

Macroalgae Blooms and their Effects on Seagrass Ecosystems

HAN Qiuying^{*}, and LIU Dongyan

Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, CAS, Shandong Provincial Key Laboratory of Coastal Zone Environmental Processes, CAS Experimental Station of Integrated Coastal Environment in Muping, Yantai Institute of Coastal Zone Research (YIC), Chinese Academy of Sciences, Yantai 264003, P. R. China

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Abstract Seagrass decline caused by the macroalgae blooms is becoming a common phenomenon throughout temperate and tropical regions. We summarized the incidence of macroalgae blooms throughout the world and their impact on seagrass beds by direct and indirect ways. The competition for living space and using resources is the most direct effect on seagrass beds when macroalgae are blooming in an aquatic ecosystem. The consequence of macroalgae blooms (e.g., light reduction, hypoxia, and decomposition) can produce significant indirect effects on seagrass beds. Light reduction by the macroalgae can decrease the growth and recruitment of seagrasses, and decomposition of macroalgae mats can increase the anoxic and eutrophic conditions, which can further constrict the seagrass growth. Meanwhile, the presence of seagrass shoots can provide substrate for the macroalgae blooms. Controlling nutrient sources from the land to coastal waters is a general efficient way for coastal management. Researching into the synergistic effect of climate change and anthropogenic nutrient loads on the interaction between seagrasses and macroalgae can provide valuable information to decrease the negative effects of macroalgae blooms on seagrasses in eutrophic areas.

Key words eutrophication; decline; seagrasses; macroalgae blooms

1 Introduction

Seagrass beds have been widely recognized as highly important coastal systems that provide valuable ecosystem services in trapping and storing nutrients and being food resource for animals (Orth *et al.*, 2006). Recently, their vast carbon sink capacity has been quantified (Duarte *et al.*, 2010). Seagrass beds worldwide can provide 19004 \$ha⁻¹ at least annually (Costanza *et al.*, 1997). Seagrass decline has been reported in recent years over the world (Orth *et al.*, 2006; Waycott *et al.*, 2009). The environmental effects of excess nutrients are one of causes of seagrass losses (Orth *et al.*, 2006; Burkholder *et al.*, 2007). Nutrient can have different effects on seagrasses based on background concentration of nutrients and seagrass species. In oligotrophic environments, nutrient enrichment can facilitate seagrass growth and biomass (Short, 1983; Alcoverro *et al.*, 1997; Peralta *et al.*, 2003; Invers *et al.*, 2004) or has no effects on seagrasses (Harlin and Thorne-Miller, 1981; Murray *et al.*, 1992; Pederson and Borum, 1993; Pedersen, 1995; Lee and Dunton, 1997). Nutrient enrichment can negatively directly or indirectly impact on seagrasses in eutrophic waters (van Katwijk *et al.*, 2010; Christianen *et al.*, 2012). Nutrients such as nitrate and ammonia can directly impact *Zostera*

marina by toxicity, resulting in decreased rhizome biomass, shoot biomass and density (Burkholder *et al.*, 1992; Short *et al.*, 1995; van Katwijk *et al.*, 2010; Christianen *et al.*, 2012). In eutrophic coastal areas, proliferation of phytoplankton, epiphytic microalgae and fast-growing drifting macroalgae usually occur, promoting light reduction, increasing the sediment organic matter load, which could induce the risk of anoxia and sulfide intrusion into meristematic areas of seagrasses (Pregnall *et al.*, 1984; Holmer and Bondgaard, 2001; Greve *et al.*, 2003), therefore restricting seagrasses growth (Twilley *et al.*, 1985; Nelson and Lee, 2001).

