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Research article

Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed

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Abstract

Relatively few studies have aimed to test if invasive species have positive effects on native species, for example via formation of habitat or by amelioration of environmental stress-conditions. The red macroalga *Gracilaria vermiculophylla,* from the West Pacific, is invading estuarine mudflat and seagrass habitats along East Pacific and East and West Atlantic coastlines. I tested if low (55-110 g WW m^{-2}) and high (220-440 g WW m^{-2}) densities of *G. vermiculophylla* have positive or negative effects on the macroinvertebrates (> 2 mm) that inhabit *Zostera marina* seagrass beds. The experiment was conducted over 34 days at both 0.5 and 2 m depth at Snaptun Harbor, Denmark. I found positive effects of *Gracilaria* on most invertebrates, with statistically significant results for "all invertebrates", "gastropods", and "bivalves", and a near-significant result for "crustaceans". Both quantitative and qualitative habitat-resource models may explain these positive effects; i.e. "more habitats" exist in the presence of *Gracilaria* and/or the "habitat differs" between *Gracilaria* and *Zostera* vegetation. Future studies should test these two general explanatory models and quantify (a) if density thresholds exists were effects shift from positive to negative, (b) specific mechanism whereby positive effects occur, (c) if *Gracilaria* provide a novel or substitute drift algal habitat, and (d) the larger-scale ecosystem implications of this invasion.

Key words: indirect effects, habitat cascade, *Gracilaria vermiculophylla*, *Zostera marina*

Introduction

It is well-known that non-native species predate on, and compete with, native biota causing species extinctions, reducing population abundances and altering community structure in ecosystems around the world (Elton 1958; Sax and Gaines 2008). While these negative effects are well documented, less is known about how invasive species may also have positive effects on native species, for example via formation of habitats, amelioration of environmental stress, mutualism, or cascading indirect effects (Rodriguez 2006; Simberloff 2006). Recently, it was shown that invasive invertebrates and seaweeds can have direct or indirect positive effects on estuarine macrofauna via "sequential biogenic habitat formation" (Thomsen et al. 2010). For example, on mudflats in Virginia the native polychaete *Diopatra cuprea* (Bosc, 1802) creates habitat for the invasive seaweed *Gracilaria vermiculophylla* (Ohmi) Papenfuss (originating from the West Pacific, hereafter *Gracilaria*), and this seaweed then create

additional habitat for bryozoans, crustaceans, polychaetes, gastropods and various algal epiphytes (Thomsen and McGlathery 2005; Nyberg et al. 2009; Thomsen et al. 2009a; Thomsen et al. 2010). This sequence of biogenic habitat formation was coined a "habitat cascade" (Thomsen et al. 2010) and it was proposed to be a general mechanism driving positive relationships between abundances of invasive species and native estuarine flora and fauna. However, invertebrates are not the only structures that potentially facilitate invasive estuarine seaweeds as (invasive and native) seaweeds may also accumulate in seagrass beds (Holmquist 1997; Cummins 2004; Huntington and Boyer 2008). Hence, there could potentially be positive effects on invertebrates when and where invasive seaweeds accumulate in seagrass beds.

Currently, *Gracilaria* is expanding its range along East Pacific and East and West Atlantic coastlines (Thomsen et al. 2006; Thomsen et al. 2007; Weinberger et al. 2008; Saunders 2009), where it can accumulate in low-energy estuarine seagrass beds. In Denmark, *Gracilaria* was found,

for the first time in Horsens Fjord in 2004, and it had since spread to several estuaries, inhabiting low energy mud-flats, stone and mussel reefs and seagrass beds (unpubl. data, Thomsen et al. 2007). In this study, I conducted a seaweed-addition field experiment over 34 summer days to test the hypothesis that *Gracilaria* has a positive net effect on the abundance and taxonomic richness of macro-invertebrates inhabiting seagrass beds.

