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Who made the world's largest green tide in China?—an integrated study on the initiation and early development of the green tide in Yellow Sea

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Abstract

To discover the original source and clarify development of the world's largest transregional green tides in the Yellow Sea, an integrated investigation covering the Subei Shoal coastal waters and the adjacent regions was carried out during March to June of 2012. The results showed that macroalgal wastes from the connecting ropes of *Porphyra* aquaculture rafts contributed significantly to the original biomass of free-floating green algae. Approximately 6500 t of *Ulva prolifera* were released into the coastal waters from mid-April to late-May when farmers were cleaning aquaculture facilities. Among the total biomass disposed, about 62.3% floated up to the sea surface, which turned into the original floating patches. The floating *U. prolifera*, with a high growth rate of 26.3% per day, dominated in the floating algal patches rapidly, moved northward under the hydrodynamic action, and formed a massive free-floating green tide near the south of Shandong peninsula in early June. The optimal sea temperature and sufficient nutrients in the Yellow Sea facilitated the formation of the green tide. No other source contributing substantially to the initial floating biomass was detected in the survey except those from the connecting ropes of rafts. Based on our field data, we concluded that the green tide in Yellow Sea is a transregional disaster stimulated directly by the unhygienic husbandry and maintenance practices of coastal aquaculture.

Green tides usually refer to blooming of opportunistic green seaweeds, such as *Ulva* spp. (Valiela et al. 1997). Most green tides occurred in the photic zone of eutrophic coastal waters (Charlier et al. 2007; Teichberg et al. 2010). Large-scale green tides can cause series of deleterious impacts to the local ecosystem, including hindrance on the growth of benthic seagrasses by increasing light attenuation, alteration in benthic fauna, disturbance in the carbon and nitrogen cycles, hypoxia resulting from degradation of blooming algae (Valiela et al. 1997). Recently, the allelopathic properties of the green-tide-forming species have been confirmed, pointing to the possible toxins from these macroalgae (Jin and Dong 2003; Nelson et al. 2003; Van Alstyne et al. 2007). Compared to the transient blooms of microalgae, the green macroalgal blooms were usually more persistent, even lasting for decades in some occasions (Bonsdorff et al. 1997).

Since 2007, green tides recurred annually from May to July in the Yellow Sea of China. The scale of the green tides, in terms of distribution area, was larger than any cases ever reported in the world (Keesing et al. 2011; Liu et al. 2013a). According to the 2008–2013 data of China Ocean Information Network (http://www.coi.gov.cn/gongbao/huanjing/), the maximum distribution area of the floating mats ranged from 2.0×10^4 to 5.8×10^4 km^2, which was approximately one-tenth of the total area of Yellow Sea. Unlike other green tides around the world, floating algal mats in the Yellow Sea were not retained in coastal water of Jiangsu province, the original blooming region, but drifted offshore to the open area (Liu et al. 2009). The floating mats drifted farther northward, reaching the south coast of Shandong peninsula, and even to the west coast of South Korea in 2008 and 2011 (Son et al. 2012). Although it was still not clear regarding the long-term ecological impact of the annual large-scale green tides, significant social and economic losses had emerged due to large amount of algal biomass piling up on beaches and coastal waters of both Shandong and Jiangsu provinces (Ye et al. 2011).

Additional Supporting Information may be found in the online version of this article.

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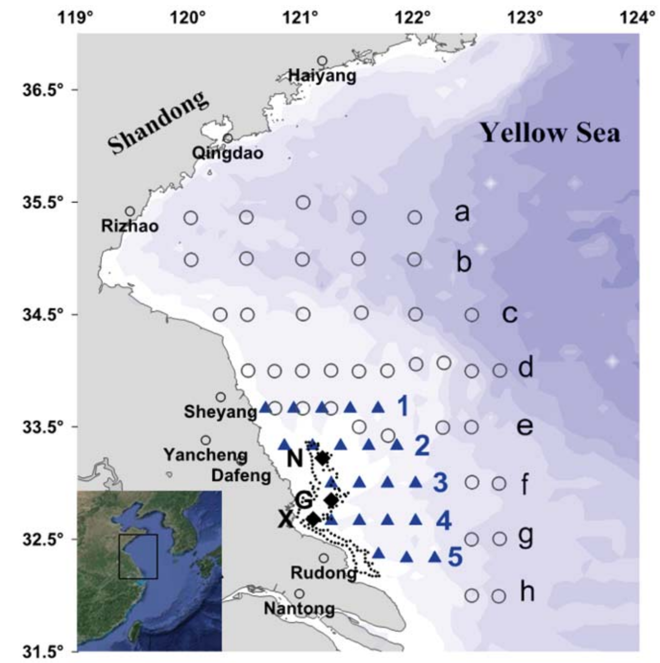

Fig. 1. Survey stations in southwestern Yellow Sea of China. Grey ○: sampling stations for the large cruises (Transect ga–gh); blue ▲: sampling stations for the small cruises (Transect S1–S5); black ◆: locations for observing the disposed macroalgae detached from the connecting ropes of *Porphyra* rafts (X, Xiaoyangkou; N, Niluosha; G, Gaoni). Dashed line indicates the recent expansion of *Porphyra* aquaculture. Geographic location of the survey area was shown in the insect at the left lower corner.

Previous researchers on the green tides in the Yellow Sea mainly focused on tracking the floating mats through satellite data and numeric modeling (Ciappa et al. 2009; Hu 2009; Hu et al. 2010; Keesing et al. 2011; Lee et al. 2011), molecular identification of ulvoid species (Leliaert et al. 2009; Liu et al. 2010b; Duan et al. 2012), ecophysiological studies on the causative algae (Lin et al. 2008, 2011; Zhang et al. 2010, 2011; Luo et al. 2012; Xu et al. 2012) etc. It was generally accepted, so far, that the floating green algae did not occur indigenously, but was originated and drifted from the Subei Shoal area (Liu et al. 2010c; Keesing et al. 2011; Cui et al. 2012). The northward transportation and offshore spreading of the floating patches was probably assisted by the seasonal monsoon and the associated surface currents (Qiao et al. 2009; Lee et al. 2011; Cui et al. 2012). Little, however, was known regarding the initiation process of the green tides at the original habitat—Subei Shoal.

