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**Nutrient limitation of
phytoplankton in
nSCS anticyclonic
eddies**

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Nutrient limitation of phytoplankton in anticyclonic eddies of the northern South China Sea

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Abstract

Baroclinic instability modulated by topography leads to the formation of two anticyclonic eddies in the northern South China Sea: the Hong Kong Southeast Anticyclonic Eddy (HKSEACE) and the Hainan Island East Anticyclonic Eddy (HIEACE). In these eddies, downwelling caused by a depressed pycnocline leads to high temperature, low salinity, impoverished nutrients, reduced Chl-*a* concentrations, and picoplankton dominance of phytoplankton assemblages in the euphotic zone. We tested the hypothesis that experimental nutrient enrichment would relieve biomass limitation of phytoplankton by opportunistic response of taxa with low nutrient affinity. Our results confirm that phytoplankton samples incubated in vitro under nutrient enriched conditions attained higher biomass, change in taxonomic dominance from dinoflagellates to diatoms, and shift in size class dominance from picoplankton to nanoplankton and netplankton. These responses were evident only when limitation to more than one nutrient was relieved. Phytoplankton in HKSEACE appeared to be co-limited by nitrogen and phosphorus, whereas at HIEACE it was co-limited by nitrogen, phosphorus and also silicon.

1 Introduction

In large areas of the tropical Pacific Ocean, the standing stock and production of phytoplankton are very low, which is the result of impoverished of essential macro-nutrients and trace metals, induced by phytoplankton consumption and poor supplement from deep layer, due to the permanent stratification of the water column (Krom et al., 1992; Van Haren et al., 2003). Changes in biomass and production of phytoplankton occur episodically when mesoscale physical phenomena increase or decrease the concentration of nutrients in the euphotic zone. Eddies are mesoscale-isolated ecosystems, which displayed physical, chemical and biological properties, pronouncedly differentiated from the surrounding waters. In the past decades increasing evidences have shown the significant role of eddy dynamics on phytoplankton biomass distribution and

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production in the oceans (e.g. Jeffrey and Hallegraeff, 1980; Angel and Fasham, 1983; Falkowski et al., 1991; McGillicuddy et al., 1998; Garcon et al., 2001; Vaillancourt et al., 2003).

Recent studies have demonstrated that monsoon-driven baroclinic eddies are one of the most common mesoscale features in the tropical and subtropical Pacific Ocean (Olaizola et al., 1993; McGillicuddy et al., 1998; Seki et al., 2001), including the South China Sea (SCS) (Chai et al., 2001a; Xu et al., 2001). Baroclinic instability leads to the formation of cyclonic eddies with a raised thermocline inducing upwelling, and anticyclonic eddies with a depressed thermocline inducing downwelling. The enhanced or decreased phytoplankton production is expected to occur in cyclonic eddies or anticyclonic eddies, respectively, resulting from higher or lower nutrient concentrations in the cyclonic or anticyclonic eddies than in the surrounding waters (Williams and Follows, 2003; Ning et al., 2004).

The most studied mesoscale processes concern upwelling in cyclonic eddies, because of its close relationship with high primary production, leading to the formation of fishing areas, due to nutrient supplement to euphotic zone from deep layer (Li and Wang, 1991; Falkowski et al., 1991; Deng et al., 1995). Since the mid 1990's, studies on downwelling and its biogeochemical effects have been a concern among marine biogeochemists, because of the importance of downwelling in anticyclonic eddies for understanding the absorption of atmospheric CO₂ by the upper ocean and the transport to the deep layer and the carbon cycles in the deep ocean (Chao et al., 1996; Williams and Follows, 2003). However, most of oceanographic studies on anticyclonic eddies in the tropical ocean, including the nSCS have been focused on physical oceanographic processes and circulation modeling (Wang et al., 2003, 2005, 2008; Cai et al., 2007; Li et al., 2007), whereas few were related to chemical oceanography in the SCS (Chen et al., 2001, 2004; Dai et al., 2008) or to biological processes related to phytoplankton biomass and primary production (Ning et al., 2004). The Hainan Island East Anticyclonic Eddy (HIEACE) and the Hong Kong Southeast Anticyclonic Eddy (HKSEACE) have been recognized and their physical features have been described (Guan, 1997;

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Yang et al., 2000; Chai et al., 2001a), but the trophodynamic responses of phytoplankton to physico-chemical coupling, i.e. the bottom-up processes of phytoplankton have not been documented, and the responses of phytoplankton growth and community structure to nutrient enrichment in these anticyclonic eddies have not been understood.

The aims of the present study at better understanding were: 1) How are the physical, chemical and biological oceanography coupling features, especially the nutrients dynamics of the two anticyclonic eddies? 2) What are the responses of phytoplankton community to nutrient enrichment in the anticyclonic eddies of the nSCS?

2 The study area

The South China Sea (SCS) is the largest semi-enclosed marginal sea in Southeast Asia with an area of about $3.5 \times 10^6 \text{ km}^2$, constituting one of the world's 50 Large Marine Ecosystems (Sherman, 2001). Our study area is the northern SCS (nSCS), bounded by the mainland of China on the north and northwest sides, Taiwan Island and Bashi Strait on the east side, Hainan Island on the west side, and south to 18° N . The nSCS is connected to the East China Sea through Taiwan Strait and to the open ocean through Luzon Strait, where a deep sill ($>2000 \text{ m}$) allows effective water exchange with the western Pacific. The topography of the area is characterized by the incline from the coast of China mainland towards the southeast, with a gradient from the coastal zone ($<50 \text{ m}$), continental shelf ($<200 \text{ m}$), the slope and open sea ($>200 \text{ m}$), to the deep sea ($>3000 \text{ m}$) (Fig. 1).

