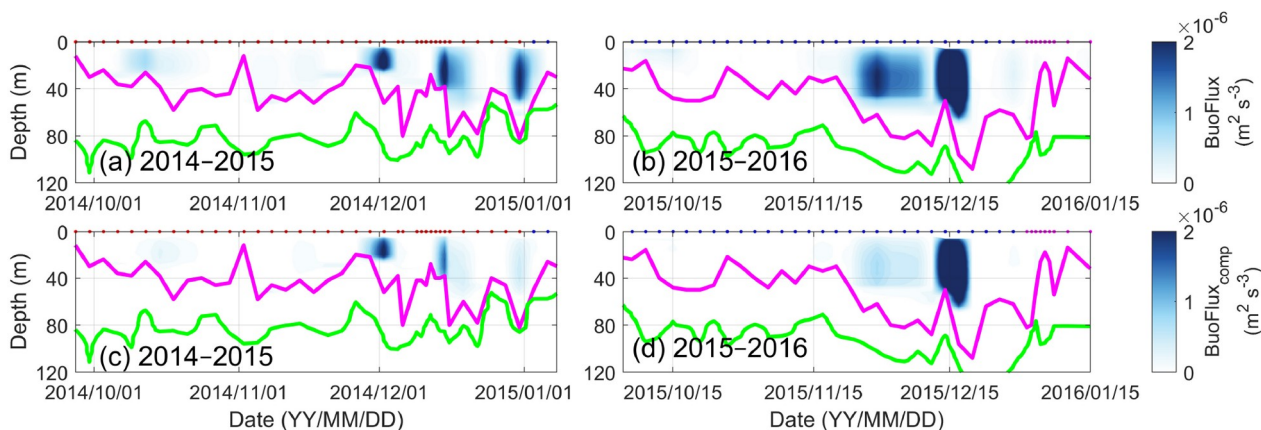


Figure 10 Along-track depth-time plots of the buoyancy flux $\overline{w'b}$ (BuoFlux; (a), (b)) and the effective buoyancy flux to T - S compensation $\overline{w'b}_{comp}$ (BuoFlux_{comp}; (c), (d)) derived from the BGC-Argo data in the northern SCS basin over the high-resolution observational periods in 2014–2015 (left panels) and 2015–2016 (right panels). Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively.

pression effect of the mesoscale anticyclone. Despite the significant deepening of the ML, the MLD remained approximately 30 m shallower than the nutricline, which was also depressed by the mesoscale anticyclone (green line in Figure 5c). The significant deepening of the ML and increasing upper-ocean M^2 (Figure 6b) led to remarkably vigorous submesoscale SI and MLI, as evidenced by the low

Ri_b and PV values (Figure 6d, 6f, and 6h) and the intense MLI-induced secondary overturning cells (Figure 7b). However, owing to the intense pycnocline below the ML base, the SI-induced slantwise convection was hard to extend beyond the nutricline and bring up nutrients into the ML, resulting in low phytoplankton carbon concentrations (Figure 2c and 2f).

Subsequently, from mid-December to early January, the vertical distance between the ML base and nutricline expanded from approximately 30 m to 60 m (Figure 2c), primarily attributed to the more significant shoaling of the ML compared to that of the nutricline. The MLD and nutricline decreased to approximately 20 m and 80 m, respectively, within a synoptic period of approximately two weeks. The significant decrease in the MLD and the strength of M^2 (Figure 6b) led to a rapid and significant weakening in the intensities of the SI and MLI, as demonstrated by the increased Ri_b and PV (Figure 6d, 6f, and 6h) and the diminished secondary circulations induced by the MLI (Figure 7b). Consequently, the SI-induced upward entrainment of deep-lying nutrients was largely limited, with only one weak near-surface phytoplankton carbon peak of approximately 40 mg m^{-3} appearing around 5 January (synoptic bloom S4, Figure 2c), which was associated with a transient proximity between the ML base and nutricline near 2 January. Subsequently, in the late winter from January to February, the ML consistently remained shallower than the nutricline, resulting in relatively low phytoplankton biomass in the upper ocean (Figure 2a).

The restricted upward entrainment of deep-lying nutrients during the second winter can also be confirmed through the BGC-Argo AOU observational data (Figure 8, also see DO in Figure S3). The data revealed that during the second winter, the AOU was significantly lower within the ML (approximately $-20 \text{ } \mu\text{mol kg}^{-1}$) compared to that in the first winter (approximately $0 \text{ } \mu\text{mol kg}^{-1}$), suggesting that high- AOU and nutrient-rich waters were largely confined below the ML base.

