

Abundance, diversity and community structure of macroinvertebrates in an Algerian stream : the Sébaou wadi

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Keywords : community structure, diversity, Algeria, benthic macroinvertebrates, mayfly, stonefly, blackfly.

We investigated the abundance, diversity and community structure of mayflies (Ephemeroptera), stoneflies (Plecoptera) and blackflies (Diptera : Simuliidae) in the Sébaou basin (Algeria). Fifty-five species were collected (i.e. 22 mayflies, 14 stoneflies and 19 blackflies species) in 18 sampling sites located in both main streams and tributaries of the Sébaou river (Great Kabylie, North Algeria). Analysis of species diversity of the three considered taxa showed an altitudinal gradient with maximal diversity in the piedmont and low altitude mountain areas (from 200 to 500 m), which provided the most heterogeneous habitats to the benthic fauna. In contrast, the low diversity of the lowland sites was due to high water temperatures, reduced summer discharge and anthropogenic disturbances. In the same way, the low diversity of the high mountain areas can be attributed either to low water temperatures or high fluctuation in daily temperature. Three species assemblage groups are revealed, the first two are related to an upstream-downstream gradient, with headwater sites characterised by stoneflies species and middle stream sites by a high mayfly and blackfly diversity and abundance. The third group was identified as spring sites characterised by a low abundance and occurrence of stonefly species.

Both altitudinal species diversity gradient and species assemblage of the Sébaou wadi were different from European and temperate areas, revealing that the accentuated North African Mediterranean climate could induce changes to both species and community structure. These results provide insights to the influence of some environmental features on aquatic insect species distribution and community structure in North African streams.

Abondance, diversité et structure des communautés de macroinvertébrés lotiques d'un cours d'eau algérien : l'oued Sébaou

Mots-clés : structure des communautés, diversité, Algérie, macroinvertébrés benthiques, Ephéméroptères, Plécoptères, Diptères Simuliidae.

L'abondance, la richesse spécifique et la structure des communautés de trois groupes de macroinvertébrés (Plécoptères, Ephéméroptères et Diptères Simuliidae) ont été étudiées dans le bassin de l'oued Sébaou (Algérie). Cinquante-cinq taxa ont été identifiés (22 Ephéméroptères, 14 Plécoptères et 19 Simulies) dans 18 stations situées sur le cours principal et les affluents de l'Oued Sébaou (Grande Kabylie, Algérie). La diversité spécifique des différentes stations révèle un gradient altitudinal avec une diversité maximale dans les zones de piémont et de basse montagne (200 à 500 m) qui constituent les zones les plus hétérogènes. Au contraire, la faible diversité des zones de plaine peut être attribuée à une température de l'eau élevée, à un faible débit ainsi qu'à l'influence des perturbations anthropiques. De même, la faible diversité des zones d'altitude semble due soit aux faibles températures, soit à la forte amplitude thermique journalière. L'étude des associations d'espèces révèle trois groupes, les deux premiers étant essentiellement déterminés par un gradient altitudinal. Les zones amont sont caractérisées par des espèces de Plécoptères alors que les zones de piémont présentent une forte abondance et une forte diversité d'Ephéméroptères et de Simuliidae. Le troisième groupe est caractéristique des sources, avec des espèces de Plécoptères peu fréquentes et peu abondantes.

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Aussi bien le gradient altitudinal de diversité que les associations d'espèces dans le bassin de l'oued Sébaou, s'avèrent différents de ceux rencontrés en Europe tempérée. Cette étude révèle que le climat méditerranéen accentué d'Afrique du Nord induit des différences de composition spécifique, mais également de structure des communautés. Ces résultats fournissent des informations quant à l'influence de variables environnementales sur la distribution des espèces et la structure des communautés d'insectes aquatiques en Afrique du nord.

1. Introduction

Since the eighties, an increasing interest was devoted to benthic stream invertebrates community structure studies (e.g. Barmuta 1989, Lugthart & Wallace 1992, Bournaud et al. 1996). However, most of the current ecological concepts were derived from studies conducted in Europe and North America and the structure and function of insect assemblages in Mediterranean and tropical streams received less attention (Omerod et al. 1994, Ramirez & Pringle 1998). Up to now, many studies of North African stream invertebrates were devoted to taxonomy or biogeography but ecological aspects are less documented (e.g. Gagneur et al. 1985, Boumaiza & Clergue-Gazeau 1986, Boumaiza & Thomas 1986, Malicky & Lounaci 1987, Bouzidi & Giudicelli 1987, Gagneur & Thomas 1988, Gagneur & Aliane 1991, Clergue-Gazeau et al. 1991, Moubayed et al. 1992, Boumaiza & Thomas 1995, Thomas 1998, Vaillant & Gagneur 1998). However, from both environmental and taxonomic point of view, North Africa differs from the Mediterranean parts of Europe, with accentuated Mediterranean climate (i.e. extreme temperature values during summer and important flooding events during scarce storms, hard rains followed by long dry periods), and fewer benthic invertebrates species in comparison to continental European Mediterranean regions (Giudicelli et al. 1985, Lounaci 1987, Lounaci-Daoudi 1996). In the same way, even though most of the species belong to Mediterranean groups, several species originate from Ethiopian and Oriental taxa and a high rate of endemism has already been observed (Vaillant 1955).

As these characteristics could induce different spatial organisation features between North African and European benthic invertebrates communities, this study, within the limits of the study area, aims to define and explain the spatial organisation of stream invertebrates according to environmental features. To reach this goal, we selected a limited part of Algeria (Djurdjura, Kabylie), including various environmental characteristics in terms of climatic attributes, elevation or distance from the sea. We first focussed on a descriptive analysis of the species abundance and occurrence of

three major taxonomic groups (Ephemeroptera, Plecoptera, Diptera : Simuliidae). Then, we investigated the upstream-downstream species diversity gradient. Finally, the species assemblage was visualised according with environmental features leading to a better understanding of the studied stream invertebrates community structure.

2. Material and methods

The Sébaou wadi (i.e. river) basin was selected as study site ; it is located at about 100 km east from the city of Algiers. The studied area ranges between the Djurdjura mountains (up to an altitude of 1680 m) to the Sébaou lowland plain downstream the city of Tizi-Ouzou (20 m above sea level).

The 18 selected sampling sites were located on both Sébaou mainstream and tributaries aiming to cover various environmental situations (Fig. 1), with a large range of altitude, discharge and topographical features (Table 1). For each of these sampling sites, 16 environmental descriptors, usually considered as ecologically relevant (Williams & Feltmate 1992, Degany et al. 1993, Wohl et al. 1995, Jacobsen et al. 1997), were used to estimate invertebrates spatial distribution : altitude expressed in meters above sea level, slope of the bottom (%), distance from the source (km), mean annual river bed width (m), mean water depth (cm), mean current velocity, bottom substrate expressed in percentage of pebbles, gravel, sand and silt according with the Cailleux (1954) classification, percentage of organic matter covering the bottom, maximal and minimal water temperature, percentage of coverage by terrestrial and aquatic vegetation, and anthropic pollution sorted in four classes ranging from pristine to highly disturbed sites considering organic pollution and river regulation.

