

Spatial distribution of macrofauna in a littoral zone with drifting macroalgae in the Neva estuary

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Abstract. This study focuses on the influence of drifting algae (*Cladophora glomerata*) and oxygen depletion on the distribution and biomass of macrofauna in the shallow stony–sandy littoral of the Neva estuary, easternmost part of the Baltic Sea. Great masses of decaying drifting algae (315–445 g dry weight m^{-2}), oxygen depletion (5.4–24.5% or 0.6–2.8 $mg L^{-1}$), and subsequent low biomass of macrofauna (0.5–2.9 g wet weight m^{-2}) were recorded in the near-shore area (5–20 m). At greater distances (30–60 m from the shore) the biomass of drifting algae decreased, hypoxia was not recorded, and no internal significant differences in the total biomass of benthic macrofauna (24.3–30.8 g wet weight m^{-2}) were found. The biomass of the macroinvertebrate community of the drifting algae reached 4.1–5.5 g wet weight m^{-2} at distances of 10–20 m from the shore, and was at least 20 times lower in the area closest to the shore (5 m). Amphipods and chironomids contributed to the total biomass 42% and 26%, respectively. Species with opportunistic life strategies and high resistance to oxygen depletion are able to survive and dominate in coastal areas of the Neva estuary with temporary hypoxia induced by macroalgal decomposition.

Key words: littoral community, benthos, metaphyton, filamentous algae, *Cladophora glomerata*, hypoxia, eutrophication, Baltic Sea.

INTRODUCTION

Coastal eutrophication enhances the growth of annual filamentous algae (Cloern, 2001; McGlathery et al., 2007), often at the expense of perennial macroalgae. The growing macroalgae together with associated epiphytes are preferred food resources for many littoral invertebrates such as crustaceans, gastropods, annelids, and insects (Jansson, 1967; Kraufvelin et al., 2006) and highly productive macroinvertebrate communities associated with these macroalgae are confirmed in several studies from different regions (Dean & Connell, 1987; Kotta & Orav, 2001; Kraufvelin & Salovius, 2004). When filamentous algae are swept away from their hard substrates by wave action, they may form a temporary drifting algal substrate (or metaphyton). The drifting algae represent a large-scale phenomenon in estuaries and lagoons with high wave activity. During decomposition the algae may cause

hypoxic conditions and further hydrogen sulphide production in underlying habitats (Lavery & McComb, 1991; Bonsdorff, 1992; Raffaelli et al., 1998).

Hypoxia is considered as one of the most serious threats to aquatic animal communities affecting their species richness and total abundance (Bonsdorff, 1992; Norkko et al., 2000; Karlson et al., 2002; Bona, 2006; Berezina et al., 2007) including those of juvenile fish (Nordström & Booth, 2007). Because the macro-invertebrates residing in the bottom sediments or colonizing the macrophytes in the shallow areas exhibit varying degrees of sensitivity and resistance to hypoxia, they could be useful as biological indicators of estuarine environment and its health (Gaston et al., 1989; Malloy et al., 2007).

The shallow Neva estuary (easternmost Baltic Sea) is dominated by the filamentous alga *Cladophora glomerata* (L.) Kütz, which produces 800–900 g C m⁻² per year (Berezina et al., 2005). This value surpasses the primary production of diverse macrophyte communities at rocky shores (Wallentinus, 1991) in the Baltic Sea and allows classifying this coastal zone as a greatly productive subsystem. An abrupt decrease in the abundance of bottom animals as a response to oxygen depletion during algal decomposition has been shown for the Neva estuary in previous studies (Berezina et al., 2007; Berezina & Golubkov, in press). The horizontal distribution of macrofauna during the time of the maximum biomass of drifting algae in the littoral zone and in other areas with a notable effect of drifting algae on littoral macrofauna remains unclear, however. Little is also known on metaphytic macrofauna and its interactions with drifting algae (Ingolfsson, 1995; Brooks & Bell, 2001; Salovius & Bonsdorff, 2004; Salovius & Kraufvelin, 2004; Salovius et al., 2005). The taxonomic composition and species dominance patterns of the animal communities of these temporary substrates are not clear either.

The present paper aims at estimating the quantitative distribution of macrofauna in the littoral zone of the Neva estuary and its dependence on drifting and attached algal biomass in areas with near-bottom hypoxia. The study also intends to compare the taxonomic composition and quantitative characteristics of the macrofauna in benthic and metaphytic communities and to find macroinvertebrate taxa that are tolerant to the prevailing environmental conditions and dominate in the studied habitats. As coastal eutrophication phenomena such as oxygen deficiency due to the decomposition of drifting algae are largely stochastic and difficult to forecast and assess in most estuaries, including the Neva estuary, I chose to study the littoral communities during a period with a maximum notable effect of the decomposition of drifting algae on the communities.

