Seaweed farms provide refugia from ocean acidification.

Article type: Research Paper

Title:

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Running Title: seaweed farming offset acidification

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Abstract

Seaweed farming has been proposed as a strategy for adaptation to ocean acidification, but evidence is largely lacking. Changes of pH and carbon system parameters in surface waters of three seaweed farms along a latitudinal range in China were compared, on the weeks preceding harvesting, with those of the surrounding seawaters. Results confirmed that seaweed farming is efficient in buffering acidification, with *Saccharina japonica* showing the highest capacity of 0.10 pH increase within the aquaculture area, followed by *Gracilariopsis lemaneiformis* (ΔpH = 0.04) and *Porphyra haitanensis* (ΔpH = 0.03). The ranges of pH variability within seaweed farms spanned 0.14-0.30 unit during the monitoring, showing intense fluctuations which may also help marine organisms adapt to enhanced pH temporal variations in the future ocean. Deficit in pCO_2 in waters in seaweed farms relative to control waters averaged 58.7 ± 15.9 μatm, ranging from 27.3 to 113.9 μatm across farms. However, ΔpH did not significantly differ between day and night. Dissolved oxygen and Ω_{arag} were also elevated in surface waters at all seaweed farms, which are benefit for the survival of calcifying organisms. Seaweed farming, which unlike natural seaweed forests, is scalable and is not dependent on suitable substrate or light availability, could serve as a low-cost adaptation strategy to ocean acidification and deoxygenation and provide important refugia from ocean acidification.

Keywords

Seaweed, aquaculture, acidification, pH, carbonate chemistry

1 INTRODUCTION

Increased atmospheric CO_2 with anthropogenic emissions is mirrored by increased CO_2 in sea-surface waters, where it displaces the equilibrium of the carbon system leading to decline in pH, a process known as ocean acidification (Gattuso and Hansson, 2011). Ocean acidification affects primarily on calcifying organisms, such as bivalves, corals, calcifying algae and, to a lesser extent, crustaceans (Kroeker et al., 2011), but also reduces the sensorial capability of fish (Bignami et al., 2013).

The ultimate solution to ocean acidification is, as for climate change, the reduction of green-house emissions. But unlike warming, ocean acidification can be locally mitigated, particularly through the photosynthetic activity of submerged macrophytes (Gattuso et al., 2018; Hurd, 2015; Mongin et al., 2016), which are net autotrophic, binding excess CO_2 and maintaining elevated pH relative to waters beyond the submerged forests (Duarte et al., 2013). Indeed, the pH of water above submerged macrophyte canopies is often elevated (Duarte et al., 2013; Koweek et al., 2017; Krause-Jensen et al., 2015; Krause-Jensen et al., 2016). Hence, seagrass meadows and algal forests have been argued to provide local refugia from ocean acidification (Gattuso et al., 2018; Hurd, 2015). While this protective role is limited to the areas where these submerged macrophytes grow, seaweed aquaculture provides a mobile platform where the protective benefits of seaweed photosynthesis can be deployed in vulnerable areas beyond wild macrophyte habitats. Hence, seaweed aquaculture has been proposed to provide protection against ocean acidification (Duarte et al., 2017; Froehlich et al., 2019), but evidence is largely lacking (Alleway et al., 2018).

Here we report evidence that seaweed aquaculture provides refugia from ocean acidification based on observations on pH and carbon system parameters on the weeks preceding harvesting of three seaweed farms along a latitudinal range in China (Fig. 1), compared to those of adjacent, unaffected waters. We hypothesized that seaweed farming increases the pH of seawater and, therefore, play a role in buffering ocean acidification on a local scale.

2 MATERIALS AND METHODS

2.1 Seaweed farms and monitoring sites

To evaluate the contribution of seaweed farming to alleviate ocean acidification, the seawaters in three large-scale seaweed farms distributed along the Chinese coast from north to south were monitored continuously, including a *Saccharina japonica* (Areschoug) C.E.Lane, C.Mayes, Druehl & G.W.Saunders farm in Lidao Bay located in the Yellow Sea, a *Porphyra haitanensis* T.J.Chang & B.F.Zheng farm in Fodu Island located in the East China Sea and a *Gracilariopsis lemaneiformis* (Bory) E.Y.Dawson, Acleto & Foldvik farm in Nan'ao Island located in the South China Sea (Fig. 1).

2.1.1 S. japonica farm in Lidao Bay

Lidao Bay is located at the easternmost end of Jiaodong Peninsula in the Yellow Sea. Lidao town is famous for its seaweed aquaculture and is known as "China's kelp city". The total area of seaweed aquaculture is approx. 5.3 km^2 in the seaweed farm where monitoring was performed (Lidao Ocean Science and Technology Co.). The breeding time of *S. japonica* is from December to June. The monitoring site inside the *S. japonica* farm was 37°14′58″N, 122°34′22″E, and the monitoring site outside the seaweed farm (control site) was 37°15′10″N, 122°37′29″E. The distance from the control site to the seaweed farm site was about 3.8 km due to the large area of this seaweed farm, where the control site was 200 meters away from the edge of the farm. The control and farm sites were distributed perpendicular to the current direction, which was north-south in summer, with an average current speed of around 30 cm s^{-1}. The tide is semidiurnal in this region, with maximum tide range of 189 cm and average tidal range of 78 cm. The average flood and ebb tide duration is 370 and 376 min, respectively. The seawater quality of this region in 2017 was class I (Inorganic Nitrogen < 0.2 mg L^{-1}, and Orthophosphate < 0.015 mg L^{-1}), which corresponds to relatively unpolluted waters, according to national monitoring annual report (SOA, 2018). The on-site monitoring was performed from June 3rd to June 12th, 2017, right before the harvest season which started on June 14th, 2017. The salinity ranged from 31.51 ‰ to 32.39 ‰, and sea surface temperature ranged from 13.98 °C to 17.89 ℃ during the monitoring period.

2.1.2 P. haitanensis farm in Fodu Island

Fudo Island is located in Zhoushan, the East China Sea, with a total area of 7.28 km^2. The cultivation area of *P. haitanensis* seaweed farm is approx. 0.1 km^2 in the eastern coast of this Island. The monitoring site inside the seaweed farm is 29°44′39″N, 122°2′14″E, and the monitoring site outside the seaweed farm as a control is 29°44′44″N, 122°2′7″E. *P. haitanensis* are cultivated in sea from September to December every year, and harvested for 3 to 5 times since November. The on-site monitoring time period was Nov. 15th to Nov. 27th, 2017, before the 3rd harvest this year. The tide of this region is regular semidiurnal, with maximum tide range of 484 cm and average tidal range of 257 cm. The average flood and ebb tide duration is 345 and 401 min, respectively. The average tidal current velocity of tide rising and falling ranged 0.36 - 1.03 m s^{-1} and 0.50 - 1.10 m s^{-1}, respectively. The dominant currents direction in November was north-south impacted by the Zhemin Coastal Current and Taiwan Current (TWC), orthogonal to the heading between the control and farm sites. According to the national monitoring annual report, the seawater quality of this region in 2017 was class III (Inorganic Nitrogen: 0.4 – 0.5 mg L^{-1}, and Orthophosphate: 0.015 – 0.03 mg L^{-1}), corresponding to highly eutrophic water (SOA, 2018). The salinity was around 24 ‰ and sea surface temperature ranged from 16 °C to 17 °C during the monitoring period.

