Limnol. Oceanogr., 55(3), 2010, 1435–1448

doi:10.4319/lo.2010.55.3.1435

Relative importance of trophic interactions and nutrient enrichment in seagrass ecosystems: A broad-scale field experiment in the Baltic–Skagerrak area

Susanne Baden,[a,*] Christoffer Boström,[b] Stefan Tobiasson,[c] Heidi Arponen,[b] and Per-Olav Moksnes[d]

[a] University of Gothenburg, Department of Marine Ecology, Kristineberg, Sweden
[b] Åbo Akademi University, Department of Biosciences, Environmental and Marine Biology, Finland
[c] Linnaeus University, School of Natural Sciences, Sweden
[d] University of Gothenburg, Department of Marine Ecology, Gothenburg, Sweden

Abstract

The interaction of eutrophication and predation in structuring seagrass *Zostera marina* L. ecosystems was assessed in a field experiment in three regions along an estuarine salinity gradient, from southern Finland to the Skagerrak area of the Swedish west coast. All regions are considered to be affected by eutrophication and overfishing but differ in the abundance of intermediate predators (e.g., small fish, shrimp, and crabs), mesograzers, and the biomass of epiphytic algae. Using transplanted *Zostera* (eelgrass), nutrient levels and intermediate predator abundance were manipulated in a full-factorial cage experiment. On the Swedish west coast, where ambient densities of mesograzers are very low, epiphytic algae responded strongly to nutrient enrichment, resulting in significantly reduced growth of eelgrass. At the Baltic sites however, where ambient densities of mesograzers are high, no significant growth of epiphytic algae was detected, and only grazer biomass responded to nutrient enrichment. Predation from small fish, shrimp, and crabs decreased the biomass of mesograzers by > 98% on the Swedish west coast, but natural predators had no significant effect on mesograzers biomass at the Baltic sites. Predation and nutrient enrichment interacted to affect the growth of eelgrass by controlling the biomass of mesograzers and nuisance algae. The differing effect of nutrient enrichment and grazing in the three regions may therefore be a result of the prevailing low and high predation pressure on mesograzers in *Zostera*. This absence or presence of predation may derive from interregional changes in trophic interactions, possibly caused by a combination of eutrophication and overfishing.

Marine eutrophication and depletion of fish stocks have been identified as two of the most serious threats to marine ecosystems worldwide (Pauly et al. 1998; Jackson et al. 2001; Diaz and Rosenberg 2008; Halpern et al. 2008). Since the 1930s, the growth and reproductive rate of populations in an ecosystem were assumed to be mainly regulated by resources (bottom-up control), in which the rate of nutrient supply enhances primary production and subsequent propagation to higher trophic levels (Banse 2007). Hairston et al. (1960) suggested that population size may also be determined by predation from higher trophic levels (top-down control). When top-down regulation involves three or more trophic levels, it has been defined as a "trophic cascade" (Paine 1980). Such trophic cascades have been found in a wide variety of terrestrial and aquatic systems (Pace et al. 1999) and appear to be particularly strong in marine benthic systems (Shurin et al. 2002). Although it has been suggested that trophic cascades are limited to simple ecosystems (Strong 1992), recent works suggest that they can also emerge in diverse communities with complex food webs if the interaction strength is skewed toward a few functionally dominant species (Pace 1999; Moksnes et al. 2008).

Seagrasses, comprising ~ 60 species, dominate coastal areas worldwide. As these systems are highly productive and support high biodiversity, they play an important ecological and economical role (Orth et al. 2006). In particular, seagrass ecosystems provide a wide range of goods and services, including protection against coastal erosion, provision of food, and a predation refuge for a variety of organisms, including several commercially important species (Duarte 2002). The global distribution of seagrasses has decreased by 29% during the past 140 yr, while 58% of remaining documented seagrass meadows is in decline (Waycott et al. 2009). Eutrophication is suggested as one of the main reasons for this loss (Orth et al. 2006). Increased nutrient supply enhances phytoplankton production and turbidity as well as that of annual fast-growing filamentous algae, reducing light and nutrient supply and thus suffocating the seagrass (Duarte 1995). In addition to eutrophication, overfishing seems to have an indirect effect on seagrass survival through trophic cascades (Heck et al. 2000; Heck and Valentine 2007). Thus, when top predators are removed, intermediate predators may increase and reduce the abundance of mesograzers (small crustaceans and gastropods that feed mainly on algae), causing a release in grazing pressure and a subsequent increase of nuisance algae. Experiments have demonstrated that enhanced nutrient loading by itself often has little negative effect on seagrass growth as long as natural mesograzer populations are present (reviewed by Hughes et al. 2004; Burkepile and Hay 2006; Valentine and Duffy 2006). Moreover, in the absence of top-down control, mesograzer populations should respond to enhanced resource availability, increase in abundance, and thus be able to control algal growth in seagrass systems also during nutrient loading (Valentine and Duffy 2006). However, if the algae are allowed to grow into thick algal

* Corresponding author: susanne.baden@marecol.gu.se

mats, hypoxic conditions may limit the growth of mesograzer populations and their ability to control further algal growth (Valiela et al. 1997). In addition, if the mesograzers also consume seagrass, a rapid increase of mesograzer populations may instead have negative effects on seagrass growth (Zimmerman et al. 2001). Thus, the interaction between bottom-up and top-down processes in seagrass systems can be complex, and the outcome may depend on the species present as well as their feeding preferences and growth dynamics. Because of a lack of studies assessing the interactive effects of predation and nutrient enrichment mediating algal and seagrass performance in field conditions, the relative role of eutrophication and cascading effects in seagrass ecosystems is still poorly known (Hughes et al. 2004; Valentine and Duffy 2006; Heck and Valentine 2007). The few field studies to date have yielded inconsistent results (Heck et al. 2000; Douglass et al. 2007; Moksnes et al. 2008). To find general answers of how eutrophication and overfishing may affect shallow coastal habitats, there is a need for more large-scale comparative studies testing the same mechanisms under different environmental conditions.

Here we present the results of a broad-scale field experiment designed to assess the relative importance of resource supply and predation and their interaction, in structuring temperate eelgrass *Zostera marina* L. communities along an estuarine salinity gradient from southern Finland in the Baltic Sea to the Skagerrak area of the Swedish west coast. The three regions assessed are all eutrophied and overfished but differ markedly in terms of abundance of small predators and mesograzers, in the biomass of ephemeral algae, and in the response of *Zostera* to eutrophication.

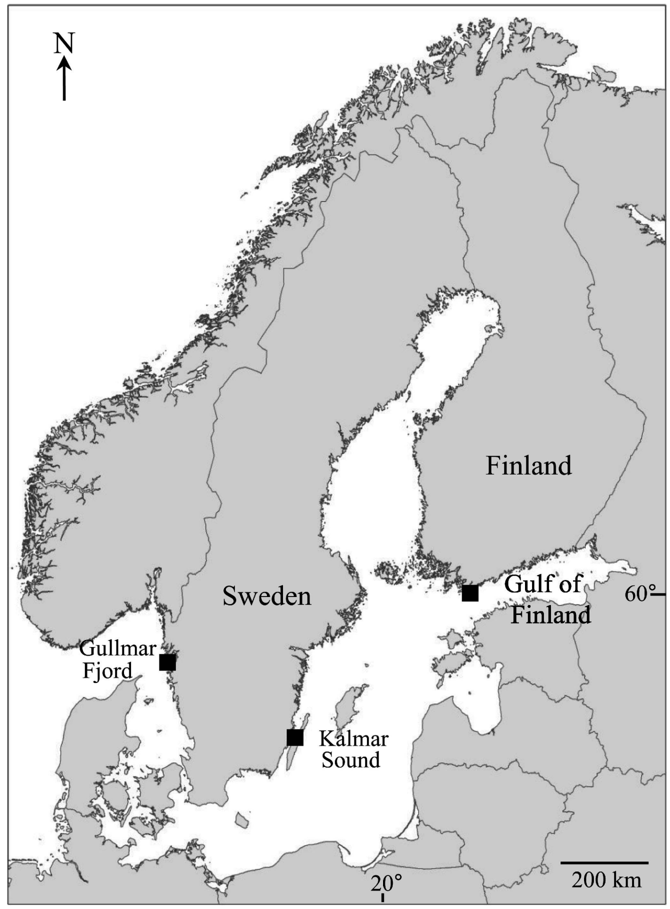

Fig. 1. Location of the three study regions.

