

Trophic role of the omnivorous grass shrimp *Palaemon elegans* in a Swedish eelgrass system

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ABSTRACT: Algal grazers are thought to play a critical role in preventing overgrowth by ephemeral algae in seagrass beds. We studied the interaction between the omnivorous grass shrimp *Palaemon elegans*, the algal grazer *Gammarus locusta* and the filamentous green alga *Ulva* sp. (syn. *Enteromorpha* sp.) to assess whether the shrimp has a positive or negative effect on the growth of ephemeral algae in eelgrass beds on the Swedish west coast. Laboratory experiments demonstrated that *P. elegans* were effective predators on gammarids <8 mm total length (TL), as well as effective grazers of filamentous *Ulva* sp. The shrimp appeared to prefer gammarid prey over algae, and only consumed significant amounts of *Ulva* sp. when the gammarid prey was too large to be consumed efficiently. The total consumption of *Ulva* sp. was positively affected by shrimp when gammarid prey were >5 mm TL, but negatively affected when *G. locusta* was smaller. In a field cage experiment, enclosed *P. elegans* decreased the abundance of gammarids by on average 68 %, causing a trophic cascade that increased the biomass of filamentous *Ulva* sp. 7-fold. These results suggest that *P. elegans* on the Swedish northwest coast feed mainly on amphipods, including the algal grazer *G. locusta*, resulting in a positive net trophic effect on the growth of filamentous *Ulva* sp. This study indicates that *P. elegans* may be an important link between overexploitation of cod in northwest Sweden and the recent increase of algal mats and loss of eelgrass in the area.

KEY WORDS: *Palaemon elegans* · Top-down effects · Trophic cascade · *Gammarus locusta* · *Ulva* sp. · Predation · Ephemeral macroalgae · Grazing

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INTRODUCTION

Eutrophication, or nutrient pollution, is a well known phenomenon having large effects on the abundance and species composition of the flora, and, consequently, the fauna in shallow water ecosystems. Due to higher nutrient supply, blooms of ephemeral algae have increased in the last 2 decades, especially blooms of filamentous *Ulva* sp. (syn. *Enteromorpha* sp.) and *Cladophora* sp. (Hardy et al. 1993, Valiela et al. 1997, 2000, Pihl et al. 1999). Simultaneously there has been a global decline of seagrass communities, strongly connected to the eutrophication (Short & Whyllie-Echeverria 1996, Duarte 2002, Green & Short 2003). Opportunistic macroalgae are favoured by the increased

nutrient supply and because of their fast growth rate they can overgrow seagrass (Valiela et al. 1997, Hughes et al. 2004) and thereby decrease the light influx causing inhibited growth and suffocation (Hauxwell et al. 2001, 2003, Havens et al. 2001).

Seagrass species form large meadows that are highly productive (Duarte 2000) and important ecosystems. They serve as nurseries and feeding grounds for several species including decapods and some commercially important fish species, such as eel and codfish. Eelgrass *Zostera marina* (L.) is the dominant seagrass on the Swedish west coast. During the last 2 decades, 58 % of the eelgrass beds have been lost from the northwest coast of Sweden (Baden et al. 2003). This decrease is thought to be associated with a general

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increase in biomass of ephemeral algal mats that cover shallow coastal areas (0 to 4 m depth), including eelgrass beds, during the summer months on the Swedish west coast (Pihl et al. 1999). These mats are dominated by filamentous *Ulva* sp., an opportunistic, fast-growing species of green algae which is positively affected by a surplus of nutrients (Wallentinus 1984, Valiela et al. 1997). Recent studies suggest that small gastropod and crustacean mesograzers play a critical role in controlling the growth of ephemeral algae (Hauxwell et al. 1998, Lotze et al. 1999, Hughes et al. 2004, Valentine & Duffy 2005), and that the present lack of such control may be related to overfishing. Removal of large fish predators may result in a trophic cascade, which implies an increase in smaller predatory organisms that reduce the abundance of algal mesograzers and thus allow ephemeral algae to grow nearly uninhibited (Heck et al. 2000, Williams & Heck 2001). On the Swedish west coast, the abundance of codfish has decreased dramatically in the last decades as a result of overfishing (Svedäng 2003, Svedäng & Bardon 2003). This loss of codfish may have increased the abundance of their prey (e.g. small fish, crabs and shrimp), which, in turn, may have increased the predation pressure on mesograzers. Consistent with this suggestion, isopod (*Idotea* spp.) and large amphipod (*Gammarus* spp.) herbivores that were common in eelgrass meadows on the Swedish west coast 20 years ago (Baden & Pihl 1984, Baden 1990) have very low abundances in these habitats today (Jephson et al. 2008, Moksnes et al. 2008). Moreover, recent cage experiments carried out in *Zostera marina* beds on the Swedish northwest coast suggest that the large amphipod *Gammarus locusta* can become very abundant and control the growth of filamentous *Ulva* sp. in the absence of predators, but that high predation rates from abundant shrimp and small fish reduce all grazer species to very low abundances in natural eelgrass beds (Moksnes et al. 2008). Moksnes et al. (2008) suggested that the shrimp *Palaemon elegans* may be a dominant predator on *G. locusta*, but demonstrated that this omnivorous shrimp also grazed *Ulva* sp., indicating that *P. elegans* may control growth of the algae. However, direct studies of the interactions between *P. elegans*, *G. locusta* and *Ulva* sp. are lacking, and it is not clear whether the net trophic effect of *P. elegans* is positive or negative for the growth of ephemeral algae.

