Research Article

GRAZING EFFECTS OF ALIEN AMPHIPODS ON MACROALGAE IN THE LITTORAL ZONE OF THE NEVA ESTUARY (EASTERN GULF OF FINLAND, BALTIC SEA)

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Abstract

It is hypothesized that the alien amphipods *Gmelinoides fasciatus* and *Pontogammarus robustoides*, which have recently invaded the eastern Gulf of Finland, are able to control macroalgae biomass. In order to test this, studies were conducted on the seasonal dynamics of amphipod populations and filamentous algae, *Cladophora glomerata*, in the Neva Estuary in 2003. The absolute abundance of the gammarids ranged from 200 to 4800 ind.m^{-2} with the maximum in June and July. The biomass of *Cladophora* increased from June to August, reaching 1.7-2.0 kgm^{-2} wet weight. Gut content analysis revealed that both gammarid species are omnivorous; however, *P. robustoides* grazed more successfully on *C. glomerata* than did *G. fasciatus.* The proportion of the algae in the *P. robustoides* diet depended on consumer body length prevailing in the diets of middle-sized (7.5–12.0 mm) specimens. The evaluation of the condition of *P. robustoides* fed different diets indicated that with the *Cladophora* diet, the clutch size was the largest but the growth rate was the lowest. The growth rate was the highest on the

mixed diet (algae and animals at a weight ratio of 1:1), which indicated that this diet was the optimal feeding strategy for consumer fitness. The data obtained clearly indicated that the grazing amphipods, *P. robustoides*, can have a dramatic impact on *C. glomerata* in the littoral zone of the eastern Gulf of Finland and perhaps control the macroalgal biomass when populations are dense.

INTRODUCTION

Disturbed ecosystems are invaded more often by new species than well-balanced, undisturbed ones (Lozon and MacIsaac 1997). Low diversity of native species, poor food webs, high nutrient levels, and changes in water salinity in disturbed habitats contribute to the invasion success of eurybiotic organisms. Recent examples are two species of gammaridean amphipods, *Gmelinoides fasciatus* (Stebbing) and *Pontogammarus robustoides* (Sars), which have established abundant, reproductive populations in the littoral zone of the inner Neva Estuary (Berezina and Panov 2003). This is one of the most eutrophic estuaries of the Baltic Sea. Primary production in this ecosystem has increased significantly over recent decades as a result of ineffective local water management in the St. Petersburg area and increased nutrient loading (Golubkov *et al.* 2003a). These changes have led to intensifying eutrophication and the stimulation of filamentous algae (mainly *Cladophora glomerata*) blooms in the coastal zone (Golubkov *et al.* 2003b). This green alga (*C. glomerata*), which develops on hard substrates, provides shelter and is an important source of food for invading gammarids (*G. fasciatus* and *P. robustoides*) and contributes to the growth of their populations. These amphipods inhabit *C. glomerata* mats in quantities that reach 4000 ind. m^{-2} locally (Berezina and Panov 2003).

Nutrients (so-called "bottom–up control") and invertebrate grazing ("top-down control") can regulate macroalgal development. Some studies indicate that top-down control plays a significant role in the control of macroalgal biomass under eutrophic conditions (Menge *et al.* 1997). Many amphipods are the most effective grazers among invertebrates due to their higher resistance to algal chemical defense mechanisms (Cronin and Hay 1996), as well as their ability to feed alternatively (Duffy and Hay 2000, Cruz-Rivera and Hay 2001). The current authors suggest that alien amphipods recently established in the littoral zone of Neva Estuary will be able to decrease *Cladophora* biomass and control algal growth. In order to verify this hypothesis, *C. glomerata* biomass and production and the density and biomass of *G. fasciatus* and *P. robustoides* were monitored. The changing diets of amphipods in one location of the Neva Estuary with high filamentous algae biomass were analyzed. The importance of different diets on consumer condition, survival, growth rate, and the clutch size

of *P. robustoides* were assessed experimentally using animals kept on algal, animal, and mixed diets.

MATERIALS AND METHODS

Description of the study site

The research was conducted at a monitoring site in the Resort District of St. Petersburg (northern Neva Estuary at 60°11´N, 29°44´E). The study site was located 25 m from the shore line. The water level throughout the observation time ranged from 0.2 to 0.6 m. The conductivity of the water fluctuated within a range of 430–1320 µS cm^{-2}. Mineral phosphorus concentrations ranged from 30 to 140 mg m^{-3}. This location is characterized as a "eutrophic zone" with oligohaline nutrient-rich water.
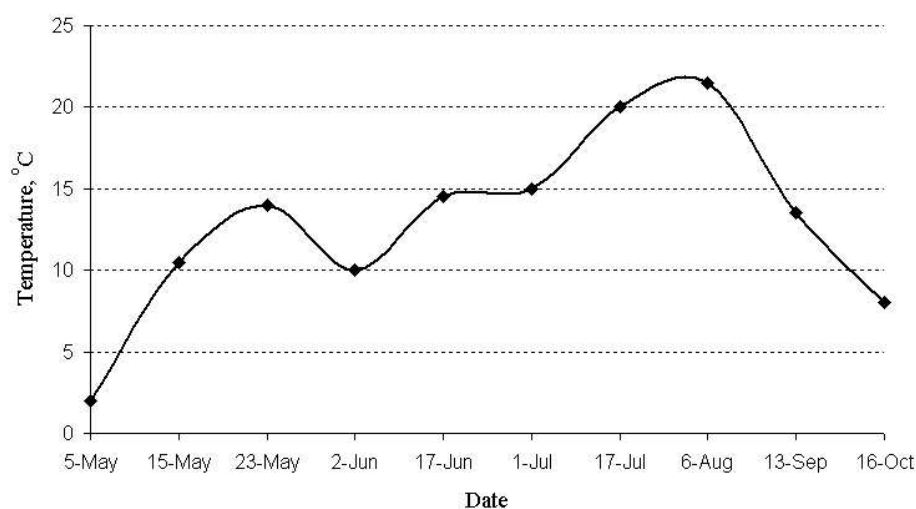

