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Long-term changes within the invertebrate and fish communities of the Upper Rhône River: effects of climatic factors

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Abstract

There is increasing evidence that the global climate change is already having measurable biological impacts. However, no study (based on actual data) has assessed the influence of the global warming on communities in rivers. We analyzed long-term series of fish (1979–1999) and invertebrate (1980–1999) data from the Upper Rhône River at Bugey to test the influence of climatic warming on both communities. Between the periods of 1979–1981 and 1997–1999, the average water temperature of the Upper Rhône River at Bugey has increased by about 1.5 °C due to atmospheric warming. In the same period, several dams have been built from 12.5 to 85 km upstream of our study segment and a nuclear power plant has been built on it. Changes in the community structure were summarized using multivariate analysis. The variability of fish abundance was correlated with discharge and temperature during the reproduction period (April–June): low flows and high temperatures coincided with high fish abundance. Beyond abundance patterns, southern, thermophilic fish species (e.g. chub, and barbel) as well as downstream, thermophilic invertebrate taxa (e.g. *Athricops*, *Potamopyrgus*) progressively replaced northern, cold-water fish species (e.g. dace) and upstream, cold-water invertebrate taxa (e.g. *Chloroperla*, *Protoneumura*). These patterns were significantly correlated with thermal variables, suggesting that shifts were the consequences of climatic warming. All analyses were carried out using statistics appropriate for autocorrelated time series. Our results were consistent with previous studies dealing with relationships between fish or invertebrates and water temperature, and with predictions of the impact of climatic change on freshwater communities. The potential confounding factors (i.e. dams and the nuclear power plant) did not seem to influence the observed trends.

Keywords: climate change, fish, freshwater, invertebrate, long-term series, Rhône River

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Introduction

The average air temperature of the Earth has increased by 0.06 °C per decade over the last century with two main periods of warming: between 1910 and 1945 and since 1976 (IPCC, 2001). Many studies have attempted to understand and predict how this warming influences ecosystems. They cover a wide range of ecosystems and taxa (e.g. plants, zooplankton, marine and terrestrial invertebrates, birds, mammals and fish; Hughes, 2000; Walther *et al.*, 2002). The two major consistent results of these studies are a change in the timing of life cycle events and spatial shifts towards higher altitudes and higher latitudes, according to thermal preferences.

Temperature is of major importance for poikilotherm aquatic organisms. It controls their physiology and behavior (Coutant, 1987) and can be considered as an ecological resource (Magnuson *et al.*, 1979). The potential impacts of global warming on aquatic organisms have been mainly documented in marine environments (Beamish, 1995; Sagarin *et al.*, 1999; Cabral *et al.*, 2001; Attrill & Power, 2002; Brooks *et al.*, 2002).

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However, the influence of global climate change could be particularly marked in freshwater bodies where movements are constrained by the environment (Shuter & Post, 1990). Many studies of climate change impacts in freshwater were predictive (Coutant, 1990; Regier *et al*., 1990; Carpenter *et al*., 1992; Meyer *et al*., 1999), and those based on actual data essentially dealt with lakes (George, 2000; Gerten & Adrian, 2000; Straile & Adrian, 2000; Scheffer *et al*., 2001; Sorvari *et al*., 2002). Few studies have assessed impacts of climate change on stream organisms (Elliott *et al*., 2000; Bradley & Ormerod, 2001), probably due to the lack of long-term data sets. This paper involves fish and invertebrate data collected between 1979 and 1999 in a segment of the Upper Rhône River at Bugey. During this period, Europe has warmed by 0.8 °C, with a greater warming rate (2 °C per century) in southern and central France (IPCC, 1997). Therefore, this data set gives us the opportunity to study the changes in stream communities at different trophic levels under climatic warming. It includes a wide range of organisms, with a large range of ecological, biological traits and niches, potentially reflecting major modifications of the aquatic ecosystem.

Since 1979, the Upper Rhône River has undergone other types of anthropogenic impacts. Hydropower schemes were built upstream from our study segment. They could affect sediment structure and discharge patterns, particularly during dam releases performed every 3 years (Bravard, 1987; Petts *et al*., 1989; Calow & Petts, 1992). On the Rhône River, schemes built before 1979 have led to an increase in winter and spring discharge rates and a decrease in summer and autumn discharge rates (Bravard, 1987). In addition, a nuclear power plant was built in 1978 in the middle of our study segment, potentially warming part of it. Such potentially confounding effects had to be considered when studying the influence of the global warming on freshwater communities at Bugey.

