

TADEUSZ FLEITUCH

Karol Starmach Institute of Freshwater Biology, Polish Academy of Sciences, 31-016 Krakow, ul. Slawkowska 17, Poland; e-mail: fleituch@zbw.pan.krakow.pl

Structure and Functional Organization of Benthic Invertebrates in a Regulated Stream

key words: regulated stream, weir, canal, benthic macroinvertebrates, trait groups

Abstract

This paper examines modifications of benthic structure and species/traits organization of macroinvertebrate communities affected by various hydro-technical structures in the regulated mountain Trzemesnia stream (southern Poland). The samples of aquatic invertebrates were collected seasonally (6 times) at: (1) one control site with natural substrate and at (2) five sites altered by sills, weirs, and canals during 1999. The stream canals, covered by *Cladophora glomerata*, were clearly distinguished from the other sites by: highest fauna density (mean of $8.5 \cdot 10^3$ ind. m^{-2}), lowest taxa richness (mean number of 4.7 taxa), and lowest diversity ($H' = 1.1$). The benthic communities consisted mainly of collector-gatherers with the highest contribution in the stream canals (range 87–96%). These results suggest that most types of stream regulations (i.e. stream bed formed by concrete bricks) negatively affect the functional organization of benthic invertebrates (collector-gatherers, predators, and scrapers).

1. Introduction

Watersheds, rivers, and stream habitats in Europe have changed dramatically over the last 100 years, as an effect of accelerated erosion, loading of pollutants from both point and non-point sources, and, in recent times, channel regulations (PETS, 1984; CRAIG *et al.*, 1987; ROUX *et al.*, 1989; YOUNT and NIEMI, 1990; DOLEDEC *et al.*, 1999). Moreover, structurally complex aquatic habitats have been directly and indirectly simplified by intensive land use and interruptions of natural biological processes. Many aquatic communities (e.g. macroinvertebrates) have gained or lost species diversity or became excessively fragmented, and both habitats and the organisms that they shelter may be less resilient when subjected to certain natural disturbances (WARD and STANFORD, 1983 a, 1983 b, 1984; ALLAN and FLECKER, 1993).

Regulated channel and uniform discharge affect the ability of an altered river system to retain and process allochthonous organic material (SPEAKER *et al.*, 1984; SNADDON, 1992). Organic matter provides a vital food source and together with mineral bed substratum, a complex habitat for aquatic invertebrates (CUMMINS and KLUG, 1979; PROCHAZKA, 1991). The benthic organisms are associated with a wide variety of substrata ranging from organic vegetation (tree debris, macrophytes, algae, and detritus) to different sizes of inorganic particulates (silt, gravel, cobble, and stones). These substrata are the most easily altered habitats when a river is regulated. Many genera or families of benthic animals have been associated with the main habitat types (MERRITT and CUMMINS, 1984; REICE, 1989).

Besides substrate, many freshwater invertebrates have precise requirements for particular current velocities or flow ranges (STATZNER *et al.*, 1988). According to EXTENCE *et al.* (1999), certain taxa may be ideal indicators of prevailing flow conditions. As well as qualitative responses to flow changes, site specific studies show that most taxa associated with slow flow

tend to increase in abundance as flows decline, whereas most species associated with faster flows exhibit the opposite response (WRIGHT, 1992; MILLER and GOLLADAY, 1996).

The effects of riverine and water management (e.g. damming or flow regulation) are usually catastrophic for most temperate rivers (WARD and STANFORD, 1979). Channel manipulation often reduces natural river variability. The majority of studies involving the impact of water barriers on freshwater invertebrates have been conducted below large reservoirs (BAXTER 1977; MUNN and BRUSVEN, 1987; ARMITAGE and BLACKBURN, 1990; VOELZ and WARD, 1990; IMBERT and STANFORD, 1996). In this respect, very few studies have concerned this effect in streams regulated by smaller water constructions (e.g. water steps and weirs, FRUTIGER, 1992; GORE and HAMILTON, 1996).

The aim of the present study was to examine modifications in benthic macroinvertebrate structure and species/traits organization affected by various hydro-technical constructions and channel modifications in a mountain stream.

2. Study Area and Methods

Trzemesnia, a second order stream, tributary of the River Raba (Upper Vistula catchment, southern Poland). Since the construction of the Dobczyce Reservoir dam (1986–87), it flows directly to the reservoir. The total length of the Trzemesnia stream is 10.2 km, mean discharge (at 270 m altitude) $0.36 \text{ m}^3 \text{ s}^{-1}$, unit catchment run-off $12.6 \text{ dm}^3 \text{ s}^{-1} \text{ km}^{-2}$, average slope 11.1‰, and catchment area 29 km^2 (PUNZET, 1969).

