

Patterns of rare fish and aquatic insects in a southwestern French river catchment in relation to simple physical variables

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Most of our current understanding of rarity has come from studies of terrestrial plants and animals, whereas freshwater habitats remain poorly documented under this topic. Here we considered the spatial distribution patterns of rarity at the river catchment scale, for five freshwater taxa (fish, Ephemeroptera, Plecoptera, Trichoptera and Coleoptera) in southwestern France. The data were collected at 554 and 155 sampling sites for fish and aquatic insects, respectively. General Linear Modelling was used to assess the influence of some typological variables (elevation, stream order, distance from source, and reach slope) on local numbers of rare species (restricted range). The relative numbers of rare species per taxa varied from 16% (Plecoptera) to 59% (Trichoptera). GLM chiefly yielded highly significant correlations between rarity and distance from the source and/or elevation for all taxa, showing that numbers of rare stream species increase towards downstream areas within the stream system. The spatial patterns in rarity for the different study taxa were rather concordant, probably as a result of similar responses to environmental conditions. By focusing on integrative variables, we emphasized the influence of river typology on the rarity of aquatic animals. Areas which carry rare species may concentrate an important fraction of the regional biodiversity. If end-users need geographic models (i.e. maps) to design river management frameworks, numerical patterning is needed to provide theoretical backgrounds: by predicting what the rarity should be like in a given area, we can provide explicit spatial schemes that may be useful to target further research, and to implement management options.

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Species richness and the presence of rare species are frequently cited criteria for site selection by conservationists (Prendergast et al. 1993, Myers et al. 2000). Local rarity may increase the likelihood that demographic and/or environmental stochasticity will wipe out populations, and a restricted spatial distribution (with individuals occurring with high or low densities) implies that populations will probably experience adverse conditions simultaneously (Gaston 1998). However, explaining rarity is often a difficult task (Pearson et al. 1983,

Magurran and Henderson 2003), as rarity may be due to random settlement, or to random predation or emigration or immigration, or to competition, or in fact to any physical factor that influence a species' distribution (Legalle et al. 2005). Many definitions of rarity exist (Rabinowitz 1981, Gaston 1994, Kunin and Gaston 1997). At regional or watershed scales "rare species" (restricted range) can be considered as those species occurring at only a few sites (Cao et al. 2001), and "rarity" can then be considered as the number of rare

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species in a given area (Lennon et al. 2004). Thus, if rarity per se cannot be directly explained, patterning and understanding the geographic variations of rarity remains a very important part of conservation biology (Chu et al. 2003).

Most of our current understanding of rarity has come from studies of terrestrial plants, birds, mammals and some insects (Thomas and Mallorie 1985, Berg and Tjernberg 1996), whereas freshwater habitats are under-represented in published studies of rarity (Chapman 1999). Rivers are increasingly affected by anthropogenic disturbance such as flow regulation or pollution, resulting in modifications of their physical and chemical conditions (Ward and Stanford 1979), disruption of natural dispersal pathways (Kruk and Penczack 2003), and, subsequently, in changes within animal communities (Dethier and Castella 2002). In most cases, such alterations of river habitats lead to losses of taxa (Brittain and Saltveit 1989), and spatial discontinuities in predictable downstream gradients (Ward and Stanford 1983). For practical management frameworks, explicit schemes such as distribution patterns of rare (or threatened) species is therefore needed to identify possible conservation areas within stream systems (Park et al. 2003). In France, for example, the Law on Water of January 1992 strengthened a governmental action plan for the delineation of natural zones of ecological, faunistic and floristic interest. The first objective of this plan was to identify areas which concentrate patrimonial values, i.e. containing rare species or endangered habitats. Similar objectives are part of the Red List indicator system proposed by the IUCN (the latter combining values concerning rarity of species with their time trends). For such purposes, several questions were asked to the scientific experts. Among these questions, two were of particular interest: 1) within a given regional system, which areas contain rare species? and 2) which environmental variables may explain spatial variations in numbers of rare species? To address these concerns, distribution patterns of rarity must be derived from environmental conditions.

