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The contribution of attached *Ulva prolifera* on *Pyropia* aquaculture rafts to green tides in the Yellow Sea

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Abstract

Green tides caused by the unusual accumulation of high floating *Ulva prolifera* have occurred regularly in the Yellow Sea since 2007. The primary source of the Yellow Sea green tides is the attached algae on the *Pyropia* aquaculture rafts in the Subei Shoal. *Ulva prolifera* and *Blidingia* (*Italic*) sp. are the main species observed on *Pyropia* aquaculture rafts in the Subei Shoal. We found that *U. prolifera* has strong buoyancy and a rapid growth rate, which may explain why it is the dominant species of green tides that occur in the China's sea area of the Yellow Sea. The growth rate of floating *U. prolifera* was about 20%–31% d^{-1}, which was much higher than *Blidingia* (*Italic*) sp. There were about 1.7×10^4 t of attached algae on the *Pyropia* aquaculture rafts in May 2012. We found that 39% of attached algae could float when the tide rose in the Subei Shoal, and *U. prolifera* accounted for 63% of the floating algae. Our analysis estimated that about 4 000 t of attached *U. prolifera* floated into the surrounding waters of the Subei Shoal during the recycling period of aquaculture rafts. These results suggest that the initial floating biomass of large-scale green tides in the Yellow Sea is determined by the *U. prolifera* biomass attached to *Pyropia* aquaculture rafts, further impacting the scale of the green tide.

Key words: attached algae, *Pyropia* aquaculture rafts, *Blidingia* (*Italic*) sp., *Ulva prolifera*, green tides

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1 Introduction

Since 2007, large-scale green tides have occurred consecutively in the China's sea area of the Yellow Sea, damaging the coastal ecology, aquaculture industry, and tourism for coastal cities in Jiangsu Province and Shandong Province (Gao et al., 2010; Wang et al., 2010; Han et al., 2013). As a consequence, green tides have become a major concern for government officials and scientists in China (Liu et al., 2009). *Ulva prolifera* has been identified as the dominant species of green tides in the Yellow Sea (Wang et al., 2008; Liu et al., 2010b; Zhao et al., 2013; Xiao et al., 2013), and numerous hypotheses have been proposed to explain the origin of green tides in the Yellow Sea. Hu et al. (2010) used MODIS and Landsat satellites to detect patches of floating green tides from 2000 to 2009, and concluded that green tide formation started in the southern areas of the Yellow Sea. Pang et al. (2010) argued that the micro-propagules in animal aquaculture ponds along the Jiangsu coastline were the source of the green tides. Zhang et al. (2010, 2011) suggested that *U. prolifera* vegetative fragments and somatic cells may serve as the source of propagules of the green tide. However, other scientists have suggested that large-scale green tides in the Yellow Sea originate from algae that are cleaned from *Pyropia* aquaculture rafts in the Subei Shoal (Liu et al., 2009; Hu et al., 2010; Keesing et al., 2011; Zhang et al., 2014), and this theory is now accepted widely. According to previous studies, there are many attached algae attached algae species name on *Pyropia* aquaculture rafts, including *Blidingia* (*Italic*) sp., *U. prolifera*, *U. linza*, *U. compressa*, *U. intestinalis* and *U. clathrat*a (Fan et al., 2015).

Despite this, the following questions remain unanswered: (1) How much does attached algae on *Pyropia* aquaculture rafts contribute to green tides in the Yellow Sea? (2) What happens as the attached algae on the rafts begins to float? (3) What properties of *U. prolifera* cause large-scale green tides, when there are many other *Ulva* species on the *Pyropia* aquaculture rafts? To address these questions, we selected three major *Pyropia* aquaculture areas in the Subei Shoal to calculate the biomass and species composition of algae on *Pyropia* aquaculture rafts in May 2012. In addition, we conducted field experiments to test the species composition of floating algae and the growth rates of floating *U. prolifera* and *Blidingia* (*Italic*) sp.

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2 Materials and methods

2.1 *Sampling locations*

Based on the distribution of *Pyropia* aquaculture area in the Subei Shoal, three sites were selected to sample attached algae in May 2012 (Fig. 1). These sites included Xiaoyangkou (32.68°N, 121.09°E), Gaoni (32.81°N, 121.22°E), and Niluosha (33.22°N, 121.17°E), and samples were collected when the biomass of attached *Ulva* species on the rafts reached the highest levels. Six rafts were randomly selected in each sampling area. Six replicate samples of green algae attached to a 30 cm long rope were collected at 10 m intervals from the ropes of each raft. A total of 36 samples were obtained at each site. The green algae samples were preserved at a low temperature of about 5°C, and transported back to the laboratory within 72 h.