The depression effect induced by the mesoscale anticyclone acted simultaneously on the vertical variations of both the MLD and nutricline. However, from mid-December to early January, the more significant shoaling of ML than the nutricline was anticipated to be influenced by the restratification effect of the remarkably intense MLI near mid-December (Figure 7b), in addition to the diminished depression effect of the mesoscale anticyclone, given the persistent net surface cooling of approximately -150 W m^{-2} (blue line in Figure 4a). This hypothesis was tested by analyzing the T - S relation (right panels in Figure 9). The results revealed that the upper-ocean lateral density gradient was also dominated by temperature in the second winter. During the ML-deepening period from late November to mid-December, the lateral temperature and salinity gradients reinforced the density fronts, with Tu less than $-\pi/4$ and C_{TS} of approximately -1 within the ML (Figure 9f and 9h). As the ML began to shoal near mid-December, C_{TS} rapidly changed from nearly -1 to 1 (Figure 7h), suggesting an evolution toward T - S compensation, which resulted in the weakening of M^2 and the shoaling of the ML (Figure 6b). Energetically,

during the ML-deepening period, the MLI-related buoyancy flux (BuoFlux , $\overline{w'b'}$) was positive and strong (Figure 10b); however, its effective component capable of inducing T - S compensation ($\text{BuoFlux}_{\text{Comp}}$, $\overline{w'b'_{\text{comp}}}$) was considerably weaker (Figure 10d). This indicated non-efficient release of the APE by the MLI, facilitating the significant ML deepening. Conversely, when the MLD reached its maximum value of approximately 110 m in mid-December, the $\overline{w'b'}$ and $\overline{w'b'_{\text{comp}}}$ signals were both remarkably strong. Thereafter, from mid-December to early January, the intensities of these signals decreased significantly (Figure 10b and 10d), indicating effective APE release by the MLI, which led to rapid T - S compensation, isopycnal slumping, and ML shoaling. Importantly, MLI-induced restratification could only influence the MLD but could not reach the depth of the nutricline. Thus, the minimal shoaling of nutricline to a depth of approximately 80 m was primarily due to the weakening of the mesoscale anticyclone (green line in Figure 5c). Notably, during the first winter, the MLI was much weaker and exerted limited influence on the vertical distance between the ML base and nutricline (Figure 7a).

In summary, the intense MLI-induced restratification played a pivotal role in the more significant shoaling of the ML compared to that of the nutricline, increasing the vertical distance between the two layers. It thus suppressed upward nutrient entrainment, hindering the occurrence of a strong winter bloom in the winter of 2015–2016.

4. Discussion

4.1 Impacts of the kuroshio intrusion

Evidently, the distinct phytoplankton carbon levels recorded by the northern BGC-Argo float across the two winters only represent differing phytoplankton biomass in the along-track regions. To further reveal the winter phytoplankton biomass throughout the northern SCS basin, Figure S5 presents two-month averaged OC-CCI sea-surface Chl-a distributions from December to January during the two winters. These data confirm that the phytoplankton biomass was overall higher in the entire northern SCS basin during the first winter of 2014–2015 (Figure S5a) compared to the second winter of 2015–2016 (Figure S5b), agreeing with the BGC-Argo observations. The relatively lower phytoplankton biomass in the second winter could be attributed to the notably intense mesoscale anticyclone. This anticyclone originated near the northeastern SCS in November (Figure S4a) and headed toward the southwest through the northern SCS basin from November to January (Figure S4b–S4d), during which it was captured by the BGC-Argo float around mid- to late-December (Figure 5c; Figure S4b and Figure S4c). As analyzed in Section 3.3, the mesoscale and submesoscale dynamics

associated with this intense mesoscale anticyclone could suppress upward nutrient entrainment, thus hindering phytoplankton growth across the entire northern SCS basin.

