LONG-TERM CHANGES IN THE EPHEMEROPTERA OF THE RIVER RHONE AT LYON, FRANCE, ASSESSED USING A FUZZY CODING APPROACH

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Ephemeroptera at one site of the Upper Rhône River (France) were examined using multivariate analyses to determine: (i) relationships among twelve species traits; (ii) the long-term temporal organization of the faunistic assemblage; (iii) the relationship between species traits and the temporal distribution of the faunistic assemblage.

Changes in the habitat mosaic from 1959 to 1982 more or less correspond to a decreasing gradient of substrate granulometry and current velocity, with more rheophilous tendencies for the ephemeropteran assemblage of the 1959-1967 period. This gradient also corresponds to a contrast between: (i) long-lived species, very demanding as far as substrate is concerned and displaying a high dissemination potential and (ii) species that exhibit a small size, a short life cycle, wide environmental requirements, but low dissemination potentialities, which should be more effective in disturbed habitats. The flush-outs of the upstream reservoirs and the completion of the Pierre-Bénite dam appear to be the determining elements of theses changes over the sampling period. They have led to a simplified redistribution of ecological niches through growing uniformity of the substratum and possible sources of food.

INTRODUCTION

The faunistic assemblage of a river ecosystem integrates the spatial and temporal variability of the habitat. Therefore, species with certain combinations of adaptations, especially traits related to survival and reproduction are assumed to be selected. Consequently, synthesis of autecological information of macro-invertebrate species based on published accounts can be used to demonstrate some of the environmental changes.

In its early stages, the ecological study of the French Upper Rhône was limited to a fragmentary inventory of the littoral fauna (LAFON, 1953). However, it soon became obvious that other methods of studying such a large and difficult to sample ecosystem would be necessary. Light traps seemed to constitute a useful source of information since adult insects, and in particular night-flying Ephemeroptera, are attracted by light. That is why systematic light trapping has been carried out in Lyon since 1959 on the banks of the Rhône, mainly at the beginning of the summer (FONTAINE, 1982; USSEGLIO-POLATERA, P. 1985). Although the light trap only sampled adults it could reflect the species composition of some benthic insect assemblages (see for example BOURNAUD *et al.* (1983) for Trichoptera).

There has been an intuitive acknowledgement that the faunistic assemblage of a river ecosystem integrates the spatial and temporal variability of the habitat. Therefore, species with certain combinations of adaptations and affinities, especially traits related to survival and reproduction, are assumed to be selected (SOUTHWOOD, 1988; LADLE & LADLE, 1992; TOWNSEND & HILDREW, 1994). Consequently, to explain the local distribution of aquatic organisms, which is a central aim of ecology, we must study the link between the traits of species and environmental variability. However, if population dynamics can be assumed to be governed essentially by autecological processes (a basic assumption of TOWNSEND & HILDREW, 1994), the dynamics of communities may be predicted from the knowledge of the species' traits of the faunistic assemblage. This can demonstrate in a complementary way some of the characteristics of the environment and bring out clear information about spatial or temporal changes in biotopes (USSEGLIO-POLATERA, 1991; 1993).

Based on such an approach, the objective of this study was to examine the ephemeropteran assemblage of the Rhône River, at Lyon, France in terms of: (i) population dynamics from 1959 to 1982; (ii) the relationships among the species' traits; (iii) the relationships between species' traits and population dynamics throughout the sampling period.

