

Introduction to the Special Issue on green tides in the Yellow Sea



Ming-Jiang Zhou ^{a,*}, Dong-Yan Liu ^b, Donald M. Anderson ^c, Ivan Valiela ^d

^a Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

^b Laboratory of Coastal Ecology, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, China

^c Woods Hole Oceanographic Institution, Woods Hole, MA 02543-1049, USA

^d Marine Biological Laboratory, Woods Hole, MA 02543, USA

ARTICLE INFO

Article history:

Received 5 June 2015

Received in revised form

17 June 2015

Accepted 19 June 2015

Available online 24 June 2015

Keywords:

Green tide

Ulva prolifera

Yellow Sea

Subei Shoal

ABSTRACT

The spectacular massive green tide of *Ulva prolifera* in the southern Yellow Sea, which has become a recurrent phenomenon in this region over the last 8 years, attracted much attention of scientists and local government. Several mechanisms have been proposed to explain the early development of green tides in the Yellow Sea, but many questions still remain to be answered. Two years after the first occurrence of massive green tide in the Yellow Sea, a project in the National Basic Research Priority Program (973 project) “Succession of Harmful Algal Blooms in the Coastal Waters of China and the Impacts on Marine Ecosystems (CEOHAB II)” supported by the Ministry of Science and Technology of China started to perform comprehensive investigations and studies on the early development of green tides in the western part of the southern Yellow Sea. In this introduction, we reviewed the progress in understanding aspects of green tide dynamics made by researchers working in the region, and highlighted remaining questions.

© 2015 Elsevier Ltd. All rights reserved.

1. Background

Blooms of fast-growing macroalgae, sometimes referred to as “green tides”, have been reported in many coastal areas in recent years (Ye et al., 2011; Smetacek and Zingone, 2013; Liu et al., 2013). Such macroalgal blooms—often associated with coastal eutrophication—frequently are detrimental to water-related human activities, such as tourism and aquaculture, and have multiple deleterious effects on natural ecosystems (Fletcher, 1996; Valiela et al., 1997; Teichberg et al., 2010; Lyons et al., 2014).

In 2007, a green tide was observed for the first time in coastal waters of Qingdao, China. A spectacular massive green tide appeared again in 2008 (Fig. 1), impaired use of beaches in the region, and posed a significant threat to the Olympic sailing events planned at the site. To protect use of beaches in Qingdao, and allow the Olympic events to take place, over 16,000 people were organized to remove the accumulated algae from the beach, and a long boom was deployed off the shore to prevent floating green algae from approaching the coast (Fig. 1). Approximately 600 boats were involved in collecting floating green algae from the sea area

surrounding Qingdao, and eventually, more than 1 million tons of green algae were removed from the coast. Despite the intensive efforts in removing accumulated algae, the green tide still significantly damaged the aquaculture industry in that region and led to substantial economic losses (Wang et al., 2012). The green tide recorded during this period was the world's largest macroalgal bloom, in terms of both affected sea area and the biomass it produced (Liu et al., 2009, 2010a). Since then, it has become a recurrent phenomenon appearing every summer, albeit at different biomass levels and area covered (Xu et al., 2014), within the Yellow Sea (Fig. 2).

The spectacular green tides in the Yellow Sea quickly attracted the attention of scientists and local government. A group of scientists was rapidly organized in 2008 to study the mechanisms and impacts of green tides, monitor the events, and devise mitigation strategies. The major macroalgal species involved in the Yellow Sea green tides was soon identified as *Enteromorpha prolifera* Müller (Chlorophyta, Ulvophyceae), based on morphological features (Zhang et al., 2008; Ding et al., 2009). The morphologically based identification was further supported by molecular biological evidence of the internal transcribed spacer (ITS) sequences of ribosomal rRNA genes and 5S rDNA spacer sequences (Leliaert et al., 2009; Wang et al., 2010; Liu et al., 2010b; Pang et al., 2010; Duan et al., 2012; Shen et al., 2012). Since the genus *Enteromorpha* had

* Corresponding author.

E-mail address: mjzhou@qdio.ac.cn (M.-J. Zhou).



Fig. 1. Massive green tide appeared in Qingdao (A, B) in 2008. Removal and containment means applied to remove (C), and limit the expansion (D) of the huge amounts of accumulated green algae.

been synonymized into the genus *Ulva* according to molecular phylogenetic analyses (Hayden et al., 2003), *Ulva prolifera* has been used in most recent publications to refer to the dominant green tide species. We also adopt that nomenclature for this Special Issue.

U. prolifera is an opportunistic bloom-forming species widely distributed around the world (Ye et al., 2011). Bloom-forming *U. prolifera* in the Yellow Sea have a complex life history, multiple reproduction modes and a high reproductive rate, the important mechanisms supporting the formation of green tides. The bloom-forming *U. prolifera* proliferates rapidly through sexual, asexual, and vegetative reproduction (Lin et al., 2008). A 1 cm² blade of *U. prolifera* can release up to 6 million spores or 27 million gametes, and 92–97 % of the spores germinate into young seedlings (Zhang et al., 2013). *U. prolifera* can efficiently take up nutrients, particularly organic forms of nitrogen, and shows extremely high growth rates (Luo et al., 2012). Mean growth rate of *U. prolifera* ranged about 10–20% per day in coastal waters of Qingdao; maximum growth rate reached 56.2% per day in an *in situ* experiment in Subei

Shoal (or Subei Bank in some previous studies) along the coast of Jiangsu province. Bloom-forming *U. prolifera* have unique morphological features (highly branched and hollow tubular thalli with monostromatic walls) that allow floating; this, combined with fast nutrient uptake and growth rates, facilitate formation of large-scale green tides.

