



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

30 1 Introduction

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

39 Water flow intensity is one of the most important factors influencing multispecies communities of aquatic and water-dependent
40 organisms (Tharme, 2003; Arthington et al., 2006; Higgisson et al., 2019). It is a parameter which shapes the morphology
41 (Michalik and Książek, 2009) and hydraulic flow conditions (water depth, flow velocity) and influences the diversity and



42 quality of habitats for fauna and flora in the active channel and in the floodplain (Allan, 1995; Poff et al., 1997; Ward and
43 Tockner, 2001; Skalski et al., 2016; Skalski et al., 2020). Furthermore, this parameter significantly influences abiotic elements,
44 such as water temperature and oxygenation, as well as nutrient cycles in the aquatic ecosystem (Monk et al., 2008; Laini et al.,
45 2019). This applies in particular to rivers subjected to strong human impact (e.g., channel regulation and incision dams, or
46 retention reservoirs, as well as a continuous increase in water discharge). Artificial restriction and control of a range of water
47 flow values leads to substantial impoverishment of biological diversity (Pander et al., 2019). Therefore, it appears crucial to
48 define ranges of environmental flows that ensure optimal habitat conditions for living organisms (Bunn and Arthington, 2002;
49 Acreman et al., 2014).

50 Environmental flow has been studied by many researchers, resulting in numerous methods for determining it. The simpler
51 ones include hydrological methods, which are based on historical hydrological data and mean annual discharge (Tennant,
52 1976; Jowett, 1997; Tharme, 2003; Rosenfeld, 2017). Analysis of such data makes it possible to specify a percentage of the
53 mean annual flow as the critical value below which severe degradation of biotic elements occurs. Unfortunately, hydrological
54 methods do not take into account the morphology of the river bed, which is a key factor shaping the river habitat (Książek et
55 al., 2020). Therefore, a number of hydraulic methods based on simple hydraulic variables such as wetted area/wetted perimeter
56 have been introduced (Książek et al., 2019). Determination of e-flow for environmental flow involves defining the breaking point
57 of the hydraulic variable discharge curves as the e-flow. Over time, hydraulic methods have developed in the direction of
58 habitat simulation methods. They have additionally focused on the habitat requirements of selected groups of model organisms,
59 most commonly water depth, flow velocity, and bed substrate (Jowett and Davey, 2007; Li et al., 2009; Muñoz-Mas et al.,
60 2016). Based on the analysis of these environmental factors, habitat-discharge curves were drawn for organisms, and from
61 these it was possible to read the optimal flows maintaining the normal ecological functions of aquatic ecosystems. Another
62 type of method, which emphasizes the importance of the natural flow regime for the entire ecosystem, is holistic methods.
63 They attempt to maintain the natural flow regime as well as flow variability. In this case, environmental flow is defined in the
64 category of deviation from the natural flow regime.

65 The methods presented above focus on the diversity and availability of habitats for freshwater macroinvertebrates, which is
66 the most important and sensitive indicator of the ecological state of the ecosystem (Jowett et al., 2008; Birk et al., 2012). The
67 diversity and taxonomic composition of aquatic organisms living in freshwater streams and rivers are used as indicators in the
68 evaluation of environmental flow (Pander et al., 2019). In many cases, macroinvertebrate assemblages are considered (Hayes
69 et al., 2014; Laini et al., 2019), as numerous studies confirm that they are relatively good indicators of ecological water quality
70 and integrity (Buss et al., 2015; Wyżga et al., 2016; Schneider and Petrin, 2017). Freshwater macroinvertebrates play an
71 important role in the processing of nutrients and organic energy in running water ecosystems, as well as in sustaining ecosystem
72 integrity. Another parameter, which is usually neglected in flow modelling, is associated with morphological channel
73 modification and incision (Wyżga et al., 2012; Skalski et al., 2016). Incision up to the bedrock simplifies the microhabitat
74 area of the river (Neachell, 2014) and can eliminate most habitats (Muñoz-Mas et al., 2016). As a consequence, to preserve
75 optimal areas with heterogeneous habitats, the environmental flow should be increased.