The aim of our study was to assess the influence of a limited set of environmental variables (elevation, stream order, distance from source, and reach slope) on the spatial distribution patterns of rarity at the river catchment scale, for different freshwater taxa. We examined whether simple (i.e. easily mapped) environmental variables are capable of predicting where rare species exist, thus allowing for easy use of successful final models by environmental managers and policy makers concerned with preservation of rare species in rivers. We focused on fish and on four insect orders (Ephemeroptera, Plecoptera, Trichoptera and Coleoptera), these five groups being commonly considered at the species level in freshwater studies, and being particularly sensitive to the impact of human activities (Oberdorff et al. 2001,

Compin and Céréghino 2003). Specifically, we thus sought to bring out explicit models which would allow to better understand the relationships between river typology, and the distribution of rarity. To this end, general linear modelling was used to assess the influence of each environmental variable on local numbers of rare species. The results obtained for fish and insects are compared, in order to identify important areas for conservation within stream systems.

Methods

Study area

The River Garonne has its source in the Maladetta Glacier (Spain), its total length is 525 km, and it slopes from the southeast to the north-west, where it reaches the Atlantic ocean through the Gironde estuary (Fig. 1). The mean annual discharge amounts to ca $545 \text{ m}^3 \text{ s}^{-1}$. The River Garonne stream system drains an area of ca $57\,000 \text{ km}^2$. Compared with other French rivers (e.g. the Seine river and the Rhône river), the Garonne river is less disturbed by industrial pollution. The climate of the region is influenced by oceanic processes, but this declines to the southeast where it undergoes the Mediterranean influence with dry winds and weaker pluviometry.

Data collection

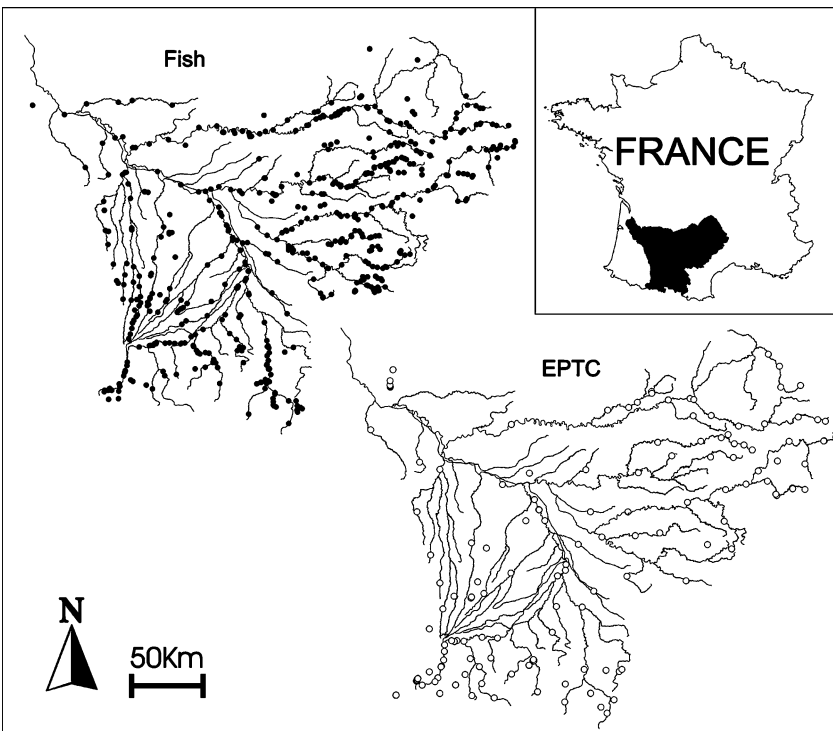
Environmental variables

Each sampling site (for fish or aquatic insects) was characterised with four environmental variables: elevation above sea level (m a.s.l.), distance from the source (km), stream order, and reach slope (per thousand). Their distribution is shown in Fig. 2. These simple variables were chosen because they relate the location of sampling sites within the stream system, they are easy to describe using maps, and their use in successful final models could therefore reduce the effort and cost of data collection for river management applications.