Studies have shown that both *Gammarus locusta* (Lotze et al. 1999, Lotze & Worm 2000) and *Palaemon elegans* (Berglund 1980) are consumers of filamentous *Ulva* sp. and thus could contribute to the reduction of algal blooms. *P. elegans* is an omnivorous shrimp (Höglund 1943, Forster 1951, Fonds et al. 1981), with a varied diet and wide habitat range (Berglund & Bengtsson 1981). In western Sweden they inhabit eel-

grass, brown algal belts and bare sand habitats. They can also be found in rockpools, where they can survive on a diet consisting of *Ulva* sp. (Berglund 1980, Berglund & Bengtsson 1981).

The aim of the present study was to investigate the effects of *Palaemon elegans* on the abundance of *Gammarus locusta* and on the growth of ephemeral algae by assessing 2 opposing hypotheses: (1) *P. elegans* have a positive effect on the growth of ephemeral algae by reducing the abundance of important grazers on ephemeral algae; or (2) *P. elegans* have a negative effect on algal growth through direct grazing of algae.

MATERIALS AND METHODS

Laboratory experiment. To assess size-specific consumption rates and food preference of *Palaemon elegans* on *Gammarus locusta* and ephemeral macroalgae, a series of laboratory experiments were carried out at Kristineberg Marine Research Station on the Swedish west coast from July to October 2005. The goals of the experiments were to (1) obtain estimates of consumption rates of juvenile and adult *P. elegans* on different size classes of gammarid prey and on filamentous *Ulva* sp., (2) assess how the shrimp's consumption rates of gammarids changed when *Ulva* sp. was present, and (3) test if the total consumption of *Ulva* sp. by *G. locusta* and *P. elegans* changed when the gammarids and omnivorous shrimp were together.

Three size classes of *Palaemon elegans* were tested as predators and/or grazers: small (3.0 to 4.9 mm carapace length from the posterior edge of the carapace to the base of the eyestalks; CL), intermediate (5.0 to 8.9 mm) and large (9.0 to 15.0 mm); and 3 size-classes of *Gammarus locusta* were used as prey: small (3.0 to 4.9 mm total length, TL) intermediate (5.0 to 7.9 mm) and large (8.0 to 11.9 mm). The size classes were chosen to represent different life stages of shrimp and gammarids, where for gammarids the 2 smallest size classes are juveniles and the large size class is adults, and for shrimp the smallest size class is juveniles and the larger 2 are adults. We tested every size class of *P. elegans* against every size class of *G. locusta*, plus treatments with only *P. elegans* or *G. locusta*, both with and without *Ulva* sp., in an orthogonal experimental design, resulting in 28 different treatment combinations. Because the results from the field experiment (see 'Results') indicated that gammarids may not consume the filamentous brown algae Ectocarpales, an additional experiment was carried out with the same design as for *Ulva* sp. which tested the consumption rate of *P. elegans* (7.0 to 10.5 mm CL) on Ectocarpales (cf. *Ectocarpus siliculosus*). In this study, only 0.1 g wet weight (WW) of algae was used, since pilot studies

found no detectable grazing when larger amounts were used. Experimental animals and algae were collected with hand nets in shallow water (0 to 1 m depth) in the study area (see details in 'Field experiment' below) and kept in the laboratory in flow-through aquaria provided with *Fucus vesiculosus* as habitat for at least 48 h (and never longer than 2 wk) before being used in a trial. Natural light entering through 2 large windows was used in the laboratory. The shrimps were fed blue mussel meat and *Ulva* sp. while being acclimated and were released back to the sea after participation. To obtain natural daily consumption rates the experimental animals were not starved before trials.

The experiment was performed in 1 l static cups provided with 1 blade of artificial eelgrass, made of plastic ribbon, as substratum in treatments with no *Ulva* sp., and filtered surface water from a nearby bay. The water temperature and salinity varied between 16 and 20°C (the majority of the trials had temperatures that varied between 17 and 19°C, with maximum 1°C difference from start to end) and 23 and 30 psu, respectively, during the experiment. This variation is well within normal for summer surface water along the west coast of Sweden, and is not expected to affect the feeding rate of the animals. One *Palaemon elegans* and either 10 small, 7 intermediate or 5 large gammarid prey were used in the predation treatments. Densities of prey were chosen to ensure that they were never limiting for consumption (pilot studies showed that 10 small gammarids were required to avoid 100% consumption by the largest predator) and to approximate natural density ratios between the 3 size classes (Moksnes et al. 2008). The prey density in the large gammarid–low density treatment was considered sufficiently high (equivalent to 630 gammarids m⁻²) to avoid any density-dependent effects on the results (e.g. that low prey density would affect the behavior of the predator and decrease the consumption rate). In the treatments with *Ulva* sp., 0.5 g WW algae was placed in the cups before the animals were added. In treatments with the smallest gammarids, only 0.3 g WW was used so that the effects of gammarid grazing still could be detectable. To provide the correct amount of algae in each cup, the algae were subjected to a standardized drying process prior to being weighed, using a small weight that pressed the algae between soft paper for 20 s. The cups were covered with a thin white net to prevent the shrimp from jumping out. Every treatment was replicated 5 times during the period from July to October. After 24 h the number of *Gammarus locusta* left in the cups was counted, the predator was released and all algae left in the cups were dried in an oven at 60°C for 24 h and then weighed. The remaining prey were frozen for later length measurement and confirmation of the species.