Methods

Study system and experimental areas—The study was carried out in 2004 in three regions (Fig. 1); the Swedish NW coast (Gullmar Fjord) in the Skagerrak, the Swedish SE coast (Kalmar Sound), and the Finnish SW coast (Gulf of Finland) in the Baltic Sea. *Zostera marina* (hereafter referred to as *Zostera*) is the dominant angiosperm throughout the northern hemisphere, extensively distributed throughout Scandinavian coastal waters (Boström et al. 2003). The broad-scale presence of *Zostera* in this region follows the 5–30 g L^{-1} salinity gradient from the northern Baltic Sea to the Skagerrak (Boström et al. 2003). On the Swedish NW coast, *Zostera* is found mainly in sheltered to moderately exposed muddy and sandy sediments at 0.7–3-m depth (Baden et al. 2003). Along the brackish south and east coasts of Sweden and in Finland, *Zostera* is distributed on more exposed, sandy sediments between 1- and 7-m depth (Baden and Boström 2001). The dominant species of algal epiphytes varies between these systems, the diversity being higher on the Swedish NW coast than in the Baltic Sea (Fredriksen et al. 2005; Jaschinski and Sommer 2008). The composition of fish and invertebrates in the *Zostera* communities changes from marine species-dominated on the Swedish NW coast to a mix of marine and limnic species in the Baltic Sea, but the diversity of small mobile invertebrates and the number of functional groups are similar in both systems (Baden and Boström 2001; Boström et al. 2003). The abundance and diversity of intermediate predators are higher on the Swedish NW coast, with 29 marine fish species and 3 common species of shrimps and crab present (Baden and Pihl 1984; Pihl et al. 2006; Jephson et al. 2008), whereas in Baltic *Zostera* beds 5 marine and 10 freshwater fish and 1 shrimp species are found (Ådjers et al. 2006). Presently, the *Zostera* communities in the three study regions differ dramatically both in terms of biomass of ephemeral algae, mesograzers, and small predators and in terms of changes in the distribution of eelgrass (Table 1). Eutrophication has significantly altered the structure and function of Swedish coastal systems (Rosenberg et al. 1996), and almost 60% of the *Zostera* meadows along the Swedish NW coast have been lost since the 1980s (Baden et al. 2003). During this period, ephemeral macroalgal mats have increased in distribution and biomass in shallow coastal habitats in the same area (Pihl et al. 1999) and now cover many *Zostera* beds during the summer months. Simultaneously, the abundance of adult cod (*Gadus morhua* L.) has decreased because of overfishing, with a decline of more than 90% experienced along the Swedish west coast (Svedäng and Bardon 2003). This loss of cod from coastal ecosystems could potentially result in a four-level trophic cascade that would promote the growth of algal mats. Consistent with this suggestion,

Table 1. Summary of the present status and relative importance of the different components of eelgrass (*Zostera marina*) food webs in the three study areas. Top predators refers to cod (*Gadus morhua*), intermediate predators to small or juvenile fish predators (gobids, labrids, sticklebacks, pipefish, perch, and gadoids) and decapod predators (grass shrimp and crabs), and mesograzers to isopod and amphipod grazers (*Idotea* spp. and *Gammarus* spp.). Annual algae refer to epiphytic and drifting ephemeral macroalgae, nutrients to winter water-column concentrations of DIN and dissolved inorganic phosphorous (DIP), and seagrass to coverage of *Zostera marina*. +, ++, and +++ refer to low, medium, and high relative importance or abundance, respectively.

Response variable	Gullmar Fjord, Skagerrak	Kalmar Sound, Baltic Sea	Gulf of Finland, Baltic Sea
Top predators	+[1]	+[2]	+[3]
Intermediate predators	+++[4,5]	+[2,6]	++[7]
Mesograzers	+ [5]	+++[5]	+++[8,18]
Annual algae	+++[9]	+[5]	++[10]
Nutrients	+++[11]	+++[12]	+++[13,14]
Seagrass	Decline[15]	No change[16]	No change[13,17]

[1] Svedäng and Bardon (2003); [2] Nilsson et al. (2004); [3] Österblom et al. (2007); [4] Pihl et al. (2006); [5] Jephson et al. (2008); [6] Nilsson et al. (2004); [7] Ådjers et al. (2006); [8] Baden and Boström (2001); [9] Pihl et al. (1999); [10] Vahteri et al. (2000); [11] Rosenberg et al. (1996); [12] Lundgren et al. (2006); [13] Boström et al. (2002); [14] Lundberg (2005); [15] Baden et al. (2003); [16] Lundgren (2004); [17] Möller and Martin (2007); [18] Gustafsson and Boström (2009).

the density of intermediate predators in *Zostera* beds on the Swedish NW coast is presently very high (2–14 fish, 5–15 crabs, and 10–70 grass shrimp m^{-2}) and appears to have increased, whereas the abundance of large mesograzers on algae (i.e., adult *Gammarus* spp. and *Idotea* spp.) in the *Zostera* beds presently is extremely low or absent, respectively, in comparison to 20 yr ago (Baden 1990; Pihl et al. 2006; Jephson et al. 2008). The gastropod community in these *Zostera* beds (dominated by rissoid micrograzers) appears not to affect the growth of epiphytic macroalgae (Moksnes et al. 2008).

The Baltic Sea ecosystems also suffer from nutrient pollution, which has resulted in extensive ecological changes including increased production of phytoplankton and ephemeral macroalgae and decreased distribution of perennial macroalgae (Rosenberg et al. 1990; Karlsson et al. 2002). However in contrast to the Skagerrak system, there is no indication that the distribution of *Zostera* beds in the Baltic is decreasing (Boström et al. 2002, 2003). Over the past 25 yr, Baltic Sea cod stocks have been decimated by around 80%, causing a shift from a cod-dominated to a clupeid-dominated ecosystem in the pelagic Baltic proper (Österblom et al. 2007; Casini et al. 2008). The potential effects of this shift on coastal ecosystem functioning are largely unknown but are suggested to differ between regions (Almesjö and Hansson 2002).

In the Kalmar Sound, there is presently an extremely low abundance of predatory fish. The availability of planktonic food for juvenile fish is thought to have decreased and may be partly responsible for several years of recruitment failure in perch *Perca fluviatilis*, pike *Esox lucius*, and roach *Rutilus rutilus* (Nilsson et al. 2004). The *Zostera* beds in this region support a high densities of mesograzers, in particular *Gammarus* spp. and *Idotea* spp., but also gastropods, such as *Theodoxus fluviatilis*, *Radix balthica*, and *Hydrobia* spp. (Jephson et al. 2008).

In contrast to the Kalmar Sound, the abundance of perch and roach in Finnish coastal waters is today relatively high (approximately 1 fish m^{-2}) and has more than doubled in the past two decades since the disappearance of cod (Ådjers et al. 2001). The *Zostera* beds in this area have a high abundance of mesograzers and low biomass of epiphytes (Boström and Mattila 1999).

Because of a lack of manipulative studies, it is largely unknown how predation pressure on mesograzers differs between regions and to what extent species interactions explain observed differences in grazer, algal, and *Zostera* biomass. The aim of the present study was to assess the relative role of bottom-up and top-down processes in structuring seagrass communities and their effect on the growth of *Zostera* in these three systems.