2.1.3 G. lemaneiformis farm in Nan'ao Island

The *G. lemaneiformis* farm located in the north east part of Shen'ao bay. Shen'ao bay is a semi-enclosed bay on the north of Nan'ao Island, the South China Sea. The sea area of Shen'ao bay is 13.3 km^2 with a tidal area of 5 km^2, and the average seawater depth is 3 meters. The semi-exchange rate of sea water (time period for exchanging half of the seawater) is 3 d. Aquaculture in this bay includes shellfish, seaweed and fish. Seaweed aquaculture accounts for 56% of the total aquaculture area in this bay; shellfish and fish accounts for 42% and 2%, respectively. *G. lemaneiformis* in the farm are cultivated in sea from December to May of the following year. The monitoring sites inside and outside the seaweed farm are 23°28′53″N, 117°6′24″E and 23°28′53″N, 117°6′31″E, respectively. The time period of on-site monitoring was from May 6th to May 14th, 2017, before the harvest season of *G. lemaneiformis*. This region has irregular semidiurnal, with maximum tide range of 279 cm and average tidal range of 129 cm. The average flood and ebb tide duration is 430 and 315 min, respectively. The heading between the farm and control sites was selected to be orthogonal to the current direction, with a prevailing southeast-northwest direction and 2 - 10 cm s^{-1} speed in this bay in spring. According to national monitoring annual report, the seawater quality of this region in 2017 was class I (Inorganic Nitrogen < 0.2 mg L^{-1}, and Orthophosphate < 0.015 mg L^{-1}) (SOA, 2018). The salinity ranged from 30 to 32 ‰, and temperature ranged from 25 to 27 °C during the monitoring period.

2.2 In-site and on-line monitoring of seawaters

At the seaweed aquaculture and control sites, two multi-parameter water analyzers (YSI EXO2, YSI Inc., USA) equipped with probes including the "EXO Optical DO", "EXO pH", "EXO Chlorophy II + BGA-PE", "EXO Turbidity" and "EXO Wiped Cond / Temp" probe etc. and two temperature and light recorders (UA-002-64, Onset HOBO Inc., USA) were deployed to perform in-site and on-line continuous monitoring. The real-time monitoring parameters included seawater temperature, salinity, dissolved oxygen (DO), pH, chlorophyll a, turbidity and conductivity. All probes were calibrated before the on-site monitoring. NIST buffer (pH 4.0, 7.0 and 10.0), FWT 25 rhodamine WT solution, turbidity standard solutions (100 NTU) and YSI 3167 Conductivity Calibrator (1000 microsiemens/cm) were used to calibrate the pH probe (Krause-Jensen et al., 2015), Chlorophyll and BGA-PE probe, turbidity probe and conductivity probe, respectively. Before calibration of DO sensors, the YSI water analyzers were put on top of purified water for 15 mins as recommended by the manufacture. After the on-site monitoring, the above methods were used again to record the deviation between the measurements and actual values, and the correction values were used to offset the monitoring deviation.

Dropping depth of YSI water analyzers were 1.5 m below sea level in Lidao bay, and 1.0 m in Nan'ao Island. In these two seaweed farms, the YSI water analyzers were attached on the float ropes for seaweed aquaculture. As for the seaweed farm in Fodu Island, since the *P. haitanensis* need daily dry-out from seawater, the YSI water analyzers were fixed on the bamboo poles that support the *Porphyra* rafts. The bottom of the YSI water analyzers were equal to the bottom of *Porphyra* raft and kept in seawater for the whole monitoring period. The distances between the sensors and seaweeds were approx. 50 cm in all the three farms. The light intensity was continuously monitored using a temperature and light recorder (Pendant UA-002-64, Onset Computer Corp, USA) with the light probe fixed horizontally to the middle of seaweed aquacultures. The monitoring time interval for both the YSI water analyzers and the temperature and light recorder was 1 minute.

2.3 Total alkalinity measurement

Seawater in both the seaweed farming area and control site were sampled simultaneously using two portable water samplers (Masterflex E/S Portable Sampler, Cole-Parmer Inc., USA). Plastic bottles (250 mL, Poly tetra fluoroethylene) for water samples storage were soaked in distilled water with 1% hydrochloric acid for 7 days and kept dry before sampling. Sampling depths of seawater were same as those of the YSI water analyzers, and the water samples were overflowed for approx. two volumes of the plastic bottle (500 ml) before taking samples in triplicates. The sampling interval was 1 hour for experiment sites of Nan'ao Island and 1 - 3 hours for Lidao Bay depending on the weather conditions during the entire monitoring period. For the experiment of *P. haitanensis* farm in Fodu Island, Zhoushan, Zhejiang Province, limited by the prolonged rainy weather, we didn’t manage to take seawater samples in an equal time interval. Totally 12 seawater samples were collected during the monitoring period.

Water samples were placed in a 4 °C incubator, and transported quickly to a laboratory inside the farms to determine the total alkalinity of seawater, following the national standard method in China - " The Specifications for Oceanographic Survey Part 4: Survey of chemical parameters in sea water" (GB / T 12763-2007). Briefly, 25 mL of seawater sample was titrated with standard hydrochloric acid solution to pH range from 3.40 to 3.90, and the pH value after titration and the volume of standard hydrochloric acid solution added were recorded. The concentration of hydrochloric acid solution was calibrated by titration method using 15 mL of 0.01mol/L $NaCO_3$ solution, with methyl red methylene blue mixed as indicator.

The total alkalinity was calculated as following:

$$\mathrm{A} = \frac{V_{HCl} \times c(HCl)}{V_W} \times 1000 - \frac{\alpha_{H^+} \times (V_W + V_{HCl})}{V_W \times f_{H^+}}$$

where A is the total alkalinity of seawater samples, mmol/L; c(HCl) is the concentration of standard hydrochloric acid solution, mol/L; V_W is the volume of seawater sample, cm^3; V_{HCl} is the volume of standard hydrochloric acid solution, cm^3; $\alpha_H{}^+$ is the activity of hydrogen ions corresponding to pH of the determined solution; $f_H{}^+$ is the activity coefficient of hydrogen ions.

2.4 Seawater carbon system (Ω_{arag}, Ω_{Cal} and pCO2)

Aragonite and calcite saturation (Ω_{arag}, Ω_{Cal}) and partial pressure of carbon dioxide (pCO_2) were calculated using the online monitoring time series data of pH and averaged value of the total alkalinity for the entire monitoring period as inputs, using the CO_2SYS Excel program version 2.1 (Krause-Jensen et al., 2015; Pierrot and Wallace, 2006).

2.5 Statistical Analysis

The obtained data were presented as mean ± standard error. Differences between groups were analyzed by t-test or Kolmogorov-Smirnov test. $p < 0.05$ was considered statistically significant. All statistical analyses were performed using the R software.

3 RESULTS

The seaweed yield in three farms varied greatly and ranged from 390 to 24000 Tons FW Km^{-2} $Year^{-1}$, with the *P. haitanensis* farm at Fodu Island supporting the lowest yield, harvested in the fall, more than five to six-fold below the yield of *G. lemaneiformis* and *S. japonica*, which were harvested in late spring (Table 1). Water temperature and salinity at the time of sampling ranged widely among seaweed farms (Table 2).