To avoid including data of shrimp that were not eating because they later showed to be in a premolt stage, 1 replicate of each size class of shrimp in treatments with no gammarids was excluded from the analysis of *Ulva* sp. consumption, and 1 replicate of large shrimp with small gammarids was excluded from the analysis of gammarid consumption. Only molting shrimps were excluded.

The effect of predator and prey size, and the presence of algae on shrimp consumption of *Gammarus locusta* were tested in a 3-factor ANOVA model using the number of *G. locusta* eaten as the dependent variable and shrimp treatment (none, small, intermediate, large), gammarid treatment (small, intermediate, large) and algal treatment (with and without) as the independent variables. Shrimp and gammarid consumption of algae was tested in a 2-factor ANOVA model using the biomass of algae consumed (mean dry weight algae in control cups without grazers minus dry weight algae left after a trial) as the dependent variable and shrimp treatment (none, small, intermediate, large) and gammarid treatment (none, small, intermediate, large) as the independent variables. Before analyses were performed, all data were tested for homoscedasticity with Cochran's *C*-test (Sokal & Rohlf 1981) and square root-transformed if variances needed to be homogenized. *A posteriori* multiple comparison tests were carried out with the Student-Newman-Keuls (SNK) test.

Field experiment. A cage experiment was performed in August and September 2005 to test if the presence of *Palaemon elegans* affected the abundance of gammarids and other amphipod grazers, and the growth of ephemeral algae. The experimental setup consisted of caged patches of artificial seagrass with a set biomass of filamentous macroalgae (*Ulva* sp.) where we assessed the effects of *P. elegans* (0 or 10 cage⁻¹; approximately 8 mm CL) and *Gammarus locusta* (0, 30 or 90 cage⁻¹; approximately 7 mm TL) on the biomass of macroalgae in an orthogonal design.

The experiment was carried out in 2 small bays, Bökevik and Lindholmen, in the Gullmarsfjord on the Swedish west coast (58° 15' N, 11° 27' E), each approximately 2 ha in area. Bökevik is a semi-exposed bay with a sandy bottom, whereas Lindholmen is more protected with a higher proportion of silt in the sediment. Dense eelgrass meadows cover the openings of both bays from about 5 to 1 m depth. Small, scattered patches of eelgrass are also found in the inner, shallow parts of the bays. Tidal amplitude is low (around 20 cm) and normally drains only a small part of the bays' edge, providing good conditions for subtidal cage experiments. The cages were made of nylon (Sefar-nitex) fibers with 1 mm mesh, measured 0.45 × 0.45 × 0.90 m (l × w × h), and were supported by an 8 mm reinforcement bar frame. The mesh size allowed

algal propagules and small mesograzers (<5 mm) to migrate through, but excluded all fish and invertebrate predators on mesograzers. Visible light penetrated the mesh to 95%. The cages were placed in a single row along shore, at approximately 0.5 m depth and 5 m apart on bare, soft bottom, and the lower end was buried 10 cm in the seabed (see Moksnes et al. 2008 for caging methods).

Artificial eelgrass, made of plastic ribbon, was used as habitat in the cages. Four blades (40 cm in length and 5 mm in width) formed a shoot and were tied to a plastic net (area 0.05 m²). An eelgrass patch contained 25 shoots and represented a shoot density of 500 shoots m⁻², equivalent to natural densities of eelgrass beds on the Swedish west coast (Baden & Pihl 1984). The patches were placed in an eelgrass bed in Lindholmen 6 wk prior to the start of the experiment to obtain a natural assemblage of algal germlings on the artificial seagrass. In addition, 15 g WW of *Ulva* sp. (approximately 1.04 g dry weight, DW) was added to each cage. To prevent the algae from being washed up the side of the cage, a soft net with a mesh size of 2.5 cm kept the algae in place, surrounding the entire patch. To ensure that nutrients would not become limiting for algal growth, 160 g commercial fertilizer (Plantacote™ 4M) were provided to all treatments in a 20 cm long net compartment (2 mm mesh size) secured to a fiberglass lever in the centre of the patch. This fertilizer provided a constant delivery of nutrients by leaching nitrogen (NO₃, NO₂ and NH₄) and phosphate (PO₄) over several months (see Worm et al. 2000 for methods). Water samples taken at the start and end of the experiment showed elevated levels of DIN (9.3 to 1.6 µM) and phosphate (0.31 to 0.13 µM) during the 3 wk experiment, approximately 4 times ambient DIN levels and 2 times ambient phosphate levels, and comparable to natural winter surface water concentrations in the area (Rosenberg et al. 1990, see Moksnes et al. 2008 for methods).

The experimental individuals were collected and kept as described for the laboratory experiment. The enclosed densities of *Palaemon elegans* (equivalent to approximately 50 shrimp m⁻²) and gammarids (equivalent to 150 and 450 ind. m⁻²) represent natural densities of eelgrass beds in the study area (Jephson et al. 2008, Moksnes et al. 2008).

Experimental treatments were randomly allocated to the patches and every treatment was replicated twice in each bay. At the start of the experiment, cages were scrubbed to remove fouling organisms, carefully emptied of all individuals using hand-held dip nets and then immediately closed at the top by rolling the net and securing it with cable ties.

