Co-occurrence and potential resource partitioning between oligochaetes and chironomid larvae in a sediment depth gradient

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Abstract

Although detritivorous Tubificinae and chironomid larvae are important groups in functioning of both, fresh and brackish water ecosystem, their co-occurrence patterns in sediment is weakly known. We carried out two-year-long research in the brackish Vistula Lagoon (southern Baltic Sea), where both Tubificinae (*Limnodrilus hoffmeisteri* and *Potamothenis hammoniensis*) and larvae of *Chironomus balatonicus* occur in high densities. Because of different source of their food, we hypothesized that the ecological interactions between those two groups of detritivores are not antagonistic, thus allowing for their co-occurrence along the depth of sediment profile with lack of competition for space. Here we show that maximum burrowing depth, occasionally reaching 25 cm was significantly affected by the total density of the each group in the entire core. Tubificinae and *C. balatonicus* showed the highest density at 0–10 cm depth, where they co-occurred most frequently, with significant co-occurrence in the layers of 0–2 cm and 2–5 cm. We propose a hypothetical model of interactions between apparently the same functional groups and the complementary role they play in sediment reworking. It points to their coexistence in the shared microhabitat, but using space and food resources differently. Also, the consequences of their activity and habitat structuring are opposite—*Chironomus* larvae mostly affect the deeper layers of the sediments, while Oligochaeta both the deeper and surface layers. Thus, their requirements and ecological roles seem not to overlap, preventing competitive exclusion and allowing for co-occurrence.

Keywords Bioturbation · Detritus-feeders · Macroinvertebrates · Vertical distribution · Zoobenthos · Baltic lagoon

Introduction

Invertebrate benthic communities inhabiting freshwater and brackish water ecosystems are composed of different taxonomic groups. Most of them live on or just below the surface of the bottom sediments, but some burrow sediments to a depth of several dozen cm. The latter particularly include Tubificinae and larvae of several species of Chironomidae, mainly from genus *Chironomus*. They are among the most globally widespread benthic invertebrates (Pinder 1995;

Timm and Martin 2015). Because they belong to so-called infauna (deep burrowers), it can be assumed that the ecological interactions can take place not necessarily in the entire inhabited sediment depth but in its specific layers (Whitlatch 1980). However, vertical distribution of these groups in sediments has been rarely studied simultaneously, and suffers the lack of quantitative analysis of the relationships between these groups (Kajak and Dusoge 1971; Milbrink 1973; Newrkla and Wijegoonaawardana 1987; Kornijów and Moss 1997). The potential impact of biotic factors driving their distribution has been therefore largely ignored, except for the effect of fish (Van de Bund and Groenendijk 1994; Kornijów 1997; Persson and Svensson 2006) and mainly abiotic factors including pollution (Mucha et al. 2004; Como and Magni 2009), and content of organic matter in sediments (Newrkla and Wijegoonaawardana 1987; Mathooko 1995; Magni et al. 2008; Beghelli et al. 2012). In fact, the traditionally perceived role of oligochaetes and chironomid larvae

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primarily involves processing of organic matter as both groups are classified as detritivores (Covich et al. 1999).

Belonging to the same trophic guild can be expected to lead to competition for food resources (Odum 1971). This also was suggested for benthic detritivores such as oligochaetes and chironomids (Brinkhurst and Kennedy 1965; Jónasson 1972; Moss and Timms 1989; Como and Magni 2009; Ojaveer 2017). Vos (2001) hypothesized the ability to avoid competitive interactions between Tubificinae and *Chironomus* larvae due to the possibility of collecting food particles of different sizes, determined by the width of the mouth. Food particles ingested by 4th larvae stage of e.g., *Chironomus balatonicus* Devai, Wuelker & Scholl indeed reach up to 500 µm (Kornijów et al. 2019), i.e. approximately at least twice the value found e.g. in *Limnodrilus* (Juget et al. 1979; Fukuhara 1987). Different source of food can also be considered as an argument precluding the possibility of competing for food. Tubificinae ingest food particles from deeper sediment layers (Davis 1974; Nogaro et al. 2007; Mermillod-Blondin 2011; Timm and Martin 2015), while *Chironomus* larvae feed primarily by filtering the overlying water or by collecting particles from the sediment surface around their burrows (Walshe 1947; McLachlan and Cantrell 1976; McCall and Tevesz 1982; Proulx and Hare 2014).

