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# Seasonal changes *in situ* grazing of the mesoherbivores *Idotea baltica* and *Gammarus oceanicus* on the brown algae *Fucus vesiculosus* and *Pylaiella littoralis* in the central Gulf of Finland, Baltic Sea

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## Abstract

The *in situ* grazing experiments were performed in the shallow water rocky habitat of the northern Baltic Sea during ice-free season 2002. In the experiments the effects of algal species and choice on the grazing of the mesoherbivores *Idotea baltica* (Pallas) and *Gammarus oceanicus* Segerstråle were tested. Salinity, temperature, concentration of nutrients in water and macroalgae and net production of macroalgae were considered as random effects in the analysis. The invertebrate feeding rate was mainly a function of the net photosynthetic activity of *Pylaiella littoralis* (L.) Kjellman and *Fucus vesiculosus* L. Feeding rate increased significantly with decreasing algal photosynthetic activity. When the two algal species were incubated together invertebrates fed primarily on *P. littoralis*. Low selectivity towards *P. littoralis* coincided with its high photosynthetic activity. The presence of *F. vesiculosus* did not modify the invertebrate feeding on *P. littoralis*. The results indicated that (1) the grazing on *F. vesiculosus* depended on the availability of *P. littoralis*, (2) the photosynthetic activity of algae explained the best the variation in grazing rate and (3) the grazers are not likely to control the early outbreak of filamentous algae in the northern Baltic Sea by avoiding young and photosynthetically active algae. The likely mechanism behind the relationship is that the increased photosynthetic activity of macroalgae coincides with their higher resistance to herbivory.

## Introduction

Benthic mesoherbivores constitute an important trophic component in coastal ecosystems where grazing by invertebrate mesoherbivores can regulate the structure and productivity of macroalgal communities (Orth & Van Montfrans, 1984; Arrontes, 1999; Engkvist et al., 2000; Adler et al., 2001). However, the relative importance of 'bottom-up control' and 'top-down' effects is thought to be highly variable between sites and seasons (Menge, 1992; Worm, 2000). In eutrophicated coastal ecosystems throughout the world mass development of filamentous algal species has been reported. Selective herbivore pressure on the ephemeral algae may indirectly sustain perennial species. If the effect of grazers is negligible then the blooms will persist through the growth season and have negative consequences on the perennial vegetation (Putman, 1986; Valiela et al., 1997; Raffaelli et al., 1998; Worm et al., 1999).

The factors affecting the feeding biology of mesograzers are poorly understood and largely qualitative. The food selection by mesograzers is determined by a number of interacting factors, such as food quality and quantity, plant morphology, shelter, access to mates (Nicotri, 1980; Hay, 1984; Putman, 1986; Jernakoff et al., 1996). It was believed earlier that mesograzers feed non-selectively on microalgae and detritus (Steneck & Watling, 1982; Bell, 1991), but many recent experimental studies on feeding preferences or diet range showed significant variation among mesograzers species (Duffy & Harvilicz, 2001; Jormalainen et al., 2001; Orav-Kotta & Kotta, 2003). Therefore, there is a need for field measurements of the feeding behaviour of mesograzers combined with the measurement of physical, chemical and ecological conditions in the study area. The functional relationships between these variables have to be estimated for different areas and different times of the year, to assess the importance of different factors on mesoherbivore grazing in the coastal ecosystem.

*Fucus vesiculosus* L. is the dominant macroalgal species in the Baltic Sea comprising up to 43% of the benthic plant biomass (Kautsky & Kautsky, 1995). In recent years the biomass of the species has notably diminished at many localities. This decline was attributed to their lower competitiveness at higher nutrient concentrations (Pedersen & Borum, 1996) and the shading effect by the filamentous alga *Pylaiella littoralis* (L.) Kjellman combined with increased herbivory by *Idotea baltica* (Pallas) (Kangas et al., 1982). However, recent studies have demonstrated the preference of grazers to feed on filamentous algae (Worm & Sommer, 2000; Orav-Kotta & Kotta, 2004) and, hence, the epiphytic food resources to be the prime factor that determines the presence of grazers in macrovegetation (Boström & Mattila, 1999). These findings correspond to the field observations of a positive relationships between epiphyte load and grazer density (Kotta et al., 2000; Worm & Sommer, 2000). Besides species composition, mesoherbivores tend to be selective in terms of algal photosynthetic activity (Paalme et al., 2002).