Excessive growth of fastgrowing macroalgae has appeared in many coastal areas (Table 1). Macroalgae blooms are controlled by physical, chemical, and biological factors (Brush and Nixon, 2010). Generally, at sheltered locations where light is not limiting, nutrients control net primary production of macroalgae in most coastal systems and macroalgal biomass is therefore usually correlated to nutrient inputs (McGlathery *et al.*, 2001). Worldwide, seagrasses experience negative effects from macroalgae blooms (Table 2), often leading to the decline of the seagrass beds. The succession from seagrasses to macroalgae can cause profound ecological changes, altering total system primary productivity, biogeochemical cycling and species composition (McGlathery, 2001). More specifically, sediments may become less stable, waters turn more turbid and nutrient turnover will increase and primary productivity, biomass as well as

^{*} Corresponding author. Tel: 0086-535-2109112
E-mail: qyhan@yic.ac.cn

nursery functions will become more fluctuating (McGlathery *et al.*, 2001, 2007; Nelson, 2009). In a recent review, Thomsen *et al.*, (2012) found that mass macroalgae have stronger affect on seagrasses than a small quantity of macroalgae, 'rooted' macroalgae has less effect than floating macroalgae, and bigger species of seagrass are more resistant than smaller species to macroalgae blooms. The negative effects of macroalgae blooms depend on the environmental variables in the region, impacting on the management of seagrass ecosystems sub-

ject to high nutrient loadings (Hessing-Lewis *et al.*, 2011). Therefore, it is necessary to study the effect of macroalgae blooms on seagrass ecosystem to further understand the causes and mechanisms of seagrass decline. Our objective is to review the reported effects of macroalgae blooms on seagrass health and discuss the mechanisms leading to these effects. In addition, we discuss the effective measure to reduce the negative effects of macroalgae blooms on seagrass ecosystems and provide further research directions in the future.

Table 1 List of macroalgae blooms recorded in literatures

| Species | Location | Reference |
|--|----------------------------------|--------------------------------|
| <i>Caulerpa</i> sp. | Mediterranean coasts | Meinesz <i>et al.</i> , 1993 |
| <i>Cladophora</i> sp. | Great Lakes, USA | Auer, 1982 |
| <i>Cladophora</i> sp. | Nahant Bay, USA | Pregnall <i>et al.</i> , 1988 |
| <i>Cladophora</i> sp. | Bermuda, USA | Lapointe and O'Connell, 1989 |
| <i>Cladophora</i> sp. | West Maui, Hawaii, USA | Smith <i>et al.</i> , 2005 |
| <i>Cladophora</i> sp. | Neva Estuary, Finland | Berezina <i>et al.</i> , 2007 |
| <i>Codium</i> sp. | Southeast Florida, USA | Lapointe <i>et al.</i> , 2005 |
| <i>Enteromorpha</i> sp. | Coos Bay, USA | Pregnall and Rudy, 1985 |
| <i>Enteromorpha</i> sp. | Ythan Estuary, Scotland | Raffaelli, 2000 |
| <i>Enteromorpha</i> sp. | North Atlantic coasts | Schories <i>et al.</i> , 2000 |
| <i>Enteromorpha</i> sp. | Mondego Estuary, Portugal | Martins <i>et al.</i> , 2001 |
| <i>Enteromorpha radiata</i> | Hayling Island, Hampshire, UK | den Hartog, 1994 |
| <i>Halimeda incrassata</i> | Florida, USA | Davis and Fourqurean, 2001 |
| <i>Ulva</i> sp. | Branford River, USA | Walsh, 1980 |
| <i>Ulva</i> sp. | Venice Lagoon, Italy | Sfriso <i>et al.</i> , 1992 |
| <i>Ulva</i> sp. | Philippines | Largo <i>et al.</i> , 2004 |
| <i>Ulva</i> sp. | Brittany, France | Merceron <i>et al.</i> , 2007 |
| <i>Ulva</i> sp. | Japan coast | Sugimoto <i>et al.</i> , 2007 |
| <i>Ulva</i> sp. | Yatsu, Japan | Yabe <i>et al.</i> , 2009 |
| <i>Ulva</i> sp. | Prince Edward Island, Canada | Schmidt <i>et al.</i> , 2012 |
| <i>Chaetomorpha</i> sp., <i>Cladophora</i> sp. | Kertinge Nor, Denmark | Hansen and Kristensen, 1997 |
| <i>Cladophora</i> sp., <i>Enteromorpha</i> sp. | Baltic Sea, Germany | Baden <i>et al.</i> , 1990 |
| <i>Cladophora</i> sp., <i>Enteromorpha</i> sp. | NW Black Sea | Zaitsev <i>et al.</i> , 1992 |
| <i>Cladophora</i> sp., <i>Gracilaria</i> sp. | Waquoit Bay, USA | Peckol <i>et al.</i> , 1994 |
| <i>Enteromorpha</i> sp., <i>Ulva</i> sp. | Southern California Estuary, USA | Kamer <i>et al.</i> , 2001 |
| <i>Chaetomorpha</i> sp., <i>Cladophora</i> sp., <i>Ulva</i> sp. | Orebetello lagoon, Italy | Lenzi <i>et al.</i> , 2003 |
| <i>Cladophora</i> sp., <i>Enteromorpha</i> sp., <i>Ulva</i> sp. | Peel-Harvey Estuary, Australia | Lavery and McComb, 1991 |
| <i>Enteromorpha</i> sp., <i>Chaetomorpha linum</i> , <i>Ulva lactuca</i> | Ythan Estuary, UK | Raffaelli <i>et al.</i> , 1998 |
| — | Great Barrier Reef, Australia | Bell, 1992 |
| Green algae | German Wadden Sea | Reise and Siebert, 1994 |
| Green algae | Damariscotta Estuary, USA | Thiel and Watling, 1998 |
| Green algae | New England | Thiel and Watling, 1998 |
| Green algae | Qingdao coast, China | Liu <i>et al.</i> , 2009 |