After 23 d, the patches, with the animals and algae, were removed with a specially designed net bag that

sampled only the artificial patch (sampled bottom area 0.07 m², mesh size 200 µm). The contents of every cage were immediately put on ice and stored deep frozen for later analysis. From each cage, the dominant algal taxa were dried separately at 60°C for 24 h before being weighed. *Gammarus locusta* were divided into 2 size classes to separate enclosed *G. locusta* from immigrated and newly hatched individuals (small gammarids 3 to 6 mm TL, large gammarids >6 mm TL), and then counted. Smaller amphipod species encountered were also enumerated.

The data were tested in a series of 2-way ANOVA models using enclosed number of shrimp and gammarids as independent variables, and number of small gammarids, large gammarids, other amphipod species and the biomass (DW) of the dominant algal taxa (*Ulva* sp., Ectocarpales and *Polysiphonia* sp.) as dependent variables. All data were square root-transformed to homogenize variances.

RESULTS

Laboratory experiment

Predation rates by *Palaemon elegans* on *Gammarus locusta* were not significantly affected by the presence of algae, but were strongly affected by the size ratio between predatory shrimp and gammarid prey. In general, consumption rates of the 3 size categories of shrimp increased with decreasing size of *G. locusta*. However, the consumption rates depended on the specific predator–prey combination, resulting in a significant interaction effect between shrimp and gammarid treatments (Table 1, Fig. 1). All shrimp sizes consumed significant amounts of the small gammarids (mean number consumed = 5.6), only intermediate and large shrimp could consume intermediate gammarids (mean number = 3.0), and the large gammarid was not signif-

Table 1. *Palaemon elegans* predation rate (lab experiment). Three-factor ANOVA model testing number of consumed *Gammarus locusta* as a function of *P. elegans* size, gammarid size and presence or absence of algae, during 24 h trials.

***p < 0.001; (ns): p > 0.05

Source of variation	df	SS	F
<i>P. elegans</i> (A)	3	228.6	20.6***
<i>G. locusta</i> (B)	2	300.6	40.7***
Algae (C)	1	4.6	1.2 (ns)
A × B	6	112.1	5.1***
A × C	3	1.3	0.1 (ns)
B × C	2	4.2	0.6 (ns)
A × B × C	6	14.8	0.7 (ns)
Residual	95	350.6	

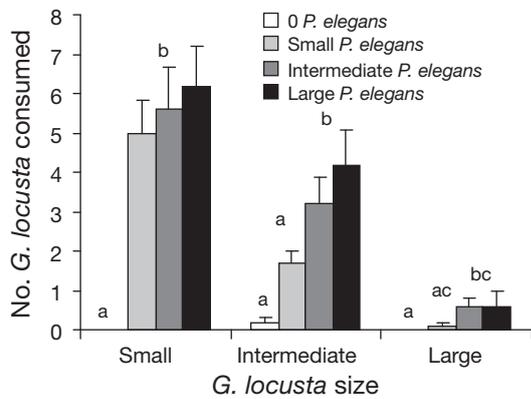


Fig. 1. *Palaemon elegans*. Predation rate (lab experiment). Mean number of consumed *Gammarus locusta* (ind.⁻¹ d⁻¹ + SE) as a function of *P. elegans* size and gammarid size, during 24 h trials. Data from the 2 algal treatments are pooled together as no significant algal effect was found. Different letters above bars indicate significantly different means at $p < 0.05$ (SNK-test)

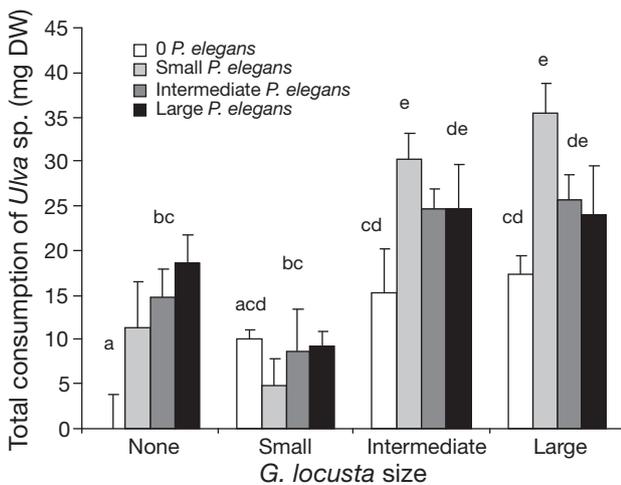


Fig. 2. *Palaemon elegans*. Total grazing rate (lab experiment). Mean total consumption of *Ulva* sp. (mg dry weight [DW] + SE) as a function of *P. elegans* size and gammarid (*Gammarus locusta*) size, during 24 h trials. Different letters above bars indicate significantly different means at $p < 0.05$ (SNK-test)

icantly consumed by any of the shrimps (SNK-test, $p < 0.05$; Fig. 1). The presence of *Ulva* sp. did not affect predation rates in any treatment (on average 2.1 and 2.4 gammarids were consumed in treatments with and without algae; Table 1).

