Browning Thomas (Orcid ID: 0000-0002-2864-6087)
Laws Edward (Orcid ID: 0000-0002-4893-9311)
Zhou Kuanbo (Orcid ID: 0000-0002-9779-3128)
Jiang Zong-Pei (Orcid ID: 0000-0002-5106-7593)
LIU Xin (Orcid ID: 0000-0002-7925-9618)
Huang Bangqin (Orcid ID: 0000-0003-2279-6241)

Stimulation of small phytoplankton drives enhanced sinking particle formation in a subtropical ocean eddy

Haoran Liu[1, 2], Thomas J. Browning[2], Edward A. Laws[3], Yibin Huang[4, 5, #], Lei Wang[6], Yiwei Shang[1, 7], Xiaogang Xing[8], Kuanbo Zhou[1], Zong-Pei Jiang[9], Xin Liu[1*], Bangqin Huang[1], Minhan Dai[1]

[1]State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, Fujian, China.

[2]Marine Biogeochemistry Division, GEOMAR Helmholtz Centre for Ocean Research, Kiel, Germany.

[3]Department of Environmental Sciences, College of the Coast and Environment, Louisiana State University, Baton Rouge, Louisiana, USA.

[4]Department of Ocean Sciences, University of California, Santa Cruz, CA, USA.

[5]NOAA/OAR Pacific Marine Environmental Laboratory, Seattle, WA, USA.

[6]Third Institute of Oceanography, Ministry of Natural Resources, Xiamen, Fujian, China.

[7]Department of Biological Sciences, University of Southern California, Los Angeles, California, USA.

[8]Second Institute of Oceanography, Ministry of Natural Resources, Hangzhou, Zhejiang, China.

[9]Ocean College, Zhejiang University, Zhoushan, Zhejiang, China.

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[#]Present address: State Key Laboratory of Marine Environmental Science, Xiamen University, Xiamen, Fujian, China.

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Email address: Haoran Liu (liuhaoran@stu.xmu.edu.cn);

Thomas J Browning (tbrowning@geomar.de);

Edward A Laws (edlaws@lsu.edu);

Yibin Huang (yibin.huang@noaa.gov); (yibin.huang@xmu.edu.cn)

Lei Wang (wanglei@tio.org.cn);

Yiwei Shang (yiweisha@usc.edu);

Xiaogang Xing (xing@sio.org.cn);

Kuanbo Zhou (kbzhou@xmu.edu.cn);

Zong-Pei Jiang (zpjiang@zju.edu.cn);

Xin Liu (liuxin1983@xmu.edu.cn);

Bangqin Huang (bqhuang@xmu.edu.cn);

Minhan Dai (mdai@xmu.edu.cn)

***Corresponding author:** Xin Liu (liuxin1983@xmu.edu.cn)

Abstract

Nutrient transfer into the sunlit surface ocean by cyclonic eddies is potentially crucial for sustaining primary productivity in the stratified subtropical gyres. However, the nature of productivity enhancements, including the flow of matter to higher trophic levels and its impact on carbon fluxes, remain poorly resolved. Here, we report a detailed assessment of the biogeochemical response to a cyclonic eddy in the subtropical Northwest Pacific via a combination of ship-based and autonomous platforms. Primary production was enhanced 2-fold within the eddy core relative to reference sites outside, whereas phytoplankton biomass even decreased. Pico-phytoplankton (<2 μm) dominated (>80 %) both phytoplankton biomass and primary production inside and outside the eddy. The stimulated primary production in the eddy core was accompanied by a ~2-fold increase in mesozooplankton abundance, a ~3-fold increase in particle formation in the deep chlorophyll maximum layer, as well as significantly enhanced surface oceanic CO_2 uptake and net community production. We suggest these observations carry important implications for understanding carbon export in the subtropical ocean, and highlight the need to include such subtropical eddy features in ocean carbon budget analyses.

1 Introduction

Carbon that is fixed into organic matter via phytoplankton photosynthesis in the euphotic zone and then transferred into deeper waters via foodweb processes, physical mixing, transport, and gravitational setting—the ocean's biological carbon pump (BCP)—is an important component of the global carbon cycle (Boyd et al., 2019; Ducklow et al., 2001). Upwelling of deep water driven by cyclonic eddies can enhance the influx of nutrients into the sunlit euphotic zone, thereby elevating phytoplankton productivity and potentially the BCP (Allen et al., 1996; Benitez-Nelson et al., 2007; Bidigare et al., 2003; Browning et al., 2021; Falkowski et al., 1991).

The subtropical Northwest Pacific is highly oligotrophic with very low chlorophyll-a (Chl *a*) and nutrient concentrations in the upper ocean (Browning et al., 2022; Wen et al., 2022). The region is perturbed by a major mesoscale eddy field, which extends across the western Pacific between 15-28 °N, and is driven by frontal instability associated with the subtropical front (Liu et al., 2012; Qiu et al., 2014). A limited number of field studies with low sampling resolution have shown weak responses of phytoplankton biomass and productivity to cyclonic eddies in this region (Huang and Xu et al., 2018; Yun et al., 2020). Chl *a* enhancements have also not been registered in satellite observations of cyclonic eddies in the region (Dufois et al., 2016; He et al., 2021). These findings challenge the potential biogeochemical importance of cyclonic eddies in this system. On the other hand, the response of standing phytoplankton stock to cyclonic eddies in oligotrophic systems might not adequately represent how much primary productivity (PP), and ultimately formation of sinking particles, is occurring (Landry et al., 2008).

