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Changes in functional biodiversity in an invaded freshwater ecosystem: the Moselle River.

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Abstract

The spread of non-indigenous species and the decline of autochthonous ones are leading to a homogenization of freshwater fauna in terms of systematic units, but the functional consequences are poorly documented. We studied the peculiar case of the lower, French section of the Moselle River where 20 invertebrate species have been introduced since 1854, with a rate increasing exponentially with time. Dredge sampling performed in 1994, 1996, 2000 and 2001 at four sampling stations allowed for an evaluation of faunal changes in terms of composition, structure and function. During this period, no structural changes were recorded in spite of multiple, new and successful introductions. The evaluation of functional modifications was based on a typology of taxa exhibiting homogeneous biological/ecological traits. Functional diversity, measured as the diversity of taxa distribution among functional groupings, revealed a significant increase between 1994/1996 and 2000/2001 because those species that were over-represented during the former period reached more equilibrated densities during the latter. The major, indirect implications of these functional changes are discussed.

Introduction

The fauna in freshwater ecosystems is being modified at unprecedented rates by human activities, resulting in a decline of local species and a spread of exotic or invasive ones. Navigable sectors of large rivers are the most affected or the most threatened aquatic ecosystems due to their multiple uses and the resulting stresses. While many studies have focused on the characteristics of successful invaders (Williamson, 1996; Ricciardi & Rasmussen, 1998; Kolar & Lodge, 2001), the impact of multiple introductions on recipient ecosystems is still poorly documented (Van der Velde *et al.*, 2000).

In this context, the main, inter-related aspects of faunal changes in a community - composition, structure and functional diversity – have to be evaluated. Composition (i.e. a list of species) and taxonomic structure (usually described with biotic indices or distribution models) are often studied, but the functional diversity of a given community, much more difficult to evaluate, is scarcely approached. However, an evaluation of functional modifications can be based on a recent, innovative functional classification of benthic macroinvertebrates assembling taxa with similar suites of biological and ecological traits in increasingly larger faunal groups (Usseglio-Polatera *et al.*, 2001). Species belonging to a given group may be considered as ‘functionally redundant’ for the major processes occurring in the ecosystem, considering that the functional effects of a taxon are output variables or consequences of its combination of traits and use of resources (Rosenfeld, 2002). From this viewpoint, three different factors were taken into account in the analysis of 22 biological and ecological traits performed by Usseglio-Polatera *et al.* (2001): (i) morphological and physiological features of taxa related to ecological processes (described with traits such as ‘feeding habits’, ‘respiration mode’ or ‘maximal size’), (ii) demographic characteristics of

populations (traits such as ‘life cycle duration’ or ‘potential number of reproduction cycles per year’), and (iii) ecological preferences influencing the functionally-relevant distribution of a taxon (traits such as ‘longitudinal distribution’ or ‘salinity preferendum’). If each taxon in a given community is replaced by its functional group, the assessment of ‘group diversity’ has the potential to provide a useful, simple measure of that community’s functional diversity.

In this context, we aimed at analysing recent faunal changes in the Moselle River, in terms of composition, structure and functioning, following a succession of uncontrolled introductions of macroinvertebrates. After a short description of the invasion pattern we focused on the consequences of repeated introductions on functional diversity.

Materials and methods

Study sites

The lower part of the Moselle River is canalized to allow for a high shipping traffic between the Rhine, the Meuse and the Saône catchments. The large number of weirs induces the presence of several diverted stretches flowing parallel to the canalized one. The present study was carried out at four sites (Figure 1): Dieulouard, Metz, Cattenom and Sierck-les-Bains, covering approximately 100 km of the lower Moselle. The sites were chosen because they represent the main environmental conditions encountered along the river, and are typical of the canalized sections (except for the Metz sampling site located 400 m upstream from a navigable section). All four sampling sites were characterised by a mineral substratum ranging from coarse sand to pebbles.

Sampling protocol

Benthic samples were collected in 1994, 1996, 2000 and 2001, at a depth of about 4 m., by dredging the bottom in a direction perpendicular to one transect. On each transect, the left side, the right side (each one at 4 metres from the bank) and the middle of the river were sampled.. This method is designed to collect the main populations living in the channel and thus representing the major part of the macrobenthic biomass. On each sampling occasion, the surface of the sampled area was evaluated according to (1) the length of the dredge draught estimated from the volume of dredged material, (2) the dredge section and (3) the sediment depth (Berly, 1989). Macroinvertebrate densities were then expressed per square metre (Table I for detailed information on the sampling protocol).

