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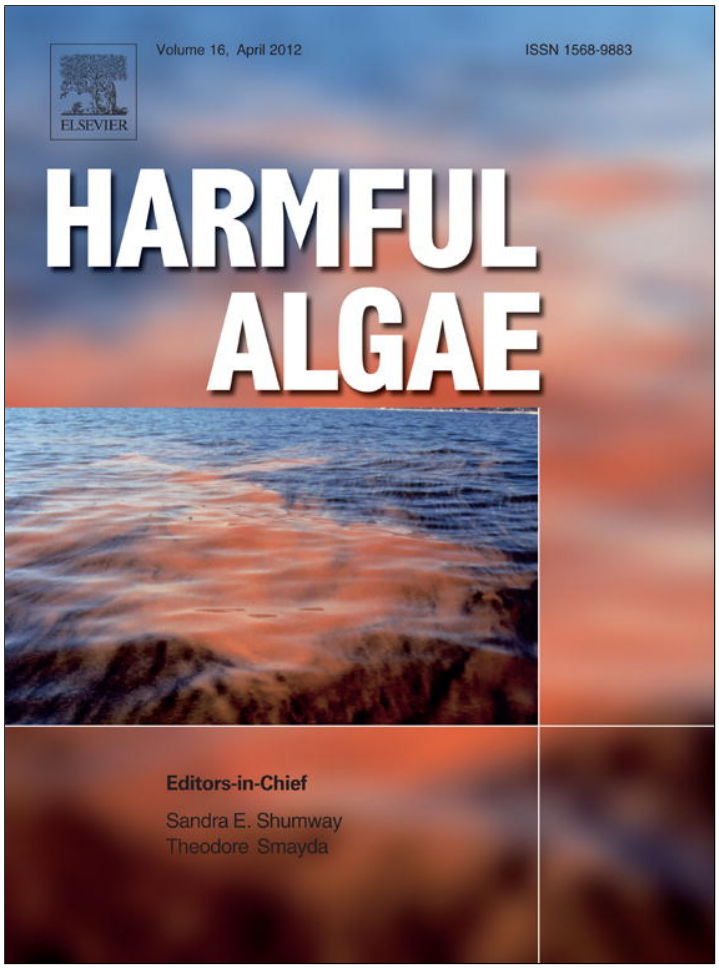

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Harmful algae are not harmful to everyone

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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.

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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 resuspension 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

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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 macroinvertebrates (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_2S) 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 $\mathrm{Log}\, x + 1$ 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

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Table 1
ANOVA results showing effects of the macroalga *Gracilaria comosa* on 'itself' and 19 abiotic and biotic responses. Significant results are in bold.

Response (* = Log x + 1 transformed)	MS	*F*	*p*
*Gracilaria comosa** (see text)	8.443	276.73	**0.000**
Error	0.031		
Halophila ovalis (Fig. 1A)	1770.86	9.96	**0.000**
Error	177.76		
Silver reduction [oxygenated depth of sediment] (Fig. 1B)	4.177	7.37	**0.002**
Error	0.567		
Multivariate invertebrate community structure (see text)	3518.5	6.03	**0.001**
Error	583.9		
Invertebrate Taxonomic Richness (Fig. 2A)	23.071	6.87	**0.003**
Error	3.36		
Invertebrate Community Evenness (Fig. 2B)	0.046	10.90	**0.000**
Error	0.004		
Invertebrate Shannon Diversity (Fig. 2C)	0.019	0.27	0.766
Error	0.072		
All invertebrate organisms (Fig. 3A)	0.937	42.73	**0.000**
Error	0.022		
Molluscs (Fig. 3B)	216.534	4.24	**0.021**
Error	51.027		
Crustaceans (Fig. 3C)	1.599	15.18	**0.000**
Error	0.105		
'Other organisms' [than mollusc/crustaceans] (Fig. 3D)	0.379	0.47	0.632
Error	0.815		
Isopods* (Fig. 3E)	1.457	11.82	**0.000**
Error	0.123		
Amphipods* (Fig. 3F)	1.047	12.20	**0.000**
Error	0.086		
Batillaria australis adults [gastropod] (Fig. 3G)	997.891	37.43	**0.000**
Error	26.663		
Batillaria australis recruits [gastropod] (Fig. 3H)	188.09	5.60	**0.007**
Error	33.574		
Nassarius spp. adults [gastropod] (Fig. 3I)	4.291	3.96	**0.027**
Error	1.083		
Nassarius spp. recruits [gastropod] (Fig. 3J)	0.018	0.06	0.946
Error	0.32		
Bedeva paivae adults [gastropod] (Fig. 3K)	0.219	3.81	**0.030**
Error	0.057		
Bedeva paivae recruits [gastropod] (Fig. 3L)	0.015	0.23	0.796
Error	0.066		
Soletellina biradiata adults [bivalve] (Fig. 3M)	0.077	1.66	0.202
Error	0.046		
Soletellina biradiata recruits* [bivalve] (Fig. 3N)	0.323	7.63	**0.002**
Error	0.042		