Benthic macroinvertebrate samples were performed from 1984 to 1998 using a standard surber net (mesh size 250 μ m, surface sampled 0.09 m²). As a complement, drift nets and visual samples allowed to catch larvae, nymphs and flying adults at each sampling occasion to check that the whole fauna was collected

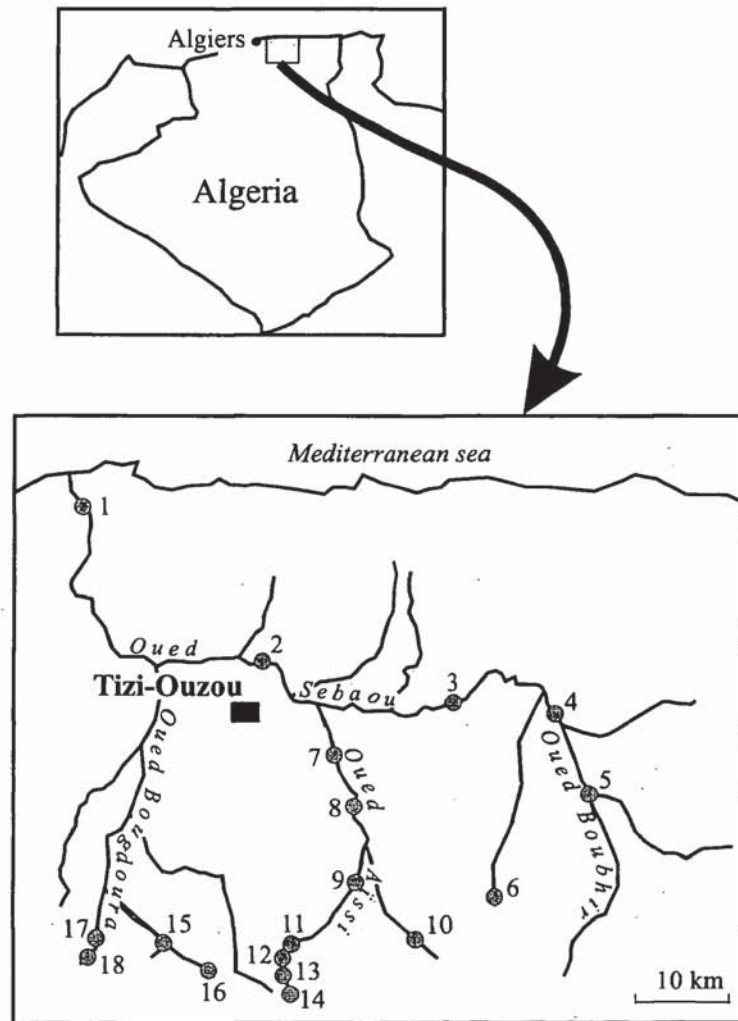


Fig. 1. Map of Algeria showing the location of the Sébaou wadi basin and of the 18 sampling sites.

Fig. 1. Carte de l'Algérie et localisation de l'oued Sébaou et des 18 stations d'échantillonnage.

using the surber-net and to provide further information for the specific determination of the larvae. Samples were fixed using five-percent formaldehyde for further analyses. In the laboratory, all the invertebrates were sorted out and determined to species level. When species level identification was not possible (i.e. no identification key available), identification was conducted to the lowest possible taxonomic level and reference individuals were sent to taxonomic experts for further analyses. This study was restricted to 3 taxonomic groups due to the taxonomic knowledge and their ecological relevance (Lenat 1988, Alder & McCreadie 1997, McCreadie et al. 1997) : mayflies (Ephemeroptera), stoneflies (Plecoptera) and blackflies (Diptera : Simuliidae).

We first made a descriptive analysis of the species abundance (mean number of individuals per m^2) and occurrence for each of the three studied taxonomic groups within the whole Sébaou wadi basin. Then, we plotted species diversity (Shannon diversity index) according to the altitude of each station. To obtain maximal ecological reliability, data was fitted with a Lo-*wess* (locally weighted regression scatterplot smoothing) (Cleveland 1979) non-parametric regression model, which is known able to visualise data tendencies and respect the natural non-linearity of data (Trexler & Travis 1993). The fraction of points used in the computation of smoothed values (i.e. tension) was set to 0.5 (default value in SPSS and Splus software), which provided a high level of accuracy.

Table 1. Characteristics of the 18 studied sites. Alt : altitude (m), Slo : slope (%), Dis : distance from the source (km), Wid : river width (m), Dep : mean water depth (cm), Vel : current velocity (4 classes from low (1) to high (4)), Peb : pebbles (%), Gra : gravel (%), San : sand (%), Sil : silt (%), Oma : organic matter covering the bottom (%), Tma : maximal water temperature (°C), Tmi : minimal water temperature (°C), Cov : riparian cover (%), Aqv : aquatic vegetation cover (%), Pol : pollution (4 classes from pristine (1) to highly disturbed (4)).

Tableau 1. Caractéristiques des 18 stations étudiées. Alt : altitude (m), Slo : pente (%), Dis : distance à la source (km), Wid : largeur du cours d'eau (m), Dep : profondeur moyenne (cm), Vel : vitesse du courant (4 classes de lent (1) à rapide (4)), Peb : galets (%), Gra : graviers (%), San : sable (%), Sil : limons (%), Oma : matières organiques déposées sur le fond (%), Tma : température maximale (°C), Tmi : température minimale (°C), Cov : couverture par la ripisylve (%), Aqv : couverture par la végétation aquatique (%), Pol : pollution (4 classes de non perturbé (1) à fortement perturbé (4)).

Sites	Environmental variables															
	Alt	Slo	Dis	Wid	Dep	Vel	Peb	Gra	San	Sil	Oma	Tma	Tmi	Cov	Aqv	Pol
1	20	0.5	90	10	40	1	10	10	40	10	30	33	13	80	100	4
2	60	0.6	75	10	40	1	15	15	30	10	30	33	12	100	100	4
3	100	0.2	45	10	40	1	15	15	30	10	30	32	11	100	100	4
4	160	1.2	40	5	30	1	40	15	20	5	20	30	11	60	50	3
5	220	2.5	25	2	20	1	50	5	15	15	15	30	9	60	25	2
6	940	30	0.4	0.5	10	4	0	50	0	50	0	13	5	40	50	1
7	140	0.8	30	10	30	3	50	15	15	10	10	31	11	60	75	2
8	200	1.4	20	8	30	3	50	15	15	10	10	27	11	60	75	3
9	300	1.5	11	5	30	3	50	15	15	10	10	27	11	60	75	3
10	1300	40	0.5	0.5	10	4	70	30	0	0	0	12	5	40	0	1
11	380	2.5	4.5	4	30	3	50	20	20	5	0	28	11	100	25	1
12	480	10	3	1.5	20	2	90	0	0	10	0	16	9	20	25	1
13	810	10	0.7	0.5	10	4	20	60	0	0	20	16	10	20	0	1
14	920	10	0.5	1	20	2	80	20	0	0	0	14	8	20	25	1
15	1680	30	1	0.5	5	3	80	20	0	0	0	19	6	100	0	1
16	1680	40	0.1	4	5	3	80	20	0	0	0	13	5	100	0	1
17	1200	20	0.8	1	10	3	80	20	0	0	0	18	6	20	0	1
18	1480	30	0.5	0.5	5	4	80	20	0	0	0	14	4	100	0	1

