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Effects of plant morphology on small-scale distribution of invertebrates

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Abstract Habitat structure influences organism communities by mediating interactions between individuals and species, affecting abundance and species richness. We examined whether variations in the morphology of soft-bottom plants affect their function as habitat and whether complex structured plants support higher macroinvertebrate abundance and species richness. Three Baltic Sea plant species were studied, together with artificial plants resembling each species. In a field collection, we found higher invertebrate abundance on the morphologically more complex plants *Myriophyllum spicatum* and *Chara baltica* than on the structurally simpler plant *Potamogeton perfoliatus*. In a colonization experiment, we found the highest invertebrate abundance on artificial *M. spicatum* but found no difference between natural plants. Invertebrate taxon richness displayed no consistent relationship with plant structural complexity. The results imply that plant morphology influences small-scale invertebrate distribution, partly supporting the hypothesis that structurally complex plants harbour higher invertebrate abundance.

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Introduction

The physical properties of habitats influence organism communities by mediating interactions between individuals and species, thus affecting abundance and species richness. In aquatic environments, habitat structures for invertebrates and fishes are frequently provided by macroscopic algae and angiosperms. On soft bottoms, angiosperms and charophytes (here referred to as plants) constitute significant three-dimensional physical structures above the sediment surface in an otherwise simply structured seascape. Generally, animal abundance and species richness are considerably higher where plants are present (e.g. Orth et al. 1984; Hemminga and Duarte 2000), as they increase the overall colonisable area and increase the structural complexity of the habitats. In addition, plant shape influences animal communities (e.g. Taniguchi et al. 2003; Warfe and Barmuta 2006). Intricate plant or algae structures have been found to harbour greater invertebrate abundance and species richness than do simple ones in marine (Hull 1997; Hauser et al. 2006), freshwater (Jeffries 1993; Warfe and Barmuta 2006; Xie et al. 2006), and terrestrial environments (Halaj et al. 2000). However, this relationship is not always found (Cyr and Downing 1988; Cremona et al. 2008) and needs further exploration. Higher animal abundance and species richness in complex versus simple plant habitats have been suggested to depend on several factors. Complexly structured habitats can increase the number of microhabitats, extending overall niche space (McNett and Rypstra 2000; Willis et al. 2005) and increasing the separation of niches within a given space (Willis et al. 2005). Plants with intricate morphologies can reduce predation pressure by reducing both prey detection and capture by predators (Warfe and Barmuta 2004). In addition, complexly structured plants can reduce

small-scale water velocity (Gregg and Rose 1982), thereby sheltering animals against hydrological disturbance. Partly as a function of altered water velocity, plants with complex morphologies support high biomasses of epiphytes and accumulate detritus (Gregg and Rose 1982; Jeffries 1993; Taniguchi et al. 2003; Warfe and Barmuta 2006, but see Cremona et al. 2008 for the opposite). Epiphytes and detritus can positively affect invertebrate abundance by providing additional structural complexity, thereby increasing shelter from predation (Hall and Bell 1988; Martin-Smith 1993; Isaksson et al. 1994). In addition, epiphytes and detritus are important food resources for many invertebrates (Kornijów et al. 1995; Bologna and Heck 1999; Orav-Kotta and Kotta 2004).

Shallow wave-protected soft-bottom areas in the Baltic Sea have a high diversity of submerged plant species of varying morphologies (Munsterhjelm 1997). These diverse plant communities constitute habitats colonized by a large number of invertebrate taxa (Hansen et al. 2008). The increased nutrient load in the Baltic Sea since the mid-twentieth century has resulted in changes in the benthic vegetation (e.g. Schramm 1996; Munsterhjelm 2005) and thereby indirectly affected the physical structure of coastal habitats. On shallow wave-protected soft-bottoms, *Chara* species have decreased in cover and distribution and in several areas been replaced by angiosperms more tolerant to nutrient-enriched conditions, such as *Myriophyllum spicatum* L., *Ceratophyllum demersum* L., *Potamogeton pectinatus* L., and *Potamogeton perfoliatus* L. (Wallentinus 1979; Blindow 2000; Munsterhjelm 2005). To predict the effects of these changes on the faunal community, it is important to evaluate whether plant species differ in their function as habitat and relate such differences to variations in plant characteristics, such as morphology. The increased nutrient load has also resulted in increased growth of filamentous and sheet-like ephemeral algae (e.g. Fletcher 1996; Schramm 1996). When these algae become detached from their substratum, they form drifting mats that are often transported to shallow soft-bottom areas (e.g. Bonsdorff 1992) where they may become trapped and entangled in large structured plants and affect the faunal community (Boström and Bonsdorff 2000). In this paper, we refer to loose-lying and attached ephemeral algae as epiphytes to distinguish them from coarsely structured algae (e.g. *Chara* spp.).

The present study aimed to investigate differences in the invertebrate community between three large structuring soft-bottom plant species in the Baltic Sea and to determine whether differences in morphological complexity between the plants affect their function as habitat. The plants studied were *Potamogeton perfoliatus*, *Chara baltica* Bruzelius, and *Myriophyllum spicatum*. We chose to define morphological complexity as the number of branches and

the perimeter of a two-dimensional image of the plants per shoot surface area, although scale differences in complexity measures must be further examined (cf. Attrill et al. 2000; Dibble et al. 2006; Warfe et al. 2008). In addition to the three natural plants, three morphologically similar artificial plastic plants were used in an attempt to isolate the effect of structure from those of other biotic characteristics of the natural plants (e.g. palatability and allelopathic substances). We further examined the effects of plant morphology on epiphytes, as such algae drifted to and were trapped in the investigated plants during the study.

We hypothesized that (I) the abundance, biomass, taxon richness, and taxon composition of plant-associated macroinvertebrates differ between the investigated plant species; (II) the macroinvertebrate abundance, biomass, and taxon richness are higher on a morphologically more complex plant than on a morphologically simpler plant; and (III) the epiphyte biomass is higher on a morphologically more complex plant than on a morphologically simpler plant.