control plots (Fig. 3G), and, combined with recruits, more abundant than all other molluscs combined. The remaining less abundant but relatively common molluscs were either slightly negatively affected by algae (adults of *Nassarius* spp, Fig. 3I, Control > Low = High) or not affected (recruits of *Nassarius* spp., Fig. 3J; adults and recruits of *B. paivae*, Fig. 3K and L). In summary, all organism pooled, crustaceans, isopods, amphipods, and *S. biradiata* increased with increasing algal density, mollusc and *B. australis* 'saturated' with increasing algal density, and *Nassarius* and *B. paivae* decreased with or were unaffected by, increasing algal density.

4. Discussion

Our hypothesis, that algae have density-dependent negative effect on the seagrass and positive effects on the associated macroinvertebrates, was supported. We found increasingly negative effects of *G. comosa* on *H. ovalis* (Hauxwell et al., 2001; Huntington and Boyer, 2008). However, this harmful alga (from the perspective of the con-trophic seagrass) also facilitated many invertebrates that inhabit the seagrass beds (Holmquist, 1997; Thomsen, 2010), either increasing or saturating their abundances with increasing algal density.

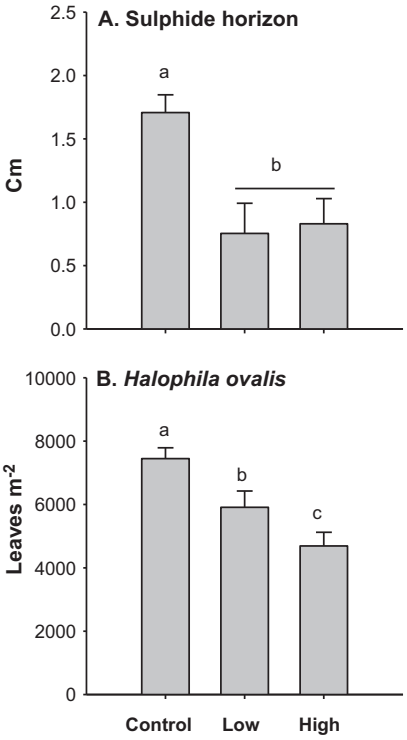

Fig. 1. Effects of the macroalga *Gracilaria comosa* on the depth of the sulphide horizon in the sediment (A; measured as reduction of Ag to Ag_2S) and green leaf density of the seagrass *Halophila ovalis* (B). Error bars are standard errors ($n = 15$). Bars = significant effects based on post hoc SNK tests.

4.1. Seagrass responses

We found that 0.7 and 1.4 kg wet weight m^{-2} of *G. comosa* reduced *H. ovalis* leaf densities by 20 and 40%, respectively, thereby supporting a recent laboratory experiment, where *H. ovalis* leaf biomass was reduced by 40–60% when stressed by 1.2 kg wet weight m^{-2} at 20 and 25 °C (Holmer et al., 2011). The similarity between field and laboratory results is at first surprising; we expected stress-impact from open (realistic) field experiments to be smaller than laboratory experiments, as stressed leaves can receive photosynthates from unaffected integrated ramets, and unaffected ramets surrounding stressed plots can colonize these via horizontal encroachment (Collier et al., 2010). However, *H. ovalis* depend less on translocated products than larger seagrasses (Hemminga and Duarte, 2000), and encroachment from adjacent clones is unlikely given the already high spatial cover of seagrasses (combined with a high areal cover of *B. australis*, see calculations below). Thus, even though this small seagrass was virtually buried by macroalgae, it still survived with >4000 leaves m^{-2} after one month of drift algal stress (a common time scale for an algal patch to persist in a seagrass bed) (Holmquist, 1992; Marcia, 2000; Irlandi et al., 2004). However, larger macroalgal patches and longer/more persistent accumulations will most likely result in more severe impact, as the relative importance of translocated photosynthates from unaffected ramets diminishes (Hauxwell et al., 2001; Cummins et al., 2004; Collier et al., 2010; Holmer et al., 2011).