The catchment is situated in the submountain area of the Pogórze Wielickie Plateau. Geologically, the area consists of Flysch rocks with weak-calcareous Istebna shally-sandstone and Godula rocks (PASTERNAK, 1969). Most of this catchment is arable (e.g. cultivated fields) with only a 40% forested area in the upper part. Mean annual air temperature is $7.9 \text{ }^\circ\text{C}$, annual range from -28 to $+35 \text{ }^\circ\text{C}$ (PUNZET, 1969). Mean annual precipitation is 800–900 mm. About 100 human settlements are distributed along the stream, while a local road adjoins it (90% of the stream length) (Fig. 1).

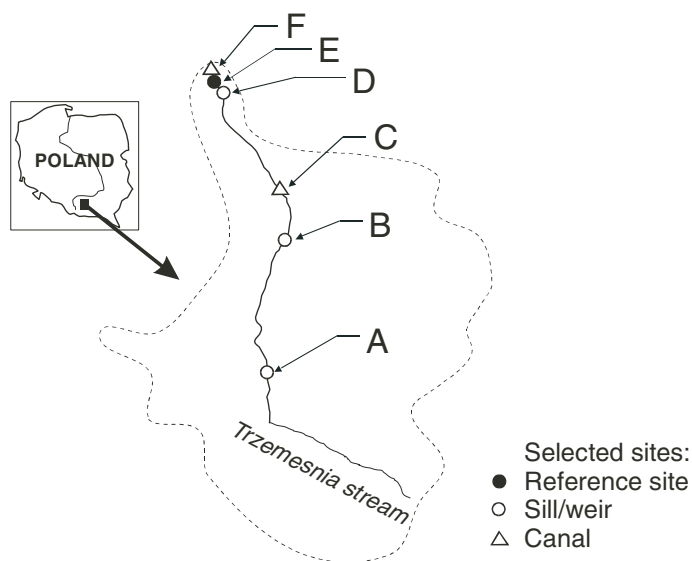


Figure 1. The location of the sampling sites.

The stream is manipulated by various structures for run-off erosion prevention (weirs) and for channel stabilization (canals). In general, its flow is interrupted by several overpouring structures (about 35 weirs) with a size range from 0.6 to 12 m of height. Additionally, the main weir sections are divided by a series of small steps that create sill/pool sequences, especially in the upper stream sections. In several regulated stretches instream concrete bricks and stones stabilize the surface of the stream bed. Parts of the stream banks are vertically protected by *in situ* cellular concrete blocks with grass (mid-stream sections) and by concrete walls (lower section). The course of the natural meandering stream is straightened in mid-reach.

For the purpose of the study five hydro-technical constructions (sites A, B, C, D, and F) and one reference site E were chosen (Fig. 1). Selected stretches 20 m in length along each site were measured and mapped. The site A was selected below the highest weir (12 m height, 10 m crest length) with a stilling basin of 100 m² at 6.8 km distance from the stream mouth. The flow at this site is very turbulent and rapid. Downstream, there are a series of low sills (0.4 m of height) with a sequence of short segments at 15 m intervals (site B, 5 km from the stream mouth). Most of the area of these segments (90%) has a stagnant flow reduced to 0.01 m/s (pool habitat). The site C was selected in the middle water-course. This stretch consists of a series of low weirs (0.35 m) with longitudinal intervals of 60 m, and water depth ranging from 0.05 to 0.15 m. The stream bed at this site is formed by concrete bricks (i.e. Gall's chains). Besides silt, there is a lack of mineral substratum and dense mats of *Cladophora glomerata* cover the stream bed. The site D (2.4 km) presents a medium-size weir (0.6 m height) with a 100 m² stilling basin. Downstream, the flow is rapid (riffle prevailed) and the water level is low (0.1–0.2 m depth). The site E (1.7 km) was selected as a reference site (non-regulated reach) with a natural substratum forming a patchy sequence of riffles (0.1–0.2 m depth) and pools (0.6 m). The site F (0.9 km from the stream mouth) represents a 3.5 m deep concrete channel. The water flow is rapid (>1 m/s) and its level does not exceed 0.1 m in depth. Only a dense algal mat along with unstable gravel covers that part of the stream. The general description of the sites is presented in Table 1.

Stream variables concurrently measured included major physical (flow, discharge, temperature, pH, specific conductance), chemical (oxygen concentration and saturation, BOD₅, nitrates, and orthophosphates), and biological components (benthic invertebrates) from May to October 1999 at monthly intervals. Detailed information concerning physico-chemical water characteristics is reported by FLEITUCH *et al.* (2000).

The stream flow was measured using a flow meter (a SCHILDKNECHT model) in three transects per site on each sampling occasion. In canals with silt, where coarser mineral substratum did not occur (sites

Table 1. General characteristics of six sites selected in the Trzemesnia stream.