Here we present a combination of ship-based and autonomous biogeochemical float observations of a cyclonic eddy in the Northwest Pacific subtropical gyre to examine biogeochemical changes within the eddy and their submesoscale variability. We find that whilst no phytoplankton biomass accumulation within the eddy in the upper 200 m was found, PP, sinking particle formation and air-to-sea CO_2 absorption were significantly enhanced. We explain this decoupling as being a result of rapid zooplankton consumption of the additional PP, which maintains phytoplankton biomass—or even decreases it—compared to background conditions.

2 Materials and Methods

2.1 Shipboard sample collection

This study was carried out during the KK1902 cruise (from 15 March to 20 April 2019) on the R/V *Tan Kah Kee* (Figure 1). Sea-surface temperature (SST) and salinity (SSS) were measured using an underway SBE21 conductivity-temperature-depth (CTD), while current speed and direction were measured by a hull-mounted Acoustic Doppler current profiling (ADCP, Workhorse 300 kHz, Teledyne). At each station, temperature and salinity were recorded by an SBE 911plus CTD. Samples for phytoplankton pigments and nutrient concentrations were collected throughout the upper 200 m. Samples for size-fractionated Chl *a*, and PP were collected at 5-6 depths within the euphotic zone. An in situ imaging system (Underwater Vision Profiler 5 HD version, UVP5), in vivo fluorescence sensor (ECO-FLNTU fluorometer, WETLabs) and photosynthetically available radiation (PAR) sensor (QCR2300-HP, Biospherical Instruments) attached to the CTD were used to measure the vertical profile of large particles (0.06-2.0 mm), fluorescence, and downwelling PAR respectively. Mesozooplankton samples were collected between 200 m depth and the surface. The deep chlorophyll-a maximum layer

(DCML) was identified by continuous chlorophyll fluorescence (Table 1). The euphotic zone (Zeu) was defined to be the depth corresponding to 1% surface PAR. As stations A35-2, A34-2, Z4, Z5, and Z7 of the transect were sampled at night, it was not possible to determine the Zeu by vertical profiles of PAR. The depth of the ship-based Zeu was therefore computed by using the relationship: $log_{10}(Zeu) = 0.72 + 0.64 \times log_{10}(DCML), r^2 = 0.49, n = 54, p < 0.01$, with the relationship computed for the daytime casts only.

2.2 Nutrient and pigments analysis

Dissolved inorganic nitrogen concentrations (nitrate and nitrite, N+N, μmol L^{-1}) were collected and analyzed onboard with a Technicon AA3 Auto- Analyzer (Bran- Lube, GmbH) following Du et al. (2017) and the detection limits were 0.01 μmol L^{-1}. A total of 4-10 L of seawater was filtered through 0.3 μm glass fiber filters (Advantec, GF-75) for diagnostic pigment analysis which were measured by high performance liquid chromatography (HPLC) (3.5 μm Eclipse XDB C8 column) following Wang et al. (2018). The filters were stored in liquid nitrogen and then kept at -80 °C when returned to the laboratory. Pigment samples were extracted in 1 mL of N, N-dimethylformamide, and then 0.6 mL of the extract was mixed with 0.6 mL of ammonium acetate in a 1.5 mL brown chromatographic bottle. Pigments including Chl *a*, fucoxanthin (Fuco), Dv-Chl *a* (DvChl*a*), and zeaxanthin (Zea) were identified based on the quantification of standards manufactured by the Danish Hydraulic Institute (DHI) Water and Environment, Hørsholm, Denmark. The pigment signatures here are selected for the major groups such as diatoms represented by Fuco, *Prochlorococcus* by DvChl*a* and cyanobacteria by Zea (Jeffrey and Vesk, 1997). Total Chl *a* (TChl*a*) was calculated as the sum of Chl *a* and DvChl*a*.

2.3 Phytoplankton productivity and size classes

Seawater was collected at depths of surface (~5 m), 50% (or 33.2%), 23.6%, 16.6%, 3.9% (or 1.9%), and 1% of surface PAR. PP was estimated from the uptake of $NaH^{14}CO_3$ in samples incubated on-deck over a 24 h period following Xie et al. (2018) and Liu et al. (2021). Briefly, seawater was distributed in 60 mL polycarbonate bottles (duplicate light bottles and one dark bottle from each depth), and spiked with 20 μCi $NaH^{14}CO_3$ in each bottle. Sunlight was screened by different combinations of neutral density and blue filters (LEE filters, UK) to stimulate submarine irradiances. The temperature in the incubator was maintained by continuous flushing of near-surface seawater. As this would artificially elevate the *in situ* temperature conditions for the subsurface samples during the incubation, the metabolic rates below the surface were corrected following Allen et al. 2005 and Huang et al. 2019 (Text S1). At the end of the incubation, samples were sequentially filtered through 20 μm, 2 μm, and 0.2 μm Nuclepore polycarbonate filters under low-vacuum pressure (<100 mm Hg) to quantify micro-, nano-, and pico-phytoplankton fractions (Sieburth et al., 1978). The filters were processed immediately on board the research vessel. The radioactivity (DPM, disintegrations per minute) on the filters was measured with a Tri-Carb 4810TR liquid scintillation counter after removing residual inorganic carbon by acid fuming overnight and immersing the filters in 4 mL of Ultima Gold scintillation cocktail (Perkin-Elmer, USA) until the filters became transparent. The depth-integrated PP (IPP) was calculated using trapezoid rule from the surface to the deepest, extrapolated to a value of zero at 200 m following Karl et al. (2021).