MATERIALS AND METHODS

Twenty nine species of Ephemeroptera were captured during the 1959-1982 period by light trapping during June and/or July of fourteen years (Fig. 1a; Appendix 1). The directional beam light trap, model n°. 1 (FONTAINE, 1982), was used. It was fitted with a Mazda MA 80 lamp emitting both visible and ultraviolet light. The trap was located in
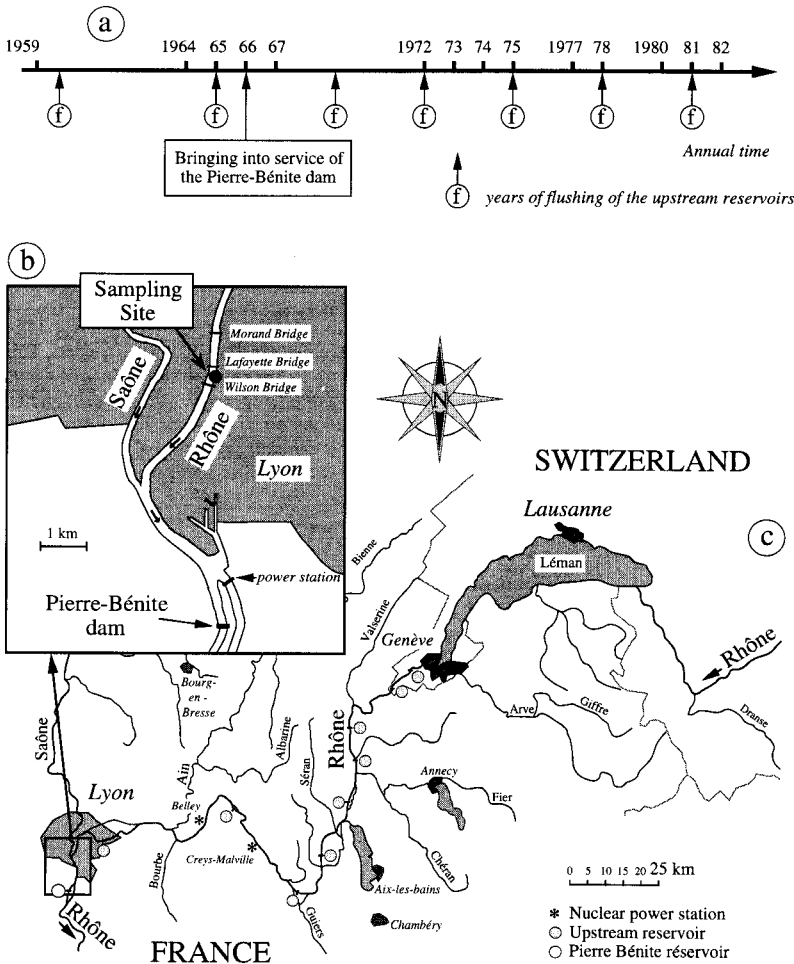
Fig. 1. Faunistic data: a: Years of the light trapping and the main disturbances of human origin in the river during the study period (also indicating the date at which the Pierre-Bénite dam was brought into service and the date of flushing of the reservoirs situated upstream from the study site); b and c: Location of the study site (two different scales).

Lyon, on a barge situated downstream from Lafayette Bridge, close to the left bank of the Rhône. At this point, the river flows between steep concrete banks. Its width is about 160 m and its mean annual discharge about 570 m³/s.

In 1966, the Pierre-Bénite dam, situated about eight kilometers downstream from the study site, was brought into service (Fig. 1b). This dam created a reservoir stretching up the Rhône as far as Morand Bridge and then caused a permanent high rise in the water level at the sampling station. The maximum depth is now between 5-6 m, instead of nearly 3-6 m before 1966. The sampling station was also submitted to regular summer flush-outs from the reservoirs situated upstream (Fig. 1c).

In this paper, autecological information was gathered from a very large and scattered literature. This information was reduced to twelve qualitative or semi-quantitative species' traits (= variables). For each of these species' traits (Table 1), the different modalities (= categories) of 19 ephemeropteran species were considered. Species extremely rare in catches (i.e. one or two individuals in only one or two monthly units) were not considered. This information was structured using a 'fuzzy coding' procedure (see USSEGLIO-POLATERA, 1991, 1993; BOURNAUD et al., 1992; CHEVENET et al., 1994), which uses positive scores to

describe the affinity of a species for different modalities of a given variable, in the following way: 0, the species had no link with a modality; 1, the species had only weak links with a modality; 2, the species had moderately strong links with the modality; and 3, the species was strongly related to the modality. As a result, the biological array consists of nineteen species x twelve species' traits, and included 49 relevant modalities (Table 1).