Site/ Parameter	A	B	C	D	E-reference	F
Site Name	Poręba	Zakościele	Łęki	Banowice	Banowice	Banowice
Distance from the stream mouth [km]	6.84	5	3–3.75	2.35	1.3–2.1	0.91
Mean depth [m]	0.1	0.4	0.15	0.2	0.25	0.08
Mean width [m]	2.0	4.0	4.0	3.5	3.0	2.5
Mean current flow [m/s]	0.47	0.09	0.66	0.42	0.41	0.91
Mean discharge [m ³ /s]	0.114	0.101	0.216	0.179	0.169	0.201
Main substrate	Gravel, stones	Stones	Canal with bricks	Stones	Stones	Concrete canal
Substrate composition	Stones, gravel, sand	Stones, gravel, sand	silt	Stones, gravel	Stones, gravel, sand	silt
Peryphiton (microphytes)	Moses, Diatoms	Diatoms	<i>Cladophora glomerata</i>	Diatoms green algae	Diatoms green algae	<i>Cladophora glomerata</i>
Riparian canopy	Mostly open	Mostly open	Open	Mostly open	Closed	Open

C and F), at remaining sites stones and gravel prevailed. During sampling (from May to October 1999) a total of seventy two benthic quantitative samples (i.e. 2 samples \times 6 sites \times 6 months) were collected using a standard SURBER sampler (with an area of 0.04 m², 250 μ m net mesh size) and preserved in the field with 4% formalin (PLATTS *et al.*, 1983; SOWA, 1975a; FLEITUCH, 1992). In the laboratory, macro-invertebrates were hand-picked using a dissecting microscope at 10 \times and 40 \times in magnitude. Where possible, invertebrates were identified to species or genus level, except for Chironomidae (unidentifiable early instars of larvae) and Oligochaeta (inadequate net mesh size for quantitative enumeration), and counted. Macroinvertebrates were examined in terms of density, species richness (Platts *et al.*, 1983), Shannon diversity (H') (MAZURKIEWICZ and FLEITUCH, 2000), functional feeding groups (FFGs, CUMMINS and KLUG, 1979; MERRITT and CUMMINS, 1984; MOOG, 1995), and benthic flow preference groups (FPG, EXTENCE *et al.*, 1999).

Cluster analysis was used to assess agglomeration hierarchy between medians (weighted pair group average method – WPGMA) of JACCARD'S similarity coefficient (JACCARD, 1908) of the benthic macro-invertebrate taxa among sites. The computations of cluster analysis and Shannon index were carried out using MVSP software.

Time intervals and site category were used as factors in the two-way analysis of variance (ANOVA) to assess the differences in total benthic density, taxon diversity, and density of functional feeding groups. When differences were significant, post-hoc comparisons were carried out by means of Tukey's test (HSD, honestly significant difference) (ZAR, 1984). Prior to analysis, data were $\log_{10}(x + 1)$ -transformed (HILL, 1979).

3. Results

The flow conditions varied significantly ($F_{(5,30)} = 17.43$, $p < 0.0001$) among six sites with the highest mean values in the canals (Fig. 2). The highest seasonal water temperature range was found at sites C (17.3–21.7 °C) and F (15.7–22.9 °C). Specific conductivity ranged from 267 to 382 μ S/cm, and pH 7.7–9.5 between sites. Oxygen saturation increased to 140% at site C in summer. Water chemistry was represented by mean nitrate (NO₃-N) level of 0.90 mg/L (seasonal range 0.57–1.38 mg/L), and range of BOD₅ from 1.0 to 3.9 mg O₂/mg/L. The mean concentration of orthophosphate (PO₄-P) was 0.2 mg/L and the maximum reported was 0.30 mg/L at site B in June.

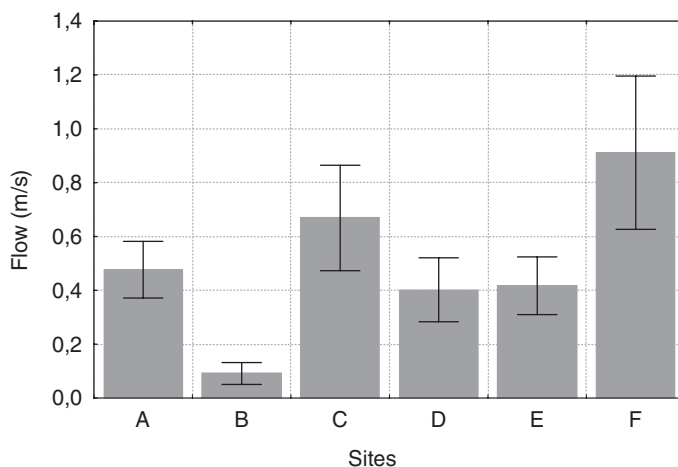


Figure 2. Flow conditions (mean and SD) at six sites during the study period (n = 12 per each bar).

