Benthic insects and fish of the Doubs River system: typological traits and the development of a species continuum in a theoretically extrapolated watercourse

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Abstract

Using the distribution patterns of benthic insects (198 species) and fishes (29 species) from 11 tributaries and the main channel of the Doubs River drainage basin (French Jura), the authors have tried to establish whether there is an organization of species into discrete, identifiable communities. Principal Component Analysis (PCA) was used to identify whether a continuum existed, and also used to select 50 least-disturbed sites, which were used to define a theoretical watercourse. The density classes of each species were projected on this longitudinal gradient and each species response was characterised by two typological traits: its typological preferendum **(tp)** and its typological amplitude **(ta),** thus creating a synthesis of ecological characteristics. In the typological index given in the appendix, the 210 species which form a biological templet are listed in alphabetical order with their **tp** and **ta** values. These typological species traits are useful contributions to a database for running waters biomonitoring.

Introduction

The present work, dealing with typological and biological qualitative assessment of running waters, was developed following two observations.

Firstly, the accelerated transformation of running waters makes interpretation of contemporary biological data increasingly difficult. Various authors argue for the establishment of biological references in every drainage and geographical area (Verneaux, 1973; Fittkau & Reiss, 1983; Verneaux, 1984, 1994; Moss et al., 1987; Reynoldson et al., 1997, Mouthon, 1999). Norris & Thoms (1999) have argued that the 'poorer conditions are usually indicated by a loss of taxa', and that fish and benthic insects, especially Plecoptera, Ephemeroptera and Trichoptera, are frequently considered as suitable indicators. Using reference biological data and comparative analyses, temporal and spatial changes in biological structures can be evaluated.

Secondly, the observed succession of species along the downstream course of streams and rivers has long been recognised as a means of classifying watercourses (Shelford, 1911; Le Roi, 1913). Fish, different groups of invertebrates and algae, mosses and higher plants have all been used to identify longitudinal or altitudinal regions (zones) in riverine ecosystems although the validity of pre-established zones has been questioned (Macan, 1963; Hynes, 1970; Hawkes, 1975). It has been generally concluded that the general change in species communities along the rivers tends to be not zonation but transition. According to the River Continuum Concept, which includes more continuous than sectioned species distribution patterns (Maitland, 1966; Ulfstrand, 1968; Verneaux & Rezzouk, 1974; Vannote et al., 1980; Gendron & Laville, 1997), the running water ecosystem is viewed as an upstream-downstream gradient that can be modified by various ecological disturbances, of natural or anthropic origin, that induce discontinuit-

Table 1. The 12 studied rivers of the Doubs river system. 117 sampling sites - S = springs

Watercourse	River site (code)	Length (km)	Altitude (m)	Drainage area (km^2)
Doubs	S 1–29	453	940–172	7700
Drugeon	S30–35	33	930–805	185
Dessoubre	S36–40	29	600–387	560
Allaine	S41–48	34	605–350	230
Audeux	S49–53	25	560–280	230
Cusancin	S54–57	9	325–280	360
Loue	S58–74	122	543–197	1900
Lison	S75–79	25	410–293	290
Furieuse	S80–88	18	575–251	100
Cuisance	S89–96	34	375–205	180
Doulonnes	S97–99	7	254–210	20
Clauge	S100–105	29	260–195	135

ies (Verneaux, 1973; Chessel et al., 1987; Angelier, 2000). Even though it may appear that species arrange themselves in discrete communities, it is considered that conditions and communities vary gradually along a theoretical watercourse or along a model watercourse, without discontinuities.

Based on the species recorded at the selected reference sites along the Doubs River and its tributaries, the above observations allowed us to establish whether there was some predictable organization in the species found. In order to establish a database which can be useful for comparative analysis, this study presents: a general biological structure in the form of a species continuum, a theoretical running watercourse, composed of reference sampling sites from different rivers, and two typological species traits used to establish a general distribution pattern of species.

Sampling sites

The Doubs river and its 11 tributaries form a 832 km-long network which extends from the Saône river plain to the Swiss mountains, in a 7700 km^2 drainage basin that overlaps the northern Jura and the southern Vosges mountains (Fig. 1).

The hydrologic conditions in the basin are the result of the alternating permeable and impermeable Jurassic strata and many karstic structures. Except for some true springs, most springs are karstic outlets.

Climatic conditions are mostly continental, somewhat influenced by oceanic inputs, altitude, orientation and morphological characteristics of the valleys. The river flow shows torrential characteristics and the

general temperature pattern of the water reaches maximum values in the months of July and August during the low-water period . Detailed descriptions of the geographical area and the various rivers were given previously (Verneaux, 1973) and we have cited here only main characteristics of the rivers and the code of the sampling sites (Table 1).

Data and methodology

The data of the water survey, periodically published by the Environment Boards, describe a deterioration in the water quality of the Doubs River system during recent decades (Agence de l'Eau, 1996, 1999). This disturbance was especially obvious in the salmonid rivers which were in good condition in the 1970s (Verneaux, 1973). The disappearance of many species (Bacchi, 1994) led to the scarcity of reference sites with biotic indices equal to or above 18/20 (IBGN, AFNOR, 1992; Observatoire Régional de l'Environnement, 1995). Because of this general change and given our aim which implies recourse to reference sites, the field data collected from 1970 to 1976 were selected for study. A major part of the same data was recently used by Doledec et al. (2000) to describe the functional diversity of communities in terms of their biological traits. These data have been updated to include recent taxonomic changes.