Cage experiments—To compare the relative importance of nutrient enrichment, algal grazing, and predation for the growth of ephemeral algae and *Zostera*, a series of 5-week-long cage experiments were performed between 20 July and 15 September 2004 in the three regions described previously (Table 1). The experimental setup consisted of patches (0.05 m^2) of live *Zostera* placed in cages within natural eelgrass beds that were subjected to different nutrient levels and mesograzer and predator abundances, in an orthogonal design. The cages measured $0.45 \times 0.45 \times 0.90$ m and $0.45 \times 0.45 \times 0.60$ m ($l \times w \times h$) in Sweden and Finland, respectively, and were made of an 8-mm galvanized steel frame covered with a nylon net (mesh size 1 mm, Sefarnitex 06-1000/57). The net allowed 95% of visible light, algal propagules, and small animals to enter through the mesh but excluded all fish and invertebrate predators on mesograzers (Moksnes et al. 2008). The experimental patches comprised 40 *Zostera* shoots (corresponding to natural densities in each region, i.e., 800 shoots m^{-2}) attached to a plastic net (mesh size 2 cm, area 0.05 m^2). At each experimental site, live plants (including intact rhizomes and root hairs) were collected by divers. To remove fauna and debris, each plant was gently rinsed in seawater. In order to measure leaf growth, each shoot was punched with a syringe (Short and Duarte 2001) and attached to the net using cable ties. The cable tie closest to the meristem was used as a marker for measurement of rhizome net growth (Short and Duarte 2001). During the entire procedure, plants were kept moist in seawater, and care was taken not to damage rhizomes, root hairs, and leaves.

Grazing and predation in the *Zostera* patches were manipulated by employing the following treatments: (1) closed cage treatment (cage with no animals added), (2) grazer treatment (cage with enclosed mesograzers), (3) fish treatment (cage with one enclosed predatory fish), (4) open cage treatment (cages with one 10 × 10-cm opening on each bottom side to allow small predators access), and (5) no cage treatment (*Zostera* patch). Possible cage artifacts were assessed by comparing the open and no cage treatments. Because juvenile mesograzers can migrate through the cage mesh (Moksnes et al. 2008), we expected a high abundance of mesograzers to appear in the closed cage treatments in areas with reproducing populations. The grazer treatment was included to ensure that the effect of mesograzers could be studied in each area and compared between regions. The treatments were combined with two levels of water-column nutrient enrichment in an orthogonal design: nutrient enrichment (dissolved inorganic nitrogen (DIN) [NO_3^-, NO_2^-, and NH_4^+] and phosphate PO_4^{3-}) and no nutrient enrichment. Nutrient levels were manipulated using a commercial, slow-release fertilizer (Plantacote™ 4M; Worm et al. 2000*b*; Moksnes et al. 2008). This fertilizer provides a constant delivery of nutrients by leaching over a period of 6–8 weeks. Nutrients were provided in the fertilization treatments by adding 300 g of Plantacote™ granules to a 20-cm-long net bag made of 1-mm plastic mesh. The net bag was attached to a rod positioned in the center of the seagrass patch (*see* below). To standardize treatments, identical empty bags were placed in the patches receiving no nutrient enrichment.

Treatments were assigned to two experimental sites in each region (10–20 km apart). At each site 20 experimental plots were placed ~ 10 m apart. Experimental treatments were then randomly assigned to the cages, allowing for two replicates of each treatment. Each region thus had four treatment replicates in total. At the start of the experiment, cages were carefully emptied of all animals using handheld dip nets. Patches were secured into the sediment using metal hooks, and the nutrient rod was placed in the middle of each eelgrass patch. Folding the net into a roll and securing it with cable ties closed the upper part of the cages.

In the grazer treatment, we enclosed a biomass of approximately 2.0 g wet weight of gammarid and isopod mesograzers in each cage. This corresponds to the natural high densities found in Finland and the Kalmar Sound (Boström et al. 2006; Jephson et al. 2008) and to those in the Gullmar Fjord 25 yr ago (Baden 1990). Gammarids and idoteids have approximately the same consumption of ephemeral green algae per body weight (Moksnes et al. 2008). The mesograzer species composition enclosed in the cages varied between regions, reflecting the respective natural assemblages. In the Gullmar Fjord, we enclosed 100 individuals of *Gammarus locusta* (7–15 mm in length). In the Kalmar Sound, 40 individuals of *Gammarus* spp. (mainly *G. locusta* but also some *G. oceanicus*, 10–15 mm in length) and 10 individuals of *Idotea* spp. (mainly *I. balthica* but also *I. chelipes*, 8–15 mm in length) were used. In the Gulf of Finland we enclosed 70 individuals of *Gammarus* spp. (mainly *G. oceanicus* but also some *G. salinus*, 7–15 mm in length) and 40 individuals of *Idotea* spp. (mainly *Idotea chelipes* but also *I. balthica*, 6–12 mm in length). The lower number of enclosed mesograzers in Kalmar Sound was due to the larger mean size of mesograzers in this region.

In the Gullmar Fjord, the enclosed predatory fish was the black goby (*Gobius niger*, 100–140 mm in length). The black goby is one of the most abundant resident fish species in eelgrass beds in the area and feeds mainly on small crustaceans (Baden and Pihl 1984; Wennhage and Pihl 2002). In the Baltic Sea, perch (*Perca fluviatilis*, 130–150 mm in length) was used, it being one of the most important predators on crustaceans in shallow vegetated habitats in the region (Lappalainen et al. 2001). At the starting date of the experiments, both mesograzers and predators were added to the treatments. To remove fouling during the course of the experiment, cages were scrubbed with brushes each week.

Sampling and analyses—Samples for water-column nutrient concentrations were taken from all closed, open, and no cage treatments at the start and at the end of the experiment. This took place approximately 10 cm downstream of the nutrient bag, using acid-washed plastic syringes equipped with a 30-cm-long plastic tube. Samples were immediately filtered through GFF filters (0.45 μm), kept on ice until stored at −60°C before finally being analyzed on an autoanalyzer (TRAACS 800) for N and P.

At the termination of the experiments, the seagrass patches were sampled by divers using a net bag (mesh size 200 μm) on a steel frame (0.071 m^2). These were carefully lowered over the *Zostera* patch and pushed into the sediment, thus sampling plants with rhizomes and associated animals intact and excluding organisms on the cage walls. During this procedure, mobile fauna clung onto the seagrass rather than swimming away (P.-O. Moksnes pers. obs.). The cages were thereafter emptied with dip nets to catch the enclosed fish and assess if any unwanted predators were present. The samples were immediately put on ice and later deep-frozen before further analysis in the laboratory. Because of rough weather conditions, five cage treatments were lost in the Kalmar Sound (two replicates of the closed and open treatments and one replicate of the fish treatment), and one open treatment was lost in Finland.

In the laboratory, the biomass of new leaf, rhizome, and root hair growth since the start of the experiment was measured to estimate above- and belowground production of *Zostera* (Short and Duarte 2001). From each treatment replicate (patch), five to eight intact seagrass plants were analyzed, and the mean was used in the statistical analysis. Total algal biomass per patch was assessed by collecting loose-lying ephemeral macroalgae and scraping all leaves from the five to eight selected plants with a scalpel. The algae were then identified to species or family under the microscope and dried to a constant weight (48 h, 60°C). The *Zostera* production and algal biomass scraped from the selected plants were converted into biomass of the total number of *Zostera* plants per patch. The mobile and sessile leaf fauna from each patch were gently removed, retained on a 200-μm sieve, and identified, measured, and enumerated. Dry weight (dry wt) was obtained by drying samples at 60°C for 48 h. To estimate mesograzer biomasses, length–dry weight relationships were developed for all species.

Table 2. Three-factor ANOVA models testing the water-column concentration of dissolved inorganic nitrogen (DIN) and phosphate (PO_4^{3-}) as a function of cage treatment, nutrient enrichment, and region at the start and end of the study. All data were $\sqrt{x}$-transformed and $\sqrt{(\sqrt{(\sqrt{x})})}$-transformed at the start and end of the experiment, respectively, to homogenize the variance. SS = sum of squares.

