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PL Reynolds

Virginia Institute of Marine Science

JP Richardson

Virginia Institute of Marine Science

JE Duffy

Virginia Institute of Marine Science

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Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance

Pamela L. Reynolds,^{a,*} J. Paul Richardson, and J. Emmett Duffy

Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, Virginia

Abstract

We tested the relative effects of nutrient loading, reduced predation, and reduced grazing on eelgrass community dynamics in Chesapeake Bay and found evidence supporting the “mutualistic mesograzers model” in which small invertebrate grazers control accumulation of epiphytic algae, buffer eutrophication effects, and thus facilitate seagrass dominance. Experimental reduction of crustacean grazers in the field stimulated a nearly sixfold increase in epiphytic algae, and reduced seagrass biomass by 65% compared to controls with grazers. Nutrient fertilization generally had much weaker effects, but an interaction with mesograzers was key in changing the sign of fertilization effects on the system: aboveground eelgrass biomass was reduced by fertilization under reduced grazing, but increased by fertilization under ambient grazing. When protected from predators in field cages, these mesograzers limited epiphyte blooms even with nutrient enrichment, and nutrients instead enhanced grazer secondary production. Crustacean mesograzers play a key role in maintaining macrophyte (seagrass) dominance in Chesapeake Bay, in buffering eelgrass against eutrophication, and in efficiently transferring nitrogen to higher trophic levels. Yet, these crustacean grazers are also highly sensitive to predator abundance. Reducing nutrient pollution alone is unlikely to restore seagrass meadows where alterations to food webs have reduced populations of algae-feeding mesograzers. Integration of both water quality and fishery management will be more effective in restoring and maintaining healthy coastal ecosystems.

A fundamental challenge in ecology is understanding and predicting how changes in the abiotic and biotic environment influence the structure and function of ecosystem processes (Gruner et al. 2008). Understanding the interplay of bottom-up and top-down processes, including the supply of nutrients and consumer pressure, is critical given ongoing perturbations to environmental condition and food-web topology (Duffy 2003; Byrnes et al. 2007). The importance of quantifying the synergistic effects of bottom-up and top-down control is well illustrated by seagrass ecosystems, which are highly threatened by both the bottom-up effects of eutrophication and the top-down effects of overfishing, among other human activities. Seagrasses provide important ecologic and economic services from provision of nursery habitat to shoreline protection against erosion and storm events to carbon sequestration (Costanza et al. 1997), but seagrasses worldwide have declined dramatically over recent decades (Orth et al. 2006b; Waycott et al. 2009).

Historically, responses to seagrass declines have focused on eutrophication, associated high turbidity, and blooms of epiphytic and planktonic algae (bottom-up control), which compete with seagrasses for light and other resources (McGlathery 1995; Hauxwell et al. 2001). Although good water quality is clearly important for seagrass vigor (Orth et al. 2006a), growing evidence also supports an important role for top-down control in seagrass systems (reviewed by Hughes et al. 2004; Baden et al. 2010; Duffy et al. 2013), with important implications for the extensive efforts and

expense devoted to seagrass management and restoration worldwide. In particular, the small invertebrate herbivores that dominate many coastal and estuarine systems often appear to play key roles in shifts between alternative community states dominated by macrophytes (e.g., seagrasses) and microalgae. These small crustacean and gastropod mesograzers are thought to function as a critical link in coastal food webs similarly to zooplankton in pelagic systems, and they can shift primary producer dominance by mediating trophic cascades (Duffy and Hay 2000; Davenport and Anderson 2007). Mesograzers are often the dominant herbivores in temperate seagrass systems (Cebrian 1999; Valentine and Duffy 2006) and, while they have been observed in select cases to act as pests and inhibit their hosts through direct consumption of seagrass tissue (Zimmerman et al. 2010; Reynolds et al. 2012), in most instances they feed preferentially and heavily on ephemeral macroalgae and microalgae (reviewed by Jernakoff et al. 1996; Valentine and Duffy 2006).

Because algae are typically competitively superior to seagrasses, especially under high-nutrient conditions, mesograzers may play a key role in preventing overgrowth of seagrasses by algae and therefore act as mutualists with their hosts, promoting seagrass growth and buffering them against algal overgrowth resulting from nutrient pollution. This “mutualistic mesograzers” model (Duffy et al. 2013) was originally based on natural history observations and lab experiments (Orth and Van Montfrans 1984) and is supported by growing field evidence (Baden et al. 2010; Cook et al. 2011; Whalen et al. 2013), although there are exceptions (Lewis and Anderson 2012).

The important role of grazing in seagrass systems raises the question of what factors control grazers and their algal resources. Invertebrate grazers, particularly crustaceans,

* Corresponding author: plreynolds@ucdavis.edu

^a Present address: Department of Environmental Science and Policy, University of California, Davis, California

are important prey for fishes (Edgar and Shaw 1995) and are highly vulnerable to predation. Thus, disturbances to upper levels of the food web, e.g., through fishing, could have pervasive effects that ripple through food webs and ecosystems (Heck and Valentine 2007). Recent evidence from the Swedish west coast supports this hypothesis, showing declines in top predators and concomitant increases in mesopredator populations coinciding with reduced grazer abundances and dramatic seagrass declines (Baden et al. 2012).

Although many lines of evidence now support a role for cascading top-down effects in vegetated marine communities, few if any studies have unequivocally documented the final links in the proposed mutualism, that is, from mesograzer reduction to algal bloom to reduced seagrass performance and biomass. It is also unclear how general this model of mesograzer control of alternate vegetation states is within estuaries (Duffy et al. 2013). In many temperate estuaries, invertebrate grazers in seagrass beds are consumed by a diverse suite of small predators including decapod crustaceans and demersal fishes (Orth et al. 1984; Teixeira and Musick 1994), most of which are generalists capable of strongly controlling grazer populations with potential consequences for algal–seagrass dynamics in this system. These small predators may be an important link in seagrass systems, since fluctuations in their populations and overall predation intensity may lead to grazer and/or algal outbreaks (Baden et al. 2010; Svensson et al. 2012). While nutrient loading has historically been attributed as the driver for shifts in seagrass to algal dominance (Harlin 1993; Orth et al. 2006b; Burkholder et al. 2007), trophic interactions are clearly also important (Heck et al. 2000; Hughes et al. 2004). In the presence of small invertebrate herbivores, fertilization alone has shown little negative effect on seagrass growth (reviewed by Hughes et al. 2004; Burkepile and Hay 2006; Valentine and Duffy 2006), and thus the question remains: can small invertebrate grazers mediate eutrophication effects in coastal food webs?