The initial density matrix is composed of 227 rows (198 species of aquatic Insecta including 43 Plecoptera, 46 Ephemeroptera, 109 Trichoptera, 28 species of fish and one Cyclostoma) and 117 columns (117 sampling sites from the Doubs river and 11 tributaries, Fig. 1). Species densities were weighted using five classes of relative density. These classes were adapted to the highest values observed in the sample for each genus of invertebrates and for each species of fish (Verneaux, 1973). This weighted method, which highlights structures using factorial analyses, has been justified by other authors (Chessel et al., 1987). Of the sites differentiated by factorial analysis, only the sites which had a biotic index (IBG Verneaux, 1982; IBGN AFNOR, 1992) above or equal to 18/20 were considered as non-or slightly disturbed from 1970 to 1976 and were thus selected as reference sites. These sites had the highest relative species richness along the entire upstream-downstream (U-D) gradient. All the species included in the matrix were present in the sample of the reference sites.
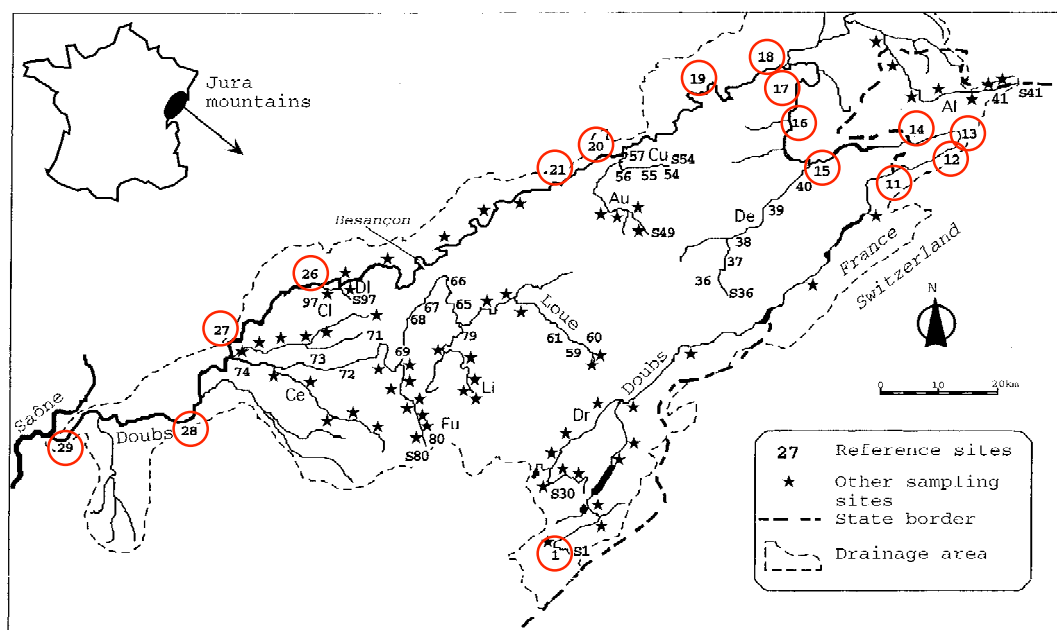
Figure 1. The drainage area of the Doubs river system – distribution of the 117 sampling sites. Aℓ: Allaine, Au: Audeux, Ce: Cuisance, Cℓ: Clauge, Cu: Cusancin, De: Dessoubre, Dℓ: Doulonnes, Dr: Drugeon, Fu: Furieuse, Li: Lison.

To take into account the density differences (Jackson, 1973), the weighted data were analysed by Principal Component Analysis (PCA) applied to the covariance matrix using ADE 4 software (Thioulouze et al., 1997).

The environmental parameters were not taken into account in establishing an environmental gradient, so that preconceptions about their effects on biological distributions could be avoided. The theoretical upstream-downstream gradient represented by a succession of reference sites, was determined only by using the biological data. Following the same principle, Mouthon (1999) divided the longitudinal gradient according to the groups of river sites which were defined using a hierarchical ascending classification (HAC). In the present study, the distances between reference sampling sites were evaluated by their angular distances, which provides a valid solution when PCA is used (Legendre & Legendre, 1984). The angles were measured from the radius joining the center of the axes to the virtual spring given by the species richness curve (Fig. 2).

The establishment of typological descriptors was based on the unimodal pattern in species response (variation in density or occurrence) to progressive change in environmental conditions (Ter braak & Verdonschot, 1995). The typological characteristics of species were therefore defined using the projection of their density classes on the theoretical U-D gradient.

Two descriptors were used to summarize the distribution of each species on the gradient: its mean position, or preferendum **(tp)** and its typological amplitude **(ta)**. In agreement with Chevenet et al. (1994) and Mouthon (1999), we chose the mean point of abundance rather than the point of maximum abundance. Thus, the specified **ta** values are equal to half the difference between the limits of the abundance distribution of each species and the **tp** values refer to the centers of gravity of the same abundance distributions (Fig. 4).

Results

Reference river sites and virtual watercourse

The sites situated in peripheral positions in the plane of a PCA (Fig. 2) make high relative contributions to the axes, and from these, 50 reference sites were selected according to their biogenic values (IBGN $\geq$ 18 and maximum relative species richness). These sites were plotted close to the curve drawn from the springs (upstream U) to the low courses (downstream D). This U-D structure represents, using PCA, a theoret-
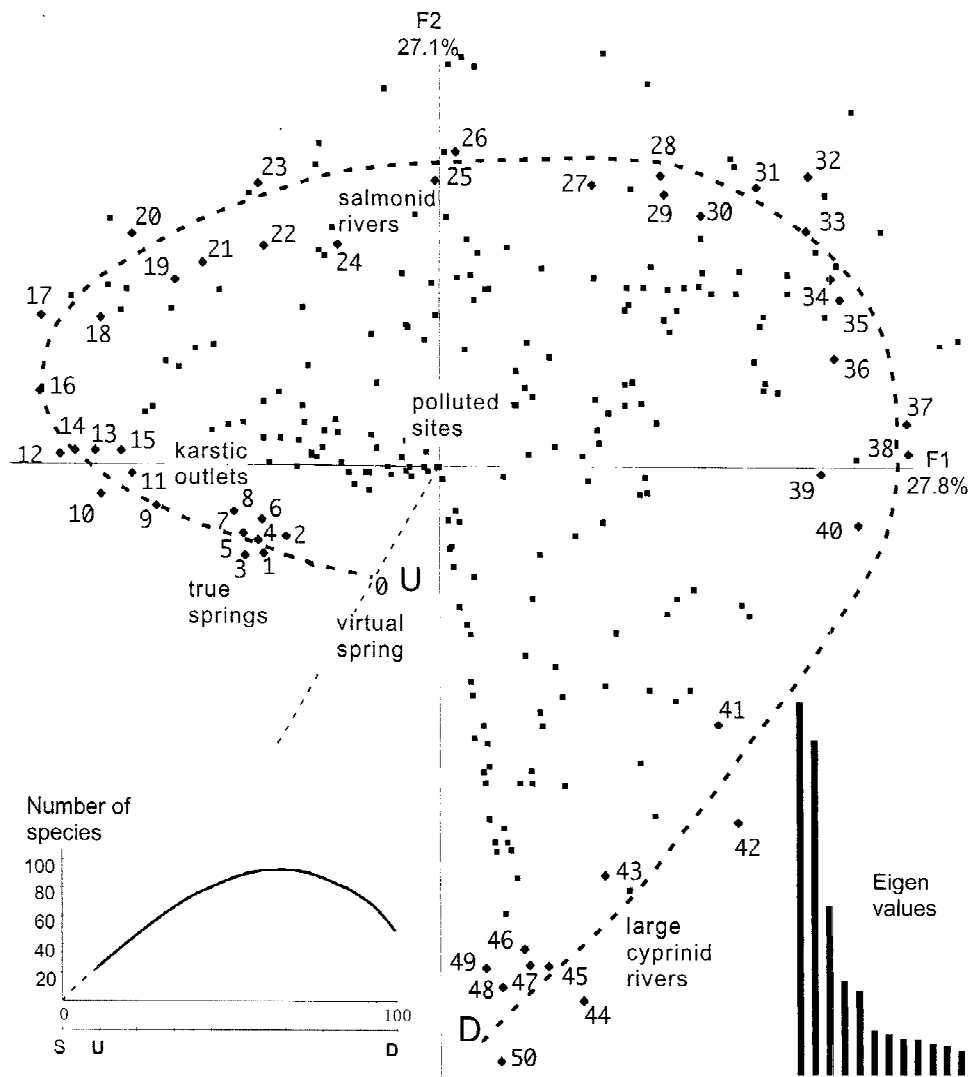
Figure 2. Ordination of the 117 sampling sites by PCA. Structural curve in the F1–F2 plane and variations of the species richness along the U-D gradient. The reference sites were numbered from 1 to 50.

ical watercourse and the sites appear in the following order:

– the true springs and brooks of the Rivers Allaine, Drugeon, Doulonnes and Furieuse (Fig. 2, sites 1–8),

– the karstic outlets and brooks of the Rivers Doubs, Dessoubre and Cusancin (Fig. 2, sites 9–14),

– the upper course of the River Loue and the lower courses of the Rivers Cusancin, Lison and Dessoubre (Fig. 2, sites 15–26),

– the middle course of the Doubs and the lower course of the Loue (Fig. 2, sites 27–41),

– the lower course of the Doubs (Fig. 2, sites 42 to 50).