Aquatic insects

We sampled 155 unstressed sites ranging from 10 to 2500 m a.s.l. Unstressed sites were defined as sites not subjected to anthropogenic impacts such as flow regulation, chemical pollution, or urban runoff (indexed by the French Water Agency: <<http://www.eau-adour-garonne.fr/>>, see also Compin and Céréghino 2003). Samples were taken from 1988 to 1998. Each site was sampled at two periods during a same year, i.e. in summer and winter. All samples were taken from the various substratum types using a standard Surber sampler (sampling area 0.1 m^2 , mesh size 0.3 mm). Ephemeroptera, Plecoptera, Trichoptera, and Coleop-

Fig. 1. The Garonne stream system, and location of the sampling sites for fish (black dots) and EPTC (open circles).



tera (EPTC) species were identified by professional taxonomists. We focused on these invertebrate taxa because EPTC are well-known to be sensitive to changes in ecosystem features (Resh and Jackson 1993); they are thus assumed to be good descriptors of the influence of spatial changes in environmental conditions. 283 EPTC species were identified, the detailed list of species was given in Céréghino et al. (2001).

Fish

We investigated 554 least impacted or fairly unstressed sites (see above) ranging from high mountain (2500 m a.s.l.) to plain or coastal (10 m a.s.l.) areas, where we recorded the composition of fish species assemblages. These sites were evenly distributed throughout the Garonne stream system. Site-specific data for fish were collected between 1980 and 2000. All sites were sampled

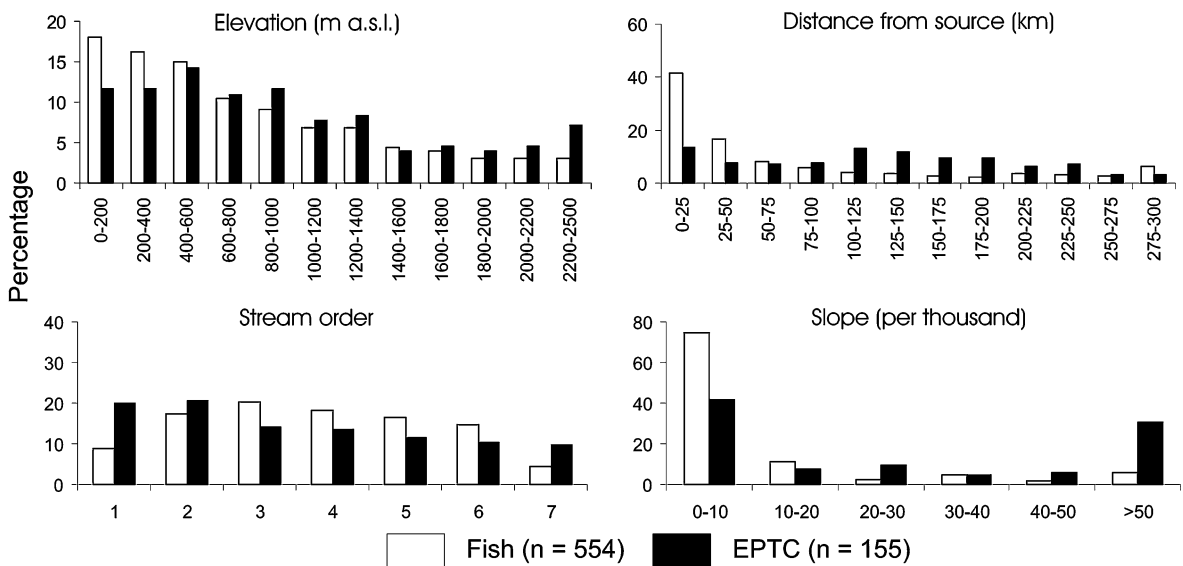


Fig. 2. Distribution of each environmental variable under consideration for fish (n=554) and EPTC sites (n=155).

once by electro fishing, during low-flow periods, using standardized methods (two-pass removal sampling, De Lury 1947, Seber and Le Cren 1967). Forty fish species were identified, among which 25 were native species (i.e. 15 exotic species). The detailed list was given in Santoul et al. (2004, 2005). In this study, it should be noticed that exotic fish were not considered when selecting rare species.

Selecting rare species

The distribution of each of the 283 EPTC species in the Garonne stream system was previously studied by C  r  ghino et al. (2001), who identified three spatial patterns: 1) local distribution, i.e. species occurring in a restricted geographic area, 2) longitudinal zonation, i.e. species occurring in different geographic areas, but within a characteristic altitudinal range, and 3) regional distribution, i.e. widespread species. Similar analyses recently conducted by Santoul et al. (2004, 2005) in our study area showed that most fish followed a longitudinal zonation pattern (as defined above), whereas few species had a local distribution. We therefore used these works to select rare species as those species having a local distribution, i.e. having a restricted range sensu Cao et al. (2001) and Lennon et al. (2004). The detailed list of species involved in this study is given in Appendix 1.

