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Seasonal variations in the grazing of *Gammarus oceanicus*, *Idotea baltica*, and *Palaemon adspersus* on benthic macroalgae

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Abstract. Grazing of *Gammarus oceanicus*, *Idotea baltica*, and *Palaemon adspersus* on benthic macroalgae was studied *in situ* using small enclosures in Kõiguste Bay, N Gulf of Riga. *Pilayella littoralis* was the prime diet of the studied invertebrates. When its biomass declined in the field, invertebrate grazing on *Fucus vesiculosus* increased. The highest grazing rates were shown by *I. baltica* followed by *G. oceanicus* and *P. adspersus*. In general invertebrate grazing was high in summer, moderate in autumn, and low in spring.

Key words: Baltic, *Gammarus*, grazing, *Idotea*, macrophytobenthos, *Palaemon*.

INTRODUCTION

Macroalgae are structurally and functionally important in coastal ecosystems. They are important primary producers (Mann, 1973; Smith, 1981; Charpy-Roubaud & Sournia, 1990) and a significant sink for anthropogenic carbon dioxide (Smith, 1981). Macrophyte communities are regulated both by nutrient loading and grazers' activity. The share of "bottom-up control" of "top-down" effects is thought to be highly variable between sites and seasons (e.g. Menge, 1992; Worm, 2000).

In recent decades, anthropogenic pollution has caused changes in plant biomasses and species composition in the whole coastal area of the Baltic Sea. The most drastic changes were the excessive growth of the filamentous macro-algae *Pilayella littoralis* (L.) Kjellm. and *Cladophora glomerata* (L.) Kütz. and the decline of perennial and slow growing *Fucus vesiculosus* L. (Kangas et al.,

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1982; Kautsky et al., 1986; Vogt & Schramm, 1991; Kotta et al., 2000). This raised the question about the role of benthic grazers: do they buffer or amplify the effect of eutrophication? The grazers are potentially able to consume a significant proportion of the macroalgal production and, hence, control the blooms of filamentous algae. On the other hand, the grazers may selectively consume perennial algae, which in turn favours the development of fast growing species and destabilize the communities.

The evidence about the effect of invertebrate grazing on macroalgae is highly variable and controversial. The prevalent benthic herbivores inhabiting the northern Baltic Sea are omnivorous (Nicotry, 1980; Franke & Janke, 1998) but they may be quite selective within food categories (Salemaa, 1978; Schaffelke et al., 1995). Besides, the effect of grazers has strong temporal and spatial variation (Kotta et al., 2000; Worm, 2000).

In the present study, *in situ* grazing rates of prevailing opportunistic herbivores on various macroalgal species were estimated in Kõiguste Bay, northern Gulf of Riga. The main questions were as follows: (1) which algal species are potentially consumed by selected invertebrates, (2) how large quantities of algae are removed by grazing, and (3) does seasonality affect the grazing pressure?

MATERIAL AND METHODS

In situ grazing experiments were performed in Kõiguste Bay (58°22.10′ N 22°58.69′ E), northeastern Baltic Sea in April, July, and October 2001. Four different macroalgal species were deployed in the experiment: the brown algae *F. vesiculosus* and *P. littoralis*, the red alga *Furcellaria lumbricalis* (Huds.), and the green alga *C. glomerata*. The specimens of *F. vesiculosus* were divided into apical (juvenile) and basal (old) parts and treatments with *F. vesiculosus* overgrown with *P. littoralis* and epiphyte-free *F. vesiculosus* were distinguished. The use of different macroalgal treatments in different seasons depended on the natural occurrence of the algae in the field (Table 1).