The samples collected in 1994, 1996 and 2000 were preserved in 4 % formaldehyde, but those from 2001 were frozen (-20°C) shortly (< 4 h) after collection. Macroinvertebrates were sorted, identified and counted under a stereomicroscope. Most taxa were identified to the genus level, except for some exotic species identified to species level, and Diptera identified only at family level. Oligochaeta and Nematoda were recorded as such.

Statistical analyses

The functional diversity of each community was calculated using the Shannon-Weaver index (Shannon & Weaver, 1963) according to the distribution of individuals (and taxa) among functional groups (Usseglio-Polatera *et al.*, 2001). The significance of temporal variations in diversity indices was tested using the non-parametric Friedman ANOVA ($\alpha=0.05$) test. The assessment of changes in functional diversity was performed using the Mann-Whitney test ($\alpha=0.05$).

Results

Biological invasion is a common phenomenon in the Moselle River, with 20 species of macroinvertebrates introduced since 1854, most of them belonging to Crustacea and Mollusca (Table II). Seven exotic species were recorded before the first half of the 20th century and thirteen thereafter. The trend in cumulative numbers of successful introductions is best described by an exponential function (Figure 2), which explains 7% more variance than a linear one.

The taxonomic composition of the fauna reveals an increase in the relative abundances of autochthonous individuals between 1994 (34.2%) and 2000 (67.1%), followed by a severe decrease in 2001 (12.1%), due mainly to a decrease in relative abundances of ‘insects’ and ‘other’ autochthonous taxa (Cnidaria, Achaeta, Nematoda and Oligochaeta). Conversely, an increase in ‘other’ exotic species can be observed, linked to the introduction of the freshwater Polychaeta *Hypania invalida*. A decline in exotic molluscs occurred in relation with a massive decrease in *Dreissena polymorpha* between 1994 and 1996. Finally, only one autochthonous crustacean *Asellus aquaticus*, present at Dieulouard, still remained in the Moselle River in 2001, while the proportion of exotic crustaceans increased with the establishment of two new species, *Dikerogammarus villosus* and *Jaera istri* (Figure 3).

During the period from 1994 to 2001, the major, structural characteristics of macrobenthic communities did not change in terms of taxonomic richness or taxonomic diversity (non-parametric Friedman ANOVA, $p=0.34$ for taxonomic richness and $p=0.054$ for taxonomic diversity; Figure 4). Conversely, in terms of functional characteristics, the functional diversity increased significantly between 1994-1996 and 2000-2001 ($p=0.005$, Figure 5). During the period from 1994 to 1996, functional diversity was very low due to the high relative abundance of taxa (such as *D. polymorpha* and *C. curvispinum*) belonging to the same

bio/ecological group (ζ). In 2000-2001, a decrease in the dominance of this group was observed (Simpson dominance, $\lambda=0.82$ in 1994, $\lambda=0.66$ in 2001; Mann Withney test, $p=0.04$), that was not counterbalanced by the establishment of several new exotic species also belonging to the group ζ (*D. villosus*, *J. istri*, *H. invalida*). The major decrease in *D. polymorpha* density in the Moselle River (Bachmann et al., 2001) seemed to play a key role in this pattern. We can also note that the increase in functional diversity was far more significant upstream than downstream, even with a decrease in the section furthest downstream at Sierck. Conversely, the other functional groups became increasingly represented along the temporal gradient (Figure 6), involving the increase in functional diversity.

Discussion

The exponential trend in the cumulative, successfully-introduced species over time in the Moselle River highlights an accelerating accumulation of exotic species during the last decade. This increase may also reflect a growing interest in biological invasions and increased knowledge of freshwater fauna. Otherwise, several hypotheses can be proposed potentially to explain this increasing rate over time: (1) an increase of propagule pressure due to the increasing development of shipping traffic, (2) a process of facilitative interactions which favors new exotic species from the same biogeographic area than previously successful introduced species (Simberloff & Von Holle, 1999) and (3) a decline in biotic resistance following the alteration of the environment and the decline of autochthonous species. Most introduced species in the Moselle River belong to Crustacea and Mollusca, a fact already observed in other freshwater ecosystems (Morton, 1997; Van der Velde *et al.*, 2000; Grigorovich *et al.*, 2002). Such taxonomic clumping of invaders can result in an over-

representation of specific traits which enhance transport, dispersal, establishment and/or massive development in a recipient ecosystem.

