



Original Articles

Long-term effects of hydromorphological stream restoration on changes in microhabitats of *Ephemera danica* (Ephemeroptera) and its population

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ABSTRACT

Relationships between various techniques of stream restoration and selected characteristics of larvae of *Ephemera danica* (Müller 1764), were investigated along a small lowland watercourse, the Kwacza (N Poland). Effects of stream restoration were assessed on the basis of abundance, biomass, and body length of mayfly larvae as well as their biological condition (i.e. relation of mean body weight and length) within a decade (2007–2017) at each of 10 various hydrotechnical constructions along a 2.5-km stretch of the watercourse. Our results show that hydromorphological changes in the stream bed were strong stress factors for the mayfly population, especially in the first year of monitoring. In the following years, the applied restoration techniques created windows of opportunity for the population of *E. danica* which were successfully used by this species, as it increased in abundance and body length and colonized the whole restored stretch of the stream. Finally, 10 years after the river bed transformation, mayfly density increased 4-fold, while larval body length and biomass increased about 40-fold, as compared with the pre-restoration period. The improved habitat conditions of *E. danica* were observed in the sections where stream banks were strengthened with tree trunks, double groynes, and double semi-palisades to protect the banks against erosion. Surprisingly, the highest increase in larval abundance was recorded in a by-pass zone, an isolated part of the stream bed, which played the role of a refuge. Using redundancy analysis (RDA), we found that the mayfly population development after the stream restoration was primarily due to modified water velocities in the transformed sections and changes in water quality (e.g. higher pH, lower concentrations of N-NO₃⁻). We inferred that the modification of the stream bed has contributed to favourable changes in the studied mayfly population, which constitutes an important food base for the fish fauna.

1. Introduction

Among all aquatic habitats, lotic ecosystems are most strongly influenced by various anthropogenic factors (Murdoch, 2011). In the 20th century, researchers noticed that further deterioration of ecological status of streams and rivers may threaten civilization growth, so many hydrotechnical measures were taken to counteract the degradation (Roni et al., 2006; Feld et al., 2011). Many stream restoration projects have been implemented worldwide, and their major objective was to restore the natural flow pattern and/or to increase habitat heterogeneity. However, the available pieces of evidence of strong and long-term positive ecological effects of hydrotechnical measures on

invertebrate fauna are generally not convincing (e.g. Palmer et al., 2010; Feld et al., 2011; Friberg et al., 2014), with few exceptions (Müller et al., 2010; Kail et al., 2015; Verdonschot et al., 2016). This results mostly from a lack of properly planned long-term monitoring of the effects of stream restoration, but even if such evaluations were conducted, the recorded changes in diversity and composition of invertebrate communities were negligible (e.g. Louhi et al., 2011; Ernst et al., 2012). In some cases a remarkable increase in habitat heterogeneity (i.e. diversity of microhabitats) in the restored watercourses was not a sufficient impulse for development of benthic macrofauna (e.g. Jähnig & Lorenz, 2008; Louhi et al., 2011). It is supposed that the stimulated hydromorphological changes in the river bed simply are not

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an impulse determining restoration of key habitat components or their spatiotemporal distribution is not compatible with the life cycles of organisms (Lorenz et al., 2009). Another problem is that monitoring is based on whole communities, which are composed of organisms with very different ecological requirements and ranges of ecological tolerance (Castella et al., 2015; Dolédec et al., 2015). Within benthic fauna, members of 3 insect orders are particularly useful for such studies: Ephemeroptera, Trichoptera or Plecoptera (Hellawell, 1986). Insect phenology is extremely varied, often very flexible, which is linked with metamorphosis (holometabolism or hemimetabolism). Particularly important is the time needed for transformation of aquatic larvae into imagines, as it is usually connected with transition from aquatic to terrestrial habitats. Many insects have only a short window of opportunity enabling survival of a local population of the given species. That is why it is so important to aim at synchronization of favourable abiotic conditions, controlled predator pressure, and suitable habitat space (i.e. habitat heterogeneity), which leads to maximization of the potential expansion of the gene pool (Sparks et al., 2010; Everall et al., 2015). During implementation of restoration techniques, researchers attempt to optimize, most often by diversification, the living conditions of aquatic organisms. Thus, the processes of reconstruction of a stream bed can be regarded as an extension of the windows of opportunity, enabling successful re-colonization of streams. Reliable evaluation of the fauna response to the restoration techniques requires long-term studies (~10 years), as reported by Lorenz et al. (2012) or Obolewski et al. (2009). In this context, detailed population research on a selected species can provide more credible results than an analysis of a whole, diverse group of aquatic organisms. Selection of an indicator species, however, should be limited to populations with well-studied ecology (Dolédec et al., 1999).

de Pauw & Hawkes (1993) determined the requirements for optimum indicator species, and in the case of the presented Kwacza watercourse, these requirements are fulfilled primarily by *Ephemera danica* (Ephemeroptera). Its larvae are typical benthic fauna, associated with communities colonizing the bottom and solid substrate. Usually they are buried in the mud, waiting for food. Very much like other mayflies, they favour well-oxygenated waters, with the bottom rich in organic matter, preferably overgrown with macrophytes (Bennett, 2007). When abundant, the larvae can be a staple food for fish constituting an important component of the food chain. This is particularly important in watercourses like the Kwacza, which are spawning grounds for threatened species, including migratory fish, e.g. trout and grayling (Dębowski et al., 2013). Thus stream restoration measures should finally lead to reconstruction of the complex interdependence of biological communities, similar to natural systems. This approach fits to the assumptions of the paradigm of hydroecology through the interdisciplinary relationship between hydrology and biology (ecology) sciences (Hannah et al., 2004).

This paper presents the spatiotemporal variation (in a period of 10 years) in population structure of larvae of *E. danica* along the restored section of the Kwacza watercourse (northern Poland). This study allowed us to verify the following hypotheses: (1) stream restoration can be a window of opportunity, stimulating the colonization of the watercourse by mayfly larvae in both spatial and temporal terms; (2) the collected biological data (larval abundance, biomass, and body length) enable quantification of the efficiency of the applied solutions, and selection of the most effective ones; and (3) hydrological parameters affect the conditions of mayfly larvae more strongly than bottom structure and physicochemical parameters of water.