The codes used on the map (Fig. 1) and the location of the sites on the longitudinal gradient are referenced in Table 2.

Species continuum and typological traits

The distribution of the 50 reference sites in the factorial plane (Fig. 2) and the correlation circle (Fig. 3) show that the succession of sites and species follows a U-D gradient similar to that presented by Aart (1973) in the plane of the first two principal components

Table 2. References of the site coding (Fig. 1) and location (gradient order) of the 50 reference sites on the upstream-downstream gradient (Fig. 2)

River sites (Fig. 2)	Code on the map (Fig. 1)	Gradient order	River sites (Fig. 2)	Code on the map (Fig. 1)	Gradient order
1	S 41	0.90	26	39	4.19
2	S 30	1.00	27	11	4.83
3	S 97	1.02	28	12	5.13
4	S 80	1.10	29	13	5.19
5	97	1.12	30	14	5.44
6	30	1.16	31	15	5.56
7	41	1.38	32	65	5.70
8	80	1.50	33	67	5.83
9	51	1.55	34	69	5.97
10	1	1.56	35	66	6.11
11	S 36	1.64	36	71	6.25
12	S 54	1.72	37	72	6.50
13	54	1.73	38	68	6.61
14	36	1.75	39	73	6.74
15	59	1.77	40	74	6.90
16	56	1.91	41	16	7.80
17	55	2.27	42	17	8.10
18	60	2.36	43	43	8.40
19	61	2.47	44	18	8.70
20	57	2.47	45	20	8.71
21	79	2.61	46	21	8.76
22	37	3.05	47	27	8.82
23	38	3.25	48	26	9.00
24	62	3.40	49	78	9.12
25	40	4.13	50	29	9.20

for a ground-vegetation circular gradient. The species follow one another from *Rhadicoleptus spinifer* to *Scardinius erythrophtalmus* (Fig. 3).

This circular U-D gradient was then adapted to a horizontal axis with a 0–10 scale, taking care that the intersite distances remained proportional to their angular distance on the PCA map. Thus each species was characterised by two typological traits: its typological preferendum **(tp)** and its typological amplitude **(ta)** (Fig. 4).

A projection of the density classes on the U-D gradient produced four different patterns (Fig. 4). *Crunoecia irrorata* (Trichoptera Limnephilidae) for example, has a distribution pattern which characterises species plotted at either end of the gradient. These species may be found either in springs and brooks, e.g. *Crunoecia irrorata*, or in slow-flowing and warmer rivers, e.g. *Scardinius erythrophtalmus*. The distribution pattern of *Ecdyonurus dispar* (Eph-

emeroptera, Heptageniidae) resembles a normal curve with a small amplitude (**ta** ≈ 30% of the scale). This pattern characterises indicator species which are typologically highly informative. The normal curve of *Baetis rhodani* is truncated downstream (**ta** ≈ 90% of the scale) and indicates that the species could also develop in large rivers. Species like *Limnephilus flavicornis*, that show a fuzzy response to the gradient, give little typological information. These results justify the elimination of two kinds of species from the biological templet: those with very low occurrence e.g. Plecoptera Perloidea, and those, e.g. *Limnephilus flavicornis*, with poorly differentiated patterns of distribution along the U-D gradient (Table 3). These species contribute little to the axes and are plotted near the center or far from the U-D curve structure. Of the species which are far from the structural curve, several belong to the genus *Limnephilus*. They are related more to a particular habitat (slow-flowing water) than
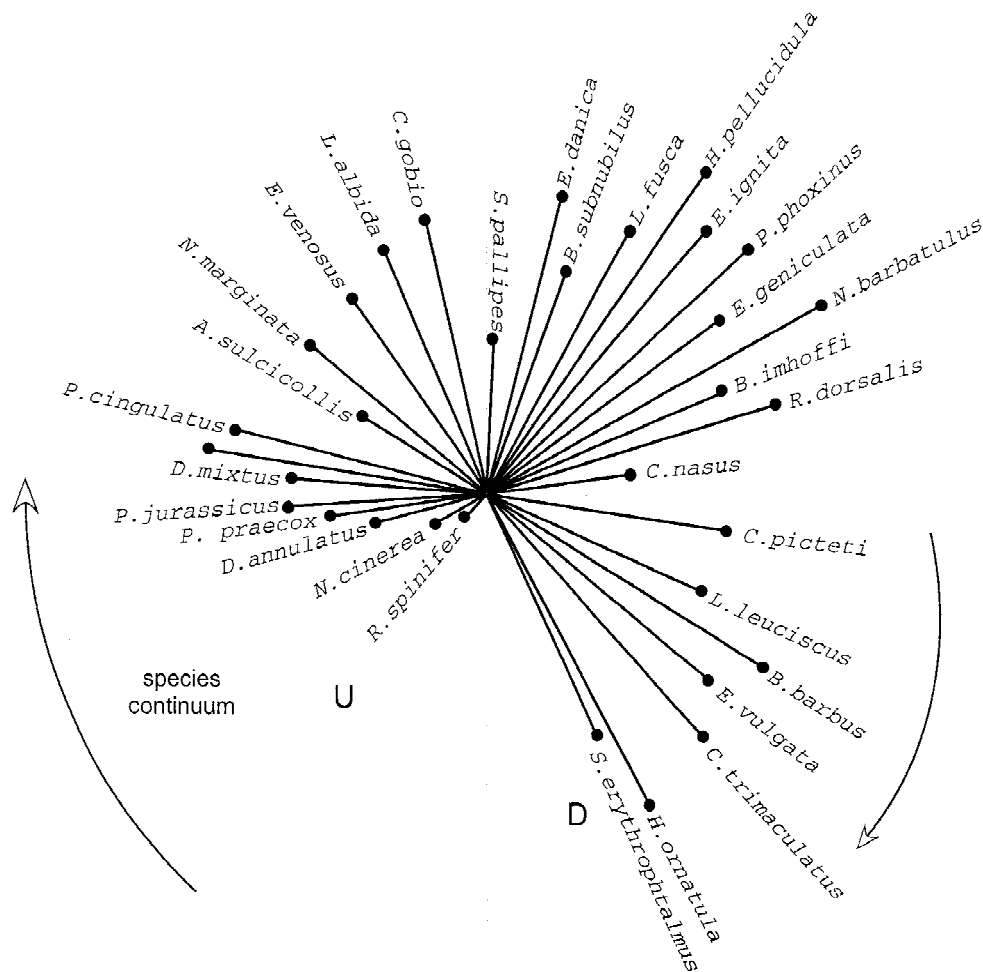
Figure 3. Correlation circle showing the species continuum from U to D. For practical reasons only a small number of species is plotted on the graph. U: upstream, D: downstream.

to a general type of water site (Verneaux, 1973). The same seems to be true for the Siphlonuridae (Ephemeroptera) and for the xylophageous species belonging to the genus *Lype* (Trichoptera). The species listed in Table 3 were not included in the species continuum.