Materials and methods

Study site

The study was conducted in July 2007 in three shallow bays near the Askö Laboratory (N58.823° E17.636°) in the north-western Baltic Proper. The colonization experiment was conducted in two bays on Askö Island (sites A and B), less than 2 km south-east of the laboratory. The field samples were collected at sites A and C, the latter bay being located approximately 10 km west of the laboratory. All sampled bays were small (2–9 ha), sheltered from wind and waves, did not exceed 3 m in depth, and had a muddy bottom substrate. The plant communities in the bays were dominated by large structuring angiosperms (e.g. *Potamogeton pectinatus* L., *Potamogeton perfoliatus*, and *Myriophyllum spicatum*) and algae (e.g. *Chara* spp. and *Fucus vesiculosus* L.). Within the bays, there were gradients in the bottom substratum and vegetation composition due to increased wave exposure towards the bay openings. In the study area, the salinity ranges from 5.8 to 7.2 psu (Wallentinus 1976) and during our study the salinity was 6.1 psu. The daytime water surface temperature was 18–20°C throughout the study period.

Field collection

To examine the occurrence of macroinvertebrates and epiphytes on the investigated plants (i.e. *Potamogeton perfoliatus*, *Chara baltica*, and *Myriophyllum spicatum*), 10 shoots of each of the three plant species were sampled at a depth of 0.8–1.8 m by a free diver. The shoots were

collected at five sampling points in each of the sites A and C. The sampling points were randomly located within an area of 0.5 ha in the two bays. At every sampling point, one shoot of each species was taken to obtain samples from abiotic conditions that were as similar as possible. During sampling, each plant shoot was covered with a 6-L plastic bag and cut with scissors just above the sediment surface. The plant shoots were kept cold during transportation and stored dark at 11°C for a maximum of 1 d before sampling the epiphytes (including large-sized phytodetritus) and invertebrates. Epiphytes and invertebrates were deep-frozen (−20°C) until later sorting and identification. Animals were identified to species level with some exceptions; Hydrachnidia, Copepoda, Cladocera, Ostracoda, *Gammarus*, and *Hydrobia* were not identified to a lower taxonomic level, and most insects were identified only to family level. Hydrozoa and Oligochaeta were not further identified, as they were damaged during freezing. Juveniles of the bivalves *Parvicardium hauniense* Petersen et Russell and *Cerastoderma glaucum* Poiret were grouped, as they were difficult to separate. The number of invertebrate individuals was counted, and together with the investigated plants and epiphytes, the animals were weighed after drying at 49–59°C to constant weight. Only the presence or absence of colonial sessile animals (hydrozoans and bryozoans) was noted.

Colonization experiment

A colonization experiment was carried out in the field, using six treatments with natural and artificial plants. The treatments were natural *Potamogeton perfoliatus*, *Chara baltica*, and *Myriophyllum spicatum* and artificial plants resembling the natural plants in morphology (Fig. 1). The plant species will hereafter be referred to as *Potamogeton*, *Chara*, and *Myriophyllum*. The experimental treatments were prepared as small plant patches of several shoots each. The natural plants used in the experiment were collected at sites A and B at a depth of 1–2 m. Before the experiment, epiphytes and fauna were carefully removed from the plants. Throughout the experimental preparations, the plants were kept in aquaria filled with sand-filtered, aerated seawater at an ambient temperature of approximately 17°C under 34 μ Einstein light conditions (measured underwater) for a maximum of 5 d. Each experimental patch of natural plants consisted of a bundle of 5–8 plant shoots, 5–25 cm in height, having a combined length of 130 cm. Each experimental patch of artificial plants consisted of a bundle of 5–6 shoots of plastic aquarium plants, 10–28 cm in height, having a combined length of 112–126 cm. The artificial plants were acquired from the manufacturer Hagen (Montreal, Canada) and were all of the same plastic material and colour. They were altered through cutting to improve their resemblance to

Fig. 1 Apical parts of natural plants (*top*) and top segments of artificial plants (*bottom*) used in the study. The *scale line* in the left corner corresponds to 1 cm
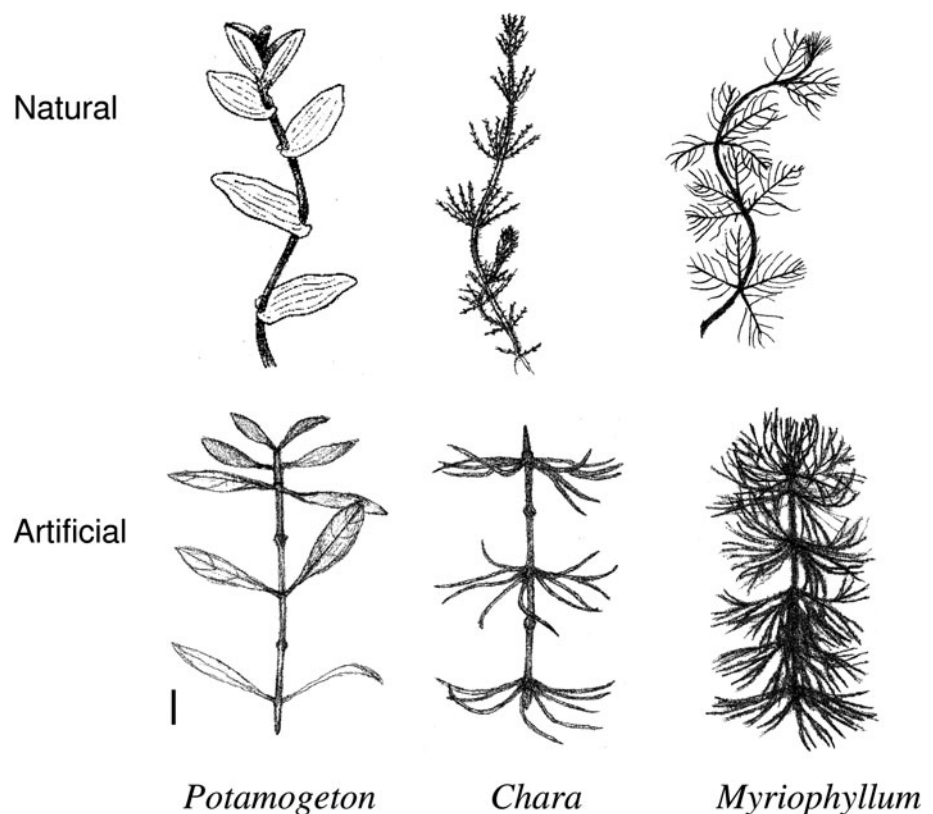
the three natural plants (Fig. 1). Each plastic plant shoot consisted of 1–4 segments of standardized shape.