The seawater pH was consistently elevated in seaweed farm compared to adjacent waters away from the farm (Figs. 2 and 3), with the difference in pH being largest for the *S. japonica* farm (mean ± SE= 0.10 ± 0.003), compared to differences of 0.026 ± 0.003 and 0.036 ± 0.003 in the *P. haitanensis* and *G. lemaneiformis* farms, respectively (Tables 1 and 2). At harvest, the biomass to water volume ratio of seaweed was 16000, 6160 and 780 g FW m^{-3} for *G. lemaneiformis*, *S. japonica* and *P. haitanensis*, respectively. This is consistent with a depletion of pCO_2 in surface waters in the seaweed farms compared to adjacent waters away from the farm (Table 2), with the deficit in pCO_2 in waters in seaweed farms relative to control waters, averaging 58.7 ± 15.9 μatm, ranging from 27.3 to 113.9 μatm across farms (Table 2, Fig. 3). The saturation state for aragonite and calcite (Ω_{arag} and Ω_{cal}) was also higher in seaweed farm waters compared to adjacent waters away from the farm (Fig. 3, Fig. 4). Both the elevated pH and reduced pCO_2 in seaweed farm waters compared to adjacent waters away from the farm did not differ between day and night samples ($p > 0.05$, Fig. 5).

Oxygen concentrations also tended to be elevated in the seaweed farms compared to adjacent waters away from the farm (Fig. 3), with the excess O_2 in the seaweed relative to control waters, which averaged 0.22 ± 0.4 mg L^{-1}, ranging from 0.02 mg L^{-1} to 0.35 mg L^{-1} across farms (Table 2). Oxygen was higher inside the seaweed farms compared to surrounding waters, although this pattern was only consistent during the day (Fig. 3).

4 DISCUSSION

4.1 The synthesized buffering effects of seaweed farming to ocean acidification

The results presented show consistent changes in carbon system parameters in the waters within seaweed farms, resulting from the photosynthetic activity of the algae. pH, Ω_{arag} and Ω_{cal} are elevated inside seaweed farms, whereas pCO_2, is reduced. Oxygen levels were also elevated within seaweed farms, although the extent of the effect was somewhat lower than that in carbon-system parameters, due to the much faster air-water equilibration for O_2 compared to CO_2. As a result, seaweed-induced changes in O_2 were equilibrated through air-sea exchange faster than those of CO_2. There were differences between species and farms. The largest pH increase was found in the *S. japonica* farm with the highest yield and photosynthesis rate. The effect was smallest for the *P. haitanensis* farm, which supported the lowest biomass and where the study was conducted in November, the time of harvest.

These results are consistent with previous reports of depleted surface pCO_2 in seaweed farms, with sea surface pCO_2 on average, 21 µatm lower in a Chinese seaweed farm compared to control areas (Jiang et al., 2013). These findings demonstrate that the net primary production of seaweed farms acts as an important sink of CO_2, supporting suggestions that seaweed farms can provide refugia from ocean acidification at reported rates of 0.017-0.027 unit per decade since the late 1980s (Duarte et al., 2017; IPCC, 2019). Calcifying organisms, including bivalves, that are particularly vulnerable to ocean acidification (Kroeker et al., 2013) can, therefore, benefit from this effect. In addition, co-culture of bivalves and seaweed aquaculture in multitrophic aquaculture systems can protect the bivalves from ocean acidification (Fernández et al., 2019; Han et al., 2020), while also mitigating the impacts associated to nutrient release from the bivalves.

4.2 The pH increases and fluctuations in seaweed farms and its environmental significance

As compared to adjacent waters away from farm, the pH within seaweed farms was elevated by all three species, by 0.026-0.100 units. A 0.1 unit of pH increase is expected to increase the calcification rate of mussel by 13.5 % (e.g., when pH increased from 7.8 to 7.9) (Wahl et al., 2018).

Respiratory CO_2 production in beds of the California mussel (*Mytilus californianus*) were reported to decrease pH by 0.010-0.029 units compared to the surrounding bulk seawater (Ninokawa et al., 2020). Therefore, seaweed farms in theory are capable to offset the impact of CO_2 production by dense assemblages of marine heterotrophic organism on pH. The pH increase within seaweed aquaculture was slightly lower than those for the benthic habitats in a subarctic fjord of Greenland, including kelp forest, vegetated tidal pools, adjacent vegetated shores etc., which was up to 0.2-0.3 unit (Krause-Jensen et al., 2015). But still, the buffer effect of seaweed in the aquaculture farms reported here would be sufficient to locally offset the pH decrease resulting from several decades of ocean acidification, reducing ocean pH at reported rates of 0.017-0.027 unit per decade since the late 1980s (IPCC, 2019). According to the IPCC, a reduction of 0.065 pH units would be expected in the end-of-century 2100 under the high mitigation future scenario (RCP 2.6), that is most consistent with the goals of the Paris Agreement (IPCC, 2019). Thus, the pH elevation capacity of seaweed farms would suffice to locally offset the predicted pH reduction. Even under a high emission future (scenario RCP 8.5), in which a 0.108 pH unit reduction would be expected by 2050 (IPCC, 2019), *S. japonica* farms would most likely balance the pH reduction in adjacent seawaters. In addition, seaweed tend to response positively to the elevated pCO_2 , which would allow for increased productivity (Krause-Jensen et al., 2016), which, in turn, would fix extra CO_2 and lead to further pH increase, providing refugia for marine organisms from ocean acidification (Hofmann et al., 2011).

Intense fluctuations in pH were observed in the seaweed aquaculture farms, which are similar to those of natural system induced by tidal water exchange. The ranges of the pH variability within seaweed farms spanned 0.14-0.30 unit during the monitoring period. These ranges are slightly lower than those reported for two kelp forests in California, which was 0.259 and 0.544 unit, respectively

(Hofmann et al., 2011). However, the seaweed aquacultures are flexible and scalable in spatial planning compared to the fixed location of natural seaweed systems. In fact, pH fluctuations are considered to offer an adaption opportunity to calcifiers, increasing their adaptive potential to a future marine environment with lower pH and/or more frequent pH fluctuations (Hendriks et al., 2015; Hurd, 2015; Ramajo et al., 2019). pH fluctuations would also help the seaweed themselves, i.e. coralline algae, to response to acidification compared to expectations under static pH condition (Cornwall et al., 2013b).

Compared to adjacent waters, the elevated pH in seaweed farm waters did not differ between day and night. This observation reflects the slow air-sea diffusion rate of CO_2, which is approximately 10 times slower than O_2, which leads to long equilibration times of CO_2 compared to O_2. Indeed, studies of the effects of coastal algal blooms on pCO_2 have demonstrated a persistent footprint, whereby the drawdown signal may persist three months following the bloom (Gazeau et al. 2005). CO_2 is consumed by seaweed during the daytime, resulting in the seawater carbonate balance moving towards a raised pH in the day. Because the seaweed farm community is autotrophic, as evidenced by the biomass accretion over time supporting the harvest, CO_2 drawdown during the daytime is not compensated by respiratory CO_2 release at night. The observation that pH remains elevated overnight implied that respiratory production during the night is lower than net photosynthetic uptake during the daytime, which follows the autotrophic nature of seaweed (Duarte et al., 1996), with the positive net production supporting growth. Indeed, field examinations of pH fluctuations in wild seaweed stands typically shows elevated values maintained through day-night fluctuations in pH (Cornwall et al., 2013a; Krause-Jensen et al., 2015; Murie and Bourdeau, 2020; Pfister et al., 2019). Therefore, the pH remains slightly higher in the farm as compared to the control area at night. Under the laboratory simulated no or low water flow (0-0.015 m s^{-1}), pH was found to rise by 0.5 pH unit under light and decrease by 0.35 pH unit in the darkness in the surface of coralline seaweed *Sporolithon durum* (Hurd et al., 2011), and the range of pH observed was 0.15 units higher in the light than the dark condition for the turf-forming coralline alga *Arthrocardia corymbosa* (Cornwall et al., 2013b). The laboratory measurement on the surface layer of algae with distance of up to 70 mm (Cornwall et al., 2013b), provide a precise micro-scale investigation into the pH variations in the concentrated diffusion boundary layer. Nested scales of pH variability have also been documented for Kobbefjord, a subarctic Greenland fjord supporting kelp beds, involving pH changes ranging from 0.2 to 0.85 units across spatial scales (Krause-Jensen et al., 2015).

