Contrasting responses of phytoplankton productivity between coastal and offshore surface waters in the Taiwan Strait and the South China Sea to ~~future CO_2-induced~~short-term seawater acidification

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Abstract

~~Future CO_2-induced ocean acidification (OA)~~Seawater acidification (SA) has been documented to either inhibit or enhance or result in no effect on marine primary productivity (PP). In order to examine effects of ~~OA~~ SA in changing environments~~under multiple drivers~~, we investigated the influences of SA~~OA~~ (a decrease of 0.4 pH_{total} units with corresponding CO_2 concentrations ranged 22.0–39.7 μM) on PP through deck-incubation experiments at 101 stations in the Taiwan Strait and the South China Sea (SCS), including ~~the coastal zone,~~ the continental shelf and slope, as well as deep-water basin. The daily ~~net~~ primary productivities in surface seawater under incident solar radiation ranged from 17–306 μg C (μg Chl *a*)$^{-1}$ d^{-1}, with the responses of PP to ~~OA~~ SA being region-dependent and the ~~OA~~SA-induced changes varying from -88~~.03~~% (inhibition) to 5~~6.87~~7% (enhancement). The ~~OA~~SA-treatment stimulated PP in surface waters of coastal, estuarine and shelf waters, but suppressed it in the South China Sea basin. Such ~~OA~~SA-induced changes in PP were significantly related to ~~NO_X (the sum of NO_3^- and NO_2^-) availability,~~ in situ pH and solar radiation in surface seawater, but negatively related to salinity changes. Our results indicate that phytoplankton cells are more vulnerable to pH drop in oligotrophic waters. Contrasting responses of phytoplankton productivity in different areas suggest that SA impacts on marine primary productivity are region-dependent and regulated by local environments.~~Considering high nutrient and low salinity in coastal waters and reduced nutrient availability in pelagic~~

zones with the progressive stratification associated with ocean warming, our results imply that future OA will enhance PP in coastal waters but decrease it in pelagic oligotrophic zones.

Keywords: CO_2; Taiwan Strait; ocean seawater acidification; photosynthesis; primary productivity; South China Sea

1 Introduction

The oceans have absorbed about one-third of anthropogenically released CO_2, which increased dissolved CO_2 and decreased pH of seawater (Gattuso et al., 2015), leading to ocean acidification (OA). This process is ongoing and likely intensifying (IPCC, 2019). OA has been shown to result in profound influences on marine ecosystems (see the reviews and literature therein, Mostofa et al., 2016; Doney et al., 2020). Marine photosynthetic organisms, which contribute about half of the global primary production, are also being affected by OA (see the reviews and literatures therein, Riebesell et al., 2018; Gao et al., 2019a). In addition to the slow change of ocean acidification, some processes, such as freshwater inputs, upwelling, typhoon and eddies, can lead to instantaneous CO_2 rising and seawater acidification (Moreau et al., 2017; Yu et al., 2020) . It is of general concern that the oceans are going to take more or less CO_2 with progressive OA, since the amount of CO_2 uptake by the oceans is essential to predict global and ocean warming trends. Therefore, Since seawater acidification occurs in many locations of ocean, it is important to understand the responses of the key players of marine biological CO_2 pump, the phytoplankton, to OAseawater acidification and other climate change drivers.

Elevated CO_2 is well recognized to lessen the dependence of algae and cyanobacteria on energy-consuming CO_2 concentrating mechanisms (CCMs) which concentrate CO_2 around Rubisco, the key site for photosynthetic carbon fixation (Raven & Beardall, 2014 and references therein; Hennon et al., 2015). The energy freed up from the down-regulated CCMs under increased CO_2 concentrations can be applied to other metabolic processes, resulting in a modest increase in algal growth (Wu et al., 2010; Hopkinson et al., 2011; Xu et al., 2017). Accordingly, elevated CO_2 availability could potentially enhance marine primary productivity (Schippers et al., 2004). For instance, across 18 stations in the central Atlantic Ocean primary productivity was stimulated by 15–19% under elevated dissolved CO_2 concentrations up to 36 μM (Hein and Sand-Jensen 1997). On the other hand, neutral effects of OA seawater acidification (SA) on growth rates of phytoplankton communities were reported in five of six CO_2 manipulation experiments in the coastal Pacific (Tortell et al., 2000). Furthermore, simulated future OA SA reduced surface PP in pelagic surface waters of Northern SCS and East China Sea (Gao et al., 2012). It seems that the impacts of OA SA on PP could be region-dependent. The varying effects of OA SA may be related to the regulation of other factors such as light intensity (Gao et al., 2012), temperature (Holding et al., 2015), nutrients (Tremblay et al., 2006) and community structure (Dutkiewicz et al., 2015).

Taiwan Strait of the East China Sea, located between southeast Mainland China and the Taiwan Island, is an important channel in transporting water and biogenic elements between the East China Sea (ECS) and the South China Sea (SCS). Among the Chinese coastal areas, the Taiwan Strait is distinguished by its unique location. In addition to riverine inputs, it also receives nutrients from upwelling (Hong et al., 2011). Primary productivity is much higher in coastal waters than that in pelagic basin zones due to increased supply of nutrients through river runoff and upwelling (Chen, 2003; Cloern et al., 2014). The South China Sea (SCS), located from the equator to 23.8 °N, from 99.1 to 121.1 °E and encompassing an area of about 3.5×10^6 km^2, is one of the largest marginal seas in the world. As a marginal sea of the Western Pacific Ocean, it has a deep semi-closed basin (with depths > 5000 m) and wide continental shelves, characterized by a tropical and subtropical climate (Jin et al., 2016). Approximately 80% of ocean organic carbon is buried in the Earth's continental shelves and therefore continental margins play an essential role in the ocean carbon cycle (Hedges & Keil, 1995). Investigating how ocean acidification affects primary productivity in the Taiwan Strait and the SCS could help us to understand the contribution of marginal seas to carbon sink under the future CO_2-increased scenarios. Although small-scale studies on OA SA impacts have been conducted in the ESC and the SCS (Gao et al., 2012, 2017), our understanding of how OA SA affects PP in marginal seas is still fragmentary and superficial. In this study, we conducted three cruises in the Taiwan Strait and the SCS, covering an area of 8.3×10^5

km^2, and aimed to provide in-depth insight into how ~~OA~~ SA and/or episodic pCO_2 rise affects PP in marginal seas with comparisons to other types of waters.

