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Three-dimensional microdistribution of *Chironomus balatonicus* larvae (Chironomidae, Diptera) in soft sediments from the Vistula Lagoon (South Baltic Sea)

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Abstract – Despite the worldwide distribution and ecological importance of *Chironomus* larvae in both freshwater and brackish water ecosystems, patterns of their spatial distribution have been rarely studied. This study was conducted in summer, spring and autumn (2010–2011) in the deep-water zone of the polymictic, strongly eutrophic Vistula Lagoon. Its objective was to test whether temporal changes in density of the larvae affect their horizontal microdistribution and burrowing depth. Horizontal distribution, as inferred from indices of dispersion and patchiness, was density-dependent. The larvae spread more regularly with increasing density. The decreased density was associated with an increase in clustered distribution. The larvae burrowed into sediments up to a depth of 25 cm. The maximum burrowing depth positively correlated with total density, but also depended on the size of the larvae. The smallest individuals ($<$ 10 mm) did not occur deeper than 5 cm. Larger larvae were encountered throughout the sediment profile. The largest larvae did not always burrow the deepest. In spring before pupation, the larvae gathered below the sediment surface.

Key words: Macroinvertebrates / vertical distribution / aggregation pattern / dispersion / size-structure

Introduction

Larvae of the non-biting midge *Chironomus* are sediment dwellers showing common worldwide occurrence in various freshwater and brackish water ecosystems (Armitage *et al*., 1995). The larvae are detritivorous, have a sedentary lifestyle, and inhabit self-made tubes, usually with vertical, more seldom horizontal orientation (Walshe, 1947; Jónasson, 1972; McLachlan and Cantrell, 1976; McLachlan, 1977b). They collect food from the surface of the sediment close to the tubes, or filter it from the water pumped through the tubes by undulating body movements (Walshe, 1947; McLachlan and Cantrell, 1976; Proulx and Hare, 2014). The larvae can burrow sediment to depths of several tens of cm (Kajak and Dusoge, 1971; Shiozawa and Barnes, 1977; Van de Bund and Groenendijk, 1994). The occurrence of the larvae deep in the sediments is believed to result from the trade-off between the energetic effort related to burrowing, and choices between better oxygenated top sediments and sediments located deeper. The latter are anoxic and possibly less nutritious, but also less accessible for fish and other predators (*e.g.*, Baker and Ball, 1995; Kornijów, 1997; Hölker and Stief, 2005; Persson and Swensson, 2006).

The activity of burrowing by *Chironomus* larvae involving digging and foraging, results in a number of alterations in the physical and chemical properties of sediments. Among others, it alters the flux of solutes and dissolved gases and modifies the concentration and distribution of sediment particles (Krantzberg, 1985; Frenzel, 1990; Svensson and Leonardson, 1996; Mermillod-Blondin, 2011). It also stimulates microbial activity, and enhances decomposition of organic matter (Hansen *et al*., 1998; Gingras *et al*., 2007).

An insight into distribution and behaviour of chironomid larvae is very important in terms of ecosystem services such as carbon metabolism, cycling of nutrients and fisheries. However, patterns of their spatial distribution have been studied rarely and with little reliance on the analysis of the actual two- or three-dimensional patterns. Previous surveys have focused on the relations between density of *Chironomus* larvae and their horizontal distribution (McLachlan, 1977a; Shiozawa and Barnes, 1977;

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Titmus and Badcock, 1981; Takacs and Tokeshi, 1994). Very few investigations have jointly considered the horizontal and vertical distributions (Takacs and Tokeshi, 1994).

The objective of this paper is to supplement knowledge regarding these issues. This 2-year project concerning the distribution of *Chironomus balatonicus* larvae in the sediments of the Vistula Lagoon aimed to test three working hypotheses that claim that there is no correlation between (i) larval density and horizontal distribution pattern and (ii) larval density and depth of burrowing, (iii) between larval size and distribution pattern or burrowing depth.