Here we investigate the interactive influence of bottom-up and top-down forcing on seagrass systems in Chesapeake Bay, Virginia. Using a combination of cageless and traditional caging methods in the field, we evaluate the potential role of small crustacean grazers in buffering this system from nutrient-mediated algal blooms and the effect of small predators (fish, shrimp, crabs) in regulating these communities. Specifically, we examined the effects of fertilization and grazer and predator exclusion on epiphyte accumulation, seagrass production, and grazer biomass in the field.

Methods

We conducted two experiments to evaluate the relative importance of top-down effects of consumers and the bottom-up influence of fertilization on the dynamics of eelgrass (*Zostera marina*) communities in the field. Historically the role of mesograzers in realistic field situations has been very difficult to address owing to the difficulty of caging them (Connell 1974; Virnstein 1978; Miller and Gaylord 2007). The first experiment used a novel cageless method to exclude grazers (Poore et al. 2009), while the

second featured cages to exclude their predators. Additionally, a predation assay was conducted in the field to assess top-down pressure on the most abundant mesograzer taxa and to confirm hypothesized food-web relationships. All experiments were conducted in a dense bed of *Z. marina* on the southeast side of the Goodwin Islands National Estuarine Research Reserve on the York River estuary near the mouth of the Chesapeake Bay in Virginia (37°13'N, 76°23'W) at 0.5 m mean-low-water depth.

Mesograzer exclusion—To test the role of grazers and nutrient additions on the seagrass community, we established experimental plots in May of 2011 using cageless methods (modified from Whalen et al. 2013). Plots were framed by three polyvinyl chloride (PVC) poles forming a 0.5 m sided equilateral triangle and randomly assigned to one of four experimental treatments in a factorial design. For the nutrient addition treatment, plots received either 0 or 300 g of the commercial, slow-release (4 month) Plantacote™ fertilizer (14 nitrogen, 14 phosphorus, 14 potassium) placed in fiberglass mesh (1 mm) bags attached 30 cm from the sediment to each plot pole, such that fertilized plots received a total of 900 g and nonfertilized plots received only empty bags (methods comparable to Moksnes et al. 2008; Baden et al. 2010). Although the fertilizer slowly leaches into the water column over a period of 6–8 weeks, to ensure consistent delivery throughout the experiment the bags were replaced with new fertilizer after 4 weeks. Prior work in the York River, Virginia, and ongoing monitoring by the Chesapeake Bay National Estuarine Research Reserve show pronounced fluctuations in nutrients and phytoplankton in patterns that are not indicative of chronic background eutrophication (Whalen et al. 2013). Our fertilizer application increased nitrogen content in the eelgrass leaves by over 20% (see Results), simulating a chronic, eutrophic condition.

Experimental reduction of mesograzers was accomplished by fitting each pole in a plot with a plaster (Ortho Plaster, 275–310 bar slow) block containing 10% carbaryl (Bayer Crop Science) by weight, which reduces crustacean grazer densities in the field (Whalen et al. 2013), attached 15 cm from the sediment. Carbaryl, a reversible acetylcholinesterase inhibitor widely used against arthropods in homes, gardens, and aquaculture in the United States, has had limited direct effects on nonarthropod taxa (such as algae) in experimental studies (Carpenter and Lodge 1986; Duffy and Hay 2000; Dumbauld et al. 2001). Supplemental studies found the concentration used here effectively reduced gammaridean amphipod densities in the field up to 60 cm away from the block, with greatly diminished effectiveness at greater distances, supporting the highly localized effects of this treatment (Whalen et al. 2013). Control plots received plaster blocks without carbaryl. Blocks were prepared with a recipe modified from Poore et al. (2009) and were replaced weekly throughout the experiment. This cageless design allows experimental exclusion of small crustacean grazers from seagrass in the field without strong modification of flow, light, and other parameters that can be compromised in traditional caging experiments (Connell 1974; Virnstein 1978).

Table 1. Mesograzer exclusion experiment: Effects of experimental treatments (deterrent and nutrient additions) on mesograzer biomass at 4 weeks, epiphyte (μg Chl *a* per gram of *Z. marina*) and epibiont load at 4 weeks, total seagrass biomass at 8 weeks, and *Z. marina* production and tissue percent nitrogen at 4 weeks. Values significant at $p < 0.05$ are listed in italic. df, degrees of freedom.

Response	df	Sum squares	<i>F</i>	<i>p</i>
Total mesograzer biomass				
Deterrent	1	2.256	7.036	<i>0.012</i>
Nutrients	1	0.001	0.001	0.972
Deterrent \times nutrients	1	0.016	0.050	0.824
Error	36	11.544		
Epiphytes				
Deterrent	1	1.754	10.836	<i>0.002</i>
Nutrients	1	0.001	0.006	0.940
Deterrent \times nutrients	1	0.396	2.449	0.126
Error	36	5.827		
Epibionts				
Deterrent	1	5.682	81.829	<i><0.001</i>
Nutrients	1	0.025	0.366	0.549
Deterrent \times nutrients	1	0.194	2.791	0.103
Error	36	2.500		
Total seagrass biomass				
Deterrent	1	0.78	43.410	<i><0.001</i>
Nutrients	1	0.032	1.760	0.193
Deterrent \times nutrients	1	0.044	2.383	0.131
Error	36	0.663		
<i>Z. marina</i> biomass				
Aboveground				
Deterrent	1	0.421	13.218	<i>0.001</i>
Nutrients	1	0.058	1.830	0.185
Deterrent \times nutrients	1	0.146	4.584	<i>0.039</i>
Error	36	1.147		
Belowground				
Deterrent	1	0.789	5.059	<i>0.031</i>
Nutrients	1	0.000	0.001	0.973
Deterrent \times nutrients	1	0.005	0.033	0.858
Error	36	5.615		
<i>R. maritima</i> biomass				
Aboveground				
Deterrent	1	1.447	7.172	<i>0.011</i>
Nutrients	1	0.081	0.340	0.531
Deterrent \times nutrients	1	0.290	1.437	0.238
Error	36	7.265		
Belowground				
Deterrent	1	1.040	7.309	<i>0.010</i>
Nutrients	1	0.427	2.998	0.092
Deterrent \times nutrients	1	0.569	3.996	0.053
Error	36	5.123		
<i>Zostera</i> production				
Deterrent	1	1.676	4.663	<i>0.038</i>
Nutrients	1	0.214	5.952	<i>0.020</i>
Deterrent \times nutrients	1	0.082	2.272	0.141
Error	34	1.222		
<i>Zostera</i> tissue % N				
Deterrent	1	0.015	3.911	0.056
Nutrients	1	0.018	4.780	<i>0.035</i>
Deterrent \times nutrients	1	0.003	0.719	0.402
Error	36	0.137		

