

# Distribution of green algae micro-propagules and their function in the formation of the green tides in the coast of Qinhuangdao, the Bohai Sea, China

Hongbin Han<sup>1,2,3</sup>, Wei Song<sup>2,3</sup>, Zongling Wang<sup>1,2,3\*</sup>, Dewen Ding<sup>1,2</sup>, Chao Yuan<sup>2,3</sup>, Xuelei Zhang<sup>2,3</sup>, Yan Li<sup>2,3</sup>

<sup>1</sup> College of Environmental Science and Engineering, Ocean University of China, Qingdao 266100, China

<sup>2</sup> Key Laboratory of Science and Engineering for Marine Ecology and Environment, First Institute of Oceanography, Ministry of Natural Resources, Qingdao 266061, China

<sup>3</sup> Laboratory of Marine Ecology and Environmental Science, Pilot National Laboratory for Marine Science and Technology (Qingdao), Qingdao 266235, China

Received 6 March 2018; accepted 13 September 2018

© Chinese Society for Oceanography and Springer-Verlag GmbH Germany, part of Springer Nature 2019

## Abstract

Since 2015, a novel green tide has been recurring in the coastal areas of Qinhuangdao at the western coast of the Bohai Sea in China, threatening the environment and ecosystem of the Beidaihe seaside holiday resort along the coast. Micro-propagules of the green algae including gametes, spores, micro-germlings and micro-vegetative fragments play an important role in the formation of green tides. They serve as a “seed source” of green macroalgae, and their distributions could reflect and influence the “algae source” of green tides. In this study, monthly surveys in the inshore and offshore areas of the Qinhuangdao coast were conducted from April to September 2016 and in January 2017 to investigate the tempo-spatial distribution patterns and the biomass variations of the green algae micro-propagules. The obtained results show that micro-propagules were mainly distributed in the inshore areas with a significantly decreasing abundance towards offshore areas. Their biomass was highest in July and August, and lowest in winter. The areas that were affected by the green tides showed a remarkably higher abundance of micro-propagules compared to other areas. These micro-propagules could serve as the “seed” source of green tides. Their distribution patterns indicate that the green tide in the coastal areas of Qinhuangdao originated locally.

**Key words:** green tides, micro-propagules, macroalgae, Qinhuangdao, Bohai Sea

**Citation:** Han Hongbin, Song Wei, Wang Zongling, Ding Dewen, Yuan Chao, Zhang Xuelei, Li Yan. 2019. Distribution of green algae micro-propagules and their function in the formation of the green tides in the coast of Qinhuangdao, the Bohai Sea, China. *Acta Oceanologica Sinica*, 38(8): 72–77, doi: 10.1007/s13131-018-1278-1

## 1 Introduction

Green macroalgal blooms, referred to as “green tides”, are mainly caused by the accumulation and bloom of fast-growing macroalgae including *Ulva*, *Chaetomorpha*, *Cladophora*, *Rhizoclonium*, *Percursaria* and *Ulvaria* (Taylor et al., 2001; Nelson et al., 2003). Over the last few decades, global and frequent occurrences of green tides have severely affected tourism, the aquaculture industry, and ecosystems, resulting to increased public attentions (Teichberg et al., 2010; Liu et al., 2013). Since 2008, the world’s largest green tide dominated by the green macroalgae *Ulva prolifera* consecutively formed blooms in the Yellow Sea. This had severe negative effects for the environment of the coastal cities of Shandong Province, China (Wang et al., 2015; Song et al., 2018). In 2015, a novel green tide began to emerge in the Bohai Sea and lasted from late April to late September. It started mainly in the adjacent sea area of the Beidaihe seaside holi-

day resort in Qinhuangdao City, Hebei Province, which is one of the busiest summer resorts in China. A variety of macroalgal species were identified in the study area, with three macroalgae, including *Ulva pertusa*, *Bryopsis plumosa*, *Ulva prolifera*, occupying more than 99.99% of the total biomass during the development of the green tides (personal communication by Song et al.). These macroalgae widely covered the coastline from the south of the Tanghe River Estuary to the north of Jinshanzui, with the biomass mostly accumulated from a distance of 0 to 100 m from the shore (personal communication by Song et al.).