Indeed, field observation, such as those reported here, reflect the actual capacity of seaweed aquaculture to affect the seawater carbonate system, under existing hydrodynamic conditions and metabolic forcing, compared to the artificial conditions in laboratory simulations. For instance, the pH increase attributable to Greenland kelp forest *in situ* of 0.15 unit was much lower than that observed in laboratory mesocosms (Krause-Jensen et al., 2016). Indeed, laboratory experiments cannot fully reproduce the large number of concurrent processes affecting both the carbon system and metabolic processes in the field, which may lead to results difficult to extrapolate to the ecosystem level (Koweek et al., 2017; Krause-Jensen et al., 2015; Wahl et al., 2018). In turn, the comparison between farm and control sites was also affected by environmental variability affecting the diffusion of CO_2 and O_2 and nutrient supply, which regulates the productivity of the seaweed.

4.3 The influence of seaweed farming on the seawater carbonate chemistry

pH variation in macroalgal habitats has been the subject of a number of studies (Cornwall et al., 2013b; Frieder et al., 2012; Hurd et al., 2011), but much less is known about the influence of macroalgae on the CO_2 system of seawater (Koweek et al., 2017; Krause-Jensen et al., 2015). Values of Ω_{arag} were over 1 for all seawaters monitored, suggesting oversaturation with respect to aragonite in general along Chinese coasts. Similar to previous studies on macrophyte habitats (Krause-Jensen et al., 2015), the seaweed farms induced an increase in the Ω_{arag} of 0.10 unit on average, consistent with changes in pH and CO_2. The values were also consistent with predicted results by a precise numerical modelling approach on seaweed farm (Mongin et al., 2016). The *S. Japonica* farming showed the largest Ω_{arag} increase of 0.29 unit, corresponding to the highest photosynthesis rate (F_v/F_m: 0.65, photosynthesis efficiency: 0.252 μmol electrons m^{-1} s^{-2}) among all three seaweed species. The other seaweed species *P. haitanensis* with high photosynthesis rate, however, showed a limited increase in Ω_{arag}, probably restricted by the extremely low biomass density (780 g FW m^{-3}) which was 5% to 12% of those for the *G. lemaneiformis* and *S. Japonica* farms. In addition, the water exchange rate in the *P. haitanensis* farm (30 – 110 cm s^{-1}) was the highest among all farming regions. The faster current velocities tend to eliminate the biological effects raised up by seaweed farming quicker. Due to the expansion of the Changjiang diluted water, the salinity of *P. haitanensis* farm (24 ‰) is dramatically lower than the other two farms (30 – 32 ‰), contributing to the highest pCO_2 in Fodu Island (480 μatm and 447 μatm for the control and seaweed site, respectively). The pCO_2 in Nan'ao Island was lowest (306 μatm and 271 μatm for the control and seaweed site, respectively), supporting by the highest water temperature and lowest latitude distribution. Therefore, the carbon limitation in Nan'ao Island would also potentially reduce the extend of pH increase in the *G. lemaneiformis* farm, in addition to the physiological restriction of this species.

The co-culture of seaweed and shellfish has been proposed to remove surplus nutrients and reduce the environmental impact of mariculture (Troell et al., 2009). Seaweed farming has been shown to efficiently absorb excess nutrient and mitigate against eutrophication (Chebil Ajjabi et al., 2018; Ge et al., 2019; Jiang et al., 2020; Wahl et al., 2018; Wei et al., 2019; Xiao et al., 2017; Xiao et al., 2019; Xie et al., 2017). However, the effects of seaweed farming on calcifying organisms mediated by their role in elevating pH and Ω_{arag} have not been yet addressed. A recent study of mussel growth in micro-patches of *Fucus* (seaweed) and *Zostera* (seagrass), reported no significant difference in pH, oxygen, and mussel growth in macrophyte habitats compared to non-vegetated sand patch (Wahl et al., 2018). However, mussel with a biomass density of 1.64 kg m^{-2} was able to decrease pH by 0.1 unit, which has counterbalanced the maximum pH increase by seaweed documented in this study. Therefore, more research is needed to test the hypothesize benefits of seaweed farming on the growth of calcifying organisms.

Likewise, field observations on the capacity of seaweed farms to buffer the ocean acidification were still lacking. Laboratory simulations can be largely biased due to simplified environmental conditions, as shown by Ninokawa et al (2020) for California mussel (*Mytilus californianus*) bed. A decrease of up to 0.1 unit of pH was documented in the lab inside the mussel bed, as compared to the surrounding bulk seawater (Ninokawa et al., 2020). However, in the field, decreases in pH of 0.010, 0.029, and 0.022 units were detected for mussel beds, are much lower than expected (0.020 - 0.126) from laboratory observations (Ninokawa et al., 2020). Hence our results, based on sampling commercial seaweed farms, provide compelling support for the hypothesized capacity of seaweed farms to remove CO_2 and raise pH and the saturation state for aragonite and calcite (Ω_{arag} and Ω_{cal}) on a local scale - but with a scalable potential. And consequently, our results support the role of seaweed farms as an instrument providing refugia and, therefore, adaptive capacity to ocean acidification due to their flexibility to be allocated to vulnerable areas in marine spatial planning

(Alleway et al., 2018; Duarte et al., 2017; Froehlich et al., 2019).

Our results involve a number of limitations that need be considered in designing future studies to further resolve the role of seaweed farms in locally mitigating ocean acidification and deoxygenation. Notably, due to the limitation of field monitoring and site conditions, only one control and farm, each characterized by a single set of sensors, were used for collection of data at each seaweed farm, therefore lacking replication, and distances from seaweed point to control point differed considerably in the three seaweed farms. In addition, the background water quality conditions differed greatly among sites, as did current conditions, which would affect the strength of the signal from the seaweed farms. These were also sampled at different seasons, imposed by the timing of maximum biomass and harvest among the cultured species, with the consequence that the proportion of light to dark hours and, consequently of dominance of photosynthesis and respiration differed substantially. For instance, the farm and control sites were set along a line orthogonal to the prevailing direction of currents, to avoid advective influences between these two sites. However, wind would impact the flow direction of the currents, and it is, therefore, possible that some advective influences between the water masses in the two stations may have occurred, which would lead to underestimating the effects of the seaweed farm. Specifically, although we set control sites 200 meters away from the edge of the farm, the distance between the farm and control sites in the Lidao Bay was ~ 3.8 km, because of the large size of the farm, which may induce considerable differences in the baseline conditions between these two sites.