This intense mesoscale anticyclone likely originated from the detachment of anticyclones from the Kuroshio loop current intruding into the SCS through the Luzon Strait (Zhang et al., 2017). The intensity of this Kuroshio intrusion, as indicated by the difference in SLA between the eastern and western sides of the Luzon Strait (Lin et al., 2024), was significantly stronger in the second winter than in the first winter (Figure S6). Consequently, in contrast to the first winter (Figure S7), the intrusion of the high-salinity Kuroshio waters was more pronounced (Figure S8) and exhibited a high spatiotemporal consistency with the intense mesoscale anticyclone that traversed the northern SCS basin in the second winter (solid contours in Figure S8). Furthermore, on the larger climatic scale, Lin et al. (2024) reported that during El Niño years, the Kuroshio intrusion tended to strengthen owing to the northward shift of the North Equatorial Current bifurcation. Therefore, the intense Kuroshio intrusion in the second winter could be associated with the strong El Niño event during that period (see Niño3.4 index in Zhang et al., 2022).

In summary, the distinct mesoscale and submesoscale dynamics, as well as the differing phytoplankton biomass, observed between the two winters in the northern SCS basin were closely associated with the intensity of the Kuroshio intrusion. Conversely, during the two winters, the low-salinity river-diluted coastal waters (salinity lower than 32 PSU) were primarily confined to the near-coastal regions owing to the intrusion of high-salinity Kuroshio waters (salinity higher than 34.5 PSU), located approximately 200–300 km away from the BGC-Argo along-track regions (Figures S7 and S8). This suggests their limited impact on the submesoscale dynamics and phytoplankton biomass in the northern SCS basin.

4.2 Biological impacts of MLI

In this study, the analysis of MLI primarily relied on the parameterization proposed by Fox-Kemper et al. (2008) (eq. (9)), wherein the MLI-induced secondary circulation and vertical velocity become zero at the base of the ML owing to the highly stable stratification barrier of the pycnocline, as indicated by the vertical structure function $\mu(z)$ (eq. (10)). However, during wintertime in the northern basin, stratification at the pycnocline significantly weakened under the strong net surface cooling (Figure 4). According to Callies et al. (2016), the vertical decay of MLI scales like kN/f , where k denotes the wavelength. Given that N^2 is relatively small below the ML in winters, MLI-induced vertical velocity may penetrate below the ML base and potentially contribute to the upward nutrient entrainment and phytoplankton subduction.

Consequently, the presence of the MLI-induced vertical velocity at the base of the ML and its decay into the ocean interior warrant further explorations based on high-resolution observations and numerical simulations.

Moreover, this study examined the biological impacts of MLIs in the low-latitude SCS basin, known for its oligotrophic and high-light waters. In this region, upper-ocean nutrient availability, rather than light intensity, serves as the predominant factor controlling primary production. Our results suggest that the remarkably intense restratification effect of the MLI can potentially suppress the upward entrainment of deep-lying nutrients, hindering phytoplankton growth in the upper ocean. This finding contradicts the findings of previous studies conducted in mid- and high-latitude regions characterized by eutrophic and low-light waters, such as the North Atlantic. In these regions, MLI-induced restratification is consistently found to promote phytoplankton blooms by trapping phytoplankton cells within the euphotic layer and increasing their light exposure (Mahadevan et al., 2012; Mignot et al., 2018). Therefore, the MLI-based modulation of phytoplankton production and export is complicated, highlighting the need for future investigations to comprehensively address the intricate biological response to the pronounced vertical velocity and restratification effect of MLI in various biogeophysical regions of the global ocean.

4.3 Comparison of the northern and central basins

In the central basin, the BGC-Argo observations revealed a notably weaker seasonality of phytoplankton biomass compared to that observed in the northern basin, with a relatively stable subsurface maximum near 60–80 m throughout the year (Figure 11). The near-surface phytoplankton carbon concentration was persistently low (approximately 10 mg m^{-3}), and no winter bloom could develop. Notably, in this region, wintertime upper-ocean mixing is driven by both net surface cooling and wind stress (Geng et al., 2019); however, the combined effect of the two processes is considerably weaker than that observed in the northern basin (Figures S9 and S10). Consequently, the MLD (less than approximately 50 m, magenta line in Figure 11a) was evidently shallower than the nutricline (80–90 m, green line in Figure 11a), with the strongly stratified pycnocline lying below the base of the ML throughout the winter (Figure S11), hindering the transport of deep-lying nutrients into the ML.