A number of researchers indicated that propagules, somatic cells and settled fragments in natural environments may play important roles during macroalgae recruitment and succession of the green tide (Zhang et al. 2010, 2011; Liu et al. 2012, 2013b), while other researchers speculated that the expansion of *Porphyra* aquaculture and the associated wastes were the major source of the large-scale floating mats (Liu et al. 2009, 2010a, 2013a; Keesing et al. 2011). None of these studies, however, provided conclusive evidences from the field to elucidate the initiation and early development of the floating green macroalgal patches, which was crucial to understand the underlying mechanism of the large-scale green tides in the Yellow Sea. The practical mitigation strategies, such as clearing algae mass from beaches and coastal waters manually, blocking drifting mats by arresting nets, are quite costly and infeasible for large-scale open waters. Thus, identification the sources of the drifting biomass and the stimuli of the blooms are the key tactics for adopting appropriate management to prevent the formation of green tides and reduce their subsequent impairment to the ecosystem.

Preliminary information on the original habitat of floating algae had been obtained through our previous surveys since 2009 (Fan et al. 2012). Consequently, an integrated ecological investigation and experiment were designed and performed in Subei Shoal and the adjacent Yellow Sea in March–June of 2012, in order to identify the original source of the floating patches and reveal the early development of the green tide. The underlying hypothesis was that the disposed macroalgal clumps or swarms of young germlings were commonly observed before or during the early formation of the green tide (Liu et al. 2009, 2010a, 2012, 2013b; Zhang et al. 2010, 2011; Keesing et al. 2011).

Material and methods

Study area and biomass measurement of the macroalgal wastes from the *Porphyra* aquaculture rafts

Subei Shoal (or Subei bank) in the nearshore water of southern Yellow Sea starts from the Yangtze River delta up to the Sheyang River, covering an area of approximately 18,000 km^2 (Wang et al. 2011). The water depth in this area is less than 10 m at high tide, and the hydrographic condition is generally featured by strong tidal force and permanent water turbidity (Zhang et al. 1999; Wang et al. 2011; Liu et al. 2013c). Over 70 sand ridges distribute alternatively with the sand grooves in the middle part of Subei Bank (Yang 1989; Wang et al. 2011). The vast intertidal mudflat is the major aquaculture area of the seaweed *Porphyra yezoensis* in China (Fig. 1).

The aquaculture rafts are usually deployed in fall (September) to seed the nets, and harvested in the following April after 6–7 months' growing. A typical *Porphyra* raft is composed of a nursery net in the middle, four vertical and two horizontal bamboo poles, and two paralleled long ropes (connecting ropes) connecting the rafts in line (Fig. 2). According to our previous surveys, the nursery nets and bamboo poles were directly moved back for recycling after the *Porphyra* crops were harvested; while the connecting ropes were cleaned on site to remove the macroalgal epiphytes, producing large amount of disposed macroalgal

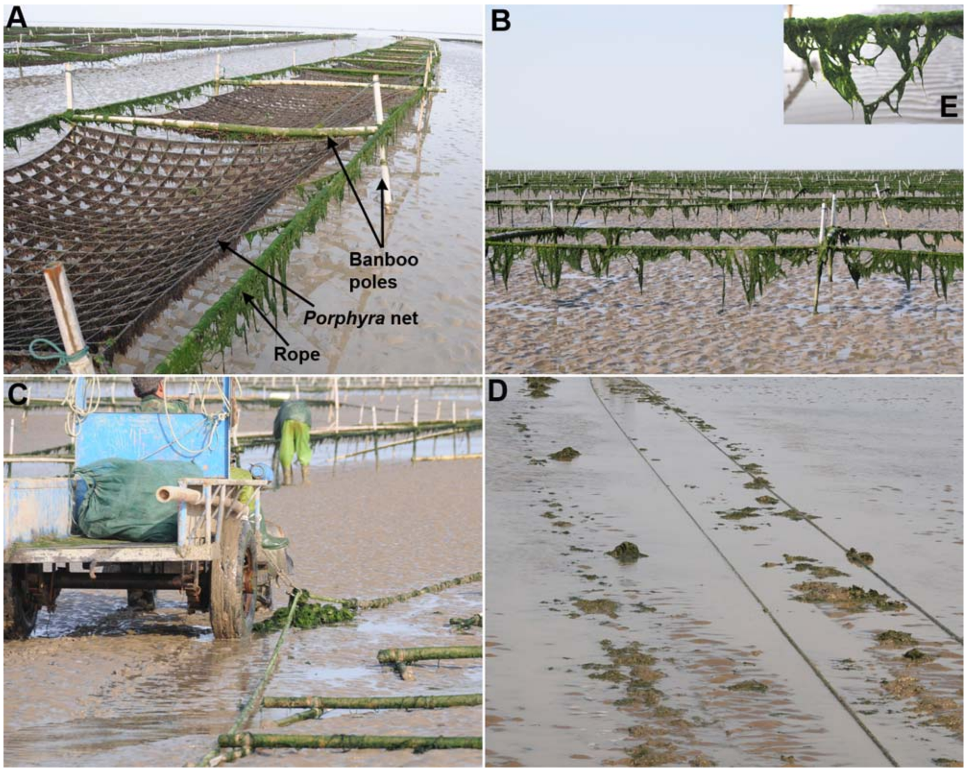

Fig. 2. Photographs of attached and disposed green macroalgae from the *Porphyra* aquaculture rafts in Subei Shoal. A: structure of *Porphyra* aquaculture rafts; B: macroalgae attached on the rafts after the *Porphyra* net was removed, a closer image of the abundant macroalgae attached on the connecting ropes (E); C: on-site cleaning the green macroalgal epiphytes from the connecting ropes by a metal hook attached to a tractor; D: macroalgae clumps left over on the muddy flat of Subei Shoal.

wastes. Species composition and biomass variation have been described in detail in the previous research (Fan et al. in press). To estimate the total *U. prolifera* biomass disposed from the connecting ropes (*TW*), the averaged macroalgal biomass on ropes was scaled up by the total rope length per hectare rafts and the total *Porphyra* aquaculture area in the Subei Shoal.

On-site observations on those disposed green algae were conducted at three locations (Fig. 1): N (Niluosha, 33.22 °N, 121.17 °E), G (Gaoni, 32.85 °N, 121.25 °E), and X (Xiaoyangkou, 32.68 °N, 121.09 °E). We recorded the process that the farmers disassembled the rafts, cleaned the connecting ropes at low tide, and also the floating process of the disposed green algae when the tide was rising. The floating patches of green algae were randomly sampled for species composition as described below.

