

# 1 Macroinvertebrate habitat requirements in rivers: overestimation of 2 environmental flow calculations in incised rivers

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15 **Abstract.** Flow variability determines the conditions of river ecosystem and river ecological functioning. The variability of  
16 ecological processes in river ecosystems gradually decreases ~~due to river channelization and incision~~. Prediction of the  
17 environmental flow allowing to keep biological diversity and river health developed as a response to the degradation of  
18 aquatic ecosystems overexploited by human. The goal of the study was to test the influence of river incision on environmental  
19 flow estimation based on the ~~macroinvertebrate biological monitoring working party macroinvertebrate BMWP\_PL~~-index.  
20 The 240 macroinvertebrate assemblages of 12 waterbodies ~~varying-differing~~ in the bed substrate, amplitude of discharge were  
21 surveyed in southern Poland. The variations in the distribution of 151 466 macroinvertebrates belonging to 92 families were  
22 analysed. The similarity of benthic macroinvertebrates reflects the typological division of the rivers into three classes:  
23 mountain Tatra streams, mountain flysch rivers, and upland carbonate and silicate rivers ~~(NMDS, ANOSIM, p<0.001)~~. As a  
24 response variable reflecting the macroinvertebrate distribution in the river, environmental parameters, BMWP\_PL index was  
25 chosen. ~~Our results show that the BMWP\_PL index reached its highest values in shallower zones (by the shores) and at high~~  
26 ~~water velocity in the Tatra Rivers or low velocity in most lowland rivers.~~ The river incision significantly increased the values  
27 of e-flow calculations in relation to redeposited channels. The area of habitat suitability ~~for macroinvertebrates~~ decreased with  
28 the bed incision intensity. In highly incised rivers, the environmental flow values are close to the mean annual flow, suggesting  
29 that a high volume of water is needed to obtain good macroinvertebrate conditions. As a consequence, the river downcutting  
30 processes and impoverishment of suitable habitats will proceed.

## 31 1 Introduction

32 Human water demand, including irrigation to increase crop productivity, dams, and reservoirs to control the timing of stream  
33 flow, and water withdrawal from rivers, has increased dramatically over the last 100 years (Vörösmarty et al., 2010; Veldkamp  
34 et al., ~~2019~~2017). Maintenance of a suitable water flow in an active river channel should not only secure human needs, but  
35 above all ensure the proper functioning of aquatic ecosystems (Anderson et al., 2006). This has become particularly important  
36 since river beds began to be perceived not only as channels filled with water, but as complex ecological systems, in which  
37 biological elements play a key role (Poff et al., 1997; Bunn and Arthington, 2002; White et al., 2016). The Water Framework  
38 Directive (WFD, European Community, 2000/60/EC) was introduced by European countries to protect and improve the state  
39 of aquatic ecosystems and formalize a water flow framework that would maintain this state (Chen and Olden, 2017).

40 ~~Water flow~~Discharge intensity is one of the most important factors influencing multispecies communities of aquatic and water-  
41 dependent organisms (Tharme, 2003; Arthington et al., 2006; Higgs et al., 2019). It is a parameter which shapes the

42 morphology (Michalik and Książek, 2009) and hydraulic flow conditions (water depth, flow velocity) and it influences the  
43 diversity and quality of habitats for fauna and flora in the active channel and in the floodplain (Allan, 1995; Poff et al., 1997;  
44 Ward and Tockner, 2001; Skalski et al., 2016; Skalski et al., 2020). Furthermore, this parameter flow significantly influences  
45 abiotic elements, such as water temperature and oxygenation, as well as nutrient cycles in the aquatic ecosystem (Monk et al.,  
46 2008; Laini et al., 2019). This applies in particular to rivers subjected to strong human impact (e.g., channel regulation and  
47 incision, dams, or retention reservoirs, as well as a continuous increase in water demand abstraction). Artificial restriction and  
48 control of a range of water flow values leads to substantial impoverishment of biological diversity (Pander et al., 2019).  
49 Environmental Flow is an amount of water required to maintain biological diversity in the river ecosystem. This definition  
50 requires to quantify ecological response of aquatic elements to flow alteration, which data are rather scarce in the literature  
51 (Poff and Zimmerman, 2010). Therefore, it appears crucial to define-estimate empirical ranges of environmental flows that  
52 ensure optimal habitat conditions for living organisms (Bunn and Arthington, 2002; Acreman et al., 2014).  
53 Environmental flow has been studied by many researchers, resulting in numerous methods for its determination~~for determining~~  
54 it. The simpler ones include hydrological methods, which are based on historical hydrological data and mean annual discharge  
55 (Tennant, 1976; Jowett, 1997; Tharme, 2003; Rosenfeld, 2017). Analysis of such data makes it-possible to specify a percentage  
56 of the mean annual flow as the critical value below which severe degradation of biotic elements occurs. Unfortunately,  
57 hydrological methods do not take into account the morphology of the river bed, which is a key factor shaping the river habitat  
58 (Książek et al., 2020). Therefore, a number of hydraulic methods based on simple hydraulic variables such as critical riffle  
59 analysis and-wetted area/wetted perimeter have been introduced (Gippel and Stewardson, 1998; Książek et al., 2019).  
60 Determination discharge values (Q) of Q for environmental flow involves defining the breaking point of the hydraulic variable  
61 discharge curves as the e-flow (Gippel and Sterwardson, 1998; Veza et al., 2012; Tare et al., 2017). Over time, hydraulic  
62 methods have developed in the direction of habitat simulation methods. They have additionally focused on the habitat  
63 requirements of selected groups of model organisms, most commonly water depth, flow velocity, and bed substrate (Jowett  
64 and Davey, 2007; Li et al., 2009; Muñoz-Mas et al., 2016). Based on the analysis of these environmental factors, habitat-  
65 discharge curves were drawn for organisms, and from these it was possible to read the optimal flows maintaining the normal  
66 ecological functions of aquatic ecosystems. Another type of method, which emphasizes the importance of the natural flow  
67 regime for the entire ecosystem, is-are holistic methods. They attempt to maintain the natural flow regime as well as flow  
68 variability. In this case, environmental flow is defined in the category of deviation from the natural flow regime (Yarnell et  
69 al., 2015).  
70 The methods presented above focus on the fish distribution and rarely on diversity and availability of habitats for freshwater  
71 macroinvertebrates, which is-are the most important and sensitive indicators of the ecological state of the ecosystem (Jowett  
72 et al., 2008; Birk et al., 2012). The diversity and taxonomic composition of aquatic organisms living in freshwater streams and  
73 rivers are used as indicators in the evaluation of environmental flow (Pander et al., 2019). In many cases, macroinvertebrate  
74 assemblages are considered (Hayes et al., 2014; Laini et al., 2019), as numerous studies confirm that they are relatively good  
75 indicators of ecological water quality and integrity (Buss et al., 2015; Wyźga et al., 2016; Schneider and Petrin, 2017).  
76 Freshwater macroinvertebrates also play an important role in the processing of nutrients and organic energy in running water  
77 ecosystems, as well as in sustaining ecosystem integrity.  
78 Another parameter, which is usually neglected in flow modelling, is associated with morphological channel modification and  
79 incision (Wyźga et al., 2012; Skalski et al., 2016). Incision and channel simplification is a global problem overwhelming most  
80 of the rivers in the mountain as well as in upland areas (Skarpich et al., 2020). During the last 100 years anthropogenic  
81 processes related to river regulation (narrowing and straitening) disturbed the fluvial processes leading to enormous river  
82 incision (Rinaldi et al., 2005; Wyźga, 2008). As a results rivers become a vertically closed systems losing the ability to store  
83 alluvial material. Moreover incision up to the bedrock simplifies the microhabitat array of the river (Neachell, 2014) and lead