Finally, the macroinvertebrates community structure was visualised using Canonical Correspondence Analysis (CCA) (ter Braak 1986) aiming to show affinities of each species for selected environmental variables (without transformation) and to determine the spatial distribution of the invertebrate community. As a complement to the two first CCA axis representation (which explained most of the relative contribution of the variables), the species assemblages within the community were determined using cluster analysis and K-means cluster procedure performed on the CCA results using the coordinates of the species on the first five CCA axes.

3. Results

Taxonomic studies of Sébaou freshwater invertebrates were conducted since 1984, leading to identify more than 400 species belonging to various zoological groups (Lounaci et al. 2000). Our study was restricted to 55 species belonging to three important taxa : mayflies (22 species), stoneflies (14 species) and blackflies (19 species).

From a quantitative point of view, abundance and occurrence of the species in the Sébaou drainage basin, considering separately each of the three taxonomic groups, revealed 3 kinds of distribution. (i) Dominant species, i.e. abundant ($> 500 \text{ ind./m}^2$) and occurrent species (present in more than 50 % of the sites) represented by mayflies such as *Baetis punicus* which is the most frequent and abundant species, and is the Algerian vicariant of *B. alpinus*, *Baetis* gr. *rhodani* and *Caenis luctuosa* (Fig. 2a) ; and blackflies such as *Simulium intermedium*, *Simulium velutinum*, and *Simulium pseudequinum* (Fig. 2b). (ii) Moderately abundant ($> 100 \text{ ind./m}^2$) and frequent (present in more than 10 % of the sites) species belonging to the three taxonomic groups : stoneflies, e.g. *Protonemura algirica* and *Protonemura* sp. (Fig. 2c) ; blackflies, e.g. *Prosimulium rufipes* and *Prosimulium albense* (Fig. 2b) ; and mayflies, e.g. *Caenis pusilla* and *Rhithrogena* gr. *germanica* (Fig. 2a). (iii) Low abundant ($< 100 \text{ ind./m}^2$) and low occurrent (less than 10 % of the sites) species, well represented in the three taxonomic groups (Fig. 2).

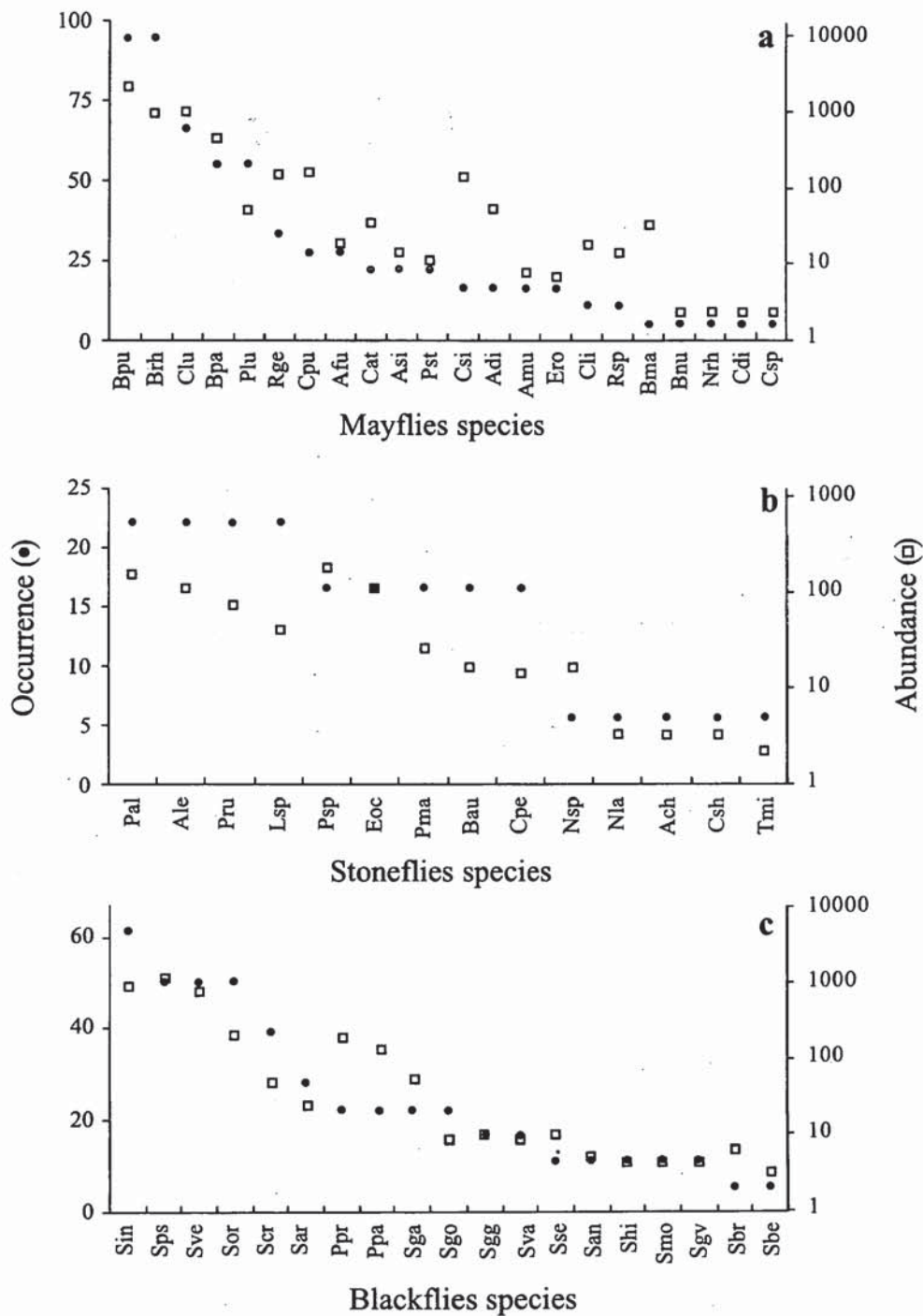


Fig. 2. Occurrence (percentage of sites where the species is present) and abundance (total number of individuals per m²) of the a) 22 mayflies species, b) 14 stoneflies species and c) 19 blackflies species. Species abundances represented in log scale to avoid undue influence of the most abundant species on the figure. See Appendix 1 for species codes.