Table 1. Different algal treatments used in the grazing experiment. Three replicates of each macroalgal treatment were used for each studied invertebrate species

Plant	April	July	October
Non-epiphytic *Pilayella littoralis*	+	+	
Basal *Fucus vesiculosus* without epiphytic *Pilayella littoralis*	+	+	+
Apical *Fucus vesiculosus* without epiphytic *Pilayella littoralis*	+	+	+
Basal *Fucus vesiculosus* with epiphytic *Pilayella littoralis*	+	+	
Apical *Fucus vesiculosus* with epiphytic *Pilayella littoralis*	+		
Loose-lying *Furcellaria lumbricalis*	+	+	+
Attached *Furcellaria lumbricalis*	+	+	+
Cladophora glomerata		+	

Idotea baltica (Pallas) and *Gammarus oceanicus* Segerstråle were collected from a shallow (1–3 m) area within the stands of *F. vesiculosus* by shaking the algae. *Palaemon adspersus* (Rathke) were caught by dredging the vegetated areas. Only adult specimens were used in the experiment.

Grazing was studied in $5 \times 5 \times 20$ cm nylon netbags of 1 mm mesh size. When available in the field, each macroalgal treatment was added either two specimens of *I. baltica*, two specimens of *G. oceanicus*, or one specimen of *P. adspersus*. Three replicates of each treatment were used. 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 plotting paper until the paper did not become wet any more. Additional three replicates of each macroalgal treatment served as control to obtain the ratio of wet to dry weight. The algae were dried at 60 °C during 48 h.

The netbags were placed at 2 m depth about 0.5 m above the bottom. Each series of the experiment lasted 10 days. In parallel to the grazing experiments, the *in situ* diurnal primary production of the studied macroalgal species was measured. Small tufts (ca. 0.05 g dw) with no macroepiphytes and grazers were placed in 600 mL glass bottles, filled with sea water, and incubated horizontally on special trays at 0.5 m depth. Bottles that did not include the algae served as controls. There were five replicates per each treatment and five controls (Kotta et al., 2000). 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. The changes in the dry weight of algae per dry weight of invertebrates in the nylon mesocosms served as the estimates of invertebrate grazing in the field. The grazing values were not compensated for the algal production in the present paper, as the production data were not yet fully available. However, earlier estimates (Kotta et al., 2000; Paalme et al., 2002) suggest that invertebrate grazing exceeds manifold the algal production in similar experimental design. Hence, the loss of algal material represents primarily invertebrate grazing.

RESULTS

The studied invertebrates consumed macroalgae the least in April when only *I. baltica* reduced the biomass of *P. littoralis* and the basal parts of *F. vesiculosus* overgrown with *P. littoralis*. The idoteid grazing in other macroalgal treatments was statistically insignificant. Similarly, the grazing of *G. oceanicus* and *P. adspersus* on the studied algae was negligible (ANOVA, $p > 0.05$) (Fig. 1).

The highest grazing level was observed in July. *G. oceanicus* and *I. baltica* consumed more macroalgae than *P. adspersus*. Among the studied macrophytes

