Short communication

Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea

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Abstract

Preference tests were performed over a two-week period in September 2001 in which isopods (*Idotea baltica*) and amphipods (*Gammarus oceanicus*) were offered choices of three common species of algae from the Baltic Sea: *Enteromorpha intestinalis, Cladophora* spp., and *Fucus vesiculosus*. After a 48-hour starvation period, 20 individuals of each grazer species were placed in aquaria containing approximately 1.0 g of each algal species. Fifteen trials for each grazer species were run for 20 hours. We found that *G. oceanicus* ate significantly more *Cladophora* spp. and *E. intestinalis* than *F. vesiculosus* ($p < 0.001$), with a preference order of: *Cladophora* spp.>*E. intestinalis*>*F. vesiculosus*. Similarly, *I. baltica* ate significantly more of both the filamentous green algae than *F. vesiculosus* ($p < 0.001$), with a preference order of: *E. intestinalis*>*Cladophora* spp.>*F. vesiculosus*. Given the preference of isopods and amphipods for filamentous green algae, we might expect these algae to be maintained at low biomass levels. However, this is clearly not the case in the Baltic Sea. Nutrient enrichment (bottom-up effects) is the accepted dominant reason for the non-controlling impact of algal grazers, but other reasons may include cascading trophic effects resulting from the removal of large piscivorous fish (top-down effects).
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1. Introduction

Algal species of the Baltic Sea have been experiencing dramatic changes over the past five decades (Elmgren and Larsson, 2001). For example, bladder wrack (*Fucus vesiculosus*), the formerly dominant algal species in shallow waters, has been decreasing in abundance since the 1940s (Rönnberg et al., 1985; Kautsky et al., 1986), and there are many hypotheses about the cause of the bladder wrack decline. Kautsky et al. (1988) attributed the decline to pulp mill effluents, but also noted that eutrophication can cause reduced light penetration, which gives *F. vesiculosus* a narrower depth range to inhabit (Kautsky et al., 1986). The impacts of ice scraping (Kiirikki and Ruuskanen, 1996), shading, and increased competition with filamentous algae may all have also reduced the spatial extent of *F. vesiculosus* belts. Salemaa (1987) and Kangas et al. (1982) suggest that overgrazing contributed as well. According to Haahtela

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(1984) the combined effects of these and several other factors are likely to have caused declining *Fucus* belts.

Opportunistic, fast-growing green algae such as *Cladophora* spp. and *Enteromorpha intestinalis* have found the changing conditions of the Baltic Sea favourable for excessive growth (Pihl et al., 1999), resulting in accumulation of mats of decomposing algae and ultimately causing anoxic conditions in benthic systems. This has caused concern not only in the scientific community, but also for residents and tourists that utilise the Baltic Sea. There are a number of grazers of filamentous algae in the Baltic Sea (i.e. Idotea baltica, Kotta et al., 2000; Gammarus spp., Denton and Chapman, 1991; Lotze and Worm, 2000; and several species of gastropods, Lotze and Worm, 2000), but these grazers are not able to control this abundant food supply.

Inherent differences in the palatability of different species of algae and the grazers' feeding preferences must play a role in the influence of grazers on the biomass of algae. *F. vesiculosus* is a long-lived, belt-forming brown algae, which is unpalatable to many herbivores due to the presence of phlorotannins (Denton and Chapman, 1991) and tough tissues (Tuomi et al., 1989). Many studies have shown, however, that tough, chemically-defended algae, such as *F. vesiculosus,* are often consumed by some herbivores (Denton and Chapman, 1991; Sommer, 1997; Malm et al., 1999; Jormalainen et al., 2001a). *I. baltica* is one grazer of *F. vesiculosus* that has been shown to have detrimental effects on mature plants (Kangas et al., 1982; Haahtela, 1984). Many grazers have feeding structures that enable them to feed on morphologically defended algal species. Grazers such as amphipods and isopods have mandibles for chewing tough algae (Hickman, 1967). Other algal species, including *Cladophora* spp. and *E. intestinalis,* are more vulnerable to herbivory due to limited investments in chemical or structural defenses (Littler and Littler, 1980). When presented with an alternative, less-defended food source, grazer preference may change.