Study site and methods

The Vistula Lagoon (54°16′N, 20°24′E) is a large (838 km^2) but shallow (mean depth 2.5 m; maximum depth 5.2 m) brackish [salinity: 1–5 PSU (practical salinity unit)] water body, separated to the north from the Baltic Sea by the Vistula Spit. The hydrology is complex owing to variable atmospheric conditions and connection to the Baltic Sea through the Strait of Baltiysk. Concentrations of nutrients in the lagoon ($N_{tot.} = 1.65–2.31$; $P_{tot} = 0.089–0.114$ $mg.dm^{-3}$) are associated with high productivity (Chubarenko and Margoński, 2008; Nawrocka and Kobos, 2011). Water transparency is low (Secchi visibility = 39–50 cm). This results not only from relatively high chlorophyll *a* concentrations (30.9–47.0 $\mu g.dm^{-3}$), but also from total suspended solids (42.7–54.5 $mg.dm^{-3}$) caused by frequent wind-driven resuspension. Phytoplankton is dominated by cyanobacteria, including the potentially toxic *Anabaena* and *Microcystis* (Nawrocka and Kobos, 2011).

The littoral zone has an intermittent belt of *Phragmites australis* (Cav.) Trin. ex Steud, *Typha* spp., or *Schoenoplectus lacustris* L. Palla, with some small patches of submerged vegetation, particularly *Potamogeton perfoliatus* L. and *Potamogeton pectinatus* L. in deeper water. No submerged macrophytes occur in the central deep-water zone. The total area with macrophytes is about 7% (Chubarenko and Margoński, 2008).

The present study was made in April, July and October, 2010, at two sampling stations in the western and middle parts of the deep-water area at a depth of approximately 2 m. Because the differences between the stations in this highly homogenous environment were negligible, the study was continued in 2011 only in the middle part of the lagoon in April, August and October. Samples were collected from a boat by means of a gravity corer (UWITEC Ltd., Austria) equipped with a drive rod. On each occasion, 7–15 sediment cores, 6 cm in diameter and at least 30 cm long were taken. After sediment collection, the tube-holding sediment was disconnected from the sampler head, and placed over a piston mounted on an extruder rod fixed to a stable base. The tube was pushed down gently, and the core was sectioned with a slicer equipped with sub-sample holder and centimetre scale (Kornijów, 2013). The upper section was 2 cm thick, the second 3 cm and each of the last five were 5 cm. Each sediment section was washed separately through 0.3 mm mesh. The retained debris was transferred to a zip-bag, and kept in a cooler without water. The humidity inside the bags prevented animals from drying out. Lack of water and low temperature made it difficult for predators to move freely and potentially consume their prey. Invertebrates were sorted live by hand on white tray filled with water, and preserved in 4% formalin.

Chironomidae were identified according to Andersen *et al*. (2013). Larvae of *Chironomus* f. l. *semireductus* from the Vistula Lagoon belong to one species – *C. balatonicus* Devai, Wülker et Scholl, 1983, as verified in the chromosome analyses by Jabłońska-Barna (2004). *Chironomus* larvae were divided into five size classes: <5, 5–10, 10–15, 15–20 and >20 mm. Their density in each layer was expressed as individuals dm^{-3} to allow comparison of invertebrate abundance in the different volumes of sediment.

The investigation of larval dispersion patterns involved the calculation of the mean (Y) and the variance (s^2) for each sample. These statistics provided the basis for the determination of the following:

Index of dispersion (ID):

$$ID = s^2/Y$$

An ID value of 1.0 corresponds with the randomness associated with a Poisson distribution. A value lower than 1.0 indicates a regular distribution pattern; while a value higher than 1.0 denotes a clustered distribution.

Level of larval aggregation, also known as the index of patchiness (IP) by Lloyd (1967):

$$IP = 1 + [(s^2 \pm Y)/Y^2]$$

Lloyd's index quantifies the occurrence of an individual in a given sample relative to an individual from a randomly distributed population with the same mean density. An IP estimate higher than 1 suggests an aggregated pattern. As IP increases, the degree of aggregation also increases, and aggregations are expected to be more distant from each other. IP lower than 1 suggests a random pattern.