Given the above, we hypothesize that the interspecific interactions between detritivorous Tubificinae and *Chironomus* larvae at both the individual and community level are not antagonistic, sensu Holland and DeAngelis (2009), allowing for their co-occurrence along the depth of sediment profile with lack of competition for space. In order to test this hypothesis, we conducted two-year-long research in soft bottom sediments of the eutrophicated Vistula Lagoon, where both Tubificinae and *C. balatonicus* larvae occur in high densities (Ezhova et al. 2005; Kornijów and Pawlikowski 2015). Specifically, we expected simultaneous presence of representatives of these groups in both, time and space along the sediment core showing the positive relationship between their densities and co-occurrence.

Materials and methods

Study site

The Vistula Lagoon located in the south-eastern part of the Baltic Sea, is large (838 km²) but shallow (mean depth 2.5 m; max. depth 5.2 m) and strongly elongated water body, oriented north-east to south-west. The western part of the lagoon with an area of 328 km² is located in the Polish territory, whereas the remaining part is in Russia. The lagoon's basin is separated from the Baltic Sea by the Vistula Spit in the north, and connected with the sea by the Baltiysk Strait.

Salinity decreases from 6.5 PSU at the Baltiysk Strait to < 1 at the mouth of the large rivers in the western basin. No regular tides occur in the lagoon. The climate is transitional, from moderate maritime to moderate continental.

Concentrations of nutrients in the water column are high ($N_{\text{tot.}} = 2.1\text{--}2.3 \text{ mg L}^{-1}$; $P_{\text{tot.}} = 0.10\text{--}0.11 \text{ mg L}^{-1}$), favouring development of cyanobacteria (Nawrocka and Kobos 2011; Kownacka et al. 2020). Water transparency is low (Secchi depth fluctuates around 50 cm). This is a result of relatively high chlorophyll-*a* concentrations ($22.9\text{--}54.3 \text{ µg L}^{-1}$), and also high concentrations of total suspended solids ($42.7\text{--}54.5 \text{ mg L}^{-1}$), caused by frequent resuspension in the shallow area exposed to wind action (Chubarenko and Margoński 2008; Piwosz et al. 2016; Kornijów 2018). Bottom sediments are primarily composed of sand in the hydrodynamic-active, shallow zone at a depth of up to 1.5–2 m. Deeper regions are dominated by fine-grained clayey silt. The near-bottom water layers are well oxygenated, even during long winters under ice cover (Kornijów et al. 2020).

The samples were collected at two sites, in the eastern (54.39190°N, 19.68360°E) and in the middle (54.35010°N, 19.48480°E) part of the open-water area of the Polish part of the lagoon at a depth of approximately 3 m, where soft sediments are composed of clayey silt (Fig. 1). Because the differences in the faunal composition between the sites in this highly homogenous environment were negligible, all the data collected were pooled.

Field survey and laboratory analyses

The field study was conducted in spring, summer, and autumn in 2010 and 2011. On each occasion, from 5 to 15 replicate standardized sediment cores 6 cm in diameter and 30 cm long were taken by means of a gravity sampler (UWITEC Ltd., Austria) equipped with a drive rod. Each core was sectioned into 7 layers with a slicer equipped with a sub-sample holder and centimetre scale (Kornijów 2013). The upper layer of the core was 2 cm thick, the second 3 cm, and the following five 5 cm thick. This interval is corresponding with individual length of worms (Matisoff et al. 1999), and at most twice as large as the length of forth instar of *Chironomus* larvae (Armitage et al. 1995). The volume of core sections ranged from 0.056 to 0.141 L. Each sediment section was washed separately through 0.3 mm mesh. Invertebrates were sorted out by eye on a white tray filled with water, and preserved in 4% formaldehyde solution. Altogether 434 sediment sections were collected and processed. The deepest sediment layer (25–30 cm) was uninhabited by invertebrates, and therefore it was excluded from analysis.

Additional 30 cm long sediment cores for analyses of organic matter and bacteria were sampled simultaneously with macroinvertebrates on each sampling date in the first and the second year, respectively. They were collected and

Fig. 1 Research area with sampling stations marked by dots. GIS layers of land cover after OpenStreetMap (2020), bathymetry according to Chubarenko (2008)—modified, and shore line after Maritime Office in Gdynia (2015)—modified

sectioned using the same equipment as in the case of benthic fauna samples. The organic matter and bacteria samples were secured in a cooler with ice immediately after sampling, and later in the laboratory were frozen and stored at -20°C until the analysis. The percentage of organic matter was calculated as a percentage weight loss during the ignition (LOI) of dried sediment burned at 550°C for 24 h. Bacteria in sediments were analysed according to Epstein and Rossel (1995). Bacterial cells from 30 fields of view were counted under $1000\times$ magnification using epifluorescent microscopy Nikon Eclipse 80i.

