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Invited feature

The world's largest macroalgal bloom in the Yellow Sea, China: Formation and implications

Dongyan Liu [a,*], John K. Keesing [a,b], Peimin He [c], Zongling Wang [d], Yajun Shi [a], Yujue Wang [a]

[a] Key Laboratory of Coastal Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, 17th Chunhui Road, Laishan District, 264003 Yantai, Shandong, PR China
[b] CSIRO Wealth from Oceans National Research Flagship, CSIRO Marine and Atmospheric Research, 6913, Wembley, Australia
[c] College of Fisheries and Life Science and Institute of Marine Science, Shanghai Ocean University, 201306, Shanghai, PR China
[d] The First Institute of Oceanography, State Oceanic Administration, 266061, Qingdao, Shandong, PR China

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ABSTRACT

The world's largest trans-regional macroalgal blooms during 2008–2012 occurred in the Yellow Sea, China. This review addresses the causes, development and future challenges in this unique case. Satellite imagery and field observations showed that the macroalgal blooms in the Yellow Sea originated from the coast of Jiangsu province and that favorable geographic and oceanographic conditions brought the green macroalgae from the coast offshore. Optimal temperature, light, nutrients and wind contributed to the formation and transport of the massive bloom north into the Yellow Sea and its deposition onshore along the coast of Shandong province. Morphological and genetic evidence demonstrated that the species involved was *Ulva prolifera*, a fouling green commonly found growing on structures provided by facilities of *Porphyra* aquaculture. Large scale *Porphyra* aquaculture (covering >20,000 ha) along the Jiangsu coast thus hypothetically provided a nursery bed for the original biomass of *U. prolifera*. *Porphyra* growers remove *U. prolifera* from the mariculture rafts, and the cleaning releases about 5000 wet weight tonnes of green algae into the water column along the coast of Jiangsu province; the biomass then is dispersed by hydrographic forcing, and takes advantage of rather high nutrient supply and suitable temperatures to grow to impressive levels. Certain biological traits of *U. prolifera* —efficient photosynthesis, rapid growth rates, high capacity for nutrient uptake, and diverse reproductive systems— allowed growth of the original 5000 tonnes of *U. prolifera* biomass into more than one million tonnes of biomass in just two months. The proliferation of *U. prolifera* in the Yellow Sea resulted from a complex contingency of circumstances, including human activity (eutrophication by release of nutrients from wastewater, agriculture, and aquaculture), natural geographic and hydrodynamic conditions (current, wind) and the key organism's biological attributes. Better understanding of the complex biological–chemical–physical interactions in coastal ecosystems and the development of an effective integrated coastal zone management with consideration of scientific, social and political implications are critical to solving the conflicts between human activity and nature.

Editor's note

The eutrophication of the World's coastal waters by human-driven nitrogen enrichment is a global-scale issue, with many distinctive local consequences. A remarkable example of these features is the subject of the Invited Feature Article in this issue.

The impressive bloom of macroalgae reviewed by Liu and colleagues was clearly fostered by the highly N-enriched waters of the coastal Yellow Sea. In addition, the blooms were made possible by local contingencies, including a ready supply of propagules generated from widespread maricultural structures, peculiar hydrodynamic aspects, and opportunistic biological attributes of the macroalgal species involved.

While local aspects conspired to generate the impressive "green tides" in the Yellow Sea, the perturbations reported by Liu and colleagues convey the sobering lesson that uncontrolled nutrient enrichment of coastal waters forces major disruptions to coastal

* Corresponding author.
E-mail address: dyliu@yic.ac.cn (D. Liu).

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ecosystems, often unforeseen in detail, but with powerful disturbances of natural ecosystems, and inexorably, on human use of these coastal environments.

1. Introduction

On 28th of June 2008, only four weeks before the opening of Beijing Olympics, a massive macroalgal bloom covering about 400 km^2 occurred along the coast of Qingdao, Shandong province, China, which was the host city for the Olympic sailing regatta (Fig. 1a–b). More than 10,000 people were involved in the cleanup, over one million tonnes of green algae were removed from the beach and coastal waters, and the Olympic sailing competition was able to proceed. Costs for cleanup and emergency response were estimated at about 200 million RMB ($\approx$30.8 million US dollars), which did not include the losses by aquaculture and tourism industries in the summer of 2008 (Ye et al., 2011).

Although the initial search for the cause of the 2008 macroalgal bloom in Qingdao focused on local coastal eutrophication and the action of tides and wind in bringing the algae ashore, a series of satellite images clearly demonstrated that the formation of the massive green tide in 2008 was a broad regional process across the Yellow Sea (Fig. 2) (Liu et al., 2009; Hu et al., 2010; Keesing et al., 2011). Small floating green algal patches originally occurred in the southern Yellow Sea near the coast of Jiangsu province in May 2008 (Fig. 2a), and these floating green algae were transported more than 200 km northwards in the Yellow Sea, from Jiangsu province to Shandong province by wind and currents. The small patches of floating green algae drifted for about one and a half months, and eventually developed into the world's largest green tide ever reported, reaching a maximum algal mat cover of 3489 km^2, scattered across an area of coastal sea of about 84,109 km^2, and producing extraordinary amounts of algal biomass (Fig. 2b). Eventually, most of these algae landed along the coast of Qingdao city (Fig. 2c) and resulted in a significant impact on the local environment and economy (State Oceanic Administration, China, 2009; Ye et al., 2011).