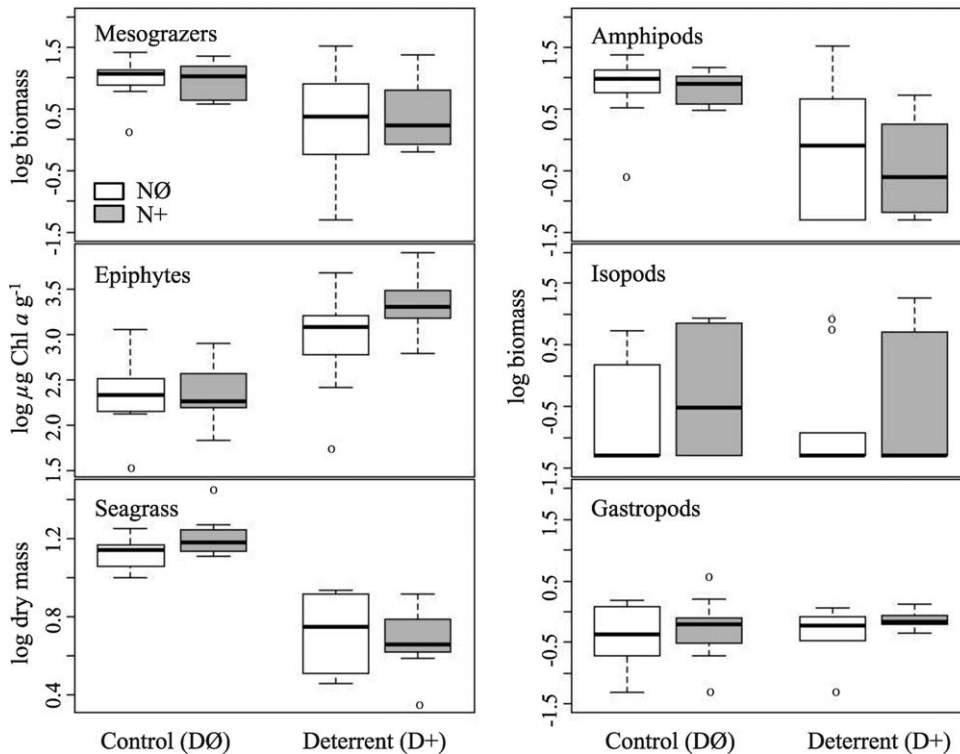


Fig. 1. Effects in mesograzers exclusion experiment of deterrent application (control, DØ; addition, D+) and nutrient additions (N+) or control (NØ) treatments on total mesograzers, amphipod, isopod, and gastropod biomass per gram of macrophyte and epiphyte load ($\mu\text{g Chl } a$ per gram of *Z. marina*) after 4 weeks, and final seagrass dry mass after 8 weeks in experimental field plots.

Four weeks after treatment application, we collected *Z. marina* shoots and associated algae and epifauna to test for treatment effects. We quantified the mesograzers community by collecting all macrophytes in approximately a 19 cm diameter circle in the center of each plot using a 300 μm mesh bag. Grazers were counted and sorted by species, as well as by size class using a stack of nested sieves. We then estimated total biomass and secondary production from the sieve size class abundance data using taxon-specific empirical equations (as in Edgar 1990). We then standardized mesograzers by the total biomass (grams of dry mass) of macrophytes collected per sample.

Additional collections of one *Z. marina* shoot per plot were made to quantify epiphytic algae (chlorophyll *a* per dry mass [g] of the scraped leaves), and four *Z. marina* shoots per plot to quantify the total mass of epibiota (pooled dry mass of all material scraped from the four leaves standardized by total leaf dry mass). We used whole shoots instead of single leaves to examine epiphyte and epibiont loading as leaf age can influence fouling accumulation. These collections were repeated after 8 weeks. After 8 weeks we also harvested all remaining seagrass per plot. This material was separated into species (*Z. marina*, *Ruppia maritima*) and into aboveground vs. belowground tissue and dried to assess differences in biomass across experimental treatments.

We quantified treatment effects on the growth rate of the *Z. marina* within the plots by punching at least five shoots (just above their respective leaf sheaths) per plot 3 weeks

after the experiment was initiated. These shoots were collected a week later (timepoint week 4) and taken back to the laboratory, where we then measured the linear extension of the leaves and calculated the rate of dry mass accumulation (g d^{-1} ; Short and Duarte 2001). Estimated growth rates from all shoots in a plot were pooled to obtain a plot-level mean, which we used to examine treatment effects on eelgrass growth rate ($\text{mm new growth extension} \times (\text{Z. marina mg} \times \text{mm}^{-1}) \times \text{duration}^{-1}$). To assess treatment effects on *Z. marina* leaf stoichiometry, at the 4 week time point we collected five shoots from the edge of each plot and removed the youngest leaf from each shoot. A 3 cm piece of each of these leaves was rinsed with deionized water, and this tissue was then pooled by plot, dried, ground, and processed on a carbon–hydrogen–nitrogen (CHN) analyzer at the Virginia Institute of Marine Science (VIMS) to assess treatment differences in leaf tissue nitrogen content. The leaf tissue nitrogen served as an integrated metric to assess nutrient availability for the eelgrass (e.g., fertilization treatment effectiveness at elevating water column nitrogen) during the field experiment (Burkholder et al. 2007). Epiphyte tissue was not available for CHN analysis, although owing to its faster turnover rates we do not necessarily expect to have been able to strongly detect fertilization effects on microalgal stoichiometry.

We tested deterrent and nutrient treatment effects on plant and epifaunal biomass, epiphyte load, and *Z. marina* growth and leaf tissue nitrogen content using two-way