Because of the complexity of the relationships among the traits of a species or between the traits and population dynamics, a multivariate approach is required for their analysis (Fig. 2). First, both faunistic and biological tables were independently processed by correspondence analysis. Separate analysis of each data table brings out a principal axis (noted F1) which is the vector direction maximizing the projected variability (or inertia) in each array independently. The species may be ordinated along these resulting axes. Then, co-inertia analysis, a simultaneous ordination of the two data tables (DOLÉDEC & CHESSEL, 1994), was used to check for a relationship between the traits of a species and population dynamics. Indeed, it may be conceivable to isolate a new axis in one multidimensional space (noted as fauna axis') and a new axis in the other multidimensional space (noted as biological axis') so that

the covariance between the two new sets of projected scores is maximal. This maximal covariance means a maximal correlation and simultaneously maximal standard deviations of both new faunistic and biological scores (Fig. 2).
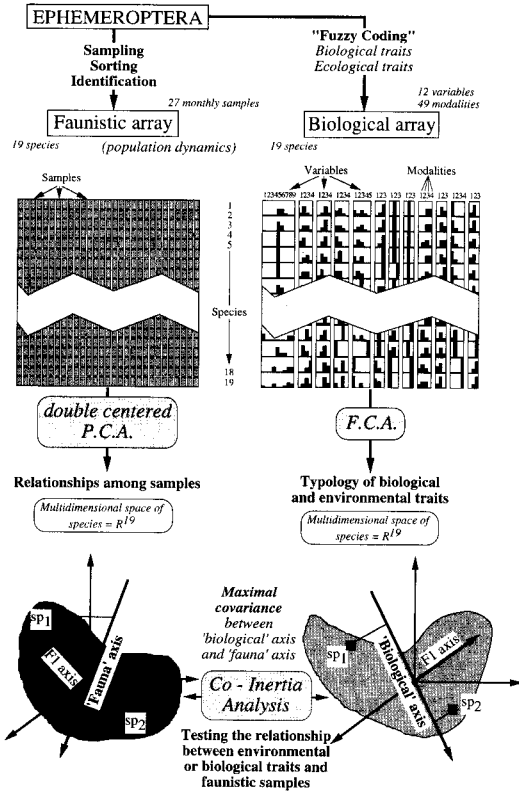
RESULTS

The faunistic data were processed by a double-centered principal component analysis (OKAMOTO, 1972). According to the eigenvalues (Fig. 3a), the two first axes are sufficient for demonstrating the structure in the data (67.9% of explained variance). The factorial plane of the two first axes arranges monthly samples in three groups according to annual time (Fig. 3b). The first group brings together the samples which were obtained

mainly before the Pierre-Bénite dam was completed (from 1959 to 1967). In this period, the Ephemeroptera assemblage was dominated by rheophilous species of Heptageniidae and *Baetis fuscatus* (Fig. 3c). This group is distinctly separated from samples of the 1978-1982 period in the F1 direction. This group is also distinctly isolated from samples of the 1972-1977 period, both in the F1 and F2 directions. The third group exhibits an Ephemeroptera assemblage dominated by Caenidae.

The biological array can also be processed by correspondence analysis, using a procedure described by CHEVENET *et al.* (1994). The two first axes explain 56% of the total inertia (Fig. 4a). The correlation ratios, which quantify the discrimination of modalities of each variable, make it possible to order the relevance of bio-

Table 1. Species' traits and modalities (= categories, plus their numbers used as labels in the figures) of Ephemeroptera used in this analysis.

Variable		Modality		Variable		Modality	
No	Name	No	Class	No	Name	No	Class
1	Substrate	1	hydrophytes	6	Potential size	1	≤ 5 mm
	(larvae)	2	algae			2	> 5-10 mm
		3	branches/roots/litter			3	> 10 mm
		4	organic detritus	7	Potential number	1	d ≤ 1000
		5	pebbles/cobbles		of descendants per	2	> 1000 - 3000
		6	gravel		reproductive cycle	3	> 3000
		7	sand	8	Potential number	1	< 1
		8	silt		of reproductive	2	1
		9	mud		cycles per year	3	≥ 2
2	Current speed	1	none	9	Dissemination	1	≤ 10 m
	(larvae)	2	low		potential	2	> 10 - 100 m
		3	intermediate		(larvae)	3	> 100 - 1000 m
		4	high			4	> 1000 m
3	Saprobity	1	xenosaprobic	10	Dissemination potential	1	≤ 100 m
		2	oligosaprobic		(imagines)	2	> 100 - 1000 m
		3	ß mesosaprobic			3	> 1000 m
		4	alpha mesosaprobic	11	Attachment to	1	clingers
4	Feeding habits	1	shredders		substrate	2	swimmers
	(larvae)	2	scrapers		(larvae)	3	burrowers
		3	deposit feeders			4	crawlers
		4	filterers	12	Body form	1	streamlined
5	Food (larvae)	1	detritus ≤ 1 mm		(larvae)	2	flattened
		2	detritus > 1 mm			3	cylindrical
		3	living plants ≤ 1 mm				
		4	living plants > 1 mm				
		5	living animals				