The experiment was set up according to a randomized complete block design. In each block, single replicates of each of the six plant treatments were placed 2 m apart in a circle. The experimental treatments were placed in a fixed order in the circles, and each circle was rotated one-sixth of a revolution in relation to the previous one in an attempt to eliminate any possible influence from the rocky bay edges. A total of 96 samples in 16 blocks were placed in the two bays, eight per bay, by SCUBA divers. The plant patches were anchored using concrete pots, which were dug into the bottom sediment in the bays. The plants were left for two weeks in the field to be colonized by fauna.

To ensure that adjacent vegetation (from which invertebrates could migrate) did not differ between treatments (i.e. to ensure that one treatment was not positioned more often adjacent to a specific vegetation type), the percentage cover of plants and algae within a 1-m radius of each sample was visually estimated. There was no significant difference in plant community composition between treatments, though there was between blocks (treatments $\chi^2 = 0.04$, $F = 0.91$, $P = 0.8$; blocks $\chi^2 = 0.88$, $F = 6.46$, $P = 0.001$; constrained canonical correspondence analysis (CCA) on fourth-root transformed data in the vegan package in R 2.10.0; Oksanen et al. 2009; R Development Core Team 2009).

At sampling, each plant patch was covered with a mesh bag (mesh size 1.0 mm) and detached from the pot, whereupon the bag was directly sealed. The samples were deep-frozen ($-20°C$) until the animals were sorted, identified, and counted. The same level of identification was used as for the samples in the field collection. Ostracoda, Copepoda, and Cladocera, however, were excluded from the experimental dataset, as these small organisms could have passed through the mesh bags after sampling. The biomass of the animals was determined by multiplying the abundance of a certain taxon by a standard weight for that taxon in a specific size class (three size classes for all common taxa). These standard weights were taken from the field collection data and previous studies of similar habitats (Hansen, unpublished data; Hansen et al. 2008). In addition, epiphytes (including large-sized phytodetritus) were identified and weighed after drying at 49–59°C to constant weight.

Plant structure

To estimate the morphological characteristics of the studied natural plants, nine additional shoots of each of the three plant species were collected from the study sites. For the artificial plants, where all replicates of the same type were identical, the morphological characteristics were measured once for each type. The plants were pressed and scanned (grey scale, 300 dpi, TIFF format). ImageJ software (Rasband 1997–2009) was used to convert all greyscale images to binary images and to analyse the total shoot surface area and perimeter. The number of branches on each shoot was also counted. The plant perimeter and number of branches were divided by the surface area and used as a measure of plant morphological complexity. In addition, the dry weight of each plant was measured to obtain a surface area to dry weight ratio for each species; the obtained ratio was used to calculate the surface area of each of the 30 plants from the field collection. For the natural plants used in the colonization experiment, surface area was instead measured separately (after sampling) by pressing and scanning, using the procedure and software described earlier.

Statistical analyses

Invertebrate taxon richness (number of taxa per individuals) was computed from the original taxon density data (number of taxa per sample), as the number of taxa generally increases with greater abundance of individuals (Gotelli and Colwell 2001). The taxon richness was calculated by rarefaction to a constant number of individuals per sample using Hurlbert's (1971) formulation in the statistical package vegan in R 2.10.0 (Oksanen et al. 2009; R Development Core Team, 2009). The rarefied taxon richness was calculated for 10 individuals in the field collection data (abundance range 2–784 individuals, three samples having < 10 individuals) and 30 individuals in the colonization experiment data (abundance range 28–423 individuals, one sample having < 30 individuals).

For the field collection data, differences in invertebrate abundance, biomass, and rarefied taxon richness, as well as differences in epiphyte biomass, between the three investigated plant species were tested using ANOVA in R 2.10.0. Besides the factor plant species, bay was also included as a factor in the analyses. In models in which the effect of plant species or its interaction with bay was significant, multiple comparisons were made using two-sided Tukey's honestly significant difference (HSD) tests.

For the colonization experiment data, differences in invertebrate abundance, biomass, and rarefied taxon richness, as well as differences in epiphyte biomass, between the investigated plants were tested using linear mixed-effects models in the nlme package in R 2.10.0 (Crawley 2007; Pinheiro et al. 2009). Plant type (natural or artificial) and plant species were used as fixed factors and experimental block as a random blocking factor. The significance of the fixed factors was tested using ANOVA (maximum likelihood). In models in which the effect of plant species or its interaction with plant type was significant, multiple

comparisons were made using two-sided Tukey contrasts (multcomp package in R 2.10.0, Hothorn et al. 2008).

To meet the assumptions of parametric tests, invertebrate abundance, invertebrate biomass, and epiphyte biomass were $\log_{10} (x + a)$ transformed, a being the lowest abundance counted or biomass measured.

To investigate whether the invertebrate taxon composition differed in relation to plant species, CCAs were conducted on invertebrate abundance from both the field collection data and the colonization experiment data. The structure of the analyses was the same as the ones used for the univariate models, i.e. including bay and plant species in the analysis of the field collection data, and including plant type and species in the analysis of the colonization experiment data. Besides, experimental block was treated as a blocking factor in the analysis of the colonization experiment data. To investigate the effect of only plant species on the invertebrate taxon composition of the field collection data, a partial CCA was additionally conducted using bay as a conditioning factor. Undue effects of rare and highly abundant taxa were reduced by removing taxa occurring in fewer than three samples, downweighting the remaining rare taxa, and fourth-root transforming the data (following recommendations for CCA by ter Braak and Šmilauer 2002). Ordinations were inspected for possible arch effects (ter Braak and Šmilauer 2002).

Results

Plant structure

The artificial plants structurally resembled the corresponding natural plants according to the factors measured (Fig. 2a,b). *Potamogeton* had the simplest structure with its broad leaves and few branches. *Chara* was of medium complexity, and *Myriophyllum* was the most complex of the three studied plant species, having a larger perimeter and more branches per surface area than did *Chara* and *Potamogeton*. Natural *Myriophyllum*, however, was more complex than its artificial version, and natural *Chara* had a higher number of branches than did artificial *Chara*.

