

1 **Contrasting responses of phytoplankton productivity between coastal and offshore**
2 **surface waters in the Taiwan Strait and the South China Sea to short-term seawater**
3 **acidification**

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13

14 **Abstract**

15 Seawater acidification (SA) has been documented to either inhibit or enhance or result in
16 no effect on marine primary productivity (PP). In order to examine effects of SA in
17 changing environments, we investigated the influences of SA (a decrease of 0.4 pH_{total}
18 units with corresponding CO₂ concentrations ranged 22.0–39.7 μM) on PP through
19 deck-incubation experiments at 101 stations in the Taiwan Strait and the South China Sea,
20 including the continental shelf and slope, as well as deep-water basin. The daily primary
21 productivities in surface seawater under incident solar radiation ranged from 17–306 μg
22 C (μg Chl *a*)⁻¹ d⁻¹, with the responses of PP to SA being region-dependent and the
23 SA-induced changes varying from -88% (inhibition) to 57% (enhancement). The
24 SA-treatment stimulated PP in surface waters of coastal, estuarine and shelf waters, but
25 suppressed it in the South China Sea basin. Such SA-induced changes in PP were
26 significantly related to in situ pH and solar radiation in surface seawater, but negatively
27 related to salinity changes. Our results indicate that phytoplankton cells are more
28 vulnerable to a pH drop in oligotrophic waters. Contrasting responses of phytoplankton
29 productivity in different areas suggest that SA impacts on marine primary productivity
30 are region-dependent and regulated by local environments.

31 **Keywords:** CO₂; Taiwan Strait; seawater acidification; photosynthesis; primary
32 productivity; South China Sea

33 **1 Introduction**

34 The oceans have absorbed about one-third of anthropogenically released CO₂, which
35 increased dissolved CO₂ and decreased pH of seawater (Gattuso et al., 2015), leading to
36 ocean acidification (OA). This process is ongoing and likely intensifying (IPCC, 2019).
37 OA has been shown to result in profound influences on marine ecosystems (see the
38 reviews and literature therein, Mostofa et al., 2016; Doney et al., 2020). Marine
39 photosynthetic organisms, which contribute about half of the global primary production,
40 are also being affected by OA (see the reviews and literatures therein, Riebesell et al.,
41 2018; Gao et al., 2019a). In addition to the slow change of ocean acidification, some
42 processes, such as freshwater inputs, upwelling, typhoon and eddies, can lead to
43 instantaneous CO₂ rising and short-term changes in carbonate chemistry, termed seawater
44 acidification (SA) (Moreau et al., 2017; Yu et al., 2020). Since SA occurs in many
45 locations of ocean, it is important to understand the responses of the key players of
46 marine biological CO₂ pump, the phytoplankton, to seawater acidification.

47 Elevated CO₂ is well recognized to lessen the dependence of algae and
48 cyanobacteria on energy-consuming CO₂ concentrating mechanisms (CCMs) which
49 concentrate CO₂ around Rubisco, the key site for photosynthetic carbon fixation (Raven
50 & Beardall, 2014 and references therein; Hennon et al., 2015). The energy freed up from
51 the down-regulated CCMs under increased CO₂ concentrations can be applied to other
52 metabolic processes, resulting in a modest increase in algal growth (Wu et al., 2010;
53 Hopkinson et al., 2011; Xu et al., 2017). Accordingly, elevated CO₂ availability could

54 potentially enhance marine primary productivity (Schippers et al., 2004). For instance,
55 across 18 stations in the central Atlantic Ocean primary productivity was stimulated by
56 15–19% under elevated dissolved CO₂ concentrations up to 36 μM (Hein and
57 Sand-Jensen 1997). On the other hand, neutral effects of seawater acidification (SA) on
58 growth rates of phytoplankton communities were reported in five of six CO₂
59 manipulation experiments in the coastal Pacific (Tortell et al., 2000). Furthermore,
60 simulated future SA reduced surface PP in pelagic surface waters of Northern South
61 China Sea and East China Sea (Gao et al., 2012). It seems that the impacts of SA on PP
62 could be region-dependent. The varying effects of SA may be related to the regulation of
63 other factors such as light intensity (Gao et al., 2012), temperature (Holding et al., 2015),
64 nutrients (Tremblay et al., 2006) and community structure (Dutkiewicz et al., 2015).

65 Taiwan Strait of the East China Sea, located between southeast Mainland China and
66 the Taiwan Island, is an important channel in transporting water and biogenic elements
67 between the East China Sea and the South China Sea. Among the Chinese coastal areas,
68 the Taiwan Strait is distinguished by its unique location. In addition to riverine inputs, it
69 also receives nutrients from upwelling (Hong et al., 2011). Primary productivity is much
70 higher in coastal waters than that in basin zones due to increased supply of nutrients
71 through river runoff and upwelling (Chen, 2003; Cloern et al., 2014). The South China
72 Sea, located from the equator to 23.8 °N, from 99.1 to 121.1 °E and encompassing an area
73 of about 3.5×10^6 km², is one of the largest marginal seas in the world. As a marginal sea

74 of the Western Pacific Ocean, it has a deep semi-closed basin (with depths > 5000 m) and
75 wide continental shelves, characterized by a tropical and subtropical climate (Jin et al.,
76 2016). Approximately 80% of ocean organic carbon is buried in the Earth's continental
77 shelves and therefore continental margins play an essential role in the ocean carbon cycle
78 (Hedges & Keil, 1995). Investigating how SA affects primary productivity in the Taiwan
79 Strait and the South China Sea could help us to understand the contribution of marginal
80 seas to carbon sink under the future CO₂-increased scenarios. Although small-scale
81 studies on SA impacts have been conducted in the East China Sea and the South China
82 Sea (Gao et al., 2012, 2017), our understanding of how SA affects PP in marginal seas is
83 still fragmentary and superficial. In this study, we conducted three cruises in the Taiwan
84 Strait and the South China Sea, covering an area of $8.3 \times 10^5 \text{ km}^2$, and aimed to provide
85 in-depth insight into how SA and/or episodic pCO₂ rise affects PP in marginal seas with
86 comparisons to other types of waters.

87 **2 Materials and Methods**

88 **2.1 Investigation areas**

89 To study the impacts of projected SA (dropping by ~0.4 pH) by the end of this
90 century (RCP8.5) on marine primary productivity in different areas (Gattuso et al., 2015),
91 we carried out deck-based experiments during the 3 cruises supported by National
92 Natural Science Foundation of China (NSFC), which took place in the Taiwan Strait (Jul
93 14th–25th, 2016), the South China Sea basin (Sep 6–24th, 2016), and the West South China

94 Sea (Sep 14th to Oct 24th, 2017), respectively. The experiments were conducted at 101
95 stations with coverage of 12 °N–26 °N and 110 °E–120 °E (Fig. 1). Investigation areas
96 include the continental shelf (0–200 m, 22 stations) and the slope (200–3400 m, 44
97 stations), and the vast deep-water basin (> 3400 m, 35 stations). In the continental shelf,
98 the areas with depth < 50 m are defined as coastal zones (9 stations).

99 **2.2 Measurements of temperature and carbonate chemistry parameters**

100 The temperature and salinity of surface seawater at each station were monitored with
101 an onboard CTD (Seabird, USA). pH_{NBS} was measured with an Orion 2-Star pH meter
102 (Thermo scientific, USA) that was calibrated with standard National Bureau of Standards
103 (NBS) buffers ($\text{pH}=4.01, 7.00, \text{ and } 10.01$ at $25.0\text{ }^{\circ}\text{C}$; Thermo Fisher Scientific Inc., USA).
104 After the calibration, the electrode of pH meter was kept in surface seawater for half an
105 hour and then the formal measurements were conducted. The analytical precision was
106 ± 0.001 . Total alkalinity (TA) was determined using Gran titration on a 25-mL sample
107 with a TA analyzer (AS-ALK1, Apollo SciTech, USA) that was regularly calibrated with
108 certified reference materials supplied by A. G. Dickson at the Scripps Institution of
109 Oceanography (Gao et al., 2018a). The analytical precision was $\pm 2\ \mu\text{mol kg}^{-1}$. CO_2
110 concentration in seawater and the pH_{Total} (pH_{T}) values was calculated by using CO2SYS
111 (Pierrot et al., 2006) with the input of pH_{NBS} and TA data.

