

Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients

ANDRÉS MELLADO DÍAZ, MARIA LUISA SUÁREZ ALONSO AND
MARIA ROSARIO VIDAL-ABARCA GUTIÉRREZ

Departamento de Ecología e Hidrología, Universidad de Murcia, Murcia, Spain

SUMMARY

1. The relationships between biological traits of macroinvertebrates and environmental characteristics were investigated in streams with contrasting physical, chemical or landscape level attributes. We used an ordination technique, RLQ analysis, which links an environmental table (R) with traits table (Q) through an abundance table (L) to investigate the relationship between habitat characteristics and biological traits.
2. A major environmental axis explaining the distribution of species and their distinctive biological features was obtained. This axis included variables of anthropogenic pressure (agricultural and urban uses) and natural variability (climatic and geologic) that are strongly intercorrelated in the study area, with a clear spatial component.
3. The attributes of species from frequently disturbed systems (small size, multivoltinism, diapause, ovoviviparity, etc.) were associated with semi-arid areas whereas traits common in more stable and favourable environments (large body size, semi-voltinism, isolated eggs, etc.) were found in upland forested areas.
4. The natural climatic variation was proposed as a *disturbance* axis of a theoretical habitat templet (driven by the intense hydrological disturbances typical of semi-arid streams), while anthropogenic pressure (mainly intensive agriculture) and high salinity, a natural consequence of geology, was proposed as an *adversity* axis. Different life-histories associated with contrasting environmental features were superimposed in this habitat templet.
5. The ecological–evolutionary scenario in which stream macroinvertebrates have evolved and by which their communities are organized, is closely linked to disturbance, environmental harshness and human pressure.

Keywords: biological traits, habitat templet, macroinvertebrates, southeast Spain, semi-arid streams

Introduction

The distribution and abundance of stream macroinvertebrates are influenced by a variety of physical and biological factors. Abiotic factors, in particular those related to disturbance (Resh *et al.*, 1988; Poff,

1992) and habitat heterogeneity (Sedell *et al.*, 1990; Scarsbrook & Townsend, 1993; Minshall & Robinson, 1998), clearly determine the composition of invertebrate communities. However, habitat factors influencing community structure differ among systems and with the spatial scale of the study (Tate & Heiny, 1995; Vinson & Hawkins, 1998; Boyero, 2003).

Ecologists have long recognized that habitat factors represent filters for biological traits, and patterns in these traits are related to spatial habitat variability as

Correspondence: Dr Andrés Mellado Díaz, Departamento de Ecología e Hidrología, Universidad de Murcia, CP 30100 Murcia, Spain. E-mail: amellado@um.es

well as to disturbance (Statzner, Hildrew & Resh, 2001a). These ideas were related to the 'habitat templet concept' of Southwood (1977, 1988). It postulates that spatio-temporal habitat variations provide a 'templet' against which differences in fundamental life history and other species traits result in differential survival and reproduction. Townsend & Hildrew (1994) thus developed a 'river habitat templet' by predicting trends of traits across spatio-temporal variability gradients. Temporal variability was understood as the frequency of disturbances, whereas spatial variability referred to the abundance of refugia buffering the effect of disturbances (Townsend & Hildrew, 1994; Townsend, Dolédec & Scarsbrook, 1997). Another proposed axis for the habitat templet was the 'adversity axis', ranging from harsh to rich habitats (Southwood, 1977). Thus, in continuously harsh environments, tolerant species would be relatively free of interspecific competition (Hynes, 1970). Greenslade (1983) termed these kinds of selective forces as 'beyond K ' selection or A -selection. More recently, Poff (1997) proposed a conceptual framework in which environmental factors act as 'filters' (from large-scale geo-climatic to microhabitat constraints), successively precluding those taxa whose characteristics are not adapted to cope with the environmental characteristics.

In recent tests of the habitat templet concept in streams, trends in species traits have often proved significant (Scarsbrook & Townsend, 1993; Resh *et al.*, 1994; Usseglio-Polatera, 1994; Statzner *et al.*, 1997; Townsend *et al.*, 1997; Merigoux, Dolédec & Statzner, 2001).

Hydrological variation is commonly viewed as an important element of the habitat templet, suggesting differences in ecosystem structure and function in streams (Poff, 1996). Mediterranean regions are characterized by high hydrological variability (Gasith & Resh, 1999), even more accentuated in Mediterranean semi-arid zones. Thus, organisms that frequently experience abiotic disturbances (floods and droughts) may respond over evolutionary time by developing morphological, physiological and/or life-history traits that minimize the impact of disturbances. A study area with a hydrological disturbance gradient determined by climate would then be good for revealing contrasts among biological traits characterizing macroinvertebrate communities.

Southeast (SE) Spain has a Mediterranean semi-arid climate with highly variable rainfall from year to year. The landscape in the Segura River basin ranges from Mediterranean humid conifer forests along mountain ranges in major nature reserves in the north-west (NW), to arid and semi-arid mediterranean shrublands further southeast. This longitudinal gradient in altitude and climate is coupled with a human pressure counterpart, the river network having forested headwaters with a low human population, agricultural midlands with intense flow regulation and a moderate population density, and densely populated cities in the lowlands. As a result of climate and land use, the hydrological regime of the rivers, especially of the smaller tributaries in the southeast, is intermittent, with the rivers being reduced to permanent pools or drying up completely (Vidal-Abarca *et al.*, 1992; Mellado *et al.*, 2002; Vidal-Abarca, Gómez & Suárez, 2004). This regime depends on climate and geomorphology, but an increasing demand for water has also modified flow regimes (Vidal-Abarca *et al.*, 2004).

In addition to these climatic and hydrological features, a major feature is that some of the tributaries in the southeastern part of the basin flow across salt-rich rocks and therefore their salinity is sometimes very high. These saline streams have marked differences in taxonomic composition compared with their freshwater counterparts in the same region (Aboal, 1989; Moreno *et al.*, 1997, 2001).

In this study, we related species traits to faunistic changes and habitat characteristics to discriminate among communities in streams of contrasting environments. We used data from 16 different stream sites classified in four distinct groups representing the environmental variability of the study area. The data set incorporated mountain forested streams, small tributaries in agricultural catchments, springs and saline streams. We used RLQ analysis (Dolédec *et al.*, 1996), a multivariate method which provides a general solution to the problem of relating species traits to habitat variables (the 'fourth-corner' problem described in Legendre, Galzin & Harmelin Vivien, 1997). The RLQ technique has been used previously to reveal trait-environment relationships in bird assemblages (Dolédec *et al.*, 1996; Hausner, Yoccoz & Ims, 2003), grassland functional groups (Barbaro *et al.*, 2000), terrestrial carabids (Ribera *et al.*, 2001) and alpine (Choler, 2005) or invasive plants (Thuiller *et al.*,

2006). This is the first study dealing with multiple functional descriptions of stream communities across a whole catchment in the Iberian Peninsula.

Specifically, we sought to test several general hypotheses:

1 The biological traits represented in macroinvertebrate communities of streams in contrasting environments are related to patterns of spatio-temporal habitat variability.

2 According to the River Habitat Templet predictions, the main traits involved in these differences are those related to life history, with attributes that favour resistance and/or resilience (e.g. multivoltinism, short-life span, small size, asexual reproduction or parthenogenesis, diapause and other resistance forms) being predominant in highly disturbed and harsh environments, such as semi-arid and saline streams, while those traits related to habitat stability and K-selection (e.g. semi-voltinism, long-life span, medium–big sizes, diverse reproductive techniques, absence of invulnerable stages) being more important in headwater mountain streams. Between these two extremes of the gradient, agricultural streams and springs will show a mixture of features.

3 The main environmental factors driving those changes in biological characteristics can act at multiple spatial scales by imposing different constraints or filters as proposed by Poff (1997). Thus, at the catchment scale, climate and geology (and its related filters such as seasonality of flow, intermittency, or drought and flood frequency, biome vegetation, salinity) will influence life-history traits, body size, feeding habits or desiccation tolerance. At this scale, human activity (with constraints such as enrichment and siltation from agriculture) will act on traits related to pollution and/or silt tolerance. At the reach/valley scale, factors such as lithology, stream size, slope and confinement, riparian condition, (with their associated constraints such as, substratum requirements, habitat volume, stream power or OM inputs) can influence traits such as, body size, relation to substratum, food preferences, feeding habits or dispersal mechanisms.

Methods

Study area and sampling design

The study sites were located in the Segura River basin, SE Spain (Fig. 1). General descriptions of the

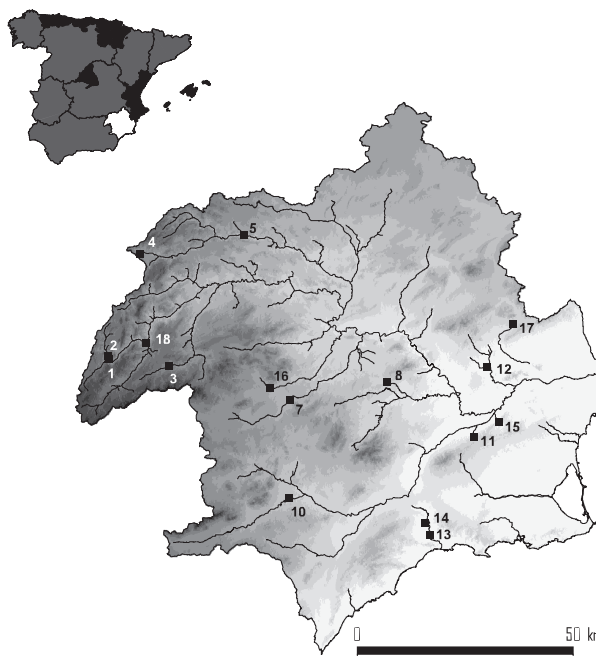


Fig. 1 Study area (inset showing its position within Spain) showing the sampling sites. Darker shading denotes higher altitude.

catchment (geology, climate, etc.) can be found in Vidal-Abarca *et al.* (1992); Mellado *et al.* (2002) and Robles *et al.* (2002). We conducted our study in 16 streams belonging to four different groups defined *a priori* on the basis of the macroinvertebrate assemblages by means of multivariate analyses (Mellado *et al.*, 2002; Mellado, 2005).