The structural complexity of the natural plants was not confounded by plant surface area. Natural *Potamogeton* had the largest surface area per sample, followed by *Myriophyllum* and *Chara* (Fig. 2c,d). Plants in the colonization experiment had a higher surface area (Fig. 2c) than did the plants in the field collection, as only one shoot was collected in each of the latter samples (Fig. 2d). The ranking of surface area between the artificial plants differed from that of the natural plants; the most complex structured plant, *Myriophyllum*, also had the largest surface area, followed by *Potamogeton* and *Chara* (Fig. 2c).
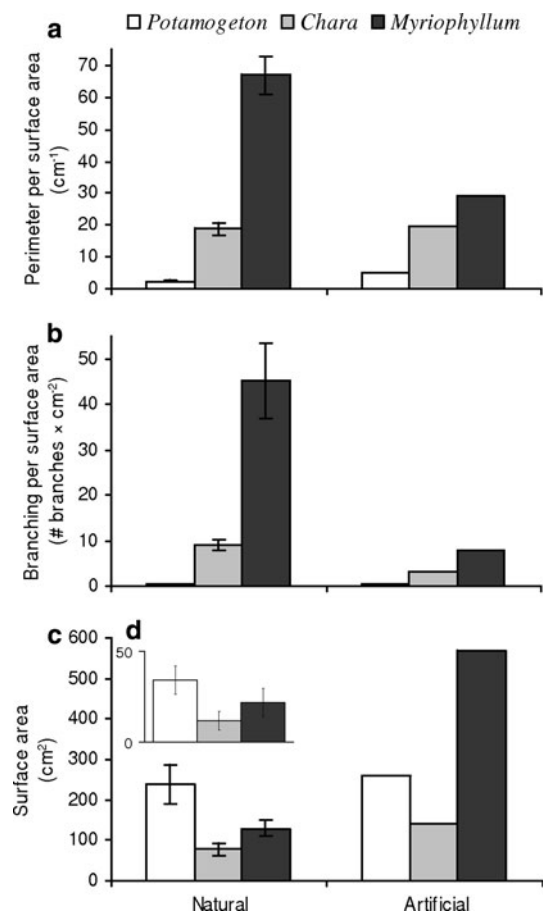

Fig. 2 Morphological characteristics of natural and artificial *Potamogeton*, *Chara*, and *Myriophyllum* used in the colonization experiment ($\bar{x} \pm CI_{95}$ for the natural plants): **a** perimeter per surface area ($n = 9$), **b** branching per surface area ($n = 9$), and **c** surface area per sample ($n = 16$). The *small inset figure* **d** shows surface area of the field collection samples ($n = 10$)

Macroinvertebrate abundance, biomass, and taxon richness

A total of 41 macroinvertebrate taxa were identified in the study (Appendix). The same faunal taxa were numerically dominant in both the field collection and colonization experiment datasets. These were Chironomidae, *Parvicardium hauniense/Cerastoderma glaucum*, *Idotea chelipes* (Pallas), and *Gammarus* spp. In addition, *Hydrobia* spp., *Theodoxus fluviatilis* (L.), *Idotea balthica* (Pallas), and *Bithynia tentaculata* (L.) were very common in the samples. As only one shoot per sample was collected in the field collection and several shoots per sample were used in the colonization experiment, the latter samples had a higher mean invertebrate abundance ($\bar{x}$ 156 ind. $\pm$ 17 CI_{95}) and biomass ($\bar{x}$ 0.23 g d.w. $\pm$ 0.04 CI_{95}) than did the former ($\bar{x}$ 96 ind. $\pm$ 61 CI_{95}; $\bar{x}$ 0.03 g d.w. $\pm$ 0.02 CI_{95}). However, the mean abundance per area, i.e. invertebrate density, was seven times lower in the colonization experiment than in

the field collection. The mean number of invertebrate taxa was higher in the colonization experiment ($\bar{x}$ 10.1 ± 0.6 CI_{95}) than in the field collection ($\bar{x}$ 5.8 ± 0.7 CI_{95}). A higher number of taxa was found for several taxonomic groups, but the sessile colonial animals *Electra crustulenta* (Pallas) and *Hydrozoa* sp. as well as the small crustaceans Copepoda, Cladocera, and Ostracoda were recorded only in the field collection due to methodological differences in sampling (see Materials and methods).

Field collection

Macroinvertebrate abundance and biomass differed between the three plant species sampled (Table 1a, b). The simply structured *Potamogeton* harboured significantly lower invertebrate abundance than did either of the complexly structured plants, *Chara* and *Myriophyllum* (Fig. 3a). The invertebrate biomass was also lower on *Potamogeton* than on *Myriophyllum* (Fig. 3b) and tended to be lower on *Potamogeton* than on *Chara* ($P = 0.085$). There was no significant difference in invertebrate abundance or biomass between *Chara* and *Myriophyllum*. Invertebrate abundance also differed significantly between the two sampled bays (Table 1a), being lower in bay

A (Log$_{10}$ $\bar{x}$ 1.4 ± 0.2 CI_{95}) than in bay C (Log$_{10}$ $\bar{x}$ 1.8 ± 0.3 CI_{95}).

For the rarefied taxon richness of invertebrates, an interaction effect was found between plant species and bay (Table 1c). The taxon richness was higher on *Potamogeton* than on *Chara* and *Myriophyllum* in one of the bays (bay C), but not in the other (bay A) (Fig. 3c).

Invertebrate taxon composition also differed between the investigated plant species, in addition to between the bays (Table 2a). The model explained 30% of the variation in taxon composition (total inertia 1.36, constrained inertia 0.41). Partialling out the effect of only plant species on invertebrate taxon composition, taking differences in taxon composition between bays into consideration (with bay as conditioning factor), the model explained 16% of the variation (total inertia 1.36, constrained inertia 0.22). Taxa with the highest abundance in the study (i.e. *Parvicardium hauniense/Cerastoderma glaucum*, Chironomidae, and *Idotea chelipes*) were more closely associated with *Chara* and *Myriophyllum* (Fig. 4). The mean abundances of these taxa were 2–35 times higher on *Chara* or *Myriophyllum* than on *Potamogeton*. The lower taxon richness found on *Myriophyllum* and *Chara* than on *Potamogeton* could be related to a more uneven distribution of taxa on these complex plants, with the numerical dominance of a few taxa. The taxa most closely associated with *Chara* were *Heterotanais oerstedi* (Krøyer), *Theodoxus fluviatilis*, and Ostracoda, while Curculionidae, *Mytilus edulis* (L.), and Cladocera were the taxa most closely associated with *Myriophyllum*. Some Curculionidae individuals associated with *Myriophyllum* were identified to the species *Eubrychius velutus* Beck. *Cataclysta* sp. and Opistho-branchia sp. were more closely associated with *Potamogeton*. Eigenvalue of the first axis of the ordination (Fig. 4) was higher (0.17) than that of the second (0.06), indicating a larger difference in invertebrate taxon assemblage between *Potamogeton* and the two other plants than between *Chara* and *Myriophyllum*.