Most of the major, recent invasive species in lowland sections of large, western-european rivers belong to the ζ group, including organisms with a unique combination of features (large-size, asexual reproduction, thermophilous, polysaprobic, affinity for silt and sand, mainly filter or deposit feeders, burrowers or permanently attached), which distinguish them clearly from taxa of other functional groups (Usseglio-Polatera *et al.*, 2001, unpublished results).

Assessing the functional consequences of a given introduction is a stimulating, challenging part of biological invasion research. Functional diversity translates the bio/ecological response of organisms to multiple environmental constraints. Its interest lies in the condensed expression of major ecological processes such as nutrient cycles or energy flows throughout different ecosystem compartments. This method, as applied to the Moselle River, is based on the study of groups of taxa with similar suites of bio/ecological traits. This approach highlights functional changes over a very short period of time following a succession of successful introductions. In 1994-1996, functional diversity was very low, illustrating the strong degradation of the river community after the demographic explosion of several new exotic species introduced in the beginning of the 1990's (Bachmann *et al.*, 1995). Recent temporal variations in the density of exotic species probably led to the more equilibrated faunal structure observed in 2000-2001, due in particular to the decline of *Dreissena polymorpha* (Bachmann *et al.*, 2001), which exhibited a very high density in the Moselle during the 1994-1996 period. As a counterpoint to the decrease in relative abundances of group ζ , an increase in relative abundance of groups β and γ_2 was observed. This phenomenon allowed a better representation of various ecological functions in the ecosystem, and contributed to the increase in the community's functional diversity between 1994-1996

and 2000-2001. The migratory corridor of invasive species, following the downstream-upstream gradient, could explain the pattern of changes in functional diversity within the four sections. For example, *J. istri*, one of the most recent invaders, was only present in Sierck in 2001, thus increasing the relative abundance of the ζ group and decreasing the functional diversity on this section.

Functional diversity takes into account the relative abundances of taxa and gives the best condensed representation of the diversity of bio/ecological trait combinations in an ecosystem. The use of evenness to track faunal changes also allows to highlight functional modifications in benthic communities before the total disappearance of a set of species with the same bio/ecological profile is observed (Chapin *et al.*, 2000).

An increase in functional diversity following several, successful invasions is not so surprising. Indeed, species introductions can increase community diversity locally, whereas they are always involved in a decrease in diversity at a global scale (Sax & Gaines, 2003). However, even at a local scale, this increase is often counterbalanced by the unpredictable impact of non indigenous species on the ecosystem, such as non-endemic pathogens. For example, the presence of *Orconectes limosus*, the American crayfish introduced in 1978 in the Moselle River, spread the crayfish plague (*Aphanomyces astaci*) which infested the very susceptible indigenous crayfish *Astacus astacus* (Van der Velde *et al.*, 2000). Moreover, most introduced species are distributed worldwide and have achieved the status of cosmopolitan species.

Navigated sectors of large rivers in Europe are more and more homogeneous both in terms of physical attributes and in terms of macrobenthic fauna. This homogenization of freshwater fauna, already reported for fishes (Rahel, 2002) and birds (McKinney & Lockwood, 1999), could lead to a decrease in the resilience of ecosystems exposed to disturbance. The spread of cosmopolitan species involves a decrease in the diversity of bio/ecological traits combinations in communities. As a result, the range of potential responses of a given community to

disturbance becomes narrower. The community is destabilized and weakened, and the ecological impacts it suffers intensify (Olden *et al.*, in press).

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Table I. Basic data for the four sites at each sampling date.