	DIN				PO_4^{3-}			
Source	df	SS	*F*	*p*	df	SS	*F*	*p*
Start								
Cage (C)	2	0.94	2.14	0.1286	2	0.08	1.05	0.3571
Nutrients (N)	1	14.9	68.22	0.0001	1	3.28	87.37	0.0001
Region (R)	2	3.38	7.71	0.0013	2	1.84	24.54	0.0001
C × N	2	0.36	0.83	0.4413	2	0.14	1.93	0.1568
C × R	4	2.21	2.52	0.0536	4	0.26	1.74	0.1583
N × R	2	1.24	2.83	0.0696	2	1.41	18.79	0.0001
C × N × R	4	1.90	2.17	0.0872	4	0.29	1.95	0.1195
Residual	46	10.1	—	—	44	1.65	—	—
End								
Cage (C)	2	0.03	3.58	0.0348	2	0.01	2.28	0.1137
Nutrients (N)	1	0.19	48.36	0.0001	1	0.10	26.21	0.0001
Region (R)	2	0.08	10.55	0.0001	2	0.18	23.28	0.0001
C × N	2	0.05	5.99	0.0046	2	0.03	4.47	0.0171
C × R	4	0.06	3.61	0.0114	4	0.02	1.27	0.2975
N × R	2	0.09	11.21	0.0001	2	0.07	9.24	0.0004
C × N × R	4	0.06	3.95	0.0071	4	0.04	2.62	0.0476
Residual	52	0.21	—	—	44	1.17	—	—

Statistical analysis—Above- and belowground production of *Zostera* over 5 weeks, total biomass of algae, and biomass, abundance, and length of dominant faunal species or groups were tested as dependent variables in a series of three-factor ANOVA models (type III) using cage treatment (five levels), nutrient treatment (two levels), and region (three levels) as fixed independent variables ($n = 4$). Before analyses were performed, all data were tested for homoscedasticity with Cochran's *C*-test and square-root transformed to homogenize variances where necessary. A posteriori multiple comparison tests were carried out using the Student–Newman–Keuls (SNK) procedure.

Results

Water-column nutrient enrichment—At the start of the experiment, average concentrations of DIN in enriched treatments were three to four times higher and significantly different from ambient nutrient treatments in all tested cage treatments in all three regions. Among the enriched treatments, DIN concentrations were significantly lower in the Gulf of Finland (2.6 μmol L^{-1}) in comparison to the Gullmar Fjord and Kalmar Sound, which did not differ (5.7 μmol L^{-1}; Table 2, SNK-test at $p < 0.05$). The phosphate concentrations in both the Gullmar Fjord and Kalmar showed a similar trend, with significantly higher values in enriched treatments compared to ambient nutrient treatments. However, this was not the case in Finland, while there was a significantly different concentration of phosphates in enriched treatments between all three regions (2.3, 1.1, and 0.43 μmol L^{-1}, respectively). In contrast, ambient DIN and phosphate concentrations showed no regional differences, being on average 1.1, 2.1, and 0.7 μmol L^{-1} DIN and 0.3−0.4 μmol L^{-1} phosphate for the Gullmar Fjord, Kalmar, and Finland, respectively.

By the end of the experiment, DIN and PO_4^- concentrations in nutrient-enriched treatments in the Gullmar Fjord and in Kalmar were comparable to their initial values (5.9 and 4.4 μmol L^{-1} DIN and 3.0 and 1.4 μmol L^{-1} phosphate, respectively) and were significantly higher than those in ambient treatments for all cage treatments (except for the no cage treatment in the Gullmar Fjord). In Finland, DIN concentrations were also significantly higher in enriched treatments (on average 1.5 μmol L^{-1}), whereas the phosphate concentration (on average 0.34 μmol L^{-1}) showed no difference from background levels (Table 2; SNK-test at $p < 0.05$). The lower nutrient concentrations at the end of the study in some treatments may be due to higher water velocities, nutrient advection rates, and possibly depletion of some nutrients, particularly in the more exposed Finnish sites and in some no cage treatments. On average, 37% and 52% of the fertilizer remained at the end of the experiment in the Baltic and in the Gullmar Fjord, respectively, corresponding to a loading rate of nitrogen (N) and phosphate (P) being 138 mmol N and 14 mmol P m^{-2} d^{-1} in the Baltic and 108 mmol N and 11 mmol P m^{-2} d^{-1} in the Gullmar Fjord, which is the double amount of P and about one-third more of N compared to seagrass field experiments carried out by Heck et al. (2000).

Zostera *production*—Both the above- and belowground production of *Zostera* were significantly higher in the Gullmar Fjord in comparison to the other regions. They were also significantly reduced in the nutrient-enriched treatment, again only in the Gullmar Fjord region, resulting in a significant interaction effect between nutrient and region (Fig. 2A; Table 3). Leaf growth was significantly lower in Finland compared to Kalmar (Fig. 2A), whereas rhizome growth was similar between these two regions (0.02 g dry wt per plant and 5 weeks) and significantly lower than in the Gullmar Fjord (0.09 g dry wt per plant and 5 weeks; Table 3; SNK-test at $p < 0.05$). No significant cage treatment effect was detected for any growth variable in any region, although a trend toward lower leaf growth was evident in the fish treatment in the Gullmar Fjord (Fig. 2B; Table 3).

Algae—Macroalgae occurred almost exclusively in the Gullmar Fjord, mainly as loose-lying algae around the upper part of the leaves with biomasses above 2.5 g dry wt per patch in enriched treatments. In contrast, only very low biomasses of epiphytic microalgae were found in Kalmar and Finland (below 0.03 g dry wt per patch in all treatments). Total algal biomass was significantly higher in the Gullmar Fjord and was significantly affected by both nutrient and cage treatment. However, this was not true in the other regions, resulting in a significant interaction effect between nutrient and region and between cage and region (Fig. 2C,D; Table 4). In the Gullmar Fjord, nutrient enrichment resulted in a significantly higher total algal