Accurately determining the original source of the green tide, including its “algae source” (vegetative) and “seed sources” (propagules), is the first step to understand the occurrence of green tides and will also help to find solutions for these ecological disasters (Pang et al., 2010). The micro-propagules, including gametes, spores, micro-germlings and micro-vegetative fragments of

Foundation item: The National Key Research and Development Program of China under contract Nos 2016YFC1402104 and 2016YFC1402106; the National Natural Science Foundation of China under contract No. 41606190; the Shandong Natural Science Foundation under contract No. ZR2016DB22; the Foundation of Key Laboratory of Integrated Monitoring and Applied Technologies for Marine Harmful Algal Blooms, SOA under contract No. MATHAB201806; the Creative Team Project of the Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology under contract No. LMEES-CTSP-2018-3.

\*Corresponding author, E-mail: [wangzl@fio.org.cn](mailto:wangzl@fio.org.cn)

green macroalgae play an important role in the formation of green tides (Hoffmann and Santelices, 1991). They are highly capable of adapting to harsh environmental conditions and act as “seed sources” of green tides in nature (Zhang et al., 2010, 2011; Liu et al., 2012). Microscopic propagules can grow into macroalgal thalli and even form algae blooms under specific conditions (Lotze et al., 2001; Worm and Lotze, 2006). Green algae micro-propagules strongly affect the biomass of mature thalli, and at the same time, their distribution indicates the potential source of green tides (Song et al., 2015a).

In case of the large-scale green tides in the Yellow Sea, the seed source has been suggested to be the micro-propagules found in both pelagic waters and sediments in the coastal areas of the Subei Shoal that are occurring throughout the year. The distribution pattern of the micro-propagules indicates that the bloom was caused by fouling green macroalgae *Pyropia* aquaculture rafts in the Subei Shoal (Song et al., 2015a, b, 2018). However, in the Bohai Sea, the source of the massive green tides remains unknown. Thus, identifying the distribution pattern of green algae micro-propagules would be conducive to determine the source of green tides. The objectives of this study are (1) to investigate the temporal and spatial distribution patterns as well as biomass variations of the micro-propagules of green algae in the coastal areas of Qinhuangdao and (2) to investigate their role in the formation of the massive green tides in the Bohai Sea.

## 2 Materials and methods

### 2.1 Selection of sampling locations

Both inshore and offshore stations of the coastal areas of Qinhuangdao were selected as sampling sites in this study (Fig. 1). The other five inshore stations were located at the major bathing beaches along the Qinhuangdao coast. The Dongshan station was near the estuary of the Xinkai River, which was northeast of the areas that were affected by the green tide. The Jinmenghaiwan station is at the Jinmenghaiwan bathing beach, which

was the worst area affected by green tides. Meanwhile, the Geziwo station is at the Geziwo bathing beach north of Jinshanzui, which is one of the affected areas of the Beidaihe Scenic Spot. The next station was the Laohushi station along the Laohushi Marine Park south of the Jinshanzui and was the only station that was not affected by the green tide. Finally, Zhongzhi station is at the Zhongzhi bathing beach, which is a key area of the Beidaihe seaside holiday resort.

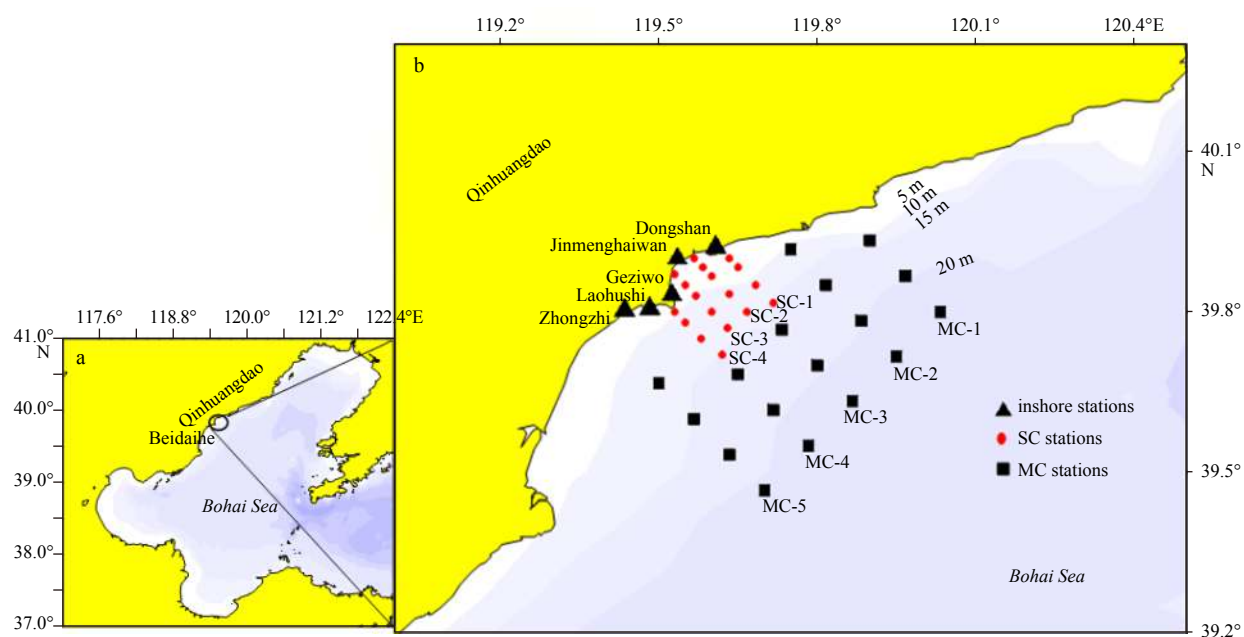
To obtain the temporal and spatial distribution patterns of the offshore micro-propagules, 36 offshore stations were established with different distances from the shore (Table 1). A total of small cruise (SC) transects composed of 18 SC stations were selected near the areas affected by the green tide. While in the offshore waters within the Bohai Sea, five major cruise (MC) transects composed of 18 MC stations were selected.