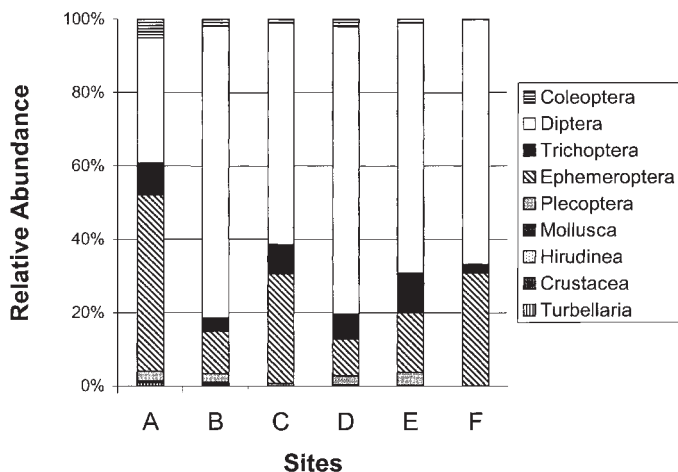


Figure 3. Mean relative abundance ($n = 12$ per each bar) of the major macroinvertebrate taxa during the study period.

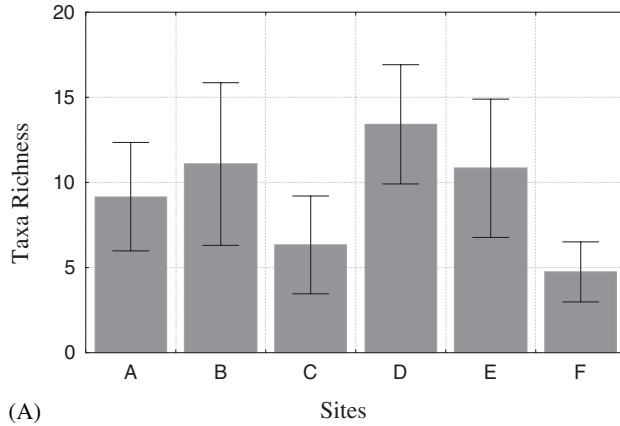
Fifty eight taxa belonging to nine aquatic invertebrate groups (Fig. 3) were identified in the Trzemesnia stream during the study period. The maximum number of accumulated taxa (42) was found at site D, the lowest ones occurring at sites C (20) and F (12). Aquatic insects accounted for most (e.g. maximum of 99,7% of site C) of the taxa density (Fig. 3). The number of taxa of Ephemeroptera and Plecoptera increased slightly at site D according to up/down stream sites, while the number of Coleoptera and Diptera decreased. In terms of mean benthic fauna density, Diptera (68%), Ephemeroptera (22%), Trichoptera (6%), and Plecoptera (1,6%) were the most numerous groups in this stream. Densities of Mollusca, Hirudinea, Crustacea and Turbellaria contributed less than 5% of the benthic community at all sites during the study period (Fig. 3).

The mean taxa richness, during the study period, showed the highest values at two sites: D (13.4) and B (11.1) (Fig. 4 A). In contrast, the lowest mean taxa richness was found in the stream canals (e.g. site F – 4,7). Total effect of time and site factors on taxa richness (ANOVA two-way test) was not significant ($F_{(25,36)} = 1.39$, $p > 0.05$).

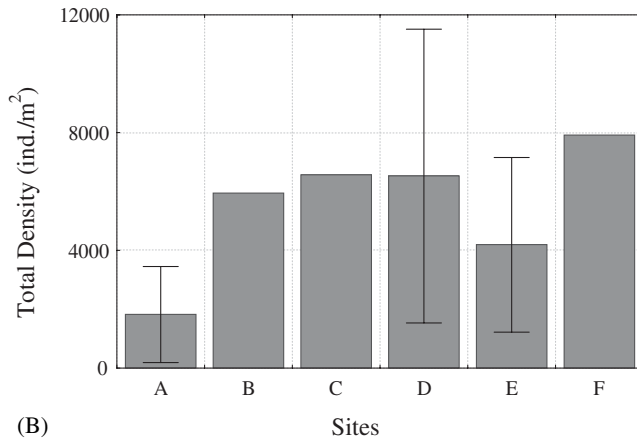
The abundance of macroinvertebrates varied longitudinally (Fig. 4 B) and was significantly different among sites (two-way ANOVA: $F = 5.37$, $p < 0.0001$). The maximal mean density was observed in canals: 6.5 and $8.5 \cdot 10^3$ ind. m^{-2} (sites C and F, respectively). Site B, where the lowest water flow was found, exhibited the greatest variation of density (mean = $5.9 \cdot 10^3$ ind. m^{-2} SD = 13.3). Site A, situated below the highest weir, showed the smallest numbers of invertebrates ($1.8 \cdot 10^3$ ind. m^{-2}). The reference site E presented an intermediate density of organisms throughout the study period (mean $4.3 \cdot 10^3$ ind. m^{-2}).