76 The goal of the study was to test the influence of river incision on environmental flow estimation based on macroinvertebrate
77 habitat preferences. Specific aims of the study were (1) to establish the habitat preferences of macroinvertebrates (240 local
78 assemblages) in mountain and lowland rivers using generalized additive models, (2) to calculate the e-flow values combining
79 the habitat requirements and hydraulic method of environmental flow calculation in relation to river hydromorphological
80 parameters (redeposition and incision) (3) to identify a scale of e-flow overestimation in relation to hydromorphological
81 modifications and hydrological regimes (Low Low Flow, Mean Low flow and Mean Annual flow). (4) to check and visualize
82 the overestimation of e-flow calculations on randomly chosen, incised, and redeposited rivers based on CCED2D model. We
83 expected that e-flow in incised rivers, allowing to obtain the shelf zone level of the river should be much higher than Mean
84 Low Flow. Such assumption could determine the consecutive higher discharges and increase the bed degradation. Firstly, we

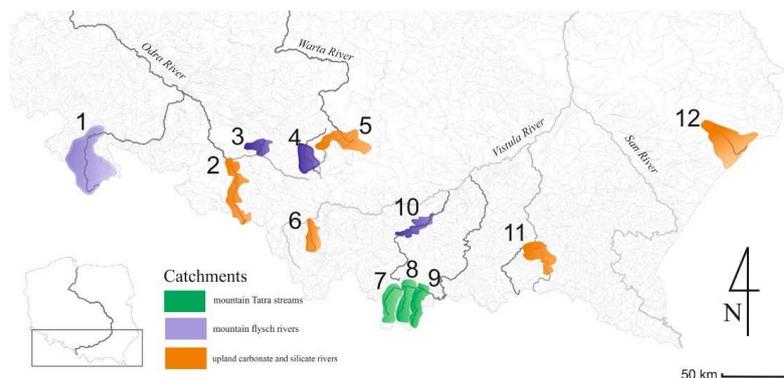


85 should restore the sedimentation processes in incised rivers to obtain a hydrodynamic balance and then manage the proper
 86 volume of water. As a consequence, suitable habitats for invertebrates and fish will be enlarged.

87 2. Materials and methods

88 2.1 Study sites

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



94
 95 Figure 1. Map of the studied mountainous rivers in Carpatho-Sudetic region of Poland.
 96

97 The first class comprises rivers located in an alpine granitoid region, characterized by calcareous and siliceous bedrock. The
 98 second group consists of rivers flowing through much lower mountain ranges (up to the timber zone), where the bedrock
 99 contains sandstone rock formations. The third group represents rivers of upland landforms with various carbonate and silicate
 100 sediments and rocks.

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

107

108 Table 1 Mean values \pm standard deviation of the physicochemical and habitat variables of the three river types, with results of
 109 one-way ANOVA.

Environmental data	Type 1		Type 2		Type 3		F	p
	Mean	St. dev.	Mean	St. dev.	Mean	St. dev.		
Physicochemical								
Water temperature [°C]	7.27	1.55	11.40	2.43	12.17	0.89	6.76	0.016
Dissolved oxygen [mgL ⁻¹]	10.73	0.45	9.33	1.34	9.15	0.79	2.39	0.150
Conductivity [μ S cm ⁻¹]	202.67	91.58	1095.60	1594.59	356.5	93.26	0.85	0.458



Water hardness [mg CaCO ₃ /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	0.000
pH _{max}	8.43	0.35	8.16	0.15	8.15	0.37	1.04	0.390
NH ₃ [mgL ⁻¹]	0.20	0.31	0.32	0.36	0.95	0.81	2.09	0.179
NO ₃ ⁻ [mgL ⁻¹]	0.60	0.20	2.11	0.93	2.25	0.92	4.16	0.052
NO ₂ ⁻ [mgL ⁻¹]	0.02	0.01	0.10	0.12	0.17	0.13	1.45	0.284
Total N [mgL ⁻¹]	0.97	0.75	3.43	1.78	4.17	2.09	3.12	0.093
PO ₄ ³⁻ [mgL ⁻¹]	0.03	0.04	0.09	0.05	0.06	0.02	2.08	0.180
Habitat								
Flow [m ³ s ⁻¹]	0.83	0.55	0.45	0.39	0.44	0.32	38.06	0.000
Depth [m]	0.29	0.14	0.54	0.34	0.50	0.33	25.89	0.000
Substrate index	22.31	5.60	7.07	5.58	6.39	3.85	422.95	0.000

110 2.2 Macroinvertebrate sampling

111 Benthic invertebrate samples were collected in two seasons: autumn (October, 2017) and spring (April, 2018). No flood waves
 112 occurred between these surveys, and the channel morphology remained the same throughout the sampling period. We collected
 113 20 subsamples (from each low-flow channel along a representative 100 m section of each river according to a sampling
 114 procedure for the BMWP_PL index (Bis and Mikulec, 2013). A total of 480 subsamples were taken from a wide range of water
 115 depths and flow velocity. Following Jowett et al. (1991) and Muñoz-Mas et al. (2016), the substrate types were converted to a
 116 single index by summing the weighted percentages of each type.