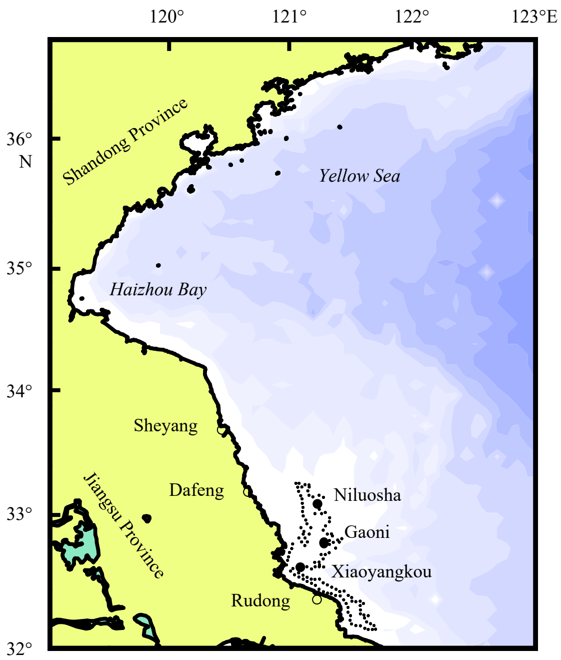

Fig. 1. Map of the three main *Pyropia* aquaculture areas located in Xiaoyangkou, Gaoni and Niluosha in the Subei Shoal.

2.2 *Species identification, separation, and biomass measurement*

Macroalgae samples were rinsed three times with sterile seawater to remove sediment, debris, and epiphytes. The green macroalgal species were identified based on the shape, branching, cell arrangement, and location of pyrenoids and chloroplasts (Tseng, 1983; Blomster et al., 1998; Ding et al., 2008; Kraft et al., 2010; Duan et al., 2012). Samples were carefully examined under the microscope using light microscopy using an Olympus CX310 microscope (KS Olympus, Tokyo, Japan). The macroalgae were dried with blotting paper and weighed using a high-accuracy electronic balance (PL203, METTLER TOLEDO Inc., Zurich, CH). The total wet weight of each sample was calculated by the sum of the biomass of all individual species (Fan et al., 2015).

2.3 *Floating experiment of attached algae on Pyropia aquaculture rafts*

Green algae samples described in Section 2.1 were dispersed in an acrylic glass tank (30 cm long × 30 cm wide × 70 cm high, in triplicate), and observed after 1 h of exposure to natural sunlight. The algae mats that floated on the water surface, suspended in the middle of the water column, and sank to the bottom of the tank were categorized as "floating", "suspension" and "sinking", respectively. Green algae in different stages were collected and dried with blotting paper, and then weighed as described above. The species composition of floating algae was measured at 1 h, 24 h, 48 h and 72 h using species identification methods described above.

2.4 *Growth experiment for U. prolifera and Blidingia (Italic) sp.*

Ulva prolifera and *Blidingia* (*Italic*) sp. were the main species found on *Pyropia* rafts in the Subei Shoal. The floating algae that were collected in the experiment described in Section 2.3 were identified as *U. prolifera* and *Blidingia* (*Italic*) sp. and different species samples separately placed in 25 L bucket (in triplicate) on shipboard for 5 d. There were three buckets were used for *Blidingia* (*Italic*) sp. and three buckets for *U. prolifera*.The seawater used for culturing was refreshed at 12:00 every day. A RBR water quality analyzer was used to measure the temperature and salinity of the seawater, and measurements were taken at 6:00, 12:00 and 18:00 every day. The daily temperature and salinity of the bucket were determined by obtaining the average across the three time points for each day. The error bars represent the variability between the three buckets.

Specific growth rate (SGR, %/d) of algae was calculated using the following formula (Metaxa et al., 2006):

$$\mathrm{SGR} = 100\,(\ln W_t - \ln W_0)\,/t,$$

where W_0 is the initial wet weight (g) of the floating algae, W_t is the wet weight (g) of the floating algae on day t, and t is the culture time (d).

2.5 *Statistics*

Datasets were analyzed by a two-way analysis of variance (ANOVA). The difference between means was analyzed by Duncan's new multiple range test followed by an ANOVA and P<0.05 was considered to be significant. Statistical analyses were performed using the SPSS 17.0 statistical program (SPSS Inc., Chicago, USA).