Data analyses

The dependent variable used in our study (rare species) corresponds to count data. The analysis of this type of data is often problematic with usual ANOVA and standard regression methods due to the violation of the assumption of normally distributed errors of the dependent variable. However, General Linear Modelling (GLM) allows a more versatile analysis of correlation than standard regression methods, because the error distribution of the dependent variable and the function linking predictors to it can be adjusted to the characteristics of the data. For analysing rare species (Crawley 1993) we fitted models using a Poisson distribution and a log link function. River was included as a random factor in the model to control pseudoreplication due to the inclusion of more than one point from each river. To correct the possible effects of under- or overdispersion on statistical tests, deviances were scaled with the square root of the ratio deviance/degree of freedom (Anon. 2000). Data were analysed with the GLIMMIX macro for SAS 8.2 (Anon. 2000), fitting a mixed effects General Linear Model (river as a random variable and environmental variables as fixed variables). Main effects were fitted using type III tests and a stepwise backwards removal procedure was used to obtain a final model containing only significant factors.

Results

Among the 283 insect species, many species (44%) were rare. Their percentage of occurrence (number of sites where the species was recorded/number of sampled sites) was <5%. The numbers of rare species per insect order are given in Fig. 3. Rarity was the highest in Coleoptera (56%) and Trichoptera (59%), and the lowest in Plecoptera (16%). Ephemeroptera were intermediate, 41% of the mayfly species being rare. Among the 25 native fish species, 20% were rare (Fig. 3), and also occurred in <5% of the sampling sites. In subsequent analyses, we focused on local numbers of rare species.

The fish model explained 50% of the total variance in numbers of rare species, as estimated by the deviance of the final model (124.3) and that of the null model (250.7). Two typological variables were negatively correlated with local numbers of rare fish (Table 1): distance from the source ($p=0.01$) and elevation ($p<0.0001$). Conversely, stream order ($p<0.0001$) was positively correlated with numbers of rare species. Finally, slope was not significantly correlated with rarity.

For the Ephemeroptera model, only distance from the source was positively correlated with the numbers of rare species ($p=0.01$). Slope, elevation and stream order were not significantly correlated with rarity of Ephemeroptera. (Table 1). In Plecoptera, no significant variables allowed to build a model. For Trichoptera and Coleoptera, elevation was negatively correlated ($p=0.01$ and $p<0.0001$, respectively) with the number of rare species. Moreover, slope was positively correlated with rarity in Coleoptera ($p=0.04$).

In summary, GLM showed that the numbers of rare stream species would tend to increase towards downstream areas within the stream system.

Discussion

Considering rarity through the number of rare species rather than in terms of species assemblages sensu stricto is likely to fit with a broader typological approach, because the resulting patterns are not expected to be region-specific (i.e. any model only referring to a region-specific list of species is more prone to have local acceptance). Under this scope, and with the aim to

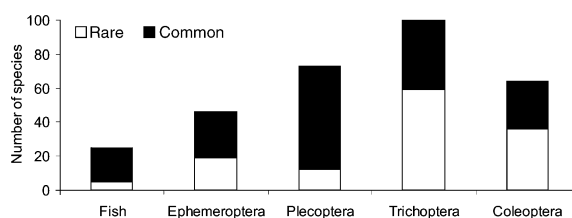


Fig. 3. Number of rare vs common species for each taxa (exotic fish species were not considered).

Table 1. Models analysing the distribution patterns of Fish (A), Ephemeroptera (B), Plecoptera (C), Trichoptera (D) and Coleoptera (E) at the stream system scale. Backwards models. Only variables with $p < 0.05$ are interpreted as statistically significant. For variables not included in the models no parameter estimate is presented and the F and p values correspond to the values when added to the final models. Deviance, and dispersion (ϕ = deviance/degree of freedom) of the final model are given for each animal group.

