

# Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a soft-bottom turbid lagoon

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**Abstract** Invasive species are often hypothesized to have superior performance traits. We compared stress tolerance (as change in biomass) of the invasive macroalgae *Codium fragile* ssp. *tomentosoides* and *Gracilaria vermiculophylla* to the native macroalgae *Fucus vesiculosus*, *Agardhiella subulata*, *Hypnea musciformis* and *Ulva curvata* in Hog Island Bay, a shallow lagoon in Virginia, USA. We hypothesized that the success of the two aliens is due to their high tolerances of turbidity, sedimentation, desiccation, grazing and nutrient enrichment. Like many lagoons, Hog Island Bay is characterized by extensive intertidal mudflats, high turbidity and sedimentation, and high densities of omnivorous mud snails. Nutrient enrichment may also become a problem as land use practices in adjacent watersheds change. Contrary to our hypothesis, *C. fragile* was less resistant to sedimentation, desiccation and grazing than other algae and had low growth at all light and nutrient

levels. This suggests that any superior performance of this invasive species compared to native algae is probably limited to microhabitats where stress is minimal and where bivalve shells facilitate recruitment and long-term persistence. In contrast, *G. vermiculophylla* was resistant to desiccation, burial and grazing, and was not negatively influenced by either high or low light or nutrient levels. These traits reflect the current success of *G. vermiculophylla* in already invaded lagoons and estuaries, and indicates that it will likely continue its spread in European and North American turbid and tidal soft-sediment systems.

**Keywords** Growth · Invasive macroalgae · Lagoon · Traits

## Introduction

Invasions of alien species are considered a major threat to global biodiversity because the invaders often outcompete, eat or infect native species (Ruiz et al. 1997; Meinesz 1999). Several marine macroalgae have caused dramatic transoceanic invasions. In particular, invasions of *Caulerpa taxifolia* (M. Vahl) C. Agardh, *Undaria pinnatifida* (Harvey) Suringar, *Sargassum muticum* (Yendo) Fensholt, *Codium fragile* ssp. *tomentosoides* (van Goor) Silva (hereafter *C. fragile*), and most recently *Gracilaria vermiculophylla* (Ohmi)

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Papenfuss, have created adverse effects worldwide by competing with native algae, altering the nursery habitat for fishes and invertebrates, reducing light penetration, changing biogeochemical cycles, and suffocating or drifting away with economically important shellfish (Chapman 1999; Meinesz 1999; Wallentinus 2002; Rueness 2005). Often the success of such cosmopolitan invaders has been related to ‘super’ traits, e.g., high growth, dispersal capacity and regenerative abilities (Rejmánek and Richardson 1996; Trowbridge 1998; Nyberg and Wallentinus 2005). It is clearly of importance to understand how these traits influence algal performance if future invasions are to be predicted, managed and prevented. Conclusions about traits that make macroalgae successful have often been interpreted from multiple single-species one-factorial laboratory experiments (e.g. Littler 1980; Wallentinus 1984; Pedersen and Borum 1997). However, to improve our understanding of invader success we also need realistic multi-species multi-factorial field experiments where the performance of invasive species is compared to native species under conditions typical of the invaded habitat (Nyberg and Wallentinus 2005).

*C. fragile* originated from Asia, and spread to the North American east coast in the 1950’s and arrived in Virginia in the 1970’s, either attached on transplanted oysters, on ship hulls or as drifting thalli from northern regions (Hillson 1976; Trowbridge 1998). Today, *C. fragile* is the fourth most common species in Hog Island Bay, a shallow turbid lagoon on the Delmarva Peninsula in Virginia (Thomsen et al. 2006). *G. vermiculophylla* is also of Asian origin, and although we do not know when it arrived in Virginia, we believe it arrived attached to transplanted oysters. Several native *Gracilaria* species are common in the western Atlantic, and because of high phenotypic plasticity and lack of definitive morphological and anatomical characteristics of unattached individuals, the presence of *G. vermiculophylla* in the Eastern Atlantic has only been discovered recently using molecular techniques (Rueness 2005; Thomsen et al. 2005). *G. vermiculophylla* is now the most abundant species in Hog Island Bay, constituting ca. 80% of the total biomass (earlier identified as *G. verrucosa*, Thomsen 2004a, b; Thomsen and

McGlathery 2005). *C. fragile* and *G. vermiculophylla* have both been described as successful invaders of shallow turbid lagoons and estuaries (Fralick and Mathieson 1973; Malinowski and Ramus 1973; Carlton and Scanlon 1985; Trowbridge 1998; Rueness 2005), a notion supported by their dominance in Hog Island Bay. We therefore expected the two aliens to have superior performance under conditions typical of such ecosystems, including low light availability due to high water column turbidity (McGlathery et al. 2001; Lawson 2003), high mesograzer densities (e.g. mud snails, Giannotti and McGlathery 2001), high sedimentation rates (Lawson 2003) and nutrient enrichment from the agricultural watershed (Goshorn et al. 2001). In addition, tidal changes create small-scale vertical gradients in desiccation stress, sedimentation and light availability (Doty 1946; Lewis 1964), whereas different distances from a mainland source of nutrients and sediments result in horizontal gradients in nutrient availability, turbidity, salinity and sedimentation levels (Castel et al. 1996; McGlathery et al. 2001). Thus, we hypothesized that to invade and persist throughout the lagoon, *C. fragile* and *G. vermiculophylla*, should perform well, in terms of biomass changes, under conditions typical of both high and low elevations and across a transect of near-mainland, mid-lagoon and near-ocean sites.

We compared performances of these two invasive species to 4 native species, typical of West Atlantic lagoon drift algal assemblages (Cowper 1978; Thorne-Miller et al. 1983; Goshorn et al. 2001): *Fucus vesiculosus* L., *Agardhiella subulata* (C. Ag.) Kraft et Wynne, *Hypnea musciformis* (Wulfen) Lamouroux, and *Ulva curvata* (Kützinger) De Toni. The 6 test species together constitute more than 90% of the biomass in Hog Island Bay and thereby reflect a simple, but realistic, model of the total drift-algal community (Thomsen 2004a).