In this paper, we analyzed the temporal changes of fish and invertebrate communities at Bugey between 1979 and 1999 and tried to identify their causes. For this purpose, we used the fish and invertebrate data sampled at Bugey each year, as well as relevant temperature and discharge data. We first evaluated the relationships between climate, discharge rate and water temperature. Then, we analyzed the structural modifications of fish and invertebrate communities, using multivariate analysis to summarize community changes. We related community patterns to environmental modifications, using statistical analyses appropriate for time series. The results were compared with previous studies dealing with the biological impacts of human activity to identify the potential influence of confounding factors.

Materials and methods

Study area

The study segment of Bugey is a 13 km long segment of the French Upper Rhône River (45.8°N; 5.2°E), upstream from the confluence of the Ain River (Fig. 1). The segment has a slope of 0.35%, a mean width of 120 m, a mean depth of 3 m and a mean annual discharge of 500 $m^3 s^{-1}$. Five hydropower schemes were built 12.5–85 km upstream from the study segment in the last 20 years (the Chautagne hydropower scheme, completed in 1981; the Belley hydropower scheme, completed in 1982; the Brégnier Cordon hydropower scheme, completed in 1984 and the Sault Brénaz hydropower scheme, completed in 1986), and a nuclear power plant (CNPE Bugey) was built in 1978 in the segment. The nuclear power plant discharges water on an average 10 °C warmer than the input water. The warmed effluent stream cools on an average of 1 °C per kilometer and only affects a narrow area 15–25 m wide along the right bank (Ginot *et al*., 1996).

The study segment was a morphologically unimpacted section, not subjected to a minimum flow and with an overall good water quality (Agence de Bassin Rhône Méditerranée Corse, 1999; see Table 1). Phosphorus (PO_4), Ammonium (NH_4) concentrations, suspended and organic matter tended to decrease during the study period. Nitrate (NO_3) concentrations were stable and relatively low (Table 1). All these data are available online on the Agence de l'eau Rhône Méditerranée Corse web site at http://rdb.eaurmc.fr.

Temperature and discharge data

During the study period, the mean daily water temperature and discharge were recorded by Electricité de France at the Bugey nuclear power plant. The temperature recorded was the input water temperature (upstream from the power plant). The mean daily air temperature (1979–1999) at Ambérieux en Bugey (20 km north from the study segment) was recorded by Météo France. To evaluate the potential water temperature and discharge modifications induced by the climatic change, for each calendar year (from daily measurements) we calculated the mean annual discharge, the mean annual water temperature and the mean annual air temperature. To evaluate the potential modification of the hydrological regime at the study segment by the hydropower schemes built during the study period, for each year (from daily measurements) we calculated the mean, the maximum and the minimum discharges during winter/spring (December–May) and summer/autumn (June–September).