### 2.2 Sample collection and field measurements

In this study, seawater samples were collected monthly in the five inshore stations from April to September in 2016, and January in 2017 (Table 1). Both temperature and salinity were determined *in situ* with a portable Multi-parameter Instrument (YSI 556, YSI Inc., Ohio, US). Seven small survey cruises (SCs) and four major cruises (MCs) were conducted to determine the temporal and spatial distribution patterns of the green algal micro-propagules in the offshore area. During the 11 cruises, surface seawater samples were collected with a water sampler (HQM-1, Juchuang Inc., Qingdao, CHN) at each station and were filtered through a 200- $\mu$ m mesh net to remove the majority of the zooplankton. Water samples were transported in coolers (4–6°C) and arrived at the laboratory within 72 h after collection.

### 2.3 Cultivation and quantification of green algae micro-propagules

A total of 1 L of each water sample was poured into a glass beaker and 20 mL polyethersulfone (PES) culture medium (Provassoli, 1963; modified by Bold and Wynne, 1978) was added to



**Fig. 1.** The bloom area of the green tide in the coastal area of Qinhuangdao, Bohai Sea, China (a); and the sampling stations (b). ▲ represents inshore stations, ● small cruise (SC) stations selected along the coastline of Qinhuangdao, and ■ major cruise (MC) stations selected in the offshore waters of the Bohai Sea.

**Table 1.** Information of inshore, small cruise (SC) and major cruise (MC) stations

Stations	North latitude	East longitude	Sampling dates
Dongshan	39°54'52.95"	119°37'13.95"	Apr. 24, May 26, Jun. 22, Jul. 23, Aug. 26,
Jinmenghaiwan	39°53'42.93"	119°32'34.49"	Sep. 24, 2016; Jan. 25, 2017
Geziwo	39°49'53.89"	119°31'31.88"	
Laohushi	39°48'44.41"	119°29'21.95"	
Zhongzhi	39°48'22.15"	119°27'10.41"	
SC-1-A	39°54'	119°38'	SCI: Apr. 26, 2016
SC-1-B	39°53'	119°39'	
SC-1-C	39°51'	119°41'	SCII: May 24, 2016
SC-1-D	39°49'	119°43'	
SC-2-A	39°54'	119°34'	SCIII: Jun. 25, 2016
SC-2-B	39°53'	119°35'	
SC-2-C	39°52'	119°36'	SCIV: Jul. 24, 2016
SC-2-D	39°50'	119°38'	
SC-2-E	39°48'	119°40'	SCV: Aug. 25, 2016
SC-3-A	39°52'	119°32'	
SC-3-B	39°51'	119°33'	SCVI: Sep. 25, 2016
SC-3-C	39°50'	119°34'	
SC-3-D	39°48'	119°36'	SCVII: Jan. 26, 2017
SC-3-E	39°46'	119°38'	
SC-4-A	39°48'	119°32'	
SC-4-B	39°47'	119°33'	
SC-4-C	39°45'	119°35'	
SC-4-D	39°43'	119°37'	
MC-1-A	39°56'	119°54'	MCI: May 27–28, 2016
MC-1-B	39°52'	119°58'	
MC-1-C	39°48'	120°02'	
MC-2-A	39°55'	119°45'	MCII: Jun. 23–24, 2016
MC-2-B	39°51'	119°49'	
MC-2-C	39°47'	119°53'	
MC-2-D	39°43'	119°57'	MCIII: Jul. 25–26, 2016
MC-3-A	39°46'	119°44'	
MC-3-B	39°42'	119°48'	
MC-3-C	39°38'	119°52'	MCIV: Aug. 26–27, 2016
MC-4-A	39°41'	119°39'	
MC-4-B	39°37'	119°43'	
MC-4-C	39°33'	119°47'	
MC-5-A	39°40'	119°30'	
MC-5-B	39°36'	119°34'	
MC-5-C	39°32'	119°38'	
MC-5-D	39°28'	119°42'	