## Material and methods

### Study site

Hog Island Bay is a ca. 100 km<sup>2</sup> lagoon on the Delmarva Peninsula on the eastern shore of

Virginia, US (McGlathery et al. 2001). The average depth is 1.5 m and ca. 80 % of the lagoon is less than 3 m deep (Oertel 2001). Seagrass became locally extinct in the lagoon in the 1930's as the result of disease and storms. Today the macrophyte community is dominated by macroalgae that either drift around with tidal currents, are attached to shells in the soft sediment (McGlathery et al. 2001; Thomsen 2004a) or incorporated into tube caps of the polychaete *Diopatra cuprea* (Thomsen et al 2005). Mud snails are present year round in high densities (e.g. ca. 80 m<sup>-2</sup> near Hog Island) in marshes and on mudflats (Giannotti and McGlathery 2001). Dissolved nitrogen in the water column is typically 15–20 µM and light extinction between 1.7 and 2.2 m<sup>-1</sup>, with highest values near the mainland and lowest near the ocean (McGlathery et al. 2001). Sedimentation, resuspension and suspended solid concentrations are high throughout the lagoon (partly due to the lack of rooted angiosperms), and storms can add or remove several centimeters of sediment within a few hours. For a map of study sites within Hog Island Bay see Thomsen (2004a).

### General procedures

Six experiments were conducted to test for the effects of sedimentation (days of burial), elevation, distance from the mainland, light availability, nutrient availability, and mud snail grazing on macroalgal biomass. Two additional experiments were conducted to test for experimental artifacts, including the twist-tie used to fix algal fragments in place (in open-plot experiments) and cage enclosure (in closed-plot experiments). Details on experimental designs are given in Table 1. Apical fragments cut from fresh algal specimens were collected from drift mats in the mid-lagoon shoal area, and allowed 24 h of wound recovery before field incubation. Initial wet weights (WW) of 0.2–2 g were used, after blotting with a towel. Performance was defined as percent change in biomass per experimental period (5–16 days, except burial experiment which lasted up to 37 days). Thus, we use 'performance', 'biomass change', 'tissue growth' (positive or negative), and 'stress tolerance' interchangeable, to include

all gain and loss-processes experienced during the experimental period.

### Burial

To test for burial tolerance, a litterbag decomposition experiment was conducted. Pre-weighed fragments were incubated in 2 mm mesh bags buried under 2–3 cm sandy sediment at a mid-lagoon mudflat (– 0.5 m MSL). This burial depth was chosen based on observations of fresh algal fragments found in sediment cores taken at the site. Sediment characteristics at the site were: 2.1% DW organic matter, 11.8 molar C:N, 1.51 g cm<sup>-3</sup> bulk density, and a mean grain diameter of 63 µm (McGlathery et al. 2001; Lawson 2003).

### Elevation

To test for the effects of vertical elevation and horizontal distance, two open-plot experiments were carried out in spring 2002 (16 and 14 days). Algae were first attached to a cable tie using a twist-tie wrapped around a small part of the fragment. Cable ties were then attached at high (0.0 m MSL) and low (– 0.8 m MSL) elevations on PVC poles, inserted at 5 near-mainland, 5 mid-lagoon and 5 near-ocean sites, where within location sites were separated by a minimum of 500 m. The second experiment was similar to the first, except that the 'high'-elevation treatment was reduced to – 0.5 m MSL. This, lower 'high-elevation' treatment was chosen to fine-tune species-specific differences in elevation tolerance (as several species were severely impacted at the high elevation of the first experiment).

### Light, nutrient and grazer effects

Cage experiments were conducted to test for the effects of shading, nutrient addition, and grazing by mud snails. Each experiment was conducted simultaneously at a near-mainland, mid-lagoon and near-ocean site (McGlathery et al. 2001; Thomsen 2004a). Allocations of fragments, treatments and positions of the cages were random. Fragments were enclosed in 22 cm transparent acrylic cages (closed with plastic caps) with

**Table 1** Summary of experiments

Test objective	Factorial design	Dates and temperature	Comments
Exp <sub>1</sub> . Burial	11 DAY × 2–8 REP	17/6 to 23/7 (24°C)	Loose fragments in litterbags covered by 2–3 cm sediment, no <i>H. musciformis</i> , only conducted at mid-lagoon site
Exp <sub>2</sub> . Elevation (high) & Distance	2 ELE × 3 DIS × 5 REP	11/3 to 27/3 (11°C)	Fixed fragments with twist tie in open plots, 0.8 versus 0.0 m below MSL, no <i>H. musciformis</i> or <i>U. curvata</i>
Exp <sub>3</sub> . Elevation (low) & Distance	2 ELE × 3 DIS × 5 REP	27/3 to 15/4 (13°C)	Fixed fragments with twist tie in open plots, 0.8 versus 0.5 m below MSL, no <i>H. musciformis</i> or <i>U. curvata</i>
Exp <sub>4</sub> . Light & Distance	2 LIG × 3 DIS × 4 REP	26/6 to 4/7 (26°C)	Loose fragments in 22 cm closed transparent cages, white versus black
Exp <sub>5</sub> . Nutrients & Distance	2 NUT × 3 DIS × 2 EXP × 4 REP	9/7 to 16/7 and 17/7 to 24/7 (26°C)	Loose fragments in 22 cm closed transparent cages, 2 vs. 0 nutrient stakes per cage, nitrogen analysis
Exp <sub>6</sub> . Grazers & Distance	2 GRA × 3 DIS × 4 REP	25/7 to 31/7 (27°C)	Loose fragments in 22 cm closed transparent cages, low (0, 2) versus high (7, 20 per cage) mud snail density, nitrogen analysis
Exp <sub>7</sub> . Twist tie & Distance	2 TWI × 3 DIS × 4 REP	19/7 to 25/7 (27°C)	Loose fragments in 22 cm closed transparent cages, twist tie versus no twist tie around algal tissue
Exp <sub>8</sub> . Caging & Distance	2 CAG × 3 DIS × 3 REP	26/7 to 31/7 (27°C)	Fixed fragments with twist tie in open plot (on rebar) versus fixed fragments with twist tie in 22 cm closed transparent cages (on rebar inside cages)