Colonization experiment

An interaction effect between plant species and type was found for macroinvertebrate abundance, biomass, and taxon richness (Table 3a–c). Invertebrate abundance was higher on artificial *Myriophyllum* than on artificial *Chara* and *Potamogeton*, but there was no significant difference in invertebrate abundance between the natural plants (Fig. 5a). Invertebrate abundance was also higher on artificial *Myriophyllum* than on natural *Chara* and *Potamogeton*, but not higher than on natural *Myriophyllum*. Like invertebrate abundance, invertebrate biomass was higher on artificial *Myriophyllum* than on artificial *Chara* and *Potamogeton* (Fig. 5b). Artificial *Myriophyllum* also harboured higher

Table 1 ANOVA testing for effects of bay and plant species on invertebrate (a) abundance, (b) biomass, and (c) taxon richness and on (d) epiphyte biomass in the field collection

Factors	Df	SS	MS	F	P
(a) Invertebrate abundance (Log$_{10}$)					
Bay	1	1.0	1.0	8.6	**0.007**
Plant species	2	4.7	2.4	19.5	**<0.001**
Bay × plant species	2	0.3	0.1	1.1	0.36
Residuals	24	2.9	0.1		
(b) Invertebrate biomass (Log$_{10}$)					
Bay	1	0.7	0.7	2.2	0.16
Plant species	2	3.0	1.5	4.8	**0.017**
Bay × plant species	2	0.1	0.1	0.2	0.86
Residuals	24	7.5	0.3		
(c) Invertebrate taxon richness (rarefied per 10 individuals)					
Bay	1	0.6	0.6	0.4	0.51
Plant species	2	10.2	5.1	4.0	**0.032**
Bay × plant species	2	12.3	6.1	4.8	**0.018**
Residuals	24	30.8	1.3		
(d) Epiphyte biomass (Log$_{10}$)					
Bay	1	2.4	2.4	10.9	**0.003**
Plant species	2	2.0	1.0	4.4	**0.024**
Bay × plant species	2	0.6	0.3	1.4	0.28
Residuals	24	5.4	0.2		

Significant effects are indicated in bold

Fig. 3 Mean ($\pm CI_{95}$) invertebrate **a** abundance, **b** biomass, and **c** taxon richness on *Potamogeton*, *Chara*, and *Myriophyllum* in the field collection. Samples from bays A and C are pooled in **a** and **b** ($n = 10$) but are shown separately in **c** ($n = 5$ per bay). *Bars topped by different letters* differ significantly (Tukey test, $P < 0.05$)
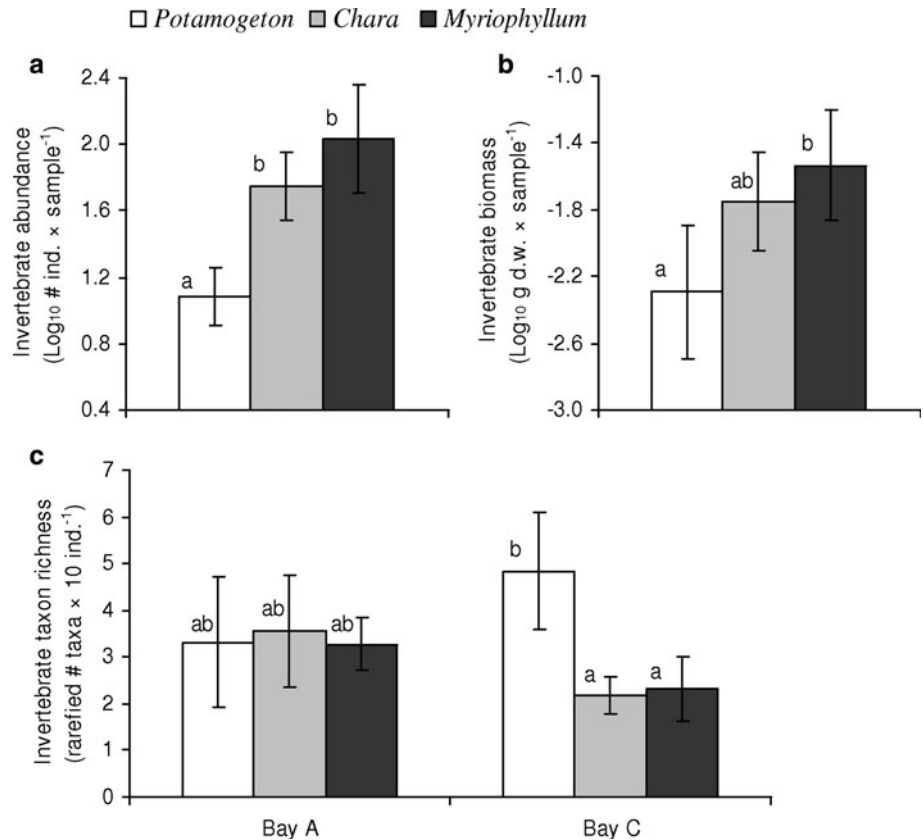

Table 2 Significance test of CCA testing for (a) the effect of bay and plant species on invertebrate taxon composition in the field collection and (b) the effect of plant type (natural or artificial) and plant species on invertebrate taxon composition in the colonization experiment

Factors	Df	χ^2	Pseudo-F	P
(a) Field collection				
Bay	1	0.10	2.5	**0.004**
Plant species	2	0.22	2.8	**0.001**
Bay × plant species	2	0.09	1.2	0.29
Residual	24	0.95		
(b) Colonization experiment				
Plant type	1	0.02	2.1	**0.007**
Plant species	2	0.03	1.5	**0.032**
Plant type × species	2	0.04	1.8	**0.009**
Residual	90	0.96		

Significant effects are indicated in bold (999 permutations). Inertia for the models are given in the text

