

**Grazing by small crustaceans
stimulates growth of *Ulva* spp. (Chlorophyta)
through preferential consumption of epiphytes**

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Abstract

Eutrophication of shallow coastal waters often leads to blooms of macroalgae. Grazing by small crustaceans, such as amphipods and isopods, can reduce macroalgal biomass accumulation. The role of grazing by small crustaceans on *Ulva* spp. biomass development was investigated in the Veerse Meer, a brackish lagoon situated in the Southwest Netherlands. Exclusion of grazing in the field did not stimulate *Ulva* spp. growth. In fact, growth rates were higher in enclosures that allowed grazers to enter. Edibility tests identified the amphipod *Gammarus locusta* (L.), and the isopods *Idotea chelipes* (Pallas) and *Sphaeroma hookeri* Leach (Lejuez) as grazers on *Ulva* spp. However, when epiphytic diatoms were present on the *Ulva* spp. thalli, *Gammarus* and *Sphaeroma* did not graze on *Ulva* tissue. Only *Idotea* continued to graze on *Ulva* spp. A laboratory growth experiment revealed a positive effect of *Gammarus* presence on *Ulva* spp. growth, probably caused by preferential removal of epiphytic diatoms from the *Ulva* spp. thalli. The growth stimulation by epiphyte removing grazers such as *Gammarus* may explain the higher growth rates in the presence of grazers observed in the field. When determining the potential role of invertebrate grazers in controlling macroalgal biomass accumulation, it is important to include an assessment of the epiphyte abundance on the macroalgae, as preferential removal of epiphytes may stimulate growth and thus have the opposite effect.

Keywords: epiphytes, grazing, growth, *Ulva* spp.

Abridged title: crustacean grazing on *Ulva* spp.

Introduction

Eutrophication of shallow coastal waters often leads to blooms of macroalgae (Vollenweider, 1992). Bloom development implies that the loss factors are much smaller than the gain factors. Thus, loss rates due to grazing, decomposition, or export should be lower than growth rates. Waterfowl can consume substantial amounts of macrophytes (Kjørboe, 1980). However, in some areas birds do not play a role until the period after the biomass build-up phase (Lodge, 1991). Grazing by small crustaceans, such as amphipods and isopods, can also reduce macroalgal biomass accumulation (Valiela *et al.*, 1997). For example in the Venice lagoon in Italy, biomass increase of *Ulva rigida* was enhanced by 4-15 % when crustacean grazers were excluded (Sfriso and Pavoni, 1994). Geertz-Hansen *et al.* (1993) showed that, in the outer part of Roskilde Fjord in Denmark, invertebrate grazing pressure on *Ulva lactuca* matched the growth rate and prevented the development of a bloom. Grazing in the inner part, however, was negligible, which allowed biomass build-up.

Invertebrate grazing on macroalgae not only involves grazing on the algal thalli, but grazing can also be restricted to associated epiphytes. Effects of grazing on epiphytes have been studied more often in seagrasses than in macroalgae. In general, removal of epiphytes on seagrass leaves by invertebrate grazers stimulates growth of seagrasses (reviews by Orth and van Montfrans, 1984 and Jernakoff *et al.*, 1996). The mechanism of growth stimulation by epiphyte removal may include both improved light conditions for the host plant, and increased nutrient supply to the plant through herbivore mediated nutrient regeneration (Jernakoff *et al.*, 1996; Fong *et al.*, 1997). Some examples of preferential consumption of epiphytes growing on macroalgae over the macroalgal thalli themselves include grazing by amphipods on *Dictyota dichotoma* (Hudson) Lamouroux

(Hay et al., 1987), *Gracilaria asiatica* Zhang and Xia (Brawley and Fei, 1987) and *Sargassum filipendula* (Duffy, 1990). Experimental evidence of growth enhancement due to the epiphyte removal is also described for macroalgae. In a microcosm study, Brawley and Adey (1981) observed that removal of the amphipod *Ampithoe ramondi* Audouin by fish predators caused heavy epiphyte overgrowth of *Hypnea spinella* (C. Agardh) Kützing and a decrease in growth rates of the plants. Furthermore, Dudley (1992) showed that epiphyte grazing by stream insects increased the biomass of *Cladophora glomerata* considerably compared to grazer-free controls. However, Duffy (1990) observed that grazing by one of the three tested amphipod species reduced the biomass of *Sargassum filipendula*, because the grazer preferred the host plant to its epiphytes. The net effect of the grazing process on the macroalgal biomass accumulation in the field depends on the preference of the grazer species for macroalgae or epiphytes and the relative abundance of the different grazer species.