2 Materials and Methods

2.1 Investigation areas

To study the impacts of projected ~~OA~~ SA (dropping by ~0.4 pH) by the end of this century (RCP8.5) on marine primary productivity in different areas (Gattuso et al., 2015), we carried out deck-based experiments during the 3 cruises supported by National Natural Science Foundation of China (NSFC), which took place in the Taiwan Strait (Jul 14th–25th, 2016), the South China Sea basin (Sep 6–24th, 2016), and the West South China Sea (Sep 14th to Oct 24th, 2017), respectively. The experiments were conducted at 101 stations with coverage of 12 °N–26 °N and 110 °E–120 °E (Fig. 1). Investigation areas include ~~the coastal zone (< 50 m),~~ the continental shelf (5~~0~~0–200 m, 22 stations) and the slope (200–~~1000~~ 3400 m, 44 stations), and the vast deep-water basin (> ~~1000~~ 3400 m, 35 stations). In the continental shelf, the areas with depth < 50 m are defined as coastal zones (9 stations).

2.2 Measurements of temperature and carbonate chemistry parameters

The temperature and salinity of surface seawater at each station were monitored with an onboard CTD (Seabird, USA). pH_{NBS} was measured with an Orion 2-Star pH meter (Thermo scientific, USA) that was calibrated with standard National Bureau of Standards (NBS) buffers (pH=4.01, 7.00, and 10.01 at 25.0 °C; Thermo Fisher Scientific Inc., USA).

After the calibration, the electrode of pH meter was kept in surface seawater for half an hour and then the formal measurements were conducted. The analytical precision was ±0.001. Total alkalinity (TA~~lK~~) was determined using Gran titration on a 25-mL sample with a TA analyzer (AS-ALK1, Apollo SciTech, USA) that was regularly calibrated with certified reference materials supplied by A. G. Dickson at the Scripps Institution of Oceanography (Gao et al., 2018a). The analytical precision was ±2 μmol kg^{-1}. CO_2 concentration in seawater and the pH_{Total} (pH_T) values was calculated by using CO2SYS (Pierrot et al., 2006) with the input of pH_{NBS} and TA~~lK~~ data.

~~2.3 Nutrient measurement~~

~~Surface seawater was collected from the Conductivity Temperature Depth (CTD) rosette/Niskin bottles with a clean 125 mL HDPE (High-Density Polyethylene) sample container. The nitrate and nitrite concentrations in seawater were then measured with a Technicon AA3 Auto-Analyzer (Bran-Lube, GmbH, Germany). The quantitative limits for nitrate and nitrite were 0.1 μmol L^{-1} and 0.04 μmol L^{-1}, respectively. We used certified reference materials (CRMS) (https://www.jamstec.go.jp/scor/) as external quality checks, and the analytical precision was better than ±1% during the whole cruise. Nutrient measurement was conducted in the cruise of the South China Sea basin. Due to the limit of human resources, it was not conducted in the other two cruises.~~

2.~~4~~ 3 Solar radiation

The incident solar radiation intensity during the cruises was recorded with an

Eldonet broadband filter radiometer (Eldonet XP, Real Time Computer, Germany). This device has three channels for PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–315 nm) irradiance, respectively, which records the means of solar radiations over each minute. The instrument was fixed at the top layer of the ship to avoid shading.

2.~~5~~ 4 Determination of primary productivity

Surface seawater (0–1m) was collected a 10 L acid-cleaned (1 M HCl) plastic bucket and pre-filtered (200 μm mesh size) to remove large grazers. To prepare high CO_2 (HC) seawater, CO_2-saturated seawater was added into pre-filtered seawater until a decrease of ~0.4 units in pH (corresponding CO_2 concentrations being 22.0–39.7 μM) was approached (Gattuso et al., 2010). Seawater that was collected from the same location as PP and filtered by cellulose acetate membrane (0.22 μm) was used to make the CO_2-saturated seawater, which was made by directly flushing with pure CO_2 until pH reached around 4.50. When saturated-CO_2 seawater was added to the HC treatment, equivalent filtered seawater (without flushing with CO_2) was also added to the AC treatment as a control. The ratios of added saturated-CO_2 seawater to incubation seawater were about 1:1000. Seawater was incubated within half an hour after they were collected~~The same amount of filtered seawater (0.22 μm) was added into the pre-filtered seawater setting as ambient CO_2 (AC) control~~. Prepared AC and HC seawater was allocated into 50-mL quartz tubes in triplicate, inoculated with 5 μCi (0.185 MBq) $NaH^{14}CO_3$ (ICN Radiochemicals, USA), and then incubated for 24 h (over a day-night cycle) under 100 % incident solar irradiances in a water bath for temperature control by running through surface seawater. Due to heating by the deck, the temperatures in the water bath were 0–2 ^{o}C higher than in situ surface seawater temperatures. TA and pH of seawater before and after 24h incubation were measured to monitor the changes of carbonate systems. After the incubation, the cells were filtered onto GF/F filters (Whatman) and immediately frozen at −20 °C for later analysis. In the laboratory, the frozen filters were transferred to 20 mL scintillation vials, thawed and exposed to HCl fumes for 12 h, and dried (55 ℃, 6 h) to expel non-fixed ^{14}C, as previously reported (Gao et al., 2017). Then 3 mL scintillation cocktail (Perkin Elmer®, OptiPhase HiSafe) was added to each vial. After 2 h of reaction, the incorporated radioactivity was counted by a liquid scintillation counting (LS 6500, Beckman Coulter, USA). The carbon fixation for 24 h incubation was taken as chlorophyll (Chl) *a*-normalized daily net primary productivity (PP, μg C (μg Chl *a*)$^{-1}$) (Gao et al., 2017). The changes (%) of PP induced by ocean acidification were expressed as $(PP_{HC}–PP_{AC})/PP_{AC} \times 100$, where PP_{HC} and PP_{AC} are the net daily primary productivity under HC and AC, respectively.

2.6 5 Chl *a* measurement

Pre-filtered (200 μm mesh size) surface seawater (500–2000 mL) at each station was filtered onto GF/F filter (25 mm, Whatman) and then stored at -80 ^{o}C. After returning to laboratory, phytoplankton cells on the GF/F filter were extracted overnight in absolute methanol at 4 ^{o}C in darkness. After centrifugation (5000 *g* for 10 min), the absorption

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values of the supernatants were analyzed by a UV–VIS spectrophotometer (DU800, Beckman, Fullerton, California, USA). The concentration of chlorophyll~~s~~ *a* (Chl *a*) was calculated according to Porra (2002).