2. Methods

2.1. Study area and restoration design

The Kwacza is a left-bank tributary of the Słupia (Fig. 1), which flows directly into the Baltic Sea. The Kwacza is a small lowland

watercourse, ca. 20 km long, and its catchment area (53.8 km²) is used mostly for farming and is characterized with a mosaic of mineral soils. Although the river in spring is fed by meltwater, whereas in summer mostly by rainwater, the high water retention capacity of its catchment result in low variation of hydrological conditions (Mrozińska et al., 2018). Because of the direct connectivity with the sea, the Kwacza has a high ichthyological potential. It is a destination of migrations of anadromous fish, especially the sea trout (*Salmo trutta* m. *trutta* L.) and salmon (*Salmo salar* L.). In the early 21st century, the level of penetration of this stream by fish significantly declined (Dębowski et al., 2013), because of both the decreased food base and the lower water flow velocity, attracting the fish migrating upstream. Before restoration, the stream bed was mostly a straight canal, shaded by tall trees, mostly alder. Water quality and biodiversity indices were similar to those recorded in degraded rivers (Mrozińska et al., 2018). Additionally, its waters are used to supply trout ponds in the upper section (above the restored section of the stream). To protect the stream against a complete loss of its most valuable ecological characteristics, a program of stream restoration was set up. In the summer of 2007, in the terminal, 2.5-km stretch of the Kwacza River, various restoration techniques were implemented (Fig. 1, sections K1–K9), except of last section (K10, near the confluence with the Słupia River) which was not subject to any restoration measures.

Some of the restoration techniques consisted in installation of both hydrotechnical as well as nature-based solutions as: (a) stone islets (K8), which modified water flow velocity by current separation; (b) wooden semi-palisades in a single (K1) and double system (K9), which forced the stream to enhance bank erosion and create meanders; (c) wooden stabilizing sills, i.e. tree trunks crossing the river bed (K4), or single (K5) and double (K6) stone-wooden groynes. The most radical forms of stream restoration were: the isolation of a 100-m stretch of the river with an inactive weir (K2), which was an obstacle for upstream migration of aquatic fauna; and reduction of the shading of a fragment of the stream by means of tree clearing (K7). The construction works in the stream bed contributed to destabilization of its banks, so in some places the banks were strengthened with tree trunks (K3).

2.2. Environmental features

Hydrological monitoring was conducted due to the importance of water flow velocity for habitat conditions of benthic species, especially for the structure of bottom sediments, which determines the development of mayfly larvae. Water flow velocity (v , m/s) was measured on the days of sample collection in each of the 10 sections along the Kwacza. Individual measurements were made in hydrometric vertical profiles spaced 1 m apart in a cross-section of the stream bed with the use of the electromagnetic open channel flow meter (model 801, Valeport, UK). In the factor analysis, mean flow velocity for each cross-section was used, calculated on the basis of mean velocities in each vertical profile within the given cross-section (Mrozińska et al., 2018).

From the bottom of each section (K1–K10), samples of undisturbed bottom sediments were taken and subjected to physical analysis. We assessed particle-size distribution and concentration of organic matter. The fractions of mineral materials were determined according to the classification of the Polish Society of Soil Science (2009) and the USDA classification system (Schoeneberger et al. 2012). The content of gravel (> 2 mm) and sand (2–0.05 mm) were determined by dry-sieving. The content of silt (0.05–0.002) and clay (< 0.002 mm) were determined by the Bouyoucos and Cassagrande aerometric method in the Prószyński modification. The results of particle-size distribution analysis (percentage of fractions) were used to draw granulometric curves and calculate main granulometric characteristics, as follows: Trask sorting coefficient (S_o), Hazen sorting coefficient (u), Knoroz grain parameter (\mathcal{E}), and Kollis domination parameter (C_d) (Radecki-Pawlik et al., 2005). These parameters can help to explain dynamics and energy of sedimentological environment in the river before and after restoration.

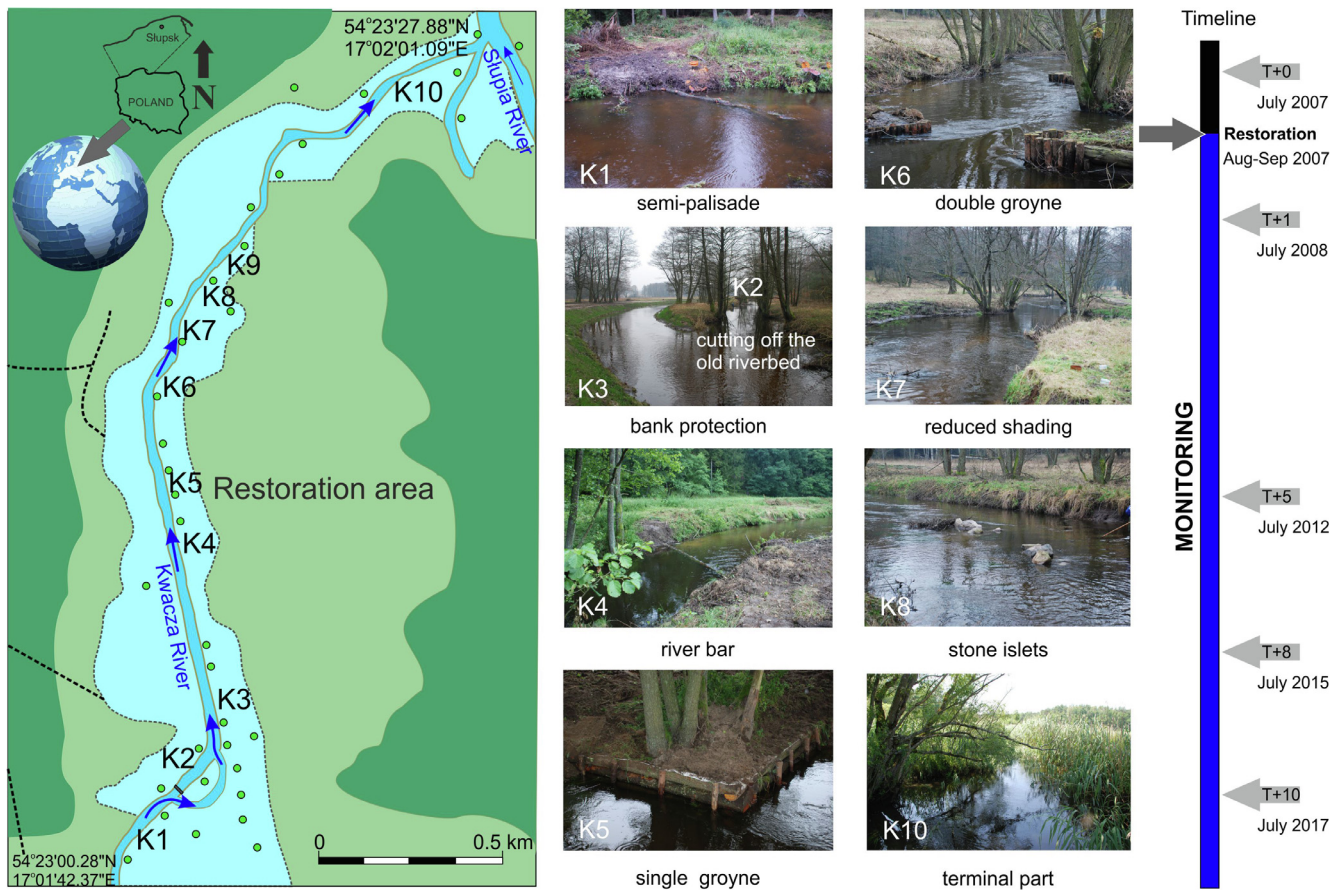


Fig. 1. Location of sampling sites with various stream restoration measures in the Kwacza River and the sampling timeline.

