Light indirectly mediates bivalve habitat modification and impacts on seagrass

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ABSTRACT

Environmental context may influence the sign, strength, and mechanisms of species interactions but few studies have experimentally tested the potential for abiotic conditions to mediate interactions through multiple co-occurring stress pathways. Abiotic conditions may mediate species interactions by directly or indirectly influencing the effects of habitat-modifying organisms that are capable of simultaneously ameliorating and exacerbating multiple stressors. It was hypothesized that light availability changes seagrass metabolism and thereby indirectly regulates bivalve habitat modification and subsequent impacts on seagrasses by shifting net effects between alleviation of nutrient stress and intensification of sulfide stress. To test this hypothesis, manipulations of light availability and blue mussel (*Mytilus edulis*) abundance were made in eelgrass (*Zostera marina*) mesocosms and biogeochemical and plant responses were measured. Light modified the effect of mussels on porewater ammonium, but eelgrass was not nutrient limited and, therefore, mussels did not enhance growth. Mussels increased sediment sulfides irrespective of light availability and, by reducing net oxygen flux (production and respiration), mussels and low light availability exacerbated sulfide intrusion of eelgrass tissues. Surprisingly, sulfide stress did not affect plant growth, survival, or energy stores. Thus, habitat modification by mussels may represent a risk to eelgrass, especially during low productivity conditions, but eelgrass can resist harm from short-term stress, even during light limitation. These findings suggest that while small-scale bivalve impacts on seagrasses may be variable in oligotrophic estuaries, they have the potential to be negative in eutrophic systems, which are increasing globally.

1. Introduction

The sign, strength, and mechanisms of interactions among species can depend on environmental context (Menge and Sutherland, 1987; Connolly and Roughgarden, 1999). Abiotic stress is an important class of environmental conditions that can shift the direction of species interactions, as predicted by the stress gradient hypothesis (Bertness and Callaway, 1994; Bertness and Hacker, 1994). This hypothesis has been especially applicable to species that physically or chemically ameliorate a single environmental stressor or increase the availability of a limiting resource (e.g., Norkko et al., 2006). Habitat-modifying organisms often simultaneously alleviate and exacerbate several stressors, creating the potential for highly complex species interactions (Kawai and Tokeshi, 2007). However, few studies have experimentally assessed the

potential for environmental context to mediate the sign or strength of species interactions through multiple co-occurring stress pathways.

Estuaries are excellent ecosystems for testing the effects of environmental conditions on habitat modification and species interactions by virtue of their dynamic abiotic gradients (e.g., salinity, nutrients, light) and numerous species that modify physical and biogeochemical conditions of the seafloor, such as suspension-feeding bivalves (e.g., Haven and Morales-Alamo, 1966; Bertness, 1984; Kautsky and Evans, 1987) and seagrasses (e.g., Frederiksen and Glud, 2006; Holmer, 2009; Castorani et al., 2014). Bivalves are common, often abundant inhabitants of temperate seagrass meadows (e.g., Peterson et al., 1984; Peterson, 1986) and may have positive, negative, or no effect on these plants. For instance, clams and mussels may facilitate seagrass growth by increasing the availability of sediment nutrients through biodeposition of feces and pseudofeces (e.g., Reusch et al., 1994; Carroll et al., 2008). However, other studies have shown that sediment enrichment by mussels can inhibit the growth of seagrasses by increasing concentrations of toxic sulfides

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(Vinther and Holmer, 2008; Vinther et al., 2012). In other instances, bivalves may have mixed (Reusch and Williams, 1998) or no (e.g., Worm and Reusch, 2000; Wagner et al., 2012) effects on seagrass growth. These variable and inconsistent effects cannot be satisfactorily explained by nutrient availability, suggesting more complex interactions. Variation in light availability—the primary determinant of seagrass productivity (Dennison and Alberte, 1985; Zimmerman et al., 1995)—might help reconcile these disparate findings.

Here, the hypothesis is tested that bivalve modification of benthic biogeochemical conditions and the sign and strength of subsequent impacts on seagrasses are indirectly mediated by light availability through changes to seagrass metabolism. It was predicted that bivalve biodeposition relieves seagrass nutrient stress by increasing sediment nitrogen, but only when light is not limiting. It was also predicted that bivalve enhancement of sediment sulfides inhibits seagrasses under light limitation, when low productivity diminishes the ability of seagrasses to maintain an oxygenated rhizosphere and resist sulfide intrusion (Pedersen et al., 2004; Holmer et al., 2005; Frederiksen and Glud, 2006). Thus, it was hypothesized that light availability mediates bivalve impacts on seagrasses by shifting the net effect between alleviation of nutrient stress and exacerbation of sulfide stress. To test these predictions, bivalve abundance and light availability were manipulated in seagrass mesocosms and biogeochemical and seagrass responses were measured.

2. Materials and methods

2.1. Study system

The blue mussel, *Mytilus edulis* L., is a suspension-feeding epibenthic bivalve that commonly co-occurs with eelgrass, *Zostera marina* L., in intertidal and shallow-subtidal zones of the temperate North Atlantic Ocean, North Sea, and Baltic Sea (e.g., Reusch et al., 1994; Reusch and Chapman, 1995; Reusch, 1998; Bologna et al., 2005). In the Baltic Sea, studies of the effects of *M. edulis* on *Z. marina* have had particularly conflicting results (e.g., Reusch et al., 1994; Worm and Reusch, 2000; Vinther et al., 2012). This study was conducted with seawater, sediments, and organisms collected from the Danish Straits, which connect the North Sea and Baltic Sea. Eelgrass and blue mussels are widely distributed within many Danish fjords and along most Danish coastlines, co-occurring in both mixed and patchy spatial distributions (Reusch et al., 1994; Worm and Reusch, 2000; Kristensen, 2002; Frederiksen et al., 2004; Vinther et al., 2012). In this region of Denmark, coastal waters are often eutrophic (median total nitrogen = 550 µg N L^{-1}; median chlorophyll a = 5.1 µg L^{-1}) and turbid (median turbidity = 10.0 mg dry L^{-1}), resulting in highly-variable benthic light availability (Secchi depth range = 0.3–17.0 m) (Nielsen et al., 2002).

