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Original Article

Harmful macroalgal blooms (HMBs) in China's coastal water: Green and golden tides

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ABSTRACT

Harmful macroalgal blooms (HMBs) have been increasing along China's coasts, causing significant social impacts and economic losses. Besides extensive eutrophication sustaining coastal seaweed tides, the stimuli and dynamics of macroalgal blooms in China are quite complex and require comprehensive studies. This review summarizes the distinct genesis, development and drifting patterns of three HMBs that have persistently occurred in China's coastal waters during recent years: transregional green tides of drifting *Ulva prolifera* in the Yellow Sea (YS), local green tides of multiple suspended seaweeds in the Bohai Sea and large-scale golden tides of pelagic *Sargassum horneri* in the YS and East China Sea. While specific containment measures have been developed and implemented to effectively suppress large-scale green tides in the YS, the origin and blooming mechanism of golden tides remain unclear due to lack of field research. With the broad occurrence of HMBs and their increased accumulation on beaches and coastal waters, it is necessary to investigate the blooming mechanism and ecological impacts of these HMBs, especially with the growing stresses of climate change and anthropogenic disturbances.

1. Introduction

With the increasing occurrence and intensive environmental impacts, macroalgal blooms are now of growing concern worldwide (Valiela et al., 1997; Ye et al., 2011; Smetacek and Zingone, 2013). The cosmopolitan seaweeds, *Ulva* (including the former *Enteromorpha*, Hayden et al., 2003) and *Sargassum*, are responsible for most macroalgal blooms (Teichberg et al., 2010; Ye et al., 2011; Smetacek and Zingone, 2013). These two genera originally colonized intertidal to sublittoral waters as primary producers, and blooms of free-floating biomass of these two taxa have recently enlarged their distribution and intensified their impacts on coastal biochemical cycling and marine benthic ecosystems.

The green tides caused by *Ulva* spp. started in Europe in the 1900s, and were widespread in temperate and tropical coastal waters along North America, Asia and other continental coasts in the 1970s–2000s (Fletcher, 1996; Valiela et al., 1997; Charlier et al., 2008; Teichberg et al., 2010; Ye et al., 2011). *Sargassum* blooms, so-called golden-brown tides, are most prominent in the regions of the Sargasso Sea, Gulf of México and Caribbean Sea (Laffoley et al., 2011; Smetacek and Zingone, 2013). *Sargassum* rafts have been floating for decades, and some species (notably *Sargassum natans* and *S. fluitans*) are believed to be holopelagic, that is, permanently drifting in the water (Parr, 1939; Amaral-Zettler et al., 2017). Recently, unusual expansions of *Sargassum* rafts have been reported along the west coasts of the northern and tropical Atlantic and even farther to the coasts of western Africa and northern Brazil in the southern Atlantic (Gower and King, 2011; Gower et al., 2013; Smetacek and Zingone, 2013; Sissini et al., 2017; Wang and Hu, 2017; Johns et al., 2020). Above all, *Ulva* spp. are prone to bloom in the photic zone of eutrophic coasts and estuaries (Charlier et al., 2008; Teichberg et al., 2010), while pelagic *Sargassum* spp. are widespread in oceanic waters (Lapointe, 1995; Teichberg et al., 2010; Ye et al., 2011; Smetacek and

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Zingone, 2013). Nevertheless, the concurrence of both seaweeds has recently been observed in the Yellow Sea (YS) of China (Xiao et al., 2020a, b). In addition to the link between coastal eutrophication and seaweed tides of *Ulva* and *Sargassum* (Valiela et al., 1997; Teichberg et al., 2010), the blooming dynamics varied significantly among the diverse causative species and in different regions (Ye et al., 2011; Smetacek and Zingone, 2013). If no containment measures are implemented, macroalgal blooms can be persistent and even last for decades on some occasions (Bonsdorff et al., 1997). Although the ecological impacts of floating seaweeds in open water are still unclear (Laffoley et al., 2011), the massive accumulation of seaweed biomass in coastal waters can cause a series of deleterious impacts on local ecosystems, including hindrance of perennial seagrass, alteration of benthic fauna, disturbance of nutrient biogeochemical cycling and hypoxia resulting from the degradation of blooming algae (Valiela et al., 1997).

In 2008, an astonishing green tide unprecedentedly inundated the coasts of Qingdao, the venue for the sailing events of the Beijing Olympics (Hu and He, 2008; Liang et al., 2008; Liu et al., 2009). Remote sensing revealed that tremendous floating green seaweed biomass covered the coasts and offshore of Shandong and Jiangsu provinces in the southern YS (Hu, 2009). The large-scale Yellow Sea green tide (YSGT) has recurred every spring to summer thereafter and resulted in significant economic losses. In terms of the distribution, coverage and production of massive floating mass, YSGT has been recognized as the world's largest green tide (Liu et al., 2009, 2010, 2013). During recent field surveys on the YSGT, pelagic brown seaweeds, comprised exclusively of a single species *Sargassum horneri*, have been increasingly observed in the YS. The widespread drifting *S. horneri* has even intruded into the southwestern YS in spring, co-occurring with the annual green tide and forming unusual bimacroalgal blooms in recent years (Kong et al., 2018; Liu et al., 2018b; Xiao et al., 2020b). Another local green tide has persisted in the coastal water off Qinhuangdao in the Bohai Sea since 2015 (Song et al., 2019a, b). Additionally, more local green tides have been reported in Yantai and Haiyang in Shandong Province, Xiamen in Fujian, Shantou and Zhanjiang in Guangdong, Haikou in Hainan and Beihai in Guangxi (Fig. 1, Fletcher, 1996; Ma et al., 2010; Cao et al., 2016), indicating that harmful macroalgal blooms (HMBs) are not a regional issue but a serious ecological nuisance that is pervasive throughout the coastal waters of China.