The phytoplankton size structure was characterized by direct size-fractionated filtration for Chl *a* analysis via fluorescence ($Chla^{Fluo}$). Briefly, seawater (1 L) was filtered through 20 μm (micro-

phytoplankton), 2 μm (nano-phytoplankton), and 0.2 μm (pico-phytoplankton) Nuclepore polycarbonate filters (Millipore, USA). The filters were stored in liquid nitrogen until further analysis. The samples were submerged in 90% acetone for Chla^{Fluo} extraction. After 16 - 24 h at -20 °C in a dark environment, the Chla^{Fluo} was measured via a Trilogy fluorometer (Turner Designs, USA) calibrated with a commercially purified Chl *a* standard (DHI Inc., Denmark). The total Chla^{Fluo} concentration summed with micro-, nano-, and pico-phytoplankton groups shows consistent results with the paired HPLC TChl*a* measurements during the cruise (TChl$a$ = 0.94 × Chla^{Fluo}; $R^2 = 0.88$; $p < 0.01$, n = 49). Here, we only used the percentage contribution of the different groups to total Chla^{Fluo} to indicate the phytoplankton size structure.

2.4 Large particles and mesozooplankton

Large particle size distributions (equivalent spherical diameter (ESD) from 0.06 to 2.0 mm) and concentrations were measured using the UVP5 HD version (Picheral et al., 2010). The UVP5 captures an image of seawater with a volume of ~1 L, and takes 6 images per second at a vertical CTD deployment speed of 0.5 m s^{-1}. For all profiles, the UVP5 acquisition sequence was set under a Pressure Protocol, therefore only the descending profiles were recorded and analyzed. We set the analyzing starting depth to 10 m, due to the interference of bubbles in surface waters that leads to an overestimate of particle counts. All UVP5 profiles were matched with the CTD profiles according to depth. Data from each individual profile was binned at a vertical resolution of 5 m. Mean averages were then taken over the samples in each vertical bin. The particles in each image were counted and sized immediately, and the data are stored in the instrument. Particle area was measured as the number of pixels (Sp) of an imaged object and can be converted to particle cross-sectional area (Sm) in square millimetres (mm^2) as follows: $Sm =$

$0.0036 \times Sp^{1.149}$. The ESD was converted according to $ESD = \sqrt{4 \times Sm/\pi}$. Further details regarding the calibration procedure are given in Picheral et al. (2010) and Kiko et al. (2022). No samples were collected in stations A35-2 and Z1 because of the poor weather conditions.

Mesozooplankton samples were collected using vertical tows with a WP2 plankton net (mesh size: 200 µm, mouth aperture: 0.25 m^2), towed vertically from a depth of 200 m to the surface at a speed of 0.5 m s^{-1}. The volume of water filtered was estimated using a flowmeter (Hydro-Bios, Kiel). After recovery, the net was rinsed from the outside using a seawater hose on a low pressure. Zooplankton attached to the collector at the cod end were gently washed off the mesh with seawater. The samples were then preserved in 10 % buffered formaldehyde (final concentration). In the laboratory, organisms were first separated into two size fractions using a 1000 µm mesh and were subsequently aliquoted using a Motoda box. The mesozooplankton abundance and composition were processed with a ZooScan digital imaging system (Gorsky et al., 2010) at a resolution of 2400 dpi. Subsamples ranged from 1/2 to 1/4 of the original sample volume to ensure that the number of zooplankton in a single scan was approximately 1500 individuals. The Ecotaxa website (https://ecotaxa.obs-vlfr.fr) was used for species identification and enumeration. Zooplankton detected were first identified automatically and subsequently sorted manually into 13 categories: Amphipoda, Chaetognatha, Copepoda, Egg, Fish larva, Foraminifera, Medusa, *Noctiluca*, Ostracoda, Polychaeta, Shrimp, Tunicate, and other zooplankton following Liu et al. 2020. The mesozooplankton abundances (ind. m^{-3}) were calculated using the following equation: abundance = number of organisms $*$ splitting ratio / net volume. The volume of water filtered through the nets was calculated by multiplying the towed depth by the net's mouth area.

2.5 Biogeochemical Argo float (BGC-Argo) observation

A BGC-Argo float (WMO ID: 2902753) was deployed in the eddy core during the cruise (March 29 2019). Synchronous with the float deployment, discrete water samples were collected for sensor calibration or validation (Figure S2; Table S3). The float was equipped with an SBE41 CTD sensor, Satlantic OCR-504 irradiance sensor, Anderaa optical dissolved oxygen (DO) sensor, Deep-Sea DuraFET pH sensor, and WETLabs MCOMS bio-optical sensor. The bio-optical sensor measured the chlorophyll fluorescence at 695 nm, which was induced by blue light at 475 nm, and particulate backscattering coefficient at 700 nm (b_{bp700}) with a scattering angle of 150°. The float profiled once per day at the beginning 4 cycles from 200 m to the surface, and then twice per day from 1000 m to surface during our study period. The vertical resolution of the float was ~ 2 m in the top 200 m.