112 **2.3 Solar radiation**

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

114 Eldonet broadband filter radiometer (Eldonet XP, Real Time Computer, Germany). This
115 device has three channels for PAR (400–700 nm), UV-A (315–400 nm) and UV-B (280–
116 315 nm) irradiance, respectively, which records the means of solar radiations over each
117 minute. The instrument was fixed at the top layer of the ship to avoid shading.

118 **2.4 Determination of primary productivity**

119 Surface seawater (0–1m) was collected a 10 L acid-cleaned (1 M HCl) plastic bucket
120 and pre-filtered (200 µm mesh size) to remove large grazers. To prepare high CO₂ (HC)
121 seawater, CO₂-saturated seawater was added into pre-filtered seawater until a decrease of
122 ~0.4 units in pH (corresponding CO₂ concentrations being 22.0–39.7 µM) was
123 approached (Gattuso et al., 2010). Seawater that was collected from the same location as
124 PP and filtered by cellulose acetate membrane (0.22 µm) was used to make the
125 CO₂-saturated seawater, which was made by directly flushing with pure CO₂ until pH
126 reached values around 4.50. When saturated-CO₂ seawater was added to the HC
127 treatment, equivalent filtered seawater (without flushing with CO₂) was also added to the
128 ambient CO₂ (AC) treatment as a control. The ratios of added saturated-CO₂ seawater to
129 incubation seawater were about 1:1000. Samples were incubated within half an hour after
130 they were collected. Prepared AC and HC seawater was allocated into 50-mL quartz
131 tubes in triplicate, inoculated with 5 µCi (0.185 MBq) NaH¹⁴CO₃ (ICN Radiochemicals,
132 USA), and then incubated for 24 h (over a day-night cycle) under 100 % incident solar
133 irradiances in a water bath for temperature control by running through surface seawater.

134 Due to heating by the deck, the temperatures in the water bath were 0–2 °C higher than in
135 situ surface seawater temperatures. TA and pH of seawater before and after 24h
136 incubation were measured to monitor the changes of carbonate systems. After the
137 incubation, the cells were filtered onto GF/F filters (Whatman) and immediately frozen at
138 –20 °C for later analysis. In the laboratory, the frozen filters were transferred to 20 mL
139 scintillation vials, thawed and exposed to HCl fumes for 12 h, and dried (55 °C, 6 h) to
140 expel non-fixed ¹⁴C, as previously reported (Gao et al., 2017). Then 3 mL scintillation
141 cocktail (Perkin Elmer®, OptiPhase HiSafe) was added to each vial. After 2 h of reaction,
142 the incorporated radioactivity was counted by a liquid scintillation counting (LS 6500,
143 Beckman Coulter, USA). The carbon fixation for 24 h incubation was taken as
144 chlorophyll (Chl) *a*-normalized daily primary productivity (PP, µg C (µg Chl *a*)⁻¹) (Gao et
145 al., 2017). The changes (%) of PP induced by SA were expressed as $(PP_{HC} -$
146 $PP_{AC})/PP_{AC} \times 100$, where PP_{HC} and PP_{AC} are the daily primary productivity under HC and
147 AC, respectively.

148 **2.5 Chl *a* measurement**

149 Pre-filtered (200 µm mesh size) surface seawater (500–2000 mL) at each station was
150 filtered onto GF/F filter (25 mm, Whatman) and then stored at -80 °C. After returning to
151 laboratory, phytoplankton cells on the GF/F filter were extracted overnight in absolute
152 methanol at 4 °C in darkness. After centrifugation (5000 g for 10 min), the absorption
153 values of the supernatants were analyzed by a UV–VIS spectrophotometer (DU800,

154 Beckman, Fullerton, California, USA). The concentration of chlorophyll *a* (Chl *a*) was
155 calculated according to Porra (2002).

156 **2.6 Data analysis**

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

163 **3 Results**

164 During the cruises, surface temperature ranged from 25.0 to 29.9 °C in the Taiwan
165 Strait and from 27.1 to 30.2 °C in the South China Sea (Fig. 2a). Surface salinity ranged
166 from 30.0 to 34.0 in the Taiwan Strait and from 31.0 to 34.3 in the South China Sea (Fig.
167 2b). The lower salinities were found in the estuaries of Minjiang and Jiulong Rivers as
168 well as Mekong River-induced Rip current. High salinities were found in the South China
169 Sea basin. Surface pH_T changed between 7.99–8.20 in the Taiwan Strait with the higher
170 values in the estuary of Minjiang River (Fig. 2c). Compared to the Taiwan Strait, the
171 South China Sea had lower surface pH (7.91–8.08) with the lowest value near the island
172 in the Philippines. TA ranged from 2100 to 2359 $\mu\text{mol kg}^{-1}$ SW in the Taiwan Strait and
173 2126 to 2369 $\mu\text{mol kg}^{-1}$ SW in the South China Sea (Fig. 2d). The lowest value occurred

174 in the estuary of Minjiang River. CO₂ concentration in surface seawater changed from
175 6.4–13.3 μmol kg⁻¹ SW in the Taiwan Strait, and 9.3–14.3 μmol kg⁻¹ SW in the South
176 China Sea (Fig. 2e). It showed an opposite pattern to surface pH, with the lowest value in
177 the estuary of Minjiang River in the Taiwan Strait and highest value in near the islands in
178 the Philippines in the South China Sea. During the PP investigation period, the daytime
179 mean PAR intensity ranged from 126.6 to 145.2 W m⁻² s⁻¹ in the Taiwan Strait and 37.3 to
180 150.0 W m⁻² s⁻¹ in the South China Sea (Fig. 2f).

181 The concentration of Chl *a* ranged from 0.11 to 12.13 μg L⁻¹ in the Taiwan Strait (Fig.
182 3). The highest concentration occurred in the estuary of the Minjiang River. The
183 concentration of Chl *a* in the South China Sea ranged from 0.037 to 7.43 μg L⁻¹. The
184 highest concentration was found in the coastal areas of Guangdong province in China.
185 For both the Taiwan Strait and the South China Sea, there were high Chl *a* concentrations
186 (> 1.0 μg L⁻¹) in coastal areas, particularly in the estuaries of the Minjing River, Jiulong
187 River and Pearl River. On the contrary, Chl *a* concentrations in offshore areas were lower
188 than 0.2 μg L⁻¹.

189 Surface primary productivity changed from 99 to 302 μg C (μg Chl *a*)⁻¹ d⁻¹ in the
190 Taiwan Strait, and from 17 to 306 μg C (μg Chl *a*)⁻¹ d⁻¹ in the South China Sea (Fig. 4).
191 High surface primary productivity (> 200 μg C (μg Chl *a*)⁻¹ d⁻¹) was found in the
192 estuaries of the Minjing River, Jiulong River, and Pearl River and areas near the East of
193 Vietnam. In basin zones, the surface primary productivity was usually lower than 100 μg

194 C ($\mu\text{g Chl } a$)⁻¹ d⁻¹.

195 A series of onboard CO₂-enrich experiments in the investigated regions were
196 conducted during three cruises. In HC treatments, pH_{total} decreased by 0.34–0.43 units,
197 while pCO₂ and CO₂ increased by 676–982 μatm and 17–25 $\mu\text{mol kg}^{-1}$ SW, respectively
198 (Table S1). Carbonate chemistry parameters after 24 h of incubation were stable ($\Delta\text{pH} <$
199 0.06 , $\Delta\text{TA} < 53 \mu\text{mol kg}^{-1}$ SW), indicating the successful manipulation (Table S1). It
200 was observed that instantaneous effects of elevated pCO₂ on primary productivity of
201 surface phytoplankton community in all investigated regions ranged from -88%
202 (inhibition) to 57% (promotion), revealing significant regional differences among
203 continental shelf, slope and deep-water basin (ANOVA, $F_{(2, 98)} = 3.747$, $p = 0.027$, Fig. 5).
204 Among 101 stations, 70 stations showed insignificant SA effects. SA increased PP at 6
205 stations and reduced PP at 25 stations. Positive effects of SA on surface primary
206 productivity were observed in the Taiwan Strait and the western South China Sea (Fig. 5,
207 red-yellow shading areas), with the maximal enhancement of 57% in the station
208 approaching the Mekong River plume (LSD, $p < 0.001$). Reductions in PP induced by the
209 elevated CO₂ were mainly found in the central South China Sea basin within the latitudes
210 of 10 °N to 14 °N and the longitudes of 114.5 °E to 118 °E (Fig. 5, blue-purple shading
211 areas), with inhibition rates ranging from 24% to 88% (Fig. 5, LSD, $p < 0.05$). These
212 results showed a region-related effect of SA on photosynthetic carbon fixation of surface
213 phytoplankton assemblages. Overall, the elevated pCO₂ had neutral or positive effects on

214 primary productivity in the continental shelf and slope regions, while having adverse
215 effects in the deep-water basin.