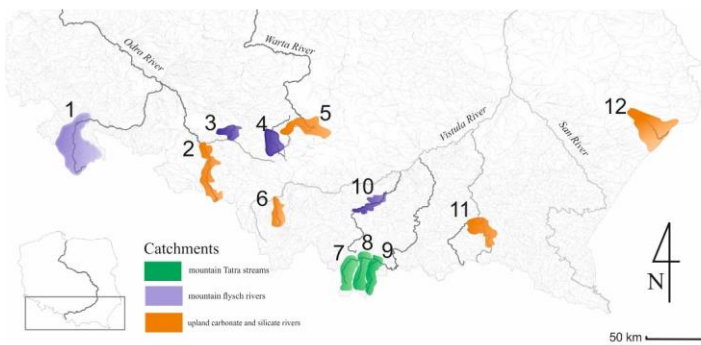
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84 to elimination most of the habitats (Muñoz-Mas et al., 2016) as well as affect ecosystem functioning (biodiversity lost and  
 85 food web network simplification, Shields et al., 1998; Jeffres et al., 2008).  
 86 Another parameter, which is usually neglected in flow modelling, is associated with morphological channel modification and  
 87 incision (Wyżga et al., 2012; Skalski et al., 2016). Incision up to the bedrock simplifies the microhabitat array of the river  
 88 (Neehell, 2014) and can eliminate most habitats (Muñoz-Mas et al., 2016). As a consequence, to preserve optimal areas with  
 89 heterogeneous habitats, the environmental flow should be vastly increased.  
 90 The goal of the study was to test the influence of river incision on environmental flow estimation based on the biological  
 91 monitoring working party macroinvertebrate index-habitat preferences. Specific aims of the study were: (1) to establish the  
 92 habitat preferences of macroinvertebrates communities (240 local assemblages) in mountain and lowland-upland rivers using  
 93 generalized additive models, (2) to calculate the e-flow values combining the habitat requirements and hydraulic method of  
 94 environmental flow calculation in relation to river hydromorphological parameters (redemption and incision), (3) to identify  
 95 reality of providing a scale of e-flow values for different hydromorphological modifications overestimation in relation to  
 96 available amount of water hydromorphological modifications and hydrological regimes (Low Low Flow, Mean Low FFlow  
 97 and Mean Annual FFlow) and )- (4) to check and visualize the e-flow values in relation to available water volume to check  
 98 and visualize the overestimation of e-flow calculations on randomly chosen, incised, and redeposited rivers based on CCED2D  
 99 model. We expected that e-flow in incised rivers, allowing to obtain the shelf zone level of the river should be much higher  
 100 than Mean Low Flow. Such assumption could determine the consecutive higher discharges and increase the bed degradation.  
 101 Firstly, we should restore the sedimentation processes in incised rivers to obtain a hydrodynamic balance and then manage the  
 102 proper volume of water. As a consequence, suitable habitats for invertebrates and fish will be enlarged.

## 103 2. Materials and methods

### 104 2.1 Study sites

105 The survey was conducted in 12 mountainous rivers assigned to three typological classes-groups according to the Polish Water  
 106 National Authority and the Water Framework Directive (Jusik et al., 2014): Tatra mountain rivers (Biały Dunajec, Dunajec,  
 107 and Białka - Type-Group 1), mountain flysch rivers (Raba, Brynica, Toszecki Potok, and Nysa Kłodzka - Type-Group 2) and  
 108 upland carbonate and silicate rivers (Solokija, Warta, Ropa, Biała, and Odra - Type-Group 3) (Fig. 1), varying in bed  
 109 modification (incision intensity or redeposition).



110  
 111 Figure 1. Map of the studied mountainous rivers in Carpatho-Sudetic region of Poland.  
 112

113 The first classgroup comprises rivers located in an alpine granitoid region, characterized by calcareous and silicate bedrock.  
 114 The second group consists of rivers flowing through much lower mountain ranges (up to the timber zone), where the bedrock  
 115 contains sandstone rock formations. The third group represents rivers of upland landforms with various carbonate and silicate

116 sediments and rocks. The typology of river channel modification was obtained from field observation and channel  
 117 measurements (cross-sections, longitudinal profile and cover, high of the floodplain). Narrow channels with downcutting to  
 118 the floodplain and simplified channel morphology were defined as incised.

119 All rivers are routinely monitored by the nearest monitoring station of the Environmental Agency (Environmental Agency  
 120 Data, 2018), and all twelve rivers have consistently been assigned a similar average chemical status in recent years. ANOVA  
 121 showed no variation between the river ~~types-groups~~ in incision bed modification ( $F=1.56$ ,  $p=0.26$ ) as well as in  
 122 physicochemical properties: dissolved oxygen, conductivity, hardness,  $pH_{max}$ ,  $NH_3$ ,  $NO_3^-$ ,  $NO_2^-$ , total N, and  $PO_4^{3-}$ . Only water  
 123 temperature and pH min significantly depended on the river ~~typegroup~~. All habitat variables (flow, depth and substrate type)  
 124 were significantly dependent on river ~~type-group~~ (Table 1), meanwhile the incision was not influenced by the parameters  
 125 variation.

127 Table 1 Mean values  $\pm$  standard deviation of the physicochemical and habitat variables of the three river ~~typesgroups~~, with  
 128 results of one-way ANOVA.

Environmental data	Type-Group 1		Type-Group 2		Type-Group 3		F	p
	Mean	St. dev.	Mean	St. dev.	Mean	St. dev.		
<b>Physicochemical</b>								
Water temperature [°C]	7.27	1.55	11.40	2.43	12.17	0.89	6.76	<b>0.016</b>
Dissolved oxygen [mgL <sup>-1</sup> ]	10.73	0.45	9.33	1.34	9.15	0.79	2.39	0.150
Conductivity [ $\mu$ S cm <sup>-1</sup> ]	202.67	91.58	1095.60	1594.59	356.5	93.26	0.85	0.458
Water hardness [mg CaCO <sub>3</sub> /l]	113.00	55.49	252.10	298.52	148.5	20.87	0.53	0.602
$pH_{min}$	7.97	0.11	7.52	0.11	7.20	0.08	47.91	<b>0.000</b>
$pH_{max}$	8.43	0.35	8.16	0.15	8.15	0.37	1.04	0.390
$NH_3$ [mgL <sup>-1</sup> ]	0.20	0.31	0.32	0.36	0.95	0.81	2.09	0.179
$NO_3^-$ [mgL <sup>-1</sup> ]	0.60	0.20	2.11	0.93	2.25	0.92	4.16	0.052
$NO_2^-$ [mgL <sup>-1</sup> ]	0.02	0.01	0.10	0.12	0.17	0.13	1.45	0.284
Total N [mgL <sup>-1</sup> ]	0.97	0.75	3.43	1.78	4.17	2.09	3.12	0.093
$PO_4^{3-}$ [mgL <sup>-1</sup> ]	0.03	0.04	0.09	0.05	0.06	0.02	2.08	0.180
<b>Habitat</b>								
Flow [m <sup>3</sup> s <sup>-1</sup> ]	0.83	0.55	0.45	0.39	0.44	0.32	38.06	<b>0.000</b>
Depth [m]	0.29	0.14	0.54	0.34	0.50	0.33	25.89	<b>0.000</b>
Substrate index	22.31	5.60	7.07	5.58	6.39	3.85	422.95	<b>0.000</b>

## 129 2.2 Macroinvertebrate sampling

130 Benthic invertebrate samples were collected in two seasons: autumn (October, 2017) and spring (April, 2018). No flood waves  
 131 occurred between these surveys, and the channel morphology remained the same throughout the sampling period. We collected  
 132 20 subsamples (1 m<sup>2</sup> each subsample) from each low-flow channel along a representative 100 m section of each river according  
 133 to a-the sampling procedure for the BMWP\_PL index (Bis and Mikulec, 2013). A total of 480 subsamples were taken from a  
 134 wide range of water depths and flow velocity. Following Jowett et al. (1991) and Muñoz-Mas et al. (2016), the substrate types  
 135 were converted to a single index by summing the weighted percentages of each type.