The Pearl River, the largest one in this region, from China mainland with a discharge of $3.3 \times 10^{11} \text{ m}^3 \text{ a}^{-1}$ occupying about 80% of total river runoff (Han et al., 1998), carries a large quantity of suspended solids ($8.3 \times 10^7 \text{ ty}^{-1}$, Han et al., 1998) and dissolved nutrients ($\text{N}=8.6 \times 10^4 \text{ ty}^{-1}$; $\text{P}=1.2 \times 10^4 \text{ ty}^{-1}$; $\text{Si}=184.3 \times 10^4 \text{ ty}^{-1}$, Wang and Peng, 1996) into the nSCS.

The meteorological forcing over the nSCS is dominated by the East Asian Monsoon (Sadler et al., 1985), and the upper ocean circulation follows closely the alternating

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monsoons (Wyrтки, 1961). During the summer southwest monsoon, the Guangdong coastal current flows eastward along the southern coast of China mainland, which eventually flows into the East China Sea through Taiwan Strait. The southwesterly winds induce Ekman transport toward offshore and coastal upwelling, including Guangdong coastal upwelling and Leizhou Peninsular and Hainan east upwelling (Chai et al., 2001a). The deep water upwells and mixes with the upper water to form the SCS intermediate water, which flows out of the nSCS into the northwestern Pacific Ocean through Luzon strait (Gong et al., 1992). On the contrary, during winter northeast monsoon, along the northern boundary, the warm and saline Kuroshio current water with oligotrophic properties intrudes through Luzon strait and flows westward along the continental margin of China to become the deep-water mass of the nSCS (Nitani, 1972; Shaw, 1991). The coastal water of the East China Sea flows southwestward through Taiwan strait into the nSCS, the northeasterly winds also induce Ekman transport toward inshore and coastal downwelling (Fang et al., 1998; Xue et al., 2004).

Meanwhile, it has been found that due to the combined effects of monsoons, topography, coastal line shape and the inertial force, the mesoscale eddies (i.e. the cyclonic cold eddies and anticyclonic warm pools) are formed in the SCS (Zeng et al., 1989; Xu et al., 2001; Chen et al., 2004), particularly the two permanent anticyclonic eddies: Hong Kong Southeast Anticyclonic Eddy (HKSEAE) and Hainan Island East Anticyclonic Eddy (HIEAE), caused by frontal instability and modulated by topography in the nSCS (Chai et al., 2001a, b).

3 Materials and methods

3.1 Satellite remote sensing observations

The studied sea area is located between 18°00' and 23°00'N in latitude and 110°00' and 118°00'E in longitude, covering a major area of the nSCS. Satellite remote sensed sea surface chlorophyll-*a* (Chl-*a*) data were derived from MODIS and processed using

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the ENVI 4.3 software, with resolution of 4×4 km. They were validated by synchronous in situ oceanographic observations (Hao et al., 2007). A global SSH anomaly dataset, compiled by the CLS Space Oceanographic Division of Toulouse, France, was used. The CLS SSH dataset has a 7-day temporal resolution and a 1/3°×1/3° spatial resolution. Both satellite remote sensed Chl and SSH datasets were used for exploring mesoscale eddies and confirming the positions of HKSEAE and HIEAE over the nSCS in summer.

3.2 In situ oceanographic survey

A summer cruise was conducted (from 26 August to 6 September 2004) on board R/V “Haijian 74”, belonging to South China Sea Branch, State Oceanic Administration, China. Two major transects (S1 and S2) were designed approximately perpendicular to the coastline, including 8 stations for Transect S1 and 6 stations for Transect S2, and 2 stations were added between each end of the 2 transects (Fig. 1).

Seawater samples were taken with a Rosette of Niskin bottles attached to a CTD (Conductivity-Temperature-Depth system, Niel Brown Mark III) probe frame. Water samples for nutrients and chlorophyll-*a* (Chl-*a*) determination were taken at surface, 10, 25, 50, 75, 100 and 150 m. Sea surface (at the depth of 2 m) water samples for nutrient enrichment experiments were taken using a Houskin water sampler with ball cap and 30 L volume at Stations S1008 and S2007, located at the Hong Kong Southeast Anticyclonic Eddy (HKSEAE) and at the Hainan Island East Anticyclonic Eddy (HIEAE), respectively.

Nutrients (NH_4^- , NO_2^- , NO_3^- , PO_4^{3-} and SiO_3^{2-}) were analyzed by standard spectrophotometric methods (Strickland and Parsons, 1972), with the detection limits being 0.04, 0.01, 0.05, 0.03 and 0.1 μmoL^{-3} , respectively. Photosynthetic pigments (Chl-*a*) were measured by the acetone extraction fluorescence method (Holm-Hansen et al., 1965) using a Turner Designs Fluorometer, Model 10, and calibrated by spectrophotometry using standard pure Chl-*a* reagent (Sigma Co.).

Before dispensing, all water samples were pre-filtered through a 200 μm mesh to

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remove large zooplankton. Water samples for the determinations of size-fractionated Chl-*a* were filtered through a 20 μm mesh (for retention of netplankton), a Nuclepore filter of 2.0 μm in pore size (for retention of nano- and net-plankton) and a Whatman GF/F filter (for retention of pico- (0.2–2.0 μm), nano- (2.0–20 μm) and net-plankton (20–200 μm)) (Ning, et al., 1996). After analyzing the content of each filter, the three fractions could be calculated. Identification of phytoplankton species and cell counts were made from 500 ml of seawater samples fixed with neutral formalin (Sournia, 1978), using an inverted microscope.

