Harmful algae are not harmful to everyone

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ABSTRACT

Seagrasses reduce sediment erosion, filter land-derived pollutants, and provide living space for numerous invertebrates, but seagrasses are increasingly threatened by bloom-forming macroalgae. We tested for density-dependent effects of the macroalga *Gracilaria comosa* on the seagrass *Halophila ovalis* and its associated invertebrates in a subtidal field experiment, in the Swan River estuary (in Perth, Western Australia). *G. comosa* had significant negative effects on *H. ovalis*, reducing leaf densities by 20 and 40% when exposed to 0.7 and 1.4 kg algal wet weight m^{-2}, respectively. By contrast, seagrass-associated invertebrates were positively affected by *Gracilaria*; taxonomic richness and densities of dominant crustacean and mollusc species increased with algal addition. More specifically, densities of surface dwelling gastropods, that utilize a 2-dimensional habitat, were saturated at 0.7 kg algal wet weight m^{-2}, whereas densities of interstitial isopods and amphipods, that utilize a 3-dimensional habitat, had highest densities at 1.4 kg algal wet weight m^{-2}. A non-native ecosystem engineer, the bioturbating gastropod *Batillaria australis*, dominated the surface dwelling mollusc community, and this invader was strongly facilitated by algal additions, being 5 times more abundant under algal mats compared to control plots. If the Swan River becomes more nutrient polluted and subsequently more algal dominated, then this ubiquitous invader may proliferate further, with difficult-to-predict system-wide ecological and biogeochemical consequences. We conclude that, in our experiment, 'harmful algae' inhibited the seagrass itself but facilitated most seagrass-associated invertebrates.

1. Introduction

Seagrasses are widely distributed coastal ecosystem engineers (Jones et al., 1997; Berkenbusch and Rowden, 2003) that alter their surrounding biotic and abiotic environment: seagrasses attenuate waves (Sánchez-González et al., 2011), control erosion and re-suspension rates (Koch, 1999), filter land derived pollutants, and provide living space for numerous seagrass-associated animals (Heck et al., 2003; Boström et al., 2006). Seagrass beds are increasingly stressed by human activities, such as global warming, coastal constructions, pollution, invasive species and eutrophication-fuelled bloom-forming macroalgae (Orth et al., 2006). Bloom-forming macroalgae is a particularly important stressor that increasingly is observed to degrade seagrass beds (McGlathery, 2001; McGlathery et al., 2007). However, their effects appear to be variable and context-dependent. For example, experiments have documented both detrimental (Holmquist, 1997; Hauxwell et al., 2001) and minimal to no effects (Marcia, 2000; Davis and Fourqurean, 2001) of macroalgae on seagrasses. Such discrepancies may be partially attributed to differences in the applied algal abundances.

To date, only two field experiments have quantified density-dependent effects of macroalgae on seagrass abundances, both studies finding increasingly negative effects on populations of the large temperate seagrass, *Zostera marina* with increasing algal stress levels (Hauxwell et al., 2001; Huntington and Boyer, 2008, these studies quantified seagrass only, not animal, responses). Importantly, these documented cases of density-dependent effects may have cascading impact beyond the seagrasses themselves, directly and/or indirectly influencing the animals that inhabit the seagrass bed (Heck et al., 2003; Boström et al., 2006). A few experimental studies have quantified how macroalgae influence animals living in seagrass beds, and these have found both positive (Holmquist, 1997; Thomsen, 2010), neutral (Marcia, 2000) and negative (Cummins et al., 2004) effects, probably reflecting

different environmental tolerances of different animal species (e.g. tolerant vs. sensitive to anoxia) (Cummins et al., 2004), different algal 'health levels' (e.g. decomposed or not) (Cummins et al., 2004) or different algal densities (Thomsen, 2010, this study quantified animal only, not seagrass, responses). However, no field experiment has tested if and how density-dependent impacts on seagrass abundances translate into density-dependent impacts on seagrass-associated fauna. We target this research gap and test for density-dependent effects of the coarsely branched red alga *Gracilaria comosa*, on the abundance of the small subtropical/tropical seagrass *Halophila ovalis* and its associated invertebrates, in the Swan River estuary (Perth, Australia). We hypothesize that algae have density-dependent negative effect on the seagrass and that this effect cascades into positive effects on the associated macro-invertebrates (Holmquist, 1997; Hauxwell et al., 2001; Huntington and Boyer, 2008; Thomsen, 2010).