Macroalgal blooms are formed by the excessive growth of some macroalgae species living in the intertidal zone, and most of these species are green algae, such as *Ulva*, *Enteromorpha*, *Chaetomorpha* and *Cladophora*. These green algal blooms have been referred to as green tides (Fletcher, 1996; Morand and Merceron, 2005). Macroalgal blooms can dramatically impact the aquatic environment and result in significant economic losses. Waterways and valuable habitats can be choked or damaged by high macroalgal biomass; noxious odors (NH_3, H_2S) and anoxic conditions produced by algal decay can impact tourism and lead to massive fish and shellfish kills (Valiela et al., 1992, 1997; Raffaelli et al., 1998; Nelson et al., 2008). The first such green tide event was reported in 1905 at Belfast Lough, North Ireland (Cotton, 1910; Letts and Richards, 1911), but such phenomena did not attract enough attention from scientists until the 1970s when green tides occurred more frequently in coastal areas, estuaries, and lakes, and caused significant negative effects on aquatic ecosystems and economic values (Fletcher, 1974; Buttermore, 1977; Klavestad, 1978). Morand and Briand (1996) listed 37 countries affected by green tides in Europe, North America, South America, Asia, and Australia, and this number has been increasing over the last decade (Morand and Merceron, 2004; Teichberg et al., 2010), indicating the deterioration of intertidal ecosystems.

The cause of green tides has generally been attributed to poor water quality, e.g., eutrophication from agricultural runoff or urban-derived pollution, which can lead to overgrowth of macroalgae (Sfriso et al., 1987; Fletcher, 1996; Valiela et al., 1992, 1997). Scientists also found that an adaptive capacity of green algae to the variable environment in the intertidal zone (e.g., temperature, salinity and light) and decreased herbivore control of algal biomass can significantly contribute to the formation of green tides (Valiela et al., 1997; Lotze et al., 2000; Worm and Lotze, 2006). It is difficult, however, to attribute the cause of green tides in the Yellow Sea completely to eutrophication because the massive green tides are a new phenomenon while coastal eutrophication has been present in the Yellow Sea for decades (Wang et al., 2003; Lin et al., 2005). Examination of satellite data from 2004 to 2010 revealed that a first green tide in the Yellow Sea appeared during 2007 (Keesing et al., 2011); this bloom reached a modest macroalgal mat cover (Fig. 3a). This bloom was also reported in the local ocean news during summer of 2007 (Jiang et al., 2008). A massive green tide occurred during summer of 2008 (Fig. 2), and has since become an annual summer event in the Yellow Sea (Fig. 3b–e), although recent years did not reach the extraordinary levels of 2008.

The green tides in the Yellow Sea have been unique in that they have developed offshore, in contrast to most reports from

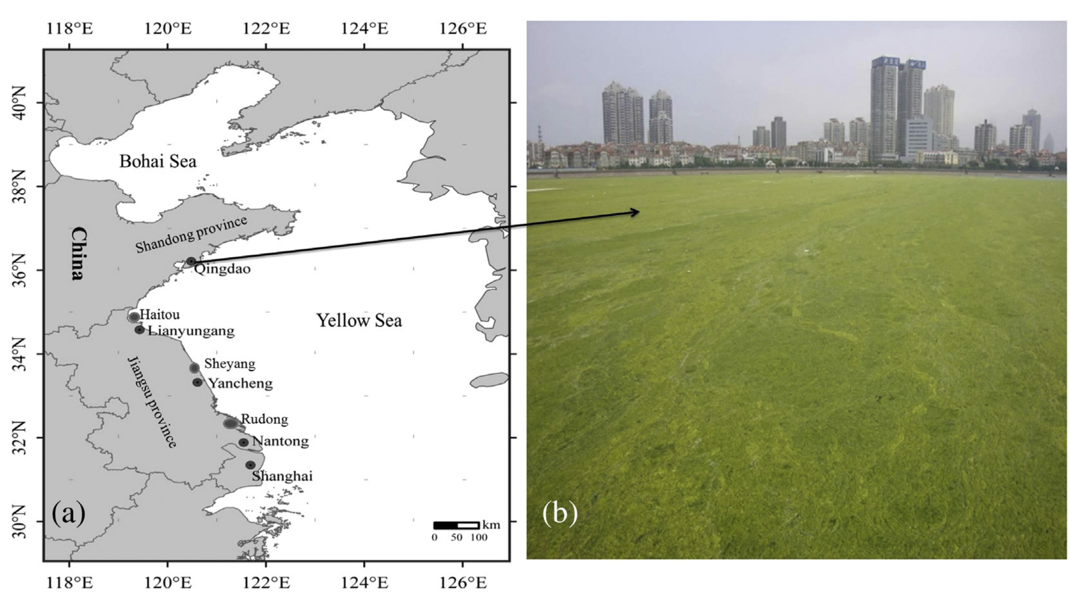

Fig. 1. 2008 summer green tide in the Yellow Sea, China: (a) geographic location of Qingdao; (b) photograph on 27th of June 2008 showing green tide at Qingdao coast.

