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INFLUENCE OF FLOW DISTURBANCES ON A MACROBENTHIC COMMUNITY IN A LOWLAND RIVER

Eliza Szczerkowska, Maria Grzybkowska, Małgorzata Dukowska, Mariusz Tszydel

Katedra Ekologii i Zoologii Kręgowców
Uniwersytet Łódzki, ul. Banacha 12/16, 90-237 Łódź
e-mail: szczerko@biol.uni.lodz.pl

Summary: The main aim of study was to describe the response of a benthic community to medium and high flow disturbance in the lowland Drzewiczka River. The studied site of the 4^{th} order river was located downstream of a dam reservoir and of a wild-water slalom canoeing track. This site may be described as a mosaic of bed patches with different stabilities and contributions to the patchy distribution of benthos; five habitats dominated at this site. In order to test which of them show the highest stability during high discharges „semi-experiments" were conducted. After two-three weeks of natural discharge amounts of water that exceeded the typical one by three times (in September), four times (in March) and sixteen times (in February) were released through the dam; this last event took place during the complete emptying of the reservoir, before its dredging. In each habitat morphometric, hydraulic and biotic parameters were measured before and immediately after water releases. Chironomidae, in terms of density, dominated at each habitat, reaching the highest abundance at the riffle habitat; other groups that played a key role in lotic assemblages included Oligochaeta, and other insects: Trichoptera and Ephemeroptera. A three to five-fold increase in discharge did not cause any substantial changes in macrobenthic density, but the sixteen-fold increase in discharge had a great influence on sediment and the river biota. However, even a spate did not cause the depletion of the entire riverbed – community stability was the highest at the submersed macrophyte habitat, dominated by macrobenthic taxa with different modes of life (epiphytic and pelophilous fauna). Thus, the macrophytic habitat of the Drzewiczka River was only partly damaged by disturbance and therefore may be classified as a refugium, from which organisms may potentially colonize the depleted sections.

Key words: river, disturbance, reservoir, canoe track, patch dynamics, benthos

INTRODUCTION

Flow regulation is considered to be the most pervasive anthropogenic change influencing rivers worldwide [Stanford *et al.* 1996]. High flows usually dramatically reduce macrobenthic density and change the structure of communities for weeks or months

[Grzybkowska and Witczak 1990, Grzybkowska *et al.* 1996, Maier 2001]. As it is well documented, animals may fare better in some patches (called refugia) than others due to differences in the disturbance – susceptibility of the physical patches or to species-specific traits that confer enhanced resistance or resilience for fauna occupying those patches [Palmer *et al.* 1995, 1997, Lake 2000, Matthaei and Towsend 2000]. Although this theory has been discussed in terms of its usefulness for mobile stream animals [Downes 1990], many ecologists supposed that the patch dynamic perspective was well suited for the explanation of processes and patterns in lotic ecosystems.

Our primary objective is to assess the response of macroinvertebrates in the lowland Drzewiczka River, which has been permanently disturbed. Firstly, because the fourth order section of this river has been dammed (since 1932-1936) and secondly due to its wild-water slalom canoeing track (W-WSCT), which was built (in 1980) just below the dam reservoir. As an effect of these discharge perturbations the section of the Drzewiczka River may be described as a mosaic of habitat patch-types; thus, resistance against these disturbances among macrobenthic groups could be expected at five dominating habitats. So the main aims were to assess any differential effects exerted on macroinvertebrates by floods of different magnitude. In order to test which of these habitats acts as a refugium and which level of discharge caused the destabilisation of particular habitats we made semi-experiments – after two-three weeks of natural flow water amounts that exceeded the natural water level three times, four times and sixteen times were released through the dam.

STUDY AREA

The studied site of the 4th order lowland Drzewiczka River was located downstream of a dam reservoir called „Drzewieckie Lake" and of a wild-water slalom canoeing track (W-WSCT) (20°28' E and 51°27' N). Both these hydroconstructions have long determined water discharge: the dam for 70 and the track for 20 recent years. For the last two decades, several times a week the discharge was increased 3-5 times in relation to the median one for two-tree hours a day.