Sampling date	Station	Number of samples	Surface (m ²)	Mean total density (ind.m ⁻²)	Individual number (ind.m ⁻²)		Taxa number	
					Exotic	Autochthonous	Exotic	Autochthonous
1994	Sierck	3	0.232	26791	9711	17081	4	15
	Cattenom	3	0.046	272456	135503	136952	3	19
	Metz	3	0.293	209292	190685	18607	4	22
	Dieulouard	3	0.084	169077	110021	59056	3	20
1996	Cattenom	1	0.144	17325	270	17055	5	14
	Metz	3	0.526	5292	4204	1088	5	20
	Dieulouard	3	0.938	12280	9444	2836	6	27
2000	Sierck	3	0.238	7306	3601	3705	6	23
	Cattenom	3	0.155	12959	3213	9745	7	18
	Metz	3	0.114	19679	7390	12290	8	22
	Dieulouard	3	0.352	5158	642	4516	6	16
2001	Sierck	3	0.310	26103	25865	238	8	7
	Cattenom	3	0.669	11547	11138	409	8	14
	Metz	3	0.747	4300	3465	834	8	14
	Dieulouard	3	0.498	32122	24633	7489	8	22

Table II. Introduced species in the French part of the Moselle River. (1: Dhur & Massard, 1995; 2: Bachmann, 2000; 3: Devin *et al.*, 2001). Functional groups were reported from Usseglio-Polatera *et al.*, 2001, and from unpublished results.

Species	Systematic unit	Introduction date	Origin	Functional group	Reference
<i>Dreissena polymorpha</i>	Mollusca: Bivalvia	1854	Ponto-Caspian	ζ	1
<i>Orchestia cavimana</i>	Crustacea: Amphipoda	First half of the 20 th century	Ponto-Caspian and Mediterranean		1
<i>Echinogammarus berilloni</i>	Crustacea: Amphipoda	First half of the 20 th century	South-Western Europe	ζ	1
<i>Atyaephyra desmarestii</i>	Crustacea: Decapoda	1920s	Mediterranean	γ2	1
<i>Physa acuta</i>	Mollusca: Gasteropoda	1920s	Mediterranean	γ1	1
<i>Branchiura sowerbyi</i>	Oligochaeta	1930s	South-Eastern Asia	ζ	1
<i>Lithoglyphus naticoides</i>	Mollusca: Gasteropoda	1931	Ponto-Caspian	γ1	1
<i>Dugesia tigrina</i>	Turbellaria: Tricladida	1950s	North America	γ2	1
<i>Potamopyrgus jenkinsi</i>	Mollusca: Gasteropoda	1976	New-Zealand	ζ	1
<i>Craspedacusta sowerbyi</i>	Cnidaria: Hydrozoa	About 1978	Asia	γ2	1
<i>Orconectes limosus</i>	Crustacea: Decapoda	1978	North America	γ2	1
<i>Cordylophora caspia</i>	Cnidaria: Hydrozoa	1987	Ponto-Caspian	ζ	1
<i>Gammarus tigrinus</i>	Crustacea: Amphipoda	1991-1992	North America	β	1
<i>Chelicorophium curvispinum</i>	Crustacea: Amphipoda	1994	Ponto-Caspian	ζ	2
<i>Corbicula fluminea</i>	Mollusca: Bivalvia	1994	Asia	ζ	2
<i>Corbicula fluminalis</i>	Mollusca: Bivalvia	1994	Asia	ζ	2
<i>Dikerogammarus villosus</i>	Crustacea: Amphipoda	1998	Ponto-Caspian	ζ	3
<i>Limnomysis benedeni</i>	Crustacea: Mysidacea	2001	Ponto-Caspian		personal observation
<i>Jaera istri</i>	Crustacea: Isopoda	2001	Ponto-Caspian	ζ	personal observation
<i>Hypania invalida</i>	Polychaeta: Ampharetidae	2001	Ponto-Caspian	ζ	personal observation

Figure captions

Figure 1: Location of the four sampling sites along the Moselle River.

Figure 2: Cumulative number of introduced species in the Moselle River since the mid-19th century. The final number of exotic species (19) is lower than that presented in the table II (20) because an introduced gammarid (*E. berilloni*) disappeared from the river before 2001. Linear and exponential adjustments were applied to describe the trend.