DIS = horizontal distance from mainland, ELE = vertical elevation level, EXP = experiment number, DAY = days of burial, LIG = light level (shading), NUT = nutrient level, GRA = grazer additions, TWI = twist tie wrapping, CAG = caging, REP = replicates

small holes that kept grazers out but fragments inside and still ensured a steady water flow. Cages reduced photosynthetic active radiation (PAR) by 11%, based on 10 readings from a sunny summer day from 10 AM to 6 PM. The mean total algal density at the start of these experiments was  $130 \text{ g WW m}^{-2}$  ( $n = 230$ ,  $SD = 33 \text{ g WW m}^{-2}$ , where densities within cages were calculated based on the area of the lower half-cylinder =  $0.028 \text{ m}^2$ ). These densities are common in Hog Island Bay (Thomsen et al. 2006). Cages were attached horizontally to floating PVC frames 15 cm below the water surface. The effect of light reduction due to water column turbidity was tested by comparing cages covered with white versus black screening, corresponding to 32 and 51% reduction in PAR. The effect of nutrients was tested by adding two fertilizer stakes to half of the cages, similar to the method used in other enrichment studies (Worm et al. 2000). A stake weighed 62 g and contained 4% available phosphate and 2%  $\text{NO}_3^-$ , 2% urea, 2% other soluble N and 7% water insoluble N (Jobe's Fertilizer Spikes™). This experiment was repeated in two consecutive weeks to reduce the high data variability observed in the first experiment and to obtain extra biomass for tissue nitrogen (N) analysis (the two nutrient addition experiments were pooled for data analysis, Exp<sub>5</sub>, Table 1). To test for the effects of grazers, the mud snail *Ilyanassa obsoleta* (Say) was added as 0, 2, 7 and 20 snails per cage following 24 h of starvation. The mud snails utilized all cage surfaces, and snail densities were calculated using the total cage surface ( $0.055 \text{ m}^2$ ) to equal 0, 36, 126 and 362 snails  $\text{m}^{-2}$ , which correspond to the range of densities commonly found in Hog Island Bay (Giannotti and McGlathery 2001). To increase the number of statistical replicates and to obtain more biomass for tissue N analysis, treatments were pooled into low (0 and 2 snails) versus high (7 and 20 snails) grazer densities. Tissue N was measured in the nutrient experiment to verify that the stakes enriched the N-limited algae (Tyler 2002), and in the grazer-experiment to determine if the grazers can facilitate growth by N excretion as has been shown in previous studies (Williams and Carpenter 1988; Fong et al. 1997). Tissue was rinsed in deionized water, oven dried

at 70°C, ground to homogeneity, and %N of the dry mass was measured in a Carlo-Erba NA 2500 Elemental Analyzer.

### Methodological artifacts

Two experiments were conducted in order to compare the cages where fragments were loose-lying and the open plots where fragments were fixed with a twist-tie. In the first experiment, the effect of the twist-tie was tested by tying half of the fragments and incubating them loose-lying within the cages. In the second experiment, the combined effect of twist-tying, spatial fixation, and cage enclosure was tested by twist-tying and fixing algal fragments onto rebar and then incubating half of the rebar inside and half outside closed cages. These experiments were also conducted simultaneously at the near-mainland, mid-lagoon and near-ocean sites.

### Data analysis

The decomposition experiment was modeled with first order kinetics of time versus remaining biomass (exponential decay model, Enriquez et al. 1993; Bourgues et al. 1996). Fixed factorial ANOVAs were conducted on all other experiments on *C. fragile* and *G. vermiculophylla* biomass change (%) and total N content per fragment (%N of  $\text{gDW} \times \text{gDW}$ ). Significant effects on the distance factor were followed by Student–Neuman–Keul (SNK) tests. Some experiments had heterogeneous variances: *C. fragile* Exp<sub>2</sub> ( $P = 0.01$ , Levene's test) and Exp<sub>6</sub> ( $P = 0.00$ ) and *G. vermiculophylla* Exp<sub>3</sub> ( $P = 0.02$ ) and Exp<sub>8</sub> ( $P = 0.01$ ). Significant effects of these tests were evaluated conservatively using  $P < 0.01$ , but note that ANOVA is relatively robust to variance heterogeneity for balanced designs with large sample sizes (Underwood 1997; Quinn and Keough 2002). We did not conduct statistical analysis that directly compared the six species performances because such responses are non-independent (Roa 1992). Instead, we make graphical comparisons, a simple method often used to analyze preference experiments (e.g. Hay et al. 1988; Camilleri 1989; Barker and Chapman 1990). We only show the pooled single factor

results, as most interactions were insignificant (Table 3) or trivial (Thomsen 2004a).

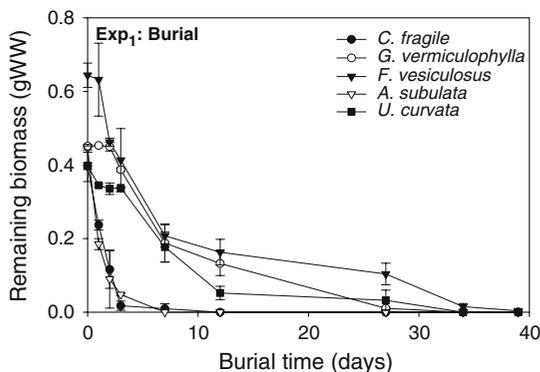
## Results

### Burial

*C. fragile* was sensitive to burial, and decomposed fast (half life = 4 days) compared to all other species except *A. subulata* that also was sensitive to burial (2 days). Decomposition rates were slower for *G. vermiculophylla* (9 days), and for the natives *U. curvata* (9 days) and *F. vesiculosus* (14 days, Fig. 1, Table 2). It should be noted that remaining biomass may not necessarily reflect recovery abilities. Although biomass was observed for *F. vesiculosus* for the longest period, its tissue structure clearly degraded relatively fast by turning soft and black, probably with poor ability to recover. In contrast, remaining *G. vermiculophylla* and *U. curvata* tissue appeared structurally intact and ‘healthy’ after several weeks of burial. Specific recovery experiments are needed to test these observations.