Thus, the aim of this study was to experimentally evaluate the grazing potential of the prevailing mesoherbivores *I. baltica* and *Gammarus oceanicus* Segerstråle on the macroalgae *F. vesiculosus* and *P. littoralis*. During the experiment salinity, temperature, concentration of nutrients in water and macroalgae and net production of macroalgae were monitored. Our hypotheses are that (1) *P. littoralis* is the prime diet of the studied grazers, (2) *F. vesiculosus* is consumed when the biomass of *P. littoralis* is reduced in the field and (3) grazing pressure increases with the decreasing photosynthetic activity of algae. That is the increased photosynthetic activity of macroalgae coincides with their higher unpalatability and/or resistance to herbivory.

## Materials and methods

The *in situ* grazing experiments were carried out along a 100-m long transect in Kakumäe Bay, the Gulf of Finland (59°30′ N 24°34′ E) monthly from April to October 2002. Transect was situated perpendicular to the shore between 0 and 5 m depth. Based on the observations made by a diver the transect was characterised by a mixture of sand, pebbles and boulders above 3-m depth. Deeper down only sandy substrate was found and, hence, the area was devoid of macrovegetation and mesoherbivores. The brown algae *F. vesiculosus* and *P. littoralis* were the prevailing macroalgal species. The coverage of the *F. vesiculosus* varied from 15% in winter to 20% in August. The coverage of *P. littoralis* varied from 0% in winter and late summer to 75% in April–May. The green alga *Cladophora glomerata* (L.) Kütz. occurred only in summer with maximum coverage at 5%. Among mesoherbivores the isopod *I. baltica* and the amphipod *G. oceanicus* prevailed in the study area. Based on the data of the Estonian Coastal Monitoring Programme their densities ranged between 250–754 ind. $m^{-2}$ and 170–610 ind. $m^{-2}$ in Kakumäe Bay in 2002, respectively.

Grazing was studied in $5 \times 5 \times 20$ cm nylon netbags of 1 mm mesh size. The meshbags had a rigid structure. Being transparent the material did not reduce the light availability to the algae (checked with an Li-Cor underwater quantum sensor). *F. vesiculosus* and *P. littoralis* were deployed separately and together. About 8 g ww (1 g dw) of *F. vesiculosus* and 2 g ww (0.5 g dw) of *P. littoralis* were added per meshbag. The use of different macroalgal treatments in different seasons depended on the natural occurrence of the algae in the field. In April–May two different cohorts of *P. littoralis* were observed at the same time. The cohorts were different in terms of plant height, colour and primary production values. As these differences might contribute to algal grazing the experiment involved the treatments of young and old generations of *P. littoralis* in April–May. The wet weight of algae was determined prior to the experiment to the nearest of 0.01 g. Before weighing, the algae were gently dried on blotting paper. Additional three replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight.

The mesoherbivores were collected from a shallow (1–3 m) hard bottom area within bushes of *F. vesiculosus* by shaking the algae. Prior to the experiment the test animals were gently placed to the Petri dish filled half with seawater and identified to the species level under a binocular microscope (20–40 × magnification). To each macroalgal treatment either two specimens of adult *I. baltica* (16–21 mm, 0.02 g dw) or two specimens of adult *G. oceanicus* (18–25 mm, 0.02–0.03 g dw) were added. The densities of mesoherbivores in the netbags corresponded to their natural occurrence in the field (i.e. 300 *I. baltica* $m^{-2}$ and 200 *G. oceanicus* $m^{-2}$). In the grazing experiments, netbags without mesoherbivores served as controls and allowed to estimate production and/or decomposition of the macroalgae. Three replicates of each treatment were used. The netbags were placed at 2-m depth about 0.5 m above the bottom. Each experiment lasted 10 days. Altogether the experiment was carried out at eight times.

