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How hydromorphological constraints and regulated flows govern macroinvertebrate communities along an entire lowland river?

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45 ABSTRACT

46 Macroinvertebrates' response to hydromorphological alterations and regulated flows along lowland
47 rivers is still poorly known despite ecohydrology's fundamental role in river science. Along the
48 Oglio River (Northern Italy), several water abstractions and dams break it into segments with
49 varying hydraulic and morphological properties. Three types of *a priori* different environments
50 were identified (dammed, downstream and free flowing sections) and macroinvertebrate
51 communities were sampled from each zone. This study aimed: I) to investigate patterns of
52 macroinvertebrate communities along a regulated lowland river by testing the *a priori* zones; II) to
53 find macroinvertebrate taxa that served as indicators of the various hydrological conditions and III)
54 to verify hydromorphological control over ecological macroinvertebrate traits resulting in different
55 trait values in each identified zone. Macroinvertebrate community was characterised in a total of 63
56 stations by means of two distinct^[sf1] quantitative approaches, each exploring a surface of 0.5 m².
57 The lowest richness values were found in dammed sites that tended toward lentic conditions.
58 Ecnomidae (dammed zones), Limoniidae (downstream zones) and Heptageniidae (free flowing
59 section) were identified as the best indicators of varying hydrological conditions. As suggested by
60 the results of 4th Corner Method environmental constraints define communities with different
61 ecological traits. These results highlight hydromorphological control over macroinvertebrate
62 community structure and reflect how regulated flows affect the Oglio River in terms of biodiversity,
63 indicator taxa and ecological traits. The authors wish to stress the importance of considering the
64 ecological effects of dams and impoundments on river systems in upstream areas as well as
65 downstream.

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70 INTRODUCTION

71 Rivers and streams are among the most vulnerable and simultaneously exploited ecological
72 systems on our planet (Allan and Castillo 2007). Humans have broadly altered river systems'
73 hydrology through impoundments and diversions to meet their water, energy, and transport needs.
74 In particular, dam construction has increased exponentially in recent decades, especially during the
75 period 1960-1990 (Rosenberg *et al.*, 2000). Rivers and streams are shaped by their hydrology,
76 which sets bottom features, the timing of flooding, transport of solids and dissolved materials,
77 metabolic rates and biological communities (Allan and Castillo 2007). Any alterations in hydrology,
78 such as those resulting from dams, have consequences for a number of lotic ecosystem properties.
79 This latter issue seems obvious, but the implications of hydrological regime, river continuity and
80 morphological conditions (together termed hydromorphology) for river and stream management
81 were scarcely considered for a long time. Currently, there is a need to understand the ecological
82 effects of a wide range of changes in physical habitat, as rivers are increasingly exploited, regulated
83 or otherwise modified through flood-defence engineering, impoundments, restoration, climate
84 change and the spread of alien species (Vaughan *et al.*, 2009). The need for studies linking
85 hydromorphology and ecological response is a priority for river research and management that
86 requires clearly stated hypotheses and adequate sampling programmes that are able to develop
87 robust flow alteration-ecological response relationship (Vaughan *et al.*, 2009; Poff and Zimmerman
88 2010).

89 Hydromorphological elements and their assessment in lotic ecosystems were introduced
90 recently in European legislation, with the Water Framework Directive (European Commission
91 2000) as a supporting tool for the comprehension of biological and chemical features. Unaltered
92 hydromorphology is generally coupled with an elevated ecological status, and vice-versa (European
93 Commission 2000).

94 Dam construction leads to a variety of demonstrated effects in stream hydraulics and
95 properties, like the alteration of sediment transport (Ward and Stanford 1983, 1987; Syvitski *et al.*,
96 2005), inundation of terrestrial systems (Nilsson and Berggren 2000), fragmentation of riparian
97 plant distribution (Jansson *et al.*, 2000), enhancement of greenhouse gas emissions (St Louis *et al.*,
98 2000), changes in thermal regimes and water chemical composition (Armitage 1984; Olden and
99 Naiman 2010; Lessard and Hayes 2003) as well as a possible regime shift, from net heterotrophy to
100 net autotrophy (Pinardi *et al.*, 2011). Furthermore, aquatic biodiversity seems to respond to
101 hydraulic disturbance by changing community structures and resistance to invasion of exotic
102 species (Stanford *et al.*, 1996; Bunn and Arthington 2002; Poff *et al.*, 2007). Different studies (Copp
103 1990; Irz *et al.*, 2006) reported a transition from lotic to lentic fish communities in dammed sites as
104 well as increased in exotic and lake-adapted taxa (Pringle *et al.*, 2000). However, there are few

105 similar studies focussing ^[sf2] on other aquatic taxa. The way the whole macroinvertebrate
106 community respond to hydromorphological alterations and regulated flows in the long term, large-
107 scale and lowland rivers has been poorly explored. Many researchers have investigated the
108 ecohydrological changes that occur below a single dam, but few studies have examined changes in
109 macroinvertebrate communities encompassing an entire river unit (Heppner and Loague 2008;
110 Zolezzi *et al.*, 2011). Hydraulic stream conditions and other hydrologic factors, including a
111 combination of current velocity, depth, surface slope and substrate roughness, instead seem to be
112 important factors for invertebrate zonation patterns (Rempel *et al.*, 2000, Brooks *et al.*, 2005,
113 Kennen *et al.*, 2010) and benthic ecology (Carling 1992). Nevertheless, the consequences of
114 streams management and invertebrate hydraulic preferences are generally better known in small
115 streams than in medium or large rivers (Mérigoux *et al.*, 2009), which is probably due to the
116 complexity of these systems (Sparks 1995).

117 The effects of dams and barriers on macroinvertebrate communities are important because of
118 the role that macroinvertebrates play in the functions and dynamics of stream ecosystems (Merritt *et*
119 *al.*, 1984; Merritt and Lawson 1992). Dam use and the intensive exploitation of rivers, particularly
120 in northern Italy, dates back to 1900. They were historically designed with little consideration for
121 ecological effects such as migration pathways, minimum flow releases or hydropeaking problems.
122 Here, as in many Mediterranean countries, rivers were converted into discontinuous systems with
123 alternating or adjacent segments characterised by varying hydrologic conditions.

124 In this study three types of environments were identified *a priori* along the course of the
125 regulated lowland Oglio River: a lentic stretch (dammed: upstream of the dams or weirs), a stream-
126 like (downstream: downstream dams or water abstraction infrastructures) and a river-like section
127 (free flowing) and macroinvertebrate communities were studied in each part. The main hypothesis
128 is that macroinvertebrate community patterns are clearly addressed by different flow conditions
129 affecting taxa richness, indicator families and ecological traits.