216 By analyzing the correlations between SA-induced PP changes and regional
217 environmental parameters (Table S2), we found that SA-induced changes in
218 phytoplankton primary productivity was significantly positively related with *in situ* pH (p
219 < 0.001 , $r = 0.379$), and PAR density ($p = 0.002$, $r = 0.311$) (Fig. 6). On the other hand,
220 the influence induced by SA was negatively related to salinity that ranged from 30.00 to
221 34.28 ($p < 0.001$, $r = -0.418$).

222 **4 Discussion**

223 In the present study, we found that the elevated pCO₂ and associated pH drop
224 increased or did not affect PP in the continental shelf and slope waters but reduced it in
225 basin waters. Our results suggested that the enhanced effects of the SA treatment on
226 photosynthetic carbon fixation depend on regions of different physicochemical conditions,
227 including pH, light intensity and salinity. In addition, coastal diatoms appear to benefit
228 more from SA than pelagic ones (Li et al., 2016). Therefore, community structure
229 differences might also be responsible for the differences of the short-term high
230 CO₂-induced acidification between coastal and basin waters.

231 SA is deemed to have two kinds of effects at least (Xu et al., 2017; Shi et al., 2019).
232 The first one is the enrichment of CO₂, which is usually beneficial for photosynthetic
233 carbon fixation and growth of algae because insufficient ambient CO₂ limits algal

234 photosynthesis (Hein & Sand-Jensen, 1997; Bach & Taucher, 2019). The other effect is
235 the decreased pH which could be harmful because it disturbs the acid-base balance
236 between extracellular and intracellular environments. For instance, the decreased pH
237 projected for future SA was shown to reduce the growth of the diazotroph *Trichodesmium*
238 (Hong et al., 2017), decrease PSII activity by reducing the removal rate of PsbD (D2)
239 (Gao et al., 2018b) and increase mitochondrial and photo-respirations in diatoms and
240 phytoplankton assemblages (Yang and Gao 2012, Jin et al., 2015). In addition, SA could
241 reduce the Rubisco transcription of diatoms, which also contributed to the decreased
242 growth (Endo et al., 2015). Therefore, the net impact of SA depends on the balance
243 between its positive and negative effects, leading to enhanced, inhibited or neutral
244 influences, as reported in diatoms (Gao et al., 2012, Li et al., 2021) and phytoplankton
245 assemblages in the Arctic and subarctic shelf seas (Hoppe et al., 2018), the North Sea
246 (Eberlein et al., 2017) and the South China Sea (Wu and Gao 2010, Gao et al., 2012). The
247 balance of positive and negative effects of SA can be regulated by other factors, including
248 pH, light intensity, salinity, population structure, etc. (Gao et al., 2019a, b; Xie et al.,
249 2022).

250 In the present study, SA increased or did not affect PP in coastal waters but reduced it
251 in offshore waters, which is significantly related to pH, light intensity and salinity (Fig. 6).
252 The effect of SA changed from negative to positive with the increase of local pH. The
253 higher pH occurred in coastal zones which may be caused by higher biomass of

254 phytoplankton (Fig. 3). Higher pH caused by intensive photosynthesis of phytoplankton
255 is accompanied with decreased CO₂ levels. In this case, CO₂ is more limiting for
256 photosynthesis of phytoplankton compared to lower pH. Therefore, SA could stimulate
257 primary productivity via supplying more available CO₂ (Hurd et al., 2019). On the other
258 hand, lower pH occurred in deep-water basin. Lower pH represents higher CO₂
259 availability. CO₂ is not limited or less limited in this case. Therefore, more CO₂ brought
260 by SA may not benefit photosynthesis of phytoplankton. Instead, decreased pH
261 accompanied by SA may inhibit photosynthesis or growth of phytoplankton, which is
262 found in cyanobacteria (Hong et al., 2017). Furthermore, the negative effects of SA are
263 particularly significant when nutrient is limited (Li et al., 2018). The nutrient levels in the
264 basin are usually lower than on the shelf (Yuan et al., 2011; Lu et al., 2020; Du et al.,
265 2021), which may exacerbate the negative effects of SA in the basin zone.

266 The negative effects of SA disappeared with increasing light intensity in this study.
267 This results in inconsistent with Gao et al (2012)' study, in which SA increased
268 photosynthetic carbon fixation of three diatoms (*Phaeodactylum tricornutum*,
269 *Thalassiosira pseudonana* and *Skeletonema costatum*) under lower light intensities but
270 decreased it under higher light intensities. The divergent findings may be due to different
271 population structure that varies in different areas. Coastal zones where nutrients are
272 relatively sufficient usually have abundant diatoms while picophytoplanktons mainly
273 *Prochlorococcus* and *Synechococcus*, dominate oligotrophic areas (Xiao et al., 2018,

274 Zhong et al., 2020). In this study, most investigated areas are oligotrophic and thus the
275 response of local phytoplankton to the combination of light intensity and SA may be
276 different from diatoms. Meanwhile, the weak correlation ($r = 0.311$) between light
277 intensity and SA effect suggests the deviation from linear relationship in the context of
278 multiple variables needs to be further illuminated in future studies. It is worth noting that
279 the samples were not mixed down in the water bath in the present study and exposed to
280 100% incident solar irradiances. Lower incident solar irradiances or some devices can be
281 used to simulate seawater mixing in future studies. A negative correlation between
282 SA-induced changes of PP and salinity was found in this study. The decrease of salinity
283 (from 35 to 30) has been shown to alleviate the negative effect of SA on photosynthetic
284 carbon fixation of a coccolithorophid *Emiliana huxleyi* (Xu et al., 2020) although the
285 potential mechanisms remain unknown. On the other hand, the change of salinity (from 6
286 to 3) did not affect effective quantum yield of microplanktonic community in the Baltic
287 Sea grown under different CO₂ levels (Wulff et al., 2018). In this study, the negative
288 relationship between salinity and SA effects seems to be an autocorrelation between
289 salinity and in situ pH (Fig. S1) because lower salinity occurred in coastal waters where
290 seawater pH was higher while the basin zone usually had higher salinities and lower pH.

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

294 (*Prochlorococcus* and *Synechococcus*), characterizing with more efficient nutrients
295 uptake, dominate the relatively stable offshore waters (Dutkiewicz et al., 2015). In
296 summer and early autumn, previous investigations demonstrated that diatoms dominated
297 in the northern waters and the Taiwan Strait (coastal and shelf regions) with high
298 abundances of phytoplankton, which is consistent with our Chl *a* data; *Prochlorococcus*
299 and *Synechococcus* dominated in the South China Sea basin and the north of South China
300 Sea (slope and basin regions) (Xiao et al., 2018, Zhong et al., 2020). In addition, it has
301 been reported that larger cells benefit more from SA because a thicker diffusion layer
302 around the cells limits the transport of CO₂ (Feng et al., 2010; Wu et al., 2014). In
303 contrast, a thinner diffusion layer and higher surface to volume ratio in smaller
304 phytoplankton cells can make them easier to transport CO₂ near the cell surface and
305 within the cells, and therefore picophytoplankton species are less CO₂-limited (Bao and
306 Gao, 2021). Therefore, different community structures between coastal and basin areas
307 could also be responsible for the enhanced and inhibitory effects of SA. It is worth noting
308 that seasonality may also lead to the differential effects of SA on primary productivity
309 since the Taiwan Strait cruise was conducted in July and the cruises of the South China
310 Sea basin and the West South China Sea were conducted in September. The SST and
311 solar PAR intensity of the Taiwan Strait in July was 2–3 °C and $22 \pm 22 \text{ W m}^{-2} \text{ s}^{-1}$ higher
312 than that in September (Zhang et al., 2008, 2009; Table S3). Although the effects of SA
313 were not related to temperature as shown in this study (Table S2), the higher solar

314 radiation in July may contribute to the positive effect of SA on primary productivity. In
315 addition, species succession of phytoplankton with season may also affect the response to
316 SA (Xiao et al., 2018).