maintain high nutrient conditions. Subsequently, 1 mL of saturated GeO<sub>2</sub> was added to the mixture to inhibit the growth of benthic diatoms. The beakers were placed in an artificial climate chamber (202728-380, Jiangnan, Inc., Ningbo, China) at 20°C with a light supply of 100 μmol photons m<sup>-2</sup> s<sup>-1</sup> and a 12 h:12 h light-dark cycle light regime. The media was replenished every five days to maintain a high nutrient level. After about 10–15 d of culture, micro-propagules of the green algae started to attach to the wall and bottom of the beakers, then further developed into germlings and could be counted by the naked eye. The number of green algal germlings was assessed as the number of green algal micro-propagules (Song et al., 2015a, b).

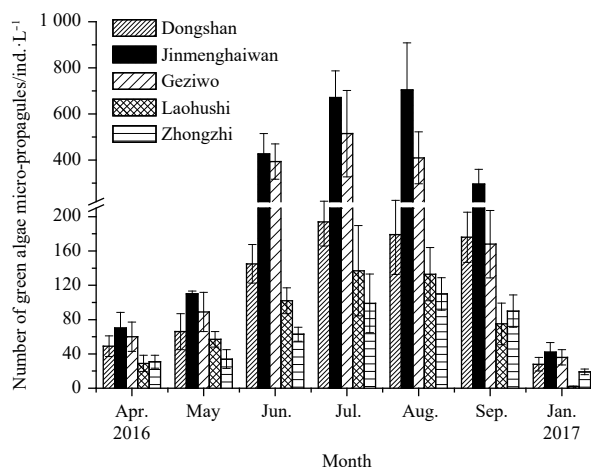
## 2.4 Statistics

Tests of homogeneity of variance were conducted, and the data were analyzed by one-way analysis of variance (ANOVA). The difference among means was analyzed with Duncan's new multiple range test followed by an ANOVA at a significance level of  $P < 0.05$ . Tests were performed in SPSS 17.0 (SPSS Inc., Chicago, USA).

## 3 Results

### 3.1 Variations in quantity of green algae micro-propagules in the inshore stations along the coastline of Qinhuangdao

Micro-propagules of the green algae were widely distributed throughout all major beaches in Qinhuangdao City. Their bio-masses in each station changed significantly at different months and locations during the survey ( $F = 6.769$ ,  $P < 0.05$ ). Biomass was highest in July and August, and was lowest in January ( $F = 6.200$ ,  $P < 0.05$ ). Specifically, the highest propagule quantity was found in the Jinmenghaiwan station throughout the entire survey period and the stations that were affected by green tides, such as Jinmenghaiwan and Geziwo, showed remarkably higher micro-propagule abundance than the other stations ( $F = 7.621$ ,  $P < 0.05$ ) (Fig. 2).