2.~~7~~ 6 Data analysis

The data of environmental parameters were expressed in raw and the data of PP were the means of triplicate incubations. Two-way analysis of variance (ANOVA) was used to analyze the effects of ~~OA~~ SA and location on PP. Least significant difference (LSD) was used to for *post hoc* analysis. Linear fitting analysis was conducted with Pearson correlation analysis to assess the relationship between PP and environmental factors. A 95% confidence level was used in all analyses.

3 Results

During the cruises, surface temperature ranged from 25.0 to 29.9 ^{o}C in the Taiwan Strait and from 27.1 to 30.2 ^{o}C in the South China Sea (Fig. 2a). Surface salinity ranged from 30.0 to 34.0 in the Taiwan Strait and from 31.0 to 34.3 in the South China Sea (Fig. 2b). The lower salinities were found in the estuaries of Minjiang and Jiulong Rivers as well as Mekong River-induced Rip current. High salinities were found in the SCS basin. Surface pH_T changed between 7.99–8.20 in the Taiwan Strait with the higher values in the estuary of Minjiang River (Fig. 2c). Compared to the Taiwan Strait, the South China Sea had lower surface pH (7.91–8.08) with the lowest value near the island in the Philippines. TA~~lK~~ ranged from 2100 to 2359 μmol ~~L~~kg^{-1} SW in the Taiwan Strait and

2126 to 2369 μmol kg~~L~~$^{-1}$ SW in the South China Sea (Fig. 2d). The lowest value occurred in the estuary of Minjiang River. CO_2 concentration in surface seawater changed from 6.4–13.3 μM kg^{-1} SW in the Taiwan Strait, and 9.3–14.3 μM kg^{-1} SW in the SCS (Fig. 1e). It showed an opposite pattern to surface pH, with the lowest value in the estuary of Minjiang River in the Taiwan Strait and highest value in near the islands in the Philippines in the South China Sea. During the PP investigation period, the daytime mean PAR intensity ranged from 126.6 to 145.2 W m^{-2} s^{-1} in the Taiwan Strait and 37.3 to 150.0 W m^{-2} s^{-1} in the SCS (Fig. 2f).

The concentration of Chl *a* ranged from 0.11 to 12.13 μg L^{-1} in the Taiwan Strait (Fig. 3). The highest concentration occurred in the estuary of the Minjiang River. The concentration of Chl *a* in the SCS ranged from 0.037 to 7.43 μg L^{-1}. The highest concentration was found in the coastal areas of Guangdong province in China. For both the Taiwan Strait and the SCS, there were high Chl *a* concentrations (> 1.0 μg L^{-1}) in coastal areas, particularly in the estuaries of the Minjing River, Jiulong River and Pearl River. On the contrary, Chl *a* concentrations in offshore areas were lower than 0.2 μg L^{-1}.

Surface primary productivity changed from 99–302 μg C (μg Chl *a*)$^{-1}$ d^{-1} in the Taiwan Strait, and from 17–306 μg C (μg Chl *a*)$^{-1}$ d^{-1} in the South China Sea (Fig. 4). High surface primary productivity (> 200 μg C (μg Chl *a*)$^{-1}$ d^{-1}) was found in the estuaries of the Minjing River, Jiulong River, and Pearl River and areas near the East of Vietnam. In ~~pelagic~~ basin zones, the surface primary productivity was usually lower than

100 μg C (μg Chl *a*)$^{-1}$ d^{-1}.

~~Through a~~A series of onboard CO_2-enrich experiments in the investigated regions were conducted during three cruises. In the high CO_2 treatments, pH_{total} had a decrease of 0.34–0.43 units, while pCO_2 and CO_2 had an increase of 676–982 μatm and 17–25 μM kg^{-1} SW, respectively (Table S1). Carbonate chemistry parameters after 24 h of incubation were stable (△pH < 0.06, △TA < 53 μmol kg^{-1} SW) , indicating the successful manipulation (Table S1). ~~we~~ It was observed that instantaneous effects of ~~the~~ elevated pCO_2 on primary productivity of surface phytoplankton community in all investigated regions ranged from -88~~.03~~% (inhibition) to 5~~6.87~~7% (promotion), revealing significant regional differences (ANOVA, $F_{(100, 404)} = 4.103$, $p < 0.001$, Fig. 5). Among 101 stations, 70 stations showed insignificant ~~OA~~ SA effects. ~~OA~~ SA increased PP at 6 stations and reduced PP at 25 stations. Positive effects of ~~OA~~ SA on surface primary productivity ~~was~~ were observed in the Taiwan Strait and the western SCS (Fig. 5, red-yellow shading areas), with the maximal enhancement of 5~~6.9~~7% in the station approaching the Mekong River plume (LSD, $p < 0.001$). Reductions in PP induced by the elevated CO_2 ~~was~~ were mainly found in the central SCS basin within the latitudes of 10 °N to14 °N and the longitudes of 114.5 °E to 118 °E (Fig. 5, blue-purple shading areas), with inhibition rates ranging from 24~~.02~~% to 88~~.03~~% (Fig. 5, LSD, $p < 0.05$). These results showed a region-related effect of ~~OA~~ SA on photosynthetic carbon fixation of surface phytoplankton assemblages. Overall, the elevated pCO_2 had neutral or positive

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effects on primary productivity in the continental shelf and slope regions ~~nearshore waters~~, while having adverse effects in the deep-water basin~~pelagic waters~~.

By analyzing the correlations between ~~OA~~SA-induced PP changes and regional environmental parameters, we found that ~~OA~~SA-induced changes in phytoplankton primary productivity was significantly positively related with *in situ* pH ($p < 0.001$, r = 0.379), ~~NOx availability (the concentrations of NO_3^- + NO_2^- at the bottom of upper mixing layers as they were unmeasurable in the surface water, p = 0.002, r = 0.727)~~ and~~,~~ PAR density (p = 0.002, r = 0.311) ~~and primary productivity (p = 0.004, r = 0.284)~~ (Fig. 6 and Table S1). On the other hand, the influence induced by ~~OA~~ SA was negatively related to salinity that ranged from 30.00 to 34.28 ($p < 0.001$, r = -0.418).

4 Discussion

In the present study, we found that the elevated pCO_2 and associated pH drop increased or did not affect PP in ~~coastal~~ the continental shelf and slope waters but reduced it in ~~pelagic~~ basin waters. Our results suggested that the enhanced effects of the ~~OA~~ SA treatment on photosynthetic carbon fixation depend on regions of different physicochemical conditions~~.~~, including pH, light intensity and salinity. ~~Higher levels of nutrients due to runoffs or upwellings should be mainly responsible for the enhancement. On the other hand, such stimulation could be related to higher UV-attenuation in these coastal waters that contain more organic matters (Hader et al., 2015), since we employed UV-transparent vessels for the incubations.~~ In addition, coastal diatoms appear to benefit more from ~~OA~~ SA than pelagic ones (Li et al., 2016). Therefore, community structure differences might also be responsible for the differences of the short-term high CO_2-induced acidification between coastal and ~~pelagic~~ basin waters.