To better understand grazer preferences, we performed choice tests in the laboratory using the most abundant mesograzers (amphipods and isopods) and three prominent algal species from the Baltic Sea. Previous food preference studies in the Baltic Sea

have only focused on one species of grazer or offered only one genus of algae (Salemaa, 1987; Schaffelke et al., 1995; Sommer, 1997; Kotta et al., 2000). We hypothesised that mesograzers would prefer the more palatable and abundant filamentous green algae rather than the tough, chemically defended algae. Knowledge of preferred food and consumption rates also allowed us to draw inferences regarding the likelihood of grazer regulation of algal growth.

2. Materials and methods

2.1. Experimental animal and food source

Isopods (*Idotea baltica*) and amphipods (*Gammarus oceanicus*) were collected from algae *(Fucus vesiculosus, Cladophora* spp., and *Enteromorpha intestinalis*) at two sites in the northwestern Åland Islands in early September 2001. Algae were collected every two days and placed in aerated seawater from Husö Bay (15–16 °C, 5.38 psu). Measurements were made of the curled lengths of amphipods in the natural position and rostrum to tip of telson of isopods. Amphipods ranged from 0.7 to 1.4 cm (avg. 1.0 ± 0.17 cm, $n = 121$) and isopods from 0.5 to 1.7 cm (avg. 1.1 ± 0.26 cm, $n = 81$). Animals were held in aquaria containing aerated seawater and rocks cleaned of biotic material for a 48-h starvation period before use in experiments. Experimental algae were cleaned of epiphytes and epibionts by hand picking through samples before use in the feeding experiments.

2.2. Feeding experiments

Experiments were conducted in $17 \times 17 \times 12$ cm plastic boxes containing 3 L of non-filtered seawater from Husö Bay. Temperature, O_2, pH, and salinity in each box were checked before and after experimental trials (Table 1). Adjacent windows allowed for natural light conditions.

Cladophora spp. and *E. intestinalis,* which had been previously cleaned, were squeezed twice to remove water and then weighed. This squeeze method was tested for repeatability and showed similar wet weights (± 0.04 g, *Cladophora*, ± 0.10 g, *Enteromorpha*) each time algae was rewetted and squeezed.

After removal of epiphytes, *F. vesiculosus* was carefully dried with a paper towel and weighed. To ensure that the results were internally consistent, the same techniques were used by the same person for all trials. The amount of algae used in each aquarium ranged from 0.7 to 1.9 g w/w. The algae were placed in the tanks at equal distances from each other (in a triangle). A small portion of the algal tuft was placed under clean rocks of equal size, to prevent algae from floating and to imitate natural conditions.

Fifteen trials were run over five days utilising 20 isopods and 20 amphipods within each trial. Experimental densities reflect those recorded by Salemaa (1978) for *I. baltica* in autumn on *Fucus* [(200 ind/1000 cm^3)]. In treatment trials, grazers were allowed to eat for 20 h. Aquaria containing algae and no consumers were used as controls and were run similar to the aforementioned. At the termination of the experiment, the algae were netted and re-weighed as before.

2.3. Statistical analysis

Differences between initial and final wet weight of algae were used to calculate percent algae consumed ($\pm$ S.E.). Any negative weights were considered as non-grazing events and analysed as zero values. Data were square-root transformed and one-way ANOVAs were performed to compare mean percentage grazing rates on the three algal species. A post hoc test (Student–Newman–Keuls) was used to find where significant differences occurred between pairs of algal species. A t-test was performed to check for differences between mean initial and mean final wet weights of controls.

There is some controversy regarding the parametric analysis of preference tests due to lack of indepen-

Table 1
Mean values ($\pm$ S.D.) of physico-chemical conditions during the experiments

		Before trial	After trial
O$_2$ (%)	Treatments	89.2 ± 17.4	65.6 ± 8.2
	Control	86.1 ± 8.1	81.9 ± 10.9
pH	Treatments	7.97 ± 0.14	7.96 ± 0.08
	Control	8.01 ± 0.10	7.97 ± 0.09
Temperature range (°C)		14.1–16.2	
Salinity (psu)		5.38	

Table 2
Comparison of control wet weights (g) with t-test results

	Fucus vesiculosus	*Enteromorpha intestinalis*	*Cladophora* spp.
Mean (± S.D.) Before	1.308 ± 0.289	1.558 ± 0.198	1.201 ± 0.282
Mean (± S.D.) After	1.313 ± 0.294	1.424 ± 0.272	1.143 ± 0.285
	t = − 0.0499, p = 0.961	t = 1.527; p = 0.133	t = 0.558; p = 0.582

dence of food types offered within the same experimental arena. This lack of independence is attributed to autogenic change during the experiments (i.e. growth, mortality, reproduction) (Peterson and Renaud, 1989). Our experiments had little autogenic change due to 20-h feeding trial and insignificant differences of control algae before and after the experiments (Table 2), thus leaving our experiment exempt of significant bias.