Fig. 1. Dynamics of water temperature at the study site in 2003.

The summer temperatures of the water were relatively low in 2003 and did not exceed 15–17 °C in June and July (Fig. 1). The substrate here consisted of gravel, stones, coarse sand, and detritus. From May to September, epiphytic and phytobenthic algae, including filamentous green alga, *Cladophora glomerata*, and red alga, *Ceramium rubrum*, grew on the hard substrates. In the July–August period, a belt of *Potamogeton spp.* developed in the location. Throughout most of the summer, the daily oxygen saturation was 80–90%. However, during the filamentous algae decomposition period, the oxygen content in the shallow water and sediments dropped to 0.5–1 mg l^{-1}.

During the observation period, the main part of the benthic community at this study site was comprised of herbivorous chironomids, amphipods, and mayflies that grazed on macroalgae. Chironomids and alien gammarids (*G. fasciatus* and *P. robustoides*) were the dominant taxa, averaging 45.5% and 37.5% of the benthic biomass, respectively. The benthos also included native species of leeches (6%), oligochaetes (3%), snails (2.5%), mayflies (2%), caddis flies (1%), and two alien species of mollusks, *Dreissena polymorpha*, and *Potamopyrgus antipodarum* (0.5%). The role of native flatworms, mysids, isopods, bivalves, and biting midges was insignificant (2%).

Study species

Gmelinoides fasciatus (Stebbing) is a gammaridean amphipod that originates from Siberia, where it is noted in the basins of the Angara, Lena, Yenisey, Irtysh, Pyasina, Tunguska, Selenga, and Barguzin rivers. *G. fasciatus* was considered to be one of the most suitable species for intentional introductions aimed at enhancing fish production in lakes and water reservoirs of the former USSR, mainly because of its high environmental plasticity and the generally high abundances within its native range (Panov and Berezina 2002). During the 1960s and 1970s, hundreds of millions of *Gmelinoides* specimens were introduced into 22 lakes and reservoirs outside its native range in Siberia and European Russia (Zadoenko *et al*. 1985). At present, *G. fasciatus* is widely distributed in the inland waters of the European part of Russia. Densities of *G. fasciatus* reach 17 500 ind. m^{-2} in some locations of Neva Bay and 4 000 ind. m^{-2} in *Cladophora* beds of the inner part of the Neva Estuary (Berezina and Panov 2003). This species is a middle-sized amphipod, with males and females attaining from 9 to 12 mm total length, respectively. Clutch sizes vary from 3 to 45 eggs depending on the body length of females.

Pontogammarus robustoides (Sars) is one of the most recent species of Ponto-Caspian origin to be discovered in the Gulf of Finland. The original distribution area of *P. robustoides* encompassed the offshore areas of the Caspian and Black seas and the lower reaches of rivers (Dediu 1980, Jazdzewski 1980, Jazdzewski and Konopacka 2000). In the 1950-1960 period, it was intentionally transferred from the Dnepr to the Kaunas reservoirs (Gasiunas 1972), where it established a successful population. During 1965–1969, crustaceans from Kaunas Reservoir were used for intentional introductions into other inland waters, including the lakes of the Leningrad Region (Gasiunas 1972, Lazauskene *et al*. 1995). It is likely that these introductions were the source of the *Pontogammarus* population that further expanded to the Neva Estuary. The introduction of *P. robustoides* to the Neva Estuary could also have been through the discharge of ballast water originating

from the southern Baltic Sea (Berezina and Panov 2003). *P. robustoides* was first noted in the Neva Bay in 1999. To date, it has established populations in the stony habitats and the *Phragmites* beds of the southern Neva Bay and the northern inner Neva Estuary, where it coexists with *G. fasciatus*. In Neva Bay, it reaches 2700 ind. m^{-2} (Berezina *et al.* in press), and the body lengths of overwintering *P. robustoides* specimens range from 16 to 18 mm (males are larger than females). Clutch sizes vary from 30 to 106 eggs per female in the body length range of 9–16 mm.

