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Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River

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Abstract We assessed the temporal changes in and the relationships between the structures of the macroinvertebrate communities and the environmental conditions of the French Rhône River (the river from Lake Geneva to the Mediterranean Sea) over the last 20 years (1985–2004). Multisite environmental and biological datasets were analysed using multiple CO-inertia analysis (MCOA) and Procrustean analysis. Changes in environmental conditions were mainly marked by an improvement in water quality between 1985 and 1991 and by an increase in water temperature from 1985 onwards due to climate change. Improvement in water quality seemed to delay changes in community structures under global warming. We then observed trends in community structures coupled with high temperatures and a decrease in oxygen content. Interestingly, we observed both gradual changes and rapid switches in community states. These shifts seemed coupled to extreme hydroclimatic events (i.e. pulse disturbances). Floods and the 2003 heatwave enhanced the development of eurytolerant and invasive taxa which were probably able to take advantage of gradual warming environmental conditions. Despite various site-specific "press" constraints (e.g. hydropower schemes, nuclear power plants), similar changes in community structures were observed along the French Rhône River. Such consistency in temporal processes at large geographical scales underlined the strength of hydroclimatic constraints on community dynamics compared to specific local disturbances. Finally, community structures did not show any sign of recovery, and their relative sensitivities to extreme hydroclimatic events seemed to increase with time. Thus, our results suggest that global changes may reduce the resilience of current community states.

Keywords Climate change · Disturbances · Heatwave · Regime shift · Ordination techniques

Introduction

The last decade was the warmest of the last millennium, and temperatures will probably continue to

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increase in the future (IPCC 2001). The different scenarios outlined by the Intergovernmental Panel on Climate Change project an increase in global mean surface air temperature relative to 1990 of 1.4–5.8 °C by 2100 (IPCC 2001). This global warming might even be higher in Europe, with an expected increase of 2–6.3 °C during the same period (Parry 2000). Besides the global warming, the frequency of extreme climatic events (e.g. storms, droughts and floods) is also likely to increase (IPCC 2001). Many studies have stressed the impact of climate fluctuations on the dynamics of organisms in various ecosystems (Stenseth et al. 2002). For instance, recent theoretical studies have highlighted the influence of changes in both means and variances of environmental variables on population growth rates (Tuljapurkar et al. 2004; Haridas and Tuljapurkar 2005). More specifically, extreme climatic events have long been viewed as strong forces that structure communities and ecosystems (Connell 1978; Boulton et al. 1992; Gardner et al. 2005). In this context, it appears crucial to consider the effects of climate change in most ecological studies, at least as a potential confounding factor.

Many studies have already attempted to understand and estimate the ecological consequences of climate change in various organisms (see Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003 and references therein). These studies have typically highlighted a change in the timing of life cycle events (and especially earlier spring events) and spatial shifts towards higher altitudes or latitudes, according to thermal preferences. However, most of these works have suffered from several difficulties. First, many of them were performed at single study sites. This hindered evaluations of the effects of confounding factors and especially of nonclimatic anthropogenic constraints on the changes observed (Parmesan and Yohe 2003). To cope with this difficulty, biologists generally selected undisturbed sites, but this ultimately led to a potential overestimation of the relative ecological effects of climate change (i.e. compared to other environmental constraints) (Parmesan and Yohe 2003). Therefore, a few authors even argued that climate change was of little importance to ecosystems (Lomborg 2001). Multiple-site studies, and more generally meta-analyses, provide a valuable approach that can be employed to overcome these problems (Parmesan and Yohe 2003; Root et al. 2003). However, most of these works have only assessed the effects of climate change at the species level and they have mainly focused on phenological and/or geographical shifts according to thermal preferences. The effect of climate change on populations is likely to be mediated by different ecological processes (e.g. density dependence, competition), leading to more complex dynamics (Stenseth et al. 2002), and effects of climate change at larger biological scales (community, ecosystem) thus remain fairly unknown (Walther et al. 2002). In this way, further joint analysis of biological and environmental time series remains essential for a better understanding of the ecological effects of climate change (Stenseth et al. 2002).

Since disturbances are common in streams and rivers, these ecosystems have been used extensively to study the impacts of disturbances on community structures (Boulton et al. 1992; Miller and Golladay 1996; Watanabe et al. 2005). However, most of these works have only focused on the effects of extreme climatic events (droughts, floods) or nonclimatic anthropogenic disturbances (e.g. dams, embankments). The ecological consequences of climate change in large river ecosystems remain largely unexplored (Pont 2003; Daufresne et al. 2004; Mouthon and Daufresne 2006). We hypothesise that climate change acts as a driving force for the dynamics of community structures at a large spatial scale. As already documented for aquatic ecosystems, gradual changes in community structures may occur as the climate gradually changes (e.g. Sorvari et al. 2002; Daufresne et al. 2004; Poulard and Blanchard 2005). This pattern may correspond to a gradual increase in relative abundances of southern and warm-water taxa and a decrease in species of northern and cold-water taxa (Daufresne et al. 2004). A second possible temporal pattern consists of rapid shifts in community structures. According to van Nes and Scheffer (2004), sudden switches to contrasting community structures would not necessarily be the consequence of major stochastic events, but may sometimes be linked to gradual environmental changes. These different patterns are not mutually exclusive and may also be mediated by other disturbances which, in rivers, are generally classified into two types: pulse and press disturbances (Bender et al. 1986). Pulse disturbances (e.g. floods) occur over a limited time period, whereas press disturbances (e.g. embankments, hydropower schemes) arise sharply and are maintained at a rather constant level over long periods of time. We can derive different hypotheses about the effects of pulse and press disturbances in the general context of climate change. For instance, climate change may reduce the basin of attraction (i.e. resilience) around current community states (van Nes and Scheffer 2004) and so lead to an increased relative sensitivity of the communities to a given pulse or press disturbance. Symmetrically, former press disturbances favouring eurytolerant taxa may decrease the relative effects of climate change on communities.

Testing these hypotheses requires long-term datasets, which are still scarce in the literature (e.g. Krzyzanek et al. 1986; Paugy et al. 1999; Weilguni and Humpesch 1999). The hydrobiological survey which has been investigating the anthropogenic regulation of the Rhône River since the beginning of the 1980s (Roger et al. 1991; Ginot et al. 1996; Fruget et al. 2001; Carrel et al. 2003) represents a unique opportunity to perform a long-term, multisite study. In this paper we focus on long-term temporal changes in environmental conditions and macroinvertebrate community structures (from 1985 to 2004) at different study sites located along the French Rhône River. First we describe the global dynamics of environmental conditions and macroinvertebrate community structures. Then we evaluate the statistical link between climate and biological dynamics. Finally we discuss the results of this work in the context of current knowledge of the effects of climate change on the dynamics of community structures.

Materials and methods

Study sites

The study was carried out using data collected along most of the 520-km long French Rhône River (Fig. 1). With a mean annual outflow of 54 km^3, the Rhône represents one of the main stream-water inputs to the Mediterranean Sea (one-sixth of the total input). Like most of the large European rivers, the French Rhône has undergone anthropogenic changes over the last 200 years, especially downstream from Lyon (Fruget and Michelot 2001). It has been subjected to chemical pollution, and embankments, hydropower schemes and nuclear power plants have been built along the river. However, the overall water quality remains relatively good for such a river (Agence de l’Eau Rhône Méditerranée Corse 1999), and the Rhône has been used extensively to improve our knowledge about large river ecosystems, with particular emphasis placed on long-term processes (Statzner et al. 1994; Dessaix et al. 1995; Dolédec et al. 1996; Fruget et al. 2001; Bady and Dolédec 2003; Daufresne et al. 2004).