3. Results

Gammarus oceanicus ate significantly ($p < 0.001$) more of the two species of filamentous algae (*Enterromorpha intestinalis* and *Cladophora* spp.) than the tougher, *Fucus vesiculosus* (Fig. 1). The grazing preference order for *G. oceanicus* based on percentage eaten was: *Cladophora* spp. (50.4 ± 4.4%)>*E. intestinalis* (30.4 ± 3.7%)>*F. vesiculosus* (0.6 ± 0.3%). *Idotea baltica* also showed a significant ($p < 0.001$) preference for filamentous algae over *F. vesiculosus* (Fig. 1). The grazing preference order for *I. baltica* based on percentage eaten was: *E. intestinalis* (37.6 ± 3.8%)>*Cladophora* spp. (21.5 ± 3.0%)>*F. vesiculosus* (4.9 ± 0.5%).

The controls showed no significant differences between mean initial and mean final wet weights (Table 2). Survival rates were high for all animals. All isopods survived the trials and only one amphipod was found dead among the 300 (15 trials × 20 animals in each trial) animals used.

The mean grazing rates for *G. oceanicus* were 19.4 mg ind^{-1} d^{-1} on *E. intestinalis,* 25.4 mg ind^{-1} d^{-1} on *Cladophora* spp., and 0.7 mg ind^{-1} d^{-1} on *F. vesiculosus*. The grazing rates for *I. baltica* were 22.6
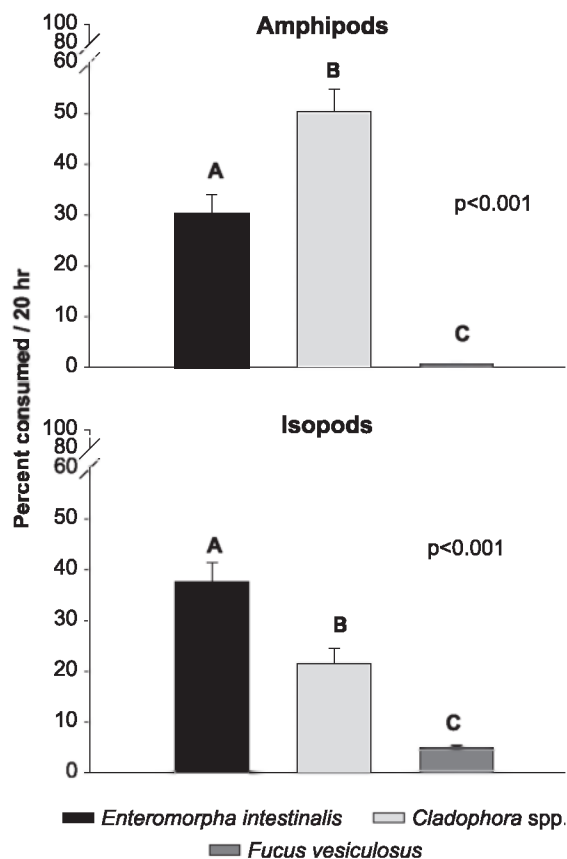
Fig. 1. The mean percentage of each algal species grazed ($\pm$ S.E.). Different capital letters denote significant differences at $p < 0.001$.

mg ind^{-1} d^{-1} on *E. intestinalis*, 11.3 mg ind^{-1} d^{-1} on *Cladophora* spp., and 4.8 mg ind^{-1} d^{-1} on *F. vesiculosus*. The grazing rates measured, however, should be interpreted within the context of our experimental conditions, which included starving animals for 48 h before use in experimental trials.

4. Discussion

4.1. Amphipod and isopod preference

Preference for the filamentous algae *Cladophora* spp. and *Enteromorpha intestinalis* is clear for both *Gammarus oceanicus* and *Idotea baltica*. *Fucus vesiculosus*, however, showed little tissue loss to grazing, although Salemaa (1987) and Engkvist et al. (2000) have suggested that large populations of *I.*

baltica could become deleterious to *F. vesiculosus*. One explanation for the lack of grazing on *F. vesiculosus* is the presence of alternative food sources in the form of filamentous algae. Salemaa (1978) has shown that juvenile *I. baltica* are important grazers of *Cladophora*, but will move off the decaying *Cladophora* in August and settle in *Fucus* belts for the winter. The lack of predators in experiments may have allowed isopods and amphipods to include different foods in their diet, thus changing their feeding behaviours.