Distribution of floating macroalgae in Subei Shoal and the adjacent waters in southern Yellow Sea

Due to the dramatic difference in water depth of Subei Shoal and the open water of southern Yellow Sea, two research vessels were used (Fig. 1). In Subei Shoal, we conducted seven cruises using a small research vessel to survey the floating macroalgae. Five parallel transects with 3–5 stations for each were surveyed using the trawling bioassay (as detailed in the following paragraph). Another five cruises were conducted through a big vessel simultaneously to survey the floating algae in the offshore water of southern Yellow Sea. According to our pioneered surveys in 2009–2011, the floating biomass was consistently originated in the area north to Subei Shoal, and has never been observed in the area further north (between 34.00 °N to the south coast of Shandong peninsula) in early April (Fan et al. 2012). Hence, the first cruise, conducted during April 8th–18th, surveyed fewer stations (18 stations) covering a region of 32.67 °–33.67 °N and 120.50 °–122.70 °E (Supporting Information Table S1).

Because of the patchy distribution, there was no recognized method to quantify the floating biomass of green tides. Satellite image data has been widely used to evaluate the distribution, coverage, and drifting patterns of floating mats in previous studies (Hu 2009; Qiao et al. 2009; Cui et al. 2012; Son et al. 2012). While, due to the resolution limit of satellite images, it is difficult to identify the small-scale mats or floating patches in the coastal waters, particularly in turbid waters of the Subei Shoal (Garcia et al. 2013). Thus, we adopted a trawling bioassay to assess the distribution and abundance of floating macroalgae in this study.

Briefly, a conical phytoplankton net (500 μm mesh size, and 80 cm of diameter in the mouth) was mounted on the side of the research vessel and was slowly towed through a certain area of surface water (*A*) at each sampling station. Wet weight of the macroalgae collected from the trawling was measured after excess water was drained. In brief, the sampled floating algae were divided into multiple groups (about two kilogram each group). Each group of algae was placed in a mesh net and shaken manually (30–50 times per min) for approximately five minutes to drain the excess seawater. The floating algae density (*D*) was then calculated as $D = W \times A^{-1}$, where *W* (g) is the total wet weight of the floating macroalgae collected from the trawling area (*A*). Species composition of the floating algae was also studied through the method described below.

In order to further test the hypothesis that environmental micropropagules may directly develop into floating mats, the vertical trawlings were conducted at each station in open water (Table S1) with the same phytoplankton net. We evaluated the prevalence and abundance of young ulvoid germlings (<10 cm) in the water column.

Species composition of floating macroalgae

We randomly tested the species composition of floating macroalgae collected in Subei Shoal and the adjacent waters. After the macroalgal samples were transported back to the laboratory in a cooler, they were immersed in DI water separately, and individual thallus was carefully sorted out and identified at species level based on morphology characterization (Tseng 1984). Each "morphological species" was further confirmed by the molecular assay described in Xiao et al. (2013). The biomass of each species group was weighted after they were tap dried on tissue paper.

On-site floating and growth experiments

Multiple sympatric ulvoid species were confirmed to exist both on the rafts and in the disposed macroalgal wastes (Shen et al. 2012; Xiao et al. 2013). In order to test the fate of the disposed macroalgae from the rafts, we conducted the on-site trials to evaluate the buoyancy and growth potential of different species. At the time of testing (April to May of 2012), the fresh macroalgae collected from the connecting ropes for the experiments consisted of a limited number of species, including *Blidingia* sp., *U. prolifera*, and *U. linza*. Thus, the three species were tested in the growth rate (GR) experiment, while *U. linza* was excluded from the buoyancy test due to insufficient material available for the test. Besides, *U. linza* could hardly dominate in the floating algae, given the apparent lower growth and nutrient uptake capacities (Luo et al. 2012, this study), and low biomass of *U. linza* on the rafts in April to May (Fan et al. in press). Therefore, we focused on the comparisons on GR and buoyancy of *Blidingia* sp. and *U. prolifera*.

Altogether 64 samples collected from four randomly selected rafts at Xiaoyangkou were tested, with each sample consisting of macroalgae carefully removed from a 1-m-rope of the raft. The fresh macroalgal sample was put in a 25-L bucket filled with ambient surface seawater after it was gently separated manually to mimic the wave effects. After about one hour exposure to the sunlight at 10:00–11:00 h, the algae were harvested based on their relative positions in the bucket. Those suspended in the middle of water column and floating on the water surface was labeled as "floating," while those sank to the bottom were labeled as "sinking." The separated algae were transported back for species identification and weight assessment as described above.

Meanwhile, an independent growth experiment was conducted on shipboard under the natural irradiance cycle to determine the on-site GR of the detached macroalgae. Approximately 50–70 g of fresh macroalgae collected in field was cultured in a 25-L bucket (in triplicate) for five days. The wet weight of each species in every testing sample was weighted before culturing and every morning at 11:00–12:00 h during culturing. And seawater for culturing was refreshed every day. Unlike the shaking method for the floating biomass in previous section, we used paper towel to remove the excess water on the algal surface and avoid injury of the thalli. The GR of the algae was calculated as: GR (% d^{-1}) = [ln (W_t/W_0)]$/t \times 100\%$ where W_0 and W_t were the wet weight of algal mass at the beginning and at day *t, t* represented the duration of the experiment in days. The proportion of *U. prolifera* in total floating biomass was also calculated and recorded every day.

Modeling the floating biomass accumulation in the coastal water of southern Yellow Sea

While multiple researchers had reported the broad coverage and affected area of the green tides (Keesing et al. 2011; Garcia et al. 2013), few studies were done to assess the total floating biomass in Yellow Sea. In this research, we simulated the floating biomass accumulation based on the initial biomass (TW) of *U. prolifera* from the *Porphyra* aquaculture rafts, on-site floating rate (FR) and GR obtained through the field trials above. We assumed the algae (TW) were disposed continuously and floated up (FR) during the one-month period (30 days) of raft cleaning, hence there was an average amount of (TW×FR)/30 drifted into the coastal water for each day. The drifting biomass consequently grew at a constant rate (GR) and expanded to large-scale floating mats. Therefore, we proposed a mathematic model as following:

$$\mathrm{TB}(t)=\sum_{1}^{t}\left(\frac{\mathrm{TW}\times\mathrm{FR}}{30}\right)\times(1+\mathrm{GR})^{t-1} \quad (0 < t \leq 30) \qquad (1)$$

$$\mathrm{TB}'(t)=\mathrm{TB}(30)\times(1+\mathrm{GR})^{t-30} \quad (t > 30) \qquad (2)$$

TW was the initial biomass of *U. prolifera* from the *Porphyra* rafts estimated by a previous research (Fan et al. in press). TB(*t*) was the total floating biomass in the Yellow Sea at Day *t* since the raft cleaning started (middle of April). After the cleaning process was completed in about 30 days (until the middle of May), the floating biomass (TB′) would undergo an exponential growth without addition of the point sources from the rafts.