Environmental data

We assessed environmental conditions through water temperature and discharge measurements as well as indices of water quality. We examined effects of water quality because it could act (1) as an indirect climatic factor (e.g. oxygen content and temperature are negatively related) and (2) as a potential confounding factor (e.g. effects of pollutions). Between 1985 and 2004, pH, conductivity (cond.), oxygen content [concentration (O_2) and percent of saturation ($O_2\%$)], biological oxygen demand (BOD_5) as well as the ammonium (NH_4), nitrite (NO_2), nitrate (NO_3) and phosphorus (PO_4) concentrations were sampled monthly at nine sampling sites distributed along the Rhône (hereafter called sites

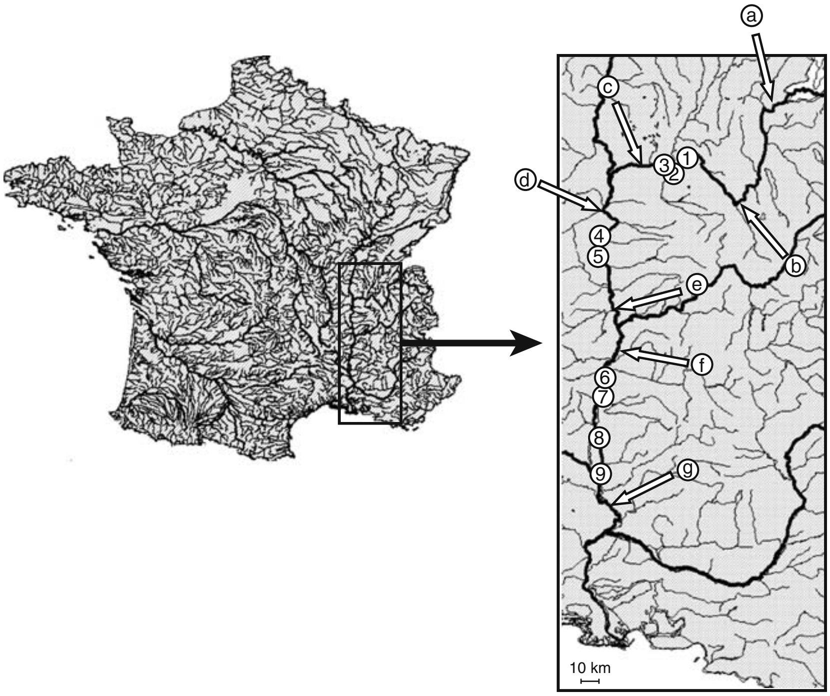

Fig. 1 Environmental (*a–g*) and biological (*1–9*) sampling sites

a–g from upstream to downstream; Fig. 1). Sampling was performed by the Agence de l'Eau Rhône Méditerranée Corse (data available at http://sierm.eaurmc.fr). During the study period, mean daily values of water temperature (T) and discharge (Q) in the vicinity of the sampling sites were provided by Electricité de France (EDF) and Banque Hydro (data available at http://www.hydro.eaufrance.fr/accueil.html). For each sampling site, all available data were averaged by year and normalised per column (to cope with the heterogeneity of the units). The environmental data finally consisted of a set of seven site-specific tables (called site-tables hereafter).

Biological data

Between 1985 and 2004, invertebrates were sampled three to four times a year at nine different sampling sites (hereafter called sites 1–9 from upstream to downstream, Fig. 1). Note that these sites were different from the sites where physical and chemical measurements were taken, but they were all included in the sites a–g river segment (Fig. 1). These data were collected by Cemagref-Lyon (sites 1–3), ARALEP (sites 4 and 5), and Cemagref-Aix (sites 6–9) in the vicinity of four nuclear power plants operated by EDF. Five sites (sites 2, 3, 5, 6 and 9) were located approximately 10 km downstream from nuclear power plants and were potentially influenced by the warmed effluents. Macroinvertebrates were sampled along the banks using artificial substrates (Roger et al. 1991; Fruget et al. 2001). Because of differences in identification levels across the study sites, we only retained the highest common taxonomic level, the family. The abundances of the different families were averaged by calendar year for each sampling site and were $\ln(X+1)$-transformed to normalize their distribution and to reduce possible heterogeneity in sampling procedures. Abundances were then centred by species. The biological data finally consisted of a set of nine site-tables of family abundances.

Statistical analyses

Summarizing environmental and biological changes

The aim of the study was to define general rules for the responses of communities to large-spatial-scale changes in environmental conditions. This implied that it was necessary to focus on common temporal dynamics in environmental and biological conditions by reducing the effects of potential site-specific confounding factors. We used multitable techniques (e.g. Escoffier and Pages 1994; Lavit et al. 1994; Chessel and Hanafi 1996) to analyse multiple time-series of invertebrate sampling and environmental (physical and chemical) conditions and to assess their similarity. Such statistical methods have only rarely been used in ecology, despite their ability to deal with the spatial and/or temporal stabilities of communities (e.g. Gaertner et al. 1998; Bady et al. 2004).

The environmental changes that occurred in the Rhône River during the 1985–2000 period were summarized using a within-class-based approach: multiple CO-inertia analysis (MCOA). MCOA was performed on the seven environmental site-tables. This method is based on covariance optimisation between several individual ordinations and a reference ordination (Chessel and Hanafi 1996, and see Supplementary material). The reference ordination can be viewed as the common structure shared by the individual ordinations. In this way, MCOA allowed the graphical representation of site-specific changes in environmental conditions compared to a reference temporal structure derived from the seven sampling site-tables. Two groups of statistics synthesised the efficiency of the MCOA. The first statistics were the squared cosines ($\cos^2$) of the angles between the first two axis scores of separate principal component analyses performed on each site-table and the first two axis scores of the reference structure. This enabled the match between the site-tables and the reference structure to be evaluated using synthetic auxiliary variables. The second statistics we used were the values of RV coefficients (Robert and Escoufier 1976) between the site-tables and the reference structure. This coefficient ranges from 0 to 1 and measures the correlation between two tables. The RV coefficients can be interpreted as classical correlation coefficients and they provided an indication of the strength of the relationship between the temporal changes within each site and the reference temporal structure.

The multiple time-series of invertebrate samples were also analysed with the MCOA procedure, allowing us to reveal the common temporal variabilities of communities at geographically distant locations, despite the spatiotemporal plasticity of biological responses to long-term changes in environmental conditions. As for the environmental variables, this analysis allowed the graphical representation of site-specific changes in biological conditions compared to a reference temporal structure derived from the nine site-tables.

Linking biological to environmental changes

To compare the reference structures of biological and environmental conditions obtained from MCOA, we used a Procrustean analysis (Gower 1971; Digby and Kempton 1987). By adjusting the two structures on a common vectorial plane, this method evaluated the concordance of the two tables (see Supplementary material for details). Moreover, a randomization test procedure was developed for Procrustean analyses (PROTEST, Jackson 1995) to evaluate the statistical significance of the link between the different tables (see Supplementary material for details). MCOA and PROTEST are implemented in the ADE4 library for R (http://www.cran.r-project.org/, Ihaka and Gentleman 1996; R Development Core Team 2006).

Results

Environmental data

Main pattern

The main physicochemical properties of the environmental sampling sites are summarized in Table 1. The overall water quality was good during the study period, though NO_2, NO_3 and PO_4 concentrations were slightly in excess of the French standard of water quality (SEQ-Eau, see Simonet 2001, available at http://sierm.eaurmc.fr/eaux-superficielles/fichiers-telechargeables/grilles-seq-eau-v2.pdf). However, the physicochemical properties highlighted a good ecological state (according to the definition of the European Framework Water Directive; Direction de l'Eau 2005). Except for the discharge, values did not present marked variations among sampling sites. Nevertheless, the water quality generally decreased steadily along the upstream–downstream gradient (Table 1).