The examined study site was 160 m long and on average 0.5 m deep. Five dominant habitat types were distinguished:

H_P – pool at the left riverbank, at the height of one of the islands, close to the end of the W-WSCT (the upper habitat).

H_S – stagnant river meander overgrown by emerged macrophytes. This habitat located along the left bank, consisted of a depositional habitat, a very low flow-area with a large amount of fine and coarse particulate organic matter and covered with emergent macrophytes (the stagnant habitat). The riparian vegetation was mainly represented by *Mentha aquatica* L. and sporadically by *Myosotis palustris* (L.) L. em. Rchb., *Rorippa amphibia* (L.) Besser and *Phalaris arundinacea* L.

H_M – the macrophyte habitat was the dominant in terms of the occupied area. Vegetation cover included large patches of *Potamogeton lucens* L. and *Potamogeton crispus* L. Small patches of *Potamogeton pectinatus* L. also covered the sand riverbed of this habitat. *Cladophora glomerata* (L.) Kutz filaments coated these macrophytes, especially in June.

H_B – along the left bank (the bank habitat). The riparian vegetation was mainly represented by *Poa trivialis* (L.) and, in decreasing order, by *Filipendula ulmaria* (L.) Maxim. The bank was rarely covered by *M. aquatica* and *Urtica dioica* L.

H_R – consisted of an erosional, high-flow area along the right bank (the lower habitat). The riparian vegetation was dominated by *Ranunculus repens* L., *U. dioica* and *F. ulmaria*. Further details of the habitats and figure of sampling site were given by Szczerkowska et al. [2003].

The trees along banks were dominated by common alder (*Alnus glutinosa* (L.) Gaetrn).

MATERIAL AND METHODS

Samples were collected at each habitat, in three seasons: autumn (September 2000), spring (March 2001) and winter (February 2002).

In each habitat 5 samples (100 cm^2 of river bottom each) were taken before (I, pre-disturbance samples) and immediately after (II, post-disturbance samples) water release, using a tubular sampler 10 cm^2 in cross section area. The depth, current velocity and area of each habitat were measured.

On the basis of the obtained samples the following characteristics were estimated:

– density and biomass of zoobenthos,

– scale of inorganic particle size classification in the form of the single inorganic substrate index – SI [Quinn and Hickey 1990],

– amounts of benthic particulate organic matter (BPOM). Using sieves and filters the organic matter was divided into two fractions: coarse (BCPOM > 1 mm) and fine particulate organic matter (BFPOM < 1 mm); see details in Petersen *et al.* [1989].

Periphyton was measured as chlorophyll *a* concentration using the Golterman *et al.* method [1978].

All statistical analyses were carried out using CCS Statistica (StatSoft 2000); see details in Grzybkowska *et al.* [2001].

RESULTS

Environmental variables

Median value of discharge in the Drzewiczka River before experiments reached 2.6 m^3s^{-1}. Discharge increased during the three experiments many times; the lowest increase was observed in September 2000 (max. 8.4 m^3s^{-1}), a higher one in March 2001 (12.0 m^3s^{-1}) while the extraordinarily high one in February 2002 (41.8 m^3 s^{-1}); this last event took place during the complete emptying of the Drzewieckie Reservoir, before its dredging.

These discharge fluctuations caused changes in numerous variables, mainly depth and current velocity, which in turn affected the scale of inorganic particle size classification (SI). These changes mostly affected both fractions of the particulate organic matter (bottom) and periphyton (chlorophyll *a*). Further details of the habitats during these studies were given by Szczerkowska *et al.* [2003].

Some areas of the streambed were essentially unaffected by the high flow, whereas others were heavily scoured. During these experiments the highest stability was observed at H_M, where no differences in benthic fine and coarse particulate organic matter or in SI were noted (Tab. 1). But even at this „macrophytic habitat" food resources of macroinvertebrates (periphyton) were also washed away.