136 Macroinvertebrate samples were collected with a D-frame net according to the Environmental Agency's sampling protocol for  
 137 biomonitoring assessment using a kicking motion for 3 minutes across all habitats (Bis and Mikulec, 2013). All collected  
 138 material was preserved in the field with 4% formaldehyde. Aquatic macroinvertebrates were separated from the rest of the  
 139 material in the laboratory using a stereoscopic microscope and then, they-Macroinvertebrates- were identified to the family  
 140 level (Tachet et al., 2000), except Oligochaeta, Porifera, and Hydrozoa, which were recorded as such. Due to the varied

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141 preferences of macroinvertebrates to habitat conditions, the BMWP\_PL index was adopted as the best qualitative index. The  
142 Biological Monitoring Working Party (BMWP) is one of the most commonly used biotic indices in various rivers and streams  
143 around the world (Roche et al., 2010; Wyżga et al., 2013). It has been adopted in many countries, including Poland (Dz.U.  
144 2019 poz. 2149, 2019). The BMWP index was originally developed to represent water quality, but subsequent studies showed  
145 that it reflects ecological quality of the waterbodies and can be also related to hydromorphological impoverishment such like  
146 incision or straightening (Mutz et al., 2013; Wyżga et al., 2013; Mikuś et al., 2021). This index best considers the sensitivity  
147 of invertebrates to environmental variables, because families with similar stress tolerances are grouped together (Armitage et  
148 al., 1983).

### 149 2.3 Data analysis

150 ANOVA was used to verify the statistical significance of the differences in environmental data between the three river groups  
151 groups (Statsoft, 2013). Non-metric multidimensional scaling (NMDS) was used to test the relationship between the  
152 macroinvertebrate taxonomic composition of the assemblages of the 12 rivers assigned to three groups (Group 1, Group 2 and  
153 Group 3) and hydromorphological variables (water velocity and depth) during the spring and autumn. Descriptive physical  
154 properties (water depth and velocity) were classified into two or three categories: Low, Medium and High. We used minimum  
155 and maximum values of depth and velocity range in each river group and divided them into 33 percentile ranges of the total  
156 value variability. In the case when the ranges were less than 0.5 m depth we have chosen two groups of 50 percentiles of the  
157 depth ranges. The significance of differences between depth and velocity classes was tested by ANOSIM (p-values of pairwise  
158 comparison with Bonferroni correction) on the Bray-Curtis dissimilarity matrix with 499 permutations of the data. PAST  
159 software (version 3.13) was used to analyse NMDS and ANOSIM (Hammer et al., 2001).

160 To develop habitat suitability functions of macroinvertebrates, reflecting the optimal conditions in the river, generalized  
161 additive models (GAMs) procedures were chosen. The advantage of the method described by Jovett and Davey (2007), is that  
162 it calculates the probability of relations between dependent biotic variables and independent flow parameters. To choose the  
163 best-fitting model, we have ranked the available models according to Akaike information criteria procedure and  $\Delta AIC_c$  values,  
164 which reflects the difference of AIC between a given model and the lowest AIC. The best fitting model, describing the  
165 relationship between independent variables (depth and velocity and its two-way interaction between them) and  
166 macroinvertebrate BMWP\_PL index, was generalized additive model with Poisson error distribution and log link function.  
167 We have also measured the accuracy of the GAM procedures (Shearer et al., 2015). The total deviance explained calculated  
168 as the relative difference between the residual and the null deviances of the model ( $[\text{null deviance} - \text{residual deviance}] / \text{null}$   
169  $\text{deviance}$ ) was adopted. The course of the regression line of the BMWP-PL and depth and velocity for each group of the bed  
170 material rivers was obtained using CurveExpert software, where the best fitted line for the set of nonlinear curves was applied  
171 and ranked. The BMWP\_PL curve maximum values were regarded as the most suitable for invertebrates and the most  
172 preferred. We were interested in calculation of optimal condition for depth and velocity separately to obtain the optimal  
173 conditions allowing to calculate the discharge which are needed for hydraulic and CCHE2D modelling. The preferred depths  
174 and velocities for each season and river bed material groups were used to calculate the hydraulic discharges which are the most  
175 suitable for BMWP\_PL variables and recognized as environmental flow.

### 176 2.3.4 Hydraulic modelling

177 We used the hydraulic method for the assessment of the environmental flow of each river because of the relationship between  
178 the hydraulic parameters of watercourses (depth and velocity) and the quality of the aquatic environment (BMWP\_PL - GAM  
179 relations). The wetted perimeter method (WPM) is based on the relationship between the wetted perimeter for a given cross  
180 section of the river and the value of flow with reference to biological requirements (Shang, 2008). We used rating curves for

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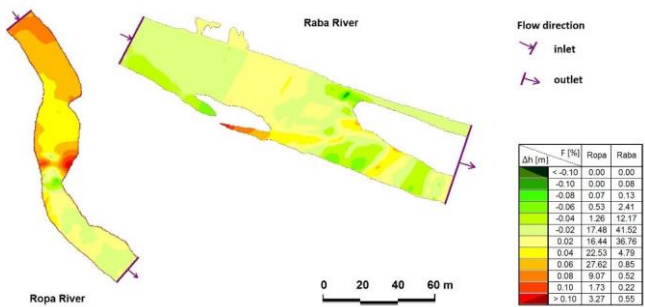
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181 each river describing the water depth – flow relations to obtain environmental flow for given optimal depth. Detailed  
 182 description of the applied hydraulic method of environmental flow calculation is given in Książek et al. (2019). To compare  
 183 the environmental flow in relation to hydromorphological parameters (incision, redeposition), we used the proportion of  
 184 Environmental flow ( $Q_{env}$ ) to mean hydraulic parameters of the minimum discharge: Low, Low Flow (LLF), Mean Low  
 185 Flow (MLF), and Mean Annual Flow (MAF). Those metrics show us the position of the calculated environmental flow  
 186 in relation to available water volume (—flow characteristics from hydrological year-to-year 1961 to 2017  
 187 observations) characteristics.

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188 **2.4.5 Case study 2D modelling methodology**

189 We provided the detailed modelling of a randomly chosen incised and redeposited river based on CCHE2D model. The  
 190 model is a depth-averaged two-dimensional numerical model for simulating unsteady, turbulent, free-surface flow in open  
 191 channels with a moveable bed. The CCHE2D model solves depth-integrated shallow water equations for all hydraulic  
 192 calculations (Wu et al., 2000; Duan et al., 2001). The CCHE2D package consists of two modules: a Mesh Generator (MG) and  
 193 a Graphical User Interface (GUI). The main function of the MG is designing a complex mesh system. The mesh is generated  
 194 based on the surveyed topography and/or Digital Terrain Model (DTM). The model was applied in two representative rivers,  
 195 varying in river bed morphology – from incised bed rock channels to a channel with natural sediment structures (with  
 196 redeposition). The mesh for each sector of the river was generated by interpolating cross sections. A total of 5,112 observations  
 197 were used: Raba – 3033 (incision) and Ropa – 2079 (redeposition). The shape of the channels was fairly regular along the  
 198 reach under study, and its pattern presented little complexity (i.e., a single channel with no islands), but riffle-pool sequences  
 199 were observed. The 153–200 m long meshes were composed of cells and nodes (length and number of nodes, respectively,  
 200 for Ropa 153 m, 49715 and Raba 200 m, 99200). Data used for the initial conditions was extracted from field measurements.  
 201 Special attention was devoted to bed roughness due to its importance for water surface level. Roughness values ranged from  
 202 0.01 in hydraulic smooth bed zones to 0.07 in rough areas. Finally, the model time step was defined at 0.1 s or 0.25 s, depending  
 203 on the model structure. The model was calibrated by comparing the measured and computed water surface levels for measured  
 204 discharges in all cells and nodes (Fig. 2).