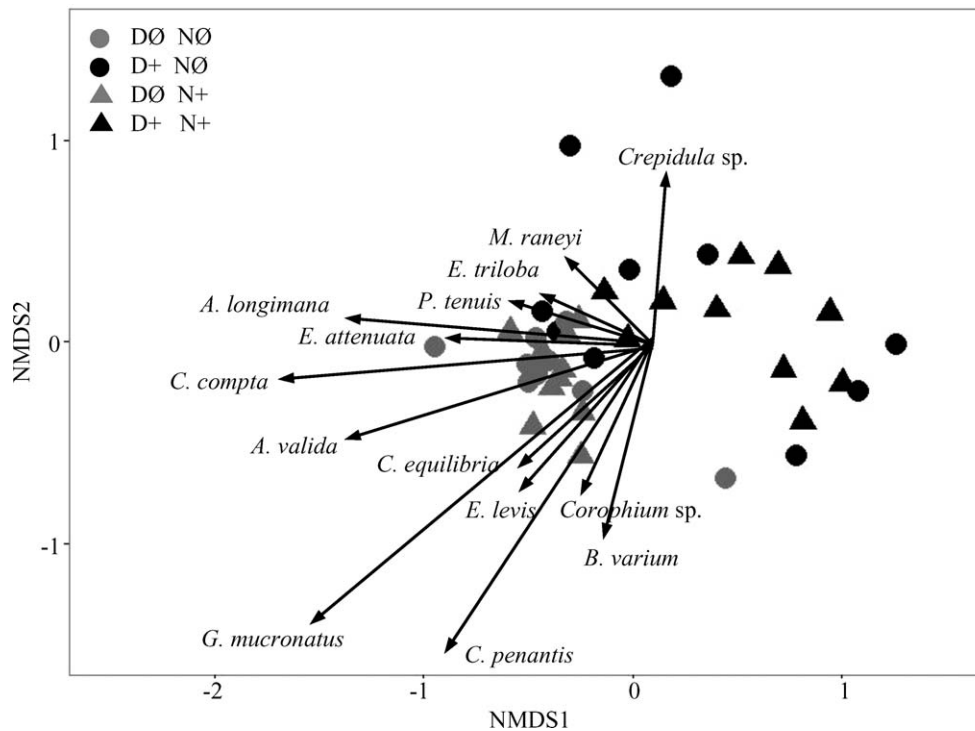


Fig. 2. Effects of nutrient addition (control, NØ; addition, N+) and mesograzzer deterrent application (D+) on mesograzzer community composition after 4 weeks in the mesograzzer exclusion experiment, illustrated via NMDS. Grazer taxa included amphipods *Ampithoe longimana*, *Ampithoe valida*, *Caprella equilibria*, *Caprella penantis*, *Corophium* sp., *Cymadusa compta*, *Elasmopus levis*, *Gammarus mucronatus*, *Microprotopus raneyi*, *Paracaprella tenuis*; isopod *Edotea triloba*; gastropods *Bittium varium*, *Crepidula* sp.

ANOVAs in R (R Development Core Team 2013, version 2.15.2) with type III sums of squares. To graphically examine changes in the mesograzzer community across experimental treatments, we used nonmetric multidimensional scaling (NMDS) based on Bray–Curtis distance with the metaMDS function in the vegan package in R. The results were plotted in two dimensions, and the envfit procedure in vegan was used to overlay species vectors.

Direct effects of chemical deterrent—To confirm whether the experimental deterrent treatment may have had direct effects on the seagrasses in the mesograzzer exclusion experiment, we conducted a mesocosm experiment at VIMS factorially manipulating seagrass species (*Z. marina*, *R. maritima*) and deterrent (none, plaster only, plaster + carbaryl) treatments ($n = 8$). Seagrasses were collected from Allen’s Island, York River, Virginia, in October 2011 and transported back to the lab on ice where they were gently defaunated by hand and rinsed in freshwater and salt water to ensure removal of all grazers. Mesocosms (18 liters) were randomly placed in tanks (blocking factor), assigned to one of the four treatments, and filled with 4.5 liters of prepared sediment (30% mud, 70% sand mixture). Mesocosms then received either 12 ± 3 g *Z. marina* or 13 ± 3 g *R. maritima* and either no block or a 50 g block composed of plaster only or plaster prepared with 10% carbaryl (deterrent treatment). Mesocosms received pulsed dumps approximately every 2 min of 150 μ m filtered

seawater from the adjacent York River and were shaded to approximate light conditions in the field. Three *Z. marina* shoots per mesocosm were punched at the leaf sheath to quantify growth rate. After 17 d we harvested all seagrass and scraped off all epibionts, which were dried and weighed to quantify epiphyte load. Barnacles were removed and dried separately to test deterrent treatment effects on this fouling invertebrate. After scraping, we then lightly rinsed and weighed all seagrass shoots. Responses were analyzed separately for the two seagrass species with one-way blocked ANOVAs in R.

Predation assay—To assess the selectivity of predation in the field, we employed a predation assay (Manyak et al. 2013) examining differences among mesograzzer taxa in vulnerability to predators in the field. Although gammaridean amphipod, isopod, and gastropod grazers are all consumed by larger invertebrates and fishes, predator selection and preferences may vary across taxa with potential effects on epiphyte–seagrass interactions depending on which grazer taxa, and their relative grazing effects, are more susceptible to predation (Best and Stachowicz 2012; Eklöf et al. 2012). To test predator effects across grazer taxa in the field, in July 2012 we used super glue to attach one mesograzzer (Ampithoid amphipod, isopod *Erichsonella attenuata*, or gastropod *Bittium varium*), or a standard prey type (10 mm piece of freeze-dried shrimp), or a control prey mimic (10 mm piece of fuzzy pipe cleaner) to

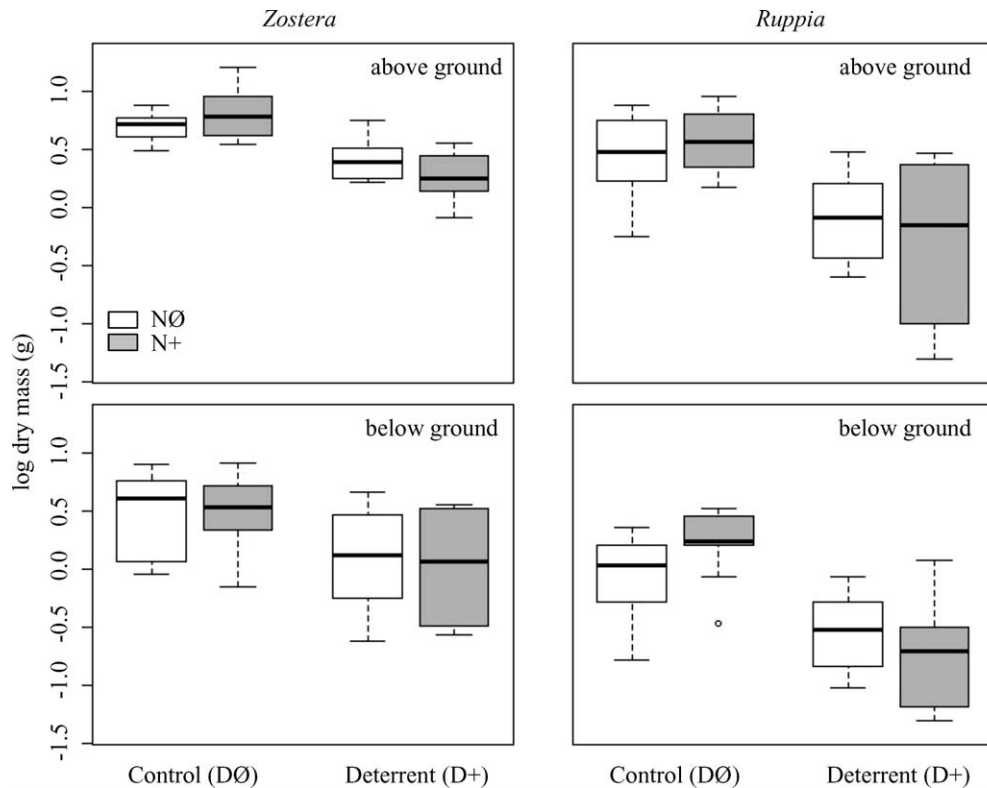


Fig. 3. Effect in mesograzzer exclusion experiment of deterrent application (D+) and nutrient additions (N+) on *Z. marina* and *R. maritima* aboveground (shoots) and belowground (roots, rhizomes) biomass after 4 weeks in the mesograzzer exclusion experiment.