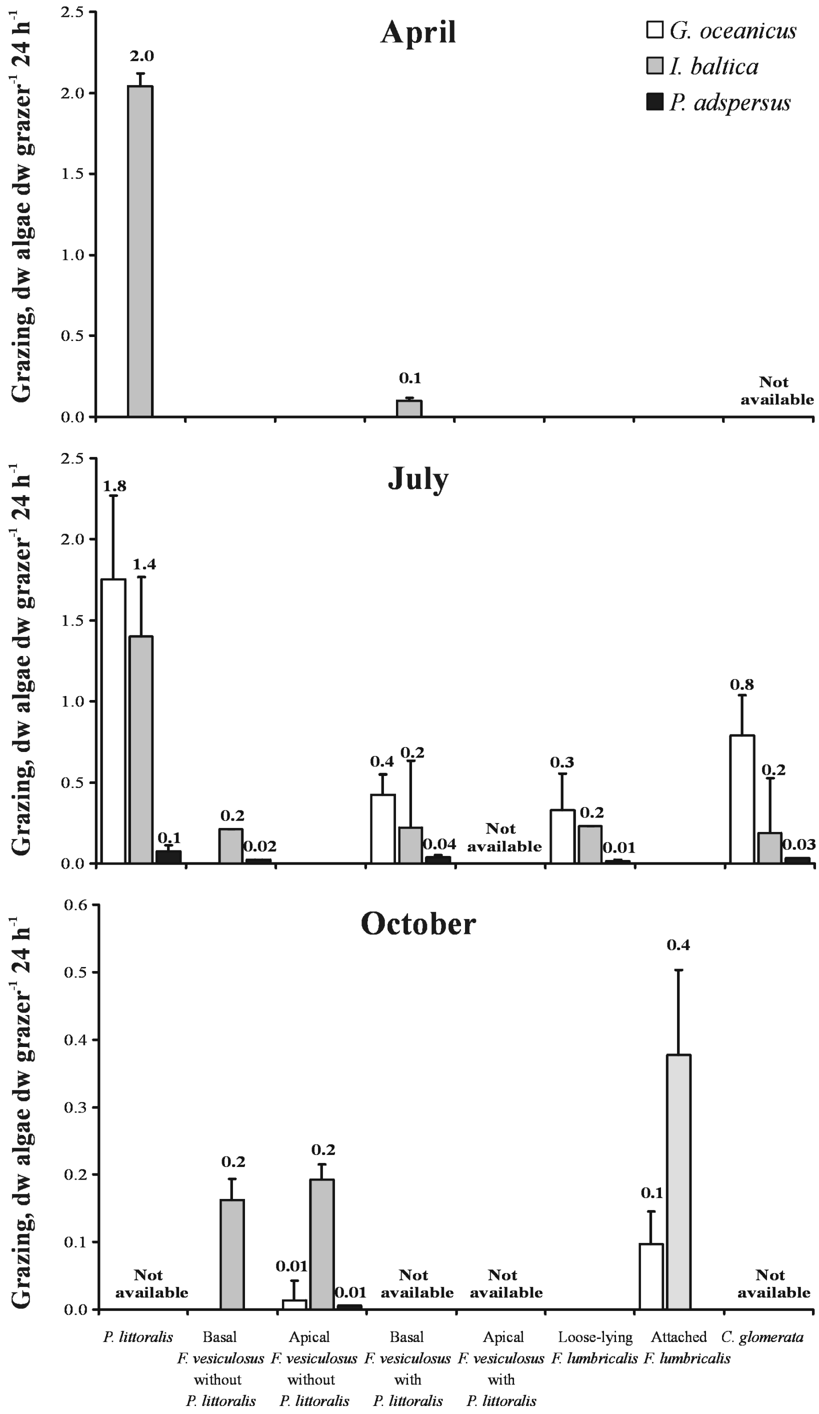

Fig. 1. Daily grazing of *Gammarus oceanicus*, *Idotea baltica*, and *Palaemon adspersus* on benthic macroalgae in April, July, and October.

the consumption of the non-epiphytic *P. littoralis* was the highest followed by *C. glomerata* and the epiphytic *P. littoralis*. *I. baltica* and *P. adspersus* also consumed the basal parts of *F. vesiculosus*. All the studied invertebrates grazed more on the loose-lying than on the attached form of *F. lumbricalis* (Fig. 1).

In October the grazing was moderate, being about two times lower than in July. As a difference of the previous seasons the attached form of *F. lumbricalis* and the epiphyte-free *F. vesiculosus* were an attractive diet for invertebrates (Fig. 1).

DISCUSSION

Our study indicated that *P. littoralis* was the prime diet of the studied grazers in Kõiguste Bay. The consumption of *F. vesiculosus* was moderate when the biomass of *P. littoralis* was reduced in the field.