3.3 Nutrient enrichment experiments

The experiments were conducted on deck of the R/V with natural light. At each station S1008 and S2007, 12 bottles were filled with 4 L seawater for each, and divided into 6 groups: a – control, and tests b – addition of NO_3^- (0.2 mol L^{-1}), c – addition of PO_4^{3-} (0.01 mol L^{-1}), d – addition of SiO_3^{2-} (0.2 mol L^{-1}), e – combining addition of NO_3^- and PO_4^{3-} at the same molarity as b and c, respectively, f – addition of $\text{NO}_3^- + \text{PO}_4^{3-} + \text{SiO}_3^{2-}$ at the same molarity as b, c and d, respectively, with 2 mL solution of each nutrient added in each bottle. Duplicate incubation bottles were set for each group. After shaking each bottle, all bottles were placed in an incubator equipped with a seawater circulation system maintaining samples at temperature same as in situ.

Subsamples were taken for measuring size-fractionated Chl-*a*, phytoplankton species identification and cell counts for each test and control bottles at time 0 h, 12 h, 24 h, 48 h, 72 h, 96 h and 108 h for the samples taken at Station S2007, and 0 h, 12 h, 24 h, 48 h and 60 h at Station S1008.

Growth rate (g , d^{-1}) of phytoplankton communities during the nutrient enrichment experiments was calculated by using equation (1) (Landry, 1993):

$$g = \ln(C_t/C_0)/t \quad (1)$$

Where biomasses C_0 and C_t were measured before start (0) of incubations and at

time (t), respectively, given in term of Chl- a unit ($\mu\text{g L}^{-1}$).

4 Results and discussion

4.1 Physical-chemical-biological properties of the two anticyclonic eddies, HKSEACE and HIEACE

5 Only a brief description of major oceanographic features in the nSCS, especially distributions of physical, chemical and biological parameters relevant to the HKSEACE and HIEACE is provided. Details about the physical features can be found else where (Chai et al., 2001a, b; Xu et al., 2004). Furthermore, the observed results at the depth of 50 m are presented, since this layer represents a mixture of the SCS surface and
10 subsurface waters (Liu et al., 2001), which is relatively stable and better reflects the mesoscale eddies forcing on phytoplankton dynamics.

The results obtained by satellite and in situ observations show that there were two pronounced patch areas with high temperature ($>25.5^{\circ}\text{C}$ and $>26^{\circ}\text{C}$, respectively) in the east of Hainan Island (HIEACE: around $18.5\text{--}20^{\circ}\text{N}$, $112\text{--}113.5^{\circ}\text{E}$) and in the south-east of Hong Kong (HKSEACE: around $19.5\text{--}21^{\circ}\text{N}$ and $115\text{--}117^{\circ}\text{E}$). In the north-
15 ern coastal area, the water temperature was low ($<23^{\circ}\text{C}$) (Fig. 2a) and salinity was high (>34.45) (Fig. 2b), reflecting the coastal upwelling, related to Ekman Transport induced by summer southwest monsoon (Xue et al., 2001a). The two anticyclonic eddies, i.e. HIEACE and HKSEACE, were clearly confirmed by satellite remote sensed sea surface altimetry (CLS SSH dataset) with average sea surface dynamic height (SSDH) larger than 10 cm (Fig. 3), and satellite remote sensed sea surface chlorophyll
20 ($<0.1 \mu\text{g L}^{-1}$, MODIS, Fig. 4). The two anticyclonic eddies were also characterized by lower salinity (<34.25 , Fig. 2b), nutrient concentration (e.g. $\text{TIN}<2.5 \text{ mol L}^{-1}$, Fig. 2c), and phytoplankton standing stock (Chl- $a<0.2 \text{ g L}^{-1}$, Fig. 2d) than those of the surrounding waters, as showed by their horizontal distribution at the 50 m layer (Fig. 2). In the
25 two anticyclonic eddies, phytoplankton communities were dominated by non-diatoms,

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e.g. dinoflagellates, Cyanophytes and Chrysophytes (Fig. 5), as well as relatively high abundance of picophytoplankton – *Synechococcus* sp. ($>8 \times 10^3$ cell mL⁻¹ in HIEACE, and $>12 \times 10^3$ cell mL⁻¹ in HKSEACE, Fig. 6). For the latter, its importance has been revealed on the trophic link with bacteria (Ning et al., 2005). Similar horizontal distribution patterns as T, S, DIN and Chl-*a* were also observed for PO₄, SiO₃ and DO (dissolved oxygen), i.e. with low concentrations of PO₄ and SiO₃, and high concentrations of DO in the two anticyclonic eddies (PO₄ < 0.15 μmol L⁻¹, SiO₃ < 4 μmol L⁻¹ and DO > 380 – 400 μmol L⁻¹). The transect profiles of these parameters unfolded pronounced downwelling in the two anticyclonic eddies with low nutrient concentration, as an example with DIN, which was < 3 μmol L⁻¹ for HKSEACE and < 2 μmol L⁻¹ for HIEACE. A strong upwelling along the coast was also seen from the profile (Fig. 7). Properties of the two anticyclonic eddies, i.e. high temperature, low salinity, low nutrient, high DO concentrations, and low phytoplankton standing stock were coinciding with the warm pools, formed by local convergence and downwelling (Su et al., 1999). The two anticyclonic eddies were formed by topography and front shearing force between the eastward Coastal Current and westward Northern Shelf Slope Current (NSSC) which was strengthened by a westward current branch separated from a current ring near Luzon strait (Chai et al., 2001b).