In parallel to the grazing experiments, the *in situ* diurnal primary production of the studied macroalgal species was measured using the oxygen method (Köhler, 1998). Small tufts (about 0.05 g dw) with no macroepiphytes and grazers (checked under a binocular microscope) were placed in 600 ml glass bottles filled with seawater and incubated horizontally on trays at 0.5-m depth. Bottles without the algae served as controls. There were five replicates per treatment (Kotta et al., 2000; Paalme et al., 2002). The bottles were large enough to guarantee that depletion of nutrients or carbon did not affect the photosynthetic activity of test algae. The changes in the dissolved oxygen concentration were measured by an oxygen meter OXI 92. At the time of the incubation the total insolation above the water surface was measured with a pyranometer. The obtained values were converted to $\mu$mol $m^{-2}$ $s^{-1}$ and transformed to photosynthetic active radiation by multiplying with a factor of 0.45 (Lüning, 1981). Based on the production estimates, all macroalgal species were photosynthetically active and no decomposition of the macroalgae occurred.

At the end of the experiment the test animals were counted and the dry weights of invertebrates and macroalgae were determined (60 °C during 48 h). The changes in the dry weight of the algae per dry weight of the invertebrates corrected for algal production served as the estimates of invertebrate grazing in the field. Parallel with the grazing experiments water temperature, salinity and concentration of nutrients in water and macroalgae from grazer cages were estimated using standard methods (Grasshoff, 1976; Solorzano & Sharp, 1980; Raimbault & Slawyk, 1991). The water samples were taken daily by a diver at 25 cm distance from the mesocosms (10 sample per experiment × 8 periods). The following fractions were analysed both for water and algae: $NO_2$, $NO_3$, total nitrogen, $PO_4$ and total phosphorus. As there were very strong correlations between different fractions of nutrients ($r > 0.9$, $p < 0.001$) for the sake of brevity the values of total nitrogen and total phosphorus are reported only.

The feeding rates by the mesograzers were analyzed using 3-way ANCOVA. Algal and mesoherbivore species and algal choice were considered as fixed effects. Factor levels of the fixed effects were as follows: animal – *G. oceanicus* and *I. baltica*, alga – *F. vesiculosus* and *P. littoralis*, choice – single (either *F. vesiculosus* or *P. littoralis*) and multiple algal choice (*F. vesiculosus* and *P. littoralis*). Salinity, temperature, total nitrogen, total phosphorus in water and macroalgae and net production of macroalgae were considered as random effects in the analysis. Prior to the analysis, Bartlett's test was used to check the assumption of homoscedasticity (Sokal & Rohlf, 1981). We employed linear and polynomial linear regression analyses to describe the relationships between the feeding rate of mesoherbivores and the studied environmental variables. Polynomial regression results are only reported if significantly better fits were achieved using this method compared with the linear model.

## Results

### *Environmental settings*

Water temperature was exceptionally high in 2002. Summer conditions (>15 °C) were observed from May to September. Salinity values were stable at 5–6 psu except for early July when the values less than 4 psu were recorded. The concentration of total nitrogen in seawater was highly variable peaking at early June and September (min = 6.7, avg = 15.4, max = 29.9 $\mu$M $l^{-1}$). The concentration of total phosphorus increased in the course of the year (min = 0.4, avg = 0.7, max = 1.1 $\mu$M $l^{-1}$). The concentration of total nitrogen and phosphorus in *F. vesiculosus* decreased gradually from April to August and then increased slightly onwards (total N: min = 4.6, avg = 8.6, max = 11.8 mg $g^{-1}$, total P: min = 1.0, avg = 1.5, max = 1.8 mg $g^{-1}$). There were no clear seasonal trends for the concentration of nutrients in *P. littoralis*. The values of total nitrogen were lowest in July and highest in April whereas the values of total phosphorus were lowest in October and highest in July (total N: min = 12.0, avg = 13.1, max = 13.9 mg $g^{-1}$, total P: min = 1.9, avg = 2.2, max = 2.9 mg $g^{-1}$).