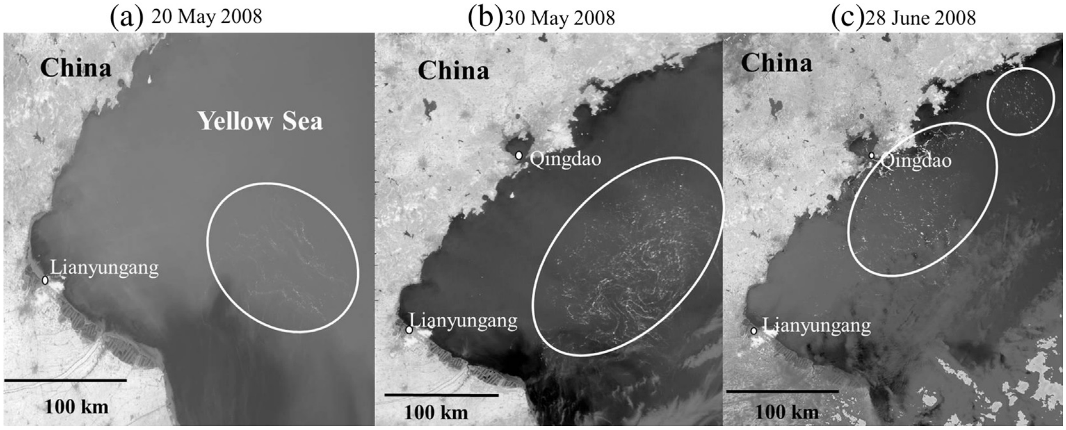

Fig. 2. Satellite images from 20 May, 30 May, and 28 June 2008, showing fast development of green tide in the Yellow Sea (white ovals indicate areas with floating green algal mats): (a) minor macroalgal mat cover off Jiangsu province coast, 20 May 2008; (b) peak macroalgal mat cover, central Yellow Sea, 30 May 2008; and (c) bloom arrived on shore of southern Shandong peninsula, 28 June 2008.

elsewhere, which took place over water columns with depths ranging from 2 to 20 m (Morand and Merceron, 2004; Merceron et al., 2007). Moreover, the offshore area provided a large expanse for the formation of a massive algal biomass and a subsequent negative impact on the marine ecosystem. The formation of green tide in the Yellow Sea is of serious concern for local government and also a challenge for scientists. Since 2008, numerous reports and scientific articles have described the causes, development and effects of the green tides in the Yellow Sea. Here we summarize these studies in regard to research from the original source of green algae, seaward transport, and context of growth that supported growth of a million tonnes of wet weight biomass in only two months.

2. Original source of green algae along the coast of Jiangsu province, Yellow Sea

2.1. Species identification of the green tides in the Yellow Sea

The morphological characteristics and the ribotype network of the nuclear encoded internal transcribed spacer (ITS) sequences both showed that *Ulva prolifera* was the species involved in the green tide of the Yellow Sea. This species was earlier known as *Enteromorpha prolifera* (O.F. Müller) (Hayden et al., 2003; and www.algaebase.org). *U. prolifera* is a green filamentous alga with tiny and multiple tubular branchlets (Zhang et al., 2008; Liu et al., 2010). Although a few other green algal species (*Ulva linza*, *Ulva intestinalis*, *Ulva compressa*, *Ulva flexuosa*) were detected in the early stages of green tides, *U. prolifera* gradually dominated in biomass while drifting and was the major contributor for the massive green tide (Liu et al., 2010; Tian et al., 2011).

2.2. Conjectures about the original sources of propagules for green tides

Although satellite imagery showed that the trajectory of the green tides in the Yellow Sea originated from the Jiangsu coast, there were different opinions about the initial source of propagules for the green tides in the Yellow Sea.

1) Liu et al. (2009, 2010) proposed that the biomass source of the bloom came from the cleaning of fouling green algae at facilities used for more than 20,000 ha of *Porphyra* aquaculture along the Jiangsu province coast (Fig. 4). These maricultural activities extend over a large region between Yancheng and Nantong, characterized by large-scale coastal sand ridges. This area supports nearly 10,000 ha of *Porphyra* aquaculture expansion, with a notable expansion that took place since 2006 (Fig. 5a).

