Abiotic factors influencing biomass accumulation of green tide causing *Ulva* spp. on *Pyropia* culture rafts in the Yellow Sea, China

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ABSTRACT

Annually recurrent green-tides in the Yellow Sea have been shown to result from direct disposal into the sea of fouling *Ulva* from *Pyropia* aquaculture. The role abiotic factors play in *Ulva* biomass accumulation on rafts was studied to find ways to mitigate this problem. Dissolved inorganic nitrogen (DIN) was very high at all sites, but the highest *Ulva* biomass was associated with the lowest DIN and anthropogenic N. Under luxuriant background nutrient conditions, variability in temperature and periods of emersion, rather than pH, light and salinity determined *Ulva* biomass. Two dominant species of *Ulva* displayed differing tolerances to temperature and desiccation which helped explain why *Ulva prolifera* dominates floating green-tides. Rather than trying to mitigate green-tides only by reducing nutrient pollution, an earlier harvest of *Pyropia* in southern Jiangsu Province especially before temperatures increase greatly above 10 °C during April, could reduce the biomass of *U. prolifera* disposed from rafts.

1. Introduction

Macroalgal blooms resulting from the excessive growth of green algae represent a major problem for the management of coastal waterways. These phenomena are not new, being reported from nutrient enriched waters in many of the world's temperate and tropical waters since the last century (e.g. Fletcher, 1996; Morand and Briand, 1996; Valiela et al., 1997; Nelson et al., 2003; Hiraoka et al., 2004; Merceron et al., 2007). However, what has characterised macroalgal blooms in the 21st century is the sheer scale of the blooms and their occurrence in coastal and offshore areas rather than just estuaries and embayments (e.g. Morand and Merceron, 2004, 2005; D. Liu et al., 2013). The striking example is the world's largest green tides in the Yellow Sea, China. There, massive blooms of *Ulva prolifera* in excess of 2000–4000 km^2 have become a recurrent feature each summer since 2008 (Keesing et al., 2011). The costs for clean-up and emergency response to the 2008 bloom were estimated at between RMB 592 million (US$96 million, Wang et al., 2009) and RMB 2 billion (US$325 million, Ye et al., 2011) and consequential losses to aquaculture production of sea cucumbers, cockles and scallops were RMB 800 million (US$130 million) and this did not include the losses to tourism (Ye et al., 2011).

Several studies have tracked the original source of the blooms from the shallow intertidal sand flats in Jiangsu Province (Shi and Wang, 2009; Hu et al., 2010; Keesing et al., 2011), where a rapid recent expansion of *Pyropia* aquaculture has occurred since 2006 (Shang et al., 2008; Liu et al., 2009). *U. prolifera* fouls the aquaculture rafts and the accumulated biomass is disposed of as waste directly into the sea where its floats and fuelled by high levels of nutrients, undergoes rapid vegetative growth and accumulate into large patches. These join and eventually form huge floating mats which are transported north as a result of wind driven surface currents ultimately washing ashore on the Shandong Peninsula more than 200 km from their source (Liu et al., 2010; Fan et al., 2012; D. Liu et al., 2013). Liu et al. (2010) showed the original biomass of 5000 tonnes of *U. prolifera* on the rafts was sufficient to seed blooms of the magnitude observed in 2008 and 2009. Other estimates of *U. prolifera* biomass on the rafts vary from 2784 tonnes (Zhang et al., 2014) to more than 10,000 tonnes (Huo et al., 2015). Therefore, in order to find ways to mitigate the Yellow Sea green tides, it is important to understand the factors that control the growth of *U. prolifera* biomass accumulation on *Pyropia* rafts throughout the geographic range of the industry.

Liu et al. (2010) found two dominant fouling *Ulva* species (*U. prolifera* and *Ulva intestinalis*) on *Pyropia* rafts, and their biomass varied latitudinally with lowest biomass accumulation in the north (ca. < 100 kg ha^{-1}) and highest in the south (ca. 200 to 600 kg ha^{-1}). In the early stages of green-tide development, several green algal species including *U. prolifera*, *U. intestinalis* and *Ulva linza* were identified from the floating algal patches, however the subsequent massive blooms were reported to be comprised almost exclusively of *U. prolifera* (Wang et al., 2008, 2010; Ding and Luan, 2009; Luo et al., 2012; Zhao et al., 2013). Fan et al. (2015) found six species of fouling green algae on *Pyropia* rafts and

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that the dominant species shifted from *Ulva compressa*, *U. intestinalis* and *Ulva clathrata* to *Blidingia* sp. and *U. prolifera* over the course of the *Pyropia* growing season. These studies showed that more than one *Ulva* species grow on the aquaculture rafts and infer that species competition and succession occurred during the growth period on raft and early stage of green tide formation. Thus, a set of abiotic factors (e.g. temperature, nutrients, light, pH and salinity) together with factors such as time of year, raft location and the influence of the tidal cycle (emersion and immersion) were evaluated in this study to understand what determines the biomass of *U. prolifera* and other fouling species on the aquaculture rafts.

2. Materials and methods

2.1. Study sites and sampling method

Based on the growth season of green algae on *Pyropia* aquaculture rafts (Liu et al., 2010), five field surveys (mid-January, mid-February, mid-March, end-March and mid-April in 2010) were conducted at three sites along the Jiangsu Province coastline of the Yellow Sea (Fig. 1). Rafts are usually removed in late April after *Pyropia* harvest (Shang et al., 2008). The sites were chosen to cover the northern (Haitou), central (Sheyang) and southern (Rudong) distribution of *Pyropia* aquaculture. At each site, the rafts at three intertidal heights: high-intertidal (closest to shore), mid-intertidal, and low-intertidal (farthest from shore) were selected for sampling.