An abbreviated version of the species continuum is presented in Figure 5 in which the species, with the limits of their typological amplitude, are classified according to their increasing typological preferendum (**tp**). Of the species studied, only 20% show a typological amplitude (**ta**) smaller than 20% of the U-D gradient so that a great number of species distributions largely overlaps (Fig. 5). The species with the narrowest typological amplitude are found mostly at both ends of the U-D gradient. In the typological index, given in the appendix, each species is listed with its

two typological traits. The typological amplitude (**ta**) is equal to half the difference between the distribution limits.

Discussion

The proposed species continuum summarises the species successions observed along various watercourses. The biological organization of a theoretical running water system takes the form of a continuum of species which replace one another along an upstream-downstream gradient. In this study, any given river site community is viewed as an arrangement of species with different preferenda, amplitudes and densities. Any species combination is *a priori* considered possible, especially when accounting for anthropo-
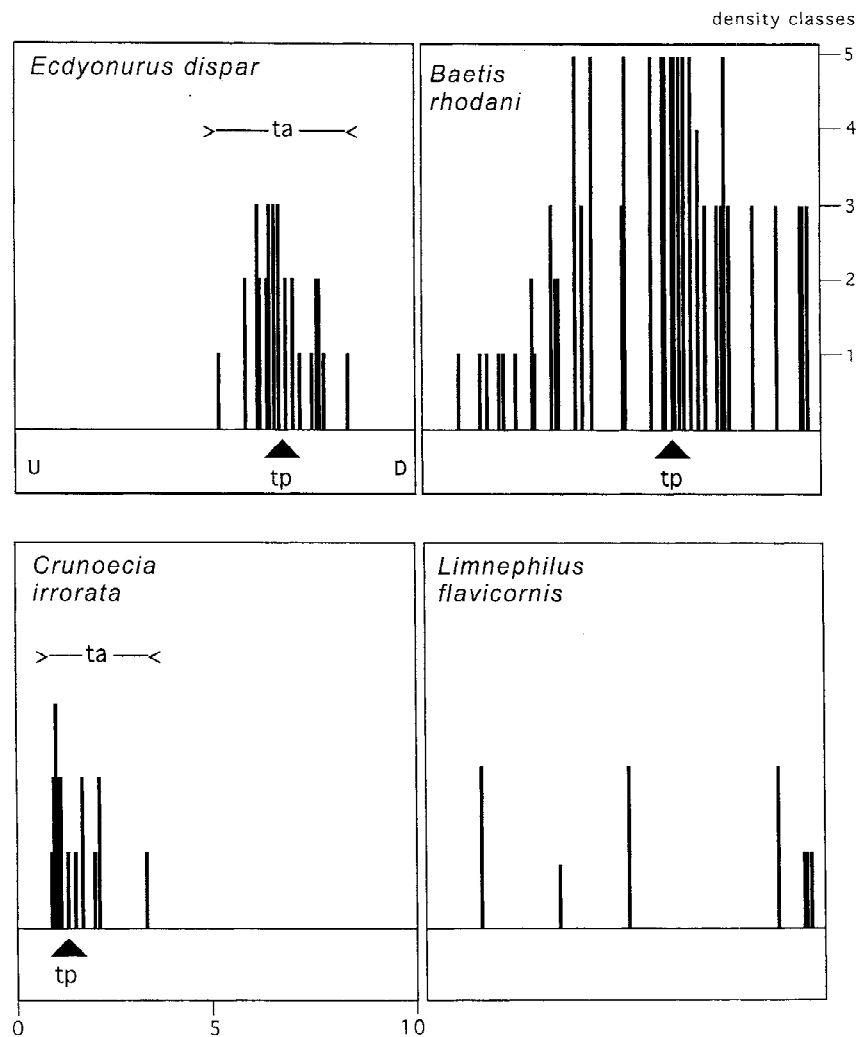
Figure 4. Invertebrate abundance patterns along the U-Dgradient. **tp:** typological preferendum (mean point of abundance), **ta:** typological amplitude.

genic inputs. However, it is always possible to split up the species continuum into ecological groups of species separated by statistical discontinuities. The classical succession Crenon-Rhithron-Potamon, (Illies & Botosaneanu, 1963) widely reported in the literature, can be plotted on the continuum but it must then be stipulated that different species combinations may be found at the same typological level. The ecological groups of species which can be defined by their typological traits (Fig. 5) are revised versions of the previously proposed 'biocenotypes' (Verneaux, 1976 a, b). Thus, the longitudinal distribution of aquatic species is generally given using approximate evaluations of occurrence or abundance in 7, 8 or 9 'zones'

(Bournaud et al., 1992; Chevenet et al., 1994; Moog et al., 1995). According to Hynes (1970), the distinctions between biological 'zones' may be valid 'in a general sense'. This generalization is produced in a virtual space: along a theoretical U-D species continuum, but the number and the placement of zones along a particular watercourse depend on the local peculiarities or disturbances encountered.