Both *Palaemon elegans* and *Gammarus locusta* consumed significant amounts of *Ulva* sp., and the total consumption of algae depended on the specific size-combination of shrimp and gammarids, giving a significant shrimp–gammarid interaction effect (ANOVA, $F_{A \times B} = 2.12$, $df = 9,63$, $p = 0.041$; Fig. 2). In the single species treatments, significant amounts of *Ulva* sp.

were consumed by all size classes of shrimp and gammarids, except the small *G. locusta* treatment that was marginally non-significant. Even though there were no significant differences between size classes (SNK-test, $p < 0.05$; Fig. 2) the results showed increasing algal consumption with increasing size class of the grazer species (on average 11.6, 14.8, 18.5 mg DW ind.⁻¹ d⁻¹ for small, intermediate and large shrimp, respectively, and 10.0, 15.3 and 17.3 mg DW treatment⁻¹ d⁻¹, for small, intermediate and large gammarids) In the mixed species treatments, the total consumption of algae was generally lower in shrimp–gammarid combinations that resulted in high rates of predation, and higher in treatments in which no predation occurred. Significantly less grazing was found in treatments with small gammarids than in treatments with intermediate or large gammarids for all shrimp sizes (SNK-test, $p < 0.05$). This effect was most pronounced in treatments with the small shrimp, which showed the overall lowest total algal consumption together with small gammarids (4.8 mg DW *Ulva* sp.) and the overall highest consumption together with large *G. locusta* (35.5 mg DW *Ulva* sp.). The total consumption of algae in the small shrimp treatment with intermediate and large *G. locusta* was significantly higher than the consumption rates of the shrimp and the gammarids in the corresponding single species treatments. This difference was not significant for the larger shrimp sizes (SNK-test, $p < 0.05$ Fig. 2).

The size-specific effect on total algal consumption was further analysed by testing the shrimp’s net effect on grazing (total consumption minus size-specific mean gammarid consumption) as the dependent variable in a 2-factor ANOVA using shrimp and gammarid size (3 levels each) as independent variables. In comparison to treatments with only *Gammarus locusta*, this analysis showed that the shrimp had a mean negative effect on algal consumption when the gammarids were small, but a significantly different and positive effect on algal consumption when *G. locusta* were of intermediate or large sizes, irrespective of shrimp size (Table 2, Fig. 3).

Table 2. Net effect of *Palaemon elegans* on *Ulva* sp. consumption (lab experiment). Two-factor ANOVA model testing the net effect of *P. elegans* on the total grazing (as total consumption minus size-specific mean gammarid consumption of *Ulva* sp.; mg DW d⁻¹) as a function of *P. elegans* size and gammarid size, during 24 h trials. **** $p < 0.0001$; (ns): $p > 0.05$

Source of variation	df	SS	F
<i>P. elegans</i> (A)	2	161.1	1.2 (ns)
<i>G. locusta</i> (B)	2	1832.8	13.6****
A × B	4	387.8	1.4 (ns)
Residual	36	2425.5	

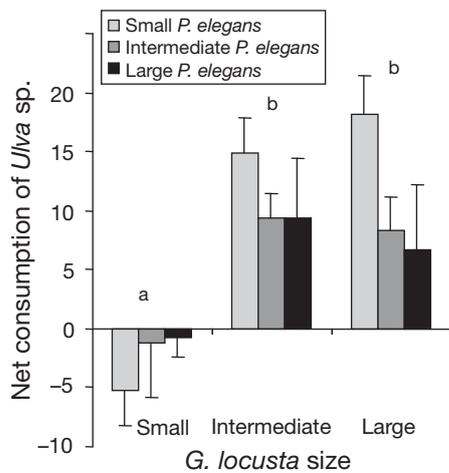


Fig. 3. *Palaemon elegans*. Net effect of *P. elegans* on *Ulva* sp. consumption (lab experiment). Mean net consumption of *P. elegans* (total consumption minus size-specific mean *Gammarus locusta* consumption of *Ulva* sp.; mg DW d⁻¹ ± SE) as a function of *P. elegans* size and gammarid size, during 24 h trials. Different letters above bars indicate significantly different means at $p < 0.05$ (SNK-test)

In the separate experiment assessing the consumption of filamentous brown algae (Ectocarpales) by intermediate to large size shrimp, no significant grazing could be detected (1-factor ANOVA, $F = 0.01$, $df = 1, 6$, $p = 0.93$).

Field experiment

During the 3 wk experiment, large numbers of juvenile gammarids and small amphipods colonized the artificial seagrass patches, and several taxa of filamentous algae bloomed in many cages. The enclosed shrimp reduced the abundance of gammarids and increased the biomass of filamentous *Ulva* sp., but did not affect other amphipod or algal species.

The abundance of *Gammarus locusta* was significantly lower in all cage treatments containing 10 enclosed *Palaemon elegans* in comparison with treatments without shrimp, indicating a strong effect of shrimp predation. This effect was significant both for *G. locusta* >6 mm TL, which includes the enclosed gammarids (on average 75% reduction), and for smaller gammarids that consisted entirely of individuals that had colonized the patches during the experi-

ment (on average 66% reduction; Table 3, Fig. 4a,b). The high colonization and growth rate of *G. locusta* was evident in the control cages that contained on average 169 gammarids per patch, including adult individuals.

The number of small juvenile gammarids was significantly higher (up to 4.6×) in cages with 30 and 90 enclosed *Gammarus locusta* in comparison with control cages (SNK-test, $p < 0.05$; Table 3, Fig. 4b). This was likely an effect of reproduction among the enclosed gammarids since *G. locusta* in the area becomes sexually mature at 8 mm TL (Andersson 2005).

