DYNAMICS OF MACROINVERTEBRATE DRIFT IN A LOWLAND RIVER

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Abstract. Macroinvertebrate drift in the fourth order section of the lowland Drzewiczka River was investigated in the main types of habitats, over the annual cycle. The percentage of macroinvertebrate biomass in the water column in the total transported organic matter was low. Terrestrial invertebrates, mainly winged insects, varied among seasons and habitats, reaching from 13.1% to 49.8% of total drift biomass. Abundance of aquatic macroinvertebrates was roughly congruent with the ranges of values reported from other rivers and differed from habitat to habitat, season to season and between season x habitat pairs (two-way ANOVA). Among agile swimmers Ephemeroptera, and among the other taxa Orthocladiinae and Tanytarsini (Chironomidae) and Naididae (Oligochaeta) showed the highest propensity to drift.

INTRODUCTION

Drift or water-borne transport of benthic invertebrates plays a key role in spatial distribution of stream macrobenthos (MÜLLER, 1954; WATERS, 1965, 1972; ELLIOTT, 1967; BRITTAiN and EiKELAND, 1988; GRZYBKOWSKA, 2000). On the one hand drift is the principal means of recolonizing an area of stream bed after a drought or heavy pollution and of the colonization of substrata suspended in the water column (distributional drift MINSHALL and PErSEN, 1985), but on the other it is a very important way for individuals to avoid the pressure of predators and to resolve the problem "to eat and not to be eaten" (PIJANOWSKA, 1999).
There is a well-known paradigm in limnology that there is no drift fauna "per se" (Waters, 1972). Thus for the recent several decades the causes of the macroinvertebrate migration in the water column have been searched by many limnologists. At the beginning of respective investigations most attention was paid to abiotic parameters; it was on their basis that several drift caused were distinguished (Müller, 1954; Waters, 1965, 1972; Elliott, 1967; Brittain and Eikerland, 1988). From numerous studies it was concluded that velocity (current speed) belongs to the most important factors determining drift and the characteristics of the streams and rivers such as presence of refugial space or bed stability play an important role in the maintenance of communities and prevention of invertebrates depletion (Borchard and Statzer, 1990; Matthaei and Townsend, 2000).

The main aim of this study is to estimate the quality and quantity of transported particulate organic matter (TPOM), including invertebrates migrating in the water column, both of aquatic and terrestrial origin, over the annual cycle. These investigations were undertaken in an undisturbed section of the lowland river.

**STUDY AREA**

The lowland Drzewiczka River is part of the Vistula River drainage basin. The Drzewiczka River rises at 248 m a.s.l., is 81.3 km long and empties into the Pilica River at 130 m a.s.l. Its catchment area is ca. 1.083 km² and the slope ranges from 2.7-2.5 ‰ in the upper reaches to 0.8-0.7 ‰ in the middle and lower course.

The study area (20°33' E i 51°29' N), in the vicinity of the village of Nieznamierowice, was established within a fourth order stream section as the control site. The investigated site was 21 km upstream of the mouth and about 10 km downstream of the dam reservoir and wild-water slalom canoeing track (W-WSCT). Due to these constructions the hydrological regime directly downstream deviated from natural conditions (Szczerkowska et al., 2003) but their functioning did not affect the flow regime of the investigated site.

In the 305 m long study site, 5 different dominant habitats were identified (Fig. 1, Table 1):

H₁ - this habitat was located along the right bank, consisted of a depositional habitat, a very low flow-area with a large amount of fine and coarse particulate organic matter - the stagnant habitat. The riparian plants were mainly represented by Mentha aquatica L., Ranunculus repens L., Poa nemoralis L., Ficaria verna Huds. and sporadically by Caltha palustris L. and Humulus lupulus L.

H₂ - close to a bridge, with sand and gravel at the bottom. The riparian plants were mainly represented by Polygonum aviculare L., Polygonum lapathifolium L., Chenopodium sp., Agrostis stolonifera L. and Ranunculus sceleratus L.
Fig. 1. The map of study area with marked sampling habitats (Hₙ).

H₁ - consisted of an erosional, high-flow area close to an island. At the gravelly-pebble bottom *Fontinalis antipyretica* HEDW. were recorded. The riparian vegetation was represented by *P. nemoralis*, *Glechoma hederacea* L. and *Solanum dulcamara* L.
Hl - the next high-flow area along the right bank (riffle). The riverside plants were mainly represented by *Urtica dioica* L., *Poa palustris* L., *G. hederacea* and *M. aquatica*.