In the Veerse Meer, a brackish lagoon situated in the Southwest Netherlands, *Ulva* spp. blooms frequently occur and show a patchy distribution (Malta *et al.*, 2000). Most grazing by birds takes place after the biomass build up, but small crustaceans are present in the lagoon during the entire growing season of *Ulva* spp. (Coosen *et al.*, 1990). This group can potentially affect biomass accumulation. Here we present results of experiments, that were carried out both in the field and in the laboratory, to study the effect of grazing by small crustaceans on *Ulva* spp. biomass accumulation.

Material and methods

Edibility tests

Four *Ulva* species, *U. scandinavica* Bliding, *U. curvata* (Kütz) De Toni, *U. rigida* C. Agardh and *U. lactuca* L. (sensu Koeman and van den Hoek, 1981), have been observed in the Veerse Meer lagoon. Identification of the different species present in the *Ulva* spp. bloom proved to be difficult, as morphological, molecular and ecophysiological characters show large overlaps (Malta *et al.*, 1999). Therefore, the species will be considered further as *Ulva* spp.. To determine which species graze on *Ulva* spp. a series of edibility tests was set up. The tests lasted 15 to 30 days. In each test, 20 individuals of one invertebrate species were placed in a beaker with an *Ulva* spp. disc (4.2 cm diameter) and one litre of lagoon water. A control beaker contained only an *Ulva* spp. disc and lagoon water. The beakers were placed in the dark at 15 °C and aerated continuously.

Three common invertebrate species from the Veerse Meer lagoon were tested: the isopods *Idotea chelipes* and *Sphaeroma hookeri*, and the amphipod *Gammarus locusta*. Separate treatments with old *Ulva* spp. discs and with young *Ulva* spp. discs were exposed to the different grazer species. In addition, clean young *Ulva* spp. discs were presented in Whatman GF/C filtered lagoon water. This treatment was included to test grazing on epiphyte free *Ulva* spp.. Prior to each test the crustaceans were starved in filtered lagoon water for 5 days. After each test the discs were visually inspected for the presence of holes in the thalli as well as the abundance of diatoms on the thalli. The latter was indicated by a brown layer. Microscopic observations confirmed that the brown layer on the *Ulva* thallus consisted of diatoms (P. Kamermans, pers. obs.). The occurrence of holes in *Ulva* spp. in the grazer treatment and the absence of holes in the control treatment indicated grazing on

Ulva spp., while clean green thalli in the grazer treatment compared to the presence of a brown layer on the disc in the control treatment indicated grazing on diatoms.

Exclosure experiment in the field

The field studies were conducted in the period from May to October at Middelplaten (51° 32' 63'' N; 3° 46' 89'' E) and Kwistenburg (51° 32' 61'' N; 3° 50' 97'' E), two shallow sites (depth 80 cm) in the Veerse Meer lagoon. Growth rates of *Ulva* spp. were determined weekly at both sites using cages that were similar to the cages employed by Geertz-Hansen *et al.* (1993). The cages were made of 20 cm long Plexiglas tubes (20 cm diameter) cut lengthways in half. The ends and bottoms of these clear roofs were covered either with 1-cm plastic-coated steel mesh (large-mesh cages that allowed grazers to enter) or with 1-mm nylon netting (small-mesh cages that prevented grazers from entering). The Plexiglas roof construction ensured that light conditions were the same in large- and small-mesh cages. The cages were fixed to ropes that were tied between poles and suspended in the water column at 50 cm above the bottom to ensure average light intensities within the cages compared with those in the free-floating *Ulva* spp. mats.