a standardized location on a leaf of a shoot of *Z. marina*. Individual grazers were collected within their most abundant size class (5–15 mm) and represent the most common mesograzzer species at the field site. The shoot was then tied to a clear acrylic rod for deployment in the field such that the shoot was oriented upright in a natural orientation. Rods were deployed at low tide and collected 24 h later. As nearly all mimics remained attached, we inferred that missing prey were likely eaten and not absent due to a loss of glue adhesion. Prey presence vs. absence data were analyzed with logistic regression in R, which took into account baseline (control) losses.

Predator exclusion—To explore top-down effects of predators on mesograzzer and cascading effects on primary producers, we conducted a 3 week field caging experiment manipulating predator access and nutrient addition in plots established in July 2012. Thirty plots were randomly assigned in a two-way factorial design to experimental nutrient addition (two levels: 0 or 300 g Plantacote™) and predator exclusion (three levels: open plot, cage control, full cage). Cages were constructed using a frame of PVC (40 × 40 × 45 cm length, width, height) wrapped in nylon mesh (0.79 mm diameter holes), which allowed access to the cage by grazers but excluded the larger predatory fishes and invertebrates. All plots were established along a seagrass patch edge and were marked with two PVC poles; cages were secured to these poles with bungee cords. Cages were filled with approximately 5 liters of coarsely defaunated mud and

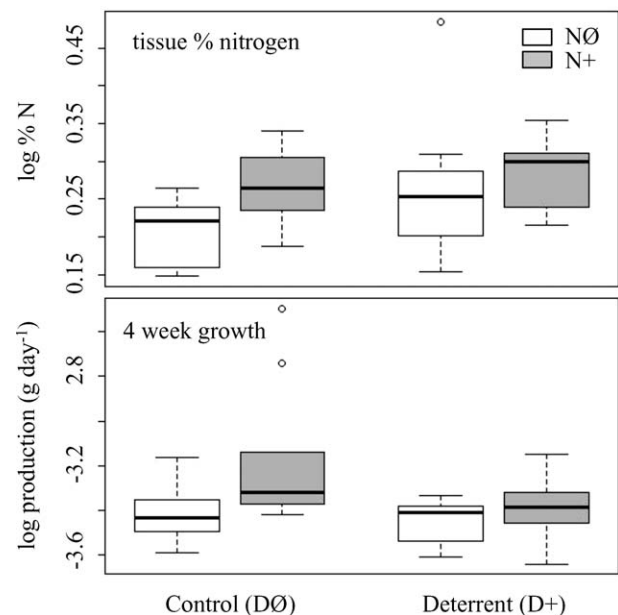


Fig. 4. Effects in mesograzzer exclusion experiment of deterrent application (D+) and nutrient additions (N+) treatments on the percentage nitrogen in new growth *Z. marina* leaf tissue, and on *Z. marina* growth rate after 4 weeks in the field.

Table 2. ANOVAs of treatment effect (control, plaster only, plaster + carbaryl) on given responses in experimental mesocosms.

Response	df	Sum squares	F	p
<i>Z. marina</i> growth				
Treatment	2	34.738	2.050	0.158
Blocking	1	18.716	2.209	0.155
Treatment × blocking	2	4.641	0.274	0.764
Error	18	152.498		
<i>Z. marina</i> growth rate				
Treatment	2	0.037	0.771	0.479
Blocking	1	0.005	0.194	0.666
Treatment × blocking	2	0.059	1.221	0.321
Error	16	0.387		
<i>R. maritima</i> growth				
Treatment	2	27.69	0.352	0.708
Blocking	1	161.82	4.118	0.058
Treatment × blocking	2	51.34	0.653	0.532
Error	18	707.39		
Barnacles on <i>Z. marina</i>				
Treatment	2	0.001	0.051	0.950
Blocking	1	0.002	0.436	0.518
Treatment × blocking	2	0.022	2.056	0.157
Error	18	0.096		
Barnacles on <i>R. maritima</i>				
Treatment	2	0.030	2.676	0.096
Blocking	1	0.000	0.001	0.970
Treatment × blocking	2	0.012	1.048	0.371
Error	18	0.102		

sand to provide substrate and assist in anchoring the cage. Open plots received a square of PVC placed on the sediment and secured to the marking poles. A circle of Vexar (30 cm diameter), to which 24 shoots of live *Z. marina* were cable tied at natural densities (initial wet mass of ~ 35 g per plot), was attached to the bottom PVC square of each plot. *Z. marina* shoots were collected with their associated rhizomes and root hairs and were gently rinsed in seawater to remove any fauna and debris prior to attachment. After the eelgrass was added, all plots were then stocked with natural assemblages of grazers (~ 75 amphipods and ~ 50 gastropods) collected by conducting two, 2 m long dipnet (13 × 14.5 cm) sweeps within the center of the seagrass bed adjacent to each plot. Nutrients were placed in mesh bags as in the mesograzers exclusion experiment and attached to one of the poles next to the cage. Plots were monitored and cages cleaned weekly throughout the experiment.

After 3 weeks, we enclosed each Vexar circle with its attached *Z. marina* and associated epifauna and predators in a mesh bag and transported them to the lab where we quantified the final dry mass of *Z. marina*, abundance and biomass of associated grazers by gross taxonomic group (gastropods, amphipods, and isopods), and identity and abundance of predators. Epiphytic algal load was quantified from one separately collected shoot per plot as in the mesograzers exclusion experiment. Since previous experiments have demonstrated that cages can introduce unintended artifacts due to reductions in light, water flow, and other factors (Connell 1974; Virnstein 1978), our interest