During the high-resolution observational period from summer to winter in 2014–2015 in the central basin, weak atmospheric forcing led to weak M^2 in the upper ocean (Figure 12a). Consequently, submesoscale instabilities were much weaker and primarily confined within the ML (see Ri_b and PV in Figure 12). With the strong stratification barrier

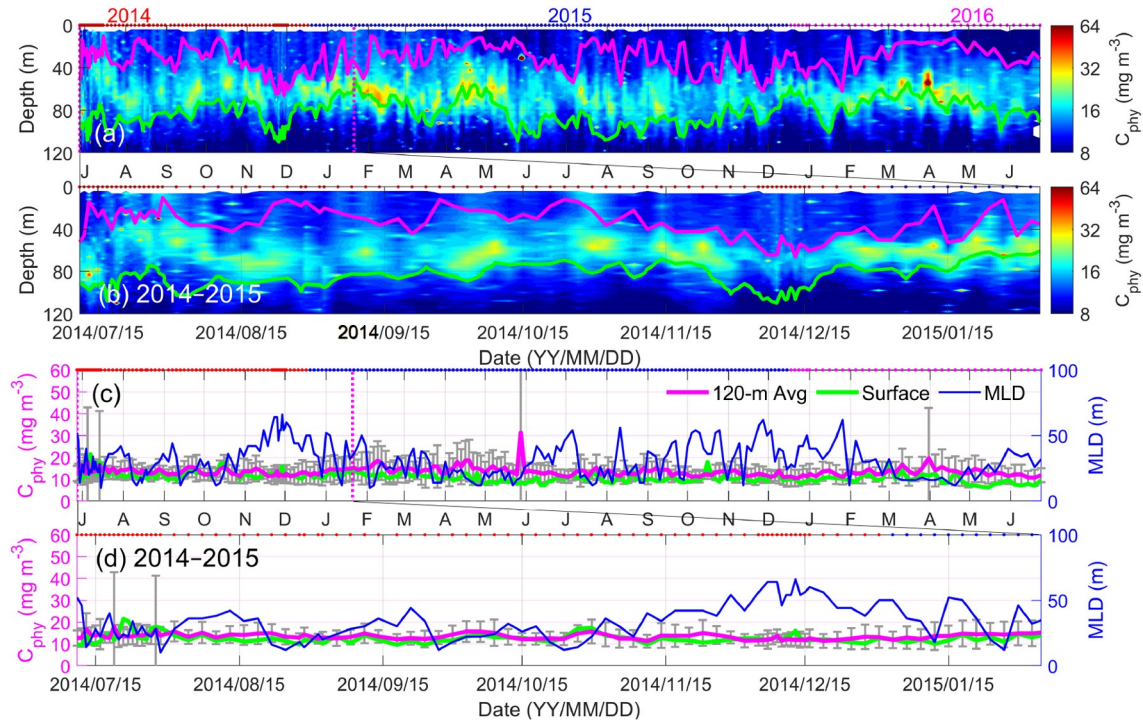


Figure 11 Along-track depth-time plot of the phytoplankton carbon concentration C_{phy} ((a), (b)) and time-series plot of the surface layer (green line) and upper 120-m averaged (magenta line) C_{phy} derived from the BGC-Argo data in the central SCS basin ((c), (d)). (a), (c) The complete two-year period. (b), (d) The high-resolution observational periods in 2014–2015. (a), (b) Magenta and green solid lines denote the MLD and nutricline depth, respectively. (c), (d) Blue line denotes the corresponding MLD. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively. Months labeled in (a) and (c) denote the middle of each month.

appearing below the base of the ML, SI-induced slantwise convection could not penetrate through the ML base and reach the nutricline, failing to contribute to the occurrence of winter bloom in the central basin (Figure 11).

4.4 Limitations and expectations of the BGC-Argo data analysis

To accurately assess the presence and intensity of submesoscale SIs and MLIs, capturing the strength of the lateral buoyancy gradients M^2 in the upper ocean is essential. However, the along-track BGC-Argo data tend to underestimate M^2 because the orientation of the BGC-Argo track is often not perpendicular to the observed submesoscale fronts. Consequently, the actual submesoscale instabilities are always more intense than those estimated using the BGC-Argo data (see detailed analysis and discussion in Thompson et al. (2016) and Tang et al. (2023)). Additionally, estimating the along-track Ekman buoyancy flux induced by the surface wind introduces additional errors as it also involves the orientation of the wind vector, along with the orientations of the BGC-Argo track and submesoscale fronts (Thompson et al., 2016). Given that net surface cooling predominantly drives upper-ocean mixing during winter in the northern SCS basin (Geng et al., 2019), the influence of surface wind has

not been considered in the associated analyses. In addition, the high-resolution BGC-Argo data can only partially resolve the vertical or slantwise plumes induced by submesoscale instabilities, given their limited spatial and temporal resolutions (approximately 3.7 km and 3 days). Therefore, the dynamical properties of water mass (e.g., Ri_b and PV) demonstrated in this study are more likely to represent an average over multiple submesoscale plumes. This limitation also contributes to the underestimation of the actual intensities of the submesoscale instabilities.