Pearson's correlation coefficients were calculated in order to identify significant associations between densities of *Chironomus* larvae, and (i) values of the IP and (ii) burrowing depth. Shapiro–Wilk tests for normal distribution and Levene tests for equal population variances were conducted. Because the tests showed unequal variances, and because the sampled sediment sections were not independent, the Friedman non-parametric analysis of variance (ANOVA) test (Chi-square) was applied. Two major analyses were conducted:

- Friedman analysis of variance by ranks (Friedman ANOVA) for differences between densities of *Chironomus* larvae found in particular sediment sections,

- Friedman analysis of variance by ranks (Friedman ANOVA) for differences between densities of particular size classes of larvae in particular sediment sections.

Furthermore, Kruskal–Wallis ANOVA test (*H*) was conducted for seasonal differences in *Chironomus* larvae densities. Statistical tests were performed with the application of StatSoft STATISTICA 10 software (StatSoft, 2011).

On each sampling occasion, an additional sediment core for the analyses of organic matter was retrieved adjacent to the faunal cores, and processed in the same way as the cores for larval distribution. The percentage of organic matter in particular sections of the core was calculated from loss on ignition of dried sediment at 450 °C.

Results

The sediment was composed of fine silt with gastropod and bivalve shells present. The uppermost oxidized sediment layer of approximately 0–5 cm was beige-brown in colour, gradually turning into grey-brown and dark grey, and into graphite-black below 15–20 cm, with a slight smell of hydrogen sulphide in the summer. The content of organic matter in the sediment profile was even and varied from 8 to 11%.

Zoobenthos was represented by six taxa: one belonging to Oligochaeta (*Potamotrix moldaviensis*), one to Gastropoda (*Potamopyrgus antipodarum*) and four to Chironomidae: *C. balatonicus* (*Chironomus* f. l. *semireductus*), *Procladius* sp., *Microchironomus* sp., *Tanytarsini* juv. The mean density of fauna varied from 8877 to 15 633 ind.m^{-2}. Chironomid larvae constituted from 31 to 65% of the benthos. The most abundant among them was *C. balatonicus*, with a contribution varying from 2.6 to 54%.

The density of *C. balatonicus* larvae changed seasonally [$H\ (5,\ N = 70) = 50.1116,\ P < 0.0001$] with a strong decrease in summer and autumn of the second year of the study (Fig. 1). The larval distribution showed aggregative behaviour, with enhanced patchiness (IP) at lowered densities (August and October 2011). However, larval distribution was regular (ID < 1) in April 2011. In other words, high density resulted in low IP (less clustered), while low density was associated with higher IP and enhanced aggregative behaviour.

There was a negative correlation between larval density and IP values ($r = -0.7113$, $P = 0.0316$), and a positive correlation between population density and the maximum burrowing depth ($r = 0.7575$, $P = 0.0176$) (Fig. 1). The maximum burrowing depth correlated significantly with IP values ($r = 0.8213$, $P = 0.005$), pointing to more aggregative larval distribution in deeper sediments.

The maximum burrowing depth also showed temporal variability. Between April 2010 and April 2011, the larvae burrowed to a depth of 20–25 cm, with significant differences between layers (Fig. 2). In August and October 2011, the burrowing depth decreased to 5–10 cm, and differences between layers were statistically non-significant (Fig. 2).

A strong relationship at both sites occurred between the length of larvae and burrowing depth (Fig. 2). The smallest individuals from the first two size classes (< 10 mm) did not occur deeper than 5 cm. Larger larvae were encountered throughout the sediment profile, and their percentage contribution in particular layers changed seasonally. The largest larvae did not always burrow the deepest. In October 2010 and April 2011, their highest percentage contribution was recorded in the surface 0–2 cm layer of the sediment.