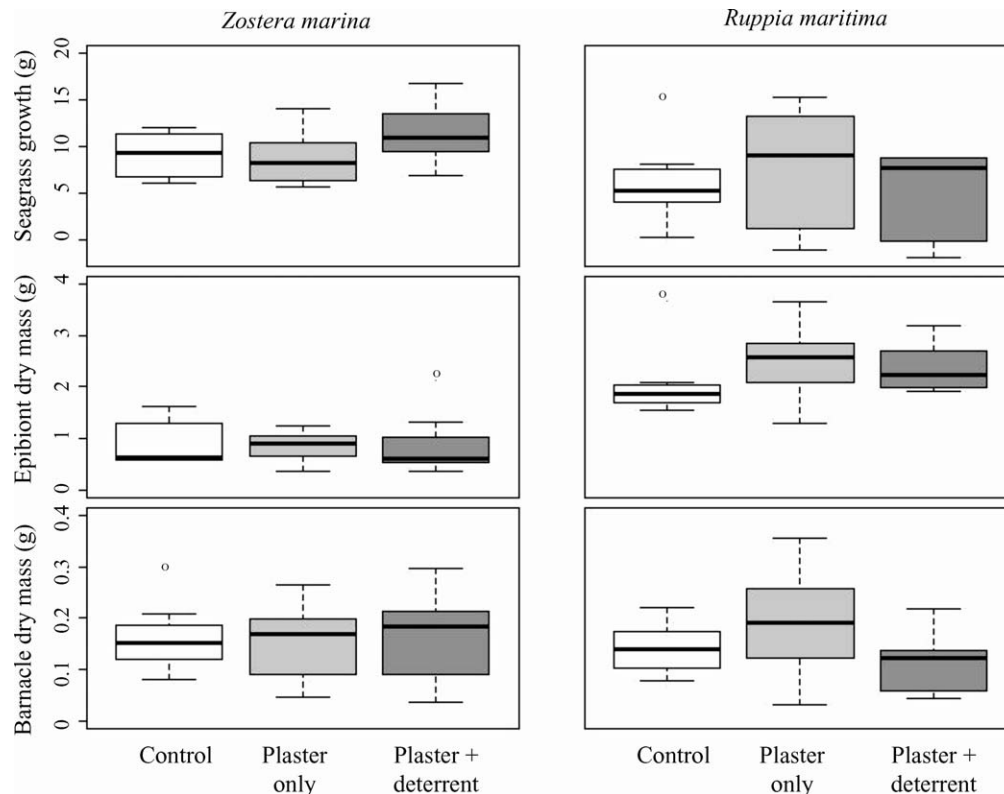


Fig. 5. Effects of plaster and deterrent (10% carbaryl) on seagrass growth and barnacle accumulation in experimental mesocosms after 17 d.

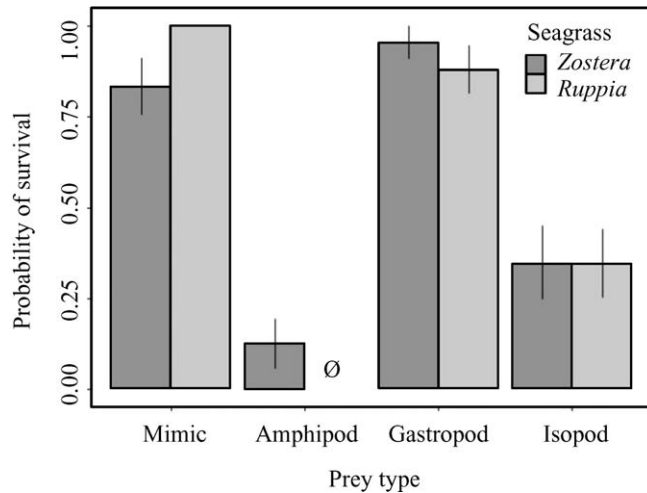


Fig. 6. Prey survivorship by mesograzer type and seagrass (habitat) type in predation assays.

was in contrasts specifically between the partial and full caging treatments, and thus analyses were performed as in Hindell et al. (2001) using a priori contrasts comparing the partial to the full treatments. Two-way ANOVAs in R were used to test for effects of nutrient addition (\pm), cage treatment (partial, full), and their interactions on epiphyte load and final *Z. marina* biomass and mesograzer wet mass in the predator exclusion experiment.

Table 3. Predator exclusion experiment: Results of a priori contrasts of experimental treatments (caging, nutrient addition) on final mesograzer biomass by taxa, epiphyte load (Chl *a* μg per gram of *Z. marina*), and *Z. marina* dry mass after 3 weeks. Standard error (SE); $\text{Pr}(>|t|) < 0.05$ are in italics.

Response	Estimate	SE	<i>t</i>	$\text{Pr}(> t)$
Crustacean grazer biomass				
Open plot vs. caging	-1.459	0.591	-2.467	<i>0.022</i>
Partial vs. full cage	-0.887	0.348	-2.546	<i>0.018</i>
Nutrient addition vs. no addition	-0.894	0.422	-2.116	<i>0.045</i>
Nutrients \times caging	-0.177	0.348	-0.508	0.616
Gastropod grazer biomass				
Open plot vs. caging	1.131	0.408	2.770	<i>0.011</i>
Partial vs. full cage	0.911	0.241	3.786	<i><0.001</i>
Nutrient addition vs. no addition	0.060	0.292	0.205	0.839
Nutrients \times caging	0.163	0.241	0.678	0.505
Total mesograzer biomass				
Open plot vs. caging	-1.040	0.537	-1.935	0.065
Partial vs. full cage	-0.674	0.317	-2.130	<i>0.044</i>
Nutrient addition vs. no addition	-0.699	0.384	-1.822	0.082
Nutrients \times caging	-0.078	0.317	-0.247	0.807
Epiphytes				
Open plot vs. caging	0.907	0.257	3.526	<i>0.002</i>
Partial vs. full caging	0.209	0.154	1.353	0.190
Nutrient addition vs. no addition	-0.004	0.186	-0.021	0.983
Nutrients \times caging	0.075	0.154	0.487	0.631
<i>Z. marina</i> dry mass (g)				
Open plot vs. caging	1.162	0.426	2.728	<i>0.012</i>
Partial vs. full caging	0.141	0.251	0.562	0.579
Nutrient addition vs. no addition	0.304	0.304	0.999	0.328
Nutrients \times caging	-0.012	0.251	-0.047	0.963

Results

Mesograzer exclusion—The dilute, slowly dissolving chemical deterrent reduced invertebrate mesograzer biomass by 76%, and this mesograzer reduction cascaded to increase epiphytic algae (chlorophyll *a* [Chl *a*]) by 590% on average after 4 weeks, which in turn reduced seagrass biomass by 65% after 8 weeks (Table 1; Fig. 1). The total biomass of epibiota on the eelgrass was positively correlated with chlorophyll *a* ($p < 0.0001$, $R^2 = 0.47$), was higher in the plots with reduced mesograzer biomass, and was thus likely largely composed of epiphytic algae. The chemical deterrent specifically reduced crustaceans, with little to no effect on gastropods (Fig. 1). The deterrent, but not the nutrient addition, substantially shifted mesograzer community composition after 4 weeks as a result of greatly reduced amphipod abundances (Fig. 2). Nutrient additions had no effect on either epiphyte load or mesograzer abundance in this experiment (Table 1; Fig. 1).