Sampling methods and laboratory procedures

Samples were taken every two weeks from May to August and monthly in September and October, 2003. Three replicates of quantitative sampling were conducted at depths of 0.5 m with a 0.03 m^2 cylindrical metal frame 0.7 m high. The cylinder was shoved into the bottom or dragged over the plants when there was macrophyte or macroalgal development. All of the hard substrates and plants in the cylinder were then transferred to a plastic container with fresh water. The water and upper bottom layer were filtered through a hand-held net (mesh size 0.25 mm) several times (for approximately 5 minutes), and then the contents were also transferred to the container. The periphyton was scraped off with a knife and washed off of the hard substrates. Then all of the sample components (content of the container) were placed in a sieve (0.25 mm) and rinsed with water. This was preserved in 4% formaldehyde and transported to the laboratory in plastic bags.

In the laboratory, all of the macrozoobenthic invertebrates (body sizes > 2-3 mm) and aquatic plants were picked out by hand and rinsed with tap water. The length of the amphipods was measured as the distance from the base of the first antenna to the base of the telson with a MBS-10 stereoscopic microscope equipped with an ocular micrometer. The animals were counted and weighed on an electro-balance to the nearest 0.01 mg. Prior to weighing; the animals were blotted with filter paper to remove water.

In order to evaluate the filamentous algae biomass at the site, hard substrates (pebbles and stones) with attached algae were collected in three to five replicates. After sampling, the algae were detached from the substrate and their dry weight was determined. Algae biomass (B) was calculated taking into account the surface areas of the substrates and projective bottom cover (90%). Primary production (P) was estimated using biomass and the P/B- coefficient in accordance with the standard technique (Golubkov *et al*. 2003b).

During sampling, the temperature, dissolved oxygen, total phosphorus, and conductivity of the water were measured. Measurements of temperature and oxygen content were conducted with a Mark-201 oxygen meter. Conductivity

(osmol μ l^{-1}) was measured with a Dist WP4 conductivity meter. To determine the total phosphorus concentrations, the water samples (100 ml) were hydrolyzed with H_2SO_4 according to standard techniques (Golterman 1969).

Gut content analysis

P. robustoides and *G. facsiatus* individuals were collected at the study site during different periods (May – June; July – August; September – October) and were used for gut content analysis. In total, 184 individuals were examined. The gut was excised from the body cavity using microneedles and microscissors under a microscope (×4). It was then transferred to a clean preparation glass. Gut fullness was evaluated visually. The contents of the gut were spread evenly in a drop of glycerin. Analyses of gut content were conducted with standard techniques. The proportion (%) of the separate food components was estimated as the value equal to the area that the component occupied on the analyzed fields of the slide glass.

Experimental methods

The value of different food was evaluated as survival, growth rate, and fecundity (clutch sizes) of amphipods (*P. robustoides*) in laboratory experiments. Precopula pairs of *P. robustoides* with equal-sized females were collected from the study site and placed in 5-L aquaria containing filtered estuarine water. After copulation, the males were removed from the females. Ovigerous females were kept in identical conditions (18ºC, continuous aeration, dark:light = 8:16, algal-animal diet, mineralization of used water of 350-400 mg l^{-1}, with water exchange each three days) during the period of egg development. After the juveniles were released, the females were removed from the aquaria. From this moment the newborn specimens in each experimental aquarium were kept on three strict diet types (algal, animal, and mixed diets). The algal diet (treatment 1) included live filaments of *C. glomerata*; the animal diet (treatment 2) included crustaceans (*Daphnia sp.*), oligochaetes (*Enchytraeidae*), and larvae of chironomids. The mixed diet (treatment 3) was composed of the components of algal and animal diets mentioned above in a 1:1 weight proportion. The survival, body length, and weight of animals were measured at 10-day intervals for 80 days. The clutch sizes of ovigerous females were determined at the end of the experiment.

Consumption rates in Pontogammarus robustoides

Specimens of *P. robustoides* were collected from Neva Bay. Animals in the size range of 6−16 mm were used in the feeding experiments. Live filamentous algae, *C. glomerata*, were used as food. The temperature and day

length corresponded to summer conditions in the littoral of Neva Bay (20±0.8°C, 8h:16h D:L). The tested animals were not fed for 12 h before the experiments in order to keep their guts empty. The fecal pellets the amphipods produced during the experiment were collected. Animals and pellets were weighed with an electro-balance to the nearest 0.01 milligram.

The consumption rate (C, mg) of the animals was calculated using the amounts of fecal pellets produced (F, mg) during exposure time (24 h), and the assimilation rate (A). The assimilation index is 0.6, as suggested by Suschenia (1975) for amphipods consuming plant food. To calculate C, the following formula was used: $A = 0.6{\cdot}C = C{-}F$, where $C = F/0.4$. Relative consumption rate (C_r) is presented as the ratio of C and the weight of the animals: $C_r = C/W$.