U. prolifera was and is the dominant species responsible for green tides in the Yellow Sea (Zhao et al., 2013), but other green algal species are present in the floating green algal canopies, such as *Ulva compressa* and *Ulva pertusa* (Duan et al., 2012). Using the ITS sequence of ribosomal rRNA genes, Jiang et al. (2008) demonstrated that the dominant floating *Ulva* species in the Yellow Sea clustered into a clade of *Ulva linza-procera-prolifera* species complex (LPP species complex), an array that differs from the major attached *Ulva* species along the coast of Qingdao. Therefore they proposed that bloom-forming *Ulva* did not derive from the local waters in Qingdao. This idea was further supported by comparisons between the floating and attached forms of *U. prolifera* (Wang et al., 2010; Duan et al., 2012).

Remote-sensing of green tides supported the idea of long-distance transport of floating algae. Satellite images, field observations, and physical oceanographic modeling all indicated that floating patches of *U. prolifera* were repeatedly formed in the near-shore water of Jiangsu province (i.e. Subei Shoal, Fig. 3A,B) along the coast of southern Yellow Sea (Sun et al., 2008; Hu, 2009; Liu et al., 2009, 2010a; Keesing et al., 2011; Qiao et al., 2011; Lee et al., 2011). Therefore, Subei Shoal is a critical area to investigate the mechanisms for the formation and early development of green tides in the Yellow Sea.

Subei Shoal is a unique intertidal mudflat zone with an area around 22,740 km² (Li, 2011). It extends over 200 km from the Sheyang River estuary to the Changjiang River estuary, and 90 km from the shoreline to open sea. Subei Shoal has radial sand ridges at the bottom that create large tidal excursions and strong tidal currents. Many rivers discharge into this shallow water region and input very substantial nutrient loads. The shallow and nutrient-rich

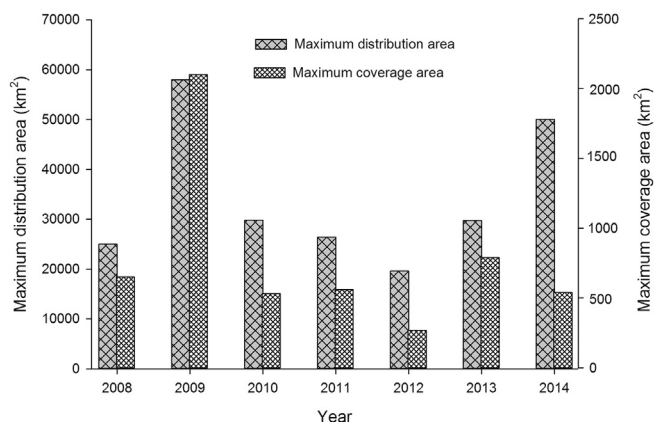


Fig. 2. Extent and cover of green tides in the Yellow Sea from 2008 to 2014 (data from the Bulletin of Marine Environmental Status of China, 2008–2014).

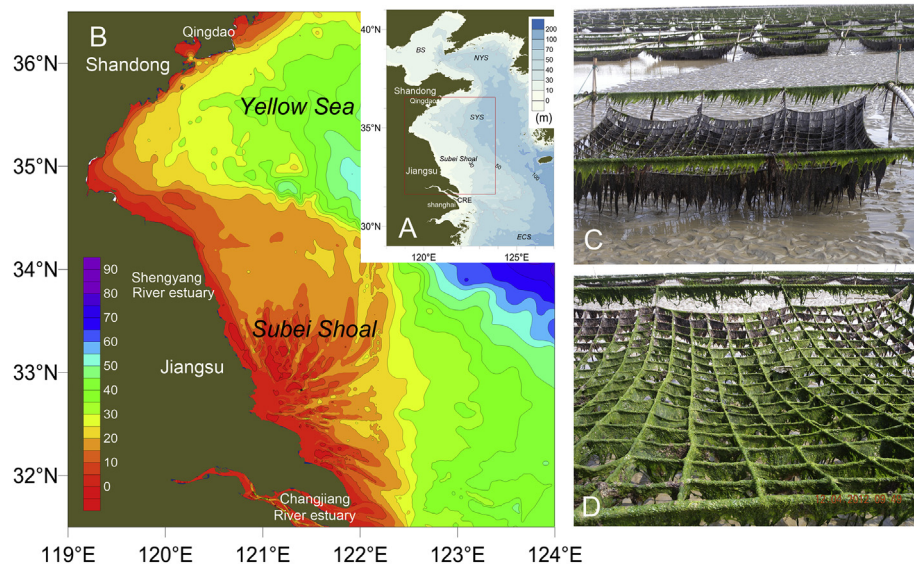


Fig. 3. Maps of the Yellow Sea (A), Subei Shoal (B) and photos of *Porphyra* aquaculture rafts located in Subei Shoal (C, D) in which green color indicated the green algae attached on the rafts.

water column makes Subei Shoal a propitious environment for cultivation of the commercially important seaweed *Porphyra yezoensis* (Fig. 3C, D). From the 2000s, the flux of nutrients from the major rivers into Subei Shoal increased significantly (Ma et al., 2010). Rapid expansion of animal aquaculture industry along the coast of Jiangsu Province also discharged large amounts of organic nitrogen into the sea (Pang et al., 2010).