Fig. 2. Design of the analysis strategy to investigate relationships among samples or biological traits and between biological traits of Ephemeroptera and faunistic samples for 19 species collected by light trapping at Lyon (France). Species sp1 and sp2 are two given stands that are to be projected on both the biological axis' and the fauna axis' of the co-inertia analysis. These projections define new scores of stands that are the most covariant (for further details, see DOLÉDEC & CHESSEL, 1994).

logical traits or ecological requirements for the various axes (Fig. 4c). By comparing the positions of modalities (Fig. 4c) and species or families (Fig. 4b), it is apparent that two faunistic groups are in opposition on axis 2 in terms of their species' traits. At the positive side of axis 2, are semivoltine species, with a large potential size and a high fecundity. Their larvae are burrowers and filterers. Only some species of Ephemeridae belong to this group. The other families of Ephemeroptera are located at the negative side of the F2 axis, with the different species organized along the F1 axis mainly based on: (i) an increasing gradient of substrate granulometry from mud at the positive side of axis 1 to pebbles at the negative side and an increasing gradient of current velocity (from no

current to high current speed); (ii) a gradient of saprobity from a mesosaprobic species to xeno-saprobic species; (iii) an increasing gradient of potential size, individual fecundity, dissemination potential of larvae and imagines. Larvae of species which are streamlined in shape, clingers and mainly scrapers at the negative side of axis 1 are opposite the larvae of species which are more often cylindrical, crawlers and deposit-feeders.

The relationship between the traits of species and their temporal distribution was then examined in a co-inertia analysis. Testing of the co-inertia axes with a permutation test (DOLÉDEC & CHESSEL, 1994) demonstrated that
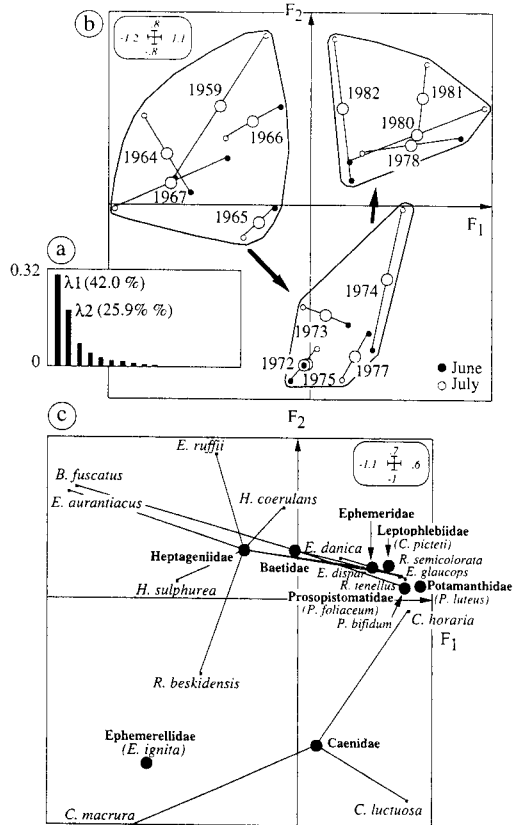

Fig. 3. Results of the double centered principal component analysis of monthly samples for 19 ephemeropteran species. a. Histogram of eigenvalues; b: Position of the monthly samples on the F1×F2 factorial plane; c: Distribution of species (the black squares) and families (the black circles) of Ephemeroptera on the F1×F2 factorial plane. Families are positioned at the weighted average of their species. Lines link species to their family.

the relationship between species' traits and population dynamics is significant only along the first co-inertia axis (p<0.05 - Fig. 5a). However we have retained axis 2 for comparison with the standard analysis of each array.

