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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

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ABSTRACT

From 2008 to 2016, massive floating green macroalgal blooms occurred annually during the summer months in the Yellow Sea. The original source of these blooms was traced based on the spatio-temporal distribution and species composition of *Ulva* microscopic propagules and settled *Ulva* vegetative thalli monthly from December 2012 to May 2013 in the Yellow Sea. High quantities of *Ulva* microscopic propagules in both the water column and sediments were found in the *Pyropia* aquaculture area along the Jiangsu coast before a green macroalgal bloom appeared in the Yellow Sea. The abundance of *Ulva* microscopic propagules was significantly lower in outer areas compared to in *Pyropia* aquaculture areas. A molecular phylogenetic analysis suggested that *Ulva prolifera* microscopic propagules were the dominant microscopic propagules present during the study period. The extremely low biomass of settled *Ulva* vegetative thalli along the coast indicated that somatic cells of settled *Ulva* vegetative thalli did not provide a propagule bank for the green macroalgal blooms in the Yellow Sea. The results of this study provide further supporting evidence that the floating green macroalgal blooms originate from green macroalgae attached to *Pyropia* aquaculture rafts along the Jiangsu coastline of the southern Yellow Sea.

1. Introduction

Over the past four decades, green macroalgal blooms, referred to as green tides, have been occurring with an increasing frequency in coastal areas worldwide. The blooms form due to excessive growth of some green macroalgal species, caused mainly by eutrophication in the intertidal zone (Hernández et al., 1997; Valiela et al., 1997; Raffaelli et al., 1998), and they negatively affect the ecology and economy of coastal environments (Fletcher, 1996; Morand and Merceron, 2005; Hiraoka et al., 2011). The world's largest green macroalgal bloom event, which was caused mainly by *Ulva prolifera* O. F. Müller (Chlorophyta, Ulvophyceae), occurred during the summer of 2008 along the coast of the southern Yellow Sea in China, and it had a serious impact on the Olympic sailing events that year. Xu et al. (2009) attributed the source of the 2008 *U. prolifera* bloom to the Yangtze River and the eutrophic condition of the Yellow Sea (Leliaert et al., 2009), which is influenced by outflows from the Yangtze River. Since 2008, green macroalgal blooms have been an annual summer event in the southern Yellow Sea (Liu et al., 2009, 2013a).

The green macroalgal blooms in the Yellow Sea are unique compared to green macroalgal blooms observed in other locations (Kamer et al., 2001; Phillips, 2006; Charlier et al., 2007; Yabe et al., 2009). Numerous hypotheses have been proposed to explain the origin of the green macroalgal blooms that occur during the summer months in the Yellow Sea. Based on a series of satellite images, some researchers postulated that these blooms originate

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from the coast of Jiangsu Province in the southern Yellow Sea (Liu et al., 2009; Hu et al., 2010; Keesing et al., 2011; Zhang et al., 2014). Several studies suggested that the huge biomass of *Ulva* species attached to the large scale *Pyropia* aquaculture rafts (covering >20,000 ha) provides the original biomass for the blooms (Liu et al., 2010; Zhang et al., 2014; Huo et al., 2015; Wang et al., 2015). Pang et al. (2010) postulated that the effluent from coastal crab and shrimp aquaculture ponds supplied *U. prolifera* thalli and germlings to the Yellow Sea, and Zhang et al. (2011) reported that the somatic cells present in marine sediments could provide a propagule bank for the *U. prolifera* blooms in the Yellow Sea.

Although it is now widely accepted that the green macroalgal blooms in the Yellow Sea arise from *Ulva* fouling the rafts used for *Pyropia* aquaculture along the coast of Jiangsu Province, little is known about the importance of the *Ulva* microscopic propagule stage. The microscopic propagules, including gametes, spores and juvenile thalli attached to small particles, and macroscopic vegetative fragments are part of the life history of opportunistic macroalgae (Worm and Lotze, 2006; Song et al., 2015a). Microscopic propagules can develop into macroalgal blades or even form algal blooms when environmental conditions are favorable (Lotze et al., 2001; Worm and Lotze, 2006). Studies have linked a high quantity of *Ulva* microscopic propagules to a relatively high biomass of mature *Ulva* species (Huo et al., 2014; Song et al., 2015a). Thus, the original source of green macroalgal blooms in the Yellow Sea can be traced based on the spatio-temporal distribution of *Ulva* microscopic propagules and mature *Ulva* species prior to green macroalgal blooms occurring.