Statistic analysis

Analysis of variance (one-way ANOVA) was performed to compare the floating capacities and GRs among the sympatric green algal species, and the variation of floating *U. prolifera* biomass in a time-series experiment. All datasets met the assumptions of normality and equal variance (Skewness and Kurtosis). A Tukey's post hoc comparison was further applied to identify the significant levels of GRs and floating *U. prolifera* biomass when the ANOVA analyses detected any significant difference ($p < 0.05$). All statistics analyses were carried out in SPSS (SPSS) and the graphs were drawn with the Origin software (OriginLab).

Results

Releasing macroalgal by-products from the connecting ropes of *Porphyra* rafts

Based on our survey, the long connecting ropes of rafts were typically cleaned-up by a semiautomatic process in which the attached green macroalgae were scraped off by a hook attached to a running tractor (Fig. 2C). Consequently, large amount of macroalgal wastes were disposed directly on the muddy flat and drifted into the coastal waters eventually. The cleaning process continued for about one month, lasting from the mid-April to mid-May. According to our previous research, the macroalgal biomass attached on the connecting ropes reached to about 124.4 g m^{-1} ± 12.0 g m^{-1} (mean ± SE, here and hereafter) during the cleaning season, comprising approximately 38.1% ± 2.9% of *U. prolifera* (Fan et al. in press). Besides, there were approximately 4500 m connecting ropes for each hectare of rafts based on our survey, and total of 3.08×10^4 ha aquaculture rafts in Subei Shoal (Liu et al. 2010a; MAFB 2011). Therefore, the macroalgal wastes were estimated to be around 1.7×10^4 t, including approximately 6500 t of *U. prolifera*.

Buoyancy and growth of the disposed macroalgae from the connecting ropes, and modeling biomass accumulation in the coastal water of Yellow Sea

Approximately 62.3% of initial *U. prolifera* biomass was floating up after one hour culturing in the ambient seawater under natural irradiance. In contrast, the FR (34.5%) of *Blidingia* sp. was significantly lower than that of *U. prolifera* (One-way ANOVA, $F_{1,126} = 27.0$, $p < 0.01$).

The growth experiment further revealed the apparent higher growth potential of *U. prolifera* in the local conditions. Specific GR of *U. prolifera* reached to 26.3% ± 3.6% d^{-1}, which was about 3- and 15-folds of the GRs of *U. linza* (9.6% ± 2.2% d^{-1}) and *Blidingia* sp. (1.7% ± 1.4% d^{-1}), respectively (ANOVA, $F_{2,6} = 23.2$, $p = 0.001$, Fig. 3B). With the advantages of higher buoyancy and GR, *U. prolifera* dominated the floating patches rapidly in all tested samples. The proportions of *U. prolifera* in the total floating biomass increased dramatically in the first day (from 38.7% ± 8.1% to 87.6% ± 10.2%, ANOVA, $F_{4,10} = 4.20$, $p = 0.030$), and then remained constantly at a high level. The averaged proportion reached to 95.3% ± 4.7% at the 4th day (Fig. 3C).

We estimated around 6500 t of *U. prolifera* were disposed from the *Porphyra* rafts during the one-month period of raft cleaning. With the averaged FR (62.3%), there were approximately 4000 t in total drifting into the water (approximately 133 t d^{-1}). When the floating (FR) and GRs in Eqs. 1 and 2 were substituted with the values from the field trials above, we obtained the following equations:

$$\mathrm{TB}(t) = \sum_{1}^{t} \left(\frac{400}{30}\right) \times (1 + 26.3\%)^{t-1} \quad (0 < t \leq 30) \tag{3}$$

$$\mathrm{TB}'(t) = \mathrm{TB}(30) \times (1 + 26.3\%)^{t-30} \quad (t > 30) \tag{4}$$

Distribution of the floating macroalgae and development of the green tide

The development of the green tide during our surveys indicated the different patterns of green tide formation among locations. The nearshore waters around Subei Shoal retained high floating biomass throughout the survey period. While, the northern open sea area showed an increasing trend both in the algal biomass and spatial coverage of floating algae. The development pattern clearly implied a northward and offshore transporting of the floating algae from the original region, the Subei Shoal. There were no or few floating green algae observed in the southeastern part of the survey area (< 32.50 °N, > 122.50 °E).

There were no floating green algae observed during the first two cruises conducted in March. Considerable amount of floating algae started at the site (E121.13 °, N33.35 °) right north to the *P. yezoensis* aquaculture area in the middle of April in 2012 (Fig. 4A), coinciding with initiation of removing and cleaning the *Porphyra* rafts. In the following cruises (late April to the beginning of May), the highest floating algal biomass was restricted around the initiation area (32.50 °–34.00 °N, 120.70 °–121.30 °E) with averaged density of 14.3 g m^{-2} (Sta. S3-1, S3-2, S3-4, S1-2, and gd-1, Fig. 5B). The other stations had much lower biomass (< 0.1 g m^{-2}). Approximately 10 days later (Fig. 4C), the floating green algae were observed at most surveyed stations (82%). At that time, the floating green algae were not only extending to the offshore area, but also dispersed northward along the transect of 121 °E. In the last cruises (from late May to early June), the floating algae drifted toward northeast and intruded the open area of northern Yellow Sea (Fig. 4D, E). Although we did not survey the Subei Shoal area at the end of May due to the adverse weather condition, the missing