The strong association between *Enteromorpha* (*Ulva*) growth and the aquaculture of *Porphyra* was reported in previous studies

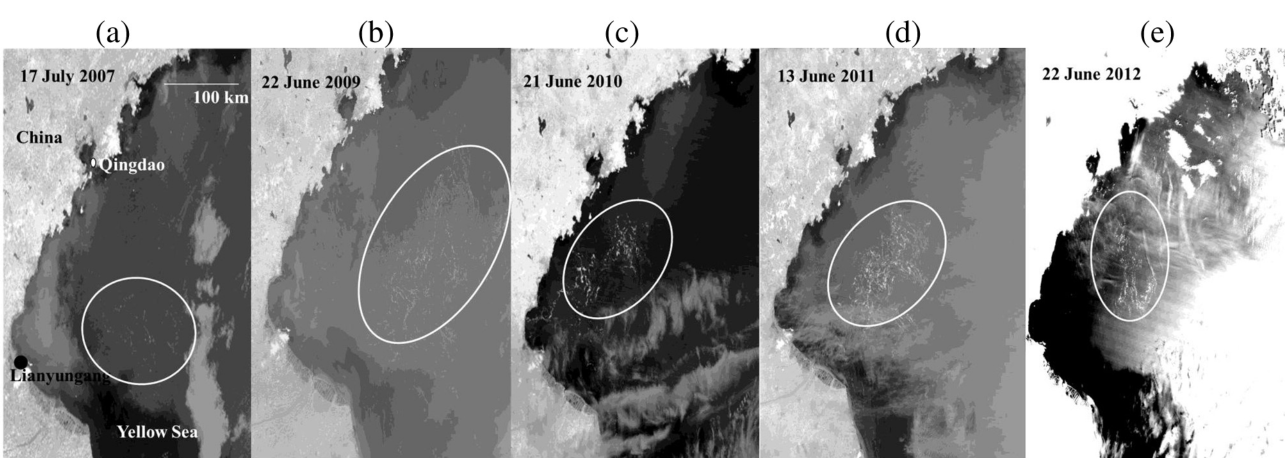

Fig. 3. MODIS satellite images showing multi-year history of green tides in the Yellow Sea during summers of (a) 2007; (b) 2009; (c) 2010; (d) 2011; and (e) 2012. White ovals indicate areas with floating green macroalgal mats.

Fig. 4. Left: *Porphyra* aquaculture structures used in Jiangu coastal region. Right: green *Ulva* fronds growing on support structures used in *Porphyra* culture are scraped off by the growers, and may then become propagules that drift out to sea and develop into the massive open-sea macroalgal mats.

(Hirano, 1986; Shang et al., 2008). The usual seeding time of *Porphyra yezoensis* along Jiangsu coast extends from mid-October to mid-November (Shang et al., 2008). Tiny green algae grow on the bamboo poles and ropes used for *P. yezoensis* aquaculture in December and January. Significant growth of the attached green algae takes place in spring (Feb. –Apr.) when weather gets warmer (Fig. 4). These green algae, including *Ulva prolifera* and *Ulva intestinalis*, are routinely scraped off the mariculture facilities after harvest of *P. yezoensis* in mid-April. The dates of routine removal green algae coincided with satellite observations during 2008–2012 that showed that the first occurrence of green tide in the Yellow Sea was from late April or early May to July (Table 2), just 2 weeks after the *Porphyra* harvest.

The biomass of the removal *Ulva prolifera* was estimated at approximately 5000 tonnes wet weight in the Jiangsu coastal region (Liu et al., 2010). This amount of macroalgae was sufficient to generate a million tonnes of green tide biomass after one and half months growth based on known growth rates of 10–37% per day (Liang et al., 2008; Liu et al., 2010).

2) Initially Pang et al. (2010) proposed that the propagule source of green tides might have been microscopic germlings of *Ulva prolifera* produced in coastal crab and shrimp aquaculture ponds situated along the coast of Lianyungang in the north of Jiangsu province (Fig. 5). However, Liu et al. (2011) compared the green algal species living in shrimp ponds with the green tide species in the Yellow Sea, using interval amplified polymorphism markers (ISSR), and found that the green macroalgal species from the shrimp ponds were different from the green tide species in the Yellow Sea. Moreover, aquaculture ponds along the coastline of Jiangsu province are located in the uppermost part of the intertidal zone, which it makes difficult to explain how green macroalgae from the ponds was exported offshore area against the reversing movement of tidal current.

More recently a new approach was proposed by Pang's laboratory (Liu et al., 2013). They found large proportion of microscopic propagules of *Ulva prolifera* (spores and gametes) in coastal waters and sediments. Particularly high biomass of *U. prolifera* propagules presented on coastal sand shoals between Yancheng and Nantong, the source locations proposed by Liu et al. (2010) and Keesing et al. (2011). These microscopic propagules were detected over winter in the sediments and seawater. Liu et al. (2013) supposed that the facilities of *Porphyra* aquaculture could be the settlement substrate for the microscopic propagules.

