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Algal mats reduce eelgrass (*Zostera marina* L.) growth in mixed and monospecific meadows

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ABSTRACT

Harmful algal blooms are considered to be one of the biggest threats to benthic vegetation. The amount of annual algal mats has increased due to eutrophication but their effects on perennial vegetation have rarely been tested in field experiments. In regions where eelgrass (*Zostera marina*) grows in mixed meadows, plant species richness may ameliorate algal-induced stress through facilitative mechanisms and improve eelgrass growth and survival. To test this, we conducted a 3 mo. field experiment at 3.5 m depth in the Baltic Sea, where we applied filamentous brown algae (300 g ww) to eelgrass monocultures and polycultures (*Z. marina*, *Ruppia cirrhosa*, *Stuckenia pectinata* and *Potamogeton perfoliatus*). The algal stress period lasted for 13 d and plots were sampled after a 5 wk recovery period. In both algal-stressed mono- and polycultures, the presence of algal mats significantly reduced eelgrass shoot and root biomass production and affected the leaf growth negatively. Plant richness did not have strong effects on eelgrass growth and eelgrass in both algal-stressed mono- and polycultures showed significantly reduced productivity. Our results clearly demonstrate that loose-lying algal mats pose a serious threat to seagrass meadows and that plant diversity cannot alone ameliorate negative effects by macroalgal mats.

1. Introduction

Seagrasses are ecosystem engineers that modify the abiotic environment of shallow coastal areas and provide multiple important ecosystem services such as habitat provisioning, sediment stabilization, carbon and nutrient trapping, and primary and secondary production (Duffy, 2006; Hemminga and Duarte, 2000; Jones et al., 1997). At present, seagrass meadows are declining globally, and this loss is mainly caused by anthropogenic pressures such as nutrient pollution, overfishing, dredging and sedimentation (Boström et al., 2011; Orth et al., 2006). With increasing eutrophication, the water quality often deteriorates and the light penetration in the water column is reduced due to increasing phytoplankton biomass. Direct shading is caused by the proliferation of competing epiphytic microalgae and the increasing occurrences of drifting filamentous macroalgal mats. All of these factors inhibit the growth and survival of seagrasses (Hauxwell et al., 2001; McGlathery, 2001). The primary mechanisms that cause algal mats to affect seagrasses negatively include shading through the covering of plants and the alteration of the biogeochemical environment (Hauxwell et al., 2001), but specific field experiments testing the interaction between macroalgal mats and seagrass health are sparse (Deegan et al., 2002; Hauxwell et al., 2001; Holmquist, 1997; Nelson and Lee, 2001).

The shading of plants leads to reduced photosynthesis, which in turn affects plant productivity and the biogeochemical environment surrounding the belowground parts (Hemminga, 1998). In seagrasses, hampered photosynthetic activity results in lowered carbohydrate production and reserve formation that supports growth, but also in reduced internal oxygen translocation from leaves to belowground tissues, which can cause root anoxia and the subsequent reduction in oxygen release from roots to the rhizosphere (Borum et al., 2006; McGlathery, 2001). The oxygen release creates an oxic layer around the roots and protects the plants from an invasion of reduced toxic compounds such as sulfides that are common in sediments (Borum et al., 2006; Holmer and Nielsen, 2007). With lowered oxygen release the protective layer diminishes or is completely lost, leading to elevated sediment sulfide concentrations and the accumulation of sulfides in the roots and rhizomes with negative implications for plant metabolism (Frederiksen and Glud, 2006; Hemminga and Duarte, 2000; Holmer and Laursen, 2002; Holmer and Nielsen, 2007). Algal mat cover also directly changes the biogeochemical environment under the mat with for example, lowered water oxygen availability at the sediment–water or water–plant interfaces. Oxygen depletion often develops because oxygen is used in algal respiration, during mat decomposition and organism metabolism (Holmer and Nielsen, 2007; Krause-Jensen et al., 1999; Middelburg and Levin, 2009). The ammonium concentration in the water underneath the mat and in the sediment porewater may also increase during algal mat decomposition (McGlathery, 2001; Zimmerman and Montgomery, 1984) and because the ammonium uptake is inhibited when plants experience root anoxia (Pregnall et al., 1984). The increased

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ammonium concentrations may thus, possibly reach toxic levels for eelgrass (van Katwijk et al., 1997).