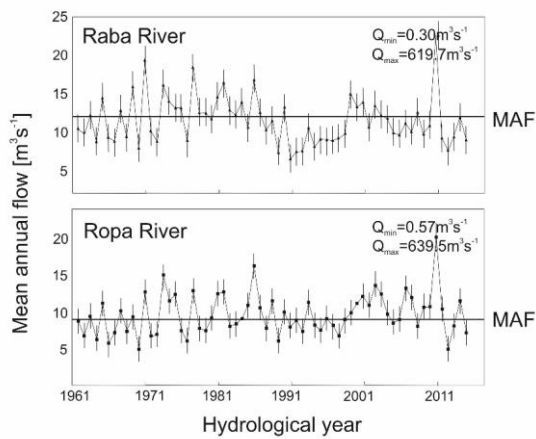


205  
 206 Figure 2. Comparison of calculated and measured water surface levels: The Ropa River for discharge  $6.71 \text{ m}^3 \text{ s}^{-1}$ , and The Raba  
 207 River for discharge  $10.29 \text{ m}^3 \text{ s}^{-1}$ : ( $\Delta h$  – difference between measured and calculated water surface level, F – area of particular  
 208 differences, percentage).

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210 In the case of the Raba River, for 70% of the calculated nodes, the difference between the calculated and measured water  
 211 surface level (WSL) was in the range  $\pm 0.02$  m. 84% of Ropa River nodes were in the range between of  $-0.02$  to  $0.06$  m. In all  
 212 described models,  $\Delta h$  in the main channel does not cross  $\pm 0.02$  m, but the visible differences are related to the horizontal layout

213 of WSL in cross-section. Evaluation of the compatibility measures of the numerical model showed very good accordance  
 214 (Książek et al., 2010) and the prepared models did not need recalibration.  
 215 The habitat suitability index was estimated in the first step by selecting a usable habitat for macroinvertebrates. For each  
 216 research section, we choose 20 points at each subsampled area sites differing in water velocity and water depth as the main  
 217 environmental variables creating habitat heterogeneity for macroinvertebrates. Then, according to the relationship between  
 218 hydromorphological habitat attributes (water depth and velocity) and the BMWP\_PL index values (describing the ecological  
 219 quality of the river), we constructed a GAM model as the best fitted method to mark out the range of hydromorphological  
 220 attributes (where the BMWP\_PL suitability index is the highest obtained from the GAM model curve is the highest). Based on  
 221 the optimal depth values environmental flow was established using rating curves.  
 222 Two rivers (located in the same Carpathian region) representing opposite bed modifications (incision and redeposition) were  
 223 chosen for the model as a case study. The modelled sectors of the river had channels with a pool-riffle sequence and fluvial  
 224 deposits, but were varied in terms of degradation of the bed structure. The hydrological characteristics of the modelled river  
 225 are presented in Fig. 3.



226  
 227 Figure 3. Changes in hydrological regime of the Raba and Ropa Rivers. The horizontal line indicates the Mean Annual  
 228 Flow (MAF).  
 229

230 The Raba was selected to represent incised channel rivers (bottom material mainly gravel and small stones, substrate index  
 231 14.9). The Dobczyce retention reservoir, which influences the hydrology and morphology of the river, is located upstream of  
 232 the examined sector of the river (12 km). Constructing of the retention reservoir in 1986 led to a significant decline in average  
 233 annual flow values (MAF values varied from 12.22 m³/s; in 1951-1985 to 10.57 m³/s in 1986-2015, F = 49.90, p < 0.0001)  
 234 and broke the continuity of the sediment transport. The reduction in flow, blockade of sediment supply and longitudinal training  
 235 work of the Raba led to incision of the riverbed and permanent compactness of the bed material. The Ropa River, chosen to  
 236 represent the redeposition processes, was located among upland, carbonate, and silicate rivers, with the lowest human impact –  
 237 agricultural land. The bottom material consists mainly of gravel and sand (substrate index 7.2), where bedload transport  
 238 remains undisturbed.

239 We also wanted to estimate minimum flow values for two rivers which were modelled using CCHE2D. The values of depth  
 240 and velocity corresponding th the highest BMWP\_PL, obtained from the GAM model for each group of river and season were  
 241 plotted against the number of pixels having values resembling suitability model. Giving those calculations we were able to  
 242 obtain the Weighted Usable Area (WUA) showing the most suitable habitat parameters (GAM depth and GAM velocity). Each

243 pixel covered 0.25 m<sup>2</sup> of total river area, so the number of counted calculated cells were the given values of velocity and depth  
 244 of each group of river were summarized and multiplied by the surface area. Based on those calculations using CCHE2D model  
 245 we were able to find the relationship between usable area and flow values. To calculate the optimal environmental flow values,  
 246 the curve between flow and suitable area was created. The optimum of environmental flow was estimated as 50% of WUA  
 247 values (Jowett et al., 2008) for CCHE2D modelled rivers.  
 248 To calculate the optimal environmental flow values (Q<sub>env</sub> optimal), a WUA vs flow curve was plotted. Optimal environmental  
 249 flow values were defined as 50% of the WUA values for both rivers. A hydraulic habitat 2D model of each river section was  
 250 used for spring and autumn as an example to estimate habitat prediction in terms of calculated environmental flow during the  
 251 season. Environmental flow that did not meet the conditions of 100% habitat suitability for macroinvertebrates was expressed  
 252 as the critical instream environmental flow value (Q<sub>env</sub> critical), below which the parameters of aquatic macroinvertebrate  
 253 communities dramatically declined.

## 254 2.5 Data analysis

255 ANOVA was used to verify the statistical significance of the differences in environmental data between the three river types  
 256 (Statsoft, 2013). Non-metric multidimensional scaling (NMDS) was used to test the relationship between the macroinvertebrate  
 257 taxonomic composition of the assemblages of the 12 rivers assigned to three types (Type 1, Type 2 and Type 3) and  
 258 hydromorphological variables (water velocity and depth) during the spring and autumn. Descriptive physical properties (water  
 259 depth and velocity) were classified into two or three categories: Low, Medium and High. The significance of differences  
 260 between depth and velocity classes was tested by ANOSIM on the Bray-Curtis dissimilarity matrix with 499 permutations of  
 261 the data. PAST software (version 3.13) was used to analyse NMDS and ANOSIM (Hammer et al., 2001).  
 262 Generalized additive modelling with Poisson distribution (GAM) was used to develop more defensible habitat preferences for  
 263 macroinvertebrates (BMWP\_PL index) based on their distribution in both dimensions: depth and velocity (Jowett and Davey,  
 264 2007). The course of the regression line was obtained using CurveExpert software, where the best fitted line for the set of  
 265 nonlinear curves was applied and ranked. To compare the variation of the proportion of environmental flow and  
 266 hydromorphological parameters (which were normally distributed) in relation to abiotic type and channel modifications,  
 267 general linear modelling was applied.