Based on the unique features of the Subei Shoal, several mechanisms have been proposed to explain the early development of green tides in this region. Liu et al. (2009, 2010a) and Keesing et al. (2011) suggested that the rapid expansion of *Porphyra* aquaculture was the major reason for the appearance of large-scale green tides. Several other surveys, however, found none or few *U. prolifera* on the *Porphyra* rafts (Pang et al., 2010; Shen et al., 2012) and hypothesized that *U. prolifera* might originate from land-based aquaculture ponds, or somatic cells, vegetative fragments and micro-propagules presented in the coastal waters or sediments etc. (Pang et al., 2010; Zhang et al., 2010, 2011; Liu et al., 2012). There are therefore arguments for different mechanisms for the origin of green tides, as well as many other questions remaining to be answered: How does *U. prolifera* recurrently develop into large-scale green tides in the Yellow Sea? What is the relationship between green tides and eutrophication and aquaculture activities in this region? Why did Subei Shoal become the most important region for the development of green tides in the Yellow Sea? To answer these questions, comprehensive multi-disciplinary investigations, including biological, chemical, ecological and oceanographic studies were needed to cover a sufficiently large area and to collect time-series data concerning the early development of green tides in the Yellow Sea.

In 2009, two years after the first occurrence of massive green tide in the Yellow Sea, a project in the National Basic Research Priority Program (973 project) “Succession of Harmful Algal Blooms in the Coastal Waters of China and the Impacts on Marine Ecosystems (CEOHAB II)” was supported by the Ministry of Science and Technology of China. One of the major tasks of this project was to elucidate the mechanisms and early development processes of green tides in the Yellow Sea. Many cruises to Subei Shoal took place, supporting comprehensive investigations on the western part of the southern Yellow Sea, and monthly investigations in Subei Shoal acquired time-series data in this region (Fig. 4). The

major findings of the project, together with recent progresses made by other relevant groups, were compiled to form this Special Issue: “Green tides in the Yellow Sea”.

2. Contributions of the Special Issue

Fifteen papers are included in this Special Issue, covering a wide variety of green tide studies, including, among other topics, a rapid method for detection of bloom-forming *U. prolifera*, adaptive strategies, physiological and life history features of *U. prolifera*, ecological processes related to onset of green tides, and the relationship between oceanographic conditions of Subei Shoal and the formation of green tides. The papers in the Issue consider new ideas

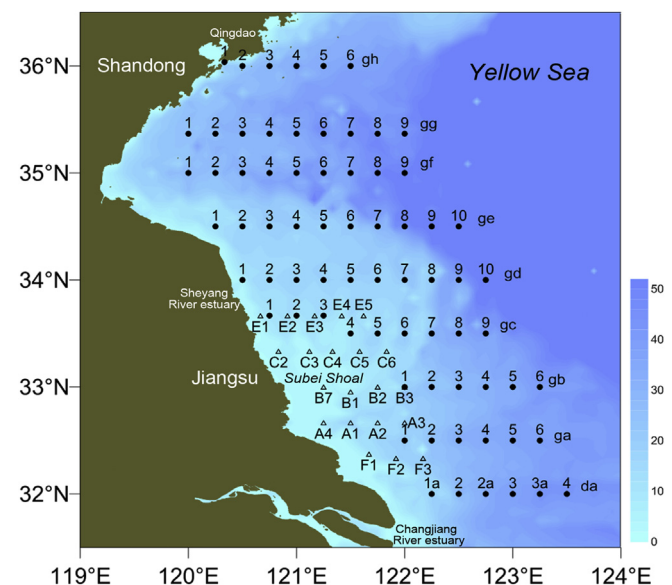


Fig. 4. Sampling stations of cruises organized by the 973 project in 2012. Black dots: stations in 8 transects (da, ga, gb, gc, gd, ge, gf, gg and gh) to investigate the dynamics and distribution of green tides in southern Yellow Sea from Apr. 16 to Jun. 8 in 2012. White triangles: stations in 5 transects (A, B, C, E, F) to investigate the distribution of floating green algae and microscopic propagules in Subei Shoal and their relationship with the raft culture of *Porphyra* in 2011 and 2012. (Color bar indicates depth, in m, in the map).

and update current understanding of the dynamics of green tides in the Yellow Sea.

2.1. Detection, development, and expansion of green tides in the Yellow Sea

Zhang et al. (2015a) developed a fluorescence *in situ* hybridization (FISH) method to detect bloom-forming *U. prolifera*. This method used a specifically-designed probe targeting the 5S spacer region of *U. prolifera*, and could rapidly identify *U. prolifera* by fluorescence microscopy and give quantitative estimates of the proportion of *U. prolifera* in a green algal sample. This method makes it possible to perform rapid analyses during the development of *U. prolifera* blooms.