130 In order to contribute to the knowledge of hydromorphological constraints and regulated
131 flows on macroinvertebrate communities, this study aims: I) to investigate patterns of
132 macroinvertebrate communities along a lowland flow regulated river, testing *a priori* zonation; II)
133 to find macroinvertebrate taxa that would serve as indicators of different hydrological conditions
134 and III) to verify environmental and hydromorphological control over macroinvertebrate ecological
135 traits resulting in different trait values in each zone.

136

137 **METHODS**

138 *Study area*

139 This study was carried out along the entire Oglio River (Lombardia, northern Italy), a man-

140 regulated watercourse of 154 km (Fig. 1). This river originates from an Alpine lake, the Lake Iseo
141 (185 m a.s.l.), and flows into the Po River (16 m.a.s.l.). Water flow in the Oglio River is regulated
142 by the Sarnico dam, at the southern extreme of Lake Iseo; regulation aims at the production of
143 electricity and the maintenance of a water reserve in the upstream lake for irrigation purposes. The
144 catchment of the Oglio River occupies an area of 3840 km², mostly exploited for agricultural
145 activities (67%) and animal farming (about 600,000 cows and over 2,100,000 pigs); the human
146 population comprises roughly 1,100,000 inhabitants.

147 The Oglio River suffers from various pressures. Briefly, intensive agriculture and farming
148 have resulted in diffuse nitrogen pollution that affects surface and groundwater (Soana *et al.*, 2011;
149 Laini *et al.*, 2011). The river itself has been heavily altered from its pristine status due to multiple
150 agricultural and industrial water uses and from the construction of hydropower plants, low head
151 dams and banks. Water diversions for irrigation date back to 1500 and are mainly located along the
152 upper 29 km long reach; the sum of their water concession equals the average historical flow of the
153 river (about 80 m³s⁻¹), which means that the water flow could be entirely diverted. The realisation of
154 hydropower plants is a more recent issue that dates back to 1950; six plants are operating at present,
155 all located in the same upper reach mentioned above where the river is generally confined to a
156 single channel, disconnected from its floodplain and with reduced sinuosity. Altered flow regime
157 and damming are probably major causes of habitat heterogeneity loss. Hydraulic infrastructures
158 result in variable riverbed widths (from <30 to about 100 m) and in variable water depths, from
159 several meters upstream from the dams, to a few centimeters downstream from the water
160 abstraction. The Oglio River has the typical features of a plain river, with gentle slopes and
161 moderate water flow. The river substrate only partially varies along the longitudinal gradient from a
162 typical gravel-dominated substrate to a fine sand-dominated substrate in the lowland areas. This is
163 due to the presence of hydraulic infrastructures in the upper sections that affect the gravel substrate
164 converting in silt and macrophyte-dominated substrate upstream from the dams.

165

166 *Macroinvertebrate and environmental data*

167 The macroinvertebrate community was sampled seasonally from July 2009 to May 2010 in a
168 number of representative sites located along the Oglio River (Fig.1). Sampling sites, seasonally
169 investigated, varied from a minimum of 15 to a maximum of 18. A few sites (mainly in dammed
170 and free flowing zones) do not present a complete seasonal series due to vandalism or excess
171 flow/floods. Sampling strategy reflected an *a priori* idea to split the water course into three
172 environment types: i) dammed sites (basins upstream hydropower plants or low head dams); ii) sites
173 immediately downstream to those described as dammed and iii) free flowing section in the lowland,
174 meandering zone. Macrofauna community was characterised in a total of 63 stations by means of

175 two distinct quantitative approaches, each exploring a surface of 0.5 m². At those sites belonging to
176 **dammed and free flowing zones** artificial substrates were employed whilst at sites belonging to
177 **downstream zones** a Surber net was used. At each station **downstream hydropower plants or dams** a
178 total of 10 Surber units (1 surber unit = 0.05 m², with 500 µm mesh size net) were collected on each
179 date by stirring and removing surface sediments and stones to remove any attached invertebrates.
180 Explored areas within each station were proportional to the relative surface of all the microhabitats
181 identified, according to Buffagni and Erba (2007).

182 Reliable and accurate collection of macroinvertebrates presents a certain degree of difficulty
183 in deep sections of upstream dams and where flows are elevated. Here, the use of artificial
184 substrates (Hester-Dendy modified e.g. Cairns and Dickson 1971; Battezzato *et al.*, 1995) can
185 represent a valid alternative to the Surber net (Solimini *et al.*, 2000; Buffagni *et al.*, 2007).
186 Multiple-plate artificial substrates (hereinafter called AS) summing a total colonisable area of 0.5
187 m², were thus employed at **dammed and free flowing stations**. These samplers were anchored and
188 suspended with ropes close to the bottom, as detailed in Buffagni *et al.* (2007). They were left *in*
189 *situ* for 1 month to allow complete colonization and thereafter carefully retrieved. Each sampler was
190 placed in a white plastic tray, and macroinvertebrates were removed with forceps from the plates
191 and trapped sediment. **The macroinvertebrates dislodged in the process of removing the AS from**
192 **the river were collected immediately downstream with a 500-µm mesh net and added to the sample.**

193 Macroinvertebrate samples and associated material, both from the Surber net or AS, were
194 preserved in 70% ethanol and then examined under a stereoscope in the laboratory. All
195 macroinvertebrate individuals were identified at family or genus level except for Hydracarina and
196 Rissoidea gastropods. The sampling and processing effort at this taxonomic level allowed all groups
197 from the invertebrate community to be investigated.

198 In all sampling dates and at all stations data on water flow, current velocity and depth were
199 collected or provided by the Oglio Consortium (member of Alpine Lakes Controller Institutions,
200 Civil Protection Department) (Table 1).

201 202 *Data analyses*

203 In this study two distinct quantitative approaches were used that contributed to the
204 compilation of a large dataset. Different sampling methods can result in varying estimations of
205 macrofauna abundance (Buffagni and Erba 2007), but they do not generally select among taxa so
206 that presence/absence data are reliable with both approaches (Bo *et al.*, 2007). However the use of
207 different sampling methods for different habitats is reported in many other studies (Gjerløv *et al.*,
208 2003; Benstead *et al.*, 2009). As a consequence, presence/absence information and not abundances
209 were used in statistical tests. Furthermore, in order to avoid drawbacks due to the different

210 taxonomic resolution, statistical analyses were generally performed by using a standardised
211 taxonomic level (family data). Information about genus was included instead to improve ecological
212 trait data analyses (see later).

213 The effects of seasonality and type of environments (predefined zones) on family richness
214 were tested by using ANOVA analysis on the log transformed data.