Furthermore, the submesoscale processes illustrated based on the BGC-Argo data represented several single independent events, rather than the complete temporal evolution of any single event, owing to the snapshot sampling patterns of the BGC-Argo floats. Moreover, we must acknowledge that our analyses only represent the development of submesoscale instabilities in particular years and along-track regions within the SCS basin, rather than the overall submesoscale dynamics in the entire SCS basin. Thus, different characteristics of the submesoscale instabilities in other periods and regions within the SCS basin are anticipated.

Despite the limitations of the BGC-Argo data mentioned above, our analyses provide a statistical overview of the occurrence frequency and spatiotemporal variability of ac-

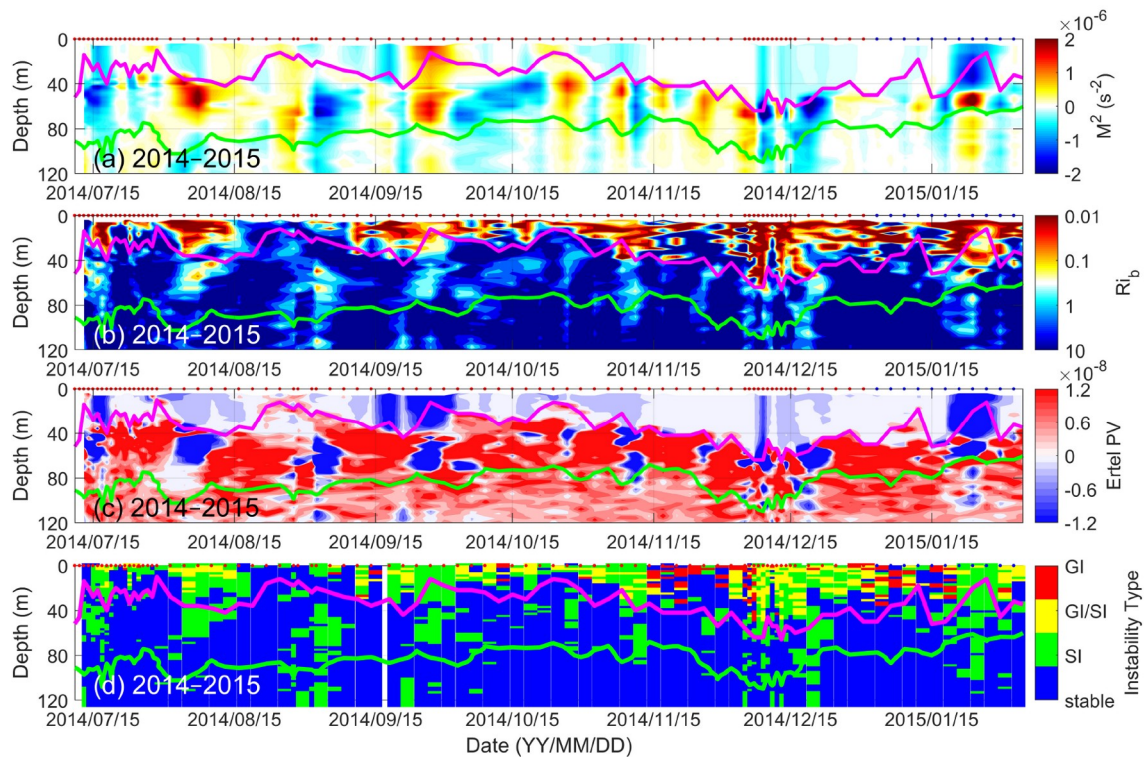


Figure 12 Along-track depth-time plot of the lateral buoyancy gradient M^2 (a), Ri_b (b), Ertel PV (c), and instability type (d) derived from the BGC-Argo data in the central SCS basin over the high-resolution observational periods in 2014–2015. Magenta and green solid lines denote the MLD and nutricline depth, respectively. BGC-Argo observations are labeled across the top using red, blue, and magenta dots denoting measurements recorded in 2014, 2015, and 2016, respectively.

tive submesoscale instabilities in the SCS basin. Moreover, the analyses offer valuable evidences on their impacts on phytoplankton production and export. These findings serve as foundations for further investigations, highlighting the need for a more extensive and accurate understanding of the submesoscale physical–biological processes occurring in the SCS basin. Future research efforts should include high-resolution field measurements and model simulations that can completely resolve submesoscale motions and cover broader regions of the SCS basin.