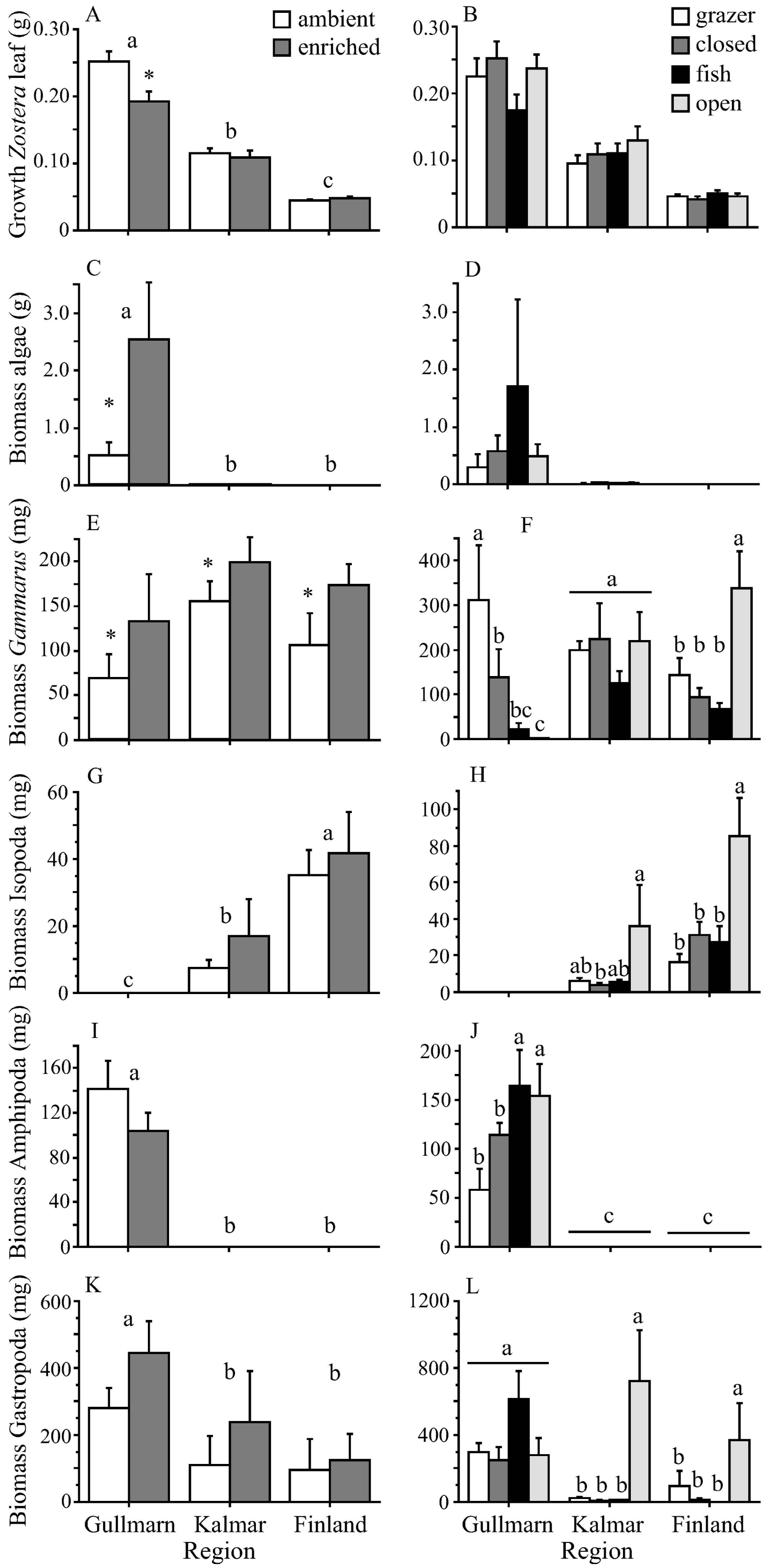

Fig. 2. Mean aboveground growth of (A, B) *Zostera marina*, (C, D) biomass of macroalgae, (E, F) *Gammarus locusta*, (G, H) isopods, (I, J) small amphipods, and (K, L) gastropods per seagrass patch (0.071 m^2) after a 5-week experiment (mean g dry weight $\pm$ SE) in three regions (Gullmar Fjord, Kalmar Sound, and Gulf of Finland). Results expressed as a function of, left column, nutrient enrichment (ambient and enriched) and, right column, four different cage treatments (grazer = enclosed mesograzers, closed = predator exclusion cage, fish = enclosed fish predator, open = cage with holes). Different letters above bars indicate significantly different means ($p < 0.05$, SNK-test).

Table 3. Three-factor ANOVA models testing above- and belowground production of *Zostera marina* (g dry wt per 5 weeks) as a function of cage treatment, nutrient enrichment, and region. Rhizome biomass was $\sqrt{x}$-transformed prior to analysis to homogenize the variance.

		Leaf biomass			Rhizome biomass		
Source	df	SS	F	p	SS	F	p
Cage (C)	4	0.01	1.12	0.35	0.00	1.03	0.40
Nutrients (N)	1	0.01	5.44	0.022	0.02	23.60	0.0001
Region (R)	2	0.62	158.00	0.0001	0.58	278.60	0.0001
C × N	4	0.01	0.71	0.58	0.01	1.21	0.31
C × R	8	0.02	1.42	0.20	0.01	1.05	0.40
N × R	2	0.02	6.20	0.003	0.03	17.10	0.0001
C × N × R	8	0.01	0.80	0.60	0.01	1.30	0.26
Residual	82	0.16	—	—	0.08	—	—

biomass compared to nonenriched treatments for all cage treatments. The total algal biomass was three to six times higher in the fish treatment compared to other cage treatments, but this difference was not significant because of the high variance of the results (Fig. 2C). The overall increase was driven mainly by the filamentous green algae *Ulva* spp. (syn. *Enteromorpha* spp.) that dominated the macroalgal assemblage (62%) and had significantly higher biomass in nutrient-enriched treatments (Table 4). In contrast, the biomass of the filamentous brown algae of the family Ectocarpales, constituting 32% of total algal biomass, was not significantly affected (Table 4). This resulted in the relative abundance of algal species responding strongly to experimental treatment. In the Gullmar Fjord, *Ulva* spp. clearly dominated in the nutrient-enriched fish and open treatments (98% and 87%, respectively) but were almost absent in nutrient grazer and closed treatments without nutrient additions (5% and 6%, respectively), which were dominated by Ectocarpales (70% and 74%, respectively).

The relatively low biomass of epiphytic algae in Kalmar (Fig. 2C,D) was dominated by Ectocarpales and *Ceramium* spp. and also by benthic microalgae (particularly *Cocconeis scutellum*) and cyanobacteria. Only propagules of filamentous red and brown macroalgae and a low abundance of benthic cyanobacteria and microalgae (again mainly *C. scutellum*) were found on *Zostera* leaves from the Gulf of Finland.

Mesograzers—The composition and abundance of mesograzers differed markedly between the Baltic regions, which contained a high abundance of large-bodied crustaceans and gastropod grazers, and the Swedish NW coast sites, which were dominated by small amphipods and gastropods. The response to experimental treatments differed dramatically between species and regions.

The biomass and composition of gammarid amphipods were strongly affected by cage treatment, with the effect also differing radically between regions. In the Gullmar Fjord, the biomass of *Gammarus locusta* was significantly affected by the presence of predators being significantly higher in the closed treatment compared to the fish and open cage treatments (Fig. 2F; Table 5). This decline was driven mainly by a complete loss of adult gammarids

Table 4. Three-factor ANOVA models testing total biomass of ephemeral macroalgae and the biomass of the green algae *Ulva* spp. and brown algae Ectocarpales (mg dry wt) as a function of cage treatment, nutrient enrichment, and region. All data were log(x + 1)-transformed prior to analysis to homogenize the variance.

Source	df	SS	F	p
Total algal biomass				
Cage (C)	4	4.4	3.0	0.023
Nutrients (N)	1	2.6	7.0	0.010
Region (R)	2	122.2	167.4	0.0001
C × N	4	0.6	0.4	0.81
C × R	8	8.8	3.0	0.005
N × R	2	5.3	7.2	0.001
C × N × R	8	1.2	0.4	0.91
Residual	84	30.7	—	—
Ulva biomass				
Cage (C)	4	3.8	3.8	0.007
Nutrients (N)	1	8.2	32.5	0.0001
Region (R)	2	71.7	142.3	0.0001
C × N	4	0.7	0.7	0.59
C × R	8	7.6	3.8	0.0008
N × R	2	17.0	33.7	0.0001
C × N × R	8	1.5	0.7	0.67
Residual	84	21.2	—	—
Ectocarpales biomass				
Cage (C)	4	3.4	1.46	0.22
Nutrients (N)	1	0.0	0.01	0.92
Region (R)	2	32.7	27.90	0.0001
C × N	4	0.6	0.27	0.89
C × R	8	6.9	1.47	0.18
N × R	2	0.01	0.01	0.99
C × N × R	8	1.3	0.27	0.97
Residual	84	49.9	—	—

($\geq$ 9 mm in length) from the fish and open treatments. There were significantly more adult gammarids in the closed treatment, which in turn was significantly lower than in the grazer treatment (Fig. 3A,B; Table 5). The abundance of juvenile gammarid amphipods was less affected by predators and differed significantly only between the grazer and open treatments (Fig. 3C,D; Table 5). This size-specific loss of gammarid amphipods resulted in a significantly higher mean size of gammarid in the grazer and closed treatments (on average 8.0 mm in length) in comparison to the fish and open treatments (average length 4.6 mm; Table 5; SNK-test at $p < 0.05$).

In Kalmar, the effect of ambient predators on gammarid amphipods (*G. locusta* and *G. oceanicus*) was the opposite. Although as on the west coast the number of adults was significantly lower in the fish than in the closed treatment, it was significantly higher in the open treatment. In contrast, the number of juvenile gammarids was significantly lower in the open treatment in comparison to the closed and grazer treatments (Fig. 3B,D; Table 5). The differing effect on adults and juveniles resulted in a significantly higher mean size of gammarid in the open (9.4 mm) in comparison to the closed and grazer treatments (on average 4.1 mm) but a similar biomass of gammarids in

Table 5. Three-factor ANOVA models testing total biomass (mg dry wt), number of adult and juveniles (< 9 mm L), and mean size (mm L) of the amphipod *G. locusta* as a function of cage treatment, nutrient enrichment, and region. Total biomass was $\sqrt{x}$-transformed and the number of adults and juveniles $\sqrt{(\sqrt{x})}$-transformed prior to analysis to homogenize the variance.