At each site the culture methods for *Pyropia* vary only slightly. Lines of rafts, perpendicular (Rudong) or parallel (Haitou and Sheyang) to the advance and retreat of the tide, consist of a culture net strung between rope and bamboo frame systems (Fig. 2). The type of raft used at Haitou and Sheyang consisted of paired rows of rafts with long narrow frames in which to string the culture nets and at Rudong the rafts are in single rows of shorter wide frames (Fig. 2 of main article). Actual dimensions of rafts used at each site are as follows: Haitou (length 6 m, width 2.9 m, height above sediment 0.8 m), Sheyang (4.5 m, 2.5 m and 0.75 m) and Rudong (3 m, 2.9 m and 0.75 m). The rafts are situated in the intertidal area and the substrate at each site (and intertidal height) was sand with no macroalgal vegetation. During high tide, the design of the rafts allows them to float at or near the surface. At low tide, vertical struts made of bamboo keep the frames and nets from touching the

Fig. 1. Map showing the three study locations along the coastline of Jiangsu Province and the location of tide gauge stations from which data was obtained.
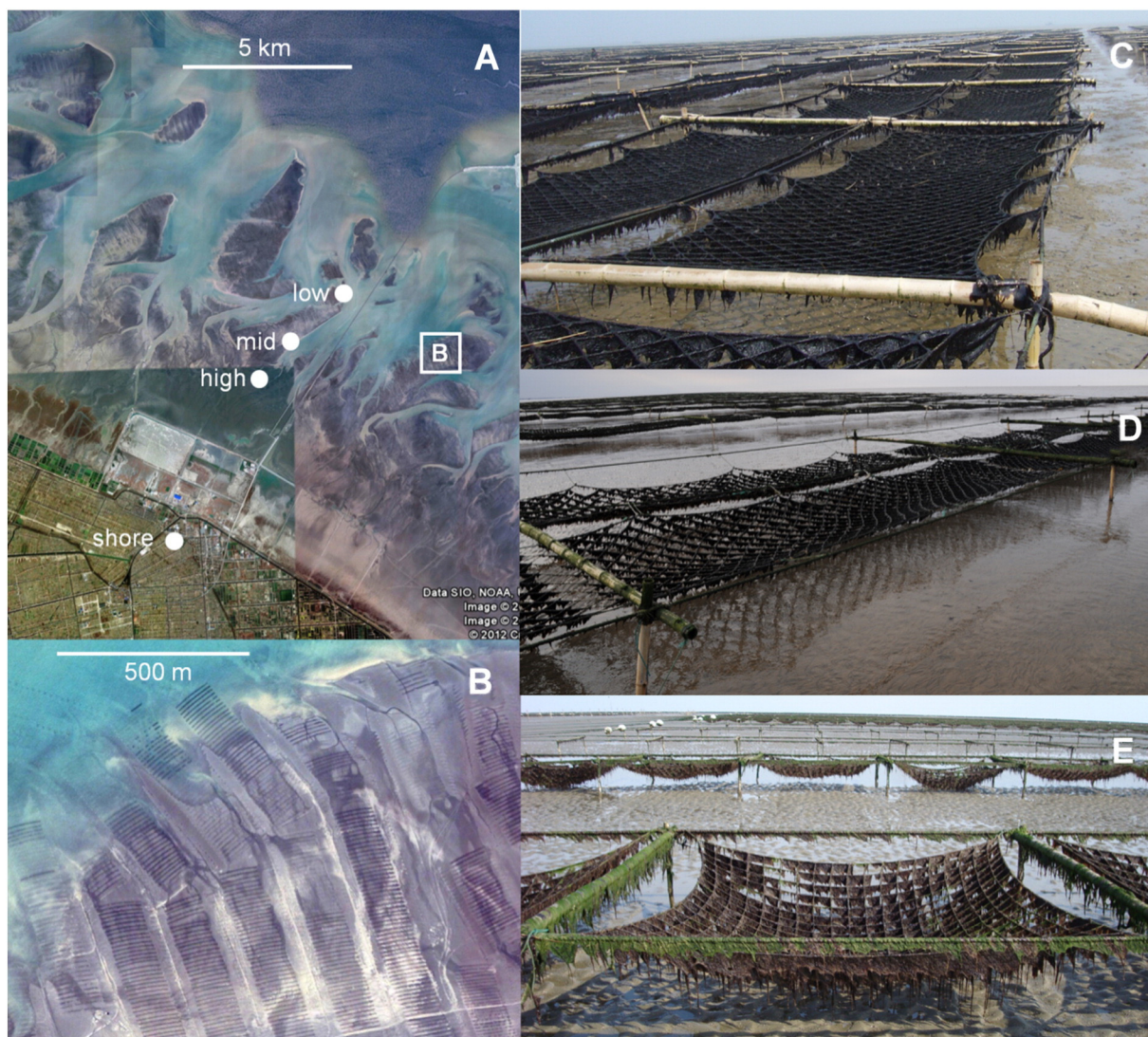
Fig. 2. Google Earth image dated 15 April 2009 showing spatial extent and concentration of *Pyropia* culture rafts off Rudong. Lower photograph B shows the detail in the inset labelled B in the upper image A. The locations of the three intertidal heights at our Rudong site are also shown as are the two types of raft construction used in *Pyropia* aquaculture at Haitou and Sheyang (C, D) and Rudong (E), respectively.

sediment. At Haitou during the neap tide the water depth at each of the high, mid and low intertidal heights was 3 m, 3.5 m and 5 m respectively. At Sheyang it was 3.5 m, 4 m and 5 m and at Rudong it was 3 m, 3.5 m and 4.5 m. The density of rafts at each site was as follows; Haitou: 300 nets per hectare, Sheyang: 270 nets per hectare and Rudong: 450 nets per hectare. The high density of rafts at Rudong extended as much as 13 km offshore (Fig. 2).

During each of the five field surveys, at each intertidal height, six rafts which had not been sampled on a previous occasion were selected at random. At Sheyang and Haitou we sampled one of the raft pairs, and at Rudong, the whole raft (Fig. 2). All green algae growing on the raft including the ropes and bamboo poles was picked or scraped off into labelled bags and placed on ice. While all sites were sampled on every field trip, not all intertidal heights could be sampled due to tide levels. The extent of sampling achieved at each site is shown as SD in Table S1. The two species of *U. prolifera* and *Ulva* cf. *intestinalis* were sorted for the measurement of wet weight, and then dried in an oven to constant weight at 60 °C for measurement of dry weight. *U.* cf. *intestinalis* sampled in this study is the same species as that described, illustrated and sequenced by Liu et al. (2010).

2.2. Measurement of temperature, light and immersion/emersion times

At the start of the experiment on 20th January 2010 we deployed four Hobo brand (model UA-002-64) light/temperature loggers at each site which recorded data every 10 min. Loggers were set on the shore above high water, and at each of the three intertidal heights (see Fig. 2). Loggers were mounted facing south on rafts at culture net height to ensure the data were collected at the same height as the algae was growing. Light sensors on the loggers were wiped clean of any fouling on a weekly basis. Logger data in lux units were converted to μmol m^2 s^{-1} using the conversion factor of 0.019 for sunlight (Sager and McFarlane, 1997) and were used to calculate the maxima, minima and mean temperature and light exposure of rafts.