Data analyses

Tubificinae and the majority of chironomid larvae were identified according to Timm (1999) and Andersen et al. (2013), respectively. The species affiliation of *Chironomus* (not distinguished morphologically) was adopted based on karyological studies by Markiyanova (2018), indicating that this genus in the central part of the lagoon is represented solely by one species, namely *C. balatonicus*.

Because the sediment layers differed in thickness (and volume), the density of invertebrates in subsequent layers was expressed per sediment L to allow comparison of invertebrates abundance (Kornijów and Pawlikowski 2016). The total density in the entire inhabited core was expressed in the most often used unit in benthos research as the number of individuals per m^2 .

Frequency of occurrence was calculated as a percentage of samples (representing a given section of sediment core) in

which one of the groups (Tubificinae or larvae of *C. balatonicus*) or two groups occurred together.

Pearson's Chi-Square Test for 2×2 tables was performed to check the significance of co-occurrence of the groups with the guidance and assumption given by Gotelli and Ellison (2013). Associations between densities of the fauna and maximum burrowing depth was identified using linear regression. Shapiro–Wilk test for normal distribution and Levene test for equal population variances were conducted. Because of an unequal variances or non-normal distribution several non-parametric tests were used:

- Kruskal–Wallis test (H) was applied for the determination of the effect of sediment depth on the content of organic matter and densities of bacteria.
- Friedman test (χ^2) was applied to test the effect of sediment depth on the density of *C. balatonicus* and Tubificinae, and Friedman post-hoc test after Nemenyi was applied for the detailed analyses.
- Wilcoxon signed-rank test (T) was applied to check the significance of differences in the densities of *C. balatonicus* and Tubificinae between two sampling years.

Statistical tests were performed with the application of STATISTICA 10 software (StatSoft 2011).

Results

Invertebrate density and distribution

The qualitative composition of benthic macroinvertebrates was very poor and consisted of only 7 taxa: *Potamothenix hammoniensis* (M.), *Limnodrilus hoffmeisteri* C. (Tubificinae), as well as larvae of *Chironomus balatonicus*, *Microchironomus tener* (K.), *Procladius* sp. and Tanytarsini juv. (Diptera; Chironomidae). Single specimens of *Potamopyrgus antipodarum* (G.) (Gastropoda) were also encountered. Most samples showed high percentage of Tubificinae and *C. balatonicus*. The mean share of *P. hammoniensis*, *L. hoffmeisteri*, and *C. balatonicus* in the total density of benthic fauna were 42, 7, and 19%, respectively.

Mean total density $\pm$ SD (Standard Deviation) of invertebrates was 7044 ± 4493 ind. m^{-2} and ranged from 2806 to 16,269 ind. m^{-2} . During the second sampling year the densities of *C. balatonicus* were significantly lower [Wilcoxon Test: $T(n=16)=23$; $p=0.02$] and those of Tubificinae did not change [Wilcoxon Test: $T(n=13)=28$; $p=0.21$].

Maximum burrowing depth differed between the taxa. Tubificinae and *C. balatonicus* were found to a depth of 25 cm, and the presence of the remaining taxa was limited to the upper 5 cm surface layer (Fig. 2). The depth below 25 cm was uninhabited by macroinvertebrates. The density of Tubificinae and *C. balatonicus* in particular core sections changed with sediment depth in most of the examined seasons (Table 1). In most cases, however, the Friedman post-hoc test did not detect significant differences in density between the particular sediment layers. The exception was *P. hammoniensis*, whose densities significantly differed between the two deepest (15–20 and 20–25 cm) and two shallower layers (2–5 and 5–10 cm) ($p \leq 0.05$). The maximum burrowing depth of both groups was correlated with their total density in the entire core (Fig. 3).

There was a positive correlation between densities of Tubificinae and *C. balatonicus* larvae (Fig. 4). Their co-occurrence was most often recorded up to a depth of 10 cm (Fig. 5) and proved to be significant in the 0–2 cm (Pearson's Chi-Square ($df=1$) = 7; $p \leq 0.008$) and 2–5 cm layers (Pearson's Chi-Square ($df=1$) = 50; $p < 0.001$). In the two deepest layers (15–20 and 20–25 cm), the frequency of both groups was much lower, and Tubificinae and *C. balatonicus* were never found together in the same sample.