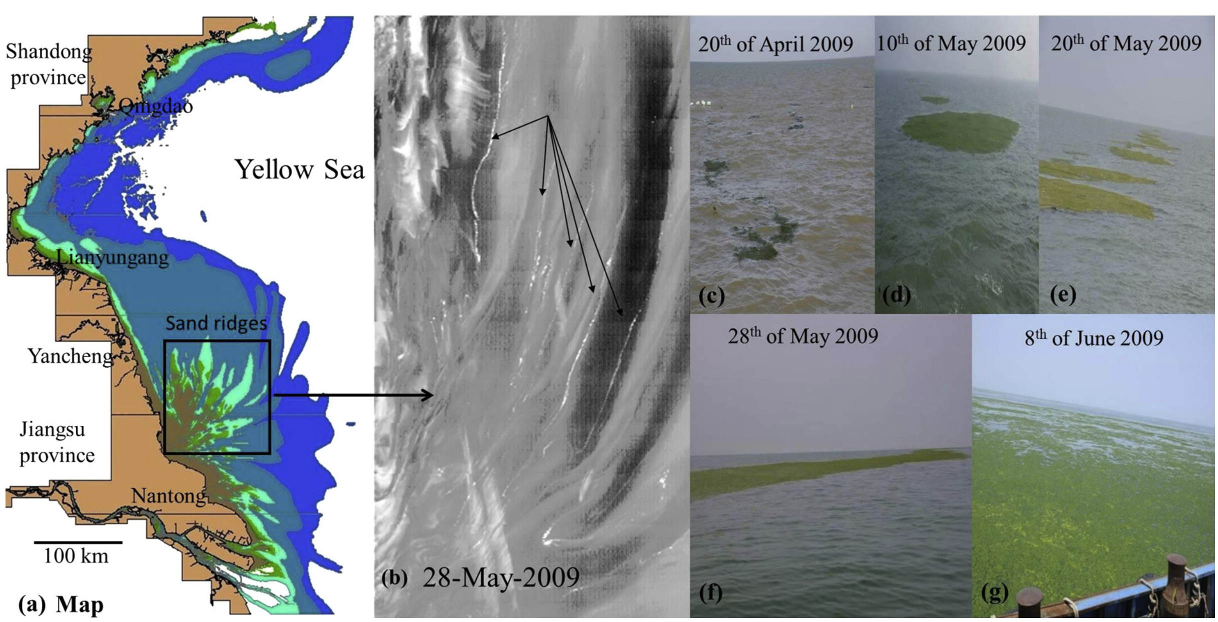

Fig. 5. Satellite and field observations in the Yellow Sea, 2009. (a): map showing regional location; (b): satellite image showing bands of green macroalgal mats near to sand shoals; (c): green macroalgal patches in coastal waters, mid-April 2009; (d–f): photographs showing expansion and aggregation of green macroalgal mats during May 2009; (g): expanse of well-developed green tide mats, center of Yellow Sea, 8 June 2009.

Table 1
Selected aspects of development of green tide mats in the Yellow Sea during 2007–2012.

Year	Period of green tide occurrence	Date	Area of green macroalgal mats (km^2)	Regional area where green algal mats were reported (km^2)	Collected biomass in Qingdao coast (million wet weight tonnes)	Reference
2007	–	17 July	82.3	10,638	–	Keesing et al. (2011)
2008	May–July	31 May	3488.7	84,109	1.4 (SOA, 2008)	Keesing et al. (2011)
2009	May–July	15 July	4993.9	70,382	0.162 (SOA, 2009)	Keesing et al. (2011)
2010	May–July	27 June	2513.2	40,211	0.029 (SOA, 2010)	Keesing et al. (2011)
2011	May–July	23 June	530	29,800	–	SOA, 2011
2012	Mid-April-July	19 July	560	26,400	–	SOA, 2012

*No information.
**SOA: State Oceanic Administration People's Republic of China, the National Bulletins of Marine Environment Quality Status 2008–2012.
***The methods for estimating the areas of green algal mats were described in Garcial et al. (2013).

We suspect that the blooms of green macroalgae are therefore linked to mariculture, but some questions remain: 1) why have green tides occurred since 2007, even though *Porphyra* and marine animal aquaculture have operated for more than 30 years along the Jiangsu coast? 2) what mechanisms support the formation and expansion of small patches of macroalgae into the world's largest green tides?

3. Why did green tide start after 2007 and continued since then?

Porphyra aquaculture on the Jiangsu coast started in the 1970s and fouling green algae always existed on the rafts, but no report of green tides were made until 2007. Keesing et al. (2011) used satellite imagery to look for floating algae from 2004 to 2010 in the Yellow Sea and also found no evidence of floating algae between 2004 and 2006. The first small bloom (191.8 km^2) was found in 2007 and then the massive blooms occurred in 2008 (3489 km^2), 2009 (4994 km^2) and 2010 (2513 km^2), respectively (Table 1). These results coincided with the first green tide at Qingdao reported by local news and scientists in the summer of 2007 (Liang et al., 2008; Li et al., 2009).

Before 2006, most *Porphyra* aquaculture took place in the intertidal zone near the coastline. Reversing movement of tidal currents dominates the hydrodynamic conditions in these areas (Yan et al., 1999), making it difficult for green algal fragments to get transported to offshore waters. However, during 2006–2008 significant expansion of the *Porphyra* aquaculture (about 10,000 ha) occurred on the sand shoals between Yancheng and Nantong, reaching distances up to 13 km from the coastline (Fig. 5a). These sand shoals are about 200 km long and 100 km wide, and feature a pinwheel shape. These sand shoals are hypothesized to have formed from the high sediment discharges by the Yellow and Yangtze Rivers (Wang et al., 2012). The unique radial geomorphology of the sand shoals affects tidal current and result in eddies forming in the deep channels between sand shoals (Du, 2012) (Fig. 5a). Combined with dominant south-east wind-driven currents and resultant upwelling between the Jiangsu coast and the western Yellow Sea during late spring (May) and summer (June–July), the green algal fragments released during the cleaning of the maricultural structures floated on surface waters and drifted offshore (Naimie et al., 2001; Moon et al., 2009; Keesing et al., 2011; Lee et al., 2011).