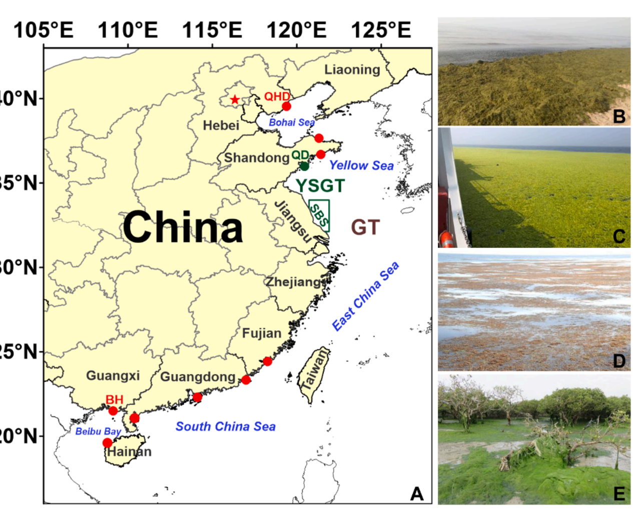

Fig. 1. Macroalgal blooms along the coasts of China. A: Locations of macroalgal blooms. Red dots and fonts indicate the locations of local green tides. The green dots, fonts and rectangle indicate the location of the transregional green tide in the Yellow Sea (YSGT). The brown font represents the schematic location of the golden tide which can affect the entire southern Yellow Sea, East China Sea and reach the northern Taiwan Strait occasionally. Abbreviations QHD, Qinhuangdao; BH, Beihai; QD, Qingdao; YSGT, transregional Yellow Sea green tide; SBS, Subei Shoal; GT, golden tide. B-E: Field photos of local green tide in QHD (July 2018), YSGT (June 2012), GT (June 2017) and local green tide in the mangrove wetland of BH (December 2015).

The dynamics of these three types of macroalgal blooms vary significantly, and the underlying mechanisms of the different blooms are not fully understood. The current knowledge on blooming mechanism indicated different research stages of these three blooms, which influenced development of their containment measures. For the large-scale green tides that have occurred periodically in the YS, the primary source of the floating *Ulva* biomass was confirmed to be closely related to marine aquaculture in the southwestern YS (Liu et al., 2010, 2013; Zhou et al., 2015). The development process, environmental drivers and intrinsic physiological characteristics contributing to the massive expansion of green tides were further elucidated through numerous long-term field observations, in situ and laboratory experiments and numerical modeling (Bao et al., 2015b; Wang et al., 2015; Liu et al., 2020a). Based on these studies, a series of countermeasures were recently executed in the source region, resulting in an overt reduction in the overall size of green tides in the YS. Additionally, general advice on the mitigation of local green tides in the Bohai Sea was proposed based on current research. While for the large-scale golden tides, the genesis, development and environmental factors leading to the massive proliferation of pelagic *S. horneri* remain unclear due to lack of sufficient field research. Hence, further comprehensive study is needed before specific prevention and control strategies can be proposed for the golden tides.

In this review, the current knowledge on the genesis and development process of the three representative macroalgal blooms and practical countermeasures to mitigate large-scale green tides are reviewed to provide an improved understanding of the biological characteristics and ecological impacts of macroalgal blooms and to highlight important directions for future research to decipher their bloom mechanisms.

2. Green tides in the Yellow Sea

2.1. Genesis of the green tides in the Yellow Sea

The green tide in the YS was first detected in 2007 when floating mats of green algae appeared along the coasts of northern Jiangsu and Haizhou Bay (34°N–35.5°N), with a maximum coverage of 100 km^2 (Keesing et al., 2011; Guo et al., 2016; Qi et al., 2016). It did not arouse much attention until 2008, when a larger green tide threatened the Olympic sailing regatta in Qingdao. Thereafter, the large-scale green tides recurred annually, with a maximum daily distribution of 58,000 km^2 and coverage of 2100 km^2 (Fig. 2, MNR, 2020; Liu et al., 2009, 2013, 2016; Keesing et al., 2011; Ye et al., 2011; Huang et al., 2014; Liu et al., 2015). Remote sensing traced the floating biomass back to the

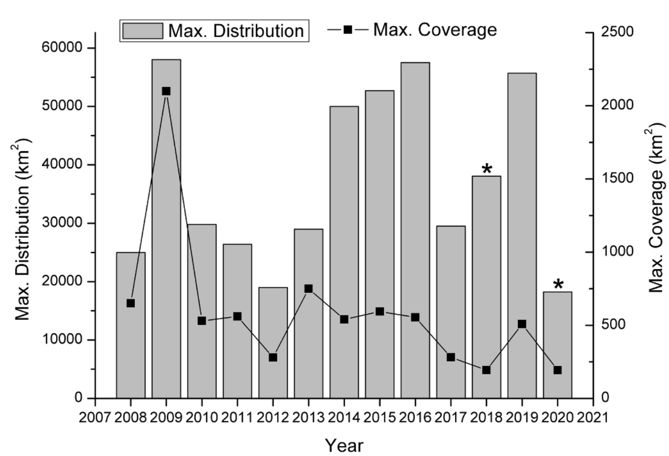

Fig. 2. Interannual variations in the maximum daily distribution and coverage of the YSGTs (MNR, 2020). Markers (*) indicate that early containment practices were conducted along the coast of Jiangsu Province (see text).

coastal water of the southwestern YS, close to the Subei Shoal (Hu, 2009; Liu et al., 2009; Hu et al., 2010; Ciappa et al., 2010; Keesing et al., 2011; Garcia et al., 2013; Bao et al., 2015b; Zhang et al., 2017). Later field observations pointed out that the macroalgal waste disposed from *Pyropia* (formerly known as *Porphyra*, Sutherland et al., 2011) aquaculture rafts in the Subei Shoal were the primary source of the initial floating biomass (Liu et al., 2013, 2016; Zhang et al., 2014; Wang et al., 2015; Zhou et al., 2015). Subsequently, intensive field research was conducted in the Subei Shoal and revealed the complicated genesis of the large-scale green tides in the YS, which were directly stimulated by extensive marine aquaculture and assisted by the favorable local hydrochemical and geophysical environment.