METHODS

This study was conducted in the shallow littoral zone within the St. Petersburg health resort area near the Zelenogorsk district (60°11' N, 29°44' E, Fig. 1), where the highest biomass of filamentous macroalgae (98% of *C. glomerata*) was recorded previously (Golubkov et al., 2003). The substrate consists of gravel, stones, and

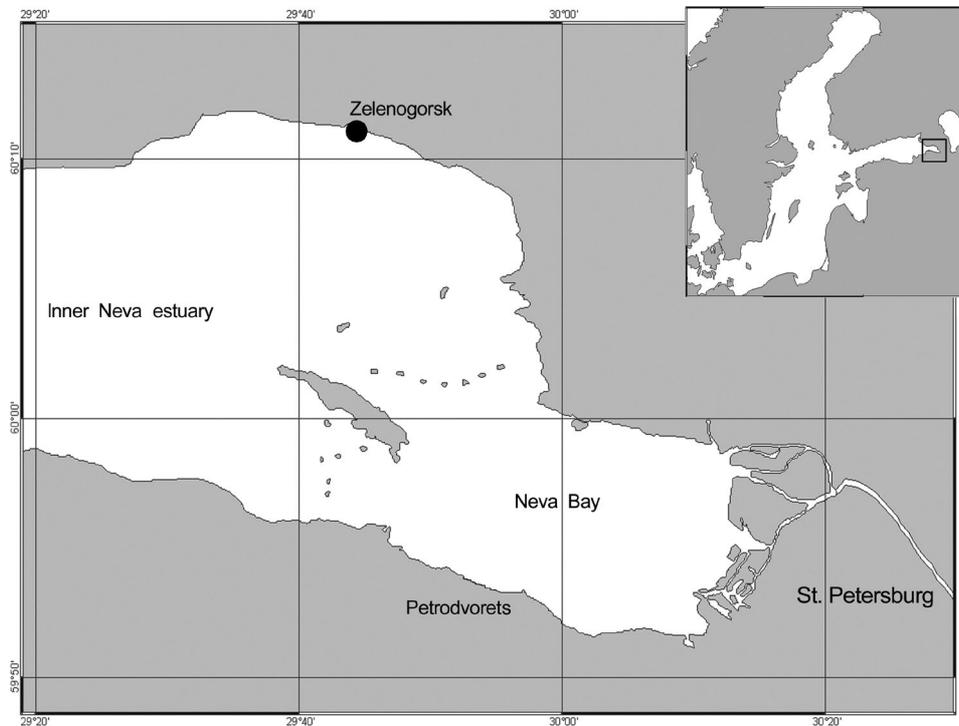


Fig. 1. Map with indication of the shallow-water area studied at the northern coast of the Neva estuary.

sand. The proportion of bottom area that is covered by hard substrates averages 90%. Drifting macroalgae usually start to decompose in July resulting in temporary deterioration of bottom environments (Berezina et al., 2007). Because the middle of the summer is a period with high water temperature and maximum biomass of macroalgae in the Neva estuary, this period was chosen for the study. All samples were collected on 14 July 2005. During the sampling (9–11 a.m.) the water temperature was 23.2–24.8°C. The average diurnal water temperature was 23.1 ± 1.1 °C, varying between 19 and 28°C. Salinity was 0.67–0.69.

Water samples for chemical analyses and biological samples (benthic animals, attached and drifting macroalgae) were collected at certain distances from the shore (5, 10, 20, 30, 40, 50, and 60 m) and in the range of depths from 0.1 to 0.7 m (Table 1). All samples were replicated thrice; altogether 66 biological samples and 21 water samples were collected.

Measurements of water temperature and oxygen content were conducted with an oxygen meter WTW Oxi-330. To get total phosphorus content 100-mL water samples were collected at each distance and preserved in glass bottles with 0.1 mL HCl. Total phosphorus was measured using the standard colorimetric method (Strickland & Parsons, 1968) at a wavelength 885 nm in a Unico-2100 spectrophotometer.

Table 1. Physical and chemical characteristics of sampling distances, density (ind. m⁻²), and biomass (g wet weight m⁻²) of macroinvertebrates in benthic (B) and metaphyton (M) communities

Distance from shore, m	Depth, m	Oxygen saturation, %	Total P, µg L ⁻¹	Density ±SE		Biomass ±SE	
				B	M	B	M
L-1 5	0.1	5.4	360	470±108	316±19	0.5±0.3	0.19±0.03
L-2 10	0.15	24.5	270	3 600±1850	4608±2700	2.9±1.5	4.13±1.55
L-3 20	0.2	38	200	14 200±1600	5280±441	10.8±1.2	4.4±1.3
L-4 30	0.25	103	176	25 880±3070	3764±641	30.1±4.7	5.5±2.5
L-5 40	0.4	125	132	26 670±4020	no data	30.8±4.3	no data
L-6 50	0.6	134	125	25 660±4340	no data	24.3±1.9	no data
L-7 60	0.7	133.6	125	19 400±2800	no data	26.7±2.8	no data

Benthic animals, from the bottom sediments and from the attached algae, were collected with a 0.03 m² cylindrical frame and a hand-held net (0.25 mm mesh size) according to the procedure elaborated earlier (Berezina et al., 2005). The frame was forced into the bottom and all the hard substrates and plants in the frame were transferred to fresh water in a plastic container. Animals were washed off the hard substrates or scraped off with a knife (for attached animals). A 3–7 cm layer of soft sediments was collected with a hand-held net of 0.25 mm mesh size for three minutes. All parts of the sample were placed in a sieve (0.25 mm) and washed with water. The macrofauna associated with drifting algae was collected from the water column using the same frame (0.03 m² area) at four distances with dense floating mats (L-1, L-2, L-3, and L-4; Table 1). The algal substrates with animals were sieved in a 0.25-mm mesh and rinsed with fresh water. The samples were preserved in 4% formaldehyde in a plastic zip-bag. In laboratory all invertebrates were picked out of the samples under stereoscopic microscope (MBS-10) and were sorted into 10 taxa (Chironomidae, Trichoptera, Amphipoda, Hirudinea, Oligochaeta, Gastropoda, Bivalvia, Ephemeroptera, Ceratopogonidae, and others). The animals were counted and weighed on an electronic balance to the nearest 0.01 mg.