Song et al. (2015a), based on time-series investigations from October 2010 to October 2011 in Subei Shoal, documented year-round abundance of green algal propagules in waters and sediments. Variation in abundance and distribution of *Ulva* propagules in Subei Shoal could be spatially linked to *Porphyra* cultivation activities in this region. With the FISH method, Zhang et al. (2015b) further confirmed the presence of *U. prolifera* propagules in Subei Shoal, and confirmed that *U. prolifera* propagules gave rise to the *U. prolifera* population attached to *Porphyra* culture rafts.

Fan et al. (2015) analyzed succession of macroalgal species attached to *Porphyra* culture rafts, and found that the dominant species in the green algal community shifted to *U. prolifera* and *Blidingia* sp. in mid-May. These results are consistent with results obtained using the FISH method by Zhang et al. (2015b). In laboratory studies, Song et al. (2015b) found that warmer water temperatures in May were associated with germination of green algae propagules and succession in the attached green algal community. These studies also offered strong evidence for the dominant position of *U. prolifera* in the green algal community attached to the *Porphyra* culture rafts in spring.

Liu et al. (2015b) sampled biomass of floating green algae during four cruises from May to June of 2012 to investigate the changes in floating green algal biomass, and trace the expansion of green tide through the southern Yellow Sea. Total biomass of floating algae quickly increased from ~2000 tons in early May to 364,000 tons in early June. They also found that free-floating patches of green algae dominated by *U. prolifera* were primarily confined to Subei Shoal in early May, and drifted gradually to the southern coast of the Shandong Peninsula in one month. No green algae were found floating into Subei Shoal from other regions of the southern Yellow Sea during the investigations. During this process, *U. prolifera* were always dominant, and dominance increased gradually during drift (Zhang et al., 2015b).

The bloom-forming *U. prolifera* must be well adapted to changes in light irradiance, particularly at the floating stage. The mechanisms involved in the high NPQ in *Ulva* were also characterized, using *U. linza* as a model organism (Zhang et al., 2015d).

2.2. Oceanographic characteristics of Subei Shoal and its relationship with green tides

Bao et al. (2015) studied trajectories of satellite-tracked surface drifters, and applied an FVCOM model forced by tides and surface winds to define driving forces for movement of floating green algae in Subei Shoal and the southern Yellow Sea. Floating algae were transported by tidal residual currents in the channels between the sand ridges in the shoal. In the southern Yellow Sea, wind became the dominant forcing underlying the drift of floating green algae. Model simulations indicated that particles drifted northward with S–SE winds, a pattern consistent with northward movement of drifters tracked by satellite.

Li et al. (2015) reviewed the historical patterns of nutrient composition and concentration in Subei Shoal, and reported a gradual increase of DIN and N/P over the last 30 years, particularly after 2008. These apparent increases are closely associated with the increasing input of nitrogen from the Changjiang River and other smaller rivers along the coast of Subei Shoal.

Sun et al. (2015) found that bloom-forming *U. prolifera* exhibited a rapid increase in uptake rates of both nitrate and phosphate when exposed to high concentration of nutrients, and *U. prolifera* could utilize multiple nutrient sources. Shi et al. (2015) further addressed the importance of land-based nutrient input in the formation of green tides, and reported high concentrations of DON in this region based on the field investigation, which could be used by *U. prolifera* when inorganic N was depleted.

2.3. Importance of *Porphyra* culture rafts in the formation of green tides

The tidal and hydrodynamic conditions, and land-derived delivery of nutrients taking place in the Yellow Sea, all favor development of the green tides. The actual sources of the propagules that generate the potential green tides seem likely linked to the *Porphyra* culture rafts deployed in this region. *Porphyra* culture rafts, including ropes, bamboo poles and nets, offer substantial surfaces for the attachment of green algal propagules that could, helped by parthenogenesis and other features of growth, be the founding sources of fronds that become floating green tides. This could be checked by genomic studies of the attached and floating fronds.

Geng et al. (2015) found that abundances of green algal propagules attached to the surface of materials used in *Porphyra* rafts (plastic, bamboo, jute rope, plastic rope, nylon and other netting) were significantly higher than those on natural surfaces (mud, sand, rocks). They concluded that *Porphyra* rafts must play an important role in the early development of green tides.

Liu et al. (2015a) suggested that parthenogenesis could play an important role in the rapid growth of attached *U. prolifera* populations. Parthenogenetic reproduction is a common feature of bloom-forming *U. prolifera* in the Yellow Sea, and unfertilized gametes could develop into both gametophytes and parthenosporophytes. This is likely to promote rapid proliferation of *U. prolifera* populations and could maintain the unique genetic features of this species.

Zhao et al. (2015) studied genetic variation and relationships at the intra-species level among floating and *U. prolifera* collected from different substrates in the shores of the Yellow Sea (but not from rafts). They found that floating samples of *U. prolifera* from the Yellow Sea, taken during the past 5 years, were genetically similar and different from non-raft surface attached samples of *U. prolifera* collected from the intertidal zone of the Southern Yellow Sea. In agreement with Wang et al. (2010) and Duan et al. (2012), Zhao et al. (2015) proposed that fronds of floating *U. prolifera* may derive from a unique ecotype. This finding might suggest that juvenile algae attached to coastal substrates might not be the source of propagules that eventually become floating green tides, and cast some doubt about the notion that coastal maricultural rafts could be involved in green tide origins. There are still unpublished results, obtained using the same methods, that suggest that *U. prolifera* attached on *Porphyra* culture rafts were genetically the same as floating samples (Zhang et al., 2015). These conflicting results suggest that only those germings attached to rafts give origin to floating green tides, a curious and unlikely prediction. Clearly, more study of these features will be needed.