~~OA~~ SA is deemed to have two kinds of effects at least (Xu et al., 2017; Shi et al., 2019). The first one is the enrichment of CO_2, which is usually beneficial for photosynthetic carbon fixation and growth of algae because insufficient ambient CO_2 limits algal photosynthesis (Hein & Sand-Jensen, 1997; Bach & Taucher, 2019). The other effect is the decreased pH which could be harmful because it disturbs the acid-base balance between extracellular and intracellular environments. For instance, the decreased pH projected for future ~~OA~~ SA was shown to reduce the growth of the diazotroph *Trichodesmium* (Hong et al., 2017), decrease PSII activity by reducing the removal rate of PsbD (D2) (Gao et al., 2018b) and increase mitochondrial and photo-respirations in diatoms and phytoplankton assemblages (Yang and Gao 2012, Jin et al., 2015). In addition, ~~OA~~ SA could reduce the ~~RuBisCO~~ Rubisco transcription of diatoms, which also contributed to the decreased growth (Endo et al., 2015). Therefore, the net impact of ~~OA~~ SA depends on the balance between its positive and negative effects, leading to enhanced, inhibited or neutral influences, as reported in diatoms (Gao et al., 2012, Li et al., 2021) and phytoplankton assemblages in the Arctic and subarctic shelf seas (Hoppe et al., 2018), the North Sea (Eberlein et al., 2017) and the South China Sea (Wu and Gao 2010, Gao et al., 2012). The balance of positive and negative effects of SA can be regulated by other factors, including pH, light intensity, salinity, population structure, etc. (Gao et al., 2019a, b; Xie et al., 2022).

In the present study, ~~OA~~ SA increased or did not affect PP in coastal waters but reduced it in offshore waters, which is~~. This is~~ significantly related to ~~nutrient availability~~pH, light intensity and salinity (Fig. 6~~d~~). The effect of SA changed from negative to positive with the increase of local pH. The higher pH occurred in coastal zones~~,~~ which may be caused by higher biomass of phytoplankton (Fig. 3). Higher pH caused by intensive photosynthesis of phytoplankton is companied with decreased CO_2 levels. In this case, CO_2 is more limited for photosynthesis of phytoplankton compared to lower pH. Therefore, SA could stimulate primary productivity via supplying more available CO_2 (Hurd et al., 2019). On the other hand, lower pH occurred in deep-water basin. Lower pH represents higher CO_2 availability. CO_2 is not limited or less limited in this case. Therefore, more CO_2 brought by SA may not benefit photosynthesis of phytoplankton. Instead, decreased pH accompanied by SA may inhibit photosynthesis or growth of phytoplankton, which is found in cyanobacteria (Hong et al., 2017). Furthermore, the negative effects of SA are particularly significant when nutrient is limited (Li et al., 2018). The nutrient levels in basin are usually lower than shelf (Yuan et al., 2011; Lu et al., 2020; Du et al., 2021), which may exacerbate the negative effects of OA in the basin zone.

The negative effects of SA disappeared with the increase of light intensity in this

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study. This results in inconsistent with Gao et al (2012)' study, in which SA increased photosynthetic carbon fixation of three diatoms (*Phaeodactylum tricornutum*, *Thalassiosira pseudonana* and *Skeletonema costatum*) under lower light intensities but increased it under higher light intensities. The divergent findings may be due to different population structure that varies in different areas. Coastal zones where nutrients are relatively sufficient usually have abundant diatoms while picophytoplanktons mainly *Prochlorococcus* and *Synechococcus*, dominate oligotrophic areas (Xiao et al., 2018, Zhong et al., 2020). In this study, most investigated areas are oligotrophic and thus the response of local phytoplankton to the combination of light intensity and SA may be different from diatoms. It is worth noting that the samples were not mixed down in the water bath in the present study and the 100% incident solar irradiances may have high light stress on cells. Lower incident solar irradiances or some devices can be used to simulate seawater mixing in future studies. Negative correlation between ~~O~~SA-induced changes of PP and salinity was found in this study. ~~While little has been documented on the relationship between salinity and OA (Wulff et al., 2018; Sugie et al., 2020; Xu et al., 2020) , lowered~~The decrease of salinity (from 35 to 30)~~ salinity~~ has been shown to alleviate the ~~impact~~negative effect of ~~O~~SA on photosynthetic carbon fixation of a coccolithorphorid *Emiliania huxleyi* (Xu et al., 2020) although the potential mechanisms remain unknown. On the other hand, the change of salinity (from 6 to 3) did not affect effective quantum yield of microplanktonic community in the Baltic Sea grown under

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different CO_2 levels (Wulff et al., 2018). In this study, Nevertheless, we presume that the enhancednegative relationship between salinity and SA effects PP couldmay be mainly be related to nutrient availabilitylocal pH because lower salinity occurred in coastal waters usually companies with high nutrient levelswhere seawater pH was higher while the basin zone had higher salinities and lower pH (Li et al., 2011).

with that the inhibitory effect was minimized when NOx availability increased. Riverine inputs, including the Minjiang River, Jiulong River, Pearl River, and Mekong River, are the primary source of nutrients in the coastal and shelf zones, resulting in higher concentrations of nutrients and lower salinity in these waters (Xiao et al., 2018). It was reported that elevated pCO_2 decreased net organic carbon production of natural plankton community in nutrient-depleted waters (Yoshimura et al., 2010). Furthermore, OA did not affect the specific growth rate of a diatom under N-replete condition but reduced it under N-limited condition (Li et al., 2018). The alleviating effect of nutrient enrichment on OA-induced stress could be multifaceted. Firstly, algae could cope with the acid-base perturbation caused by OA through active proton pumps (McNicholl et al., 2019). The operation of such proton pumps need some essential proteins, such as plasma membrane H^+-ATPase, whose synthesis is nutrient-dependent (Taylor et al., 2012; Xu et al., 2017). Secondly, it has been shown that nutrient enrichment could accelerate the repair rate of PSII via synthesizing the key proteins such as PsbA (D1), and PsbD (D2) (Geider et al., 1993; Li et al., 2015). Thirdly, nitrogen