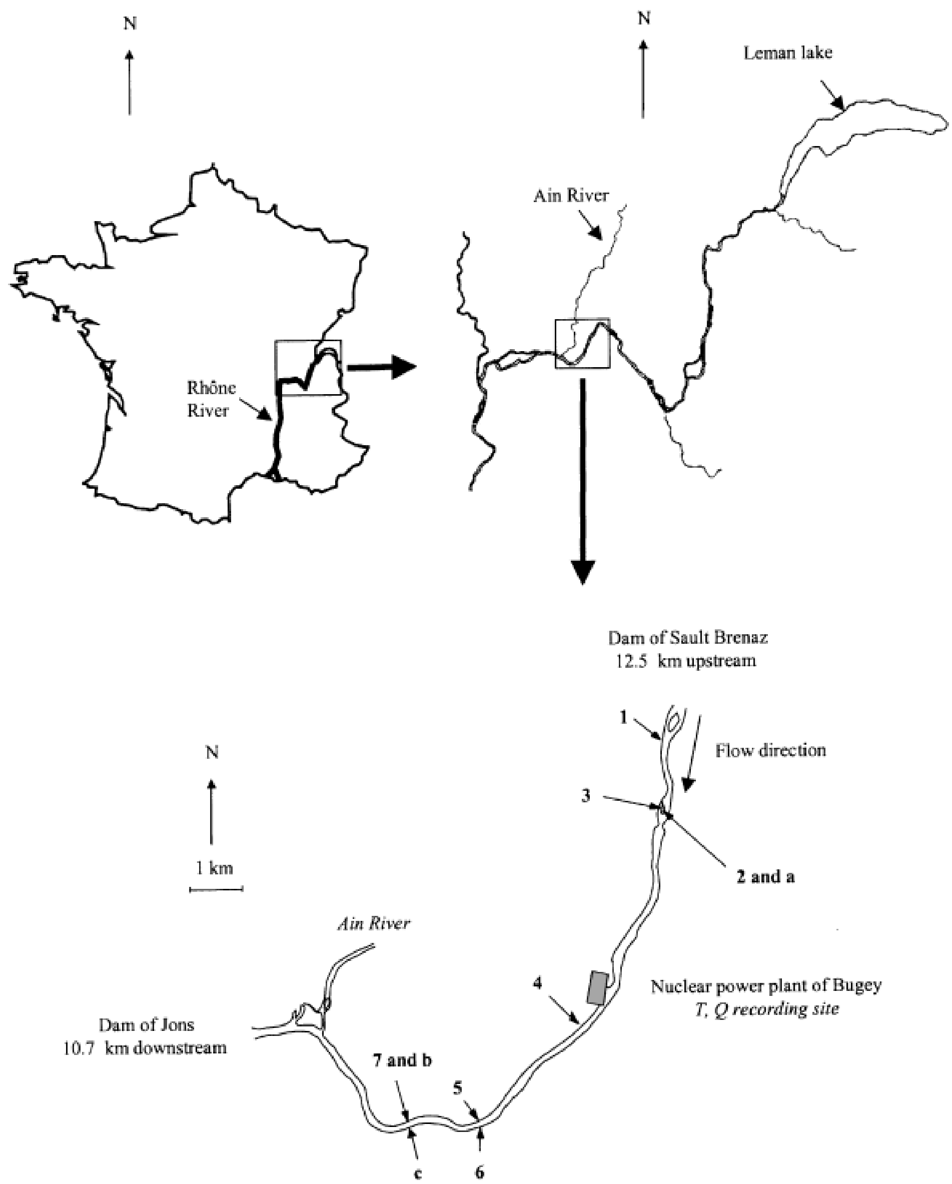

Fig. 1 Study area and location of the fish sampling sites (1–7), the invertebrate sampling sites (a–c) and the temperature (T) and discharge (Q) recording sites.

Finally, to link environmental changes to fish and invertebrate community changes, for each year (from daily measurements) we calculated the mean water temperature and mean discharge during limiting periods of the life cycles of fish and invertebrate. Periods considered for fish were the reproduction (from April to the end of June; Mann, 1996) and early growth of the Young of the Year (YOY) (from July to the end of October; Cattanéo *et al.*, 2001). Both directly influence the recruitment and, as a consequence, the strength of cohorts (Cragg-Hine & Jones, 1969; Mann, 1974; Philippart, 1981; Mills & Mann, 1985). The growth period includes summer and could also influence the survival of juveniles and adults. For invertebrates, the large number of different invertebrate taxa made it impossible to define the key periods influencing the whole invertebrate community (Hynes, 1970). A biological year was defined beginning on 1 October of the calendar year n and ending on 30 September of the calendar year $n + 1$. These dates were chosen according to the ecology of most of the taxa present in the invertebrate community of the Upper Rhône River (Hynes, 1970). In summary, we used the six seasonal variables defined above to link environmental changes to the changes in fish and invertebrate communities (Table 2): the mean annual reproduction temperature;

the mean annual reproduction discharge; the mean annual growth temperature; the mean annual growth discharge; the mean temperature calculated for the invertebrate biological year; and the mean discharge calculated for the invertebrate biological year.

Table 1 Mean, median and standard deviation of BOD5, conductivity and NH_4, NO_2, NO_3, PO_4, chlorophyll *a* and O_2 concentrations at Jons (10.7 km downstream the study segment)

	Mean	Median	SD	Trend
NH_4 (mg L^{-1})	0.13	0.10	0.11	–
NO_2 (mg L^{-1})	0.07	0.06	0.04	–
NO_3 (mg L^{-1})	3.74	3.50	1.36	~
O_2 (mg L^{-1})	10.16	10.20	1.17	~
BOD5 (mg L^{-1})	1.80	1.60	0.96	–
PO_4 (mg L^{-1})	0.15	0.12	0.1	–
Chlorophyll *a* (μg L^{-1})	3.95	2.65	3.92	–
Conductivity (μS cm^{-1})	312.73	310.00	41.90	~

BOD5, 5-day biological oxygen demand; ammonium, NH_4; nitrite, NO_2; nitrate, NO_3; phosphorus, PO_4; dissolved oxygen, O_2; SD, standard deviation.
Statistics are derived from the data collected by the Agence de l'eau Rhône Méditerranée Corse (available at http://rdb.eaurmc.fr). Data were collected on average 12.5 times a year (SD = 8.5), except for chlorophyll *a*, which were sampled 12, 6 and 6 times during 1981, 1987 and 1988, respectively, and on average 7.1 times a year (SD = 2.7) since 1993. Values strictly below the detection limit were considered as equal to the detection limit (Helsel, 1990). Trend refers to the decrease (–) or stability (~) of values since 1971 (1981 for chlorophyll *a*).