Fig. 2. Fréquence (pourcentage de stations où l'espèce considérée a été inventoriée) et abondance (nombre total d'individus par m²) pour les a) 22 espèces d'Ephéméroptères, b) 14 espèces de Plécoptères, et c) 19 espèces de Simulies. Les abondances ont été représentées en échelle logarithmique de manière à éviter une influence excessive des espèces dominantes sur la figure. Voir l'Annexe 1 pour les codes des espèces.

Considering the species diversity (Shannon diversity index), Fig. 3 shows a clear upstream-downstream gradient. Diversity was low for the lowland sites, but the slope of the Lowess curve showed a straight increase, reaching maximal values in intermediate altitude, i.e. between 200 and 500 metres. Then, diversity slightly decreased up to an elevation of 800 metres. Finally, above this altitude, diversity still decreased but the Lowess slope was gentle.

Considering the spatial distribution of the species according to the 16 environmental descriptors, some variables accounted for a well known upstream-downstream gradient of physical and biological features (Illies & Botosaneanu 1963, Vannote et al. 1980, Wasson 1989), therefore, a highly significant Pearson correlation ($r > 0.5$, $p < 0.001$) was found between 9 of the 16 variables. As these correlated variables could add noise and bias the statistical analyses (ter Braak & Looman 1995), they were removed from the data matrix. The seven remaining variables were four micro-scale topographical variables, i.e. percentage of pebbles, gravel and silt, and water current velocity; two biological variables, i.e. aquatic and terrestrial vegetation cover; and one macro-scale variable (i.e. altitude) acting as an integrator of the longitudinal gradient. The CCA was thus realised on 55 species, 7 en-

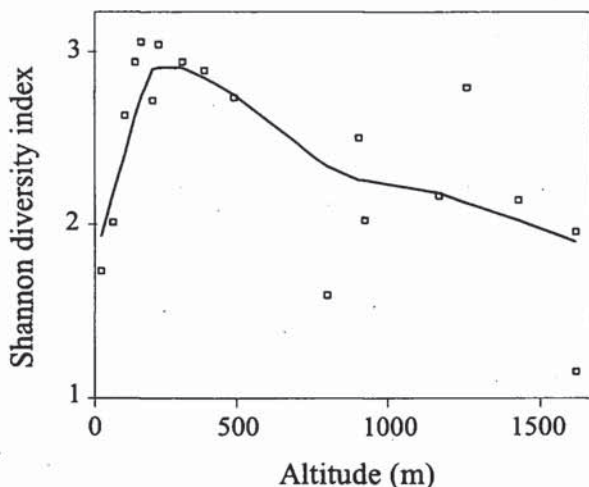


Fig. 3. Invertebrate diversity (Shannon diversity index) in the 18 stations ranked according to increasing altitude. Smoothing was performed using Lowess non-parametric smoother (solid line) with tension $f = 0.5$ (see text for detail).

Fig. 3. Evolution de la diversité spécifique (indice de Shannon) de 18 stations en fonction de l'altitude. L'ajustement a été réalisé par une fonction non-paramétrique de type Lowess (trait continu) avec une tension $f = 0.5$ (voir texte pour plus de détail).

vironmental variables and 18 stations. The consideration of the species assemblage using multivariate statistical methods (CCA and hierarchical classification) showed different species groups on the CCA F1-F2 plane (Fig. 4) representing the spatial distribution of the species according to the environmental features considered. Considering F1-F2 CCA plane, axis 1 represented mainly a longitudinal gradient, showing positive values for lowland and piedmont species and negative values for altitude related species. Axis 2 exhibited more complex features and we can assume that it represented a specialisation factor according to substrate size and the streambed coverage by terrestrial vegetation (Fig. 4a). Considering the species assemblage, the ordination diagram allowed three main groups to be distinguished (Figs. 4b & 4c) and statistically identified by the K-means cluster procedure, with a maximal convergence of the three classes centers ($p < 0.001$) obtained after five K-means iterations. Group 1 represented species mainly restricted to head-water mountain streams with large substrates and high current velocity, and only *Cloeon dipterum* exhibited a different habitat, as this species is exclusive of slow flowing warm streams. The other species belonging to this group can be considered as rheophilous. This assemblage was characterised by the abundance of stoneflies, with 6 species within the 14 species belonging to the group 1. The second group was less distinct from the previous one (Fig. 4c) and composed by a more diverse species assemblage. It is characterised by deposited substrates (silt) and aquatic vegetation. This group was mainly composed of mayflies and blackflies, and only two stoneflies species were recorded. The third group was associated with terrestrial vegetation coverage, large substrates (pebbles). This six species assemblage was mainly composed by stoneflies (five species), and only one blackfly species (*Simulium monticola*) was recorded. Finally, among the entire assemblage, some species were found independent from the three groups and can therefore be considered i) as ubiquitous when species are located in the middle of the CCA plane (e.g. *Baetis punicus* or *Simulium* gr. *variegatum*), or ii) with a narrow spatial distribution highly influenced by one or several environmental variable (e.g. *Caenis* sp.).

4. Discussion

The Sébaou stream invertebrates fauna was characterised by lower species diversity than European streams (Lounaci-Daoudi 1996), which could be due to the high water temperatures, allowing therefore a larger spatial distribution of eurythermous taxa usually