The Subei Shoal is a large intertidal muddy flat with an area of approximately 18,000 km^2, covering the northern Yangtze River Estuary (32°N) to the Sheyang River (34°N) and extending from the eastern coastline of Jiangsu Province to 90 km offshore (Wang et al., 2011). With its unique hydrogeochemical characteristics, Subei Shoal has been the largest nursery ground for *Pyropia* aquaculture since the 1970s (Cao, 2006). Typically, *Pyropia* aquaculture starts in fall (September – October) when rafts with *Pyropia* seeded nets are set up in the field. After approximately half-year culture until the following spring (April – May), the nursery nets are collected back for the *Pyropia* crops, while the remaining facilities (bamboos and connecting ropes) are cleaned in situ and recycled for the next fall (Fig. 3). A series of studies suggested that vast *Ulva* micropropagules, including the blooming species *U. prolifera*, existed in the water and sediment of the Subei Shoal (Fang et al., 2012; Liu et al., 2018a; Miao et al., 2020a, b). The raft structures (bamboos, ropes and nets) provided the best fouling substrata for the micropropagules (Geng et al., 2015). The species composition of the macroalgal community on the rafts succeeded with the fluctuating temperatures from fall to winter and the next spring (Fan et al., 2015; Keesing et al., 2016). In particular, *U. prolifera* grew rapidly when the temperature increased to above 15 °C and accounted for 40% of the total epiphytic macroalgal biomass during the *Pyropia* harvest season (April to May, Li et al., 2015b; Fan et al., 2015; Song et al., 2015). During the cleaning process after the harvest of *Pyropia* crop, the epiphytic green macroalgae were inadvertently disposed on the muddy flats (Fig. 3) and eventually drifted into the coastal waters, becoming the primary source of the floating green tides. It was estimated that over 250 km^2 of *Pyropia* rafts produced approximately 16,000 tonnes of macroalgae waste, among which 40% were *U. prolifera* (Wang et al., 2015). With its strong buoyancy and growth rate (Fu et al., 2019; Hao et al., 2020), *U. prolifera* dominated the floating patches rapidly and proliferated into large-scale floating mats within a month.

Additional efforts were made to test hypotheses on the other sources of floating *Ulva* macroalgae, including direct germination from environmental micropropagules and discharge from coastal aquaculture ponds (Pang et al., 2010; Liu et al., 2012). Although green macroalgal micropropagules could be detected in the entire southern YS even in winter without green tides (Zhang et al., 2010, 2011; Liu et al., 2012, 2018a), field surveys did not detect swarms of germlings, the intermediate stage linking the environmental micropropagules with the abundant floating biomass (Wang et al., 2015). In addition, various laboratory studies indicated that these environmental micropropagules need to attach to certain substrata to grow into thalli (Liu et al., 2012, 2018a; Zhang et al., 2013a). Meanwhile, no *Ulva* algae discharge was found in the coastal aquaculture ponds of shrimps or crabs before or during the blooming period (Wang et al., 2018). Further genetic screening on the attached populations of *U. prolifera* throughout the coastal waters of China confirmed the existence of the ‘floating’ ecotype only in the Subei Shoal, which was the strain responsible for the large-scale green tide in the YS (Zhao et al., 2015). This strain has not been identified in other surveyed regions (Zhang et al., 2018), and no other source has been observed or confirmed.

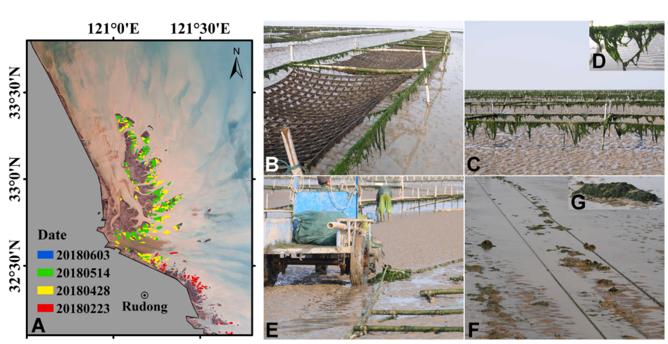

Fig. 3. Raft distribution based on high-resolution satellite images showing the raft removal process during February–June 2018 (A) and field pictures of fouling green macroalgae on the rafts (B–D) and the raft cleaning process (E–G, Wang et al., 2015).

2.2. Drifting and expansion

In addition to the impacts of *Pyropia* aquaculture, the unique topography of the Subei Shoal played an important role in transporting the initial floating biomass. Both field observations and drifting simulations found that the initial floating biomass accumulated along deep grooves and formed long, narrow floating slicks. The unusual microcirculation induced by the topography of the shoal coupled with the seasonal monsoon assisted the formation and transport of algal slicks (Xia, 2009; Bao et al., 2015a, b). The source biomass derived from the northern and eastern raft regions contributed significantly to the formation of green tides in open waters (Bao et al., 2015b; Huang et al., 2014; Zhang et al., 2017; Xiao et al., unpubl.). Due to the increasing demand for *Pyropia* from Japan in 2005 (Cao, 2006), the culture rafts almost doubled in 2007 along the Jiangsu coast, especially in the northern and offshore regions of the Subei Shoal (Fig. 4). Computational simulation and drifter experiments also indicated that the *Ulva* biomass derived from the northern and eastern offshore regions of the shoal can readily drift out of the shoal with the assistance of strong tidal forces and northward winds (Bao et al., 2015b; Zhang et al., 2017; Xiao et al., unpubl.).

Unlike the green tides in other coastal regions around the world, the floating macroalgal biomass of the YSGT was not restricted to the original source area (Subei Shoal) but expanded extensively into offshore and open waters, which was resulted not only from favorable environmental conditions but also from the inherent physiological advantage of floating *U. prolifera*. Multiple field drifter experiments coupled with the numerical modeling corroborated that the seasonal monsoon and its associated surface currents in spring and summer drove the northward drifting of the floating macroalgal mats, and likely determined the geographic range that the YSGT was distributed and the amount of biomass washed ashore (Liu and Hu, 2009; Qiao et al., 2009; Ciappa et al., 2010; Qi et al., 2016). The nutrients in the western YS were sufficient to sustain the rapid growth of floating *U. prolifera* (Li et al., 2015a; Shi et al., 2015; Wang et al., 2019; Zhang et al., 2020), and the availability of various types of nitrogen (dissolved inorganic nitrogen, DIN vs. dissolved organic nitrogen, DON) favored the amplification and persistence of floating biomass at different blooming stages in different regions (Li et al., 2016, 2019; Zhang et al., 2020). The massive loads of wastewater, manure, fertilizer and atmospheric deposition provided the most nutrients consumed by the large-scale green tides in the YS (Valiela et al., 2018). In addition, high nutrient uptaking and assimilation capability and the C_4 photosynthetic pathway also enhanced photosynthesis and rapid biomass accumulation of floating *U. prolifera* exposed to fluctuating irradiance intensity and CO_2 availability when drifting in open water (Luo et al., 2012; Xu et al., 2012; Zhang et al., 2013b; Valiela et al., 2018; Wang et al., 2019; Liu et al., 2020a). Furthermore, Wang et al. (2020a) hypothesized that the sporangium and in situ germination of floating *U. prolifera* thalli and grazing of