Dissolved oxygen (DO), water temperature, conductivity (EC), Cl^- , pH, and salinity were measured *in situ* by the calibrated, portable, multiparametric YSI 6600V2 sonde (YSI, USA).

Water samples for laboratory analyses were collected from the depth of 10–20 cm to 5-litre polyethylene bottles, washed earlier with 2 M hydrochloric acid and rinsed several times with distilled water. Water samples taken from each section of the Kwacza as well as from the Stupia River were analysed against nitrate nitrogen (N-NO_3^-), ammonium nitrogen (N-NH_4^+), orthophosphates (P-PO_4^{3-}), and total phosphorus (TP) according to international standards (APHA, 1998).

2.3. Biological traits

Benthic invertebrates were sampled according to the protocol recommended by the European Union in the European Water Framework Directive (WFD) (Haase et al. 2004). The first series of samples was collected before stream restoration in 2007 (T + 0), and next after a year (T + 1), 5 years (T + 5), 8 years (T + 8), and 10 years (T + 10) from the time of restoration (Fig. 1). We established 10 sections (K1–K10), whose location overlapped with the applied hydrotechnical constructions. At each of them, 15 subsamples were taken: 5 from the middle of the stream, and 5 from each bank. They were collected with a manual tool (shovel) with mesh size of 500 μm . Each sample covered an area of 20 cm \times 20 cm (thickness 10–15 cm, depending on sediment thickness), so in total at each section we collected material from 0.6 m² of the river bottom. The material was next rinsed and transferred to labelled glass jars and preserved with 4% formaldehyde in field conditions. In the laboratory, we isolated from the subsamples the larvae of *E. danica*, and determined their abundance (no. of individuals collected in the section), frequency, density, biomass (to the nearest 0.01 g), and body length (to the nearest 0.01 mm). Biological condition of larval (BC

index) was assessed on the relation of mean body weight and length (Froese 2006), using the formula:

$$BC = \sqrt{Bb \cdot Lb}, \text{ where}$$

Bb – mean body weight (mg),
Lb – mean body length (mm).

We assumed that the increase in body weight and length of *E. danica* is determined by improved environmental conditions, resulting from stream restoration. Values of this index reflected the condition of the population and were associated with effectiveness of the various restoration techniques. We also calculated a reference value, i.e. the mean value for individual years, but also for the pre- and post-restoration periods. To facilitate quantification of the effects of individual restoration measures on the mayfly population, we calculated BC index values for individual sections during the monitoring.

2.4. Data analyses

Differences in environmental predictors (water flow velocity, particle-size distribution, physico-chemical parameters of water) and biological ones (abundance, biomass, body length) between pre-restoration (T + 0) and post-restoration (T + 1, T + 5, T + 8 and T + 10) periods were subjected to analysis of variance (ANOVA) with Kruskal-Wallis test by ranks and then a Dunn post-hoc test at significance level $p < 0.05$. At that stage, the data were tested for normality (Shapiro-Wilk test) and homoscedasticity (Levene test). To diminish the effects of extreme values, the variables (except pH) were $\log(x + 1)$ transformed (ter Braak and Šmilauer, 2002).

The relationship between larval biomass and body length was

assessed using linear correlation. The analyses concerned individual study years and changes in individual sections of the restored watercourse. For each period, the coefficient of determination R^2 was calculated to assess how the data fit the pattern. This allowed us to determine how strongly larval biomass was associated with body size in successive years after stream restoration. We also took into account Pearson's coefficient of linear correlation (r) between those variables.

Next, we analysed the associations between environmental factors and characteristics of mayfly larvae on the basis of redundancy analysis (RDA, ter Braak, 1986). To reduce co-linearity, we used manual selection of parameters, choosing those that influenced the quality of the model at a level of at least 10% ($p \leq 0.1$, Magnan, 1994). We also applied the inflation index (VIF) to exclude co-linearity of the included variables (ter Braak & Šmilauer, 2002). The p values were determined using Monte-Carlo permutation test (Hope, 1968). The whole procedure was performed using CANOCO 5.10 software. To illustrate the statistically significant relationships between the studied characteristics of larvae and environmental variables, we also generated t -value biplots with Van Dobben circles, based on the RDA of physicochemical properties of water and parameters of *E. danica*. The t -value biplots are based on reduced rank regression, link many regressions between the abundance of taxa and specified descriptors and a model defined by RDA with the use of Monte Carlo permutation test ($p < 0.05$), (Manly, 2006). Van Dobben circles indicated the larval parameters that to a large extent reacted to the tested factor (value of $t < |2|$) (ter Braak and Looman, 1994).

3. Results

3.1. Hydrological situation

Before the restoration measures (T + 0), the studied stretch of the Kwacza was straight, and showed a nearly trapezium-shaped cross-section. The small slope of the bottom (0.2‰) resulted in slow water flow (on average $v = 0.23$ m/s). At that time, the stream was no longer an attractive habitat for migratory fish, which provided an incentive to change the situation (Fig. 2). As a result of implementation of various hydrotechnical constructions within the river bed, which changed the geometry of its cross-section, the water flow dynamics remarkably increased, particularly beneath the structures installed. The previously linear course of the current was modified, e.g. in the case of the stone islets (K8) it forked, while in the case of double groyne (K6), as a result of narrowing and impoundment of the river bed, the current was moved to its central part. In those sections, mean water flow velocity was the highest (mean $v = 0.61$ m/s), whereas the lowest velocity in the post-restoration period was recorded at K2, i.e. in the isolated part of the stream bed (mean $v = 0.10$ m/s) (Fig. 2).