317 **5 Conclusions**

318 By investigating the impacts of the elevated pCO₂ on PP in the Taiwan Strait and the
319 South China Sea, we demonstrated that such short SA-treatments induced changes in PP
320 were mainly related to pH, light intensity and salinity based on Pearson correlation
321 coefficients, supporting the hypothesis that negative impacts of SA on PP increase from
322 coastal to basin waters (Gao et al., 2019a). In addition, phytoplankton community
323 structures may also modulate SA induced changes. In view of ocean climate changes,
324 strengthened stratification due to global warming would reduce the upward transports of
325 nutrients and thus marine primary productivity. The negative effect of SA in basin zones
326 may further reduce primary productivity. Meanwhile, PP in some coastal waters may be
327 increased by SA.

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

329 *Author contributions.* KG and TW developed the original idea and designed research.

330 TW and JS carried out fieldwork. GG provided statistical analyses and prepared figures.

331 GG, KG, and XZ wrote the manuscript. All contributed to revising the paper.

332 *Competing interests.* The contact author has declared that neither they nor their

333 co-authors have any competing interests.

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344 **References**

345 Bach, L. T., and Taucher, J.: CO₂ effects on diatoms: a synthesis of more than a decade of
346 ocean acidification experiments with natural communities, *Ocean Sci.*, 15,
347 1159-1175, 2019.

348 Bao, N., and Gao, K.: Interactive effects of elevated CO₂ concentration and light on the
349 picophytoplankton *Synechococcus*, *Front. Mar. Sci.*, 8, 1-7, 2021.

350 Boyd, P. W., Strzepek, R., Fu, F. X., and Hutchins, D. A.: Environmental control of open-
351 ocean phytoplankton groups: Now and in the future, *Limnol. Oceanogr.*, 55,
352 1353-1376, 2010.

353 Chen, C. T. A.: Rare northward flow in the Taiwan Strait in winter: A note, *Cont. Shelf*

354 Res., 23, 387-391, 2003.

355 Cloern, J. E., Foster, S.Q. and Kleckner, A. E.: Phytoplankton primary production in the
356 world's estuarine-coastal ecosystems, *Biogeosciences*, 11, 2477-2501, 2014.

357 Doney, S. C., Busch, D. S., Cooley, S. R., and Kroeker, K. J.: The impacts of ocean
358 acidification on marine ecosystems and reliant human communities, *Annu. Rev. Env.*
359 *Resour.*, 45, 83-112, 2020.

360 Du, C., He, R., Liu, Z., Huang, T., Wang, L., Yuan, Z., Xu, Y., Wang, Z. and Dai, M.:
361 Climatology of nutrient distributions in the South China Sea based on a large data
362 set derived from a new algorithm. *Prog. Oceanogr.*, 195, 102586, 2021.

363 Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T., and
364 Berman-Frank, I.: Impact of ocean acidification on the structure of future
365 phytoplankton communities, *Nat. Clim. Change*, 5, 1002-1006, 2015.

366 Eberlein, T., Wohlrab, S., Rost, B., John, U., Bach, L. T., Riebesell, U., and Van de Waal,
367 D. B.: Effects of ocean acidification on primary production in a coastal North Sea
368 phytoplankton community, *Plos One*, 12, 1-15, 2017.

369 Endo, H., Sugie, K., Yoshimura, T., and Suzuki, K.: Effects of CO₂ and iron availability
370 on *rbcL* gene expression in Bering Sea diatoms, *Biogeosciences*, 12, 2247-2259,
371 2015.

372 Feng, Y., Hare, C. E., Rose, J. M., Handy, S. M., DiTullio, G. R., Lee, P. A., Smith, W. O.,
373 Peloquin, J., Tozzi, S., Sun, J., Zhang, Y., Dunbar, R. B., Long, M. C., Sohst, B.,

374 Lohan, M., and Hutchins, D. A.: Interactive effects of iron, irradiance and CO₂ on
375 Ross Sea phytoplankton, *Deep-Sea Res. PT. I*, 57, 368-383, 2010.

376 Gao, G., Xu, Z. G., Shi, Q., and Wu, H. Y.: Increased CO₂ exacerbates the stress of
377 ultraviolet radiation on photosystem II function in the diatom *Thalassiosira*
378 *weissflogii*, *Environ. Exp. Bot.*, 156, 96-105, 2018b.

379 Gao, G., Jin, P., Liu, N., Li, F. T., Tong, S. Y., Hutchins, D. A., and Gao, K. S.: The
380 acclimation process of phytoplankton biomass, carbon fixation and respiration to the
381 combined effects of elevated temperature and pCO₂ in the northern South China Sea,
382 *Mar. Pollut. Bull.*, 118, 213-220, 2017.

383 Gao, G., Qu, L., Xu, T., Burgess, J.G., Li, X. and Xu, J.: Future CO₂-induced ocean
384 acidification enhances resilience of a green tide alga to low-salinity stress. *ICES J.*
385 *Mar. Sci.*, 76, 2437-2445, 2019b.

386 Gao, G., Xia, J. R., Yu, J. L., Fan, J. L., and Zeng, X. P.: Regulation of inorganic carbon
387 acquisition in a red tide alga (*Skeletonema costatum*): The importance of phosphorus
388 availability, *Biogeosciences*, 15, 4871-4882, 2018a.

389 Gao, K. S., Beardall, J., Häder, D. P., Hall-Spencer, J. M., Gao, G., and Hutchins, D. A.:
390 Effects of ocean acidification on marine photosynthetic organisms under the
391 concurrent influences of warming, UV radiation, and deoxygenation, *Front. Mar.*
392 *Sci.*, 6, 1-18, 2019a.

393 Gao, K. S., Xu, J. T., Gao, G., Li, Y. H., Hutchins, D. A., Huang, B. Q., Wang, L., Zheng,

394 Y., Jin, P., Cai, X. N., Hader, D. P., Li, W., Xu, K., Liu, N. N., and Riebesell, U.:
395 Rising CO₂ and increased light exposure synergistically reduce marine primary
396 productivity, *Nat. Clim. Change*, 2, 519-523, 2012.

397 Gattuso, J. P., Gao, K. S., Lee, K., Rost, B., and Schulz, K. G.: Approaches and tools to
398 manipulate the carbonate chemistry, pp 41-52. Guide to best practices for ocean
399 acidification research and data reporting, edited by: Riebesell, U., Fabry, V. J.,
400 Hansson, L., and Gattuso J.-P., Luxembourg: Publications Office of the European
401 Union, 2010.

402 Gattuso, J. P., Magnan, A., Bill é R., Cheung, W. W. L., Howes, E. L., Joos, F., Allemand,
403 D., Bopp, L., Cooley, S. R., Eakin, C. M., Hoegh-Guldberg, O., Kelly, R. P., Portner,
404 H. O., Rogers, A. D., Baxter, J. M., Laffoley, D., Osborn, D., Rankovic, A., Rochette,
405 J., Sumaila, U. R., Treyer, S., and Turley, C.: Contrasting futures for ocean and
406 society from different anthropogenic CO₂ emissions scenarios, *Science*, 349,
407 aac4722, 2015.

408 Hedges, J. I., and Keil, R. G.: Sedimentary organic matter preservation: an assessment
409 and speculative synthesis, *Mar. Chem.*, 49, 81-115, 1995.