Hp - this habitat consisted of a low-flow area due to a fallen tree (pool). The bank was covered with riverside plants, particularly *Cardamine amara* L., *P. nemoralis*, *U. dioica*, *M. aquatica*, *R. repens* and *G. hederacea*.

It is worth noting that the Drzewiczka River flows through agricultural land overgrown by numerous grasses; the riparian trees consisted mainly of *Alnus glutinosa* (L.) GaERTN. and *Salix alba* L.

The mean annual water temperature in the Drzewiczka River was 12.1°C.

**MATERIAL AND METHODS**

Benthic samples from the five sampling habitats were collected in the Drzewiczka River monthly, in the morning, from November 2000 to October 2001. Ten samples were collected with a 10 cm² (100 cm² of stream-bed area) tubular sampler at each habitat (Hn). The sampler was pushed into sediment to a depth of 15 cm and also through vegetation if it was present.

In each habitat (Hn) temperature, depth, current speed and area of the habitat were measured. Additional samples were taken to analyse the composition of particulate inorganic matter according to Cummins (1962). This method divided the dry sediments into size classes that are of ecological significance. The analysis of size fraction was made on a weight basis. To aid statistical analysis of the substrate, field data on particle size distribution were transformed into the single substrate index (SI) by summing up the mid point values of size classes weighted by their percentage cover (Quinn and Hickey, 1990). These samples were also used to determine the organic matter content in the bottom sediment. For this purpose a 1 mm sieve was used to segregate particulate organic matter (POM) into a fraction > 1 mm (coarse - CPOM) and a fraction < 1 mm (fine - FPOM). The size classes of POM followed those used by Petersen et al. (1989). Benthic organic matter was then dried at 60°C for two days, weighed, ashed at 600°C for two hours and reweighed.

Benthic samples of 50 cm² each were also taken at each habitat in order to estimate chlorophyll *a* concentration. The benthic material was rinsed. The obtained solution was centrifuged and a supernatant was used for determining chlorophyll *a* concentration by spectrophotometry (Golterman et al., 1978).

In order to estimate amounts of both fine and coarse transported particulate organic matter (TFPOM and TCPOM) and number of drifting macroinvertebrates three nets (mesh size 400 mm) 1.5 m in length were mounted on 0.5 x 0.7 m frames; they were put into each habitat for ten minutes; see details in Grzybkowska (1992). In the laboratory macroinvertebrates captured in the nets were sorted, identified, counted and then recalculated for 100 m³. Detrital materials were selected into two fractions: coarse (TCPOM > 1 mm) and fine particulate organic matter (TFPOM < 1 mm). Benthic organic matter was then dried at 60°C for two days, weighed, ashed at 600°C for two hours and reweighed.
To measure total amounts of transported organic matter (TPOM) triplicate water samples were collected in 10 l plastic bags. These samples were filtered through Whatman filters and mass of TFPOM was added to the mass of organic matter caught in the frames.

The proportion of benthos in the drift (U %) was calculated by the formula

\[ U = \frac{x \cdot D \cdot 100}{X - x \cdot D} \]

where: \( x \) is the number of drifting individuals per m\(^3\), \( X \) is the number of benthic individuals (m\(^2\)), and \( D \) is the average water depth (Elliott, 1967).

Data were log transformed \((x + 1)\), when necessary, to satisfy the requirement of normality and homogeneity of variance. Analysis of variance (two-way ANOVA) was used to examine spatial and temporal variance of benthic and transported organic matter, inorganic substratum, chlorophyll \(a\), hydraulic parameters as well as the density of drifting macroinvertebrates. Pearson correlation coefficients were calculated to examine relationships between the densities of particular invertebrate groups and given biotic and abiotic parameters. The canonical correlation was used to examine the relationship between the densities of all macrobenthic groups and all environmental variables.

All statistical analyses were carried out using CCS Statistica (StatSoft, 2000).

RESULTS

Environmental variables

Characteristics of the investigated habitats in the Drzewiczka River are shown in Table 1.