5 CONCLUSIONS

In conclusion, our field observations of seawater carbonate chemistry characteristics confirmed the capacity of seaweed farming to raise pH, O_2 and Ω_{arag} and remove CO_2 in seawater in a natural large-scale setting. The most efficient farm was that of the *S. Japonica* due to their high photosynthetic rate and high biomass density, raising seawater pH by 0.100 within the seaweed farm. Thus, our research supports the hypothesis that seaweed farming can provide local adaption to ocean acidification and deoxygenation.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (21677122 & 21876148) and Fundamental Research Funds for the Central Universities (2019QNA4051) to X.X., Long-Term Observation and Research Plan in the Changjiang Estuary and the Adjacent East China Sea Project (LORCE, 14282) to J.Z. We thank Mr. Xiaojun Yang and staffs at the Shandong Li'dao Marine Technology Co., Ltd., Mr. Shixiang Ke and staffs at the Zhoushan Risheng Mariculture Co., Ltd., staffs at the Nan'ao coastal laboratory of Shantou University for support in performing on-site measurements and water sample collection, and Dr. Anzhou Cao at Ocean College, Zhejiang University for support in the oceanographical background information of the seaweed farms.

AUTHOR CONTRIBUTIONS

CMD and XX conceptualized the study. YY, YH, WC, CL, JH, KL, FW, YL, ZC, SL, JL and WW contributed original survey data. XX, YY, SA and CMD performed the statistical analyses and wrote the original draft of the manuscript. All authors reviewed and edited the manuscript.

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Table 1. The initial cultivation density, biomass, yield and harvest time of seaweed in three seaweed farms and the timing of on-site monitoring.

	Nan'ao Island	Lidao Bay	Fodu Island
Seaweed species	*G. lemaneiformis*	*S. japonica*	*P. haitanensis*
Initial Density (T FW km^{-2})	3200	1190	NA [1]
Biomass (T FW $farm^{-1}$)	60	82000	39
Yield (T FW km^{-2} $Year^{-1}$)	24000	15400	390
Yield (T DW km^{-2} $Year^{-1}$)	2540	2200	39
Biomass density (g FW m^{-3})	16000	6160	780
F_v/F_m [2]	0.44	0.65	0.60
Photosynthetic efficiency α (μmol electrons m^{-1} s^{-2})	0.160	0.252	0.250
FW/DW [3]	9.45	7.00	10.00
Starting date of harvest	15th, May	14th, Jun	28th, Nov
Dates of monitoring	10th-14th, May	3rd-12th, Jun	15th-27th, Nov

[1] The seed of *Porphyra* were on the rope and too small to estimate the density.

[2] The maximum PSII photochemical efficiency.

[3] Data derived from either our experiment or estimation from seaweed farm.

Table 2. The physical and chemical characteristics of seawater in the seaweed aquaculture and control sites in three seaweed farms.

		Total [2]		Day [2]		Night [2]	
		Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Nan'ao control	Temperature (°C)	25.69 ± 0.00	24.97-26.53	25.72 ± 0.01	25.09-26.53	25.66 ± 0.01	24.97-26.23
	Salinity(‰)	30.13 ± 0.01	28.55-31.47	30.09 ± 0.01	28.55-31.47	30.17 ± 0.01	28.70-31.07
	pH	8.12 ± 0.00	8.02-8.21	8.12 ± 0.00	8.02-8.21	8.12 ± 0.00	8.03-8.18
	DO ($mg \cdot L^{-1}$)	7.25 ± 0.01	5.56-9.12	7.31 ± 0.01	5.56-9.12	7.17 ± 0.01	5.67-8.38
	Total alkalinity ($\mu mol\ Kg^{-1}$)	2021.14 ± 5.48	1957.49-2258.41	2017.4 ± 4.9	1957.56-2090.74	2026.84 ± 11.65	1977.88-2258.33
	pCO_2 (μatm)	305.84 ± 0.48	232.87-405.23	304.41 ± 0.69	232.87-405.23	307.23 ± 0.65	253.39-389.28
	Ω_{Cal}	5.07 ± 0.01	4.19-6.04	5.09 ± 0.01	4.19-6.04	5.04 ± 0.01	4.32-5.71
	Ω_{arag}	3.31 ± 0.00	2.72-3.94	3.32 ± 0.00	2.72-3.94	3.29 ± 0.00	2.82-3.72
Nan'ao seaweed farm	Temperature (°C)	25.73 ± 0.00	25.08-26.96	25.75 ± 0.01	25.09-27.03	25.72 ± 0.01	25.08-26.21
	Salinity(‰)	29.92 ± 0.01	28.64-30.71	29.91 ± 0.01	28.64-30.71	29.94 ± 0.01	28.74-30.63
	pH	8.15 ± 0.00	8.04-8.31	8.16 ± 0.00	8.04-8.31	8.14 ± 0.00	8.05-8.21
	DO ($mg \cdot L^{-1}$)	7.41 ± 0.01	5.67-10.34	7.57 ± 0.02	5.67-9.86	7.19 ± 0.01	5.86-8.15
	Total alkalinity ($\mu mol\ Kg^{-1}$)	1973.97 ± 9.3	1725.99-2129.99	1960.39 ± 11.46	1726.01-2090.84	1995 ± 14.79	1912.93-2129.96
	pCO_2 (μatm)	270.66 ± 0.54	177.65-588.21	265.10 ± 0.77	177.65-481.88	277.28 ± 0.71	226.79-588.21
	Ω_{Ca}	5.26 ± 0.01	4.23-6.57	5.33 ± 0.01	4.23-6.57	5.17 ± 0.01	4.31-5.76
	Ω_{arag}	3.43 ± 0.00	2.75-4.29	3.48 ± 0.01	2.75-4.29	3.37 ± 0.00	2.80-3.76
	ΔpH [1]	0.04 ± 0.00	-0.03-0.19	0.04 ± 0.00	-0.05-0.18	0.03 ± 0.00	-0.03-0.10
Lidao control	Temperature (°C)	16.66 ± 0.00	15.65-17.89	16.68 ± 0.00	15.65-17.89	16.63 ± 0.00	15.73-17.40
	Salinity(‰)	32.23 ± 0.00	31.89-32.39	32.23 ± 0.00	31.97-32.39	32.23 ± 0.00	31.89-32.35
	pH	8.02 ± 0.00	7.91-8.12	8.02 ± 0.00	7.92-8.12	8.02 ± 0.00	7.91-8.11
	DO ($mg \cdot L^{-1}$)	8.63 ± 0.00	7.37-9.94	8.67 ± 0.01	7.38-9.94	8.56 ± 0.01	7.37-9.79
	Total alkalinity ($\mu mol\ Kg^{-1}$)	2291.8 ± 3.9	2158.61-2360.01	2292.69 ± 4.59	2172.77-2347.62	2290.43 ± 7.12	2158.6-2360