Considering that the proposed typological traits are in agreement with the ecological valency (typological amplitude) and the ecological affinity (typological preferendum) of species, these descriptors give synthetized ecological information which can be added to
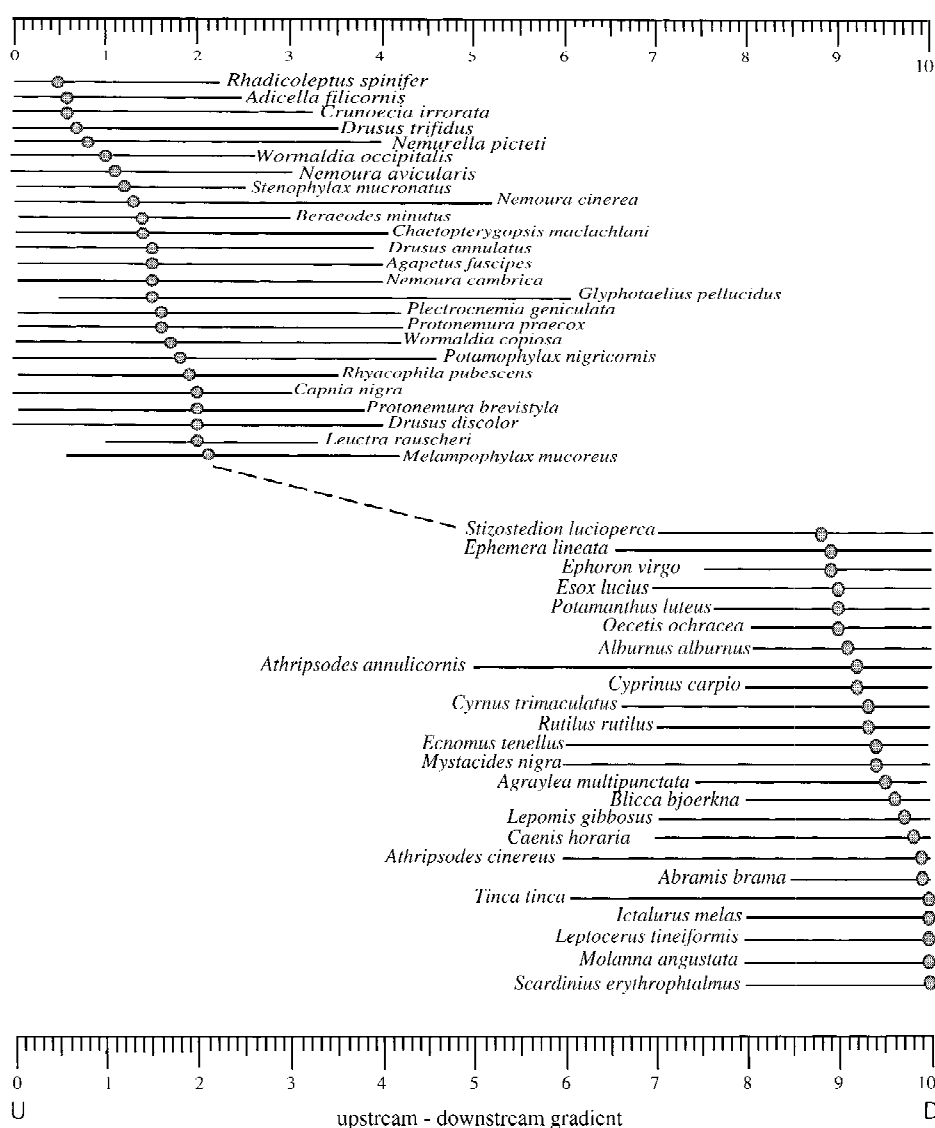
Figure 5. The species continuum of the Doubs river system. Species of insects and fishes are arranged according to their **tp** and **ta** values. o: typological preferendum, ——: typological amplitude.

biological species traits (Charvet et al., 1998; Doledec et al., 2000) in a database for running waters studies.

Even though the proposed species pattern was initially used for the peri-alpine area, the wide bio-geographical distribution of many species inventorised makes the Doubs pattern a suitable framework which can be expanded to include cool-temperate Middle Europe. In this area the specified species accounted for 25–50% of the species potential and, near the limits, especially southwards, only 10–40% of them disappeared. The Mollusc communities of the refer-

ence sites are presently being analysed. Because of the common set of species found in Middle Europe, other groups of animals accruing from other drainage areas can be included in the templet. Accurate studies, such as those by Vinçon & Ravizza (2001) and Sipahiler (2000) underline the importance of endemism and argue for a regional adjustment of the reference species organizations.Studies, such as the one by Cayrou et al. (2000) on the macrobenthos of the Adour-Garonne drainage basin (France) are very useful for enlar-

Table 3. List of the 17 species with low occurrence in the sample, or with fuzzy distribution on the U-D gradient. ctr 1–2 = contributions to the 1–2 axes of the PCA

	Occ (%)	Ctr 1+2 (%)		Occ (%)	Ctr 1+2 (%)
Plecoptera			Ephemeroptera		
Dictyogenus alpinus	4	0.7	*Leptophlebia marginata*	7	0.0
Perla maxima	6	1.7	*Siphlonurus aestivalis*	41	1.9
			Siphlonurus lacustris	18	1.5
Trichoptera			Trichoptera		
Grammotaulius atomarius	7	0.4	*Limnephilus lunatus*	12	0.6
Holocentropus dubius	13	0.1	*Limnephilus politus*	6	0.2
Ironoquia dubia	5	0.3	*Limnephilus rhombicus*	9	0.4
Limnephilus centralis	4	0.2	*Lype reducta*	4	0.1
Limnephilus decipiens	3	0.1	*Sericostoma pedemontanum*	5	0.0
Limnephilus flavicornis	24	1.5	*Tinodes pallidulus*	5	0.0

ging the reference structure and extending its field of application.

References

Aart Van der, P. J. M., 1973. Distribution analysis of wolfspiders (Aracae Lycosidae) in a dune area by means of principal component analysis. Neth. J. aquat. Zool. 23: 266–329.

AFNOR, 1992. Essais des Eaux. Détermination de l'indice biologique global normalisé (IBGN). NFT 90–350. AFNOR, Paris. 9 p.

Agence de l'Eau Rhône, Méditerranée, Corse, 1996. Carte de la Qualité des cours d'eau. Synthèse des données acquises de 1988 à 1994.

Agence de l'Eau Rhône, Méditerranée, Corse, 1999. Réseau National de Bassin - Qualité des cours d'eau - Résultats 1997, 76 p.

Angelier, E., 2000. Ecologie des eaux courantes. Tec. & Doc., Paris: 199 pp.

Bacchi, M., 1994. Recherches sur la macrofaune benthique de la Haute Loue. Evolution des peuplements depuis 1973. Mém. DESS Eaux Continentales, Univ. Fr. Comté, Besançon. 41 p et annexes.

Bournaud, M., P. Richoux & P. Usseglio-Polatera, 1992. An approach to the synthesis of qualitative ecological information issued from aquatic Coleoptera communities. Regul. Rivers 7: 165–180.

Cayrou, J., A. Compin, N. Giani & R. Céréghino, 2000. Associations spécifiques chez les macroinvertébrés benthiques et leur utilisation pour la typologie des cours d'eau. Cas du réseau hydrographique Adour-Garonne (France). Ann. Limnol. 36 (3): 189–202.

Charvet, S., A. Kosmala & B. Statzner, 1998. Biomonitoring through biological traits of benthic macroinvertebrates: perspectives for a general tool in stream management. Arch. Hydrobiol. 142 (4): 415–432.

Chessel, D, J. D. Lebreton & N. Yoccoz, 1987. Propriétés de l'analyse canonique des correspondances; une illustration en hydrobiologie. Rev. Stat. Appl. 35: 55–72.

Chevenet, F., S. Doledec & D. Chessel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. Freshwat. Biol. 31: 295–309.

Doledec, S., J. M. Olivier & B. Statzner, 2000. Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effects of taxonomic and spatial resolution. Arch. Hydrobiol. 148 (1): 25–43.

Fittkau, E. J. & F. Reiss, 1983. Versuch einer Rekonstruktion der Fauna europäischer Ströme und ihrer Auen. Arch. Hydrobiol. 97: 1–6.

Gendron, J. M. & H. Laville, 1997. Les Chironomidés (Diptera) de l'Aude, rivière méditerranéenne des Pyrénées orientales: étude biocénotique et typologique. Ann. Limnol. 33: 93–106.