Statistical differences between particular habitats of the Drzewiczka River were recorded for all variables, except for chlorophyll \(a\) and TFPOM (Table 2). In contrast, such statistical differences among seasons were noted for a lower number of parameters. Two-way ANOVAs showed that only one parameter, transported coarse organic matter, varied among habitats and seasons.

Terrestrial invertebrates in transported organic matter

The largest portion of the macroinvertebrate drift in the total transported organic matter was noted at \(H_r\) - 0.002% while it was 0.56% in TCPOM. In the other habitats the percentage of invertebrates in TPOM and TCPOM were: 0.0007% TPOM and 0.0160% TCPOM at \(H_s\), 0.0005% TPOM and 0.1200% TCPOM at \(H_b\), 0.0008% of TPOM and 0.1700% of TCPOM at \(H_p\), and 0.0009% TPOM and 0.3100% TCPOM at \(H_i\).

Annual biomass contribution of terrestrial invertebrates to the total biomass of drift in the Drzewiczka River was high (Fig. 2). Winged insects, such as Diptera (mainly chironomids but rather little contributing to total biomass), Coleoptera, Hymenoptera, and Heteroptera dominated although Araneina and Oligochaeta rinsed from ecotone zones were also noted.
Table 1
Mean ($\bar{x}$) and ranges (R) of selected characteristics of the investigated habitats ($H_n$) of the Drzewiczka River, downstream of Lake Drzewnieckie, over the investigated period.

<table>
<thead>
<tr>
<th>Variables</th>
<th>$H_s$</th>
<th>$H_b$</th>
<th>$H_i$</th>
<th>$H_r$</th>
<th>$H_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (m)</td>
<td>0.60</td>
<td>0.50</td>
<td>0.46</td>
<td>0.55</td>
<td>0.71</td>
</tr>
<tr>
<td>R</td>
<td>0.36-0.75</td>
<td>0.39-0.70</td>
<td>0.28-0.62</td>
<td>0.20-0.90</td>
<td>0.58-0.90</td>
</tr>
<tr>
<td>Current velocity (m s$^{-1}$)</td>
<td>0.02</td>
<td>0.32</td>
<td>0.52</td>
<td>0.42</td>
<td>0.46</td>
</tr>
<tr>
<td>R</td>
<td>0.00-0.17</td>
<td>0.18-0.66</td>
<td>0.30-0.76</td>
<td>0.14-0.91</td>
<td>0.21-0.90</td>
</tr>
<tr>
<td>SI (mm)</td>
<td>0.44</td>
<td>6.27</td>
<td>13.24</td>
<td>9.53</td>
<td>3.09</td>
</tr>
<tr>
<td>R</td>
<td>0.22-1.55</td>
<td>1.50-9.93</td>
<td>0.29-40.90</td>
<td>0.55-47.42</td>
<td>0.60-8.11</td>
</tr>
<tr>
<td>BFPOM (g m$^{-2}$)</td>
<td>1793-16627</td>
<td>363-1956</td>
<td>364-3153</td>
<td>836-10143</td>
<td>225-4016</td>
</tr>
<tr>
<td>R</td>
<td>9028</td>
<td>1122</td>
<td>2068</td>
<td>4061</td>
<td>1646</td>
</tr>
<tr>
<td>BCPOM (g m$^{-2}$)</td>
<td>3009</td>
<td>52</td>
<td>896</td>
<td>2183</td>
<td>1006</td>
</tr>
<tr>
<td>Chlorophyll $a$ (mg m$^{-2}$)</td>
<td>167.9</td>
<td>161.6</td>
<td>106.4</td>
<td>159.6</td>
<td>140.8</td>
</tr>
<tr>
<td>R</td>
<td>32.8-475.1</td>
<td>41.0-499.7</td>
<td>16.3-352.2</td>
<td>16.4-548.8</td>
<td>24.6-385.0</td>
</tr>
<tr>
<td>TFPOM (g m$^{-3}$)</td>
<td>25.07</td>
<td>15.77</td>
<td>25.72</td>
<td>22.41</td>
<td>17.64</td>
</tr>
<tr>
<td>R</td>
<td>7.83-62.94</td>
<td>0.11-36.22</td>
<td>2.45-121.70</td>
<td>1.92-90.91</td>
<td>0.43-29.45</td>
</tr>
<tr>
<td>TCPOM (g m$^{-3}$)</td>
<td>1.193</td>
<td>0.065</td>
<td>0.078</td>
<td>0.081</td>
<td>0.078</td>
</tr>
<tr>
<td>R</td>
<td>0.035-4.460</td>
<td>0.006-0.184</td>
<td>0.014-0.122</td>
<td>0.020-0.206</td>
<td>0.009-0.230</td>
</tr>
</tbody>
</table>