The pH and DO sensors were manually calibrated by the shipboard samples collected at the same time from the hydrographic cast conducted during float deployment using the spectrophotometric method (Jiang et al., 2019) (Figure S2; Table S3). The quality control procedures for float-measured backscattering follows the protocol outlined in the BGC-Argo quality control manual for particles backscattering (Schmechtig et al., 2017). Briefly, the process begins by excluding raw b_{bp} data that falls outside the global range (<-0.000025 m^{-1} or >0.1 m^{-1}). Subsequently, a series of tests and procedures were applied to eliminate negative and positive spikes, as well as identify and remove any potential bad offsets. A detailed description is provided in Supporting Information Text S1. The despiked b_{bp700} corresponds to the bulk population of small particles, whose diameter is smaller than 100 μm and mostly between 0.5 to 30 μm (Galí et al., 2022). The

raw fluorescence was adjusted by subtracting a background signal (minimum fluorescence measured between 200 and 300 m), and then an extra non-photochemical quenching (a phenomenon whereby phytoplankton exposed to high light exhibit reduced fluorescence per unit chlorophyll) correction was further applied to the daytime profile (Long et al., 2021; Xing et al., 2012). The processed fluorescence data was converted into the Chl *a* concentration using the conversion factor derived from the paired comparison against ship-collected HPLC samples. Quality-controlled float data were interpolated to a 1 m vertical resolution and smoothed over time with a 5-point (which equates to ~2.5 days per group) running mean to filter out the short-term fluctuations (Huang et al., 2022).

The daily air-sea CO_2 gas flux (F_{CO_2}) alongside the float trajectory was computed as follows:

$$F_{CO_2} = k \times K_0 \times (pCO_{2\_sea} - pCO_{2\_air}) \quad \text{Eq. 1}$$

where k is the gas exchange velocity parameterized from remotely sensed 10-m wind speeds, K_0 is the temperature and salinity dependent CO_2 solubility (Weiss, 1974), pCO_{2_sea} and pCO_{2_air} are partial CO_2 values at the sea surface (from float measurements) and atmosphere (from the NOAA Greenhouse Gas Marine Boundary Layer Reference), respectively. The 10 m wind stress and speed were retrieved from https://manati.star.nesdis.noaa.gov/datasets/ASCATData.php. The atmospheric pCO_2 was available from https://gml.noaa.gov/ccgg/mbl/mbl.html. pCO_{2_sea} was computed from float-measured pH paired with estimates of total alkalinity using the CANYON-B neural network algorithm from float tempeture, salinity and oxygen measurements (Bittig et al., 2018), and validated against discrete collected samples. To elucidate the underlying mechanism driving the seawater pCO_2 change, we quantified the effects of thermal and

nonthermal effects on float-measured pCO_{2_sea}, according to the scheme proposed by Takahashi et al. (2002) (details provided in Text S1). Nonthermal effects include the imprint of dissolved inorganic carbon (DIC) concentration change induced by biological activity and physics (i.e., vertical transport and sea-air CO_2 exchange) (Fassbender et al., 2018).

Biologically mediated O_2 change ($\frac{dO_2}{dt}_{bio}$, net community production, NCP) was estimated as a residual by subtracting a set of physically induced oxygen fluxes from the float observed oxygen change ($\frac{dO_2}{dt}_{obs}$) following Bushinsky and Emerson (2015) and Huang et al. (2022):

$$\frac{dO_2}{dt}_{bio} = \frac{dO_2}{dt}_{obs} - \frac{dO_2}{dt}_{Gas} - \frac{dO_2}{dt}_{mixing} \quad \text{Eq. 2}$$

where $\frac{dO_2}{dt}_{Gas}$ and $\frac{dO_2}{dt}_{mixing}$ represents the oxygen change induced by air-sea gas change and vertical mixing (a sum of vertical transport attributed by entrainment, diapycnal diffusion, and vertical advection), respectively. Parametrizations of physical terms and their associated uncertainty estimate are detailed in Text S1. The oxygen-based NCP estimate was converted into the carbon unit based on C:O ratio of 1.4 (Laws, 1991). Not accounting for horizontal advection in the oxygen budget in the present study results in a limited impact on the accuracy of oxygen-based NCP estimates, because our float approximates Lagrangian observations, and horizontal oxygen gradients in the upper ocean layers are relatively small due to vigorous O_2 air-sea gas change (Bushinsky and Emerson, 2015; Huang et al., 2018).

The research vessel was navigated to track the eddy core while the BGC-Argo followed the quasi-Lagrangian drift (Figure 1d). The radius, center position, and amplitude of the studied cyclonic eddy were obtained from the satellite eddy trajectory product (version 3.1 for delayed-time), which was distributed by AVISO+ and can be downloaded from https://doi.org/10.24400/527896/a01-2021.001. The amplitude was defined as the magnitude of the height difference between the extremes of sea surface height (SSH) within the eddy and the SSH around the effective contour defining the eddy edge in the product. As the eddy pumping causes a shallowing of isopycnals coincided with a DCML (Figure 2c), based on the distance to the eddy core relative to eddy radius (r/R) and the DCML variation (Figures 4, S4, Table 3), float data were partitioned into three sectors: eddy core (cycle 3-13) (DCML $\leq$ 113 m and r/R < 0.7), eddy edge (cycle 14-33) (119 m $\leq$ DCML $\leq$ 131 m and 0.7 < r/R < 1) and background stations in the absence of eddy influence (cycle 34-53) (131 m $\leq$ DCML $\leq$ 153 m and 1 < r/R < 2.5), respectively.

The daily sea level anomaly in our study area was obtained from the Copernicus Climate Change Service, Climate Data Store (https://doi.org/10.24381/cds.4c328c78). The climatological eddy kinetic energy product was distributed by AVISO+ and can be downloaded from https://tds.aviso.altimetry.fr/thredds/catalog/dataset-duacs-climatology-global/delayed-time/monthly_clim/eke/catalog.html.