	pCO_2 (μatm)	432.84 ± 0.38	328.89-577.41	430.05 ± 0.47	328.89-562.53	437.66 ± 0.64	338.04-577.41
	Ω_{Ca}	3.60 ± 0.00	2.00-4.41	3.61 ± 0.00	1.96-4.41	3.56 ± 0.00	2.91-4.31
	Ω_{arag}	2.30 ± 0.00	1.87-2.83	2.32 ± 0.00	1.89-2.83	2.28 ± 0.00	1.87-2.76
Lidao seaweed farm	Temperature (℃)	14.98 ± 0.00	13.98-16.05	14.95 ± 0.01	13.98-16.05	15.03 ± 0.01	13.99-15.98
	Salinity(‰)	31.90 ± 0.00	31.51-32.29	31.90 ± 0.00	31.51-32.29	31.90 ± 0.00	31.55-32.18
	pH	8.12 ± 0.00	8.00-8.18	8.12 ± 0.00	8.00-8.18	8.12 ± 0.00	8.09-8.17
	DO ($mg \cdot L^{-1}$)	8.83 ± 0.00	8.18-9.93	8.82 ± 0.00	8.18-9.93	8.84 ± 0.01	8.30-9.62
	Total alkalinity (μmol Kg^{-1})	2322.92 ± 3.42	2184.66-2388.69	2325.54 ± 4.29	2248.85-2388.68	2316.4 ± 7.12	2184.67-2383.14
	pCO_2 (μatm)	325.78 ± 0.15	276.27-393.33	326.98 ± 0.18	276.27-393.33	323.76 ± 0.24	284.13-355.37
	Ω_{Ca}	4.05 ± 0.00	3.12-4.56	4.04 ± 0.00	2.32-4.56	4.08 ± 0.00	3.77-4.48
	Ω_{arag}	2.59 ± 0.00	2.24-2.91	2.58 ± 0.00	2.24-2.91	2.60 ± 0.00	2.40-2.86
	ΔpH	0.10 ± 0.00	-0.03-0.21	0.10 ± 0.00	-0.03-0.20	0.11 ± 0.00	0.01-0.21
Fodu control	Temperature (℃)	17.54 ± 0.01	8.42-20.98	17.82 ± 0.02	8.42-20.98	17.30 ± 0.02	8.66-19.56
	Salinity(‰)	24.15 ± 0.00	19.52-24.94	24.17 ± 0.00	19.52-24.94	24.16 ± 0.00	20.34-24.86
	pH	8.03 ± 0.00	7.98-8.08	8.02 ± 0.00	7.98-8.08	8.03 ± 0.00	7.99-8.08
	DO ($mg \cdot L^{-1}$)	8.14 ± 0.00	7.47-10.00	8.10 ± 0.00	7.47-10.24	8.18 ± 0.00	7.66-10.13
	Total alkalinity (μmol Kg^{-1})	2298.98 ± 47.52	2122.15-2461.87	2283.67 ± 71.68	2122.25-2461.98	2329.5 ± 40.55	2288.95-2369.95
	pCO_2 (μatm)	480.80 ± 0.16	406.81-543.25	482.54 ± 0.22	406.81-543.25	479.76 ± 0.23	407.04-527.94
	Ω_{Ca}	3.41 ± 0.00	2.34-3.96	3.44 ± 0.00	2.34-3.96	3.39 ± 0.00	2.67-3.62
	Ω_{arag}	2.13 ± 0.00	1.41-2.50	2.15 ± 0.00	1.41-2.50	2.11 ± 0.00	1.63-2.27
Fodu seaweed farm	Temperature (℃)	16.11 ± 0.02	8.41-24.87	17.00 ± 0.03	8.41-24.87	15.35 ± 0.03	8.41-19.54
	Salinity(‰)	24.12 ± 0.01	15.03-24.96	24.21 ± 0.00	22.66-24.96	24.04 ± 0.01	15.03-24.93
	pH	8.05 ± 0.00	7.97-8.11	8.05 ± 0.00	7.99-8.11	8.06 ± 0.00	7.97-8.11
	DO ($mg \cdot L^{-1}$)	8.45 ± 0.00	7.48-10.18	8.36 ± 0.01	7.53-11.10	8.53 ± 0.01	7.48-10.11
	Total alkalinity (μmol Kg^{-1})	2308.55 ± 50.36	2121.75-2420.76	2271.39 ± 69.41	2121.87-2420.9	2383.11 ± 27.68	2355.43-2410.8
	pCO_2 (μatm)	447.37 ± 0.26	376.83-558.19	455.18 ± 0.33	379.85-529.21	441.10 ± 0.39	376.83-558.19

Ω_{Ca}	3.43 ± 0.00	2.54-4.37	3.50 ± 0.00	2.54-4.37	3.37 ± 0.00	2.66-3.76
Ω_{arag}	2.13 ± 0.00	1.55-2.78	2.18 ± 0.00	1.55-2.78	2.09 ± 0.00	1.63-2.36
ΔpH	0.03 ± 0.00	-0.04-0.11	0.02 ± 0.00	-0.03-0.08	0.03 ± 0.00	-0.04-0.11

[1] ΔpH represents the pH difference between seaweed aquaculture and control sites.

[2] Total, day and night represent for the entire monitoring period, day and night period, respectively.

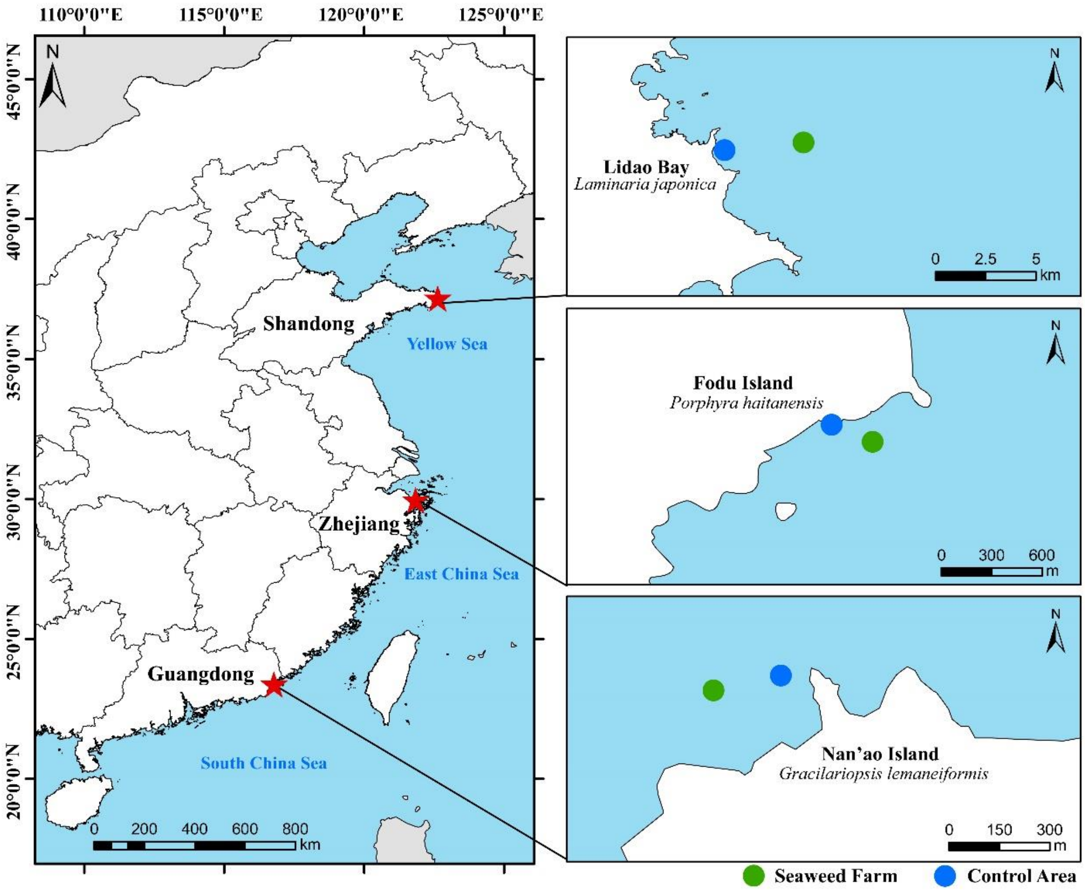

Figure 1. Locations of seaweed farms, including a *S. japonica* farm in Lidao Bay, a *P. haitanensis* farm in Fodu Island and a *G. lemaneiformis* farm in Nan'ao Island (green dots: the monitoring sites inside seaweed aquaculture area, blue dots: the control sites).

