Helgol Mar Res (2004) 58:71–76
DOI 10.1007/s10152-003-0170-2

ORIGINAL ARTICLE

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Seasonal variation in invertebrate grazing on *Chara connivens* and *C. tomentosa* in Kõiguste Bay, NE Baltic Sea

Received: 19 March 2003 / Revised: 1 December 2003 / Accepted: 2 December 2003 / Published online: 15 January 2004

Abstract Charophytes are a highly endangered group of algae. In the Baltic Sea, the number of species, distribution area and biomass of charophytes have significantly decreased in recent decades. Although eutrophication triggers their initial decline, the mechanism of the final extinction of charophyte populations is not fully understood. An in situ experiment was performed to study the role of the mesoherbivores *Idotea baltica*, *Gammarus oceanicus* and *Palaemon adspersus* in the decline of charophytes in the north-eastern Baltic Sea. Invertebrate grazing showed a clear seasonality: grazing pressure was low in April, moderate in July, and high in October. Grazing on charophytes by *P. adspersus* was negligible, whereas *I. baltica* and *G. oceanicus* significantly reduced the biomass of charophytes in the field. Low photosynthetic activity (high decomposition rate) of the charophytes favoured grazing. The invertebrates studied preferred *Chara tomentosa* to *C. connivens*. Low consumption of *C. connivens* may reflect its non-native origin. The experiment suggests that, under moderately eutrophic conditions, grazers are not likely to control charophyte populations. However, grazers have the potential to eliminate charophytes in severely eutrophic systems under the stress of filamentous algae.

Communicated by H.D. Franke

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Keywords *Chara* · *Gammarus* · Grazing · *Idotea* · Photosynthetic activity

Introduction

Charophytes are a highly developed and diverse group of algae. They are widely distributed in freshwater, brackish and marine habitats from tropical to polar regions (Wood and Imahori 1965). Of 314 species, only six have been reported from all continents. Recent species prefer freshwater environments while the majority of fossil species occurred in brackish waters: even marine species were quite common. Charophytes often reach deeper than submerged angiosperms yet can also prevail in shallow waters (Chambers and Kalff 1985). In the Baltic Sea this group of algae inhabits sheltered coastal areas where their distribution pattern is primarily controlled by exposure, sediment type and salinity regime (Schubert and Yousef 2001a; Torn et al. 2004).

In recent decades, number of species, distribution area and biomass of charophytes have significantly declined in virtually the whole Baltic Sea (Dekere 2001; Koistinen and Munsterhjelm 2001; Martin 2001; Schubert and Yousef 2001b; Sinkevièienë and Jurgilaitë 2001). This decline has been attributed to increased nutrient loads resulting in higher productivity of phytoplankton, epiphytic algae and angiosperms. The reduction in available light intensity leads to an upward shift of the depth limit of charophytes and the replacement of the charophyte-dominated community by phanerogams and filamentous algae (Moss 1989; Scheffer at al. 1992; Yousef et al. 1997; Schubert and Yousef 2001b). The results, however, cannot explain the extinction of charophytes in shallower waters but this knowledge is essential for the effective protection of this highly endangered group of algae (HELCOM 1998).

Invertebrate herbivory is considered to be a major factor determining the structure and development of macroalgal assemblages (e.g. Paine 1974; Lubchenco 1978, 1982; Hawkins and Hartnoll 1983; Brawley 1992;

Vadas and Elner 1992). As the mass development of epiphytic algae triggers an increase in grazer density (Kangas et al. 1982; Salemaa 1987; Malm 1999; Kotta 2000; Kotta et al. 2000), it is likely that the shading effect of filamentous algae, combined with an increased grazing rate, may be involved in the decline of charophytes in the Baltic Sea.

At present there are no experimental studies dealing with the effect of grazers on charophytes in the Baltic Sea. In our study, in situ grazing by prevailing mesoherbivores on two charophyte species was estimated in Kõiguste Bay, in the northern part of the Gulf of Riga. The main questions were: (1) Do selected invertebrates graze on *Chara connivens* and *C. tomentosa*?; (2) What quantities of alga are removed by grazing during different seasons?; and (3) Is the photosynthetic activity of the algae related to grazing pressure?

Methods

In situ grazing experiments were performed in Kõiguste Bay (58°22.10′N 22°58.69′E), north-eastern Baltic Sea in April, July and October 2001 (Table 1). Kõiguste Bay is typified by a wide coastal zone with a diverse bottom topography and macrophyte community. Boulders predominate in areas shallower than 3 m, pebbles at 3–8 m depth, and clay bottoms mixed with gravel and pebbles in deeper areas. Depending on the water exchange between the Gulf of Riga and the open Baltic Sea, salinity in Kõiguste Bay ranges from 6 to 7 psu. The region is ranked among the less eutrophic ones in the Estonian coastal sea (Suursaar 1995; Astok et al. 1999).