Two benthic particulate organic matter (BPOM) fractions: coarse (BCPOM) and fine (BFPOM) and two transported particulate organic matter fractions (TPOM): coarse (TCPOM) and fine (TFPOM) are presented; SI - granularity of inorganic substrate index, chlorophyll $a$ - concentration in periphyton.

Table 2
Summary of two-way ANOVAs comparing the chosen characteristics of the Drzewiczka River between five habitats (df=4; 40), sampling periods (seasons, df=3; 40) and habitat x season (df=12; 40); explanations as in Table 1.

<table>
<thead>
<tr>
<th>Variables</th>
<th>Statistics</th>
<th>Habitat</th>
<th>Season</th>
<th>Habitat x Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth (m)</td>
<td>F: 5.646*</td>
<td>0.001*</td>
<td>3.104*</td>
<td>0.037*</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>Current velocity (m s$^{-1}$)</td>
<td>F: 20.198*</td>
<td>0.000*</td>
<td>2.498</td>
<td>0.073</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>SI (mm)</td>
<td>F: 6.759*</td>
<td>0.000*</td>
<td>2.304</td>
<td>0.092</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>BFPOM (g m$^{-2}$)</td>
<td>F: 15.996*</td>
<td>0.000*</td>
<td>0.594</td>
<td>0.623</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>BCPOM (g m$^{-2}$)</td>
<td>F: 40.709*</td>
<td>0.000*</td>
<td>0.859</td>
<td>0.470</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>TFPOM (g m$^{-3}$)</td>
<td>F: 0.864</td>
<td>0.494</td>
<td>4.261*</td>
<td>0.011*</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.040</td>
<td>0.040</td>
<td>0.040</td>
<td>0.040</td>
</tr>
<tr>
<td>TCPOM (g m$^{-3}$)</td>
<td>F: 22.493*</td>
<td>0.000*</td>
<td>6.673*</td>
<td>0.001*</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
<td>0.000*</td>
</tr>
<tr>
<td>Chlorophyll $a$ (mg m$^{-2}$)</td>
<td>F: 1.698</td>
<td>0.169</td>
<td>8.699*</td>
<td>0.000*</td>
</tr>
<tr>
<td>R</td>
<td>P: 0.169</td>
<td>0.169</td>
<td>0.169</td>
<td>0.169</td>
</tr>
</tbody>
</table>
Fig. 2. Seasonal dynamics of the terrestrial and aquatic invertebrate biomass in the drift in the investigated habitats ($H_n$) of the Drzewiczka River.
The highest percentages of terrestrial drift were recorded at H₁, reaching 49.8% of total biomass, while the lowest ones were noted at H₅, where their contribution to the total biomass was 13.1%.

Seasonal dynamics of terrestrial insect biomass in the drift was also noted. Their highest biomass was recorded in spring and autumn.

**Seasonal dynamics of density and biomass of macroinvertebrate drift**

Seasonal dynamics of given macroinvertebrate taxa biomass at habitats is shown in Fig. 3 while mean annual densities of the dominant taxa are presented in Fig. 4.

The distribution of invertebrate biomass varied from habitat to habitat as indicated in Fig. 3; this was mainly caused by chironomids. Significant statistical differences in total invertebrate biomass among sampling dates reflected fluctuations in the population abundance of all taxa except Heteroptera, Trichoptera and predatory Tanypodinae. Significant "habitat x season" interaction effects noted only for two taxa of Orthocladiinae and Tanytarsini indicated a strong microdistribution shift of these small-size species (Table 3).

The Pearson "r" correlation was used to examine the relationship between abiotic parameters and biomass of given macroinvertebrate taxa (Table 4). Chironomini, Tanytarsini and Orthocladiinae were correlated with the highest number of riverine parameters. In contrast, current velocity among hydraulic parameters and amount of benthic and transported organic matter were those that mostly determined the abundance of the dominant macroinvertebrate taxa.