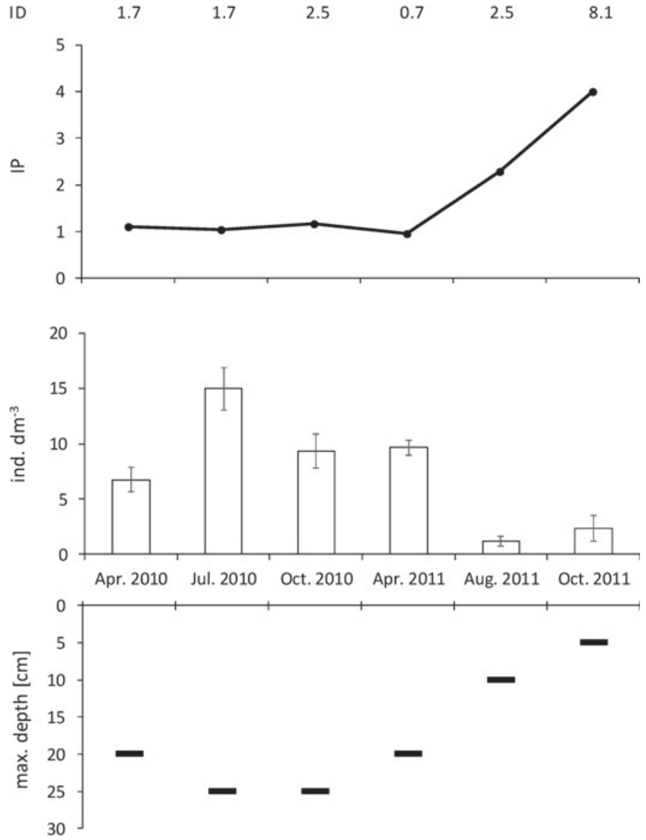

Fig. 1. Seasonal changes in density of *Chironomus* larvae (ind.dm^{-3}), their ID, IP and maximum depth of burrowing into the sediment in the Vistula Lagoon. Whiskers denote SE. For *n* values (number of cores analysed); see Figure 2.

Discussion

The diversity of zoobenthos in the Vistula Lagoon was very low. This might be associated with the nature of the sediment, fine-grained and strongly homogenized, as a result of frequent resuspension (Mathooko, 1995). In the second year of the study, the abundance of *C. balatonicus* decreased considerably. The decrease did not concern other taxa of Chironomidae, *e.g.*, *Procladius* which is more sensitive to severe oxygen conditions (Jónasson, 1972).