Methods

The experiment was conducted in *Zostera marina* Linnaeus seagrass beds south of Snaptun Harbor, in East Jutland, Denmark (55°49'4.02"N, 10°3'12.84"E). *Gracilaria* was observed for the first time near this location in 2004 (Thomsen et al. 2007). Unattached *Gracilaria* were collected from the local seagrass bed. Algae were brought ashore, shaken to release mobile macro-invertebrates, closely inspected for remaining clinging invertebrates (which were then hand-picked) and compiled to low (ca. 10 g WW) and high (ca. 40 g WW) drift algal treatments. Low and high treatments were added to 0.3×0.3m plots (corresponding to ca. 110 and 440 g WW m^{-2}) and compared to control plots without *Gracilaria*. The experiment was conducted at both a shallow and an adjacent deeper site, because local invertebrate abundances differ between depth levels (pers. obs). The final design was as follow; 2 depth levels (0.5, 2.0 m) × 3 invader densities (0, low, high) × 8 replicates = 48 plots in total. A few replicate plots were lost so I ended up with 6-8 replicates for any specific depth × invader density combination.

Gracilaria thalli were entangled around 10 thin U-bend metal-pegs per plot (similar to, although much thinner than, standard tent-pegs). The pegs were then pushed into the sediment to avoid sediment-surface protruding structures that may capture drifting objects or otherwise create environmental artefacts. This algal fixation method leaves only the algal thalli as a visible structure in each plot. A similar number of pegs but without entangled algae were inserted into the control plots. This method simulate drift algae that are entangled around seagrass stems with minimal experimental artefacts above the sediment surface (e.g., with no changes to local light conditions, hydrodynamics, sedimentation levels and without trapping drifting or fouling objects/organisms). The experiment ran for 34 days (June 30th 2006 to August 3rd), a commonly

applied stress-duration for drift algal-seagrass studies, and reflecting the relatively short time that drift algae typically persist in individual seagrass plots (e.g., Marcia 2000; Nelson and Lee 2001; Cardoso et al. 2004; Irlandi et al. 2004; Holmer and Nielsen 2007; Martínez-Lüscher and Holmer 2010). Water temperature varied from ca. 17 to 22C° during the experiment. Initial seagrass shoot densities were higher, but with lower biomass, in the shallow compared to the deep site (density: 521.34 shoots m^{-2} ± 36.31 SEM, n= 8 vs. 370.38 ± 34.71, n = 8, p = 0.009, $F_{1,15}$ = 9.17; shoot biomass: 0.587 gWW shoot^{-1} ± 0.141, n=10 vs. 1.862 ± 0.418 gWW, n=10, p < 0.001, $F_{1,19}$ = 16.94 on log-transformed data; variances were homogeneous). At the termi-nation of the experiment, the control plots were still free of drift alga demonstrating that control pegs did not capture algae, but ca. half of the seaweed biomass was lost in both the low and high algal treatments. Hence the true stress levels were in-between 55-110 and 220-440 g WW m^{-2} over the time-course of the experiment for the low and high stress levels, respectively. Changes to algal biomass is common in these field experiments caused by algal decay and fragmentation, grazing, biotic disturbances, and hydrodynamic stress (e.g., Nelson and Lee 2001; Cardoso et al. 2004; Cummins 2004; Huntington and Boyer 2008). On August 3rd, algae, seagrass and macro-invertebrates above the sediment (i.e. not including infauna) were collected from the centre of each plot in a 0.025 m^2 frame. In the laboratory, invertebrates retained on a 2 mm sieve were identified, counted and individual species sorted into two size classes depending on whether it was larger or smaller than half its maximum size as listed for Danish marine invertebrates by Køie et al. (here referred to as recruits and adults respectively, 2000).

Factorial PERMANOVA (Anderson et al. 2008) was used to test the effect of the presence of *Gracilaria* and depth (fixed factors) on the multivariate invertebrate community structure (log x+1 transformed data, Bray Curtis similarity coefficient, 4999 permutations). Factorial ANOVA was used to test univariate responses on "total densities" for each of the two size groups and on size-pooled data for "gastropods", "bivalves", "echinoderms", and "crustaceans" (constituting >95% of counted taxa). Species-specific size-groups could not be analysed separately because of high data variability, many more zero values, and strong violations of

ANOVA assumptions for these high-resolution data. Taxonomic richness had homogenous variance on untransformed raw-data. Remaining variables were log x+1 transformed to fulfil the variance homogeneity assumption (Levene's tests, p > 0.05, except for test on echinoderms that could not be successfully transformed due to a total lack of individuals at the shallow site site only). Significant effects of *Gracilaria* were followed by Student-Neuman-Keuls (SNK) post hoc tests.