These parameters were derived for periods of night and day (light > 0 μmol m^2 s^{-1}) and immersion and emersion for each sampling interval. The periods of emersion and immersion were calculated by comparing light and temperature data for loggers on the rafts with those on shore and using tide tables. Tide heights and times used were for nearby ports: Lianyungang Harbour (close to Haitou), Sheyang River mouth (Sheyang) and Xiaoyang Harbour (Rudong).

2.3. Measurement of pH, salinity and nutrients and algal nitrogen isotopic signatures

Replicate 200 mL seawater samples were collected at each intertidal height at each site on each sampling occasion. Where the tide was low the water sample collected from tidal pools as close to the sampled intertidal height as possible. During April, samples of the two *Ulva* spp. and *Pyropia* were collected at each site from high, mid and low-intertidal rafts to analyse for nitrogen isotopic content. Opportunistic sampling of water quality and of floating algae offshore in the Yellow Sea was also carried out. Seawater samples were analysed for pH using a pH meter (METTLER TOLEDO FE20, Switzerland), salinity using a salinity meter (JENCO3173, U.S.A.) and nutrients (dissolved inorganic nitrogen: $NH_4 + NO_3 + NO_2$, and dissolved inorganic phosphorus: PO_4^{-3}). using an auto-analyser (Seal AA3, Germany). Algal samples were analysed for the stable isotope ^{15}N in order to calculate $\delta^{15}N$. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany). Reference gas was calibrated against International Reference Materials (IAEA-N1, IAEA-N2 and IAEA-600 for nitrogen). Results are expressed relative to atmospheric N_2 for $\delta^{15}N$ in the δ ‰ notation (e.g., $\delta^{15}N$ sample $= [(^{15}N/^{14}N_{sample})/(^{15}N/^{14}N_{standard}) - 1] \times 1000$). Replicate measurements of a laboratory standard (acetanilide, Thermo Scientific) analysed with the samples indicated that analytical errors were <0.1‰.

2.4. Statistical procedures

Temperature, light, nutrients and algal biomass data were analysed using ANOVA and were limited to where data sets had equal variances between factors (Levene's test p > 0.05). Multiple comparisons used Tukey's HSD ($\alpha = 0.05$). Where data could not be transformed to adequately correct variance structure, multi factor analyses were split into single factor analyses or non-parametric comparisons (Kruskal and Wallace test) were made. Bonferroni levels of significance ($p_{crit} = 0.05/$number of tests) were used to guard against Type I errors. Greater detail is given as SD.

3. Results

3.1. Spatial and temporal variability in Ulva biomass accumulation

Three trends in *U. prolifera* biomass accumulation are evident (Fig. 3). Firstly, biomass was lowest at the northern site of Haitou (mean of 6.6 gDW per raft) and then becomes progressively greater at Sheyang (50 gDW) and is highest at the southern site of Rudong (103 gDW). Secondly, in general, biomass accumulated progressively during the study with the greatest occurring in late-March and early April. Thirdly, biomass accumulation was lowest at the low intertidal height, although there was only sufficient data to analyse for this effect at Rudong. Biomass accumulation was highest at the mid intertidal height at Haitou and at the high intertidal height at Sheyang. Only the Rudong site had sufficient samples across all intertidal heights and all sampling dates for a rigorous comparison of the effect of date and intertidal height. ANOVA showed both these main effects were highly significantly different (date: $F_{(4112)} = 16.63$, p < 0.0001; intertidal height $F_{(2112)} = 13.06$, p < 0.0001) and that end-March and mid-April were both significantly higher than January, February and mid-March (p = 0.003 to < 0.0001). Biomass on the low-intertidal rafts was significantly lower than on either the high or mid intertidal rafts (p = 0.0001). The mid and intertidal rafts varied in depth by only 0.5 m while the mid and low rafts varied by a depth of 1 m.

U. cf. *intestinalis* was absent in samples from Haitou, rare among samples from Sheyang (maximum of 0.23 gDW per raft) and common at Rudong (up to 47 gDW) (Fig. 3). The variance structure in these samples prevented statistical analysis, but in contrast to *U. prolifera*, *U.* cf. *intestinalis* biomass was highest on the low-intertidal rafts (except in January and April) and lowest in the high-intertidal rafts. During the mid to late-March period of greatest algal growth, the mean biomass of *U.* cf. *intestinalis* was 47.0 gDW on the low-intertidal rafts compared to 20.0 gDW for *U. prolifera*. In the same period the mean biomass of *U.* cf. *intestinalis* was just 3.4 gDW on the high-intertidal rafts compared to 84.6 gDW for *U. prolifera*. However, there was a sharp decline in biomass of *U.* cf. *intestinalis* (47 gDW to 4 gDW) at the low intertidal height at Rudong between late-March and mid-April.

3.2. Comparison of temperature and light within and among sites

Among-site comparisons of temperature were limited to mid intertidal height data (Fig. 4). Day temperatures over the whole study period were highest at Rudong by almost 2° (mean 8.50 °C) compared with Sheyang (6.49 °C) and Haitou (6.66 °C). Differences in night temperatures were less, with Rudong the highest by just 0.7° (mean 6.30 °C) compared with Sheyang (5.56 °C) and Haitou (4.47 °C). Significant among-factor differences in variances (p < 0.0001) precluded an overall analysis of variance so analyses were conducted for each sampling time (Tables summarising the statistical analyses of temperature are given in Tables S2 and S3 of SD).

With only two exceptions, mean temperature increased with every sampling date at every site and was progressively higher at each site from north to south within each sampling period (Table 1). Mean temperatures varied from 2.4 to 10.3 °C at Haitou compared to 5.3 to 10.5 °C at Rudong. The most marked change in temperature at all sites (2.7–3.2 °C) was between mid and late-March (Table 1). Sheyang and Haitou differed in temperature significantly on only two occasions.