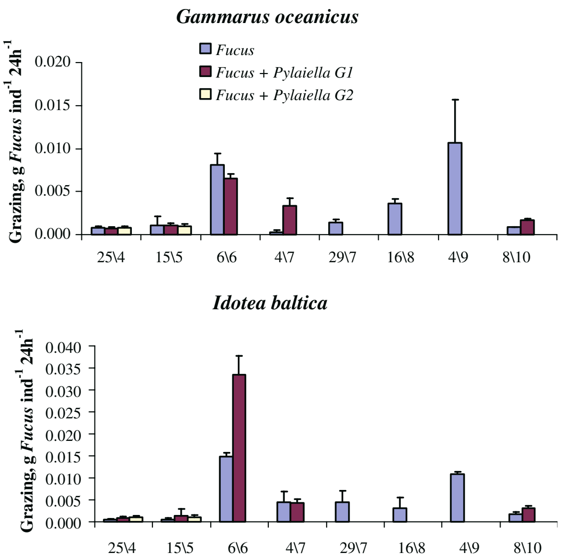


*Figure 1.* Seasonal changes in the grazing rate of mesoherbivores on *F. vesiculosus* in single and multiple choice treatments. G1 and G2 refer to the older and younger cohorts of *P. littoralis*, respectively.

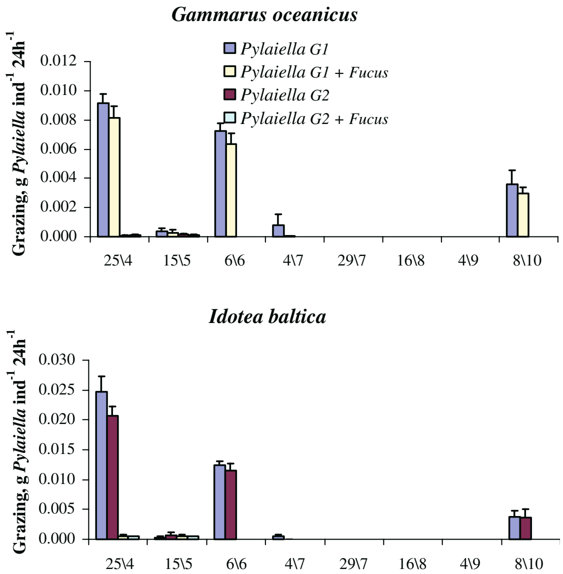


*Figure 2.* Seasonal changes in the feeding rate of mesoherbivores on *P. littoralis* in single and multiple choice treatments. G1 and G2 refer to the older and younger cohorts of *P. littoralis*, respectively.

When water temperature was below 15 °C the maximum net production of *F. vesiculosus* was stable at 0.5 mg $O_2$ g $dw^{-1}$ $h^{-1}$. At higher temperatures in May–September the values were high and stable at 2.1–2.4 mg $O_2$ g $dw^{-1}$ $h^{-1}$. The diurnal primary production of *F. vesiculosus* followed the trend of its maximum net production. The daily dry weight increment of *F. vesiculosus* was 0.1–0.4% at low temperatures and 1.3–1.8% at high temperatures. The maximum net production of *P. littoralis* gradually decreased from 2.2–2.6 mg $O_2$ g $dw^{-1}$ $h^{-1}$ in April to 1.3–1.6 mg $O_2$ g $dw^{-1}$ $h^{-1}$ in October. The diurnal primary production of *P. littoralis* was variable at 0.8–2.6% inc. dw 24 $h^{-1}$ between April–July and low at 0.4% inc. dw 24 $h^{-1}$ in October.

### *Grazing rates*

The invertebrate grazing on *F. vesiculosus* was highest in early June and September and lowest in April. The grazing on *P. littoralis* was highest in late April, early June and early October. *P. littoralis* was not found in the study area from the mid July to the late September. When the grazers had a choice of older and younger generations of *P. littoralis*, the latter was practically not consumed. The maximum grazing values were 0.4 and 0.3 g dw algae ind.$^{-1}$ 24 h$^{-1}$ for *F. vesiculosus* and *P. littoralis*, respectively (Figs. 1 and 2).

Algal choice and interaction of alga × algal choice had an effect on the grazing rate of mesoherbivores. Grazing was significantly reduced with decreasing net production of *F. vesiculosus* ($p < 0.001$) and *P. littoralis* ($p < 0.001$). Water temperature, salinity and concentration of nutrients in water and macroalgae did not correlate with the feeding rates of the studied mesoherbivores (linear correlation analysis, $p > 0.05$) (Table 1).