Although *Palaemon elegans* could not control the total abundance of gammarids, the shrimp caused a strong and significant positive effect on the biomass of filamentous *Ulva* sp. that was on average 7× higher in treatments with enclosed shrimp. No significant effect of the gammarid treatments was detected, although the interaction effect was only marginally non-significant ($p = 0.052$; Table 3, Fig. 4c). The biomass of *Ulva* sp. at the end of the experiment consisted almost entirely of new growth found attached mainly to the supportive net that covered the patches; little remained of the enclosed loose *Ulva* sp.

At the end of the experiment, the algal biomass was dominated by different species of the filamentous brown algae Ectocarpales (59%) that bloomed in many

Table 3. Field experiment. Two-factor ANOVA models testing the number of *Gammarus locusta* >6 mm TL and those 3 to 6 mm (TL), and the biomass of *Ulva* sp., as a function of cage treatments. All data were square-root (x)-transformed. ** $p < 0.01$; (ns): $p > 0.05$

Source of variation	df	<i>G. locusta</i> >6 mm		<i>G. locusta</i> 3 to 6 mm		<i>Ulva</i> sp.	
		SS	F	SS	F	SS	F
<i>P. elegans</i> (A)	1	146.0	28.6 **	214.3	8.4**	2232.9	20.0**
<i>G. locusta</i> (B)	2	30.5	3.0 (ns)	318.5	6.3**	259.1	1.2 (ns)
A × B	2	0.8	0.1 (ns)	83.2	1.6 (ns)	784.4	3.5 (ns)
Residual	18	91.7		458.4		2010.3	

Table 4. Cage experiment. Two-factor ANOVA models testing the biomass of Ectocarpales algae, *Polysiphonia* sp. and number of amphipods (*Erichtonius* sp., *Corophium* sp. and *Microdeutopus* sp.) as a function of cage treatments. All data were square-root (x)-transformed. (ns): $p > 0.05$

Source of variation	df	Ectocarpales		<i>Polysiphonia</i> sp.		Amphipods	
		SS	F	SS	F	SS	F
<i>P. elegans</i> (A)	1	3574.6	2.0 (ns)	564.9	3.7 (ns)	55.1	0.1 (ns)
<i>G. locusta</i> (B)	2	1507.2	0.4 (ns)	607.9	2.0 (ns)	5.9	0.0 (ns)
A × B	2	1253.2	0.4 (ns)	896.0	2.9 (ns)	206.6	0.1 (ns)
Residual	18	31 728.0		2736.1		13 320.2	

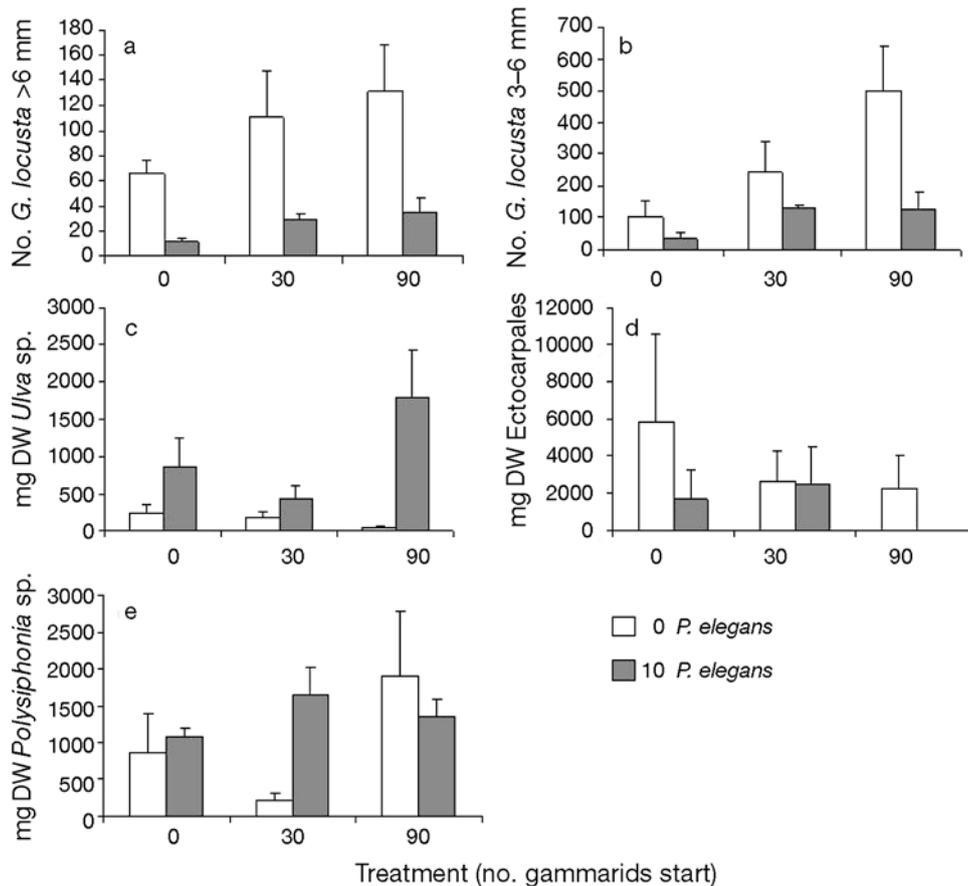


Fig. 4. *Palaemon elegans* and *Gammarus locusta*. Field experiment. Mean number per cage of *G. locusta* (a) >6 mm TL and (b) 3 to 6 mm TL, and mean biomass (mg DW) per seagrass patch of (c) *Ulva* sp., (d) Ectocarpales and (e) *Polysiphonia* sp. (+SE) after 23 d, as a function of initial density of *P. elegans* and *G. locusta*