5. Conclusions

In the northern basin of the oligotrophic SCS, near-surface winter blooms are known to occur seasonally, accompanied by a deepened ML under strong net surface cooling. However, the intensities and durations of these winter blooms exhibit evident interannual variability, with significantly stronger and weaker blooms captured by the BGC-Argo float during the first (2014–2015) and second (2015–2016) winters of the observational period. Based on the high-resolution BGC-Argo observations (approximately 3.7 km), this study investigated the potential effects of submesoscale SI and MLI on the distinct phytoplankton growth and export ob-

served during wintertime over the two consecutive years. In the first winter, a month-long bloom was triggered as the deepened ML contacted the uplifted nutricline, owing to an intense mesoscale cyclone in the late winter. Active SI-induced slantwise convection provided a clear mechanism for the upward entrainment of deep-lying nutrients when the MLD was approximately 20–30 m shallower than the nutricline in the early winter, thus initiating the winter bloom 20–30 days earlier than that expected solely by surface cooling and mesoscale eddies. The SI also facilitated the export of fixed phytoplankton carbon from within the ML to deeper layers. Conversely, in the second winter, the ML and nutricline were suppressed by an intense mesoscale anticyclone, leading to remarkably intense MLI. This induced significant ML shoaling but left the nutricline relatively undisturbed, creating a larger vertical distance between the ML base and nutricline. Consequently, the upward injection of deep-lying nutrients and phytoplankton bloom were inhibited, and carbon export was also suppressed. In comparison, in the central SCS basin, the phytoplankton biomass was significantly weaker, and no winter bloom could develop. This was primarily attributed to the significantly shallower MLD and weaker submesoscale instabilities that were predominantly confined within the ML, compared to those in the northern basin.

Thus, this study provides valuable observational evidence for the influence of submesoscale instability processes on phytoplankton growth and export during wintertime in the SCS basin. These findings can be extended to the broader oligotrophic and high-light low-latitude oceans, enhancing our understanding of the complex submesoscale physical-biological processes occurring within the global ocean.

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Conflict of interest The authors declare that there are no conflicts of interest.