When mesoherbivores were provided single macroalgal species the grazing on *F. vesiculosus* and *P. littoralis* declined with the increasing net production of the named algae (Fig. 3). In multiple choice treatments *P. littoralis* was often preferred to *F. vesiculosus*. Invertebrate grazing on *F. vesiculosus* was stronger when the net photosynthetic activity of *P. littoralis* was higher and that of *F. vesiculosus* was lower. The presence of *F. vesiculosus* did not modify the grazing on *P. littoralis*, and the grazing on *P. littoralis* was only related to its net photosynthetic activity (Figs. 4 and 5).

## Discussion

This study showed that the photosynthetic activity of macroalgae was universal factor that was related to the feeding rate and selectivity of benthic mesoherbivores in the northern Baltic Sea. The experiments on the feeding activity of mesoherbivores on decomposing macroalgae suggest that the algae are unpalatable or resistant to herbivory when they are photosynthetically active i.e. at the beginning of their decomposition (Birch et al., 1983; Paalme et al., 2002). Later stages of the decomposition cell walls break down, concentration of nutrients increases in the decomposing material as a result of increased microbial activity and algae become more attractive for benthic invertebrates (Boyd, 1970; Byren & Davies, 1986; Mann, 1988; Buchsbaum et al., 1991). On another hand the rising nutrient concentration in seawater may also improve the quality of algae as food, thereby increasing the pressure of grazers on the algae (Hemmi & Jormalainen, 2002). However, when the isopod *I. baltica* were provided natural and powdered algae of the same species, the preference with artificial food did not parallel those

*Table 1.* Results of 3-way ANCOVA for the analysis of mesoherbivore grazing on macroalgae

| Effect | *df* | *F* | *p* |
|---|---|---|---|
| Animal | 1 | 2.503 | 0.117 |
| Alga | 1 | 0.690 | 0.408 |
| **Choice** | 1 | 6.893 | **0.010** |
| Animal × Alga | 1 | 2.250 | 0.137 |
| Animal × Choice | 1 | 1.359 | 0.246 |
| **Alga × Choice** | 1 | 9.090 | **0.003** |
| Salinity | 1 | 0.237 | 0.627 |
| Temperature | 1 | 0.899 | 0.345 |
| Total N water | 1 | 2.737 | 0.101 |
| Total P water | 1 | 0.694 | 0.407 |
| Total N *Fucus* | 1 | 3.155 | 0.078 |
| Total P *Fucus* | 1 | 0.009 | 0.921 |
| Total N *Pylaiella* | 1 | 0.080 | 0.778 |
| Total P *Pylaiella* | 1 | 1.724 | 0.192 |
| **Net production *Fucus*** | 1 | 12.969 | **< 0.001** |
| **Net production *Pylaiella*** | 1 | 16.510 | **< 0.001** |
| **Intercept** | 1 | 13.412 | **< 0.001** |

Factor codes of the fixed effects are as follows: Animal – *G. oceanicus* and *I. baltica*, Alga – *F. vesiculosus* and *P. littoralis*, Choice – single and multiple algal choice. Significant effects are marked in bold. Salinity, temperature, total nitrogen, total phosphorus in water and macroalgae and net production of macroalgae were considered as random effects in the analysis.