Statistics

The measured parameters were expressed as mean ±SE (standard error). Possible differences in the survival, body length, weight, and clutch size of gammarids among the different treatments were analyzed with two-way ANOVA. Pearson's correlation coefficient served to test the relationship between the feeding rates and body weights of the animals.
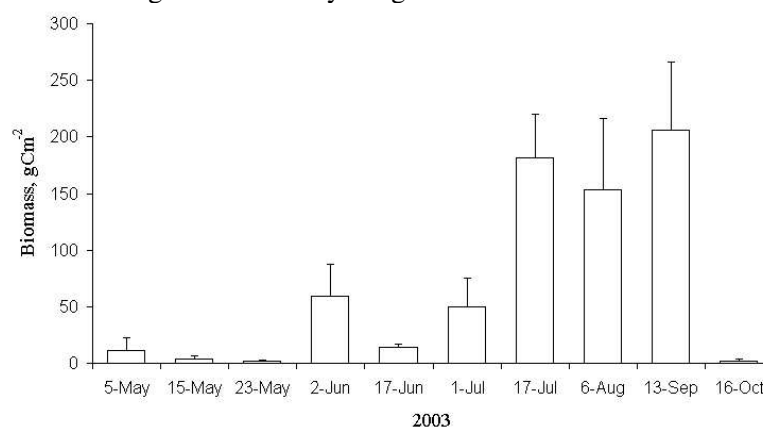

Fig. 2. Seasonal dynamics of *Cladophora glomerata* biomass at the study sites.

RESULTS

Dynamics and production of *Cladophora glomerata* ***biomass at the study site***

The development of *C. glomerata* at the study site was different during the period of observation. The average biomass of the algae was 136±50 g of dry weight per m^2 or 68±25 g C m^{-2}. The maximum biomasses (181.5–206.0 g C m^{-2}) were observed from July to September (Fig. 2). These values

correspond to 0.36–0.42 kg of algae dry weight per 1 m^2 of bottom. The average primary production of *C. glomerata* was estimated as 7 g C m^{-2} per day (24 h), reaching the maximum value (21 g C m^{-2} d^{-1}) in the middle of September.
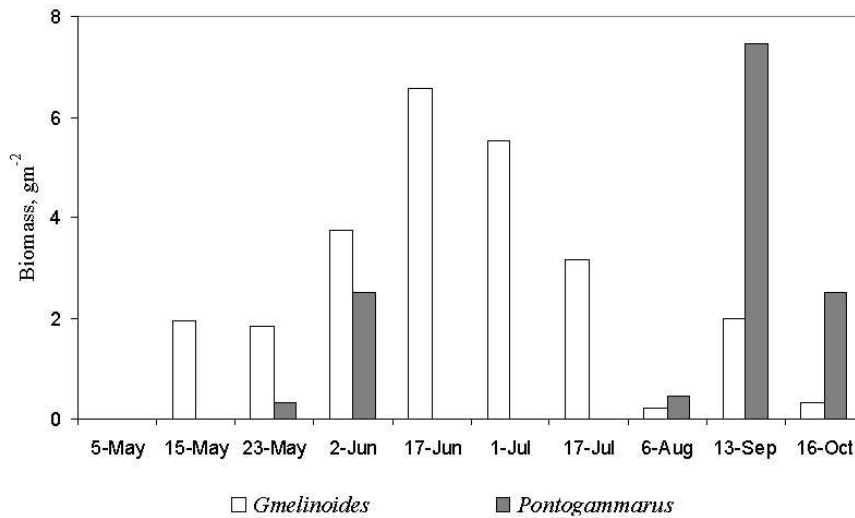

Fig. 3. Population dynamics of alien amphipods in the stone littoral with *Cladophora glomerata*.

Population dynamics of alien gammarids at the study site

Coexisting populations of *G. fasciatus* and *P. robustoides* were observed at the study site of the Neva Estuary. At the beginning of the ice-free period (mid May) the gammarids migrated from the deep-water to the shallow-water zones. In late September and October, when the water temperature was less than 5°C, densities of these amphipods in the littoral zone declined due to their migrations to deep-water habitats. The density of amphipods as well as chironomids and other insects was also low during the intensive decomposition of filamentous algae (August).

At the site *G. fasciatus* comprised 86.6% of the total gammarid density and 66% of the biomass (Fig. 3). The average density and biomass of *G. fasciatus* exceeded 1240±552 ind. m^{-2} and 2.53±0.71 g m^{-2}, respectively. The maximum density (3500–5150 ind. m^{-2}) and biomass (up to 6.56 g m^{-2}) were noted in June–July as a result of intensive reproduction.

The average density (131±74 ind. m^{-2}) and biomass (1.32±0.75 g m^{-2}) of *P. robustoides* were low during summer. The biomass of this species increased

significantly (up to 8 g m^{-2}) only during September 2003, the period of intensive juvenile release.

Table 1

Food items and their frequency of occurrences (%) in the diet of *Gmelinoides fasciatus*. Size groups: I – 3.0–6.9 mm; II – 7.0–12.0 mm.