A statistically significant correlation was recorded between all investigated environmental variables and total macrobenthic biomass (canonical R = 0.964, test Chi² (121) = 312.29, P<0.000). TCPOM among riverine variables and Orthocladiinae among animal variables showed the highest positive relationship with factor 1.

**Chironomidae in the drift**

At each habitat of the Drzewiczka River orthocladi midges dominated in terms of density but not biomass, reaching from 8.6% density of the total drifting individuals at H₅ to 20.6% at H₁. Because this subfamily includes rather small-size individuals its share in the biomass of drift is lower (Figs 3, 4). At each habitat a maximum of abundance was observed in March, May and September-October, with the highest peak at H₁ (180 inds 100 m⁻³ and 39.1 mg 100 m⁻³).

At H₁ Tanytarsini (about 29.7% of density and 27.2% of chironomid biomass and 9.6% of density and 12.4% of biomass of the total invertebrate drift) and Chironomini were co-dominants beside Orthocladiinae (30.0% and 26.5% of total Chironomidae and 9.7% and 12.0% of the total drift, respectively).

Tanypod predators reached from 2.9% of density to 3.2% of total chironomid biomass at H₁ to respectively 9.5% of density and 10.6% of biomass at H₅, but their contribution to total abundance of drifting macroinvertebrates was lower (Figs 3, 4). A maximum of tanypod abundance was noted at Hs in April (27 inds 100 m⁻³ and 3.26 mg 100 m⁻³).
Fig. 3. Seasonal biomass dynamics (lines) and the percentages (histograms) of the main invertebrate taxa in drift in the investigated habitats ($H_n$) of the Drzewiczka River.
Fig. 4. Mean annual density of the main invertebrate taxa in benthos (inds 100 cm$^{-2}$) and drift (inds 100 m$^{-3}$) in the investigated habitats ($H_n$) of the Drzewiczka River; benthic data after Borysewicz (2003).

Table 3
Summary of two-way ANOVAs comparing biomass of the selected macroinvertebrate groups between five habitats (df=4; 40), sampling periods (seasons, df=3; 40) and habitat x season (df=12; 40).

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Statistics</th>
<th>F</th>
<th>P</th>
<th>F</th>
<th>P</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligochaeta</td>
<td>0.874</td>
<td>0.488</td>
<td></td>
<td>3.610  *</td>
<td>0.021 *</td>
<td>0.514</td>
<td>0.893</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>1.633</td>
<td>0.185</td>
<td></td>
<td>3.383  *</td>
<td>0.027 *</td>
<td>0.648</td>
<td>0.788</td>
</tr>
<tr>
<td>Heteroptera</td>
<td>1.587</td>
<td>0.197</td>
<td></td>
<td>0.159</td>
<td>0.923</td>
<td>0.750</td>
<td>0.695</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>2.556</td>
<td>0.053</td>
<td></td>
<td>1.239</td>
<td>0.308</td>
<td>1.719</td>
<td>0.699</td>
</tr>
<tr>
<td>Simuliidae</td>
<td>0.905</td>
<td>0.470</td>
<td></td>
<td>4.619  *</td>
<td>0.007 *</td>
<td>0.620</td>
<td>0.813</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>2.863      *</td>
<td>0.035</td>
<td></td>
<td>21.779 *</td>
<td>0.000 *</td>
<td>0.751</td>
<td>0.694</td>
</tr>
<tr>
<td>Orthocladiinae</td>
<td>7.665      *</td>
<td>0.000</td>
<td></td>
<td>19.926 *</td>
<td>0.000 *</td>
<td>3.362</td>
<td>0.002 *</td>
</tr>
<tr>
<td>Tanypodinae</td>
<td>1.283</td>
<td>0.293</td>
<td></td>
<td>1.593</td>
<td>0.206</td>
<td>0.617</td>
<td>0.815</td>
</tr>
<tr>
<td>Chironomini</td>
<td>15.853     *</td>
<td>0.000</td>
<td></td>
<td>3.741  *</td>
<td>0.018 *</td>
<td>1.890</td>
<td>0.658</td>
</tr>
<tr>
<td>Tanytarsini</td>
<td>15.465     *</td>
<td>0.000</td>
<td></td>
<td>10.292 *</td>
<td>0.000 *</td>
<td>10.489</td>
<td>0.000 *</td>
</tr>
<tr>
<td>Total</td>
<td>2.705      *</td>
<td>0.044</td>
<td></td>
<td>4.153  *</td>
<td>0.012 *</td>
<td>0.881</td>
<td>0.573</td>
</tr>
</tbody>
</table>
Larvae of Diamesinae and Prodiamesinae were sporadically observed; the former subfamily mainly at H_r, while the latter one at H_p, H_s and H_r.