117 Macroinvertebrate samples were collected with a D-frame net according to the Environmental Agency's sampling protocol for
 118 biomonitoring assessment using a kicking motion for 3 minutes across all habitats (Bis and Mikulec, 2013). All collected
 119 material was preserved in the field with 4% formaldehyde. Aquatic macroinvertebrates were separated from the rest of the
 120 material in the laboratory using a stereoscopic microscope. Macroinvertebrates were identified to the family level (Tachet et
 121 al., 2000), except Oligochaeta, Porifera, and Hydrozoa, which were recorded as such. Due to the varied preferences of
 122 macroinvertebrates to habitat conditions, the BMWP_PL index was adopted as the best qualitative index. The Biological
 123 Monitoring Working Party (BMWP) is one of the most commonly used biotic indices in various rivers and streams around the
 124 world (Roche et al., 2010; Wyzga et al., 2013). It has been adopted in many countries, including Poland (Dz.U. 2019 poz.
 125 2149, 2019). This index best considers the sensitivity of invertebrates to environmental variables, because families with similar
 126 stress tolerances are grouped together (Armitage et al., 1983).

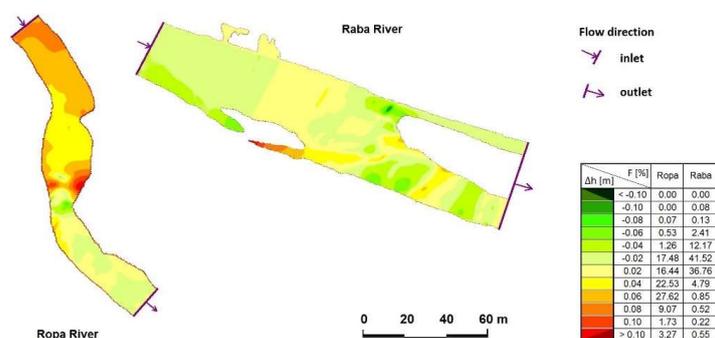
127 2.3 Hydraulic modelling

128 We used the hydraulic method for the assessment of the environmental flow of each river because of the relationship between
 129 the hydraulic parameters of watercourses (depth and velocity) and the quality of the aquatic environment (BMWP_PL GAM
 130 relations). The wetted perimeter method (WPM) is based on the relationship between the wetted perimeter for a given cross
 131 section of the river and the value of flow with reference to biological requirements (Shang, 2008). Detailed description of the
 132 applied hydraulic method of environmental flow calculation is given in Książek et al. (2019). To compare the environmental
 133 flow in relation to hydromorphological parameters (incision, redeposition), we used the proportion of Environmental flow
 134 (Qenv) to mean hydraulic parameters of low, low flow (LLF), mean low flow (MLF), and mean annual flow (MAF). Those
 135 metrics show us the position of the calculated environmental flow in relation to flow characteristics from hydrological year-
 136 to-year characteristics.

137 2.4 Case study 2D modelling methodology



138 We provided the detailed modelling of a randomly chosen incised and redeposited river based on CCED2D model. The model
139 is a depth-averaged two-dimensional numerical model for simulating unsteady, turbulent, free-surface flow in open channels
140 with a moveable bed. The CCHE2D model solves depth-integrated shallow water equations for all hydraulic calculations (Wu
141 et al., 2000; Duan et al., 2001). The CCHE2D package consists of two modules: a Mesh Generator (MG) and a Graphical User
142 Interface (GUI). The main function of the MG is designing a complex mesh system. The mesh is generated based on the
143 surveyed topography and/or Digital Terrain Model (DTM). The model was applied in two representative rivers, varying in
144 river bed morphology – from incised bed rock channels to a channel with natural sediment structures (with redeposition). The
145 mesh for each sector of the river was generated by interpolating cross sections. A total of 5,112 observations were used: Raba
146 – 3033 (incision) and Ropa – 2079 (redeposition). The shape of the channels was fairly regular along the reach under study,
147 and its pattern presented little complexity (i.e., a single channel with no islands), but riffle-pool sequences were observed. The
148 153–200 m long meshes were composed of cells and nodes (length and number of nodes, respectively, for Ropa 153 m, 49715
149 and Raba 200 m, 99200). Data used for the initial conditions was extracted from field measurements. Special attention was
150 devoted to bed roughness due to its importance for water surface level. Roughness values ranged from 0.01 in hydraulic smooth
151 bed zones to 0.07 in rough areas. Finally, the model time step was defined at 0.1 s or 0.25 s, depending on the model structure.
152 The model was calibrated by comparing the measured and computed water surface levels for measured discharges in all cells
153 and nodes (Fig. 2).