Under the influence of changes in river bed geometry, we observed

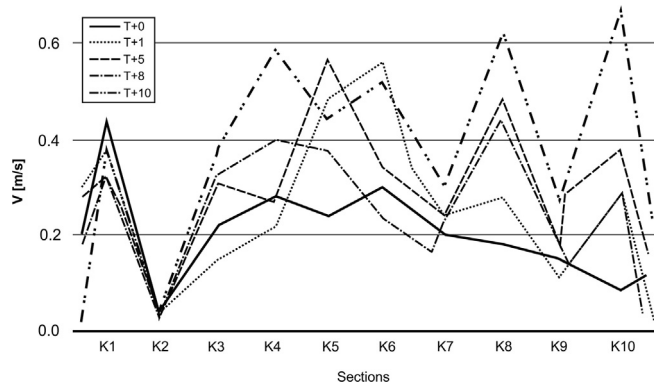


Fig. 2. Water flow velocity (v , m/s) in the Kwacza River during the summer between 2007 (T + 0) and 2017 (T + 10).

an immediate (already in T + 1) statistically significant increase in water flow dynamics in the whole studied stretch of the stream (one-way ANOVA, $p < 0.05$). In later years, the erosion evoked by flowing water contributed to variable hydrodynamic conditions. The stabilization of water velocity conditions in individual sections K1–K10 appeared between T + 8 and T + 10, with mean $v = 0.30 \pm 0.14$ m/s. It increased nearly 2-fold when compared to average value recorded in T + 0 ($p < 0.001$).

3.2. Physical properties and granulometric parameters of sediments

During this study, in the particle-size distribution of bottom sediments of the Kwacza, the mean share of the sand fraction decreased from 95% before restoration to 83% post-restoration period (Table 1). Also the percentage share of the gravel fraction was reduced by half, and a rapid decline was observed mostly in T + 1. In later years, the contribution of this fraction in the river sediments was stabilized. The decrease in proportion of gravel was accompanied by a highly significant increase in the silt fraction ($p < 0.0001$). The analysed sediments were characterized by good sorting and high uniformity, as indicated by values of Trask sorting coefficient ($S_o < 2.5$), Hazen sorting coefficient ($u < 5$), Knoroz grain parameter ($E \leq 4$), and Kollis domination parameter ($C_d \cong 1$). Only the Knoroz grain parameter fluctuated significantly in the study period ($p = 0.04$).

The physical structure of sediments after restoration differed depending on the applied technical solutions. The greatest changes were observed at K2 (the isolated part with a weir), where large amounts of organic matter were accumulated (Appendix 1). Also near the stone islets (K8), we observed a remarkable accumulation of this fraction.

The increase in water flow velocity was accompanied by washing away of the finer fractions of the sediments and an increase in the gravel fraction. Such a situation was observed near groynes, where the share of the silt fraction declined, whereas near the double semi-palisade (K9), the bottom was deepened in the central part of the river bed. Substantial changes were recorded also near the tree trunks crossing the river bed (K4): deepening of the bottom downstream from the impoundment and the increased share of the sand fraction (0.02–0.002 mm), while the proportion of the gravel fraction decreased (Appendix 1).

3.3. Physicochemical parameters of water

The selected physicochemical parameters analysed in individual years after restoration varied remarkably (Table 2). The greatest changes were observed in T + 1, whereas in later years the concentrations of many parameters were stabilized. Functioning of the new hydrodynamic system affected some water quality parameters (Table 2). This applies primarily to the mineral forms of nitrogen, N-NH_4^+ in particular, as its concentration increased highly significantly ($p < 0.0001$) and oxygen content was also elevated. In contrast, N-NO_3^- concentration declined ($p < 0.0001$): already in T + 1 it was 34% lower and in T + 10 it was 58% lower than in the pre-restoration period. In the case of conductivity and pH, fluctuations were also significant ($p < 0.001$): a substantial decline in T + 1, followed by an increase in later years of the study. The applied restoration techniques did not have any significant effect on water temperature, concentrations of phosphorus compounds, and salinity.

Restoration caused significant changes in water quality in the isolated part with a weir (K2), near the single semi-palisade (K1), and groynes (K5 and K6). Among the predictors whose concentrations changed markedly during this study, N-NH_4^+ and N-NO_3^- concentrations were the highest at K2 and K5, while pH and conductivity clearly increased at K1. Water aeration was markedly affected by stone islets (K8) and river bar (K4). No remarkable changes in water quality were observed in the untransformed terminal part of the Kwacza, near its confluence with the Słupia (K10).

Table 1

Physical properties (mean \pm standard deviation, SD) and granulometric parameters of bottom sediments of the Kwacza River. Abbreviation: p = significance of differences between years (one-way ANOVA test).

	unit	Pre-restoration					p
		T + 0 n = 30	T + 1 n = 30	T + 5 n = 30	T + 8 n = 30	T + 10 n = 30	
Gravel	%	8 \pm 1	4 \pm 0	5 \pm 0	5 \pm 0	4 \pm 0	0.59
Sand	%	91 \pm 9	95 \pm 8	93 \pm 9	83 \pm 8	83 \pm 8	0.63
Silt	%	1 \pm 0	1 \pm 0	2 \pm 0	12 \pm 1	13 \pm 1	< 0.0001
S_o		0.55 \pm 0.05	0.55 \pm 0.05	0.45 \pm 0.04	0.56 \pm 0.06	0.55 \pm 0.05	0.19
u		0.28 \pm 0.03	0.26 \pm 0.03	0.22 \pm 0.02	0.26 \pm 0.03	0.25 \pm 0.03	0.61
\mathcal{E}		0.09 \pm 0.01	0.09 \pm 0.01	0.06 \pm 0.01	0.09 \pm 0.01	0.08 \pm 0.01	0.25
C_d		1.48 \pm 0.15	1.32 \pm 0.13	0.95 \pm 0.09	0.83 \pm 0.08	1.28 \pm 0.13	0.04

3.4. Effects of restoration on *E. Danica* larvae

In total, 762 larvae of *E. danica* were collected in this study (Appendix 2). In the pre-restoration period they were found in 23% of subsamples, but in T + 1 their frequency declined dramatically. In the later years, intensive colonization of other parts of the watercourse was observed, so that finally, in T + 10, nearly all the sampling sites were inhabited by them (Table 3). Long-term analyses of the studied characteristics of the population of mayfly larvae show significant differences between years. Before restoration, the mean density of the larvae in the Kwacza was 5.4 indiv. m⁻², and mean biomass reached 14.4 mg m⁻², while in the post-restoration period they were on average 2- and 12-fold higher, respectively. Even greater changes were observed in body length and body weight, as they on average increased 15- and 13-fold, respectively, as compared with the pre-restoration period. Mean body weight and body length tended to increase continuously, in contrast to population density and biomass. After the restoration (T + 1), larval density decreased to only 1/7 of the initial value, and biomass to 2/3 of the initial value, but mean body length increased. In later years, the collected data indicated that larval abundance and body length gradually increased, reaching the highest values in T + 10 (Table 3). Thanks to this, their abundance was finally 4-fold higher, biomass 43-fold higher, and body length 34-fold higher in the studied population than in the pre-restoration period.