3 Results

3.1 *The species composition and biomass of attached algae on the rafts in May 2012*

We collected green macroalgal species from *Pyropia* aquaculture rafts during May 2012, and detected the presence of *Blidingia* (*Italic*) sp., *U. prolifera*, *U. compressa*, *U. intestinalis* and *U. clathrata*. Among them, *Blidingia* (*Italic*) sp. and *Ulva prolifera* were the main macroalgal species on the *Pyropia* aquaculture rafts. *Ulva compressa*, *U. intestinalis* and *U. clathrata* had low biomass and were only detected in some sampling sites. Given their low prevalence, we combined the results for these three species and refer to these samples as *Ulva* spp. The attached total algae biomass at Xiaoyangkou, Gaoni and Niluosha were 214.2, 153.4 and 53.0 g/m, respectively (Fig. 2).

3.2 *Morphology of U. prolifera and Blidingia (Italic) sp.*

Ulva prolifera attached to the rafts were light green with multiple slender branchlets on the boughs. The diameter of the side branch was smaller than the chief branch, and chief branch was hollow and tubular (Figs 3a and b). There was a small gap between the two cells of the green algae with a flat air sac (Fig. 3c). *Blidingia* (*Italic*) sp. attached to the rafts were dark green with

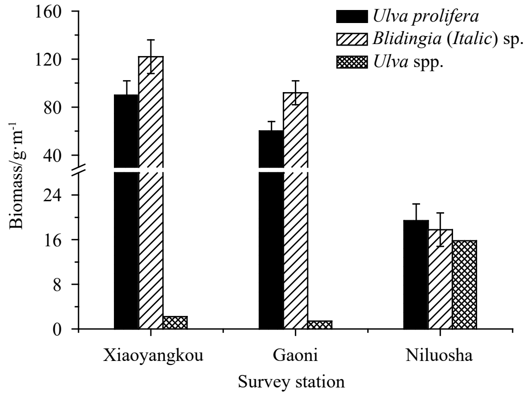

Fig. 2. Biomass of green macroalgae on the *Pyropia* aquaculture rafts.

thin tubular, unbranched, and single layered cells (Figs 3d and e). *Blidingia* (*Italic*) sp. were small and closely arranged (Fig. 3f).

3.3 *The state of attached algae and species composition of floating algae*

We placed algae from the *Pyropia* aquaculture rafts in a tank and found that 39% of the algae floated on the water surface after 1 h of being dispersed (Fig. 4). *Ulva prolifera* accounted for about 63% of the floating algae and the percentage gradually increased and reached 91.3% after 24 h. The proportion of *U. prolifera* accounted for floating algae was greater than 98% after 72 h (Fig. 5).

3.4 *The SGR of U. prolifera and Blidingia (Italic) sp.*

The SGR of *U. prolifera* ranged from 20%–31% d^{-1} during the test period, and this was much higher than *Blidingia* (*Italic*) sp., which ranged from 1.7%–3.4% d^{-1} (Fig. 6). Taken together, the SGR of *U. prolifera* was about 15 times greater than *Blidingia* (*Italic*) sp. The average daily seawater temperatures ranged from 20.5 to 23.5°C, and the average salinity varied over time (P>0.05) with values ranging from 30.5 to 30.9, which was not a dramatic change (Fig. 7).

4 Discussion

The *Pyropia* rafts usually begin to be collected in April. The culture nets will be transported back for the *Pyropia* crops, while the connecting ropes and bamboo poles will be cleaned *in situ* before they are moved back for next year's construction. And the harvesting starts from near-shore region and progresses to the east. The cleaning process usually takes for about one month,