215 The quality of taxa inventory generated by seasonal sampling along the entire Oglio River
216 and for the 3 groups of stations was checked using accumulation's curves. This approach is widely
217 used to evaluate the representativeness of collected information (Soberón and Llorente 1993) and
218 represents how the number of taxa within a geographical area varies as a function of the collection
219 effort (Colwell and Coddington 1994). The slope of the curve decreases with sampling effort and
220 reaches a hypothetical value of 0 when all taxa are detected. As the taxon richness is probably the
221 main variable describing community diversity (Gaston 1996), accumulation's curves allow one to
222 set reference terms for taxa richness given a fixed number of replicate samples. Different types of
223 functions were fitted to family accumulation curves and the Weibull function provided the best
224 match. The same function was demonstrated as a good compromise between the number of
225 parameters to be fitted and also results in other studies on invertebrates (Jimenez-Valverde *et al.*,
226 2006; Tjørve 2003). The Weibull function was fitted to smoothed data and the asymptotic value
227 (i.e., the taxa richness predicted for an ideally infinite sample size) was computed. The ratio of
228 recorded to predicted richness (asymptotic score) was used as a proxy of representativeness of the
229 database (in the three pre-defined zones and for the whole river).

230 A nonmetric multidimensional scaling (nMDS) analysis was performed to identify
231 distribution patterns among the macroinvertebrate communities of the different sampled sites.
232 NMDS is regarded as one of the most robust unconstrained ordination methods (Oksanen 2011) and
233 is robust from deviation from multi-normality. Bray-Curtis distance was used as dissimilarity
234 measure and stress was used to test the goodness of fit. The threshold above which the ordination
235 was not considered reliable was set at 20%. Linear fittings were performed between the
236 hydrological data (discharge, velocity and depth) and the output of nMDS ordination in order to
237 identify environmental factors driving macroinvertebrate distribution. Analysis of similarities
238 (ANOSIM) using Bray-Curtis distance was carried out to test whether there was a significant
239 difference between the *a priori* proposed zones in terms of macroinvertebrate communities. This
240 test was developed by Clark (1993) as a method for testing the significance of the groups that had
241 been *a priori* defined. Prior to multivariate analysis, hydrological variables were transformed (log-
242 transformation for quantitative variables) and standardised to improve linear relationships among
243 variables, reduce distribution skewness and avoid distortions due to the effect of different
244 transformations and magnitudes.

IndVal analysis was carried out to select the indicator family for each river zone (Dufrêne and Legendre 1997). This analysis evaluates the affinity of each taxon for one of the three environment types defined *a priori* (the Indicator Value: IV). Such an affinity is calculated on the basis of the frequency of each taxon in the identified groups. To take into account the unequal size of the sampling sites within each group the group-equalized IV was calculated according to De Cáceres and Legendre (2009). The significance of IV was tested using a Monte-Carlo test (999 runs) and Alpha level was set at 0.05. Taxa selected by IndVal should present environmental-specific ecological traits to allow their presence; the “4th Corner Method” (Legendre *et al.*, 1997) was used to check for differences in ecological traits between the different tested zones and flow conditions.

The matrix of ecological traits was built considering the traits and relative subgroups described by Usseglio-Polatera *et al.* (2000) and Tachet *et al.* (2002). The ecological characteristics used include the 7 traits related with hydrology and physical habitat, with a total of 37 possible modalities. The purpose of this method is to relate the ecological traits of the organisms to the habitat characteristics of the sites in which they live. The calculation is made possible by using traits, presence/absence (or abundance) and environmental matrices. Within the 5 models proposed by Dray & Legendre (2008) model number 2 “Environmental control over species assemblage” was chosen. In this model, the hypothesis is that taxa assemblages depend on the environmental feature characterising the sites where they were found. As shown by some authors (Bournaud *et al.*, 1996; Dolédec *et al.*, 1998) higher taxonomic levels can be suitable for an ecological study, so the first step was to select the families and genus collected in the Oglio River from the database. For the macroinvertebrate groups in which genus data were available, only the genus recovered in Oglio River were used. The second step was to calculate the relative frequency of each subgroup (i.e. lowlands, piedmont level or alpine level) belonging to a category (i.e. *Altitude*). The sum of the frequencies of the subgroup within a category is equal to 1.

All statistical analyses were performed using the statistical computing software R (R-Development core-team, 2010) with packages “Vegan” (Oksanen 2011), “ade4” (Chessel 2011) and “indicspecies” (De Cáceres 2011).

Results

Assessment of macroinvertebrate richness among different sampling methods

Results from ANOVA analysis (Table 2) suggested that the zone ($p < 0.01$) and the season ($p < 0.05$) were statistically significant variables affecting macroinvertebrate family richness along the Oglio River but not the interaction zone:season ($p = 0.09$). During the study period (1 year) about 40,000 organisms were identified to family or genus level and a total of 72 families were identified.

Focussing on the different sampling methods used: more than 75% of the recorded families were presented in Surber samples and also in AS samples. Concretely 62 families were detected using AS while 57 using Surber net and 47 were presented using both methods. The families recorded by exclusively a method were rare and were found in only few sites.

Assessment of macroinvertebrate inventory completeness and richness estimations along the three proposed zones

Downstream and free flowing zones hosted the richest sampling stations, with a total of 61 and 55 families recorded. On the other hand, stations within dammed zones exhibited the lowest richness, with 37 families recorded. Accumulation's curves showed the representative sampling effort for the 3 selected zones (Fig 2). This result suggested that the sampling effort accounted for at least 75% of the total families estimated for each zone (Table 3). Family richness seemed to increase slightly more rapidly in the downstream sites compared to the other zones. Moreover, dammed sites presented clearly lower family richness values compared to the other zones that appeared to be rather similar. Using data from all pooled sampling stations, the ratio between the recovered (72) and theoretical number of families predicted by accumulation's curves (78) equalled 92%.

Importance of hydromorphological environmental variables in determining macroinvertebrate communities

In the ordination space of the first 3 axes of non-multidimensional scaling the samples were arranged according to the *a priori* identified zones (Fig.3) and presented a stress value of 16%. Moreover, vector fitting among nMDS axes and hydromorphological parameters highlighted the importance of hydrological factors as drivers of the macroinvertebrate communities. The nMDS plot established three distinct groups that essentially consisted of the proposed *a priori* hypothesis. Considering axes 1 and 2, "dammed stations" appeared well-clustered on the right side of the plot while "downstream stations" were placed on the bottom and "free flowing section" essentially on the top left of the plot.

In detail (Fig. 3), downstream stations seemed to be characterised by reduced discharge and depth and partially by high velocity, while dammed ones were related to higher levels of depth. On the other hand, stations in the free flowing section were mainly characterised by high discharges and velocity. All variables presented a linear fitting statistically significant ($p < 0.01$) between selected zones. Furthermore, the ANOSIM test showed there were significant differences ($R = 0.522$, $p < 0.001$) in macroinvertebrate assemblage composition among the three pre-defined zones.