Sites 1, 2, 3 and 4 are first and second order, high altitude stream reaches (950–1040 m) located in mountainous conifer-forested areas in a nature reserve, in the humid NW part of the basin. Sites 5 and 18 are third and fourth order reaches at medium altitudes (650 and 720 m) located in forested areas inside or near the nature reserve limits, similar to sites 1, 2 and 3. All of these sites were classified as *mountain streams*.

Sites 7, 8, 10 and 16 are medium altitude reaches belonging to four streams (420–780 m and first–third order) in extensive agricultural areas in the middle part of the Segura river basin, and are affected to some extent by agriculture runoff, water abstraction and diversions for irrigation, livestock grazing and/or recreational activities. These sites were grouped, along with a slightly saline lowland stream (site 13), in the *agricultural streams* type. The apparent reason of

the grouping of site 13 is that its low salinity (in comparison with the other saline streams), coupled with a high diversity of habitats (with a well developed and rich macrophyte community) and the presence of a tiny freshwater spring flowing into the stream, make the community structure of this stream similar to that of the fresher waterbodies forming the *agricultural streams* group.

Sites 11 and 17 are first and third-order spring-fed stream reaches at low altitudes (350 and 340 m) with some signs of impairment because of recreational activities or canalization, in the first case, and to water abstractions and livestock grazing, in the second. These two sites formed the *springs* type.

Finally, sites 12, 13, 14 and 15 are low altitude (100, 60, 140 and 100 m) saline streams (mean measured conductivities ranged from *c.* 9000 at site 13 up to more than 50 000 $\mu\text{S cm}^{-1}$ at site 12) in semi-arid areas of the southeastern part of the catchment characterized by salt-rich Miocene marls. Sites 13 and 14 are littoral streams, site 12 is a hyper-saline stream that flows into a reservoir and site 15 is a small intermittent saline tributary of the Segura River near Murcia. All these sites were classified as *saline streams*, with the exception of site 13, included in the *agricultural streams* type.

Macroinvertebrate sampling

One hundred and five macroinvertebrate samples were taken from the 16 streams on seven occasions from 1999 to 2001: April 1999, July 1999, November 1999, February 2000, April–May 2000, July 2000 and December 2000–February 2001. Some sites were not sampled on all seven dates because of technical problems (site 13 was not sampled in July 2000; site 18 was later added to the study, in July 2000) or because of the drying of some sites in summer (site 15 dried out during summer in 1999 and 2000; site 4 dried in summer 1999). One single multi-habitat semi-quantitative kick-sample (using a hand net with a 0.5 mm mesh), as described by Zamora-Muñoz & Alba-Tercedor (1996), was taken on each sampling occasion from a 100 m reach. Macroinvertebrates were live-sorted in the field from white trays with a portable aspirator in an attempt to get a representative sample of the community and to maximize the species list, including rare taxa. The area sampled was not estimated, but the time was standardized to 1 h per

site. Samples were preserved in 70% ethanol and invertebrates were identified in the laboratory to the lowest taxonomic level (usually genus) except for some dipterans (identified to families, subfamilies or tribes), Hydrachnidia, Tricladida, Oligochaeta and Nematoda. A total of 208 taxonomic units were used in this study (see Appendix). Each sampling unit was defined as a site-date sampling event and treated independently in the subsequent analyses.

Biological traits

We used 62 categories of 11 biological traits to describe the functional composition of invertebrate communities (Table 1). The selection of traits and their categories was dictated by the information available. The database used here was that of Tachet *et al.* (2000), which described the averaged affinity of each genus to each category. It assigned an affinity score (1–5) of each genus to each trait category using a fuzzy coding approach (Chevenet, Dolédec & Chessel, 1994). The functional structure of communities is conserved, if taxonomic levels higher than species are used (Dolédec, Olivier & Statzner, 2000; Gayraud *et al.*, 2003), especially when analysed with multivariate methods.

For some taxa identified at coarser levels of taxonomic resolution, affinity scores were calculated by summing the affinity scores of the genera belonging to this taxonomic group and known from our region and re-scaling the results to a 1–5 scale. The opposite was the case, for example, when we identified a genus (mostly dipterans) with no information at that level in Tachet *et al.* (2000). In those cases, we assigned the subfamily or family affinities for that genus. However, there were some southern taxa that could not be used, as they were not included in Tachet *et al.* (2000). The snails *Melanopsis* sp., *Mercuria* sp. and *Pseudamnicola* sp. and the beetles *Coelostoma* sp. and *Herophydrus* sp. were among these taxa. We did not use them in further analyses, and neither did we include those individuals that could not be identified to genus because of their small sizes.

Environmental variables

A total of 39 environmental variables were used in this study (Table 2). Twelve physicochemical parameters including conductivity, discharge, water

Table 1 Biological traits and categories (=‘modalities’) for taxa considered in the present study. ‘Code’ is the label used in the figures for trait categories. Traits and categories were those defined by Tachet *et al.* (2000)

Biological traits	Modalities	Code
Maximal size	<0.25 cm	<0.25
	>0.25–0.5 cm	0.25–0.5
	>0.5–1 cm	0.5–1
	>1–2 cm	1–2
	>2–4 cm	2–4
	>4–8 cm	4–8
	>8 cm	>8
Life-cycle duration	≤1 year	1
	>1 year	>1
Potential no. reproductive cycles per year	<1	<1
	1	1
Aquatic stages	>1	>1
	Egg	Egg
Reproduction	Larva	lar
	Pupa	pu
	Adult	ad
	Ovoviviparity	ov
	Isolated eggs, free	efr
	Isolated eggs, cemented	ec
	Clutches, cemented or fixed	cfx
Dissemination	Clutches, free	cfr
	Clutches, in vegetation	cv
	Clutches, terrestrial	ct
	Asexual reproduction	asx
	Aquatic passive	aqp
	Aquatic active	aqa
	Aerial passive	aep
Resistance form	Aerial active	aea
	Eggs, statoblasts	ee
	Cocoons	co
	Cells against desiccation	cdes
Food	Diapause or dormancy	dia
	None	no
	Fine sediment + microorganisms	s-m
	Detritus < 1 mm	fde
	Plant detritus > 1 mm	cde
	Living microphytes	lmph
	Living macrophytes	lMph
	Dead animal > 1 mm	sdan
	Living microinvertebrates	lminv
	Living macroinvertebrates	lMinv
Feeding habits	Vertebrates	ver
	Absorber	ab
	Deposit feeder	depf
	Shredder	shr
	Scraper	scr

Table 1 (Continued)

Biological traits	Modalities	Code
Respiration	Filter feeder	fil
	Piercer (plants or animals)	pier
	Predator (carver/engulfer/swallower)	pred
	Parasite	par
Locomotion and substratum relation	Tegument	teg
	Gill	gi
	Plastron	plst
	Spiracle (aerial)	spi
Locomotion and substratum relation	Flier	fli
	Surface swimmer	sswim
	Full water swimmer	fswim
	Crawler	craw
	Burrower (epibenthic)	bur
	Interstitial (endobenthic)	int
	Temporarily attached	tatt
Permanently attached	patt	

temperature, suspended solids, dissolved oxygen, pH, alkalinity and nutrient concentrations were measured on each sampling occasion.

Seven geographical or geomorphologic variables were estimated at each site from topographical maps and a geographical information system: geographical coordinates, altitude, stream order, sub-catchment area upstream from a sampling site, and the percentage of calcareous and marl/alluvial lithology in that sub-catchment.

Five land-use variables were estimated at each sampling site using a geographical information system, the CORINE-land cover database modified to some simple indicative layers (CEC, 1993) and a hydrological model that accounted for the effects of precipitation and discharge on the influence of land-use area at the receiving stream site. These parameters were the percentages of urbanized, industrial, agriculture/pasture, unmodified and forested land plus unmodified areas in the sub-catchment, multiplied by a specific correction factor derived from the hydrological model for each site, thus obtaining the final land-use ratios.