2. Materials and methods

The experiment was conducted in a seagrass bed (ca. 60% cover of *H. ovalis*) at 1.5 m depth at Waylen Bay (115°50′23.79″E, 32°0′14.84″S) in the Swan River, near the centre of Perth, Western Australia. On October 30, 2010, 45 plots were established and each randomly allocated to one of 3 macroalgal treatments. The native alga, *G. comosa*, was added as 0, 50, and 100 g wet weight to cover a 15 cm radius (0.07 m^2) from the plot centre (=0, 0.7 and 1.4 kg m^2), being fixed with 10 thin u-bend metal pegs, pushed in flush with the sediment surface to avoid trapping particles and organisms. Pegs were also added to the control plots to avoid confounding treatments by the presence of metal. We added *G. comosa* because this species is one of the most abundant algae in Swan River (Astill and Lavery, 2004), and is common in seagrass beds (Thomsen and Wernberg, 2009), on mudflats (Astill and Lavery, 2001), and attached to mollusc shells (Thomsen et al., 2010a). Biomass of *G. comosa* is typically highest in the main estuarine basin in spring and summer, and often exceeds 1 kg wet weight m^{-2} in patches (Thomsen unpubl. data; Astill and Lavery, 2001). Our manipulated algal levels therefore represent patchy, but commonly encountered densities of *G. comosa* in spring and summer. The experiment ran for ca. 1 month, a common residence time for a specific macroalgal patch and a common time interval to run impact studies on seagrasses (e.g., Marcia, 2000; Astill and Lavery, 2001; Nelson and Lee, 2001; Irlandi et al., 2004; Holmer and Nielsen, 2007; Holmer et al., 2011). The experiment was conducted during early summer, coinciding with *G. comosa*'s main population growth (added algae are therefore more likely to remain in the plots and not decay, thereby avoiding difficult-to predict indirect effects (Cummins et al., 2004)). Water temperatures ranged from 18 to 22 °C, salinities from 25 to 32 psu (Swan River Trust data) and secchi-depths from 2 to 4 m (personal observation). We have previously, at this location, quantified typical secchi-depths of 2.7 m with corresponding light extinction coefficients of −0.75 (Wernberg et al., 2008). We measured the depth to the sulphide horizon in the sediment by inserting a 5 cm silver stick (1.2 mm diameter, 99% Ag) 4 cm into the sediment in each plot centre on November 27. All sticks were collected 24 h later, and the distance to the blackened part (a result of reduction of Ag to Ag$_2$S) measured with a ruler to nearest millimetre distance. After the silver sticks were removed we collected a circular 10 cm diameter core (0.008 m^2) from each plot centre (one high algal treatment plot was lost). The content of the core was rinsed through a 1 mm sieve. A freezer malfunction destroyed the structural integrity of preserved algal samples and we did therefore not quantify algal biomass at the end of the experiment. However, the biomass of *G. comosa* appeared to be similar between initial and final levels, no algae entered control plots (see also Section 3) and we were still able to quantify relative algal abundances as percentage cover after spreading thalli out evenly in a white tray. Live (green) seagrass leaves were counted and all macroinvertebrates, except small soft sedentary polychaetes which tended to disintegrate during sieving, were identified and counted. Molluscs and decapods were identified to species; other invertebrates to broad taxonomic groupings. The most common mollusc, *Batillaria australis*, *Nassarius* spp. (*N. burchardi* and *N. pauperatus*), *Bedeva paivae* and *Soletellina biradiata* were further separated into two size classes, where small ('recruits') and large ('adults') individuals were defined as being smaller or larger than half the length of the length reported in Wells and Bryce (2000) for that particular species (recruits were visually much smaller than adults). We calculated taxonomic richness, Pielou's evenness, Shannon's diversity and total abundances of broad taxonomic groupings. Univariate responses were analyzed with ANOVA (on Log $x + 1$ transformed data when necessary to ensure variance homogeneity) and the multivariate community structure with PERMANOVA on 4th root transformed data (Bray–Curtis similarity coefficient. 4999 permutations) (Clarke et al., 2006; Anderson et al., 2008). In the community analyses, we treated recruits as separate taxa, because they might reflect different types of responses to the treatments (but the results were very similar when data were analyzed without size groupings). We used Student–Newman–Keul (SNK) and permutation based *t*-tests to identify subgroups within significant treatments, for univariate and multivariate responses, respectively.

3. Results

The algal addition treatment worked according to intentions. No algae colonized control plots, addition plots appeared to contain the same biomass that was added, and we documented clear differences in algal-cover among treatment at the end of the experiment (Table 1; SNK comparisons; control = 0% ± 0 SE < Low = 12% ± 1 SE < high = 35% ± 4 SE). Algal additions significantly decreased the distance to the sulphide horizon (Table 1, Fig. 1A; sulphide horizon of control > low = high) high) and seagrass leaf densities (Table 1, Fig. 1B; control > low > high), where low and high algal abundances caused ca. 20% and 40% reduction in leaf density, respectively. Algae also changed the multivariate invertebrate community structure (Table 1); control and low treatments and control and high treatments were significantly different (*t* = 2.48 and 2.05, respectively, *p* < 0.002) whereas communities of low and high algal treatments were similar (*t* = 1.25, *p* = 0.184). Species richness increased with algal density (Fig. 2A, control = low < high; note that richness was, non-significantly, higher in the low than the control plots), whereas evenness decreased with algal density (Fig. 2B, control > low > high). However, algal addition did not affect diversity (Table 1, Fig. 2C).

Algal addition had an impact on most of the dominant invertebrate taxa. Algal addition had a significant positive effect on all organism pooled (Table 1, Fig. 3A, control < low < high) – a result depending on strong positive effects on both crustaceans (Fig. 3B, control < low < high) and molluscs (Fig. 3C, control < low = high), but not 'other taxa' (Fig. 3D; a few echinoderms and errant polychaetes occurring in very low densities; control = low = high). The pattern observed for crustaceans was driven by increases in densities of both isopods (predominantly sphaeromoids, Fig. 3E, control < low < high) and amphipods (Fig. 3F, control < low < high). The pattern observed for molluscs was driven by a large increase in *B. australis* (Fig. 3G and H, Recruits and Adults; control < low = high) and smaller increases in *S. biradiata* (Fig. 3M and N, Recruits; control < low < high; Adults; similar, but not significant, trend). In particular, adult *B. australis* were ca. 5 times more abundant under algal mats compared to