2 Mechanisms Underlying the Negative Effect of Macroalgae Blooms on Seagrasses

2.1 Direct Effect of Macroalgae Blooms on Seagrasses

The direct effects of macroalgae on seagrass ecosystems include the competition for space or resources (Druehl, 1973; Williams, 1990; Fourqurean *et al.*, 1995; Ceccherilli and Cinelli, 1997). Competition between seagrasses may have more effects than competition between seagrass and other species at high densities of seagrass (Rose and Dawes, 1999). Multer (1988) found that high biomass of macroalgae appears under the conditions of

low and moderate seagrass shoot density, indirectly demonstrating the competitive relationship between seagrasses and macroalgae. When nutrient availability is low, competitive dominance of seagrasses over rhizophytic macroalgae occurs (Fourqurean *et al.*, 1995), and rhizophytic macroalgae could even accelerate seagrass beds in their early successional stage, while in the later stage of bed development, the density of macroalgae declines as the seagrass bed is rebuilt, indicating the acceleration and competition for space between seagrasses and macroalgae (Williams, 1990). Davis and Fourqurean (2001) also demonstrated that under the condition of macroalgae removal, the ratio between C and N in leaf tissue of seagrass is significantly lower, suggesting competition mechanism for N between two species.

Table 2 Overview of effects of macroalgal blooms on seagrass

| Seagrass Species examined | Location | Macroalgae bloom species | Parameters | Comments on efficacy | Reference |
|---|--|---|--|---|------------------------------------|
| <i>Thalassia testudinum</i> | John Pennekamp Coral Reef State Park, Florida, USA | <i>Halimeda incrustata</i> | Growth rate and C/N of seagrass | Macroalgae impact on seagrasses less than seagrasses on macroalgae. | Davis and Fourqurean, 2001 |
| <i>Thalassia testudinum</i> | Biscayne Bay, Florida, USA | Drift algae and epiphyte | Above-ground biomass, below-ground biomass, shoot density | Moderate macroalgae mats may have negative effects on seagrasses. | Irlandi <i>et al.</i> , 2004 |
| <i>Thalassia testudinum</i> | Port Aransas, Texas, USA | Drift macroalgae | Leaf chlorophyll, sediment sulfide | Seagrasses can regrow after macroalgae were removed. | Lamote and Dunton, 2006 |
| <i>Zostera</i> sp. | Hayling Island, Hampshire, UK | <i>Enteromorpha radiata</i> | Bed area, shoot density | Macroalgae can disturb the seagrasses and living seagrasses were not healthy. | den Hartog, 1994 |
| <i>Zostera marina</i> | Waquoit Bay, Massachusetts, USA | Drift macroalgae | Shoot density, recruitment, growth rate, aboveground net production | The new growing shoots of seagrasses were destroyed because of macroalgae mats. | Hauxwell <i>et al.</i> , 2001 |
| <i>Zostera marina</i> | Waquoit Bay, Massachusetts, USA | <i>Gracilaria</i> sp. | Recruiting shoots, growth rate, biomass, density | Seagrasses declined by macroalgae mats. | Hauxwell <i>et al.</i> , 2001 |