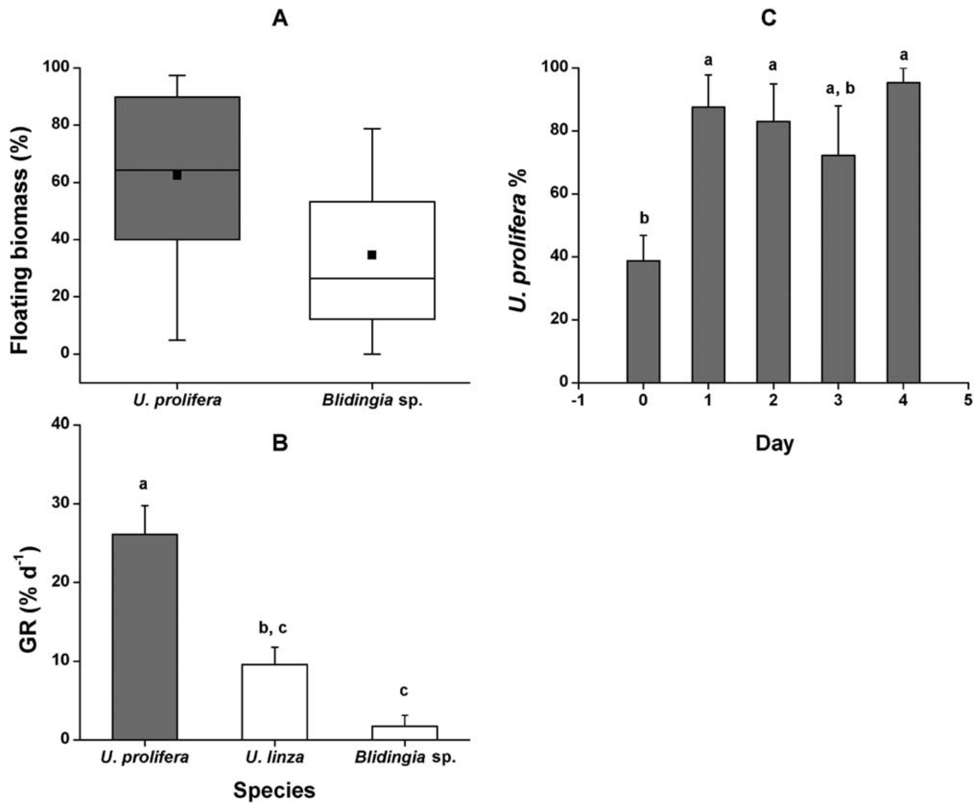

Fig. 3. Buoyancy and growth rates of green macroalgae collected from the connecting ropes of *Porphyra* rafts and from the coastal water of Subei Shoal. A: Significant difference of FRs of *U. prolifera* (gray) and *Blidingia* sp. (white) after one hour culturing (ANOVA, $F_{1,126} = 27.0$, $p < 0.01$). The line within the box was the median, and square symbol was the mean. The boxes span the 25–75% quartiles and the vertical lines span the 10–90%. Sixty-four samples were tested for each species. B: GRs (% d^{-1}) of *U. prolifera* (gray column), *U. linza* and *Blidingia* sp. (white columns) in a four-day culturing test. Error bar = SE ($n = 3$). C: variation of the *U. prolifera* proportion in the floating algal biomass at each day during the four-day culturing test. Error bar = SE ($n = 3$). Different lower case letters on the bars indicate significant difference based on Tukey's multiple comparisons ($p < 0.05$).

data in this region did not affect the overall distribution of floating macroalgae at this time (Fig. 4D).

At the beginning of the green tide in April, the floating algae presented mostly as small isolated patches ($< 0.1\,m^2$) with irregular shapes (Fig. 5A). With the development, the patches accumulated and aggregated into long-large floating mats. In the open area, nearly all the floating macroalgae were observed in linear bands ranged from hundreds of meters to tens of kilometers (Fig. 5).

Species composition of floating green algae

The tests on the species composition showed evident dominance of *U. prolifera* in the floating algae. *U. prolifera* percentages ranged between 90% and 100%, and 129 out of 145 tested samples consisted of exclusively *U. prolifera*. The minor species, including *U. linza* and *Blidingia* sp., were with low proportions at the early stage (from April 27th to May 6th). With the development of green tide, the number of samples with minor species decreased rapidly. During the end of May to early June, all the floating samples were composed of nearly 100% of *U. prolifera*.

Furthermore, the samples with minor species were mostly collected in and round the Subei Shoal (Fig. 6), consistent with the initiation of floating algal mats described above. Above all, the community composition of the floating algae revealed an evident time and spatial development pattern, which was concordant with the source of the floating mats and development of green tide.

Germlings in the coastal water of southern Yellow Sea

During the initial three small cruises conducted in March and middle of April, there were few individual thalli detected in the water of Subei Shoal. Less than 50 germlings (< 10 cm in length) were observed in 10 horizontal trawlings covering approximately 3.2×10^4 m^2 of the sampling area. Similarly, there was no considerable amount of young germlings observed at the five big cruises conducted in April, May, and June. Only a few individual germlings were found sporadically in 31 out of total 145 stations. The abundance was around 0.65 ind. $trawling^{-1}$ or 0.046 ind. L^{-1} water, and the majority of positive samples (90%) were observed in the three cruises conducted after the middle of May.