Attached algae and drifting algae were collected also from a 0.03 m² area at each distance in order to estimate algal biomass. The algae were rinsed with fresh water and any associated animals were removed from them. In laboratory the algae were dried at 60°C for 96 h to constant weight and weighed. The carbon content in *C. glomerata* contributes 50% of the dry weight or 10% of the wet weight of the algae (Gubelit & Berezina, in press).

The abundance and biomass of animals (in wet weight, the shells of molluscs included) and biomass of algae (in dry weight) were estimated as an arithmetical mean ±SE (standard error) from all sample replicates and then re-calculated per 1 m² of bottom area.

Possible differences in biomasses of macroinvertebrates and macroalgae between distances were analysed by one-way analysis of variance (ANOVA).

Prior to the analysis the data were tested for homogeneity and the data were $\lg(x+1)$ -transformed in the case of heterogeneous variances. If the overall ANOVA tests were significant the Tukey HSD post-hoc test was performed to elucidate pair-wise differences. When homogeneity of variances was not obtained even with logarithmic transformation, Kruskal–Wallis’ non-parametrical test was used. Pearson’s correlation coefficient (r) served to test the relationships between the biomasses of zoobenthos (and its taxa) and algae and oxygen and phosphorus contents. Normality of the data was checked before performing correlation analysis.

RESULTS

Oxygen saturation and phosphorus content in near-bottom areas

Table 1 summarizes the results for dissolved oxygen saturation and total phosphorus concentration in water near the bottom at the study distances. The total phosphorus concentration ranged between 125 and 360 $\mu\text{g L}^{-1}$, reaching the maximum at site L-1. During daytime the dissolved oxygen levels ranged from 5.4% to 134% (Table 1). Hypoxia (5.4–38% or 0.6–2.8 mg L^{-1}) was recorded mainly in the near-shore area to 20 m distance from the shore at sites L-1, L-2, and L-3. The diurnal oxygen measured at L-5 (without the influence of drifting algae) fluctuated between 55.9% and 125.5% ($n = 7$), averaging $99.4 \pm 7.7\%$. A highly significant negative correlation between oxygen and total phosphorus concentrations was found ($r = -0.97$, $p < 0.01$; Table 2).

Table 2. Correlation coefficient and significance between oxygen, phosphorus content, biomass of attached *Cladophora glomerata*, biomass of drifting algae, and biomasses of different benthic taxa

	Oxygen	Phosphorus	Attached algae	Drifting algae
Oxygen	–	–0.97**	0.94**	–0.81*
Phosphorus	–	–	0.93**	0.89**
Attached algae	–	–	–	–0.78*
Oligochaeta	0.84*	–0.79*	ns	ns
Hirudinea	0.75*	ns	ns	ns
Gastropoda	ns	ns	ns	ns
Bivalvia	ns	ns	ns	–0.86*
Amphipoda	0.86*	–0.94**	0.82*	–0.86*
Isopoda	ns	ns	ns	ns
Chironomidae	0.92**	–0.88**	0.87*	ns
Trichoptera	0.85*	–0.82*	0.78*	–0.81*
Ephemeroptera	ns	ns	ns	ns
Ceratopogonidae	ns	ns	ns	ns
All benthic taxa	0.99**	–0.94**	0.89**	0.93**

Biomass of attached and drifting macroalgae

The biomass of the drifting algae differed between the distances (one-way ANOVA, $df = 6$, $MS = 73\,772$, $F = 39.1$, $p < 0.001$) and decreased with increasing distance from the shore. The biomass reached $445\text{ g dry weight m}^{-2}$ at L-1 (5 m from the shore) and 315 g m^{-2} at L-2 (10 m from the shore; Fig. 2). The differences in the biomass of drifting algae were not significant at L3–L5 (20–40 m distances from the shore), where it averaged from 102 to 134 g m^{-2} (post hoc test, all $p > 0.05$). At L-6 and L-7 (>50 m) the drifting biomass was significantly lower (all $p < 0.01$) than at the other distances reaching only $14\text{--}35\text{ g m}^{-2}$. Hypoxia (conditions with oxygen saturation of 5–38%) was recorded at distances with the highest biomass of drifting algae ($315\text{--}445\text{ g m}^{-2}$). At a drifting algal biomass of $100\text{--}134\text{ g m}^{-2}$, the oxygen saturation was 103–134% (normoxia). The negative relationships between the biomass of drifting algae and oxygen saturation were confirmed by the significant correlation ($r = 0.81$, $p < 0.05$; Table 2).