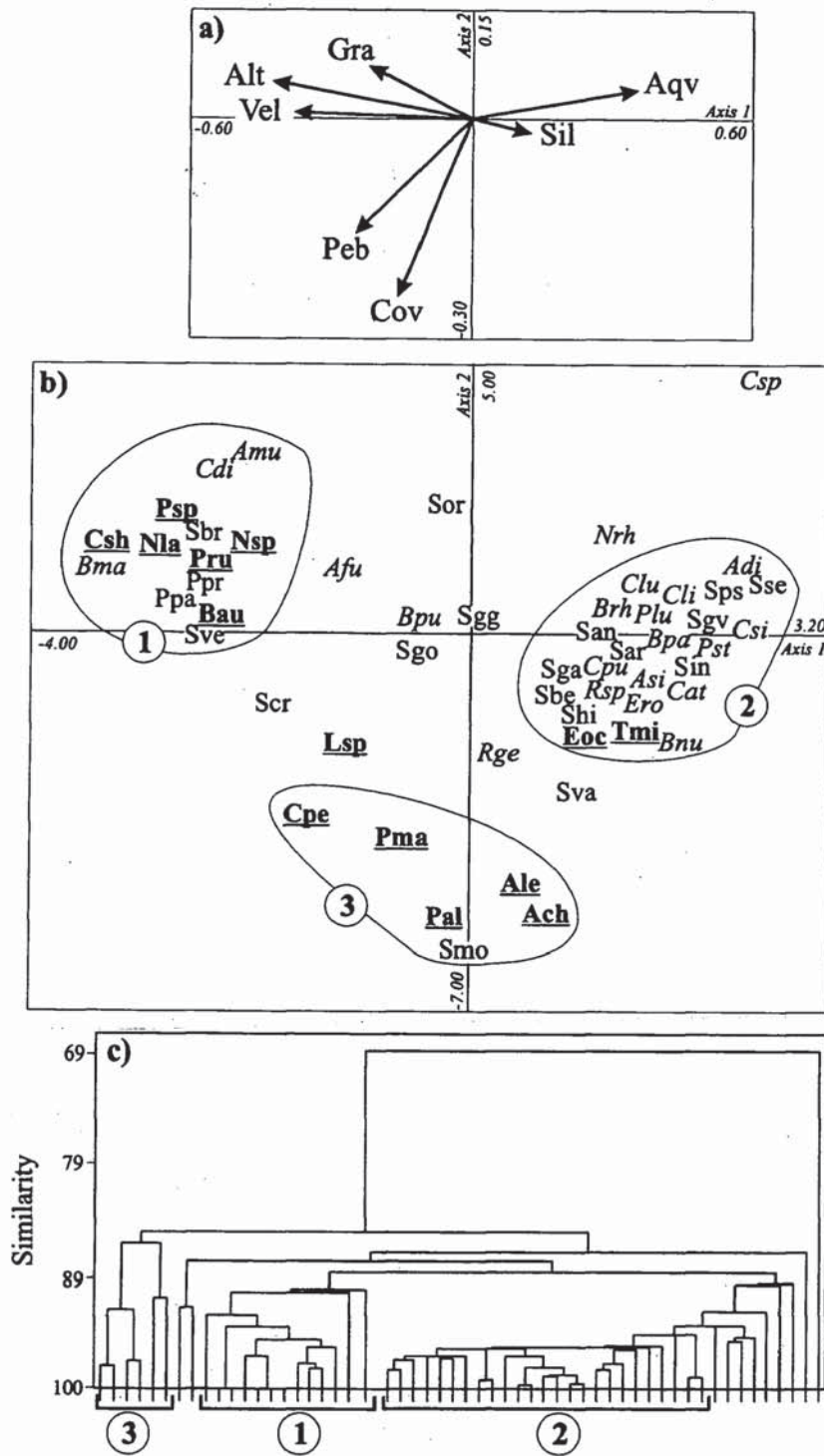


Fig. 4. F1x2 plane of the canonical correspondence analysis (CCA) between insect species abundances and the 7 selected environmental variables. a) representation of environmental variables (see Table 1 for variables codes). b) representation of species assemblage according to environmental variables, normal font : blackflies ; italic font : mayflies ; bold and underlined font : stoneflies (see Appendix 1 for species codes). The 3 species groups identified by cluster analysis are reported on the CCA plane. c) cluster analysis of the 2 first axis coordinates of CCA showing the 3 species groups, other species are dispersed across the similarity gradient.

Fig. 4. Plan F1x2 de l'analyse canonique des correspondances (CCA) entre les abondances des espèces d'insectes et les 7 variables environnementales retenues. a) représentation des variables environnementales (voir Tableau 1 pour les codes des variables). b) représentation des associations d'espèces en fonction des variables environnementales, caractères normaux : Simulidé ; italique : Ephéméroptères ; gras et souligné : Plécoptères (voir l'Annexe 1 pour les codes des espèces). Les 3 groupements d'espèces identifiés par la classification hiérarchique ont été reportés sur le plan F1x2. c) Classification hiérarchique des coordonnées des espèces sur les deux premiers axes de la CCA montrant les 3 groupements d'espèces, les autres espèces sont dispersées au sein du gradient de similarité.

restricted to the European lowland plains streams. For example, the stoneflies and mayflies genus *Habrophlebia*, *Cloeon*, *Perla* and *Leuctra*, usually colonise European piedmont and lowland waters (Williams & Feltmate 1992, Giller & Malmqvist 1998), whereas they were found in the Sébaou headwaters mountain streams (Fig. 4). As a consequence, fewer habitats are vacant for stenothermous species, inducing lower species diversity due to the lack of potential habitats and to the presence of competitors. In the same way, the upstream-downstream species replacement known in temperate streams (Allan 1975, Ward 1986) did not or scarcely occurred in the Sébaou streams (Lounaci 1987, Lounaci-Daoudi 1996). However, according with Giudicelli (1984) and Giudicelli et al. (1985), the North African particular climatic high altitude characteristics induce an adaptation of some headwater taxa, inducing a high rate of endemism, i.e. 36 % of the mayfly species and 21 % of the stonefly species in the Sébaou basin (Appendix 1).

Considering the spatial distribution of the species, stream macroinvertebrates are known to be greatly affected by their biotic and abiotic environment (Dobson & Hildrew 1992, Williams & Feltmate 1992). In the same way, the community structure attributes (i.e. species composition and diversity, abundance or occurrence of the species) are also influenced by environmental patterns (Wohl et al. 1995, Bournaud et al. 1996, Hawkins et al. 1997, Jacobsen et al. 1997). Therefore, the knowledge of the relationships between organisms and their environment are of crucial importance to understand the functioning of ecological systems (Begon et al. 1996).

The altitudinal species diversity gradient we found in the Sébaou wadi basin (i.e. species diversity decrease with altitude) (Fig. 3) was already reported in tropical and temperate streams (Hynes 1971, Williams & Hynes 1971, Allan 1975, Ward 1986) and usually attributed to the temperature lowering with altitude (Allan 1995, Jacobsen et al. 1997). However, a more detailed study of the results showed more complex features: The low diversity obtained in the downstream lowland plain of the Sébaou wadi can be explained by the interaction of several phenomena. Owing to the accented Mediterranean climate, rivers are subjected to high water temperatures (> 30° C) acting as a restricting factor for the fauna (Williams & Feltmate 1992). In the same way, high water temperature induces a high evaporation rate inducing low current velocities and therefore low topographical heterogeneity in these deposition areas (Lounaci 1987), leading to low habitat diversity, and consequently to a reduced diversity. Mo-

reover, these lowland plains are subjected to high disturbances induced by scarce but violent floods and anthropogenic pollution. In these densely populated areas, the pollution is enhanced by reduced flow rate and only few pollutotolerant species can survive. Therefore these areas are colonised by eurythermous and widespread mayfly species such as *C. luctuosa*, *B. gr. rhodani*, (Fig. 2a) and *Caenis* sp. which is characteristic of these areas (Fig. 4b). Some pollutotolerant blackflies were also found (*S. pseudequinum*, *S. intermedium*, *S. velutinum*), as high load of particulate organic matter provided abundant feeding resources to these species, sustaining therefore high individual densities (Fig. 2b) but low diversity (Fig. 3).