410 Hein, M., and Sand-Jensen, K.: CO₂ increases oceanic primary production, *Nature*, 388,
411 526-527, 1997.

412 Hennon, G. M. M., Ashworth, J., Groussman, R. D., Berthiaume, C., Morales, R. L.,
413 Baliga, N. S., Orellana, M. V., and Armbrust, E. V.: Diatom acclimation to elevated

414 CO₂ via cAMP signalling and coordinated gene expression, Nat. Clim. Change, 5,
415 761-765, 2015.

416 Holding, J. M., Duarte, C. M., Sanz-Martín, M., Mesa, E., Arrieta, J. M., Chierici, M.,
417 Hendriks, I. E., Garcia-Corral, L. S., Regaudie-de-Gioux, A., Delgado, A., Reigstad,
418 M., Wassmann, P., and Agusti, S.: Temperature dependence of CO₂-enhanced
419 primary production in the European Arctic Ocean, Nat. Clim. Change, 5, 1079-1082,
420 2015.

421 Hong, H. S., Chai, F., Zhang, C. Y., Huang, B. Q., Jiang, Y. W., and Hu, J. Y.: An
422 overview of physical and biogeochemical processes and ecosystem dynamics in the
423 Taiwan Strait, Cont. Shelf Res., 31, S3-S12, 2011.

424 Hong, H. Z., Shen, R., Zhang, F. T., Wen, Z. Z., Chang, S. W., Lin, W. F., Kranz, S. A.,
425 Luo, Y. W., Kao, S. J., Morel, F. M. M. and Shi, D. L.: The complex effects of ocean
426 acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*. Science,
427 356, 527-530, 2017.

428 Hopkinson, B. M., Dupont, C. L., Allen, A. E., and Morel, F. M.: Efficiency of the
429 CO₂-concentrating mechanism of diatoms, P. Natl. Acad. Sci. USA., 108, 3830-3837,
430 2011.

431 Hoppe, C. J. M., Wolf, K. K. E., Schuback, N., Tortell, P. D., and Rost, B.: Compensation
432 of ocean acidification effects in Arctic phytoplankton assemblages. Nat. Clim.
433 Change, 8, 529-533, 2018.

434 Hurd, C.L., Beardall, J., Comeau, S., Cornwall, C.E., Havenhand, J.N., Munday, P.L.,
435 Parker, L.M., Raven, J.A. and McGraw, C.M.: Ocean acidification as a multiple
436 driver: how interactions between changing seawater carbonate parameters affect
437 marine life. *Mari. Freshwater Res.*, 71, 263-274, 2019.

438 IPCC, 2019: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate
439 [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E.
440 Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama,
441 N.M. Weyer (eds.)]. In press.

442 Jin, P., Gao, G., Liu, X., Li, F. T., Tong, S. Y., Ding, J. C., Zhong, Z. H., Liu, N. N., and
443 Gao, K. S.: Contrasting photophysiological characteristics of phytoplankton
444 assemblages in the Northern South China Sea, *Plos One*, 11, 1-16, 2016.

445 Jin, P., Wang, T. F., Liu, N. N., Dupont, S., Beardall, J., Boyd, P. W., Riebesell, U., and
446 Gao, K. S.: Ocean acidification increases the accumulation of toxic phenolic
447 compounds across trophic levels, *Nat. Commun.*, 6, 1-6, 2015.

448 Li, F. T., Wu, Y. P., Hutchins, D. A., Fu, F. X., and Gao, K. S.: Physiological responses of
449 coastal and oceanic diatoms to diurnal fluctuations in seawater carbonate chemistry
450 under two CO₂ concentrations, *Biogeosciences*, 13, 6247-6259, 2016.

451 Li, F. T., Beardall, J., and Gao, K. S.: Diatom performance in a future ocean: interactions
452 between nitrogen limitation, temperature, and CO₂-induced seawater acidification,
453 *ICES J. Mar. Sci.*, 75, 1451-1464, 2018.

454 Li, H. X., Xu, T. P., Ma, J., Li, F. T., and Xu, J. T.: Physiological responses of
455 *Skeletonema costatum* to the interactions of seawater acidification and the
456 combination of photoperiod and temperature, *Biogeosciences*, 18, 1439-1449, 2021.

457 Lu, Z., Gan, J., Dai, M., Zhao, X. and Hui, C. R.: Nutrient transport and dynamics in the
458 South China Sea: A modeling study. *Prog. Oceanogr.*, 183, 102308, 2020.

459 Moreau, S., Penna, A. D., Llorc, J., Patel, R., Langlais, C., Boyd, P. W., Matear, R. J.,
460 Phillips, H. E., Trull, T. W., Tilbrook, B. and Lenton, A.: Eddy-induced carbon
461 transport across the Antarctic Circumpolar Current. *Global Biogeochem. Cy.*, 31,
462 1368-1386, 2017

463 Mostofa, K.M., Liu, C.Q., Zhai, W., Minella, M., Vione, D., Gao, K., Minakata, D.,
464 Arakaki, T., Yoshioka, T., Hayakawa, K. and Konohira, E.: Reviews and Syntheses:
465 Ocean acidification and its potential impacts on marine ecosystems, *Biogeosciences*,
466 13, 1767-1786, 2016.

467 Pierrot, D., Wallace, D.W. R., and Lewis, E.: MS Excel program developed for CO₂
468 system calculations. ORNL/CDIAC-105a, Carbon Dioxide Information Analysis
469 Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge,
470 Tennessee, USA., 2006.

471 Porra, R. J.: The chequered history of the development and use of simultaneous equations
472 for the accurate determination of chlorophylls a and b, *Photosynth. Res.*, 73,
473 149-156, 2002.

474 Raven, J. A., and Beardall, J.: CO₂ concentrating mechanisms and environmental change,
475 *Aquat. Bot.*, 118, 24-37, 2014.

476 Schippers, P., Lüring, M., and Scheffer, M.: Increase of atmospheric CO₂ promotes
477 phytoplankton productivity, *Ecol. Lett.*, 7, 446-451, 2004.

478 Shi, D. L., Hong, H. Z., Su, X., Liao, L. R., Chang, S. W., and Lin, W. F.: The
479 physiological response of marine diatoms to ocean acidification: Differential roles of
480 seawater pCO₂ and pH, *J. Phycol.*, 55, 521-533, 2019.

481 Tortell, P. D., Rau, G. H., and Morel, F. M. M.: Inorganic carbon acquisition in coastal
482 Pacific phytoplankton communities, *Limnol. Oceanogr.*, 45, 1485-1500, 2000.

483 Tremblay, J. E., Michel, C., Hobson, K. A., Gosselin, M., and Price, N. M.: Bloom
484 dynamics in early opening waters of the Arctic Ocean. *Limnol. Oceanogr.*, 51,
485 900-912, 2006.

486 Riebesell, U., Aberle-Malzahn, N., Achterberg, E. P., Algueró-Muñiz, M.,
487 Alvarez-Fernandez, S., Arístegui, J., Bach, L. T., Boersma, M., Boxhammer, T.,
488 Guan, W. C., Haunost, M., Horn, H. G., Loscher, C. R., Ludwig, A., Spisla, C.,
489 Sswat, M., Stange, P., and Taucher, J.: Toxic algal bloom induced by ocean
490 acidification disrupts the pelagic food web, *Nat. Clim. Change*, 8, 1082-1086, 2018.

491 Wu, Y., Gao, K., and Riebesell, U.: CO₂-induced seawater acidification affects
492 physiological performance of the marine diatom *Phaeodactylum tricornutum*,
493 *Biogeosciences*, 7, 2915-2923, 2010.

494 Wu, Y., Campbell, D. A., Irwin, A. J., Suggett, D. J., and Finkel, Z. V.: Ocean
495 acidification enhances the growth rate of larger diatoms. *Limnol. Oceanogr.*, 59,
496 1027-1034, 2014.

497 Wulff, A., Karlberg, M., Olofsson, M., Torstensson, A., Riemann, L., Steinhoff, F. S.,
498 Mohlin, M., Ekstrand, N., and Chierici, M.: Ocean acidification and desalination:
499 Climate-driven change in a Baltic Sea summer microplanktonic community, *Mar.*
500 *Biol.*, 165, 1-15, 2018.