Among the various hydrotechnical solutions, the strongest influence on larval abundance was exerted by single and double groynes (K5 and K6). Initially (T + 0), in the places where groynes were planned, no larvae of *E. danica* were found, whereas in T + 10, as many as 90 individuals were collected (Table 4). A dramatic increase in larval abundance was recorded in the isolated part of the river bed, with the inactive weir (K2). Simultaneously, in T + 10, their abundance was reduced in the section where shading of the river bed was reduced by tree felling (K7) and near single semi-palisade (to 1/9 and 1/2 of the initial value, respectively) (Table 4). A systematic increase in larval

biomass was observed in nearly all parts of the river, but finally (T + 10) it was the highest near the double semi-palisade (K9) and in the section with reduced shading of the river bed (K7) (Table 4). At the end of the study period, the longest individuals were found near various types of semi-palisades, tree trunks protecting the banks against lateral erosion, and in sunny parts of the river bed.

We also assessed the condition of mayfly larvae on the basis of the BC index. First, we performed an analysis of linear regression, attempting to estimate the expected value of the index, for the known values of biomass and body length in individual years (Fig. 3). In all the study years, both predictors were strongly correlated. Similarly, the calculated coefficient of determination (R^2) indicated very good (T + 0, T + 1, and T + 8), and good (T + 10) fit of the model. In T + 5, the goodness of fit was only satisfactory.

Mean values of the BC index of the *Ephemera* population showed an increase after stream restoration (Fig. 4). In the pre-restoration period, the mean level of this index was 0.63, but after restoration it increased 10-fold (Fig. 4A). In successive years after restoration, values of this index increased from 105% (T + 1) to 1600% (T + 10), as compared with the pre-restoration period. Before restoration, only in the initial (K1-K3) and terminal sections (K7 and K9) larval condition was good (higher than the mean for this period). After restoration, larval condition was always high in the section where river banks were protected by tree trunks (K3). In some sections, larval condition was constantly lower than average, e.g. in the unshaded part (K7) or in the terminal section, near the Stupia River (Fig. 4A).

A decrease in larval condition after restoration was observed primarily in T + 1, and mainly in the sections with semi-palisades (K1 and K9), and in the separated fragment (by-pass) with the weir (K2). In later years, reduced BC values were observed in 1–2 sections: K7 and K8 in T + 5; K5 and K8 in T + 8; and only K9 (double semi-palisade) in T + 10 (Fig. 4B). We recorded also much greater positive changes in this index. The applied restoration measures caused a permanent increase in larval condition (from T + 5) in the section with stabilized

Table 2

Physicochemical properties (mean \pm standard deviation, SD) of water in the Kwacza River before and after restoration. Abbreviations: Tw = water temperature; EC = electrolytic conductivity; DO = dissolved oxygen; p = significance of differences between years (one-way ANOVA).

	Unit	Pre-restoration					p
		T + 0 n = 30	T + 1 n = 30	T + 5 n = 30	T + 8 n = 30	T + 10 n = 30	
T_w	°C	16.2 \pm 0.2	15.8 \pm 0.4	15.2 \pm 0.3	15.3 \pm 0.3	14.5 \pm 0.3	0.38
EC	$\mu\text{S cm}^{-1}$	307 \pm 31	273 \pm 27	291 \pm 29	299 \pm 30	312 \pm 31	< 0.001
pH	–	7.68 \pm 0.77	7.36 \pm 0.74	7.47 \pm 0.75	7.66 \pm 0.77	7.69 \pm 0.77	< 0.001
DO	mg L ⁻¹	9.47 \pm 0.95	7.70 \pm 0.77	7.82 \pm 0.78	7.83 \pm 0.78	7.79 \pm 0.78	< 0.01
DO	%	89.4 \pm 8.9	72.8 \pm 7.3	73.9 \pm 7.4	74.0 \pm 7.4	73.6 \pm 7.4	< 0.01
N-NH ₄ ⁺	mg L ⁻¹	0.301 \pm 0.030	0.712 \pm 0.071	0.587 \pm 0.059	0.537 \pm 0.540	0.471 \pm 0.047	< 0.0001
N-NO ₃ ⁻	mg L ⁻¹	0.346 \pm 0.035	0.229 \pm 0.023	0.185 \pm 0.019	0.169 \pm 0.017	0.147 \pm 0.015	< 0.0001
P-PO ₄ ³⁻	mg L ⁻¹	0.259 \pm 0.026	0.252 \pm 0.025	0.224 \pm 0.022	0.251 \pm 0.025	0.232 \pm 0.023	0.25
TP	mg L ⁻¹	0.778 \pm 0.078	0.756 \pm 0.076	0.672 \pm 0.067	0.753 \pm 0.075	0.696 \pm 0.070	0.26
Cl ⁻	mg L ⁻¹	13.7 \pm 0.7	14.2 \pm 0.9	14.1 \pm 0.4	14.6 \pm 0.5	14.2 \pm 0.4	0.33
Salinity	g L ⁻¹	0.168 \pm 0.017	0.179 \pm 0.018	0.172 \pm 0.017	0.161 \pm 0.016	0.179 \pm 0.018	0.23

Table 3

Comparison of changes in mean parameters (\pm standard error, SE) of the population of *Ephemera danica* in subsequent years of the study. Abbreviations: F = frequency (%); D = mean density (indiv. m⁻²); B = mean biomass (mg m⁻²); Bb = mean body weight (mg), Lb = mean body length (mm); p = significance of differences between years (one-way ANOVA).

		T + 0 n = 30	T + 1 n = 30	T + 5 n = 30	T + 8 n = 30	T + 10 n = 30	p
F	%	23	13	43	47	87	-
D	$\bar{x} \pm SE$	5.4 \pm 0.5	0.8 \pm 0.1	1.7 \pm 0.1	10.4 \pm 0.6	24.0 \pm 1.2	0.01
B	$\bar{x} \pm SE$	14.42 \pm 0.93	9.44 \pm 1.02	27.61 \pm 2.00	41.96 \pm 1.68	619.67 \pm 26.48	0.0002
Bb	$\bar{x} \pm SE$	0.92 \pm 0.07	1.83 \pm 0.21	7.56 \pm 0.55	8.10 \pm 0.52	30.81 \pm 0.73	0.0001
	range	0.08–8.40	2.80–30.00	1.30–82.00	0.06–64.00	6.20–97.67	
Lb	$\bar{x} \pm SE$	0.43 \pm 0.03	0.95 \pm 0.09	5.12 \pm 0.24	4.50 \pm 0.31	14.93 \pm 0.27	< 0.0001
	range	0.41–3.06	4.83–12.69	3.45–22.16	0.65–39.00	5.52–27.02	

banks (K3) and near the system of double groyne (K6). In the latter section, larval condition was the best (BC \sim 36), and it increased dramatically between T + 8 and T + 10 (Fig. 4B).