Table 1. A one-way ANOVA was used to determine significant differences of given environmental parameters of the Drzewiczka River habitats (H) between three sampling dates (df = 5; 24)

Tabela 1. Wyniki analizy wariancji ANOVA użytej do określenia różnic w parametrach abiotycznych i biotycznych między trzema terminami poborów prób w poszczególnych siedliskach (H) rzeki Drzewiczki

Habitats – Siedliska / Variables – Zmienne		H_P	H_S	H_M	H_B	H_R
Depth – Głębokość	F	59.510	50.439	22.372	47.111	11.245
(m)	p	0.000	0.000	0.000	0.000	0.000
Current velocity – Szybkość nurtu	F	44.006	97.514	65.723	28.988	10.796
($m\ s^{-1}$)	p	0.000	0.000	0.000	0.000	0.000
Chlorophyll *a*	F	195.744	136.325	47.962	12.527	140.862
($mg\ m^{-2}$)	p	0.000	0.000	0.000	0.000	0.000
SI	F	6.486	5.600	2.203	11.915	13.802
(mm)	p	0.001	0.001	0.087	0.000	0.000
FPOM	F	9.771	3.596	1.635	6.858	10.724
($g\ m^{-2}$)	p	0.000	0.014	0.189	0.001	0.000
CPOM	F	4.848	13.775	2.290	14.911	11.407
($g\ m^{-2}$)	p	0.003	0.000	0.078	0.000	0.000

df – number of degrees of freedom, F – statistics, p – significance level
df – liczba stopni swobody, F – wartość testu, p – poziom prawdopodobieństwa

Results of ANOVA showed that it was only the high level of discharge (in February) that caused changes of inorganic substrate at the stagnant habitat (depositon of sand). The Tukey's post-hoc test showed that the differences in two BPOM fractions, BFPOM and BCPOM, were both the effect of season and increase in discharge (Tab. 1). Similarly to the „macrophytic habitat" changes in periphyton were also noted during the experiments.

The habitat close to the bank was characterized by both dislodgement and sedimentation of fine sand, which influenced SI. This process affected both BPOM and periphyton (Tab. 1). Atypical riffle habitat, with the highest current velocity and inorganic substrate heterogeneity, was characterized by dislodgement of both inorganic and organic matter during each „flood". At pool habitat each change in discharge caused removal of benthic CPOM.