The Pearson "r" correlation was used to examine the relationship between particular abiotic variables and the biomass of the dominant taxa drift (Table 4).

Table 4
Pearson "r" correlation coefficients between riverine parameters and drift macroinvertebrate biomass in the investigated habitats; explanations as in Table 1.

<table>
<thead>
<tr>
<th>TAXA</th>
<th>TCPOM*, chlorophyll a*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oligochaeta</td>
<td>TCPOM*, chlorophyll a*</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>TCPOM*, chlorophyll a*</td>
</tr>
<tr>
<td>Heteroptera</td>
<td>-temp.*</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>cur. vel.<em>, -BFPOM</em>, -temp.*</td>
</tr>
<tr>
<td>Simuliidae</td>
<td>-temp.***</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>-cur. vel.<em>, BFPO**, TCPOM</em>**, temp.<em>, chlorophyll a</em></td>
</tr>
<tr>
<td>Orthocladiinae</td>
<td>-cur. vel.<em><strong>, TCPOM</strong></em>, chlorophyll a*</td>
</tr>
<tr>
<td>Tanypodinae</td>
<td>TCPOM***</td>
</tr>
<tr>
<td>Chironomini</td>
<td>-cur. vel.<em><strong>, BFPO</strong></em>, BCPOM*, TCPOM***, -SI**, temp.*</td>
</tr>
<tr>
<td>Tanytarsini</td>
<td>-cur. vel.<strong>, BFPO</strong>, TCPOM***, -SI*, chlorophyll a*</td>
</tr>
<tr>
<td>Total</td>
<td>TCPOM*</td>
</tr>
</tbody>
</table>

Significance level of correlation coefficient: *P<0.05, **P<0.001, ***P<0.001.

Proportion of benthos in drift
In the Drzewiczka River the highest propensity to drift was recorded for midges: Orthocladiinae and Tanytarsini (Fig. 4). Over the investigated period the high values of U were sometimes recorded for Oligochaeta (0.3620% at H_s in May) and Simuliidae (0.6511% at H_r in November).

The annual mean of proportion of total benthos in the total drift was the highest at H_r (0.0121%) while lower at the other habitats, reaching 0.0019% at H_s, 0.0012% at H_b, 0.0020% at H_i and 0.0033% at H_p.

DISCUSSION

Macroinvertebrate drift in total transported organic matter
Water with high quality food, including zooplankton and macroinvertebrate drift, can support high numbers of both fish and benthic filter feeders; thus collector-filterers are important in linking processes that occur in the water column with those that occur on the stream bed (Wallace and Merritt, 1980; Palmer and O’Keefe, 1990). But despite its important role in the trophic webs (Allen, 1951; Allen, 1978) and maintenance of lotic community structure, macroinvertebrate drift little contributes to the total mass of transported organic matter. Data from the fourth section of the Drzewiczka River are congruent with
the statements from the other streams and rivers (O'Hop and Wallace, 1983; Grzybkowska et al., 1990; Waringer, 1992). However sometimes in rivers the percentage of drift in TPOM is higher, reaching from 0.2% (Benke et al., 1991) to 6% (low order stream section in Canada, Dance et al., 1979).

In north temperate streams a seasonal variability of this share was observed in a mountain stream, where the lowest biomass of macroinvertebrate drift occurred in March (0.001%), while the highest in November (5%, Fleituch, 1994). Such a pattern was not recorded in the Drzewiczka River.