Fish data

Fish were sampled at seven sites at different seasons, on average 3.7 times a year (SD = 1.2). Four sites (4, 5, 6 and 7, Fig. 1) were from 0.250 to 13 km downstream from the nuclear power plant. The other sites were from 4.5 to 6.25 km upstream from the nuclear power plant (Fig. 1). Descriptions of site morphology are given by Ginot *et al*. (1996). The sampling of site 6 began in 1980, whereas the other sites were sampled since 1979.

Fish were collected at each site by continuous electrofishing from a boat, drifting downstream along banks, always starting at the same point (Allardi *et al.*, 1975; Carrel & Rivier, 1996). The average sampling duration was 27.6 mn (SD = 6.9). A site was 300–400 m long (depending of the sampling duration) and 2–4 m wide. Sampling was performed using a Dream Electronics apparatus (type: Heron DC; 300–400 V; 2–3 A, Pessac, France). Captured fish were identified to the species, measured to the nearest millimeter, and released.

The species abundance was expressed as catch per unit effort (CPUE) calculated for each sample (site × season), i.e., the number of fish of a given species captured for a 20 mn period (to be consistent with other studies on the Rhône River using the same protocol; Cattanéo *et al.*, 2001; Grenouillet *et al.*, 2001). Fish

Table 2 Trend test (trend *P*) for air temperature (T_{air}) water temperature (T_{water}) and discharge (*Q*) seasonal variables used in the paper

Variables			Trend *P*	Use
Annual	Mean	T_{air}	*	Detecting the influence of climate change on water temperature and discharge
		T_{water}	*	
		Q	NS	
Summer	Min.	Q	NS	Detecting discharge modification at Bugey due to hydropower schemes
	Mean	Q	NS	
	Max.	Q	NS	
Winter	Min.	Q	NS	
	Mean	Q	NS	
	Max.	Q	NS	
Reproduction	Mean	T_{water}	**	Detecting the influence of environment on fish community
		Q	*	
Growth	Mean	T_{water}	*	
		Q	NS	
Invertebrate	Mean	T_{water}	*	Detecting the influence of environment on invertebrate community
		Q	NS	

Annual, Summer, Winter, Reproduction, Growth and Invertebrate refer to, respectively, calendar year (January–December), summer (June–September), winter (December–May), fish reproduction period (April–June), growth period of young of the year fish (July–October) and invertebrate biological year (October–September). Min. and Max. designate minimum and maximum values, respectively. We indicate how the different variables were used.
*$P < 0.05$, **$P < 0.01$, NS, non-significant.

species accounting for less than 5% of sampled fish CPUE were excluded from the study. CPUE were $\ln(x+1)$ transformed to normalize their distributions, and averaged by year $\times$ site. Note that year was defined from the fish biological year (from 1 July of the calendar year n to 30 June of the calendar year $n+1$). These dates were defined according to the 'average' hatching date of most of the cyprinid species (Spillmann, 1961; Mann, 1996; Bruslé & Quignard, 2001; Keith & Allardi, 2001) present in fish community of the upper river Rhône (Ginot *et al.*, 1996). An ANOVA performed on ln(CPUE + 1) data (before yearly averaging) indicated that only 3.1% of the total variance was due to different sampling seasons (vs. 19% for years) justifying our averaging by year $\times$ site. The fish abundance data set finally contained eight columns (species) and 146 rows (site $\times$ year combinations). The proportion of YOY in the abundance data set was evaluated for each species. We used size limits derived from analysis of general books or papers dealing with the ecology of European freshwater fish (Pattée, 1988; Persat, 1988; Bruslé & Quignard, 2001; Keith & Allardi, 2001). Individuals with a length strictly below 50 mm for bleak, barbel and roach, below 60 mm for stream bleak, gudgeon and chub, below 65 mm for nase and below 80 mm for dace were considered as YOY.