The biomass of attached macroalgae also varied significantly between distances (one-way ANOVA, $df = 6$, $MS = 21\,943$, $F = 3.65$, $p = 0.02$). It increased with the distance from the shore/depth (Fig. 3). The differences in the mean algal biomass were not significant at distances L2–L4 (varying from 49 to 82 g m^{-2}) and at distances L5–L7 ($196\text{--}218\text{ g m}^{-2}$, post hoc tests, all $p > 0.05$). At the near-shore distance (L-1) it was only 10 g m^{-2} , which is significantly less than at the greater distances (all $p < 0.01$).

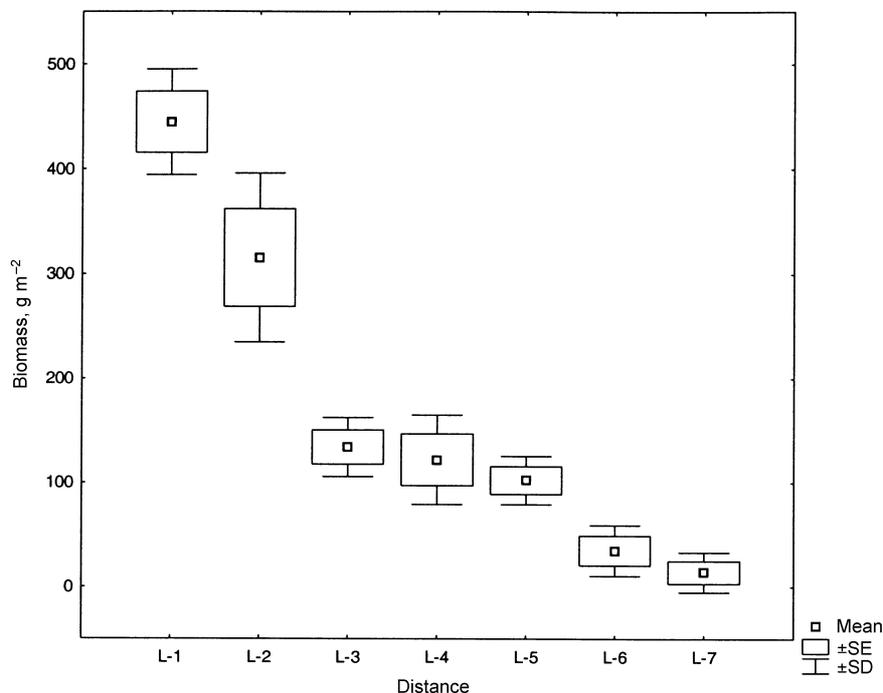


Fig. 2. Biomass distribution ($\text{g dry weight m}^{-2}$) of drifting algae in the study area.

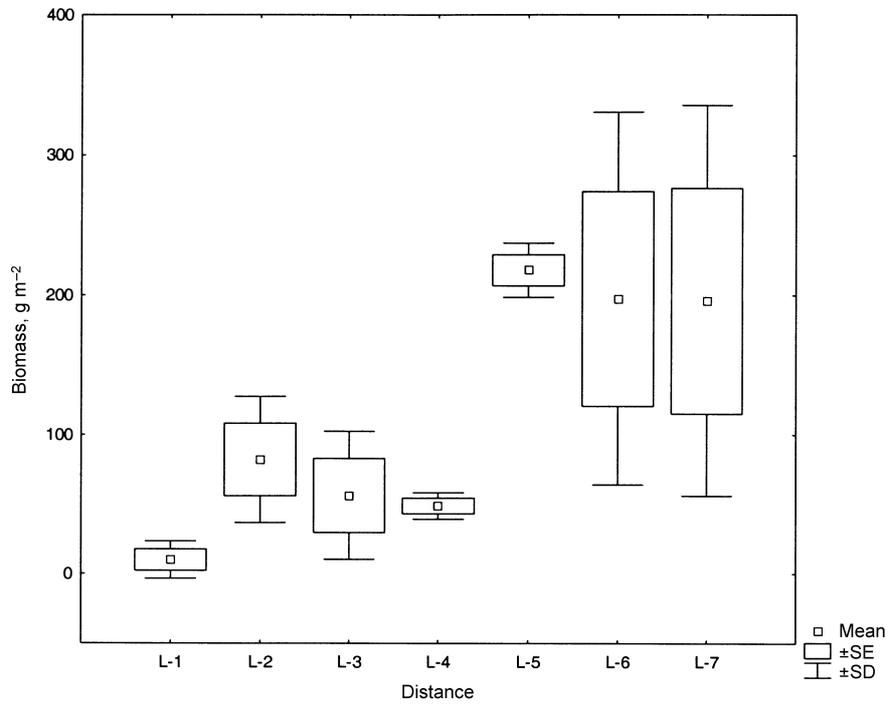


Fig. 3. Biomass distribution of attached algae (g dry weight m⁻²) in the study area.