Piedmont areas showed the higher diversity (Fig. 3). This assemblage was mainly composed of mayflies and blackflies (Fig. 4). These areas were characterised by moderate water temperatures and velocities, gentle slope, aquatic vegetation and intermediate flooding disturbance amplitude and frequency. They can be considered as the mid-reaches of the watercourse with an invertebrate community which was typically composed by grazers and collectors (Vannote et al. 1980). These characteristics, according with the intermediate disturbance hypothesis (Connell 1978, Resh et al. 1988), allowed a large range of habitats and therefore the colonisation by numerous species (i.e. between 15 and 20 species of the three considered taxonomic groups per station) corresponding essentially to the group 2 previously defined (Fig. 4). The species assemblage was characterised by low altitude (< 400 m) and piedmont species avoiding the warm lowland waters such as *Potamanthus luteus*. In the same way, *Simulium argenteostriatum* was found in these intermediate sites, whereas this species colonise lowland waters in Europe. The observed distribution can therefore be considered as an avoidance of warm Algerian lowland waters where conductivity is often very high (Gagneur & Thomas 1998). Finally, *Eoperla ochracea* and *Tyrrhenoleuctra minuta* exhibited an unusual habitat for stoneflies, as these species are usually restricted to coldwater streams (Williams & Feltmate 1992).

Headwaters streams showed a low diversity (Fig. 3) mainly due to the high daily and seasonal amplitude of temperature, which constitutes one of the most restricting factors for the benthic macroinvertebrates (Jacobsen et al. 1997), leading to low abundances (Fig. 2) and growth rates (Allan 1995). This species assemblage was represented by the group 1 (Fig. 4) which is composed of few rheophilous species and dominated by stoneflies. These species are characteristic of cold headwaters streams (> 1000 m) with steep slopes (20

to 40 %) and large substratum (boulders, pebbles, gravel).

However, the altitudinal gradient, did not explain the entire community structure, as the group 3 was found to be independent from altitude (Fig. 4). These species, mainly belonging to stoneflies can be considered as a particular assemblage even if two species (*Leuctra* sp. and *Simulium cryophilum*) were also found in headwater streams. This assemblage occurs in cold-water springs. These areas typically have low diversities due to their high environmental and chemical stability (Williams & Feltmate 1992). These species are principally associated to terrestrial vegetation and large substrates (pebbles) with a moderated association with altitudinal characteristics.

Within the limits of the study material (mayflies, stoneflies and blackflies), these results sustained Townsend's (1989) hypotheses stipulating that no single model adequately describe all communities. The assemblage patterns we found showed the complexity of the Sébaou river invertebrates community assemblage, which was ruled by various biotic and abiotic factors. Within these characteristics and according to Gagneur (1994), and Gagneur & Thomas (2000), thermal regime of the streams, high summer temperatures as well as reduced water discharge in summer induce differences between European and North African invertebrates assemblages attributes. We can therefore hypothesise that species life histories as well as biotic interactions ruling the community structure are different from Europe and should be studied in more detail, aiming to a better understanding of the ecological functioning of North African streams.

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References

- Alder P.H. & McCreadie J.W. 1997. — The hidden ecology of black flies : sibling species and ecological scale. *Amer. Entomol.*, 43 : 153-161.
- Allan J.D. 1975. — Faunal replacement and longitudinal zonation in an alpine stream. *Verh. Internat. Verein. Limnol.*, 19 : 1646-1652.
- Allan J.D. 1995. — *Stream ecology, structure and function of running waters*. Chapman & Hall, London : 338p.
- Barmuta L.A. 1989. — Habitat patchiness and macrobenthic community structure in an upland stream in temperate Victoria, Australia. *Freshwater Biol.*, 6 : 229-538240.
- Begon M., Harper J.L. & Townsend C.R. 1996. — *Ecology : individuals, population, and communities*, Third edit., Blackwell Science, Oxford : 1068p.
- Boumaiza M. & Clergue-Gazeau M. 1986. — Le peuplement simuliidien de la Tunisie. I - Inventaire faunistique et biogéographique (Diptera, Nematocera). *Annl. Limnol.*, 22 : 31-39.
- Boumaiza M. & Thomas A.G.B. 1986. — Répartition et écologie des Ephéméroptères de Tunisie (1^{ère} partie) (Insecta, Ephemeroptera). *Archs Inst. Pasteur Tunis*, 63 (4) : 567-599.
- Boumaiza M. & Thomas A.G.B. 1995. — Distribution and ecological limits of Baetidae vs the other mayfly families in Tunisia : a first evaluation (Insecta, Ephemeroptera). *Bull. Soc. Hist. nat. Toulouse*, 131 : 27-33.
- Bournaud M., Cellot B., Richoux P. & Berrahou A. 1996. — Macroinvertebrate community structure and environmental characteristics along a large river : congruity of patterns for identification to species or family. *J. N. Am. Benthol. Soc.*, 15 : 232-253.
- Bouzidi A. & Giudicelli J. 1987. — Contribution à l'étude faunistique et écologique des Simulies du Maroc (Diptera, Simuliidae). II - *Simulium (Obuchovia) marocanum* n.sp. et les espèces méditerranéennes d'*Obuchovia* Rubzov. *Annl. Limnol.*, 23 : 185-195.
- Cailleux A. 1954. — Limites dimensionnelles des noms des fractions granulométriques. *Bull. Soc. Geol. Fr.*, 4 : 643-646.
- Clergue-Gazeau M., Lek S. & Lek S. 1991. — Les Simulies d'Afrique du Nord. Nouvelles données sur la répartition de la faune du Maroc et biogéographie des espèces maghrébines (Diptera, Simuliidae). *Rev. Hydrobiol. Trop.*, 24 : 47-59.
- Cleveland W.S. 1979. — Robust locally-weighted regression and scatterplot smoothing. *J. Amer. Statist. Assn.*, 74 : 829-836.
- Connell J.H. 1978. — Diversity in tropical rainforests and coral reefs. *Science*, 199 : 1302-1310.
- Degani G., Herbst G.N., Ortal R., Bromley H.J., Levanon D., Netzer Y., Harari N. & Glazman H. 1993. — Relationship between current velocity, depth and the invertebrate community in a stable river system. *Hydrobiologia*, 263 : 163-172.
- Dobson M. & Hildrew A.G. 1992. — A test of resource limitation among shredding detritivores in low order streams in southern England. *J. Anim. Ecol.*, 61 : 69-77.
- Gagneur J. 1994. — Flash floods and drying up as major disturbances upon benthic communities in North-African wadis. *Verh. Internat. Verein. Limnol.*, 25 : 1807-1811.
- Gagneur J. & Aliane N. 1991. — Contribution à la connaissance des plécoptères d'Algérie. In : J. Alba-Tercedor and A. Sanchez-Ortega (eds). *Overview and strategies of Ephemeroptera and Plecoptera*. Sandhill crane Press, Gainesville : 311-323.
- Gagneur J. & Thomas A.G.B. 1988. — Contribution à la connaissance des Ephéméroptères d'Algérie. I. Répartition et écologie (1^{ère} partie) (Insecta, Ephemeroptera). *Bull. Soc. Hist. nat. Toulouse*, 124 : 213-223.
- Gagneur J. & Thomas A.G.B. 2000. — Factors influencing the repartition of aquatic diptera in north-western Algerian wadis. *Verh. Internat. Verein. Limnol.*, 27 : (in press).
- Gagneur J., Thomas A.G.B. & Vitte B. 1985. — Première citation d'une espèce du genre *Paraleptophlebia* en Afrique du Nord. *Bull. Soc. Hist. nat. Toulouse*, 121 : 141-143.
- Giller P.S. & Malmqvist B. 1998. — *The biology of streams and rivers*. Oxford university press, Oxford, New York, Toronto : 296 p.
- Giudicelli J. 1984. — Les sources du Moyen Atlas et du Rif (Maroc) : faunistique (description de deux espèces nouvelles de Trichoptères), écologie, intérêt biogéographique. *Bijdr. Dierk.*, 54 : 83-100.
- Giudicelli J., Dakki M. & Dia A. 1985. — Caractéristiques abiotiques et hydrobiologiques des eaux courantes méditerranéennes. *Verh. Internat. Verein. Limnol.*, 22 : 2094-2101.