### Elevation

There were significant effects of elevation on both *C. fragile* and *G. vermiculophylla* (Exp<sub>2</sub>, Table 3, Fig. 2A) at all sites (Fig. 2B) in the first elevation



**Fig. 1** Effect of burial time on macroalgal biomass. Error bars are Standard errors ( $n = 2-8$ ). Regressions of Log-transformed biomass versus burial time are reported in Table 2. *H. musciformis* was not present in sufficient material at the time of sampling

experiment (0.8 m vertical difference). Performance was highest at the low elevation, a pattern also observed for the two native species (but less obvious for *F. vesiculosus*). In contrast, in the second experiment (0.3 m vertical difference, Exp<sub>3</sub>, Table 3, Fig. 2C) there was a negative effect of elevation only on *C. fragile*. Again, there were no effects of distance (Fig. 2D). For the native species, there was a strong negative effect of high elevation on *A. subulata*, whereas there was no effect on *F. vesiculosus*.

### Light, nutrients and grazer effects

In the light experiment, there were no significant effects of either shading or distance from the mainland on *C. fragile* or *G. vermiculophylla* biomass (Exp<sub>3</sub>, Table 3, Fig. 3A, B). In comparison, *A. subulata*, *H. musciformis* and *U. curvata* all had highest performance in the high light treatments and at the mid-lagoon site, demonstrating that the reduction in PAR from 51 to 32% of surface levels can indeed limit growth of these species. Similarly, nutrient additions did not influence the performance of either of the two invasive species, although there was a tendency for *G. vermiculophylla* to have higher growth in the high-nutrient treatments (Exp<sub>4</sub>, Table 3, Fig. 3C, D). In this experiment, there was a significant effect of distance from the mainland on *C. fragile*, where growth was lowest at the near-mainland site and highest at mid-lagoon and near-ocean sites (SNK test). Again, *H. musciformis* and *U. curvata*, outgrew the two alien species, both with and without nutrient additions, and again with highest growth at the mid-lagoon site. In the grazer experiments, high densities of mud snails significantly influenced the biomass of *C. fragile* and *G. vermiculophylla* (Exp<sub>6</sub>, Table 3, Fig. 3E), but in opposite directions. Thus, whereas *C. fragile* was negatively affected, *G. vermiculophylla* was positively affected, as were most native species (except *F. vesiculosus*). In this experiment there were no distance effects although there was a tendency for *G. vermiculophylla* to have highest growth at the mid-lagoon site, a pattern somewhat more obvious for *A. subulata*, *H. musciformis* and *U. curvata* (Fig. 3F).

**Table 2** Burial experiment. Regressions of remaining biomass (Log gWW) versus days of burial

Species	<i>n</i>	Intercept	Slope	DF	SS	<i>r</i> <sup>2</sup>	<i>P</i>
<i>C. fragile</i>	11	– 0.63	– 0.19		3.20	0.47	<b>0.019</b>
<i>G. vermiculophylla</i>	25	– 0.22	– 0.08	23	2.00	0.78	<b>0.001</b>

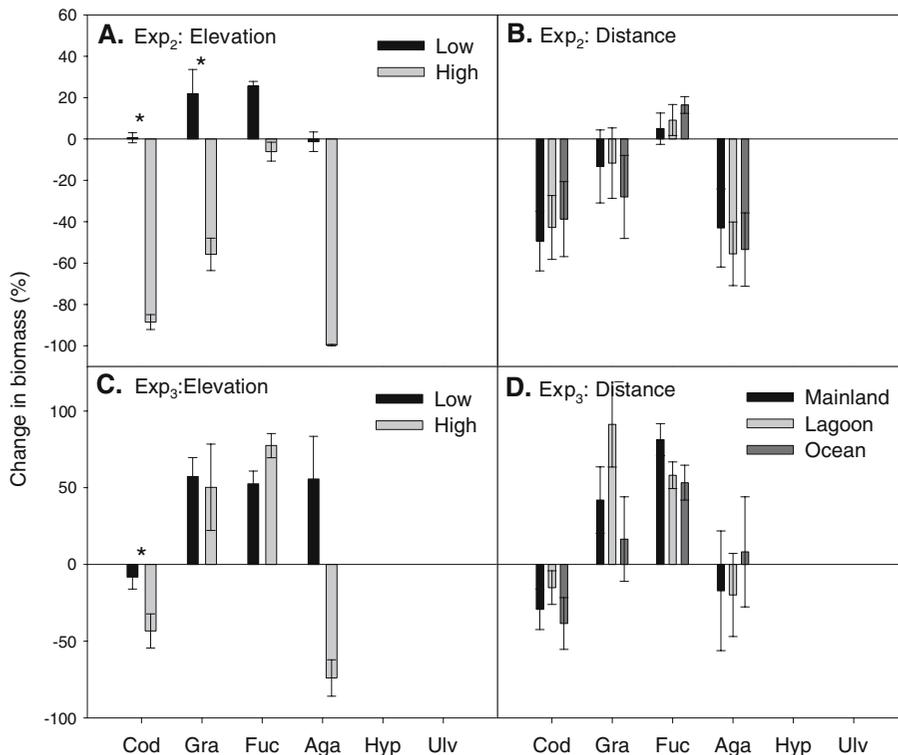
**Table 3** ANOVA results on *C. fragile* and *G. vermiculophylla* performances