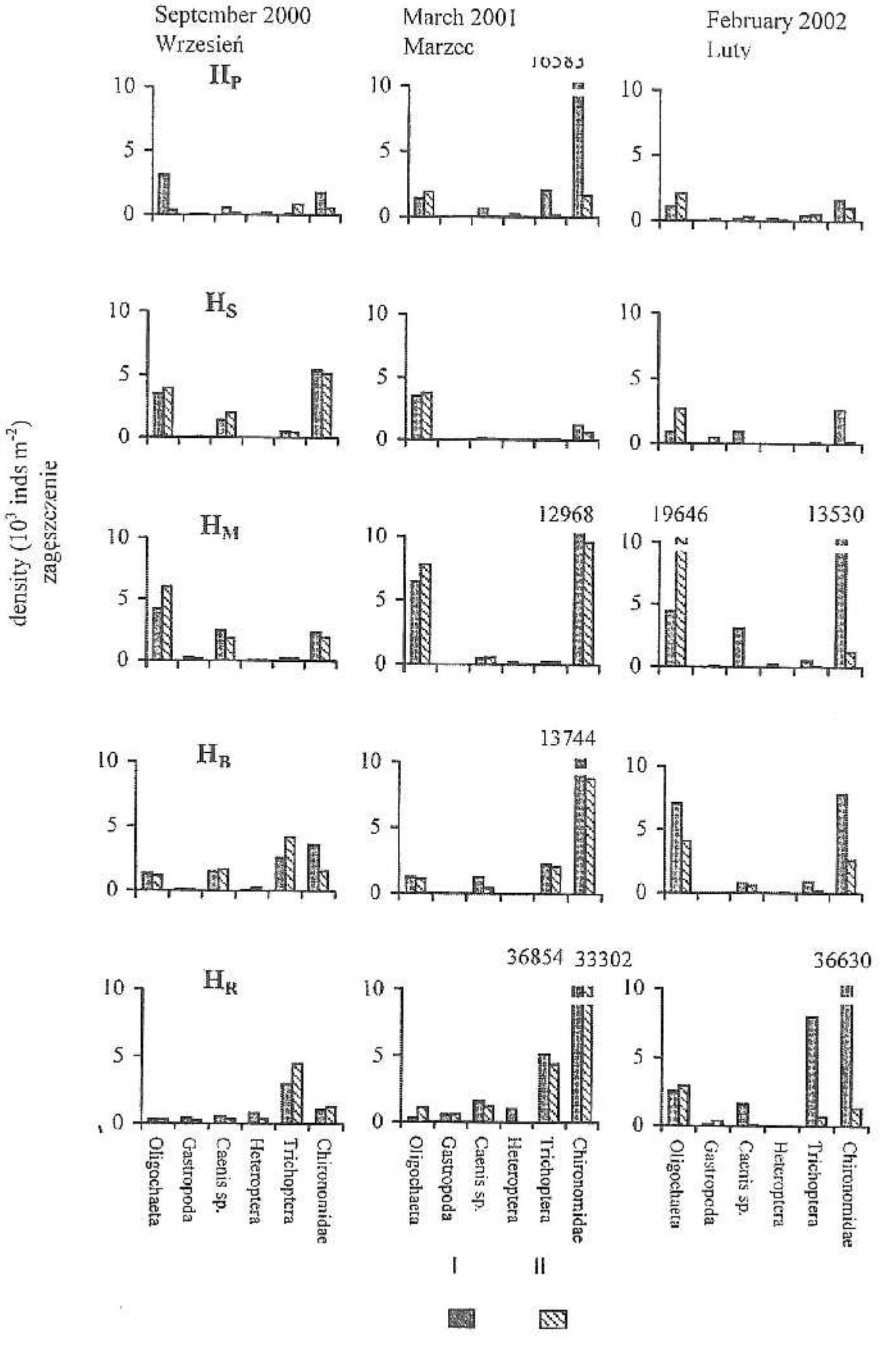

Fig. 1. The mean densities of the dominant macrobenthic taxa at studied habitats (H) of the Drzewiczka River before (I – the first period) and immediately after (II – the second one) the „experiment"

Rys. 1. Zagęszczenie dominujących taksonów bezkręgowców w poszczególnych siedliskach (H) Drzewiczki przed (I) i bezpośrednio po silnym uwalnianiu wody (II)

Benthic community

The most favourable habitat for zoobenthos was characterised by high current and oxygen levels, average amounts of fine particulate organic matter, low amounts of BC-POM, and the presence of microspaces for invertebrates and surfaces for algal (chlorophyll *a*) development (Fig. 1).

Table 2. A one-way ANOVA was used to determine significant differences of given dominant macrobenthic taxa at habitats (H) of the Drzewiczka River between three sampling dates (df = 5; 24)

Tabela 2. Wyniki analizy wariancji ANOVA użytej do określenia różnic w zagęszczeniu dominujących bezkręgowców w poszczególnych siedliskach rzeki Drzewiczki (H) między trzema terminami poborów prób

Habitats – Siedliska / Variables – Zmienne		H_P	H_S	H_M	H_B	H_R
Oligochaeta	F	2.142	4.846*	3.417*	3.442*	2.953*
	p	0.095	0.003*	0.018*	0.017*	0.032*
Gastropoda	F	0.642	8.127*	8.614*	1.474	0.704
	p	0.670	0.000*	0.000*	0.235	0.626
Caenis sp.	F	1.792	19.224*	10.797*	1.654	1.717
	p	0.153	0.000*	0.000*	0.184	0.169
Heteroptera	F	2.909*	0.606	3.137*	7.573*	7.979*
	p	0.034*	0.696	0.026*	0.000*	0.000*
Trichoptera	F	6.362*	12.155*	1.108	10.112*	31.203*
	p	0.001*	0.000*	0.382	0.000*	0.000*
Chironomidae	F	8.711*	14.843*	15.652*	19.261*	103.893*
	p	0.000*	0.000*	0.000*	0.000*	0.000*
Total – Razsem	F	5.987*	6.367*	3.829*	5.168*	77.469*
	p	0.001*	0.001*	0.011*	0.002*	0.000*