As in-stream habitat variables we used a set of eight metrics included in a physical habitat multi-metric index (IHF), similar to the British River Habitat Survey (National Rivers Authority, 1995) and the US-EPA rapid bioassessment protocol (Barbour *et al.*, 1999), and fully described by Pardo *et al.* (2002). These

Table 2 Environmental variables used in the present study, organized by variable types, and their respective scores on the first RLQ axis ('code' is the label used in the figures)

Environmental variable	Variable type	Code	RLQ score
Total suspended solids	Physicochemical	SS	-0.059
Ammonium	Physicochemical	Ammo	-0.040
Nitrite	Physicochemical	Nitri	-0.057
Nitrate	Physicochemical	Nitra	-0.108
Phosphate	Physicochemical	Phos	-0.045
Alkalinity	Physicochemical	Alk	-0.042
Dissolved oxygen	Physicochemical	Ox	0.027
Oxygen saturation	Physicochemical	Ox%	-0.015
pH	Physicochemical	pH	0.062
Water temperature	Physicochemical	T	-0.083
Electric conductivity (25 °C)	Physicochemical	Con	-0.128
Discharge	Physicochemical	Q	0.093
Longitude (East)	Geomorphological	E	-0.131
Latitude (North)	Geomorphological	N	0.092
% calcareous subcatchment area	Geomorphological	calc	0.115
% marls subcatchment area	Geomorphological	marl	-0.098
Altitude	Geomorphological	Alt	0.113
Stream order (Strahler)	Geomorphological	Ord	-0.005
Subcatchment area	Geomorphological	Area	0.012
Average channel width	Instream habitat	Wid	0.067
Substratum type	Instream habitat	Sub	0.061
Fluvial Habitat Index (IHF)	Instream habitat	IHF	0.010
IHF – embeddedness	Instream habitat	emb	-0.058
IHF – riffle frequency	Instream habitat	rf	0.043
IHF – substratum heterogeneity	Instream habitat	sb	-0.047
IHF – velocity–depth regimes diversity	Instream habitat	vd	0.047
IHF – shaded channel	Instream habitat	sh	0.056
IHF – heterogeneity elements	Instream habitat	het	0.058
IHF – macrophyte cover	Instream habitat	co	-0.017
Riparian forest quality index (QBR)	Riparian forest	QBR	0.083
QBR – vegetation cover	Riparian forest	QBRc	0.004
QBR – vegetation cover structure	Riparian forest	QBRs	0.063
QBR – riparian forest quality composition	Riparian forest	QBRq	0.092
QBR – riparian forest naturalness	Riparian forest	QBRn	0.051
Urban use ratio (subcatchment)	Land use	Rurb	-0.066
Industrial use ratio (subcatchment)	Land use	Rind	-0.033
Agricultural use ratio (subcatchment)	Land use	Ragr	-0.106

Table 2 (Continued)

Environmental variable	Variable type	Code	RLQ score
Natural use ratio (subcatchment)	Land use	Rnat	0.116
Percentage natural subcatchment area	Land use	Nat	0.112

metrics, estimated in a 100 m reach, included substratum embeddedness, substratum particle size heterogeneity, riffle frequency, variability of velocity/depth regimes, shading of the channel, heterogeneity elements (roots, wood, debris dams, etc.) and macrophyte cover heterogeneity, as well as the final IHF score. We calculated the IHF metrics on three sampling occasions and used averaged values. Similarly, to depict riparian forest we used the four components included in the QBR index, an index of riparian quality, described in Munné *et al.* (2003), as well as the final QBR score. This index has recently been applied in the study area and some modifications were proposed to adapt semi-arid catchment conditions (Suárez Alonso & Vidal-Abarca, 2000). It is based on four additive metrics: riparian vegetation cover (proportion of the riparian area covered by trees and shrubs), cover structure (proportion of riparian vegetation composed by trees and shrubs separately), riparian quality (number of trees or shrub species and absence of introduced species, and other human impacts in riparian vegetation) and channel alterations (absence of human impacts altering channel form). It also takes into account differences in the geomorphology of the river from its headwaters to the lower reaches. We calculated the QBR index metrics on a single sampling occasion.

Statistical analyses

Three separate ordinations of the R (environmental variables), L (taxonomic composition) and Q (biological traits) tables were performed prior to the RLQ analysis. First, correspondence analysis (CA) was conducted on the taxonomic composition table (L), providing an optimal simultaneous ordination of samples and taxa. In this case, we used log-transformed abundance data to downweight the high abundances. A principal component analysis (PCA) was conducted using log-transformed environmental

variables. To interpret this analysis we used the loadings of each environmental variable on the components of the PCA. Next, the trait table Q was investigated by fuzzy correspondence analysis (FCA, Chevenet *et al.*, 1994). To select traits which best explained the variance on a given axis, we compared correlation ratios (i.e. the ratio between the between-category variance and the total variance, see Chevenet *et al.*, 1994).

An RLQ analysis is a double constrained ordination that must be compared with the unconstrained ordination provided by CA to measure how much of the total macroinvertebrate community structure is associated with environmental variables and biological traits. The general mathematical model of RLQ analysis, which basically consists of the eigenanalysis of the matrix $R^T L Q$, is fully explained in Dolédec *et al.* (1996): 147). The significance of the relationship between the environmental attributes and the biological traits was investigated by a permutation test with 1000 random permutations of the rows of both the species traits and the environmental characteristics tables (Dolédec *et al.*, 1996). To evaluate the strength of these relationships, the constrained ordination resulting from the three tables in the RLQ analysis was compared with the unconstrained separate analyses of R, L and Q. The percentage of variation in each separate analysis taken into account by RLQ analysis was calculated for the first two axes in analysis of R, L and Q tables. Finally, to assess the relative contribution of each environmental variable to the new ordination we used the factor loadings on the main RLQ axes. Similarly, the main biological traits responsible of the observed variability in the RLQ ordination were assessed by their relative position along the first RLQ axis. All analyses were made using the ADE-4 package (Thioulouse *et al.*, 1997) for the R software, version 1.9.0 (R Development Core Team, 2004).

Results

Separate ordination of the tables

Faunistic table (L) Total variability in the macroinvertebrate data was 4.07, and the first four axes of a CA performed on log-abundance table explained 27.3% of this variability, with 18.3% in the first two axes. The first axis explained 11.7% while the second

Table 3 Results of the separate analyses involved in the RLQ analysis

CA-taxa-samples table (table 'L')				
Eigenvalues (1–4)	0.47	0.27	0.20	0.16
Variance (%)	11.65	6.61	5.02	4.02
PCA-environmental variables (table 'R')				
Eigenvalues (1–4)	11.81	4.43	3.25	3.18
Variance (%)	30.29	11.37	8.34	8.16
FCA-biological traits table (table 'Q')				
Eigenvalues (1–4)	0.22	0.20	0.18	0.13
Variance (%)	10.84	9.86	8.69	6.41

CA, correspondence analysis; PCA, principal correspondence analysis; FCA, fuzzy correspondence analysis.

axis explained 6.6% (Table 3). Additional axes were not considered further in the RLQ analysis. The first eigenvalue corresponding to the first canonical correlation was 0.69 (the square root of 0.47). This value was the best possible correlation within the species abundance table. The projection of samples on the factorial map showed a clear arch effect (Fig. 2) typical of marked environmental gradients, but also a clear grouping of samples in the four stream types defined previously, with a small overlap between springs and agricultural streams.

Environmental table (R) The first two axes of the PCA of the environmental characteristics of the sites accounted for 41.7% of the total variance, with axes 1 and 2 explaining 30.3% and 11.4% of the total variance respectively (Table 3). The first axis was positively associated (loadings higher than 0.75) with the agricultural land-use ratio, nitrates, percentage of marl/alluvial sub-basin, the eastern coordinate and conductivity, and negatively associated with the natural land-use ratio, the percentage of calcareous area, the forest-natural land-use ratio, altitude, the riparian forest QBR index and the riparian quality (Fig. 3). These were all variables highly correlated with altitude ($r > 0.59$ in all cases). Altitude was also highly correlated with longitude, latitude, dominant geology and land use.

The second axis had the highest correlations (loadings >0.63) with sub-catchment area (Area), stream order and the in-stream habitat quality index (IHF) and negative correlations occurred at the opposite side with oxygen concentration and saturation (loadings >0.5) (Fig. 4). *Mountain streams* and *saline streams* were clearly isolated along the first axis, with the former group occupying a negative position and the

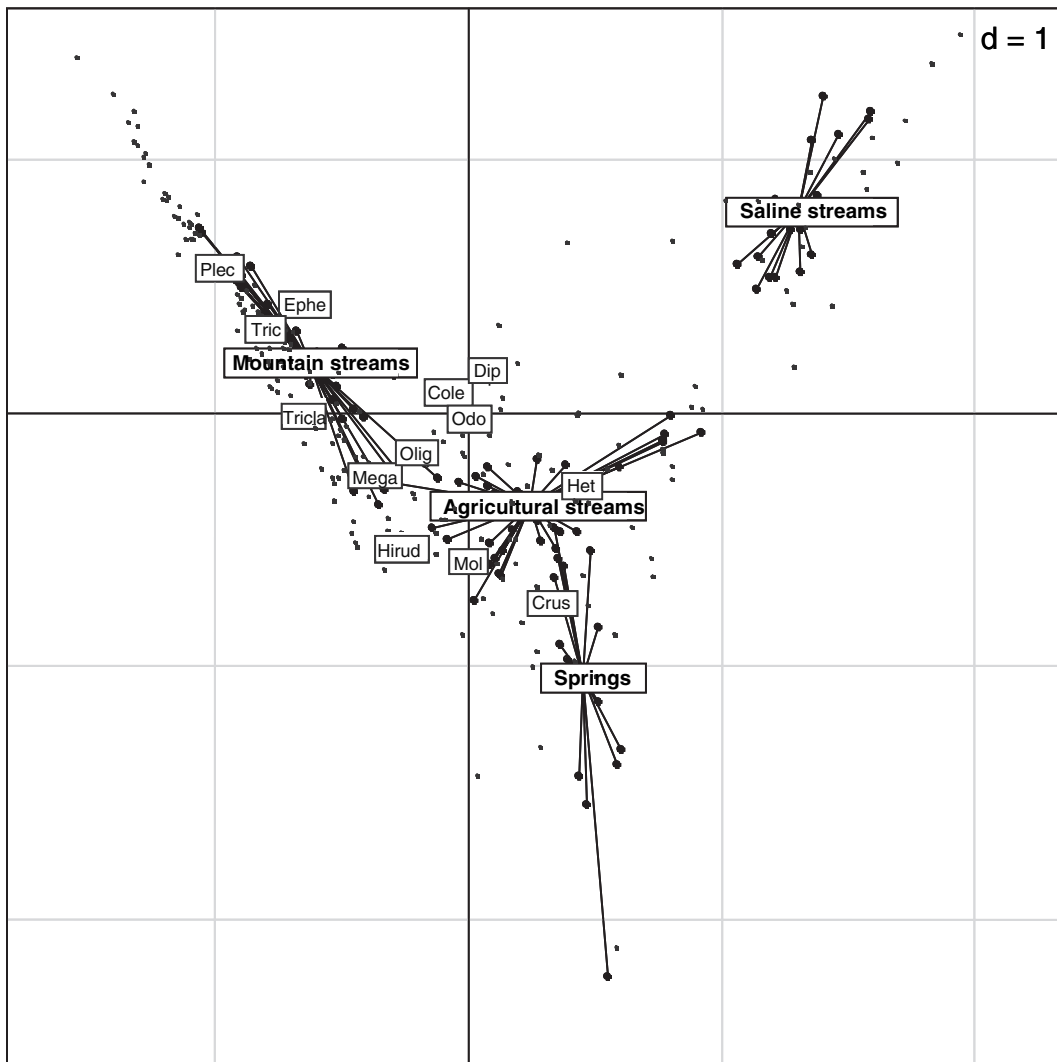


Fig. 2 Correspondence analysis of the faunistic table showing the samples grouped by stream types and taxa grouped by main orders. Ordination plot scale (i.e. the length of the main divisions, 'd') is indicated.