As already observed in the vicinity of Lyon (France) (Daufresne et al. 2004; Mouthon and Daufresne 2006) and more generally in Europe (Webb 1996), the water temperature increased between 1985 and 2004 (Fig. 2A). In particular, year 2003 was the warmest of the study period and was characterized by a summer heatwave (Stott et al. 2004). Conversely, the discharge fluctuated around an average value (927 m^3 s^{-1}), but no particular trend could be detected (Fig. 2B). Four floods occurred during the study period (Banque Hydro 2006): in October 1993 (e.g. 10- and 50-year return floods at sites b and g, respectively), January 1994 (only affecting the Lower Rhône; e.g. 50-year return flood at site g), March 2001 (e.g. 5- and 20-year return floods at sites b and g, respectively) and November 2002 (e.g. 10- and 50-year return floods at sites b and g, respectively).

Temporal changes in environmental conditions

Square cosines (ranging from 0.89 to 0.95 and from 0.74 to 0.97 for the first and second axes of the reference structure, respectively) were high and homogeneous. Thus, angles between the factorial axes of the PCA performed on the different site-tables and the factorial axis of the reference structure were low. This highlighted the strong match between the site-table structures and the reference structure. Similarly, RV values (ranging from 0.82 to 0.95; Fig. 3 panels C–I) attested to the strong correlation between the temporal changes within the different sites and the reference

Table 1 Main physicochemical properties of the environmental sampling sites

	Site a	Site b	Site c	Site d	Site e	Site f	Site g
Q	413 (57)	461 (89)	611 (121)	1031 (227)	1065 (237)	1383 (300)	1529 (308)
T	11.3 (0.4)	12.0 (0.4)	13.5 (0.7)	13.8 (0.6)	14.8 (0.7)	13.4 (0.8)	14.8 (0.7)
Cond.	284 (24)	299 (24)	318 (25)	376 (24)	390 (23)	402 (26)	400 (24)
pH	8.11 (0.08)	8.07 (0.08)	8.09 (0.05)	8.03 (0.08)	7.99 (0.09)	7.99 (0.09)	7.95 (0.17)
O_2 (6)	10.3 (0.3)	10.1 (0.3)	10.1 (0.2)	10.0 (0.3)	9.7 (0.4)	9.9 (0.3)	9.7 (0.6)
O_2% *(70)*	96.8 (3.4)	96.5 (2.8)	98.8 (2.2)	98.5 (2.9)	96.5 (3.1)	97.1 (2.9)	97.9 (5.3)
BOD_5 *(6)*	1.70 (0.59)	1.43 (0.61)	1.24 (0.42)	1.73 (0.52)	1.54 (0.44)	1.42 (0.41)	1.88 (1.12)
NH_4 *(0.5)*	0.21 (0.08)	0.17 (0.07)	0.10 (0.09)	0.24 (0.08)	0.30 (0.13)	0.24 (0.10)	0.14 (0.06)
NO_2 *(0.3)*	0.04 (0.01)	0.06 (0.01)	0.06 (0.01)	0.08 (0.01)	0.11 (0.01)	0.10 (0.01)	0.12 (0.08)
NO_3, *(50)*	2.29 (0.32)	2.77 (0.34)	3.94 (0.49)	6.13 (0.81)	6.90 (0.77)	6.41 (0.59)	6.56 (0.64)
PO_4 *(0.5)*	0.11 (0.06)	0.14 (0.08)	0.12 (0.05)	0.21 (0.06)	0.37 (0.25)	0.30 (0.16)	0.28 (0.19)

Mean values were calculated over the study period. Standard deviations are given in brackets. Values in italics represent the upper (for NH_4, NO_2, NO_3 and PO_4) or lower (for O_2 and O_2%) limits currently defining a good ecological state for French rivers according to the European Water Framework Directive (Direction de l'Eau 2005)

Q discharge, *T* temperature, *Cond.* conductivity, O_2 oxygen, O_2% percentage of oxygen saturation, BOD_5 five-day biological oxygen demand; NH_4 ammonium, NO_2 nitrite, NO_3 nitrate, PO_4 phosphorus. All values are expressed as mg L^{-1} except for Q (m^3 s^{-1}), T (°C), Cond. (μS cm^{-1}) and pH

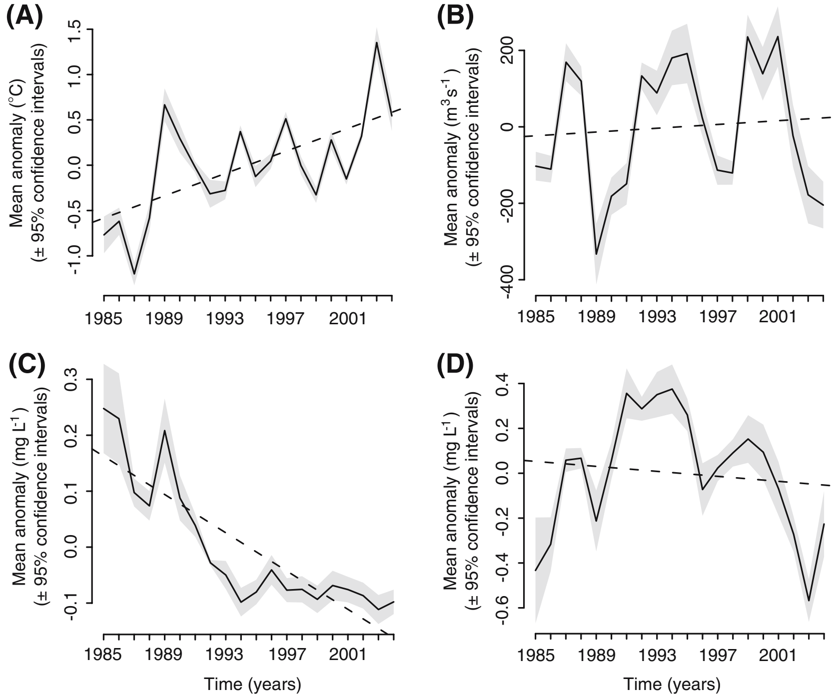

Fig. 2A–D Annual mean anomalies. **A** Water temperature, **B** discharge, **C** PO_4 concentration, **D** O_2 concentration. For each environmental sampling site the anomalies were calculated relative to mean 1985–2004 values. In *grey*: 95% confidence intervals. Trends are shown ($Y(t) = at + b$)

temporal structure. As consequences, (1) the reference structure accurately described general changes in environmental conditions (homogeneous RV and $\cos^2$ values), (2) changes were similar at all of the sites (high RV and $\cos^2$ values), and hence (3) the influence of site-specific factors on environmental dynamics was weak.