At both sites, five cages with large mesh and five cages with small mesh were used. Each cage contained five *Ulva* spp. discs (4.2 cm diameter) that were punched from *Ulva* spp. thalli with a sharpened stainless steel tube. The cages were cleaned at intervals of 4 to 7 days. Every week, the growth rate was determined with new discs cut out of fresh *Ulva* spp. thalli. Before incubation, the total WW of the five discs in each cage was determined. Each week, the DW of fifteen extra discs was determined as described above to establish the WW to DW conversion factor. After one week, total WW per cage was

measured and growth was calculated as the increase in DW per cage with the following formula of Geertz-Hansen *et al.* (1993):

$$(\ln W_t - \ln W_0) / t$$

where W_0 is the initial and W_t the final DW after t days of incubation.

Grazer abundance in the field

In July and August, the abundance of invertebrate grazers was determined at the two study sites. Potential invertebrate grazers reach their greatest densities in these months (Nienhuis and van Ierland, 1978; Nienhuis and Groenendijk, 1986). A 0.16 m² bottomless cylinder (diameter 45 cm, height 45 cm) with a 1-mm net attached to the top was randomly placed on the bottom. The net could be opened at the top and all material inside the cylinder (macroalgae and invertebrates) was collected with a 1-mm dip net. Per site three cylinder samples were taken. Potential invertebrate grazers, as based on Geertz-Hansen *et al.* (1993), Horne *et al.* (1994) and our own edibility tests, were sorted from the samples and their numbers counted. The samples were dried for 48 h at 60 °C and weighed, after which they were combusted at 550 °C for 2 h and weighed again. From this, the ash-free dry weight (AFDW) was calculated.

Flow experiment

It can be argued that experimental set-ups with cages will alter the environment within the cages in such a way that factors other than grazing will also have an effect on the growth rate of the *Ulva* discs. Flow conditions may be better in the large-mesh cages compared to the small-mesh cages supplying more nutrients to the discs in the large-mesh cages. To study this possibility, growth rate of *Ulva* spp. discs was determined in an experiment without grazers. In each of two outside basins (2.5 x 1.2 x 0.5 m) six cages

were placed. The cages consisted of 17 cm long Plexiglas tubes with a diameter of 11 cm. The ends of the tubes were covered with 1-cm plastic-coated steel mesh (large-mesh treatment) or with 1-mm nylon netting (small-mesh treatment). Each basin contained three large-mesh cages and three small-mesh cages. The basins were filled with seawater from the Oosterschelde estuary, which was replaced every week. In one basin water was pumped around at a speed of 7 cm s^{-1} (flow treatment), while the water in the other basin was not moved (no-flow treatment). In an experiment, Parker (1981) showed that a current speed of 7.5 cm s^{-1} enhanced growth rates more than speeds of 15.0 or 22.5 cm s^{-1} . Per cage, two *Ulva* spp. discs were cut, introduced in the cages and processed as described above for the enclosure experiment. The flow experiment was conducted in September and October and lasted 5 weeks. To avoid specific effects caused by the basin, the pump was alternated between the basins at the beginning of each growth trial.

Laboratory growth experiment

The net effect of grazing by invertebrates on *Ulva* spp. growth was studied in an experiment carried out in May. About 1 gram wet weight of *Ulva* spp. was placed in each of six beakers with 400 ml aerated unfiltered lagoon water. In two beakers 15 *Idotea* were added, in two beakers 15 *Gammarus* were added and two beakers remained as control. The beakers were placed at a temperature of $15 \text{ }^{\circ}\text{C}$ and an irradiance level of $100 \mu\text{E m}^{-2} \text{ s}^{-1}$ with a cycle of 12 h light and 12 h dark. *Ulva* spp. WW was determined on day 0, 3 and 8.