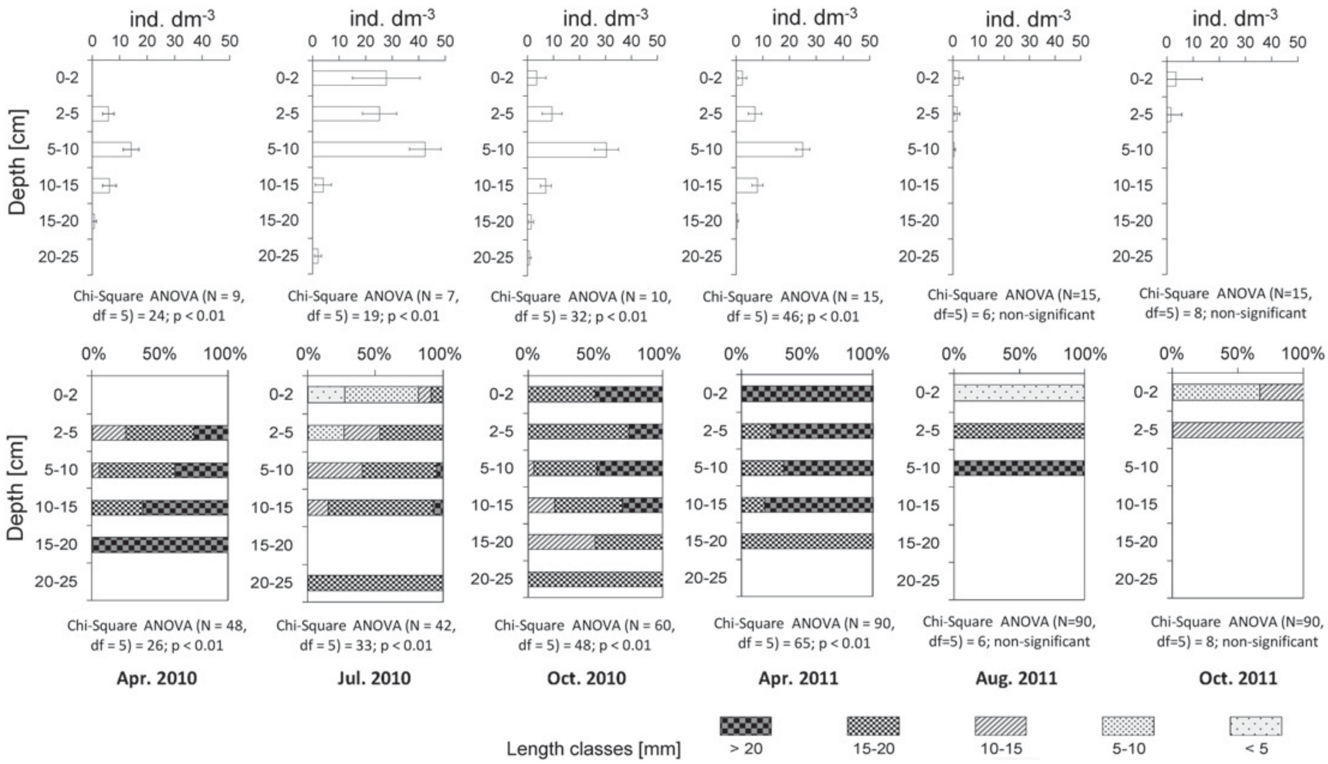

Fig. 2. Seasonal changes in the vertical distribution patterns of Chironomus larvae as individuals dm^{-3} for all size classes together (top), and as per cent of individuals in each size class (bottom). Whiskers denote SE.

This suggests that factors other than oxygen conditions caused a decrease in the abundance of *C. balatonicus* larvae.

The larvae burrowed into bottom sediments to a maximum depth of 25 cm, which is within the range determined for other species of the genus (Shiozawa and Barnes, 1977; Takacs and Tokeshi, 1994; Kornijów, 1997). *Chironomus* larvae are known to be uniquely successful in exploiting sediments depleted of oxygen due to certain adaptations. They possess the high-affinity respiratory pigment haemoglobin, which can bind oxygen for storage in anoxic conditions (Walshe, 1950; Czeczuga, 1960; Weber, 1980; Frank, 1983; Heinis *et al.*, 1994; Int Panis *et al.*, 1996a,b). They have also developed other physiological (Frank, 1983; Penttinen and Holopainen, 1995; Hamburger *et al.*, 1996; Anderson *et al.*, 2008), morphological (Nagell and Orrhage, 1981) and behavioural (Brundin, 1950; Walshe, 1950; Nagell and Orrhage, 1981; Frank, 1983; Penttinen and Holopainen, 1995; Kornijów and Moss, 2002; Gingras *et al.*, 2007; Anderson *et al.*, 2008) adaptations to hypoxia. Another adaptation to hypoxic conditions is building by the larvae interconnected tubes (Jónasson and Kristiansen, 1967; Jónasson, 1972). This presumably increases the cumulative effect of ventilation (McLachlan and Ladle, 2009). According to Pinder (1995), the anastomoses may additionally allow for a degree of cooperation, whereby a proportion of larvae are free to feed while others irrigate the tube network. Some adaptations to hypoxia have also been found in pupae (Rossaro *et al.*, 2007).

The costs associated with adaptations for deep borrowing are compensated by lower pressure of usually size-selective predators, and simultaneously, also of outright competition for food with numerous younger *Chironomus* larvae and other benthic species (Tokeshi, 1995). Deeper-burrowing individuals are also subject to lower mortality than those living on or right under the surface of sediments from sudden changes in near-bottom water layers, particularly in estuaries, with fluctuating salinity (Dauer *et al.*, 1987).