df – number of degrees of freedom, F – statistics, p – significance level

df – liczba stopni swobody, F – wartość testu, p – poziom prawdopodobieństwa

Chironomidae (Diptera, dominated at the studied site of the Drzewiczka River. The other groups, such as Oligochaeta and insects, *Trichoptera* and *Ephemeroptera*, also played a important role in the benthos (Fig. 1). Midges were very numerous at the riffle habitat in March in terms of absolute (over 60 000 inds m^{-2}) and relative abundance (over 85% of the total macrobenthic density); this finding was obtained during the first period. The absolute and relative highest abundance of oligochaetes was noted in riverbed area covered by submersed macrophytes (H_M), where they reached over 19000 inds m^{-2}; this value constituted over 88% of the total macrobenthic abundance. But this extraordinary high abundance of Oligochaeta was only observed during the second period of studies in February thus, many organisms might have been dislodged from the other habitats of the river as well as from the reservoir; in both these cases macrophytes acted as a trap for drifting macroinvertebrates.

Table 3. Pearson r correlation coefficient between dominant macrobenthic taxa and abiotic and biotic environmental variables of the Drzewiczka River

Tabela 3. Korelacja (współczynnik Pearsona r) między zagęszczeniem makrobezkręgowców a wybranymi parametrami środowiskowymi Drzewiczki

Taxa – Taksony	Abiotic and biotic variables – Abiotyczne i biotyczne zmienne
Oligochaeta	cur.vel.***, SI*, chl.*, BFPOM**, BCPOM***
Gastropoda	cur.vel.*
Caenis sp.	BFPOM*
Heteroptera	cur.vel.***, depth.**, SI*, -BFPOM***, -BCPOM***, CPOM**
Trichoptera	cur.vel.**, depth.*, SI**, -BCPOM***
Chironomidae	-cur.vel.***, BFPOM**
Total – Razem	BFPOM*

chl. – chlorophyll *a*; cur.vel. – current velocity; SI – substrate inorganic index; BPOM – benthic particulate organic matter, fine (BFPOM) and coarse (BCPOM) fractions.
Significance level of correlation coefficient: * $P<0.05$, ** $P < 0.01$, *** $P <0.001$
chl. – chlorofil *a*; cur.vel. – szybkość prądu; SI – granulacja nieorganicznego podłoża; BPOM – bentoniczna materia organiczna, drobnocząsteczkowa (BFPOM) i gruboczasteczkowa (BCPOM) frakcja.
Poziom istotności współczynnika: * $P< 0{,}05$, ** $P< 0{,}01$, *** $P<0{,}001$

The loss in zoobenthos during the studies reflected major decreases in the abundance of chironomids and oligochaetes (mainly Naididae), taxa often found in the drift (materials in preparation).

Abundance of Chironomidae changed at habitats between sampling periods (Fig. 1, Tab. 2). At H_P the differences in chironomid density between the first, March, and other periods were observed (the post-hoc Tukey test). High abundance of these midges may be the effect of their life history (sampling period before the emergence of imagines). At stagnant habitat chironomids reached a low density, and the lowest one was recorded during the flood. Macrophyte habitat was characterized by high abundance of midges, especially in autumn and winter, but it was only the flood that caused a significant decrease in these insects. A trend similar to that described at H_M was observed at the bank habitat (Fig. 1). At the riffle habitat the extraordinarily high density of chironomids was observed in March, while an incredible decrease of midges was noted during the flood, in February.

As analysis of ANOVA showed, differences between sampling periods in terms of Oligochaeta density were not noted only at the pool habitat (Tab. 2). At the stagnant habitat the lowest abundance of Oligochaeta was observed before the flood, but during high discharge (in February) colonization by these organisms was observed. Macrophytes acted as traps for Oligochaeta – each increase in discharge was correlated with increase in abundance of these invertebrates. At the bank and riffle habitats a similar trend was observed, the highest densities were recorded in February while the lowest ones either in September and March (at H_R) or only in March (at H_B).

Trichoptera did not change in terms of their density only at the macrophyte habitat (ANOVA, Tab. 2). The caddis flies did not reach high density both at pool and stagnant habitats (Fig. 1). The flood caused a statistically significant (Tukey test) decrease in Trichoptera both at the bank and riffle habitats.