## 268 3. Results

### 269 3.1 Environmental flow based on benthic invertebrates distribution in relation to river hydromorphology

270 A total of 151 466 individuals belonging to 92 benthic invertebrate families from 480 macroinvertebrate assemblages were  
 271 identified. High variation was shown in the taxonomic composition of aquatic invertebrates depending on the  
 272 hydromorphological parameters (water depth and velocity) and the season (Fig. 4). In the case of rivers classified as **Type**  
 273 **Group 1**, water velocity was found to significantly affect the taxonomic composition of the macroinvertebrates in both spring  
 274 and autumn (Table 2).

275 Table 2 Results of ANOSIM analysis comparing macroinvertebrate assemblages between classes of velocity and depth  
 276 measured for three river **types-groups** in the spring and autumn season. **Values below the diagonal are dissimilarity indices,**  
 277 **and the above are p-values (p<0.05 in bold).**

		Velocity			Depth		
		Low	Medium	High	Low	Medium	High
Spring	Type 1	Low	<b>0.043</b>	<b>0.023</b>	-	0.543	-
	Medium	0.10	-	<b>0.002</b>	-	-0.01	-
	High	0.10	0.21	-	-	-	-
	Low	-	<b>0.009</b>	<b>0.0002</b>	-	-	0.632
	Medium	-	-	-	-	-	<b>0.001</b>
	High	-	-	-	-	-	-

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Type 2	Medium	0.09	-	<b>0.006</b>	-	-0.01	-	<b>0.0003</b>
	High	0.16	0.09	-	-	0.13	0.16	-
	Low	-	<b>0.026</b>	<b>0.244</b>	-	-	0.161	<b>0.0002</b>
Type 3	Medium	0.07	-	<b>0.004</b>	-	0.02	-	<b>0.045</b>
	High	0.04	0.12	-	-	0.26	0.08	-
	Low	-	0.138	0.067	-	-	0.356	-
Type 1	Medium	0.04	-	<b>0.030</b>	-	0.0001	-	-
	High	0.06	0.09	-	-	-	-	-
	Low	-	<b>0.0004</b>	<b>0.0001</b>	-	-	<b>0.017</b>	<b>0.0001</b>
Type 2	Medium	0.15	-	<b>0.0001</b>	-	0.07	-	<b>0.0004</b>
	High	0.25	0.39	-	-	0.30	0.13	-
	Low	-	0.119	0.139	-	-	0.186	<b>0.008</b>
Type 3	Medium	0.04	-	0.154	-	0.03	-	0.365
	High	0.03	0.03	-	-	0.11	0.01	-

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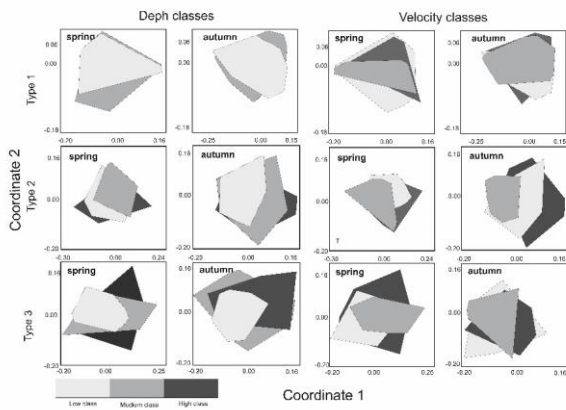
		Velocity			Depth		
		Low - Medium	Medium - High	High - Low	Low - Medium	Medium - High	High - Low
Spring	Group 1	<b>0.1*</b>	<b>0.21**</b>	<b>0.1*</b>	-0.01	-	-
	Group 2	<b>0.09**</b>	<b>0.09**</b>	<b>0.16***</b>	-0.01	<b>0.13**</b>	<b>0.16***</b>
	Group 3	<b>0.07*</b>	0.01	<b>0.12**</b>	0.02	<b>0.26***</b>	<b>0.08*</b>
Autumn	Group 1	0.04	0.06	<b>0.09*</b>	0.0001	-	-
	Group 2	<b>0.15***</b>	<b>0.25***</b>	<b>0.39***</b>	<b>0.07*</b>	<b>0.3***</b>	<b>0.13***</b>
	Group 3	0.04	0.03	0.03	0.03	<b>0.11**</b>	0.01

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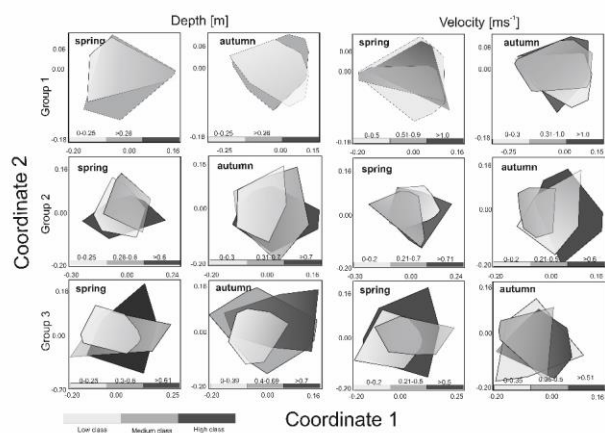
278 Significance level (p with Bonferroni correction): \*p<0.05, \*\* p<0.01, \*\*\* p<0.001

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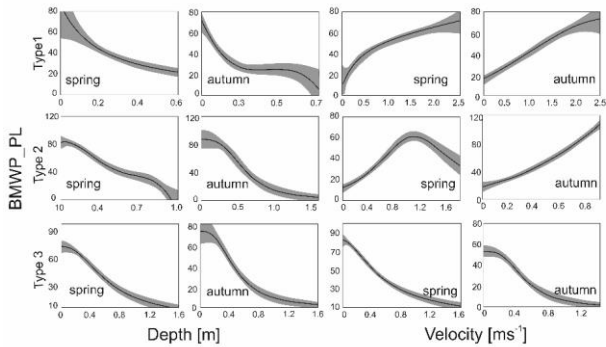
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282 Figure 4. Non-metric multidimensional scaling (NMDS) of macroinvertebrates taxonomic composition of three types-groups  
 283 of rivers (Type-1, Type-2, and Type-3) in the spring and autumn season according to velocity and depth ranges.

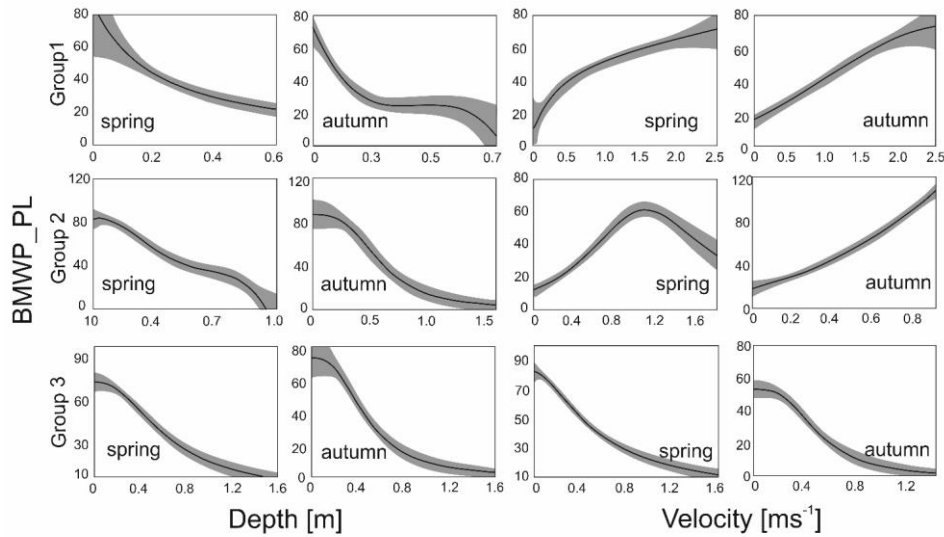
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285 In spring, there were significant differences between velocity classes (low and high and medium and high), while in autumn,  
 286 before overwintering, significant differences were only noted for medium and high classes. In neither season, the differences  
 287 noted in taxonomic composition depending on the range of depth were statistically significant in the case of rivers of the second  
 288 abiotic type-group (Type-Group 2), more significant differences were observed between velocity and depth classes (three depth  
 289 classes were adopted due to the greater amplitude of these parameters). In the spring, significant differences were visible in all  
 290 velocity classes, while in the case of depth they were noted only in the comparison of the low and middle depth classes. In  
 291 autumn, differences were found for all classes in the case of variation in both velocity and depth. In the case of Type-Group 3  
 292 rivers (carbonate and silicate fine sediments and rocks), the velocity parameter taxonomically differentiated macroinvertebrate  
 293 communities only in the spring between the high and medium velocity classes. In the case of depth, differences were observed  
 294 in both seasons – in spring between the deepest and shallowest environments and those with medium depth, and in autumn  
 295 only between the deepest and the shallowest zones (Table 2).