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enrichment could significantly increase the synthesis and content of photosynthetic pigments including Chl *a*, phycocyanin, and phycoerythrin (Johnson & Carpenter, 2018; Gao et al., 2019b), contributing to high photosynthetic activity under stressful environmental conditions. Negative correlation between OA-induced changes of PP and salinity was found in this study. While little has been documented on the relationship between salinity and OA (Wulff et al., 2018; Sugie et al., 2020; Xu et al., 2020), lowered salinity has been shown to alleviate the impact of OA on a coccolithorphorid (Xu et al., 2020). Nevertheless, we presume the enhanced PP could mainly be related to nutrient availability because lower salinity in coastal waters usually companies with high nutrient levels (Li et al., 2011). In addition, local pH may be another factor that affects the impacts of OA. There are diurnal and seasonal fluctuations of pH in coastal waters and phytoplankton that adapt well to the fluctuant pH environments would be tolerant to the decreased pH caused by OA (Flynn et al., 2012, Li et al., 2016). On the other hand, the surface pH in the ocean basin is relatively stable, with a varied range of only ~0.024 over a month (Hofmann et al., 2011). Therefore, the phytoplankton cells living in these environments could be more sensitive to pH drop due to elevated pCO_2 (Li et al., 2016).

The specific environmental conditions have profound effects on shaping diverse dominant phytoplankton groups (Boyd et al., 2010). Larger eukaryotic groups (especially diatoms) usually dominate the complex coastal regions, while picophytoplanktons

(*Prochlorococcus* and *Synechococcus*), characterizing with more efficient nutrients uptake, dominate the relatively stable offshore waters (Dutkiewicz et al., 2015). In summer and early autumn, previous investigations demonstrated that diatoms dominated in the northern waters and the Taiwan Strait (coastal and shelf regions) with the high abundance of phytoplankton, which are consistent with our Chl *a* data; *Prochlorococcus* and *Synechococcus* dominated in the SCS basin and the north of SCS (slope and basin regions) (Xiao et al., 2018, Zhong et al., 2020). In addition, it has been reported that larger cells benefit more from ~~OA~~ SA because a thicker diffusion layer around the cells limits the transport of CO_2 (Feng et al., 2010; Wu et al., 2014). In contrast, a thinner diffusion layer and higher surface to volume ratio in smaller phytoplankton cells can make them easier to transport CO_2 near the cell surface and within the cells, and therefore picophytoplankton species are less CO_2-limited (Bao and Gao, 2021). Therefore, different community structures between coastal and ~~pelagic~~ basin areas could also be responsible for the enhanced and inhibitory effects of ~~OA~~SA. It is worth noting that seasonality may also lead to the differential effects of SA on primary productivity since the Taiwan Strait cruise was conducted in July and the cruises of the South China Sea basin and the West South China Sea were conducted in September. The SST and solar PAR intensity of the Taiwan Strait in July was 2–3 ^{o}C and 22 ± 22 W m^{-2} s^{-1} higher than that in September (Zhang et al., 2008, 2009; Table S3). Although the effects of SA were not related to temperature as shown in this study (Table S2), the higher solar radiation in July may contribute to the positive effect of SA on primary productivity.

5 Conclusions

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By investigating the impacts of the elevated pCO_2 on PP in the Taiwan Strait and the SCS, we demonstrated that such short ~~OA~~SA-treatments induced changes in PP were mainly related to ~~NOx availability~~pH, light intensity and salinity based on Pearson correlation coefficients, supporting the hypothesis that negative impacts of ~~OA~~ SA on PP increase from coastal to ~~pelagic~~ basin waters (Gao et al., 2019a). In view of ocean climate changes, strengthened stratification due to global warming would reduce the upward transports of nutrients and ~~further reduce nutrient availability~~thus marine primary productivity. The negative effect of SA in basin zones would further reduce primary productivity~~, consequently, leading to exacerbating impacts of OA on PP in pelagic zones~~. Meanwhile, PP in coastal ~~and/or upwelled~~ waters would be increased by SA. ~~stimulated or non-affected by OA with continuous discharges of nutrients from terrestrial environments, which may imply higher PP and enhance frequency of harmful algal blooms in future oceans~~.

Data availability. All data are included in the article or Supplement.

Author contributions. KG and TW developed the original idea and designed research. TW and JS carried out fieldwork. GG provided statistical analyses and prepared figures. GG, KG, and XZ wrote the manuscript. All contributed to revising the paper.

Competing interests. The contact author has declared that neither they nor their co-authors have any competing interests.

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Figure captions

Fig. 1 Sampling stations for the incubation experiments in the Taiwan Strait and the South China Sea during three cruises. Taiwan Strait cruise was conducted in July 2016 (red dots), South China Sea Basin cruise were conducted in September 2016 (blue dots) and Western South China Sea cruise was conducted in September 2017 (black dots). ~~The arrows represent surface circulation fields in summer in the vicinity of Vietnam coast based on Lan et al. (2006).~~

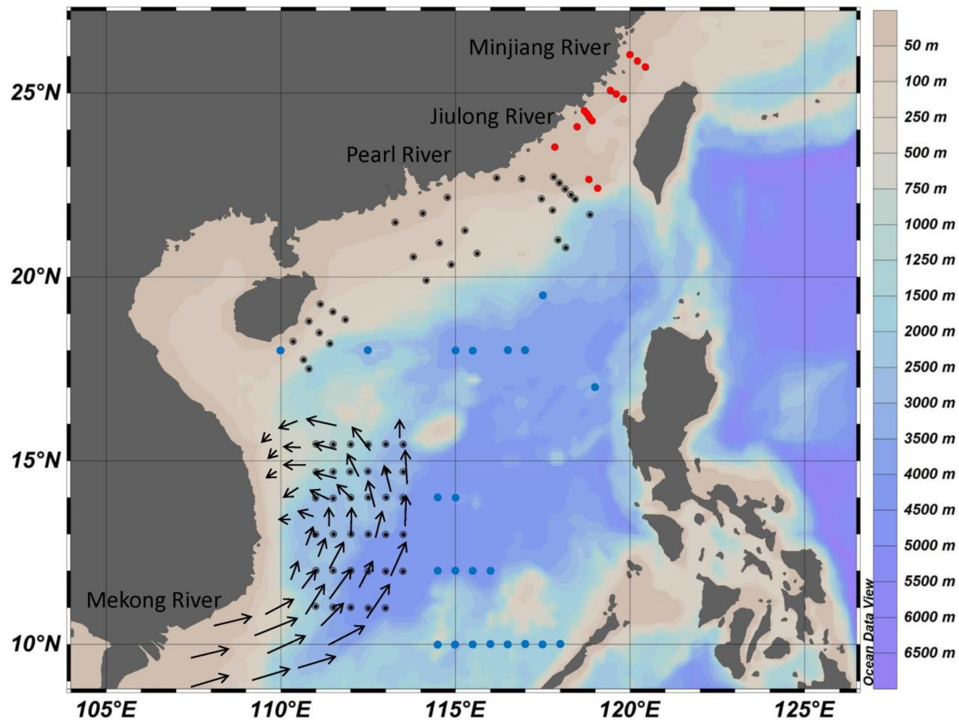
Fig. 2 Temperature (^{o}C, panel a), salinity (panel b), pH (panel c), total alkalinity (μmol L^{-1}, panel d), and CO_2 (μmol kg^{-1} SW, panel e) in surface seawater and mean PAR intensity (W m^{-2} s^{-1}, panel f) during the PP incubation experiments.