References

- Bachman S D, Fox-Kemper B, Taylor J R, Thomas L N. 2017. Parameterization of frontal symmetric instabilities. I: Theory for resolved fronts. *Ocean Model*, 109: 72–95
- Barkan R, McWilliams J C, Molemaker M J, Choi J, Srinivasan K, Shchepetkin A F, Bracco A. 2017. Submesoscale dynamics in the Northern Gulf of Mexico. Part II: Temperature-salinity relations and cross-shelf transport processes. *J Phys Oceanogr*, 47: 2347–2360
- Bidigare R R, Kennicutt II M C, Brooks J M. 1985. Rapid determination of chlorophylls and their degradation products by high-performance liquid chromatography I. *Limnol Oceanogr*, 30: 432–435
- Boccaletti G, Ferrari R, Fox-Kemper B. 2007. Mixed layer instabilities and restratification. *J Phys Oceanogr*, 37: 2228–2250
- Brannigan L. 2016. Intense submesoscale upwelling in anticyclonic eddies. *Geophys Res Lett*, 43: 3360–3369
- Brannigan L, Marshall D P, Naveira Garabato A C, Nurser A J G, Kaiser J. 2017. Submesoscale instabilities in mesoscale eddies. *J Phys Oceanogr*, 47: 3061–3085
- Callies J, Ferrari R, Klymak J M, Gula J. 2015. Seasonality in submesoscale turbulence. *Nat Commun*, 6: 8
- Callies J, Flierl G, Ferrari R, Fox-Kemper B. 2016. The role of mixed-layer instabilities in submesoscale turbulence. *J Fluid Mech*, 788: 5–41
- Chen Y L, Chen H Y. 2006. Seasonal dynamics of primary and new production in the northern South China Sea: The significance of river discharge and nutrient advection. *Deep Sea Res Part I-Oceanogr Res Papers*, 53: 971–986
- Chen Y L, Chen H Y, Karl D M, Takahashi M. 2004. Nitrogen modulates phytoplankton growth in spring in the South China Sea. *Cont Shelf Res*, 24: 527–541
- Erickson Z K, Thompson A F. 2018. The seasonality of physically driven export at submesoscales in the Northeast Atlantic Ocean. *Glob Biogeochem Cycle*, 32: 1144–1162
- Fang G, Wang G, Fang Y, Fang W. 2012. A review on the South China Sea western boundary current. *Acta Oceanol Sin*, 31: 1–10
- Fang M, Ju W, Liu X, Yu Z, Qiu F. 2015. Surface chlorophyll-a concentration spatio-temporal variations in the Northern South China sea detected using MODIS data. *Terr Atmos Ocean Sci*, 26: 319–329
- Field C B, Behrenfeld M J, Randerson J T, Falkowski P. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science*, 281: 237–240
- Fox-Kemper B, Ferrari R, Hallberg R. 2008. Parameterization of mixed layer eddies. Part I: Theory and diagnosis. *J Phys Oceanogr*, 38: 1145–1165
- Geng B, Xiu P, Shu C, Zhang W, Chai F, Li S, Wang D. 2019. Evaluating the roles of wind-and buoyancy flux-induced mixing on phytoplankton dynamics in the northern and central South China Sea. *J Geophys Res-Oceans*, 124: 680–702
- Haine T W N, Marshall J. 1998. Gravitational, symmetric, and baroclinic instability of the ocean mixed layer. *J Phys Oceanogr*, 28: 634–658
- He Q, Zhan H, Cai S, He Y, Huang G, Zhan W. 2018. A new assessment of mesoscale eddies in the South China Sea: Surface features, three-dimensional structures, and thermohaline transports. *J Geophys Res-Oceans*, 123: 4906–4929
- Hoskins B J. 1974. The role of potential vorticity in symmetric stability and instability. *Quart J R Meteorol Soc*, 100: 480–482
- Hu J, Wang X H. 2016. Progress on upwelling studies in the China seas. *Rev Geophys*, 54: 653–673
- Kanamitsu M, Ebisuzaki W, Woollen J, Yang S K, Hnilo J J, Fiorino M, Potter G L. 2002. NCEP-DOE AMIP-II reanalysis (R-2). *Bull Amer Meteor Soc*, 83: 1631–1644
- Lévy M, Franks P J S, Smith K S. 2018. The role of submesoscale currents in structuring marine ecosystems. *Nat Commun*, 9: 16
- Lin H, Liu Z, Hu J, Menemenlis D, Huang Y. 2020. Characterizing meso-to submesoscale features in the South China Sea. *Prog Oceanogr*, 188: 102420
- Lin K, Han T, Zhang Y, Shen C, Lee S, Wang J, Mohtar A T, Huang K, Chiang H, Chen Y, Wang X. 2024. Influences of East Asian winter monsoon and El Niño-Southern Oscillation variability on the Kuroshio intrusion to the South China Sea over the past 60 years. *Geophys Res Lett*, 51: e2023GL104155
- Mahadevan A. 2016. The impact of submesoscale physics on primary productivity of plankton. *Annu Rev Mar Sci*, 8: 161–184
- Mahadevan A, D'Asaro E, Lee C, Perry M J. 2012. Eddy-driven stratification initiates North Atlantic spring phytoplankton blooms. *Science*, 337: 54–58
- McWilliams J C. 2016. Submesoscale currents in the ocean. *Proc R Soc A*, 472: 20160117
- Miao M F, Zhang Z W, Qiu B, Liu Z Y, Zhang X C, Zhou C, Guan S D, Huang X D, Zhao W, Tian J W. 2021. On contributions of multiscale dynamic processes to the steric height in the Northeastern South China Sea as revealed by moored observations. *Geophys Res Lett*, 48: e2021GL093829
- Mignot A, Ferrari R, Claustre H. 2018. Floats with bio-optical sensors reveal what processes trigger the north Atlantic bloom. *Nat Commun*, 9: 1834
- Ni Q, Zhai X, Wilson C, Chen C, Chen D. 2021. Submesoscale eddies in the South China Sea. *Geophys Res Lett*, 48: e2020GL091555
- Omand M M, D'Asaro E A, Lee C M, Perry M J, Briggs N, Cetinić I, Mahadevan A. 2015. Eddy-driven subduction exports particulate organic carbon from the spring bloom. *Science*, 348: 222–225
- Park J, Farmer D. 2013. Effects of Kuroshio intrusions on nonlinear internal waves in the South China Sea during winter. *J Geophys Res-Oceans*, 118: 7081–7094
- Qiu C, Yang Z, Wang D, Feng M, Su J. 2022. The enhancement of submesoscale ageostrophic motion on the mesoscale eddies in the South China Sea. *J Geophys Res-Oceans*, 127: e2022JC018736
- Rudnick D L, Ferrari R. 1999. Compensation of horizontal temperature and salinity gradients in the ocean mixed layer. *Science*, 283: 526–529
- Sabine C L, Feely R A, Gruber N, Key R M, Lee K, Bullister J L, Wanninkhof R, Wong C S, Wallace D W R, Tilbrook B, Millero F J, Peng T H, Kozyr A, Ono T, Rios A F. 2004. The oceanic sink for anthropogenic CO₂. *Science*, 305: 367–371
- Su J. 2004. Overview of the South China Sea circulation and its influence on the coastal physical oceanography outside the Pearl River Estuary. *Cont Shelf Res*, 24: 1745–1760
- Tang H, Shu Y, Wang D, Xie Q, Zhang Z, Li J, Shang X, Zhang O Y W, Liu D. 2023. Submesoscale processes observed by high-frequency float in the western South China sea. *Deep Sea Res Part I-Oceanographic Res Papers*, 192: 103896
- Tang S, Liu F, Chen C. 2014. Seasonal and intraseasonal variability of surface chlorophyll-a concentration in the South China Sea. *Aquat EcoSyst Health Manage*, 17: 242–251