Test	<i>C. fragile</i>				<i>G. vermiculophylla</i>				
	SS	DF	<i>F</i>	<i>P</i>	SS	DF	<i>F</i>	<i>P</i>	
Exp <sub>2</sub>	ELE	55447.1	1	433.41	<b>0.000*</b>	43423.5	1	30.81	<b>0.000</b>
	DIS	521.8	2	2.04	0.154	1395.2	2	0.50	0.616
	ELE × DIS	124.4	2	0.49	0.621	3522.1	2	1.25	0.306
	Error	2814.5	22			31002.0	22		
Exp <sub>3</sub>	ELE	9026.3	1	6.66	<b>0.017</b>	1046	1	0.19	0.671
	DIS	1720.1	2	0.63	0.540	22066	2	1.96	0.166
	ELE × DIS	1839.1	2	0.68	0.518	24812	2	2.20	0.136
	Error	28450.0	21			118447	21		
Exp <sub>4</sub>	LIG	255.3	1	1.42	0.252	387.8	1	1.14	0.299
	DIS	15.1	2	0.04	0.959	813.1	2	1.20	0.324
	LIG × DIS	1096.6	2	3.06	0.077	420.8	2	0.62	0.549
	Error	2692.0	15			6099.2	18		
Exp <sub>5</sub>	NUT	4.2	1	0.05	0.830	721	1	0.67	0.416
	DIS	1246.1	2	7.02	<b>0.002</b>	102	2	0.05	0.954
	NUT × DIS	61.1	2	0.34	0.711	2500	2	1.17	0.321
	Error	3727.9	42			45004	42		
Exp <sub>5</sub> Nit	NUT	1.026	1	4.63	<b>0.037</b>	0.681	1	6.30	<b>0.016</b>
	DIS	0.191	2	0.43	0.653	0.524	2	2.42	0.102
	NUT*DI	0.172	2	0.39	0.681	0.157	2	0.73	0.489
Error	9.314	42			4.105	38			
Exp <sub>6</sub>	GRA	15387.7	1	10.07	<b>0.005*</b>	44558	1	21.32	<b>0.000</b>
	DIS	2213.6	2	0.72	0.498	4559	2	1.09	0.357
	GRA × DIS	1778.7	2	0.58	0.569	1467	2	0.35	0.709
	Error	27498.7	18			37612	18		
Exp <sub>6</sub> Nit	GRA	0.006	1	0.71	0.415	3.368	1	23.35	<b>0.000</b>
	DIS	0.077	2	4.23	<b>0.038</b>	0.590	2	2.05	0.158
	GRA*DIS	0.006	2	0.31	0.737	0.706	2	2.45	0.115
Error	0.118	13			2.596	18			
Exp <sub>7</sub>	TWI	41.7	1	1.10	0.310	47.9	1	0.24	0.627
	DIS	488.4	2	6.42	<b>0.008</b>	330.5	2	0.84	0.447
	TWI × DIS	14.1	2	0.19	0.833	446.9	2	1.14	0.343
	Error	646.9	17			3331.1	17		
Exp <sub>8</sub>	CAG	57.4	1	0.65	0.434	43321.8	1	26.23	<b>0.000*</b>
	DIS	893.6	2	5.09	<b>0.025</b>	5510.4	2	1.67	0.230
	CAG × DIS	600.5	2	3.42	0.067	3466.4	2	1.05	0.380
	Error	1053.2	12			19820.8	12		

Significant results (*P* < 0.05 for homogeneous and *P* < 0.01 for heterogeneous variances, shown with asterisk) are in bold. Confer Table 1 for abbreviations and description of test designs. Nit = test on total tissue Nitrogen content

The tissue N content was highest for all species in the nutrient addition cages (Fig. 4A), indicating that the enrichment treatment was effective. Growth of the two invasive species (as well as *A. subulata* and *F. vesiculosus*) did not appear to be N limited since there was no increase in growth rates associated with the enhanced tissue N content. In contrast, growth of *H. musciformis*

and *U. curvata* were higher in thalli that had elevated N content, suggesting N limitation for these species. In the grazing experiment, N excretion did however appear to facilitate growth of *G. vermiculophylla* (and *A. subulata* and *U. curvata*), as indicated by significantly higher growth and tissue N content in the cages with high snail densities (Fig. 4C).



**Fig. 2** Effect of elevation (A = 0 to  $-0.8$  m MSL; B =  $-0.5$  to  $-0.8$  m MSL) and distance (B, D) on biomass changes. Cod = *C. fragile*, Gra = *G. vermiculophylla*, Fuc = *F. vesiculosus*, Aga = *A. subulata*, Hyp = *H. musciformis*, Ulv = *U. curvata*. Errors bars are standard errors,

cf. Table 1 for number of replicates and design description. *U. curvata* and *H. musciformis* were not present in sufficient material at the time of sampling. Letters and asterisk's designate statistically different groups for *C. fragile* and *G. vermiculophylla*