This significant result implies that Ephemeroptera species having particular species trait modalities display particular temporal distributions. The projection of axes of inertia of the separate analyses on the co-inertia axes
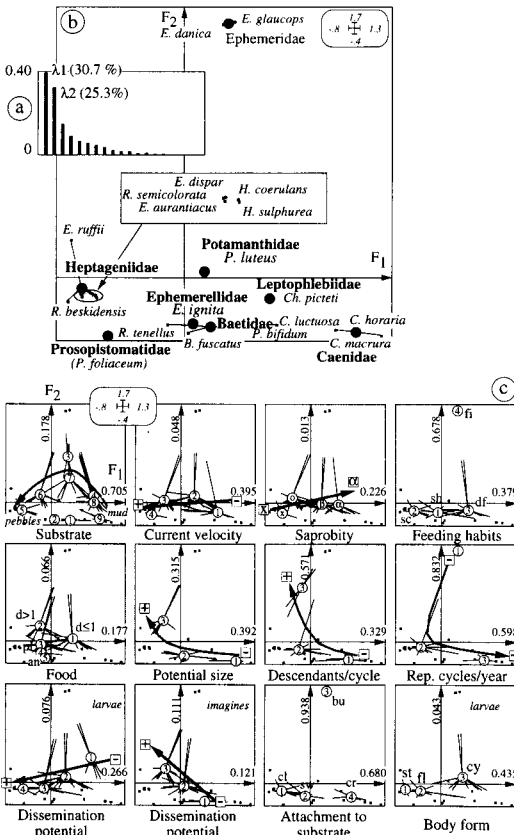