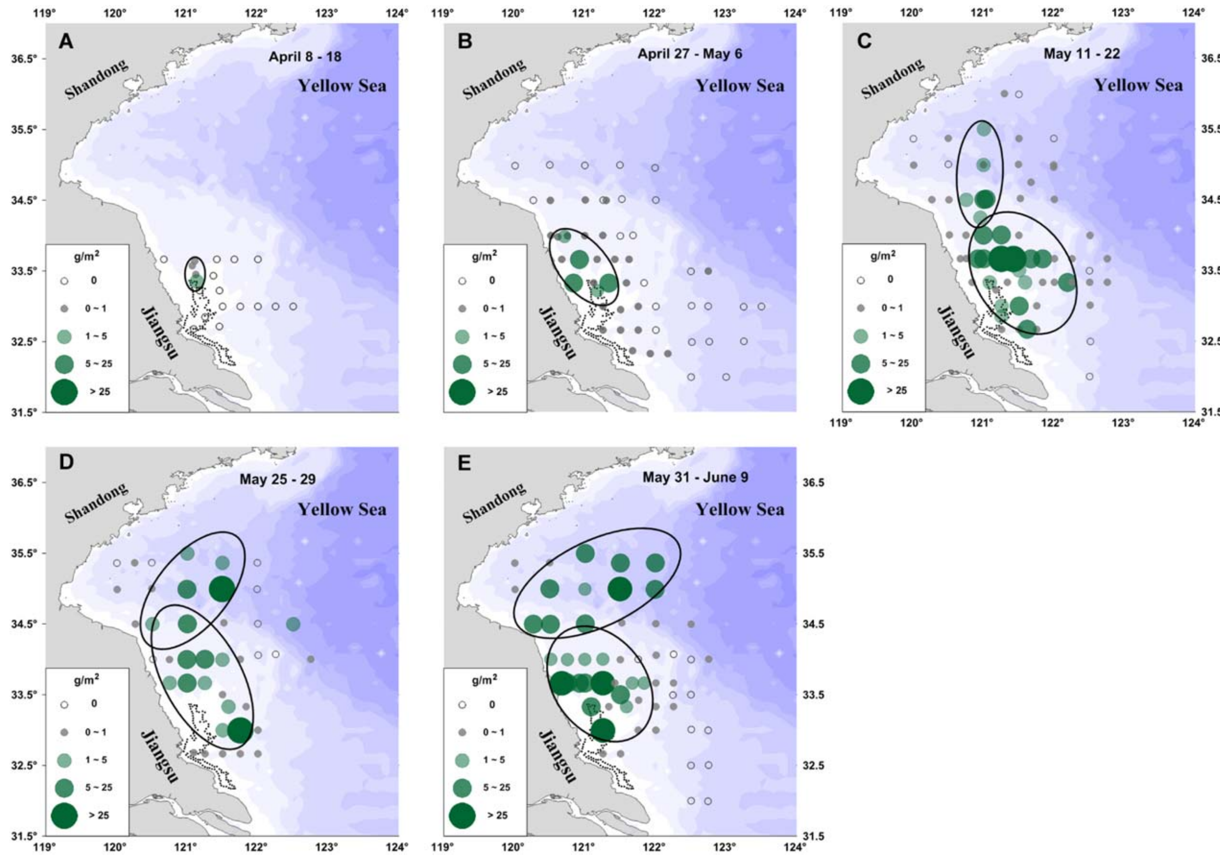

Fig. 4. Spatial and temporal development of floating green algal biomass in 2012. The black ovals denoted the major distribution and the drifting patterns of the floating biomass within each survey period.

Fig. 5. Photos showing the development process of green tide in the Yellow Sea in 2012. A: initial floating algae (black arrows) in Subei Shaol on April 26th; B: aggregated floating algae with a closer image of the individual floating patch (C) on May 6th; D: a long band of floating algal mat in June; E: a large-scale floating mat in open water of the Yellow Sea in June of 2012.

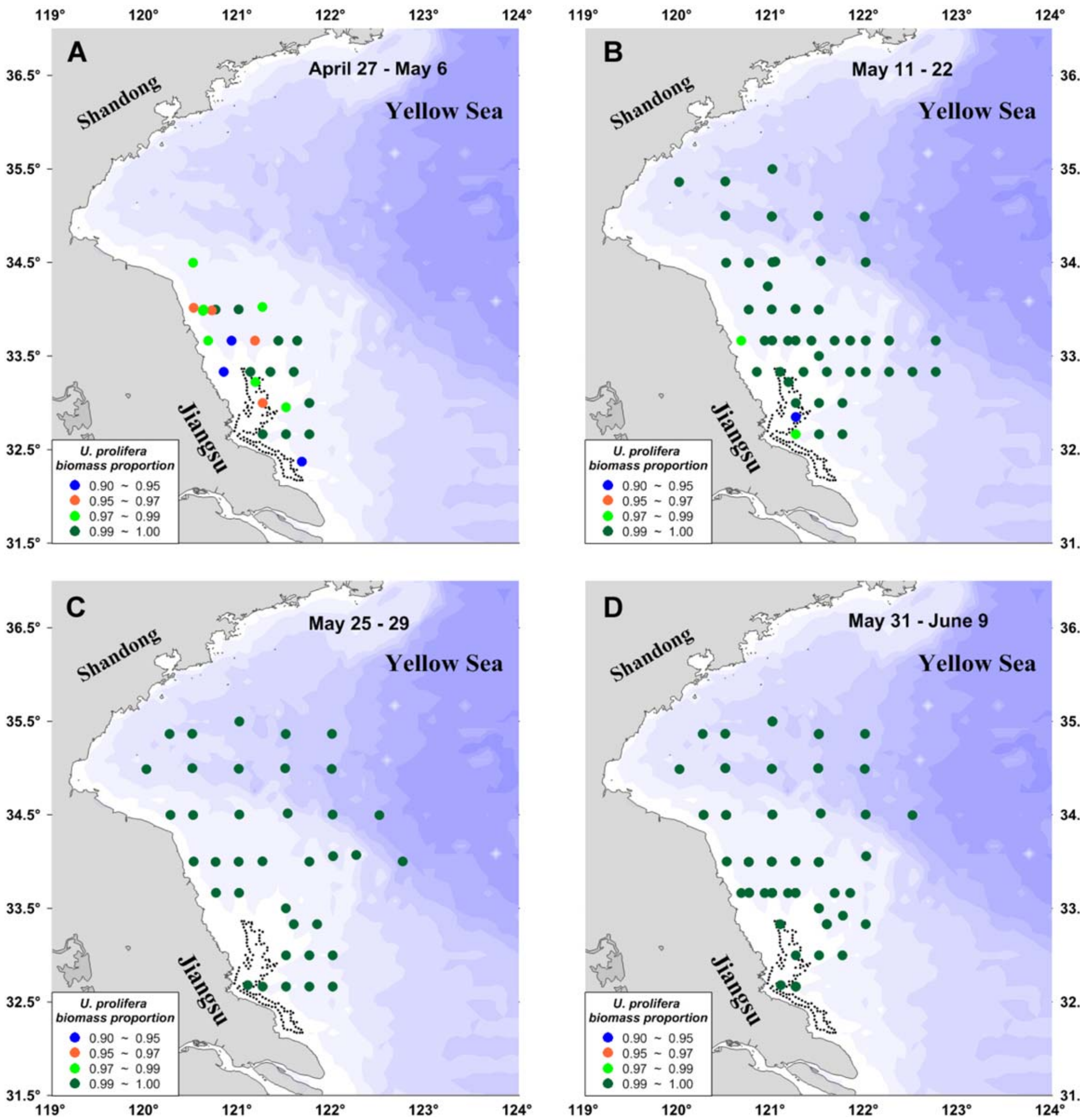

Fig. 6. Proportions of *U. prolifera* biomass in the floating algal patches sampled in and around the Subei Shoal water during the four cruises.

We noticed that none of these germlings had the complete structure as those developed from micropropagules in the laboratory. Through a dissecting microscope, these samples did not have the rhizoid structure, which is a key organ for the micropropagules attaching to the small particles and developing into visible individuals in the laboratory (Liu et al. 2012). They were either broken fragments from the floating algae, or some young progenies developed directly from an ulvoid parental tissue. The gross morphology of these samples varied from single thin tabular or ribbon-like thalli to the tubular thalli with or without dense branches.