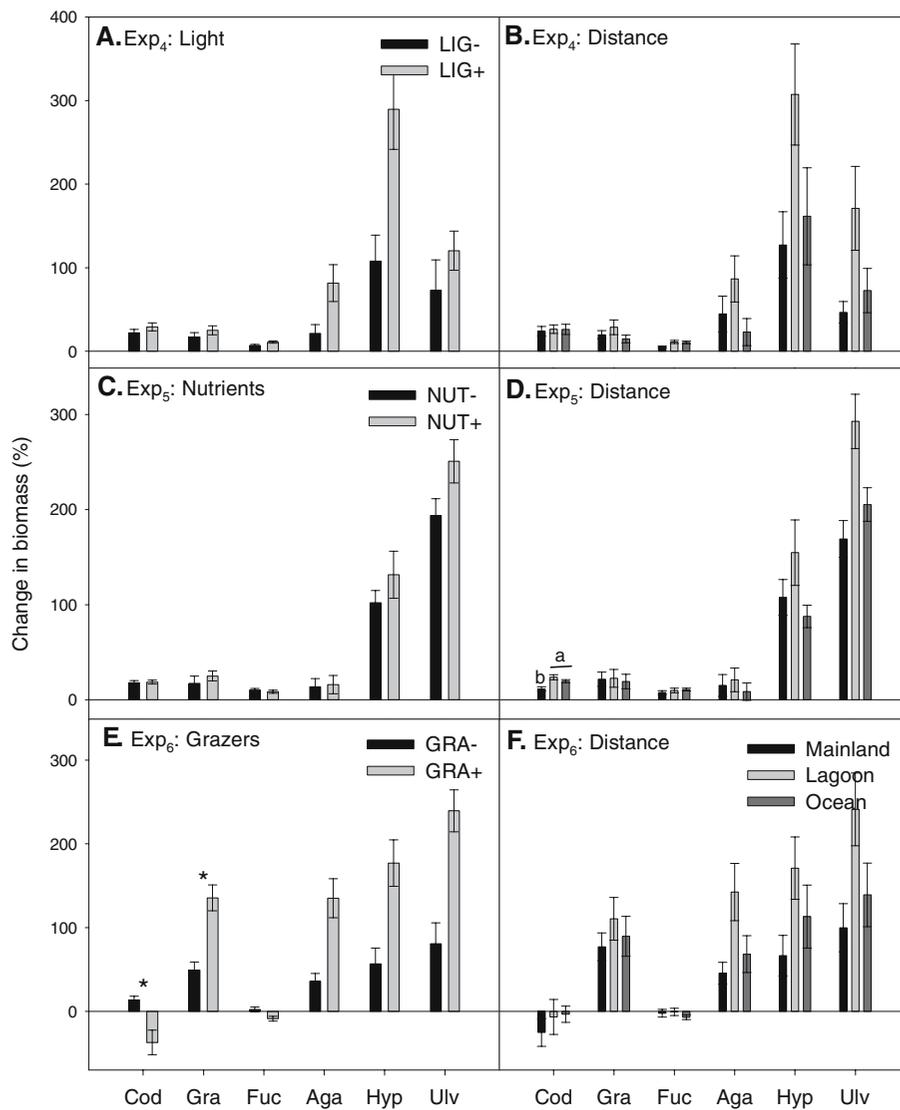
### Methodological artifacts

The twist tie procedure is a reasonable approach to obtain 'open plot' performance data. There was no effect of the twist ties on either *C. fragile* or *G. vermiculophylla* (Exp<sub>7</sub>, Table 3, Fig. 5A), whereas *A. subulata*, *H. musciformis* and *U. curvata* showed a 10–20% growth reduction in twist-tie treatments. Caging did not affect *C. fragile* (or *F. vesiculosus* or *A. subulata*), but *G. vermiculophylla* (and *H. musciformis*, *U. curvata*) were affected significantly, with higher growth in open plots (Exp<sub>8</sub>, Table 3, Fig. 5C). This suggests that these species are limited by caging, e.g. due to nutrient or light reduction, particularly in experiments like this where physical disturbance, sedimentation and grazing was likely minimal (attached to floating structures just below the surface). In the caging experiment, *C. fragile* was once more significantly affected by distance, and

again with low growth at the near-mainland site and high growth at mid-lagoon and near-oceans sites (Fig. 5D).

### Discussion

We document that, contrary to our hypothesis, *C. fragile* did not have higher stress-tolerances than native species under conditions that are characteristic of Northwest Atlantic coastal lagoons. Instead, *C. fragile* had relatively low growth under benign conditions (high light, low grazing, low elevation) and high biomass loss under stressful conditions (high grazing, sediment burial, high elevation, i.e. desiccation). This susceptible to burial, grazing and desiccation likely prevent it from becoming more dominant in Hog Island Bay. In contrast, *G. vermiculophylla* was considered a successful stress-tolerant invader,



**Fig. 3** Effect of Light reduction (A), nutrient addition (C), grazer additions (E) and distances from mainland (B, D, F) on biomass changes. Errors bars are standard errors, cf. Table 1 for number of replicates and design description,

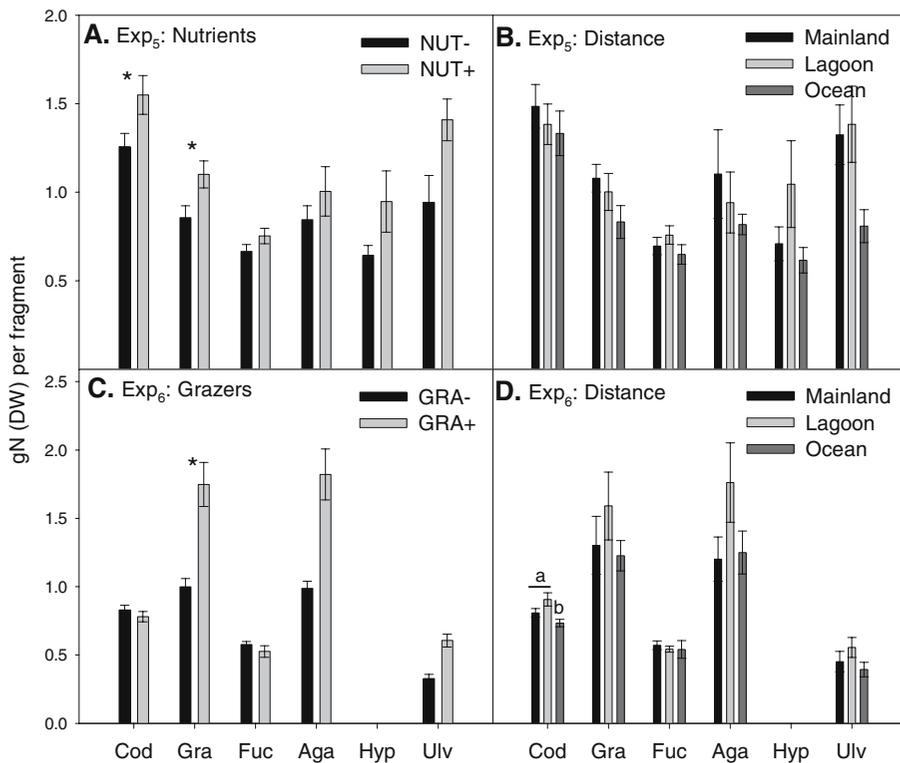
and Fig. 2 for species abbreviations. Letters and asterisk's designate statistically different groups for *C. fragile* and *G. vermiculophylla*

with high resistance to sedimentation, desiccation, grazing as well as low light and low nutrients. This tolerance reflects its dominance at most locations in the lagoon, including both intertidal and shallow subtidal elevations.