We did not manipulate the underlying mechanisms whereby macroalgae affect seagrasses, but negative impacts are likely to reflect competition for light and nutrients and from accumulations of waste products in the sediments below the algal mat, potentially with toxic levels of sulphides (Hemminga and Duarte, 2000; McGlathery, 2001; Holmer et al., 2005). We have previously measured ca. 60% light reductions below 200 g wet weight *G.*

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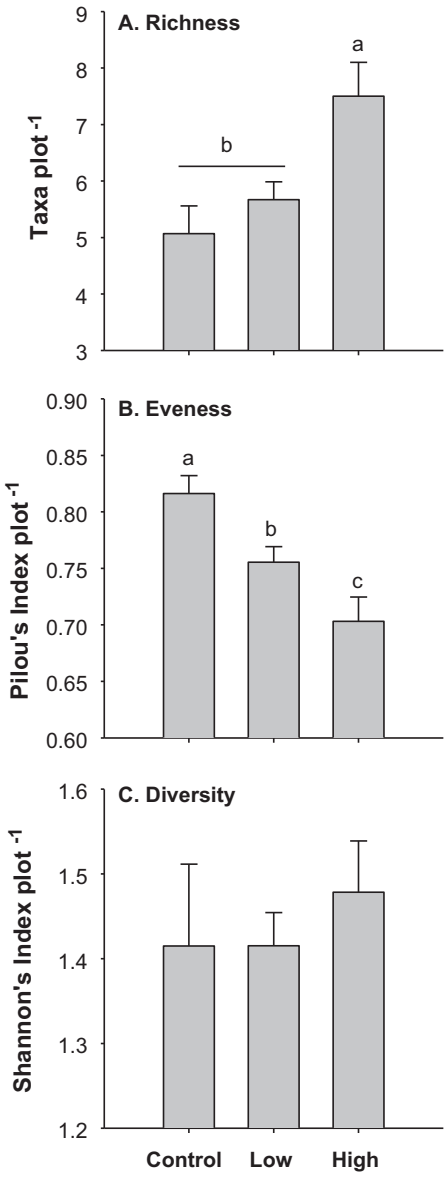

Fig. 2. Effects of the macroalga *Gracilaria comosa* on taxonomic richness (A), evenness (B) and diversity (C) of macroinvertebrate communities inhabiting a *Halophila ovalis* seagrass bed. Error bars are standard errors ($n = 15$). Bars = significant effects based on post hoc SNK tests.

comosa m^{-2} (Thomsen and Wernberg, 2009) and Huntington and Boyer (2008) recorded >90% reduction below 1.7 kg m^{-2} of morphologically similar *Gracilariopsis* sp. Indeed, there is ample studies that have documented light reduction under algal canopies (e.g., Krause-Jensen et al., 1996; Astill and Lavery, 2001; Wernberg et al., 2005). We estimate that up to 60 μE m^{-2} s^{-1} can reach the seagrass canopy below the dense algal mat during typical summer conditions (assuming 90% reduction by the mat; $0.1 \times 2000\ \mu E\ m^{-2}\ s^{-1} \times e^{-0.75\ m \times 1.5\ m}$) (Wernberg et al., 2008). This incident light is above *H. ovalis*' compensation point of ca. 40 μE m^{-2} s^{-1} (Hillman et al., 1995), partially explaining how *H. ovalis* survived with >4000 leaves m^{-2} even at the highest algal stress level. In addition, during summer months, precipitation, land-run-off and river flow are low (Brearley, 2005) and aquatic plants may be nutrient limited. Experimental work suggests that seagrasses often are nutrient limited (Hughes et al., 2004; Burkepile and Hay, 2006) and a preliminary experiment conducted at our study location suggests that addition of nutrients can enhance *H. ovalis* biomass by 5–20% below an algal mat (Thomsen and Wernberg, 2009). Finally, here we documented a decrease in the depth of the sulphide horizon in the sediment below the algal mats (=increase in sediment porewater sulphide; Fig. 1A), a likely common phenomenon (Martinez-Luscher and Holmer, 2010; Hoeffle et al., 2011; Holmer et al., 2011). Sulphide is an enzyme inhibitor and therefore a phytotoxin, and high porewater sulphide levels have previously been shown to reduce seagrass growth (Koch et al., 2007; Kilminster et al., 2008). Thus, a combination of light reduction (Hauxwell et al., 2003; Brun et al., 2008), competition for nutrients (Hughes et al., 2004; Burkepile and Hay, 2006) and accumulation of sulphides in the sediment (Koch and Erskine, 2001; Holmer et al., 2005; Koch et al., 2007) are likely mechanisms whereby *G. comosa* reduces the abundance of *H. ovalis*. However, to identify the exact limiting mechanisms, their relative importance, and possible threshold loadings will require sophisticated experiments.