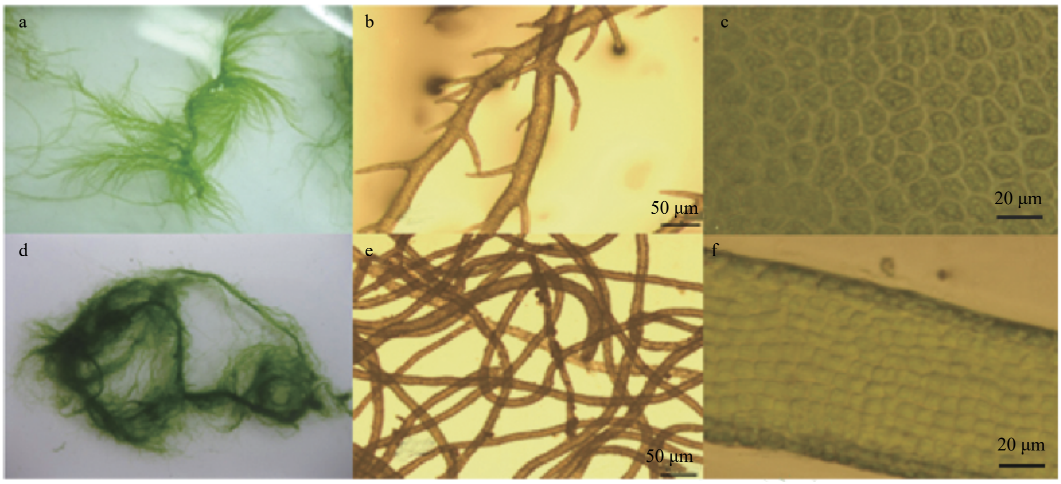

Fig. 3. The main green macroalgae species on *Pyropia* aquaculture rafts. a–c. *Ulva prolifera* morphological characteristics, microstructure and cell rank characteristics; and d–f. *Blidingia* (*Italic*) sp. morphological characteristics, microstructure and the cell arrangement characteristics.

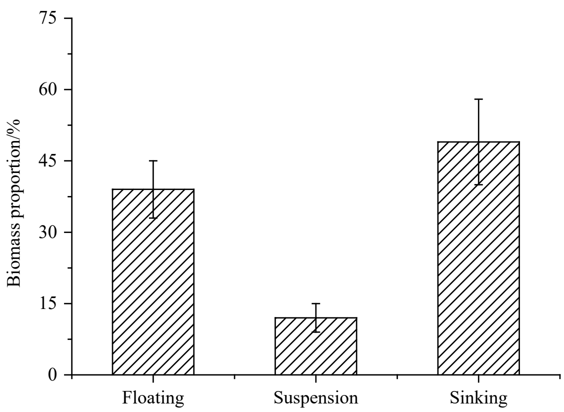

Fig. 4. Biomass proportion of attached algae after 1 h of being dispersed.

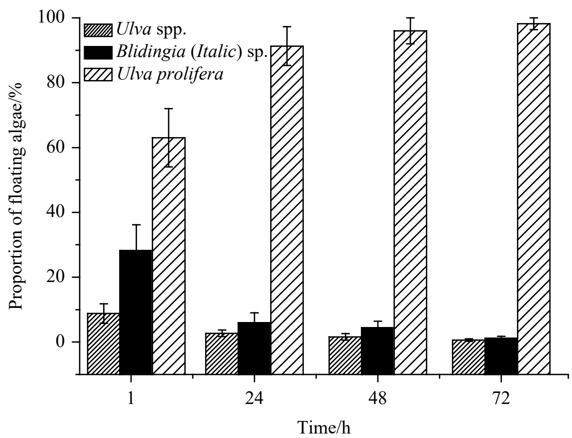

Fig. 5. Variability in species composition of floating green algae over a 72 h culture period.

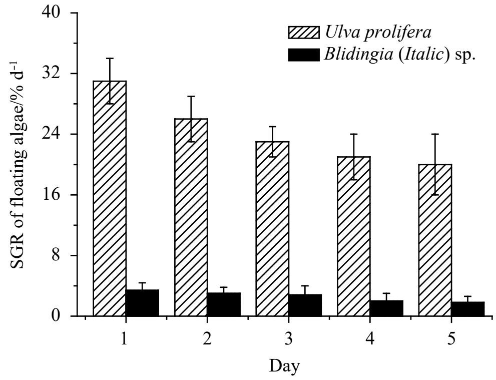

Fig. 6. The SGR of floating green algae during the culture period.

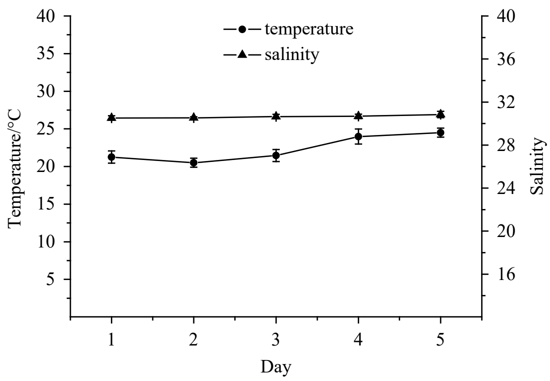

Fig. 7. Temporal variability of temperature and salinity in the culture experiment.