The mean diversity index (H') of benthic community at sites A and B was high ($H' = 2.12$ and 2.28 , respectively) in comparison with the canals (sites F and C, $H' = 1.11$ and 1.57 respectively, Fig. 4C). The reference site did not show the maximum fauna diversity in the Trzemesnia stream. The H' diversity differences among sites were statistically significant (two-way ANOVA: $F = 1.84$, $p < 0.05$).

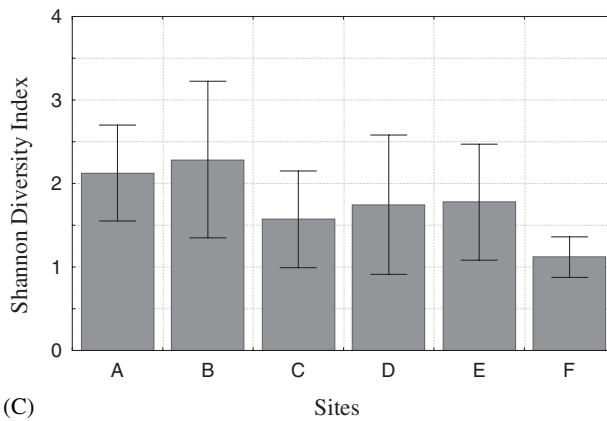
In the Trzemesnia stream collector-gatherers dominated at each site (Fig. 5A). A reduction in shredders mean abundance was observed at sites C and F. While comparing absolute values of density of functional feeding groups (two-way ANOVA; factors: time and site) significant differences were found for collector-gatherers ($F_{(25,36)} = 2.56$, $p < 0.005$), predators



(A)



(B)



(C)

Figure 4. A – Taxa richness, B – Density of macroinvertebrates, and C – Shannon diversity versus density at six sites in the Trzemesnia stream based on samples taken from May to October (for each site n = 12).

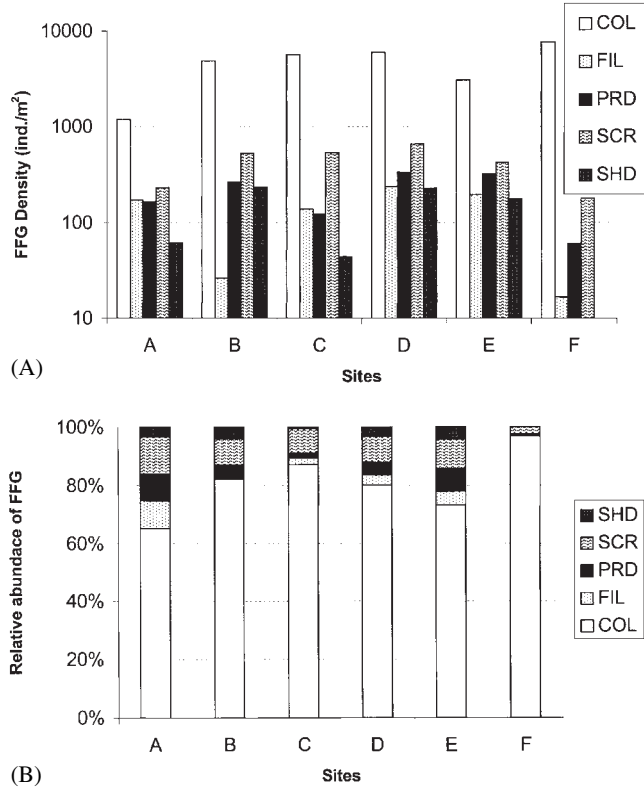


Figure 5. Mean absolute (A) and relative (B) abundance (for each site n = 12) of functional feedings groups (FFG): COL – collector-gatherers, FIL – filterers, PRD – predators, SCR – scrapers, and SHD – shredders during the study period.

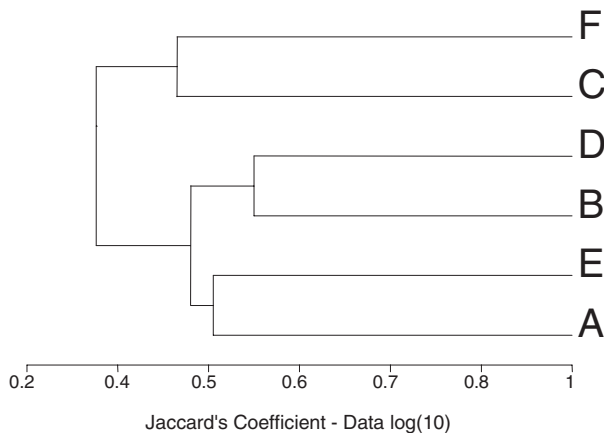


Figure 6. Site groupings from cluster analysis based on taxa densities (see methods for details).