3.5. Relationships between *E. Danica* larvae and microhabitat composition

Using RDA we verified which of all the analysed environmental factors (flow velocity, temperature, EC, pH, DO, DO%, N-NH₄⁺, N-NO₃⁻, P-PO₄³⁻, TP, salinity, gravel, sand, silt, S₀, u, ε) significantly affect mayfly occurrence. As a result of forward analysis, we selected a final set of 4 explanatory variables that markedly influenced the quality of the model: flow velocity, pH, EC, and N-NO₃⁻ (Table 5).

In the generated RDA model, the first axis explained 27.4% of the variance, while the second axis explained 1.6% of the variance (in total 29% of the total variance) of the studied mayfly characteristics, and all the canonical axes were significant (Monte Carlo test, p = 0.002). The first component (RDA 1) was strongly linked with hydrological conditions, whereas the second one (RDA 2) was associated with trophic state (N-NO₃⁻) and water mineralization (EC) (Fig. 5A).

The t-value biplot for mean flow velocity (Fig. 5B) indicates that the studied characteristics of mayfly larvae were within the positive response area of this variable. This shows general preferences of the larvae for microhabitats with faster water flow. The same analysis demonstrates that mean water pH was positively correlated with the biomass and body length of larvae, and moderately with their abundance (Fig. 5C). The location of N-NO₃⁻ within the negative response area designated by Van Dobben circles (Fig. 5D), indicates that nitrates are among the factors linked with a significant decrease in larval biomass and body length.

4. Discussion

Our first hypothesis was that the changes caused by stream restoration stimulated *Ephemera* to colonize new fragments of the Kwacza watercourse. The linear river bed with invariable low flow velocity

(v_{avr} \sim 0.2 m/s) in the pre-restoration period was not favourable for mayfly species (Bennett, 2007). This changed significantly in the post-restoration period, when increased larval dispersal was observed in both spatial and temporal terms (Table 3). In the pre-restoration period, *E. danica* was detected in only 7 sampling sites monitored along the Kwacza watercourse. After five years since the restoration, number of sites colonized increased to 13, and after a decade, larvae of *E. danica* were found in nearly the whole restored stretch of the stream (Appendix 2). Undoubtedly the species made use of the possibility of expansion, caused by hydromorphological changes in the stream bed, which indicates its ability to adaptation to the changing environmental conditions. Restoration processes bring about many hydroecological changes, which can result in windows of opportunity, mentioned by many authors (Vander Zanden et al., 2005; Obolewski et al., 2018). The appearance of new ecological niches allows a rapid growth of populations of some species, which within a relatively short time become crucial components of ecosystems. As a result, many initially unfavourable sites were colonized and environmental resources were maximally used. Thus, restoration techniques can potentially play a major role in improving the biodiversity of river ecosystems (Verdonschot et al., 2016).

During the restoration of the Kwacza, many various hydrotechnical solutions were used, and their effects on larval condition varied, as observed in individual sections of the watercourse. In the transformed sections, water flow was slow (K2) or fast (K5 and K6), water depth was markedly increased (K4) or shallow (K8), or shading was minimized (K7). Such a mosaic of microhabitats suggested that the system was optimal and allowed the development of aquatic organisms. This was confirmed by the calculated BC index (the weight-length relation), reflecting biological condition of larvae in individual habitats (Froese, 2006). Before restoration it was relatively low (BC \approx 0.6), but in the post-restoration period it increased about 10-fold on average, reaching a maximum in T + 10 (Fig. 4A). The weight-length relation in the studied population shows that among the applied solutions, particularly the reduction of shading (K7) and the untransformed terminal section,

Table 4

Values of characteristics of the population of *Ephemera danica* in subsequent years of the study: A = abundance (no. of individuals collected in the section); Bb = mean body weight (mg); Lb = mean body length (mm).

	T + 0			T + 1			T + 5			T + 8			T + 10		
	A	Bb	Lb	A	Bb	Lb	A	Bb	Lb	A	Bb	Lb	A	Bb	Lb
K1	21	2.51	1.75	0	0	0	3	16.50	12.57	25	0.80	0.03	11	18.80	3.21
K2	6	0.83	2.53	0	0	0	0	0	0	0	0	0	181	19.62	0.18
K3	5	2.80	0.61	3	1.89	2.04	3	10.50	10.53	20	1.18	1.3	17	45.14	3.41
K4	0	0	0	4	0.92	1.21	5	5.67	4.09	7	2.40	0.62	17	28.25	3.08
K5	0	0	0	0	0	0	5	7.53	2.92	1	-	-	70	20.36	0.38
K6	0	0	0	0	0	0	5	1.67	1.42	13	0.68	0.13	20	60.32	3.23
K7	45	0.27	0.01	2	10.00	5.02	0	0	0	55	0.63	0.03	5	21.00	7.63
K8	10	1.83	0.22	0	0	0	5	27.78	5.61	1	-	-	31	10.67	0.59
K9	11	0.97	0.12	5	5.47	0.98	2	3.33	4.02	56	15.68	0.37	6	57.44	12.84
K10	0	0	0	0	0	0	3	2.67	2.02	9	18.31	3.34	74	26.53	0.60