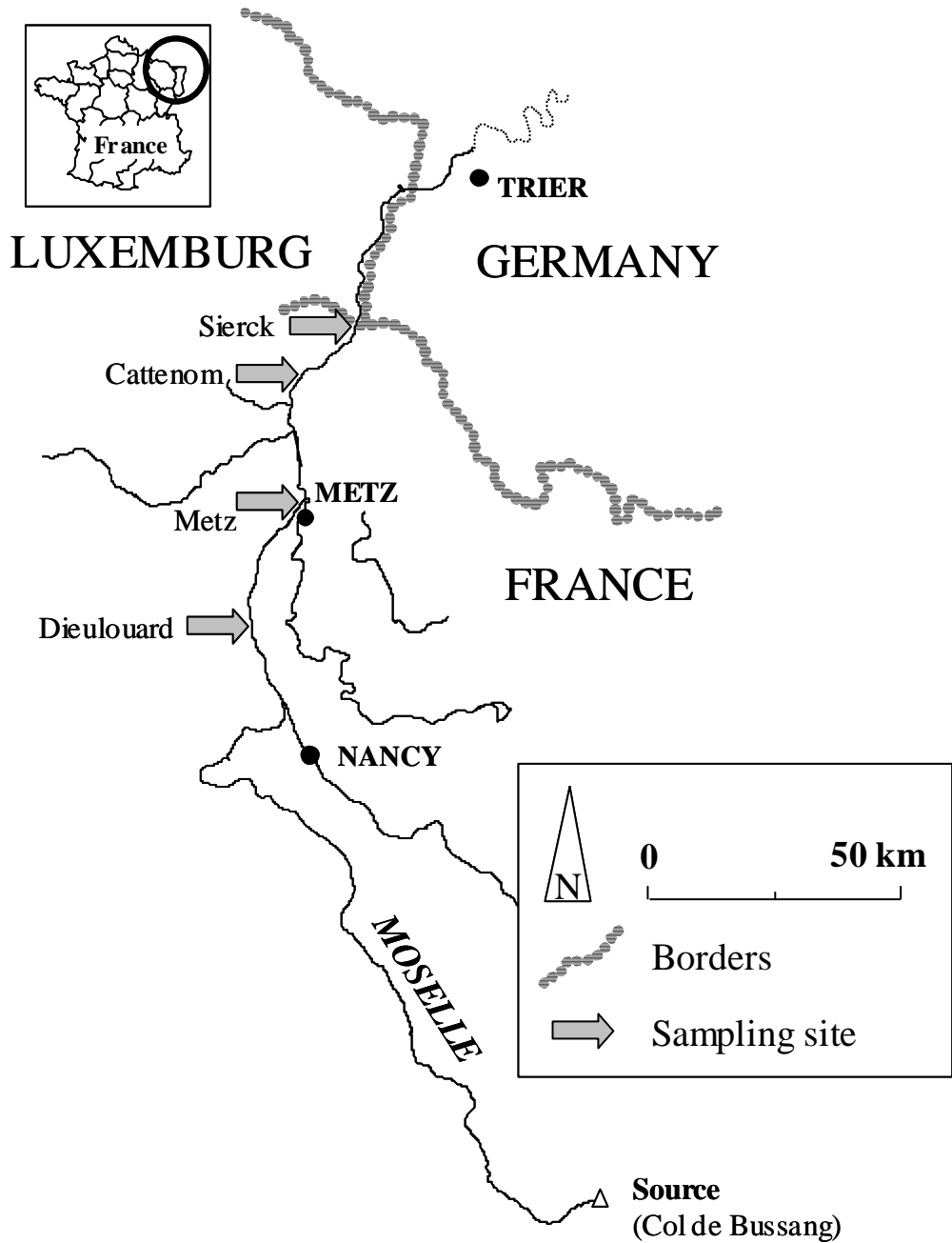
Figure 3: Relative abundances of the main taxonomic groups in the Moselle River sections studied between 1994 and 2001. See table I for the abundances.

Figure 4: Variation of the mean (\pm standard deviation) taxonomic richness per sample (a) and diversity (b) in the Moselle River section studied between 1994 and 2001. See Table I for the number of samples per year.