The globally spread *C. tomentosa* L. occurs in brackish waters only in the Baltic Sea (Olsen 1944; Björkman 1947) where it is distributed along virtually all coasts which provide wind- and wave-sheltered localities. The species is more frequent in the northern and central Baltic Sea (Pankow et al. 1990; Nielsen et al. 1995). In Europe, *C. connivens* Salzm. has been recorded from Scandinavia to Portugal and also in a few scattered localities in Britain and Ireland (Corrillion 1957; Moore 1986). In the Baltic Sea, *C. connivens* Salzm. is rare (Olsen 1944; Trei 1991; Nielsen at al. 1995) and considered as non-indigenous to the area (Luther 1979). According to recent data, the species is found only in Estonian and Swedish waters (Blindow 2000; Torn et al. 2004).

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

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 and Mann 1980; Franke and Janke 1998). Gammarids are considered to be 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). *Palaemon* spp. are omnivorous, feeding on algae, moss, debris and small arthropods (Berglund 1980). Other studies have suggested the prevalence of carnivorous habits (Sitts and Knight 1979; Siegfried 1982).

Grazing was studied in 5×20 cm nylon net bags (~400 cm^3) of 1 mm mesh size. To each macroalgal treatment was added either two specimens of *I. baltica*, two specimens of *G. oceanicus* or one specimen of *P. adspersus*. Net bags without grazers served as control. Three replicates of each treatment were run. The wet weight of algae was determined prior to the experiment to the nearest 0.01 g. Before weighing, the algae were gently dried on blotting paper until the paper did not become wet anymore. An additional three replicates of each macroalgal treatment served as controls to obtain the ratio of wet to dry weight. The algae were dried at 60°C for 48 h.

The net bags 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 dry weight) with no macroepiphytes and grazers were placed in 600 ml glass bottles, filled with seawater and incubated horizontally on special trays at 0.5 m depth. Bottles which did not include any algae served as controls. There were five replicates per treatment and five controls (Kotta et al. 2000; Paalme et al. 2002).

At the end of the experiment the test animals were counted and the dry weights of invertebrates and macroalgae were determined for each net bag. The changes in the dry weight of algae relative to dry weight of invertebrate served as an estimate of invertebrate grazing in the field. The control treatment was used to compensate the grazing values with respect to algal production and/or decomposition.

Results

Invertebrate grazing on charophytes showed a clear seasonality (Table 2; Fig. 1). The effect depended on both algal and invertebrate species. The grazing of *P. adspersus* on charophytes was negligible, whereas *I. baltica* and *G. oceanicus* significantly reduced the biomass of charophytes in the field.

Table 2 Two-way ANOVAs for the grazing on *Chara tomentosa* and *C. connivens*. Factor 1: season; factor 2: species of grazer. *Bold* numbers indicate significant differences

C. connivens Factor	*df*		*F*	*P* level
	Effect	Error		
1	2	12	93.4	**0.000**
2	1	12	1.6	0.232
1×2	2	12	1.6	0.244
C. tomentosa Factor	*df*		*F*	*P* level
	Effect	Error		
1	2	12	30.0	**0.000**
2	1	12	0.7	0.418
1×2	2	12	3.7	**0.049**

Table 1 Average duration of daylight, surface irradiance and water temperature in the study area during incubation

Month	Duration of daylight (h)	Surface irradiance (μE m^{-2} s^{-1})			Water temperature (°C)
		daylight mean	diurnal mean	midday max	
April	15.0	475	297	1,210	9.1±1.5
July	17.5	649	473	1,370	21.8±0.2
October	11.7	387	189	1,228	12.5±0.1

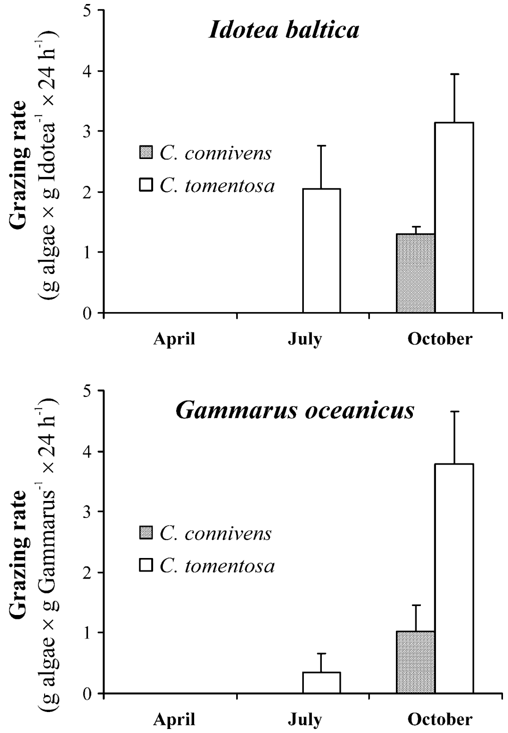

Fig. 1 Seasonal variation in invertebrate grazing on charophyte species (means and SE)