296 Each of the hydromorphological parameters was evaluated by the GAM model, which provided the best fit to the data (Table  
 297 3). There were significant effects of depth and velocity and its combination on variation of BMWP\_PL index. Generally, the  
 298 percentage of the total deviance was the highest for the combination of both hydrological parameters, however depth parameter  
 299 alone described similar level of the total deviance. Velocity explained 38.1 and 44.5 % of the total deviance of BMWP\_PL  
 300 variation in the mountain rivers (Group 1) for spring and autumn respectively. In other river groups the total deviance  
 301 described for velocity varied between 6 to 29 % . Bringing into consideration that both hydrological parameters alone described  
 302 more of the total deviance, we regarded them in further analyses separately. The curves of the generalized additive models for  
 303 the biotic index BMWP\_PL in spring and autumn are presented in Fig. 5.



304



305

306 Figure 5. Habitat suitability curves using Generalized Additive Models models of BMWP\_PL index for water velocity and  
 307 depth in spring and autumn season for three river types/groups.

308

309 These models were made for each of the three river types/groups: calcareous and silica bedrock alpine rivers (Type-Group 1),  
 310 sandstone mountain rivers (Type-Group 2), and carbonate and silicate upland rivers (Type-Group 3). In the first typegroup,  
 311 with a gravel bottom, the BMWP\_PL index reached its highest values at high water velocity and in shallower zones (by the  
 312 shores). In the second type-group of river, the BMWP\_PL index was highest at medium velocities in spring and at high  
 313 velocities in autumn. In both seasons, higher values for the biotic index were associated with shelf environments, as in the case  
 314 of Type-Group 1. Similar relationships with depth were noted in the Type-Group 3 rivers, where BMWP\_PL values were  
 315 highest in the shallow low-depth environments at low velocity in both spring and autumn (Fig. 5).

316

317 Table 3 Summary of the Generalized Additive Models for BMWP\_PL according to velocity and water depth ranges  
 318 parameters in three river types-groups for spring and autumn season. Res. dev. – residual deviance; % deviance – percentage  
 319 of total deviance; Res. df. – residual degrees of freedom; p – significance value.

		Spring			Autumn		
		Type 1	Type 2	Type 3	Type 1	Type 2	Type 3
Velocity [ms <sup>-1</sup> ]	F	17.49	5.05	9.48	11.62	26.97	13.76
	p	<b>0.000</b>	<b>0.01</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
	AIC	324.06	1243.75	655.12	982.35	3552.36	1429.16
Depth [m]	F	2.8	14.49	3.28	0.28	24.33	5.47
	p	<b>0.06</b>	<b>0.000</b>	<b>0.04</b>	0.163	<b>0.000</b>	<b>0.003</b>
	AIC	479.81	4061	763.05	1198.16	3650.93	1589.24

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		Spring			Autumn		
		Group 1	Group 2	Group 3	Group 1	Group 2	Group 3
Null	Res.dev.	2676	1324	2334	2717	2632	1971
	% deviance explained	0	0	0	0	0	0
	Res. d.f.	99	99	99	99	99	99
	F	-	-	-	-	-	-
	p	-	-	-	-	-	-
Velocity [ms <sup>-1</sup> ]	Res.dev.	1655	1250	2031	1508	1890	1570
	% deviance explained	38.1	6.6	12.9	44.5	28.2	20.3
	Res. d.f.	97	96.9	96.9	97	96.9	96.9
	F	30.66	3.01	7.9	41.46	18.41	12.1
	p	<0.0001	0.005	0.0005	<0.0001	<0.0001	<0.0001
Depth [m]	Res.dev.	1098	762	1879	1231	979	1467
	% deviance explained	58.9	42.4	19.4	54.6	62.7	25.5
	Res. d.f.	97	96.9	96.9	97	97	97
	F	73.3	36.86	13.11	64.93	78.6	17.15
	p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Velocity [ms <sup>-1</sup> ] x Depth [m]	Res.dev.	979	672	1781	1007	858	1284
	% deviance explained	63.4	49.2	23.6	62.9	67.4	34.8
	Res. d.f.	95	94.9	95	94.9	94.9	95
	F	43.41	23.63	8.45	45.04	49.2	13.48
	p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

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Using the optimal depth characteristics reflecting the habitat suitability (Fig. 5), the environmental flow based on hydraulic method (rating curve) was defined the wetted perimeter method was calculated. The results are shown in Table 4.

Table 4 Environmental flow and flow proportion (S) in different abiotic and bed modification types (I- incision, R- redeposition) of 12 mountainous rivers.

River name	Ab. type	River bed mod.	Environmental flow (Q <sub>env</sub> ) [m <sup>3</sup> s <sup>-1</sup> ]		Hydrological characteristics [m <sup>3</sup> s <sup>-1</sup> ]			Environmental flow proportion (S)					
			spring	autumn	LLF	MLF	MAF	SLLF spring	SLLF autumn	SMLF spring	SMLF autumn	SMAF spring	SMAF autumn
Biały Dunajec	I	I	0.89	1.10	0.22	0.54	2.26	4.02	4.97	1.66	2.05	0.39	0.49
Dunajec	I	R	0.64	0.86	0.19	0.68	3.09	3.43	4.62	0.94	1.27	0.21	0.28
Białka	I	R	0.78	0.98	0.27	0.65	3.88	2.90	3.64	1.20	1.51	0.20	0.25
Brynica	II	I	0.17	0.10	0.02	0.13	0.77	6.89	4.05	1.34	0.79	0.22	0.13

Raba	II	I	4.80	3.60	0.30	3.53	11.45	16.00	12.00	1.36	1.02	0.42	0.31
Toszecki Potok	II	I	0.27	0.18	0.02	0.11	0.59	14.35	9.56	2.43	1.62	0.46	0.30
Biała	II	I	1.20	1.05	0.31	0.96	2.69	3.89	3.41	1.25	1.09	0.45	0.39
Nysa Klodzka	II	I	1.90	1.50	0.14	0.61	3.68	13.37	10.55	3.12	2.46	0.52	0.41
Solokija	II	R	0.36	0.50	0.25	0.72	1.34	1.42	1.97	0.50	0.69	0.27	0.37
Warta	III	I	1.75	1.65	0.22	0.96	2.07	8.09	7.63	1.83	1.73	0.85	0.80
Odra	III	R	7.40	7.00	4.22	9.54	42.26	1.75	1.66	0.78	0.73	0.18	0.17
Ropa	III	R	2.15	2.00	0.58	1.79	9.64	3.73	3.47	1.20	1.12	0.22	0.21

LLF- Low Low Flow, MLF- Mean Low Flow, MAF- Mean Annual Flow

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There is a high variation of the  $Q_{env}$ , related to its own channel properties and volume of water. To obtain the relation to hydraulic river parameters, the mean  $Q_{env}$  relative similarity to MAF, MLF, and LLF were measured. There was no relation to the abiotic **type-group** of river (Table 5). The only significant relation was linked to channel modification (Fig. 6). In all cases, the relative similarity of flow was significantly higher in incised channels than redeposited ones.