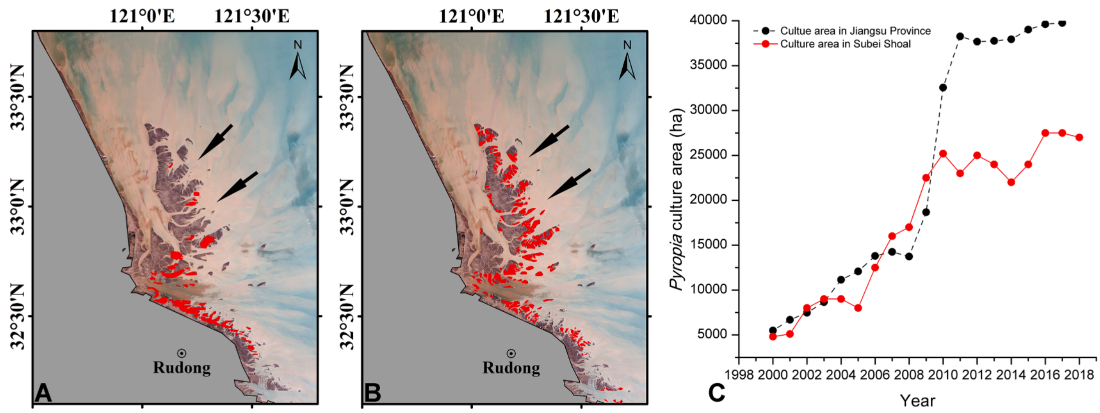

Fig. 4. The increase of *Pyropia* aquaculture rafts in the Subei Shoal. A-B: Comparison of the raft distributions in 2004 (A) and 2007 (B) based on remote sensing, showing a clear increase of rafts in the northern and offshore regions (arrows). C: The increasing trend of culture area along the Jiangsu coast (black symbols and dashed line, BFMARA, 2019) and in the Subei Shoal (red symbols and solid line, Xing et al., 2019) during the last two decades.

herbivorous zooplankton assisted the rapid proliferation and massive expansion of drifting mats, which needs further field investigation. Facilitated by all these bio-, geochemical factors, a few thousand tonnes of initial floating biomass were amplified into millions of tonnes of macroalgal mass in approximately one to two months. Such massive macroalgal mass widespreading over the entire western YS is hard to be controlled or cleaned by the traditional countermeasures (see below).

2.3. Prevention and control practices

To provide a suitable environment for the sailing events of the 29th Olympic Game in 2008, more than 16,000 people, 1600 fishing boats and 1000 trucks were emergently organized and implemented in response to the sudden outbreak of large-scale green tides in the near-shore water of Qingdao, and approximately 1 million tonnes of fresh *Ulva* algal mass was manually removed from the beaches and coastal waters (Ye et al., 2011). This primitive method with such dramatic inputs was apparently infeasible as a long-term response to the green tides. Subsequently, a series of emergent tactics were developed to prevent the *Ulva* algal mass from piling up on the recreational beaches and to protect the shoreline and coastal facilities. Countermeasures, such as blocking drifting mats with arresting nets and collecting algal masses through automatic processing line have been widely adopted by multiple coastal cities of Shandong Province and have partially mitigated the adverse impacts of green tides on marine aquaculture and environment. However, these measures can only protect the limited areas along the coastline and are quite costly and infeasible for open waters. For example, a total of 80 km arresting nets were implemented along the coasts of Shandong (55 km in Qingdao, Fig. 5, 10 km in Yantai, 5 km in Weihai, 10 km in Rizhao) in 2019. Approximately 12,000 fishery boats were deployed, and over 1.8 million tonnes of algae mass were collected. This cleaning battle directly cost over 70 million RMB (Wang et al., 2020c). Another concern related to these obligatory cleaning tactics is the potential land pollution resulting from disposal or burial of the massive algal mass collected in such a short period (~ 2 months). It took years for the landfill of *Ulva* waste to recover from the toxic hydrogen sulfide (H_2S) and heavy metal pollution carried from the sea. The specific equipment and technology were developed to stabilize and utilize the algal mass. For example, a private company (Qingdao Seawin Biotech Group Co., Ltd) equipped with pressing machines and a fertilizer line, was able to consume 10,000 tonnes of fresh *U. prolifera* per day. The bioproducts (e.g., fertilizers, cosmetics and food additives) transformed from harvested seaweeds could partially counteract the significant economic losses (Cai et al., 2016; Zhang et al., 2019c), while their economic value is greatly impaired by the high cost of collecting and transporting the very large biomass from the sea.

Since the source region of the Yellow Sea green tides (YSGTs) has been confirmed by various studies (Zhou et al., 2015; Wang et al., 2015; Liu et al., 2016; Zhang et al., 2017), containment strategies in the source region are believed to be more efficient and cost-effective due to the relatively limited geographic range and lower amount of initial algal mass (Wang et al., 2020c). The source-controlling measures focused on the three key stages involved in the early development process of the YSGTs, the *Ulva* algae attached to the rafts, the disposed algal mass and

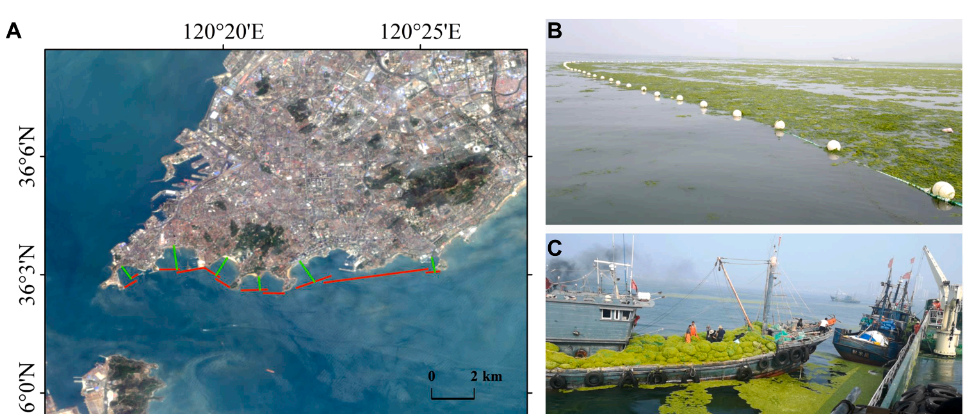

Fig. 5. Schematic of the arresting nets (red lines) deployed along the coastline of Shinan and Laoshan districts of Qingdao to block floating *Ulva* biomass (A), field pictures of the arresting nets (B) and ship-based removal of floating *Ulva* biomass (C).