Invertebrate data

Invertebrates were sampled at three sites at different seasons, on average 3.5 times a year (SD = 0.7), from March 1980 to September 1999. Two sites (b and c, Fig. 1) were 6.8 km downstream from the nuclear power plant, and the other site was 5.25 km upstream from the nuclear power plant (Fig. 1). Sites were sampled using cylindrical artificial substrates (30 cm diameter $\times$ 15 cm high) according to the IQBP protocol (Verneaux *et al.*, 1976). At each site, a pair of artificial substrates was left on the streambed along banks, one in a lotic zone, the other in a lentic zone. They remained 21 days to allow macro-invertebrates to colonize. Because of hydrological conditions (floods), this time could be extended by up to 4 days. Then, substrates were washed and invertebrates were collected in a 0.5 mm mesh net. All specimens were identified to the genus level except chironomids, Limnephilidae, other Diptera (identified to the subfamily or family level) and the species *Dugesia tigrina*. Oligochaeta and Hydracarina (accounting, respectively, for 3.6% and 0.01% of the total abundance) were not included in the analysis because of difficulties in their identification. One taxon (*Gammarus*) largely dominated the community (it could account for more than 90% of the abundance of a sample; Roger *et al.*, 1991). Thus, in our analysis we included all taxa with more than five individuals sampled during the whole study. CPUE values were not calculated for invertebrate data because the sampling effort was constant across samples. The abundance of taxa was $\ln(x+1)$ transformed to normalize their distributions, and averaged by invertebrate biological year $\times$ site. An ANOVA performed on ln(abundance + 1) data (before yearly averaging) indicated that only 5.7% of the total variance was due to different sampling seasons (vs. 19.7% for years), justifying our averaging by year $\times$ site. The invertebrate abundance data set finally contained 74 columns (taxa) and 60 rows (site $\times$ year combinations).

Summarizing interannual biological variations

We first calculated the proportion of variance due to the year and site for fish and invertebrate abundance data and tested the significance of the effects using permutation tests (ADE4 software; Thioulouse *et al.*, 1997). Then, we studied the annual variations of data in the different sites. To reduce the number of analyses, we summarized separately fish and invertebrate changes in all sites as multivariate axes. A centered principal component analysis was performed on fish abundance data (ADE4 software; Thioulouse *et al.*, 1997). The resulting axes are independent linear combinations of mean species ln(CPUE + 1). The temporal changes in fish community structure were represented by time series of annual factorial scores at each site. For invertebrates, the large domination in the abundance of *Gammarus* led us to choose correspondence analysis rather than principal component analysis. Instead of dealing with variability in the abundance of taxa, this allowed us to focus on the variability of community structure (relative abundances). As for fish, the temporal changes in invertebrate community structure were represented by the time series of annual factorial scores at each site. All community trends were compared between sites located downstream and upstream of the nuclear power plant to assess the potential impact of the warm effluent.

Trend analysis

To detect trends in time series, we used a modified Mann–Kendall trend test developed by Hamed & Rao (1998). This non-parametric test (based on ranks) looks for temporal trends once autocorrelation effects are removed. Tests were performed using S-plus software (S-plus2000, 2000).

Link between variables

The potential relations between temperature and discharge variables were assessed using Pearson's correlation coefficients. Then, we estimated the correlation between biological axes and environmental variables. To cope with autocorrelation effects in our correlation tests, we adjusted the number of degrees of freedom by a modified Chelton method, using the autocorrelation estimator proposed by Chatfield (1989). Unlike smoothing or prewhitening, this method deals with the increase of type I error rate without increasing the type II error rate (see Pyper & Peterman, 1998 for details). For each factorial axis and each environmental variable, we used a global Fisher's test (Fisher, 1950) (combining all sites) to assess the influence of environmental conditions on communities. The proportion of community variability explained by each environmental variable was evaluated by the Pearson's correlation coefficient between mean scores by site × year and the environmental variable. All tests were performed using S-plus software (S-plus2000, 2000), and corrected for their multiplicity using Bonferroni procedures (Sokal & Rohlf, 1998).

Results

Temperature and discharge data

Between 1979 and 1999, the mean annual air at Ambérieux en Bugey and water temperatures upstream the nuclear power plant increased, respectively, from 10.7 °C to 11.7 °C and from 11.3 °C to 11.9 °C. Three years were warm for both air and water temperatures: 1982, 1989 and 1994 (Fig. 2a). In the same period, discharge fluctuated around its mean annual discharge (500 $m^3 s^{-1}$) without exhibiting particular cycles or trend (Fig. 2b).