cages, and by filamentous red algae, mainly *Polysiphonia* sp. (28%), whereas *Ulva* sp. only constituted 14% of the total biomass on average. However, neither Ectocarpales nor *Polysiphonia* sp. were significantly affected by the cage treatments, despite the large variation in gammarid abundance (Table 4, Fig. 4d,e). High abundances of 3 smaller (2 to 6 mm TL) amphipod species (*Erichtonius* sp, *Corophium* sp and *Microdeutopus* sp.) were found in all treatments (on average 2611 amphipods patch⁻¹), but none were significantly affected by experimental treatments (Table 4).

DISCUSSION

This study suggests that the omnivorous shrimp *Palaemon elegans* has a positive net trophic effect on the growth of filamentous green algae in the study area by reducing the abundance of the dominant algal grazer *Gammarus locusta*. In our field cage experiment, the shrimp reduced the number of gammarids by

on average 68%, causing a trophic cascade that increased the biomass of filamentous *Ulva* sp. 7×, on average. This result is consistent with earlier cage experiments which demonstrated that *G. locusta* can become very abundant in the absence of predation and control the growth of filamentous *Ulva* sp., but that the abundance of gammarids is reduced to very low levels in the presence of local predators (which were dominated numerically by *Palaemon* shrimp), resulting in increased growth of algae (Moksnes et al. 2008). The high abundance of gammarids in the cage control treatment in the present study is equivalent to approximately 3105 ind. m⁻². The abundance of *G. locusta* in natural eelgrass in the study area is 14 to 68× lower, and consists mainly of small juveniles (Jephson et al. 2008, Moksnes et al. 2008). These results suggest that high rates of predation limit the abundance of *G. locusta* in northwest Sweden, and that *P. elegans* is a dominant predator.

The laboratory experiment demonstrated that both juvenile and adult *Palaemon elegans* are omnivores

acting as effective predators of gammarids <8 mm TL as well as effective grazers of filamentous *Ulva* sp., which is consistent with earlier studies (Höglund 1943, Forster 1951, Berglund 1980, Fonds et al. 1981). However, the shrimp appeared to prefer gammarid prey, as the consumption of *Gammarus locusta* was not affected by the presence of algal food, whereas significant amounts of *Ulva* sp. were only consumed by shrimp in the presence of *G. locusta* when the gammarid prey was too large to be eaten effectively by the shrimp (e.g. in treatments with juvenile shrimp and *G. locusta* >5 mm TL). Although *P. elegans* can survive on *Ulva* sp. when trapped in tidal pools (Berglund & Bengtsson 1981), the growth of the shrimp is very poor on a strict vegetarian diet, and they need to consume animal meat constituting more than 13% of their body weight (DW) per day to gain weight (Fonds et al. 1981). This dependence on animal prey for growth likely explains their preference for gammarids, and suggests that *P. elegans* may have a stronger predatory role in the seagrass community than the grass shrimp *Palaemonetes pugio* that primarily consumes epiphytic algae and detritus (Morgan 1980).

In our laboratory experiment, the size ratio between the shrimp predator and the gammarid prey determined whether *Palaemon elegans* had a net positive or negative effect on algal biomass. In comparison to treatments with only *Gammarus locusta*, the total consumption of *Ulva* sp. increased in the presence of *P. elegans* when the gammarid prey was >5 mm TL (see Fig. 3), likely as a result of complementary grazing from the shrimp that was high enough to compensate for the loss of gammarid grazers. However, in the presence of smaller gammarid prey, the shrimp appeared to mainly consume gammarids, and the total consumption of algae was lower. The clear positive net effect on *Ulva* sp. biomass in the field experiment was therefore probably a result of the high abundance of both juvenile gammarids and other small amphipod species that likely constituted important prey for the enclosed shrimp. Although we did not detect any treatment effects on the abundance of smaller amphipod species, earlier caging experiments and stomach analyses demonstrate that they are consumed by both *P. elegans* and adult *G. locusta* (Moksnes et al. 2008). The lack of an effect in the present study may have been a result of high abundance of either adult *G. locusta* or *P. elegans* in all treatments, canceling any treatment effects. Thus, the high abundance of small amphipod prey in eelgrass beds on the Swedish west coast appears to allow *P. elegans* to act mainly as a predator in the food web, resulting in an indirect positive effect on palatable green algae. Consistent with these suggestions, stable isotope studies demonstrated that *P. elegans* in the study area mainly consume amphipod

prey and are found one trophic level above the gammarids. Moreover, in eelgrass beds on the south coast of Sweden in the Baltic Sea, which lack the small tube-building amphipod species that are abundant on the west coast, and where the mean size of gammarids is 7 mm TL, *P. elegans* was found to consume mainly filamentous algae (Jephson et al. 2008), indicating that the availability and size of prey determines the trophic role of this opportunistic omnivore.