We were able to distinguish time periods that were associated with different environmental conditions (Figs. 2, 3B). From 1985 to 1991, interannual variability in environmental conditions was mainly due to changes in PO_4, NH_4 and NO_2 concentrations, and in BOD_5, oxygen contents and pH. We especially observed a general decrease (given as the mean change between 1985 and 1991 ± 95% CI) in PO_4 (-0.21 ± 0.12 mg L^{-1}), NH_4 (-0.17 ± 0.07 mg L^{-1}) and NO_2 (-0.04 ± 0.06 mg L^{-1}) concentrations, and in BOD_5 (-1.43 ± 0.92 mg L^{-1}). Concomitantly, for the same period we observed an increase in the oxygen contents ($+0.79 \pm 0.29$ mg L^{-1} for concentration and $+6.03 \pm 3.08\%$ for saturation) and pH ($+0.11 \pm 0.11$). Hydrological variability was also quite influential on changes in environmental conditions and the very low flow conditions in 1989 and 1990 were clearly observable in the reference structure (the factorial scores of these years on the first two axes were opposed to the factorial scores of the discharge variable, Fig. 3 panels A, B). It is important to note that these patterns represented the greatest relative changes in environmental conditions according to the MCOA. This of course did not imply that other variables remained stable during the same period. In this way, despite a positive trend in temperature, the thermal constraints were not particularly relevant to the observed environmental changes during this first period. After 1991, environmental changes were mainly driven by a decrease in oxygen content (Fig. 2d) and an increase in water temperature (negatively related to axis F2, Fig. 3), especially from 1995 onwards. During a short transition period (1991–1994), the decrease in PO_4 (Fig. 2c), NH_4, NO_2 concentrations and BOD_5 and the increase in pH still influenced the temporal patterns. However, these changes were quantitatively extremely weak (given as the mean change between 1985 and 1991 ± 95% CI): -0.12 ± 0.06 mg L^{-1} for PO_4, -0.04 ± 0.05 mg L^{-1} for NH_4, -0.01 ± 0.01 mg L^{-1} for NO_2, -0.63 ± 0.36 mg L^{-1} for BOD_5, $+0.11 \pm 0.02$ for pH. Finally, year 2003 appeared to be very unusual, due to its particularly high temperatures.

Biological data

Main pattern

The main properties of biological sampling sites are given in Table 2. We observed a gradual decrease in the total number of samples as well of the family richness along the upstream–downstream gradient. However, the average family richness per sample remained stable among the sampling sites.

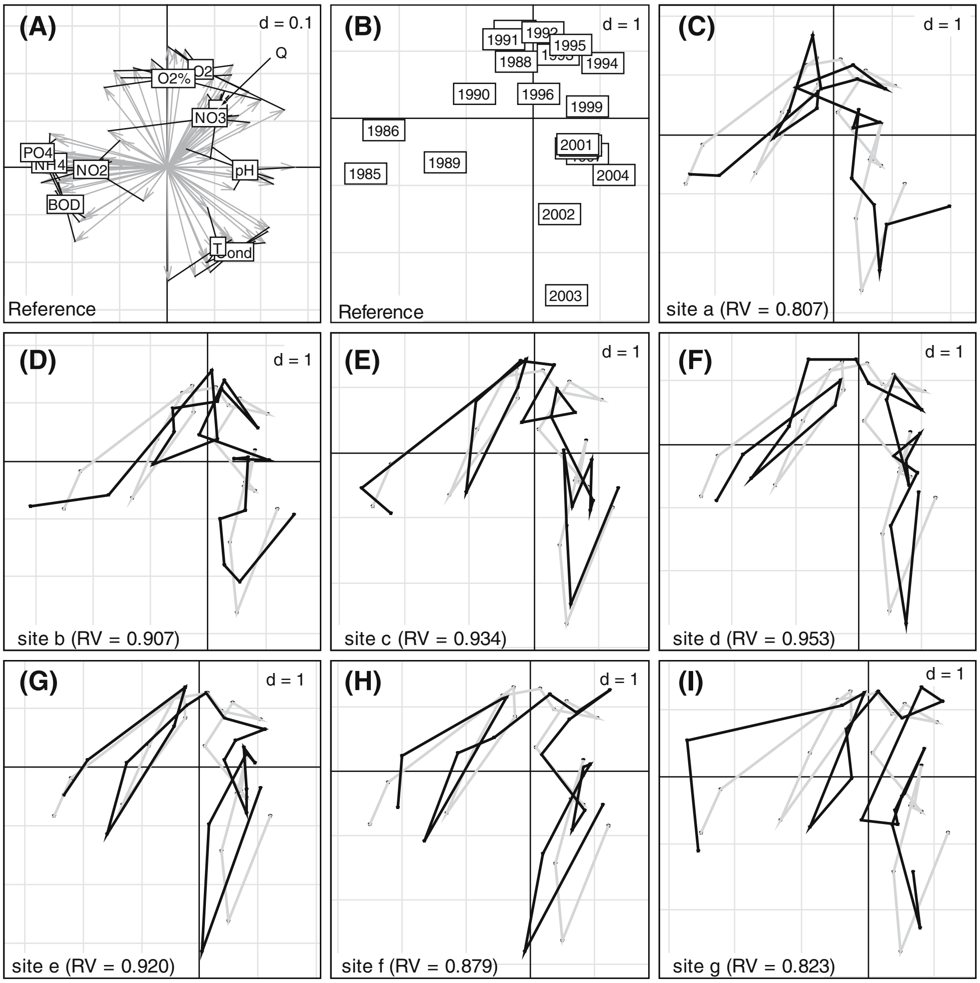

Fig. 3A–I Results of the MCOA performed on the environmental data. **A** Factorial scores for the environmental variables on the reference structure. **B** Reference temporal structure. **C**–**I** *Grey lines* show reference temporal structure scores and *black lines* show scores for each sampling site for the years covered

Table 2 Main features of the biological sampling sites

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9
Mean no. of samples per year (SD)	4.5 (1.1)	4.5 (0.9)	4.5 (1.1)	4.3 (0.5)	4.5 (0.7)	2.1 (0.3)	2.1 (0.3)	2.6 (0.5)	2.6 (0.5)
Total no. of individuals	788,266	555,595	547,009	550,143	305,522	94,830	105,769	65,287	45,253
Total FR	76	71	72	60	66	50	47	49	46
Mean FR per sample	22.7 (9.1)	19.1 (7.3)	20.4 (8.2)	23.7 (8.9)	31.6 (12.7)	23.4 (4.4)	21.7 (4.6)	19.8 (4.9)	17.3 (4.2)

FR family richness, *SD* standard deviation

Temporal changes in community structures

Square cosines were high, ranging from 0.62 to 0.95 and from 0.77 to 0.91 for the first and second axes of the reference table, respectively. Again, this result revealed a strong match between the site-tables and the reference structure. Similarly, RV values were high (ranging from 0.63 to 0.91; Fig. 4 panels B–J), suggesting a strong match between the temporal changes within the different sites and the reference temporal structure. Just as for the environmental conditions, these results suggested that the reference structure accurately described general changes in community structures (homogeneous RV and $\cos^2$ values). Moreover, changes were similar overall at all of the sites (high RV and $\cos^2$ values), suggesting weak effects of site-specific factors (e.g. sample procedures, local disturbances) on community dynamics.