from the mid-April to mid-May (Wang et al., 2015; Huo et al., 2015). So, there are still quite a few *Pyropia* rafts left on the Subei Shoal in May, especially at the east edge of Subei Shoal. As indicated by the detailed description of macroalgal assemblage on the rafts, there were large amount of *Ulva* on the rafts and could reach the highest in May after rapid growing of the attached algae with favorable temperature (Fan et al., 2015; Liu et al., 2016). So we collected the samples in May, when the green tide began to form. Our results showed that *U. prolifera* and *Blidingia* (*Italic*) sp. were the dominant species on *Pyropia* aquaculture rafts during the harvesting season in Subei Shoal. We found that *U. prolifera* accounted for 63% of the floating algae when algae samples from rafts were placed in a tank for 1 h. *Ulva prolifera* represented 91.3% of the floating algae by 24 h of culturing samples in a tank. In constrast, our field investigations found that *U. prolifera* represented more than 95% of the floating algae in the Subei Shoal (Song, 2014). The percentage of *U. prolifera* continued to increase as macroalgae drifted offshore, reaching 99% or higher in the algal patches of the central Yellow Sea (Liu et al., 2016). The ocean waves may stir and scatter *U. prolifera* and *Blidingia* (*Italic*) sp., which are initially mixed together, and this may underlie the difference we observed between the field and simulation experiments. Therefore, the percentage of *U. prolifera* in the field was higher over a short period of time. The resulted showed tha buoyancy capacity of *U. prolifera* was higher than other attached algae on *Pyropia* aquaculture rafts, which may be one of the reasons it has become the dominant species in the green tides of the Yellow Sea.

The growth of *U. prolifera* is controlled by many environmental factors (Agrawal, 2009). Wang et al. (2007) found that 20–25°C was the appropriate temperature range for *U. prolifera* and Cui et al. (2015) showed that the growth rate of *U. prolifera* was higher than other floating algae at 20°C. The average daily SGR of green algae along the Rudong coast is approximately 23.2%–26.3% (Zhang et al., 2013). In our experimental conditions, the daily temperature was between 20.5°C and 23.5°C with salinity of around 30, which match with conditions that are optimal for *U. prolifera* growth. The daily SGR in our tank experiments was 20%–31% every day for *U. prolifera*, which was much higher than *Blidingia* (*Italic*) sp. the other dominnat algae species found on the *Pyropia* aquaculture rafts. In our study, the ambient seawater was used for culturing and refreshed every day. So the nutrients concentrations in the culturing water should be similar to the ambient seawater. With the substantial nutrient inputs from the rivers surrounded, e.g., Changjiang (Yangtze) River, Sheyang River and Guan River, high nutrients were generally found in the Subei Shoal over the past decades (Keesing et al., 2011). It was almost certainly sufficient for the *U. prolifera* blooms (Liu et al., 2013; Zhou et al., 2015). Similarly, the culture experiment was performed on the shipboard under the nature light. The light intensity of the sea surface was below 30 μmol/(m^2·s) on the rainy days, 30–300 mol/(m^2·s) on cloudy days, and generally above 300 μmol/(m^2·s) on sunny days (Cui et al., 2015). Cui et al. (2015) noted that *U. prolifera* has better tolerance to high temperature and light intensity than the other three species. Our algae culture experiment are on the sunny days and the growth rate of *U. prolifera* were higher than the *Blidingia* (*Italic*) sp.

We observed an increase in the percentage of *U. prolifera* among the floating algae over time, and a concurrent decrease in the presence of other algae. The rapid growth rate of *U. prolifera* is an important reason why this species has become the dominant species of green tide in the Yellow Sea (Zhang et al., 2014; Cui et al., 2015). In our experiment, when the attached algae began to float, *U. prolifera* quickly became the dominant species due to its buoyancy and rapid growth rate. The other green algae could not compete with *U. prolifera*, and *U. prolifera* became the dominant species within two days. Under the influence of the southeast monsoon, *U. prolifera* can float northward and reach the sea area of Qingdao (Keesing et al., 2011).

Blidingia (*Italic*) sp. was a high percentage of the attached algae on *Pyropia* aquaculture rafts in May 2012. However, the species of algal micro-propagules in Subei Shoal mainly consisted of the genus *Ulva*, and there were only low amounts of *Blidingia* (*Italic*) sp. micro-propagules (Song et al., 2015). Therefore, we hypothesized that attached *Ulva* and *Blidingia* (*Italic*) sp. had different growth modes. We observed regularly arranged oval or long cylindrical germ cell cytocysts of *U. prolifera* under the microscope, where germ cells were clearly seen in the germ cell cytocysts (Fig. 3c). However, *Blidingia* (*Italic*) sp. were shaped differently and appeared transparent and closely arranged under the microscope. Interestingly, these *Blidingia* (*Italic*) sp. cells did not contain germ cell cytocysts (Fig. 3f). Therefore, we hypothesized that attached *U. prolifera* and *Blidingia* (*Italic*) sp. may mainly depend on reproductive and vegetative growth modes, respectively.