154
155 Figure 2. Comparison of calculated and measured water surface levels: The Ropa River for discharge 6.71 m³s⁻¹, and The
156 Raba River for discharge 10.29 m³s⁻¹.

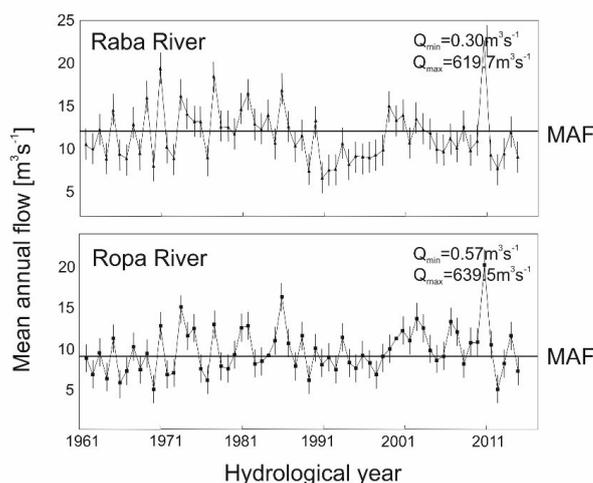
157
158 In the case of the Raba River, for 70% of the calculated nodes, the difference between the calculated and measured water
159 surface level (WSL) was in the range ± 0.02 m. 84% of Ropa River nodes were in the range between -0.02 to 0.06 m. In all
160 described models, Δh in the main channel does not cross ± 0.02 m, but the visible differences are related to the horizontal layout
161 of WSL in cross-section. Evaluation of the compatibility measures of the numerical model showed very good accordance
162 (Książek et al., 2010) and the prepared models did not need recalibration.

163 The habitat suitability index was estimated in the first step by selecting a usable habitat for macroinvertebrates. For each
164 research section, we choose 2 s differing in water velocity and water depth as the main environmental variables creating
165 habitat heterogeneity for macroinvertebrates. Then, according to the relationship between hydromorphological habitat
166 attributes (water depth and velocity) and the BMWP_PL index values (describing the ecological quality of the river), we
167 constructed a GAM model as the best fitted method to mark out the range of hydromorphological attributes (where the
168 BMWP_PL suitability index is the ).

169 Two rivers (located in the same Carpathian region) representing opposite bed modifications (incision and redeposition) were
170 chosen for the model as a case study. The modelled sectors of the river had channels with a pool-riffle sequence and fluvial



171 deposits, but varied in terms of degradation of the bed structure. The hydrological characteristics of the modelled river
172 are presented in Fig. 3.



173
174 Figure 3. Changes in hydrological regime of the Raba and Ropa Rivers. The horizontal line indicates the mean annual flow
175 (MAF).

176

177 The Raba was selected to represent incised channel rivers (bottom material mainly gravel and small stones, substrate index
178 14.9). The Dobczyce retention reservoir, which influences the hydrology and morphology of the river, is located upstream of
179 the examined sector of the river (12 km). Constructing of the retention reservoir in 1986 led to a significant decline in average
180 annual flow values (MAF values varied from 12.22 m³/s; in 1951-1985 to 10.57 m³/s in 1986-2015, $F = 49.90$, $p < 0.0001$).
181 The reduction in flow and longitudinal training work of the Raba led to incision of the riverbed and permanent compactness
182 of the bed material. The Ropa River, chosen to represent the redeposition processes, was located among upland, carbonate,
183 and silicate rivers, with the lowest human impact. The bottom material consists mainly of gravel and sand (substrate index
184 7.2), where bedload transport remains undisturbed.