At present, the Baltic Sea suffers from serious eutrophication (Gustafsson et al., 2012). In the northern regions, the water transparency has decreased significantly during the past 70 years (drop from 9 m to 4 m, Fleming-Lehtinen et al., 2009), while the occurrence of both cyanobacterial and filamentous macroalgal blooms has increased dramatically (HELCOM, 2009). In the archipelago areas of the northern Baltic Sea, drifting algal mats may cover vast areas of the seafloor (Norkko and Bonsdorff, 1996; Vahteri et al., 2000). The mat thickness varies from 5 to 40 cm (Vahteri et al., 2000), with average biomasses commonly ranging between 300 and 500 g DW m^{-2} (Norkko and Bonsdorff, 1996; Salovius and Bonsdorff, 2004), but biomasses of over 800 g DW m^{-2} have also been recorded (Bonsdorff, 1992). Such drifting algal mats can cover areas ranging from 2 to 29 ha (Norkko and Bonsdorff, 1996; Vahteri et al., 2000) and occur from days to several weeks (Norkko and Bonsdorff, 1996).

For littoral ecosystems, the consequences of increased eutrophication include reduced light availability, sediment organic enrichment and increasing amounts of suffocating drift algal mats followed by anoxia (Norkko and Bonsdorff, 1996; Vahteri et al., 2000). Consequently, the Baltic Sea eelgrass (*Zostera marina* L.) populations are subjected to increasing stress caused by nutrient pollution but simultaneously, they grow in naturally multispecific meadows where facilitative interactions among plants may alleviate the algal mat-induced stress (Gustafsson and Boström, 2013).

Positive and negative species interactions such as facilitation and competition greatly influence ecosystem functioning and the stability of both ecosystems and individual species (Loreau, 2000; Mulder et al., 2001). In the Baltic Sea, eelgrass *Z. marina* commonly grows in mixed plant communities consisting of 2–4 co-occurring species, though the total plant species richness in these meadows may total >10 species (Kautsky, 1988). Previous studies have shown that neighboring plant species affect the temporal stability of eelgrass, as well as enhance the resistance of eelgrass to shading (Gustafsson and Boström, 2011, 2013). The underlying mechanisms may arise from e.g. the enhanced oxygen release of heterospecifics such as *Potamogeton perfoliatus* (L.) (Caffrey and Kemp, 1991). This may lead to a greater availability of NO_3^- through enhanced nitrification (Caffrey and Kemp, 1990; Marbá et al., 2006; Touchette and Burkholder, 2000a) and increased oxygenation of the reduced rhizosphere, which in turn ameliorates the anoxic conditions and decreases sulfide intrusion (Bertness and Callaway, 1994; Gustafsson and Boström, 2013). The morphological complexity of submerged aquatic vegetation ranges from short straplike leaves (*Z. marina*) to tall, complex canopies (*Potamogeton* spp., *Myriophyllum* spp.). This influences both invertebrate richness (Gustafsson and Boström, 2009), as well as algal entanglement (Jeffries, 1993; Gustafsson and Boström, 2009; Hansen et al., 2010), and thus, potentially the duration of the algal cover and effect of the algal mat on the canopy with subsequent indirect negative effects on eelgrass.

Many of the experiments investigating the effects of algal mat cover on seagrasses have been conducted in outdoor mesocosms or in the laboratory (listed in Rasmussen et al., 2013a). While useful, the shortcomings of such approaches include limited realism due to the lack of natural sediment and hydrodynamic conditions and the lack of natural epi- and infaunal communities, which are known to interact with algae (Lotze and Worm, 2000; Nordström et al., 2006) In this paper, we wanted to quantify the effects of macroalgal mats on eelgrass growth in the field. As the general consensus is that algal mats have negative effects on seagrass growth and survival due to shading and altered biogeochemical processes (Hauxwell et al., 2001; Holmer and Nielsen, 2007; McGlathery, 2001), we firstly hypothesized that algal mat cover would hamper eelgrass biomass accumulation and growth. Secondly, we hypothesized that algal mat cover would decrease the water oxygen availability beneath the algal mat and increase the porewater ammonium concentrations. Lastly, as facilitative interactions can alleviate stress and thus, influence individual species' growth and stability positively during stress (Gustafsson and Boström, 2013; Mulder et al., 2001), we hypothesized that the presence of co-occurring angiosperm species would improve algal stress tolerance in eelgrass.