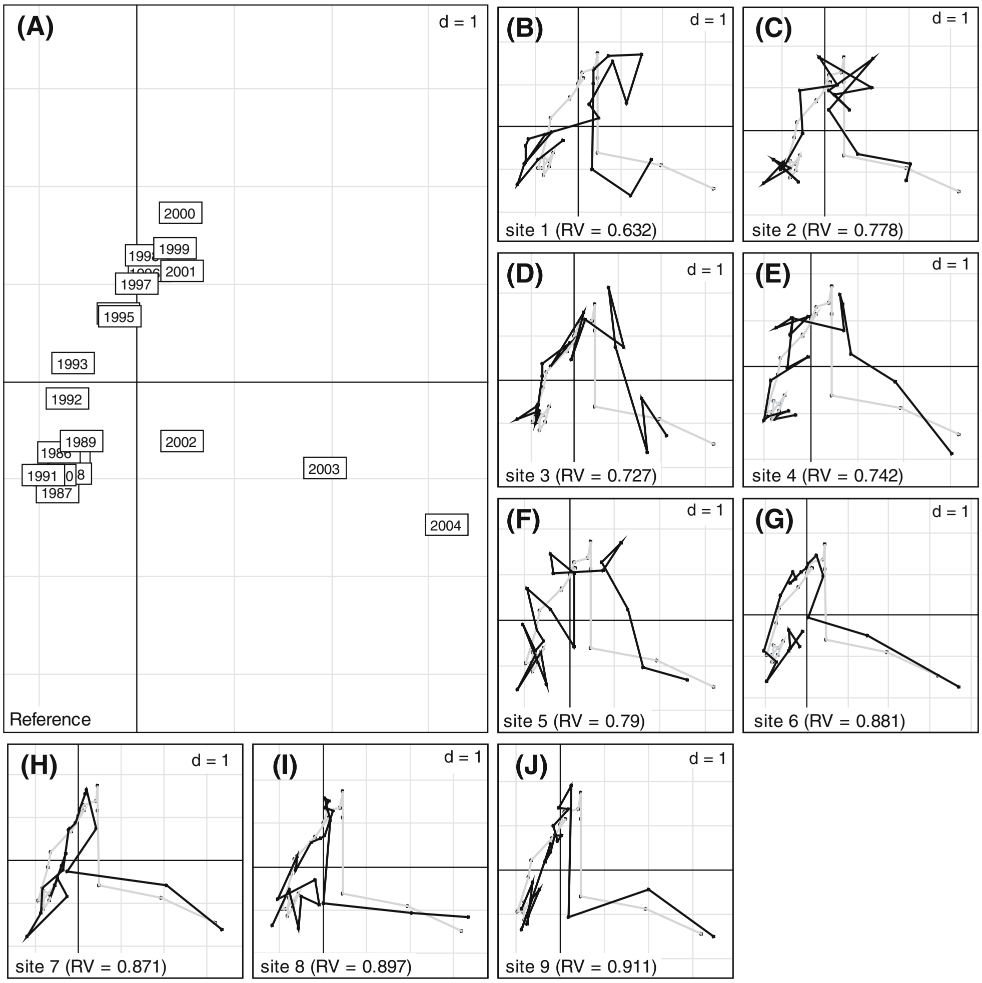

Fig. 4A–J Results of the MCOA performed on the biological data. **A** Reference temporal structure. **B–J** *Grey lines* reference the temporal structure and *black lines* show the scores for each site for the years covered

According to the reference temporal structure, we could distinguish three main time periods in terms of biological conditions (Figs. 4, 5): from 1985 to 1991, from 1991 to 2000 and from 2000 onwards. During the first period, the community structures remained particularly stable (no trends in the scores on axes F1 and F2; Fig. 5a, b). The second period appeared to show a temporal change in these structures. From 1991 to 1993, changes in the community structures were only highlighted by axis F2 of the reference structure (Fig. 5b). Then, from 1993 to 2000, changes were visible on both F1 and F2 of the reference structure (Fig. 5a, b). A marked shift (i.e. notable geometric distances between year scores on the reference structure, Fig. 5c) in community structures occurred between 2000 (which can be viewed as an inflexion point in the time series of factorial scores on axis F2; Fig. 5b) and 2002. This shift was only visible on axis F2 of the reference structure, and was especially clear between 2001 and 2002. A second shift (particularly visible on axis F1) occurred later, between 2002 and 2004.

During the first period (1985–1991), community structures were dominated by families such as Rhyacophilidae and Chloroperlidae at most upstream sites (1–3) and by Valvatidae or Physidae in the median and downstream ones (Fig. 6). The second period was characterized by an increase in the abundances of Corbiculidae over all sites. The abundances of Baetidae and Ecnomidae also increased at sites 1–3 and 4–9, respectively. During this period, some families such as Physidae or Dugesiidae tended first to increase their numbers at downstream sites (7–9). Later, the abundances of these families started to decrease at these sites and to develop at the most upstream ones (site 5 first and then 1–4). The 2000–2002 shift was mainly due to an increase in the abundances of Gammaridae (mainly due to the invasive species *Dikerogammarus villosus*) in sites 4–9 and Ancylidae at the most downstream

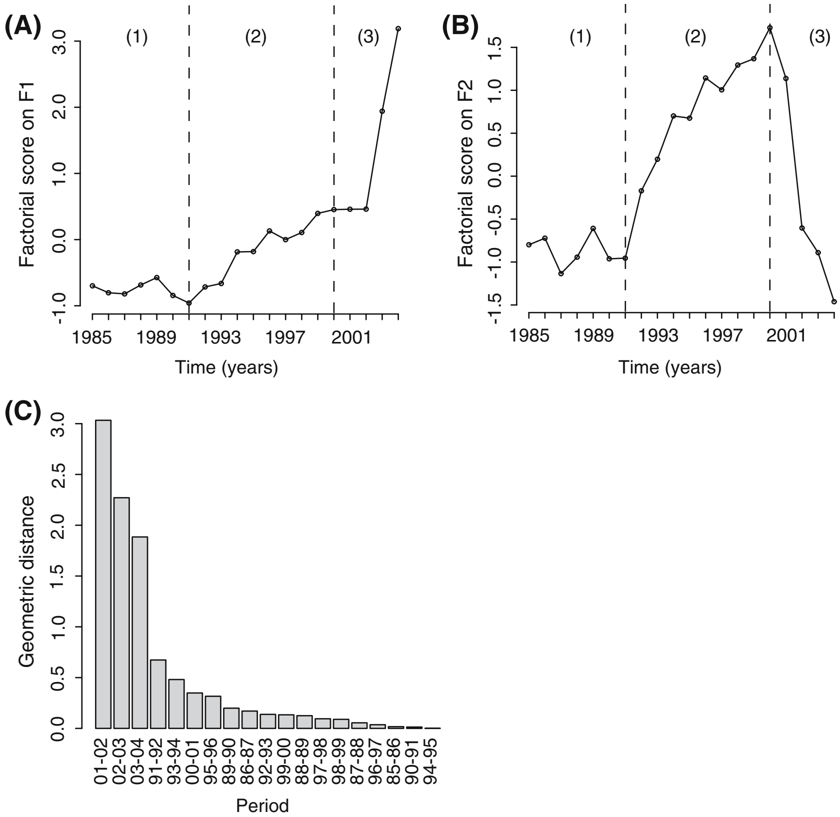

Fig. 5A–C Details of the biological reference temporal structure. **A** Time series of the scores for the years on the F1 axis of the biological reference structure. **B** Time series of the scores for the years on the F2 axis of the biological reference structure. The three main periods of biological change defined in the text are represented. **C** Geometric distances between the scores of two consecutive years on the F1 × F2 plane of the biological reference structure. Geometric distance is calculated as the square-root of the sum of the squared differences between scores

sites (6–9), and a decrease in the abundances of Baetidae and Ancylidae at the upstream sites (1–3). Finally, the 2002–2004 shift prompted (1) increasing abundances of Hydroptidae and decreasing abundances of Glossiphoniidae at all the sites, (2) decreasing abundances of Erpobdellidae at the median and downstream sites (4–9), (3) increasing abundances of Physidae and Dugesiidae at the upstream sites (1–3), (4) increasing abundances of Caenidae and Ferrissiidae at the median and downstream sites (4–9) and a substantial decrease in the abundances of Asellidae in sites 4–7, (5) increasing abundances of exotic and invasive species belonging to families Atyidae, Ampharetidae and Mysidae at all median and downstream sites (Fig. 6).