Effect	Estimate $\pm$ standard error	F	DF	p
A–Fish				
Intercept	-0.904 ± 0.811			
Slope		0.24	1.510	0.62
Distance source	-1.450 ± 0.582	6.19	1.511	0.01
Elevation	-0.014 ± 0.002	43.71	1.511	<0.0001
Stream order	0.765 ± 0.188	16.42	1.511	<0.0001
Deviance	124.31			
ϕ	0.69			
B–Ephemeroptera				
Intercept	-4.190 ± 0.549			
Slope		0.22	1.85	0.64
Distance source	1.985 ± 0.397	4.99	1.86	<0.0001
Elevation		0.10	1.85	0.76
Stream order		0.04	1.85	0.85
Deviance	52.23			
ϕ	0.47			
C–Plecoptera				
Intercept				
Slope		0.00	1.86	0.99
Distance source		0.62	1.86	0.43
Elevation		0.03	1.86	0.85
Stream order		0.05	1.86	0.82
D–Trichoptera				
Intercept	0.249 ± 0.315			
Slope		0.33	1.85	0.57
Distance source		0.31	1.85	0.58
Elevation	-0.0007 ± 0.0002	2.56	1.86	0.01
Stream order		0.29	1.85	0.59
Deviance	112.62			
ϕ	0.85			
E–Coleoptera				
Intercept	0.240 ± 0.399			
Slope	0.642 ± 0.301	2.13	1.85	0.04
Distance		0.00	1.84	0.98
Elevation	-0.0025 ± 0.0005	4.68	1.85	<0.0001
Stream order		3.11	1.84	0.08
Deviance	85.86			
ϕ	0.68			

address the first question of areas concentrating rare species, we provided models of longitudinal gradients in numbers of rare species. Rarity was related to the downstream location of sampling sites within the stream system: it primarily increased with distance from the source, or declined with elevation. In our study area, two recent works described the spatial distribution patterns of fish (Santoul et al. 2004, 2005) and aquatic insects (C  r  ghino et al. 2003) species richness, thus providing models which may help to highlight our own results. C  r  ghino et al. (2003) reported that EPTC richness peaked in the intermediate section of the downstream continuum of the Garonne stream system, i.e. at intermediate stream order (3rd and 4th) and intermediate elevations (500–1200 m). Therefore, common species

would create most of the spatial structure in richness patterns of EPTC. In fish, local species richness increased towards downstream areas, as a result of downstream additions of species (Santoul et al. 2004). Therefore, common and (to a lesser extent) rare species would both contribute to the spatial structure in richness patterns of fish.

The spatial patterns in rarity for the different study taxa were rather concordant. This pattern may result from: 1) random mechanisms, 2) biotic interactions among different taxa, 3) common environmental determinants, or 4) spatial covariance in different environmental factors that independently account for diversity variation in different taxa (Gaston 1996). If local systems were compared, it is likely that a high degree of concordance could be generated through biotic factors (Paszkowski and Tonn 2000). However, at broader spatial scales such as the Garonne stream system, congruent patterns of rarity between fish and aquatic insects orders are almost certainly a result of similar responses by different taxa to environmental conditions rather than to biotic interactions (Heino 2002). Nevertheless, the comparison of the results we obtained for the various taxonomic groups allows to refine and moderate the longitudinal gradient model of rarity. Rare fish, E, P, T, and C occurred in all sampled rivers. However, Plecoptera were mostly confined to the upper mountainous sections of the stream system (see also Cayrou et al. 2000). Their habitat range was thus lower than in other taxa, with regards to the environmental variables we considered. Consequently, if the longitudinal pattern is broadly acceptable, Plecoptera would not be relevant organisms for patterning rarity within large watersheds. The numbers of rare Coleoptera species followed a longitudinal gradient, but in addition, the significant relationship with slope suggested that local conditions (e.g. erosive forces generated through the combination of slope with other variables such as water depth and current velocity) have a greater importance when explaining rarity in this taxa. Fish rarity was negatively correlated with both distance from the source and elevation. Although these results seem contradictory, they suggest the importance of local conditions, especially when streams take their source at low elevations (i.e. in piedmont areas), and thus carry rare species at low distance from the source.