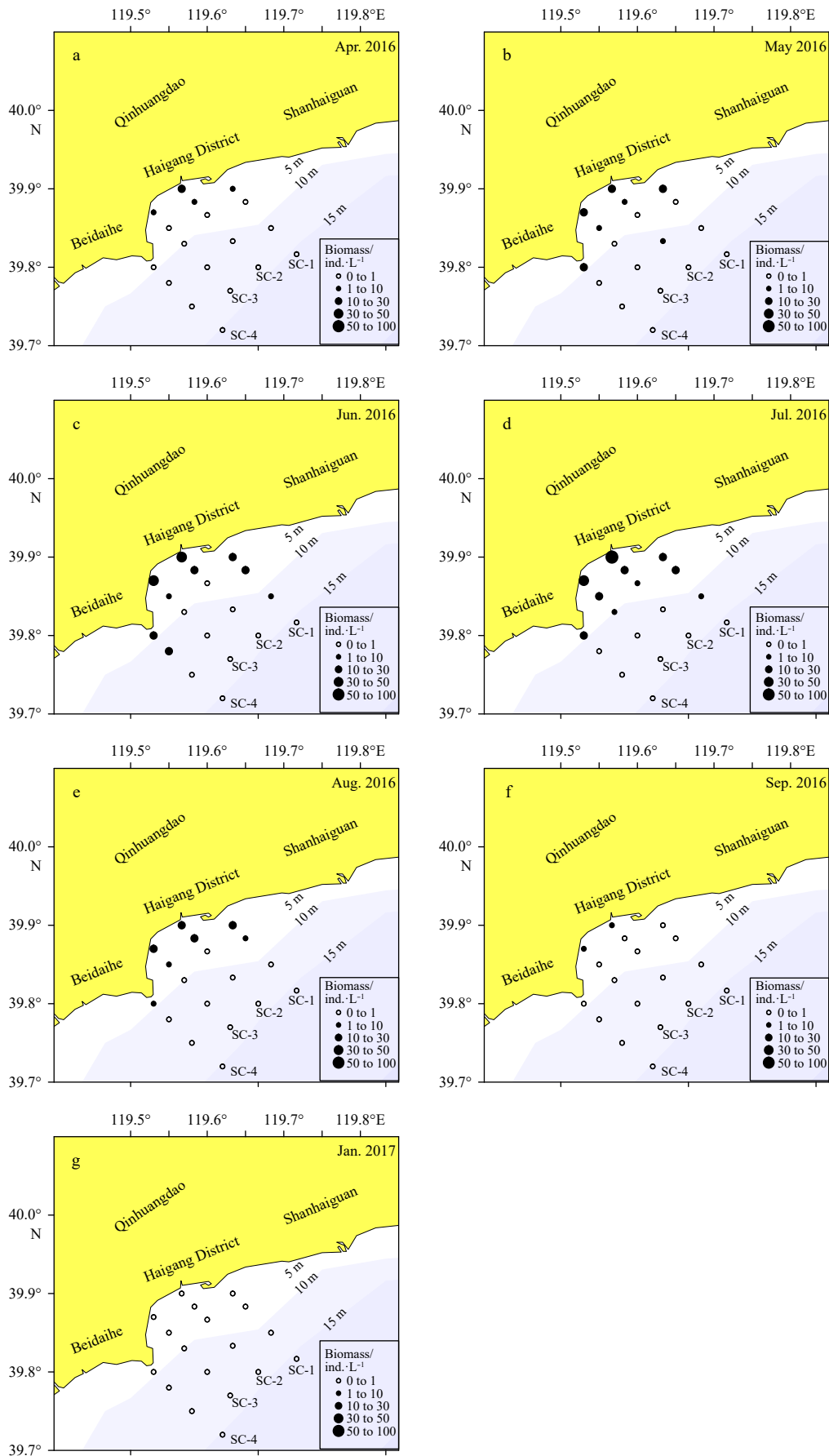
**Fig. 2.** Micro-propagule biomass in the inshore stations during the survey. Values are presented as means+SD ( $n=3$ ).

### 3.2 Tempo-spatial distribution of green algae micro-propagules in the offshore areas

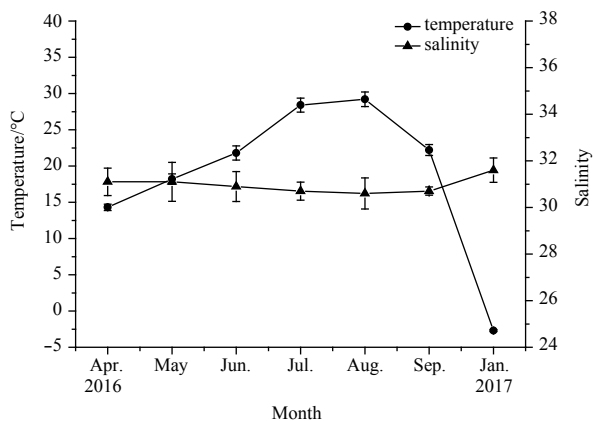
The tempo-spatial variation in the distribution of the micro-propagules of the green algae in the offshore stations is shown in Fig. 3. In the SC stations, green algal micro-propagules were mainly concentrated in areas closer to the shore ( $F = 5.814$ ,  $P < 0.05$ ), while no micro-propagules were observed in MC stations.

### 3.3 Changes in coastal temperature, salinity and correlation analysis

Seawater temperature showed significant seasonal variation in the inshore stations ( $F = 1.948$ ,  $P < 0.05$ ). However, variations in the average salinity were less evident during the survey period ( $P > 0.05$ ) (Fig. 4). Furthermore, correlation analysis showed a significant correlation between the biomass of the micro-propagules and the coastal temperature ( $P < 0.05$ ). However, the density of the micro-propagules was not significantly correlated with salinity ( $P > 0.05$ ).