Fig. 3 Chl *a* concentration (μg L^{-1}) in the Taiwan Strait and the South China Sea during research cruises.

Fig. 4 Surface primary productivity (μg C (μg Chl $a)^{-1}$ d^{-1}) in the Taiwan Strait and the South China Sea during research cruises.

Fig. 5 Ocean acidification (pH decreases of 0.4 units) induced changes (%) of surface primary productivity in the Taiwan Strait and the South China Sea. Red-yellow shading represents a positive effect on PP and blue-purple shading represents a negative effect. ~~Positive effect was found in coastal waters and estuary affected waters, such as the Taiwan Strait, the Pearl River plume, Mekong River induced Rip current in West China Sea. Negative effect was found in surface of oligotrophic waters like SCS Basin.~~

Fig. 6 Ocean acidification (pH decreases of 0.4 units) induced changes (%) on surface primary productivity in the South China Sea as a function of ~~salinity (a), PAR (b),~~ ambient pH (~~c~~a), PAR (b), and salinity (c)~~nitrate plus nitrite concentration (d)~~. The dotted lines represent 95% confidence intervals.



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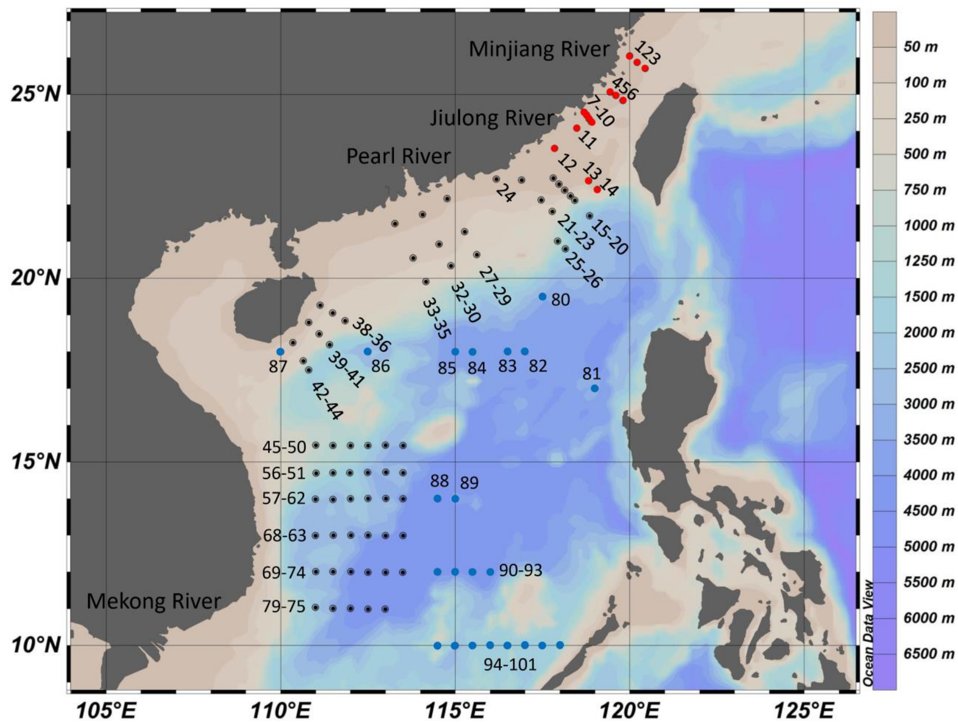

Fig. 1

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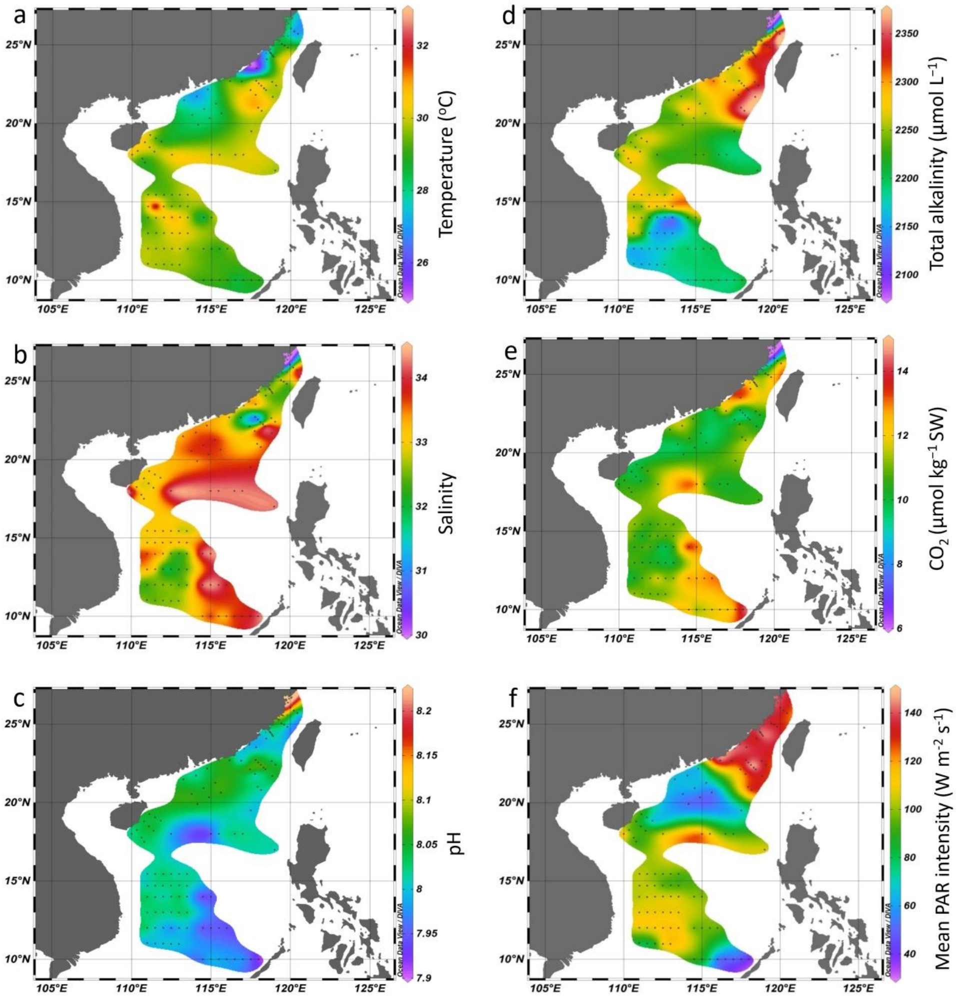