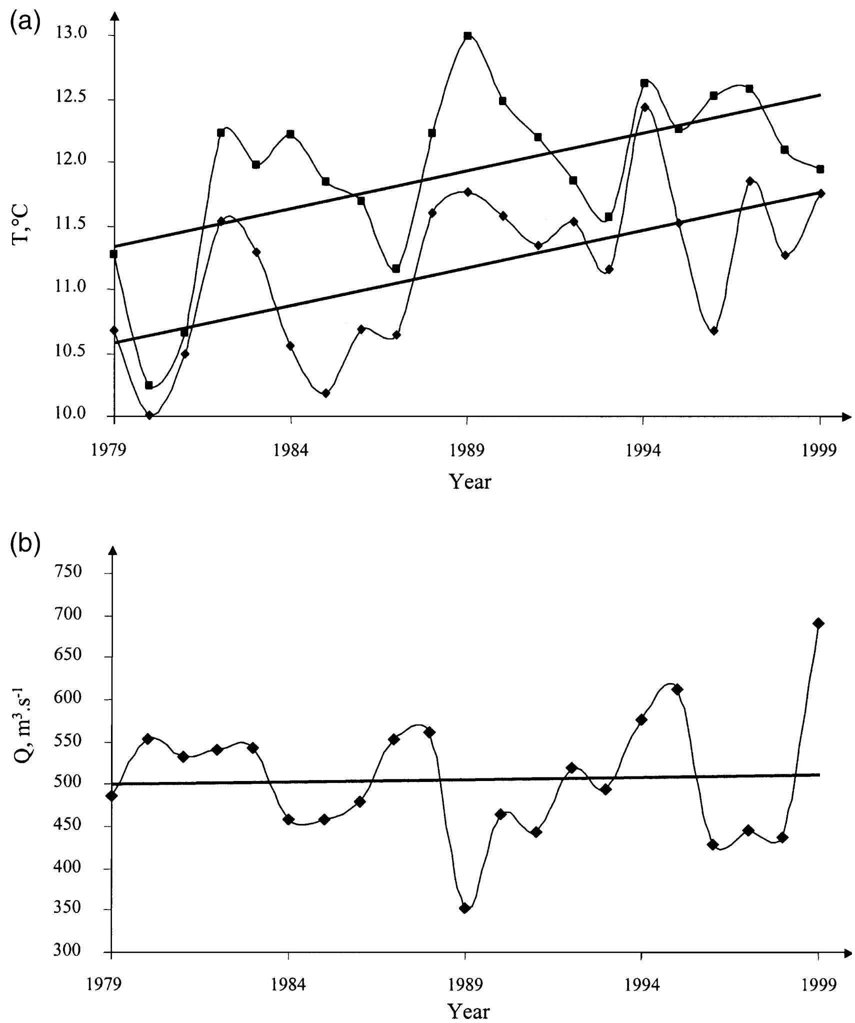

Fig. 2 Mean annual daily water (◆) and air (■) temperature (a) and mean annual daily discharge (b) at Bugey between 1979 and 1999. Trends are shown ($Y(t) = at + b$).

Fish data

Between 1979 and 1999, a total number of 58 090 fish of 37 species were caught (from 12 to 25 species per year). The fish community was dominated by a set of eight species accounting for 95.3% of sampled fish CPUE: chub (*Leuciscus cephalus* Linnaeus, 1758), stream bleak (*Alburnoides bipunctatus* Bloch, 1782), dace (*Leuciscus leuciscus* Linnaeus, 1758), bleak (*Alburnus alburnus* Linnaeus, 1758), barbel (*Barbus barbus* Linnaeus, 1758), roach (*Rutilus rutilus* Linnaeus, 1758), nase (*Chondrostoma nasus* Linnaeus, 1758) and gudgeon (*Gobio gobio* Linnaeus, 1758), which accounted, respectively, for 26.7%, 17.2%, 16.4%, 10.9%, 7.8%, 6.0%, 5.2% and 5.1% of sampled fish CPUE. 66.9% of the sampled fish CPUE were caught in the sites 4, 5, 6 and 7 downstream of the nuclear power plant. Most fish were more than 1 year old even though the percentage YOY represented about 1/3 of the nase CPUE, about 1/4 of the stream bleak CPUE and about 1/5 of the bleak and dace CPUE. The total proportion of YOY was high in the warm years (e.g. proportion of YOY in the total abundance = 45.6% the biological year 11 (1988–1989) and 30.4% in biological year 12 (1989–1990) compared with only 17% in biological year 2 (1979–1980)).