- Hawkins C.P., Hogue J.N., Decker L.M. & Feminella J.W. 1997. — Channel morphology, water temperature, and assemblage structure of stream insects. *J. N. Am. Benthol. Soc.*, 16 : 728-749.
- Hynes H.B.N. 1971. — Zonation of the invertebrate fauna in a West Indian stream. *Hydrobiologia*, 38 : 1-8.
- Illies J. & Botosaneanu L. 1963. — Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes considérées surtout du point de vue faunistique. *Mitt. Int. Verein. Theor. Angew. Limnol.*, 12 : 1-57.
- Jacobsen D., Schultz R. & Encalada A. 1997. — Structure and diversity of stream invertebrate assemblages : the influence of temperature with altitude and latitude. *Freshwater Biol.*, 38 : 247-261.
- Lenat D.R. 1988. — Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. *J. N. Am. Benthol. Soc.*, 7 : 222-233.
- Lounaci A. 1987. — Recherches hydrobiologiques sur les peuplements d'invertébrés benthiques du bassin de l'oued Aïssi (Grande Kabylie). Thèse de Magister, Université d'Alger : 133 p.
- Lounaci-Daoudi D. 1996. — Travaux sur la faunistique, l'écologie et la biogéographie des insectes aquatiques du réseau hydrographique du Sébaou. Thèse de Magister, Université de Tizi-Ouzou, 152 p.
- Lounaci A., Brosse S., Ait Mouloud S., Lounaci-Daoudi D. & Mebarki N. 2000. — Current knowledge of benthic invertebrate diversity in an Algerian stream : a species check-list of the Sébaou River basin (Tizi-Ouzou). *Bull. Soc. Hist. nat. Toulouse*, 136 : (in press).
- Lugthart G.J. & Wallace J.B. 1992. — Effects of disturbance on benthic functional structure and production in mountain streams. *J. N. Am. Benthol. Soc.*, 11 : 138-164.
- Malicky H. & Lounaci A. 1987. — Beitrag zur Taxonomie und Faunistik der Köcherfliegen von Tunesien, Algerien und Marokko (Trichoptera). *Opusc. Zool. Flumin.*, 14 : 1-20.
- McCreadie J.W., Adler P.H. & Burger J.F. 1997. — Species assemblages of larval black flies (Diptera:Simuliidae) : random or predictable? *J. N. Am. Benthol. Soc.*, 16 : 760-770.
- Moubayed J., Ait-Mouloud S. & Lounaci A. 1992. — Les Chironomides (Diptera) d'Algérie. I. Bassin de l'oued Aïssi (Grande Kabylie). *Nachr. Bl. Bayer. Ent.*, 41 : 21-29.
- Omerod S.J., Rundle S.D., Wilkinson S.M., Daly G.P., Dale K.M. & Juttner I. 1994. — Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. *Freshwater Biol.*, 32 : 309-322.
- Ramirez A. & Pringle C.M. 1998. — Structure and production of a benthic insect assemblage in a neotropical stream. *J. N. Am. Benthol. Soc.*, 17 : 443-463.
- Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. 1988. — The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.*, 7 : 433-455.
- ter Braak C.J.K. 1986. — Canonical Correspondence Analysis : a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67 : 1167-1179.
- ter Braak C.J.F. & Looman C.W.N. 1995. — Regression. *Data analysis in community and landscape ecology*. Jongman R.G.H., ter Braak C.J.F. & Van Tongeren O.F.R. (Eds), Cambridge University Press 29-77.
- Thomas A.G.B. 1998. — A provisional checklist of the Mayflies of North Africa (Ephemeroptera). *Bull. Soc. Hist. nat. Toulouse*, 134 : 13-20.
- Townsend C.R. 1989. — The patch dynamics concept of stream community ecology. *J. N. Am. Benthol. Soc.*, 8 : 36-50.
- Trexler J.C. & Travis J. 1993. — Non-traditional regression analyses. *Ecology*, 74 : 1629-1637.
- Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. 1980. — The river continuum concept. *Can. J. Fish. Aquat. Sci.*, 37 : 130-137.
- Vaillant F. 1955. — Recherches sur la faune macrolé (hydropétrique s.l.) de France, de Corse et d'Afrique du Nord. *Mem. Mus. Natn. Hist. Nat., Paris, Sér. A*, 11 : 1-258.
- Vaillant F. & Gagneur J. 1998. — The diptera Empididae Hemerodrominae from western Algeria and the middle Atlas of Morocco. *Ann. Soc. Entomol.*, 34 : 365-384.
- Ward J.V. 1986. — Altitudinal zonation in a Rocky mountain stream. *Arch. Hydrobiol.*, 74 : 133-199.
- Wasson J.G. 1989. — Eléments pour une typologie fonctionnelle des eaux courantes. 1. Revue critique de quelques approches existantes. *Bull. Ecol.*, 20 : 109-127.
- Williams D.D. & Feltmate B.W. 1992. — *Aquatic insects*. CAB International : 358 p.
- Williams T.R. & Hynes H.B.N. 1971. — A survey of the fauna of streams on Mount Elgon, East Africa, with special reference to the Simuliidae (Diptera). *Freshwater Biol.*, 1 : 227-248.
- Wohl D.L., Wallace J.B. & Meyer J.L. 1995. — Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). *Freshwater Biol.*, 34 : 447-464.