Statistical analyses

All data were tested for heteroscedacity with a Bartlett's test for homogeneity of variances (Sokal and Rohlf, 1995). Grazer abundance and biomass determined in the field,

as well as *Ulva* spp. growth in the enclosure and flow experiments scored as significant. The data continued to give significant results after several transformations. Therefore, these data were tested non-parametrically with Mann-Whitney U-tests. The data of the growth experiment in the laboratory did not score as significant in Bartlett's test. A two-way ANOVA was used to test the effect of time and treatment, as well as the interaction between time and treatment, on *Ulva* spp. weight (Sokal and Rohlf, 1995). The significance of differences between the separate treatments was determined with the Tukey-Kramer pairwise comparison test (Sokal and Rohlf, 1995). A significance level of 5% was used in all tests. The statistical analyses were conducted using the STATISTICA programme.

Results

Edibility tests

The edibility tests revealed that all 3 species investigated (*Idotea chelipes*, *Gammarus locusta* and *Sphaeroma hookeri*) consumed *Ulva* spp. (Table I). *Idotea* was the only species that consumed *Ulva* spp. under all circumstances (Table I). *Ulva* spp. in unfiltered seawater was not ingested by *Gammarus* and *Sphaeroma*, but diatoms present on the thalli were grazed by these species (Table I). Only when clean young *Ulva* spp. was presented in filtered seawater did *Gammarus* and *Sphaeroma* graze on the macroalga (Table I). These results indicate that *Gammarus* and *Sphaeroma* consumed *Ulva* spp. only when epiphytic diatoms were not present on the *Ulva* spp. thalli.

Exclosure experiment and grazer abundance in the field

Growth rates of *Ulva* spp., as established by the exclosure experiment, were high in May and June and declined thereafter (Fig. 1). At both sites, significantly higher growth rates were frequently observed in the large-mesh cages (Fig. 1). This indicates that exclusion of grazing did not stimulate growth. In contrast, growth was higher in the cages in which grazers were allowed to enter.

The occurrence of crustacean grazers showed large variability between species, samples and sites (Table II). *Gammarus locusta* was the dominant species in July, while *Idotea chelipes* and *Sphaeroma hookeri* were the most abundant species in August. In only three cases, significant differences between sites were observed. At Middelplaten, a significantly higher biomass of *Idotea* was found in July. This site also showed a significantly higher density and biomass of *Gammarus* in July. The density of *Sphaeroma*,

however, was significantly lower at Middelpalten in July. In general, potential invertebrate grazer density did not show large differences between sites.

Flow experiment

Maximal *Ulva* spp. growth rates observed in the flow experiment were similar to rates observed in the enclosure experiment in the field in September and October (compare Fig. 1 and Fig. 2). Occasionally, negative growth rates were found. This could be attributed to discs that were in a bad condition at the end of the growth trial, as they were slimy and showed decolorations. Higher *Ulva* spp. growth rates were found in the basin without current (Fig. 2). Contrary to the expectation, growth rates in the small-mesh cages were generally, and in some cases significantly, higher than in the large-mesh cages (Fig. 2). This indicates that the small mesh of the cages does not hamper growth.

Laboratory growth experiment

The growth experiment showed a slight increase in *Ulva* spp. biomass in the control treatment, indicating that the experimental conditions favoured growth of *Ulva* spp. (Fig. 3). A significant effect of treatment was found (Table IIIa). The presence of *Idotea* resulted in a significant reduction in *Ulva* spp. biomass (Fig. 3, Table IIIb). The presence of *Gammarus*, however, had the opposite effect, a significant increase in biomass compared to the control treatment was found (Fig. 3, Table IIIb). The clean green thalli in the *Gammarus* treatment appeared to be free of epiphytes. The differences between treatments increased as time progressed. This produced a significant interaction between duration of the experiment and treatment (Table IIIa). These results demonstrate a positive effect of *Gammarus* presence on *Ulva* spp. growth, probably caused by removal of epiphytic diatoms from the *Ulva* spp. thalli.