**Fig. 3.** Tempo-spatial distribution patterns of green algae micro-propagules in SC stations.



**Fig. 4.** Line graph showing the mean salinity and temperature of the inshore stations during the survey. Values are presented as means+SD ( $n=5$ ).

#### 4 Discussion

Based on the known life-cycle of green macroalgae, the density of green algal micro-propagules mainly depends on the mature thalli (Huo et al., 2014). In addition, the motility of the micro-propagules is weak, leading to a higher concentration in the area of their original source. Thus, the distribution pattern of the micro-propagules in this study provided a good reflection of the biomass of the green macroalgae in the area, which were also the source of the green tides (Huo et al., 2016). In this study, the micro-propagule levels were highest in the inshore stations. The number of micro-propagules showed a significant decrease in density from inshore to offshore and they were not detected in the MC stations. This indicates that the original source of the micro-propagules were the mature thalli present in the inshore areas of the Qinhuangdao coastline. Furthermore, the micro-propagules that originated in the inshore areas could be transported to the outer rims through the oceanic current, and during this process, seawater would sharply dilute the dense population of the micro-propagules (Song et al., 2015a).

One of the functions of the green algae micro-propagules is their distribution could also reflect the location of the algae source of the green tide (Huo et al., 2016; Song et al., 2015a). Li et al. (2014) argued that the distribution of the micro-propagules could also be used as a reflection of the developmental stage in the establishment of green tides. In the case of the large-scale Yellow Sea green tides, areas with high micro-propagules density and areas with floating mature thalli were similar (Li et al., 2014; Wang et al., 2015). In contrast, in this study, high densities of micro-propagules were always detected at the inshore stations, especially in the green tide-affected Jinnenghaiwan and Geziwo stations. In addition, in the seven SCs and four MCs, horizontal and vertical trawling did not detect green macroalgal thalli (personal communication by Song et al.). This result indicates that unlike the remotely originating Yellow Sea green tides, the green tides in the coast of Qinhuangdao originated locally, with the algae source located near the areas that are affected by the green tide.

The abundance of green algal micro-propagules was mainly affected by the biomass of mature thalli at the area of their origin (Song et al., 2015a). The Jinnenghaiwan bathing beach was most severely affected by the green tides, which could well explain why during the algal bloom, this station detected significantly higher levels than other inshore stations. In addition, salinity, temperat-

ure, and nutrient level also affected the release of the green algal micro-propagules (Taylor et al., 2001; Agrawal, 2009).

Poor seawater quality (specifically eutrophication) has been indicated as the major cause of most green tides all over the world (Valiela et al., 1997; Raffaelli et al., 1998; Teichberg et al., 2010). Dissolved nutrients, and particularly dissolved inorganic nitrogen (DIN), are important factors driving the growth of marine macroalgae (Fong et al., 1996). High nutrient concentrations have been reported to promote the release of green algae micro-propagules (Li et al., 2009). The affected areas of the Bohai Sea were adjacent to the estuary of the Tanghe River, where eutrophication was very severe. These hypereutrophic conditions stimulated the rapid growth of macroalgae and the release of micro-propagules.

The variation in salinity in the inshore areas of Qinhuangdao was not large and was well within the suitable range for the growth of *Ulva prolifera*, which is the causative species of green tide (Taylor et al., 2001; Fan et al., 2015). Thus, no significant correlation was found between salinity and density of micro-propagules.

Statistical analysis further indicated that the biomass of micro-propagules was significantly correlated with sea temperature. Numerous studies confirmed temperature as the key factor influencing the release of micro-propagules in green algae in addition to changing in the biomass of mature thalli (Taylor et al., 2001; Agrawal, 2009; Liu et al., 2012; Song et al., 2015a). During the blooms from April and September, changes in sea temperature may affect both the biomass and the species composition of the mature thalli in the inshore areas and also influenced the release of micro-propagules. During winter, the low sea temperature inhibited the growth of green macroalgae and the release of micro-propagules (Agrawal, 2009), causing a significant decline in the number of micro-propagules.

The other function of the micro-propagules is to cope with harsh conditions and act as a survival stage and “seed” for the next bloom (Zhang et al., 2010; Song et al., 2015a). In favorable environmental conditions, the micro-propagules of green algae attach to suitable substrates and develop into a thalli, which now become the “algal source” for future blooms (Santelices et al., 1995; Lotze et al., 2001; Worm et al., 2001). Fang et al. (2012) reported that even after one year of low-temperature and dark treatments, about 20% of the green algal micro-propagules were still germinated and developed into mature thalli. Thus, we can conclude that a small part of *Ulva* microscopic propagules in the inshore areas could live through the winter and represented a large “seed bank”. When environmental conditions in terms of temperature, salinity, nutrient levels and the presence of suitable attached substrates became favorable for *Ulva* species, it resulted in the development of green tide in the coast of Qinhuangdao, Bohai Sea.