It is important to note that *Palaemon elegans* had a positive effect on the growth of filamentous *Ulva* sp. only. No direct or indirect effect on the biomass of filamentous brown and red algae was found in the present study, in which Ectocarpales and *Polysiphonia* sp. algae bloomed in many cages despite high abundances of gammarids or shrimp. Laboratory experiments have demonstrated that both *P. elegans* (this study) and *Gammarus locusta* (Andersson 2005) are less efficient grazers on Ectocarpales algae than on *Ulva* sp. Ectocarpales algae likely contain anti-herbivore substances (Hay & Fenical 1988), which may explain why they often replace fast growing, grazer-susceptible species such as *Ulva* spp. when grazers are abundant (Lotze & Worm 2000, Lotze et al. 2001, Moksnes et al. 2008). However, the mats of ephemeral algae that cover many shallow habitats along the Swedish west coast today are dominated by filamentous *Ulva* species (Pihl et al. 1999), likely because filamentous *Ulva* species are dominant space competitors in the absence of grazers (Lotze et al. 2000, Moksnes et al. 2008).

Heck et al. (2000) proposed that overfishing of large fish predators in coastal areas worldwide (J. B. C. Jackson et al. 2001, Myers & Worm 2003) may have resulted in trophic cascades in which small predators have increased in number and, in turn, reduced the abundance of mesograzers, releasing ephemeral algae in seagrass beds from herbivory. The strong top-down control of dominant mesograzers in eelgrass beds on the Swedish west coast (Moksnes et al. 2008, this study) indicates that changes in the abundance of large fish predators may be involved in the recent increase of ephemeral algal mats in the area, and that the loss of eelgrass beds may be an effect of the combination of nutrient enrichment and overfishing. This is supported by the well documented overfishing and dramatic decrease of both inshore and offshore stocks of gadoid fish in Kattegatt and eastern Skagerrak, especially of cod *Gadus morhua* from the northwest coast of Sweden (Svedäng 2003, Svedäng & Bardou 2003). This has occurred concurrently with the increase of ephemeral algal mats. Eelgrass beds constitute an important juvenile and foraging habitat for 0-year and 1-year cod, respectively (Pihl et al. 2006), and stomach content analyses (Fjøsne & Gjørseter 1996,

Wennhage & Pihl 2002) and stable isotope analyses (Jephson et al. 2008) suggest that small fish and decapods common in eelgrass beds, including *Palaemon* shrimp, are important prey items of cod. The decrease in abundance of large fish predators, in combination with a decreased foraging success in eelgrass with higher coverage of filamentous algae (Isaksson et al. 1994), has likely increased the abundance of smaller predators, and, in turn, the predation pressure of small algal grazers in eelgrass beds. Consistent with an increased predation pressure on grazers is the change in population structure of large grazer species in eelgrass beds over the last 20 years. In the 1980s, adult *Gammarus locusta* and large isopod species (*Idotea* spp.) were abundant in the eelgrass beds of the study area (on average 50 and 27 ind. m⁻², mean size 9.5 [n = 95] and 10.6 mm TL [n = 922], respectively) (Baden & Pihl 1984, Baden 1990, S. Baden unpubl. data). *G. locusta* found in the same eelgrass beds today consist almost entirely of juvenile individuals (on average 130 ind. m⁻², mean size 4.1 mm TL), and isopods are missing from the system (Jephson et al. 2008, Moksnes et al. 2008). Large-bodied prey species are more vulnerable to visual predators and the loss of large individuals and species from a mesograzer assemblage appear to be a common community response to size-selective fish predation (Edgar & Aoki 1993). In the assessed seagrass system, *Gobius niger*, a dominant fish in Swedish eelgrass beds (Baden & Pihl 1984), selectively feed on adult *G. locusta* and can reduce their abundance by >90% in cage enclosures, causing a 70× increase in *Ulva* biomass (Moksnes et al. 2008). Thus, in the eelgrass beds along the northwest coast of Sweden, complementary predation from small fish and shrimp appear to control the biomass of algal grazers.

Palaemon elegans and *P. adspersus* (which have a similar role in the food web as *P. elegans*; Berglund 1980, Jephson et al. 2008) are the most abundant potential predators on mesograzers in eelgrass beds on the Swedish west coast (10 to 77 shrimps m⁻²; Baden & Pihl 1984, Jephson et al. 2008, Moksnes et al. 2008). The present study has demonstrated that *P. elegans* is an efficient predator on the dominant algal grazer *Gammarus locusta*, and that natural densities of shrimp can promote the growth of the dominant algal species in algal mats through a trophic cascade. These results therefore suggest that *Palaemon* shrimp constitute a possible link between overfishing and macroalgal blooms on the Swedish west coast. However, it is not clear whether the abundance of *Palaemon* shrimp or other small predators have increased in Skagerrak in the last decades. Further studies are needed to assess how variation of the gadoid stock affects the abundance of small predators in shallow coastal habitats, and how natural eelgrass responds to enhanced

nutrient and predation levels, to establish whether overfishing plays a critical part in the current eelgrass decline on the Swedish west coast. Because eelgrass beds are an important nursery habitat for 0-year cod, large-scale changes in the distribution of grass beds may affect the recruitment and population size of cod (Gotceitas et al. 1997, Pihl et al. 2006, reviewed by E. L. Jackson et al. 2001). The present loss of seagrass beds in northwest Sweden may therefore create a negative feedback loop that further decreases the abundance of cod and, through the trophic cascade, accelerates the loss of eelgrass.

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