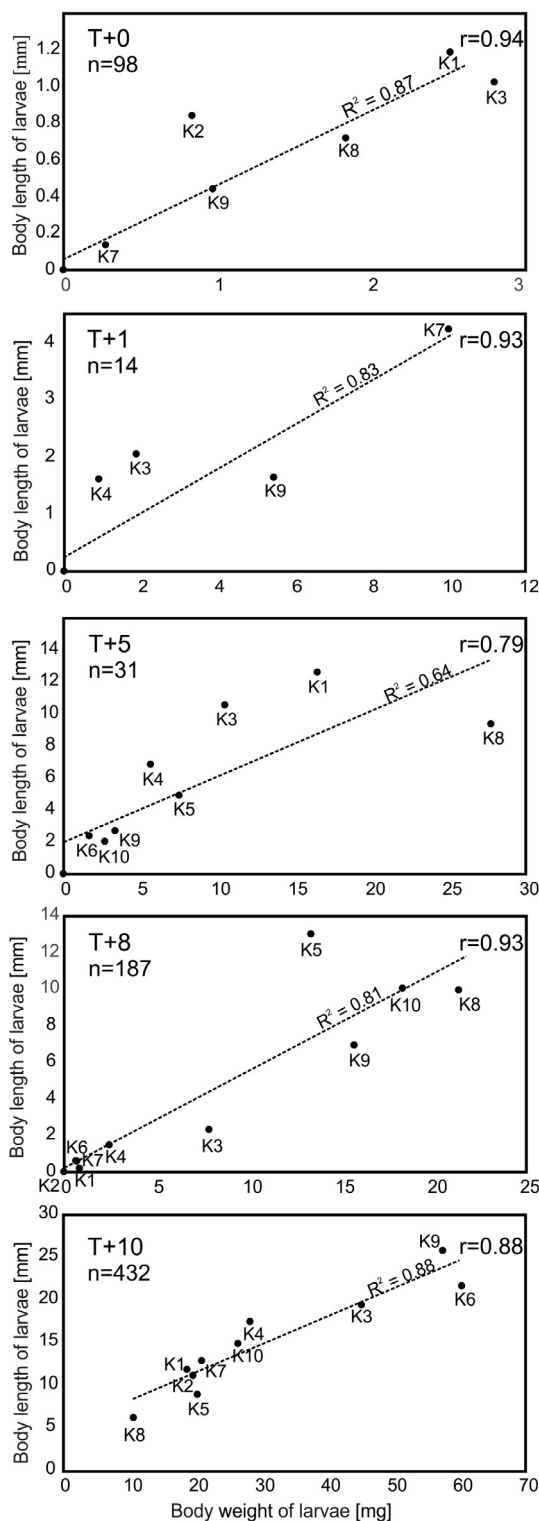


Fig. 3. Coefficients of correlation between mean body weight and mean body length of *Ephemera danica* larvae (mm) at the sampling sites in the study years.

near the confluence with the Słupia (K10) were not favourable for this species. An opposite, most positive effect, was recorded in the sections where river banks were strengthened with tree trunks (K3) or with systems of groynes (Fig. 4B). This indicates that our second hypothesis, about usefulness of biological data for evaluation of effectiveness of various restoration measures, was true.

Our third hypothesis, about the major importance of hydrological parameters, was not confirmed in this study. The sudden increase in

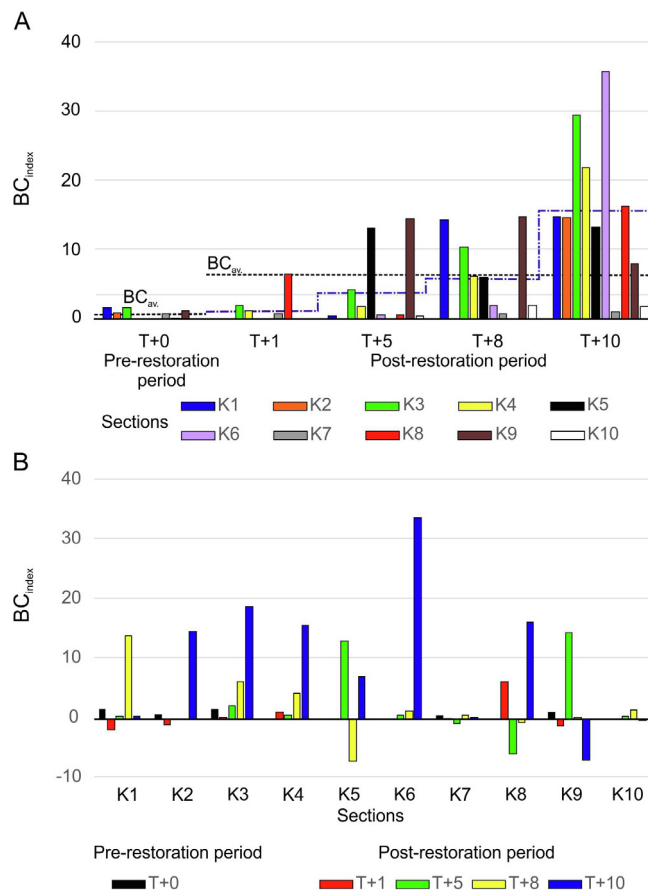


Fig. 4. Evaluation of the condition of *Ephemera danica* larvae with the BC index during the study period (A) and its changes in the sections only in the study period in relation to time (B).

Table 5

Selected explanatory variables that represent a significant relationship between the groups (marginal and conditional effects). Abbreviation: EC = electrolytic conductivity.

Variable	Marginal effects	Conditional effects		
	λ_1	λ_A	p value	F - ratio
Flow velocity (v)	0.08	0.08	0.002	25.68
N-NO ₃ ⁻	0.08	0.07	0.002	23.02
pH	0.03	0.01	0.006	5.86
EC	0.04	0.02	0.026	4.25

Lambda A denotes the amount of variability in the groups of data that would be explained by a constrained ordination model using that variable as the only explanatory variable. Statistically non-significant variables are not shown in the table.

water flow in some sections of the stream increased erosion and changed particle-size distribution (Table 1). This should have an impact on the mayfly population, as an unstable substrate makes its colonization by macroinvertebrates difficult (e.g. Larsen et al., 2011; Jones et al., 2012). Surprisingly, in our study such a correlation was not confirmed empirically. Changes in particle-size distribution were not a significant stress factor for the population of *Ephemera* larvae (Fig. 5A, Table 5). As reported by Bennett (2007), mud accumulation and appearance of aquatic plants in habitats is preferred by *E. danica*, and such changes were observed during restoration of the Kwacza. This may indicate that interactions between substrates and organisms in restored watercourses are of minor importance, as compared to the dynamics of hydrological conditions and water quality, and that is why they were