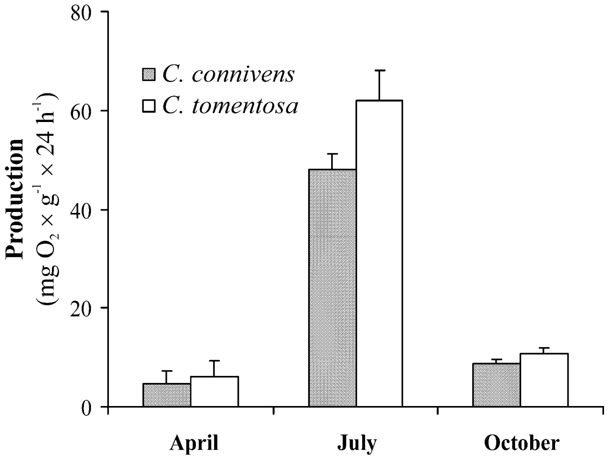

Fig. 2 Seasonal variation in algal production (means and SE)

Charophytes were not consumed in April. In July, grazing was moderate and only *C. tomentosa* was consumed. *I. baltica* had significantly higher grazing rates than *G. salinus* in July. Grazing was highest in October. The consumption of *C. tomentosa* by *G. oceanicus* was then about ten times as high as in July. Similarly, idoteid grazing on *C. tomentosa* was higher, though the difference was not statistically significant. In October, *C. connivens* was grazed by both *I. baltica* and *G. oceanicus*. The grazing pressure of the studied invertebrates on *C. connivens* was moderate and their values were not statistically different.

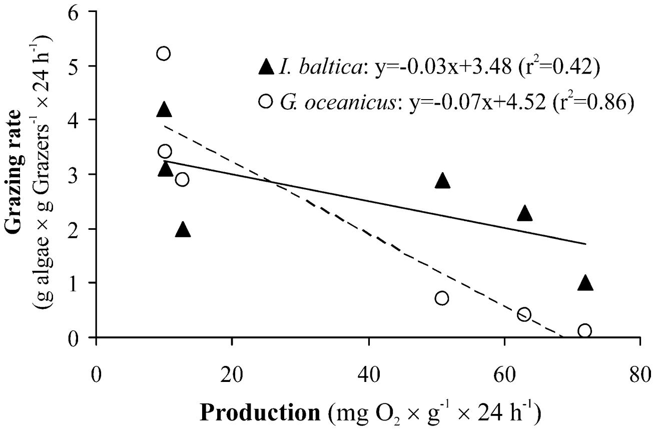

Fig. 3 Relationships between algal production and grazing rate. The zero grazing values are excluded from the analysis

There was a negative linear relationship between the photosynthetic activity of *C. tomentosa* and invertebrate grazing, provided that water temperature was above 10°C (Figs. 2, 3). According to visual observations, the photosynthetic activity of the charophyte was inversely related to the state of algal decomposition.

Discussion

Grazing on charophytes in April was probably limited by low temperature. The significance of temperature for the activity of grazers has been demonstrated earlier in the field (Valiela et al. 1997; Lotze and Worm 2002). The activity of herbivores is negligible when water temperature is below 10°C in the north-eastern Baltic Sea (Orav-Kotta and Kotta 2003b). Hence, the recruitment of charophytes is likely to be affected more by climate (e.g. temperature, solar radiation) than by grazers.

The low grazing pressure in summer may be explained by the good condition of the charophytes as is indicated by their high photosynthetic activity. The protection against grazers may involve either morphological resistance (Steneck and Watling 1982; Hay et al. 1994) or chemical defence (Hay and Fenical 1988; Hay et al. 1994; Amsler 2001; Paul et al. 2001). The results of this experiment suggest that *C. connivens* is more resistant to herbivores than *C. tomentosa*. Besides, the mass development of filamentous alga which are the preferred food for the studied grazers in the area (Orav-Kotta and Kotta 2003a, 2003b) may explain why the grazing rate on charophytes is low in summer.