Fig. 4. Results of the fuzzy correspondence analysis of twelve species traits for 19 ephemeropteran species. a. Histogram of eigenvalues; b: Distribution of species (the black squares) and families (the black circles) of Ephemeroptera on the F1×F2 factorial plane. Families are positioned at the weighted average of their species. Lines link species to their family; c: Distribution of modalities (the number in the circle) of biological variables on the F1×F2 factorial plane, with correlation ratios for each variable indicated on the axes (see Fig. 2 for full labels of variable modalities, for variables that exhibit a gradient, modality no. 1 is at the lowest end of the gradient). Small squares represent the species. Each modality is positioned at the weighted average of species representing this modality. Lines link species to their modalities but are only 50% of their total length for readability; lines are omitted if a species contributed less than 1% to the modality distribution.
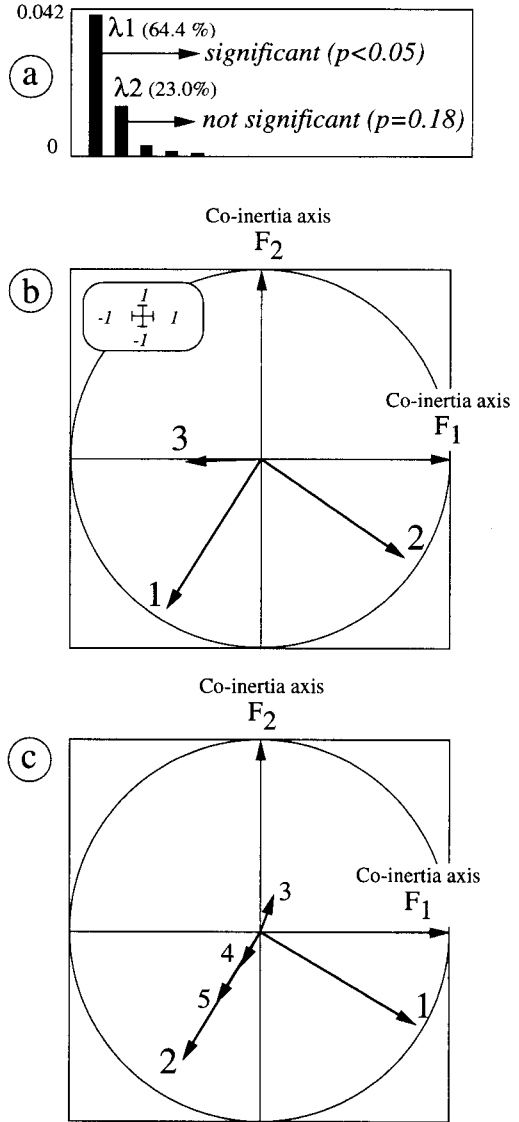
Fig. 5. Co-structure between species traits and temporal distribution of species by co-inertia analysis. a. Histogram of eigenvalues; b and c: Relationships between separate analyses and co-inertia analysis. Each arrow represent an axis number of the standard analysis (b. monthly samples and c. species' traits) that are projected on to the co-inertia axes (F1 and F2).
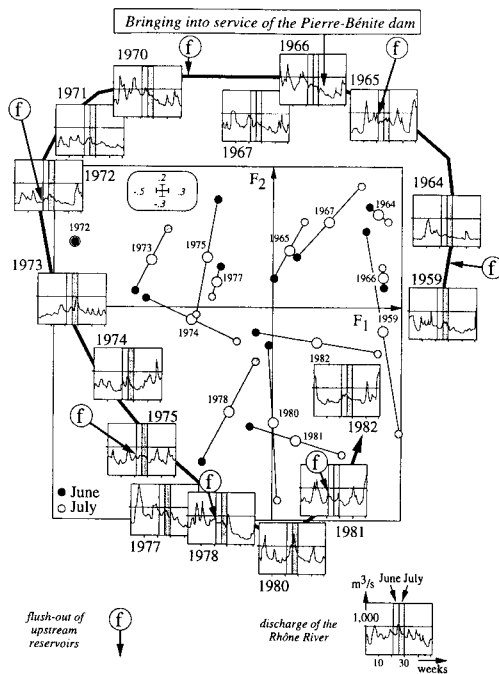
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Fig. 6. Co-structure between species traits and temporal distribution of species by co-inertia analysis. Distribution of modalities (the number in the circle) of biological variables on the F1×F2 co-inertia plane (see Fig. 2 for full labels of variable modalities). Small squares represent the species. Each modality is positioned at the weighted average of species representing this modality. Lines link species to their modalities but are only 50% of their total length for readability; lines are omitted if a species contributed less than 1% to the modality distribution.
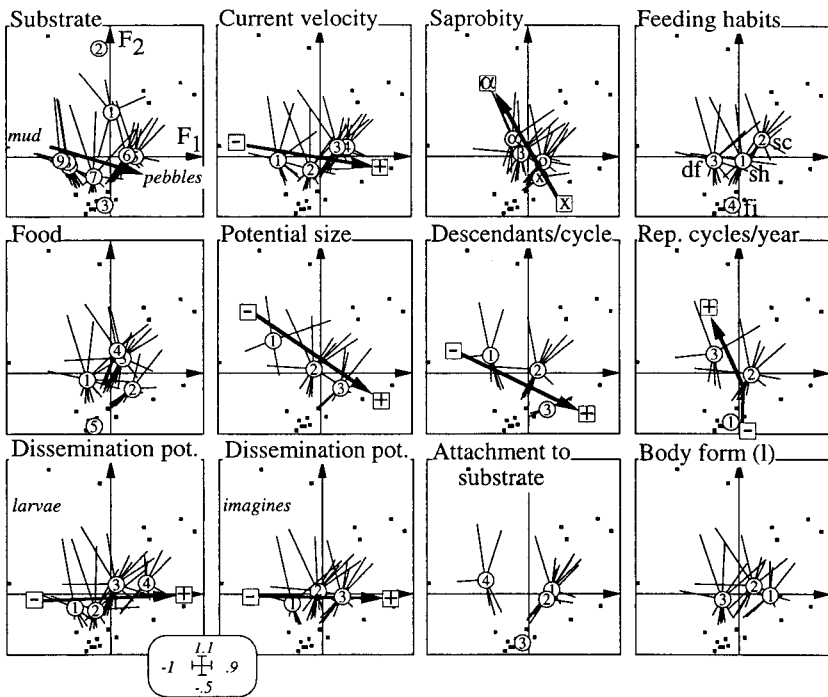
indicates that the plane (F1×F2) of co-inertia analysis mainly expresses the structure of plane F1×F2 for the species' traits and for the temporal distribution of species (Figs 5b, c).

Comparing the positions of trait modalities (Fig. 6), monthly samples (Fig. 7), and species vectors (Fig. 8) on the first factorial plane summarizes the results of the co-inertia analysis. Again, the samples are ordinated close to their temporal position. The opposition of samples of the 1959-1967 and of the 1972-1977 periods more or less corresponds to a decreasing gradient of substrate granulometry and current velocity, with more rheophilous tendencies for species of the first group. Furthermore, the observed gradient (along the F1 axis) also corresponds to a contrast between: (i) species that in general exhibit a small size, a short life cycle, wide environmental requirements, but low dissemination potentialities which should be more effective in disturbed habitats (at the negative side of F1) and (ii) long-lived species, very demanding as far as substrate is concerned and displaying a high dissemination potential.