#### References

- Agrawal S C. 2009. Factors affecting spore germination in algae-*review*. *Folia Microbiologica*, 54: 273–302, doi: [10.1007/s12223-009-0047-0](https://doi.org/10.1007/s12223-009-0047-0)
- Bold H C, Wynne M J. 1978. *Introduction to the Algae: Structure and Reproduction*. Englewood Cliffs, NJ: Prentice Hall Press, 571–578
- Fan Shiliang, Fu Mingzhu, Wang Zongling, et al. 2015. Temporal variation of green macroalgal assemblage on *Porphyra* aquaculture rafts in the Subei shoal, China. *Estuarine, Coastal and Shelf Science*, 163: 23–28, doi: [10.1016/j.ecss.2015.03.016](https://doi.org/10.1016/j.ecss.2015.03.016)
- Fang Song, Wang Zongling, Li Yan, et al. 2012. The dynamics of micro-propagules before the Green tide (*Ulva prolifera*) outbreak

- in the southern Huanghai Sea and Changjiang (Yangtze) River Estuary area. *Haiyang Xuebao* (in Chinese), 34(4): 147–154
- Fong P, Boyer K E, Desmond J S, et al. 1996. Salinity stress, nitrogen competition, and facilitation: what controls seasonal succession of two opportunistic green macroalgae?. *Journal of Experimental Marine Biology and Ecology*, 206(1–2): 203–221, doi: [10.1016/S0022-0981\(96\)02630-5](https://doi.org/10.1016/S0022-0981(96)02630-5)
- Hoffmann A, Santelices B. 1991. Banks of algal microscopic forms: hypotheses on their functioning and comparisons with seed banks. *Marine Ecology Progress Series*, 79(1): 85–194
- Huo Yuanzi, Han Hongbin, Hua Liang, et al. 2016. Tracing the origin of green macroalgal blooms based on the large scale spatio-temporal distribution of *Ulva* microscopic propagules and settled mature *Ulva* vegetative thalli in coastal regions of the Yellow Sea, China. *Harmful Algae*, 59: 91–99, doi: [10.1016/j.hal.2016.09.005](https://doi.org/10.1016/j.hal.2016.09.005)
- Huo Yuanzi, Hua Liang, Wu Hailong, et al. 2014. Abundance and distribution of *Ulva* microscopic propagules associated with a green tide in the southern coast of the Yellow Sea. *Harmful Algae*, 39: 357–364, doi: [10.1016/j.hal.2014.09.008](https://doi.org/10.1016/j.hal.2014.09.008)
- Li Yan, Song Wei, Xiao Jie, et al. 2014. Tempo-spatial distribution and species diversity of green algae micro-propagules in the Yellow Sea during the large-scale green tide development. *Harmful Algae*, 39: 40–47, doi: [10.1016/j.hal.2014.05.013](https://doi.org/10.1016/j.hal.2014.05.013)
- Li Ruixiang, Wu Xiaowen, Wei Qinsheng, et al. 2009. Growth of *Enteromorpha Prolifera* under different nutrient conditions. *Advances in Marine Science* (in Chinese), 27: 21–216
- Liu Dongyan, Keesing J K, He Peimin, et al. 2013. The world's largest macroalgal bloom in the Yellow Sea, China: formation and implications. *Estuarine, Coastal and Shelf Science*, 129: 2–10, doi: [10.1016/j.ecss.2013.05.021](https://doi.org/10.1016/j.ecss.2013.05.021)
- Liu Feng, Pang Shaojun, Zhao Xiaobo, et al. 2012. Quantitative, molecular and growth analyses of *Ulva* microscopic propagules in the coastal sediment of Jiangsu province where green tides initially occurred. *Marine Environmental Research*, 74: 56–63, doi: [10.1016/j.marenvres.2011.12.004](https://doi.org/10.1016/j.marenvres.2011.12.004)
- Lotze H K, Worm B, Sommer U. 2001. Strong bottom-up and top-down control of early life stages of macroalgae. *Limnology and Oceanography*, 46(4): 749–757, doi: [10.4319/lo.2001.46.4.0749](https://doi.org/10.4319/lo.2001.46.4.0749)
- Nelson T A, Nelson A V, Tjoelker M. 2003. Seasonal patterns in ulvoid algal biomass, productivity, and key environmental factors in the northeast pacific. *Botanica Marina*, 46: 263–275