Satellite and field observations in 2009 confirmed the specific location and time of the drift events (Fig. 5a–g). The first small slicks of floating green algae occurred over the sand shoals during mid-April 2009, just after the *Porphyra* had been harvested (Fig. 5a and b). Field observations in coastal waters between Yancheng and Nantong further demonstrated the accuracy of satellite observations (Fig. 5c–g). In mid-April 2009, numerous small green algal patches were found in coastal waters (Fig. 5c) and these patches kept growing and aggregating during drifting (Fig. 5d–g) and later in June 2009 they coalesced to a massive green tide in the center of the Yellow Sea (Fig. 3b).

4. What mechanisms could turn small patches of macroalgae into the world's largest green tide?

We hypothesize that a number of circumstances—beyond the hydrodynamic transport out to sea— conspired to create conditions favorable for generation of the remarkable green tides seen in the Yellow Sea. The mechanisms that might be involved include favorable temperatures, high nutrient supply, high rates of nutrient uptake, growth, and photosynthesis, and diverse reproductive strategies.

4.1. Optimal temperature conditions

Sea surface temperature (SST) in the Yellow Sea during 2004–2009 was obtained from NASA data distribution system (http://oceancolor.gsfc.nasa.gov) and analyzed by Keesing et al. (2011). SST in April generally ranged between 6 and 12 °C with a gradient of cooler water in the north near the Shandong peninsular and warmer in the south near Shanghai; in May, SST was warmer, ranging from 10 to 18 °C, but mostly 12–16 °C; in June, SST increased to 15–24 °C; and in July, SST ranged from 20 to 28 °C but mostly between 22 and 26 °C. Previous studies on eight marine algal species associated with green tides found that temperature plays a vital role in controlling their growth rate; for example, *Enteromorpha linza* (=*Ulva linza*) grows optimally at 15 °C at a rate of 14% per day (Taylor et al., 2001; Largo et al., 2004). SST in the Yellow Sea during May–June are optimal for the growth of *Ulva prolifera*, which has been estimated to grow at a rate of 10–37% per day in the field and was measured to grow at 23% per day under laboratory conditions at temperatures greater than 15 °C (Liang et al., 2008; Li et al., 2009; Tian et al., 2010).

Ambient temperatures could favor the ability of macroalgal propagules to maintain buoyancy. Mesocosm experiments (Peimin He, unpublished data) showed that the green algae only floated when temperature was higher than 10 °C and light intensity was above 20 μmol photos m^{-2} s^{-1}. This experiment also indicated that the tubular filaments of *Ulva prolifera* needed adequate gas (CO_2 or O_2) produced by respiration and photosynthesis to support floating, thus enabling continuous growth. The green algae can float and grow well under the conditions when SST reached 15–25 °C and light intensity was 60–140 μmol photos m^{-2} s^{-1} during May–June (Keesing et al., 2011). Thus, suitable SST and light intensity combined with favorable wind and current during May–June, created oceanographic conditions which aided the flotation and formation of a green tide in the Yellow Sea.

4.2. High nutrient supply

In general, *Ulva* spp. associated with most green tide events display a close positive correlation to dissolved inorganic nitrogen (DIN), where growth increased with increasing DIN concentration (Sfriso et al., 1987; Valiela et al., 1997; Morand and Merceron, 2004;

Table 2
Comparison of $\delta^{15}N$ signatures in the green macroalgal biomass, and DIN concentrations in seawater from Jiangsu coast and offshore Yellow Sea (unpublished data).

Sampling sites	DIN concentration in seawater (μM)	Green macroalgal species	$\delta^{15}N$ (‰)
Offshore Qingdao, Shandong	0.65–16.1	*U. prolifera*	3.53–6.47
Offshore Yellow Sea, central Yellow Sea	0.73–5.78	*U. prolifera*	3.87–4.99
Porphyra rafts, coast of Haitou, Jiangsu, impacted	12.2–80.1	*U. prolifera*	16.1–17.5
by wastewater discharge		*U. intestinalis*	14.0–14.5
Porphyra rafts, coast of Sheyang, Jiangsu, impacted	10.1–69.1	*U. prolifera*	22.5–25.5
by wastewater discharge and discharges from Sheyang River		*U. intestinalis*	14.6–20.5
Porphyra rafts, offshore intertidal on shoals, Rudong,	5.3–35.3	*U. prolifera*	6.1–7.09
Jiangsu, an area much less affected by wastewater discharge		*U. intestinalis*	2.75–4.05

Teichberg et al., 2010). Over the last decade, nutrient enrichment occurred in most of coastal waters in the Yellow Sea, characterized by high nitrogen concentrations. For example, official monitoring of nutrients in the Yellow Sea by the State Oceanic Administration (2008–2012) shows that dissolved inorganic nitrogen (DIN) in more than 50% of the areas sampled exceeded 14 μM since 2003. Moreover, about 50,000 tonnes of fermented chicken manure used for coastal animal aquaculture ponds between Lianyungang and Sheyang, enriched the local seawaters after wastewater from ponds was discharged into the coastal waters (Liu et al., 2013). These, plus other nutrient inputs, could have supported the bloom of *Ulva prolifera*.