While much remains to be learned as to the primary origin and mechanisms creating green tides, we can preliminarily argue, with the information presented in this Special Issue, that early

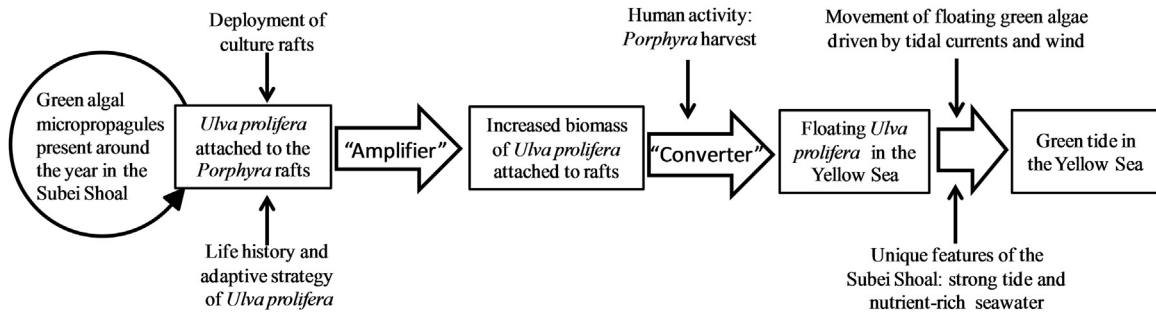


Fig. 5. A conceptual model of development of green tides in southern Yellow Sea. Green algal propagules, including those of bloom-forming *Ulva prolifera*, are present around the year in Subei Shoal. After deployment of *Porphyra* culture rafts in autumn in the Shoal, propagules of *U. prolifera* start to attach to the rafts and gradually dominate the attached green algal community in late April to early May in the following year. The attached green algae are removed from rafts during the process of *Porphyra* harvesting and became a floating algal canopy. Supported by nutrient-rich seawater in Subei Shoal, the floating green algae proliferate rapidly, and move northward driven by the tidal currents and wind, with the end result being the “world’s largest” green tide. During this process, the *Porphyra* culture rafts act as an “amplifier” that spurs early macroalgal abundance and growth, and a “converter” that releases the attached macroalgal fragments into the sea in floating form.

development of green tide in Subei Shoal and the southern Yellow Sea (Fig. 5) may begin as green algal propagules—present year-round in Subei Shoal—that start to germinate and attach, most likely, to *Porphyra* culture rafts when the rafts are established on Subei Shoal during autumn. The attached propagules grow and gradually dominate the attached green algal community by late April to early May in the following year, as water temperature turns warm (aquaculture rafts act as an “amplifier” that spurs early macroalgal abundance and growth). After the attached green algae are removed from the rafts as the farmers clean them, fragments of fronds of *U. prolifera* become floating (the role of aquaculture rafts now changes to that of a “converter” that releases the originally attached macroalgal fragments into floating form in the sea). The biomass of *U. prolifera* rapidly increases during floating in nutrient-rich surface seawater, supported by the remarkably abundant nutrient supply in Yellow Sea surface waters, and the biomass then drifts widely as a result of residual tidal currents and wind in the Yellow Sea, with the end result being the “world’s largest” green tide.

3. Unknown questions and research perspectives

Although the work reported in this Issue has led to a much better understanding of green tides in the Yellow Sea, many questions still remain. For example, results presented in this Issue suggested that bloom-forming *U. prolifera* consist of a unique ecotype, different from the populations of *U. prolifera* attached to shore areas along the coast of Jiangsu, Shandong and Zhejiang provinces. To what extent is this true? Where did this unique *U. prolifera* ecotype come from? Is it a modified version of the original ecotype (i.e., a result of ecophenotypic variation) or an invasive population of *U. prolifera*?

The green tides in the Yellow Sea generally last for a long time (nearly two months) and affect a large sea area. The extensive macroalgal canopy must alter nutrient and other biogeochemical conditions in the water column, and perhaps in the benthos, in a variety of ways and lead to changes in microbial (Zhang et al., 2015c) and other communities. The macroalgae seems quite likely to compete with phytoplankton producers as well. What other ecological consequences result from the recurrence of green tides in the Yellow Sea? What may be the fate of the considerable biomass involved in the green tide phenomenon? The rather large amount of floating algae must be exported somewhere, or the biomass must decay and affect the lower layers of the water column and the sediments below; both these aspects are currently unknown.

The results reported in this Issue make an initial sortie into potential ways to develop mitigation strategies, but none have been tested. Once further research resolves some of these remaining problem areas, we will be in a more effective position to develop potential mitigation measures that aim to lower incidence of green tides. Developing such management strategies will not be simple, and will need to integrate best science results as well as other cultural and economic imperatives. Application of the basic studies contained in this Issue will be essential to design useful coastal water quality maintenance plans in the Yellow Sea region.