later on the opposite side. *Agricultural streams* and *springs* samples occupied a central position and overlapped moderately with site 17 samples grouped with the *agricultural streams* samples. The second component (11.4% of extracted variance) of the PCA did not discriminate stream types, but it separated sites within stream types (all but saline streams) mainly on the basis of stream size (catchment area, order).

Biological traits table (Q) The first two axes of a FCA performed on the biological traits-taxa table accounted for 20.7% of the total variance (= 2.05, Table 3). The first axis (10.8% of variance) was mainly

correlated with feeding habits and food type and to a lesser extent with maximal size, life-cycle duration, potential number of reproductive cycles per year and reproductive strategy (Fig. 5). The second axis (9.9% of variance) was mainly correlated with types of respiration, reproductive strategy and maximal size. Categories of feeding habits were also separated on this axis but not as much as on the first axis (Fig. 5). The third axis (8.7% of variance) was positively correlated with reproduction and feeding habits, so that it did not add new information to the analysis and was not further considered.

Long-lived taxa with large maximal body size occupied the positive side along both axes (Fig. 5).

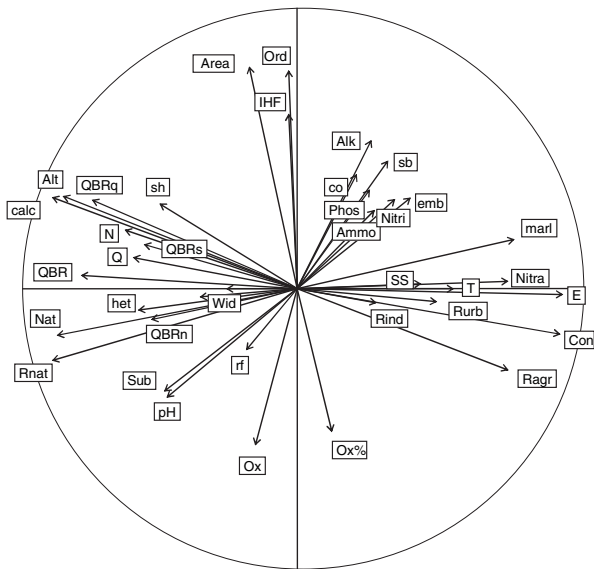


Fig. 3 Principal component analysis (PCA) correlation circle of the 39 environmental variables. Short vectors have not been labelled for clarity. For environmental variable codes see Table 2.

They were mainly, though not exclusively, predators feeding on macroinvertebrates, laying isolated eggs (both free and cemented) and with gill respiration. Invertebrates in this group comprised Odonata, the Megaloptera *Sialis* sp., some Plecoptera (*Perla* sp. and *Dinocras* sp.), Trichoptera (*Rhyacophila* sp.) or crustacea (Decapoda) as well as Tricladida and Hirudinea (Fig. 6). The upper-left quadrant (negative values on the first and positive values on the second axis) was mainly occupied by medium sized filter-feeders and deposit-feeders feeding on detritus, fines and microorganisms. They were short-lived taxa (1 year or less), and had sexual reproduction using free clutches. The mode of respiration included breathing through the tegument or gills. Ephemeroptera, Trichoptera, Diptera and Plecoptera formed the bulk of this group, along with some bivalves such as *Pisidium* sp (Fig. 6). On the negative side of the second axis occurred smaller taxa with either short or long life spans. Reproductive modes included sexual reproduction with fixed terrestrial and endophytic clutches. Scrapers, organisms feeding on living macrophytes, and piercers of small invertebrates or vertebrates were the main functional feeding guilds. Respiration was mainly by plastron or aerially by spiracles. Coleoptera and Heteroptera dominated this group, along with some Mollusca and Diptera.

RLQ: simultaneous analysis of biological traits, environmental variables and taxonomic composition

The first two axes extracted 78.3% and 8.9%, respectively, of the total variance in the table that crosses the site environmental characteristics and the biological traits of the genera (Table 4). The permutation test was significant ($P = 0.001$, 1000 random permutations). The first RLQ axis accounted for 98.5% of the variability in the first axis in the separated PCA of environmental variables (i.e. ratio between the variance of the habitat characteristics accounted for in RLQ (11.6) and that of the separate analysis (11.8), see Tables 3 & 4). Similarly, it accounted for 51.9% of the variability in the first axis of the biological traits. The two new sets of sites and taxon scores had a correlation of 0.40 along the first RLQ axis (Table 4), a value that can be compared with the highest possible correlation between sites and taxa, given by the square root of the first eigenvalue of the CA (0.69, see Results: separate ordination). Thus, the first RLQ axis explained 58.0% of the variability in the faunistic table (L). Because of the low variance explained by the second RLQ axis, it was not considered further.

Environmental variable loadings on the first RLQ axis are presented in Table 2. Nitrate, water temperature, conductivity, eastern longitude and agricultural use were negatively correlated with the first RLQ axis, while calcareous geology, altitude, riparian quality, natural land use and northern latitude were at the opposite side.

Taxa, biological trait modalities and sampling sites, as well as scores of environmental variables on the first RLQ axis, were plotted together to summarize the results derived from the analysis (Fig. 7). To facilitate the interpretation of the graph, taxon scores were plotted according to higher taxonomic groups (usually order) and environmental factors were grouped into physicochemical, in-stream habitat, riparian forest, geo-morphological and land-use variables (Table 2). Samples were also classified by stream types. Looking at the positive extreme of the RLQ axis gradient (Fig. 7), it is apparent that sites within forested and/or natural catchments tend to have well preserved riparian forests (QBR, QBRq), a high frequency of riffles, rocky substratum, shaded channels and heterogeneity elements, such as twigs, roots or debris dams and a variety of velocity/depth regimes. They are located at high altitudes in

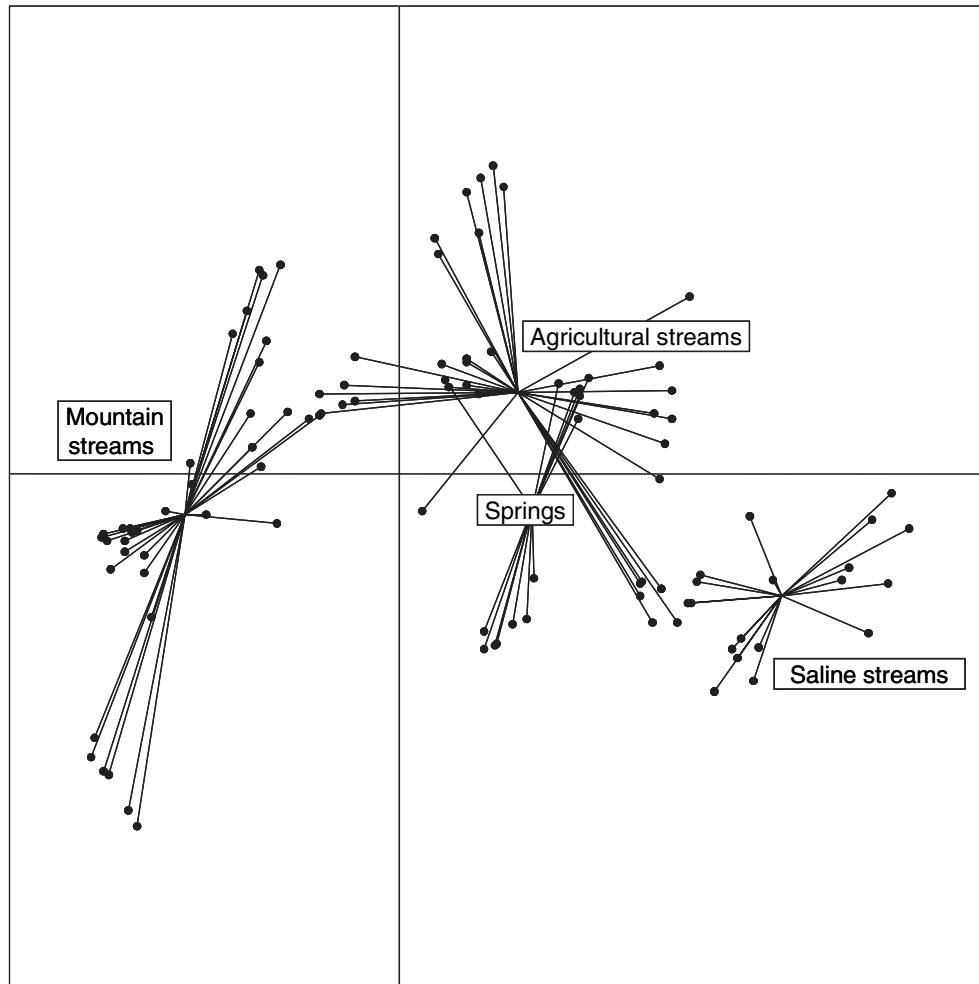


Fig. 4 Principal component analysis (PCA) plot of the samples, grouped by stream types. Lines link samples to their stream types. Ordination plot scale (i.e. the length of the main divisions, 'd') is indicated.