**Burial**

Sediment deposition and burial are fundamental characteristics of coastal lagoons and estuaries

(Schoellhamer 1996; McManus 1998; Thomsen 2004a). In Hog Island Bay, sediment cores often contain a top layer with embedded small algal fragments and a deeper black organic-rich layer indicating past burial events (Pers. obs.). Hence, it is clearly important for macroalgae in lagoons to be resistant to burial. Our results suggest that *C. fragile* tissue is inferior to many native species in burial resistance. We found that *C. fragile* (and *A. subulata*) decomposed fast compared to other



**Fig. 4** Effect of nutrient addition (A), grazer additions (C) and distances from mainland (B, D) on nitrogen content per species. Errors bars are standard errors, cf. Table 1 for number of replicates and design description,

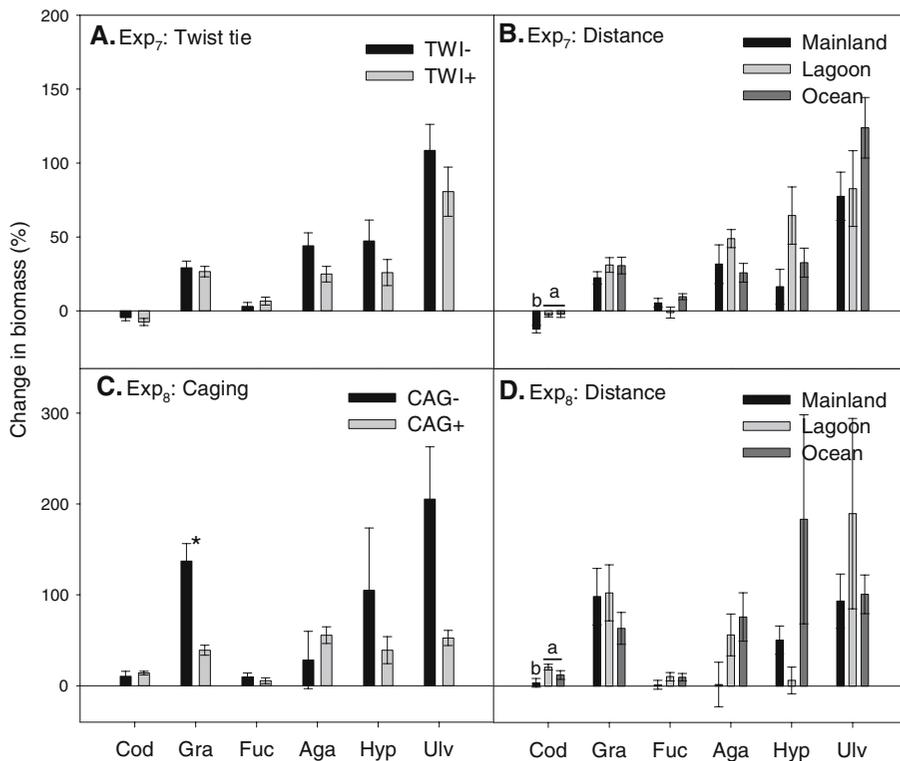
algae (this study, Santelices et al. 1984; Trowbridge 1996; Kamermans et al. 1998). In particular, *C. fragile* decomposed faster than *U. curvata*, even though a high SA:V ratio, simple and thin structure, high protein content, and low C:N ratio theoretically should make *U. curvata* susceptible to rapid breakdown (Duarte 1992; Enriquez et al. 1993). In comparison, *G. vermiculophylla* decomposed more slowly, and its tissue appeared structurally intact and healthy even after a week of complete burial, an observation confirmed by pulse-amplified modulated fluorescence that showed this material to be viable of photosynthesis (Thomsen 2004a). Clearly, *G. vermiculophylla* is well adapted to high-sedimentation habitats.

### Light

Lagoons typically are turbid habitats and it should be advantageous to perform well in low

and Fig. 2 for species abbreviations. Letters and asterisk's designate statistically different groups for *C. fragile* and *G. vermiculophylla*. Tissue samples of *H. musciformis* were lost from the grazer experiment

light conditions. Both *C. fragile* and *G. vermiculophylla* gained biomass in low and high light treatments, and with no apparent negative effect of shading, suggesting that they are not light limited at the low level. *C. fragile* is photosynthetically efficient at low light levels (Ramus et al. 1976a, b). However, in our experiment *C. fragile* did not have higher growth compared to *G. vermiculophylla* or native macroalgae under low light levels (51% PAR reduction). It is possible that greater light reduction would benefit the aliens since *G. vermiculophylla* can take up organic molecules (as *G. tikvahiae*, Tyler 2002) and survive for long periods in darkness (unpubl. data, Wallentinus et al. 2004), and *C. fragile* is positively buoyant potentially covering and shading other species with negative buoyancy. Such potential advantages are not reflected in our short-term tissue-based comparisons. It is interesting that *U. curvata* and *H. musciformis* had higher growth in the low-light treatment than the alien



**Fig. 5** Effect of twist-tie wrapping (A) and caging (C) and distances from mainland (B, D) on biomass changes. Errors bars are standard errors, cf. Table 1 for number of

replicates and design description and, Fig. 2 for species abbreviations. Letters and asterisk's designate statistically different groups for *C. fragile* and *G. vermiculophylla*

species, even though they are considered to be high-light adapted species with high SA:V ratios and high metabolic rates (Littler 1980; Pedersen 1995; Pedersen and Borum 1997; Krause-Jensen and Sand-Jensen 1998).