Acknowledgments

We gratefully acknowledge the National Basic Research Priority Project (2010CB428700) supported by the Ministry of Science and Technology of China, the Strategic Priority Research Program (XDA11020304) supported by the Chinese Academy of Science, and projects (41121064, U1406403) supported by the National Natural Science Foundation of China. Support for D. M. Anderson was provided through the Woods Hole Center for Oceans and Human Health, National Science Foundation Grant OCE-1314642 and National Institute of Environmental Health Sciences Grant 1-P01-ES021923-01. We deeply appreciate the outstanding efforts of the scientists and crews during the CEOHAB II cruises. Special thanks also to Judith L. Kleindinst, Rencheng Yu, Qingchun Zhang, and officers of ECSS for their significant contributions to the production of this Special Issue.

References

- Bao, M., Guan, W.B., Yang, Y., Cao, Z.Y., Chen, Q., 2015. Drifting trajectories of green algae in the western Yellow Sea during spring and summer 2012. *Estuar. Coast. Shelf Sci.* 163, 9–16. <http://dx.doi.org/10.1016/j.ecss.2015.02.009>.
- Ding, L.P., Luan, R.X., 2009. The taxonomy, habit and distribution of a green alga *Enteromorpha prolifera* (Ulvaes, Chlorophyta). *Oceanol. Limnologia Sinica* 40, 68–71 (in Chinese, with English Abstract).
- Duan, W.J., Guo, L.X., Sun, D., Zhu, S.F., Chen, X.F., Zhu, W.R., Xu, T., Chen, C.F., 2012. Morphological and molecular characterization of free-floating and attached green macroalgae *Ulva* spp. in the Yellow Sea of China. *J. Appl. Phycol.* 24, 97–108.
- Fan, S.L., Fu, M.Z., Wang, Z.L., Li, Y., Liu, G.X., Liu, X.Q., Song, W., Wang, X.N., Xie, J., Zhu, M.Y., 2015. Temporal variation of green macroalgal assemblage on *Porphyra* aquaculture rafts in the Subei Shoal, China. *Estuar. Coast. Shelf Sci.* 163, 23–28. <http://dx.doi.org/10.1016/j.ecss.2015.03.016>.
- Fletcher, R.L., 1996. The occurrence of ‘green tide’. In: Schramm, W., Nienhuis, P.H. (Eds.), *Marine Benthic Vegetation—recent Changes and the Effects of Eutrophication*. Springer Verlag, Berlin, pp. 7–43.
- Geng, H.X., Yan, T., Zhou, M.J., Liu, Q., 2015. Comparative study of the germination of *Ulva prolifera* gametes on various substrates. *Estuar. Coast. Shelf Sci.* 163, 89–95. <http://dx.doi.org/10.1016/j.ecss.2014.12.026>.
- Hayden, H.S., Blomster, J., Maggs, C.A., Silva, P.C., Stanhope, M.J., Waaland, J.R., 2003.