2.2. Experimental design

To determine the role of light availability in mediating blue mussel habitat modification and impacts on eelgrass, mussel abundance (present vs. absent) and light availability (high vs. low) were manipulated in a factorial design for 37 days in an indoor mesocosm experiment at the University of Southern Denmark (Odense, Denmark; 55° 22′ 9″ N, 10° 25′ 40″ E). Mesocosms consisted of transplanted sediments and eelgrass in 5.4 L plastic buckets (20 cm diameter × 17 cm tall; n = 6 buckets per treatment). Eelgrass mesocosms were housed in two aquaria (each 1.1 m length × 0.7 m width × 0.6 m height) that were respectively illuminated at high and low light availability. Aquaria shared flowing seawater (total vol. ≈ 1200 L; connected through a sump with plastic filtration media) that was collected unfiltered from the Marine Biological Research Centre (Kerteminde, Denmark; 55° 27′ 11″ N, 10° 39′ 54″ E) and partially (15% = 175 L) replaced weekly to prevent nutrient accumulation. To maintain 100% air-saturation of the water, 14 air stones were distributed evenly across each aquarium. Both aquaria were illuminated on a 12 h:12 h day:night cycle using Philips SGR 140/400 W lamps (three HQT-BT/D bulbs in high-light aquarium vs. one bulb in low-light aquarium; Royal Philips, Amsterdam, The Netherlands). To further reduce light in the low-light aquarium, the top of this aquarium was shaded with neutral-density black plastic netting.

To characterize abiotic conditions, temperature and light availability were measured every 15 min using a data-logging pendant sensor (HOBO UA-002-64, Onset Computer Company, Bourne, Massachusetts, United States of America (USA)) in each aquarium, attached to stands at eelgrass canopy height (30 cm above the sediment (see below) and 13 cm below the air-water interface). Illuminance readings were calibrated to photosynthetically-active radiation (PAR; 400–700 nm) measured with a PAR sensor (LI-COR LI-250A light meter with LI-193 Underwater Spherical Quantum Sensor, LI-COR Biosciences, Lincoln, Nebraska, USA). During daytime, mean canopy-height irradiance in high-light and low-light aquaria was 574 ± 289 (SD) and 97 ± 70 µmol photons s^{-1} m^{-2}, respectively (high variability in measured irradiance was due to air bubbles periodically crossing the sensor and occasional fouling of the sensor surface). These irradiance levels were chosen to represent light conditions within the range experienced by natural eelgrass communities and at which light availability typically does or does not limit eelgrass growth (i.e., above and slightly below the light-saturation point, P_{max}), respectively (Dennison and Alberte, 1985). At night, both aquaria were completely dark. Aquaria had similar flow (1200 L h^{-1}), temperature (14.4 °C), salinity (13.4 ± 0.8), water-column oxygen air-saturation (100%), and water-column nutrients (18.5 ± 1.7 µg NO$_3^-$ L^{-1}; 11.5 ± 7.7 µmol NH$_4^+$ L^{-1}).

2.3. Field collections

In February and March 2013, sediments and eelgrass were collected from haphazardly-selected patches at a shallow (0–2 m depth) subtidal site at Svenstrup Beach in western Funen, Denmark (55° 28′ 7″ N, 9° 45′ 17″ E). Sediments were excavated from the upper 15 cm by shovel, sieved to remove fauna and detritus >1 mm, homogenized by hand, and stored in the recirculating seawater system until planting (3 days). Sediments were sandy (porosity: 30 ± 3%) and low in organic matter (0.42 ± 0.12%). Eelgrass was carefully uprooted, rinsed of sediments, and transported in coolers to the laboratory (<2 h). To reduce thermal shock, eelgrass was kept in a temperature-controlled room, with aerated seawater and intermediate light (150–250 µmol photons s^{-1} m^{-2}), in which the temperature was increased gradually (+1 °C d^{-1}) from 1 °C to 14 °C, the typical seawater temperature in coastal Denmark in the spring and early summer, when eelgrass productivity is high (Olesen and Sand-Jensen, 1994a,b; due to time constraints, plants could not be collected in the spring or summer). Next, undamaged terminal shoots (leaf length > 10 cm and rhizome length ≥ 2 cm, with 3–5 internodes, intact roots, and no lateral shoots) were selected and carefully removed of senescent tissues. Then, each mesocosm was filled with sediment (10 cm layer) and 28 shoots were transplanted in haphazard arrangement (=891 leaf shoots m^{-2}, corresponding to eelgrass densities typically observed in mixed eelgrass–mussel patches (Reusch et al., 1994; Vinther et al., 2012)). Transplanted eelgrass was allowed two weeks to establish under intermediate light (150–250 µmol photons s^{-1} m^{-2}) and then each mesocosm was randomly assigned a light and mussel treatment.

In March 2013, mussels were gathered by hand from haphazardly-selected floating docks at the Marine Biological Research Centre and medium-sized mussels (51.9 ± 5.1 mm length, a typical size for mussels from local mixed eelgrass–mussel beds; HF Vinther, unpublished data) were retained. Mussels were transported to the laboratory and acclimated using the same procedure as for eelgrass. To half of the mesocosms, 28 mussels (=891 mussels m^{-2} or 27.6 ± 3.6 g dry soft tissue per mesocosm) were carefully added in their natural orientation,