Negative relationships were found between the biomass of attached and drifting algae ($r = -0.78$, $p < 0.01$; Table 2). Figure 4 outlines the percentage proportion of attached and drifting algal biomass at the studied distances. The

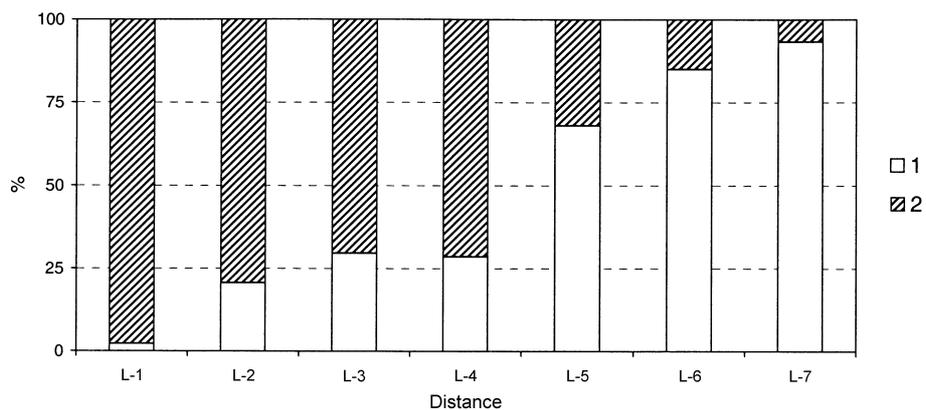


Fig. 4. Biomass proportion (%) of the attached (1) and drifting algae (2) in the study area vs distance from the shore.

drifting algae contributed the main part (70–98%) of the total algal biomass at shorter distances from the shore (5–30 m) and to a smaller extent (7–32%) at greater distances (40–60 m from the shore).

Biomass of zoobenthos

The biomass of benthic macrofauna differed significantly between the distances (one-way ANOVA, $df = 6$; $MS = 1.02$, $F = 21.4$, $p < 0.001$). The differences in the biomass between distances L-1, L-2, and L-3 were significant (post hoc tests, all $p > 0.05$) increasing from 0.5 to 10.8 g m^{-2} (Table 1, Fig. 5). However, significant differences (post hoc tests, all $p > 0.05$) were found at larger distances from the shore L-4–L-7 (24.3–30.8 g m^{-2} ; Fig. 5), where the total biomasses were at least two times higher than at distances L-1–L-3 (post hoc tests, all $p < 0.05$).

The macrobenthic community was in terms of biomass and density dominated by the following taxa: oligochaetes *Stylaria lacustris* (L.), *Limnodrilus hoffmeisteri* Claparède, and species of the genus *Nais*; the hirudineans *Erpobdella octoculata* (L.) and *Glossiphonia complanata* (L.); the amphipods *Gmelinoides fasciatus*

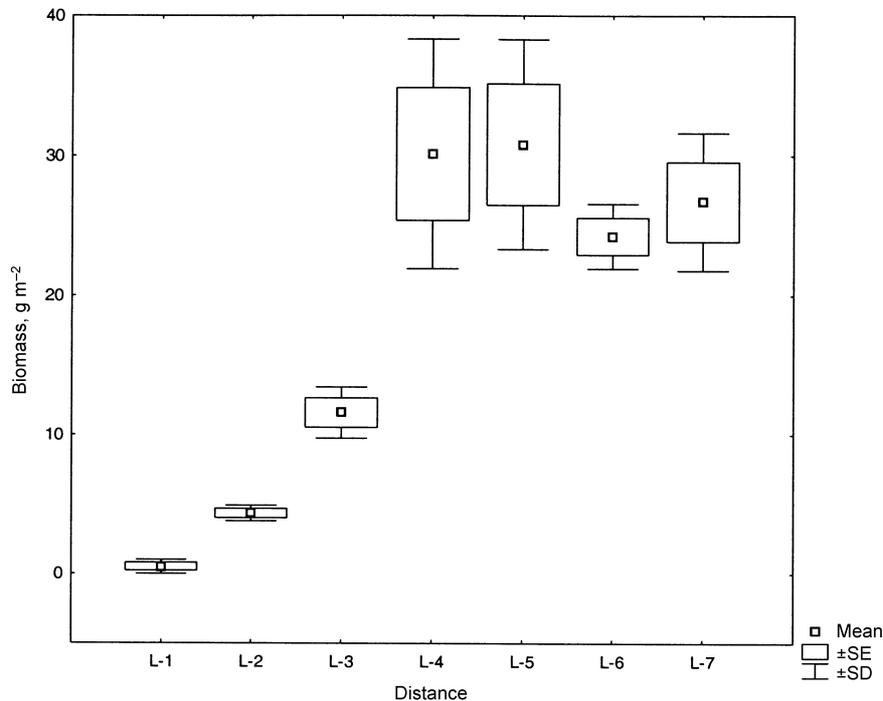


Fig. 5. Biomass distribution ($\text{g wet weight m}^{-2}$) of benthic macrofauna in the study area.

(Stebbing) and *Pontogammarus robustoides* (Sars); the ephemeropterans *Caenis* spp. and *Ephoron virgo* (Oliv.); the trichopterans *Agraylea multipunctata* Curtis and *Hydropsyche contubernalis* MacLachlan; and some species of chironomids (*Demicryptochironomus vulneratus* (Zetterstedt), *Tanytarsus medius* Reiss et Fittkau, *Paratanytarsus quintuplex* Kieffer, *Cricotopus* sp., *Rheotanytarsus* sp., and *Polypedilum* sp.).