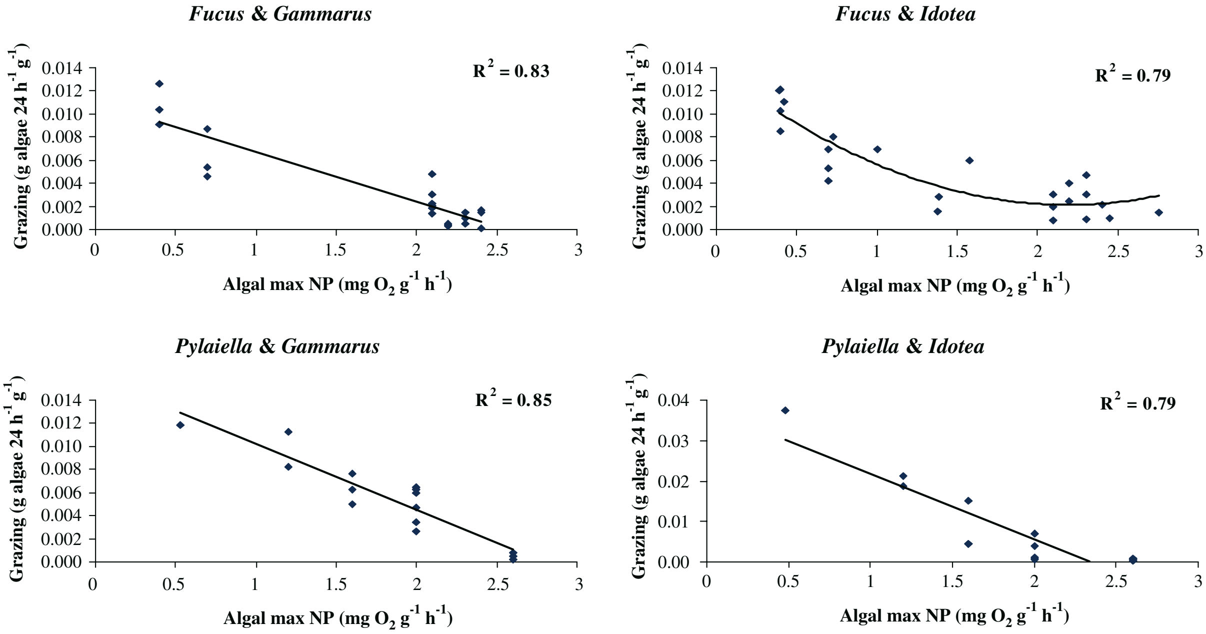


*Figure 3*. Relationships between maximum net production of algae and grazing of invertebrates in single choice treatments.

with natural algae. It was concluded that chemical quality of alga is not the major determinant of feeding preferences of the isopod (Jormalainen

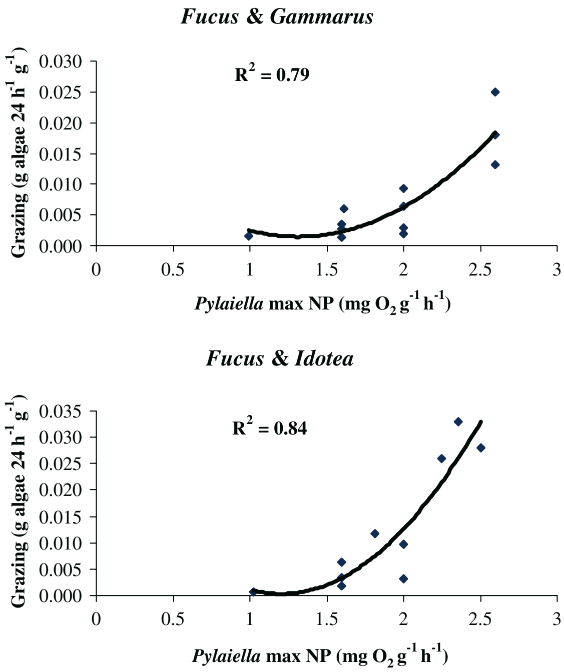


*Figure 4*. Relationships between maximum net production of *P. littoralis* and grazing of invertebrates on *F. vesiculosus* in multiple choice treatments.

et al., 2001). Similarly, nutrient enhancement of the algae did not influence the fitness components of the adult herbivores (Hemmi & Jormalainen, 2004) leaving morphological structure as the prime factor affecting the feeding rates of mesoherbivores.