Results

There were no significant 'Gracilaria × depth' interaction effects in any test and so single factor effects of *Gracilaria* and depth could be interpreted independently (Table 1). The multivariate test showed that community structure differed between depth levels, but not between *Gracilaria* treatments. There were also significantly higher taxonomic "richness" and higher densities of "echinoderms", but lower densities of "bivalves", at the deep site compared to the shallow site (Figure 1A, E, G). There were no significant effects of *Gracilaria* additions on "richness" or densities of "adults-only", "echinoderms", or "crustaceans" (Figure 1A, C, E, H). However, in most of these cases the highest densities were still found associated with high *Gracilaria* biomass; only "richness" and "crustaceans" at the shallow depth-site did not follow this pattern (and for crustaceans this was

Table 1. Impacts of the invasive drift macroalgae *Gracilaria vermiculophylla* on native invertebrates at two depth levels in a *Zostera marina* seagrass bed, Snaptun Harbor, Denmark. The "Community" test was conducted with PERMANOVA (Anderson et al. 2008). Remaining tests were conducted with factorial ANOVA. All test-data, except "Richness" were log x+1 transformed to ensure variance homogeneity (although the "Echinoderm" test still had minor variance heterogeneity despite this transformation). Significant results (p < 0.05) are in bold and near-significant results (p < 0.10) in bold and brackets. See figure 1 for graphical representation of results.

| Test	Treatment	SS	Df	F	P
Community	*Gracilaria*	1536	2	1.287	0.269
	Depth	12959	1	21699	**0.001**
	Gracilaria × Depth	485	2	0.406	0.877
	Error	20903	35		
Richness	*Gracilaria*	0.028	2	2.227	0.123
(Fig. 1A)	Depth	0.034	1	5.430	**0.026**
	Gracilaria × Depth	0.014	2	1.107	0.342
	Error	0.222	35		
Total	*Gracilaria*	0.601	2	4.299	**0.021**
(Fig. 1B)	Depth	0.001	1	0.001	0.982
	Gracilaria × Depth	0.084	2	0.598	0.555
	Error	2.444	35		
Adults	*Gracilaria*	0.133	2	1.808	0.179
(Fig. 1C)	Depth	0.081	1	2.207	0.146
	Gracilaria × Depth	0.052	2	0.709	0.499
	Error	1.288	35		
Recruits	*Gracilaria*	0.786	2	4.599	**0.016**
(Fig. 1D)	Depth	0.007	1	0.085	0.772
	Gracilaria × Depth	0.079	2	0.460	0.635
	Error	2.990	35		
Echinoderms	*Gracilaria*	0.282	2	2.571	**(0.091)**
(Fig. 1E)	Depth	6.028	1	109.987	**0.000**
	Gracilaria × Depth	0.263	2	2.395	0.106
	Error	1.918	35		
Gastropods	*Gracilaria*	0.429	2	3.556	**0.034**
(Fig. 1F)	Depth	0.141	1	2.341	0.135
	Gracilaria × Depth	0.082	2	0.677	0.515
	Error	2.112	35		
Bivalves	*Gracilaria*	0.708	2	3.175	**0.049**
(Fig. 1G)	Depth	2.562	1	22.98	**0.001**
	Gracilaria × Depth	0.045	2	0.203	0.817
	Error	3.902	35		
Crustaceans	*Gracilaria*	0.263	2	1.539	0.229
(Fig. 1H)	Depth	0.027	1	0.318	0.576
	Gracilaria × Depth	0.161	2	0.943	0.399
	Error	2.996	35		
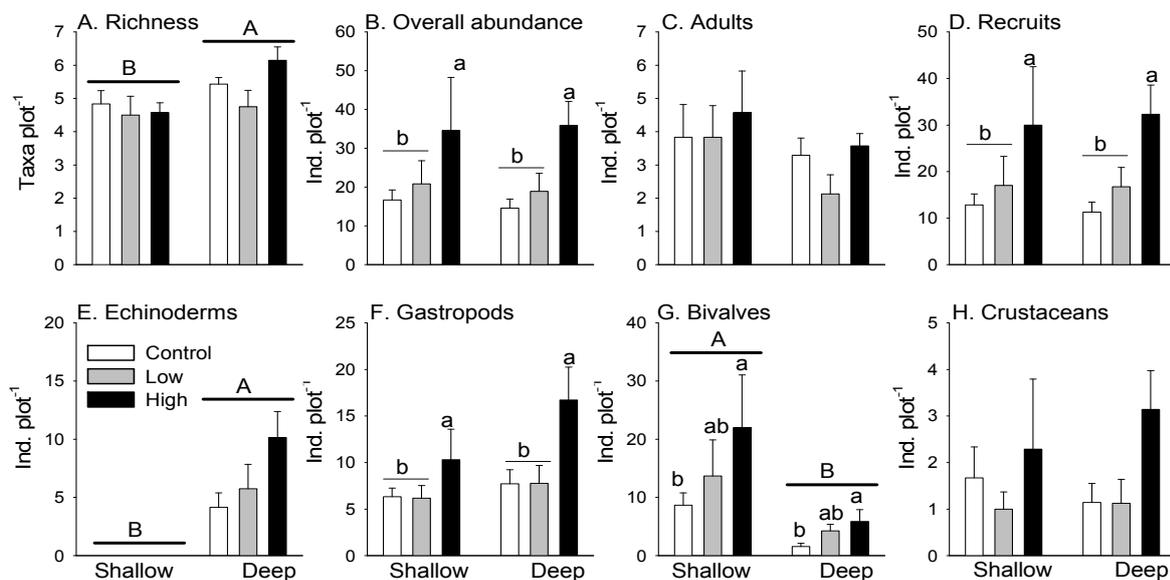
Figure 1. Impacts of the invasive drift macroalgae *Gracilaria vermiculophylla* on native invertebrates at two depth levels in a *Zostera marina* seagrass bed, Snaptun Harbor, Denmark; Capital vs. lower case letters correspond to significant different depth and drift algal effects, respectively (SNK tests for *Gracilaria* treatments). Data variability = 1 SEM, n = 6-8 per depth × drift algal treatment-combination. The low algal density treatment correspond to 110 (initial) to 55 (final) gWW m^{-2} and the high algal density treatment to 440 (initial) to 220 (final) gWW m^{-2}. Deep site = 2 m and Shallow site = 0.5 m. See table 1 for ANOVA results.