185 To calculate the optimal environmental flow values (Q_{env} optimal), a WUA's flow curve was plotted. Optimal environmental
186 flow values were defined as 50% of the WUA values for both rivers. A hydraulic habitat 2D model of each river section was
187 used for spring and autumn as an example to estimate habitat prediction in terms of calculated environmental flow during the
188 season. Environmental flow that did not meet the conditions of 100% habitat suitability was expressed as the critical instream
189 environmental flow value (Q_{env} critical), below which the parameters of aquatic macroinvertebrate communities dramatically
190 declined.

191 2.5 Data analysis

192 ANOVA was used to verify the statistical significance of the differences in environmental data between the three river types
193 (Statsoft, 2013). Non-metric multidimensional scaling (NMDS) was used to test the relationship between the macroinvertebrate
194 taxonomic composition of the assemblages of the 12 rivers assigned to three types (Type 1, Type 2 and Type 3) and
195 hydromorphological variables (water velocity and depth) during the spring and autumn. Descriptive physical properties (water
196 depth and velocity) were classified into two or three categories: Low, medium and High. The significance of differences
197 between depth and velocity classes was tested by ANOSIM on the Bray-Curtis dissimilarity matrix with 499 permutations of
198 the data. PAST software (version 3.13) was used to analyse NMDS and ANOSIM (Hammer et al., 2001).



199 Generalized additive modelling with Poisson distribution (GAM) was used to develop more defensible habitat preferences for
 200 macroinvertebrates (BMWP_PL index) based on their distribution in both dimensions: depth and velocity (Jowett and Davey,
 201 2007). The course of the regression **line** was obtained using CurveExpert software, where the best fitted line for the set of
 202 nonlinear curves was applied and ranked. To compare the variation of the proportion of environmental flow and
 203 hydromorphological parameters (which were normally distributed) in relation to abiotic type and channel modifications,
 204 general linear modelling was applied.

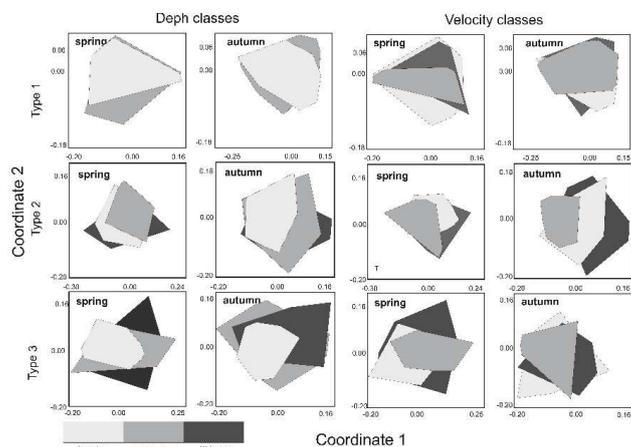
205 3. Results

206 3.1 Environmental flow based on benthic invertebrates distribution in relation to river hydromorphology

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

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

		Velocity			Depth			
		Low	Medium	High	Low	Medium	High	
Spring	Type 1	Low	0.043	0.023		0.543	-	
		Medium	0.10	0.002	- 0.01		-	
		High	0.10	0.21	-	-		
	Type 2	Low	0.009	0.0002		0.632	0.001	
		Medium	0.09	0.006	- 0.01		0.0003	
		High	0.16	0.09	0.13	0.16		
	Type 3	Low	0.026	0.244		0.161	0.0002	
		Medium	0.07	0.004	0.02		0.045	
		High	0.01	0.12	0.26	0.08		
Autumn	Type 1	Low		0.138	0.067	0.356	-	
		Medium	0.04		0.030	0.0001	-	
		High	0.06	0.09		-	-	
	Type 2	Low	0.0004	0.0001		0.017	0.0001	
		Medium	0.15		0.0001	0.07	0.0004	
		High	0.25	0.39		0.30	0.13	
	Type 3	Low		0.119	0.139		0.186	0.008
		Medium	0.04		0.154	0.03		0.365
		High	0.03	0.03		0.11	0.01	