In our study algal choice and interaction between algal species and choice had an effect on the feeding rate of mesoherbivores. The presence of *F. vesiculosus* did not modify the grazing rates of *P. littoralis* whereas the *P. littoralis* had significant effect on the grazing of *F. vesiculosus*. It suggests that the filamentous alga was often the first choice for the studied invertebrates. The role of epiphytes as a prime food for mesoherbivores has been well demonstrated (Cruz-Rivera & Hay, 2000; Orav-Kotta & Kotta, 2004 but see also Jormalainen et al., 2001). Although *F. vesiculosus* is poor food it provides stability for mesoherbivores in highly seasonal environment of the northern Baltic Sea e.g. in the seasons when annual algae are lacking or then the annual algae are photosynthetically active. During the most time of the year a diverse assemblage of annual algae are observed in the canopy of *F. vesiculosus* (Kiirikki, 1996) offering the potential for the food choices of mesoherbivores. In the experiment by Lotze & Worm (2002) the grazers that commonly hid under the thally of

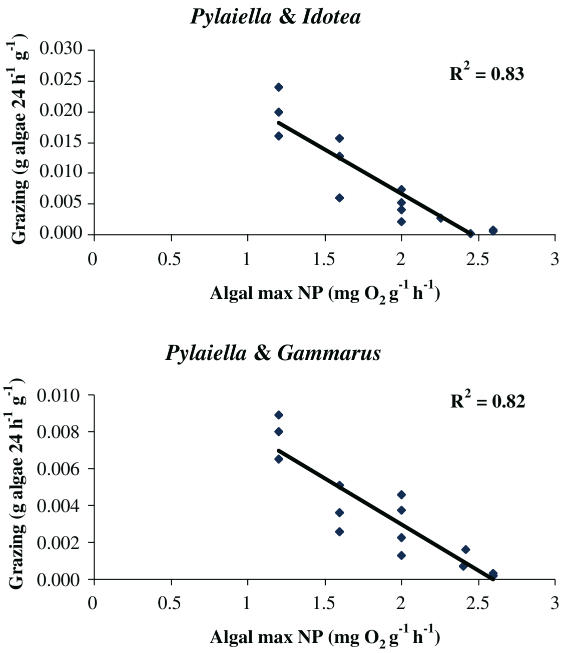


*Figure 5.* Relationships between maximum net production of algae and grazing of invertebrates in multiple choice treatments.

*F. vesiculosus* did not consume the brown alga but the annual species.

Surprisingly, the water temperature within the range of our study (4–21 °C) did not affect the feeding rate of mesoherbivores as compared to the results of earlier studies (Shacklock, 1991; Lotze & Worm, 2002). The feeding rate of mesoherbivores coupled with the seasonality in the photosynthetic activity of macroalgae. The algal species used in the experiment differ in their seasonality. After a mild winter, the filamentous algal zone is first dominated by *P. littoralis*, which degenerates and detaches before summer (Kiirikki, 1996). Depending on the temperature and light conditions, several blooms of *P. littoralis* are observed in our study area till early August (Martin et al., 2003). Hence, the population of *P. littoralis* is likely in bad condition during mid spring, early summer and early autumn coinciding the peaks of invertebrate feeding on *P. littoralis*. The seasonal changes in the photosynthetic activity of *F. vesiculosus* are less variable except for lower values during winter (Paalme & Mäkinen, 1997; Lehvo et al., 2001). The invertebrate feeding on *F. vesiculosus* is higher in summer when *P. littoralis* is absent in the study area.

The present study indicates that grazers can not control the blooms of annual algae in the northern Baltic Sea. As photosynthetic activity of *P. littoralis* decrease with age the invertebrate grazing increases when annual algae have already achieved high densities and start to decompose. In that respect the grazers are not important in buffering eutrophication effects at the earlier stages of the blooms. They may, however, inhibit the recruitment of annual algae (Lotze & Worm, 2002) and protect perennial macroalgae from ephemeral epiphytes at the later stages of the blooms (Worm et al., 2000). In a large-scale field survey the cover of *F. vesiculosus* significantly increased with grazer densities and decreased with annual algal cover (Worm et al., 1999). Consequently, they release macrophytes from competition with annual algae and contribute to the stability of coastal ecosystem (Worm, 2000).

To conclude, the results of this study indicated that (1) the grazing on *F. vesiculosus* depended on the availability of *P. littoralis*, (2) the photosynthetic activity of algae explained the best the variation in grazing rate and (3) the grazers are not likely to control the early outbreak of filamentous algae by avoiding young and photosynthetically active algae.

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