Both eelgrass and widgeongrass (*R. maritima*) declined on average in plots exposed to the deterrent (Table 1; Fig. 3). This change was evident in both the aboveground (leaves) and belowground (roots and rhizomes) components of both seagrass species after 8 weeks in the field. Deterrent (D) and nutrient (N) treatments interactively affected *Z. marina* aboveground biomass, since greater leaf biomass was observed in fertilized plots with the intact ambient mesograzer community (D \emptyset N+ treatments).

While fertilization promoted *Z. marina* production, mesograzers had the opposite effect (Fig. 4). Nitrogen content of new *Z. marina* tissue was 9% higher in fertilized plots and correlated with the increased growth rate in those treatments (Fig. 4).

Direct effects of chemical deterrent—*Z. marina* and *R. maritima* seagrasses grew by 9.7 and 7.6 g in wet mass, on average, across all mesocosms during the experimental test of potential direct effects of the chemical deterrent treatment. No treatment (control, plaster only, plaster + deterrent), blocking, or blocking by treatment interaction effects were observed on the growth of *Z. marina* or *R. maritima*, the growth rate of *Z. marina*, or the accumulation of barnacles on each seagrass type (Table 2; Fig. 5).

Predation assay—Prey survivorship differed strongly among prey taxa (amphipod, isopod, gastropod) and seagrass habitats (*Z. marina*, *R. maritima*; $\chi^2 = 11.42$, $p = 0.010$). Gammaridean amphipods were completely removed by predators, whereas gastropods were largely untouched (Fig. 6). Losses due to abrasion or weakened glue adhesion in the field (measured as losses of the mimic) were minimal in the eelgrass habitat and not observed at all in the widgeongrass.

Predator exclusion—Few predators were recorded in the full cages at the end of the experiment compared with the partial cages ($F_{1,28} = 2.234$, $p = 0.018$), confirming that the experiment reduced predator pressure in the full cage treatments. Predator exclusion increased crustacean but reduced gastropod biomass (a priori contrast of partial vs. full cage, Table 3; Fig. 7). Caged mesograzers were dominated by gammaridean amphipods that are known to be strong algal grazers (e.g., *Ampithoe longimana*, *Cymadusa compta*, *Gammarus mucronatus*, Fig. 8). Nutrient additions increased crustacean biomass but had no effect on gastropod biomass (Table 3; Fig. 7). Neither predator exclusion nor nutrient additions affected epiphyte load (Chl *a* per gram of *Z. marina*) or the final mass of *Z. marina* (a priori contrasts), although we did observe an effect of caging itself (Table 3; Fig. 7).

Discussion

Our results provide direct field experimental confirmations of the mutualistic mesograzers hypothesis, i.e., that mesograzers promote seagrass dominance by cropping algal competitors that otherwise reduce seagrass performance (Orth et al. 1984; Duffy et al. 2013). Specifically, experimental reduction of crustacean grazers stimulated a nearly sixfold increase in epiphytic algae in the field, which in turn strongly reduced seagrass growth and biomass (by 65% compared with controls). In general, we found stronger evidence of top-down than of bottom-up control in this system, although there were important effects of fertilization on grazer production. In particular, the two field experiments demonstrated that grazers substantially promoted eelgrass, nutrient loading enhanced biomass of crustacean grazers but not of algae, and that

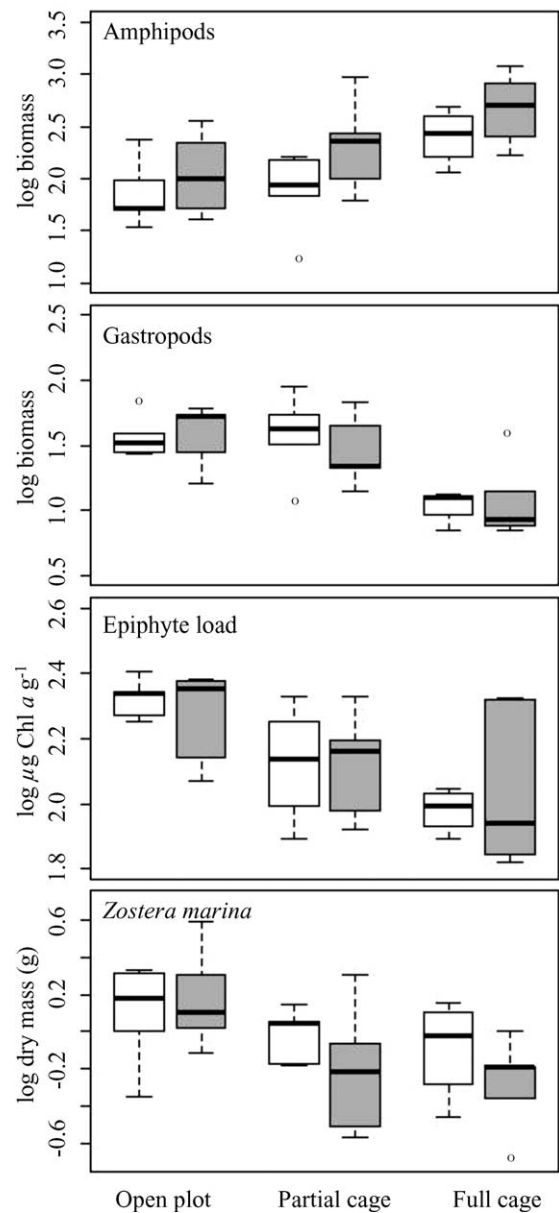


Fig. 7. Effects in predator exclusion experiment of caging (open, partial, full) and nutrient addition (N+) on crustacean and gastropod mesograzers biomass, epiphyte load, and *Z. marina* dry mass after 3 weeks.

crustacean grazers were highly sensitive to the abundance of predators. These results corroborate similar evidence of mesograzers control of algae in laboratory and mesocosm studies (reviewed by Jernakoff et al. 1996; Hughes et al. 2004; Valentine and Duffy 2006) as well as a growing number of field experiments in eelgrass (Moksnes et al. 2008; Baden et al. 2010; Whalen et al. 2013) and other seagrass systems (Cook et al. 2011; Myers and Heck 2013). But few previous studies have made the final connection from reduced grazing to ephemeral algal blooms to reduced seagrass fitness.