There were no significant differences in biomass between benthic taxa (chironomids, trichopterans, amphipods, hirudineans, oligochaetes, gastropods, bivalves, ephemeropterans, and others) at the studied distances (one-way ANOVA, $df = 6$, $MS = 1.8$; $F = 3.14$; $p < 0.001$, post hoc comparisons, ns). Chironomids and amphipods constituted respectively 20–53% and 5–54% of the total biomass. The biomass proportions of trichopterans and hirudineans were also high reaching 8–26% and 5–31% at the studied distances (Fig. 6). The biomass of oligochaetes, hirudineans, amphipods, chironomids, trichopterans as well as the total biomass increased significantly with increasing oxygen content in near-bottom areas (Table 2). Positive correlations between the biomass of macroinvertebrates (amphipods, chironomids, and trichopterans) and attached algae were found (Table 2). The lowest biomasses of amphipods (0.22–0.28), trichopterans (0.05–0.76), and chironomids (0.16–2.3 g wet weight m^{-2}) were also found at distances L-1 and L-2 with the highest biomass of drifting algae (300–450 g dry weight m^{-2}). The negative relationships between the biomass of benthic macrofauna and the biomass of drifting algae were further confirmed by the significant correlations (Table 2).

Biomass of macroinvertebrates colonizing drifting algae

The chironomids (species of the genera *Cricotopus* and *Polypedilum*), oligochaetes (mainly Naididae), the hirudinean *Erpobdella octoculata*, the trichopteran

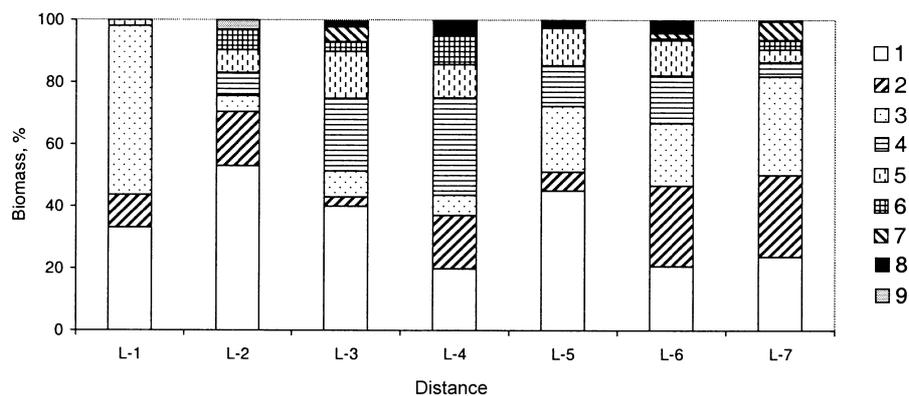


Fig. 6. Taxonomic composition of zoobenthos at the studied distances and percentage contribution to total biomass. 1 – Chironomidae, 2 – Trichoptera, 3 – Amphipoda, 4 – Hirudinea, 5 – Oligochaeta, 6 – Gastropoda, 7 – Bivalvia, 8 – Ephemeroptera, and 9 – Ceratopogonidae.

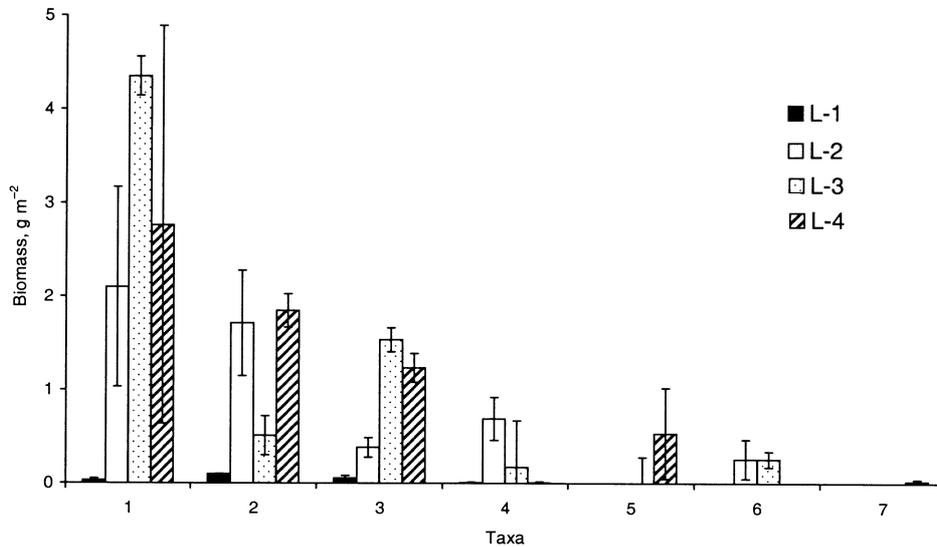


Fig. 7. Average biomass (\pm SE) of different invertebrates colonizing drifting algae and their percentage contribution to total biomass. 1 – Amphipoda, 2 – Chironomidae, 3 – Trichoptera, 4 – Oligochaeta, 5 – Hirudinea, 6 – Ephemeroptera, 7 – Ceratopogonidae.