likely due to a total absence of individuals). Finally, I found consistent support for the habitat-formation hypothesis on "all invertebrates" (recruits and adults combined), "recruits-only", "gastropods", and "bivalves", with significantly highest densities at both depth levels associated with high *Gracilaria* biomass (Figure 1B, D, F, G).

Discussion

Most invertebrate groups were positively affected by the presence of *Gracilaria* in the *Zostera marina* habitat. Thus, this study provides experimental evidence of positive effect of invasive seaweed in seagrass bed (Rodriguez 2006; Williams 2007; Thomsen et al. 2009b). These data also represent a novel habitat cascade that was not described in a recent review over facilitation and habitat cascades (Thomsen et al. 2010). Here, the seagrass provides a *basal biogenic habitat* for invertebrates and *Gracilaria*, and *Gracilaria* subsequently provide an *intermediate embedded biogenic habitat* to support additional fauna. Although this may be the first experiment to demonstrate that invasive

drift algae can have positive effects on seagrass inhabiting macro-invertebrates under field conditions, several other experiments have shown that native drift algae can facilitate invertebrate abundances in seagrass beds. For example, higher densities of the snails *Potamopyrgus antipodarum* (J. E. Gray, 1853) (Cummins 2004) and *Hydrobia ulva* Pennant (Cardoso et al. 2004) and, more generally, invertebrate richness and total invertebrate abundances (Holmquist 1997) have been found when native drift algae have been added to seagrass habitats. However, these studies also reported negative effects on different invertebrate taxa and discussed how drift algae can have negative impacts on the seagrass itself, via competition for light and nutrients and by increasing anoxia, sulphide and ammonia levels in the water column or sediment pore-water. Such negative effects can result in long-term reductions in the stability of the habitat cascade where drift algae ultimately destroy the seagrass habitat (Holmquist 1997; McGlathery 2001; Hauxwell et al. 2003), causing detrimental effect to the seaweed itself (loss of protection from tidal currents and storm waves) and the entire