501 Xiao, W. P., Wang, L., Laws, E., Xie, Y. Y., Chen, J. X., Liu, X., Chen, B. Z., and Huang,
502 B. Q.: Realized niches explain spatial gradients in seasonal abundance of
503 phytoplankton groups in the South China Sea, *Prog. Oceanogr.*, 162, 223-239, 2018.

504 Xie, S., Lin, F., Zhao, X. and Gao, G.: Enhanced lipid productivity coupled with carbon
505 and nitrogen removal of the diatom *Skeletonema costatum* cultured in the high CO₂
506 level. *Algal Res.* 61, 102589, 2022.

507 Xu, J. K., Sun, J. Z., Beardall, J., and Gao, K. S.: Lower salinity leads to improved
508 physiological performance in the coccolithophorid *Emiliania huxleyi*, which partly
509 ameliorates the effects of ocean acidification, *Front. Mar. Sci.*, 7, 1-18, 2020.

510 Xu, Z. G., Gao, G., Xu, J. T., and Wu, H. Y.: Physiological response of a golden tide alga
511 (*Sargassum muticum*) to the interaction of ocean acidification and phosphorus
512 enrichment, *Biogeosciences*, 14, 671-681, 2017.

513 Yang, G. Y., and Gao, K. S.: Physiological responses of the marine diatom *Thalassiosira*

514 *pseudonana* to increased $p\text{CO}_2$ and seawater acidity, Mar. Environ. Res., 79,
515 142-151, 2012.

516 Yu, P., Wang, Z. A., Churchill, J., Zheng, M., Pan, J., Bai, Y., and Liang, C.: Effects of
517 typhoons on surface seawater $p\text{CO}_2$ and air-sea CO_2 fluxes in the northern South
518 China Sea. J. Geophys. Res-Oceans, 125, p.e2020JC016258, 2020.

519 Yuan, X., He, L., Yin, K., Pan, G., and Harrison, P. J.: Bacterial distribution and nutrient
520 limitation in relation to different water masses in the coastal and northwestern South
521 China Sea in late summer. Cont. Shelf Res., 31, 1214-1223, 2011.

522 Zhang, C., Zhang, X., Zeng, Y., Pan, W., Lin J.: Retrieval and validation of sea surface
523 temperature in the Taiwan Strait using MODIS data. Acta Oceanol. Sin., 30, 153-160,
524 2008.

525 Zhang, C., Ren, Y., Cai, Y., Zeng, Y., and Zhang, X.: Study on local monitoring model for
526 SST in Taiwan strait based on MODIS data. J. Trop. Meteorol., 25, 73-81, 2009.

527 Zhong, Y. P., Liu, X., Xiao, W. P., Laws, E. A., Chen, J. X., Wang, L., Liu, S. G., Zhang,
528 F., and Huang, B. Q.: Phytoplankton community patterns in the Taiwan Strait match
529 the characteristics of their realized niches, Prog. Oceanogr., 186, 1-15, 2020.

530 **Figure captions**

531 **Fig. 1** Sampling stations for the incubation experiments in the Taiwan Strait and the
532 South China Sea during three cruises. Taiwan Strait cruise was conducted in July 2016
533 (red dots), South China Sea Basin cruise were conducted in September 2016 (blue dots)
534 and Western South China Sea cruise was conducted in September 2017 (black dots).

535 **Fig. 2** Temperature ($^{\circ}\text{C}$, panel a), salinity (panel b), pH_{total} (panel c), total alkalinity (μmol
536 kg^{-1} SW, panel d), and CO_2 ($\mu\text{mol kg}^{-1}$ SW, panel e) in surface seawater and mean PAR
537 intensity ($\text{W m}^{-2} \text{s}^{-1}$, panel f) during the PP incubation experiments.

538 **Fig. 3** Chl *a* concentration ($\mu\text{g L}^{-1}$) in the Taiwan Strait and the South China Sea during
539 research cruises.

540 **Fig. 4** Surface primary productivity ($\mu\text{g C } (\mu\text{g Chl } a)^{-1} \text{ d}^{-1}$) in the Taiwan Strait and the
541 South China Sea during research cruises.

542 **Fig. 5** Seawater acidification (pH decreases of 0.4 units) induced changes (%) of surface
543 primary productivity in the Taiwan Strait and the South China Sea. Red-yellow shading
544 represents a positive effect on PP and blue-purple shading represents a negative effect.

Fig. 6 Seawater acidification (pH decreases of 0.4 units) induced changes on surface primary productivity (%) in the South China Sea as a function of ambient pH_{total} (a), PAR (b), and salinity (c). The dotted lines represent 95% confidence intervals.