4.2. Invertebrate responses

In contrast to the negative effects of macroalgae on the seagrass, we detected many positive effects on invertebrates living in the seagrass bed. Taxonomic richness, total abundances, and abundances of mollusc and crustaceans were highest in algal addition plots. We are aware of two drift algal experiments that have found analogous community-wide invertebrate facilitation in seagrass beds; in Florida *Laurencia poiteaui* increased richness and abundances of many invertebrates in a mixed *Thalassia*/*Halodule*/*Syringodium* bed (where *L. poiteaui* had a detrimental impact on the seagrass) (Holmquist, 1997), and in Denmark invasive *G. vermiculophylla* increased the abundance of molluscs and crustaceans in a *Z. marina* bed but did not affect community structure or taxonomic richness (this study only sampled epifauna and did not report impact on the seagrass) (Thomsen, 2010).

We found no species that were restricted to the macroalgal (or seagrass habitat), suggesting that the higher number of taxa in the presence of algae was due to an increased likelihood of finding a species already living in the seagrass bed, rather than colonization of a new species from outside the meadows (Virnstein and Howard, 1987; Holmquist, 1997; Thomsen, 2010). The high abundance – and increased dominance – by a few species in the algal treatments caused a low evenness in these treatments, and because high richness counteracts low evenness, there was a no-effects on Shannon's diversity. Adult *Nassarius* spp., were the only taxa that appeared to be negatively affected by *G. comosa*. *Nassarius* spp. are the second most abundant group of snails in Swan River seagrass beds (Thomsen et al., 2010b), where they are deposit feeders and scavengers feeding on organic material at the sediment surface, i.e., they mainly occupy a 2-dimensional habitat (Brearley, 2005). We expected *Nassarius* spp. to be facilitated by decomposing plant material below the *G. comosa* mats, and the negative effect observed may have been indirectly caused by co-varying high *B. australis* densities. In the seagrass bed *B. australis* is also a surface dwelling deposit feeder, and this species was strongly facilitated by low and high algal levels, probably feeding on decomposing plant material. In the algal addition plots this invasive snail occupied ca. half of the entire surface area [(2000 adults $m^{-2} \times 0.002\ m^{-2}$ $adult^{-1}$) + (2000 recruits $\times$ 0.00005 m^{-2} $recruit^{-1}$) = 0.5 m^2 = 50% of surface] (snail surface data from Thomsen et al., 2010b), corresponding to a similar or larger spatial cover than the seagrass itself. This high snail density and cover could represent a carrying capacity of intensive intra- and inter-specific competition for space and food between deposit feeding surface dwellers, explaining why *B. australis* densities did not differ between low and high algal treatments and why *Nassarius* spp. did not benefit from algal addition. In contrast to *Nassarius*, *B. paivae*, the third most common surface dwelling gastropod in Swan