Green macroalgae are scraped and thrown away by farmers in Subei Shoal during the *Pyropia* harvesting season in May (Liu et al., 2010a, 2016; Zhang et al., 2014; Wang et al., 2015). In our study, 39% of the attached algae floated after 1 h and over 98% of the floating algae were *U. prolifera* after 72 h of culture. We suspect that the changes in the floating state of *U. prolifera* may affect its growth pattern. Li et al. (2014) observed morphological differences between attached and floating *U. prolifera*, where floating *U. prolifera* has significantly more branching than attached *U. prolifera*. Lin et al. (2008) found that the reproductive cells of floating *U. prolifera* contained unreleased micro-propagules that could germinate and grow directly to create more branches. Lin et al. (2008) also found that *U. prolifera* relies on vegetative growth when it is in a floating state. Ye et al. (2008) suggested that *U. prolifera* could rapidly grow through the asexual propagation of somatic cells during floating. Zhang et al. (2016) observed four different growth and reproductive strategies of floating *U. prolifera*, including: (1) tubular diameter becoming larger, (2) formation of new branches, (3) release of zoids, and (4) polarized growth. The diversified reproduction strategies of *U. prolifera* may also underlie its dominance during green tide events at the Yellow Sea.

The algae attached to *Pyropia* aquaculture rafts are considered to be the origin of the green tides in the Yellow Sea (Liu et al., 2009, 2010a; Keesing et al., 2011; Huo et al., 2015; Zhang et al., 2014). Farmers begin to recycle aquaculture rafts in May and when the macroalgae are scraped off, the attached algae begin to float to form initial green tides in Subei Shoal as the tide rises (Liu et al., 2010a; Huo et al., 2015). Then, the initial green tides drifts offshore, resulting in the rapid increase in floating biomass and the formation of large-scale green tides in the Yellow Sea (Liu et al., 2010a, 2013). Our study quantitatively analyzed the contribution of attached algae to green tides in the Yellow Sea. Based on our data and the total *Pyropia* aquaculture area (3.8×10^4 hm^2) in the Subei Shoal (Shang et al., 2008), we estimated the raft-fouling biomass of the green macroalgae to be about 1.70×10^4 t in May 2012. Our results showed that 39% of the attached algae could float and *U. prolifera* accounted for 63% after 1 h. Taken together, about 4 000 t *U. prolifera* may have began floating once the rafts were harvested in May. In the floating process, *U. prolifera* experienced a rapid growth rate of 20%-31%, and after 30 d of floating, *U. prolifera* likely reached 237 times of the initial biomass based on a daily growth rate of 20% (Fig. 8). This is enough to form a large-scale green tide of one million tons in the Yellow Sea by the end of June. Taken together, our findings highlight that the biomass of *U. prolifera* attached on *Pyropia* aquaculture rafts can affect the scale of green tide in the Yellow Sea.

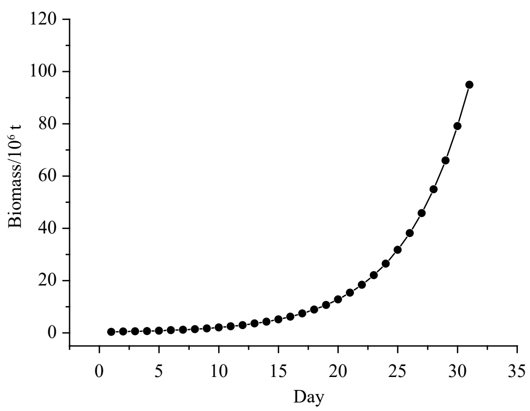

Fig. 8. Temporal variability of total biomass of floating macroalgae based on a 20% growth rate.

References

Agrawal S C. 2009. Factors affecting spore germination in algae—review. Folia Microbiologica, 54(4): 273–302, doi: 10.1007/s12223-009-0047-0

Blomster J, Maggs C A, Stanhope M J. 1998. Molecular and morphological analysis of *Enteromorpha intestinalis* and *E. compressa* (Chlorophyta) in the British Isles. Journal of Phycology, 34(2): 319–340, doi: 10.1046/j.1529-8817.1998.340319.x

Cui Jianjun, Zhang Jianheng, Huo Yuanzi, et al. 2015. Adaptability of free-floating green tide algae in the Yellow Sea to variable temperature and light intensity. Marine Pollution Bulletin, 101(2): 660–666, doi: 10.1016/j.marpolbul.2015.10.033

Ding Lanping, Luan Rixiao, Huang Bingxin, et al. 2008. The taxonomical study on Capsosiphonaceae (Ulvales, Chlorophyta) from Huanghai-Bohai Seas of China. Haiyang Xuebao (in Chinese), 30(2): 169–174

Duan Weijun, Guo Lixin, Sun Dong, et al. 2012. Morphological and molecular characterization of free-floating and attached green macroalgae *Ulva* spp. in the Yellow Sea of China. Journal of Applied Phycology, 24(1): 97–108, doi: 10.1007/s10811-011-9654-7