| Food items	May-June		July-August		September-October	
Size groups	I	II	I	II	I	II
Detritus	100	100	100	100	100	100
Blue-green algae		15		45		20
Unicellular green algae	65	60	75	70	50	60
Colonial green algae		10	30	15		20
Filamentous green algae		20		100		
Macrophytes			10	10	20	40
Crustacea		10			10	10
Infusoria	15	40	10	45		10
Oligochaeta	5	20				20
Chironomidae	1	40		30		
Rotatoria				15		5
Nematoda				15		
Sediments	80	100	60	80	65	80
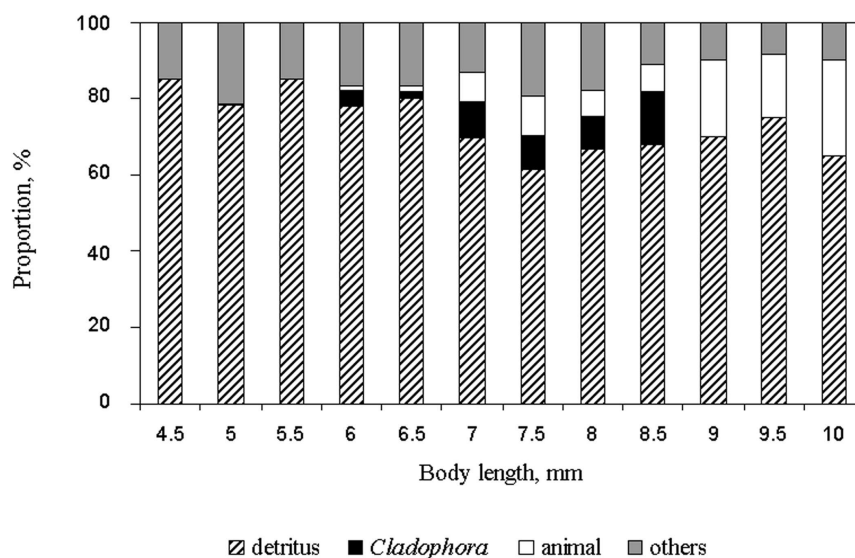
Fig. 4. Role of different food items in the diet of *Gmelinoides fasciatus* according to body lengths.

Gut contents of alien gammarids from the study site

Microscopic analysis of gut content indicated that the main items in the diet of *G. fasciatus* were plant-derived food and detritus (frequency of occurrences were 100% of the tested specimens, Table 1). Filamentous algae (*C. glomerata*) were noted only in the gut of *G. fasciatus* specimens with body lengths of 7–12 mm. It is important that the proportion of *Cladophora*-fed specimens increased from 20% in June to 100% in July. Among other components unicellular green algae were noted frequently (50–75%) as well as infusorians (up to 45%) and chironomids (up to 40%). The most abundant component in *G. fasciatus* guts was detritus (Fig. 4). Filamentous algae presented in small amounts only in the guts of specimens with body lengths of 7.5–9.0 mm ranging from 1 to 10% of the total food mass. Animal-derived food was also not high in the *G. fasciatus* diet (not more than 18%).

Table 2

Food items and their frequency of occurrences (%) in the diet of *Pontogammarus robustoides.* Size groups: I – 3.0–6.9 mm; II – 7.0–12.9 mm; III – 13.0–17.0 mm.

Food items	May – June		July – August		September – October		
Size groups	II	III	I	II	I	II	III
Detritus	100	100	100	100	100	100	100
Blue-green algae		50	20	80	25	25	
Unicellular green algae			100	60	100	65	75
Colonial green algae				20	25	30	70
Filamentous green algae	100	80	25	100	50	100	70
Macrophytes			30	20	50	30	70
Crustacea				40		10	15
Infusoria	50	30	60	40	20	60	75
Oligochaeta		100	60	60	50	50	50
Chironomidae	50	80	30	40	25	60	70
Insecta (Ephemeroptera, Coleoptera, Trichoptera)				40	20	15	20
Rotatoria				10			
Nematoda				20			
Sediments	100	100	80	60	70	65	50

The food spectrum of *P. robustoides* was richer than that of *G. fasciatus* (Table 2). Among the different items, detritus and filamentous and unicellular green algae presented in the diet of most of the tested specimens. Variability in food composition between different months was not revealed. However, significant differences were noted between the diets of crustaceans of different sizes. For example, algae *C. glomerata* presented in diets of 100% of the tested specimens with body lengths of 7.0–12.9 mm. The frequencies were significantly lower for larger and smaller specimens (70–80 and 25–50%, respectively). In contrast, animal food (oligochaetes, chironomids) was included

in the diets of larger specimens more often than in the case of smaller specimens.
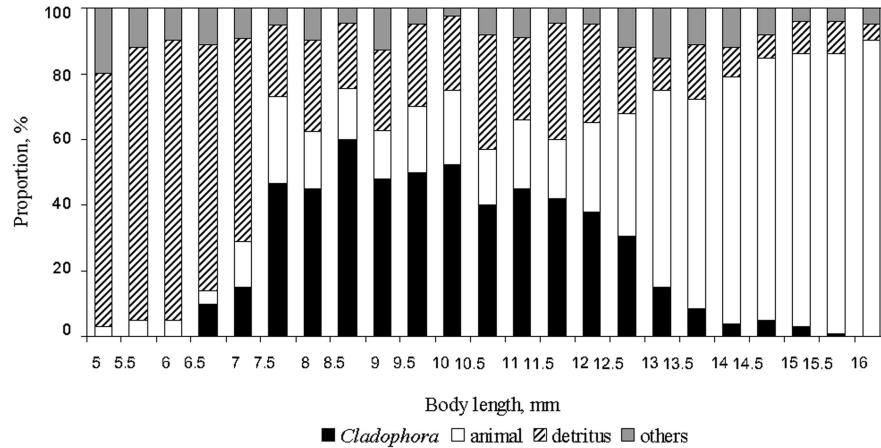

Fig. 5. Role of different food items in the diet of *Pontogammarus robustoides* according to body lengths.