The maximum depth of burrowing by the larvae in the Vistula Lagoon depended on their total density. This result should be interpreted with caution, however, because the link coincided with a change in the size–structure of the larval population (Fig. 2). Smaller larvae, with length < 10 mm, gathered in the upper 5 cm layer of the sediment. Larger larvae generally occurred throughout the sediment profile. The positive correlation between the depth of burrowing and size of larvae was earlier determined for *Chironomus* larvae and other chironomid taxa (Brundin, 1950; Kajak and Dusoge, 1971; Shiozawa and Barnes, 1977; Shobanow, 1984; Olafsson, 1992; Van de Bund and Groenendijk, 1994; Int Panis *et al.*, 1996a; Kornijów, 1997). It is explained by the fact that larger larvae can make more powerful undulating movements to ventilate their tubes, which have larger diameters, thereby increasing the depth to which oxygen-rich water can be pumped. This way, larvae are able to modify more efficiently the microenvironment in their dwelling. In addition, larger individuals and those burrowing deeper, have higher concentrations of haemoglobin (Czeczuga, 1960; Int Panis *et al*., 1996a).

It is worth emphasizing that in the Vistula Lagoon, the largest larvae did not always occur the deepest. In spring 2011, many of the largest larvae, > 20 mm, were concentrated near the surface of the sediments. The migration of the larvae from deeper to surface layers was presumably related to preparation for transformation into the next (pupal) development stage. Subsequently, small larvae appeared near the surface, probably originating from summer hatch. Therefore, the depth of sediment burrowing is not always positively correlated with the size of larvae. It also depends on their development stage. This pattern has been so far overlooked.

The depth of burrowing by *Chironomus* larvae in the Vistula Lagoon changed seasonally. This aspect has been very rarely investigated before. Considerable seasonal changes in the distribution of *Chironomous* larvae, synchronized with larval development, were observed among others in the Rybinsk Reservoir (Shobanow, 1984). In the Neusiedler See, seasonal changes in depth of burrowing by *Tanypus punctipennis* were recorded, but not by *Chironomus* (Wolfram, 1996). In the Low Litton Reservoir, no patterns in seasonal distribution were noticed (Olafsson, 1992). This could have resulted from the analysis ignoring the abundance of particular species, but taking all species together, including plant-associated *Endochironomus albipennis*, migrating from macrophytes to sediments in autumn (Kornijów, 1992).

Chironomus larvae in the Vistula Lagoon clearly tended to aggregate at lower densities. Again, however, when in summer and autumn 2011 their density decreased, and patchiness increased, the larvae were particularly represented by small individuals. Therefore, it cannot be excluded that aggregation would also occur if the larvae were very abundant during that time. Such a situation was recorded by Shiozawa and Barnes (1977) in Lake Utah, where the contagious distribution of *Chironomus* occurred during periods of high densities of the 1st and 3rd instars.

Lack of consideration of the size of the larvae could have been the reason for different results obtained by various authors investigating correlations between the density of larvae and their horizontal distribution. At low abundance, *Chironomus* larvae were strongly aggregated in the Saidenbach Reservoir (Hempel, 2011). In a gravel-pit lake, *Chironomus* larvae were randomly distributed (Titmus and Badcock, 1981), while in Lough Neagh they showed a tendency towards regular distribution regardless of the density (Takacs and Tokeshi, 1994). The latter authors assumed that neither food resources for larvae mostly feeding on detritus nor the living space available was a limiting factor. When detritus was spread uniformly, which seldom occurs (Downing and Rath, 1988; Downing, 1991), an apparent random distribution could be expected (Titmus and Badcock, 1981), or random distribution at low densities and regular at high densities (Takacs and Tokeshi, 1994). The discussion seems to consider the biology and behaviour only of large larvae of the 3rd and 4th instars. The biology of early larval stages is little known.

In conclusion, an increase in density may contribute to an increase in burrowing depth only when large larvae are present. An increase in density, irrespective of the size, will affect the horizontal distribution, making it more regular. This probably results from an increase in competition for food and space, and the related territorialism of larvae (McLachlan and Cantrell, 1976; McLachlan and Ladle, 2009).

The results of this study suggest that the response of *Chironomus* larvae to changes in density, involving horizontal or vertical movements, largely depends on the size of the larvae. This characteristic, very rarely considered in analyses of microdistribution (Shiozawa and Barnes, 1977), seems to be of basic importance for the understanding of the behaviour and distribution of the larvae, which differ at various stages of their development. In view of the above, all three hypotheses proposed in the paper are rejected.

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