Caenis (Ephemeroptera) were recorded mainly in autumn, reaching the highest density (over 2400 inds. m^{-2}) at the macrophyte habitat and below 2000 inds. m^{-2} at the stagnant habitat (Fig. 1). Small increases in discharge (in September and March) had no effect on the abundance of *Caenis* but flood had a catastrophic influence on this ephemeropteran taxon – these organisms were flushed downstream.

Heteroptera were recorded in greater numbers in autumn and spring, mainly at the riffle habitat, reaching over 700 inds. m^{-2} in September and over 1000 inds. m^{-2} in March (Fig. 1). Results of ANOVA showed that at this habitat the significant decrease in Heteroptera abundance was noted in March; during the February sampling period Heteroptera were observed sporadically.

Mollusca constituted a small part of the total macrobenthic density (Fig. 1), but taking into account their biomass (materials in preparation) their percentage would change.

Values of Pearson r correlation between the macrobenthic dominant groups and riverine biotic and abiotic parameters are presented in Table 3.

DISCUSSION

Benthic particulate organic matter, especially its fine fraction (FPOM), is important in distributing energy and associated nutrients within streams at multiple spatial and temporal scales [Minshall *et al.* 2000]. According to Brady and Cowell [2003], FPOM is being colonized by macroinvertebrates rather for its nutritional value but not as a refuge from predation. However, Corkum [1992] stated detritus is rather a poor indicator of total macrobenthic density. Detritus may be so abundant that it exerts no influences on the distributional pattern of macroinvertebrates [Minshall 1984]; thus, the relationship between total macroinvertebrate density and detritus may be stronger at the river sites with reduced detrital levels [Corkum 1992]. In turn, Egglishaw [1964] tried to explain a lack of association between macrobenthic density and detritus in spring as the effect of the redistribution of fauna caused by life history of insects: emergence on the one hand and oviposition and subsequent hatch of larvae on the other. In the Drzewiczka River the amount of BFPOM was correlated with density of typical pelophilous taxa: Oligochaeta (mainly associated with macrophyte habitats, both emerged and submerged ones) and Chironomini (Chironomidae). This last taxon included both pelophilous and psammophilous forms. Among the other taxa Caenis (Ephemeroptera) was correlated with fine BPOM.

Periphyton is considered to be the dominant source of energy for macroinvertebrates, especially for grazers; this feeding group was numerously represented by Orthocladiinae (Chironomidae) and *Psychomyia pusilla* (Trichoptera) at the high-flow area of the Drzewiczka River [Grzybkowska *et al.* 2001, Tszydel *et al.* 2003]. Besides, invertebrate grazing factors controlling periphyton loss include high shear stress/turbulence and sediment instability [Nikora *et al.* 1997]. A three- and five-fold increase in discharge in the Drzewiczka caused a decrease in periphyton but it seemed to have no effect on grazers that reached very high density at every period studied, except flood (in February), which affected both grazers and their food resources.

In freshwater ecosystems submerged macrophytes are known to impede water flow and circulation. They form one of the most important habitats for many invertebrates. This is because in comparison with often unstable and unprotected bottom substrates they offer relatively stable and deposit-free surfaces on which it is easy to forage (epiphyton) and/or construct larval cases [Cardinale *et al.* 1977, Tokeshi and Pinder 1985]. Macrophytes may also create favourable conditions for pelophilous zoobenthos by trapping fine particulate organic matter on the bottom [Cogerino *et al.* 1995]. Vascular plants were also very important in the disturbed site of the Drzewiczka River – this part of area of the riverbed was affected by the higher flow to the lowest degree. It is probable that this less disturbed area acts as refugia for macroinvertebrates in which some drifting organisms, such as Oligochaeta, may cumulate (retention and/or passive deposition of animals).