Hawkes, H. A., 1975. River zonation and classification. In Whitton, B. A. (ed.), River Ecology. Studies in Ecology, Blackwell Scientific Publication, Oxford: 312–374.

Hynes, H. B. N., 1970. The Ecology of Running Waters. Liverpool University Press: 555 pp.

Illies, J. & L. Botosaneanu, 1963. Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. Mitt. int. Ver. Limnol. 12: 1–57.

Jackson, D. A., 1973. Multivariate analysis of benthic invertebrate communities: the implication of choosing particular data standardization, measure of association and ordination methods. Hydrobiologia 268: 9–26.

Legendre, L. & P. Legendre, 1984. Ecologie numérique. 2. La structure des données écologiques. Masson, Paris: 335 pp.

Le Roi, O., 1913. Zur Kenntnis der Plecopteren von Rheinland-Westfalen. Sber. naturh. Ver. preuss. Rheinl. Westf: 25–51.

Macan, T. T., 1963. Freshwater Ecology. Longmans, London: 358 pp.

Maitland, P. S., 1966. Studies on Loch Lomond. II – The Fauna of the River Endrick. Backie & Son, Glasgow: 194 pp.

Moog, O. & coll., 1995 Fauna Aquatica Austriaca. A Comprehensive Species Inventory of Austrian Aquatic Organisms with Ecological Notes. Bundesministerium für Land und Forstwirtschaft-Wasserwirtschaftskataster, Wien: 195 pp.

Moss, D., M. T. Furse, J. F. Wright & P. D. Armitage, 1987. The prediction of the macroinvertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshwat. Biol. 17: 41–52.

Mouthon, J., 1999. Longitudinal organisation of the mollusc species in a theoretical French river. Hydrobiologia 90: 117–128.

Norris, R. H. & M. C. Thoms, 1999. What is river health? Freshwat. Biol. 41: 197–209.

Observatoire Régional de l'Environnement de Franche-Comté. 1995. Qualité des eaux superficielles. 7 p.

Reynoldson, T. B., R. H. Norris, V. H. Resh, D. E. Day & D. Rosenberg, 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water quality impairment using benthic macroinvertebrates. J. n. am. Benthol. Soc. 16: 833–852.

Shelford, V. E., 1911. Ecological succession. I. Stream fishes and the method of physiographic analysis. Biol. Bull. mar. biol. Lab. Woods Hole 21: 9–35.

Sipahiler, F., 2000. New Ryacophila (Trichoptera Rhyacophilidae) species from France and Spain. Aquatic Insects 22: 138–147.

Ter braak, C. F. J. & P. F. M. Verdonschot, 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat. Sci. 7: 255–289.

Thioulouse, J., D. Chessel, S. Doledec & J. M. Olivier, 1997. ADE4: a multivariate analysis and graphical display software. Stat. Computing 7: 75–83.

Ulfstrand, S., 1968. Benthic animal communities in Lapland streams. Oikos, suppl. 10: 1–120.

Vannote, R. L., G. W. Minshall, K. W. Cummins, S. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Can. J. Fish. aquat. Sci. 37: 130–137.

Verneaux, J., 1973. Cours d'eau de Franche-Comté (massif du Jura). Recherches écologiques sur le réseau Hydrographique du Doubs – essai de biotypologie. Ann. Scient. Univ. Fr. Comté, Biol. Anim. 3 (9): 1–260.

Verneaux, J. & M. Rezzouk, 1974. Les structures d'un grand cours d'eau à Salmonidés: la Loue (Massif du Jura) - Essai typologique et problèmes des relations entre espèces et milieu. Ann. Limnol.10 (2): 131–162.

Verneaux, J., 1976a. Biotypologie de l'écosystème 'eau courante'. La structure biotypologique. C.R. Acad. Sc. Paris 283: 1663–1666.

Verneaux, J., 1976b. Biotypologie de l'écosystème 'eau courante'. Les groupements socio-écologiques. C.R. Acad. Sc. Paris 283: 1791–1793.

Verneaux, J., 1982. Une nouvelle méthode pratique d'évaluation de la qualité des eaux courantes. Un indice biologique de qualité générale (I.B.G.). Ann. Scient. Univ. Fr. Comté, Biol. Anim. 4 (3): 11–21.

Verneaux, J., 1984. Méthodes biologiques et problèmes de la détermination des qualités des eaux courantes. Bull. Ecol. 15 (1): 47–55.

Verneaux, J., 1994. Le macrobenthos et 'l'état de santé' des eaux douces. Fondements contraintes et perspectives: 215–227. In Etat de Santé des Écosystèmes Aquatiques. Les Variables Biologiques Comme Indicateurs. Actes du séminaire national Hydrosystèmes. Cemagref, Paris: 298 pp.

Vinçon, G. & C. Ravizza, 2001. Leuctridae (Plecoptera) of the Pyrénées. Ann. Limnol. 37 (4): 293–322.

Appendix 1 - Typological index: list of the 210 species which compose the reference 'species continuum' of the Doubs river system. The two typological traits are indicated for each species: the typological preferendum (**tp**) and the typological amplitude (**ta**)

Species	Typological preferendum	Typological amplitude limits		
	tp	Min	Max	**ta**
Abramis brama Linné	9.9	8.5	10.0	0.7
Adicella filicornis Pictet	0.5	0.0	2.5	1.2
Agapetus delicatulus Mc Lachlan	6.3	4.2	7.3	1.5
Agapetus fuscipes Curtis	1.5	0.0	4.0	2.0
Agapetus ochripes Curtis	5.4	3.8	6.9	1.5
Agraylea multipunctata Curtis	9.5	7.4	10.0	1.3
Alainites muticus Linné	4.2	1.5	7.60	3.0
Alburnoides bipunctatus Bloch	7.5	6.5	9.00	1.2
Alburnus alburnus Linné	9.1	8.0	10.0	1.0
Allogamus auricollis Pictet	4.6	2.8	7.0	2.1
Amphinemura sulcicollis Stephens	2.5	0.0	6.1	3.0
Amphinemura triangularis Ris	3.3	0.0	6.4	3.2
Anabolia nervosa Curtis	4.9	0.8	8.7	3.9
Athripsodes albifrons Linné	7.1	4.0	10.0	3.0
Athripsodes aterrimus Stephens	8.2	4.0	10.0	3.0
Athripsodes bilineatus Linné	7.2	5.0	10.0	2.5
Athripsodes cinereus Curtis	9.9	6.0	10.0	2.0
Baetis alpinus Pictet	2.9	1.8	5.6	1.9
Baetis buceratus Eaton	7.6	4.0	9.0	2.5
Baetis fuscatus Linné	6.6	4.2	8.3	2.0
Baetis lutheri Müller-Liebenau	5.4	3.5	7.5	2.0
Baetis rhodani Pictet	6.0	0.0	9.0	4.5
Baetis scambus Eaton	5.0	1.0	8.5	3.7
Barbus barbus Linné	7.6	5.5	8.4	1.4
Beraeodes minutus Linné	1.4	0.0	3.0	1.5
Besdolus imhoffi Pictet	6.6	5.0	7.3	1.1
Blicca bjoerkna Linné	9.6	8.0	10.0	1.0
Brachycentrus montanus Klapalek	3.4	2.4	5.5	1.5
Brachycentrus subnubilus Curtis	5.5	4.0	7.0	1.5
Brachyptera risi Morton	4.1	1.5	7.0	2.7
Caenis horaria Linné	9.8	7.0	10.0	1.5
Caenis luctuosa Burmeister	7.4	5.6	10.0	2.2
Caenis rivulorum Eaton	6.3	3.4	9.1	2.8
Capnia bifrons Newman	3.0	1.0	4.0	1.5
Capnia nigra Pictet	2.0	0.0	3.0	1.5
Centroptilum luteolum Müller	5.5	2.1	8.5	3.2
Ceraclea alboguttata Hagen	8.6	6.0	10.0	2.0
Ceraclea annulicornis Stephens	9.2	5.0	10.0	2.5
Ceraclea dissimilis Stephens	7.7	6.0	10.0	2.0
Chaetopterygopsis maclachlani Stein	1.4	0.0	4.0	2.0
Chaetopteryx villosa Fabricius	3.8	1.5	7.9	3.2
Cheumatopsyche lepida Pictet	6.3	4.2	7.0	1.4
Chimarra marginata Linné	6.1	4.0	8.0	2.0
Chloroperla tripunctata Scopoli	6.5	4.0	8.0	2.0
Chondrostoma nasus Linné	7.0	6.0	9.0	1.5
Chondrostoma toxostoma Vallot	7.0	6.0	9.0	1.5
Choroterpes picteti Eaton	7.4	6.0	8.5	1.2
Cloeon dipterum Linné	8.3	4.0	10.0	3.0
Cloeon simile Eaton	7.0	3.2	8.5	2.6
Cottus gobio Linné	3.5	1.0	6.0	2.5
Crunoecia irrorata Curtis	0.5	0.0	3.2	1.6
Cyprinus carpio Linné	9.2	8.0	10.0	1.0