- Pang Shaojun, Liu Feng, Shan Tifeng, et al. 2010. Tracking the algal origin of the *Ulva* bloom in the Yellow Sea by a combination of molecular, morphological and physiological analyses. *Marine Environmental Research*, 69(4): 207–215, doi: [10.1016/j.marenvres.2009.10.007](https://doi.org/10.1016/j.marenvres.2009.10.007)
- Provasoli L. 1963. Growing marine seaweeds. In: *Proceedings of the 4th International Seaweed Symposium*. Oxford: Pergamon Press, 9–17
- Raffaelli D G, Raven J A, Poole L J. 1998. Ecological impact of green macroalgal blooms. *Oceanography and Marine Biology*, 125: 37–97
- Santelices B, Hoffmann A J, Aedo D, et al. 1995. A bank of microscopic forms on disturbed boulders and stones in tide pools. *Marine Ecology Progress Series*, 129: 215–228, doi: [10.3354/meps129215](https://doi.org/10.3354/meps129215)
- Song Wei, Jiang Meijie, Wang Zongling, et al. 2018. Source of propagules of the fouling green macroalgae in the Subei Shoal, China. *Acta Oceanologica Sinica*, 37: 102–108
- Song Wei, Li Yan, Fang Song, et al. 2015a. Temporal and spatial distributions of green algae micro-propagules in the coastal waters of the Subei Shoal, China. *Estuarine, Coastal and Shelf Science*, 163: 29–35, doi: [10.1016/j.ecss.2014.08.006](https://doi.org/10.1016/j.ecss.2014.08.006)
- Song Wei, Peng Keqin, Xiao Jie, et al. 2015b. Effects of temperature on the germination of green algae micro-propagules in coastal waters of the Subei Shoal, China. *Estuarine, Coastal and Shelf Science*, 163: 63–68, doi: [10.1016/j.ecss.2014.08.007](https://doi.org/10.1016/j.ecss.2014.08.007)
- Taylor R, Fletcher R L, Raven J A. 2001. Preliminary studies on the growth of selected 'green tide' algae in laboratory culture: effects of irradiance, temperature, salinity and nutrients on growth rate. *Botanica Marina*, 44(4): 327–336
- Teichberg M, Fox S E, Olsen Y S, et al. 2010. Eutrophication and macroalgal blooms in temperate and tropical coastal waters: nutrient enrichment experiments with *Ulva* spp. *Global Change Biology*, 16(9): 2624–2637
- Valiela I, McClelland J, Hauxwell J, et al. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography*, 42: 1105–1118, doi: [10.4319/lo.1997.42.5\\_part\\_2.1105](https://doi.org/10.4319/lo.1997.42.5_part_2.1105)
- Wang Zongling, Xiao Jie, Fan Shiliang, et al. 2015. Who made the world's largest green tide in China?—an integrated study on the initiation and early development of the green tide in Yellow sea. *Limnology and Oceanography*, 60(4): 1105–1117, doi: [10.1002/lno.10083](https://doi.org/10.1002/lno.10083)
- Worm B, Lotze H K. 2006. Effects of eutrophication, grazing, and algal blooms on rocky shores. *Limnology and Oceanography*, 51: 569–579, doi: [10.4319/lo.2006.51.1\\_part\\_2.0569](https://doi.org/10.4319/lo.2006.51.1_part_2.0569)
- Worm B, Lotze H K, Sommer U. 2001. Algal propagule banks modify competition, consumer and resource control on baltic rocky shores. *Oecologia*, 128(2): 281–293, doi: [10.1007/s004420100648](https://doi.org/10.1007/s004420100648)
- Zhang Xiaowen, Wang Hongxia, Mao Yuze, et al. 2010. Somatic cells serve as a potential propagule bank of *Enteromorpha prolifera* forming a green tide in the Yellow Sea, China. *Journal of Applied Phycology*, 22(2): 173–180, doi: [10.1007/s10811-009-9437-6](https://doi.org/10.1007/s10811-009-9437-6)
- Zhang Xiaowen, Xu Dong, Mao Yuze, et al. 2011. Settlement of vegetative fragments of *Ulva prolifera* confirmed as an important seed source for succession of a large-scale green tide bloom. *Limnology and Oceanography*, 56(1): 233–242, doi: [10.4319/lo.2011.56.1.0233](https://doi.org/10.4319/lo.2011.56.1.0233)