Fan Shiliang, Fu Mingzhu, Wang Zongling, et al. 2015. Temporal variation of green macroalgal assemblage on *Porphyra* aquaculture rafts in the Subei Shoal, China. Estuarine, Coastal and Shelf Science, 163: 23–28, doi: 10.1016/j.ecss.2015.03.016

Gao Shan, Chen Xiaoyuan, Yi Qianqian, et al. 2010. A strategy for the proliferation of *Ulva prolifera*, main causative species of green tides, with formation of sporangia by fragmentation. PLoS One, 5(1): e8571, doi: 10.1371/journal.pone.0008571

Han Wei, Chen Liping, Zhang Jianheng, et al. 2013. Seasonal variation of dominant free-floating and attached *Ulva* species in Rudong coastal area, China. Harmful Algae, 28: 46–54, doi: 10.1016/j.hal.2013.05.018

Hu Chuanmin, Li Daqiu, Chen Changsheng, et al. 2010. On the recurrent *Ulva prolifera* blooms in the Yellow Sea and East China Sea. Journal of Geophysical Research, 115(C5): C05017

Huo Yuanzi, Han Hongbin, Shi Honghua, et al. 2015. Changes to the biomass and species composition of *Ulva* sp. on *Porphyra* aquaculture rafts, along the coastal radial sandbank of the southern yellow sea. Marine Pollution Bulletin, 93(1–2): 210–216, doi: 10.1016/j.marpolbul.2015.01.014

Keesing J K, Liu Dongyan, Fearns P, et al. 2011. Inter- and intra-annual patterns of *Ulva prolifera* green tides in the Yellow Sea during 2007–2009, their origin and relationship to the expansion of coastal seaweed aquaculture in China. Marine Pollution Bulletin, 62(6): 1169–1182, doi: 10.1016/j.marpolbul.2011.03.040

Kraft L G K, Kraft G T, Waller R F. 2010. Investigations into southern Australian *Ulva* (Ulvophyceae, Chlorophyta) taxonomy and molecular phylogeny indicate both cosmopolitanism and endemic cryptic species. Journal of Phycology, 46(6): 1257–1277, doi: 10.1111/j.1529-8817.2010.00909.x

Li Yan, Song Wei, Xiao Jie, et al. 2014. Tempo-spatial distribution and species diversity of green algae micro-propagules in the Yellow Sea during the large-scale green tide development. Harmful Algae, 39: 40–47, doi: 10.1016/j.hal.2014.05.013

Lin Apeng, Shen Songdong, Wang Jianwei, et al. 2008. Reproduction diversity of Enteromorpha prolifera. Journal of Integrative Plant Biology, 50(5): 622–629, doi: 10.1111/j.1744-7909.2008.00647.x

Liu Dongyan, Keesing J K, Dong Zhijun, et al. 2010a. Recurrence of the world's largest green-tide in 2009 in Yellow Sea, China: *Porphyra yezoensis* aquaculture rafts confirmed as nursery for macroalgal blooms. Marine Pollution Bulletin, 60(9): 1423–1432, doi: 10.1016/j.marpolbul.2010.05.015

Liu Dongyan, Keesing J K, He Peimin, et al. 2013. The world's largest macroalgal bloom in the Yellow Sea, China: formation and implications. Estuarine, Coastal and Shelf Science, 129: 2–10, doi: 10.1016/j.ecss.2013.05.021

Liu Dongyan, Keesing J K, Xing Qianguo, et al. 2009. World's largest macroalgal bloom caused by expansion of seaweed aquaculture in China. Marine Pollution Bulletin, 58(6): 888–895, doi: 10.1016/j.marpolbul.2009.01.013

Liu Feng, Pang Shaojun, Chopin T, et al. 2010b. The dominant *Ulva* strain of the 2008 green algal bloom in the Yellow Sea was not detected in the coastal waters of Qingdao in the following winter. Journal of Applied Phycology, 22(5): 531–540, doi: 10.1007/s10811-009-9489-7

Liu Xiangqing, Wang Zongling, Zhang Xuelei. 2016. A review of the green tides in the Yellow Sea, China. Marine Environmental Research, 119: 189–196, doi: 10.1016/j.marenvres.2016.06.004

Metaxa E, Deviller G, Pagand P, et al. 2006. High rate algal pond treatment for water reuse in a marine fish recirculation system: water purification and fish health. Aquaculture, 252: 92–101, doi: 10.1016/j.aquaculture.2005.11.053