4.2 Responses of phytoplankton community to nutrient enrichment in the two anticyclonic eddies

4.2.1 Initial concentrations of nutrients

In the two anticyclonic eddies, HKSEACE and HIEACE, represented by Stations S1008 and S2007, respectively, the initial Chl-*a* concentrations were very close (0.28 and 0.26 μg·L⁻¹), but the nutrient concentrations were very different. At Station S2007, DIN was less than 2 μmol·L⁻¹, PO₄³⁻ undetectable, and SiO₃²⁻ was only 1.1 μmol·L⁻¹, which were lower than the low limit concentrations of N (5.71 μmol L⁻¹, Chu, 1949),

P ($0.48 \mu\text{mol L}^{-1}$, Zhao et al., 2000) and Si ($4.40 \mu\text{mol L}^{-1}$, Harvey, 1957), being suitable for diatom growth. At Station S1008, DIN was 2.84, PO_4^{3-} 0.01, and SiO_3^{2-} $6.81 \mu\text{mol L}^{-1}$; but except for Si, concentrations of N and P were lower than the low limits of suitable concentration for diatom growth. On the whole, except for Si concentration in HKSEACE, all the other key nutrients were limiting factors for diatom growth in the two anticyclonic eddies. Concentrations of both these nutrients and Chl-*a* were lower than in the surrounding waters of the two anticyclonic eddies (Fig. 2).

4.2.2 Responses of Chl-*a* concentration to nutrient enrichments

For the experimental series at Station S2007, Chl-*a* increased after a potential period of 72 h only in the N+P+Si enriched nutrients test group, and it reached up to $3.84 \mu\text{g}\cdot\text{L}^{-1}$ in 96 h, and $14.40 \mu\text{g}\cdot\text{L}^{-1}$ in 108 h, which was about 50 times higher than the initial concentration, while the growth rate was 2.67d^{-1} . Chl-*a* concentrations in control and other nutrient test groups did not change much (Fig. 8a). At Station S1008, only in the two N+P and N+P+Si enriched nutrients test groups, Chl-*a* increased after 48 h potential period, reaching up to $1.07 \mu\text{g}\cdot\text{L}^{-1}$ and $1.19 \mu\text{g}\cdot\text{L}^{-1}$ in 60 h, respectively, which was about 3 times higher than the initial concentration. The growth rates were 2.68d^{-1} and 2.9d^{-1} , respectively, similar to results (3.0d^{-1}) obtained by Yin et al. (2000) in the water nearby Hong Kong, whereas Chl-*a* concentrations in control and other experimental groups did not change pronouncedly (Fig. 8b). Although the incubation period for Station S1007 was short, the growth trend of phytoplankton for each group was clear. From these experimental results we concluded that phytoplankton was limited by N, P and Si at the HIEACE and by N and P at the HKSEACE.

4.2.3 Responses of size structure of Chl-*a* to nutrient enrichments

Size fractionated measurements of Chl-*a* led to significant results. In the initial water samples phytoplankton size structure was dominated by picoplankton ($0.2\text{--}2.0 \mu\text{m}$), which occupied 84.6% of the total biomass at Station S2007 and 86.5% at Station

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S1008. Nanoplankton (2–20 μm) only occupied 11.9% and 11.0%, and netplankton (20–200 μm) 3.5% and 2.5%, respectively, at Stations S2007 and S1008 (Fig. 8). Within the Station S2007 experimental series, phytoplankton biomass developed only in the N+P+Si combining nutrients enriched group, in which proportions of nanoplankton and netplankton increased up to 55.3% and 35.4%, respectively, whereas picoplankton decreased to 9.3% at the end of the experiment (Fig. 9a). Within the Station S1008 experimental series, phytoplankton biomass developed well in both N+P and N+P+Si enriched groups, in which the proportion of nanoplankton increased up to 46.6% and that of picoplankton decreased down to 51.5%, respectively, in N+P enriched group; they were 56.6% and 37.7%, respectively, in N+P+Si enriched group; whereas that of netplankton remained at a low level (1.9%) in N+P group, and increased one time (5.7%,) in the N+P+Si group at the end of the experiments (Fig. 9b). From these results we concluded that nutrient enrichments led phytoplankton size to shift from picoplankton to nanoplankton and netplankton in the two anticyclonic eddies, due to high nutrient half saturation constant, i.e. Michaelis-Menten constant of the nutrient responses for the large-size phytoplankton (Parsons and Takahashi, 1973). However, there was a major difference in the proportion of netplankton in the N+P+Si group between the two stations, i.e. the proportion of netplankton was about 6 times higher at S2007 than at S1008. It probably resulted from the shorter experimental period at S1008, so that netplankton had not developed adequately.

4.2.4 Shifts of dominant group, species and abundance in phytoplankton communities after nutrient enrichment

Initial phytoplankton communities in both Stations S2007 and S1008 were mainly dominated by dinoflagellates, which occupied 62.5% and 60% of total phytoplankton abundance. Phytoplankton dominant species were *Prorocentrum dentatum*, *Nitzschia* sp., etc. at Station S2007 and *Gyrodinium spirale*, *Nitzschia* sp., *Prorocentrum dentatum*, etc., at Station S1008, respectively (Tables 1 and 2). At the end of experiments, diatoms became the most dominant phytoplankton in the N+P+Si groups of both Sta-

tions S2007 and S1008 test series, reaching up to 90.3% and 94% of the total phytoplankton abundance, respectively (Table 1). The major species were *Cylindrotheca closterium*, *Leptocylindrus minimus*, *Chaetoceros curvisetus*, *Pseudonitzschia delicatissima*, etc. for the N+P+Si group of the Station S2007 series, and *Cylindrotheca closterium*, *Pseudonitzschia delicatissima*, etc. for that of the Station S1008 series (Table 2). In the N+P group samples of the Station S1008 series, the dominant species were *Pseudonitzschia delicatissima*, *Scrippsiella trochoidea*, *Gyrodinium spirale*, *Cylindrotheca closterium*, *Nitzschia* sp. etc. (Table 2). However, for N+P group of the Station S2007 series, phytoplankton could not grow. Comparing field and experimental results suggested that initial nutrient conditions in the field at both Stations S2007 and S1008 were not suitable to diatom growth, rather more favorable to dinoflagellates, which are known to be not Si limited.