Table 2. Taxa list with differences in density (two-way ANOVA test) among six sites of the Trzemesnia stream.

TAXON	F(5,36)	P	TAXON	F(5,36)	P
TURBELLARIA			TRICHOPTERA		
<i>Dendrocoelum</i> sp.	3,610	0,010	<i>Rhyacophila nubila</i> (ZETTERSTEDT)	1,787	NS
ISOPODA			<i>Rhyacophila tristis</i> PICTET	1,000	NS
<i>Asellus aquaticus</i> L.	1,000	NS	<i>Hydropsyche pellucidula</i> CURTIS	7,253	0,000
AMPHIPODA			<i>Hydropsyche contubernalis</i> MCLACHLAN	0,435	NS
<i>Gammarus fossarum</i> KOCH	3,130	0,019	<i>Hydropsyche instabilis</i> (CURTIS)	1,000	NS
HIRUDINEA			<i>Polycentropus flavomaculatus</i> (PICTET)	1,071	NS
<i>Eprobaddella octoculata</i> L.	0,604	NS	<i>Hydroptila</i> sp.	9,702	0,000
<i>Eprobaddella monostriata</i> (LINDENFELD et PIETRUSZYNSKI)	1,780	NS	<i>Psychomyia pusilla</i> FABRICIUS	3,781	0,007
<i>Glossiphonia complanata</i> L.	0,804	NS	<i>Sericostoma personatum</i> (SPENCE)	1,000	NS
MOLLUSCA			<i>Odontocerum albicorne</i> (SCOPOLI)	0,804	NS
<i>Ancylus fluviatilis</i> O. F. MÜLLER	0,428	NS	<i>Silo nigricornis</i> (PICTET)	0,800	NS
Other Gastropoda	0,801	NS	<i>Halesus digitatus</i> SCHRANK	0,895	NS
<i>Pisidium</i> sp.	1,000	NS	<i>Drusus</i> sp.	1,302	NS
PLECOPTERA			<i>Limnephilus</i> sp.	0,800	NS
<i>Leuctra hippopus</i> KEMPNY	4,470	0,003	<i>Potamophylax</i> sp.	0,611	NS
<i>Nemoura</i> sp.	0,817	NS	DIPTERA		
<i>Protonemura</i> sp.	2,339	NS	Simuliidae	5,433	0,001
<i>Perlodes</i> sp.	1,942	NS	Chironomidae	25,855	0,000
<i>Isoprela grammatica</i> (PODA)	2,325	NS	Ceratopogonidae	6,401	0,000
<i>Pera</i> sp.	0,664	NS	<i>Antocha virripennis</i> MEIGEN	1,998	NS
EPHEMEROPTERA			<i>Atherix</i> sp.	16,146	0,000
<i>Ephemerella danica</i> O. F. MÜLLER	0,814	NS	Limoniidae	3,000	0,023
<i>Beatis lutheri</i> MÜLLER-LIEBENAU	4,817	0,002	<i>Tabanus</i> sp.	1,000	NS
<i>Torleya</i> sp.	0,824	NS	<i>Dicranota bimaculata</i> SCHUMMEL	1,485	NS
<i>Ephemerella ignita</i> PODA	19,370	0,000	HYDRACARINA		
<i>Ecdyonurus venosus</i> (FABRICIUS)	2,869	0,028	COLEOPTERA		
<i>Rhythrogena semicolorata</i> CURTIS	1,874	NS	<i>Elmis</i> sp.	4,964	0,001
<i>Habroleptoides confusa</i> SARTORI et JACOB	6,524	0,000	<i>Stenelmis</i> sp.	1,046	NS
<i>Leptophlebia</i> sp.	5,670	0,001	Ditiscidae	1,000	NS
<i>Caenis</i> sp.	3,028	0,022	<i>Hydropus</i> sp.	1,787	NS
ODONATA			<i>Haliplus</i> sp.	1,000	NS
<i>Coenagrion</i> sp.	1,000	NS	<i>Laccophilus</i> sp.	1,000	NS
			<i>Gyrinus</i> sp.	1,000	NS
			<i>Haliplus</i> sp.	1,000	NS

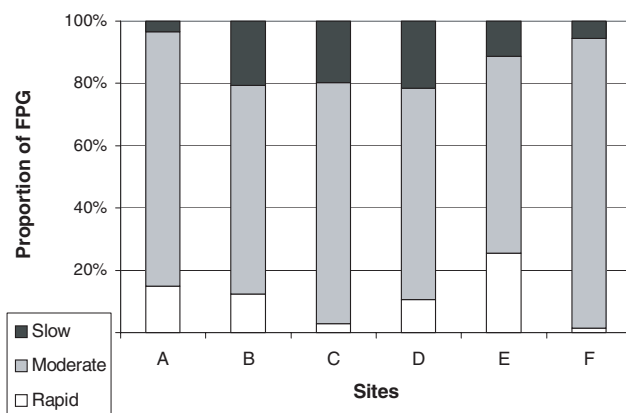


Figure 7. Proportion of flow preference groups (FPG) based on macroinvertebrate density. Categories: rapid flow, moderate flow, and slow flow groups.