a
Temperature (°C)
b
Salinity
c
pH
d
Total alkalinity (μmol L⁻¹)
e
CO2 (μmol kg⁻¹ SW)
f
Mean PAR intensity (W m⁻² s⁻¹)

Fig. 2

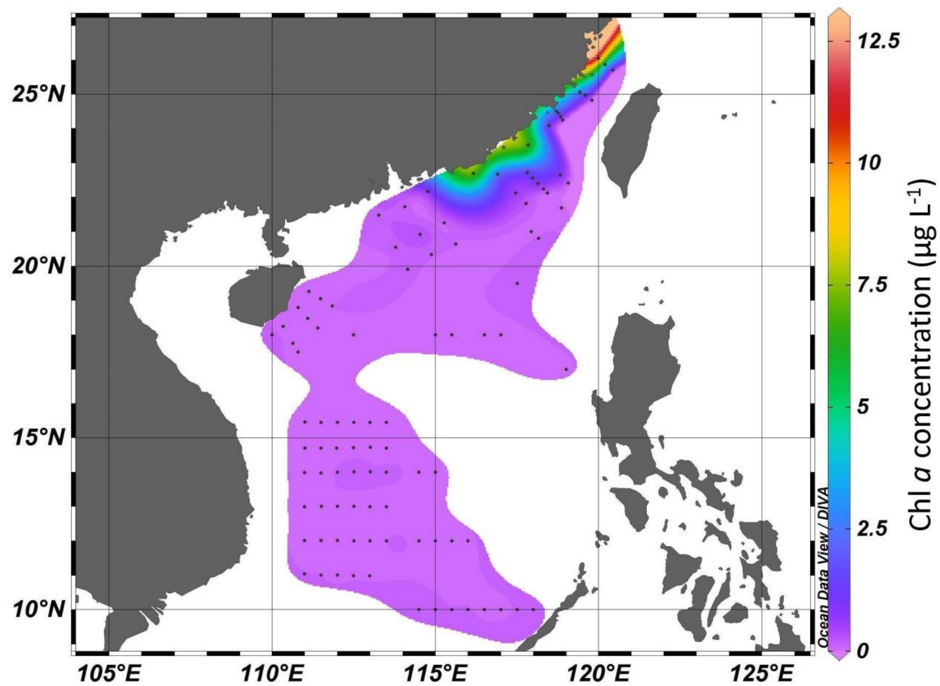
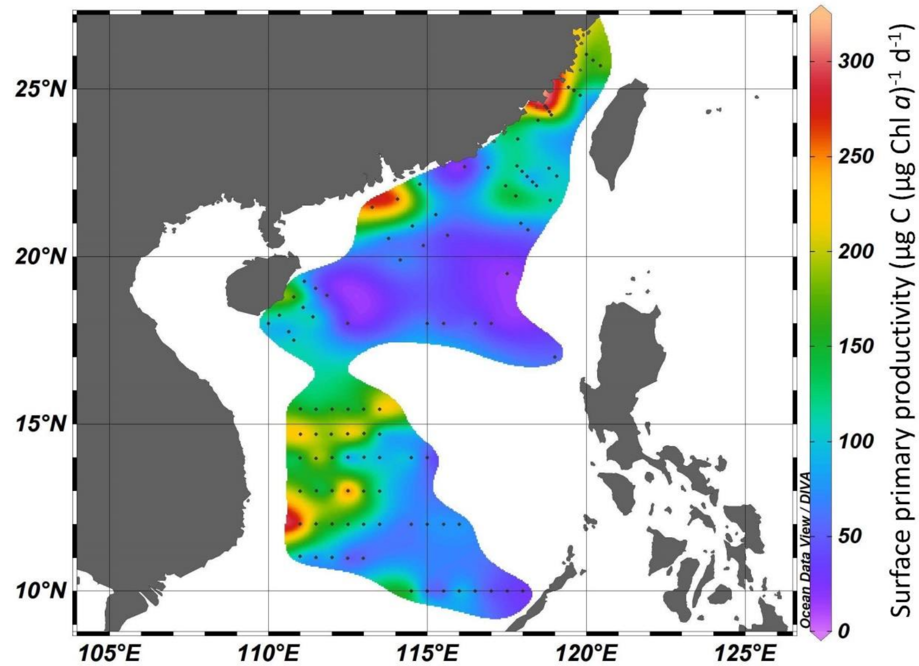

25°N
20°N
15°N
10°N
105°E
110°E
115°E
120°E
125°E
Ocean Data View / DIVA
12.5
10
7.5
5
2.5
0
Chl a concentration (μg L-1)