2.6 Statistical analyses

All statistic analyses were performed in R (R Development Core Team, 2022). A Pearson's correlation coefficient was applied to detect correlations between pairs of variables (R function

"cor.test"). The significance of differences (for TChl*a*, IPP, and nitrate concentration) between inside the eddy (core plus transit plus edge stations) and outside the eddy (reference stations) was quantified by a t-test with a significance level of 0.05 (R function "t.test"). To test for the differences in BGC-Argo derived air-sea CO_2 flux, NCP, b_{bp700}, and Chl*a* among eddy core (cycles 3-13), edge (cycles 14-33), and outside (cycles 34-53), a one-way analysis of variance (ANOVA) was conducted with a significance level of 0.05 (R function "aov"). This was followed by a Tukey posthoc test, using the "HSD.test" function in the R package "agricolae".

3 Results

3.1 Hydrographic and biogeochemical conditions

Our study region was located at the western North Pacific Subtropical Countercurrent (STCC) area, a region with high eddy frequencies in a region of elevated eddy kinetic energy (Figure 1a; Qiu et al., 2014; Ramp et al., 2017). The ship's high-resolution sampling transect crossed a cyclonic eddy core, as indicated by the decreased SLA and sea surface current from satellite and shipboard ADCP-derived observations (Figure 1d). Station A35-2 and Z7 were located at the outside of the cyclonic eddy and used as "background" reference sites. Note that A35-2 was influenced by the adjacent anti-cyclonic eddy (ACE) (Figure 1d). Underway SST in the eddy core (Z2, A34-2) was ~2 °C colder than the counterpart in edge waters (Z1 and A32-2), whilst SSS was elevated by ~0.3 in the eddy core and core-edge transit (Z6) (Figure 1c), implying eddy pumping of colder, more saline subsurface water. The cyclonic eddy propagated westward for 145 days (26 January - 19 June 2019) (Figures 1a, black line) and was sampled in its well-developed mature (1/3 – 2/3 of lifespan) stage (Figure 1b) (Sweeney et al., 2003).

The N+N concentration was depleted (<0.1 μmol L^{-1}) in surface waters (<70 m) both inside and outside of the eddy, but significantly increased in the eddy core below the DCML, with the nitracline shoaling into the euphotic zone between Stations Z2 to Z5 (ranging 0.13-0.64 μmol L^{-1} at 100 m) (Figure 2a). Higher salinity subsurface water was uplifted to the surface within the eddy (Figure 2b), but an exception was the fresher surface water from Stations Z3 to Z5, resulting from the advection of a filamentous intrusion (Hu et al., 2023) (Figure 1c, 2b). The TChl*a* concentrations at the surface were low (< 0.1 mg m^{-3}). TChl*a* concentrations at DCML were relatively stable between eddy core and outside of the eddy (Figure 2c). However, the 0-200 m depth-integrated TChl*a* concentrations decreased significantly within the eddy compared to outside of the cyclonic eddy (Figures 2c, Table 2). Further BGC-Argo observations (see discussion below) suggested that the restricted Chl*a* changes between inside and outside of the eddy were due to the combination of differential photoacclimation within and outside of the eddy (Figure S4) and carbon biomass changes. However, in line with the shoaling nitracline, the isopycnal surface associated with the DCML (23-23.5 kg m^{-3}) shoaled from ~140 m at the eddy edge to ~100 m within the euphotic zone at the core (Figure 2c).

3.2 Phytoplankton productivity and size structure

Pico-phytoplankton, contributing 80-95% of the TChl*a*, consistently dominated the phytoplankton community, with elevated contributions in the eddy core (Figure 2g-i). Furthermore, concentrations of DvChl*a*, the pigment exclusive to *Prochlorococcus*, was the most abundant detected pigment, with the 0-200 m integrated concentrations decreasing from the core (10.52±0.92 mg m^{-2}) to the outside the cyclonic eddy stations A35-2 and Z7 (14.91±0.22 mg m^{-2}; Figure 2f). The distribution of Zea, a marker pigment for all cyanobacteria, did not show clear

trends, although the integrated concentration slightly decreased from the core (3.22±0.45 mg m^{-2}) to the outside station A35-2 and Z7 (4.58±0.09 mg m^{-2}; Figure 2e). Concentrations of Fuco, a marker pigment often associated with diatoms, were ubiquitously low (<0.6 mg m^{-2}) but increased ~2-fold at the eddy core (Z2) relative to the outside stations (Figures 2d, Table 2).

Whilst standing integrated TChl*a* concentrations decreased in the eddy compared with outside the eddy, PP clearly increased in the eddy core, with the eddy core station A34-2 double that of the outside station Z7 (211.4 and 108.5 mg C m^{-2} d^{-1}, respectively) (Figures 2j-l, Table 2). Although stations Z3-Z5 were closer to the eddy core, PP was general lower in these filament influenced stations (142.6±27.3 mg C m^{-2} d^{-1}) than the core-edge transit station Z6 (190.1 mg C m^{-2} d^{-1}) (Figures 2j-l, Table 2). PP was consistently dominated by the picophytoplankton (> 80%) both within (micro-PP: 4.9±1.4 mg C m^{-2} d^{-1}, nano-PP: 21.7±5.3 mg C m^{-2} d^{-1}, pico-PP 151.4±27.4 mg C m^{-2} d^{-1}) and outside (micro-PP 2.8±0.6 mg C m^{-2} d^{-1}, nano-PP 17.5±8.1 mg C m^{-2} d^{-1}, pico-PP 83.3±1.6 mg C m^{-2} d^{-1}) of the eddy (Figures 2j-l, Table 2).