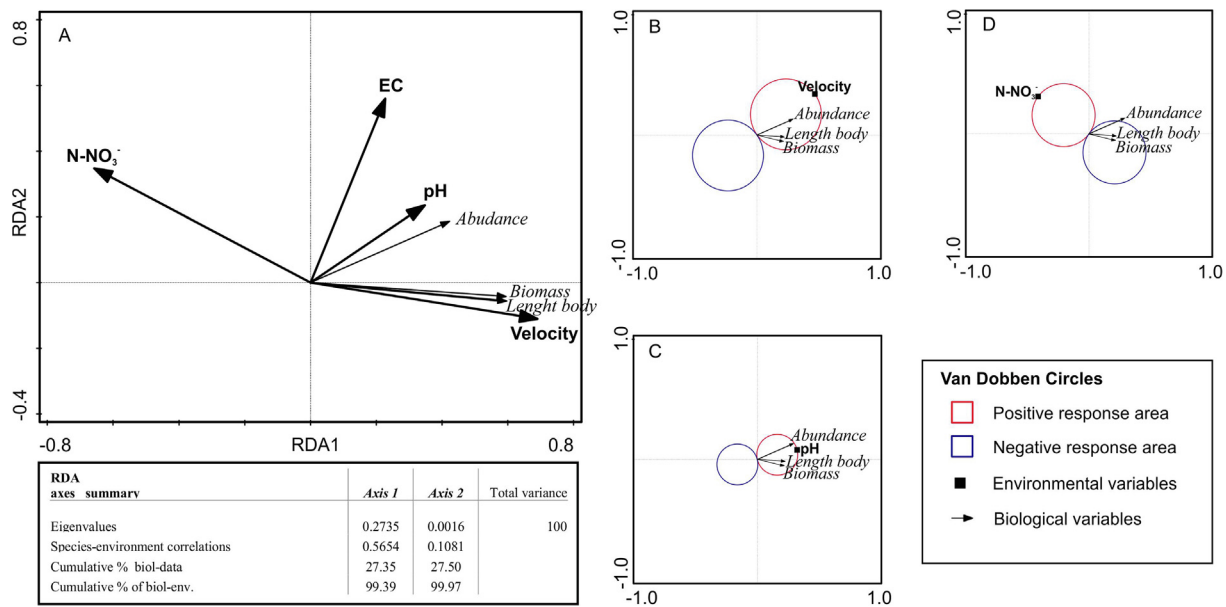


Fig. 5. Results of redundancy analysis (RDA): (A) a biplot of significant environmental variables and parameters of *Ephemera danica* larvae ($p < 0.05$); and t -value biplots with Van Dobben circles based on the RDA of environmental variables and parameters of *E. danica* larvae: (B) Van Dobben circles for discharge; (C) Van Dobben circles for pH; and (D) Van Dobben circles for N-NO_3^- .

not noticeable in our study. Another striking observation was the appearance of abundant mayfly larvae in T + 10 in the isolated part of the river bed (K2, Table 4). After restoration, the relatively slow water flow in this section (Fig. 2) did not create comfortable conditions for development of larvae of *E. danica* (Bennett, 2007). Despite this, the isolated fragment played a role of a mayfly refuge during dramatic changes in the river bed, e.g. rising water level, causing dislocation and/or death of mayfly larvae. In this way, the separated fragment of the watercourse, very much like areas located near the river bed, proved to be the most important for preservation of the gene pool in the river system (Dittrich et al., 2016). The large accumulation of larvae at K2 could be caused by a lack of pressure of predatory fish of fast-flowing waters (e.g. *Salmo trutta*, *Thymallus thymallus*, *Salmo solar*) that migrate upstream the Kwacza (Dębowski et al., 2013).

The ability of *E. danica* to colonize the restored watercourse implies an increase in habitat heterogeneity. This applies not only to hydrological parameters but also to particle-size distribution and physicochemical parameters (Tables 1 and 2). Results of ordination analyses (RDA) show that generally the major factor responsible for larval dispersal and condition of *E. danica* is water flow velocity (Fig. 5B, Table 5). However, such a favourable influence was observed only in the period of stabilization of conditions after the restoration ($\geq T + 5$). Rapidly enforced changes in water flow velocity in the river bed can be regarded as a stress factor that can effectively shape the population size of mayfly larvae (e.g. Dewson et al., 2007; Wagner et al., 2011). In this study, it was also visible, when in T + 1 the abundance (although not body size) of mayfly larvae was markedly reduced (Table 3). This effect was deepened by changes in physicochemical conditions, reflected in fluctuating concentrations of the studied parameters (Table 2). Sudden changes in environmental conditions in individual sections could imply physiological reactions of aquatic organisms (Boaventura et al., 1997; Livingstone, 2001, 2003). Recent research has shown that the presence of some enzymes – superoxide dismutase (SOD), glutathione peroxidase (GPx), and glutathione (GSH) in bodies of mayfly larvae – predisposes them as biomarkers for assessment of early reactions of aquatic organisms to changes in environmental conditions (Hook et al., 2014). In this study we also found that an increase in N-NO_3^- concentrations is associated with a lower abundance and body size of *Ephemera* larvae (Fig. 5D). The increase, however, is not due to stream restoration but

mostly to trout culture in the Kwacza River upstream from the restored sections. Božanić et al. (2018) clearly showed that discharge of nutrient-rich water from fish ponds used for trout culture is connected with a decline of mayfly abundance in watercourses. In contrast, fluctuations of water pH have a potential stimulating effect on larval condition (Fig. 5C). Although the range of fluctuations was still within the highest class of water quality, effects of water pH on many ecological processes were significant. This contrasts with other reports, which do not show any such relationship or even suggest that pH and EC do not affect mayfly development (Bispo et al., 2006). It appears that changes in stream hydrodynamics may cause unexpected effects and behaviour of aquatic organisms, often not confirmed by studies conducted in stabilized ecological systems.

The systematic increase in biometric characteristics of larvae of *E. danica*, reflecting the condition of this species, indicates that stream restoration can be important also for health of migratory fish populations, for which a relatively small watercourse, such as the Kwacza, is a natural spawning ground. Domagała et al. (2015) reported that remarkable differences in smolt growth rate in streams result from differences in densities of benthic invertebrates. Another, equally significant parameter, is body size of the consumed organisms, as mean size of predators and their prey are always positively correlated (Cohen et al., 1993; Klemetsen et al., 2003). Hence, body size (which reflects condition) is one the major environmental factors affecting food selection (Schmidt-Nielsen, 1984; Reiss, 1989). This issue is particularly important when attempting to restore populations of salmonid fish. Thus, apart from their role as a bioindicator of changes caused by stream restoration, mayfly larvae can be crucial for achieving the objective of the restoration programme, i.e. the restoration of the fish fauna and increase in biodiversity in the Słupia catchment area.

5. Conclusions

Stream restoration is a strong stress factor affecting the ecosystems of watercourses, initially leading to disturbance of the ecological balance and having a negative effect on local mayfly populations. Nevertheless, within a short time *Ephemera danica* can adapt to new conditions and start to colonize newly created sites in the transformed river bed. Larvae of *E. danica* can thus be treated as a bioindicator of the

general effectiveness of the applied restoration measures. It can be particularly useful in the evaluation of effects of individual hydro-technical solutions on the habitat conditions of the studied species.

The set of factors that determine the population growth of *E. danica*, apart from the rather obvious role of the major hydrological factor (flow velocity), includes also water pH and mineralization (EC), which were marginalized in other reports. Another surprising result of our study was the negligible role of particle-size distribution of benthic sediments, although many other reports confirmed such a relationship. Anyway, our most striking finding was that larvae of *Ephemera* used as a refuge the isolated stretch of the river, which theoretically was the least likely to be colonized by organisms that prefer fast-flowing waters. This confirms that stream restoration is a very complicated process and its results are hard to predict, but this does not undermine the validity of restoration measures, aimed at biodiversity protection in river valleys.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105810>.

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