**Nutrients**

Lagoons are naturally nutrient-rich systems, and successful algae should be able to canalize high nutrient concentrations into growth (Pedersen and Borum 1996). Nutrient rich soft-bottom systems have been susceptible to invasion by both *C. fragile* (Hanisak 1979a, b; Trowbridge 1998) and *G. vermiculophylla* (Rueness 2005), and enrichment has been suggested to be of importance for their invasive success. However, we found that short-term nutrient enrichment did not increase the biomass of either alien, even though

tissue N concentrations increased. Instead, the growth response scaled with the SA:V ratio, with the largest growth effects for *H. musciformis* and *U. curvata* (Wallentinus 1984; Pedersen and Borum 1997). Nevertheless, the alien species increased their tissue N, providing storage to sustain growth if nutrients becomes depleted which may an advantage in coastal lagoons where the nutrient supply is often pulsed (Pedersen and Borum 1996; Pedersen and Borum 1997).

**Grazing**

Algal biomass in temperate lagoons can be controlled by grazing of crustaceans and gastropods (Duffy and Hay 1991; Geertz-Hansen et al. 1993; Giannotti and McGlathery 2001; Rosinski 2004). Here, the omnivorous mud snail *I. obsoleta* inhibited growth of *C. fragile* but facilitated

*G. vermiculophylla* and native species with high SA:V ratios. This snail is one of the most ubiquitous gastropods in West Atlantic lagoons (Kelaher et al. 2003) and can potentially influence growth over large geographical regions. The facilitation was likely caused by algal uptake of N-rich compounds excreted by the snails, a hypothesis supported by tissue-N data (Fong et al. 1997; Giannotti and McGlathery 2001). The grazing experiment was conducted late in the summer season, when the nutrient supply typically becomes limiting in the lagoon (McGlathery et al. 2001; Tyler et al. 2001; Tyler and McGlathery 2003). The contrasting inhibition of *C. fragile* was surprising because (a) alien species often are successful due to grazer escape (Boudouresque and Verlaque 2002; Myers and Bazely 2003), (b) *C. fragile* is considered a poor food for generalist herbivores (Trowbridge 1998; Scheibling and Anthony 2001), (c) alternative foods (e.g. *U. curvata*) with high tissue N content and low structural complexity were offered simultaneously (Geertz-Hansen et al. 1993; Cebrián and Duarte 1994). It is possible that the strong grazer effect is related to the siphonous cell structure of *C. fragile*, potentially making it vulnerable to abrasion.

#### Elevation gradient

Marine organisms have variable performances at different tidal elevations because they differ in their tolerances to desiccation (Stephenson and Stephenson 1949), biological interactions are constrained by time of inundation (Connell, 1961a; b; Paine 1966), and physical disturbances are linked to the water level (Paine and Levin 1981; Denny and Gaines 1990). *C. fragile* can occur in dense intertidal stands (Trowbridge 1998), and was thus expected to perform well in the intertidal zone. However, *C. fragile* lost biomass at both 0.0 and -0.5 m MSL, a pattern confirmed in additional experiments and reflecting its distribution in Hog Island Bay (Thomsen 2004a). Thus, invasions in Virginia should be limited to the lower intertidal zone, where desiccation stress is reduced. In contrast, *G. vermiculophylla* performed well at -0.5 m MSL, suggesting that this species is relatively

tolerant to desiccation, and consistent with its high abundance on intertidal mudflats in Hog Island Bay (Thomsen et al. 2006). The elevation gradient is of particular importance in flat tidal habitats, because minor differences in tidal level affect large horizontal areas. For example, if strong offshore winds coincide with a spring tide, up to 80% of the Hog Island Bay can become emergent. If such low water co-occurs with high temperatures, effects could be detrimental for the desiccation-prone *C. fragile* (and *A. subulata*), potentially contributing to large seasonal and annual variability in its distribution patterns (Thomsen 2004a).

#### Distance gradient

Oceanic influences increase and terrestrial inputs decrease with distance from the mainland, typically with near-mainland sites having highest nutrient concentrations and lower salinities, poorer light conditions and finer and more organic sediments (McGlathery 1992; Taylor et al. 1995; Castel et al. 1996; Thomsen 2004a). By crossing manipulative treatments with a distance gradient we could test for interaction effects and thereby facilitate predictions about the likelihood of success by the invaders in other lagoons. *G. vermiculophylla* had high performance at all sites, matching its wide distribution in Hog Island Bay (Thomsen et al. 2006) and supporting the view of this species as being highly stress tolerant (Yokoya et al. 1999; Wallentinus et al. 2004; Rueness 2005). In contrast, *C. fragile* showed poor performance at near-mainland sites despite a reported tolerance to high nutrients, low salinity and low light (Malinowski and Ramus 1973; Hanisak 1979a; Trowbridge 1998), suggesting that invasions are unlikely in these locations. The native species often also had low performance at the near-mainland sites, indicating generally poor growth conditions. Despite the covariation between multiple factors, the most likely stressors at near-mainland sites are high concentrations of suspended solids, reduced light penetration and sediment smothering, (McGlathery et al. 2001; Lawson 2003; Thomsen 2004a).

## Perspectives

For *C. fragile*, persistence in Hog Island Bay is likely accomplished by minimizing biomass loss during adverse conditions alternating with relatively low, but steady, growth when conditions are benign, and by occupying ‘micro-habitats’ where stressors are minimal. This hypothesis was supported by long-term experiments showing *C. fragile* to be a successful recruiter around mid-lagoon sites from – 0.60 to – 0.90 m MSL where bivalve shells are abundant (i.e. around oyster reefs) (Thomsen and McGlathery, 2006). *G. vermiculophylla* is clearly a stress-tolerant species that can grow in most lagoonal locations, can tolerate burial, is insensitive to different light and nutrient conditions, and performs well in the presence of high snail densities. These field-based conclusions correlate with laboratory data that show strong tolerance to darkness, and to temperature and salinity variation (Yokoya et al. 1999; Wallentinus et al. 2004; Rueness 2005). Of particular interest in West Atlantic lagoons, is facilitation by an ubiquitous polychaete *D. Cuprea* that incorporates *G. vermiculophylla* into its surface protruding tube-caps and thereby provides spatial fixation and reduced tidal flushing in soft-sediment systems (Thomsen 2004b; Thomsen and McGlathery 2005). In conclusion, we suggest that *G. vermiculophylla*, due to its stress tolerance, will spread further and become dominant in invaded European and North American turbid and shallow soft-bottom systems.

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