the initial floating mass in the Subei Shoal (Wang et al., 2020c). Tactics developed to avoid the attachment of *Ulva* spores and reduce the epiphytic green algal mass on the rafts included replacing the traditional bamboos and ropes with new antifouling materials for rafts, freezing pretreatment, using modified clays to deposit and reduce micro-propagules from water and spraying acid to eliminate the green algae on the rafts (Geng et al., 2015; Li et al., 2017; Liu et al., 2020b). From November 2019 to May 2020, a large-scale field trial was conducted to reduce the epiphytic green macroalgae in the entire *Pyropia* raft region in the Subei Shoal. The initial measure was to eliminate the attached algae using sodium hypochlorite (NaOCl) detergent. Approximately 1500 tonnes of solution (2%) was sprayed on the rafts in November 2019, and additional 400 tonnes were applied from March to April 2020. Over 2000 tonnes of attached algae were estimated to be eliminated through this measure; however, the potential adverse impacts of this chemical on the *Pyropia* crops and the benthic organisms, as well as the rapid recruitment of attached green algae with increasing temperature, suspended the further implementation of this measure. Then, two more approaches (early-raft-removal and rope embedding) were proposed to reduce the potential amount of algal mass disposed on the muddy flat. To avoid rapid proliferation of epiphytic green algae in May, especially the bloom-forming *U. prolifera* (Fan et al., 2015), local fishermen were required to remove all the rafts from the shoal (without any cleaning effort) before early May, which was about one month earlier than the regular operation. Then the connecting ropes of *Pyropia* rafts were settled on the flat and embedded into mud with the assistance of strong tidal forces. The epiphytic green algae on the ropes were allowed to decay naturally before being released into the water column (Wang et al., 2020c). Although the rope-embedding approach was not widely implemented in 2020, it is easy to carry out in the future and could be an effective supplement for the measure of early-raft-removal. With all the practical approaches, the size of the green tide in 2020 was the smallest within the last five years (Fig. 2). The maximum coverage of the green tide in 2020 (192 km^2) was comparable to that of 2018 (193 km^2, Fig. 2), when a previous large-scale field trial of controlling initial floating macroalgae was conducted (described below).

Based on the transport pattern of floating algal slicks, an efficient algae-removal strategy was proposed to reduce the initial free-floating algal mass from the Subei Shoal (the third key stage, Wang et al., 2020c; Xiao et al., unpubl.). This strategy was implemented in 2018 to secure marine environmental safety during the Shanghai Cooperation Organization (SCO) Summit in Qingdao. Approximately 3000 tonnes of the initial floating algal mass were removed from the Subei Shoal and the adjacent coastal water (Jiangsu Fishery Bureau, personal communication). Contemporaneous field observations indicated that the green macroalgae attached on the rafts and initial floating biomass were much higher in 2018 than that in previous years (Xiao et al., 2020a), while the scale of the green tide (193 km^2 maximum coverage) was the lowest since 2013 (Fig. 2). These field trials corroborated the origin and source of the large-scale green tides in the YS and validated the feasibility and efficiency of these source control strategies on abating the overall scale of the YSGT and mitigating its significant ecological and social impacts.

3. The green tide in the Bohai Sea

In 2015, another local green tide occurred in the coastal water of Qinhuangdao of the western Bohai Sea (Fig. 1), and it has recurred every April to September since then. During the blooms, vast macroalgae accumulated primarily on the Jinmenghaiwan bathing beach at the estuary of the Tang River (39°54′19.36″N, 119°33′54.90″E), spread rapidly throughout the three adjacent beaches, Jinwu, Qianshuiwan and Geziwo, and reached Jinshanzui (39°49′54.69″N, 119°31′30.50″E, approximately 12 km south of the initial location, Fig. 6). The bloom was restricted to the photic zone of the shallow intertidal and subtidal