On the figure in which each species is defined as a vector (Fig. 8) plotted between its position according to species' traits (the beginning of the

Fig. 7. Co-structure between species traits and temporal distribution of species by co-inertia analysis. Distribution of monthly samples on the F1×F2 factorial plane and the relationship between the location of monthly samples on the F1×F2 co-inertia plane and the water discharge of the Rhône River at Lyon.

arrow) and its position according to its population dynamics (the end of the arrow), the high number of long arrows indicates that most of ephemeropteran species have only a limited co-structure between species' traits and temporal distribution, because there is a limited superposition of the species when positioned by species traits and by temporal distribution. In contrast, *Ecdyonurus ruffii, E. aurantiacus* and *Heptagenia coerulans* which are representative of the 1959-1967 period and *Caenis luctuosa* which is representative of the 1972-1977 period, exhibit a fairly strong co-structure between species' traits and historical distribution, because their arrows are all rather short. A group of species including *Caenis horaria, Choroterpes picteti, Procloeon bifidum, Raptobaetopus tenellus, Potamanthus luteus, Ephemera glaucops, Ecdyonurus dispar* and *Rhithrogena semicolorata*, whose catches are often low and scarce, display similar historical distribution (because the ends of the arrows are close together) but very different species' traits.

DISCUSSION

The distribution in time and space of benthic invertebrates in a section of river is the result of a series of responses to a set of complex interactions between the variables represented by current, substrate, depth, food resources and competition. The observed changes in captured species assemblages will thus depend more or less directly on the changes in these different parameters over the studied period. Two series of factors appear to be at the origin of the observed changes in Ephemeroptera assemblages over the studied period. Firstly, the regular summer flush-outs of the upstream reservoirs release large quantities of fine sediment which clog interstitial spaces, thus reducing the circulation of water and oxygenation of hyporheic microhabitats (PERRIN, 1978; BOURNAUD *et al.*, 1987; CELLOT & BOURNAUD, 1988). The second factor is the bringing into service of the Pierre-Bénite dam, which slowed down the flow of the Rhône River and therefore created a more uniform and lentic environment. From 1966 onwards, fine sediments were deposited in the slowed waters of the Rhône, at the sampling station level. In this way,

Ephemeroptera became more sensitive to periodic flush-outs, especially when the releases of dams upstream were followed by a long period of low discharge (for example, in 1972, 1973 and 1974 after the flush-out of June 1972 - Fig. 7). Thus the combined action of sedimentation and water level has contributed towards the reduction, especially since 1966, of a whole series of lotic microhabitats. These habitats were formed by rapid current zones even at low-water, shallow water levels with limited turbidity, composed mainly of banks of loose pebbles that allow strong growth of algae and bryophytes and hence the development of a typical rheophilous fauna of scrapers.

In conclusion, several points emerged from this synthesis. Based on autecological information obtained from the literature, the graphical expression of the biological and ecological significance of a faunistic assemblage allowed, by means of indicator species, to reconstitute part of the biotope traits from a faunistic table. Even if species traits are rather similar throughout the Ephemeroptera, the sampling and the biological indicator value of 19 species of Ephemeroptera allowed us to express reliable assumptions on the evolution of the Rhône River at Lyon, over 25 years. This process opens up new perspectives in the synthesis of long-term ecological research.
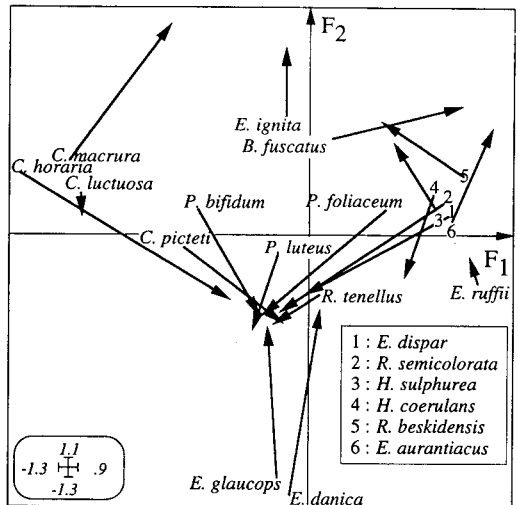

Fig. 8. Co-structure between species traits and temporal distribution of species by co-inertia analysis. Species vectors on the F1 x F2 co-inertia plane (see text for further details).