Discussion

Grazing by some species of small crustaceans can reduce macroalgal biomass (Geertz-Hansen et al., 1993; Sfriso and Pavoni, 1994; Duffy, 1990). Other invertebrate species feed preferentially on epiphytes occurring on the macroalgae and, as a result, may have a positive effect on macroalgal growth (Brawley and Adey, 1981; Dudley, 1992). The enclosure experiment in the Veerse Meer lagoon indicates that the negative effect of crustacean grazing on *Ulva* spp. was negligible. In fact, growth rates were higher in the cages that allowed grazers to enter. Exclusion of grazing by the small mesh produced lower *Ulva* spp. biomass increase. The results of the flow experiment do not provide evidence for reduced growth conditions for *Ulva* spp. in the small-mesh cages. In this flow experiment, growth was higher in the small-mesh cages than in the large-mesh cages. In some cases, weight loss instead of weight increase was found. In the flow experiment, the disc were constantly exposed to flow, while in the field periods without flow are not uncommon. The continuous flow may have been suboptimal for the *Ulva* spp. disc in the cages. This is supported by the bad condition of some of the disc at the end of the growth trials. In the basin without flow, the growth rates were generally similar between cages. Thus, the small-mesh cages did not reduce conditions for *Ulva* spp. growth.

Results from the enclosure experiment suggest that the presence of grazers had a positive effect on *Ulva* spp. growth. Data from the laboratory experiments offer a possible explanation for this observation. The edibility tests identified *Idotea chelipes* as the only invertebrate grazer that will consume *Ulva* spp. together with its epiphytes. *Gammarus* and *Sphaeroma* will only graze on *Ulva* tissue when epiphytes are not present. The grazing experiment in the laboratory indicates that cleaning of the *Ulva* spp. thalli by *Gammarus* had a positive effect on *Ulva* spp. growth. In the field, the amphipod

Gammarus and the isopod *Sphaeroma* will probably limit their consumption to epiphytic diatoms present on the *Ulva* spp. thalli. Consequently, the thalli can receive more light and grow faster.

Calculations with data from our laboratory grazing experiment show that one *Idotea* can consume an average of 0.036 g WW per day, which is 3 % of the initial *Ulva* spp. disc weight, while one *Gammarus* can stimulate *Ulva* spp. growth with an average of 0.002 g WW per day, which is 0.2 % of the initial *Ulva* spp. disc weight. Growth stimulation will most likely be larger in the field, because in the laboratory, light conditions were reduced compared to the field situation (respectively 100 $\mu\text{E m}^{-2} \text{s}^{-1}$ in the lab and on average 250 $\mu\text{E m}^{-2} \text{s}^{-1}$ in the field; Malta and Verschuure, 1997). In the field, part of the actual increase in biomass is probably consumed by *Idotea*. The ratio between *Idotea* density and the density of epiphyte removing grazers such as *Gammarus*, and the size of the individuals, determines whether the *Ulva* spp. biomass will increase or decrease. Furthermore, *Gammarus* will feed on epiphytes when they are present, but may switch to macroalgal biomass when epiphytes are scarce or absent. Thus, the abundance of epiphytes also affects the grazer impact by *Gammarus*.

Horne *et al.* (1994) found consumption of *Ulva* sp. by *Gammarus mucronatus* in an estuary with a low nutrient loading rate and not in an estuary with a high nutrient loading rate. When we relate these results to our data, this observation suggests that, under high nutrient conditions, *Gammarus* was not grazing on *Ulva*, but on its epiphytes. Epiphytes are generally more abundant at high than at low nutrient loading (Sand-Jensen and Borum, 1991).

In conclusion, *Ulva* spp. growth rate was enhanced by the presence of *Gammarus*. This probably resulted from preferential removal of epiphytic diatoms attached to *Ulva* spp. thalli. When determining the potential role of grazers in controlling macroalgal

biomass accumulation, it is important to include an assessment of the epiphyte abundance on the macroalgae, as preferential removal of epiphytes may stimulate growth and thus have the opposite effect.

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Table I. Edibility of different food items for invertebrates from the Veerse Meer lagoon, + indicates that item was consumed - indicates that item was not consumed.