Link between environmental and biological changes

The environmental and biological reference structures presented a strong and significant link (PROTEST; observed value = 0.7653, $p = 0.001$), revealing a clear statistical relationship between temporal changes in both environmental and biological conditions in the French Rhône. Procrustean projection highlighted particularly strong similarities in the temporal patterns between 1990 and 2001 (Fig. 7). The match between the two dynamics seemed less marked between 1985 and 1989 and from 2002 onwards than between 1990 and 2001.

Discussion

About using MCOA and Procrustean projection to analyse multisite and multitaxon datasets

Ordination techniques have long been viewed as powerful tools for describing community structures without focusing on particular taxa (see Jongman et al. 1995; Legendre and Legendre 1998). In particular, MCOA allows the common temporal variability of communities with different structures to be analysed. This property sounds extremely interesting when looking for general rules about the response of communities to climate change. Indeed, such an investigation requires the analysis of consistent multisite and multitaxon surveys covering extensive periods of time. In particular, MCOA enabled us to focus on common dynamics and to reduce the influence of site-specific confounding factors. As a consequence, this method, based on a within-class approach, presents some limitations. When performing a MCOA, it is especially

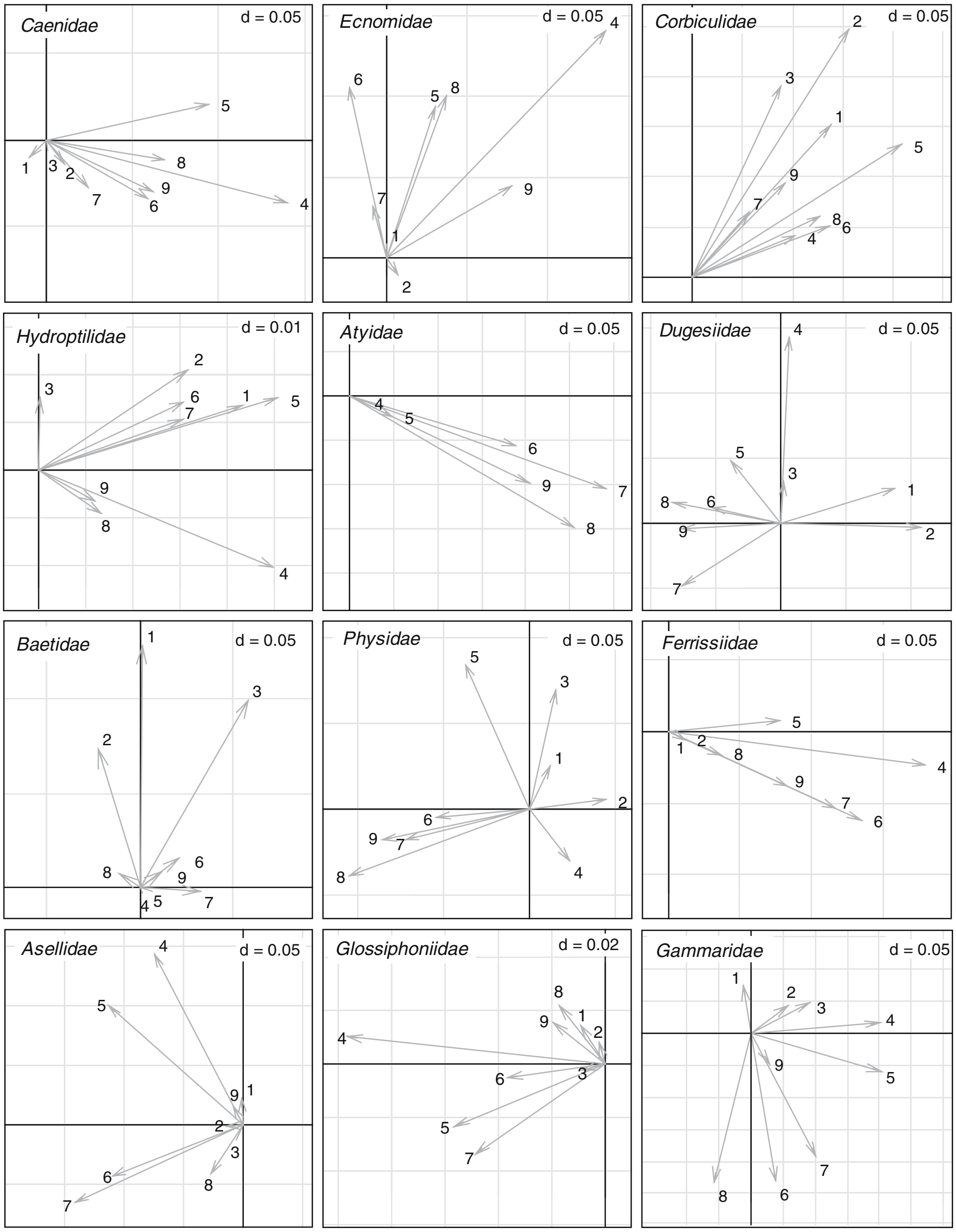

Fig. 6 Factorial scores of some informative macroinvertebrate families on the first two axes of the biological reference structure. The numbers (ranging from 1 to 9) are those of the sampling sites

important to check (1) that all of the different communities contribute equally to the set-up of the common structure, and (2) that this common structure is close to the individual structures of the communities. Hence, interpretion of the reference structure as a global structure is only valuable when both RV and $\cos^2$ values are high. Similarly, performing a MCOA on environmental variables enables general changes rather than particular variables to be focused upon. Moreover, it allows the variables that exert most influence on environmental changes at different periods to be identified. This represents an important asset when analysing environmental dynamics. Finally, the PROTEST enables the statistical link between environmental and biological changes to be assessed. As a consequence, coupling MCOAs and a PROTEST provide interesting tools for investigating the causal links between biological and environmental patterns, which are obviously (as for any statistical tests) not directly related to the statistical relationship. In addition, the implementation of these methods and the interpretation of the results are easy for users familiar with even simple ordination techniques (e.g. principal component analysis).

A consistent change in the community structure

During the study period, we observed definite and significantly linked changes in both environmental conditions and macroinvertebrate community structures. These changes were consistent across the different sampling sites despite heterogeneous habitat conditions and contrasting anthropogenic histories. However, it was important to distinguish between *absolute* and *relative* changes. For instance, all of the environmental study sites underwent similar *absolute* changes in their environmental conditions (factorial scores for the environmental variables on the reference structure were similar for the different sampling sites; Fig. 3). This means that each environmental variable showed a consistent decrease at all of the sites. This was mainly because initial differences among the sampling sites were only due to differences in absolute values (Table 1). Since the community structures presented obvious initial differences along the upstream–downstream gradient, we only observed consistent *relative* biological changes (some factorial scores of the families on the reference structure were heterogeneous for the different sampling sites; Fig. 6). This result means that a family could show different changes (increase or decrease) at different sites. Hence, the consistency in biological changes underlined consistent ecological responses to similar (*absolute*) environmental changes at the community scale, but not necessarily at the family scale.