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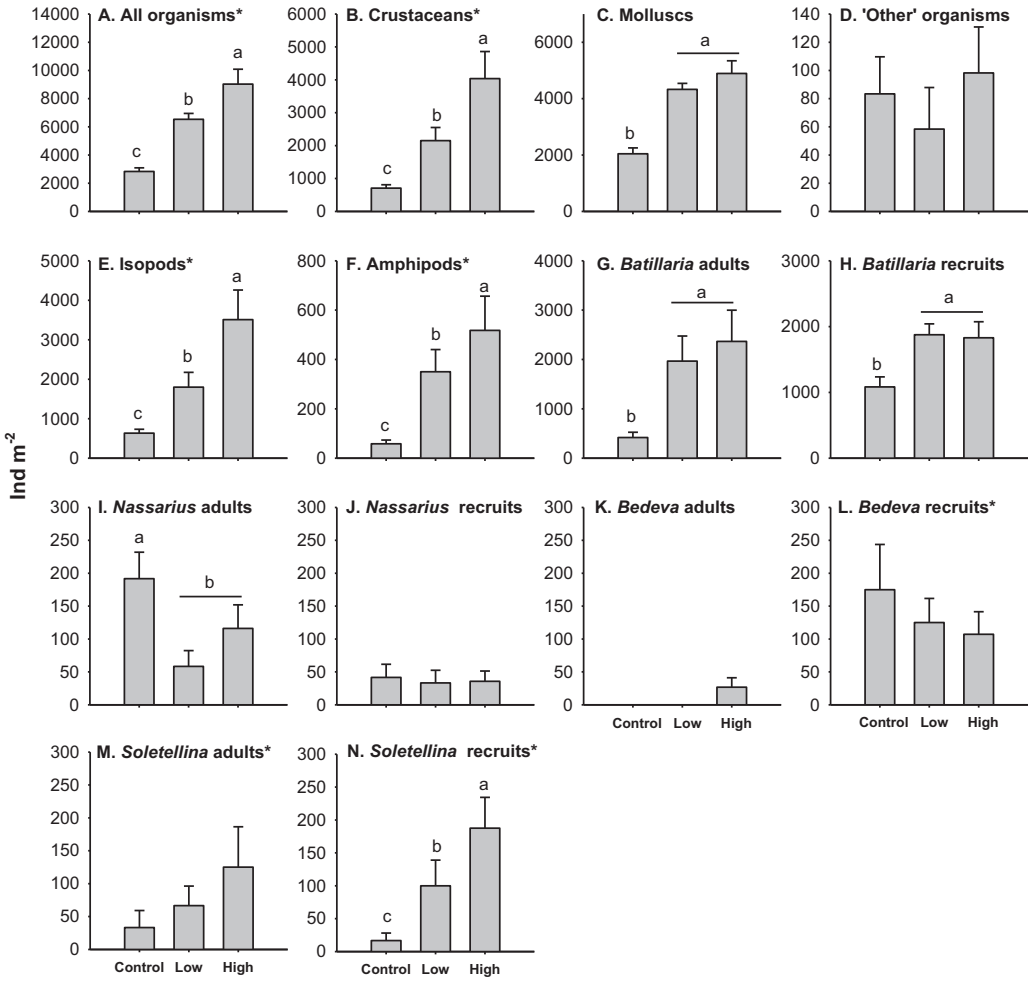

Fig. 3. Effects of the macroalga *Gracilaria comosa* on densities of macroinvertebrates inhabiting a *Halophila ovalis* seagrass bed. Error bars are standard errors (n = 15). Variables marked with * were Log x + 1 transformed to ensure variance homogeneity. Bars = significant effects based on post hoc SNK tests.

River seagrass beds (Thomsen et al., 2010b), was not affected by *G. comosa* (or high co-varying *B. australis* levels). However, *B. paivae* is a predatory driller that does not compete for food, and can climb onto (i.e. does not compete for space), and maybe even predate on, *B. australis*, even if their hard shells would make this a time-consuming effort (Thomsen et al., 2010b).

We also found strong positive effects of macroalgae on amphipods and isopods, probably reflecting a complex combination of increasing escape from predators (e.g. abundant blowfish and sea perches in the Swan River) (Brearley, 2005), increased food (grazing on macroalgae, their epiphytes, and decomposing plant material), or simply more space to live in and on (Heck and Wetstone, 1977; Holmquist, 1997; Lauringson and Kotta, 2006). These crustaceans are interstitial species (sensu Huston, 1994), that live on and between seagrass leaves and *G. comosa* branches. This increase in crustacean abundances thereby correspond with an increase in the 3-dimensional habitat (alga) they occupy. A similar positive algal density-dependence was observed for the infaunal bivalve *S. biradiata* (Fig. 3M and N). This species is likely to be a deposit feeder like *B. australis* and *Nassarius* spp. (Matthews and Fairweather, 2008) but inhabit the sediment profile, i.e. a 3-dimensional habitat, like the isopods and amphipods. In short, within the experimental context tested here increasing algal densities had no or saturating effect on surface dwellers that utilize a 2-dimensional habitat (*Nassarius* spp. exempted), but continuous positive effect on most of the species that utilize a 3-dimensional habitat.