Isotopic N signatures of samples of green tide thalli confirmed the sources of nutrients present in the Yellow Sea and that were available to the macroalgae. During January–April 2010, DIN concentrations in the Jiangsu coastal waters and $\delta^{15}N$ signatures in the thalli of green algae attached to the mariculture rafts were surveyed by Keesing et al. (unpublished data) (Table 2). The results showed that DIN concentrations of seawater in Haitou near Lianyungang (12.2–80.1 μM) and Sheyang in the north of Yancheng (10.1–69.1 μM) were much higher than these in Rudong near to sand shoals (5.3–35.3 μM), Yellow Sea offshore (0.73–5.78 μM) and at the Qingdao coast (0.65–16.1 μM). Previous studies found that anthropogenically enriched organic matter from farm runoff, animal, and human wastes can result in elevated levels of isotopically heavy nitrate in seawater ($\delta^{15}N$ = 10–25‰) and could leave a signature in the thalli of algae (McClelland and Valiela, 1998; Cole et al., 2005; Teichberg et al., 2010). Much heavier $\delta^{15}N$ signatures in the thalli of *Ulva prolifera* and *U. intestinalis* in Haitou and Sheyang were detected (Table 2). The results show the significant impact of aquaculture, agriculture, and wastewater discharges on coastal water quality in the Yellow Sea. As the enriched waters moved southward with the coastal current, dilution reduced the signal of anthropogenic nitrogen in the seawater, so that lighter $\delta^{15}N$ values could be found in thalli collected from offshore areas.

Berglund (1969) found that optimal growth of *Ulva linza* occurred at 14 μM DIN and that growth was inhibited at 21 μM DIN. However, *Ulva prolifera* displays extraordinary tolerance of high nitrogen concentrations in laboratory culture experiment. The optimal growth of *U. prolifera* occurs at 50 μM and the wet weight increased 59.1% after 22 days culture at 20 °C, but it also can grow well when DIN reaches 500 μM and the wet weight increased 25.8% (Li et al., 2010a,b). Thus, the eutrophic seawaters in the Yellow Sea coast and offshore are entirely likely to be able to support the remarkably high growth rates for *U. prolifera*, and that resulted in the green tides.

4.3. High nutrient uptake rates

Fast growing marine algae associated with most algal blooms have higher nitrogen demand than slow growing species (Valiela et al., 1997; Pedersen and Borum, 1997), as seen in laboratory culture experiments with *Ulva prolifera* in the Yellow Sea (Table 3). V_{max} of nitrate uptake by *U. prolifera* was higher than other *Ulva* species (Luo et al., 2012). The V_{max} of ammonium uptake in *U. prolifera* was lower than in *Ulva lactuca*. However, Tian et al. (2010) found that V_{max} increased with increased ammonium concentrations and reached a maximum of 421 μmol g^{-1} DW h^{-1}. Moreover, V_{max}/K_m values of *U. prolifera* were much higher than in other *Ulva* species, suggesting a significant competitive advantage to uptake from the water column.

4.4. Effective photosynthesis

Algae are known to generally perform C_3 photosynthesis, but recent metabolic labeling and genome sequencing data found that they may also perform C_4 photosynthesis (Kremer and Küppers, 1977; Keeley, 1999; Roberts et al., 2007). By transcriptome sequencing, Xu et al. (2012) found that both C_3 and C_4 photosynthesis genes occur in *Ulva prolifera* and the key enzymes of C_4 metabolism are also discovered. Theoretically, these biological advantages can enhance the algal capacity for carbon fixation, biomass accumulation and environmental adaptation (von Caemmerer and Furbank, 2003; Roberts et al., 2007; Xu et al., 2012).

Table 3
Inorganic nitrogen uptake for five *Ulva* species in laboratory culture; V_{max} (μmol g^{-1} DWh^{-1}): maximum uptake rate; K_s (μM): half-saturation constant.

Species	Nitrate			Ammonium			Reference
	V_{max}	K_m	V_{max}/K_m	V_{max}	K_m	V_{max}/K_m	
U. prolifera	124.3	15.2	8.2	284.6	25.1	11.3	Luo et al., 2012
U. prolifera	122.2	7.81	22.67	138.4	8.53	15.92	O'Brien and Wheeler, 1987
U. linza	109.1	22.9	4.75	250.3	36.9	6.77	Luo et al., 2012
U. lactuca	225.5	20.5	10.99	20	5	4	Pedersen and Borum, 1997
U. lactuca	116	34	3.47	427	85	5.1	Runcie et al., 2003
U. rigida	68.6	38.04	1.80	–	–	–	Naldi and Viaroli, 2002
U. rigida	71.89	25.68	2.80	–	–	–	Lavery and McComb, 1991
U. intestinalis	64.65	17.22	3.75				Rees, 2003

4.5. Diverse reproductive strategy

Ulva prolifera has a diverse reproductive system, including sexual, asexual and vegetative propagation (Lin et al., 2008); and propagation of vegetative fragments and asexual zoospores are effective and important reproductive routes to guarantee growth rate during the green tide formation (Ye et al., 2008; Zhang et al., 2011).