Biological consequences of changes in environmental conditions

We found that the biological and environmental changes were statistically significantly linked (PROTEST, $p = 0.001$). We could distinguish different periods regarding changes in both environmental and biological conditions. The first period ranged from 1985 to 1991. Despite an increase in water temperature (Fig. 2A), the greatest common environmental change was an improvement in the water quality (Figs. 2C, D, 3). This improvement probably mainly resulted from changes in water quality treatments in France, but probably also partially from the re-oligotrophication of Lake Geneva (Anneville et al. 2005), at least for the French Upper Rhône. Despite this improvement, the community structures remained very stable during this period (Figs. 4, 5). One could argue that such stability was due to the level of improvement. In fact, changes in pH, O_2, O_2% and NO_2 were low, at least with regard to the relative sensitivities of the different families to these factors. Actually, initial values of these parameters were rather good, with no particular detrimental effect on aquatic life (Direction de l'Eau 2005). Similarly, while the decrease in BOD_5 may seem more important, its mean value (±95% CI) in 1985 was already low (2.92 ± 0.75 mg L^{-1}). However, the decreases in PO_4 and NH_4 were more substantial. For instance, mean concentrations (±95% CI) of PO_4 and NH_4 were respectively 0.46 mg L^{-1} (±0.2) and 0.40 mg L^{-1} (±0.08) in 1985 and 0.26 mg L^{-1} (±0.10) and 0.23 mg L^{-1} (±0.08) in 1991. Such changes, in addition to both a slight increase in oxygen content and a decrease in NO_2 concentration, may have slightly influenced the community structure (Emerson et al. 1975; Russo 1985; Arthur et al. 1987). Actually, it seems likely that the increase in water temperature and consecutive warm and dry years (1989 and 1990) overwhelmed the positive ecological effects of the improvement in water quality. Indeed, temperature increases chemical kinetics and the metabolic rates of organisms which, in turn, generally result in a greater sensitivity of biota to chemicals (Cairns et al. 1978; Alcaraz and Espina 1995; Augspurger et al. 2003; Kir et al. 2004; Kroupova et al. 2005). In this way, temperature increase is generally considered detrimental to water quality (Agence de l'eau Rhône Méditerranée Corse 1999; Simonet 2001).

The second period (1991–2000) corresponded to gradual changes in community structures (Figs. 4, 5). Regarding physicochemical conditions, the mean annual temperature was higher than during the first period (ca. 0.8 °C warmer than during the 1985–1988 period; Fig. 2A) and the improvement in water quality ceased (Figs. 2C, 3). These two facts led to a gradual decrease in oxygen content (Figs. 2D, 3). As already shown in the French Upper Rhône (Daufresne et al. 2004) and in the Saône River (Mouthon and Daufresne 2006), the high temperatures associated here with decreasing oxygen contents seemed to induce changes in the community structures. Such changes have already been shown to be significantly correlated with water temperature at sites 1–3 during the 1979–1999 period and they corresponded to a decrease in relative abundances of lotic and cold-water taxa versus an increase in those of lentic and warm-water taxa (Daufresne 2004; Daufresne et al. 2004). Conversely, one could argue that we instead observed a delayed effect of water quality improvement. However, the significant match between biological and environmental changes seemed particularly strong during this period

(1991–2000, Fig. 7). In addition, regarding the ecological impacts of chemicals over observed ranges (Direction de l’Eau 2005; Table 1), the levels of improvement in the water (between 1985 and 1991 but also between 1991 and 1995) were too low to explain such major changes alone. Finally, developing taxa (e.g. Ecnomidae, Corbiculidae) are not considered sensitive to water quality (Tachet et al. 2000). Nonetheless, as described above, it seems likely that the improvement in water quality hindered the impact of global warming on changes in community structure at the beginning of the study period.

Interestingly, we could distinguish two subperiods between 1991 and 2000: before and after 1993. The 1991–1993 period was characterized by an increase in the abundance of families such as Ecnomidae in the Lower Rhône and Baetidae in the French Upper Rhône. The functional interpretation of such changes is not easy. The coding of most ecological traits of macroinvertebrates in rivers has been based on a general classification strongly influenced by the upstream–downstream gradient (e.g. Tachet et al. 2000). For example, most of the invertebrates inhabiting downstream zones are considered lentic and thermophilic. Hence, it was difficult to evaluate the relative ecological preferences of invertebrates at a given sampling site. However, Ecnomidae, and particularly *Ecnomus tenellus* found in the Rhône and inhabiting slow-flowing rivers (Meurisse-Genin et al. 1987; Tachet et al. 1988), may be considered to be more lentic and thermophilic than the Valvatidae or Physidae that characterized the community structure between 1985 and 1991. Baetidae generally inhabit epipotamic zones of large rivers (i.e. flowing zones with coarse substrate and moderate water temperature), although some species can support warmer and more lentic conditions (Tachet et al. 2000). The concomitant decrease in abundance of Chloroperlidae (inhabiting cold water zones, Tachet et al. 2000) at the most upstream sites also support the hypothesis of an effect of higher temperatures. In addition to the warming, it is important to note that changes between 1991 and 1993 may also be the consequence of particularly warm and dry conditions during 1989 and 1990. The slight shift observed in 1993–1994 (Figs. 4, 5C) was probably due to the two consecutive floods of 1993 and 1994 (Cattanéo et al. 2001; Fruget et al. 2001). More than producing major changes in community structures, this shift particularly corresponded to the first appearance of Corbiculidae (only represented by *Corbicula fluminea* in the Rhône) at most biological sampling sites. This family is known to be invasive and eurytolerant (Araujo et al. 1993). Corbiculidae were found from 1990 onwards at sampling sites 1–3, but at rather low abundances (mean abundances ±95% CI between 1990 and 1992; 1.27 ± 0.97 indiv. per sample). Corbiculidae then tended to develop at all of the sites and were mainly responsible for changes in community structures until 2000 (Figs. 4, 5). Interestingly, we also noticed some alternative appearance/disappearance patterns along the downstream-upstream gradient during the 1991–2000 period (e.g. for Physidae or Dugesiidae; Fig. 6). Such patterns probably resulted from ecological processes that were similar to those involved in altitudinal or latitudinal shifts in the geographical ranges of some species under global warming (Walther et al. 2002).

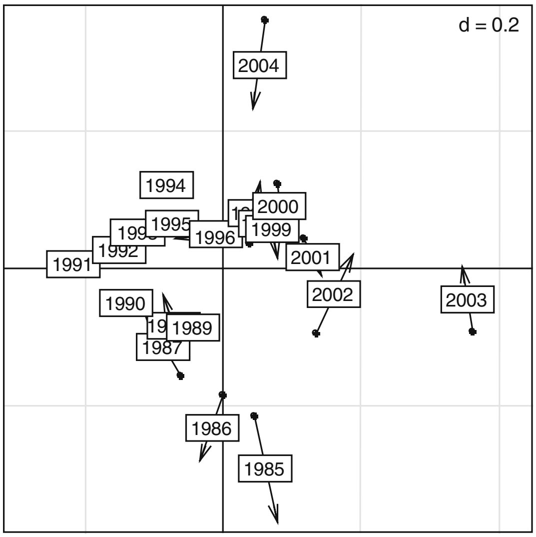

Fig. 7 Scores for the different years plotted on the common vectorial plan of the Procrustean projection of the biological and environmental reference structures. *Arrows* indicate the mismatch between the two reference structures

The third main period (2000–2004) corresponded to two major shifts in community structures. The first shift, visible on axis F2 of the biological reference structure (2000–2001–2002; Figs. 4, 5), may be attributed to the floods of March 2001 and November 2002. The mismatch between the environmental and biological reference structures in 2002 (Fig. 6) was probably related to the fact that the mean discharge used in the analysis did not properly reflect floods. These extreme events only induced decreases in the abundances of a few families such as Baetidae at the most upstream sites (1–3). However, as for Corbiculidae in 1994, these floods seemed to be beneficial to eurytolerant and invasive taxa (e.g. the gammarid *Dikerogammarus villosus*) at the median and downstream sampling sites (4–9).