Comparison of light levels among sites and dates was limited to the mid intertidal height rafts (Fig. 5). As a result of variance structure, ANOVA was limited to the main *Ulva* growing periods from early March to mid-April where square root transformation corrected the variance structure (p = 0.058). Mean values ranged from 475 to 570 µmol m² s⁻¹ at Haitou, 114 to 209 µmol m² s⁻¹ at Sheyang and 323 to 532 µmol m² s⁻¹ at Rudong. Significant differences existed among sites ($F_{(2,1087)} = 112.48$, p < 0.0001) but not dates ($F_{(2,1087)} = 2.59$, p = 0.075) and that there was no significant interaction ($F_{(4,1087)} = 2.33$, p = 0.055). Multiple comparisons confirmed that light levels at Sheyang were significantly lower (p < 0.0001) than at both Haitou and Rudong. However this was shown to be an artefact of the farmer at Sheyang not cleaning the light loggers at regular intervals. Evidence for this is that at Sheyang the ratio of the land based logger to the mid intertidal loggers 1.7:1 for the first fortnight and thereafter ranged from 3:1 to 14:1 while at Haitou and Rudong the range during the whole study was just 1.5:1 to 2.8:1. The Sheyang light data was not used further in this study.

Comparisons of light levels among the last three sampling dates and intertidal height at Rudong using ANOVA showed main factors of intertidal height ($F_{(2,1071)} = 7.14$, p = 0.001) and date ($F_{(2,1071)} = 6.37$, p = 0.002) were significant with no interaction among factors ($F_{(4,1071)} = 1.18$, p = 0.320). Multiple comparisons showed that mid intertidal rafts (mean = 430 µmol m² s⁻¹) experienced greater light than the low intertidal rafts (298 µmol m² s⁻¹) (p = 0.001) but not the high intertidal rafts (335 µmol m² s⁻¹) (p = 0.027, Bonferroni $p_{crit} = 0.05/3 = 0.017$). The high intertidal and low intertidal rafts did not differ from each other (p = 0.558). Overall, high-intertidal rafts had larger temperature ranges than mid and low-intertidal rafts and there was an extended period of cold and low light (<1000 µmol m² s⁻¹) from 26 February to 7 March which was especially evident at Rudong (Figs. S1 and S2 in SD provided a fuller picture of the temperature and light contrasts spatially and temporally).
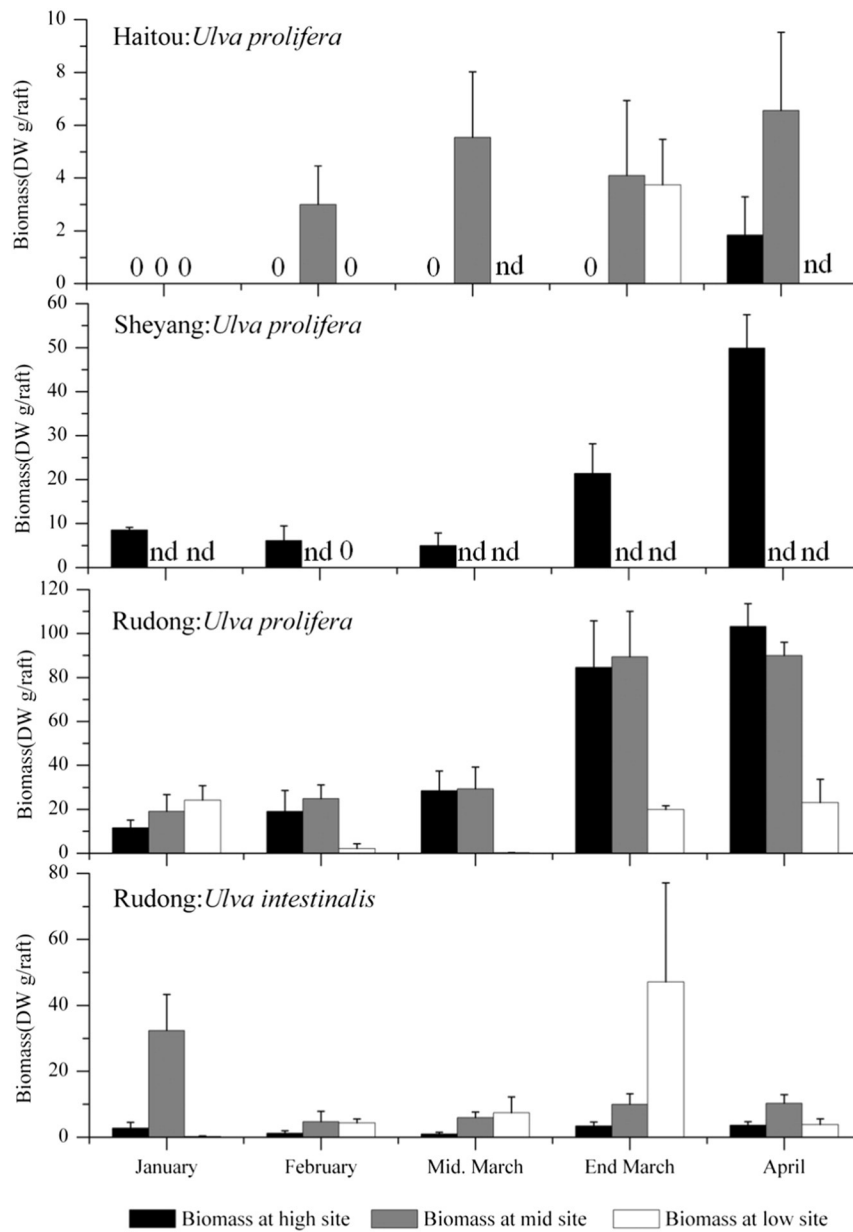
Fig. 3. Biomass accumulation of *Ulva prolifera* at Haitou, Sheyang and Rudong on rafts at each intertidal height. Biomass of *Ulva* cf. *intestinalis* at Rudong is also shown. nd = no data, 0 = data value of 0 ± 0, bars are means of N samples ± 1 standard error (N is shown in SD, Table S1).

3.3. Impact of tide on immersion/emersion times

The tidal cycles for each of the Ports closest to the study sites were compared for the period of our study. The tidal range was greatest at the Rudong site; over 8.5 m ranging from − 14 cm to 852 cm (average
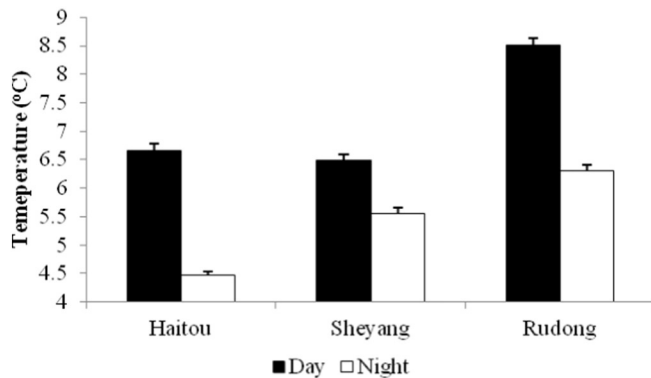

Fig. 4. Mean temeperatures experienced by aquaculture rafts at each of the three sites during day and night over the period from January 24 to April 14, 2010. Bars show means and standard errors of 965 to 1021 observations for day and night times per site.