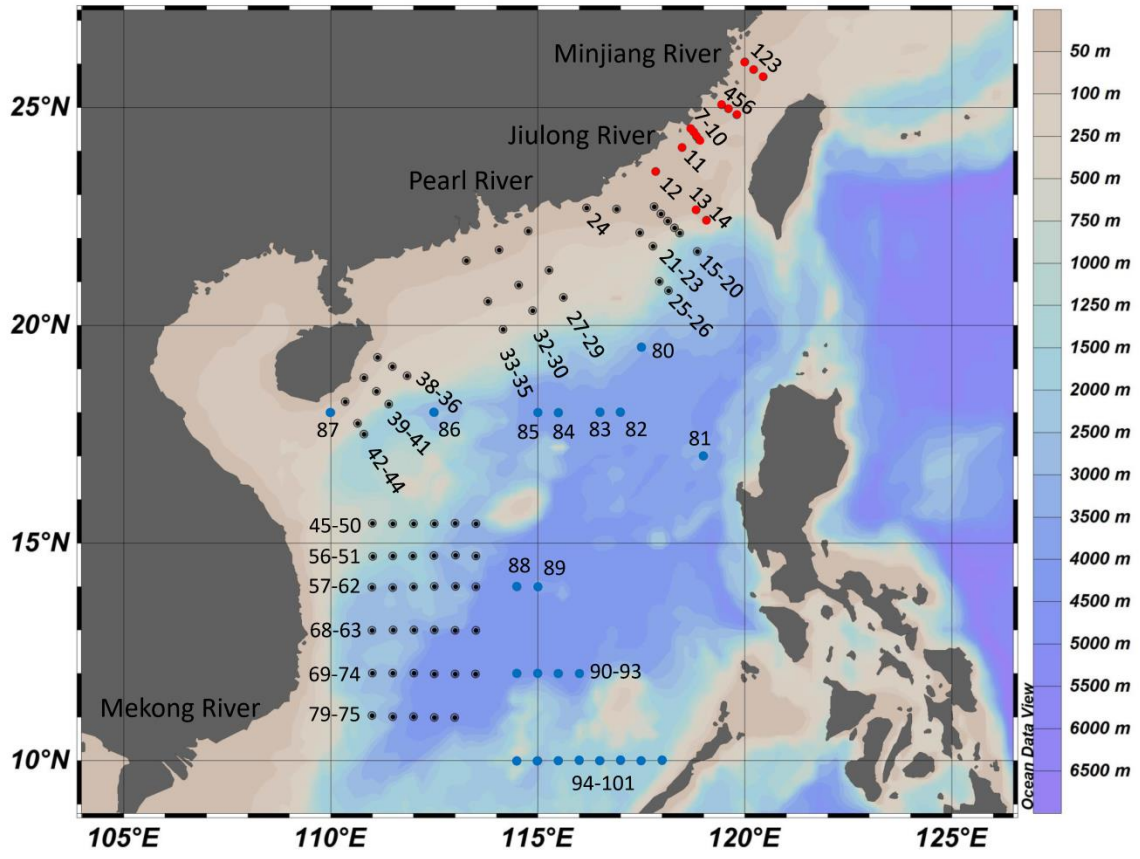


Fig. 1

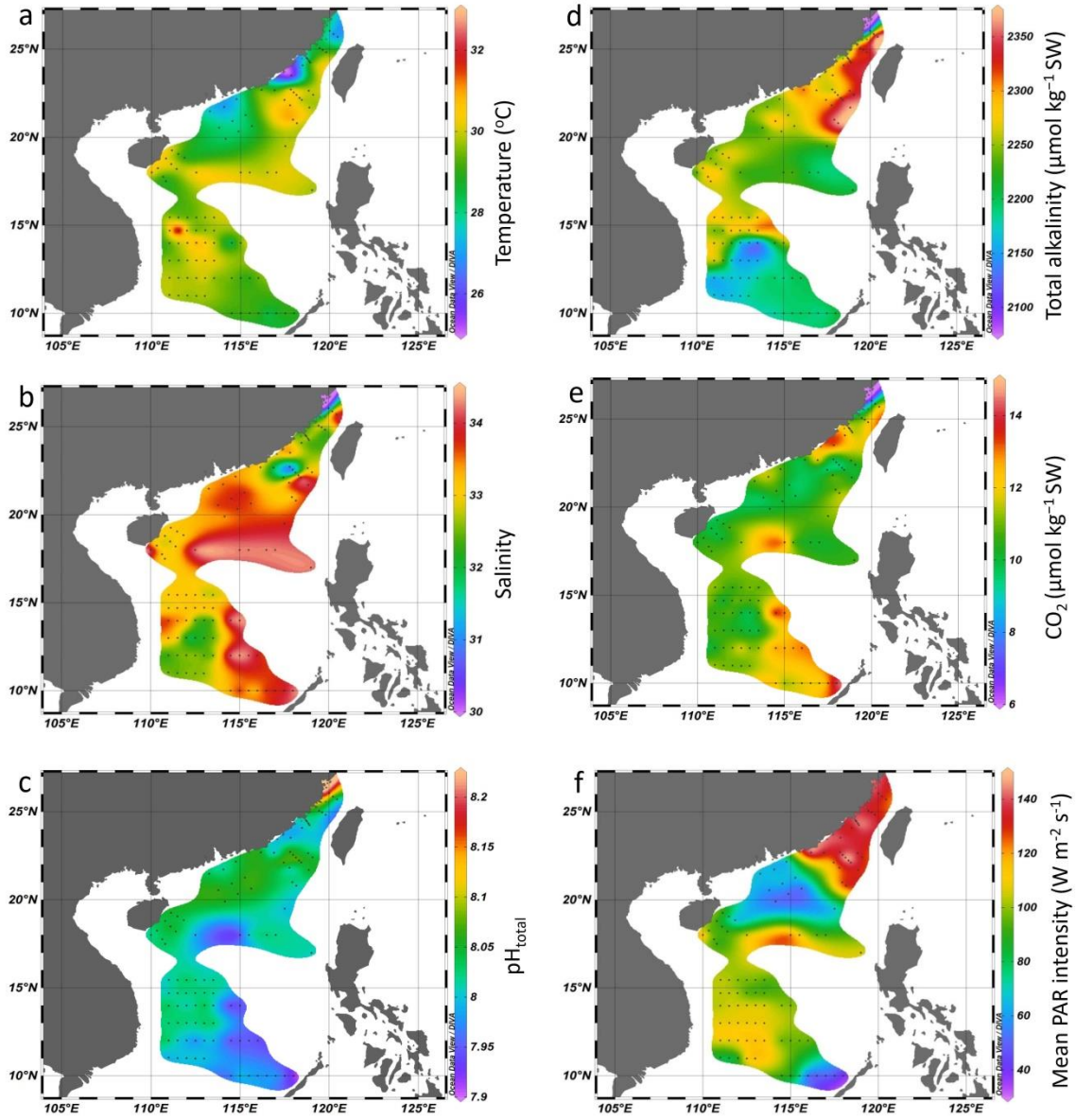


Fig. 2

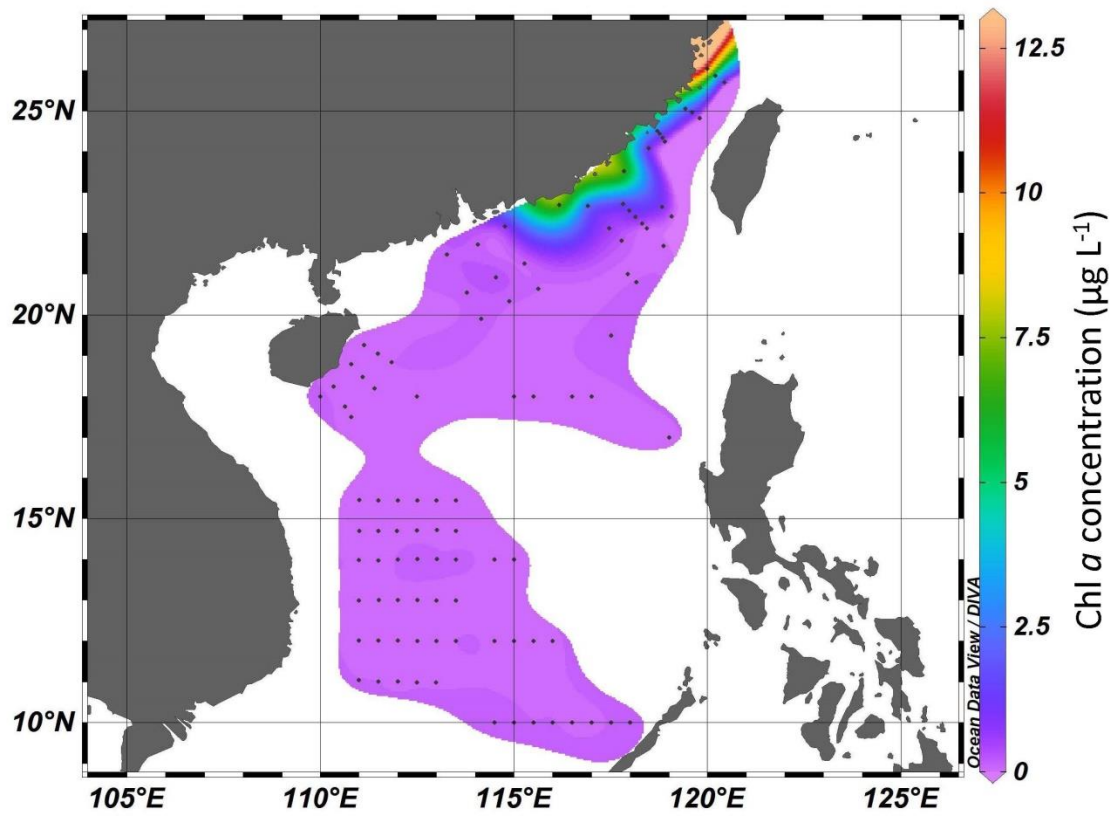


Fig. 3