316 IndVal analysis identified indicator taxa for the three **environment types** proposed (Table 4).
317 Five families were significant indicators for dammed **sites**: Ecnomidae, Coenagrionidae,
318 Viviparidae, Lymnaeidae and Limnephilidae. Some authors (Bonada *et al.*, 2008, following Dufrêne
319 and Legendre, 1997) considered an IV > 25 as key value to consider adequate an indicator taxa, so
320 the first two presented an important IV value and great significance level ($p < 0.001$). Stations
321 included in the **downstream zones** presented a heterogeneous list composed by fourteen indicator
322 families: Limoniidae, Psychomyidae, Lumbricidae, Baetidae, Neritidae and Rhyacophilidae with
323 the best significance level ($p < 0.001$). These stations presented a heterogeneous clustering of taxa,
324 with different ecological characteristics and varying taxonomic positions. Finally, seven families
325 were good indicators for the free flowing section with Heptageniidae (essentially genus
326 *Heptagenia*) with the highest IV followed by Calopterygidae (genus *Calopteryx*), Gammaridae,
327 Platycnemidae, Hydropsychidae, Gomphidae and lastly Tubificidae.

328 Results from the “4th Corner Method” showed distinct patterns of ecological traits in the
329 three different *a priori* hypothesised zones: dammed, downstream and free flowing stretch (Table
330 5). When focussing upon ecological traits like *transversal distribution*, *longitudinal distribution* or
331 *current velocity* it is very interesting to note that the three pre-**defined zones** presented
332 macroinvertebrate communities with different ecological traits. In these cases, dammed and
333 downstream **zones** presented almost always opposite and complementary values. In particular,
334 analysing *transversal distribution* in dammed zones presented a macroinvertebrate community with
335 negative correlation with habitats like river channel and a strong and positive relation with habitats
336 like ponds and pools (0.25; $p < 0.01$) and also with lakes (0.07; $p < 0.01$). On the other hand,
337 macroinvertebrate communities inhabiting downstream zones presented a negative relationship with
338 habitats like lakes (-0.09; $p < 0.01$) and ponds (-0.11; $p < 0.05$) and positive value with banks habitats
339 (0.12; $p < 0.01$). In free flowing section significant and negative relationships were obtained with
340 ponds (-0.10, $p < 0.05$) and temporary waters (-0.09; $p < 0.01$). Focussing on *longitudinal distribution*
341 dammed zones presented negative relationship with crenon and epirhithron zones (-0.11 and -0.21;
342 $p < 0.01$) and positive relationship with metapotamon habitats (0.17; $p < 0.01$). Again, downstream
343 zones presented opposite values compared with dammed stations (except for estuary value) with
344 positive relationships with crenon and epirhithron areas (0.09 and 0.12; $p < 0.01$) and negative
345 relationships with epipotamon (-0.08; $p < 0.01$) and metapotamon (-0.08; $p < 0.05$). In this ecological
346 trait free flowing sites presented complex results with positive relationships with metarhithron
347 zones (0.11; $p < 0.01$) and negative with estuary (-0.12; $p < 0.01$) and metapotamon (-0.06; $p < 0.05$).

348 Also considering *altitude* trait, **macroinvertebrate communities inhabiting** dammed and
349 downstream zones presented opposite signs between lowlands, piedmont and alpine levels.

350 Observing *substrate preference* dammed zones were essentially related to microphytes and
351 macrophytes (0.14 and 0.12; $p < 0.01$), while downstream zones with flags, twigs and roots (0.07 and
352 0.09; $p < 0.01$) and silt (-0.09; $p < 0.01$). The free flowing section was positively related to silt, sand
353 and gravel (0.14; 0.12; 0.09 with $p < 0.01$). Furthermore, considering *current velocity*, dammed zones
354 presented negative and significant relationships with medium and fast velocity (-0.18 and -0.24;
355 $p < 0.01$) while **the others** presented a positive relation, although less significant. Analysing the
356 *trophic status*, it was interesting to note that dammed zones were positively related with eutrophic
357 conditions (0.13; $p < 0.01$) while **the other ones** presented opposite results with negative relationship
358 with eutrophic conditions. The *temperature* trait seemed important because dammed zones
359 presented a negative and significant relationship with psychrophilic, i.e. cold-stenothermal
360 organism (-0.099; $p < 0.01$) and a positive relationship with eurythermic conditions (0.06; $p < 0.01$),
361 while other zones did not present significant values.

362

363 Discussion

364 Species level resolution is preferable in ecohydrological researches when it is available
365 (Monk *et al.* 2012). However, the present study considered the taxonomic level used as adequate in
366 order to characterise the ecological traits of most groups with respect to riverine hydrology and a
367 good compromise between classification effort and gathered information (Marchant *et al.*, 1995;
368 Bournaud *et al.*, 1996; Dolédec *et al.*, 1998). Also, macroinvertebrate family richness generally
369 presents a high correlation with species richness in Mediterranean areas (Sánchez-Fernández *et al.*,
370 2006) as well as in boreal systems (Heino and Soininen, 2007) which seems to suggest how species-
371 level assemblage patterns could be reproduced by using genus- and family-level data. Furthermore,
372 recently Belmar *et al.* (2012) focussed on hydrological variables found a relatively strong
373 relationship between community composition and flow regimes at different taxonomic levels, from
374 species to family level.

375 In this study, the decision to work on the presence/absence of families and not on abundance
376 is justified first by the necessity of using two distinct sampling techniques which were demonstrated
377 to recover the same group of organisms. Additionally, outputs from the NMDS analysis were likely
378 to provide a similar qualitative data ordination when performed on abundance (after data
379 transformations as Wisconsin double standardization) and on presence/absence.

380 At the scale of the entire river, the seasonal samplings and the number of stations
381 investigated were adequate in order to provide a reliable inventory of the macroinvertebrate
382 community. In fact, according to the outputs of the accumulation's curves, more than 80% of the
383 total families were censused, and only a few families were missing in order to reach the asymptotic
384 theoretical richness value. Focussing on each **environment type**, about 78% of the expected families

385 were found in dammed stations, and it is likely that sampling efforts could have been slightly
386 improved in order to reach higher completeness values (Jiménez-Valverde and Hortal 2003;
387 Sánchez-Fernandez *et al.*, 2008). Highly representative family inventories were instead realised for
388 downstream and free flowing stations.