Nutrient enrichment induced both shifts of dominant group and species and cell abundance of phytoplankton (Tables 1 and 2). Diatom abundance increased 45 times in the N+P+Si group of the S2007 series after 108 h incubation. It increased 7 and 45 times in the N+P and N+P+Si groups, respectively, of the S1008 series after 60 h incubation, which suggested that diatoms at Station S1008 water were still limited somewhat by Si, induced by that the original Si was much consumed by diatoms without any supplementation. Dinoflagellates abundance increased only 1.4 times in N+P+Si group of S2007 series, and increased 0.4 times in N+P and decreased about one half in N+P+Si groups, respectively, of the S1008 series, for the latter case, it was probably resulted from species competition between diatoms and dinoflagellates in phytoplankton community, i.e. addition of Si combining N and P promoted diatoms fast growth, inhibiting dinoflagellates.

Comparing the results on shift of size fractionated Chl-*a* with that of dominant group and species after the nutrient enrichment experiments, it was found that the most dominant fraction of Chl-*a* was always nanoplankton (Fig. 8), which did not fit the results obtained from identification and cell counting in the phytoplankton dominated by diatoms, which belong mostly to netplankton. After checking the size of

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the diatom species, we found that the most dominant species belonged to *Nitzschia* genus with cell shape-like needle, or other genus with very thin and fragile cells. Cell size (width×length) was 2–6 μm×40–80 μm for *Cylindrotheca closterium*, 1.5–2.5 μm×59–140 μm for *Pseudonitzschia delicatissima*, 1.5–5 μm×12–40 μm for *Lep-
5 tocyllindrus minimus*, and 7–30 μm×35–150 μm for *Chaetoceros curvisetus*. These could very easily pass through the 20 μm mesh into nanoplankton fraction, when size-fractionation was performed, although without any vacuum, resulting in the overestimation of nanoplankton and underestimation of net plankton biomasses.

5 Conclusions

10 In the present studies the existence and location of the Hong Kong Southeast Anticyclonic Eddy and Hainan Island East Anticyclonic Eddy formed by front shearing force and topography were confirmed. The physico-chemical and biological oceanographic coupling properties of the two eddies were revealed by satellite and in situ observations. The two eddies exhibited higher temperature, lower salinity, oligotrophic
15 property, and lower phytoplankton stock than the surrounding waters. Picoplankton and non-diatom species were dominant in these phytoplankton communities, resulting from multi-key nutrients limitation, probably induced by convergence of the sea surface water and downwelling driven by pycnocline depression. Simulated in situ nutrient enrichment experiments resulted in succession of dominant species of phytoplankton
20 communities from non-diatoms to diatoms, and shifts of the dominant size fraction from picoplankton to netplankton and nanoplankton, due to high Michaelis-Menten constant of the nutrient responses for the large sized phytoplankton. For better understanding of the temporal and spatial variations of phytoplankton trophodynamics in these anticyclonic eddies, longer periods for experiments and seasonal observations are needed
25 in the future.

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Table 1. Shifts of dominant group in phytoplankton communities after nutrient enrichment for the water samples collected at Stations S1008 and S2007, representing HKSEACE and HIEACE, respectively.

	S2007				S1008					
	Original		+NPSi		Original		+NP		+NPSi	
	cells-L ⁻¹	(%)	cells-L ⁻¹	(%)	cells-L ⁻¹	(%)	cells-L ⁻¹	(%)	cells-L ⁻¹	(%)
Diatoms	128	37.5	5915	90.3	255	40	2042	73.9	11660	98.6
Dinoflag.	213	62.5	511	7.8	383	60	553	20	170	1.4
Others	–	–	128	1.9	–	–	170	6.1	–	–
Total	341		6554		638		2765		11830	

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Table 2. Shifts of dominant species and abundance (cells·L⁻¹) in phytoplankton communities after nutrient enrichment for the water samples collected at Stations S1008 and S2007.

S2007				S1008					
Original		+NPSi		Original		+NP		+NPSi	
<i>Prorocentrum dentatum</i>	170	<i>Cylindrotheca closterium</i>	2043	<i>Gyrodinium spirale</i>	213	<i>Pseudonitzschia delicatissima</i>	1617	<i>Cylindrotheca closterium</i>	10851
<i>Nitzschia</i> sp.	85	<i>Leptocylindrus minimus</i>	1702	<i>Nitzschia</i> sp.	128	<i>Scrippsiella trochoidea</i>	212	<i>Pseudonitzschia delicatissima</i>	723
		<i>Chaetoceros curvisetus</i>	1702	<i>Prorocentrum dentatum</i>	85	<i>Gyrodinium spirale</i>	170		
		<i>Pseudonitzschia delicatissima</i>	255			<i>Cylindrotheca closterium</i>	85		
						<i>Nitzschia</i> sp.	85		