associated invertebrate assemblages. However, under most natural circumstances this chain of negative cascading interactions is unlikely for *Gracilaria* invasion into the Danish seagrass beds. There were no apparent visible effects of *Gracilaria* on *Zostera* seagrass leaf size or density (pers. obs.) and experimental studies have failed to detect negative impacts of *Gracilaria* (or the morphologically similar *Gracilariopsis*) on *Zostera* at ambient temperatures and algal densities (but extreme densities/temperatures can cause negative effects) (Huntington and Boyer 2008; Martínez-Lüscher and Holmer 2010; Hoeffle 2010). Clearly, future studies should focus on the environmental threshold conditions where invasive (and native) drift algal effects shift from positive or neutral to negative on the seagrass as well as the associated invertebrate community. Such thresholds are likely to depend on a complex mixture of seagrass attributes (size, clonal integration, morphology, strategy, health), algal attributes (density, areal extent and time of coverage, morphology, life-strategy, form-functional attributes, respiration rates), and environmental conditions (temperature, salinity, nutrients, desiccation, light, hydrodynamics, sedimentation).

The experiment provides causal evidence of positive effects of an invader on invertebrate abundances, but revealed little about the specific mechanisms whereby this occurs. There are two likely, and not mutually exclusive, explanations; positive effects are driven by *quantitative* and/or *qualitative* differences in habitat attributes and resource provision between the invader and the seagrass (Thomsen et al. 2010). It is likely that *Gracilaria* provides shelter from predators, food for grazers and/or attachment space for recruits (stress amelioration is less likely in subtidal habitats) (Norkko et al. 2000; Cardoso et al. 2004; Nyberg et al. 2009). The experiment was conducted as an "addition-design" to reflect a typical invasion process (Thomsen et al. 2009b). It may therefore be that the increase in "total habitat", i.e. associated increase in shelter, food and attachment space, drive the patterns irrespective of the species-identity of the invader. Thus, if *Zostera* (or native drift algae) for whatever reason was able to increase its biomass, similar positive effects could occur. The alternative model emphasizes that *Gracilaria* differ *qualitatively* from *Zostera* regarding resource provision. For example, *Gracilaria* is positioned horizontally on the

sediment, has cylindrical branching laterals that are not "shed" (but asexual reproduction may occur via fragmentation) and is relatively palatable. In contrast, *Zostera* leaves are linear, flat and unbranched, stand up, are shed regularly during ontogenesis, and are less palatable. Perhaps these qualitative differences cause invertebrates to be positively affected by *Gracilaria*. Thus, small bivalves were typically found attached to algal branches (e.g. *Mytilus edulis* Linnaeus, 1758), snails (e.g., *Littorina littorea* Linnaeus, 1758) may respond to increased food (Thomsen et al. 2007), and small sea stars (*Asterias rubens* Linnaeus, 1758) may utilize both additional food (e.g. snails and bivalves) and predation refuge from large crabs (e.g., *Carcinus maenas* Linnaeus, 1758) (Falls 2008). Ultimately, more advanced experiments are needed to distinguish between these models, by combining multiple densities of both the seagrass and invasive algae with orthogonal resource manipulations, e.g. using mimics that do not provide food subsidy, and cages to exclude predators. Extrapolation of the present results to larger spatio-temporal scales will depend on whatever *Gracilaria* eventually reduce seagrass habitats (discussed above) and/or replace native drift algae. For example, in Danish estuaries native algae such as *Fucus vesiculosus* Linnaeus, *Ulva lactuca* Linnaeus, and *Chaetomorpha linum* (O.F. Müller) Kützing can occur in seagrass beds. Thus, it is also important to quantify if *Gracilaria* provides a novel algal habitat or substitute native algal habitat, within seagrass beds.

In conclusion, there were positive effects of the invasive *Gracilaria* on native invertebrate abundances inhabiting seagrass beds, but particular so for gastropods and bivalves. Follow-up studies should quantify (a) thresholds were positive or neutral effects of invaders on seagrasses and associated invertebrates shift to negative effects, (b) the mechanism whereby positive effects occurs (quantity vs. quality of habitat/resource provision), (c) if *Gracilaria* provide a novel habitat in invaded seagrass beds or if it displaces native drift algae, and (d) the larger ecosystem implications of these three points.

Acknowledgements

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