389 The representativeness of the macroinvertebrate community for the entire river and for the
390 three groups of *a priori* selected reaches is an important requirement for the analyses performed and
391 guarantees the robustness of the main outputs. Results from the present study clearly suggest that
392 hydrological parameters and regulated flows play a key role in structuring macroinvertebrate
393 communities in a regulated lowland river. This outcome has a high degree of novelty as, to current
394 knowledge, similar results focussing on large scale and entire river units, specifically on
395 macroinvertebrate communities and ecological traits are very scarce in the literature, at least in
396 ecohydrology research and similar geographic areas.

397 The sequence of hydropower plants, low head dams and water abstraction infrastructures has
398 created a discontinuum of hydrological conditions in the Oglio River with alternating lentic-like and
399 strictly lotic-like reaches near upstream and downstream infrastructures. As a consequence,
400 macroinvertebrate communities do not present an upstream-downstream gradient along the
401 rivercourse, as predicted by river continuum theories (Vannote *et al.*, 1980). Rather, the presented
402 results clearly describe identifiable and alternating lentic and lotic communities along the
403 rivercourse. The results of NMDS analysis match the proposed *a priori* grouping of the investigated
404 stations according to three distinct hydrological features. Differences in terms of taxonomic
405 composition among the proposed zones were also reflected in the ANOSIM test while
406 environmental types (predefined zones) and the season seems to be important factors affecting
407 macroinvertebrate richness values.

408 These different zones will be discussed separately later. The macroinvertebrate community
409 structure is probably shaped by factors such as the substrate, vegetation and chemical gradients at
410 the microscale (i.e. dissolved oxygen availability in porewaters), that are directly related with local
411 hydrology. Furthermore, hydrological change and interaction with substrate may affect the
412 availability of potential microhabitats to some species while increasing habitat availability for
413 others (Statzner *et al.*, 1988). Gore et al. (2001) stressed that aquatic organisms are probably
414 restricted to those combinations of velocity, depth, and substrate that allow morphological and
415 behavioural resistance to flow to be exceeded by energetic gains and predicted an increasing
416 emphasis on incorporating hydraulic variables as a part of bioassessment. A dynamic and natural
417 hydrological connectivity among waterbodies, in terms of space and time, has been proven to drive
418 patterns of macroinvertebrate biodiversity and ecosystem functions in different floodplain rivers
419 (Amoros and Bornette 2002; Leigh and Sheldon 2009).

420 *Dammed stations*

421 This group included sites characterised by features typical of shallow lakes of a few meters
422 depth, no apparent water velocity, soft substrate and dense macrophyte stands. Here, hydrology and
423 depth were the main drivers for the ordination of data (cluster on the right of the nMDS plot).
424 Indicator taxa like *Ecnomus tenellus* (Ecnomidae) or Coenagrionidae, Viviparidae and Lymnaeidae
425 were in agreement with this output, with absence of water current and high depth as selecting
426 factors for the taxa colonizing dammed stations. Ecological trait analysis added further evidence in
427 this respect, as recovered macroinvertebrate communities are generally related to lentic habitats like
428 ponds or lakes with null current velocity and macro and microphytes substrate. Among
429 macrophytes, *Vallisneria spiralis* was abundant in all dammed stations. Despite the fact that they
430 were located in the upper zone of the Oglio River these sites did not present invertebrate
431 communities typical of rhithron zones. This is in part due to the natural conditions of the lowland
432 river, but considering the hydromorphologic variable values, it seems to be clear that regulated
433 flows and dams act as alterations within the natural river continuum.

434 Here, the Oglio River is also often disconnected from its floodplain, although the ecological
435 importance of this area as part of a river ecosystem has been recognised (Burt *et al.*, 2008; Burt *et*
436 *al.*, 2010).

437 Stations upstream from hydropower plants and low head dams had poorer measured and
438 estimated biodiversity, probably due to net habitat loss during the shift from a lotic to an artificial
439 lentic system (Bonada *et al.*, 2005; Ribera 2008) that included reduced sinuosity and the loss of
440 meandering zones loss (Garcia *et al.*, 2012). Aquatic environments such as rivers display large
441 habitat heterogeneity, including pool-riffle sequences (Vannote *et al.*, 1980; Allan and Castillo
442 2007) as well as a number of different micro-habitats at reach scale (Cogerino *et al.*, 1995; Allan *et*
443 *al.*, 1997; Boyero 2003). The habitat heterogeneity of lotic ecosystems may allow the presence of a
444 higher number of taxa in comparison to ponds or lakes, although under natural conditions, these
445 environments generally contribute to the presence of rare and unique species (Williams *et al.*,
446 2003). Furthermore, dammed stations, essentially in the upper zone of Oglio River, presented
447 macroinvertebrate communities negatively related with psychrophilic conditions, which seems to
448 emphasise the importance of thermal regimes (Olden and Naiman 2010) in environmental flows
449 assessments.

450

451 *Downstream stations*

452 Current velocity, reduced depth and type of substrate (mainly flags or mesolital) suggested
453 that stations downstream from the dams or water abstraction structures had those features that
454 characterise pristine, rhithral and stream-like environments. This is another artificial condition

455 which is a consequence of a sudden decrease in water flow for multiple water uses. The reversal of
456 lentic-like features and the re-establishment of lotic characteristics were described in the Serial
457 Discontinuity Concept (SDC) (Ward and Stanford 1983) and in other studies (Odum 1997). The
458 SDC viewed dams as clear discontinuities within the river continuum and proposed that rivers have
459 a tendency to reset ecological conditions toward unregulated or natural conditions as distance
460 downstream from the point of regulation increases (Stanford and Ward 2001).

461 In downstream stations, selected indicator families like Psychomyidae, Ephemerellidae
462 (*Ephemerella*) or Rhyacophilidae were typical of rhithral ecosystems, while other families provided
463 multiple and often unclear information with respect to environmental features. For example, the
464 presence of Neritidae (*Theodoxus*) and other Mollusca could be an indicator of an hyporhithral or
465 potamal environment, while that of *Dreissena polymorpha* does not, and its presence is probably
466 due to a drift effect from dammed upstream coupled with the high dispersive capacity of this
467 invasive species.

468 The ecological traits analysis, and in particular the traits *transversal distribution*,
469 *longitudinal distribution*, *current velocity* and *altitude* suggested negative relationships between
470 macroinvertebrate communities of downstream stations with lakes, potamal zones and null velocity
471 and positive relation with alpine level altitude, fast velocity and rhithron zones, features that are
472 generally typical of stream-like environments with limited water discharge.

473

474 *Free flowing stations*

475 These stations characterised a lowland, ~100 km long free-flowing river course which was
476 devoid of infrastructures that created longitudinal discontinuities of relevant water flow variations.
477 Flows and water velocity were constant or tended to increase and the upstream-downstream
478 variations of chemical and biological features probably followed the predictions of the Vannote *et*
479 *al.* (1980) conceptual model.