Hydrographic conditions

The sea surface temperature (SST) increased steadily during the survey period (approximately 2 °C every two weeks), starting from approximately 5.5 °C in early March to 20.5 °C in the middle of June. The floating macroalgae started to appear when SST increased to 13.0 °C, and blooming of the large-scale floating algae was observed when SST was over 15.0 °C, which was consistent with our previous observations (Fan et al. 2012). During the survey, surface salinity varied from 27 psu to 31 psu in the sampling area, with a gradual increasing trend from coastal water to the offshore area.

Discussion

Our results clearly showed the primary contribution of macroalgal wastes from the *Porphyra* aquaculture rafts to the initial floating biomass of the following green tides in the Yellow Sea. In addition, a complete development process was described that the disposed macroalgae drifted into the coastal waters in/around Subei Shoal of southwestern Yellow Sea, and finally developed into large-scale floating mats. Details of the key processes during the green tide formation were discussed as following.

Macroalgal wastes from the connecting ropes

Infrastructure of green macroalgae on *Porphyra* rafts has been studied by multiple surveys. Initial survey found the wide presence of *U. prolifera* on the rafts, and suggested that the macroalgae on the rafts was likely the major source of the large-scale floating mats in the Yellow Sea (Liu et al. 2009; 2010a). However, the following analyses, mostly based on molecular phylogenies, raised large discrepancies on whether there was *U. prolifera* on rafts and/or genetic variations among attached and floating *U. prolifera* populations. The discrepancies resulted in more confusion on the inherent linkage between attached macroalgae and the floating populations (Pang et al. 2010; Zhang et al. 2011; Duan et al. 2012; Shen et al. 2012). Our previous research confirmed the existence of *U. prolifera* on the rafts when the bloom started in spring, and revealed a significant seasonal fluctuation in the species composition (Xiao et al. 2013). Further research affirmed the significant temporal and spatial variation in the species composition, and ultimately assessed the total *U. prolifera* biomass that could contribute to the initial floating biomass (Fan et al. in press).

In this survey, we described the detailed process that *U. prolifera* derived from the connecting ropes of *Porphyra* rafts was released into the coastal water, and confirmed the above hypothesis. The macoralgal wastes were manually detached from their original substrata (the connecting ropes of the aquaculture rafts) and disposed on the muddy flat during removing and cleaning the aquaculture facilities. These disposed macroalgal clumps were readily suspended and float up in the surface water by the wave effect at the rising tide. Both our field observations and on-site floating experiment showed the floating process for the detached macroalgae, especially *U. prolifera*.

Domination of *U. prolifera* during floating

Another unresolved linkage between disposed and floating algae was how and when *U. prolifera* overgrew the other sympatric species and became dominant in the floating patches. High species diversity has been reported in the macroalgae community on the *Porphyra* rafts (Liu et al. 2010b; Shen et al. 2012; Xiao et al. 2013), and the disposed macroalgae clumps on the muddy flats as well (Xiao et al. 2013). In contrast, the floating algae were uniformly dominated by the single filamentous species, *U. prolifera*, as shown in this study (Fig. 6) and reported previously including those identified through the molecular methods (Leliaert et al. 2009; Liu et al. 2010b). The other floating *Ulva* algae (e.g. *U. linza* and *Blidingia* sp.) were only detected in the patches in and around the origination region and at the early stage of the green tide. The relative biomass of these minor species was much lower ($<10\%$) compared to that of *U. prolifera*, and they "disappeared" rapidly with the floating mats moving to offshore. Besides, the time that the minor floating *Ulva* species "disappeared" was consistent with the cessation of point source of disposed macroalgal wastes (at around the end of May). This development pattern of the floating algal community confirmed the major contribution of the disposed macroalgae to the initial floating biomass of green tides.

Then dramatic shift on the species composition should occur when the detached macroalgae started the free-floating stage. We speculated two possible ways for this community shift: one was that the other coexisting species were physically not suitable for floating, hence sunk to the bottom while most detached *U. prolifera* started to float; the other was that the *U. prolifera* algae physiologically preferred the floating environment, and accumulated biomass rapidly, and consequently overgrew the other sympatric green algal species. Both hypotheses were confirmed by our contemporary on-site experiments which revealed both stronger buoyancy potential and a significantly higher GR of *U. prolifera* (Fig. 3). Previous research also reported the physiological advantages of *U. prolifera* over the other sympatric species during floating, including high nutrient absorption, photosynthesis and fast growing, implying the bloom tendency of this species in the region of southern Yellow Sea (Liu et al. 2010b; Lin et al. 2011; Wang et al. 2012; Huo et al. 2013). Our experiment and field observation further proved this hypothesis, and provided solid field data on the floating and GRs of *U. prolifera* which connected the green macroalgae detached from the rafts with the floating biomass.

The early development process of the green tide in the Yellow Sea

Previous research, mostly based on the laboratory culture, reported a relatively higher GR of *U. prolifera* (16%–55% d^{-1}, Hiraoka and Oka 2008; Liu et al. 2010b, 2010c) compared with the other ulvoid species, such as *U. linza, U. compressa* and *U. lactuca* ($<22\%$ d^{-1} in general, Taylor et al. 2001; Largo et al. 2004; Ale et al. 2011; Kim et al. 2011). It was, however, extremely difficult to make the side-by-side comparisons among these species and made any consensus on the GR based on literatures, because the GRs were strongly affected by the different culture conditions (e.g., nutrients, irradiance). The various life stages and strains of these tested materials may further confound the comparison (Hiraoka and Oka 2008; Lüning et al. 2008). Our field tests directly demonstrated the significantly higher GR of the blooming species than the other coexisting species under the local conditions. Although a little lower than the maximum GR of the local strain of *U. prolifera* (up to 36% d^{-1}) in the laboratory (Liu et al. 2010b, 2010c), the on-site GR (around 26.3% d^{-1}) was at a relatively high level (Luo et al. 2012), indicating that the environmental conditions in this region was favored for the growing of *U. prolifera*. The on-site GR was also consistent with the rate of field biomass accumulation at early stage of the bloom (Fan et al. 2012; Liu et al. in press). Therefore, we applied this on-site GR of *U. prolifera* into our biomass accumulation model (Eqs. 3 and 4).

Based on our model, this high GR was sufficient for the initial 4000 t of floating *U. prolfiera* expanded into million tonnes of biomass within one month. In addition to the vegetative growth, the diversified modes of macroalgal reproduction were also reported and hypothesized contributing to the vast biomass accumulation (Lin et al. 2008, 2011; Gao et al. 2010; Liu et al. 2010b; Wang et al. 2012). Sporulation of *U. prolifera* was commonly observed both in the laboratory culture and field samples (Lin et al. 2008, 2011; Liu et al. 2010b). It was, however, difficult to distinguish the algal thalli developed through different proliferation pathways (e.g., vegetative growing vs. sporulation). Therefore, it needs further investigation to assess how the various proliferation pathways contributed to the accumulation of floating biomass.