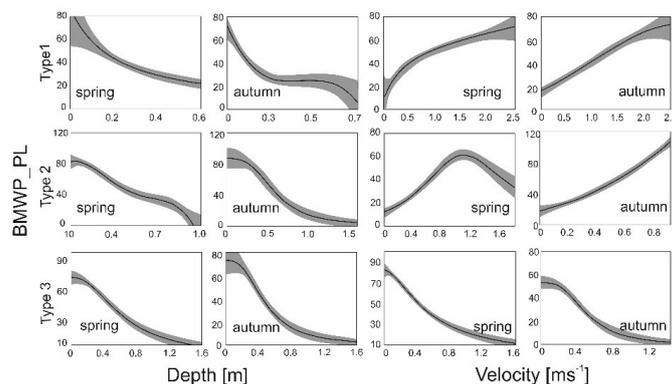
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216 Figure 4. Non-metric multidimensional scaling (NMDS) of macroinvertebrates taxonomic composition of three types of rivers
 217 (Type 1, Type 2, and Type 3) in the spring and autumn season according to velocity and depth ranges.

218

219 In spring, there were significant differences between velocity classes low and high and medium and high, while in autumn,
 220 before overwintering, significant differences were only noted for medium and high classes. In neither season, the differences
 221 noted in taxonomic composition depending on the range of depth were statistically significant in the case of rivers of the second
 222 abiotic type (Type 2), more significant differences were observed between velocity and depth classes (three depth classes were
 223 adopted due to the greater amplitude of these parameters). In the spring, significant differences were visible in all velocity
 224 classes, while in the case of depth they were noted only in the comparison of the low and middle depth classes. In autumn,
 225 differences were found for all classes in the case of variation in both velocity and depth. In the case of Type 3 rivers (carbonate
 226 and silicate fine sediments and rocks), the velocity parameter taxonomically differentiated macroinvertebrate communities
 227 only in the spring between the high and medium velocity classes. In the case of depth, differences were observed in both
 228 seasons – in spring between the deepest and shallowest environments and those with medium depth, and in autumn only
 229 between the deepest and the shallowest zones (Table 2).

230 Each of the hydromorphological parameters was evaluated by the GAM model, which provided the best fit to the data (Table
 231 3). The curves of the generalized additive models for the biotic index BMWP_PL in spring and autumn are presented in Fig.
 232 5.



233



234 Figure 5. Habitat suitability models of $BMWP_{PL}$ for water velocity and depth in spring and autumn season for three river
 235 types.

236

237 These models were made for each of the three river types: calcareous and silica bedrock alpine rivers (Type 1), sandstone
 238 mountain rivers (Type 2), and carbonate and silicate upland rivers (Type 3). In the first type, with a gravel bottom, the
 239 $BMWP_{PL}$ index reached its highest values at high water velocity and in shallow zones (by the shores). In the second type
 240 of river, the $BMWP_{PL}$ index was highest at medium velocities in spring and at high velocities in autumn. In both seasons,
 241 higher values for the biotic index were associated with shelf environments, as in the case of Type 1. Similar relationships with
 242 depth were noted in the Type 3 rivers, where $BMWP_{PL}$ values were highest in low-depth environments at low velocity in
 243 both spring and autumn (Fig. 5).

244

245 Table 3 Summary of the generalized additive models for $BMWP_{PL}$ according to velocity and water depth ranges in three
 246 river types for spring and autumn season.

		Spring			Autumn		
		Type 1	Type 2	Type 3	Type 1	Type 2	Type 3
Velocity [ms^{-1}]	F	17.49	5.05	9.48	11.62	26.97	13.76
	p	0.000	0.01	0.000	0.000	0.000	0.000
	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	0.06	0.000	0.04	0.163	0.000	0.003
	AIC	479.81	1061	763.05	1198.16	3650.93	1589.24

247

248 Using the optimal depth characteristics reflecting the habitat suitability, the environmental flow based on the wetted perimeter
 249 method was calculated. Results are shown in Table 4.

250

251 Table 4 Environmental flow and flow proportion (S) in different abiotic and bed modification types of 12 mountainous rivers.