480 Due to its length, this reach included a number of different habitats whose features could partially
481 overlap those characterising downstream stations (i.e. the substrate, at its beginning) as well as
482 those characterizing dammed stations (i.e. water depth, toward its end). Such heterogeneity is
483 reflected by the results of the IndVal and Ecological traits analyses. In fact, selected
484 macroinvertebrate indicators taxa of free flowing stations like Gammaridae, *Heptagenia* or different
485 taxa of Odonata are essentially related with lowland rivers. However, results from the ecological
486 trait analysis, and in particular those related to the trait *longitudinal distribution*, suggested a
487 rhithral more than potamal macrofauna community. In terms of altitude traits, this section presented
488 a macroinvertebrate fauna more related with a piedmont level community than with a lowland level.

489 The use of different analysis (IndVal and traits analysis) can improve the quality of the results

490 bringing additional ecohydrological information. This section that would be expected to present
491 macroinvertebrate communities closely related with a potamon condition, really presented
492 heterogeneous communities that may be partially associated with an alteration of the rhithron-
493 potamon boundary. The topic regarding a possible shift in the rhithron-potamon boundary was in
494 part stressed by Stanford *et al.* (1996) who suggested that in rivers that are free flowing for long
495 distances downstream from large dams, the position of the rhithron-potamon transition could be
496 predicted from the operational mode of the dams relative to the influence of tributaries. Furthermore
497 this topic is quite specific and necessarily requires supplementary researches.

498

499 *Final considerations*

500 The relationship between habitat alteration and river ecology is finally receiving increasing
501 attention (Vaughan *et al.*, 2009; Poff and Zimmerman 2010) and specific macroinvertebrate index
502 or invertebrate preferences research, related to flow alteration and hydroecology topics, have been
503 recently developed (Extence *et al.*, 1999; M rigoux *et al.*, 2009; Armanini *et al.*, 2011a, Armanini *et*
504 *al.*, 2011b). However, biomonitoring activities by environmental agencies and scientific interest
505 focus widely on the impact of dams and hydroelectric plants on downstream sections (Ligon *et al.*,
506 1995; Power *et al.*, 1996; Galbraith and Vaughn 2011) while less attention to the macroinvertebrate
507 communities is generally devoted for upstream, dammed stations. Here, drastic changes in
508 macroinvertebrate communities can occur, as demonstrated by the present study in terms of
509 indicator taxa and selection of different macroinvertebrate ecological traits. The authors suggest that
510 monitoring activities should also prioritise those zones where human intervention has created river
511 reaches with lentic features. Pringle (1997), focussing on fish communities, had already stressed the
512 importance of considering the upstream as well as downstream effects of dams and impoundments
513 because disturbances can also be transmitted upstream.

514 Results from the present study also suggest altered macrofauna communities in zones
515 located upstream and downstream from barriers or dams. For example, abundant densities of exotic
516 invertebrates like *Dreissena polymorpha*, *Corbicula* or *Orconectes limosus* characterising dammed
517 and downstream stations, are likely a consequence of flow alteration (Bunn and Arthington 2002)
518 coupled with other anthropogenic causes. Upstream, invertebrate communities suffer stagnation and
519 habitat loss, resulting in biodiversity loss (Stanford *et al.*, 1996) as more exigent, strictly lotic taxa
520 such as most EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) cannot cope with such conditions.
521 Downstream, macroinvertebrate communities suffer highly artificial variable flows, resulting in
522 habitat instability that promotes the presence of communities with numerous indicator taxa.

523 Results from the IndVal analyses may represent an effective monitoring tool when the
524 effects of river flow regulations or the realisation of infrastructures must be evaluated. Particularly

525 informative, with this respect, are those macroinvertebrate taxa characterised by high indicator
526 values.

527 Ecohydrological research and sustainable water flow management should be central in the
528 present and near future in order to achieve the quality targets set by the Water Framework Directive
529 (Acreman and Ferguson 2010; Boon *et al.*, 2010) as well as for modified waterbodies such as the
530 Oglio River. This is particularly important also because hydroclimatic models predict that European
531 rivers will collectively show reduced discharge and seasonally would have lower summer flow
532 (Arnell 1999). Moreover, flow management may even be relatively ineffective in restoration
533 solutions or environmental conservation when provided in the absence of pollution abatement,
534 riparian management and habitat restoration (Arthington *et al.*, 2010).

535 Renöfalt *et al.* (2010) have suggested prioritising among different restoration actions,
536 starting with projects that have positive effects on the largest areas or on projects and actions that
537 can serve as learning experiences through scientific experimentation and testing. In this perspective,
538 the investigated area from a human-dominated landscape should be exploited as useful test case
539 (Jackson *et al.*, 2009) for the sustainable management of environmental flow and restoration of
540 floodplains in other similarly altered areas.

541

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549

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900 **Table 1.** Environmental and hydrological variables measured and used in the analysis.
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Variables	Dammed stations	Downstream stations	Free flowing stations
Discharge ($\text{m}^3 \text{s}^{-1}$)	42.88 ± 27.72	21.23 ± 14.33	86.23 ± 54.53
Depth (m)	3.10 ± 0.75	1.13 ± 0.49	1.96 ± 0.84
Velocity (m s^{-1})	0.23 ± 0.22	0.51 ± 0.32	0.95 ± 0.31

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944 **Table 2.** Summaries of ANOVA used to assess the effects of Zone, Season and the interaction on
945 macroinvertebrate richness. df: degrees of freedom. *** $p<0.001$; ** $p<0.01$; * $p<0.05$
946

Variables	df	Mean Sq	F-value.	p-value
Zone	2	0.7403	6.206	0.00387 **
Season	3	0.3712	3.112	0.03425*
Zone: Season	6	0.2283	1.914	0.09634

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948 **Table 3.** Number of stations sampled (Stations), number of observed (S obs) and estimated families
949 (S exp) for each Oglio zone (obtained by Accumulation's Curves). For each zone the completeness
950 degree (% Compl) is also displayed.
951

	Stations	S exp	S obs	% Compl
Dammed stations	14	47	37	78
Downstream stations	24	69	61	89
Free flowing stations	25	65	55	84
Oglio River (total)	63	78	72	92