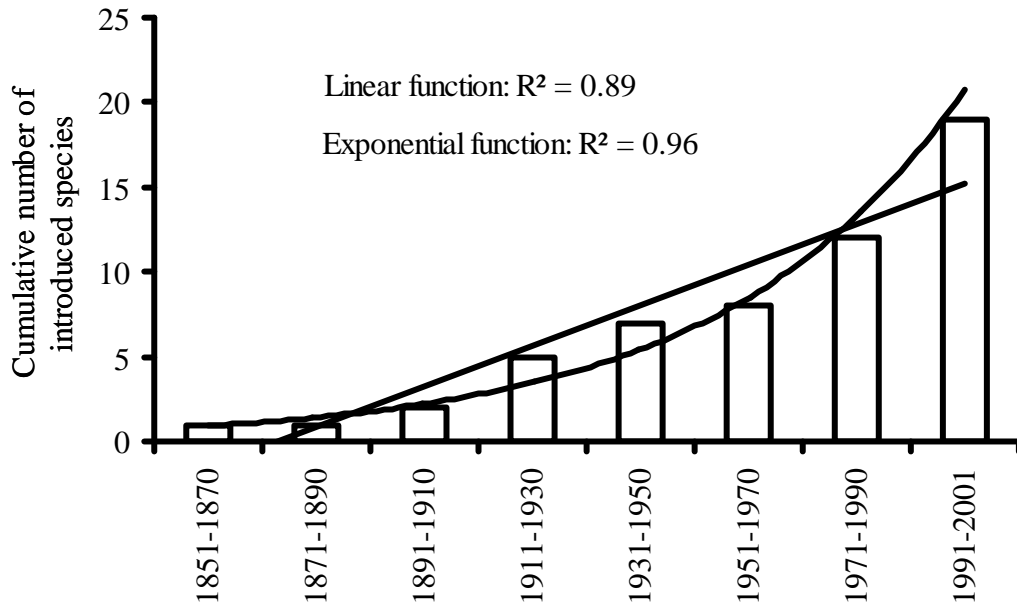
Figure 5: Functional diversity of four Moselle River sections between 1994 and 2001. (Shannon-Weaver index was calculated on distribution of individuals among functional groups defined by Usseglio-Polatera *et al.*, 2001).

*: The Sierck station was not sampled in 1996

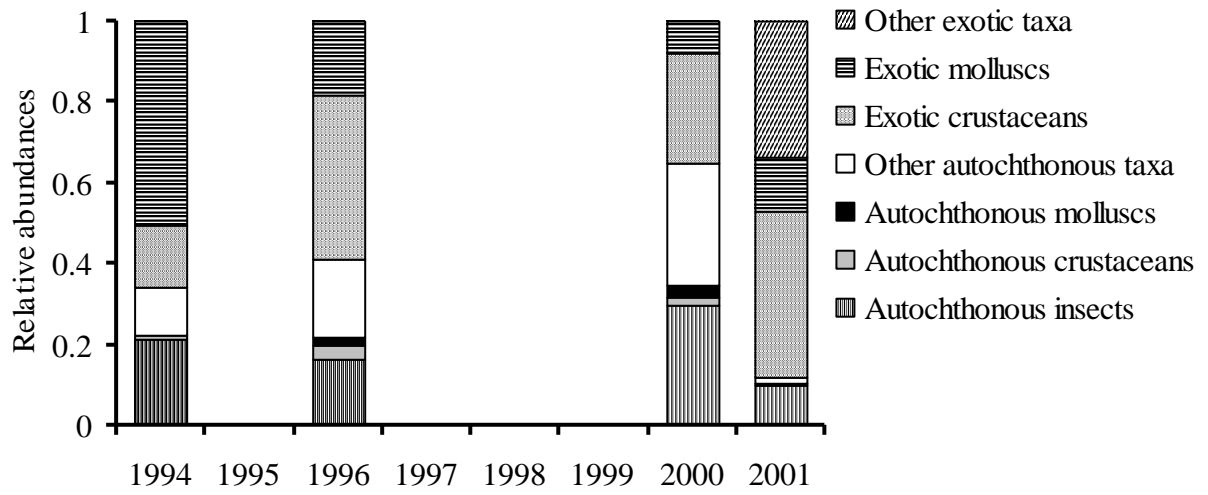
Figure 6: Relative abundances of functional groups (excluding the ζ group) in the benthic community of four Moselle River sections. Two groups were not shown on this graph because of their low relative abundance (see Usseglio-Polatera *et al.*, 2001 for further details on mean bio-ecological profiles of groups).