The changes in community structures that occurred after 2002 were the largest that occurred over the whole study period (because they were particularly marked on axis F1 of the biological reference structure; Figs. 4, 5). As already shown for mollusc communities of the Saône River, these patterns could be due to the 2003 heatwave (Mouthon and Daufresne 2006). The changes observed (e.g. overall decrease in Glossiphoniidae, decreases in Erpobdellidae and Asellidae at the median and downstream sites, overall increase in Caenidae, Heptageniidae or Hydroptilidae) thus probably partially reflected a relative sensitivity of some families to extreme temperatures and low discharge conditions. However, regarding the time scale of our study and the sampling frequency, we cannot exclude a cumulative effect of the November 2002 flood. Again, this period was characterized by the development of exotic and invasive taxa (e.g. *Atyaephyra desmarestii*, *Hypania complanata* and *Hemimysis anomala* belonging to the families of Atyidae, Ampharetidae and Mysidae, respectively) in the Middle and Lower Rhône (sites 4–9) or eurytolerant taxa such as Dugesiidae at the most upstream sites (1 and 2). The heatwave also seemed to be beneficial to the gammarid *Dikerogammarus villosus* in the median zones (sites 4–5). Such changes persisted in 2004, underlining the strength of the heatwave constraint.

Interpreting changes in the general context of disturbance theory

Disturbances have long been considered important structuring forces in populations, communities and ecosystems (Pickett and White 1985; Pickett et al. 1989). They typically reinitiate a succession and/or colonization sequence (Reice 1985; Glenn-Lewin and van der Maarel 1992) by releasing resources and creating open spaces (Connell and Slatyer 1977). The ecological consequences of disturbances have been studied extensively in rivers. Pulse disturbances such as floods and droughts have received particular attention (Boulton et al. 1992; Miller and Golladay 1996; Watanabe et al. 2005). Some of our results matched the general rules for the dynamics of communities undergoing such disturbances. For instance, changes in community structures systematically occurred after each pulse disturbances (major floods of 1993–1994 and 2001–2002, heatwave of the 2003 summer). In addition, the development of invasive exotic species (e.g. *Atyaephyra desmarestii*, *Corbicula fluminea*, *Dikerogammarus villosus*, *Hypania complanata*, *Hemimysis anomala*) clearly showed that these events opened up new space for subsequent colonization. Finally, the pulse disturbance globally favoured eurytolerant taxa that are more resistant to changes in environmental conditions.

Conversely, some patterns we found did not fit the expected dynamics following pulse disturbances. For instance, the recovery time of a macroinvertebrate community structure after a disturbance (pulse or press) is generally less than a decade (Fuchs and Statzner 1990; Niemi et al. 1990; Watanabe et al. 2005). Community structures of the Rhône did not show any signs of recovery after pulse disturbances, which could be due to the perennial establishment of exotic species. However, changes did not exclusively result from invasion processes. Between 1985 and 2004, the decrease in abundance of indigenous families like Valvatidae or old invaders like *Physella acuta* (Physidae) at the downstream site and of Rhyacophilidae and Chloroperlidae at the most upstream sites (1–3) was the main contribution to changes in community structures. In the same way, Daufresne et al. (2004) showed that a decrease in the relative abundances of *Chloroperla* sp. and *Protonemura* sp. was one of the most important changes in community structures in the 1979–1999 period at sites 1–3.

We found that the biological and environmental reference structures were statistically linked (PROTEST, $p = 0.001$; Fig. 7) despite a sampling frequency and a temporal (interannual) scale that were not appropriate for the statistical evaluation of the instantaneous effects of pulse disturbances. In this way, even if some biological effects of pulse disturbances were visible, our study chiefly underlined the effect of the gradual environmental changes. This could explain the mismatch between observed patterns and the classical assumption about pulse disturbance effects. Lake (2000) named such long-term environmental changes “ramp disturbances”. Unlike press or pulse disturbances, the strength of a ramp disturbance increases steadily over time and space. Global changes, and especially global warming, fit such definition perfectly. Only some recent and largely theoretical works have attempted to account for ramp disturbance in community dynamics analyses (Scheffer et al. 2001; Scheffer and Carpenter 2003; van Nes and Scheffer 2004). Recent work has highlighted that systems may switch rapidly to alternative attractors in response to a small change in external conditions. In this context, a gradual change in environmental conditions should induce gradual changes in community structures disrupted over time by rapid shifts (van Nes and Scheffer 2004). Gradual environmental change leads to a reduction in the basin of attraction around a current community state, and when approaching a bifurcation point the attraction basin shrinks and a small stochastic event may induce a shift to an alternative attractor. Dynamics of the macroinvertebrate community structures in the Rhône with alternating gradual changes and rapid shifts could match such a hypothesis. In particular, this viewpoint could explain the commonly observed switches in community structures (Fig. 4, panels B–J) under different strengths of pulse disturbances. Actually, if floods affected the whole river, their strengths were systematically smaller and relatively common at the median and most upstream sites (ca. 5- to 10-year return). Symmetrically, this hypothesis could explain the different changes in community structures under comparable pulse disturbances (1993–1994 vs. 2001–2002 floods). Changes in community structures after 1993–1994 were not drastic compared to those occurring between 2001 and 2003. Following van Nes and Scheffer's (2004) hypothesis, community structures in 1993 were probably far from a catastrophic bifurcation point, in contrast with community structures in year 2001. In this way, the relative sensitivities of communities to floods may have increased during the study period due to global changes. The most important shift, occurring after the 2003 heatwave, probably resulted from a similar process.

Finally, it is interesting to note that dynamics were altogether similar across the sites, despite different press disturbance histories. Initial community structures in our study were the consequence of more than a hundred years of anthropogenic constraints (Dessaix et al. 1995; Dolédec et al. 1996; Fruget et al. 2001; Fruget and Michelot 2001). Compared to a natural state, press disturbances (e.g. embankments, hydropower schemes) typically decrease biodiversity and favour lentic taxa. However, the strengths of press disturbances were heterogeneous among the sites (distance from hydropower schemes, presence or not of embankments, sites located upstream or downstream from nuclear power plants etc.). Despite these differences and their relative consequences for initial states, community dynamics were close. Such consistency is strong evidence in favour of the power of hydroclimatic constraints to shape aquatic ecosystem dynamics. Nevertheless, MCOA is a within-class type approach and does not focus on differences among sites. Among-class analysis should be a more appropriate approach for comparing site-specific dynamics and for deeply studying the effects of nonclimatic anthropogenic constraints. However, it is important to note that working at a smaller spatio-temporal scale with such raw data would not be easy. The sampling protocol (e.g. frequency) and determination level (family) would probably hinder the discrimination of effects of site-specific factors.

Conclusion

As previously shown in large rivers (Daufresne et al. 2004; Mouthon and Daufresne 2006), we observed gradual changes in macroinvertebrate community structures under climate change. However, our analysis underlines that improvements in water quality may hinder the effects of global warming. In addition, this study stresses the substantial effects of hydroclimatic events (which are likely to increase in frequency with global warming) on community dynamics. For instance, we showed that the 2003 heatwave (possibly coupled with the 2002 flood) caused the greatest changes in community structures. More specifically, we clearly documented that all strong hydroclimatic events (the 2001 and 2002 floods for example) systematically led to the development of eurytolerant and invasive taxa. In contrast to expectations, we did not observe any sign of recovery, and the relative sensitivities of communities to extreme hydroclimatic events seemed to increase with time. As a consequence, it appears difficult to predict changes in the dynamics of communities in the context of global changes. As well as a gradual change in community structure, we emphasise that hydroclimatic events can produce shifts of unpredictable magnitude in macroinvertebrate communities.

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