- Linnaeus was right all along: *Ulva* and *Enteromorpha* are not distinct genera. *Eur. J. Phycol.* 38, 277–294.
- Hu, C., 2009. A novel ocean color index to detect floating algae in the global oceans. *Remote Sens. Environ.* 113, 2118–2129.
- Jiang, P., Wang, J.F., Cui, Y.L., Li, Y.X., Lin, H.Z., Qin, S., 2008. Molecular phylogenetic analysis of attached Ulvaceae species and free-floating *Enteromorpha* from Qingdao coasts in 2007. *Chin. J. Oceanol. Limnol.* 26, 276–279.
- Keesing, J.K., Liu, D.Y., Fearn, P., Garcia, R., 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. *Mar. Pollut. Bull.* 62, 1169–1182.
- Lee, J.H., Pang, I.C., Moon, I.J., Ryu, J.H., 2011. On physical factors that controlled the massive green tide occurrence along the southern coast of the Shandong Peninsula in 2008: a numerical study using a particle-tracking experiment. *J. Geophys. Res.* 116, C12036.
- Leliaert, F., Zhang, X., Ye, N., Malta, E.J., Engelen, A.H., Mineur, F., Verbruggen, H., De Clerck, O., 2009. Research note: identity of the Qingdao algal bloom. *Phycol. Res.* 57, 147–151.
- Li, H.M., Zhang, C.S., Han, X.R., Shi, X.Y., 2015. Changes in concentrations of oxygen, dissolved nitrogen, phosphate, and silicate in the southern Yellow Sea, 1980–2012: Sources and seaward gradients. *Estuar. Coast. Shelf Sci.* 163, 44–55. <http://dx.doi.org/10.1016/j.ecss.2014.12.013>.
- Li, M.G., 2011. Advances in the research and development of the radial sandbanks. *J. Waterw. Harb.* 32, 229–243 (in Chinese, with English abstract).
- Lin, A.P., Shen, S.D., Wang, J.W., Yan, B.L., 2008. Reproduction diversity of *Enteromorpha prolifera*. *J. Integr. Plant Biol.* 50, 622–629.
- Liu, D.Y., Keesing, J.K., Xing, Q.G., Shi, P., 2009. World's largest macroalgal bloom caused by expansion of seaweed aquaculture in China. *Mar. Pollut. Bull.* 58, 888–895.
- Liu, D.Y., Keesing, J.K., Dong, Z.J., Zhen, Y., Di, B.P., Shi, Y.J., Fearn, P., Shi, P., 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. *Mar. Pollut. Bull.* 60, 1423–1432.
- Liu, D.Y., Keesing, J.K., He, P.M., Wang, Z.L., Shi, Y.J., Wang, Y.J., 2013. The world's largest macroalgal bloom in the Yellow Sea, China: formation and implications. *Estuar. Coast. Shelf Sci.* 129, 2–10.
- Liu, F., Pang, S.J., Chopin, T., Xu, N., Shan, T.F., Qin, S., Sun, S., 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. *J. Appl. Phycol.* 22, 531–540.
- Liu, F., Pang, S.J., Zhao, X.B., Hu, C.M., 2012. Quantitative, molecular and growth analyses of *Ulva* microscopic propagules in the coastal sediment of Jiangsu province where green tides initially occurred. *Mar. Environ. Res.* 74, 56–63.
- Liu, Q., Yu, R.C., Yan, T., Zhang, Q.C., Zhou, M.J., 2015a. Laboratory study on the life history of bloom-forming *Ulva prolifera* in the Yellow Sea. *Estuar. Coast. Shelf Sci.* 163, 82–88. <http://dx.doi.org/10.1016/j.ecss.2014.08.011>.
- Liu, X.Q., Li, Y., Wang, Z.L., Zhang, Q.C., Cai, X.Q., 2015b. Cruise observation of *Ulva prolifera* bloom in the southern Yellow Sea, China. *Estuar. Coast. Shelf Sci.* 163, 17–22. <http://dx.doi.org/10.1016/j.ecss.2014.09.014>.
- Luo, M.B., Liu, F., Xu, Z.L., 2012. Growth and nutrient uptake capacity of two co-occurring species, *Ulva prolifera* and *Ulva linza*. *Aquat. Bot.* 100, 18–24.
- Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queiros, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P., 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. *Glob. Change Biol.* 20, 2712–2724.
- Ma, H.R., Chen, J.F., Cui, Y., Zhao, J., Ma, S.S., Yang, F., 2010. Analysis of water quality and assessment of major pollutants input to the sea from the Guan River and Sheyang River. *Prog. Fish. Sci.* 31, 92–99 (in Chinese, with English abstract).
- Pang, S.J., Liu, F., Shan, T.F., Xu, N., Zhang, Z.H., Gao, S.Q., Chopin, T., Sun, S., 2010. Tracking the algal origin of the *Ulva* bloom in the Yellow Sea by a combination of molecular, morphological and physiological analyses. *Mar. Environ. Res.* 69, 207–215.
- Qiao, F.L., Wang, G.S., Lu, X.G., Dai, D.J., 2011. Drift characteristics of green macroalgae in the Yellow Sea in 2008 and 2010. *Chin. Sci. Bull.* 56, 2236–2242.
- Shen, Q., Li, H.Y., Li, Y., Wang, Z.L., Liu, J.S., Yang, W.D., 2012. Molecular identification of green algae from the rafts based infrastructure of *Porphyra yezoensis*. *Mar. Pollut. Bull.* 64, 2077–2082.
- Shi, X.Y., Qi, M.Y., Tang, H.J., Han, X.R., 2015. Spatial and temporal nutrient variations in the Yellow Sea and their effects on *Ulva prolifera* blooms. *Estuar. Coast. Shelf Sci.* 163, 36–43. <http://dx.doi.org/10.1016/j.ecss.2015.02.007>.
- Smetacek, V., Zingone, A., 2013. Green and golden seaweed tides on the rise. *Nature* 504, 84–88.
- Song, W., Li, Y., Fang, S., Wang, Z.L., Xiao, J., Li, R.X., Fu, M.Z., Zhu, M.Y., Lei, Z.X., 2015a. Temporal and spatial distributions of green algae micro-propagules in the coastal waters of the Subei Shoal, China. *Estuar. Coast. Shelf Sci.* 163, 29–35. <http://dx.doi.org/10.1016/j.ecss.2014.08.006>.