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954 **Table 4.** Results of INDVAL analysis for each zone. Indicator Value and significant *p*-value are
 955 displayed.
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Dammed stations			
Order	Family	I.V.	<i>p</i>-value
TRI	Ecnomidae	64.3	0.001
ODO	Coenagrionidae	38.6	0.001
ARC	Viviparidae	25.5	0.004
PUL	Lymnaeidae	25.0	0.024
TRI	Limnephilidae	14.3	0.039
Downstream stations			
Order	Family	I.V.	<i>p</i>-value
DIT	Limoniidae	54.8	0.001
TRI	Psychomyidae	53.7	0.001
OPI	Lumbricidae	53.3	0.001
EFE	Baetidae	46.0	0.001
NER	Neritidae	42.0	0.001
EFE	Ephemerellidae	40.7	0.002
VEN	Dreissenidae	40.2	0.011
TRI	Rhyacophilidae	39.9	0.001
TRI	Lepidostomatidae	37.5	0.003
DIT	Empididae	33.6	0.005
ARH	Erpobdellidae	30.6	0.045
HEM	Naucoridae	25.5	0.005
VEN	Corbiculidae	24.1	0.044
DIT	Tipulidae	17.4	0.04
Free flowing stations			
Order	Family	I.V.	<i>p</i>-value
EFE	Heptageniidae	74.3	0.001
ODO	Calopterygidae	49.0	0.001
ANP	Gammaridae	48.0	0.004
ODO	Platycnemidae	44.4	0.001
TRI	Hydropsychidae	43.8	0.035
ODO	Gomphidae	42.9	0.001
TUB	Tubificidae	23.2	0.033

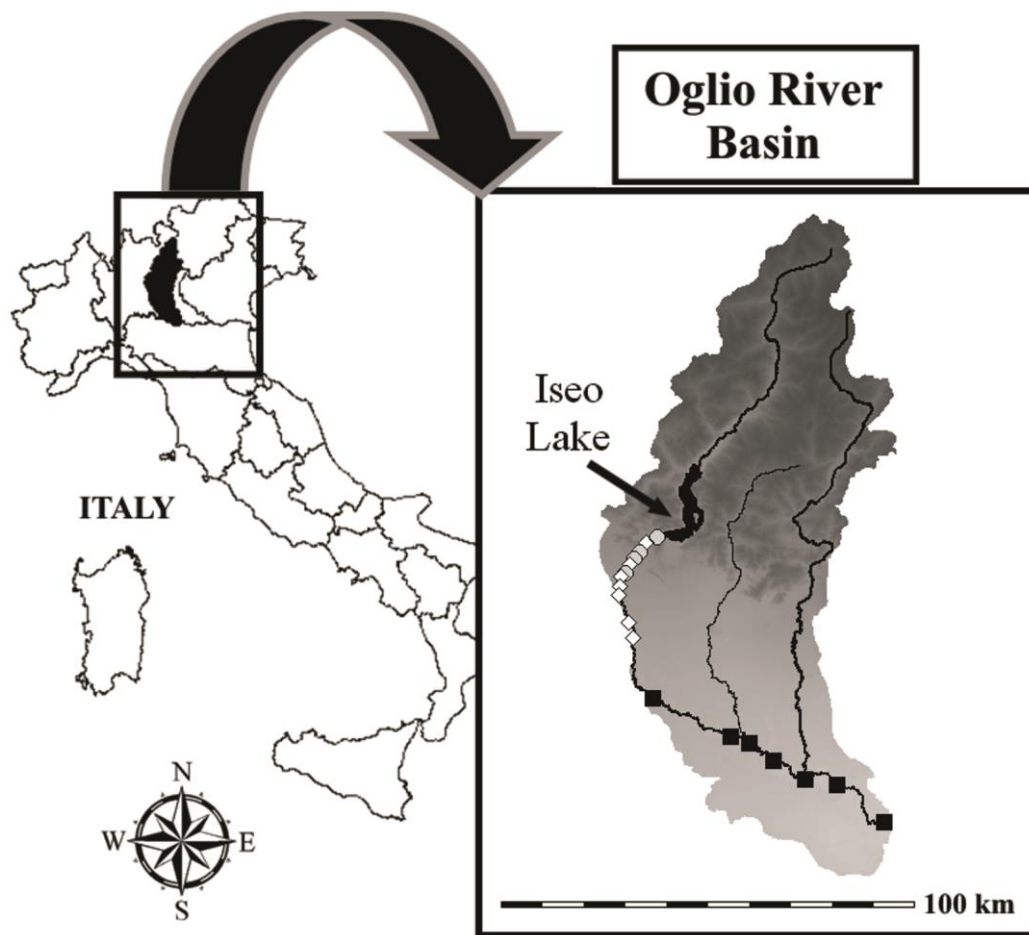
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960 **Table 5.** Summaries of ecological traits results following the traits description of Usseglio-Polatera
961 et al. (2000). The results from the global test (F) and their significance p obtained by permutations
962 in the “4th Corner Method” are presented (Legendre *et al.*, 1997). For dammed, downstream and
963 free flowing sites, the r-values from the correlation traits-habitat matrix are given. The significance
964 of r-value was also tested by permutations (999 runs). All p -values include Holm correction. ***
965 $p < 0.001$; ** $p < 0.01$; * $p < 0.05$
966

Ecological Traits	F-test	<i>p</i> -value		Dammed		Downstream		Free flowing	
				r-value		r-value		r-value	
<i>Transversal distribution</i>									
river_channel	13.705	0.001	***	-0.159	0.003	0.054	0.034	0.072	0.016
banks_	15.167	0.001	***	-0.160	0.003	0.116	0.003	0.008	0.408
ponds_pools	36.554	0.001	***	0.255	0.003	-0.107	0.014	-0.095	0.014
marshes_peat_bogs	1.284	0.126		0.026	0.282	0.027	0.282	-0.049	0.084
temporary_waters	4.066	0.001	***	0.032	0.098	0.060	0.016	-0.088	0.003
lakes	4.702	0.001	***	0.071	0.004	-0.087	0.003	0.034	0.113
groundwaters	2.813	0.001	***	0.016	0.208	-0.071	0.003	0.061	0.003
<i>Longitudinal distribution</i>									
crenon	8.075	0.001	***	-0.113	0.003	0.093	0.003	-0.005	0.417
epirhithron	24.772	0.001	***	-0.210	0.003	0.120	0.003	0.045	0.106
metarhithron	21.290	0.001	***	-0.191	0.003	0.038	0.120	0.114	0.003
hyporhithron	6.407	0.001	***	-0.110	0.003	0.051	0.032	0.035	0.068
epipotamon	4.446	0.009	**	0.073	0.014	-0.082	0.009	0.026	0.194
metapotamon	15.750	0.001	***	0.171	0.003	-0.080	0.022	-0.055	0.034
estuary	8.242	0.001	***	0.040	0.037	0.088	0.003	-0.124	0.003
outside_river_system	17.688	0.001	***	0.175	0.003	-0.118	0.003	-0.019	0.293
<i>Altitude</i>									
lowlands	9.678	0.001	***	0.135	0.003	-0.056	0.052	-0.050	0.052
piedmont_level	10.184	0.001	***	-0.135	0.003	0.033	0.129	0.075	0.008
alpine_level	5.319	0.002	**	-0.091	0.003	0.077	0.004	-0.006	0.413
<i>Substrate (preferendum)</i>									
flags	3.083	0.005	**	-0.001	0.487	0.069	0.004	-0.071	0.003
gravel	7.247	0.001	***	-0.099	0.003	-0.013	0.324	0.093	0.003
sand	12.812	0.001	***	-0.137	0.003	-0.005	0.451	0.115	0.003
silt	10.609	0.001	***	-0.064	0.004	-0.085	0.004	0.140	0.003
macrophytes	8.486	0.001	***	0.120	0.003	-0.019	0.230	-0.078	0.006
microphytes	10.592	0.001	***	0.141	0.003	-0.060	0.044	-0.052	0.044
twigs_roots	4.278	0.001	***	-0.054	0.010	0.088	0.003	-0.049	0.011
organic_detritus	0.774	0.164		0.032	0.153	-0.033	0.153	0.009	0.325
mud	2.024	0.059	.	0.027	0.151	-0.062	0.018	0.043	0.134
<i>Current velocity (preferendum)</i>									
null	31.875	0.001	***	0.239	0.003	-0.087	0.013	-0.103	0.008
slow	6.559	0.001	***	0.107	0.003	-0.020	0.200	-0.066	0.004
medium	35.694	0.001	***	-0.246	0.003	0.056	0.068	0.140	0.003
fast	19.390	0.001	***	-0.189	0.003	0.087	0.008	0.062	0.022
<i>Trophic status (preferendum)</i>									
oligotrophic	9.936	0.001	***	-0.133	0.003	0.086	0.006	0.018	0.266