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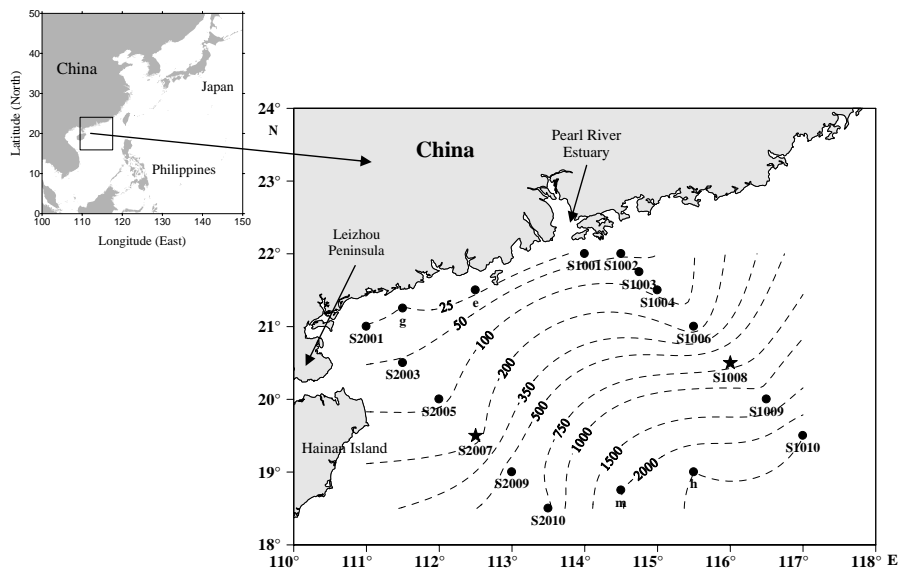


Fig. 1. Locations of transects and sampling stations and topography of the northern South China Sea. “*” shows the sampling stations for nutrients enrichment experiments. Station S1008 is located in the Hong Kong Southeast Anticyclonic Eddy (HKSEACE), and Station S2007 is located in the Hainan Island East Anticyclonic Eddy (HIEACE).

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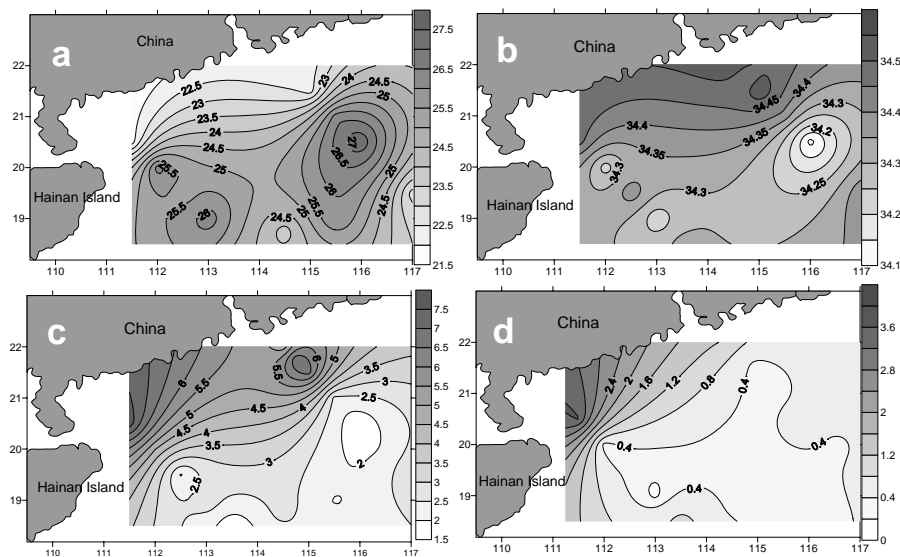


Fig. 2. Horizontal distributions of environmental features at 50m depth of the nSCS in summer 2004. **(a)** Water temperature ($^{\circ}$), **(b)** Salinity, **(c)** TIN ($\mu\text{mol L}^{-1}$), and **(d)** Chl-*a* ($\mu\text{g L}^{-1}$), showing the oceanographic features of the 2 anticyclonic eddies, HKSEACE and HIEACE.

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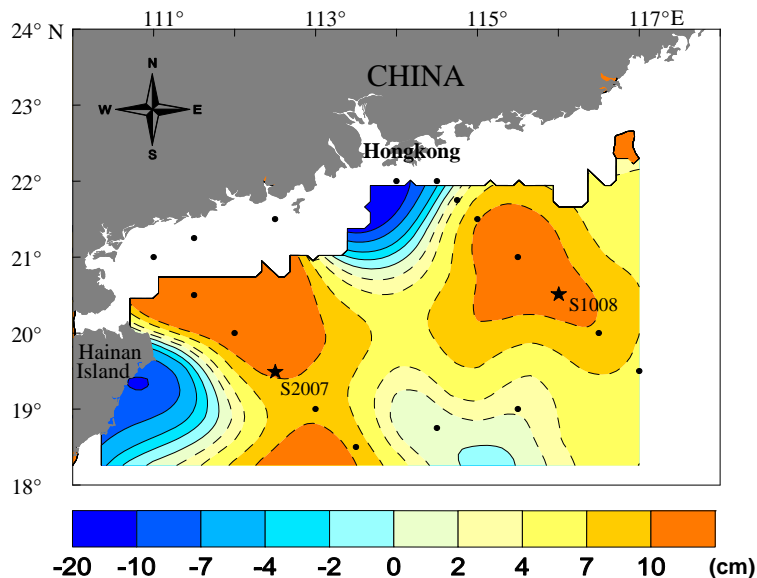


Fig. 3. Satellite image of average sea surface dynamic height (SSDH) derived from CLS dataset with a 7-day temporal resolution and a $1/3^\circ \times 1/3^\circ$ spatial resolution, compiled by the CLS Space Oceanographic Division of Toulouse, France, was used for exploring HIEACE and HKSEACE of the nSCS during 25–31 August 2004.