Fig. 4 CCA ordination of invertebrate taxon composition in relation to the three plants *Potamogeton*, *Chara*, and *Myriophyllum* in the field collection. The ordination was conducted using bay as a conditional factor (eigenvalue of the first axis 0.17 and of the second axis 0.06). See text for details. Abbreviations of full taxonomic names of animals (*underlined*) in taxonomic order: Hexapoda: Curculionidae, Chironomidae, and *Cataclysta* sp.; Crustacea: Copepoda, Cladocera, *Gammarus* spp., *Idotea chelipes*, *Heterotanais oerstedi*, and Ostracoda; Gastropoda: *Bithynia tentaculata*, *Hydrobia* spp., *Theodoxus fluviatilis*, and Opisthobranchia sp.; and Bivalvia: *Mytilus edulis* and *Parvicardium hauniense/Cerastoderma glaucum*

invertebrate biomass than did the natural plants. Among the natural plants, invertebrate biomass was lower on *Chara* than on *Potamogeton*. Invertebrate taxon richness was higher on natural *Potamogeton* than on natural *Chara* and *Myriophyllum* (Fig. 5c), while among the artificial plants, invertebrate taxon richness was instead higher on *Myriophyllum* than on *Potamogeton*.
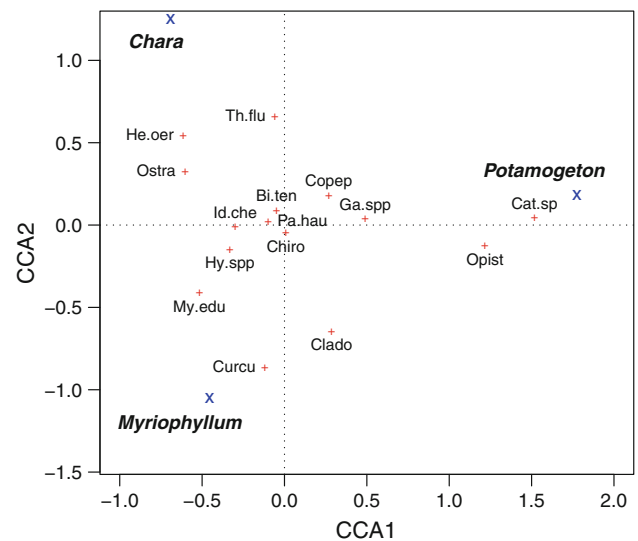
Table 3 ANOVA table of mixed-effects models testing for effects of plant type (natural or artificial) and plant species on invertebrate (a) abundance, (b) biomass, and (c) taxon richness and on (d) epiphyte biomass in the colonization experiment

Factors	nDf	dDf	F	P
(a) Invertebrate abundance (Log$_{10}$)				
Intercept	1	75	2829.0	**<0.001**
Plant type	1	75	0.1	0.77
Plant species	2	75	17.6	**<0.001**
Plant type × species	2	75	4.0	**0.023**
(b) Invertebrate biomass (Log$_{10}$)				
Intercept	1	75	321.6	**<0.001**
Plant type	1	75	20.5	**<0.001**
Plant species	2	75	31.5	**<0.001**
Plant type × species	2	75	22.8	**<0.001**
(c) Invertebrate taxon richness (rarefied per 30 individuals)				
Intercept	1	75	646.4	**<0.001**
Plant type	1	75	1.3	0.26
Plant species	2	75	1.9	0.16
Plant type × species	2	75	11.9	**<0.001**
(d) Epiphyte biomass (Log$_{10}$)				
Intercept	1	75	17.0	**<0.001**
Plant type	1	75	0.3	0.60
Plant species	2	75	9.1	**<0.001**
Plant type × species	2	75	0.3	0.78

Significant effects are indicated in bold

An interaction effect between plant species and type was also found for invertebrate taxon composition (Table 2b). The model explained only 8.6% of the variation in taxon composition (total inertia 1.05, constrained inertia 0.09). The variation in invertebrate taxon composition in relation to plant species was also explored separately for the natural and artificial plants, but these models explained less of the variation in taxon composition than did the full model including both natural and artificial plants. This indicates very small and little systematic differences in faunal composition between the plant species in the colonization experiment.

Epiphytes

The epiphytes examined on the studied plants consisted mostly of loose-lying algae and phytodetritus entangled in the plants, but also included some attached algae. Epiphytes consisted mainly of filamentous algae (i.e. *Ceramium tenuicorne* (Kützing) Wærn, *Polysiphonia* spp., *Dictyosiphon foeniculaceus* (Hudson) Greville, *Ectocarpus* spp./*Pylaiella littoralis* (L.) Kjellman, *Cladophora* spp., and other uniseriate Chlorophyta and Cyanophyceae). Detritus occurred only in small amounts. Samples in the
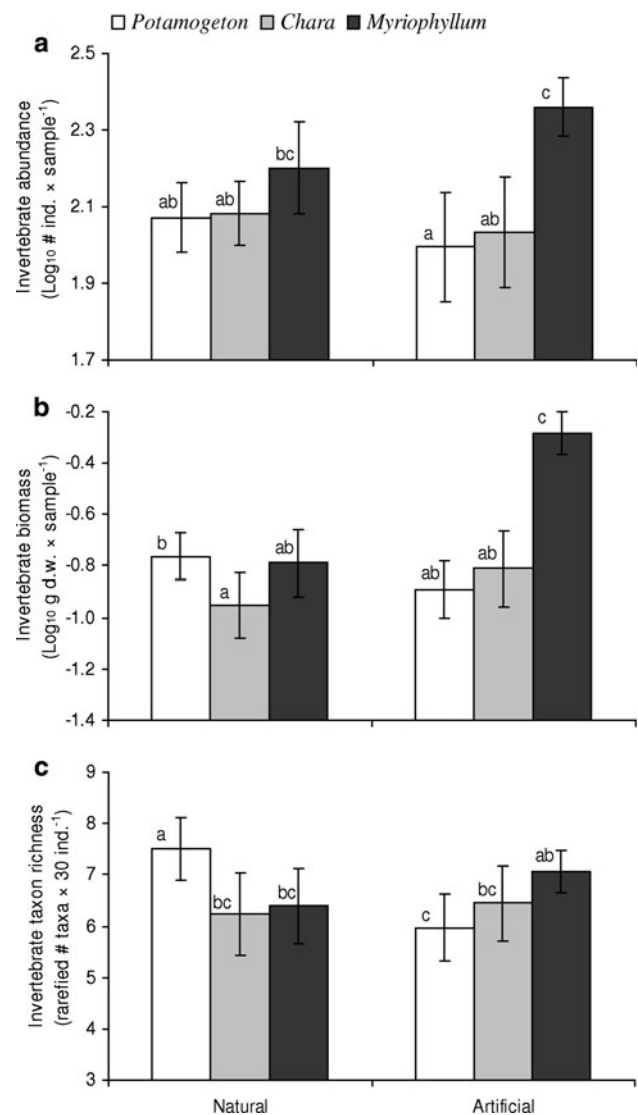

Fig. 5 Mean (±CI$_{95}$) invertebrate **a** abundance, **b** biomass, and **c** taxon richness in the colonization experiment using natural and artificial *Potamogeton*, *Chara*, and *Myriophyllum* (n = 16). *Bars* topped by *different letters* differ significantly (Tukey test, $P < 0.05$)

colonization experiment had a higher ratio of loose-lying to attached epiphytes than did samples in the field collection, and also included small proportions of non-filamentous algae (i.e. *Chorda filum* (L.) Stackhouse, *Furcellaria lumbricalis* (Hudson) Lamouroux, and *Ulva* spp.).