limestone geology catchments of the humid north western part of the basin, being hard-water sites with relatively high discharge and well oxygenated waters. Samples on this position matched the *mountain streams* type sites (Fig. 7). Distinctive biological traits (Fig. 7) characterizing the faunistic assemblages are: large body size (2–4 and 4–8 cm classes) and semi-voltinism; sexual reproduction laying cemented eggs; eggs and statoblasts as resistant stages; a tendency for aquatic dispersal (either passive or active); consumers of plant debris or fine sediment and microorganism, with scrapers and filter-feeders as the main functional feeding guilds; tegument respiration; and, finally, permanent attachment, burrowing or crawling as the principal locomotion and substratum relationships (Fig. 7). All the Plecoptera and most of the Epheme-

roptera and Trichoptera occupied the right-hand side of the axis, along with *Ancylus* sp., *Ferrisia* sp., *Austropotamobius* sp., anisoptera (such as Gomphidae and *Cordulegaster* sp.) and most Elmidae. Contrastingly, sites located in the semi-arid southeastern part of the study area were characterized mainly by agricultural land use and also included the most urbanized catchments. The dominant geology was marl with quaternary alluvial deposits and the altitude was low at most of sampling sites. Riparian forests and stream channel morphology were of poor quality (with introduced species and human alterations of vegetation and/or channel form). Among in-stream habitat variables, high substratum embeddedness, visually estimated as the degree of interstitial filling of the substratum by fine particles and

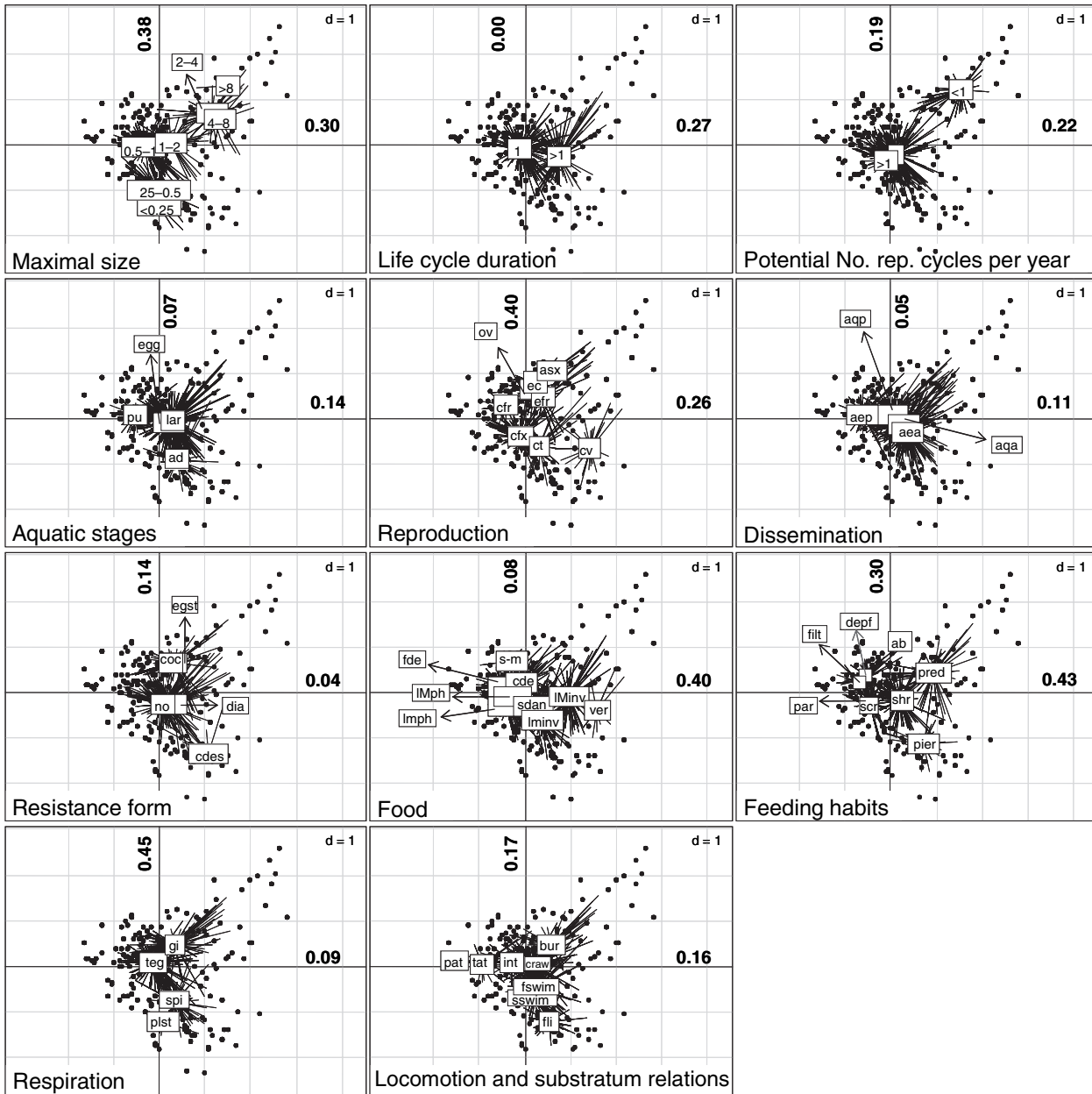


Fig. 5 Distribution of categories (white labels) of the biological traits on the first two axes of the fuzzy correspondence analysis (FCA). Each modality label was positioned at the weighted average of the taxon positions (solid squares, compare Fig. 7) representing this modality. Numbers indicated the correlation ratios with the first axis (horizontal numbers) and second axis (vertical numbers) (see Chevenet *et al.*, 1994). Some labels have been moved for clarity and their actual position is indicated by arrows. Ordination plot scale (i.e. the longitude of the main divisions, 'd') is indicated (see Table 1 for codes used for trait modalities).

substratum particle size heterogeneity were the main features characterizing this part of the gradient. Physicochemical attributes included high conductivity and nitrate concentration, high temperature and high suspended solids. Samples from sites classified as *saline streams* were associated with these environ-

mental features, being located at the negative extreme of the gradient (Fig. 7).

Common biological traits of macroinvertebrates inhabiting these semi-arid saline streams were: either very high or low small body size (<0.25 and >8 cm), multivoltinism, aquatic adults, ovoviparity and