Appendix 1. Mean summer densities of the ephemeropteran species collected during the 1959-1982 period by light trapping. The densities, expressed as the mean number of individuals for a period of 10 nights, correspond to the mean of the densities observed during the months of June and July for each year. Species extremely rare in catches (*) were not considered in the analysis.

Species			Years of sampling													
			1959	1964	1965	1966	1967	1972	1973	1974	1975	1977	1978	1980	1981	1982
Heptagenia coerulans	Rostock, 1877		22.9	7.2	0.8	1.7	2.3	-	-	0.8	1.1	0.2	-	-	1.4	1.5
Heptagenia flava	Rostock, 1877	*	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
Heptagenia sulphurea	(Müller, 1776)		183.2	315.9	77.9	77.2	194	15	166.3	17.3	51.7	50.6	10.6	15.4	17.1	91.8
Electrogena lateralis	(Curtis, 1834)	*	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-
Ecdyonurus aurantiacus	(Burmeister, 1839)		42.8	97	15.5	19.9	112.3	2.1	68.2	0.2	1.5	-	0.6	0.2	0.7	0.2
Ecdyonurus dispar	(Curtis, 1834)		1.4	1.1	0.8	1.1	0.5	-	-	0.6	-	0.2	-	-	-	0.2
Ecdyonurus insignis	(Eaton, 1870)	*	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Ecdyonurus ruffii	(Grandi, 1953)		61.1	40.6	2.2	7.1	9.8	-	-	0.8	0.5	1.2	-	1.7	0.9	2.8
Ecdyonurus venosus	(Fabricius, 1775)	*	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhithrogena beskidensis	Alba-Tercedor & Sowa, 1987		68.3	57.7	57.4	49.7	113.9	-	14.1	13.1	71.3	72.6	3.5	4.9	1.8	8.9
Rhithrogena semicolorata	(Curtis, 1834)		0.2	0.3	-	2	-	-	-	-	-	-	-	-	-	-
Baetis fuscatus	(Linné, 1761)		215.5	321.5	77.6	129.3	560.5	55.7	26.6	17.1	11.9	3.5	19.9	21.5	3.9	78.7
Baetis rhodani	(Pictet, 1843)	*	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Cloeon dipterum	(Linné, 1761)	*	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-
Procloeon bifidum	(Bengtsson, 1912)		0.2	-	0.3	0.2	-	-	-	-	-	-	-	-	-	-
Raptobaetopus tenellus	(Alharda, 1878)		1.6	-	-	-	-	-	-	-	-	-	-	-	-	-
Caenis horaria	(Linné, 1758)		0.3	-	-	-	-	-	2.8	-	-	-	-	-	-	0.3
Caenis macrura	Stephens, 1835		119.8	124.9	70.2	20.3	228	483.4	112.8	36.9	108.3	35.6	6.8	3.5	1.5	7.2
Caenis luctuosa	(Burmeister, 1839)		2.8	1.7	3.8	0.6	3.7	17.9	14.7	24.2	13.8	15.7	1.3	1	0.2	0.3
Ephemerella ignita	(Poda, 1761)		103.2	95.1	22.7	28.5	63.7	66.4	15.9	17.4	193.8	70.4	0.9	5.2	1.8	6.2
Ephemera danica	Müller, 1764		7.6	0.9	-	0.4	1.5	-	-	-	1	-	-	-	-	-
Ephemera glaucops	Pictet, 1843		1.1	-	-	-	-	-	-	-	-	-	-	-	-	-
Ephemera vulgata	Linné, 1758	*	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2
Potamanthus luteus	(Linné, 1767)		0.9	-	-	-	-	-	-	1.7	-	-	-	-	-	-
Prosopistoma foliaceum	Fourcroy, 1785		0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Habroleptoides confusa	Sartori & Jacob, 1986	*	0.2	0.3	-	-	-	-	-	-	-	-	-	-	-	-
Habrophlebia fusca	(Curtis, 1834)	*	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-
Habrophlebia lauta	Eaton, 1884	*	-	-	-	-	-	-	0.3	-	-	0.2	-	-	-	-
Choroterpes picteti	Eaton, 1871		2.2	0.6	-	-	-	-	-	-	-	-	-	-	-	-

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