The proportions of different food items in the diets of *P. robustoides* were varied and related to consumer body size (Fig. 5). Juveniles (5–7 mm) fed on detritus as their main food, while the proportion of *C. glomerata* was low (0–15%) in the diets. In the diet of adult specimens (8.0–12.5 mm), the role of filamentous algae increased significantly reaching 60% of the total food mass. Specimens with body lengths of 13–16 mm consumed less (1–10%) as a result of an increase in animal food in their diets. The largest specimens (15–16 mm) were characterized mainly as predators.

The results of gut content analyses of *G. fasciatus* and *P. robustoides* indicate significant differences between the species regarding the proportions of filamentous algae in the diets (Fig. 4, 5). Proportions of *C. glomerata* in the *P. robustoides* diet were from two- to three-fold higher than in the *G. fasciatus* diet. Additionally, the size scope of *G. fasciatus* specimens that fed on *Cladophora* was significantly narrower than in the case of *P. robustoides*. Thus, *P. robustoides* grazed more effectively on filamentous algae than did *G. fasciatus*.

Consumption rates of Pontogammarus robustoides
The diurnal food consumption of *P. robustoides* foraging on filamentous algae varied from 1.1 to 3.8 mg of *DW* or 0.6-2 mg C. Relative consumption

rates decreased from 0.2 to 0.7 (or from 20 to 70%) depending on the body weight of the amphipods. The relationship between consumption rates (C_R) and wet weight (*WW*, mg) of the consumer body was approximated by the exponential function $C_R = 1.38\ WW^{-0.43}$ (*R*= −0.81, *P* − 0.001, Fig. 6). As demonstrated above, *C. glomerata* prevailed in the diet of specimens with body lengths (or weights) in the range of 8.0–12.5 mm (7.8–31.5 mg). Consumption rates of this size group were 30-50% of body weight per day according to the regression obtained.
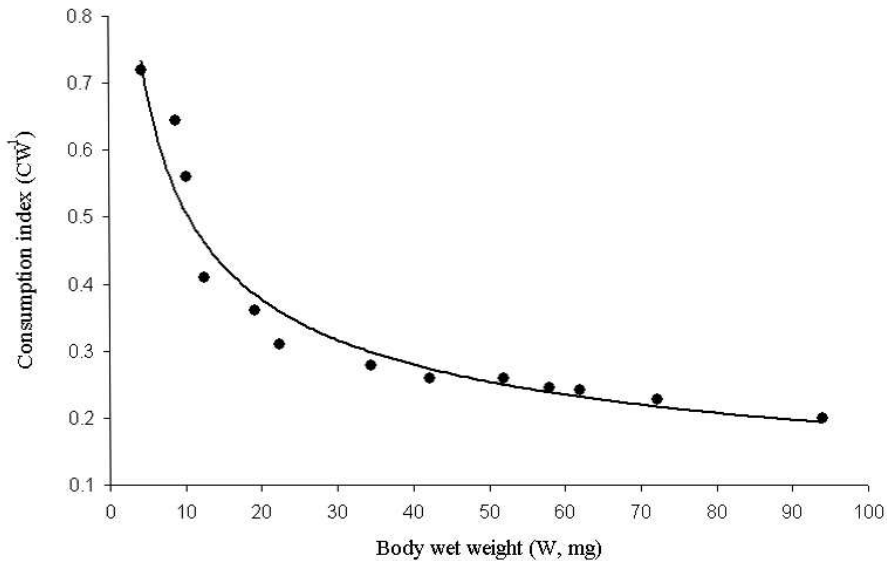

Fig. 6. Consumption rates of *Pontogammarus robustoides* according to body weight during feeding on filamentous algae.

Table 3

Average (X±SE) length, weight, and clutch size of female *Pontogammarus robustoides* from different experimental treatments.

Treatment	Length, mm	Weight, mg	Clutch size, eggs/ female
1	13.02±0.47	33.62±2.74	34.25±4.65
2	13.07±0.61	34.38±3.31	23.14±1.62
3	13.86±0.48	41.41±3.89	30.25±1.71

Survival, growth rates, and clutch sizes of *Pontogammarus robustoides* ***on different diet types***

The survival of animals was 85% on the algal and mixed diets and slightly lower (66%) on the animal diet.