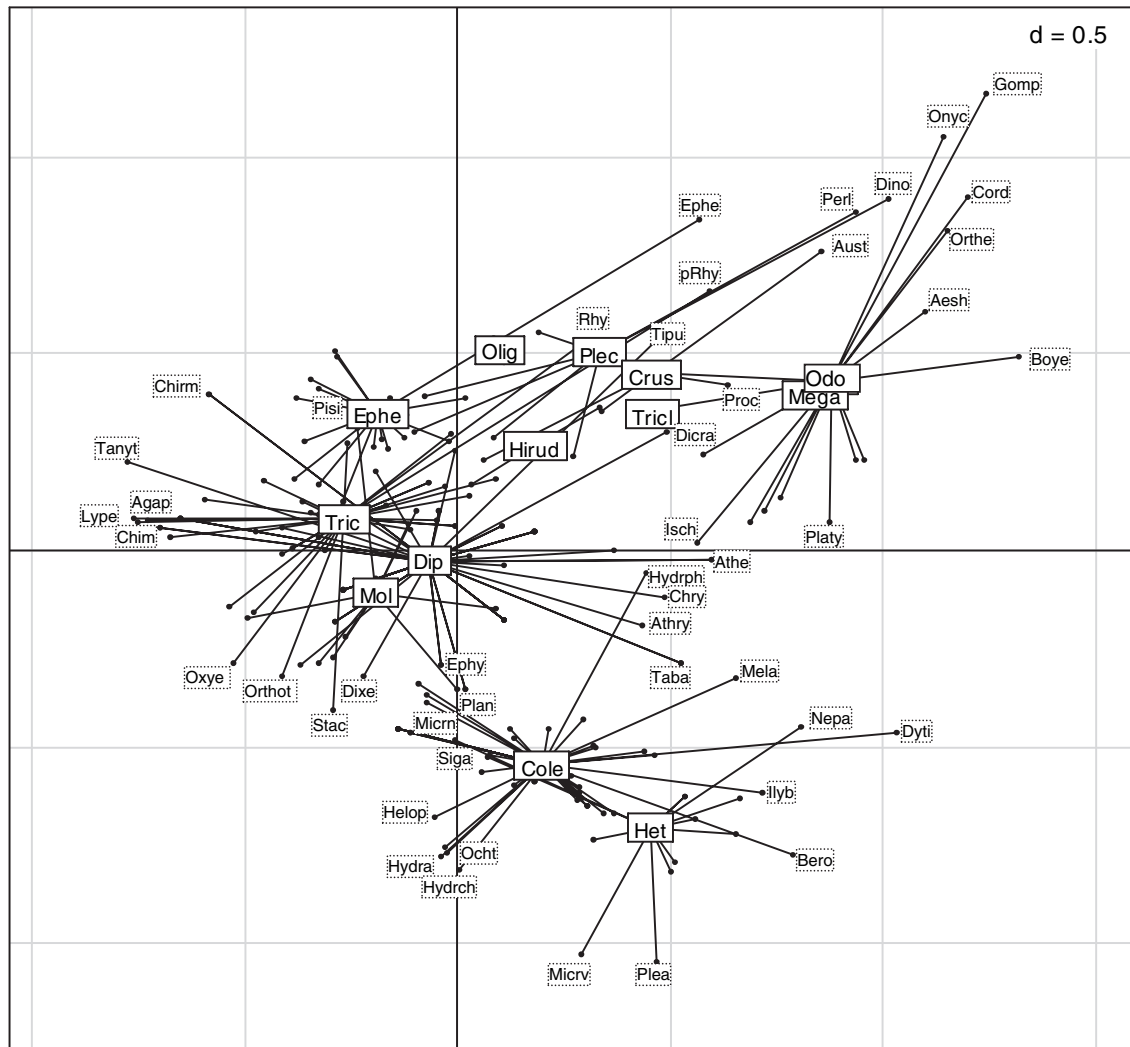


Fig. 6 Distribution of faunistic groups (usually orders) on the first two axes of the fuzzy correspondence analysis of biological traits. Faunistic groups (white square labels) are positioned at the weighted average of their component taxa (solid circles); Those taxa having extreme scores relative to their groups are indicated (dotted square labels). For taxon codes, see Appendix. Ordination plot scale (i.e. the longitude of the main divisions, 'd') is indicated.

Table 4 Summary of the RLQ analysis

Eigenvalues	eig 1	eig 2
RLQ analysis	0.21	0.02
Variance (%)	78.30	8.90
R/RLQ	eig 1	eig 1 + 2
Variance	11.64	14.80
Variance ratio (%)	99	91
L/RLQ	eig 1	eig 2
Variance	0.40	0.24
Variance ratio (%)	58	47
Q/RLQ	eig 1	eig 1 + 2
Variance	0.12	0.24
Variance ratio (%)	52	58

endophytic clutches; relative affinity for aerial dispersion, behavioural adaptations to desiccation (aestivating in 'cells' in the soil) and diapause or dormancy as resistance strategies, living microinvertebrates or vertebrates as the main food sources, parasitic or predatory (piercers) feeding behaviour, aerial respiration through spiracles and the ability to swim, (both in the water column or on the surface). The majority of the Heteroptera, the hydrophilid *Berosus* sp. (and to a lesser degree *Haliphus* sp. or *Ilybius* sp.), some dipterans in the Culicidae and snails such as *Potamopyrgus* sp. dominated the negative side of the RLQ axis, as well as *Cleoon* sp.

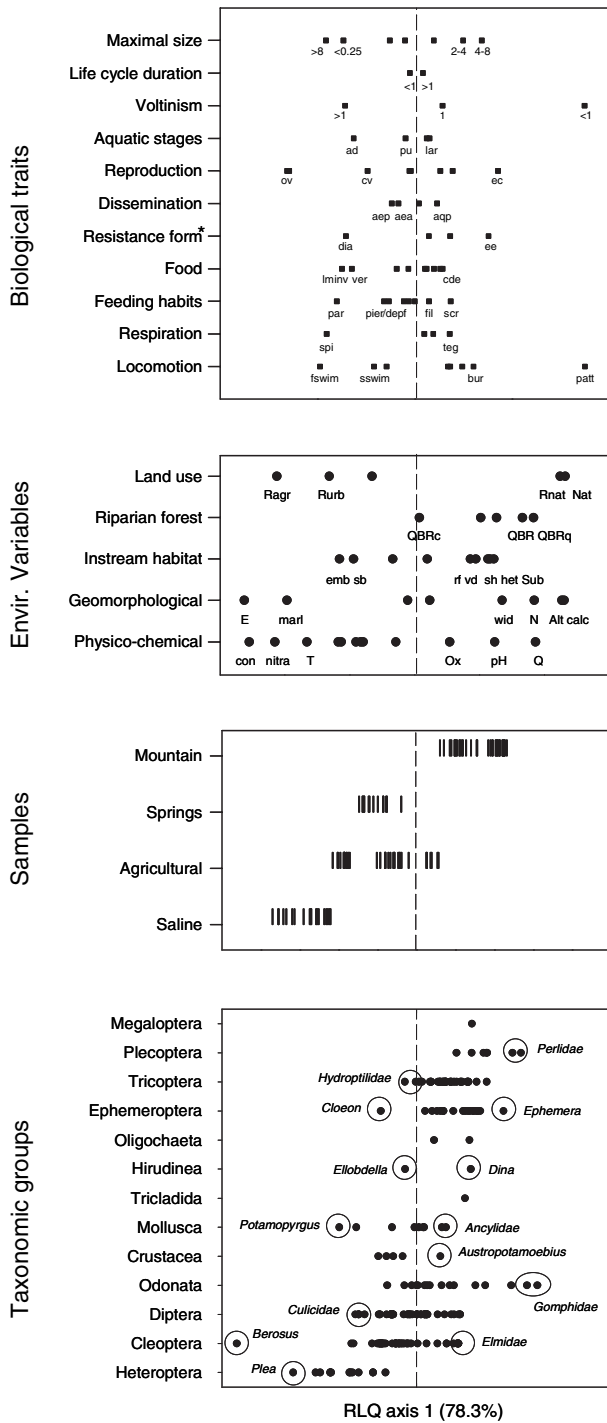


Fig. 7 Biological trait categories, environmental variables, sites and taxon scores along the first RLQ axis. Categories are grouped by trait, environmental factors are grouped by variable type, sites are grouped by stream type and taxa are grouped by faunistic groups. (*) Because of the very negative value of the category 'cells against desiccation' in trait 'resistance form' (around -4), the scale of the graph was shortened to (-2,2) to separate more effectively the other trait categories along this axis.

Discussion

Environmental factors driving community characteristics

In this study, we found a variety of environmental factors that were related to the observed community structure and biological attributes. The most influential variables (i.e. those that showed the highest or lowest values along the RLQ axis) were the areas under agriculture and natural/forest, riparian forest quality, surficial geology and altitude. There was also a strong spatial influence, with geographical coordinates (and especially longitude) as correlates. Conductivity, nitrate, water temperature and discharge also exerted major influences. Among the in-stream habitat variables, those related to substratum particle size and heterogeneity were the most influential, but to a lesser degree in comparison with the other variables. Contrastingly, among the less influential variables (those positioned near the centre of the axis) were riparian cover, the in-stream habitat index, macrophyte cover, stream order, catchment area and oxygen content.

When viewed across relatively large spatial scales, much variation in species distributions can be attributed to patterns of variation within the landscape (Townsend *et al.*, 2003). Large-scale landscape attributes, such as land use, surficial geology, altitude and hydrology were found by Richards, Johnson & Host (1996) to have the greatest influence on macroinvertebrate assemblages. However, Richards *et al.* (1997) found that reach-scale physical features were more strongly related to the life history and behavioural attributes of macroinvertebrates than were catchment-scale variables, suggesting that species traits exhibit strong relationships with local environmental conditions. Our results suggest that a variety of factors, acting at different scales and hierarchically organized (e.g. agricultural land use and the percentage of marl determine conductivity and nitrate concentration and also influence the riparian habitat and/or the substratum), control the functional organization of communities at our study scale, as pointed out by Poff (1997).

Biological traits and environmental attributes

Major natural environmental variables and anthropogenic alterations important to stream communities were revealed, as well as the biological traits responding to these properties. We found a highly

significant relationship between biological traits, expressed by sets of life history/behavioural/physiological characters and the environmental features of the habitat, as measured by the main underlying environmental gradient.

The first RLQ ordination axis accounted for a large fraction of the total variance explained, indicating the existence of a strong environmental gradient structuring the characteristics of the sites and taxa. The ordination of sites along this axis matched closely our *a priori* biotic classification of stream types. *Saline streams* were located to the extreme left of the gradient, while *agricultural streams* and *springs* occupied more central (but still negative) positions (Fig. 7). The nature of the environmental factors that dominate this part of the gradient (disturbed land use, no riparian forests, southeast coordinates, high nutrient loadings, marl geology, high conductivity, etc.) would indicate an area under high anthropogenic pressure that threatens these ecosystems (Gómez *et al.*, 2005). At the same time, these semi-arid streams encompass a natural disturbance regime characterized by extreme floods and droughts, these events being the most important natural disturbance agents in such ecosystems (Fisher & Grimm, 1991). Both factors, along with a high tolerance to salinity, determine the structure and function of the whole aquatic ecosystem and influence the traits of the biota in these streams. This region of the gradient matched some of the biological traits cited in the literature as providing resilience and/or resistance to disturbance (i.e. small body size and many generations per year) (Southwood, 1977, 1988; Townsend & Hildrew, 1994). Other biological features that reduce the impact of environmental fluctuations were: the presence of adults able to cope with drought episodes by occupying cells in the soil (such as the hydrophilid water beetle *Berosus*), diapausing stages and the laying of endophytic eggs. The presence of aquatic adults that can survive inland for some time by flying, or the making of burrows by crayfish, also enables recolonization after floods or droughts. In this sense, the aquatic adults of Heteroptera and Coleoptera are among the best colonizers of ephemeral waters and exemplify the adaptativeness of this life style (Ortega *et al.*, 1991; Wissinger, 1997 and references therein; Velasco, Suarez & Vidal-Abarca, 1998; Bilton, Freel & Okamura, 2001). The prevalence of ovoviviparity as a reproductive strategy was due mainly to the presence of the introduced

freshwater snail *Potamopyrgus antipodarum* (Gray). This trend has been noted by others (Dolédec, Statzner & Bournaud, 1999; Usseglio-Polatera & Beisel, 2002). These authors observed that there was a greater variety of parental care at reference sites, with four types of egg deposition predominant, while ovoviviparity and regeneration were more common at frequently disturbed sites. *Potamopyrgus antipodarum* often shows parthenogenetic reproduction, which we interpret as a factor conferring resilience in disturbed habitats, because of the great number of descendants. The dominance of fliers in the more stressed environments could reflect the value of being able to disperse immediately in the face of sudden disturbances, such as floods and droughts (Lytle & Poff, 2004).