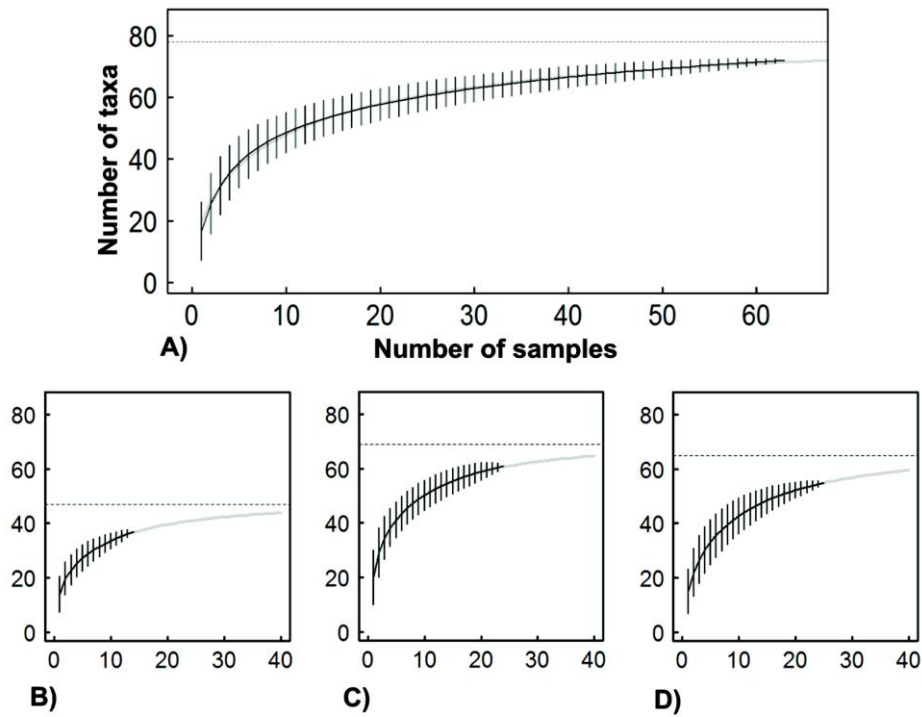
mesotrophic	3.372	0.008	**	0.050	0.058	-0.078	0.009	0.041	0.059
eutrophic	9.031	0.001	***	0.130	0.003	-0.047	0.041	-0.056	0.024
<i>Temperature</i>									
psychrophilic	5.234	0.001	***	-0.099	0.003	0.043	0.062	0.036	0.066
thermophilic	0.409	0.411		0.024	0.333	0.003	0.446	-0.022	0.333
eurythermic	2.153	0.032	*	0.063	0.006	-0.037	0.126	-0.013	0.318

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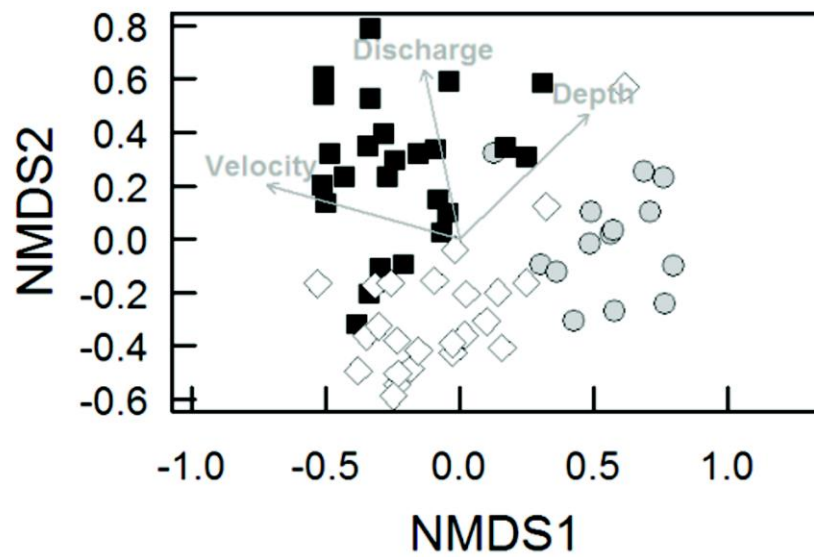
Fig 1. Map of Oglio basin (Northern Italy) and sampling sites along the river. In grey circles the dammed sites, in white downstream sites and in black squares the sites belonging to the free flowing section.



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980 **Fig 2.** Accumulation's Curves in the Oglio River (A). The three zones separately are also displayed:
981 Dammed stations (B), Downstream stations (C) and free flowing section (D). Expected asymptote is
982 always displayed. The numbers of samples are always displayed on the x-axis while the number of
983 taxa on the y-axis.

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 988 **Fig 3.** NMDS plot and the *a priori* identified zones coloured. In black color sites belonging to the
 989 free flowing section, in grey dammed sites and in white downstream sites (stress=0.16).
 990 Hydromorphological variables marked are also displayed.
 991 [sf3]