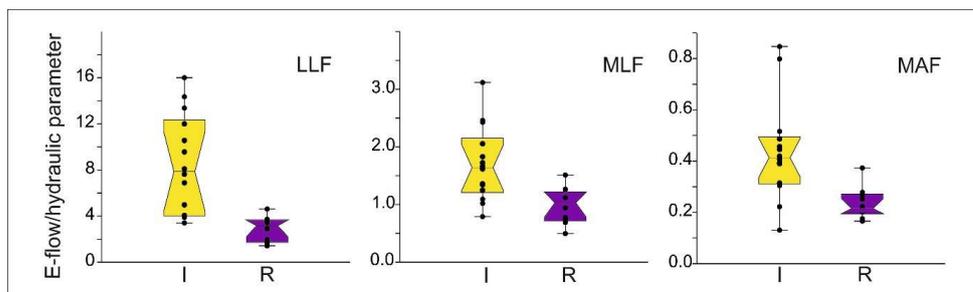
River name	Ab. type	River bed mod.	Environmental flow (Q_{env}) [m^3s^{-1}]		Hydrological characteristics [m^3s^{-1}]			Environmental flow proportion (S)					
			spring	autumn	LLF	MLF	MAF	SLLF spring	SLLF autumn	SMLF spring	SMLF autumn	SMAF spring	SMAF autumn
Bialy Dunajec	I	I	0.89	1.10	0.22	0.54	2.26	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
Bialka	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 Kłodzka	II	I	1.90	1.50	0.14	0.61	3.68	13.37	10.55	3.12	2.46	0.52	0.41
Sołokija	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

252

253 There is a high variation of the Q_{env} , related to its own channel properties and volume of water. To obtain the relation to
 254 hydraulic river parameters, the mean Q_{env} relative similarity to MAF, MLF, and LLF were measured. There was no relation



255 to the abiotic type of river (Table 5). The only significant relation was linked to channel modification (Fig. 6). In all cases, the
 256 relative similarity of flow was significantly higher in incised channels than redeposited ones.



257
 258 Figure 6. The distribution of e-flow proportion to LLF, MLF, and MAF in relation to river bed modification. I – incision, R –
 259 redeposition.

260

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

265

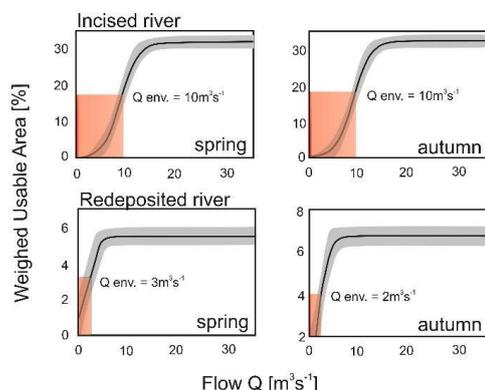
266 Table 5 General linear modelling results for hydrological flow similarity (S) in relation to bed modification (incision and
 267 redeposition), season, and abiotic river type.

Parameter	SS	d.f.	MS	F	p
LLF_{sim}					
Intercept	648.66	1	648.66	54.09	0.00
Incision	101.13	1	101.13	8.43	0.01
Type	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		
MLF_{sim}					
Intercept	41.19	1	41.19	138.07	0.00
Incision	3.14	1	3.14	10.52	0.00
Type	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		
MAF_{sim}					
Intercept	2.70	1	2.70	126.31	0.00
Incision	0.32	1	0.32	15.04	0.00
Type	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		

268

269 3.2 Case study

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

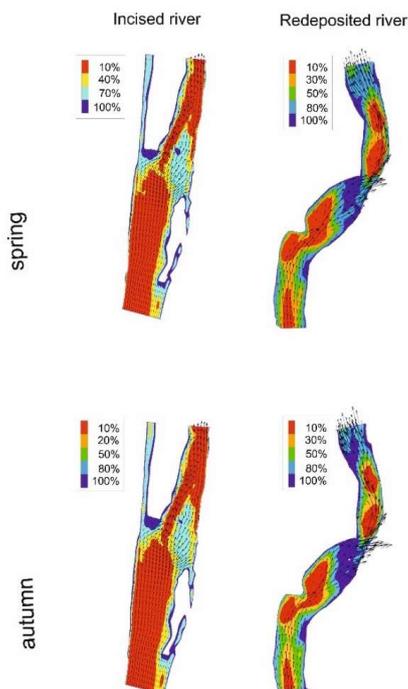


273

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

276 The environmental flow was defined as Q_{env} corresponding to 50% of the value of the usable area, which ensures optimal conditions
 277 for the development and functioning of aquatic macroinvertebrates, and thus the maintenance of the good ecological state of
 278 the river. Analysis of the curves for the Raba River shows a 50% reduction in the usable area at the flow of about $10 \text{ m}^3\text{s}^{-1}$
 279 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
 280 flow of about $2 \text{ m}^3\text{s}^{-1}$ in spring and $3 \text{ m}^3\text{s}^{-1}$ in autumn (Table 6).