| <i>Zostera marina</i> | Blakely Island, USA | <i>Ulvaria obscura</i> | Shoot density | The macroalgae bloom can reduce the shoot density of seagrasses | Nelson and Lee, 2001 |
| <i>Zostera marina</i> | Waquoit Bay, Massachusetts, USA | Drift macroalgae | Growth rate, shoot densities, bed area | Macroalgae canopies can disturb the seagrass shoots. | Hauxwell <i>et al.</i> , 2003 |
| <i>Zostera marina</i> | Iwakuni, the Seto Inland Sea, Japan | <i>Ulva</i> sp. | Shoot density, seedling density, survival rate, growth rate | Macroalgae blooms decreased seagrass function. | Sugimoto <i>et al.</i> , 2007 |
| <i>Zostera marina</i> | Tomales Bay, California, USA | <i>Gracilariopsis</i> sp. | Shoot density, growth rate, biomass | Seagrass shoot density was decreased by macroalgae due to the light reduction. | Huntington and Boyer, 2008 |
| <i>Zostera marina</i> | Island of Fyn, Denmark | <i>Gracilaria vermiculophylla</i> | Shoot survival rate, leaf dark respiration and leaf net photosynthesis | Macroalgae reduced the seagrass survival. | Martínez-Lüscher and Holmer, 2010 |
| <i>Zostera marina</i> | Wadden Sea | <i>Ulva</i> sp., <i>Gracilaria</i> sp., <i>Chaetomorpha</i> sp. and <i>Enteromorpha</i> sp. | Seed | Macroalgae led to the death of generative shoots before the seeds were ripe. | van Katwijk <i>et al.</i> , 2010 |
| <i>Zostera marina</i> | Coos Bay, USA | <i>Ulva</i> sp. | Seagrass biomass, density and length | The additions of macroalgae did not impact on the seagrass in the marine area, but induced seagrass decline in the river areas. | Hessing-Lewis <i>et al.</i> , 2011 |
| <i>Zostera marina</i> | Prince Edward Island, Canada | <i>Ulva</i> sp. | Seagrass aboveground and belowground tissue N and C content, length, shoot density | Seagrass leaf length increased and shoot density declined. | Schmidt <i>et al.</i> , 2012 |
| <i>Halophila ovalis</i> , <i>Zostera capricorni</i> , <i>Ruppia megacarpa</i> | Tuggerah Lakes Estuary, New South Wales, Australia | <i>Enteromorpha intestinalis</i> | Seagrass biomass, components of the infauna | Macroalgae mats decreased benthos biodiversity. | Cummins <i>et al.</i> , 2004 |

2.2 Indirect Effects of Macroalgae Blooms on Seagrass: Light Reduction

Light availability is a vital environmental factor affecting seagrass and macroalgae growth. Light reduction by the macroalgae may reduce the growth and recruitment of seagrasses and further affect seagrass ecosystem health. The result of light reduction induced by macroalgae blooms decreases the growth depth of seagrasses (Krause-Jensen *et al.*, 2000; McGlathery, 2001). In highly eutrophic waters, macroalgae species can obtain the highest biomass of 0.5 kg m⁻² and 0.5 m canopy height (McGlathery, 2001). In Hiroshima Bay (Japan), floating *Ulva* canopy height can attain 20–30 cm (Sugimoto *et al.*, 2007). Under the conditions of *Cladophora vagabunda* and *Gracilaria tikvahiae* blooms, more than 95% of light

intensity is reduced from 6 to 8 cm cover (Krause-Jensen *et al.*, 2000). In 3–4 cm ulvoid canopies, over 90% of photosynthetic photon flux density is attenuated (Sugimoto *et al.*, 2007).