2. Materials and methods

2.1. Site characteristics and plant community

The field experiment was conducted at Ängsö Island in the Archipelago Sea, northern Baltic Sea (66°75,405′N, 20°60,15′E). The annual surface water temperature range is 0–22 °C and the salinity between 5.5 and 7. During the experiment, the water temperature ranged between 11 °C in June and 22 °C in July. The experimental area is 3–5 m deep and occasionally exposed to S-SW winds. The vegetation consists of a *Z. marina*-meadow (mean shoot density 311 shoots m^{-2}, Boström et al., 2006) with stands of co-occurring *Stuckenia pectinata* (L.) Börner (L.), *P. perfoliatus*, *Zannichellia palustris* (L.) and *Ruppia cirrhosa* (Petagna). Unvegetated, sandy patches intersperse the meadow. The sediment is mainly a mixture of medium-sized (~40% 0.25 mm), coarse (~24% 0.5 mm) and fine sand (~18% 0.125 mm) with low organic content (0.5%) (Boström et al., 2006). During the summer months (June–August) the seagrass meadow is typically exposed to an algal cover averaging 430 g DW m^{-2} (authors' unpublished data).

2.2. Experimental setup and sampling

The experimental plant species were *Z. marina*, *P. perfoliatus*, *Stuckenia pectinata* and *R. cirrhosa*. We used a replacement design (Harper, 1977), with a standardized initial shoot density (total 24 individuals; six individuals of each species in polycultures). All experimental plants were collected from the area and transplanted within 6 h. Plants were gently tied to 30 × 30 cm plastic grids (mesh size 30 mm) and kept submerged during all handling. In polycultures, neighboring individuals were always heterospecific. The following *Z. marina* (hereafter *Zm*) treatments ($n = 6$) were deployed: (1) *Zm* monoculture + algae, (2) *Zm* monoculture (control), (3) *Zm* polyculture + algae, and (4) *Zm* polyculture (control). To investigate *Z. marina* root and rhizome growth, plants were tied to the grid at the youngest rhizome internode.

Plots were planted ~5 cm deep into the sediment using SCUBA in an unvegetated area within the natural meadow in a completely randomized design. The distance between plots was 2.5 m. To investigate the effects of algal mats we deployed roofless cages (∅ 65 cm, height 50 cm) made of plastic grids (30 mm mesh size) around all plots and added 300 g wwt algae (~940 g wwt m^{-2}) to treatments subjected to algal stress, whereas control plots received no algae. The amounts of drift algae in the natural eelgrass meadow varied between 600 and 5600 g wwt m^{-2} (corresponding to ~50–550 g DW m^{-2}) ($n = 3$). The algal mat consisted of a natural mixture of *Ectocarpus*/*Pylaiella* spp., *Dictyosiphon*/*Stictyosiphon* spp. *Ulva intestinalis* (L.), *Chorda filum* (L.) Stackhouse and *Ceramium tenuicorne* (Kützing) Waern. The experiment ran from June 18 to September 8, including a 5 wk initial establishment period, where after an algal mat was deployed to treatment plots for 13 d corresponding to natural temporal scales of algal disturbance (Norkko and Bonsdorff, 1996). After removing both cages and algae, the plots were left to recover for 5 wks. There were two set-ups of the previously mentioned four treatments and unique plots were sampled destructively at two occasions (24 plots sampled at every sampling); 5 wks after the establishment (Pre-algal) and 5 wks after the algae were removed (Resilience). The Pre-algal sampling was done to investigate if natural differences had arisen between treatments prior to the deployment of the stress factor. The recovery time of 5 wks (Resilience) was chosen to investigate whether plants had regained their biomass toward the end of their growth season (mid-September, Boström et al., 2004), with