Nevertheless, some traits usually predicted in more stable and benign conditions were also present in this negative part of the habitat gradient: large body size and predation on vertebrates. However, the introduced American crayfish *Procambarus clarkii* (Girard) was the largest taxon (>8 cm), and was found mainly in agricultural streams. This species shows characteristics such as opportunistic omnivory, resistance to pollution and extreme environmental conditions such as drought, fast growth and high reproduction potential. It requires a productive aquatic ecosystem, and is common in other disturbed sites, which make this species particularly suitable for invading eutrophic streams (Angeler *et al.*, 2001; Gil-Sanchez & Alba-Tercedor, 2002). Predation on vertebrates was shown by *Agabus*, *Dytiscus*, *Ilybius*, *Meladema*, *Rhantus*, *Nepa*, *Notonecta*, *Anax*, *Aeshna*, *Boyeria*, *Procambarus* and *Helobdella*, typical taxa typically inhabiting lentic or sluggish waterbodies, as in our agricultural streams.

In contrast, the right-hand side of the RLQ habitat-traits gradient (Fig. 7) was occupied mainly by samples from stream sites in semi-pristine conditions, located in the intact nature reserves of the humid north-western upper catchment. These samples corresponded to the *mountain stream* typology, and the biological traits highlighted were large body size and less than one reproductive cycle per year. These features have commonly been treated indicating relatively stable habitats with a low frequency and intensity of disturbances (MacArthur & Wilson, 1967; Southwood, 1988; Stearns, 1992; Townsend & Hildrew, 1994). Other characters, such as the production of cemented isolated eggs, could be explained because they represent a lesser investment in parental care in a

more stable environment. Statzner *et al.* (2001b) found that streams affected by sewage had fewer taxa producing isolated cemented eggs compared with reference sites. We hypothesize that the relatively greater surface area of single eggs (compared with clutches) could make them more vulnerable to toxins and preclude oviposition in polluted reaches.

Statzner *et al.* (2001b) hypothesized that, compared with reference conditions, streams affected by sewage (with a reduced oxygen concentration) would favour aerial respiration. They also argued that agricultural land use (causing increased erosion and silting) would not favour interstitial organisms. The removal of riparian woodland (thus reducing coarse particulate organic matter input to streams) would also be deleterious to shredders (Anderson & Sedell, 1979; Cummins *et al.*, 1989). We found evidence to support all of these hypotheses, with all the cited traits being predominant in the left-hand side of the RLQ axis. Aerial respiration was probably related to factors other than low oxygenation (such as low flows or high temperature and salinity), however, because all the streams were well-oxygenated. On the other hand, aerial respiration mainly characterizes the Coleoptera, Heteroptera and Diptera, and the dominance of lentic habitat in *agricultural* and *saline* streams may favour the occurrence of these taxa and thus this trait in such streams. We also found that filter-feeders dominated *mountain streams*. Organisms with permanent attachment to the substratum, burrowers and interstitial animals were also more abundant in *mountain streams*. Usseglio-Polatera & Beisel (2002) found a switch from swimmers and/or crawlers upstream to interstitial animals or burrowers downstream in the River Meuse. They also found a change in feeding habits (piercers and scrapers to filter-feeders or deposit feeders) that matches our results.

A 'habitat templet' for streams in SE Spain

One previous habitat templet, originally developed by Greenslade (1983), was applied to lentic waters in semi-arid regions in Australia (Williams, 1985), with axes being the 'predictability of drought' (the main disturbance factor in temporary streams) and 'salinity'. Our results appeared to fit this model, with the RLQ axis being equivalent to the diagonal of the templet (Fig. 8). Nevertheless, it is difficult to express the longitudinal axis of the templet in terms of a single

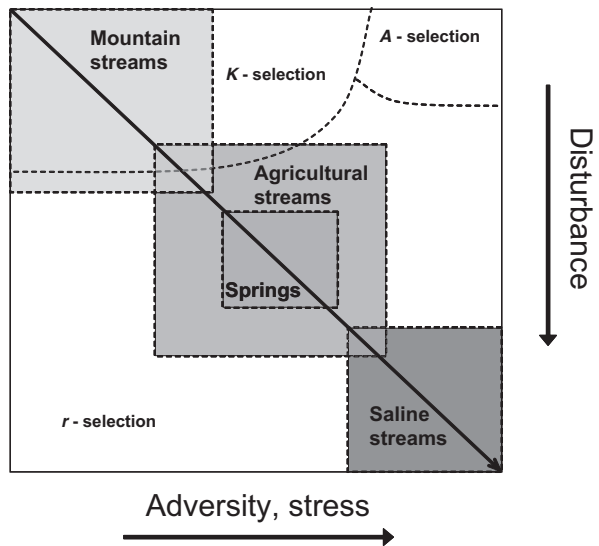


Fig. 8 Proposed theoretical habitat templet for Segura catchment streams. The stream types studied are located along the adversity axis and the disturbance axis (frequency and intensity). The main selection models acting in each region of the templet are also indicated. The main diagonal corresponds to the obtained first RLQ axis.

variable (namely salinity), because of the variety of confounding factors that correlate along the main gradient in our catchment (e.g. altitude and climate, geology and land use). Therefore, we opted to consider this axis as an 'adversity axis', *sensu* Greenslade (1983), along which natural stressors (i.e. salinity and drying) are accentuated by human pressures (agricultural land use and its corollaries: organic enrichment, water abstraction and physical channel alteration). Natural climatic variation corresponds to the disturbance axis of our habitat templet (driven by the intense disturbance regime typical of semi-arid streams, with normal drying periods and spates, whereas anthropogenic pressures (mainly driven by intensive agriculture), in addition to natural sources of salinity, correspond to the adversity axis (Fig. 8). The variations of biological traits along the axes of this templet are in agreement with the concept of *r*- and *K*-selection, as initially stated by MacArthur & Wilson (1967). We did not find evidence of *A*-selected type organisms (Grime, 1977; Greenslade, 1983) that theoretically should be found in stable but harsh environments (Fig. 8), presumably because of the lack of such systems in our study. Moreover, to our knowledge, there are no species in the regional pool showing these adversity traits.

Future use of species traits as basis for monitoring human impacts

Ecological theory predicts different life-history strategies for different levels of disturbance or spatio-temporal heterogeneity (Poff & Ward, 1990; Townsend & Hildrew, 1994), and thus different life-history traits can also indicate different intensities of human impact (Dolédéc *et al.*, 1999).

An RLQ analysis has been used as an effective tool for identifying species traits that respond to impacts of land use change at different scales. In the initial stages of a monitoring programme, it is advisable to select indicator species with traits directly linked to specific ecological processes modified by human intervention (Hausner *et al.*, 2003).

With regard to human impacts in streams from the Segura river basin, we found changes in land use (mainly agriculture, with the alteration of riparian corridors, water abstraction and nutrient enrichment) to have the strongest impact on invertebrate assemblages at the catchment scale. Nevertheless, the confounding effects of geology, altitude and climate precluded any selection of traits corresponding to environmental impacts.

Intensive agriculture is the most destructive human activity (more than traditional fruit cultivation) in the former riparian woodlands of the semi-arid SE Spain (Salinas, Blanca & Romero, 2000) and the expansion of intensive irrigation in Murcia over the past few decades has been widely documented, as well as its consequent environmental impacts (Martínez-Fernández, Esteve-Selma & Calvo-Sendín, 2000, 2002; Vidal-Abarca *et al.*, 2004). Moreover, Ortega *et al.* (2004) found that intensive agriculture (measured as its surrogate, potential nitrogen export) was the most important factor affecting the ecological integrity of semi-arid wetlands in SE Spain. Nevertheless, the effects of intensive agriculture on stream macroinvertebrate communities have not yet been addressed sufficiently, although semi-arid saline 'ramblas' of SE Spain are among the most threatened aquatic ecosystems in Spain and probably in Europe (Sánchez-Fernández *et al.*, 2004; Abellán *et al.*, 2005; Gómez *et al.*, 2005).

It would be desirable to investigate the effects of this land use change separately, eliminating other confounding effects (such as altitude, climate and geology) as far as possible, perhaps selecting

catchments *a priori*, with similar altitude, climate and geology but contrasting land use (from forest to extensive dryland agriculture and intensive irrigation). Manipulative experimental designs might be possible but would be costly. Further, streams in these semi-arid regions are rare and fragile habitats and the experimental manipulation of whole catchments, even for scientific purposes, would be unacceptable for conservation reasons. Thus, until we are capable of disentangling the influence of natural factors such as climate, geology or altitude, from those of anthropogenic activities, it will be difficult to find traits suitable for biomonitoring, at least in the case of changes in agriculture at the basin scale.