Invertebrate data

A total of 1 282 230 invertebrates (92 taxa) were captured during the study period. The proportion of *Gammarus* averaged across sites was 87.4%. Chironimidae (4% of the total invertebrate abundance), Oligochaeta (3.6%), *Hydropsyche* (2.3%), *Heptagenia* (1.1%), molluscs such as *Theodoxus*, *Potamopyrgus* and *Corbicula* (0.4%, 0.2%, 0.1%, respectively), *D. tigrina*, *Ephemerella* and Simulidae (0.2%, 0.1%, 0.1%, respectively) were the other most abundant taxa. Invertebrate abundance was higher in site a (42% of the total invertebrate abundance) than in sites b (30%) and c (28%), located downstream of the nuclear power plant.

Interannual variability of fish and invertebrates data

41.3% ($P < 0.001$) of the total variance in fish abundance data was due to temporal (between year) effects (compared with 20.1% ($P < 0.001$)) for spatial, between-site effects). Similarly, for invertebrate abundance data, interannual variance represented 51.5 % ($P < 0.001$) of the total variance (compared with 7.2% ($P < 0.001$) for spatial effects).

Temporal changes of fish community structure

The first two axes of the principal component analysis accounted for 59% of the total variability of fish abundance data (37% for the first axis and 22% for the second axis). Time series of multivariate scores were calculated for each site. However, to clarify figures, we only represented scores averaged across all sites, across sites downstream of the nuclear power plant and across sites upstream of the nuclear power plant (Fig. 3a, c).

The first axis reflected the overall abundance variability. For each site, there was a strong correlation between factorial scores and the sum of species CPUE per year (r^2 values from 0.86 to 0.95). Therefore, factorial scores of each site for each year represented the overall fish abundance sampled at the site. As a consequence, the first axis did not discriminate fish species (Fig. 3b). Site scores confirmed that fish density was higher in sites downstream of the nuclear power plant, especially between the biological years 8 and 11 (i.e. from July 1985 to June 1989) (Fig. 3a). However, temporal changes of the site factorial scores were comparable in all sites, including those upstream the nuclear power plant.

The second axis opposed in each site species with increasing relative CPUE over time (such as chub and barbel) to those with decreasing relative CPUE over time (such as dace and bleak) (Fig. 3d). Between biological years 1 and 21, the mean annual CPUE of chub increased by three times and that of barbel by 5.6 times (Fig. 4). Meanwhile, the mean annual CPUE of dace decreased by 2.9 times. The mean annual CPUE of stream bleak was stable until biological year 19 and rapidly increased between biological years 19 and 21 (multiplied by 2.1). This last change was not revealed by the principal component analysis. Site factorial scores on the second axis reflected the relative CPUE of chub and barbel compared with the relative CPUE of dace and bleak in each site (Fig. 3c). Temporal changes of the site factorial scores were comparable in all sites, including those upstream from the nuclear power plant (Fig. 3c).

Temporal changes in invertebrate community structure

The first axis of the correspondence analysis accounted for (18%) of the invertebrate data inertia. This axis opposed taxa that tend to appear and increase during the study period (e.g. *Athricops*, *Potamopyrgus*, *Corixa* and *Lepidostoma*) to taxa that instead tended to decrease or disappear (e.g. *Chloroperla*, *Protonemura* and *Nemoura*) (Fig. 5). As for fish, we only represented factorial scores time series averaged across all sites, across sites downstream of the nuclear power plant and across sites upstream of the nuclear power plant (Fig. 6). The factorial scores of sites located upstream and downstream the nuclear power plant showed similar temporal patterns.