Our data suggest that herbivores have the highest impact on *Chara* stands in autumn. A similar seasonal pattern of herbivory has been reported for freshwater habitats, though waterbirds were considered in these experiments (Van den Berg 1999; Noordhuis et al. 2002). Visual observations indicate that strong grazing pressure is related to the onset of algal decomposition. This is also indicated by an inverse relationship between algal photosynthetic activity and invertebrate grazing.

By October, the density of filamentous algae had notably declined in the study area. The abundant population of herbivores which had relied on these algae were forced to switch to an alternative diet. As compared to other macroalgae in the area, the decomposing charophytes seemed to be the most rewarding food for the studied invertebrates, especially for *G. oceanicus* (Orav-Kotta and Kotta 2003b). The consumption of *C. tomentosa* by *I. baltica* was significantly higher than consumption of *F. vesiculosus* (Orav-Kotta and Kotta 2003b), even though the brown alga is ranked after the filamentous *Pilayella littoralis* as the second most important diet for this isopod in the northern Baltic Sea (Orav-Kotta and Kotta 2003a).

The utilisation of macrophytes is dependent on plant condition and nutritional quality (Hutchinson 1975; Wetzel 1983). As shown in this study, and also for other brackish (Paalme et al. 2002) and freshwater environments (Pöckl 1995), gammarids prefer decaying food to fresh algae. The low levels of herbivory are related to the unpalatability or resistance of the algae. According to Hunter (1976), fresh *Chara* are heavily calcified, which may greatly reduce their appeal to herbivores (but see Noordhuis et al. 2002). In the course of decomposition the cell walls of the algae become less resistant to herbivory (Birch et al. 1983) and the concentration of nutrients increases in the decomposing material as a result of increased microbial activity (Boyd 1970; Hunter 1976; Byren and Davies 1986; Buchsbaum et al. 1991). As a consequence, the algae become more attractive to benthic invertebrates (Mann 1988). The relationship between the rate of algal decomposition and grazing was not so straightforward for *I. baltica*, probably due to the different feeding mode of the isopod (e.g. Salemaa 1987). We observed that *I. baltica* was able to consume fresh alga. However, when provided with algae in different state of decomposition, *I. baltica* feeds selectively on more degraded parts of the algae (Salemaa 1987; Paalme et al. 2002). As for *P. adspersus*, this experiment demonstrated that charophytes (even when partly decomposed) do not belong to the diet of this species. The results support earlier findings of the prevalence of carnivorous habits in *P. adspersus* in the north-eastern Baltic Sea. In the absence of prey, *P. adspersus* may feed on filamentous algae such as *Pilayella littoralis* and *Cladophora glomerata* (L.) Kütz (Orav-Kotta and Kotta 2003b).

Why did the studied invertebrates prefer the coarse *C. tomentosa* over the fine *C. connivens*? It has been suggested that *C. connivens* has been introduced to western Europe and the Baltic Sea as an aquatic ballast plant. The known ranges coincide with port areas where, in earlier times, ballast sand was unloaded (Luther 1979). Hence, one possible explanation for low grazing pressure by *I. baltica* and *G. oceanicus* on *C. connivens* is that the native grazers may not be well adapted to feed on the introduced charophyte species. Only in October, when *C. connivens* had low photosynthetic activity and began to degrade, moderate grazing was observed. Often, the success of an introduction event is related to the absence of natural enemies (i.e. grazers or predators) in the recipient region (e.g. Moyle and Light 1996; Williamson and Fitter 1996). Consequently, the establishment of *C. connivens* in the Baltic Sea was probably favoured by an effective vegetative reproduction of the species (Luther 1979) and the absence of grazing during the productive season.

The relationship between photosynthetic activity of the charophytes and grazing may explain the disappearance of the charophyte populations. Under moderately eutrophic conditions, the charophyte populations are unlikely to be controlled by mesoherbivores. The grazers may partly reduce the vegetative production of the charophytes through an effective removal of algal biomass in autumn. However, in severely eutrophic conditions, when covered by filamentous algae, the photosynthetic activity of charophytes decreases and, hence, the algae become more attractive to herbivores. The high numbers of mesograzers in eutrophic areas (Kangas et al. 1982; Kotta et al. 2000) may then eliminate the charophytes. The grazers are likely to affect *C. tomentosa* more than *C. connivens*. We suggest that this difference reflects the non-native nature of *C. connivens*.

Acknowledgements The study was financed by the Estonian Governmental Program No. 0182578s03 and Estonian Science Foundation grant No. 5103. The experiments comply with the current laws of the country in which they were performed.

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