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Appendix List of macroinvertebrate taxa. Codes appearing in the figures are included

Taxonomic unit (Code)	Taxon	Code
Coleoptera (Col)	<i>Agabus</i>	Agab
	<i>Anacaena</i>	Anac
	<i>Aulonogyrus</i>	Aulo
	<i>Berosus</i>	Bero
	<i>Bidessus</i>	Bide
	<i>Cyphon</i>	Cyph
	<i>Deronectes</i>	Dero
	<i>Dryops</i>	Dryo
	<i>Dytiscus</i>	Dyti
	<i>Elmis</i>	Elmi
	<i>Elodes</i>	Elod
	<i>Enochrus</i>	Enoc
	<i>Esolus</i>	Esol
	<i>Graptodytes</i>	Grap
	<i>Gyrinus</i>	Gyri
	<i>Halipilus</i>	Hali
	<i>Helochaers</i>	Heloc
	<i>Helophorus</i>	Helop
	<i>Hydraena</i>	Hydra
	<i>Hydrochus</i>	Hydrch
	<i>Hydrocyphon</i>	Hydrcy
	<i>Hydroglyphus</i>	Hydrg
	<i>Hydrophilus</i>	Hydrph
	<i>Hydroporus</i>	Hydrpo
	<i>Hygrotus</i>	Hygr
	<i>Hyphidrus</i>	Hyph
	<i>Ilybius</i>	Ilyb
	<i>Laccobius</i>	Laccb
	<i>Laccophilus</i>	Laccp
	<i>Limnebius</i>	Limnb
	<i>Limnius</i>	Limni
	<i>Meladema</i>	Mela
	<i>Nebrioporus</i>	Nebr
	<i>Normandia</i>	Norm
	<i>Ochthebius</i>	Ocht
	<i>Orectochilus</i>	Orec
	<i>Oreodytes</i>	Oreo
	<i>Oulimnius</i>	Oulim
	<i>Paracymus</i>	Parac
	<i>Peltodytes</i>	Pelt
	<i>Pomatinus</i>	Poma
<i>Rhantus</i>	Rhan	
<i>Riolus</i>	Riol	
<i>Stenelmis</i>	Stene	
<i>Stictonectes</i>	Sticn	
<i>Stictotarsus</i>	Stict	
<i>Yola</i>	Yola	
Heteroptera (Het)	<i>Anisops</i>	Anis
	<i>Aquarius</i>	Aqua
	<i>Gerris</i>	Gerr
	<i>Hydrometra</i>	Hydrm
	<i>Mesovelis</i>	Mesov
	<i>Micronecta</i>	Micrn
	<i>Microvelia</i>	Micrv

Appendix (Continued)

Taxonomic unit (Code)	Taxon	Code
Ephemeroptera (Ephe)	<i>Naucoris</i>	Nauc
	<i>Nepa</i>	Nepa
	<i>Notonecta</i>	Noto
	<i>Plea</i>	Plea
	<i>Sigara</i>	Siga
	<i>Velia</i>	Veli
	<i>Baetis</i>	Baet
	<i>Centroptilum</i>	Cent
	<i>Cloeon</i>	Cloe
	<i>Procloeon</i>	Procl
	<i>Pseudocentroptilum</i>	Pseuc
	<i>Caenis</i>	Caen
	<i>Paraleptophlebia</i>	Paral
	<i>Habroleptoides</i>	Habr1
<i>Habrophlebia</i>	Habrp	
Odonata (Odo)	<i>Chorotherpes</i>	Chor
	<i>Serratella</i>	Serr
	<i>Torleya</i>	Torl
	<i>Ephemer</i>	Ephe
	<i>Ecdyonurus</i>	Ecdy
	<i>Heptagenia</i>	Hept
	<i>Rithrogena</i>	Rith
	<i>Epeorus</i>	Epeo
	<i>Electrogena</i>	Elec
	<i>Potamanthus</i>	Potama
	<i>Anax</i>	Anax
	<i>Aeshna</i>	Aesh
	<i>Boyeria</i>	Boye
	<i>Sympetrum</i>	Symp
<i>Crocothemis</i>	Croc	
Trichoptera (Tric)	<i>Orthetrum</i>	Orthe
	<i>Cordulegaster</i>	Cord
	<i>Gomphus</i>	Gomp
	<i>Onychogomphus</i>	Onyc
	<i>Coenagrion</i>	Coen
	<i>Ceriatrion cf</i>	Ceri
	<i>Ischnura</i>	Isch
	<i>Pyrrhosoma</i>	Pyrr
	<i>Lestes</i>	Lest
	<i>Platycnemis</i>	Platy
	<i>Calopteryx</i>	Calo
	<i>R.(Pararhyacophila)</i>	pRhy
	<i>R.(Rhyacophyla)</i>	Rhy
	<i>Hydropsyche</i>	Hydrps
<i>Cheumatopsyche</i>	Cheu	
<i>Polycentropus</i>	Poly	
<i>Plectrocnemia</i>	Plect	
<i>Cyrnus</i>	Cyrm	
<i>Chimarra</i>	Chim	
<i>Lype</i>	Lype	
<i>Tinodes</i>	Tino	
<i>Agapetus</i>	Agap	
<i>Hydroptila</i>	Hydrpt	
<i>Oxyethira</i>	Oxye	
<i>Stactobia</i>	Stac	

Appendix (Continued)

Taxonomic unit (Code)	Taxon	Code
	<i>Ithytrichia</i>	Ithy
	<i>Orthotrichia</i>	Orthot
	<i>Micrasema</i>	Micra
	<i>Drusus</i>	Drus
	<i>Limnephilus</i>	Limne
	<i>Potamophylax</i>	Potamo
	<i>Halesus</i>	Hale
	<i>Stenophylax</i>	Steno
	<i>Mesophylax</i>	Meso
	<i>Allogamus</i>	Allo
	<i>Lasiocephala</i>	Lasi
	<i>Ceraclea</i>	Cera
	<i>Oecetis</i>	Oece
	<i>Athripsodes</i>	Athri
	<i>Setodes</i>	Seto
	<i>Mystacides</i>	Myst
	<i>Sericostoma</i>	Seri
	<i>Sericostomatidae</i>	SeriN
	<i>Beraeidae NID</i>	Bera
	<i>Calamoceras</i>	Cala
Plecoptera (Plec)	<i>Perla</i>	Perl
	<i>Dinocras</i>	Dino
	<i>Isoperla</i>	Isop
	<i>Nemoura</i>	Nemou
	<i>Protonemura</i>	Prot
	<i>Capnioneura</i>	Capn
	<i>Leuctra</i>	Leuc
Megaloptera (Mega)	<i>Sialis</i>	Sial
Diptera (Dip)	<i>Psychodidae NID</i>	PsycN
	<i>Pericoma</i>	Peri
	<i>Psychoda</i>	Psyc
	<i>Berdeniella</i>	Berd
	<i>Tonnoiriella</i>	Tonn
	<i>Dixa</i>	Dixa
	<i>Dixella</i>	Dixe
	<i>Culicidae NID</i>	Culi
	<i>Culex</i>	Cule
	<i>Culiseta</i>	Culis
	<i>Anopheles</i>	Anop
	<i>Simuliidae NID</i>	SimuN
	<i>Simulium</i>	Simu
	<i>Eusimulium</i>	Eusi
	<i>Dasyhelea</i>	Dasy
	<i>Ceratopogoninae</i>	Cerat
	<i>Atrychopogon</i>	Atry
	<i>Chironomini</i>	Chir
	<i>Chironomus</i>	Chirm
	<i>Orthoclaadiinae</i>	Orthoc
	<i>Tanypodinae</i>	Tanyp
	<i>Tanytarsini</i>	Tanyt
	<i>Corynoneurinae</i>	Cory
	<i>Tipula</i>	Tipu
	<i>Antocha</i>	Anto
	<i>Dicranota</i>	Dicr
	<i>Helius</i>	Heli

Appendix (Continued)

Taxonomic unit (Code)	Taxon	Code
	<i>Hexatoma</i>	Hexa
	<i>Pseudolimnophila</i>	Pseul
	<i>Eloeophyla</i>	Eloe
	<i>Paradelphomyia</i>	Parad
	<i>Eriopterini</i>	Erio
	<i>Hemerodromiinae</i>	Heme
	<i>Clinocerinae</i>	Clin
	<i>Dolichopodidae</i>	Doli
	<i>Atherix</i>	Athe
	<i>Ibisia</i>	Ibis
	<i>Athrychops</i>	Athry
	<i>Tabanidae NID</i>	TabaN
	<i>Tabanus</i>	Taba
	<i>Stratyomyiinae NID</i>	StraN
	<i>Oxycera</i>	Oxyc
	<i>Nemotelus</i>	Nemot
	<i>Stratyomis</i>	Stra
	<i>Odontomyia</i>	Odon
	<i>Syrphidae</i>	Syrp
	<i>Ephydriidae NID</i>	EphyN
	<i>Ephydra</i>	Ephy
	<i>Sciomyzidae</i>	Scio
	<i>Ilione</i>	Ilio
	<i>Anthomiidae NID</i>	Anth
	<i>Limnophora</i>	Limno
	<i>Chrysopilus</i>	Chry
Crustacea (Crus)	<i>Echinogammarus</i>	Echi
	<i>Crangonyx</i>	Cran
	<i>Atyaephira</i>	Atya
	<i>Austropotamoebius</i>	Aust
	<i>Procambarus</i>	Proc
Mollusca (Mol)	<i>Pisidium</i>	Pisi
	<i>Ancylus</i>	Ancy
	<i>Ferrisia</i>	Ferr
	<i>Theodoxus</i>	Theo
	<i>Lymnaea</i>	Lymna
	<i>Physella</i>	Phys
	<i>Potamopyrgus</i>	Potapy
	<i>Planorbis</i>	Plan
Tricladida (Tricl)	<i>Tricladida NID</i>	Tric
Hirudinea (Hirud)	<i>Helobdella</i>	Helob
	<i>Dina</i>	Dina
Oligochaeta (Olig)	<i>Oligochaeta</i>	Olig
	<i>Eisseniella</i>	Eiss