Appendix 1 contd.

Cyrnus flavidus Mc Lachlan	7.5	4.6	10.0	2.7
Cyrnus trimaculatus Curtis	9.3	6.6	10.0	1.7
Dinocras cephalotes Curtis	3.2	2.2	5.0	1.4
Dinocras megacephala Klapalek	5.0	3.5	7.0	1.7
Drusus annulatus Stephens	1.5	0.0	3.9	1.9
Drusus discolor Rambur	2.0	0.0	4.0	2.0
Drusus mixtus Pictet	2.5	2.0	5.2	1.6
Drusus trifidus Mc Lachlan	0.7	0.0	3.5	1.7
Ecclisopteryx guttulata Pictet	3.5	0.7	6.2	2.7
Ecdyonurus aurantiacus Kimmins	6.5	4.0	7.5	1.7
Ecdyonurus dispar Curtis	5.5	3.4	7.3	1.9
Ecdyonurus insignis Eaton	7.3	5.2	8.5	1.6
Ecdyonurus macani Thomas & Sowa	4.5	3.0	6.3	1.6
Ecdyonurus picteti Meyer-Dür	3.0	1.0	4.5	1.7
Ecdyonurus submontanus Landa	3.5	1.0	5.0	2.0
Ecdyonurus torrentis Kimmins	3.7	1.9	5.2	1.6
Ecdyonurus venosus Fabricius	3.9	3.0	6.0	1.5
Ecnomus tenellus Rambur	9.4	6.0	10.0	2.0
Electrogena lateralis Curtis	5.7	3.5	7.2	1.8
Epeorus assimilis Eaton	4.5	2.5	6.5	2.0
Ephemera danica Müller	5.0	1.5	7.0	2.7
Ephemera lineata Eaton	8.9	6.5	10.0	1.7
Ephemera vulgata Linné	8.0	6.5	10.0	1.7
Ephoron virgo Olivier	8.9	7.5	10.0	1.2
Esox lucius Linné	9.0	7.0	10.0	1.5
Euleuctra geniculata Stephens	6.6	5.6	9.0	1.7
Glossosoma bifidum Mc Lachlan	2.8	2.5	5.5	1.5
Glossosoma conformis Neboiss	4.0	3.0	7.0	2.0
Glyphotaelius pellucidus Retzius	1.5	0.5	6.0	2.7
Gobio gobio Linné	7.7	6.0	9.5	1.7
Goera pilosa Fabricius	6.1	4.6	7.8	1.6
Gymnocephalus cernuus Linné	8.4	7.0	10.0	1.5
Habroleptoides confusa Sartori & Jacob	4.4	0.0	7.0	3.5
Habrophlebia fusca Curtis	3.5	0.0	7.0	3.5
Habrophlebia lauta Eaton	5.5	3.0	8.0	2.5
Halesus digitatus Schrank	4.8	2.5	7.0	2.2
Halesus radiatus Curtis	4.5	2.0	7.0	2.5
Halesus tesselatus Rambur	6.6	3.0	7.6	2.3
Heptagenia sulphurea Müller	7.8	6.0	9.0	1.5
Hydatophylax infumatus McLachlan	4.3	3.0	7.0	2.0
Hydropsyche angustipennis Curtis	4.5	3.0	7.4	2.2
Hydropsyche exocellata Dufour	8.7	8.0	10.0	1.0
Hydropsyche instabilis Curtis	3.5	2.5	7.0	2.2
Hydropsyche ornatula Mc Lachlan	8.1	7.0	10.0	1.5
Hydropsyche pellucidula Curtis	5.8	2.5	8.5	3.0
Hydropsyche siltalai Döhler	5.5	3.0	7.0	2.0
Hydroptila forcipata Eaton	6.5	4.5	9.3	2.4
Hydroptila sparsa Curtis	7.0	5.0	10.0	2.5
Hydroptila vectis Curtis	6.0	3.0	10.0	3.5
Ictalurus melas Rafinesque	10.0	8.0	10.0	1.0
Isoperla grammatica Poda	4.5	3.7	7.6	1.9