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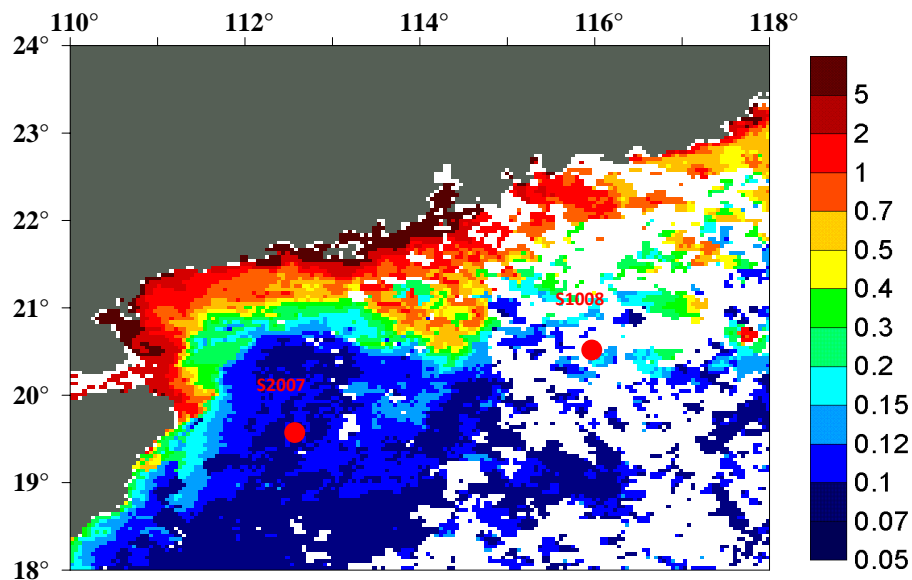


Fig. 4. Satellite image of average sea surface chlorophyll ($\mu\text{g L}^{-1}$) derived from MODIS during 24 d (from 14 August to 7 September 2004) in the nSCS, with a spatial resolution of 4×4 km. White areas were cloud coverage.

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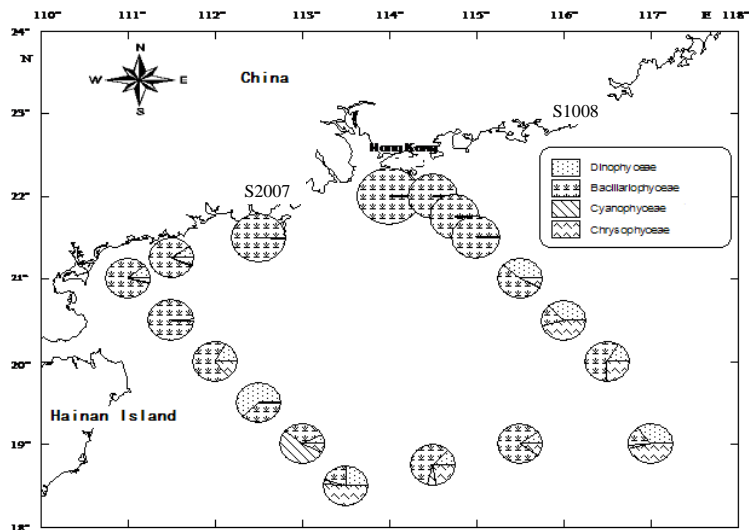


Fig. 5. The species group composition of phytoplankton communities at the various sampling stations of the nSCS during summer 2004, showing the shifts of the dominant group from diatoms nearshore to non-diatoms offshore, and the proportions of dinoflagellates in the two anti-cyclonic eddies, at Stations S1008 and S2007.

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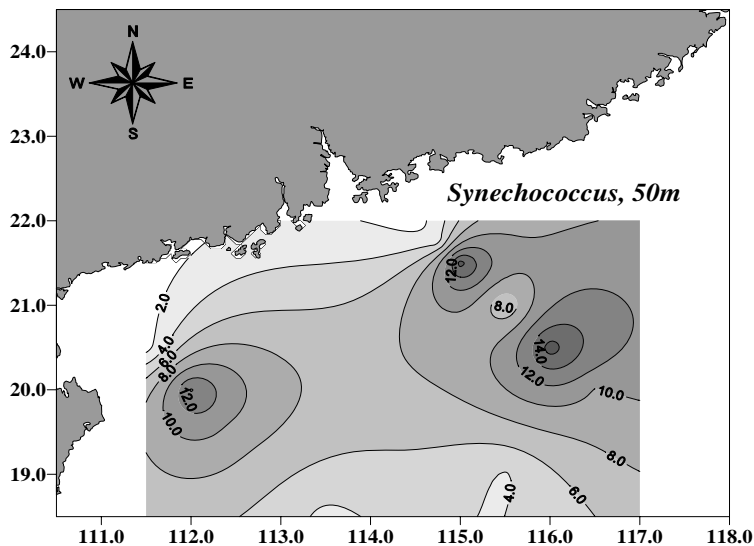


Fig. 6. Horizontal distribution of *Synechococcus* abundance ($\times 10^3$ cell mL⁻¹) at 50 m depth of the nSCS during summer 2004, showing that the highest value was encountered in the two anticyclonic eddies.