I. baltica is omnivorous, feeding on benthic microalgae, filamentous algae, macroalgae, detritus, small invertebrates, and even its conspecifics (Naylor, 1955; Sywula, 1964; Ravanko, 1969; Nicotry, 1980; Robertson & Mann, 1980; Franke & Janke, 1998). Despite its omnivory, *I. baltica* is rather selective within food categories (Salemaa, 1978; Schaffelke et al., 1995). Its dietary choice involves selection between different algal species (Schaffelke et al., 1995; Schramm et al., 1996) but likely also between different parts of the algal thallus (Salemaa, 1987). In the northern Baltic Sea, however, *F. vesiculosus* is considered the main source of food for *I. baltica* (Salemaa, 1987).

Earlier literature does not provide a definite answer to the question whether *I. baltica* select *F. vesiculosus* for shelter or food, as the experiments about the microhabitat choice of idoteids usually involved only a single macroalgal species (e.g. Salemaa, 1987; Merilaita & Jormalainen, 2000). Our experiments indicated the prevalence of *P. littoralis* as a main food for *I. baltica*. In the absence of *P. littoralis*, *I. baltica* fed on *F. vesiculosus* and *C. glomerata*. Hence, in the light of these results, the former hypothesis is more likely.

Gammarids are considered selective omnivores. Their diet consists of decaying organic matter with its microbial community, macroalgae but also other animals such as other invertebrates, fish eggs, wounded fish (e.g. Macneil et al., 1997). The utilization of macrophytes is dependent on plant species, their condition, plant particle size, microbial activity on the plant material, and nutritional quality (Hutchinson, 1975; Wetzel, 1983). The growth of the limnic gammarids *Gammarus fossarum* Koch and *Gammarus roeseli* Gervais is affected by the type of diet, being high on naturally decaying leaves and fine organic detritus and low on green algae (Pöckl, 1995). Flesh supplements to an algal diet accelerate the growth and maturation of gammarids (Vassallo & Steele, 1980).

Our study demonstrated that besides *P. littoralis*, *Gammarus* spp. consumed significant amounts of the green alga *C. glomerata*. An earlier study with the limnic gammarids showed that among a large variety of food, the growth and survival of the amhipods are poorest with *Cladophora* sp. (Pöckl, 1995). The difference between these observations might be attributed to the condition of *Cladophora*. Our earlier studies demonstrated that the attractiveness of *Cladophora* to invertebrate grazing is highly dependent on the physiological state of the filamentous algae (Paalme et al., 2002).

Palaemon spp. are omnivorous, feeding on algae, moss, debris, and small arthropods (Berglund, 1980). Other studies suggest the prevalence of carnivorous habits (Sitts & Knight, 1979; Siegfried, 1982). Our study showed that *P. adspersus* consumed relatively high quantities of *P. littoralis* and basal parts of *F. vesiculosus*. However, the consumption rates were manifold lower as compared to *I. baltica* and *Gammarus* spp.

The results of this study give an indication of the invertebrate grazing in the study area. Our next step will be to combine the estimates of algal production and invertebrate densities with the grazing rates. This will allow us to detect whether benthic grazers are potentially able to regulate the macroalgae in the northern Baltic Sea.

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Sesoonsed muutused *Gammarus oceanicus*'e, *Idotea baltica* ja *Palaemon adspersus*'e toitumisel makrovetikatest

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Gammarus oceanicus'e, *Idotea baltica* ja *Palaemon adspersus*'e toitumisaktiivsust uuriti Kõiguste lahes, kasutades selleks nailonist mesokosme. Nimetatud selgrootud toitusid peamiselt pruunvetikast *Pilayella littoralis*. Kui selle vetika biomass uurimisalal vähenes, suurenes teise pruunvetika (*Fucus vesiculosus*'e) tähtsus selgrootute toidus. Kõige suurema koguse vetikatest tarbis *I. baltica*, järgnesid *G. oceanicus* ja *P. adspersus*. Üldjuhul oli selgrootute toitumisintensiivsus suurim suvel, keskmine sügisel ning vähim kevadel.