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



286



287 Figure 8. Numerical modelling of incised (Raba), and redeposited (Ropa) rivers for visualization distribution of
288 macroinvertebrates habitat suitability index for calculated Q_{env} in spring and autumn season.

289

290 A comparison of the Q_{env} values (optimal and critical) and means: annual flow (MAF) and low flow (MLF) for the two types
291 of rivers is presented in Table 7. In the highly incised river (Raba River), the Q_{env} optimal requirement for spring was lower
292 but for autumn was higher than MAF, and Q_{env} critical was always higher than MLF. In the redeposited Ropa River, in spring
293 as well as in the autumn season, Q_{env} optimal requirements were much lower than MAF, and MLF was higher than Q_{env} critical.
294 Both findings are congruent with the former hydraulic calculations for all rivers.

295

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

Season	Flow type [m^3s^{-1}]	River bed modification	
		Incision	Redeposition
		Raba	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
Year	MAF	11.45	9.64
	MLF	3.53	1.79
	LLF	0.3	0.58

298

299 4. Discussion

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

313 Linkage between mean annual flow and environmental flow estimation has been the subject of consideration for many years
314 (Tennant, 1976), based on the assumption that to obtain good stream environment conditions, some percentage of the average
315 flow is required (Richter et al., 2012; Van Niekerk et al., 2019). According to Tennant (1976), 10% of the average flow is the
316 minimum flow recommended to sustain short-term survival habitat for most aquatic life forms. Thirty percent was



317 recommended as a base flow to sustain good survival biota conditions. Sixty percent provides excellent to outstanding habitat
318 for most aquatic life forms during their primary periods of growth and for most recreational uses. However, what about strongly
319 channelized and incised rivers, which are the most common channel types in Europe? Our survey indicated that to obtain
320 macroinvertebrate diversity, we need a much higher volume of water than 10% of MAF. In the case of incision, a high volume
321 of water is needed to cover the shelves and sediment storage, which are the principal elements of macroinvertebrate habitats
322 and refuges in a dynamic river system (Duan et al., 2009; Anim et al., 2018).

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

331 The biotic integrity of rivers is primarily restricted by downstream transport of sediments controlling the integrity of fluvial
332 ecosystems (Katano et al., 2009; White et al., 2016). Substrate characteristics such as size, stability, compactness, quality, and
333 dynamics are a key parameter determining the occurrence and variation in macroinvertebrate communities. High substrate
334 stability, substrate heterogeneity, and low compactness determine high macroinvertebrate diversity (Beisel et al., 2000; Duan
335 et al., 2009). On the other hand, fine sediments can be regarded as a potential stressor for macroinvertebrates (Meißner et al.,
336 2019). In highly incised sectors of the river, a deficiency of sediment and its compactness as well as a lack of food sources
337 (Jowett, 2003) lead to impoverishment of the taxonomic composition of macroinvertebrates and favour taxa adapted to high
338 flow only (Wyźga et al., 2013). Our modelling indicates that prevention of optimal conditions requires more volume of water
339 which exceeds the mean annual flow. This suggestion can be dangerous, because increased discharge augments incision
340 processes. We can thus fall into a kind of ecological trap. A solution may be to pay careful attention to the bed morphology,
341 especially in the case of incised channels. We then have two options to preserve the high biodiversity of invertebrates according
342 to the EU water directive: to vastly increase the water volume or to restore sedimentation processes to obtain a hydrodynamic
343 balance. As a consequence, suitable habitats for invertebrates and fish will be enlarged. The second option seems much more
344 realistic. Only then we will be able to successfully maintain the diversity of aquatic biota.

345 5. Conclusions

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

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353 Writing - review & editing; Kłonowska-Olejniak Małgorzata: Data curation; Dumnicka Elżbieta: Data curation; Woś
354 Agnieszka: Investigation; Wyrębek Maciej: Investigation, Resources, Visualization; Książek Leszek: Investigation,
355 Methodology, Resources, Validation, Writing - review & editing; Paweł Madej: Funding acquisition, Project administration;
356 Grela Jerzy: Funding acquisition, Project administration; Skalski Tomasz: Conceptualization, Formal analysis, Investigation,
357 Methodology, Software, Supervision, Visualization, Writing - original draft.



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