($F = 1.77$, $p < 0.05$), and scrapers ($F = 5.44$, $p < 0.0001$) among the six sites. The highest relative contribution of collector-gatherers (e.g. *Baetis lutheri* MÜLLER-LIEBENAU., *Ephemera ignita* PODA, *Leptophlebia* sp., and *Hydroptila* sp.) was found at sites C and F (87% and 96%, respectively, Fig. 5B). Scrapers (e.g. *Ancylus fluviatilis* O. F. MÜLLER, *Psychomyia pusila* FABRICIUS) exhibited changing distribution patterns with maximum abundance at the head-water site A (12.7%), and in the middle reaches as well (site E – 10%). Shredders (e.g. *Gammarus fossarum* KOCH, *Nemoura* sp., *Protonemura* sp., *Leuctra hippopus* KEMPNY, *Elmis* sp., *Halesus digitatus* SCHRANK, and *Sericostoma personatum* SPENCE) and filterers (e.g. Simuliidae, *Hydropsyche pellucidula* CURTIS, and *H. instabilis* CURTIS) were practically absent at greatly altered sites (i.e. sites C and F). The relative contribution made by predators (i.e. *Dicranota bimaculata* SCHUMMEL, *Isoperla grammatica* PODA) decreased from sites A to C and again increased at the reference E site (*Rhyacophila nubila* ZETTERSTEDT, *Hydracarina*, *Dicranota bimaculata* SCHUMMEL, and *Polycentropus flavomaculatus* PICTET). In the stream canals predators represented always less than 2% of the benthic community.

Results of the cluster analysis (based on the taxa abundance) are shown in Fig. 6. In the first group sites C and F (stream canals dominated by Baetidae, Rhyacophilidae and Chironomidae) were clearly separated from the second group (sites A, B, D, and E). Species contribution at site A was more similar to that found at sites D or E than that at site F. For example, three mayflies (*Habroleptoides confusa* SARTORI et JACOB, *Ecdyonurus venosus* (FABRICIUS), and *Rhitrogena semicolorata* (CURTIS)) were common at sites A, D, and reappeared in the downstream reach (site E), whereas they were absent at stream canals (sites C and F). Significant differences in taxa distribution among sites were also confirmed for the most taxa of Ephemeroptera and Diptera in the stream (Table 2).

Most of the stream taxa were assigned to three flow-association categories: rapid flow, moderate flow, and slow flow groups. In this study, taxa associated with moderate stream flows dominated (mean range 63–93%) at all the sites (Fig. 7). Among all groups only the moderate flow group was significantly related to the current velocity ($r^2 = 0.74$; $F = 15.33$; $p < 0.01$). The highest contribution of taxa that prefer rapid flows was found at the reference site E (25%), whereas in stream canals this group exhibited only a small proportion, ranging from 1% (site F) to 3% (site C). The lowest proportion of invertebrates associated with slowly flowing water was observed at site A (3%) and at site F (5%).

4. Discussion

The benthic communities, especially in canals of the Trzemesnia stream, exhibited low taxa richness, low diversity and high density when compared with the reference site (Figs. 4A, B and C) or with other regulated watercourses of the same rhithron zone in Poland (FLEITUCH, 1992). This effect of the stream regulation was also confirmed by the cluster analysis and site grouping (Fig. 6). Similar observations have been confirmed by other studies (ARMITAGE, 1984; CAZAUBON and GIUDICELLI, 1999; WARD and STANFORD, 1979).

The trophic structure of the macroinvertebrate communities, based on FFGs (MERRITT and CUMMINS, 1984), was altered by the stream regulation. The abundance of predators and to a lesser extent, shredders was reduced in the regulated sites when compared with the reference site (Fig. 5A). Reductions in Nemouridae (e.g. *Nemoura* sp. and *Protonemura* sp.) and shredding caddisflies (e.g. *Halesus digitatus* and *Sericostoma personatum*) accounted for the lower relative abundance of shredders, while the absence of stonefly predator (e.g. Perlidae) accounted for the reduction in predators. The specific distribution of FFGs among the Trzemesnia sites emphasised the significance of diversity of habitats as a template for stream organisms (*sensu* SOUTHWOOD, 1977). Collector-gatherers dominated in all habitats, predators occurred in small numbers in canals, while scrapers were rare, occurring predominantly at the natural site E, where stones were covered by periphyton.