**Composition and abundance of drift**

Generally, the drift abundance of the Drzewiczka River appears to be consistent with the literature data collected from the north temperate streams (Cellot, 1989; Anderwald et al., 1991). This statement also concerns terrestrial invertebrates which are the regular components of macroinvertebrate drift in streams (Edwards and Huryn, 1995; Kołodziejczyk, 1999); their taxonomic composition and abundance depends on the ecotone and the seasons (Elliott, 1967; Edwards and Huryn, 1995; Grzybkowska, 2000). Generally terrestrial invertebrates are a small fraction of the total drift in the rivers (Shannon et al., 1996). One of the highest percentages of this fraction was recorded in a high Andean stream, where terrestrial invertebrates contributed as much as 16% to total drift biomass, mainly insects (Thysanoptera and Heteroptera) and spiders (Turcote and Happer, 1982). In central Poland, but in a higher order section of a river flowing across an agricultural catchment, terrestrial animals, mainly winged insects, little contributed to the total drift (Grzybkowska et al., 1987). In the investigated site of the Drzewiczka River terrestrial invertebrates were also represented mainly by winged insects, primarily Chironomidae and Heteroptera, but their abundance reached about a dozen percent of the drift and changed with habitats and seasons; the highest values were recorded both in spring and autumn.

Some taxa of aquatic invertebrates are more common in the drift than others; among insects there are Ephemeroptera, some Plecoptera and Trichoptera, some Diptera and among Crustacea - Isopoda and Amphipoda. Their frequent occurrence in drift may be the effect of their exceptional drift abilities; they can easily enter and leave the water column (agile swimmers, Elliott, 1967; Bishop and Hynes, 1969; Skinner, 1985; Benke et al., 1986; Obi and Conner, 1986; Grzybkowska et al., 1987). Their movement may be also interpreted in a behavioral context based upon foraging opportunities and predator avoidance. Invertebrate predators are very important in determining drift density while fishes in determining the timing of drift (Kołodziejczyk, 1999). Among agile swimmers Ephemeroptera (Baetis, Leptophlebia) considerably contributed to drift in the Drzewiczka River.

As we mentioned above in many papers special attention was paid to crustaceans and insects in the water column while very few data sets are available for other groups, such as Oligochaeta; according to Dumnicka (1996) this group was even ignored in drift studies. Such approach of many workers may be the effect of choosing lotic ecosystems as study objects; in them
endobenthic tubificids with low propensity to displacement dominated in the benthos. In turn another Oligochaeta family, Naididae, linked to epilithon and periphyton (Learner et al., 1978) may more significantly contribute to drift (Cellot and Juget, 1998). In the Drzewiczka River Naididae also dominated in the water column. Whether their abundant occurrence in May may be explained by their life cycle (asexual reproduction), as it was in the Rhône River (Cellot and Juget, 1998), will be shown by future investigations. Thus Naididae in the drift may represent production in excess of the carrying capacity of the benthic substrate (production-compensation model proposed by Waters, 1981).

Some other taxa, without legs (such as Simuliidae and some Chironomidae (Orthocladiinae)), also constituted a significant proportion of the drift. This phenomenon may be explained by the simuliid and orhoclad mode of life; larvae of these dipterans are rather mobile during the larval stage and often exposed to current, thus more likely to enter water flow. Note, that two taxa of Chironomidae: Chironomini and Orthocladiinae represent alternative strategies for active dispersal. Sedentary existence of the late instar of Chironomini requires that they actively colonise a habitat at early instars, while mobile Orthocladiinae may be able to seek and colonize stream bed after a spate (Grzybkowska et al., 1996), drought or heavy pollution (Brittain and Eikeland, 1988) throughout their whole larval life (Ferrington, 1984; Storey and Pinder, 1985; Williams, 1989; Grzybkowska et al., 1993). Data from the Drzewiczka River were congruent with this statement; Orthocladiinae belong to drift-prone macroinvertebrates.

In the Drzewiczka River many of tanypod predators were also noted in the drift. Such an abundant presence of predators in the drift is exceptional in lotic ecosystems (Williams, 1989; Grzybkowska, 1992).

In this lowland river differences in the composition and abundance of drift were recorded, similarly as it was in benthic sediments (Borysewicz, 2003). Difference observed are a resultant of the behavioral properties of given taxa and environmental variables, especially current velocity and amount of transported coarse organic matter. In the literature of the subject correlation between amount of suspended matter and propensity of macroinvertebrates to migration was also noted (Dog and Mileage, 1991).