Table 1
Comparison of mean temperatures experienced by mid-intertidal rafts at each of the three sampling sites over all sampling dates. N for each cell ranges from 192 to 384 temperature records.

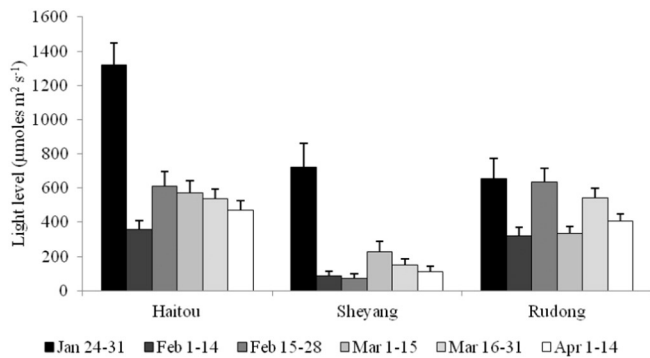| Sample date	Haitou °C	Sheyang °C	Rudong °C
Jan 24–31	2.43	3.79	5.35
Feb 1–14	2.72	3.84	5.26
Feb 15–28	4.46	4.52	6.81
Mar 1–15	4.52	5.06	6.13
Mar 16–31	7.66	7.74	9.24
Apr 1–14	10.34	9.94	10.52

Fig. 5. Mean light levels (μmol m^2 s^{-1}) experienced by mid intertidal aquaculture rafts at each of the three sites during the sampling periods from January 24 to April 14, 2010. Bars show means and standard errors of 111 to 129 observations per period per site (except January 64 to 88 observations).

434 cm). By contrast the tide range at Sheyang to range was just a little over 3 m (between -14 cm and 294 cm, average 157 cm). Tides at Haitou varied over 5.3 m from -9 cm to 529 cm, averaging 281 cm.

Low-intertidal rafts at Rudong remained submerged for an average of 15.3 and 17.1 h day^{-1} during the late-March April sampling periods respectively (Fig. 6). This is 13 to 16% more than the high-intertidal rafts which were submerged on average 13.7 and 14.7 h day^{-1} over the same period. Only low-intertidal rafts remained submerged over neap tide cycles. Periods of emersion were greater at night (Fig. 6) and low-intertidal rafts were submerged for an average of 7.6 to 8.6 h (9 to 15% longer) during daylight periods during end-March to mid-April compared to an average of 7.0 to 7.5 h for high-intertidal rafts (Fig. 6). Mid-intertidal rafts had similar emersion and immersion times as high-intertidal rafts as a result of the small (ca. 0.5 m) differences in depth (ca. 0.5 m) relative to the total tide range of more than 8.5 m.

3.4. Influence of immersion/emersion cycles on temperature and light

Day temperatures of exposed rafts were consistently higher than those of submerged rafts during both mid-March and April (Fig. 7A), but this difference was only significant in mid-March (p < 0.0001, April p = 0.415). There was no significant difference in temperature among exposed rafts at the three intertidal heights in either mid-
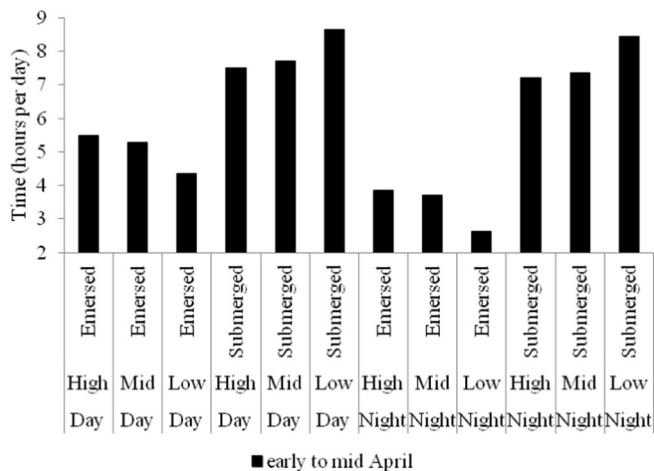

Fig. 6. Mean hours aquaculture rafts were exposed and submerged during day and night periods at each intertidal height at Rudong during the early to mid-April (14 days) 2010 sampling period. Bars are average hours day^{-1} for each period. The mid-late-March period which exhibited a similar pattern is not shown.
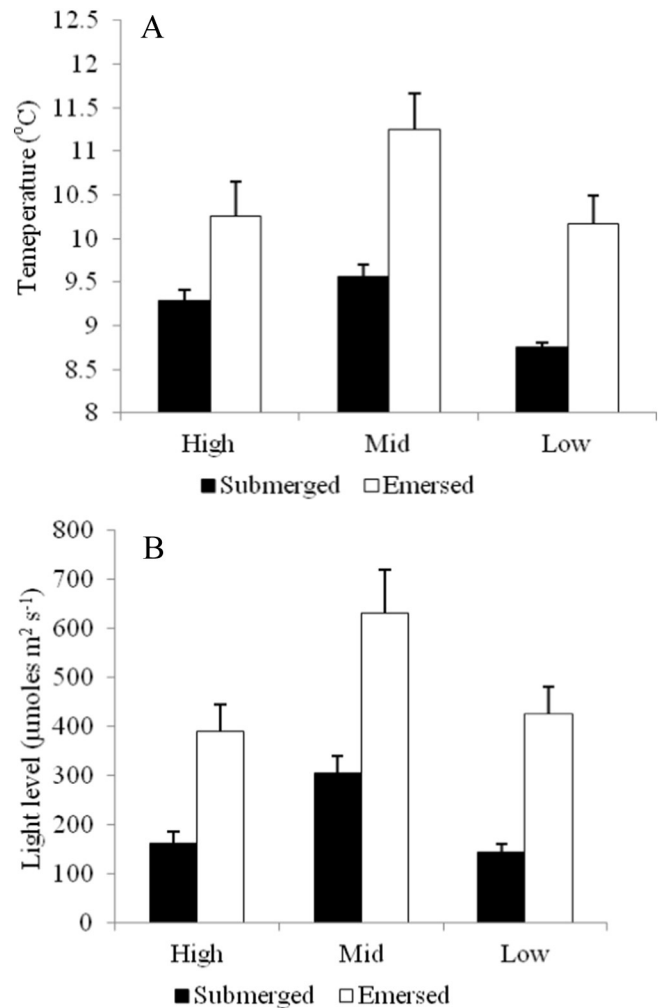

Fig. 7. Comparative day time temperatures (A) and light (B) experienced by submerged and exposed aquaculture rafts at each intertidal height at Rudong during the mid to late-March 2010 sampling period. Bars show means and standard errors of 74 to 96 observations. The early to mid-April period which exhibited similar patterns is not shown.