In this respect, ENGLUND and MALMQVIST (1996) have found that the functional feeding groups respond differently to flow modifications in regulated rivers. In their studies, increased flow and its variability have negative effects on the abundances of collectors, grazers and predators, while no effects are observed on filter feeders and shredders.

Differences in feeding behaviour may explain the diverse trait group responses. Grazers occurring on the top of stones with their food (algae) are exposed to the current while the collectors are associated with fine particulate organic matter. The animals with fine detritus can easily be eroded by high flows in the studied canals. The predators, a diverse group, may be exposed to the current (i.e. active forages – family Rhacophilidae – site C), or less exposed to current (i.e. sit-and-wait forages – Erpobdellidae – site B). The high current speed with increased bed stability and corresponding habitat alternations (mats of *Cladophora* sp.) may have reduced microcurrent velocities in the stream canals. The fine detritus cumulated in the mats may explain high densities of collector-gatherers in the canals (e.g. *Baetis lutheri* at site C). A lack of natural substrate in the stream canals and the reduction of current velocity in algal mats may justify the low contribution of the rapid flow preference group at these sites (Fig. 7).

In the Trzemesnia stream the benthic communities consisted of eurythermal and stenothermal species. The eurythermal species are polyvoltine and are present throughout the year (BOURNARD *et al.* 1982; PLESCOT, 1958; SOWA, 1975b). Examples of these found in the present study were the Hydropsychidae, Caenidae, and Baetidae. Among the stenothermal species that are adapted to the new thermal conditions of the channelled stream, the monovoltine species with short life cycles occurred. An example of that cycle in the Trzemesnia stream was the mayfly *Ephemerella ignita* (PODA). According to SOWA (1975b) this species usually spends about 10 months in the egg stage in the Carpathians and grows rapidly after hatching in late spring. The high summer water temperatures in the stream canals (2–5 °C higher when comparing with the remaining sites, FLEITUCH *et al.*, 2000) can explain the absence of some stenothermic taxa, which usually inhabit the rhithron zone (e.g. the family of Heptageniidae, and *Isoperla grammatica*). These species, which complete a generation in one year (SOWA, 1975b), have disappeared from the canal sections of the stream. It seems that the contrasted thermal regime and high summer temperatures in July have the most important effect on aquatic invertebrates in these sections (FLEITUCH *et al.*, 2000).

Most of the caddisflies represented a group of poorly synchronous univoltine species (e.g. *Rhyacophila nubila*, *Psychomyia pusila*, *Hydropsyche pellucidula*). All the larval instars of

these species live side by side for most of the year in the Carpathian Mountains (SZCZĘSNY, 1986). The two species *Hydropsyche instabilis* and *H. pellucidula*, commonly presented in this stream, are adapted to progressively higher summer temperatures (EDINGTON and HILDREW, 1981). Another species, *Polycentropus flavomaculatus* (Trichoptera), numerous at sites B and D, is very tolerant high temperatures and decreased oxygen concentrations (PHILIPSON and MOORHOUSE, 1976). *Rhyacophila* larvae that prevailed in the canal with a stream bed covered with bricks (site C), are the caddies most restricted to conditions of high current speed (SCOTT, 1958; DORIER and VAILLANT, 1954). This flow preferences may explain the high abundance of *Rhyacophila* in the canals.

The stream bed of two channelled reaches (sites C and F) was characterized by a lack of natural substratum (i.e. stones, gravel, or cobble). However, at these sites, the bed was densely covered by epiphytes – *Cladophora glomerata*. This species is a widely distributed, filamentous green alga (DODDS, 1991) adapted to resisting high water temperatures and fast flowing water. This alga does not directly provide nutrition to macroinvertebrates in rivers (STEVENS *et al.*, 1997). Rather it provides cover and habitat structure for the algal diatoms that comprised the main diet of those invertebrates (SHANNON *et al.*, 1994). The bed at site E exhibited a natural stony habitat which was probably reflected in high contribution of rapid flow group. The smallest number of slow flow group at site A, below the highest weir, and the lowest fauna density were caused probably by a flushing effect of this type of stream construction. Similarly, the smallest numbers of this group was observed at site F, represented the highest flows in the stream.

The non-regulated river stretches (e.g. the reference site in this study) may provide an important colonisation pathway for benthic species to enter the regulated and semi-regulated up- and downstream reaches. This mechanism seems to be important in river restoration and management.

Water resource development can give rise to dramatic changes in the character of riverine ecosystems. In order to assess the environmental flow requirements for a specific ecosystem, it is important to understand how aspects of the physical environment affect the various components of the ecosystem. For the Trzemesnia stream, it is imperative to maintain both the natural flow and habitat variability. Indeed, physical, chemical and biological factors operate in conjunction with each other to produce unique systems, both in terms of their character and functioning. The integrity of river ecosystems relies on a balance among all parameters. This fact is often neglected, with a tendency to focus on 'flows' in the management of our streams and rivers.

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