3.3 Large particles and mesozooplankton

Large particle concentrations derived from the UVP5 were elevated at the DCML in the eddy core, leading to a significant positive relationship between size-specific particle abundance and CTD measured fluorescence in the eddy core ($r \geq 0.37$). This was especially the case for the particles in the range of 0.06 – 0.5 mm ($r \geq 0.51$; Figure 3a), which indicated that the large particles in the eddy centre were closely associated with phytoplankton and tended to result in large particles between 0.06 and 0.5 mm. Smaller large particles (0.06 - 0.5 mm) abundance accounted for >97 % of the total large particles and showed a clearer trend throughout the eddy,

with ~3-fold higher concentrations at the DCML of the eddy core station Z2 (132 ind. L^{-1}) relative to outside station Z7 (Figure 3c). The vertical distribution of such larger particles (0.5 - 2.0 mm) appeared to be related to diel vertical zooplankton migration or fecal pellets, with enhanced concentrations at the surface at night time (Figure 3d).

Mesozooplankton (> 0.2 mm) abundances within the eddy core (station Z2) reached a peak value of 296.2 ind. m^{-3}, which were ~2 times higher than the outside station Z7 (Figure 3b). These were dominated by copepods (averaging 89% contribution to the mesozooplankton community for all stations).

3.4 BGC-Argo float observation

In line with the shipboard observations, observations from the BGC-Argo float deployed in the eddy core captured more consistent spatial trend from eddy core to edge and showed initially elevated salinity, lower temperature waters, and shoaled DCML depths (Figures 4a, S3). Consistent with Xiu and Chai (2020), two proxies of phytoplankton biomass, Chl *a* and b_{bp700}, were both elevated at the DCML in the eddy core relative to background conditions by 1.36 and 1.17-fold, respectively (Figures 4b, S3). There was no apparent trend between in and outside of the eddy in terms of the 0-200 m integrated Chl *a*. However, the 0-200 m integrated b_{bp700}, which reflects small particle signals mostly associated with the phytoplankton, was significantly decreased within the eddy core (Figure S3b, Table 3). BGC-Argo-derived NCP, an indicator of carbon export potential that represents the excess amount of organic carbon production over the consumption (Ducklow and Doney, 2013; Li and Cassar, 2017), was significantly elevated either within the MLD or Zeu in the eddy core (50.63 ± 22.17, 175.16± 48.00 mg C m^{-2} d^{-1}) compared

with the eddy edge (27.11 ± 8.90, 25.19 ± 23.62 mg C m^{-2} d^{-1}) and background (6.88 ± 11.34, 43.05 ± 19.52 mg C m^{-2} d^{-1}) (Figures 4d, S3).

Aligning with previous results (Takahashi et al., 2002), air-sea CO_2 flux in the background stations (average wind speed 5 m s^{-1}) yielded a weak CO_2 sink (2.32 ± 2.1 mg C m^{-2} d^{-1}) during the spring in the Subtropical North Pacific. However, the eddy core region, where measurements coincided with intense winds (maximum of 11 m s^{-1}, Figure S5a), exhibited a major enhancement of oceanic CO_2 uptake (45.8 ± 16.68 mg C m^{-2} d^{-1}) (Figures 4c, S3), matching the trends expected from the lower temperatures, enhanced PP and sinking particles observed in the shipboard survey. To elucidate the role of different wind speeds in driving the observed air-sea CO_2 difference, we conducted a sensitivity analysis by adjusting a constant wind speed of 5 m s^{-1} (an average value in the reference sites) for all profiles to reconstruct the air-sea CO_2 flux within the eddy core. As expected, the reconstructed air-sea CO_2 flux in the eddy core substantially decreased, which confirms the important role of intensifying wind speed in driving enhanced CO_2 uptake in the eddy core. However, the reconstructed air-sea CO_2 flux in the eddy core still yielded a stronger sink for atmospheric CO_2 relative to the reference sites (Figure S3c), the implication being that other factors, such as the air-to-sea pCO_2 gradient within and outside eddy core, was another key factor responsible for the observed difference in air-sea CO_2 flux. We further separated the thermal and nonthermal (e.g., physical mixing, biological activity, and air-sea gas exchange) forcing on aqueous pCO_2, and found the variability in surface pCO_{2_sea} was mainly driven by the thermal effect over the nonthermal effect in the eddy (Figure S5b). When the temperature effect is removed, the remaining variability would characterize a source of CO_2 from the ocean to the atmosphere (Figure S5b).

4 Discussion

4.1 Dominance of picophytoplankton in a cyclonic eddy ecosystem

In contrast to previous studies near Hawaii that found elevated productivity within the cores of cyclonic eddies to be associated with enhanced Chl *a* biomass and a dominant contribution of larger phytoplankton (diatoms and prynmnesiophytes) (Benitez-Nelson et al., 2007; Bidigare et al., 2003; Brown et al., 2008), we observed a cyclonic eddy core that hosted a decreased overall phytoplankton biomass and a persistent dominance of small picophytoplankton (Figures 2, S3, and Tables 2, 3). The float-measured b_{bp700} signal aligned well with the ship-board HPLC TChl*a* observations, with both indicating a decrease in phytoplankton within the eddy core; however, the float-measured Chl*a* exhibited a relatively stable pattern within and outside the cyclonic eddy. The inconsistency in Chl*a* trends between float and shipboard observations may result from the use of a fixed fluorescence to Chl*a* correction factor (derived from the paired comparison of the samples collected from the ship during the float deployment) for the float Chl*a* computation over a period of almost a month. Modified environmental conditions in response to eddy evolution may have altered the phytoplankton taxonomic composition and physiological acclimation mechanisms, leading to a potential change in the fluorescence to Chl*a* relationship (Roesler et al., 2017).