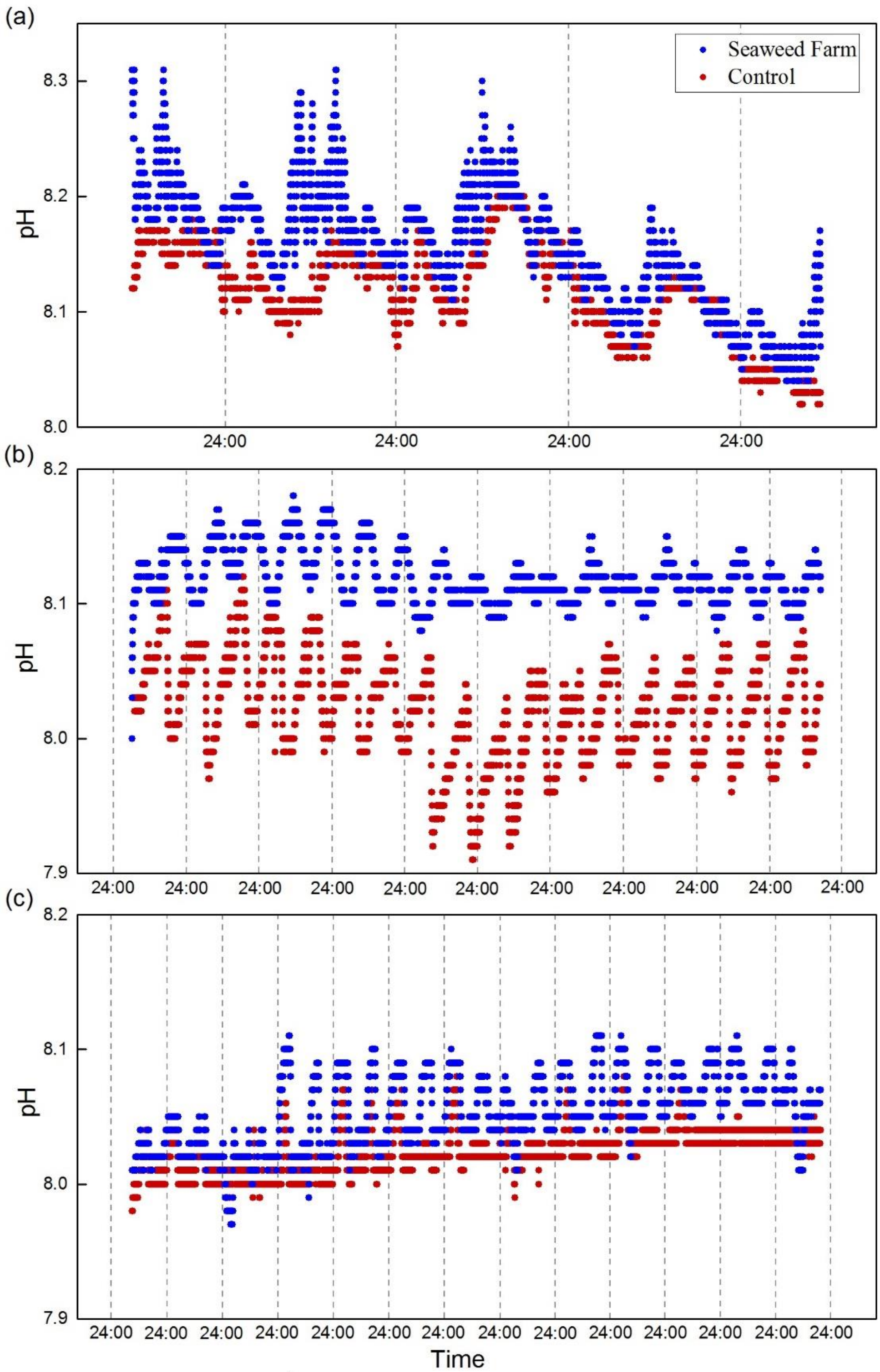

Figure 2. Time line of pH in control and seaweed for three seaweed farms (a: Nan'ao Island, b: Lidao Bay and c: Fodu Island).

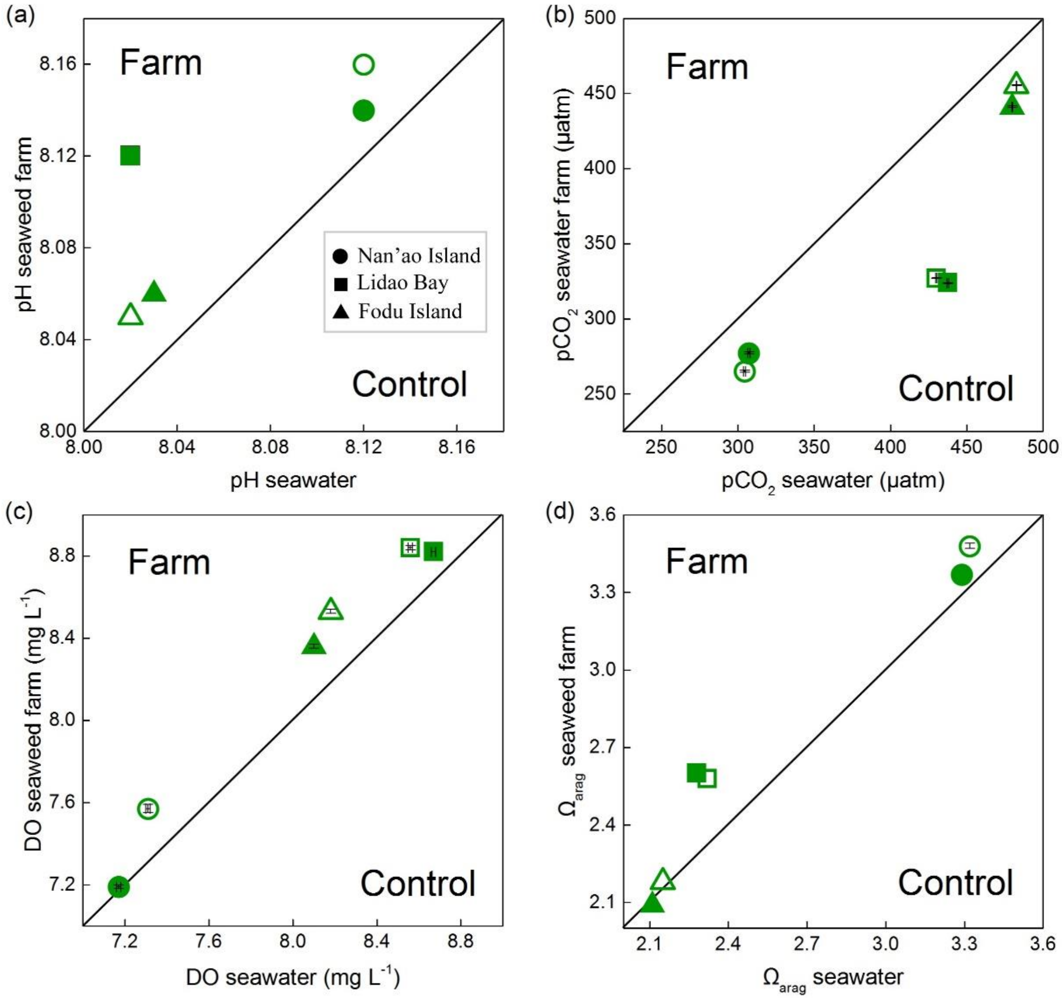

Figure 3. The relationship between water properties of seawaters in seaweed farms and control sites in Nan'ao Island (●), Lidao Bay (■) and Fodu Island (▲). The four water properties are pH (panel a), pCO_2 (b), DO (c) and Ω_{arag} (d). Open and closed symbol represent day and night values, respectively. The solid lines show the 1:1 lines. The dots above the solid line: values of the seawater properties in farm > control site; below the solid line: values of the seawater properties in farm < control site.