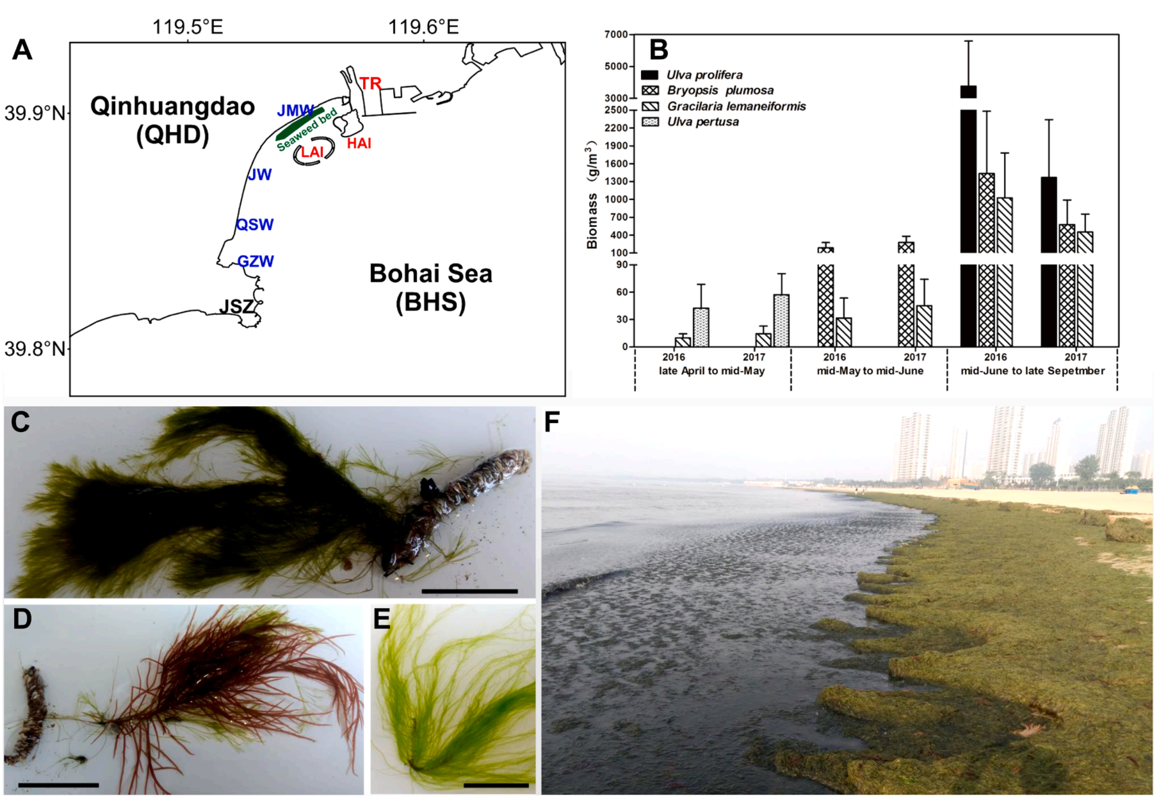

Fig. 6. Local green tides in the Bohai Sea. A: Map of the coastline of Qinhuangdao (see Fig. 1 for the location of QHD). JMW, Jinmengwan bathing beach; JW, Jinwu bathing beach; QSW, Qianshuiwan bathing beach; GZW, Geziwo bathing beach; JSZ, Jinshanzui marine protected area; TR, Tang River; LAI, Lianhua artificial island; HAI, Hailuo artificial island. B: Variations in biomass and species composition during the three phases of the green tide. C, D and E: Attached *Bryopsis plumose, Gracilaria lemaneiformis* and *Ulva prolifera* from the seaweed bed, respectively. F: Field picture of a green tide on Jinmengwan beach. Scale bars in C–E are 5 cm.

inshore water (approximately 0–10 m from the shoreline and 0–2 m depth, Song et al., 2019a, b) The blooming macroalgae, comprising Multiple species (see below), were suspended throughout the water column, which was distinct from the YSGTs. Although the size of the green tide in the Bohai Sea (approximately 0.12 km^2) was 3–4 orders of magnitude lower than that of YSGTs (100–2100 km^2 in coverage), it also caused significant economic losses and social impacts to multiple important tourist attractions and a national marine protecting area.

Field research on bloom dynamics confirmed the independence of this local green tide to the YSGTs. The blooming macroalgae comprised M. species and showed evident species succession during the bloom. Approximately 8 species (7 families in 3 phyla) were identified, including *Ulva prolifera, U. pertusa, Bryopsis plumose, Gracilaria lemaneiformis* and *Codium fragile* (Song et al., 2019b). Field surveys revealed that the entire blooming process could be divided into 3 phases based on the dominant species: I, low biomass was dominated by *U. pertusa* from late April to mid-May; II, the growing biomass was dominated by the red algae *B. plumosa* during mid- May to mid-June; III, *U. prolifera* proliferated rapidly and became dominant since mid-June, and the biomass of *U. prolifera* along with the other two common species *B. plumose* and *G. lemaneiformis* remained high until late September (Fig. 6).

The two major blooming species, *B. plumosa* and *U. prolifera*, were identified only in the natural seaweed bed located in the inshore water of Jinmengwan, and the species succession of the macroalgal community on the seaweed bed was highly consistent with that of the suspending macroalgae of the green tides. Interestingly, these blooming species preferred different substrata, *G. lemaneiformis* was mainly attached to the dwelling tubes of benthic Polychaeta, while *U. prolifera* and *B. plumosa* preferred the gravels (Fig. 6). Combined with field experiments, it was concluded that the attached macroalgae on the seaweed beds provided the original algal source for the green tides in the Bohai Sea (Song et al., 2019a). The blooming *U. prolifera* in the Bohai Sea was genetically distinct from the floating *U. prolifera* in the YS, which further confirmed the independence of these two types of green tides (Zhao et al., 2015; Han and Song, unpublished data). Long-term monitoring showed that the DIN concentration in the coastal water of Qinhuangdao increased from 0.1 mg L^{-1} to 0.15 mg L^{-1} during 2006 to 2016, while the DIP decreased from 0.03 to 0.015 mg L^{-1} (CNEMC, 2016), suggesting a general eutrophication with the high N/P ratio at this coast. Additional numerical modeling indicated that substantial coastal construction (e.g., two artificial islands, HAI and LAI, constructed in 2014) altered the hydrodynamics of the coastal water, which reduced the water exchange and hampered the nutrient dispersal, and hence assisted the blooming of the benthic macroalgae (Song et al., 2019a). Countermeasures, such as decreasing the nutrient input and increasing the water flush in the sensitive sea area, were proposed to prevent the formation of this local green tide.

4. Golden tides in the Yellow and East China seas

The golden tide caused by *Sargassum horneri* in the East China Sea (ECS) has been noted and reported since the 2000s. Abundant *Sargassum* seaweeds were originally detected drifting in the eastern ECS since the early 2000s (Komatsu et al., 2007, 2008, 2014a; Filippi et al., 2010), while only sporadic pelagic *S. horneri* was observed in the YS with no significant ecological and economic impacts to the coastal areas (Xiao et al., 2020a). From the winter of 2016 to spring 2017, an unprecedented golden tide inundated the southwestern YS and seriously impaired the marine aquaculture in the Subei Shoal. The dense and heavy drifting algal mats destroyed 20%–70% of *Pyropia* aquaculture rafts and caused significant economic losses (Xing et al., 2017; Liu et al., 2018b). Decadal field observations indicated that the inundation events in this shallow coastal water were recorded as early as 2013 and have recurred every spring since 2017 (Xiao et al., 2020a). The drifting *Sargassum* was often tangled with the *Ulva* algal mass and formed unusual bi-macroalgal blooms in the shoal and adjacent coastal water (Xiao et al., 2020a, b). By satellite remote sensing, Hu et al. (2010) reported the first detection of an annual macroalgal bloom in the western ECS since 2000, which was originally misidentified as a green tide, but proved to be a golden tide in the following research (Qi et al., 2017). Satellite remote sensing revealed a much larger geographic distribution of the floating *Sargassum*, from the northern Taiwan Strait to the entire southern YS, from the western coastline to the eastern boundary of the continental shelf of the ECS (Hu et al., 2010; Komatsu et al., 2014a; Qi et al., 2017). The scale of golden tides, in terms of distribution, coverage and total biomass, has increased significantly in recent years (Qi et al., 2017). In both 2017 and 2020, for example, a substantial amount of drifting *S. horneri* was observed during multiple shipboard surveys from April to June in the western YS (Xiao et al., 2020a, b; Yuan et al., unpubl.). Subsequent remote sensing analyses found that pelagic *Sargassum* was widespread in the entire southern YS and open waters of the ECS and the geographic distribution of golden tides was even broader than the contemporary green tides (Fig. 7). The golden tide of *S. horneri* has become the second transregional macroalgal bloom along the coasts of China after the YSGTs and poses serious threats to the coastal ecosystems and economy (Liu et al., 2018b; Byeon et al., 2019; Choi et al., 2020).