Asymptotic wet weight was attained by *P. robustoides* in all studied conditions, and the weight/age data fit well into a sigmoid or "S-shaped" curve (Fig. 7). Significant differences in the growth rates of the amphipods between treatment 1 and treatments 2 and 3 were noted according to ANOVA (*MS* = 421.21, *F* = 13.24, *P* - 0.0004). The growth rate of *P. robustoides* was highest on the mixed diet (treatment 3). The growth rate of animals fed on *Cladophora glomerata* filaments (treatment 1) were significantly lower (1.1% of body wet weight or 0.5 mgd^{-1}) than in treatments 2 and 3. The growth rate of *P. robustoides* in treatment 2 (1.5% of wet weight per day or 0.69 m g d^{-1}) were slightly higher than in treatment 3 (1.6% or 0.83 m g d^{-1}).
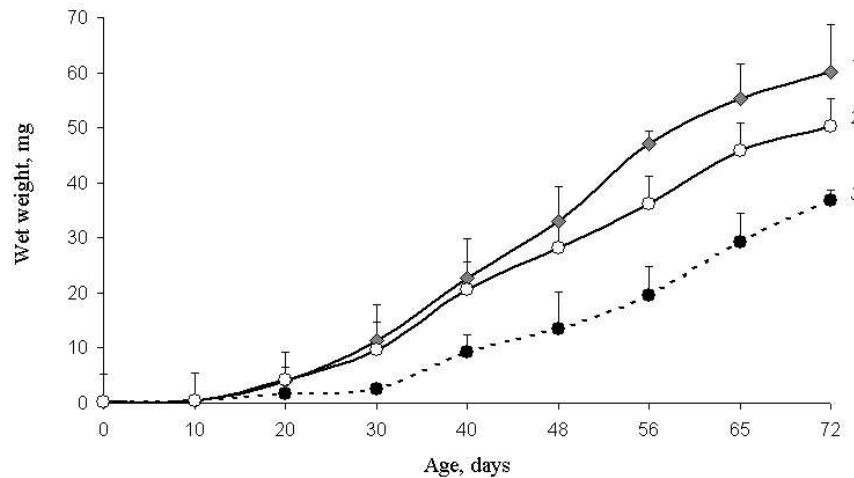

Fig. 7. Growth rates of *Pontogammarus robustoides* on different diets. *1* - mixed diet (treatment 3), *2* - animal diet (treatment 2), *3* - algal diet (treatment 1).

Specimens of *P. robustoides* reached sexual maturity at an age of 60-70 days, when they attained body lengths of 11.5-15 mm. Table 3 outlines the results for the average sizes (body length and weight) of ovigerous females and the number of eggs in clutches. The length and weight of the females varied significantly between treatments 1 and 3 (*F*=30.7, *P* <0.001; *F*=6.25, *P* – 0.04) while their clutch sizes did not differ significantly. In treatment 1, ovigerous females were smaller than in treatment 3, in which there was the lowest growth rate (Fig. 7). Lengths (*F*=26.4, *P* – 0.001) and clutch sizes (*F*=17.9, *P* – 0.004) varied significantly between treatment 2 and treatment 3. While average lengths and weights of ovigerous females were not significantly different in treatments 1

and 2, their clutch sizes were significantly different (F=6.86, P – 0.034). The maximum numbers of eggs in the clutches were noted in females that were fed only *C. glomerata*, while the minimum clutch sizes were noted for the group fed animal food.

DISCUSSION

It was concluded from the results of gut content analysis that *G. fasciatus* and *P. robustoides* use a mixed feeding strategy as grazers, collector-gatherers, and predators. In the conditions of the Gulf of Finland littoral zone, they are typically omnivorous animals. The comparison of the feeding strategies of these species in the Neva Estuary with those in ancestral areas reveals similar traits. Filamentous algae (*Cladophora sp.*) were present in the diets of *P. robustoides* in the northern Caspian Sea (Briskina 1952), the Don River (Ioffe and Maximova 1968), the Dnepr basin (Kititsina 1977), and the lakes of Lithuania (Gasiunas 1972). The diet of *P. robustoides* specimens collected in *Phragmites* beds with a high biomass of attached *Cladophora* filaments (Don River) includes algae as the main food item and chironomids, oligochaetes, and copepods (Ioffe and Maximova 1968). In habitats without *Cladophora*, the amphipods fed mainly on macrophytes and detritus. The gut content analysis of *P. robustoides* juveniles (2-6 mm) also revealed differences in the diets that correspond with the results obtained in the current study. Newborn specimens fed mainly on epiphytes that had developed on macroalgae. After reaching a body length of 6 mm, they began to graze on *Cladophora* tissue.

The grazing activity of crustaceans depends on many factors including species characteristics. *G. fasciatus* prefers detritus as its main food item and avoids *Cladophora*, while *P. robustoides* actively grazes on this alga. The amphipod *Gammarus locusta* grazed on epiphytes but not algae tissue, while the isopod *Idotea chelipes* foraged on *Ulva sp.* (Kamermans *et al.* 2000). Moore (1977) reported that *Cladophora* was never eaten by *Gammarus lacustris* and *Monoporeia affinis* and is perhaps a reflection of the relative strength of its cell wall.

The growth rates obtained for *P. robustoides* (1.1% of mass per day at 20ºC) indicates that filamentous algae provided sufficient nutritional value for animal fitness, although growth rates in this species were the lowest on the *Cladophora* diet in comparison with the other diets. Similarly, the lowest growth rates (0.93-2.25% day^{-1} at 16ºC) of the amphipods *Gammarus fossarum* and *G. roeseli* were noted when *Cladophora* sp. was offered as food (Pöckl 1995). For comparison, *Gammarus pulex* growth rates were high (4.6% day^{-1} at 15ºC) when they grazed on algae *Nitella* sp. as well as on decaying elm leaves (Willoughby 1983).

Clutch sizes in amphipods are regulated by the interrelated effects of body length, metabolism, food availability, oxygen content, and temperature. Increased *P. robustoides* clutch sizes in the presence of *Cladophora* can be attributed to the more favorable conditions that exist with these algae. *Gammarus duebeni* females also produce many small eggs when the biomass of aquatic plants is high (during summer), while those in habitats without plants produce relatively few large eggs (Sheader 1983). Similar traits were noted in the amphipod *Gammarus minus* in springs with aquatic plants (Glazier 1999).