The epiphyte biomass differed significantly between plant species in both the field collection and the colonization experiment (Tables 1d and 2d). The epiphyte biomass was significantly lower on *Potamogeton* than on *Chara* in the field collection (Fig. 6a) and lower on *Potamogeton* than on both *Chara* and *Myriophyllum* in the colonization experiment (Fig. 6b). Epiphyte biomass also differed between the sampled bays in the field collection, being lower in bay C (Log$_{10}$ $\bar{x}$ − 1.6 ± 0.3CI$_{95}$) than in bay
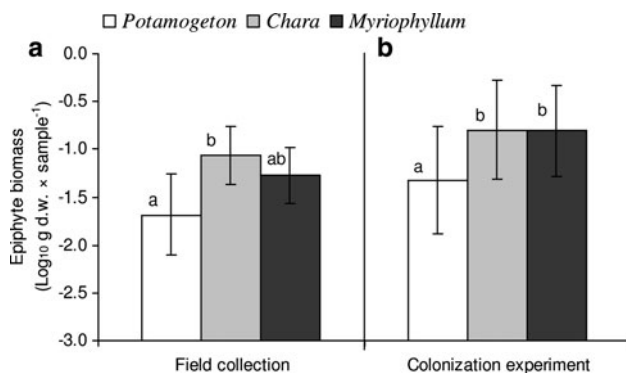
Fig. 6 Mean ($\pm CI_{95}$) epiphyte biomass of *Potamogeton*, *Chara*, and *Myriophyllum* in **a** the field collection and **b** the colonization experiment. Samples from bays A and C are pooled in (**a**) ($n = 10$), and samples of natural and artificial plants are pooled in (**b**) ($n = 32$). *Bars* topped by *different letters* differ significantly (Tukey test, $P < 0.05$)

A ($Log_{10} \bar{x} - 1.1 \pm 0.2CI_{95}$). There was no difference in epiphyte biomass between natural and artificial plants in the colonization experiment.

Discussion and conclusions

The present study demonstrates that the species identity of large structuring plants in soft-bottom habitats affects the plant-associated macroinvertebrate community. In accordance with our first hypothesis, we found a difference in faunal community response variables between the studied plants in our field collection (Figs. 3a–c, 4). Differences in invertebrate abundance, species richness, and community composition between various aquatic plant species have been reported in several cases (e.g. Cyr and Downing 1988; Taniguchi et al. 2003; Xie et al. 2006).

Results from the field collection also partly support our second hypothesis: that plants with more complex morphology (e.g. *Myriophyllum* and *Chara*) should have a higher abundance and biomass of invertebrates than should plants with simpler morphology (e.g. *Potamogeton*) (Fig. 3a, b). However, we found no increase in invertebrate abundance or biomass with increased complexity between *Chara* and *Myriophyllum*. Invertebrate abundance and biomass were also highest on the complexly structured artificial *Myriophyllum* in the colonization experiment (Fig. 5a, b). A higher abundance of invertebrates in more structurally complex habitats is in accordance with many previous studies (e.g. Jeffries 1993; Taniguchi et al. 2003; Hauser et al. 2006). Increased invertebrate abundance with greater habitat complexity can depend on an increase in the amount and range of exploitable microhabitats (e.g. McNett and

Rypstra 2000; Willis et al. 2005). Under conditions of resource limitation, complex structured plant habitats could facilitate the coexistence of species and individuals through niche partitioning, as resources and microhabitats can be used in a greater number and variety of ways in complex than in simple structures. In addition, complex habitats can facilitate shelter from both physical disturbance (i.e. reduced water velocity, Gregg and Rose 1982) and predation (e.g. Warfe and Barmuta 2004).

Results from the colonization experiment partly contrasted the field collection results. Invertebrate abundance and biomass were not significantly higher on the complexly structured natural *Myriophyllum* and *Chara* than on the simpler structured natural *Potamogeton* (Fig. 5a, b). Invertebrate biomass was even lower on natural *Chara* than on natural *Potamogeton*, although this difference was small.

Plants in the colonization experiment may still have been in a colonization phase at the time of sampling, two weeks after being placed in the field. This possibility is supported by the low invertebrate densities on the plants in the colonization experiment versus on the plants in the field collection. In comparison, Boström and Bonsdorff (2000) reported that invertebrate colonization occurred on artificial seagrasses throughout the 2 months of an experiment in the northern Baltic Sea, and Edgar (1991) reported that the most rapid invertebrate colonization of artificial algae occurred between 8 and 24 days in the East China Sea. Virnstein and Curran (1986), however, reported that invertebrate colonization of artificial seagrasses levelled off after just 4 days in an experiment in the Indian River lagoon, Florida. Interactions between individuals and species may have been weaker in the more sparsely occupied plants in the colonization experiment than in the more densely occupied plants in the field collection. At low invertebrate density, the effect of habitat complexity on the invertebrate community may be less profound, explaining why we did not find higher invertebrate abundance and biomass on more complexly structured natural plants in the experiment.

In accordance with our second hypothesis, the rarefied invertebrate taxon richness was higher on the more complexly structured artificial *Myriophyllum* than on the simpler structured artificial *Potamogeton* in the colonization experiment (Fig. 5c). However, the difference was small, and the results for the natural plants contradicted our hypothesis. The rarefied invertebrate taxon richness was lower on the complex natural *Myriophyllum* and *Chara* than on the simpler *Potamogeton* in the colonization experiment (Fig. 5c) and in one of the bays in the field collection (Fig. 3c). These results contradict previous findings of higher invertebrate species richness on more

complexly structured plants (Taniguchi et al. 2003; Hauser et al. 2006; Warfe et al. 2008). Consequently, our results imply that the relationship between structural complexity of plants and species richness of invertebrates is itself complex and does not always respond to general predictions.