Agraylea multipunctata, the ephemeropteran *Caenis* sp., and the amphipods *Gmelinoides fasciatus* and *Pontogammarus robustoides* colonized the drifting algae (Fig. 7). The total biomass of metaphytic macroinvertebrates was very low (0.2 g m^{-2}) at L-1 and significantly higher at L-2–L-4 (10–30 m distance) varying between 4.1 and 5.5 g m^{-2} (one-way ANOVA, post hoc comparison, all $p < 0.05$; Table 1). The differences in macroinvertebrate biomass between distances L-2–L-4 were not significant (one-way ANOVA, $p > 0.05$). Amphipods constituted 42% of the total biomass of this temporary community, chironomids 26%, and oligochaetes 10%. The trichopteran *A. multipunctata* and the hirudinean *E. octoculata* contributed to the total biomass with 15% and 5% each.

DISCUSSION

In the Neva estuary thick mats of drifting algae are often accumulating in the shallow littoral in summertime, they cover around 20% of all shallow habitats with depths from 0 to 1 m (Berezina & Golubkov, in press). In coastal areas of other parts of the Baltic Sea, drifting algae and mats are a widely distributed phenomenon. For example, in Kõiguste Bay, northeastern Baltic Sea, drifting algal patches were found to be on average 0.5–1 km wide and to cover about 25% of the total bottom area with their biomass varying between 35 and 1391 g dry

weight m^{-2} (Lauringson & Kotta, 2006). Furthermore, macroalgae with a severe influence on shallow habitats have been recorded in 30% of the sheltered and 60% of the exposed bays in the Åland Islands, northern Baltic Sea (Berglund et al., 2003). Algal mats also cover about 30% to 50% of shallow soft-sediment habitats during summer in embayments on the west coast of Sweden (Pihl et al., 1999; Sundbäck et al., 2003). In some other cases macroalgal accumulations weighing up to 400 kg wet weight m^{-2} have been reported (Morand & Briand, 1996).

According to the obtained results at an experimental site in the Neva estuary the occurrence and biomass of drifting algae depend on distances from the shore and water depth. Macroalgae had a rather large biomass (above 400 g dry weight m^{-2}) at short distances from the shore (5–10 m). The biomass decreased significantly with increasing distance from the shore (to 14 g dry weight m^{-2} at 60 m distance).

Decaying drifting algae induce temporary hypoxia in covered areas. In this study it was found that the effect of drifting algae on oxygen levels and zoobenthic biomass were related to algal biomass. The severest impacts were recorded at shorter distances from the shore with 300–450 g dry weight m^{-2} of decaying drifting algae. At distances with a macroalgal biomass of 14–122 g dry weight m^{-2} no oxygen depletion and significant changes in benthic biomass were found. Similar results were reported from the Åland Archipelago, in the northern Baltic Sea, where signs of reduced oxygen saturation were observed at an algal biomass of 832 ± 60 g dry weight m^{-2} , while no effects of oxygen saturation were found at 150 ± 19 g m^{-2} (Bonsdorff, 1992).

A decrease in the abundance of benthic animals as a result of oxygen depletion during the decomposition of algae was recorded with the maximum effect at near-shore distances with thickest accumulations of decaying algae. At least a ten-fold decrease in the abundance of benthic animals due to high mortality was observed in July–August during hypoxic conditions (<3 mg L^{-1}) in near-bottom areas beneath drifting algae in different locations in the Neva estuary (Berezina et al., 2007; Berezina & Golubkov, in press). The same phenomena have been described in many eutrophied estuaries and lagoons of other coastal regions (Norkko & Bonsdorff, 1996; Powilleit & Kube, 1999; Cardoso et al., 2004; Rosenberg & Nilsson, 2005; Jones & Pinn, 2006; Bona, 2006).

For sea bottom areas rich in organic matter it has been confirmed that *r*-selected species (opportunistic species) can occupy stressed coastal environments despite oxygen deficiency (Cognetti, 1992). The stressed habitats consisting of drifting algae in the Neva estuary were colonized by eurybiotic taxa (chironomids, oligochaetes, hirudineans), locally adapted populations of stenobiotic species of trichopterans and ephemeropterans, typical of the studied habitat, as well as some recently introduced species of amphipods (*Gmelinoides fasciatus*, *Pontogammarus robustoides*). A high dominance of a few taxa as chironomids and amphipods was found. Chironomids were recorded as the dominating taxon in the coastal zone of

the Venice Lagoon with proliferating nuisance seaweeds and temporary oxygen depletions (Tagliapietra et al., 1998; Bona, 2006). Also, an invertebrate fauna dominated by Chironomidae was reported at a high biomass of filamentous algae in the northernmost part of the Baltic Sea (Råberg & Kautsky, 2007).

The obtained results show that hypoxia affected not only sensitive taxa but also some opportunistic taxa (primarily annelids, amphipods, chironomids), resulting in a reduction of their biomass. The biomass of the benthic macrofauna in the studied site was strongly dependent on the oxygen level and amount of drifting algae. Likewise, the oxygen level and percentage of organic matter in the sediment influence the horizontal distribution of species in the Orbetello Lagoon, Mediterranean Sea, after macrophyte blooms followed by severe dystrophic crises with high fish mortality (Lardicci et al., 1997).