Our results also support pioneering work in the Baltic region, where experiments and time series also showed that

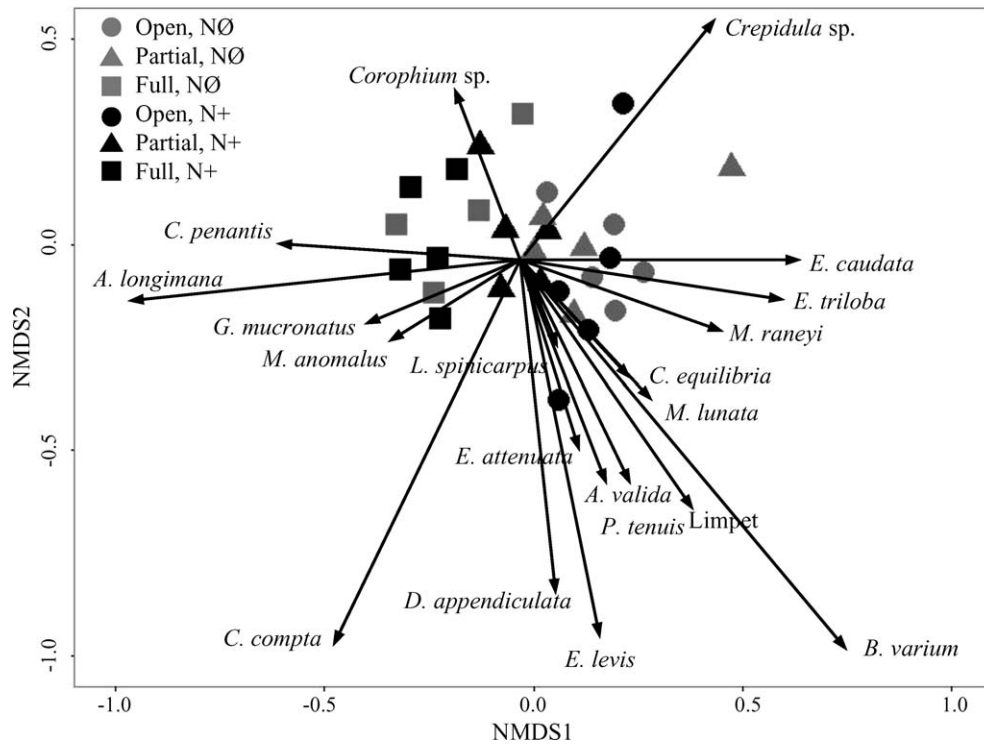


Fig. 8. Effects of nutrient addition and cage type (open, partial, full) on mesograzzer community composition in the predator exclusion experiment after 3 weeks in the field, illustrated via NMDS. Grazer taxa included species listed in Fig. 2 as well as amphipods *Dulichieilla appendiculata*, *Lembos spinicarpus*, *Microdeutopus anomalus*; isopod *Paracerceis caudata*, gastropod *Mitrella lunata*, and an unidentified limpet.

mesograzers are a key link in eelgrass food webs, potentially mediating the transition between macrophyte- and algal-dominated systems (Moksnes et al. 2008; Baden et al. 2010, 2012). Our results thus confirm the emerging generalization that temperate seagrass beds are much more sensitive than historically assumed to perturbations to coastal food webs. As in the Baltic region, however, the top-down control we documented interacts in important ways with bottom-up forcing. Specifically, in both systems, small crustacean grazers play an important role in buffering seagrass against eutrophication and improving seagrass health, as evidenced by the interaction between fertilization treatment and mesograzzer presence on eelgrass biomass. In our study, nutrient loading increased eelgrass biomass when mesograzers were present but tended to reduce eelgrass biomass when mesograzers were excluded; fertilization enhanced eelgrass growth in both presence and absence of grazers in our short-term assay. Similarly, experimentally enhanced nutrient levels on the Swedish west coast resulted in blooms of macroalgal mats and decreased growth of eelgrass in the absence of mesograzers but had no effect under historically high mesograzzer densities (Baden et al. 2010). Likewise, nutrient enrichment had no effect on shoalgrass biomass in a recent field experiment (Myers and Heck 2013), although there was a negative effect on leaf length in protected sites where amphipod abundances were low. These interactions between grazing and nutrient loading mirror many previous experiments conducted in the laboratory and mesocosms

(Hughes et al. 2004), which showed that mesograzers controlled the growth of ephemeral algae, even under elevated nutrient conditions.

Seagrass ecology and the management strategies based on it have historically focused almost exclusively on water quality (specifically turbidity and nutrient loading). However, several of the studies discussed above from temperate seagrass beds found that experimental fertilization had little effect on epiphytic algae, whereas experimental mesograzzer reduction had stronger effects than fertilization (Heck et al. 2000; Hughes et al. 2004; Spivak et al. 2009). Nutrient limitation was supported in our study, however, by the positive effect of nutrient enrichment on mesograzzer biomass in the predator exclusion study. This finding that fertilization effects bypassed standing stock of primary producers to elevate secondary production is similar to that observed in a field caging experiment in the Baltic, where ambient densities of grazers are high (Baden et al. 2010).

The key role of invertebrate grazers raises the question of what controls their abundance. Both our study and experiments in the Baltic region show that ambient predator abundances exert strong top-down control on grazers (Moksnes et al. 2008; Baden et al. 2010) and that this pattern is overlain on, and interacts with, a base of bottom-up control. Our field experiment confirmed previous mesocosm findings of a bottom-up influence on grazers as nutrient loading was transmitted efficiently up the food web to increase mesograzzer biomass in mesocosm experiments in

Chesapeake Bay (Spivak et al. 2009) and field experiments in Sweden (Moksnes et al. 2008). This bottom-up signal is consistent with patterns in time-series data from our site showing that correlations across trophic levels are more often positive than negative (Douglass et al. 2010).

Although our data suggest that patterns of trophic control are similar in eelgrass beds on both sides of the North Atlantic, quite different processes can occur in other seagrass systems (*see* review in Duffy et al. 2013), where, for example, algal grazing by omnivorous fishes (Heck et al. 2000) or destructive grazing of eelgrass tissue by invertebrates (Zimmerman et al. 2010; Reynolds et al. 2012) has variable consequences for seagrasses when food webs are perturbed. The relative strengths of top-down and bottom-up control and their system-level consequences are thus mediated by species- and system-specific factors, including palatability of primary producers, food preference and vulnerability of mesograzers (Best and Stachowicz 2012), omnivory of mesopredators (Heck and Valentine 2006), and differences in recruitment dynamics on different trophic levels (Svensson et al. 2012). Similar to prior work in Sweden (Baden et al. 2010), we found strong cascading top-down control, likely because the most abundant epifauna were effective algal grazers (primarily amphipods). These taxa were in turn highly vulnerable to the ambient predator community, as evidenced by the intense predation upon this group in field predation assays (Fig. 6) as well as their dominance in communities in which their predators were excluded (full field cages, Fig. 8).

Our results add growing support for the hypothesis that changes in both nutrient regimes and coastal food-web structure often interact to have a fundamental effect on seagrass ecosystems. Reducing nutrient pollution alone is unlikely to restore seagrass meadows if there have been pervasive alterations to food webs that have resulted in reduced populations of algal mesograzers. In these areas, management of water quality would best be integrated with fishery management to restore the abundance of large predators and improve coastal ecosystems.

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