According to literature data the relation drift - benthos is rather insignificant in small rivers; the value of 0.01% calculated in several studies reviewed by Waters (1972) being typical. As it was stated by McLay (1970) and Benke et al. (1986, 1991) high drift/benthos ratios (from 0.1 to 1.9%) may be explained by increase in drift distance in large rivers. Thus the values obtained in the Drzewiczka River are rather congruent with those in small rivers.

While interpreting the data from the Drzewiczka River some methodical limitations (ensuing from the techniques of sampling in this river) should be taken into account. First of all drift samples underestimated density much more than biomass. This was a result of applying a fine mesh net, which for certain did not allow us to capture the youngest (finest) developmental stages. However, most studies cited above suffered from the same limitation, hence the very comparisons of respective data from the present and literature studies are unbiased.
As we mentioned earlier the drift phenomenon is a result of not only hydraulic pressure but also the individual response of an organism, which makes it possible to avoid the intra- or/ and interspecific interactions and the predation pressure (Brittain and Eikeland, 1988; Peckarsky et al., 2001). Note that individuals may modify their drift behavior in response to other characteristics of a river, for example the presence of refugia accessible to individuals (Raeder and McArthur, 1995). This aspect of the drift was not analysed in the Drzewiczka River.

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DYNAMIKA DRYFU BEZKRĘGOWCÓW W RZECE NIZINNEJ

STRESZCZENIE

Badania dryfu podjęto w czwartorzędowym odcinku nizinnej rzeki Drzewiczki, około 10 km poniżej tamy i sztucznego toru kajakowego, a więc w odległości, w której nie odnotowano już oddziaływania obu tych budowli na biocenozę rzeki.

Materiał zbierano w pięciu różnych siedliskach rzeki; różniły się one pod względem głębokości, prędkości przepływu, granulacji nieorganicznego podłoża, ilości obu frakcji BPOM oraz unoszonej grubocząsteczkowej POM.

Dryfujące bezkręgowce miały niewielki udział w całkowitej masie unoszonej materii organicznej (od 0,0005 do 0,002 %); wartości te były głównie odzwierciedleniem zmian w ilości innych frakcji unoszonej materii organicznej, a w mniejszym stopniu bezkręgowców. Odnotowano znaczącą biomasę bezkręgowców lądowych, głównie uszkrydłonych owadów; wiele z nich to postacie doskonale merolimnicznych owadów takich jak Chironomidae czy inne muchówki. Frakcja ta reprezentowana była także przez organizmy bądź wypłukane (skaposzczety) bądź strącone do wody (pluskwiaki) ze strefy ekotonowej.

Obfitość dryfujących organizmów w Drzewiczce jest porównywalna z danymi z innych ekosystemów lotycznych. Wodne organizmy unoszone z prądem były reprezentowane głównie przez kilka taksonów, spośród bezkręgowców o wysokiej skłonności do dryfowania odnotowano Ephemeroptera (Leptophlebia, Paraleptophlebia i Baetis, w zależności od siedliska), a o morfologii nie predytynującej do dryfu Oligochaeta (głównie Naididae), oraz muchówki: Simuliidae i Chironomidae, głównie Orthocladiinae i Tanytarsini. Częsta obecność Orthocladiinae w tonii wodnej to wynik ich behawioru - larwy tego taksonu są ruchliwe przez cały okres rozwoju, podczas gdy dominujące w bentosie Chironomini w II - IV stadium żyją zagrzebane w dnie, często w wytworzonych przez siebie rurkach.
Stwierdzono znaczną sezonową zmienność obfitości transportowanych zwierząt we wszystkich badanych siedliskach. Z analizy korelacji kanonicznej wynika, że zależności między wybranymi parametrami rzeki a obfitością taksonów bezkręgowców są istotne statystycznie (R=0,943, Chi²(121)= 282,41, P<0,000). Najważniejszymi czynnikami z analizowanych parametrów rzeki była obfitość TCPOM, a z bezkręgowców Orthocladiinae.

Najwyższą obfitością charakteryzowała się fauna unoszona w płytkim siedlisku o żwirowo-piaszczystym podłożu i wysokiej prędkości przepływu. Potwierdziła to analiza korelacji "r" Pearsona; istotne statystycznie dane stwierdzono między zagęszczeniem Chironomidae: Chironomini, Tanytarsini i Orthocladiinae a ich bazą pokarmową (POM, peryfiton) oraz prędkością przepływu.

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