Macroalgae are probably important as a habitat and food resource for macrofauna enhancing the re-colonization of previously defaunated sediments by macroinvertebrates (Österling & Pihl, 2001; Salovius & Kraufvelin, 2004; Salovius et al., 2005). Transport of the drifting algae is in addition an important dispersal mechanism for both the plants and their associated fauna along a medium-ranged (regional) scale (Biber, 2007). Benthic invertebrates are most likely able to utilize the extra organic material (Raffaelli, 2000), but diverse taxa differ considerably in their ability to utilize the filamentous algal drift. Macroalgae, for example, can provide an extra refuge from predation for mobile species (Kulczycki et al., 1981). Lauringson & Kotta (2006) found that drifting algae favour several detritivorous, herbivorous, and carnivorous species as a result of increased habitat complexity in otherwise poorly vegetated coastal areas of the northeastern Baltic Sea.

Consumption of algal matter by grazers (crustaceans and insects) may damage growing algae and regulate biomass (Duffy & Hay, 2000; Edgar & Klumpp, 2003; Berezina et al., 2005). The infaunal impact has been suggested to be of great importance especially at low algal biomass (Raffaelli, 2000; Kraufvelin et al., 2006) as denser and more intense blooms are highly likely to result in primarily negative effects on the infauna (Raffaelli et al., 1998 and references therein). However, some researches show that grazers (mainly crustaceans) play an important role in the decomposition of algal detritus (Harrison, 1977; Kotta et al., 2000).

In the case of the Neva estuary the invasive amphipods *Pontogammarus robustoides* and *Gmelinoides fasciatus* were the most abundant taxa in decaying drifting algae even at the lowest oxygen content (0.6 mg L^{-1}). Evidently, these amphipods use the decaying algae as a food resource and additional habitat. In another study amphipods (*Monoporeia affinis*) were classified as 'very sensitive' to hypoxia (Modig & Ólafsson, 1998). The mechanism that allows amphipods to play a central role in the decomposition of decaying algae in habitats with temporary hypoxia remains unclear. It is likely that amphipods are able to tolerate the threats caused by algal decomposition over prolonged periods until they

eventually migrate to areas with more favourable conditions. This behavioural adaptation can be considered as a mechanism facilitating amphipod dominance in the shallow coastal zone of the Neva estuary.

Chironomids were another abundant taxon among the metaphyton colonizers in the study area. Chironomids have been recorded as a highly abundant taxon in drifting algae and loose lying mats in other regions as well (Kingsford & Choat, 1985; Raffaelli et al., 1998; Salovius et al., 2005). Oligochaetes were found as a common but not abundant component in algae in a case study of another part of the Baltic Sea (Salovius et al., 2005). At the same time, gastropod molluscs, which have been reported as a common component of this temporary community in other regions (Norkko et al., 2000; Salovius & Kraufvelin, 2004), were a very rare taxon in the case study, obviously due to deoxygenation. Thus, in the conditions of the Neva estuary drifting algae were initially colonized and further dominated by opportunistic and mobile taxa such as crustaceans and aquatic insects.

The biomass of the animals in the drifting algae was 5–6 times lower than in the benthic community associated with attached macroalgae in areas undisturbed by drifting algae. Similarly, the abundance, biomass, and diversity of the macrofauna in *Cladophora glomerata* were reported to drop when algae detached from the substrate and started to drift and decay (Salovius & Kraufvelin, 2004). It can be explained not solely by negative effects of temporary hypoxia induced by algae during decomposition but also by some specific traits of the behaviour and life cycles of algal colonizers. The invertebrates associated with macroalgae have longer life spans than the algae themselves and many of them can leave the algae when the algae detach from the hard substrate and start to decay.

The number of species and the number of individuals depend on their different degrees of adaptability to a specific environmental factor in the studied habitat. Species with opportunistic life strategies and high resistance to oxygen depletion will be able to survive in coastal areas of the Neva estuary with recurrent oxygen depletion phenomena. In the future the ongoing eutrophication may result in decreased species diversity and even a tendency of ‘homogenization’ in benthic community succession, when a few highly adaptive species are dominating in the benthic biomass.

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Põhjaloomastiku levik Neeva estuaari kinnitumata vetikamattidega rannikumeres

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On käsitletud kinnitumata makrovetika (*Cladophora glomerata*) mõju põhjaloomastiku biomassi levikule Neeva estuaari rannikumere liivastel-kivistel põhjadel. Kinnitumata vetikamati massiline esinemine (315–445 g kuivkaalus m⁻²) ja sellest tulenev hapnikudefitsiit (5,4–24,5% või 0,6–2,8 mg L⁻¹) vähendas põhjaloomastiku biomassi (0,5–2,9 g märgkaalus m⁻²). Väiksemate vetikamati biomasside juures hapnikudefitsiiti ei esinenud ja vetikamattide mõju põhjaloomastiku kooslustele puudus. Suurselgrootute biomass vetikamatis oli 4,1–5,5 g märgkaalus m⁻² 10–20 m kaugusel rannajoonest ja need väärtused olid vähemalt 20 korda väiksemad 5 m kaugusel rannajoonest. Kirpvähilised ja surusäased moodustasid vastavalt 42 ning 26% põhjaloomastiku üldbiomassist. Vaid madalat hapnikusisaldust taluvad oportunistlikud liigid on võimelised ellu jääma ja domineerima Neeva estuaari rannikumere kinnitumata vetikamati koosluses.