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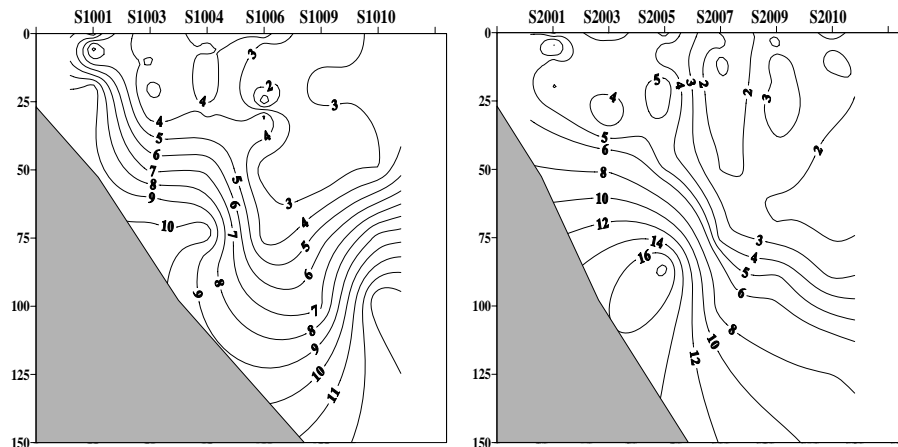


Fig. 7. Vertical distribution of total inorganic nitrogen (TIN) along the Transects S1 and S2 during summer 2004 in the nSCS, showing the high concentration ($>5 \mu\text{mol L}^{-1}$) in the coastal upwelling and low concentration ($<3 \mu\text{mol L}^{-1}$) occurring in the two anticyclonic eddies.

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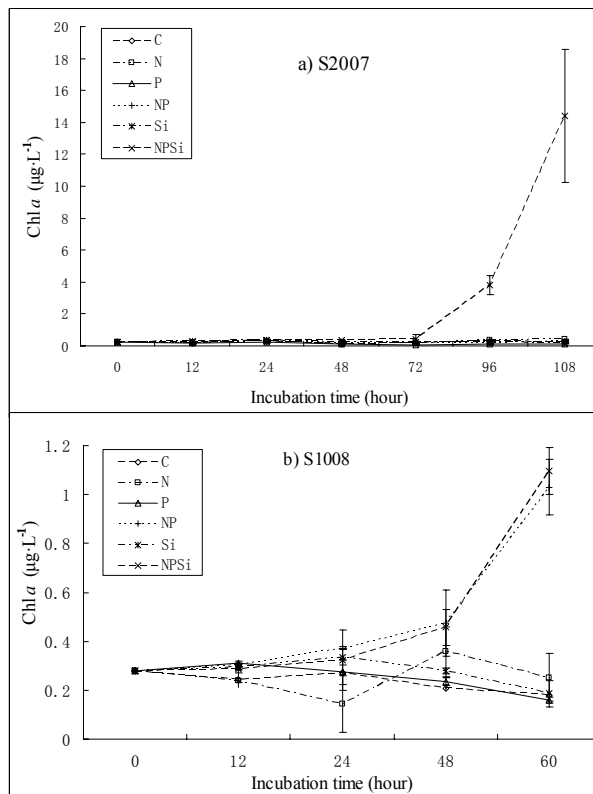


Fig. 8. Responses of Chl-*a* to nutrient enrichments. **(a)** at Station S2007, only increase in Chl-*a* appeared in N+P+Si combining addition group; **(b)** at Station S1008, only increase in Chl-*a* appeared in N+P and N+P+Si combining addition groups. Significant changes were not detected for other groups.

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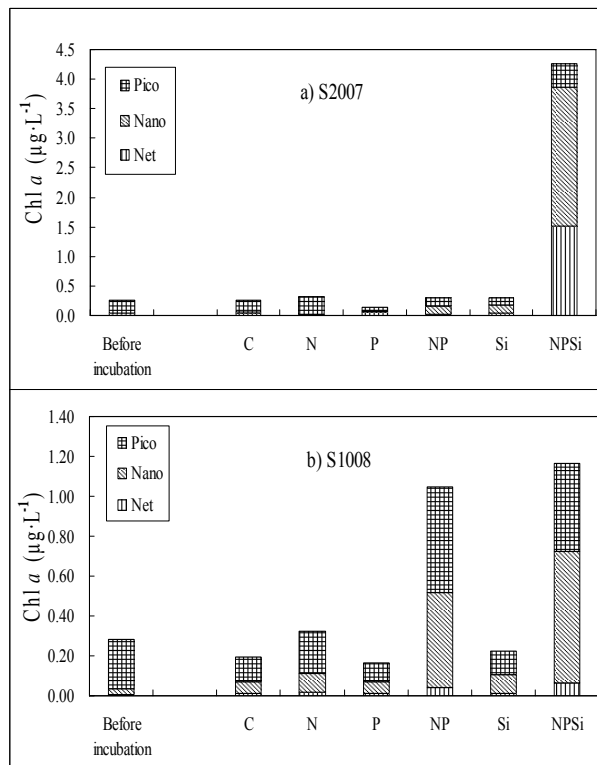


Fig. 9. Shifts of dominant size class of phytoplankton biomass following the nutrient enrichment. **(a)** At Station S2007 the shift was from picoplankton to nanoplankton and netplankton fractions, with the proportion rank being nano>net>pico in the N+P+Si combining addition group, and **(b)** At Station S1008 the shift was from picoplankton to nanoplankton fraction, with the proportion rank being nano>pico>net in N+P and N+P+Si combining addition groups.

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