Light limitation may reduce photosynthetic activity of seagrasses. For example, light availability reduction because of macroalgae blooms leads to the shoot density decline of eelgrass in Hamblin Pond (Hauxwell *et al.*, 2001). The macroalgae blooms leading to light reduction for seagrasses are correlated to the duration of the macroalgal cover. Shoot growth does not increase over 10 days after the macroalgae are removed from the seagrass bed, and growth of *Thalassia testudinum* does not decrease over 10 days when macroalgae are present, suggesting that improving and declining light availability by drift algae does not affect the short-term growth of seagrasses

(Irlandi *et al.*, 2004). It may be because the shaded and unshaded shoots of seagrass can utilize the resources together. But in a long period, the macroalgae can significantly decrease the seagrass biomass. For example, under the conditions of 100% macroalgae canopy for 2–3 months, 25% above-ground biomass of seagrass is reduced (Irlandi *et al.*, 2004).

Carbon translocation and storage capacity between leaves, rhizomes and roots can control the ecological success of seagrasses under light reduction conditions (Lee and Dunton, 1996; Alcoverro *et al.*, 1999; Touchette and Burkholder, 2000; Brun *et al.*, 2002; Peralta *et al.*, 2002). Ammonium assimilation into amino acids and other nitrogen-organic compounds requires carbon skeletons and energy, which are from photosynthesis or mobilized from carbon-reserves in seagrasses (Brun *et al.*, 2008; Villazán *et al.*, 2013). Light reduction from macroalgal blooms may increase the toxicity of ammonium on seagrasses (Brun *et al.*, 2008; Villazán *et al.*, 2013).

2.3 Indirect Effects of Macroalgae Blooms on Seagrasses: Increasing Water-Column and Sediment Hypoxia

Macroalgae may release 39% of gross production of themselves after most of the remaining fixed carbon is released (Albert and Valiela, 1994). Decomposition of macroalgae mats may release enormous dissolved organic matter into environment, which may increase biological oxygen demand and lead to the anoxia in eutrophicated waters. Extended hypoxia conditions increase energy requirements of seagrass for photosynthesis and further constrict the seagrass growth. The anoxia condition caused by dense macroalgae mats may change sulfide and nutrient cycles (McGlathery *et al.*, 2007). High sulphide concentration resulting from the anoxia by macroalgal canopies in the seagrass beds can lead to sulphide intrusion into meristematic areas of seagrass, which decreases the maximum photosynthetic rate of seagrass and has an effect on leaf growth (Pedersen *et al.*, 2004). In addition, sulfide concentrations in the pore water rise when plant photosynthesis decreases the oxygen supply to the roots (Jørgensen, 1982). Sulfide accumulation in the sediments may further result in the decrease of the seagrass biomass or mortality (Koch *et al.*, 2007; van der Heide *et al.*, 2012).

Hypoxia and high sulphide may also decrease productivity of seagrasses by negatively affecting nutrient absorption (Pregnall *et al.*, 1984). Because of the ability to fast absorb nutrients, fast-growing macroalgae can regenerate the nutrient from ambient environment, which can result in the temporary retention of nutrients (McGlathery *et al.*, 1997). High respiration rates may cause a significant release of nutrients from both the sediments and decomposing algae (Sfriso *et al.*, 1987). Under higher releasing rates of nutrients, macroalgae absorbing nutrients from water displace plants uptaking nutrients from sediments. The macroalgae bloom can bring more anthropogenic inputs of nitrogen into seagrass ecosystems, such as

that from ammonia (Nelson, 2009). Higher ammonium concentration in ambient water has the deleterious effects on seagrasses (van der Heide *et al.*, 2008). For example, the ammonia levels ($>25 \mu\text{mol L}^{-1}$) may negatively impact on *Zostera marina* (van Katwijk *et al.*, 1997), and high ammonium concentration ($125 \mu\text{mol L}^{-1}$) can lead to the seagrass shoots reduction and seagrass death (Huntington and Boyer, 2008).