Fig. 3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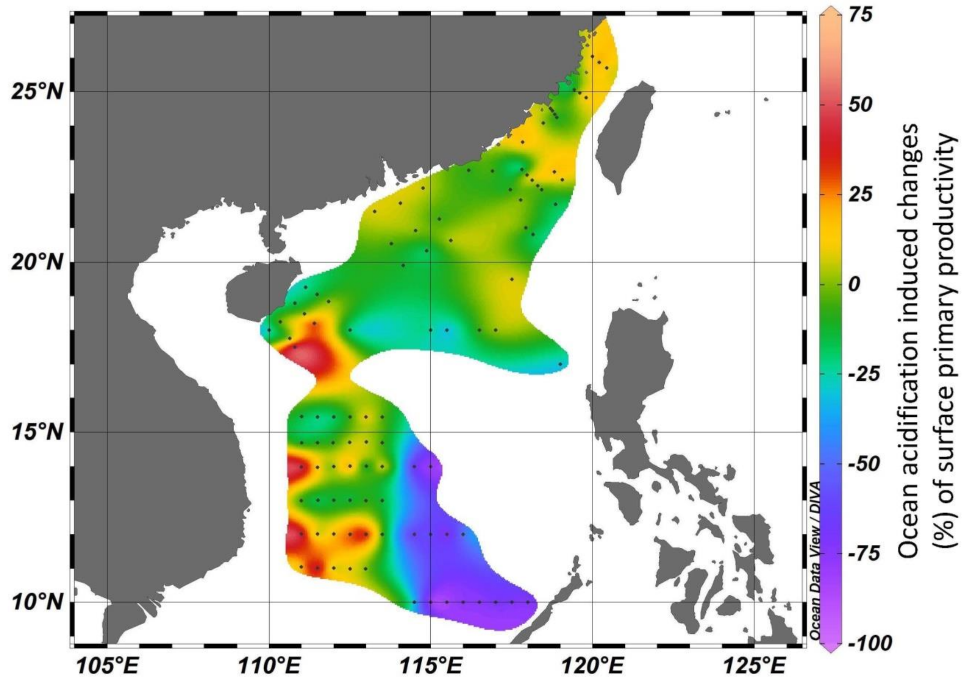
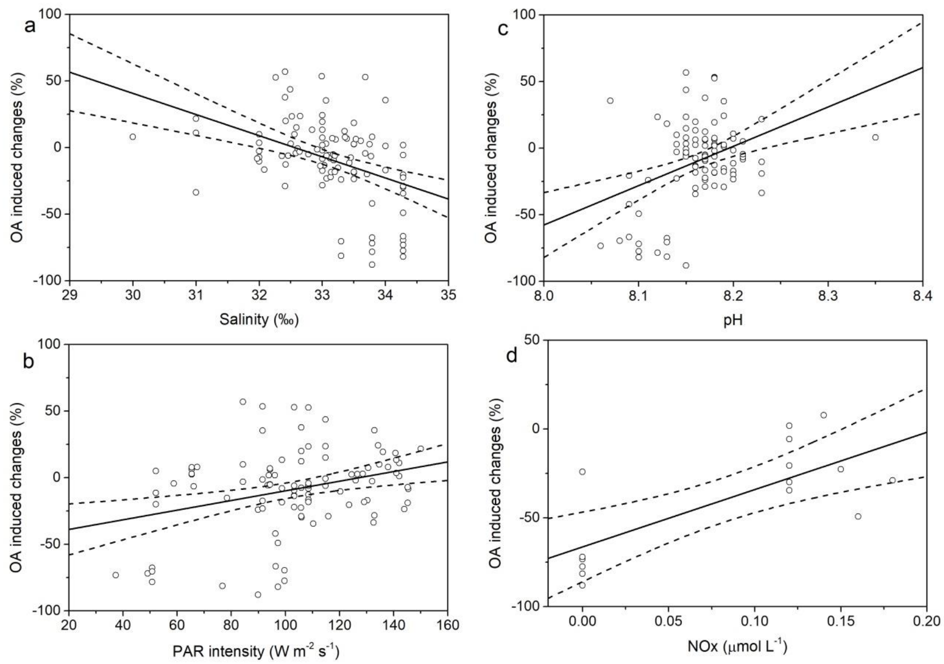
105°E
110°E
115°E
120°E
125°E
Ocean Data View / DIVA
300
250
200
150
100
50
0
Surface primary productivity (μg C (μg Chl a)-1 d-1)

Fig. 4



25°N
20°N
15°N
10°N
105°E
110°E
115°E
120°E
125°E
75
50
25
0
-25
-50
-75
-100
Ocean acidification induced changes
(%) of surface primary productivity
Ocean Data View / DIVA

Fig. 5


a
b
c
d
OA induced changes (%)
Salinity (‰)
PAR intensity (W m-2 s-1)
pH
NOx (μmol L-1)
100
50
0
-50
-100
29
30
31
32
33
34
35
20
40
60
80
100
120
140
160
8.0
8.1
8.2
8.3
8.4
0.00
0.05
0.10
0.15
0.20

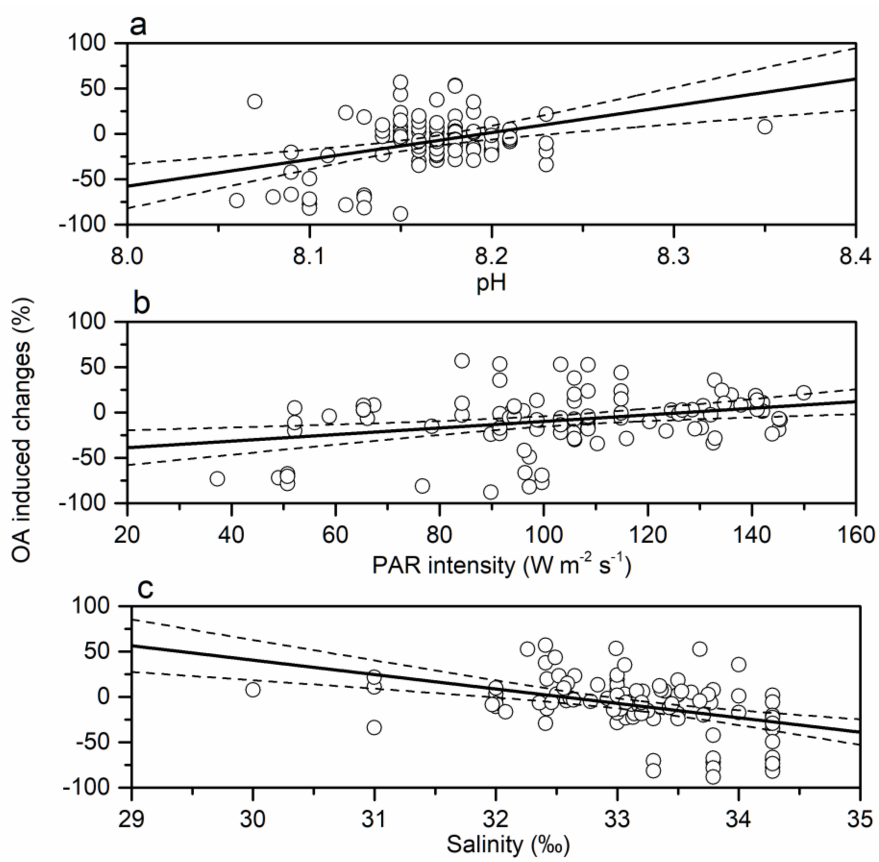


Fig. 6

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