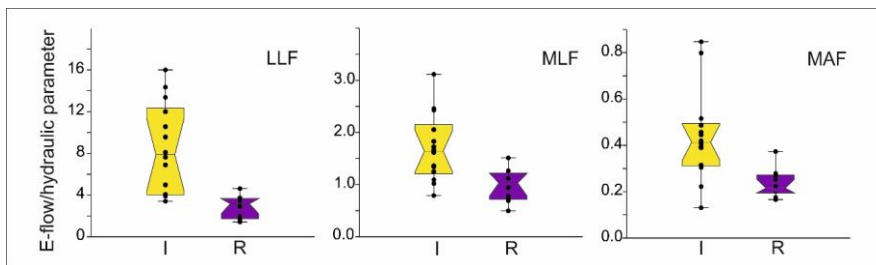


Figure 6. The distribution of **mean values  $\pm$  SE (box) and whisker length (one sigma) with distribution of jitter of e-flow proportion to Low Low Flow (LLF), Mean Low Flow (MLF), and Mean Annual Flow (MAF) in relation to river bed modification: (I – incision, R – redeposition).**

In each type of flow (MAF, MLF, LLF), the relative similarity was higher in incised rivers than redeposited, showing that the incised rivers needed much more volume of water to sustain appropriate conditions for macroinvertebrates compared with the redeposited ones. More detailed analysis and visualization of spatial modelling were predicted by 2D modelling of randomly chosen rivers presented below as a case study.

Table 5 General linear modelling results for hydrological flow similarity (S) in relation to bed modification (incision and redeposition), season, and abiotic river **typegroup**. **SS – sum of squares; d.f. – degrees of freedom; MS – mean square.**

Parameter	SS	d.f.	MS	F	p
<b>LLF<sub>sim</sub></b>					
Intercept	648.66	1	648.66	54.09	0.00
<b>Incision</b>	<b>101.13</b>	<b>1</b>	<b>101.13</b>	<b>8.43</b>	<b>0.01</b>
<b>TypeGroup</b>	11.28	2	5.64	0.47	0.63
Season	6.32	1	6.32	0.53	0.48
Error	227.86	19	11.99		
<b>MLF<sub>sim</sub></b>					
Intercept	41.19	1	41.19	138.07	0.00
<b>Incision</b>	<b>3.14</b>	<b>1</b>	<b>3.14</b>	<b>10.52</b>	<b>0.00</b>
<b>TypeGroup</b>	0.50	2	0.25	0.84	0.45

Season	0.10	1	0.10	0.33	0.57
Error	5.67	19	0.30		
<hr/>					
MAF <sub>sim</sub>					
Intercept	2.70	1	2.70	126.31	0.00
<b>Incision</b>	<b>0.32</b>	<b>1</b>	<b>0.32</b>	<b>15.04</b>	<b>0.00</b>
TypeGroup	0.11	2	0.06	2.60	0.10
Season	0.00	1	0.00	0.14	0.71
Error	0.41	19	0.02		

LLF<sub>sim</sub> – Low Low Flow similarity, MLF<sub>sim</sub> – Mean Low Flow similarity, MAF<sub>sim</sub> – Mean Annual Flow similarity

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### 3.2 Case study

We calculated the detailed 2D modelling for two randomly chosen incised and redeposited rivers. According to the GAM macroinvertebrate habitat suitability model, WUA-flow curves were calculated for river-s with varying intensity of bed modification, Raba (incised) and Ropa (redeposited), as shown in Fig. 7.

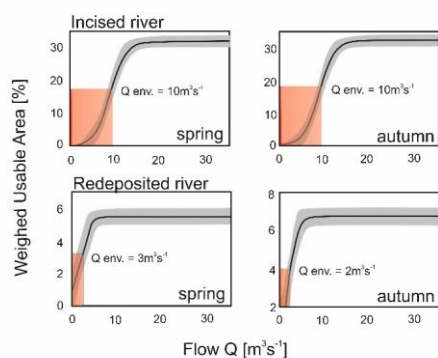


Figure 7. Weighted Usable Area (WUA) - flow relation curves (spring and autumn season) of the rivers varying in bed modification: Raba River with incision and Ropa River with redeposition.

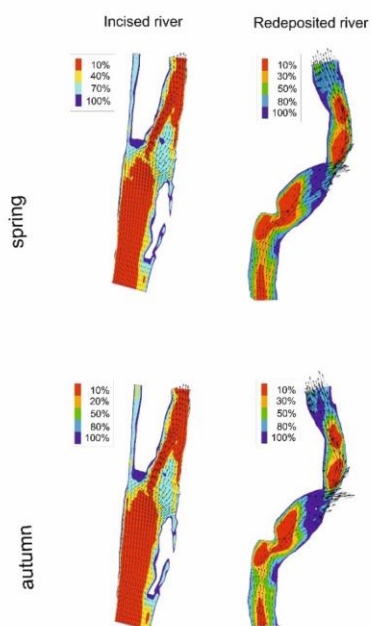
The environmental flow was defined as the lowest flow corresponding to 50% of the value of the usable area, which ensures minimum optimal conditions for the development and functioning of aquatic macroinvertebrates (Jowett et al., 2008), and thus the maintenance of the good ecological state of the river. Analysis of the curves for the Raba River shows a 50% reduction in the usable area at the flow of about  $10 \text{ m}^3 \text{ s}^{-1}$  for both spring and autumn. In the case of the Ropa River, the WUA-flow curves show a 50% reduction in the usable area at the flow of about  $2 \text{ m}^3 \text{ s}^{-1}$  in spring and  $3 \text{ m}^3 \text{ s}^{-1}$  in autumn (Table 6).

A spatial visualization of macroinvertebrate habitat suitability for  $Q_{\text{env}}$  optimal conditions is presented in Fig. 8. In the case of the strongly incised Raba River, a very small suitable habitat area was observed, covering only the shelf zone. In the case of the Ropa River, where sediment transportation occurs, a river with undisturbed sediment transport, the usable areas constitutes more than 20% of the environmental flow area. The modelling was also used to determine  $Q_{\text{env}}$  critical, at which the most valuable areas in terms of habitat (over 80% suitability) disappear (Fig. 8, Table 6). Below this  $Q_{\text{env}}$  critical value, a dramatic decline in macroinvertebrate diversity would have to be expected.

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 368 **Figure 8.** Probability of habitat suitability calculated as a percentage of optimal conditions occurrence of macroinvertebrates  
 369 habitat suitability for calculated  $Q_{env}$  in spring and autumn season in incised (Raba), and redeposited (Ropa) rivers. **Figure 8.**  
 370 Numerical modelling of incised (Raba), and redeposited (Ropa) rivers for visualization distribution of macroinvertebrates  
 371 habitat suitability index for calculated  $Q_{env}$  in spring and autumn season.