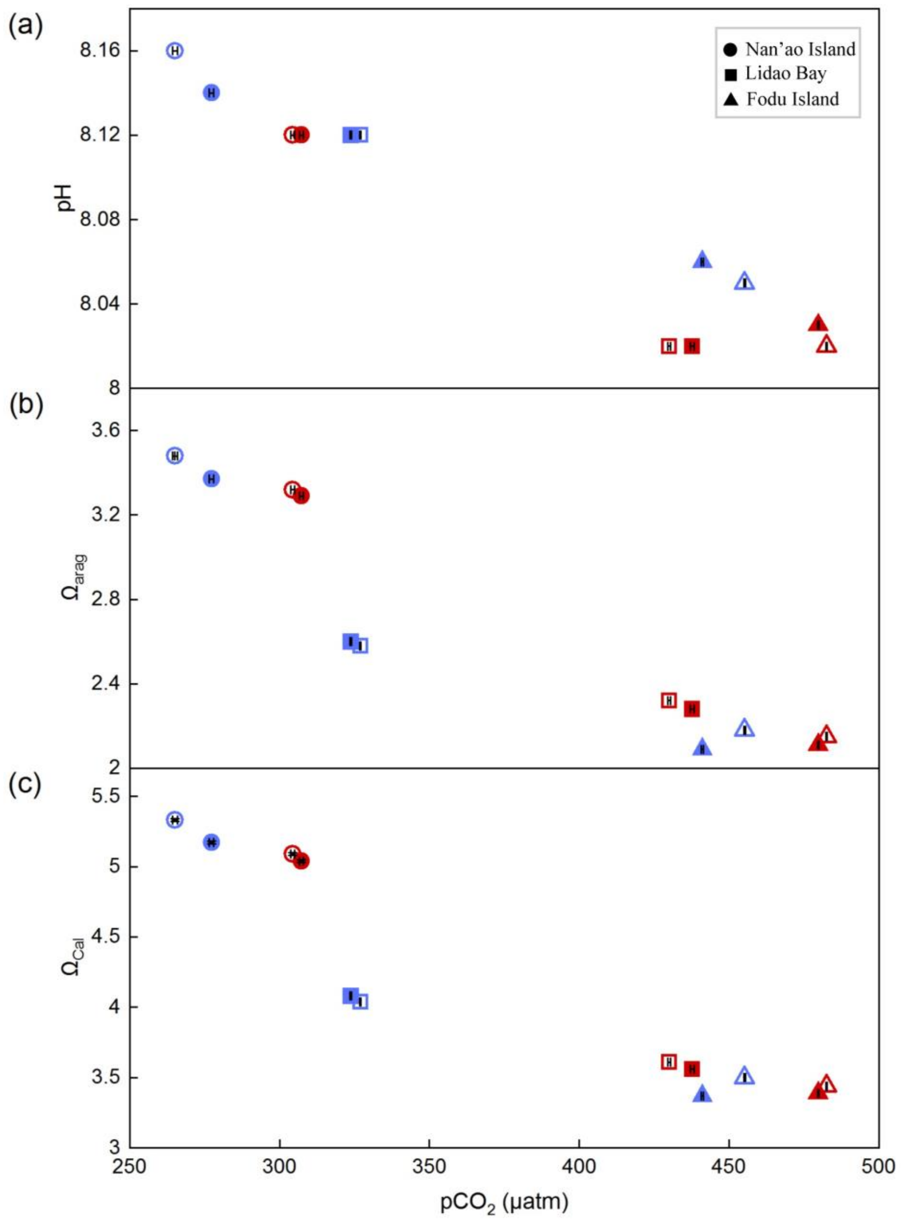

Figure 4. (a) The relationship between the pH and the pCO_2 in control and seaweed area for three seaweed farms. (b) The relationship between the Ω_{arag} and the pCO_2 in control and seaweed area for three seaweed farms. (c) The relationship between the Ω_{ca} and the pCO_2 in control and seaweed area for three seaweed farms. Open and closed symbol represent day and night values, respectively.

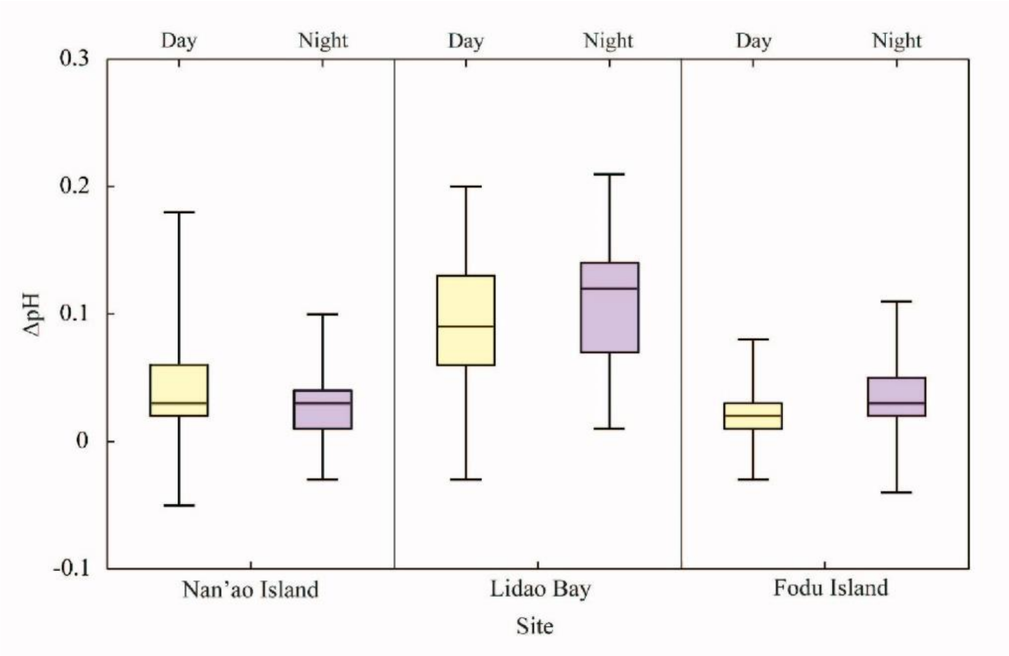

Figure 5. Boxplot of the pH difference between seaweed aquaculture and control sites (ΔpH) during day and night period in the three seaweed farms (left: Nan'ao Island, middle: Lidao Bay and right: Fodu Island). The sample size in Nan'ao Island, Lidao Bay and Fodu Island are 57065, 13635, and 17887, respectively. The line in the boxes represents the median, the boxes extend to the 25% and 75% quartiles of the data and the whiskers extend to the 95% quartiles.