Pang Shaojun, Liu Feng, Shan Tifeng, et al. 2010. Tracking the algal origin of the *Ulva* bloom in the Yellow Sea by a combination of molecular, morphological and physiological analyses. Marine Environmental Research, 69(4): 207–215, doi: 10.1016/j.marenvres.2009.10.007

Shang Zhaotang, Jiang Mingshu, Pu Meijuan. 2008. Analysis of the general situations of laver culture in Jiangsu Province and its climatic suitability. Journal of Anhui Agricultural Sciences (in Chinese), 36(13): 5315–5319

Song Wei. 2014. Studies on species identification, physiological characteristics and community succession of attached green algae on Subei Shoal [dissertation]. Changsha: Hunan Agricultural University

Song Wei, Peng Keqin, Xiao Jie, et al. 2015. Effects of temperature on the germination of green algae micro-propagules in coastal waters of the Subei Shoal, China. Estuarine, Coastal and Shelf Science, 163: 63–68, doi: 10.1016/j.ecss.2014.08.007

Tseng C K. 1983. Common Seaweeds of China (in Chinese). Beijing: Science Press

Wang Jinfeng, Jiang Peng, Cui Yulin, et al. 2010. Molecular analysis of green-tide-forming macroalgae in the Yellow Sea. Aquatic Botany, 93: 25–31, doi: 10.1016/j.aquabot.2010.03.001

Wang Chao, Qiao Hongjin, Pan Guanghua, et al. 2008. Studies on the parameters of physiology of *Enteromorpha prolifera* collected from the Qingdao Olympic sailing center. Marine Sciences (in Chinese), 32(8): 13–15

Wang Zongling, Xiao Jie, Fan Shiliang, et al. 2015. 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. Limnology and Oceanography, 60(4): 1105–1117, doi: 10.1002/lno.10083

Wang Jianwei, Yan Binlun, Lin Apeng, et al. 2007. Ecological factor research on the growth and induction of spores release in *Enteromorpha prolifera* (Chlorophyta). Marine Science Bulletin (in Chinese), 26(2): 60–65

Xiao Jie, Li Yan, Song Wei, et al. 2013. Discrimination of the common macroalgae (*Ulva* and *Blidingia*) in coastal waters of Yellow Sea, northern China, based on restriction fragment-length polymorphism (RFLP) analysis. Harmful Algae, 27: 130–137, doi: 10.1016/j.hal.2013.05.003

Ye Naihao, Zhang Xiaowen, Mao Yuze, et al. 2008. Life history of *Enteromorpha prolifera* under laboratory conditions. Journal of Fishery Sciences of China (in Chinese), 15(5): 853–859

Zhang Jianheng, Huo Yuanzi, Wu Hailong, et al. 2014. The origin of the *Ulva* macroalgal blooms in the Yellow Sea in 2013. Marine Pollution Bulletin, 89(1–2): 276–283, doi: 10.1016/j.marpolbul.2014.09.049

Zhang Jianheng, Huo Yuanzi, Yu Kefeng, et al. 2013. Growth characteristics and reproductive capability of green tide algae in Rudong coast, China. Journal of Applied Phycology, 25(3): 795–803, doi: 10.1007/s10811-012-9972-4

Zhang Jianheng, Kim J K, Yarish C, et al. 2016. The expansion of *Ulva prolifera* O. F. Müller macroalgal blooms in the Yellow Sea, PR China, through asexual reproduction. Marine Pollution Bulletin, 104(1–2): 101–106, doi: 10.1016/j.marpolbul.2016.01.056

Zhang Xiaowen, Wang Hongxia, Mao Yuze, et al. 2010. Somatic cells serve as a potential propagule bank of *Enteromorpha prolifera* forming a green tide in the Yellow Sea, China. Journal of Applied Phycology, 22(2): 173–180, doi: 10.1007/s10811-009-9437-6

Zhang Xiaowen, Xu Dong, Mao Yuze, et al. 2011. Settlement of vegetative fragments of *Ulva prolifera* confirmed as an important seed source for succession of a large-scale green tide bloom. Limnology and Oceanography, 56(1): 233–242, doi: 10.4319/lo.2011.56.1.0233

Zhao Jin, Jiang Peng, Liu Zhengyi, et al. 2013. The Yellow Sea green tides were dominated by one species, *Ulva* (*Enteromorpha*) *prolifera*, from 2007 to 2011. Chinese Science Bulletin (in Chinese), 58(19): 2298–2302

Zhou Mingjiang, Liu Dongyan, Anderson D M, et al. 2015. Introduction to the Special Issue on green tides in the Yellow Sea. Estuarine, Coastal and Shelf Science, 163: 3–8, doi: 10.1016/j.ecss.2015.06.023