Fig. 2 Density of Tubificinae and *Chironomus balatonicus* larvae along the sediment profile in the Vistula Lagoon. Values are means $\pm$ SEM (Standard Error of the Mean) for sampling occasions

Table 1 Friedman Chi-Square (χ^2) test for the effect of sediment depth on the density of *Chironomus balatonicus* and Tubificinae in the Vistula Lagoon

	Apr 2010	Jul 2010	Oct 2010	Apr 2011	Aug 2011	Oct 2011
<i>Chironomus balatonicus</i>	$\chi^2 (n=9, df=5)=24$; $p < 0.01$	$\chi^2 (n=7, df=5)=19$; $p < 0.01$	$\chi^2 (n=10, df=5)=32$; $p < 0.01$	$\chi^2 (n=15, df=5)=46$; $p < 0.01$	$\chi^2 (n=15, df=5)=6$; NS	$\chi^2 (n=15, df=5)=8$; NS
Tubificinae	$\chi^2 (n=9, df=5)=29$; $p < 0.0001$	$\chi^2 (n=3, df=5)=9$; $p < 0.1$	$\chi^2 (n=5, df=5)=21$; $p < 0.0007$	$\chi^2 (n=15, df=5)=52$; $p < 0.0001$	$\chi^2 (n=15, df=5)=50$; $p < 0.0001$	$\chi^2 (n=15, df=5)=49$; $p < 0.0001$

NS not significant

Fig. 3 Linear regression analysis of the relationship between invertebrate density in entire sediment core and maximum burrowing depth in the Vistula Lagoon

Fig. 4 Relationship between the densities of Tubificinae and *Chironomus balatonicus* larvae in sediment cores

Proxies for nutritional conditions in the sediments

Values of organic matter content in the sediment profile ranged from 8 to 11%, and were aligned in the sediment profile [Kruskal–Wallis H ($n=21$) = 6; $p=0.39$]. The concentration of bacteria seemed to be the highest between 15

and 25 cm, but differences between the layers were insignificant [Kruskal–Wallis H ($n=21$) = 6; $p=0.42$].

Discussion

The habitat conditions in the Vistula Lagoon, including high concentrations of nutrients and low transparency due to resuspension and the development of phytoplankton corresponded to those in other Baltic coastal shallow and highly eutrophic lagoons and estuaries. Their organic matter-rich silty sediments are beneficial particularly for non-selective detritivorous Oligochaeta and chironomid larvae, known to build high densities (Ezhova et al. 2005; Gasiunaite et al. 2008; Radziejewska and Schernewski 2008; Wolnomiejski and Witek 2013; Kornijów and Pawlikowski 2015; Golubkov et al. 2019). However, the mutual distribution of these invertebrates in the sediment is very little known.

In our study the maximum burrowing depth by Tubificinae and *C. balatonicus* larvae in the Vistula Lagoon positively correlated with their densities (Fig. 3). A similar relationship was found for Tubificinae living in rivers (Brinkhurst and Kennedy 1965) and lakes (McCall and

Fig. 5 Frequency (%) of occurrence of Tubificinae alone, *Chironomus balatonicus* alone, or both groups together along the sediment profile in the Vistula Lagoon

Fisher 1980), as well as in experimental conditions (Robbins et al. 1979). According to McCall and Tevesz (1982), deeper burrowing may be related to the rate of exploitation of food resources. At low densities, the rate is low and there is no need for burrowing deeper. The opposite situation might occur at high densities, when food shortage in superficial layers can sooner or later appear. Such situations could take place in the studied lagoon, where the highest density of bacteria was recorded deeper than that of the majority of invertebrates. This could force animals to exploit deeper sediment layers.

The relationship between density and burrowing depth by *Chironomus* larvae might be related to the larval size structure. Because larger individuals tend to burrow deeper (Kajak and Dusoge 1971; Kornijów and Pawlikowski 2015), in a larger population the probability of occurrence of big individuals can be assumed to be greater, and therefore deeper burrowing can be expected.

A general positive relationship was found between densities of Tubificinae and *C. balatonicus* (Fig. 4). The density and joint frequency of occurrence of both groups were highest in the upper 10 cm sediment (Figs. 5 and 6). In addition, only in this depth range co-occurrence proved to be significant. The results suggest lack of antagonistic interactions between Tubificinae and *C. balatonicus*, including lack of competition for space, which supports our hypothesis. A similar conclusion was drawn based on the established correlation between the density of *Chironomus plumosus* (L.) larvae and Tubificinae (mainly *Potamothrix hammoniensis*) in a long-term series of more than twenty years of research in other large and shallow water bodies, namely in the southern Baltic Szczecin Lagoon by Wolnomiejski (1994) and in Estonian Lake Võrtsjärv by Kangur et al. (1998).