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372  
 373 A comparison of the  $Q_{env}$  values (optimal and critical) and means: Annual Flow (MAF) and Low Flow (MLF) for the two  
 374 types of rivers is presented in Table 7. In the highly incised river (Raba River), the  $Q_{env}$  optimal requirement for spring was  
 375 lower but for autumn was higher than MAF, and  $Q_{env}$  critical was always higher than MLF. In the redeposited Ropa River, in  
 376 spring as well as in the autumn season,  $Q_{env}$  optimal requirements were much lower than MAF, and MLF was higher than  $Q_{env}$   
 377 critical. Both findings are congruent with the former hydraulic calculations for all rivers.

378  
 379 Table 6 Environmental optimal and critical flow based on macroinvertebrate habitat suitability models of two mountainous  
 380 rivers with mean MAF, MLF, and LLF in relation to the seasons.

Season	Flow type [ $m^3s^{-1}$ ]	River bed modification	
		Incision Raba	Redeposition Ropa
Spring	$Q_{env}$ optimal	10	2
	$Q_{env}$ critical	<6	<1
	MAF	14.79	12.94
	MLF	5.20	2.93
Autumn	$Q_{env}$ optimal	10	3
	$Q_{env}$ critical	<6	<1
	MAF	7.86	5.81
	MLF	3.80	1.96
	MAF	11.45	9.64

Year	MLF	3.53	1.79
	LLF	0.3	0.58

381

#### 382 4. Discussion

383 The present study showed that river bed transformation, disturbing sedimentation processes and increasing the incision of the  
384 river bed vastly increases the environmental flow values for macroinvertebrates habitat suitability. This is important because  
385 incision processes are common in most European rivers (Gore, 1996). Channel incision decreases the area of suitable habitat  
386 for macroinvertebrates and increases the potential environmental flow to an extremely high level to obtain the minimum  
387 beneficial habitat capacity for macroinvertebrates (Bravard et al., 1997; Skalski et al., 2020). In incised channels, the degree  
388 of lateral connectivity of between the river and floodplain is reduced, and the degree of modification of the substrate material  
389 is higher (Wyźga et al., 2012). As a consequence of channelization and incision, the continuity of the floodplain and shelf zone  
390 along the river is disrupted (Walther and Whiles, 2008; Kędzior et al., 2016; Anim et al., 2018; dos Reis Oliveira et al., 2019).  
391 Moreover, incision results in a concomitant decrease in sediment supply to the channels, reducing the microhabitat diversity  
392 and the quality of macroinvertebrate habitats (Wyźga, 2007; McKenzie et al., 2020). During the incision process,  
393 morphological changes in the channel, especially in the case of highly incised rivers, decrease the area of shelf habitat, and  
394 fluvial deposits are drastically reduced. Thus, to keep areas wet, flow requirements must be much higher than the mean annual  
395 flow and associated with inundation hazards.

396 Linkage between mean annual flow and environmental flow estimation has been the subject of consideration for many years  
397 (Tennant, 1976), based on the assumption that to obtain good stream environment conditions, some percentage of the average  
398 flow is required (Richter et al., 2012; Van Niekerk et al., 2019). According to Tennant (1976), 10% of the average flow is the  
399 minimum flow recommended to sustain short-term survival habitat for most aquatic life forms. Thirty percent was  
400 recommended as a base flow to sustain good survival biota conditions. Sixty percent provides excellent to outstanding habitat  
401 for most aquatic life forms during their primary periods of growth and for most recreational uses. However, what about strongly  
402 channelized and incised rivers, which are the most common channel types in Europe? Our survey indicated that to obtain high  
403 macroinvertebrate diversity, we need a much higher volume of water than 10% of MAF. In the case of incision, a high volume  
404 of water is needed to cover the shelves and sediment storage, which are the principal elements of macroinvertebrate habitats  
405 and refuges in a dynamic river system (Duan et al., 2009; Anim et al., 2018).

406 It is obvious that macroinvertebrates are closely linked to the substrate, which is highly variable in terms of particle size  
407 (Bravard et al., 1997; Merz and Ochikubo Chan, 2005; Duan et al., 2009). Alluvial processes are strongly disturbed in an  
408 incised river, leading to deepening of the channel and bed degradation (Wyźga, 2007). The areas shown in Fig. 7, which are  
409 100% suitable for macroinvertebrates, are extremely low-narrow in incised rivers throughout the spring and autumn. In most  
410 rivers with an augmented bed, the sedimentation process is disturbed, and thus only habitats located closer to the surface,  
411 where lateral erosion occurs, provide a suitable habitat for macroinvertebrates. Modern restoration efforts often involve the  
412 artificial addition of sediments to sand (dos Reis, Oliveira et al., 2019) or modification of channel morphology to restore the  
413 sedimentation process (Violin et al., 2011; Anim et al., 2018).

414 The biotic integrity of rivers is primarily restricted by downstream transport of sediments controlling the integrity of fluvial  
415 ecosystems (Katano et al., 2009; White et al., 2016). Substrate characteristics such as size, stability, compactness, quality, and  
416 dynamics are a key parameter determining the occurrence and variation in macroinvertebrate communities. High substrate  
417 stability, substrate heterogeneity, and low compactness determine high macroinvertebrate diversity (Beisel et al., 2000; Duan  
418 et al., 2009). On the other hand, fine sediments can be regarded as a potential stressor for macroinvertebrates (Meißner et al.,  
419 2019). In highly incised sectors of the river, a deficiency of sediment and its compactness as well as a lack of food sources  
420 (Shields et al., 1994; Jowett, 2003) lead to impoverishment of the taxonomic composition of macroinvertebrates and favour



421 taxa adapted to high flow only (Wyżga et al., 2013). Our ~~modelling results~~ indicates that prevention of optimal conditions  
422 requires more volume of water which exceeds the mean annual flow. ~~This conclusion seems paradoxical and rather dangerous,~~  
423 ~~because increase discharge augments incision processes. This suggestion can be dangerous, because increased discharge~~  
424 ~~augments incision processes.~~We can thus fall into a kind of ecological trap. A solution may be to pay careful attention to the  
425 bed morphology, especially in the case of incised channels. ~~There is still a problem to gather information on flow ecological~~  
426 ~~response od any organisms and extend the survey in international context should be done (Poff and Zimmermann, 2010;~~  
427 ~~Fornaroli et al., 2015).~~ We then have two options to preserve the high biodiversity of invertebrates according to the EU water  
428 directive: to vastly increase the water volume or to restore sedimentation processes to obtain a hydrodynamic balance. As a  
429 consequence, suitable habitats for invertebrates and fish will be enlarged. The second option seems much more realistic. Only  
430 then we will be able to successfully maintain the diversity of aquatic biota.

## 431 5. Conclusions

432 In habitat modelling, careful attention should be paid to the morphology of the modelled river, its geometry, and the fluvial  
433 processes in the active channel. In incised channels where sedimentation processes are altered, for example, by dam reservoirs  
434 or bedrock downcutting, the area of suitable habitat is limited. Macroinvertebrate habitat preferences are strongly linked to  
435 shelf habitats, where sediment storage and redeposition of bed material is the highest. In that case, the recolonization pattern  
436 of invertebrates requires much higher flows, even higher than the mean annual flow. As a consequence, the river is endangered  
437 by downcutting processes and impoverishment of suitable habitats.

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439 Writing - review & editing; Kłonowska-Olejnik Małgorzata: Data curation; Dumnicka Elżbieta: Data curation; Woś  
440 Agnieszka: Investigation; Wyřebek Maciej: Investigation, Resources, Visualization; Książek Leszek: Investigation,  
441 Methodology, Resources, Validation, Writing - review & editing; Paweł Madej: Funding acquisition, Project administration;  
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