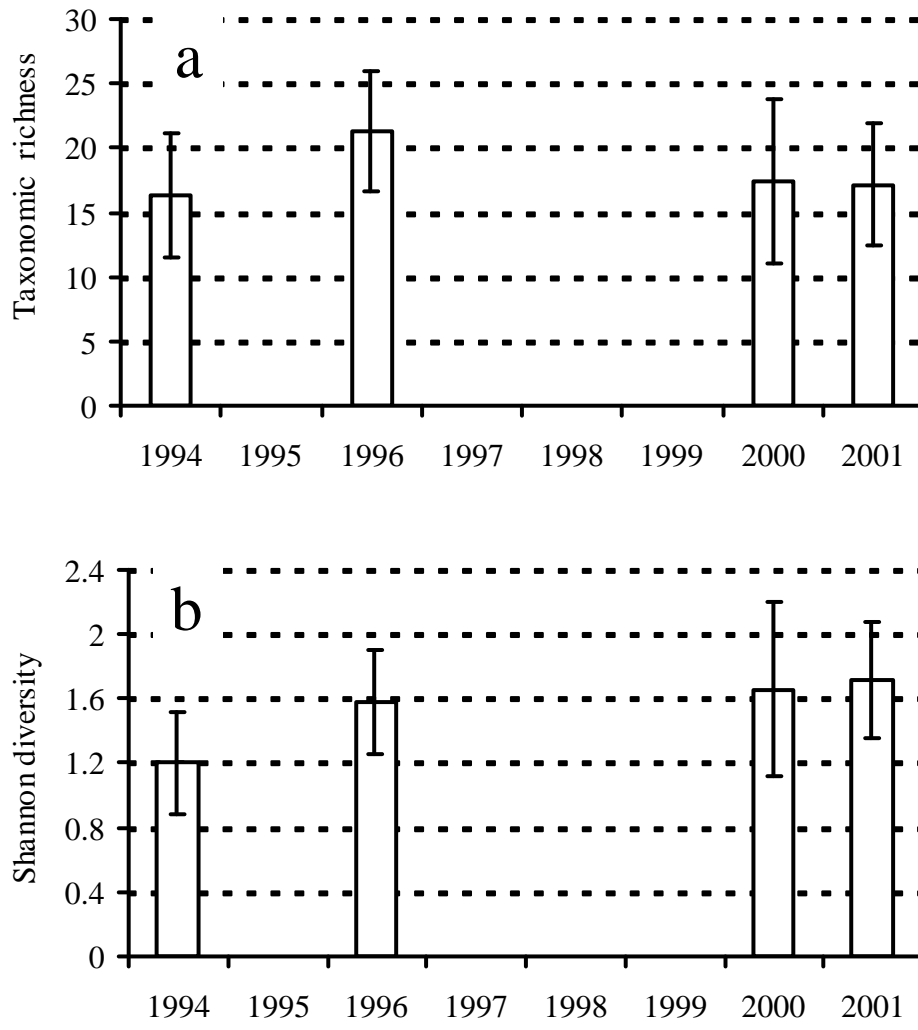
Devin et al. Figure 1.



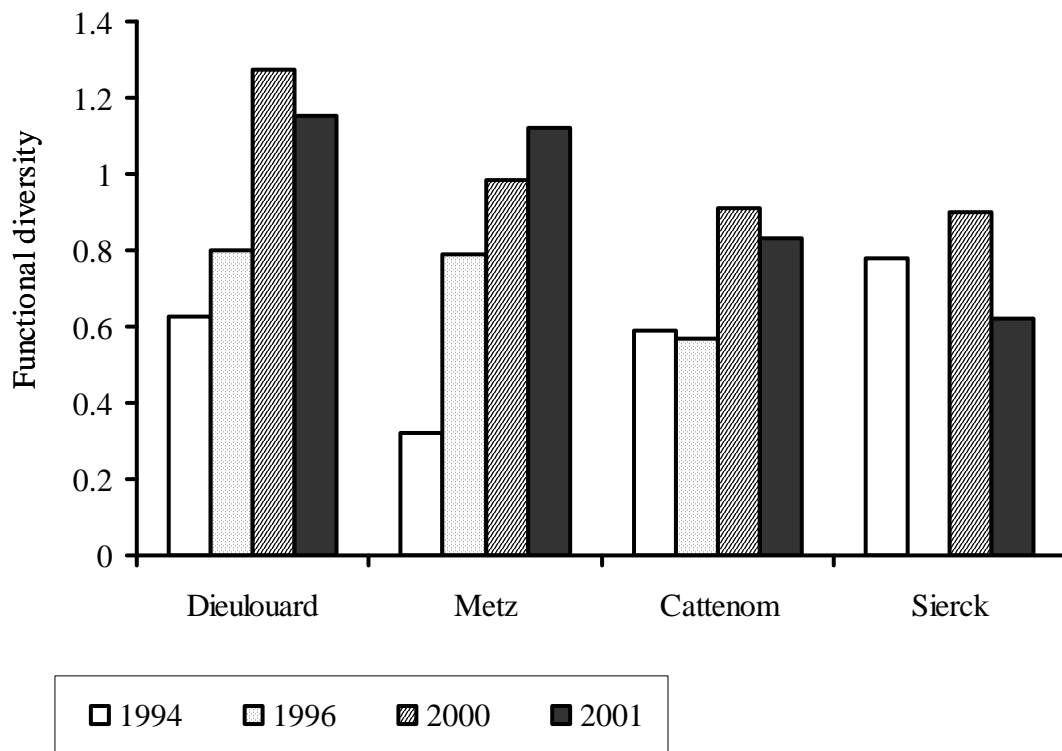
Devin et al. Figure 2.