The extraordinary macroalgal blooms in the Yellow Sea since 2008 seem to have resulted via a chain of complex circumstances, where human activities (eutrophication by wastewater, aquacultural, and agricultural discharges) interacted with natural geohydrodynamic and climatic conditions (sand shoals, currents, temperature), in ways that allowed a species, *Ulva prolifera*, that happened to have a series of adaptations that allowed very fast growth under the unusual circumstance (efficient photosynthesis, fast growth ability, high nutrient uptake, and diverse reproductive strategies), to proliferate sufficiently to generate a massive green tide.

5. Challenges in management and science

Green tides challenge management and science. For example, in the case of *Ulva* spp. blooms in Lannion (Brittany, France), removal of macroalgal biomass cost € 7.60 to €122 per tonne removed (Charlier et al., 2007). Costs using cleanup and the emergency response during the 2008 green tide in the Yellow Sea were estimated at about 200 million RMB, which does not include the losses by aquaculture and tourism industries (Ye et al., 2011). Ye et al. (2011) estimated that the green tide caused about 800 million RMB (≈123 million US dollars) loss for the aquaculture economy in Shandong province an important aquaculture base in the north of China for scallops, abalones, sea cucumbers, and clams. This included a 300–400 million RMB (≈46–61.5 million US dollars) losses for *Apostichopus japonicus* (sea cucumber) aquaculture in Haiyang, and 160 million RMB (≈24.6 million US dollars) loss for *Placopecten magellanicus* (scallop) and 300 million RMB (≈46 million US dollars) loss for *Ruditapes philippinarum* (clam) aquaculture in Rushan. In 2009, the total economic loss caused by the green tide was estimated at 641 million RMB (≈98.6 million US dollars) (State Oceanic Administration, China, 2009).

Following five successive years of green tides in the Yellow Sea, it is difficult to see this situation changing, in the absence of measures to prevent algal propagules from *Porphyra* aquaculture rafts entering the sea, or a dramatic improvement in the water quality, particularly in lowered nutrient concentrations. It is important for scientists to clarify the different opinions on the source of green tide in the Yellow Sea and set up an integrated scientific program for managers and farmers. Liu et al. (2009, 2010) proposed a management policy advising the disposal of the waste algae by burial on land rather than disposal into the sea. These measures are already practiced in the northern Jiangsu province (e.g., at Haitou) where rafts are located just a few meters from the high water mark. At the end of the harvest season farmers bring the ropes and bamboo poles ashore and clean them or bury them over the summer to remove the algae (Liu and Keesing, pers. obs.). However, burial on land does not assure complete removal, because nutrients in the algae could readily be transported down below the water table into groundwater, which could then further transport nitrogen into adjacent coastal waters.

With the successive occurrence of annual green tides, it may become possible for scientists to develop models to predict timing and intensity of macroalgal bloom events, and identify options to minimize damage. Such a predictive capacity (Valiela et al., 2000) can enable adaptation and strategic planning to organize cleanups and control conditions before a green tide can develop. Measures could include protecting tourist beaches and aquaculture leases with large booms, such as those used to protect against oil spills (these have previously been applied to microalgal blooms, Hrudey et al., 1999) or ensuring that vulnerable aquaculture crops, such as kelp and sea cucumber, are harvested ahead of blooms.

Alternative uses of biomass to profit from the green tide events were proposed in previous studies, including animal food, fertilizers, biodiesel, pharmaceutical or nutraceutical products (Bolton et al., 2009; Vijayavel and Martinez, 2010; Wang et al., 2010; Maceiras et al., 2011). *Ulva prolifera* is mainly used as food or for medical purposes, because it is rich in polysaccharides, proteins, and essential mineral elements for human health, and also has low content of fats and cellulose (Cai et al., 2009). Some green algae from *Porphyra* aquaculture rafts have been mixed with *Porphyra yezoensis* thalli and made into seaweed sheets similar to the health food Nori sheets (Peimin He, pers. obs.). Lately, a few scientists explored the uses of *U. prolifera* for bio-oil production, considering the tremendous biomass in the green tides of the Yellow Sea (e.g., Li et al., 2010a,b; Zhou et al., 2010, 2012; Zhuang et al., 2012). *U. prolifera* is converted to bio-oil by hydrothermal liquefaction, and the bio-oil yield up to 23.0 wt% (calculated on the feed) was obtained at 300 °C, with a reaction time of 30 min and the addition of 5 wt% Na_2CO_3 (Zhou et al., 2010, 2012). Obviously, *U. prolifera* is a good raw material for bioenergy, but more work is needed to improve the yield and quality of bio-oil.

Commercial exploitation of the biomass produced in green tides would only partly offset the bill for environmental damage, particularly in the case of the Yellow Sea, which would require an economic use that could operate efficiently with super-abundance for just a few weeks each year. In future, with the elucidation of the basic facts in the green tides of the Yellow Sea, increasingly large pilot scale projects can be undertaken, which will allow for better prediction of ecological risk in the intertidal zone and the true potential of macroalgae.

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