- Taylor J R, Ferrari R. 2009. On the equilibration of a symmetrically unstable front via a secondary shear instability. *J Fluid Mech*, 622: 103–113
- Taylor J R, Ferrari R. 2010. Buoyancy and wind-driven convection at mixed layer density fronts. *J Phys Oceanogr*, 40: 1222–1242
- Taylor J R, Thompson A F. 2023. Submesoscale dynamics in the upper ocean. *Annu Rev Fluid Mech*, 55: 103–127
- Thomas L N, Taylor J R, Ferrari R, Joyce T M. 2013. Symmetric instability in the Gulf stream. *Deep Sea Res Part II-Topical Stud Oceanogr*, 91: 96–110
- Thompson A F, Lazar A, Buckingham C, Naveira Garabato A C, Damerell G M, Heywood K J. 2016. Open-ocean submesoscale motions: A full seasonal cycle of mixed layer instabilities from gliders. *J Phys Oceanogr*, 46: 1285–1307
- Xing X, Qiu G, Boss E, Wang H. 2019. Temporal and vertical variations of particulate and dissolved optical properties in the South China Sea. *J Geophys Res-Oceans*, 124: 3779–3795
- Xing X, Boss E, Chen S, Chai F. 2021. Seasonal and daily-scale photo-acclimation modulating the phytoplankton chlorophyll-carbon coupling relationship in the mid-latitude Northwest Pacific. *J Geophys Res-Oceans*, 126: e2021JC017717
- Xue H, Chai F, Pettigrew N, Xu D, Shi M, Xu J. 2004. Kuroshio intrusion and the circulation in the South China Sea. *J Geophys Res*, 109: 2002JC001724
- Zhang W, Wang H, Chai F, Qiu G. 2016. Physical drivers of chlorophyll variability in the open South China Sea. *J Geophys Res-Oceans*, 121: 7123–7140
- Zhang Y, Zhao Z, Liao E, Jiang Y. 2022. ENSO and PDO-related inter-annual and interdecadal variations in the wintertime sea surface temperature in a typical subtropical strait. *Clim Dyn*, 59: 3359–3372
- Zhang Z, Zhao W, Qiu B, Tian J. 2017. Anticyclonic eddy sheddings from kuroshio loop and the accompanying cyclonic eddy in the northeastern South China Sea. *J Phys Oceanogr*, 47: 1243–1259
- Zhao Z, Oey L, Huang B, Lu W, Jiang Y. 2022. Off-coast phytoplankton bloom in the Taiwan Strait during the northeasterly monsoon wind relaxation period. *J Geophys Res-Oceans*, 127: e2022JC018752

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