The density of *P. robustoides* was low at the study site. However, in other locations of the southern part of the Neva Estuary the species established denser populations. In 2002, the maximum *P. robustoides* density and biomass were 2000 ind. m^{-2} and 48 g m^{-2}, respectively (Berezina *et al.*, in press). The biomass of specimens larger than 6 mm was about 40 g m^{-2}. According to consumption rates of *P. robustoides* noted in this study, this population is able to consume up to 4-5 g d^{-1} (dry weight) or 1.9-2.4 g C m^{-2} d^{-1} of algae. These values are two- to three-fold lower than the average production of *C. glomerata* evaluated at the study site. Thus, it is likely that after a further rise in *P. robustoides* density, the grazing impact on *Cladophora* will be rather strong.

However, the further success of *P. robustoides* depends on environmental conditions. The current status of the littoral zone of the Neva Estuary is characterized by high phosphorus content in the water which indicates increased eutrophication. The primary production of filamentous algae exceeded the production of phytoplankton by at least two-fold in the open waters of the Neva Estuary; thus, eutrophication in the littoral zone is more intense than in the open waters (Golubkov *et al.* 2003b). Eutrophication also increased as a result of decaying filamentous algae detached from hard substrates during storms that accumulated in very high biomass in the littoral zone. The algae can substantially modify nutrient dynamics in the water and sediments (Lavery and McComb 1991, Peckol and Rivers 1996). During the decomposition process (35 days), 40-65% of the tissue phosphorus was released by the decaying mats of *C. glomerata* (Paalme *et al*. 2002). Rapid decomposition also provides an important additional supply of organic and inorganic compounds that are potentially available for recycling in the water.

Strong storms that affected the littoral zone of the Neva Estuary along with the pollution of the coastal zone from decaying filamentous algae in August 2003 resulted in a significant decline of gammarid density. Strong drops in the oxygen content of underlying sediments to 0.5–1.0 m g l^{-1} could be the real reason for the high mortality of *G. fasciatus* and *P. robustoides*. Hypoxia negatively influences the survival of oxiphylic invertebrates, including potential grazers. As a result, the density of amphipods and chironomids strongly declined

(Berezina *et al.*, in press). It is known that in nature the survival of amphipod species is limited by water oxygen concentrations of approximately 2 m g l^{-1} (Dediu 1980, Panov and Berezina 2002). Lethal oxygen concentrations were determined experimentally to be 0.5 and 0.3-0.4 mg O l^{-1} at 20ºC for *G. fasciatus* (Bekman 1962) and *P. robustoides* (Ioffe and Maximova 1968), respectively. A similar tendency is observed in other parts of the Baltic Sea where drifting algae mats stressed the benthic communities by inducting hypoxia and even anoxia in the sediments (Arroyo *et al.* 2003). Decaying macroalgae are recognized as being capable of inducing widespread mortality among benthic invertebrates, seriously affecting higher trophic levels, and destabilizing the whole shallow-water ecosystem (Everett 1994, Cummins *et al.* 2004, Norkko and Bonsdorff 1996, Hansen and Kristensen 1997). At the same time, the effect of herbivores on decaying algae was insignificant in most cases (Kotta *et al.* 2000). Thus, amphipods, which are effective grazers of the filamentous algae *C. glomerata,* decreased significantly in number due to high mortality or migration from "polluted" habitats.

At present, the problem of grazing control of macroalgae is being discussed broadly, but opinions are often contradictory. It was demonstrated that grazing plays a significant role in controlling macroalgal biomass (Menge *et al.* 1997, Duffy and Hay 2000). An in situ experiment revealed amphipods had a strong impact on the abundance of red, brown, and green filamentous algae. When the amphipod *Ampithoe longimana* was present in mesocosms*,* the green algae was cropped to a sparse turf, but when the amphipods were removed, the filamentous algae developed rapidly (Duffy and Hay 2000). In contrast, some experiments (Morgan *et al*. 2003) revealed that the top-down effect caused by grazers was insignificant compared to the effects of nutrients (bottom-up effect). When nutrients were abundant, the amphipods did not graze on *Cladophora* tissue but on its epiphytes since they are generally more abundant at high than at low nutrient loads (Sand-Jensen and Borum 1991). A similar effect was revealed in the experimental study of *Gammarus* grazing on *Ulva* sp. (Horne *et al*. 1994, Kamermans *et al.* 2000). At the same time, grazing on epiphytes can be considered a positive effect that stimulates filamentous algae growth (Kamermans *et al.* 2000). The mechanism of growth stimulation by removing epiphytes may include both improved light conditions for the host plant and increased nutrient supply to the plant through herbivore mediated nutrient regeneration (Fong *et al.* 1997). The gammarid *Gammarus oceanicus* also had weak grazing effects and favored algal recruitment through excretion (Lotze and Worm 2002).

In conclusion, the current study indicates that the grazing amphipods *G. fasciatus* and *P. robustoides* play a significant role in the functional

organization of the littoral communities of the Gulf of Finland and can be considered as important factors, along with nutrients, of macroalgal bloom control through food web interactions.

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