- Song, W., Peng, K.Q., Xiao, J., Li, Y., Wang, Z.L., Liu, X.Q., Fu, M.Z., Fang, S.L., Zhu, M.Y., Li, R.X., 2015b. Effects of temperature on the germination of green algae micro-propagules in coastal waters of the Subei Shoal, China. *Estuar. Coast. Shelf Sci.* 163, 63–68. <http://dx.doi.org/10.1016/j.ecss.2014.08.007>.
- Sun, K.M., Li, R.X., Li, Y., Xin, M., Wang, Z.L., Tang, X.X., Xiao, J., Pang, M., 2015. Responses of *Ulva prolifera* to short-term nutrient enrichment under light and dark conditions. *Estuar. Coast. Shelf Sci.* 163, 56–62. <http://dx.doi.org/10.1016/j.ecss.2015.03.018>.
- Sun, S., Wang, F., Li, C.L., Qin, S., Zhou, M.J., Ding, L.P., Pang, S.J., Duan, D.L., Wang, G.C., Yin, B.S., Yu, R.C., Jiang, P., Liu, Z.L., Zhang, G.T., Fei, X.G., Zhou, M., 2008. Emerging challenges: massive green algae blooms in the Yellow Sea. *Nat. Preced.* hdl:10101/npre. 2008.2266.1.
- Teichberg, M., Fox, S.E., Olsen, Y.S., Valiela, I., Martinetto, P., Iribarne, O., Muto, E.Y., Petti, M.A.V., Corbisier, T.N., Soto-Jimenez, M., Paez-Osuna, F., Castro, P., Freitas, H., Zitelli, A., Cardinale, M., Tagliapietra, D., 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Glob. Change Biol.* 16, 2624–2637.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnol. Oceanogr.* 42, 1105–1118.
- Wang, C., Yu, R.C., Zhou, M.J., 2012. Effects of the decomposing green macroalga *Ulva (Enteromorpha) prolifera* on the growth of four red-tide species. *Harmful Algae* 16, 12–19.
- Wang, J.F., Jiang, P., Cui, Y.L., Li, N., Wang, M.Q., Lin, H.Z., He, P.M., Qin, S., 2010. Molecular analysis of green-tide-forming macroalgae in the Yellow Sea. *Aquat. Bot.* 93, 25–31.
- Xu, Q., Zhang, H.Y., Ju, L., Chen, M.X., 2014. Interannual variability of *Ulva prolifera* blooms in the Yellow Sea. *Int. J. Remote Sens.* 35, 4099–4113.
- Ye, N.H., Zhang, X.W., Mao, Y.Z., Liang, C.W., Xu, D., Zou, J., Zhuang, Z.M., Wang, Q.Y., 2011. 'Green tides' are overwhelming the coastline of our blue planet: taking the world's largest example. *Ecol. Res.* 26, 477–485.
- Zhang, J.H., Huo, Y.Z., Yu, K.F., Chen, Q.F., He, Q., Han, W., Chen, L.P., Cao, J.C., Shi, D.J., He, P.M., 2013. Growth characteristics and reproductive capability of green tide algae in Rudong coast, China. *J. Appl. Phycol.* 25, 795–803.
- Zhang, Q.C., Liu, Q., Kang, Z.J., Yu, R.C., Yan, T., Zhou, M.J., 2015a. Development of a fluorescence in situ hybridization (FISH) method for rapid detection of *Ulva prolifera*. *Estuar. Coast. Shelf Sci.* 163, 103–111. <http://dx.doi.org/10.1016/j.ecss.2014.09.004>.
- Zhang, Q.C., Liu, Q., Yu, R.C., Kang, Z.J., Guo, W., Ding, Y.M., Chen, J.H., Wang, Y.F., Li, Y., Yan, T., Zhou, M.J., 2015b. Application of a fluorescence in situ hybridization (FISH) method to study green tides in the Yellow Sea. *Estuar. Coast. Shelf Sci.* 163, 112–119. <http://dx.doi.org/10.1016/j.ecss.2014.09.005>.
- Zhang, X.L., Song, Y.J., Liu, D.Y., Keesing, J.K., Gong, J., 2015c. Macroalgal blooms favor heterotrophic diazotrophic bacteria in nitrogen-rich and phosphorus-limited coastal surface waters in the Yellow Sea. *Estuar. Coast. Shelf Sci.* 163, 75–81. <http://dx.doi.org/10.1016/j.ecss.2014.12.015>.
- Zhang, X.W., Mao, Y.Z., Zhuang, Z.M., Liu, S.F., Wang, Q.Y., Ye, N.H., 2008. Morphological characteristics and molecular phylogenetic analysis of green tide *Enteromorpha* sp. occurring in the yellow Sea. *J. Fish. Sci. China* 15, 822–829 (in Chinese, with English Abstract).
- Zhang, X.W., Mou, S.L., Cao, S.N., Fan, X., Xu, D., Ye, N.H., 2015d. Roles of the transthylakoid proton gradient and xanthophyll cycle in the non-photochemical quenching of the green alga *Ulva linza*. *Estuar. Coast. Shelf Sci.* 163, 69–74. <http://dx.doi.org/10.1016/j.ecss.2014.09.006>.
- Zhang, X.W., Wang, H.X., Mao, Y.Z., Liang, C.W., Zhuang, Z.M., Wang, Q.Y., Ye, N.H., 2010. Somatic cells serve as a potential propagules bank of *Enteromorpha prolifera* forming a green tide in the Yellow Sea, China. *J. Appl. Phycol.* 22, 173–180.
- Zhang, X.W., Xu, D., Mao, Y.Z., Li, Y.X., Xue, S.Y., Zou, J., Lian, W., Liang, C.W., Zhuang, Z.M., Wang, Q.Y., Ye, N.H., 2011. Settlement of vegetative fragments of *Ulva prolifera* confirmed as an important seed source for succession of a large-scale green tide bloom. *Limnol. Oceanogr.* 56, 233–242.
- Zhao, J., Jiang, P., Liu, Z.Y., Wei, W., Lin, H.Z., Li, F.C., Wang, J.F., Qin, S., 2013. The Yellow Sea green tides were dominated by one species, *Ulva (Enteromorpha) prolifera*, from 2007 to 2011. *Chin. Sci. Bull.* 58, 2298–2302.
- Zhao, J., Jiang, P., Qin, S., Liu, X.J., Liu, Z.Y., Lin, H.Z., Li, F.C., Chen, H.X., Wu, C.H., 2015. Genetic analyses of floating *Ulva prolifera* in the Yellow Sea suggest a unique ecotype. *Estuar. Coast. Shelf Sci.* 163, 96–102.