	Total biomass				Number of adults				Number of juveniles				Size			
	df	SS	*F*	*p*	df	SS	*F*	*p*	df	SS	*F*	*p*	df	SS	*F*	*p*
Cage (C)	4	451.7	4.6	0.002	4	26.5	24.2	0.0001	4	6.2	2.6	0.04	4	101.2	11.7	0.0001
Nutrients (N)	1	152.2	6.3	0.014	1	0.5	1.8	0.18	1	7.1	11.7	0.0009	1	17.7	8.2	0.006
Region (R)	2	783.0	16.1	0.0001	2	24.7	45.2	0.0001	2	45.4	37.6	0.0001	2	5.1	1.2	0.31
C × N	4	101.1	1.0	0.39	4	1.0	0.9	0.44	4	1.5	0.6	0.65	4	14.8	1.7	0.15
C × R	8	965.9	4.9	0.0001	8	23.8	10.9	0.0001	8	21.8	4.5	0.0001	8	235.8	13.7	0.0001
N × R	2	15.9	0.3	0.72	2	0.5	1.0	0.38	2	2.7	2.2	0.11	2	1.7	0.4	0.67
C × N × R	8	119.2	0.6	0.77	8	1.7	0.8	0.63	8	4.2	0.8	0.55	8	21.0	1.2	0.30
Residual	84	2044	—	—	84	23.0	—	—	84	50.7	—	—	73	157.4	—	—

all cage treatments (Fig. 2F; Table 5; SNK-test at $p < 0.05$).

In the Gulf of Finland, the number of adult gammarids (*G. oceanicus* and *G. salinus*) was significantly higher in the open than in the fish and closed treatments, which did not differ from each other. The number of juveniles was not significantly affected by cage treatment, in contrast to the results from the Kalmar Sound (Figs. 2F, 3B,D; Table 5). This resulted in a significantly higher biomass and mean size of gammarid in the open treatment in comparison to the fish and closed treatments (Fig. 2F; Table 5; SNK-test at $p < 0.05$).

The biomass and mean size of gammarid in the open treatments were significantly lower in the Gullmar Fjord in comparison to the Baltic sites. However, in the closed treatments the biomass was similar in all regions, and the mean size of gammarid was in fact larger in the Gullmar Fjord than that of the sites in the Baltic Sea (Fig. 2F; Table 5; SNK-test at $p < 0.05$).

Nutrient treatments also affected the biomass and composition of gammarids, but in contrast to cage treatment, the effect was the same in all regions. Enriched treatments had significantly higher biomass but a lower mean size of gammarid in all cage treatments in all regions (Fig. 2E; Table 5; SNK-test at $p < 0.05$). The size effect was caused by a significantly higher abundance of juvenile gammarids in nutrient-enriched compared to ambient treatments in all regions, whereas the effect on adult gammarids, although positive, was not significant (Fig. 3A,C; Table 5).

Idoteids were absent from the investigated *Zostera* meadows in the Gullmar Fjord but were numerous in the

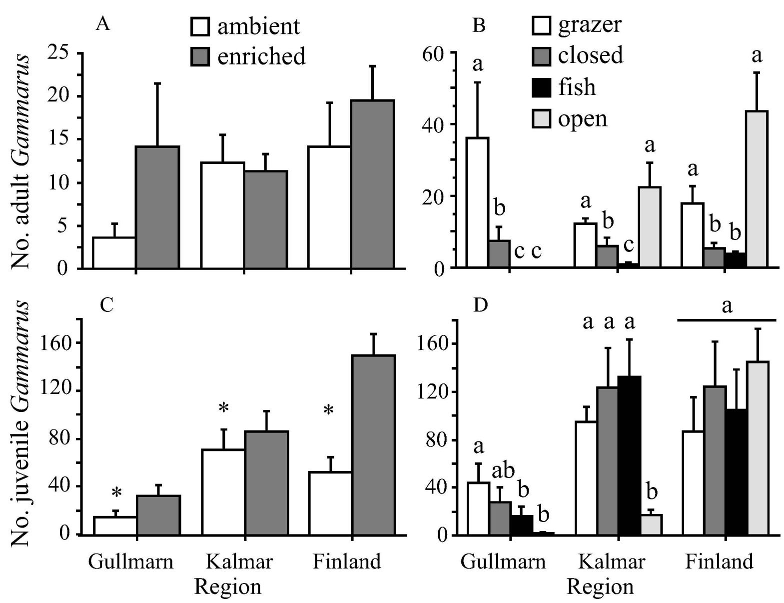

Fig. 3. Mean number of (A, B) adult and (C, D) juvenile (≤ 9 mm in length) *Gammarus locusta* (± SE) per seagrass patch (0.071 m²) after a 5-week experiment in three regions (Gullmar Fjord, Kalmar Sound, and Gulf of Finland). Results expressed as a function of (A, C) nutrient enrichment (ambient and enriched) and (B, D) four different cage treatments (grazer = enclosed mesograzers, closed = predator exclusion cage, fish = enclosed fish predator, open = cage with holes). Different letters above bars indicate significantly different means ($p < 0.05$, SNK-test). Asterisks denote significant differences between nutrient treatments.

Table 6. Three-factor ANOVA models testing total biomass of isopods, small tube-building amphipods, and gastropods (mg dry wt) as a function of cage treatment, nutrient enrichment, and region. Biomass of isopods and small amphipods were $\sqrt{(\sqrt{x})}$-transformed and the biomass of gastropods $\sqrt{x}$-transformed prior to analysis to homogenize the variance.

Source	df	SS	*F*	*p*
Isopod biomass				
Cage (C)	4	8.5	7.5	0.0001
Nutrients (N)	1	0.7	2.6	0.11
Region (R)	2	124.8	220.7	0.0001
C × N	4	0.9	0.8	0.54
C × R	8	6.3	2.8	0.009
N × R	2	0.6	1.0	0.37
C × N × R	8	1.9	0.7	0.55
Residual	84	23.7	—	—
Small amphipod biomass				
Cage (C)	4	0.9	1.22	0.31
Nutrients (N)	1	0.1	0.42	0.52
Region (R)	2	110.1	315.50	0.0001
C × N	4	0.4	0.59	0.67
C × R	8	4.6	3.26	0.028
N × R	2	0.2	0.43	0.65
C × N × R	8	0.9	0.65	0.73
Residual	84	14.7	—	—
Gastropod biomass				
Cage (C)	4	3759	12.8	0.001
Nutrients (N)	1	120	1.6	0.20
Region (R)	2	2275	15.5	0.0001
C × N	4	176	0.6	0.66
C × R	8	2497	4.3	0.0002
N × R	2	37	0.3	0.77
C × N × R	8	355	0.6	0.77
Residual	84	3759	12.8	0.001

Baltic Sea. In Finland, the total biomass of *Idotea* spp. (dominated by *I. chelipes* and *I. balthica*, with a few *I. granulosa*) was significantly higher than in the other regions and here also significantly higher in the open treatment compared to the other treatments, which did not differ from each other (Fig. 2H; Table 6). The same trend was also evident in Kalmar, even though the total biomass of isopods in the open treatment differed significantly only from the closed treatment (Fig. 2H; Table 6). Similar to the gammarid response, nutrient treatments appeared to support a higher biomass of isopods compared to the ambient treatments (on average 44% higher; Fig. 2G), although the overall effect of enrichment was not significant (Table 6).

Small tube-building species of amphipod were very abundant on the *Zostera* leaves in the Gullmar Fjord (dominated by *Ericthonius difformis*, *Corophium insidiosum*, and *Microdeutopus gryllotalpa*) but absent in the Baltic regions, where the isopod *Jaera albifrons* was the only other crustacean mesograzer species found on the eelgrass leaves. The total biomass of small amphipod species was therefore significantly higher in the Gullmar Fjord in comparison to the other regions and here also significantly higher in the fish and open treatments than in the grazer and closed treatments, resulting in a significant interaction effect between cage and region (Fig. 2J; Table 6). No significant nutrient effect was detected, although a trend toward a lower biomass was indicated in enriched treatments (Fig. 2I; Table 6).