Remote sensing analyses and computational modeling revealed variable drifting pathways of the floating *S. horneri* in the YS and ECS. Field investigations and computational simulations suggested that the drifting *S. horneri* was likely originated from the western coasts of the ECS (the coasts of Zhejiang Province) and was transported by water currents to the convergence zone of the continental shelf and the Kuroshio Front (Komatsu et al., 2007, 2014a, b; Filippi et al., 2010). Furthermore, unusual expansion of drifting *Sargassum* was occasionally observed in certain years, which could be ascribed to meteorological anomalies, global warming or unusual water currents (Filippi et al., 2010; Komatsu et al., 2014b). Qi et al. (2017) re-examined the drifting pathways and interannual variation of golden tides in the ECS and found that pelagic *Sargassum* was widespread from the western coastline to the eastern continental shelf of the ECS. The distribution and coverage areas of floating *Sargassum* have increased since 2012 and even exceeded the sizes of most *Ulva* green tides in 2017, with an overall coverage of 160, 000 km^2. Similar to previous studies, particle tracking simulations indicated floating *Sargassum* was originated from the Zhejiang coast in early spring and then transported to the eastern offshore of the ECS and farther north into the southern YS through the Kuroshio Current and Taiwan Warm Current (Qi et al., 2017). Later, Xing et al. (2017) reported another drifting path of floating *Sargassum* in the western YS, in which the floating *Sargassum* was initiated from the eastern tip of the Shandong Peninsula in fall 2016, drifted southward along coasts and

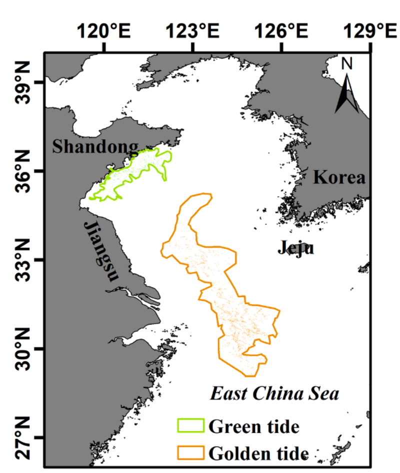

Fig. 7. Distributions of green and golden tides on June 22nd and April 24th, 2020, respectively, based on satellite remote sensing (Yuan et al., unpublished data).

accumulated in the shallow water off the Subei Shoal in winter 2016. Although the size of the winter bloom (~ 8.8 km^2 in coverage) was much smaller than that in the ECS, this southward progression in winter was consistently detected in the following years (Yuan et al., unpubl.). Compared to the consistent point source and drifting pathway of the green tides in the YS, the variable drifting pattern of the golden tides in the YS and ECS in different seasons suggested possibly multiple sources of the floating *Sargassum*, which remains to be clarified.

The current hypotheses on the source and origin of the golden tides were mainly derived from satellite remote sensing analyses and numerical modeling, while little field work has been done to confirm their potential link to any benthic population of *S. horneri*. Indeed, some discrete benthic populations have been identified along the coasts of Liaoning, Shandong and Zhejiang provinces (Tseng and Chang, 1959; Tseng, 1984; Sun et al., 2008, 2009; Hu et al., 2011; Bi et al., 2016; Huang et al., 2018; Lv et al., 2018; Ding et al., 2019), but little is known about their abundance, population sizes, seasonality and life cycle. It was speculated that anthropogenic disposal or natural break-off of *S. horneri* from mussel aquaculture rafts in northern coastal waters of Zhejiang Province contributed to the large-scale golden tide in offshore water of the ECS (Ding et al., 2019; Zhang et al., 2019b; Zhuang et al., 2021). Other research (Huang et al., 2018) indicated that the winter bloom at the end of 2016 was originated from the Bohai Strait and the adjacent coastal water. Phylogenetic analyses revealed a high genetic homogeneity of the drifting *S. horneri* in both the YS and ECS (Hu et al., 2011; Liu et al., 2018b; Lv et al., 2018). Sensible molecular markers (e.g., microsatellites, novel mtDNA noncoding regions) have been recently developed to discriminate a few haplotypes within *S. horneri* (Su et al., 2017; Liu et al., 2018b; Byeon et al., 2019; Zhuang et al., 2021), while the genetic affinity of pelagic *S. horneri* with any benthic population has yet to be determined. In addition, it is far from being understood that how much benthic populations may contribute to the different seasonal golden tides, as well as what caused the wide geographic distribution and significant biomass accumulations in some regions. These questions are even more complex since current knowledge on the physiology and reproduction of floating *S. horneri* is also very limited. To date, mature receptacles, young seedlings, new branchlets growing from the receptacle and holdfasts have been observed on floating *S. horneri* seaweeds during blooms (Komatsu et al., 2008; Liu et al., 2018b; Xiao et al., 2020b), but it is still unclear whether *S. horneri* could complete its life cycle and remain holopelagic, like the floating *S. fluitans* and *S. natans* in the Sargasso Sea (Laffoley et al., 2011).

5. Impacts of large-scale macroalgal blooms

Previous studies on the local green tides around the world indicated that increasing nitrogen loading to shallow estuaries favored blooming of ephemeral macroalgae, which, in turn, altered the biogeochemical cycles of nutrients and prompted significant changes in the benthic fauna and primary producers (mainly replacing the seagrass beds with seaweed mats, Valiela et al., 1997). The ecological consequences of large-scale macroalgal blooms, such as the YSGTs and golden tides in the YS and ECS, were likely more complicated, from the profound changes in geochemical cycling to instant fluctuations in planktonic and benthic organisms. At the same time, the influences could vary significantly among the distinct ecosystems and at different stages of the green tides. At the early stage of the green tides, floating *U. prolifera* actively assimilated inorganic carbon to support its rapid growth, resulting in an increase in pH and dissolved oxygen (DO) in the water column, which was commonly observed in the Subei Shoal and the coast of southern Jiangsu Province during April to May (Zhang et al., 2019c; Miao et al., 2020b). However, the massive *U. prolifera* algal mass was piled up and washed ashore along the coast at the descending stage of the green tides. Algal decomposition released loads of C, N and P and consumed a mass of oxygen from the water, resulting in deleterious water quality, low DO and even hypoxia (e.g., local waters of Qingdao in July to August, Lin et al., 2017; Feng et al., 2020).