Salemaa (1978) found that colour morphs of *I. baltica* are important in *Fucus* belts for avoidance of predators. On the other hand, Boström and Mattila (1999) showed that *I. baltica* would choose food over shelter in experiments with seagrass. Jormalainen et al. (2001a) performed preference tests in which *I. baltica* was shown to prefer *F. vesiculosus* over five other algae including *E. intestinalis*. However, *I. baltica* showed reduced growth rates on *F. vesiculosus* and Jormalainen et al. (2001a) concluded that predator avoidance was more important than the chemical composition and food value of the algae.

Vegetative parts of *Fucus vesiculosus*, which were offered in our trials, have been shown to be chemically defended (Tuomi et al., 1989). Though data are inconsistent, chemical defences have been shown to play a part in deterrence of some herbivores (Hay and Fenical, 1988; Schnitzler et al., 2001) and thus could have been the reason for the low rates of herbivory in this experiment. But, according to Jormalainen et al. (2001a), the more phlorotannins seaweeds contained, the more preferred they were by *I. baltica*. We did observe some bite marks on *F. vesiculosus* after *I. baltica* trials, but the amounts of tissue lost were insignificant.

4.2. Factors affecting rates of herbivory

The bottom-up effect of nutrient loading is well known to stimulate algal growth and is thought to be the cause of the excessive filamentous algae in the Baltic Sea (Bonsdorff et al., 1997; Elmgren and Larsson, 2001). Grazers have been shown to play an important part in consuming algal overgrowth. Hillebrand et al. (2000) have shown that herbivores and nutrients can have a balancing effect on marine benthic algal community structure, and that herbivore presence can even dampen effects of nutrient enrichment. Worm

and Sommer (2000) suggest that mesoherbivores can play an important role in buffering moderate eutrophication effects, but extreme eutrophication cannot be controlled because grazers cannot keep up with the growth of algae (Worm et al., 1999). Geertz-Hanzen et al. (1993) found that grazing pressure in a Danish estuary matched the growth rates of the macroalgae *Ulva lactuca* in the summer and exceeded it in the fall. On the other hand, Kamermans et al. (2002) showed that herbivores such as amphipods and isopods stimulated growth of *Ulva* spp. in an estuary in the Netherlands through the consumption of epiphytes causing an opposite and non-controlling effect on algal overgrowth. Porter (1976) has also shown that nutrients regenerated by grazers can stimulate algal blooms.

A second factor affecting the rates of herbivory in the Baltic Sea could involve top-down effects which control small grazer densities. Both eutrophication and over-harvesting of piscivorous fish (Lehtonen, 1985) such as large perch (*Perca fluviatilis*), pike-perch (*Stizostedion lucioperca*), and pike (*Esox lucius*), can lead to a reduction in predation pressure on smaller fish species such as stickleback (*Gasterosteus aculeatus* and *Pungitius pungitius*), black goby (*Gobius niger*), and small perch (*Perca fluviatilis*), all of which prey on isopods and amphipods (Salemaa, 1978). Fish catches from 1963–1982 show an increase in large pike-perch catch (Lehtonen, 1985), and Rajasilta et al. (1999) also found that over the past 20 years shores that were once rich in fish fauna were now without abundant fish species such as sticklebacks and minnows. Jormalainen et al. (2001b) suggest that population densities of *I. baltica* may be strongly regulated by predation and Geertz-Hanzen et al. (1993) found that reduced grazer pressure was responsible for the mass accumulation of macroagla (*Ulva lactuca* L.) in a eutrophic Danish estuary.

With the evidence addressed above, future research on the greening of the Baltic Sea should address the evidence that there is simultaneous top-down and bottom-up control of algal biomass (Hillebrand and Kahlert, 2001).

5. Conclusions

A significant preference for fast-growing, opportunistic green algae (*Cladophora* spp. and *Enteromorpha intestinalis*) over the brown alga *Fucus vesiculosus* was found for both amphipods (*Gammarus oceanicus*) and isopods (*Idotea baltica*). Top-down effects and bottom-up effects may both play a part in explaining the overgrowth of the preferred filamentous green algae affecting the Baltic Sea.

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