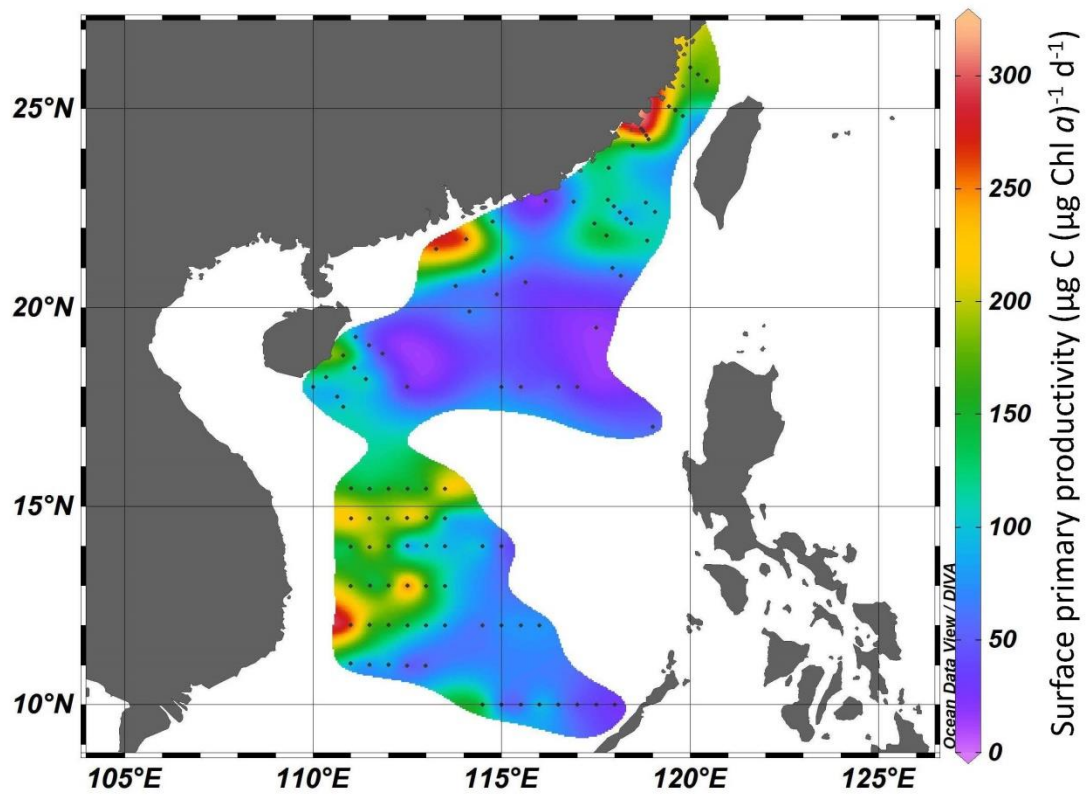


Fig. 4

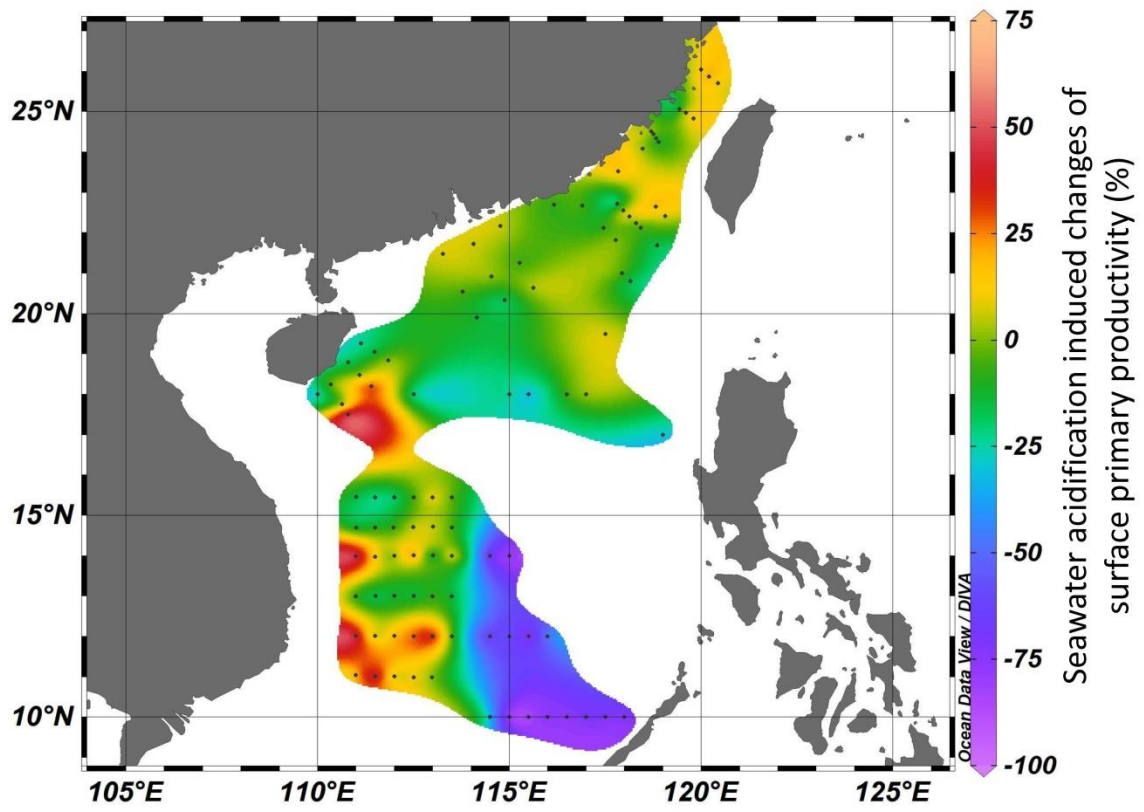


Fig. 5

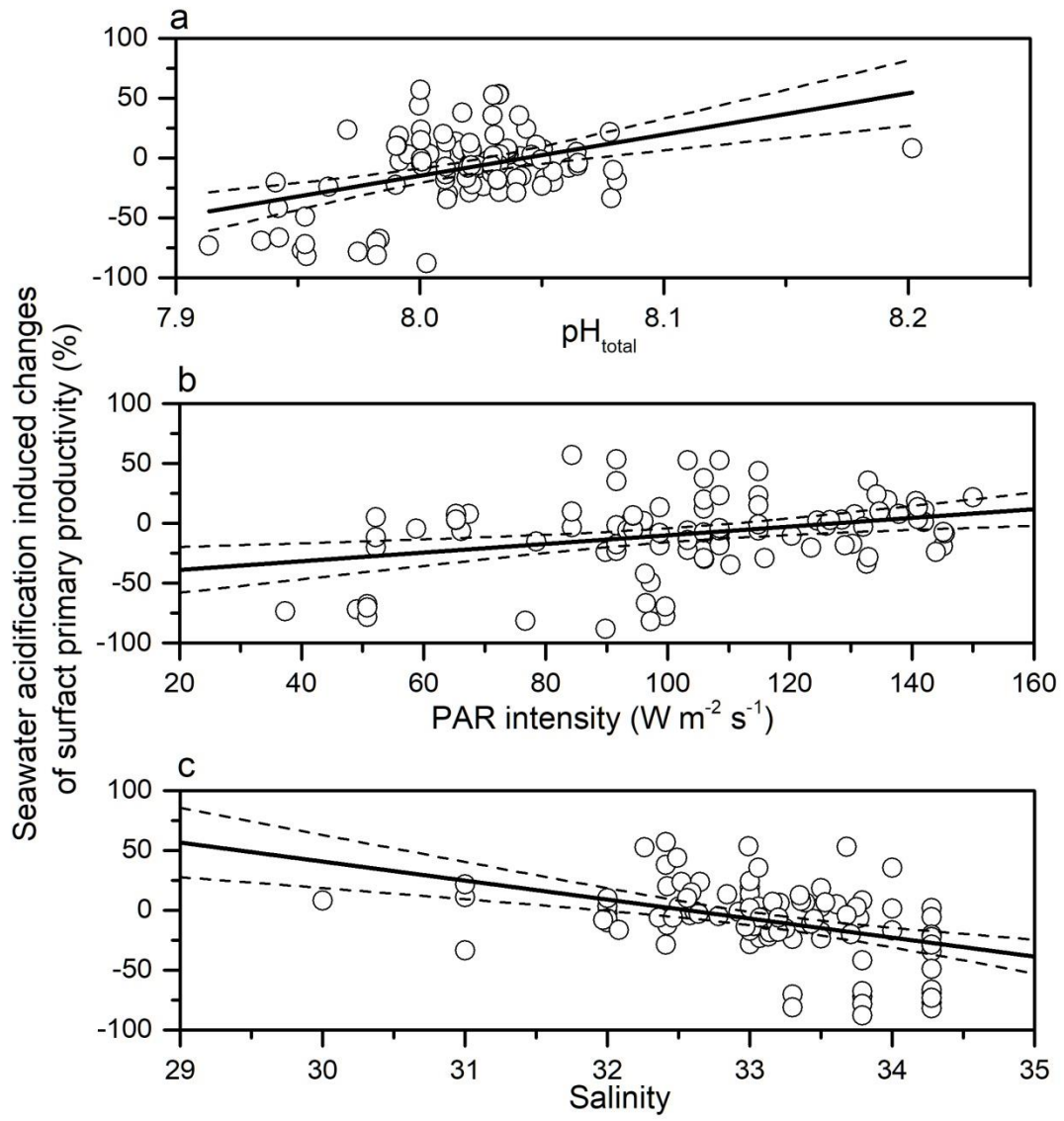


Fig. 6