Phytoplankton community structure is expected to change in response to changes in nutrient availability (Irwin et al., 2006). The strong dominance of picophytoplankton was maintained under cyclonic eddy conditions, which might be attributed to the overall weak upward inputs of nutrients. In this study, the integrated nitrate within the eddy core increased by only

approximately 2-fold (Table 2), compared to the ~4-fold increase observed by Benitez-Nelson et al. (2007) for a cyclonic eddy near Hawaii that eventually induced a diatom bloom. The relatively lower nutrient supply into the euphotic zone in the cyclonic eddy observed during the present study therefore appeared insufficient for the accumulation of large phytoplankton such as diatoms. Similar picophytoplankton dominant communities under cyclonic eddy conditions were reported by Yun et al. (2020) in this region.

4.2 Tight trophic transfer regulates phytoplankton stand stock

In contrast to the limited shifts in phytoplankton community structure and even decreased integrated TChl*a* and b_{bp700}, ^{14}C integrated primary productivity (IPP) was significantly enhanced within the eddy core and core-edge transit stations relative to background levels (Figure 2j-l). Similar to our observations, an earlier data synthesis has noted that the Chl *a* anomalies within eddies are relatively small in the North Pacific subtropical gyre (Huang and Xu, 2018), implying the decoupling between phytoplankton biomass and productivity we observed could be common in this region. Mass conservation implies that the enhanced primary production rates without phytoplankton biomass accumulation within the eddy core must be largely compensated by corresponding consumption and/or sinking rates. The 2-fold enhancement in mesozooplankton abundance within the eddy core suggested that overall grazing pressure was indeed enhanced (Figure 3c; Landry et al., 2008), with the picophytoplankton responsible for the majority of the enhanced production presumably consumed by smaller microzooplankton that were not identified here (Calbet and Landry,1999).

The much shorter generation times of microzooplankton in comparison to larger zooplankton means that the microzooplankton can increase in abundance quickly and increase grazing pressure following increases in their prey, in this case, picophytoplankton. We suggest the decline in phytoplankton concentrations within the eddy core was therefore likely the result of tightly coupled phytoplankton growth and zooplankton grazing pressure. Moreover, our findings suggest that the simultaneous elevation of zooplankton grazing is expected to facilitate the formation of large particles, and fecal pellets within the eddy core, prompting the overall potential enhancement of sinking particles observed (Figure 3). Thus, these results support the view, via trophic transfer, that small picophytoplankton can be also critical to carbon export in oligotrophic oceans (Richardson and Jackson, 2007, Puigcorbé et al., 2015; Stukel and Landry 2010).

The development of the eddy stage might also further impact the biological responses observed, resulting from variability in the supply of new nutrients from depth (Rii et al., 2008; Sweeney et al. 2003). According to Sweeney et al. (2003), the cyclonic eddy stage can be divided into three stages: intensification (less than one-third of the eddy lifetime), mature (between one-third and two-thirds of the eddy lifetime), and decay (greater than two-thirds of the eddy lifetime). These stages are based on the lifespan of the eddy, and during the intensification and mature stages, there is an upwelling of nutrients and stimulation of biological response. However, vertical nutrient supply stops and biological response decreases during the decay stage of the eddy. In a previous study by Yun et al. (2020), it was shown that neither Chl*a* nor PP in a decaying cyclonic eddy was significantly different from that in a reference site in a similar region. However, in the current study the observed cyclonic eddy was in its well-developed mature

stage, with a higher eddy amplitude and associated nutrient input compared to Yun et al. (2020). Despite both studies showing a picophytoplankton dominated community, the present study thus found an increase in PP with a tightly coupled link to higher trophic levels.

4.3 Potential contribution to ocean CO_2 uptake

Based on the biogeochemical Argo float (BGC-Argo) observations we assessed the capacity of the subtropical cyclonic eddy to modify oceanic carbon sequestration. Our results are in agreement with Ford et al. (2022), who reported that a cyclonic eddy enhanced the sink of atmospheric CO_2 in the South Atlantic Ocean based on satellite and in-situ observations. Our analysis revealed that the cyclonic eddy-induced thermal effect was a key driver of the enhanced CO_2 sink in the eddy core, due to cooler SST increasing CO_2 solubility. In addition, the elevated wind speeds at the eddy core increased gas transfer and stimulated the air-sea CO_2 flux (Figure S3, S5). The sensitivity to SST and wind speed indicated that the ability of mesoscale eddies located in subtropical gyres to modify the CO_2 flux may also vary seasonally (Song et al., 2016; Ford et al., 2022). Our study confirmed enhanced biological production and potential carbon export in the eddy core through various independent measurements, including UVP5 observations, ^{14}C-PP, and the calculation of net community production (NCP) from an oxygen tracer budget. Consequently, the elevated biological production plays a significant role in reducing pCO_2 by consuming more seawater DIC. However, we found the cyclonic eddy could act as a CO_2 source from the ocean to the atmosphere in the eddy core after removing the temperature effect (Figure S3), this is likely because the additional DIC transported vertically upward by the eddy outweighs the increased DIC consumption due to elevated biological production (Chen et al., 2007).

Consistent with the large particle formation observed, our results also indicated a significant increase in the float-estimated NCP within the eddy core (Figure 4). The increased NCP reflects the carbon export potential of particulate organic carbon (POC), dissolved organic carbon (DOC) (Emerson 2014), and also zooplankton-mediated transport (Boyd et al., 2019). Efficient DOC production has been found in the oligotrophic ocean (Roshan and DeVries 2017; Huang et al., 2023). Moreover, enhanced zooplankton grazing is expected to result in more DOC production via sloppy feeding and excretion (Moran et al., 2022). Previously, Chen et al. (2008) found the enhanced NCP inside the cyclonic eddy appears to have accumulated as DOC rather than exported as POC to the mesopelagic in the subtropical North Pacific Gyre. As 97 % of the total large particles we observed were smaller particles (0.06-0.5 mm) (Figure 3c-d), with slower sinking speeds and more efficient remineralization (Benitez-Nelson et al., 2007), further study in relation to quantifying the export flux of POC to the deep ocean in the eddy is still needed.