Theoretically, the total floating biomass can reach up to 5.6×10^5 t in 30 days (mid-April to mid-May). This estimation was not surprisingly higher than that from the field survey data (Fan et al. 2012; Liu et al. in press). In the model, the biomass loss due to sinking, predation, and GR variation was not considered. Besides, we assumed that the hydraulic conditions were stable and favored by growth of the floating macroalgae, which may vary in reality. The biomass variation at the late stage of green tide was even more difficult to simulate because more complicated processes started to be involved, such as natural degradation, sinking, anthropogenic clean-up, and dispersing.

As derived from our model, the field GR and total time period for growth of the floating biomass were the most critical parameters affecting the total amount of floating biomass. The total floating biomass after one-month growing could be reduced to 10% if the GR was reduced by half, or the growing period was shortened to 20 days (data was not shown), indicating a feasible strategy to mitigate the negative impact of green tides in the Yellow Sea. The other practical countermeasures, such as collecting the disposed macroalgae when cleaning the rafts, may reduce the floating biomass more efficiently, while requiring the collaborative dedications from the government and local farmers.

The source of the initial floating biomass for the green tides in the Yellow Sea

As the seed source for recruitment in the following spring, propagules are the important overwinter life-stage of intertidal macroalgae (Clayton 1992; Lotze et al. 2000; Sousa et al. 2007). *U. prolifera* micropropagules were identified in the sediments of major bloom region (Zhang et al. 2010; Liu et al. 2012, 2013b; Song et al. in press). According to the laboratory observations, Liu et al. (2012) hypothesized a "floating germination" mechanism in which the environmental propagules could attach to the floating sand particles, germinated and directly formed the floating mats. This hypothesis was further tested in our field surveys through multiple vertical trawlings. Given the widespread of floating algae in the bloom region, large amount of young germlings, the intermediate stage between propagules and floating mats, should be observed before or at the beginning of the blooms. Surprisingly, no such considerable amount of young germlings was observed in the vertical trawlings conducted from March to June. Our previous field observations in 2009 and 2011 did not support the hypothesis either. Additionally, the morphology of the small amount of individual "germlings" found in our trawling survey did not match the "floating germination" hypothesis. The germlings collected through our trawlings did not contain any rhizoids, a structure typical for the young *Ulva* individuals germinated from the environmental micropropagules in the laboratory (Hiraoka and Oka 2008; Liu et al. 2012). They were either broken fragments from the floating mass or directly germinated from a floating parental *Ulva* tissue.

Furthermore, the widespread of the environmental propagules in a wide geographic range in the Yellow Sea (Zhang et al. 2010, 2011; Liu et al. 2012) were in conflict with the consistent narrow initiation location of the green tides and developing pattern observed in multiple years (Keesing et al. 2011; Fan et al. 2012). As stated above, the constant high floating algal biomass and consistent starting point of green tides suggested a persistent point source of floating algae in and around the Subei Shoal (Keesing et al. 2011; Fan et al. 2012; this study). Without more field details on the developing process, it is implausible that the environmental propagules could turn directly into floating mats and contribute substantially to the initial floating biomass of the green tides.

In contrast, our field investigations demonstrated a complete process of green tide formation in the Yellow Sea, in which the large amount (approximately 4000 t) of *U. prolifera* disposed from the *Porphyra* rafts were able to dominate the floating algae promptly and accumulated into massive biomass under optimal environmental conditions. Thus, *U. prolifera* disposed from the *Porphyra* rafts contributed significantly to the early development of green tides and was the primary source of the initial floating biomass which developed into large-scale green tides annually in the Yellow Sea.

Environmental factors affecting the early development of the green tides

The classic conceptual model predicts high nutrient loading is the most important stimuli for the macroalgal blooms in shallow temperate estuaries (Valiela et al. 1997; Teichberg et al. 2010). And a number of biotic and abiotic factors, such as grazing and water residence time, may also be associated with the anomalous blooming of opportunistic marine macroalgae (Valiela et al. 1997; Worm and Lotze 2006; Korpinen et al. 2007; Nelson et al. 2008). Our contemporary surveys in the

Yellow Sea and a number of other researchers did indicate evidently high nutrient levels in this region, with a decreasing gradient from the coastline toward offshore waters (Huo et al. 2013; Shi et al. unpubl.). However, the consistent initiation location of the floating mats at the north edge of Subei Shoal (Keesing et al. 2011; Fan et al. 2012; this study) was controversial to the general high nutrients all over along the coasts of Jiangsu province. In fact, the eutrophic status of this area can be dated back to 1990s, and no prominent change in nutrient levels were noticed since 2007 or 2008 when the green tides broke out and started to be pervasive in the Yellow Sea (Wang et al. 2003; Keesing et al. 2011). It is well accepted that high nutrient level can facilitate and sustain the large-scale bloom of *Ulva* macroalgae (Valiela et al. 1997; Wang et al. 2012). However, the annual large-scale blooming of *U. prolifera* in the Yellow Sea cannot be attributed solely to eutrophication or other commonly mentioned factors. A persistent "source" was apparently prerequisite for the initiation of the large-scale green tides in Yellow Sea.

Concluding remarks

We surveyed the distribution and composition of the floating macroalgae, and studied the GR and buoyancy of the detached macroalgae through on-site trials. The series of research demonstrated the primary contribution of macroalgal wastes from the connecting ropes of *Porphyra* rafts to the green tides in the Yellow Sea, and the early development process of the green tide was revealed as well. The large amount of *U. prolifera* algae flourished on the *Porphyra* aquaculture rafts in Subei Shoal region, and the biomass reached maximum (approximately 6500 t in total) after the *Porphyra* crops were harvested. Due to the improper cleaning of the aquaculture facilities, these macroalgae were inadvertently disposed on the muddy flats of Subei Shoal and eventually drifted into the coastal waters, becoming the primary source of the initial floating biomass. With the prominent advantages on buoyancy and GR, *U. prolifera* dominated the floating patches rapidly and proliferated into large-scale floating mats within a month. The favored environmental conditions (SST and eutrophication) in southern Yellow Sea boosted the blooms of floating green algae. No other source was observed or confirmed by our survey. Thus, we concluded that the green tide in the Yellow Sea is an ecological disaster stimulated directly by the unhygienic husbandry and maintenance practices of coastal aquaculture.

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