Also other factors besides plant structure can, of course, mediate the invertebrate community in plant habitats. Two such factors are plant palatability and plant-secreted allelopathic substances. Baltic Sea invertebrate herbivores have been observed to feed on both fresh angiosperms and charophytes (Kotta et al. 2004; Boström and Mattila 2005). Some species may even specialize on certain plant species, as in the case of *Eubrychius velutus* (Culculionidae), which feeds and completes all its life stages on *Myriophyllum* (Newman et al. 2006). Allelopathic substances have been documented for *Myriophyllum spicatum* (Gross 2003) and *Chara baltica* (Wium-Andersen et al. 1982), and decreased survival or changed behaviour of some invertebrate taxa has been observed in the presence of *M. spicatum* or extracts of the plant (dipteran larvae, Dhillon et al. 1982; mysids, Lindén and Lehtiniemi 2005). Allelochemicals are rare among submerged *Potamogeton* species (Gross 2003) and, to the best of our knowledge, have not been reported for *Potamogeton perfoliatus*. The interaction effect between plant type and plant species on invertebrate abundance and biomass in the colonization experiment could possibly be explained by negative effects on invertebrates by allelochemicals secreted by natural *Myriophyllum*. In that case, the positive effect of high structural complexity is counteracted by the repellent effect of allelochemicals of this species. Artificial *Myriophyllum*, however, also had a larger surface area, which additionally could explain the higher abundance and biomass found on the plant.

During the study, filamentous algae drifted into the bays and became entangled in the plants. The algae accumulation differed between the plants, and in accordance with our third hypothesis, the simply structured *Potamogeton* accumulated the lowest biomass of epiphytes (Fig. 6). Lower biomass of epiphytes and detritus on structurally simple than on complex plants has been found in several studies (Gregg and Rose 1982; Jeffries 1993; Taniguchi et al. 2003; Warfe and Barmuta 2006). As epiphytes can affect invertebrate distributions, plant morphology may indirectly affect invertebrate communities through differences in their capacity to trap and accumulate drifting plant material. We suggest that complex structured plants harbour higher invertebrate abundance and biomass partly because they accumulate more epiphytes and detritus.

Several previous studies have investigated the role of drifting mats of filamentous algae and found both positive (Norkko 1998; Norkko et al. 2000; Lauringson and Kotta 2006) and negative effects (Norkko and Bonsdorff 1996a, 1996b; Norkko et al. 2000) on invertebrates. The potential positive effects of epiphytes on invertebrate abundance and biomass found in the present study could be caused by the transport, via drifting algae, of animals to plants (Salovius et al. 2005), by increased shelter against predators from the additional structures of algae (Isaksson et al. 1994; Norkko 1998), and by increased food availability (Lauringson and Kotta 2006). Baltic Sea invertebrate herbivores often prefer feeding on epiphytes rather than on coarsely structured plants and algae (Orav-Kotta and Kotta 2004; Goecker and Kåll 2003; Boström and Mattila 2005).

To conclude, this study demonstrates that the species identity of large structuring soft-bottom plants can influence the small-scale distribution of plant-associated macroinvertebrates. Changes in aquatic vegetation communities, due to factors such as eutrophication, may induce changes in faunal communities as the plant habitat structure is altered. We found some support for higher invertebrate abundance and biomass, but not taxon richness, in morphologically more complex plant habitats than in simpler plant habitats. Results from our field collection data indicate that a changed vegetation community with decreased cover and distribution of the suggested eutrophication-sensitive taxon *Chara*, and increased cover and distribution of the more eutrophication-tolerant *Potamogeton perfoliatus*, would result in lower invertebrate abundance and biomass, potentially affecting higher trophic levels. A change in vegetation composition to increased cover and distribution of the eutrophication-tolerant *Myriophyllum spicatum* would, according to our field collection data, not result in changed invertebrate abundance and biomass. Our results also indicate that the effect of plant morphology on the invertebrate community may partly be explained by the plants' different capacities to accumulate drifting and epiphytic algae, which in turn influence invertebrates.

Appendix

See Table 4.

Table 4 Invertebrates found in the present study in three shallow soft-bottom bays in the north-western Baltic Proper

Invertebrate taxa	Presence in no. of samples	Total abundance
Chironomidae	123	5,131
Parvicardium hauniense Petersen & Russell/*Cerastoderma glaucum* Poiret	123	5,087
Idotea chelipes (Pallas)	118	2,901
Theodoxus fluviatilis (L.)	97	662
Hydrobia spp.	87	972
Gammarus spp.	85	1,250
Bithynia tentaculata (L.)	74	306
Idotea balthica (Pallas)	70	659
Radix balthica (L.)[a]	56	232
Hediste diversicolor (O.F. Müller)	31	89
Leptocheirus pilosus Zaddach	30	117
Hydroptilidae[a]	28	56
Potamopyrgus antipodarum Gray	27	58
Opisthobranchia unid. sp.	26	43
Mytilus edulis L.	19	37
Cyanophthalma obscura (Schultze)[a]	16	71
Lymnaea stagnalis (L.)[a]	16	19
Jaera albifrons spp. Leach	14	22
Limapontia capitata (O.F. Müller)[a]	11	24
Cataclysta sp.	11	20
Electra crustulenta (Pallas)[b]	11	
Copepoda[b]	9	19
Curculionidae	8	12
Macoma balthica (L.)	8	12
Hydrozoa unid. sp.[b]	8	
Corophium volutator (Pallas)[a]	7	7
Praunus inermis (Rathke)[a]	6	11
Hydrachnidia[a]	5	6
Limnephilidae	4	4
Piscicola geometra (L.)	4	4
Ostracoda[b]	3	5
Haliplidae[a]	3	4
Heterotanais oerstedi (Krøyer)	3	4
Ceratopogonidae[a]	3	3
Cladocera[b]	3	3
Palaemon adspersus Rathke[a]	2	2
Palaemon elegans Rathke[a]	1	2
Oligochaeta unid. sp.	1	2
Coenagrionidae[a]	1	1
Dytiscidae[a]	1	1
Mya arenaria (L.)[a]	1	1

The species are ranked according to their presence in number of samples and total abundance. In total, 126 samples were sorted

[a] Only found in the colonization experiment data

[b] Only recorded in the field collection data (see "Materials and methods")

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