The periodic inundations of macroalgal biomass covered up to 2.6% of the sea surface in these marginal seas (Qi et al., 2017; Zhang et al., 2019a). It could undoubtedly affect every component of coastal ecosystems in addition to the biogeochemical processes (Norkko et al., 2000; Wang et al., 2011, 2020b; Zhang et al., 2019c). Although laboratory experiments notified the allelopathic effect of macroalgae on various microalgae species (Tang and Gobler, 2011; Gao et al., 2018; Cai et al., 2019), microalgal red tides (e.g. *Karenia mikimotoi, Heterosigma akashiwo* and *Noctiluca scintillans*) were observed co-occurring with green and golden tides in the Bohai Sea and YS (Kong et al., 2018). It was also commonly found that abundant herbivorous amphipods (*Ampithoe* spp.) grazed on the drifting *U. prolifera* and *S. horneri* and proliferated within these drifting mats (Wang et al., 2020a; Xiao and Fan, unpubl.). Furthermore, substantial epiphytic benthic organisms, juvenile fishes and fish eggs were detected in the pelagic mats of *S. horneri* in the YS (Xiao and Fan, unpubl.). Nonetheless, there has been little systematic research on the trophic responses and nutrient cycling of these marine organisms under the long-lasting impacts of these prevailing transregional seaweed tides.

The Yellow Sea, enclosed by the Chinese mainland, Korean Peninsula and Yangtze River Estuary, has undergone significant environmental changes in recent decades (Lin et al., 2011; Huang et al., 2012; Li et al., 2015a; Valiela et al., 2018; Song and Duan, 2019). The increasing rate of annual mean sea surface temperature (SST) in the southern YS reached 0.025 $^{\circ}C\ yr^{-1}$ in winter and 0.009 $^{\circ}C\ yr^{-1}$ in summer, while the SST in the northern YS increased by approximately 0.048 $^{\circ}C\ yr^{-1}$ in winter and 0.004 $^{\circ}C\ yr^{-1}$ in summer (Huang et al., 2012; Song and Duan, 2019). Ocean acidification was also enhanced along with increased eutrophication and temperature in the YS, with pH decreasing by 0.003–0.005 yr^{-1} (Song and Duan, 2019). As a response to environmental changes, *Pyropia* aquaculture has moved northward, expanding from the northern offshore region of the Subei Shoal (described in 2.2) to the coast of Haizhou Bay (between northern Jiangsu Province and southern Shandong). *Pyropia* aquaculture has developed rapidly along the coasts of Shandong Province since 2017–2018 (Tan et al., 2018). The floating ecotype of *U. prolfiera* (the major genetic strain responsible for the YSGTs, Zhao et al., 2015) was recently detected in the benthic *Ulva* populations along the coasts of Qingdao with a relatively low abundance of 0.3%, indicating the risk of bioinvasion (Miao et al., 2018; Zhao et al., 2018). In addition, the nuisance jellyfish blooms in the YS and northern ECS impaired the diversity and structure of demersal and pelagic fishes in the YS (Dong et al., 2011; Shan et al., 2013), which could also impact the abundance and community structure of macroalgae through the top-down effect (Lotze et al., 2000; Eriksson et al., 2009). The persistent large-scale green tide in the YS, increasing golden tides and frequent local tides directly reflected the significant pressure of growing anthropogenic disturbances and climate changes, which in turn influenced the progression and blooming patterns of these macroalgal blooms (Keesing et al., 2016; Qi et al., 2016; Johns et al., 2020)

6. Summary and perspective

This review summarizes the recent research progress on the three types of macroalgal blooms along the coasts of northern China, covering the distinct genesis, development and drifting processes and impacts of these blooms. Similar to the harmful algal blooms caused by dinoflagellates and diatoms, macroalgal blooms are becoming frequent ecological nuisances impairing the coastal ecosystem and local economy throughout the coasts of China. Thus, more research is needed to reveal the bloom mechanisms and the ensuing environmental consequences in coastal ecosystems, especially under the pressures of climate change and anthropogenic disturbance. In particular, systemic monitoring techniques and ecological models are needed to depict the interannual variations of large-scale macroalgal blooms and propose ecologically friendly containment measures.

Compared to the local green tides, the transregional macroalgal blooms (e.g., the green tides in the YS and the golden tides in the YS and ECS) pose more challenges to monitoring and management. Satellite remote sensing coupled with shipboard field surveys has been widely used in long-term monitoring since the first occurrence of large-scale green tides in the YS. Other multispatial sensors, such as unmanned aerial vehicles (UAVs) and autonomous underwater vehicles (AUVs), have also facilitated specific regional scale observations (Xu et al., 2018; Xing et al., 2019). The recent occurrence of bimacroalgal (*U. prolifera* and *S. horneri*) blooms in the western YS has caused more difficulties on detecting and monitoring both blooms through satellite remote sensing, and multidimensional sensors and technologies have become increasingly important. In addition, an ecological model simulating the complete blooming dynamics is necessary for future research on the interannual variations in environmental drivers of and efficiency of containment measures for large-scale macroalgal blooms. Hu et al. (2017) and Xiao et al. (2019) took into account the unevenness of drifting macroalgae and estimated the floating biomass of green tides in the YS, which partially overcame the shortage of the current one-dimensional spatial parameters (e.g. maximum distribution and coverage), but still counted on instant daily remote sensing data. The ecological model should be able to simulate and assess the cumulative floating biomass throughout the bloom and the inundated biomass in a specific area or time frame.

Efficient emergent responses and long-term management are needed to counteract the detrimental social and economic impacts of these harmful macroalgal blooms. As described above, a series of emergent mitigation strategies have been developed and implemented in response to massive *Ulva* algal mass accumulated along the coasts of the southwestern YS. These labor-intensive strategies are very costly and probably impractical for long-term implementation. In comparison, the early containment measures are promising for cutting down the initial biomass in the Subei Shoal and hence reducing the total floating biomass in the YS (Wang et al., 2020c). More research is still needed to investigate the feasible approach and key technology that can effectively prevent and control green tides at the early stage to secure hygienic *Pyropia* aquaculture and, more importantly, systematic improvements of the coastal environment. The benthic and drifting *S. horneri* are generally considered as habitats and refugees for various fishes and other littoral animals (Komatsu et al., 2007, 2008). However, recent massive inundation and beaching events have caused significant economic losses and detrimental environmental impacts (Xing et al., 2017; Liu et al., 2018b; Byeon et al., 2019; Choi et al., 2020). Thus, continued monitoring and comprehensive field research are needed to delineate the origin and drifting of pelagic *S. horneri* and to develop proper containment measures to prevent its transition into undesirable harmful golden tides.

Declaration of Competing Interest

We declare there is no conflict of interest.

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