Appendix.

	code	sites																	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Mayflies																			
<i>Acentrella sinaica</i> Bogoescu	Asi	0	0	0	2	1	0	0	2	0	0	1	0	0	0	0	0	0	0
<i>Afrotiptum dimorphicum</i> Soldan & Thomas (*)	Adi	0	0	4	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alainites gr. muticus</i>	Amu	0	0	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	2
<i>Baetis gr. rhodani</i>	Brh	4	2	5	5	5	4	3	2	4	0	3	2	3	2	3	2	4	3
<i>Baetis maurus</i> Kimmins	Brna	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
<i>Baetis numidicus</i> Soldan & Thomas (*)	Bnu	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Baetis pavidus</i> Grandi	Bpa	2	2	2	4	5	0	4	4	3	0	4	0	0	0	0	0	0	1
<i>Baetis punicus</i> Thomas, Boumaiza & Soldan (*)	Bpu	3	2	3	5	5	2	2	4	5	5	5	4	5	4	5	5	5	0
<i>Caenis luctuosa</i> (Burmeister)	Clu	5	4	4	4	5	0	3	2	5	0	5	2	0	0	4	0	0	2
<i>Caenis pusilla</i> Navas	Cpu	0	0	0	0	0	0	3	4	3	0	4	1	0	0	0	0	0	0
<i>Caenis sp.</i>	Csp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Choroterpes (C.) atlas</i> Soldan & Thomas (*)	Cat	0	0	0	4	2	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Choroterpes (E.) lindrothi</i> Peters (*)	Cli	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cloeon dipterum</i> (L.)	Cdi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cloeon gr. simile</i>	Csi	0	0	4	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ecdyonurus rothschildi</i> Navas (*)	Ero	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0
<i>Habrophlebia gr. fusca</i>	Afu	0	0	0	0	0	0	0	0	0	0	2	1	1	0	2	0	0	1
<i>Nigrobaetis rhiithralis</i> (Soldan & Thomas) (*)	Nrh	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Potamanthus luteus</i> (L.)	Plu	1	1	2	1	3	0	2	2	2	0	2	0	1	0	0	0	0	0
<i>Procloeon stagnicola</i> Soldan & Thomas (*)	Pst	0	0	2	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Rhithrogena gr. germanica</i>	Rge	0	0	0	2	2	0	0	0	0	0	4	4	3	4	0	0	0	0
<i>Rhithrogena sp.</i>	Rsp	0	0	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0
Stoneflies																			
<i>Afroperlodes lecerfi</i> (Navas)	Ale	0	0	0	0	0	0	0	0	0	2	4	0	1	0	0	0	1	0
<i>Amphinemura chiffensis</i> (Aubert) (*)	Ach	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Brachyptera auberti</i> (Consiglio)	Bau	0	0	0	0	0	2	0	0	0	2	0	0	0	0	0	0	2	0
<i>Capnionemura petitipterae</i> Aubert (*)	Cpe	0	0	0	0	0	1	0	0	0	2	0	0	0	2	0	0	0	0
<i>Capnopsis schilleri</i> (Rostock)	Csh	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Eoperla ochracea</i> (Kolbe)	Eoc	0	0	0	0	0	0	4	3	3	1	0	0	0	0	0	0	0	0
<i>Leuctra sp.</i>	Lsp	0	0	0	0	0	0	0	0	0	0	2	0	2	3	0	0	2	0
<i>Nemoura lacustris</i> Pictet	Nla	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
<i>Nemoura sp.</i>	Nsp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
<i>Perla marginata</i> (Panzer)	Pma	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0
<i>Protonemura algirica</i> (Aubert) (*)	Pal	0	0	0	0	0	2	0	0	0	0	0	4	0	4	0	0	2	0
<i>Protonemura ruffoi</i> Consiglio	Pru	0	0	0	0	0	1	0	0	0	4	0	1	0	0	3	0	0	0
<i>Protonemura sp.</i>	Psp	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1	4
<i>Tyrhenoleuctra minuta</i> (Klapalek)	Tmi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Blackflies																			
<i>Prosimulium (P.) albense</i> Rivosecchi	Ppa	0	0	0	0	0	0	0	0	0	4	0	0	0	0	3	0	4	2
<i>Prosimulium (P.) rufipes</i> (Meigen)	Ppr	0	0	0	0	0	0	0	0	0	4	0	0	0	0	3	0	4	2
<i>Simulium (E.) gr. aureum</i>	Sga	0	0	0	0	0	0	0	2	4	0	3	0	0	0	0	0	1	0
<i>Simulium (E.) velutinum</i> (Santos Abreu)	Sve	2	1	5	5	5	0	2	2	4	0	3	0	0	0	0	0	0	0
<i>Simulium (N.) angustitarse</i> (Lundström)	San	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0
<i>Simulium (N.) brevidens</i> (Rubzov)	Sbr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
<i>Simulium (N.) cryophilum</i> (Rubzov)	Scr	0	0	0	0	0	0	0	0	0	3	0	2	2	2	2	2	2	0
<i>Simulium (N.) gr. vernum</i>	Sgv	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Simulium (S.) argentostriatum</i> Strobl.	Sar	0	0	0	1	1	0	0	2	2	0	2	0	0	0	0	0	0	0
<i>Simulium (S.) gr. ornatum</i>	Sgo	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1
<i>Simulium (S.) gr. variegatum</i>	Sgg	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	0
<i>Simulium (S.) hispaniola</i> Grenier	Shi	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Simulium (S.) intermedium</i> Roubaud	Sin	0	5	3	5	2	0	2	5	5	0	3	2	0	0	1	2	0	0
<i>Simulium (S.) monticola</i> Friederichs	Smo	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>Simulium (S.) ornatum</i> Meigen	Sor	0	4	2	0	3	2	0	0	0	0	2	0	0	0	3	2	2	4
<i>Simulium (S.) variegatum</i> Meigen	Sva	0	0	0	0	0	0	0	2	1	0	0	2	0	0	0	0	0	0
<i>Simulium (T.) bezii</i> Corti	Sbe	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
<i>Simulium (W.) pseudequinum</i> Seguy	Sps	5	5	4	5	5	0	2	3	5	0	3	0	0	0	0	0	0	0
<i>Simulium (W.) sergenti</i> Edwards	Sse	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 1. Mean abundance/m² of the species for each of the 18 sites and species codes used in the figures; abundances were sorted in five classes : 0 : absent, 1 : 1 to 50 individuals/m², 2 : 51 to 200 individuals/m², 3 : 201 to 500 individuals/m², 4 : 501 to 2000 individuals/m², 5 : > 2000 individuals/m². (*) endemic species of North Africa.

Annexe 1. Abondance moyenne par m² des espèces pour les 18 stations et codes utilisés dans les figures ; cinq classes d'abondance ont été considérées : 0 : absent, 1 : 1 à 50 individus/m², 2 : 51 à 200 individus/m², 3 : 201 à 500 individus/m², 4 : 501 à 2000 individus/m², 5 : > 2000 individus/m². (*) espèces endémiques de l'Afrique du Nord.