Besides the availability of food resources very important biotic mechanisms of lotic habitats that can affect benthic assemblages are competition and predation [Minshall and Robinson 1998]. Among abiotic factors local current velocity, water depth, and inorganic substratum composition are known to most strongly influence the microdistribution of lotic macroinvertebrates [Matthaei and Towsend 2000, Jowett 2003]. These variables impose different frequencies and intensities of disturbance or differences in inter-habitat characteristics [Minshall and Robinson 1998]. According to Matthaei *et al.* [2003], spates in streams leave a small-scale mosaic of bed patches with different stabilities and contribute to the patchy distribution of benthos. For over two decades highly frequent high-flow events caused the development of a bed patch mosaic in the Drzewiczka River downstream of the dam and canoeing track. While the 3-5-fold increase in discharge may be included in the factors sustaining high abundance and diversity of macrobenthos, the extraordinarily high discharge (in February) disturbed sediment and subsequently washed away particulate organic matter, affected the distribution, composition and abundance of the zoobenthos; plenty of individuals as well as their food were washed downstream. However, community stability varied significantly between habitats. But even a spate did not cause depletion of the entire riverbed – community stability was highest at the submersed macrophyte habitat dominated by macrobenthic taxa with different modes of life (epiphytic fauna and pelophilous). Thus, according to the definition of refugia given by Lake [2000], macrophytes habitat in the Drzewiczka River may be ascribed to the 2nd class – it applies to biotas that were only partly damaged by disturbance; these biotas could potentially colonize the depleted river sections.

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WPŁYW ZWIELOKROTNIONEGO PRZEPŁYWU NA ZOOBENTOS NIZINNEJ RZEKI

Streszczenie. Poznanie funkcjonowania czwartorzędowego odcinka nizinnej rzeki Drzewiczki (prawostronny dopływ Pilicy) w warunkach silnych zakłóceń spowodowanych piętrzeniem (jego efekt to 84-hektarowe Jezioro Drzewieckie) i użytkowaniem sztucznego górskiego toru kajakowego (W-WSCT) było celem podjętych badań. Wieloletni specyficzny rytm uwalniania wody zdeterminowany funkcjonowaniem tych konstrukcji spowodował silną heterogenność (mozaikowość) warunków środowiskowych odcinka rzeki poniżej zbiornika.

Na stanowisku bezpośrednio poniżej tamy i W-WSCT przeprowadzono badania w trzech sezonach: jesienią, wiosną i zimą. W każdym z sezonów pobierano próby, każdorazowo przed i bezpośrednio po silnym uwalnianiu wody ze zbiornika, przekraczającym we wrześniu trzykrotnie medianę przepływu, pięciokrotnie w marcu, natomiast szesnastokrotnie w lutym. O ile upust wody ze zbiornika jesienią i wiosną był zbliżony do wysokości przepływu generowanego na potrzeby treningowe kajakarzy, to zimowy był nietypowy, zdeterminowany opróżnianiem zbiornika przed jego planowanym bagrowaniem. W każdym z sezonów zbierano materiał po 2-3-tygodniowej stabilizacji przepływu na naturalnym poziomie.

W pięciu dominujących i wyraźnie różniących się siedliskach rzeki szacowane były: parametry morfometryczne, hydrauliczne oraz podstawowe parametry populacyjne bentofauny. W zoobentosie wszystkich siedlisk dominowały ochotkowate (Chironomidae, Diptera), które osiągnęły najwyższe zagęszczenie w nurcie rzeki. Spośród innych taksonów stwierdzono znaczny udział Oligochaeta oraz innych owadów: Trichoptera i Ephemeroptera (*Caenis*).

Trzykrotny i pięciokrotny wzrost przepływu nie powodował zmian w zagęszczeniu bezkręgowców, natomiast ostatni, najwyższy przepływ był przyczyną silnej destabilizacji podłoża; wiele osobników bentofauny wraz z ich zasobami pokarmowymi zostało wymytych. Jednakże nawet ten katastroficzny przepływ nie spowodował podobnych zmian w całym odcinku rzeki – najmniejszą destabilizację odnotowano w środku koryta rzeki, porośniętego zanurzonymi makrofitami (rdestnice). W istniejących warunkach środowiskowych rozwinęła się bardzo bogata i zróżnicowana biocenoza z dominującą fauną naroślinną oraz organizmami pelofilnymi, wykorzystującymi BFPOM „chwytaną" przez makrofity. Siedlisko to można zatem uznać za refugium dla bentofauny.

Słowa kluczowe: rzeka, zakłócenia, piętrzenie, tor kajakowy, bentos