Previous researchers developed models to evaluate the impact of *Ulva* microscopic propagules on the productivity of adult macroalgae in massive green macroalgal blooms (Martins et al., 2007; Martins et al., 2008). Liu et al. (2012) suggested that *Ulva* microscopic propagules turn directly into floating biomass when temperature, irradiance and nutrients together meet the required levels. Zhang et al. (2015) inferred that microscopic propagules of *U. prolifera* contributed significantly to the dramatic increase of attached *U. prolifera* on *Pyropia* rafts, and the germination of *U. prolifera* microscopic propagules on *Pyropia* rafts promoted the proliferation of attached *U. prolifera* on the rafts, which release more microscopic propagules into seawater and sediments after they became mature. However, it remains uncertain whether *Ulva* microscopic propagules can directly develop into mature *Ulva* vegetative thalli by attaching to sand particles and subsequently accumulate into large-scale floating green macroalgal mats.

Several researchers previously described the distribution and species composition of *Ulva* microscopic propagules in the Yellow Sea. Huo et al. (2014) reported the abundance and distribution of *Ulva* microscopic propagules during a green tide that occurred from April to August 2012, and Li et al. (2014) conducted eight cruises to identify the distribution and species diversity of *Ulva* microscopic propagules from late April to early June 2012. Song et al. (2015a) investigated small scale distributions of *Ulva* microscopic propagules in the coastal waters of Subei Shoal monthly from 2010 to 2011. However, sufficient and convincing evidence for the origin of green macroalgal blooms based on the large scale distributions and species compositions of *Ulva* microscopic propagules is still scarce. Furthermore, little is known about whether the settled mature *Ulva* vegetative thalli in coastal regions of the southern Yellow Sea can provide a propagule bank for the green macroalgal blooms.

In the present study, six cruises were conducted monthly from December 2012 to May 2013 to investigate the spatio-temporal distribution and species composition of *Ulva* microscopic propagules and settled mature *Ulva* vegetative thalli in both seawater and sediments simultaneously prior to the occurrence of a green macroalgal bloom in the southern Yellow Sea. The aims of this study were to trace the original source of green macroalgal blooms in the Yellow Sea and to evaluate the contribution of *Ulva* microscopic propagules to these blooms.

2. Materials and methods

2.1. Study area and survey methods

The coastline of Jiangsu Province (30°44′–35°4′N) is suitable for *Pyropia* aquaculture, which is cultivated from October to April. The aquaculture rafts are set up in September and removed the following May (Fig. 1A and B). Large scale investigations were conducted monthly from December 2012 to May 2013 in this

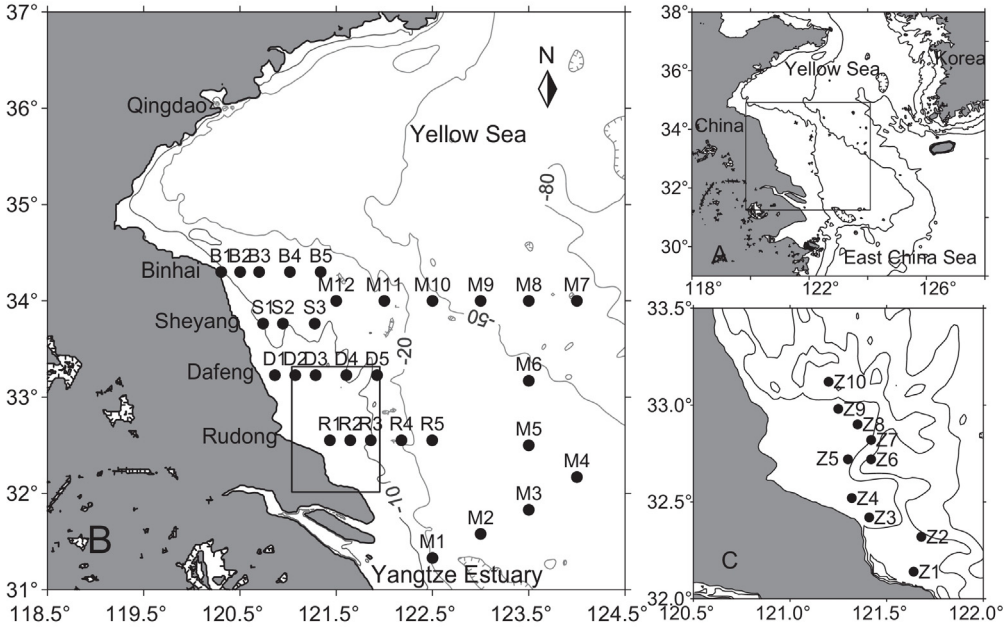

Fig. 1. (A) The square indicates the study area in the southern Yellow Sea during the period from December 2012 to May 2013. (B) Sampling transects and sites along the coast, with the *Pyropia* aquaculture area indicated by the square. (C) Sampling sites in the *Pyropia* aquaculture area. The numbers on the contour map indicate isobaths.