The total biomass of gastropods was significantly higher in the Gullmar Fjord compared to Kalmar and Finland. Again there was no visibly significant nutrient effect, although a trend to higher biomass in enriched treatments was seen in all regions (Fig. 2K; Table 6). Biomass was significantly higher in the open compared to other treatments in Kalmar and Finland, while in the Gullmar Fjord, the fish treatment showed a borderline-significant higher biomass compared to others in this region (Fig. 2L; Table 6). The gastropods in the Gullmar Fjord were smaller, more numerous (mean 381 ± SE 65 per cage), and dominated by *Rissoa membranacea* and *R. albella* (both with a mean height < 3 mm). In Kalmar, small *R. membranacea* and *Hydrobia* spp. occurred together with the larger limnic species *Theodoxus fluviatilis* and *Lymnaea peregra* (mean height 5.8 mm), with a mean abundance of 48 ± SE 8.5 per cage. In Finland, the gastropod species (mean abundance 12 ± SE 3 per cage) were dominated by *T. fluviatilis*, whereas *Hydrobia* spp. and *L. peregra* were sparse.

Cage artifacts—We tested cage artifacts such as reduced light and water flow by comparing our response variables between the open cage with the no cage treatment and found no consistent difference. The water-column DIN level was significantly lower in the no cage treatment at the end of the study in Gullmar Fjord, possibly as a result of higher flow and nutrient advection rates. However, this artifact was not found at the start of the experiment or in the same treatment in the other two regions. In the Gullmar Fjord, the biomass of filamentous algae and the mesograzer *Gammarus locusta* were significantly lower in the open compared to the no cage treatment. At the end of the experiment, algae were found entangled on the rods of the fertilizer bags of some no cage treatments, increasing the algal biomass of the patches, but were prevented from doing so in the open treatments because of the small cage openings. The higher biomass of gammarids in the no cage treatment was driven by two replicates that had acquired this mass of drifting algae. Thus, these differences appear to have been caused by algal drifts and not by artifacts associated with changes in light conditions and water flow. In the Kalmar Sound, the biomass of *Gammarus* spp. was instead significantly higher in the open compared to the no cage treatment. Cage artifacts were not detected in the Gulf of Finland.

Discussion

Our results suggest that differences in predation pressure on mesograzers play a key role in explaining regional differences not only in the composition and abundance of mesograzers but also in the biomass of ephemeral algae and the effect of eutrophication on *Zostera* growth. Although all regions are expected to be similarly influenced by eutrophication, *Zostera* growth was negatively affected only by nutrient enrichment on the Swedish NW coast. Here a numerous assemblage of small predators excluded algal mesograzers, allowing ephemeral algae to overgrow *Zostera* plants during nutrient enrichment. In contrast, the Baltic seagrass sites supported a comparatively low number of predators, allowing an abundant mesograzer assemblage to prevent algal growth even during enhanced nutrient conditions. To our knowledge, this is the first broad-scale manipulative study revealing the relative importance of nutrient pollution, herbivory, and predation in seagrass beds.

Baltic Zostera *systems*—Because of the salinity gradient running from the brackish Baltic Sea (on average 6–8 g L^{-1} in Finland and Kalmar) to the more saline Swedish NW coast (20–30 g L^{-1}), the regions investigated differ naturally in terms of species composition and growing conditions for *Zostera*. The Finnish *Zostera* populations are at the border of salinity tolerance (Boström et al. 2004), a fact demonstrated in the present study by the four- to five-times lower growth rate here compared to populations on the Swedish NW coast. At the Finnish sites, *Zostera* growth is thought to be limited by nutrients (Boström et al. 2004) and carbon availability (Hellblom and Björk 1999). However, in this study, *Zostera* production at the Baltic sites was not enhanced by water-column nutrient enrichment. This suggests either that other factors limited growth or that *Zostera* utilize primarily sediment nutrient pools (Worm and Reusch 2000). Although the Finnish populations are growing under salinity stress and could be expected to be more vulnerable to anthropogenic disturbances, these meadows, as well as Estonian populations, have not been negatively affected by the increased eutrophication experienced in the past few decades (Boström et al. 2002, 2003; Möller and Martin 2007). The present results suggest that the abundance of mesograzers found in the two Baltic regions may prevent nutrient-induced overgrowth of ephemeral algae, a process that has severely affected the distribution of seagrass in many other areas (Short and Wyllie-Echeverria 1996; Greve et al. 2005). In the Baltic *Zostera* meadows, we found a very low biomass (< 0.5 g dry wt m^{-2}) of epiphytes for all treatments, including during nutrient enrichment that did not increase algal biomass significantly. Instead, we found a significant increase of mesograzer biomass in nutrient-enriched treatments in both regions, suggesting that although nutrients did indeed increase algal growth, this extra production was probably rapidly grazed down. Stable isotope analyses from the Kalmar Sound support the assumption that the gammarids feed mainly on ephemeral macroalgae, whereas idoteids feed on a mixture of ephemeral macroalgae and detritus (Jephson et al. 2008). Gammarids and isopods have high grazing capacities on ephemeral macroalgae (Kotta et al. 2006; Moksnes et al. 2008; Andersson et al. 2009). Consequently, the extremely high abundance of mesograzers present in the two Baltic regions (980–7000 gammarids and isopods m^{-2} in the open seagrass patches) could easily limit the development of epiphytic macroalgae. In addition, at exposed sites like those in the Baltic, physical erosion through leaf movement possibly acted to prevent epiphytic biomass accumulation on seagrass leaves (Lavery et al. 2007). The importance of this mechanism in relation to bottom-up and top-down mechanisms warrants further investigation.

Although not present in seagrass beds at the time of sampling, as a result of eutrophication, drifting mats of filamentous algae have increased dramatically on sublittoral soft bottoms in the Baltic Sea in recent decades (Vahteri et al. 2000). In contrast to the Swedish NW coast, these mats originate mainly from rocky shores but may also grow in the seagrass meadows. These algal mats are concentrated close to the sediment and have a negative effect on benthic infauna but may simultaneously constitute a food resource for mesograzers (Norkko et al. 2000). Little is known about the effects of drift algal accumulation on Baltic seagrass populations, but their effect on the performance of *Zostera* appears less severe compared to the Skagerrak area.

In periods with a lack of palatable algal food sources, mesograzers (especially idoteids) could potentially consume *Zostera* (Boström and Mattila 1999; Zimmerman et al. 2001; Vesakovski et al. 2008). However, we found no negative effect of mesograzers on *Zostera* productivity, as very few grazing marks were recorded on leaves. Additionally, the growth of *Zostera* was not lower in the open treatments, where mesograzer biomass was significantly higher.

The high abundance and large mean size of mesograzers in the Baltic *Zostera* meadows suggest that predation pressure from primary predators is very low in these systems. In the present study this assumption was supported, as we found no significant negative effects from local predators on the biomass or mean size of any group of mesograzers in both Baltic regions. In fact, the biomass and size of all mesograzers were higher in the treatments giving access to local predators. The lack of predation on mesograzers in Kalmar Sound is consistent with recent reports of extremely low abundance of perch (*Perca fluviatilis*) in the area (Nilsson et al. 2004). In confirmation of this, during more than 200 man-hours of underwater fieldwork in the area, we observed no fish and encountered only a few grass shrimp.

In the Gulf of Finland, we expected a stronger predation effect since the abundance of perch in the coastal zone has more than doubled in recent decades (Ådjers et al. 2006). However, the abundance of perch in Finnish seagrass meadows remains 10–100 times lower than the abundance of intermediate predatory fish and crustaceans on the Swedish NW coast (Pihl et al. 2006) and appears to be too low to control local mesograzer populations. During fieldwork in Finland, the only predators observed were small transient schools of perch. Although perch are considered an important predator on crustaceans (Jormalainen and Tuomi 1989; Boström and Mattila 1999), they were much less efficient as predators on mesograzers in the present study compared to the black goby (Moksnes et al. 2008; this study) and grass shrimp (Persson et al. 2008), which dominate on the Swedish NW coast. The only significant effect of enclosed perch in this study was a reduction of adult gammarids in the Kalmar Sound.