The second step of such studies, i.e. identifying the environmental variables which actually explain spatial variations in numbers of rare species remains a difficult task. Indeed, species' distribution is influenced by a large number of environmental factors, such as the geological history of the area, environmental stability (Ward and Stanford 1979), ecosystem productivity (Lavandier and D  camps 1984), habitat heterogeneity and suitability (Gorman and Kar 1978), and competition and predation (Pianka 1978). Moreover, these factors operate at several

spatial and temporal scales, e.g. geologic history affects the biogeography of species at a regional scale, whereas physical characteristics of microhabitats may influence local distributions (Hastie et al. 2000). By focusing on integrative variables (e.g. elevation, stream order), we emphasized the influence of river typology on the rarity of aquatic animals, with a marked concentration of rare species in large and high-ordered streams. This scheme remains likely to provide insights to both managers and ecologists, because the underlying local conditions which are associated to such global river typologies are well known (see e.g. the River Continuum Concept by Vannote et al. 1980). For example, the literature supports the idea that elevation influences the distribution of stream species through water temperature (Vannote and Sweeney 1980, Newbold et al. 1994), because temperature governs population dynamics through growth and fecundity (Gillet et al. 1995), by acting as a physicochemical habitat filter (sensu Poff 1997) with respect to species traits such as metabolism and energetic demands.

Most species in biological communities are rare (Lennon et al. 2004), and this is true of aquatic animal communities (Marchant et al. 1999). Rarity is sometimes omitted in ecological studies, because rare species are believed to contribute little to the interpretation of spatial and temporal patterns of biodiversity (Cao et al. 2001), and/or because they may add noise to statistical analyses (Cayrou et al. 2000). On the other hand, rare species are of special interest to both conservationists and environmental managers (Rey Benayas et al. 1999), whereas areas which carry rare species may concentrate an important fraction of the regional biodiversity (this study). If end-users need geographic models (i.e. maps) to design river management frameworks, numerical patterning is needed to provide theoretical backgrounds (Whittier et al. 1988): by predicting what the rarity should be like in a given area, we can provide explicit spatial schemes that may be useful to target further research, and to implement management options.

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Appendix 1. List of the rare species involved in this study.

Fish

Barbus meridionalis (Risso, 1826)
Rhodeus sericeus (Pallas, 1776)
Salaria fluviatilis (Asso, 1801)
Gasterosteus aculeatus Linnaeus, 1758
Pungitius pungitius (Linnaeus, 1758)

Ephemeroptera

Acentrella sinaica Bogoescu, 1931
Alainites albinatii Sartori & Thomas, 1989
Alainites muticus (Linnaeus, 1758)
Baetis pavidus Grandi, 1949
Caenis luctuosa (Bürmeister, 1839)
Caenis pusilla Navas, 1913
Choroterpes picteti (Eaton, 1871)
Cloeon dipterum (Linnaeus, 1761)
Ecdyonurus aurantiacus (Bürmeister, 1839)
Ecdyonurus insignis (Eaton, 1870)
Electrogena lateralis (Curtis, 1834)
Ephemera lineata Eaton, 1870
Ephoron virgo (Olivier, 1791)

Habroleptoides confusa Sartori & Jacob, 1986
Habrophlebia fusca (Curtis, 1834)
Nigrobaetis niger (Linnaeus, 1761)
Procloeon bifidum (Bengtsson, 1912)
Procloeon pennulatum (Eaton, 1870)
Rhithrogena germanica Eaton, 1885

Plecoptera

Brachyptera braueri (Klapalek, 1900)
Capnia bifrons (Newman, 1839)
Capnioneura mitis Despax, 1932
Dictyogenus imhoffi (Pictet, 1841)
Isoperla ambigua (Despax, 1936)
Leuctra albida Kempny, 1899
Leuctra flavomaculata Mosely, 1935
Leuctra major Brink, 1949
Nemoura linguata Navas, 1918
Nemoura marginata Pictet, 1835
Perla burmeisteriana Claassen, 1936
Taeniopteryx nebulosa (Linnaeus, 1758)