Isoperla obscura Zetterstedt	6.8	6.0	8.0	1.0
Isoperla oxylepis Despax	3.0	2.0	5.0	1.5
Isoperla rivulorum Pictet	2.5	1.0	5.0	2.0
Ithytrichia lamellaris Eaton	5.5	3.0	7.6	2.3
Lampetra planeri Bloch	3.3	1.5	6.4	2.4
Lasiocephala basalis Kolenati	5.6	3.6	7.2	1.8
Lepidostoma hirtum Fabricius	5.8	4.0	7.0	1.5
Lepomis gibbosus Linné	9.7	7.0	10.0	1.5
Leptocerus interruptus Fabricius	10.0	8.0	10.0	1.0
Leptocerus tineiformis Curtis	10.0	8.0	10.0	1.0
Leuciscus cephalus Linné	7.7	4.0	10.0	3.0
Leuciscus leuciscus Linné	6.9	5.0	9.4	2.2
Leuciscus souffia Risso	6.2	4.0	7.3	1.6
Leuctra albida Kempny	4.2	1.0	7.2	3.1
Leuctra alpina Kühtreiber	3.0	0.0	4.0	2.0
Leuctra fusca Linné	5.7	3.0	8.0	2.5
Leuctra hexacantha Despax	3.5	2.0	5.0	1.5
Leuctra hippopus Kempny	4.5	1.0	6.5	2.7
Leuctra inermis Kempny	2.3	0.0	6.0	3.0
Leuctra major Brink	6.0	3.0	8.4	2.7
Leuctra rauscheri Aubert	2.0	1.0	3.3	1.1
Lota lota Linné	6.6	4.0	9.0	2.5
Melampophylax mucoreus Hagen	4.3	2.5	6.5	2.0
Micrasema setiferum Pictet	5.9	4.0	7.0	1.5
Molanna angustata Curtis	10.0	8.0	10.0	1.0
Mystacides azurea Linné	8.0	6.0	10.0	2.0
Mystacides nigra Linné	9.4	6.0	10.0	2.0
Nemacheilus barbatulus Linné	6.0	4.0	7.8	1.9
Nemoura avicularis Morton	1.1	0.0	3.0	1.5
Nemoura cambrica Stephens	1.5	0.0	4.4	2.2
Nemoura cinerea Retzius	1.3	0.0	5.1	2.5
Nemoura marginata Pictet	2.5	0.0	7.0	3.5
Nemoura mortoni Ris	2.2	1.0	5.4	2.2
Nemurella picteti Klapalek	0.8	0.0	4.0	2.0
Neureclipsis bimaculata Linné	7.9	6.0	10.0	2.0
Nigrobaetis niger Linné	5.6	4.0	8.5	2.2
Notidobia ciliaris Linné	4.5	2.0	7.0	2.5
Odontocerum albicorne Scopoli	4.5	2.0	7.0	2.5
Oecetis notata Rambur	8.3	7.0	10.0	1.5
Oecetis ochracea Curtis	9.0	8.0	10.0	1.0
Oecetis testacea Curtis	7.6	7.0	10.0	1.5
Oligoneuriella rhenana Imhoff	6.4	5.2	8.0	1.4
Oligoplectrum maculatum Fourcroy	4.5	3.0	6.5	1.7
Oxyethira flavicornis Pictet	8.5	7.0	10.0	1.5
Paraleptophlebia submarginata Stephens	5.3	2.0	8.2	3.1
Perca fluviatilis Linné	8.5	7.0	10.0	1.5
Perla bipunctata Pictet	5.2	4.0	7.0	1.5
Perla burmeisteriana Claassen	6.0	4.2	7.3	1.5
Perla marginata Panzer	4.5	2.5	6.0	1.7
Perlodes jurassicus Aubert	3.2	2.0	5.4	1.7
Philopotamus ludificatus Mc Lachlan	3.1	2.0	6.0	2.0
Philopotamus montanus Donovan	2.2	1.0	5.0	2.0
Phoxinus phoxinus Linné	4.6	2.3	7.0	2.3

Plectrocnemia conspersa Curtis	2.5	0.0	6.2	3.1
Plectrocnemia geniculata Mc Lachlan	1.6	0.0	4.2	2.1
Polycentropus flavomaculatus Pictet	6.7	3.0	9.2	3.1
Polycentropus multiguttatus Mosely	8.5	6.0	10.0	2.0
Potamanthus luteus Linné	9.0	7.6	10.0	1.2
Potamophylax cingulatus Stephens	3.2	1.0	5.1	2.0
Potamophylax latipennis Curtis	5.9	3.5	7.0	1.7
Potamophylax luctuosus Piller Mitterpacher	4.5	2.0	7.0	2.5
Potamophylax nigricornis Pictet	1.8	0.0	4.5	2.2
Potamophylax rotundipennis Brauer	6.5	3.0	7.4	2.2
Protonemura brevistyla Ris	2.0	0.0	3.8	1.9
Protonemura lateralis Pictet	2.5	0.0	4.8	2.4
Protonemura meyeri Pictet	3.5	2.0	6.0	2.0
Protonemura nimborum Ris	4.0	3.0	6.5	1.7
Protonemura nitida Pictet	3.5	1.0	6.5	2.7
Protonemura praecox Morton	1.6	0.0	4.2	2.1
Protonemura risi Jacobson & Bianchi	2.3	1.0	5.0	2.0
Pseudocentroptilum pennulatum Eaton	6.7	4.0	9.0	2.5
Psychomyia pusilla Fabricius	6.5	2.0	8.5	3.2
Rhadicoleptus spinifer Mc Lachlan	0.5	0.0	2.2	1.1
Rhithrogena carpatoalpina Klonowska & al.	4.0	2.0	6.6	2.3
Rhithrogena germanica Eaton	5.5	5.0	8.0	1.5
Rhithrogena iridina Kolenati	3.6	2.5	7.2	2.3
Rhithrogena picteti Sowa	2.5	1.5	5.0	1.7
Rhithrogena semicolorata Curtis	5.1	3.5	7.5	2.0
Rhodeus sericeus Pallas	8.7	7.5	10.0	1.2
Rhyacophila dorsalis Curtis	6.0	3.0	8.0	2.5
Rhyacophila fasciata Hagen	4.2	2.0	7.4	2.7
Rhyacophila pubescens Pictet	1.9	0.0	3.5	1.7
Rhyacophila tristis Pictet	2.6	0.0	5.1	2.5
Rhyacophila vulgaris Pictet	3.5	2.0	6.5	2.2
Rutilus rutilus Linné	9.3	7.0	10.0	1.5
Salmo trutta fario Linné	4.8	1.0	7.3	3.1
Scardinius erythrophtalmus Linné	10.0	8.0	10.0	1.0
Sericostoma personatum Kirby & Spencer	4.0	1.5	6.5	2.5
Serratella ignita Poda	5.6	1.0	8.5	3.7
Silo nigricornis Pictet	3.0	0.0	4.0	2.0
Silo pallipes Fabricius	4.5	2.0	7.0	2.5
Silo piceus Brauer	6.0	4.0	7.0	1.5
Siphonoperla torrentium Pictet	2.6	1.0	5.7	2.3
Stenophylax mucronatus Mc Lachlan	1.2	0.0	2.5	1.2
Stizostedion lucioperca Linné	8.8	7.0	10.0	1.5
Taeniopteryx kühtreiberi Aubert	6.0	3.0	7.0	2.0
Taeniopteryx nebulosa Linné	7.8	6.4	9.0	1.3
Taeniopteryx schoenemundi Mertens	6.8	5.0	8.0	1.5
Thymallus thymallus Linné	6.0	4.0	7.0	1.5
Tinca tinca Linné	10.0	6.0	10.0	2.0
Tinodes dives Pictet	2.7	1.0	6.5	2.7
Tinodes rostocki Mc Lachlan	4.7	3.0	7.7	2.3
Tinodes waeneri Linné	7.0	3.0	8.5	2.7
Torleya major Klapalek	5.5	3.5	7.5	2.0
Wormaldia copiosa Mc Laclan	1.7	0.0	4.2	2.1
Wormaldia occipitalis Pictet	1.0	0.0	2.6	1.3