Grazer species	old Ulva in unfiltered lagoon water	young Ulva in unfiltered lagoon water	diatoms on young unfiltered lagoon water	old Ulva	and in filtered lagoon water	young Ulva in filtered lagoon water
<i>Idotea chelipes</i>	+	+	+			+
<i>Sphaeroma hookeri</i>	-	-	+			+
<i>Gammarus locusta</i>	-	-	+			+

Table II. Occurrence of invertebrate grazers at Middelplaten and Kwistenburg. Values are mean +SD (n = 3). Significantly higher values at sites, as determined by Mann-Whitney U-tests, are indicated: * = P < 0.05.

grazer species	date	Density (# m ⁻³)	Density (# m ⁻³)	Biomass (g m ⁻³)	Biomass (g m ⁻³)
	10 July	Middelplaten	Kwistenburg	Middelplaten	Kwistenburg
<i>Idotea chelipes</i>		91 (31)	57 (35)	0.25 (0.05) *	0.07 (0.02)
<i>Sphaeroma hookeri</i>		42 (33)	255 (64) *	0.10 (0.06)	0.22 (0.06)
<i>Gammarus locusta</i>		633 (362) *	289 (36)	0.64 (0.40) *	0.28 (0.01)
	29 Aug	Middelplaten	Kwistenburg	Middelplaten	Kwistenburg
<i>Idotea chelipes</i>		984 (367)	7555 (11555)	1.58 (0.71)	2.55 (2.97)
<i>Sphaeroma hookeri</i>		1453 (244)	810 (1021)	0.73 (0.31)	0.80 (0.76)
<i>Gammarus locusta</i>		68 (73)	34 (40)	0.10 (0.11)	0.05 (0.09)

Table IIIa. Statistical evaluation of the effect of treatment (no grazers present as control, or either *Idotea chelipes* or *Gammarus locusta* as grazers) on *Ulva* biomass in the laboratory growth experiment. Values are degrees of freedom (df), mean square (MS) and probability (P) of two-way ANOVA.

Source	of	df	MS	P
variation				
Treatment	2	0.212	0.000	
Time	2	0.005	0.166	
Treatment x Time	4	0.091	0.000	
Error	9	0.002		

Table IIIb. Matrix of pairwise comparison probabilities of Tukey-Kramer post-hoc test.

Treatment	<i>Idotea</i>	<i>Gammarus</i>	Control
<i>Idotea</i>	1.000		
<i>Gammarus</i>	0.000	1.000	
Control	0.000	0.002	1.000

Figure legends

Fig. 1. Growth rates (d^{-1}) of *Ulva* spp. discs at Middelplaten (a) in large-mesh cages (closed circles) and small-mesh cages (open circles) and at Kwistenburg (b) in large-mesh cages (closed squares) and small-mesh cages (open squares). Values are mean +SD (n = 5). Occasionally, the mesh became detached from the roofs and discs escaped from the cages. Growth rates were then based on means of less than 5 cages. This was the case for large-mesh cages at Middelplaten in week 1 n = 4, week 4,5 n = 3; small-mesh cages at Middelplaten in week 1,6,8 n = 4, week 4 n = 3, week 5 n = 2; large-mesh cages at Kwistenburg in week 2,22 n = 4, week 5 n = 3, week 4 n = 2; small-mesh cages at Kwistenburg in week 1,6,10,23,24 n = 4, week 4,5 n = 3. Significant differences in *Ulva* growth rates between large and small mesh-size cages as determined by Mann-Whitney U-tests are indicated with * = $P < 0.05$.

Fig. 2. Growth rates (d^{-1}) of *Ulva* spp. discs at Middelplaten (a) in large-mesh cages (closed circles) and small-mesh cages (open circles) in the flow basin and (b) in large-mesh cages (closed squares) and small-mesh cages (open squares) in the no-flow basin. Values are mean +SD (n = 3). Significant differences in *Ulva* growth rates between large and small mesh-size cages as determined by Mann-Whitney U-tests are indicated with * = $P < 0.05$.

Fig. 3. Biomass ($g\ WW\ beaker^{-1}$) of *Ulva* spp. in an experiment with different grazer treatments: no grazers as control (open diamonds), and the grazers *Gammarus locusta* (closed squares) and *Idotea chelipes* (closed circles). Values are mean +SD (n = 2).