Trichoptera

Agapetus ochripes Curtis, 1834
Agraylea multipunctata Curtis, 1834
Allogamus ligonifer (McLachlan, 1876)
Allogamus uncatu (Brauer, 1857)
Apatania meridiana (McLachlan, 1880)
Apatania stylata Navas, 1916
Athripsodes albifrons (Linnaeus, 1758)
Beraea maura (Curtis, 1834)
Beraea pullata (Curtis, 1834)
Beraeodes minutus (Linnaeus, 1761)
Brachycentrus subnubilus Curtis, 1834
Ceraclea dissimilis (Stephens, 1836)
Chaetopteryx gonospina Marinkovic, 1966
Cheumatopsyche lepida (Pictet, 1834)
Crunoecia irrorata (Curtis, 1834)
Cyrnus trimaculatus (Curtis, 1834)
Drusus bolivari (McLachlan, 1880)
Ecnomus tenellus (Rambur, 1842)
Enoicyla pusilla (Burmeister, 1839)
Ernodes vicina (McLachlan, 1879)
Glossosoma boltoni Curtis, 1834
Glyptotaelius pellucidus (Retzius, 1783)
Goera pilosa (Fabricius, 1775)
Hydropsyche angustipennis (Pictet, 1834)
Hydropsyche siltalai Dohler, 1963
Hydroptila angulata Mosely, 1922
Hydroptila vectis Curtis, 1834
Ithytrichia lamellaris Eaton, 1873
Lepidostoma hirtum (Fabricius, 1775)
Limnephilus centralis Curtis, 1834
Limnephilus rhombicus (Linnaeus, 1758)
Limnephilus sparsus Curtis, 1834
Lithax obscurus (Hagen, 1859)
Lype reducta (Hagen, 1868)
Melampophylax mucoreus (Hagen, 1861)
Mystacides nigra Linnaeus, 1758
Oecetis testacea (Curtis, 1834)
Oxyethira falcata Morton, 1893
Plectrocnemia brevis McLachlan, 1871
Plectrocnemia conspersa (Curtis, 1834)
Plectrocnemia laetabilis (McLachlan, 1880)
Plectrocnemia scruposa (McLachlan, 1880)
Polycentropus kingi (McLachlan, 1881)
Potamophylax cingulatus (Stephens, 1837)
Potamophylax latipennis (Curtis, 1834)
Rhyacophila laevis Pictet, 1834
Rhyacophila nubila (Zetterstedt, 1840)
Rhyacophila obliterata (McLachlan, 1863)
Rhyacophila philopotamoides (McLachlan, 1879)

Rhyacophila rupta (McLachlan, 1879)
Sericostoma flavicorne Schneider, 1845
Setodes argentipunctellus (McLachlan, 1877)
Setodes viridis (Fourcroy, 1785)
Silo graellsii Pictet, 1865
Silo nigricornis (Pictet, 1834)
Tinodes assimilis (McLachlan, 1865)
Tinodes dives (Pictet, 1834)
Triaenodes bicolor Curtis, 1834
Wormaldia triangulifera (McLachlan, 1878)

Coleoptera

Dryops lutulentus (Erichson, 1847)
Elmis latreillei Bedel, 1878
Hydraena pulchella Germar, 1824
Haliphilus ruficollis (De Geer, 1774)
Hydraena angulosa Mulsant, 1844
Hydraena cordata Schaufuss, 1833
Hydrovatus simplex Sharp, 1880
Hygrotus inaequalis (Fabricius, 1777)
Hymenodes metallescens Rosenhauer, 1847
Laccophilus hyalinus (De Geer, 1774)
Limnebius nitidus (Marsham, 1802)
Peltodytes caesus (Duftschmid, 1805)
Scarodytes halensis (Fabricius, 1787)
Yola bicarinata (Latreille, 1804)
Brychius elevatus (Panzer, 1794)
Dryops viennensis (Castelnau, 1840)
Haliphilus fulvicollis Erichson, 1837
Hydroporus pubescens (Gyllenhal, 1808)
Limnius intermedius Fairmaire, 1881
Peltodytes rotundatus (Aubé, 1836)
Potamonectes griseostriatus (De Geer, 1774)
Agabus undulatus (Schrank, 1776)
Esolus parallelepipedus (Müller, 1806)
Hydraena pygmaea Waterhouse, 1833
Helodes marginata Fabricius, 1777
Hydrocyphon deflexicollis (Müller, 1821)
Enicocerus exscultus Stephens 1829
Hydraena nigrata Germar, 1824
Hydraena riparia Kugelann, 1794
Macronychus quadrituberculatus Müller, 1806
Eubria palustris Germar, 1818
Platambus maculatus (Linnaeus, 1758)
Limnius muelleri (Erichson, 1847)
Riolus illiesi Steffan, 1958
Orectochilus villosus (Müller, 1776)
Ochthebius dilatatus Stephens, 1829