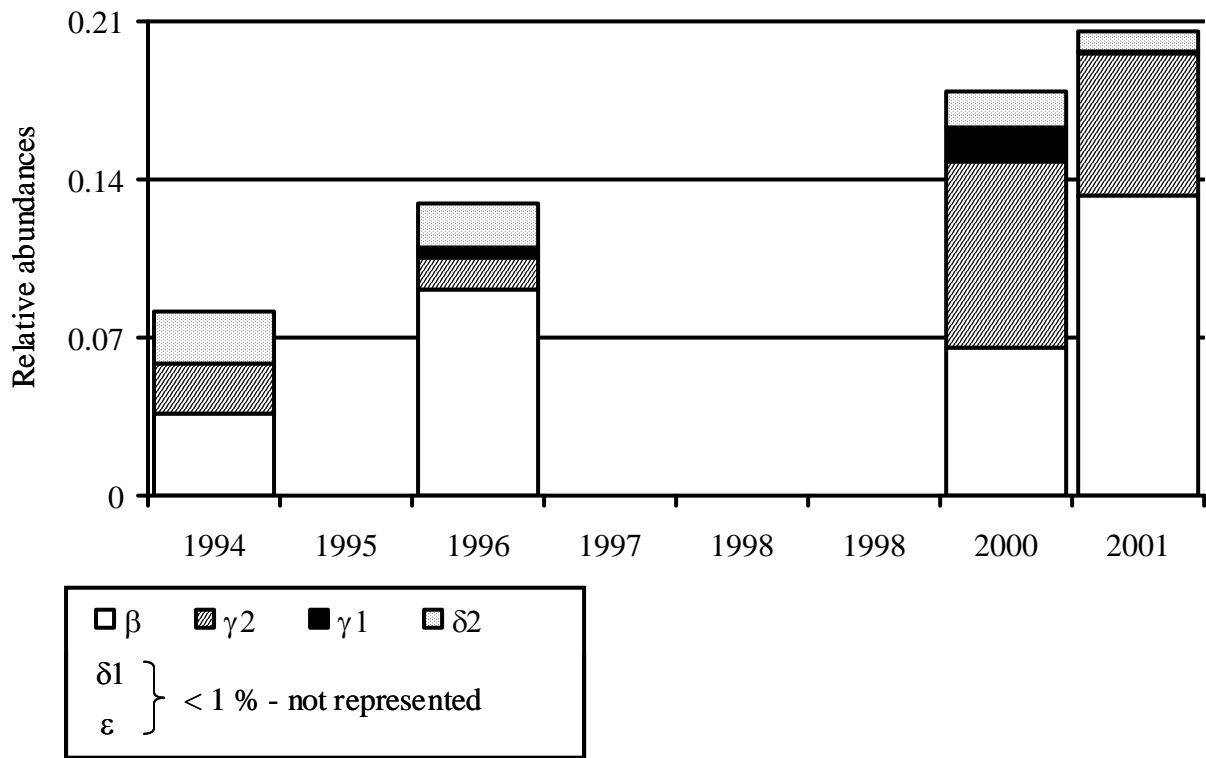
Devin et al. Figure 3.



Devin et al. Figure 4.



Devin et al. Figure 5.



Devin et al. Figure 6.