Thus, in the Baltic, the effect of overfishing on coastal ecosystems appears complex. The 80% reduction of cod is thought to have changed the pelagic food web (Casini et al. 2008), which in the Kalmar Sound may have led to a decrease in planktonic food for juvenile fish and a collapse of local populations of intermediate fish predators (Nilsson et al. 2004). In the Finnish coastal areas, the decrease of cod may have contributed to increased perch populations—although other factors, such as increased temperature and eutrophication, are probably more important (Ådjers et al. 2006). Since juvenile cod are more efficient predators on *Gammarus* and *Idotea* spp. than perch (Olovsson 2000), decreased cod populations could also potentially have a direct positive effect on mesograzer abundance in the area. However, the role of juvenile cod in Baltic seagrass systems is not yet known.

Skagerrak Zostera *systems*—Compared to the Baltic regions, the *Zostera* system on the Swedish NW coast responded dramatically differently to all experimental treatments. A nutrient enrichment of three to four times the background concentration in the Gullmar Fjord increased the biomass of ephemeral algae more than fourfold (equivalent to over 50 g dry wt algae m^{-2} in enriched treatments) and decreased the growth of *Zostera* by over 20% in all cage treatments. This decreased growth was likely a result of shading (Krause-Jensen et al. 2008), but the thick algal mats present at the end of the experiment may have also caused leaf mortality and population decline through hypoxia and sulfide invasion (Holmer and Bondgaard 2001). Concurrent measurement of total sulfur content and stable isotopic composition in *Zostera* plants from the three study regions showed high sulfide invasion in the Gullmar Fjord sites but low invasion in the Baltic regions (Holmer et al. 2009), indicating stressful growing conditions for the declining Skagerrak populations (Baden et al. 2003). The nutrient-induced algal growth is consistent with earlier experiments in the Gullmar Fjord area (Moksnes et al. 2008), and its negative effect on *Zostera* growth in the Skagerrak provides new evidence that the extensive loss of *Zostera* here has a direct link to eutrophication. These results are also supported by similar findings in the German Kiel Fjord, southern Baltic Sea (Jaschinski and Sommer 2008).

However, our experiments strongly suggest that top-down processes are also involved in the proliferation of algal mats along the Swedish NW coast. In contrast to the insignificant predation effects on mesograzers at the Baltic sites, intense predation pressure appears to exclude the dominant algal grazers *Gammarus locusta* and idoteids from *Zostera* beds in the Gullmar Fjord area. This strong effect on mesograzers is consistent with earlier cage experiments in the same location (Moksnes et al. 2008; Persson et al. 2008). Interestingly, in closed cages juvenile gammarids thrived and later reproduced and reached biomasses similar to those of the Baltic regions. However, in the fish treatment, the biomass of gammarids was 84% lower. As no adult gammarids were found in this treatment, this was likely a result of size-selective predation by the black goby. Moreover, in the presence of an abundant and diverse assemblage of intermediate predators in the open cage treatments (dominated by grass shrimp, gobid fish, and shore crab), only a few juvenile gammarids were found, and the overall biomass of gammarids was $>$ 98% lower in comparison to the closed cage treatment. These results strongly suggest a much more pronounced role for top-down processes in the Skagerrak compared to the Baltic Sea. In the Gullmar Fjord area, intertidal *Fucus* belts are rich in adult gammarids. Since adults are absent from *Zostera* meadows in the area today (Jephson et al. 2008; Moksnes et al. 2008), the *Fucus* likely harbor important source populations.

The gammarids strongly affected algal community structure. In the fish and open treatments, filamentous *Ulva* spp. dominated the algal assemblage, whereas algae in the closed and grazer treatments with high biomass of gammarids consisted almost entirely of the less palatable annual brown and red algae. In these treatments, the total algal biomasses were 66% and 83% lower, respectively, in comparison with the fish treatment (although not significantly different statistically). This result is consistent with experimental work on seaweed communities showing strong selective grazing by amphipods (Duffy and Hay 2000). The relatively low biomass of algae in the open treatment was likely a result of grazing by the omnivorous grass shrimp *Palaemon adpersus* and *P. elegans*, which were unusually abundant at the study site at the end of the experiment (on average 280 individuals m^{-2}). The grass shrimp prefer to feed on small crustaceans and are therefore important predators on juvenile gammarids, but where there is a lack of animal prey, they are also efficient grazers on ephemeral algae. However, in contrast to gammarids, they appear not to be able to control algal growth, and their overall effect on the system promotes the growth of algal mats (Jephson 2008; Moksnes et al. 2008; Persson et al. 2008).

In the Gullmar Fjord area, predation on gammarids also increased the biomass of small tube-building amphipods significantly. This result is in accordance with earlier studies suggesting that competition and predation from the omnivorous *G. locusta* negatively affect smaller mesograzer species (Moksnes et al. 2008). The large amount of amphipod tubes on the leaves may further add to impaired photosynthesis. Thus, on the Swedish NW coast the high predation pressure on large mesograzers appears to increase fouling on *Zostera* through both growth of epiphytic macroalgae and coverage by amphipods tubes. The suggested interactive role of top-down and bottom-up factors in the Swedish eelgrass beds are supported by a correlative study from Baja California describing a trophic cascade where low abundance of small predatory fish govern the success of *Zostera* in eutrophic areas (Jorgensen et al. 2007).

The present study adds support to the increasing number of studies pointing at the importance of top-down effects in shallow benthic ecosystems, in particular the important role of mesograzers in controlling algal growth in seagrass ecosystems (Worm et al. 2000*a*; Hughes et al. 2004; Burkepile and Hay 2006; Valentine and Duffy 2006), and suggests that nutrient enrichment and predation interact in affecting the growth of *Zostera* in the Baltic–Skagerrak area. Mesograzers appear to provide a positive feedback mechanism for the *Zostera* ecosystem by preventing the proliferation of ephemeral algae and may thus increase resilience to eutrophication, as indicated in the Baltic study areas. However, these large-bodied mesograzers are vulnerable to predation, and in Skagerrak intermediate predators appear to control their abundance and composition. In this region, overfishing may play an important role in the decline of *Zostera*.

In the 1980s the distribution of *Zostera* in the Skagerrak was much broader than today and not overgrown by algae despite elevated nutrient levels since the 1970s (Baden 1990; Rosenberg et al. 1990; Baden et al. 2003). The present loss of *Zostera* (Baden et al. 2003) has instead coincided with an increase in algal mats (Pihl et al. 1999) and loss of both cod and other large predatory fish from the coastal areas and loss of idoteids and gammarids from the *Zostera* beds (Baden 1990; Svedäng and Bardon 2003; Jephson et al. 2008). Although the effect of cod predation on the abundance of intermediate predators has not been studied, stomach content analyses suggest that intermediate predators are important prey (Fjøsne and Gjøsæter 1996; Wennhage and Pihl 2002). Today, the high abundance of intermediate predators plays a significant role in reducing the density of seagrass mesograzers, which in turn release algae from grazer control to bloom in response to elevated nutrient levels (Moksnes et al. 2008, this study). The present field experiments provide new support to the hypothesis that overexploitation of top predators can contribute to seagrass decline under certain trophic conditions (Heck et al. 2000) and suggest a comanagement of the fisheries and nutrient pollution.

Acknowledgments
We thank Susanna Andersson, Tina Iveslätt, Therese Jephson, Olof Lövgren, Maj Persson, Erik Pihl, Camilla Roos, Kentaroo Tryman, and Anna Villnäs for excellent assistance in the field and laboratory; Aleksandra Zgrunda, University of Gdańsk, for help with identification of diatoms; and William Thorndyke for English grammar corrections. This research was funded by grants from the Swedish Environmental Protection Agency (SEPA contract I-55-03 to S. Baden and I-58-03 to P.-O. Moksnes) within the national project Marine Biodiversity Patterns and Processes (MARBIPP), from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS contract 21.5/2003-0213 to S. Baden); Wåhlströms minnesfond för den Bohuslänska havs- och insjömiljön (S. Baden and P.-O. Moksnes); the Academy of Finland (project 209265 to C. Boström); Maj and Tor Nessling Foundation; Ministry of Environment (both to H. Arponen); and Åbo Akademi Foundation.

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Associate editor: Anthony Larkum

Received: 10 August 2009
Accepted: 29 January 2010
Amended: 15 March 2010