The vertical distribution of *C. balatonicus* and Tubificinae in bottom sediments, their distinct diets and modes of physical disturbance suggests their complementary role in the processing of organic matter. A hypothetical model for such role, based on the data of the present study and literature review, is presented in Fig. 7. Tube-dwelling chironomid larvae live in self-ventilated U-shaped, J-shaped, or Y-shaped tubes, and feed on filtered suspension or particles collected from the sediment. A substantial fraction of the detrital material is not assimilated by the animals, and the undigested remains are excreted deeper in the sediment. This applies not only to detritus particles, but partly also to bacteria and certain groups of algae (Kajak and Warda 1968; Baker and Bradnam 1976; Hirabayashi and Wotton 1998). In this way, the larvae, acting as downward conveyors (Mermillod-Blondin 2011; Kristensen et al. 2012), contribute to the transport and decomposition of organic matter to deeper sediment layers. The subsurface sediment enriched by chironomid larvae is in turn a feeding place of Tubificinae. Worms are believed to feed in the upper 15 cm sediment layer (Davis 1974; McCall and Fisher 1980; Fukuhara 1987). They selectively digest some organic components, transport them vertically upward through their gut, and defecate at the sediment surface (biodeposition) (Davis 1974; Fukuhara 1987; Nogaro et al. 2007; Timm and Martin 2015). They are considered upward belt-conveyors enriching the surface sediment layer with fine organic matter (Andersson et al. 1988), which might be of potential importance for chironomid surface collectors. Therefore, *Chironomus* larvae and Tubificinae, representing basically the same trophic guild (detritivores), live in a shared habitat, but use space and food resources differently, and the consequences of their burrowing and feeding behaviour are opposing. As a result of the activity of tube-dwelling *Chironomus* larvae,

Fig. 6 Percentage of organic matter (LOI) and concentrations of bacteria along the sediment profile in the Vistula Lagoon. Values are means $\pm$ SEM for sampling occasions

Fig. 7 Conceptual scheme of activity and relationships between Tubificinae and tube-dwelling *Chironomus* larvae, and the resulting direction of matter circulation (arrows). Bio-processing signifies activity of shredders, fungi and bacteria

the nutritional value of surface sediment layers decreases while that of deeper located sediments increases (Lewandowski and Hupfer 2005; Hölker et al. 2015). The effect of worms' activity is the opposite; the top of the sediment becomes covered by fecal pellets, and the underlying layers become more silt-clayish (Timm and Martin 2015). Thus, their requirements and ecological roles (called niches) seem not to overlap, preventing competitive exclusion and allowing for co-occurrence.

It is uncertain to what extent the invertebrates' activity and their environmental structural effect are important for both groups. *Chironomus* larvae are probably less dependent on oligochaetes than vice versa, because they can take food not only from the sediments (enriched by the activity of worms), but also from the water column. Oligochaetes may in turn benefit from sediment enrichment only after the abandoned tubes decay and fecal pellets are processed by meiofauna and bacteria (McLachlan et al. 1979; Van de Bund et al. 1994). Therefore, this relationship can be extended in time. This may explain the fact that in the Vistula Lagoon a strong decrease of the density of *C. balatonicus* larvae in the second year of this study did not result in a simultaneous decrease of the Tubificinae population.

Frequently observed strong dominance, or even the exclusive occurrence of one of the groups, may not to be a result of biotic interactions such as opportunistic predation

by *Chironomus* larvae, as suggested by Loden (1974) and Jónasson and Thorhauge (1976), or competition for food, claimed by other authors (Brinkhurst and Kennedy 1965; Jónasson 1972; Moss and Timms 1989). Assuming the constant pressure by fish and invertebrate predators, it may be determined by specific local habitat conditions (e.g. quantity and quality of food, inorganic pollution or organic matter loads and resulting water and sediment oxygenation), to which various invertebrates respond differently. This would be justified by the fact that the density ratio between chironomids and oligochaetes is used in predictive ecology to estimate pollution and/or eutrophication in estuaries (Como and Magni 2009; Silva et al. 2012), lakes (Wiederholm 1980; Lang 1999; Burlakova et al. 2018), and rivers (Goodnight 1973; Rosa et al. 2014; Gorzel et al. 2018). This suggests that research on different drivers of species co-occurrence might be not only of theoretical interest, but can also be a source of new information on the functioning of benthic communities and ecological status of an ecosystem (Cazelles et al. 2016).

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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