March or April (p = 0.165, p = 0.506 respectively), but there were differences among submerged rafts. During mid-March and April, the low-intertidal rafts were significantly cooler (p < 0.0001, p < 0.0001 respectively) when submerged than both the high and mid-intertidal rafts which did not differ from each other (p = 0.089, p = 0.944 respectively).

Light levels of exposed rafts were consistently significantly higher (more than double) than those of submerged rafts during both mid-March and April (p < 0.0001, p < 0.0001 respectively) (Fig. 7B). Despite differences in some means of more than 200 μmol m^2 s^{-1}, due to high variability in light levels within treatments, there was no significant difference in the light levels among exposed rafts at each of the three intertidal heights in either mid-March or April (p = 0.525, p = 0.280 respectively). Differences in light among submerged rafts at different intertidal heights were significant. Mid-intertidal rafts were subject to significantly more light in both mid-March and April (p = 0.0003, p = 0.007 respectively) than high and low-intertidal rafts which did not differ from each other (p = 0.995, p = 0.949 respectively).

3.5. Comparison of pH, salinity and nutrients within and among sites

Graphs showing pH, salinity and nutrients at all sites and times are provided as SD, Figs. S3 and S4). Water pH was consistent at all sites

and sampling periods and varied between 7.76 and 8.57. Salinity at Haitou and Rudong varied between 26.5 and 30.4. Salinity at Sheyang was lower than the other sites due to the discharge of Sheyang River and varied greatly between 22.7 in January and 12.0 in late-March. Average DIN concentrations were high (8.9–61.4 μM) but variable at all sites in all sampling periods while dissolved inorganic phosphorus (DIP) levels were comparatively low (0.08–0.59 μM). At Haitou mean DIN levels ranged from 20.0 μM in mid-March to 59.6 μM in late-March. At Sheyang DIN was highest (61.4 μM) in January and down to a low of 10.4 μM in mid-April. The lowest levels of DIN were at Rudong (24.7 μM in January to 8.9 μM in April). DIN in mid-April was significantly lower than January at Rudong and Sheyang ($p = 0.040$ to 0.007). Within factor comparisons by ANOVA and multiple comparisons showed that DIN was significantly lower at Rudong than either or both Haitou and Sheyang in all months ($p = 0.001$ to 0.012). Ratios of DIN to DIP (N:P) exceeded Redfield ratios (16:1) greatly at all times and also varied greatly (48:1 to 259:1) among sites and intertidal heights at different times. N:P ratios greater than 162:1 only occurred at Sheyang due to high DIN concentrations.

Nitrogen content of tissue varied little among sites within each species; 3.5 to 4% (*U. prolifera*), 3.7 to 4.3% (*U.* cf. *intestinalis*) (Fig. 8). In a comparison, the two species sampled from the rafts had much higher N content than that sampled from offshore areas (1.3 to 1.7%), indicating the difference of nitrogen levels between coastal and offshore waters. Meanwhile, the $\delta^{15}N$ signature of *U. prolifera* from offshore in the northern Yellow Sea was only 3.9 to 5.0‰ (Fig. 8) and this was similar to that at Rudong (3.6 to 6.3‰), while much higher levels were recorded at both Haitou (12.3 to 17.0‰) and Sheyang ($\delta^{15}N$ 17.4 to 23.3‰). These data responded to the water DIN concentrations among sites, Haitou and Sheyang were characterised by heavier nitrogen pollution than Rudong.
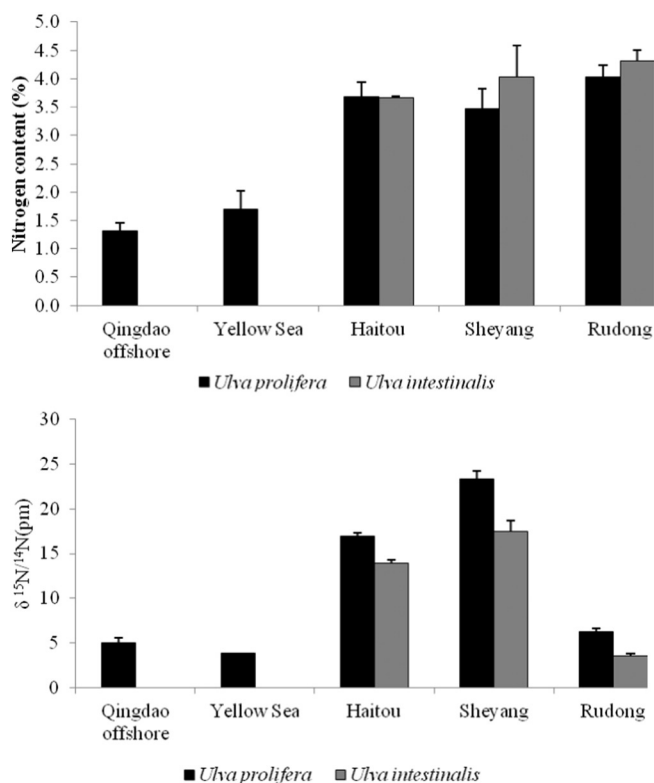

Fig. 8. Nitrogen content [%] (upper) and N_{15} isotope measurements [δ 15 N/14 N (‰)] (lower) in *Ulva prolifera*, *Ulva* cf. *intestinalis* and *Pyropia yezoensis* on aquaculture rafts at Haitou (N = 4), Sheyang (N = 4) and Rudong (N = 6) between 15 to 16 April 2010 and in offshore waters of the Yellow Sea at two locations collected on 1 June 2011 (Yellow Sea N = 5) and 22 June 2011(Qingdao offshore N = 3). Bars show means and standard errors.

4. Discussion

In this study, biomass accumulation of *U. prolifera* and *U.* cf. *intestinalis* on rafts grown in coastal waters with high background nutrient levels displayed significant relationships with temperature and periods of emersion, while variations in pH, light and salinity were not associated with biomass accumulation. Moreover, the highest biomass accumulation occurred at the site (Rudong) with the lowest DIN and lowest anthropogenic nitrogen levels.

