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Macroalgae Blooms and their Effects on Seagrass Ecosystems

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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 synergistical effect of climate change and anthropognic nutrient loads on the interaction between searsasses 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

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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 subject 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
Caulerpa sp.	Mediterranean coasts	Meinesz *et al*., 1993
Cladophora sp.	Great Lakes, USA	Auer, 1982
Cladophora sp.	Nahant Bay, USA	Pregnall *et al*., 1988
Cladophora sp.	Bermuda, USA	Lapointe and O'Connell, 1989
Cladophora sp.	West Maui, Hawaii, USA	Smith *et al*., 2005
Cladophora sp.	Neva Estuary, Finland	Berezina *et al*., 2007
Codium sp.	Southeast Florida, USA	Lapointe *et al*., 2005
Enteromorpha sp.	Coos Bay, USA	Pregnall and Rudy, 1985
Enteromorpha sp.	Ythan Estuary, Scotland	Raffaelli, 2000
Enteromorpha sp.	North Atlantic coasts	Schories *et al*., 2000
Enteromorpha sp.	Mondego Estuary, Portugal	Martins *et al*., 2001
Enteromorpha radiata	Hayling Island, Hamspshire, UK	den Hartog, 1994
Halimeda incrassata	Florida, USA	Davis and Fourqurean, 2001
Ulva sp.	Branford River, USA	Walsh, 1980
Ulva sp.	Venice Lagoon, Italy	Sfriso *et al*., 1992
Ulva sp.	Philippines	Largo *et al*., 2004
Ulva sp.	Brittany, France	Merceron *et al*., 2007
Ulva sp.	Japan coast	Sugimoto *et al*., 2007
Ulva sp.	Yatsu, Japan	Yabe *et al*., 2009
Ulva sp.	Prince Edward Island, Canada	Schmidt *et al*., 2012
Chaetomorpha sp., *Cladophora* sp.	Kertinge Nor, Denmark	Hansen and Kristensen, 1997
Cladophora sp., *Enteromorpha* sp.	Baltic Sea, Germany	Baden *et al*., 1990
Cladophora sp., *Enteromorpha* sp.	NW Black Sea	Zaitsev *et al*., 1992
Cladophora sp., *Gracilaria* sp.	Waquoit Bay, USA	Peckol *et al*., 1994
Enteromorpha sp., *Ulva* sp.	Southern California Estuary, USA	Kamer *et al*., 2001
Chaetomorpha sp., *Cladophora* sp., *Ulva* sp.	Orebetello lagoon, Italy	Lenzi *et al*., 2003
Cladophora sp., *Enteromorpha* sp., *Ulva* sp.	Peel-Harvey Estuary, Australia	Lavery and McComb, 1991
Enteromorpha sp., *Chaetomorpa linum*, *Ulva lactuca*	Ythan Estuary, UK	Raffaelli *et al*., 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 *et al*., 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; Ceccherlli 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
Thalassia testudinum	John Pennekamp Coral Reef State Park, Florida, USA	*Halimeda incrassata*	Growth rate and C/N of seagrass	Macroalgae impact on seagrasses less than seagrasses on macroalgae.	Davis and Fourqurean, 2001
Thalassia testudinum	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 *et al*., 2004
Thalassia testudinum	Port Aransas, Texas, USA	Drift macroalgae	Leaf chlorophyll, sediment sulfide	Seagrasses can regrow after macroalgae were removed.	Lamote and Dunton, 2006
Zostera sp.	Hayling Island, Hamspshire, UK	*Enteromorpha radiata*	Bed area, shoot density	Macroalgae can disturb the seagrasses and living seagrasses were not healthy.	den Hartog, 1994
Zostera marina	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 *et al*., 2001
Zostera marina	Waquoit Bay, Massachusetts, USA	*Gracilaria* sp.	Recruiting shoots, growth rate, biomass, density	Seagrasses declined by macroalgae mats.	Hauxwell *et al*., 2001
Zostera marina	Blakely Island, USA	*Ulvaria obscura*	Shoot density	The mcaroalgae bloom can reduce the shoot density of seagrasses	Nelson and Lee, 2001
Zostera marina	Waquoit Bay, Massachusetts, USA	Drift macroalgae	Growth rate, shoot densities, bed area	Macroalgae canopies can disturb the seagrass shoots.	Hauxwell *et al*., 2003
Zostera marina	Iwakuni, the Seto Inland Sea, Japan	*Ulva* sp.	Shoot density, seedling density, survival rate, growth rate	Macroalgae blooms decreased seagrass function.	Sugimoto *et al*., 2007
Zostera marina	Tomales Bay, California, USA	*Gracilariopsis* sp.	Shoot density, growth rate, biomass	Seagrass shoot density was decreased by macroalgae due to the light reduction.	Huntington and Boyer, 2008
Zostera marina	Island of Fyn, Denmark	*Gracilaria vermiculophylla*	Shoot survival rate, leaf dark respiration and leaf net photosynthesis	Macroalgae reduced the seagrass survival.	Martínez-Lüscher and Holmer, 2010
Zostera marina	Wadden Sea	*Ulva* sp., *Gracilaria* sp., *Chaetomorpha* sp. and *Enteromropha* sp.	Seed	Macroalge led to the death of generative shoots before the seeds were ripe.	van Katwijk *et al*., 2010
Zostera marina	Coos Bay, USA	*Ulva* 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 *et al*., 2011
Zostera marina	Prince Edward Island, Canada	*Ulva* sp.	Seagrass aboveground and belowground tissue N and C content, length, shoot density	Seagrass leaf length increased and shoot density declined.	Schmidt *et al*., 2012
Halophila ovalis, *Zostera capricorni*, *Ruppia megacarpa*	Tuggerah Lakes Estuary, New South Wales, Australia	*Enteromorpha intestinalis*	Seagrass biomass, components of the infauna	Macroalgae mats decreased benthos biodiversity.	Cummins *et al*., 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 nutrogen-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 macroalgl 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 macoralgae 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 (Jøgernsen, 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 μmol L^{-1}) may negatively impact on *Zostera marina* (van Katwijk *et al*., 1997), and high ammonium concentration (125 μmol 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 macoalgae growth on the soft sediments (Tweedley *et al*., 2008). Macroalgae bloom can result in the sediment erosion, increasing the turbidiy 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. Macralgae 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 searsasses and macroalgae in eutrophic areas, which can provide valuable information to decrease the negative effects of macroalgae bloom on seagrasses.

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