We found enhanced picophytoplankton productivity, large paricle formation, and ocean CO_2 uptake within a Subtropical North Pacific cyclonic eddy, even though the standing stocks of phytoplankton were not enhanced. Considering that cyclonic eddies such as the one studied here are common across subtropical gyres (Chelton et al., 2011; Qiu et al., 2014), we suggest they could play an important role in mediating the regional BCP and fueling higher trophic levels in these systems, even where overall Chl *a* concentrations remain similar to background levels (Chang et al., 2018; Huang and Xu, 2018). It is also pertinent that such eddy-stimulated productivity and subsequent sinking carbon fluxes would not be registered in typical satellite algorithms that depend only on surface Chl *a* biomass, light, and temperature (Behrenfeld and

Falkowski, 1997). More detailed studies in the future will shed light onto how widespread and representative our results are, both for other eddies in this region and throughout different phases of eddy maturity (Sweeney et al., 2003).

5 Conclusions

By combining high-frequency, ship-based measurements and multi-sensor BGC-Argo float observations, we assessed in detail the impact of a subtropical cyclonic eddy on plankton and the BCP. We found that eddy pumping of deeper waters with elevated nutrients within the eddy core enhanced picophytoplankton primary production, but that the tightly coupled transfer to higher trophic levels meant that the enhanced production was not accompanied by a buildup of phytoplankton biomass. These processes also resulted in net oceanic CO_2 absorption, large particle formation, and potential sinking carbon export in the eddy core. The impacts of decreased SST, and DIC drawdown by the enhanced biological activity likely collectively exceeded the upward vertical transport of carbon-rich deeper water, resulting in a net CO_2 drawdown from the atmosphere. Exactly how much sinking POC was exported was not possible to quantify with our observations. Better resolution of such mesoscale features would improve estimates of the global ocean carbon budget.

Data availability statement

Shipboard data can be found at https://doi.org/10.17632/sstdmfyt6h.1.

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Figure 1. Study area and sampling stations. (a) Annual eddy kinetic energy averaged over the year 1993-2020. Black line in panel a represents the study cyclonic eddy trajectory. NEC, north equatorial current; STCC, subtropical countercurrent. (b) Amplitude of the study eddy during its whole lifetime, the yellow and grey shadow indicates the biogeochemical Argo (BGC-Argo) and ship-based study high-resolution transect periods, respectively. (c) Underway sea surface temperature (SST) and salinity (SSS) of the study high-frequency sampling transect, core stations are marked in red. (d) Enlarged map of high-resolution transect with a background of sea level anomaly on 4 April 2019. Arrows are satellite-derived surface current velocities (background field) and mean 50–100 m ADCP-derived current velocities (cruise track). Color circles indicate the trajectory of the BGC-Argo float and the studied eddy center position.

Figure 2. Biogeochemical response along the high-resolution transect. (a) nitrate plus nitrite (N+N), (b) salinity, (c) total Chl *a* (TChl*a*), key taxon-specific pigments include (d) fucoxanthin (Fuco, Diatom), (e) zeaxanthin (Zea, all cyanobacteria) and (f) dv-Chl *a* (DvChl*a*, *Prochlorococcus* spp.), Chl*a* percentage of (g) Micro-phytoplankton (Micro-Chl*a,* >20 μm), (h) Nano-phytoplankton (Nano- Chl*a,* 2-20 μm), and (i) Pico-phytoplankton (Pico-Chl*a,* <2 μm) to TChl*a*; phytoplankton primary production of (j) Micro-phytoplankton (Micro-PP), (k) Nano-phytoplankton (Nano-PP), and (l) Pico-phytoplankton (Pico-PP). The white lines represent the 1% light level Zeu. The red (in the panel a) and black lines indicate nitracline depth (0.1 μM) and isopycnic surfaces, respectively. The stations marked in red indicate the eddy core.

Figure 3. Large particles and mesozooplankton. (a) Heatmap of statistical relationships between CTD fluorescence and size-specific particle abundance (0.06 -2.0 mm equivalent spherical

diameter, ESD) measured by the UVP5 coupled with the CTD. The numbers and colors represent estimated Pearson correlations (p values always <0.01). (b) Mesozooplankton abundance (circles) and taxonomic composition (bar graph). Particle distribution of (c) 0.06–0.5 mm and (d) 0.5-2.0 mm size classes obtained by the UVP5. Nighttime periods are shaded grey. Black lines indicate the depth of the isopycnic surfaces. The station marked in red indicates the eddy core.

Figure 4. (a-b) Time series of float measured chlorophyll-a (Chl*a*), and backscattering at 700 nm (b_{bp700}); (c-d) average air-sea carbon dioxide (CO_2) flux and depth-integrated net community production (NCP) above the mixed layer (MLD) and euphotic-zone (Zeu) in three locations relative to the eddy center, including eddy core (cycles 3-13), eddy edge (cycles 14-33), and background stations (cycles 34-53). The black and white in panels a-b indicate the MLD and Zeu, respectively. The vertical bar in panels c-d represents the propagated error. BG: background stations in the absence of eddy impact. The positive value in panel c represents oceanic CO_2 uptake.