4.1. Temperature and periods of emersion

Temperature has a strong influence on *Ulva* germination and vegetative growth (Woodhead and Moss, 1975). Optimal temperatures for growth of *Ulva* (including *U. prolifera*) are 15 to 20 °C and favourable temperatures are 10 to 22 °C (e.g. Taylor et al., 2001; Largo et al., 2004; Liang et al., 2008; Luo et al., 2012). In this study, at Rudong, where *Ulva* growth was the greatest, temperature was significantly warmer during the day (by about 2 °C) than Sheyang and Haitou. During the main period of *Ulva* growth from mid-March to mid-April, temperatures were higher with daytime averages of 10.4 to 11.3 °C at Rudong, 8.1 to 10.1 °C at Sheyang and 8.3 to 11.0 °C at Haitou. Maximum temperatures were also much higher at Rudong (23.1 to 24.0 °C) in the same period compared with 17.7 to 16.9 °C at Haitou and 16.8 to 15.2 °C at Sheyang. Our result matched the observation of Liu et al. (2010), which showed a trend of increasing *Ulva* biomass accumulation from north to south along the Jiangsu coastline. Thus a very strong association exists between the warmest site and the highest biomass of *U. prolifera* on the rafts.

When we compared with the biomass data between 2009 (Liu et al., 2010) and 2010 (our result), the levels of *U. prolifera* accumulation in 2010 are lower by between 90% at Haitou and 29% at Rudong than those measured in the same months in 2009. This might be related to the differences temperatures between years. 2010 was one of the coldest years on record in China, highlighted by the complete freezing of the surface of the Bohai Sea (Guo et al., 2011; Sun et al., 2011). The average air temperature in Jiangsu in March and April 2010 was 1.7 and 3.8 °C cooler respectively in 2010 than in 2009 (Table 2). Temperature data from the harbours nearest to our study sites (Table 2) show the main *Ulva* growing period was colder at all sites in 2010 than in 2009. Average water temperatures in 2010 were 4.1, 3.8 and 1.4 °C cooler at Lianyungang, Yancheng and Nantong respectively in early to mid-April (Table 2). Thus the greatest temperature differential between years was in the north where we also found the greatest reduction in biomass accumulation between years.

Although our analysis of the influence of tidal height on biomass was limited to just the Rudong site, emersion over the tidal cycle displayed a clear impact on the growth of *U. prolifera*. During the main period of *Ulva* growth, low-intertidal rafts spent 1.6 to 2.4 h day^{-1} (13 to 16%) longer submerged than high-intertidal rafts. The latter had significantly

Table 2
Comparison of average daily water temperatures (°C) at three harbours in Jiangsu Province close to out three study sites in March and April in 2009 and 2010 (source: web site of Ocean and Fishery Bureau of Jiangsu Province, China http://www.jsof.gov.cn/) and monthly provincial average air temperatures for Jiangsu (source: web site of Meteorological Bureau of Jiangsu Province, China http://www.jsmb.gov.cn/).

Location	2009 °C	2010 °C	Difference °C
Lianyungang water (Mar 16–31)	8.69	6.81	−1.88
Yancheng water (Mar 16–31)	9.42	8.12	−1.30
Nantong water (Mar 16–31)	9.58	9.51	−0.07
Jiangsu air (March)	9.1	7.6	−1.50
Lianyungang sea (Apr 1–14)	11.51	7.38	−4.13
Yancheng sea (Apr 1–14)	12.45	8.65	−3.80
Nantong sea (Apr 1–14)	12.11	10.66	−1.44
Jiangsu air (April)	15.6	11.9	−3.70

higher algal biomass accumulation suggesting the period of emersion, or a related environmental variable, e.g. desiccation, temperature, light or ecological process (e.g. grazing), may be important. Intertidal algae are able to tolerate desiccation and *Ulva* spp. are well adapted to desiccation stress in comparison with other species (e.g. Johnson et al., 1974; Quadir et al., 1979; Einav et al., 1995; Abe et al., 2001; Guo and Dong, 2008; Nelson et al., 2010). Partial desiccation can elevate photosynthesis (e.g. Dring and Brown, 1982). *U. prolifera* has been shown to be tolerant of desiccation by Zou (2001) who found no change in photosynthesis rates after 25% water loss and net positive photosynthesis continued to at least 70% desiccation. Beer and Eschel (1983) made similar findings in an *Ulva* sp. in the Mediterranean. Zou and Gao (2003) and Zou et al. (2007) showed that *U. lactuca* increased photosynthesis after desiccation but that this was highly temperature dependent. Benefits were lower at 30 °C but at temperatures experienced in our study, photosynthetic rates were enhanced during desiccation by up to 22% for 1.9 h at 10 °C (11% for 1 h at 20 °C) remaining net positive for 4.4 h (3.4 h). Consistent with the physiological studies, the result at the Rudong site demonstrated the emersion over the tidal cycle is the predominant factor responsible for the higher growth of *U. prolifera* on mid and high-intertidal rafts relative to deeper rafts.

4.2. Influence of light, pH and salinity on algal biomass

From mid-March to mid-April light at Haitou (475 to 570 μmol m^2 s^{-1}) was significantly higher than at Rudong (323 to 532 μmol m^2 s^{-1}), but biomass accumulation of *U. prolifera* was significantly lower at Haitou. This suggests that light levels between sites cannot explain differences in biomass. Light levels at both sites exceeded the optimal light requirements recorded for *Ulva*. Taylor et al. (2001) found the growth response of four species of *Ulva* (*U. compressa*, *U. linza*, *Ulva curvata*, *Ulva rigida*) reach a maximum after light exceeded 18 to 44 μmol m^{-2} s^{-1}. Most intertidal algal species reach light saturation at 400 to 600 μmol m^{-2} s^{-1} (Lobban et al., 1985). Zou (2001) showed *U. prolifera* in China reaches light saturation at about 425 μmol m^{-2} s^{-1}.

pH varied from 7.78 to 8.57 among sites and dates but is not considered a factor in explaining spatial variability in the growth of *U. prolifera*. Salinity at the sites of both lowest (Haitou) and highest (Rudong) algal growth was similar (26.5 to 30.4) while salinity at Sheyang was lower and varied greatly (12.0 to 22.7) consistent with the rainfall seasonality and the close proximity (8 km) of the mouth of the Sheyang River. Salinity can affect the growth of *Ulva*, but they tolerate a wide range (Martins et al., 1999; Taylor et al., 2001; Nelson et al., 2008). We did not find any evidence that salinity explained *Ulva* biomass patterns in this study.