3 Other Effects

Because sediment is deposited on seagrass beds due to their ability to decrease current velocities and weaken wave energy (Gambi *et al.*, 1990), seagrass presence may actually enhance macroalgae growth on the soft sediments (Tweedley *et al.*, 2008). Macroalgae bloom can result in the sediment erosion, increasing the turbidity of water under the condition of weak wind and wave action (Canal-Vergés *et al.*, 2010). The turbidity and erosion may lead to the loss of eelgrass meadows by decreasing the light availability (van der Heide *et al.*, 2008) and increasing the risk of seagrass rhizome being uprooted by water (Duarte, 2002; Han *et al.*, 2012). In spring or summer, the degradation of huge amounts of macroalgae results in the break-down of the biological balance in the seagrass ecosystem. Macroalgae with fast nutrient turnover rate can faster decompose than seagrass, which invokes nutrient releasing into water and consequently increases the concentration of nutrient, therefore further supporting macroalgae growth (McGlathery *et al.*, 2001). All three effects above-mentioned will result in non-linear responses and favour macroalgae, thus accelerating the replacement of seagrasses by macroalgae. Thus, it is important to study the biomass thresholds of macroalgae that induces the seagrass beds decline for the seagrass ecosystem protection.

4 Future Needs and Management Implications

In the future, measures to decrease the negative effects of macroalgae blooms on seagrass ecosystems should be taken. Controlling nutrient sources from land to coastal waters is a general efficient way for management. Eutrophication is serious in many coastal areas due to agriculture, industry, aquaculture waste water. The occurrence of nutrients in excess is necessary for the macroalgae bloom (Hodgkin *et al.*, 1980). There are some reports that seagrass ecosystem restoration is successful after reducing the nutrient loading into coastal areas, in Orbetello lagoon (Italy) (Lenzi *et al.*, 2003), Mondego estuary (Portugal) (Cardoso *et al.*, 2005) and southwest Florida (USA) (Tomasko *et al.*, 2005).

Climate changes, such as increased temperature and sea level rise effects on seagrasses and macroalgae have been studied (Santos, 1993; Short and Neckles, 1999; Sousa-Dias and Melo, 2008). Higher temperature could facilitate certain macroalgal species growth, especially

species inducing blooms (Sousa-Dias and Melo, 2008). Increased temperature has different effects on different seagrass species (Marsh *et al.*, 1986). Warmer species increase photosynthesis and respiration with higher temperature, but temperate species reach their photosynthesis optimum below the highest seasonal temperature (Short and Neckles, 1999). Sea level rise may decrease the light level for seagrasses, therefore negatively impacting seagrass productivity and functional values (Short and Neckles, 1999; Hauxwell *et al.*, 2001; Irlandi *et al.*, 2004). Sea level rise may increase water flow or enhance tidal circulation, which could accelerate flushing of the macroalgae, and therefore reduce the negative effects of macroalgae bloom on seagrass ecosystems (Flindt *et al.*, 1997; Lenzi *et al.*, 2003). Sea level rise will draw in seawater into estuaries and rivers, resulting in salinity change, which in turn may alter competitive situation between seagrasses and macroalgae. Global climate change acceleration can be expected in the future. It is necessary to research into the synergistical effect of climate change and anthropogenic nutrient loads on the interaction between seagrasses and macroalgae in eutrophic areas, which can provide valuable information to decrease the negative effects of macroalgae bloom on seagrasses.

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