4.3. Implications

Our findings have two key implications for management and future research. First, our study emphasises that 'harmful organisms' typically are harmful only to a specific group of organisms within a density-dependent context. We found negative density-dependent effects on the con-trophic seagrass, likely mediated via increasing levels of competition for light, nutrients and oxygen, but positive and sometimes density-dependent effects on inter-trophic invertebrates, that probably utilize the additional plant material as habitat and food. This community-wide facilitation of invertebrates represents a 'habitat cascade' (Thomsen et al., 2010a; Dijkstra et al., in press), where one habitat-former (here seagrass) provides living space and hydrodynamic protection for another habitat-former (here macroalgae) thereby increasing species richness and animal abundances of the ecosystem. Similar indirect positive effects between co-existing ecosystem engineers, are common in marine and terrestrial systems, but few scientific studies have investigated them (Thomsen et al., 2010a; Dijkstra et al., in press). More studies are therefore needed to better understand how biodiversity, species abundances and productivity are maintained by these co-existing ecosystem engineers. Specifically, feedback loops between the alga and the seagrass will eventually determine longer and larger scale effects. For example, increasing accumulations of persistent algal mats may eventually kill off entire seagrass beds (Hauxwell et al., 2001), and unattached drift algae thereby loose hydrodynamic protection (provided by

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the seagrass, Bell et al., 1995; Bell, 1997), resulting in beach-casting by waves and currents, and ultimately a collapse of the entire habitat cascade. From a management perspective it is clearly essential to know such point-of-no return drift algal stress thresholds, and, to identify these, future experiments should apply more and higher algal densities, larger plots sizes and/or longer run-times.

Second, we found a strong facilitation of *B. australis* from algal addition treatments. *B. australis* was, also in the absence of macroalgae, orders of magnitudes more abundant than native molluscs found in these seagrass beds. This snail is a classic example of an invasive ecosystem engineer (Jones et al., 1997; Gutierrez et al., 2003; Sousa et al., 2009) because of its longevity, size, bioturbation (e.g., sediment movements), metabolism (e.g., excretion of ammonia) and production of hard and resistant shells, which represent additional habitat for sessile organisms (Thomsen et al., 2010a,b). This finding highlights that an ecologically 'positive effect' can be opposite to cultural or economically 'beneficial/wanted effect' (Thieltges et al., 2006). Very little is known about how this ubiquitous invader has impacted the Swan River ecosystem, but our results suggest that the snail population has potential to grow orders of magnitude larger than currently high densities, for example if the estuary becomes more eutrophic and drift algae mats subsequently more prolific as it would be expected with the current economic and demographic growth of Perth. We have previously calculated a total population size of ca. 3.6 billion snails in the Swan River (Thomsen et al., 2010b). If the snail population double or triple from that, this invasion will likely not only result in system-wide difficult-to predict effects on native species and ecosystem properties, but also a significantly increased probability of spread to adjacent non-invaded estuaries in Western Australia. Managers can therefore, at least partially, reduce localized invasion impacts and likelihood of spreading, by managing drift algal populations. It is important that future studies test how the invader impacts native seagrasses and invertebrates, e.g., if and how it may uproot seagrass seedlings, convert organic material to inorganic nutrients, rework sediments, affect sediment biogeochemistry, e.g. sulphide pools, provide shells for sessile organisms to attach to, and whether activities, behaviours, metabolism and impacts change along environmental gradients.

4.4. Conclusion

We conclude that the macroalgae *G. comosa* had a negative impact on the seagrasses *H. ovalis*, but a positive impact on macroinvertebrates, in particular isopods, amphipods and the invasive ecosystem engineer *B. australis*. Management of drift algal levels could therefore simultaneously support the persistence of seagrass beds, invertebrate community structure and secondary productivity, and reduce the risk of invaders spreading to nearby estuaries.

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