4.3. Influence of nutrients on algal biomass

Ulva biomass is known to show a direct link with nitrogen concentrations (Poole and Raven, 1997). The highest DIN concentrations were at Sheyang (10.4 to 61.4 μM followed by Haitou (20.0 to 59.6 μM) while at Rudong, the site of the highest algal growth, DIN was 8.9 to 24.7 μM. Isotope data indicated significant anthropogenic enrichment of the nitrogen source for *Ulva* at Haitou (δ^{15}N: 13.9 to 17.0‰) and Sheyang (δ^{15}N: 17.4 to 23.3‰), compared with Rudong (δ^{15}N: 3.6 to 6.3‰). There are numerous direct and indirect sources of anthropogenic nitrogen input along the Jiangsu coastline including the Sheyang River and 50,000 tonnes of animal manure is applied annually to coastal fish and crustacean aquaculture ponds near to Haitou and Sheyang (F. Liu et al., 2013).

Although the highest biomass did not match the gradient of DIN along the sites, we found that the levels of DIN in Jiangsu coastline were high and sufficient to the growth of *Ulva* at all sites. Teichberg et al. (2010) suggested that other factors are important especially under luxuriant nutrient conditions. This could explain why the abiotic factors determining *Ulva* biomass in this study are temperature and tidal effects rather than nutrient concentrations. We considered the

possibility of nitrogen limitation in our study, but do not believe it was a factor. Berglund (1969) reported that optimal growth of *U. linza* occurred at 14 μM DIN and that growth was inhibited at 21 μM DIN; Kamer and Fong (2001) found that the growth of *U. cf. intestinalis* could respond positively up to 80 μM DIN. Published data on the response of *U. prolifera* to different nutrient levels is limited. Li et al. (2009) cultured *U. prolifera* from the 2008 Qingdao green-tide which grew at 3.85% day^{-1} without additional nutrients in seawater sourced with the algae containing 5.4 μM DIN) at 20 °C. They found adding 10 μM DIN increased growth to 6.31% day^{-1} but that increasing it by 50 μM DIN had no greater effect (6.32% day^{-1}).

During the *Ulva* floating period in the Yellow Sea, DIN concentrations in offshore (e.g. 1–15 μM DIN in 1997–1999 by Wang et al. (2003) and 0–42 μM DIN in 2006–2007 by Fu et al. (2009)) were much lower than coastal waters. Nitrogen contents of *Ulva* tissue (1.3 to 1.7%) in offshore were also much lower than on the rafts (3.5 to 4.3%) (Fig. 8). This demonstrates that the nitrogen in the Yellow Sea is sufficient enough to support high biomass of *U. prolifera*. It is more likely low phosphorus rather than high nitrogen affected growth in our study. With N:P ratios ranging from 48:1 to 259:1 (means 104:1 to 160:1), phosphorus was limiting in all situations sampled. Phosphate limitation in Chinese seas has been documented previously (Harrison et al., 1990). It is evident that more research is needed on the growth response of *U. prolifera* to varying nutrients in controlled field experiments.

4.4. Comparison of U. cf. intestinalis and U. prolifera

There was a striking contrast in growth of *U. cf. intestinalis* and *U. prolifera* on mid/high and low-intertidal rafts. Mean abundance of *U. cf. intestinalis* was 47 gDW per raft (low) and 3 gDW (high) and that of *U. prolifera* was 20 gDW (low) and 85 gDW (high). This pattern could be interpreted as being either due to *U. cf. intestinalis* favouring less light and/or being less tolerant to desiccation than *U. prolifera* (see above). We often found *U. cf. intestinalis* in refuges of pools of water in the tops of bamboo uprights when it was absent from other parts of the rafts. Indeed the biomass recorded for *U. cf. intestinalis* on mid and high-intertidal rafts came mostly from such refuges. Dromgoole (1980) showed that at higher ratios of surface area to volume the more rapidly algae became desiccated. Guo and Dong (2008) found that *Ulva pertusa* had significantly higher growth (27%) and photosynthetic rate (13 to 32%) after 0.5 to 2 h desiccation but that *U. linza* did not show the same response noting that the morphology of *U. pertusa* makes it more resistant to desiccation. *U. cf. intestinalis* has broader thalli and a more gracile morphology than *U. prolifera* (Liu et al., 2010) which will make the former more susceptible to desiccation. The characteristics of *U. prolifera* of tolerance to desiccation and high temperature can help us to understand why it can dominate other *Ulva* species on the rafts (Fan et al., 2015) and subsequently during the floating growth stage of bloom formation (Wang et al., 2008, 2010; Zhang et al., 2008; Ding and Luan, 2009). The reduction in biomass of *U. cf. intestinalis* between the mid-March and April samples might also be at least partly explained by a susceptibility to desiccation as temperatures warmed significantly between these dates.

4.5. Summary and conclusions

The spatial and temporal patterns of green algae growing on the *Pyropia* aquaculture rafts indicated that, in the high background DIN waters of the Yellow Sea coastline, temperature and periods of emersion are the most important abiotic factors determining the biomass accumulation and species succession, rather than pH, light and salinity. Dissolved inorganic nitrogen (DIN) levels were high at all sites, but the highest biomass accumulation occurred at the site with the lowest anthropogenic nitrogen levels. The result suggests that other abiotic factors (e.g. temperature, emersion period) can be more important under conditions where nitrogen is not limiting.

In a previous study (Liu et al., 2010), we suggested two approaches for mitigating the green tides in the Yellow Sea. One is reducing nutrient pollution which is a long-term target, and the other is requiring that the fouling algae were cleaned up onshore to prevent them being disposed of into the sea. Based on this study, an earlier harvest of *Pyropia* in the southern sites could also be helpful, by significantly reducing the biomass accumulation of *U. prolifera* on rafts, because rapid growth of *U. prolifera* only occurred late-March and April when temperature increases greatly and higher than 10 °C.

Acknowledgments

Appendix A. Supplementary Data

Supplementary content (SD) in the form of additional detail on methods and additional tables and figures related to this article can be found accompanying the online version of this paper. Supplementary data associated with this article can be found in the online version, at doi:http://dx.doi.org/10.1016/j.marpolbul.2016.02.051.

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