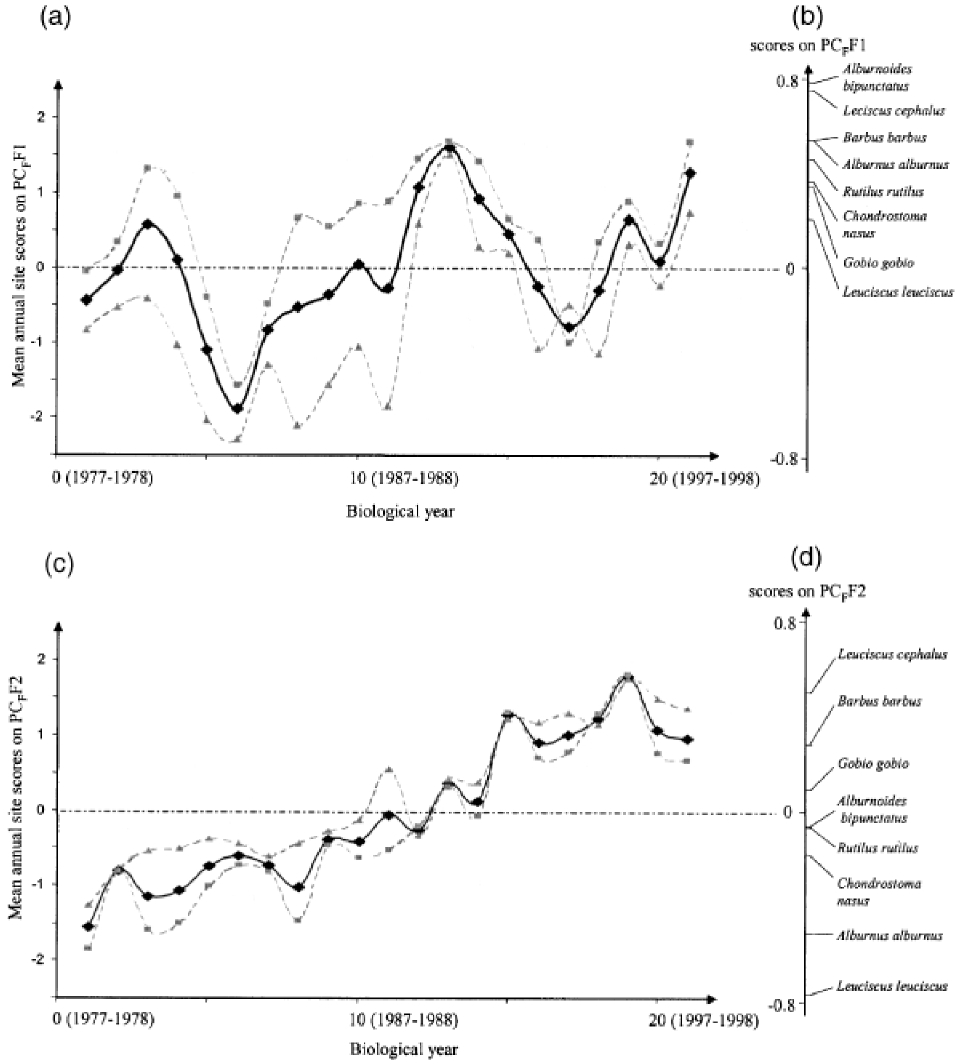

Fig. 3 Time series of sites scores on the two first axes of the principal component analysis of fish data (PC_FF1 (a) and PC_FF2 (c)). Scores are averaged across all sites (◆, continuous line), across sites downstream from the nuclear power plant (■, dashed line) and across sites upstream from the nuclear power plant (▲, dashed line). Species contributions on PC_FF1 (b) axis and PC_FF2 (d) axis are given. Note that *Y*-axis scales of (a) and (b) ((c) and (d), respectively) are different.

Trend analysis

The mean annual air and water temperature time series showed significant positive trends ($P<0.05$) (Fig. 2, Table 2). These trends were not sensitive to extreme years: they remained significant at the 0.05 level when we removed the 1982, 1989 and 1994 warm years. Similarly, the mean temperature during fish reproduction period, fish growth period and invertebrate biological year increased significantly during the study. Discharge variables show weak trends. Only mean discharge during the reproduction period decreased ($P<0.05$) (Table 2).

For fish, the factorial scores on the first axis of the principal component analysis of five sites (1, 2, 3, 6, 7) showed significant positive trends (Table 3). However, trends of factorial scores of sites 1 and 3 did not remain significant when we removed the extreme biological years 3, 13 and 21. Two sites located downstream from the nuclear power plant (4, 5) did not exhibit significant trend. On average, the total fish abundance did not show any major increase (see Fig. 3a). Factorial scores of all sites on the second axis showed strong significant positive trends ($P<0.05$ for site 4, $P<0.01$ for site 7, $P<0.001$ for all other sites) (Table 3). Chub and barbel thus progressively replaced bleak and dace in all the sites including those upstream from the nuclear power plant. This pattern was continuous throughout the study period (Fig. 3).

With respect to invertebrates, time series of site scores on the first axis of the correspondence analysis also

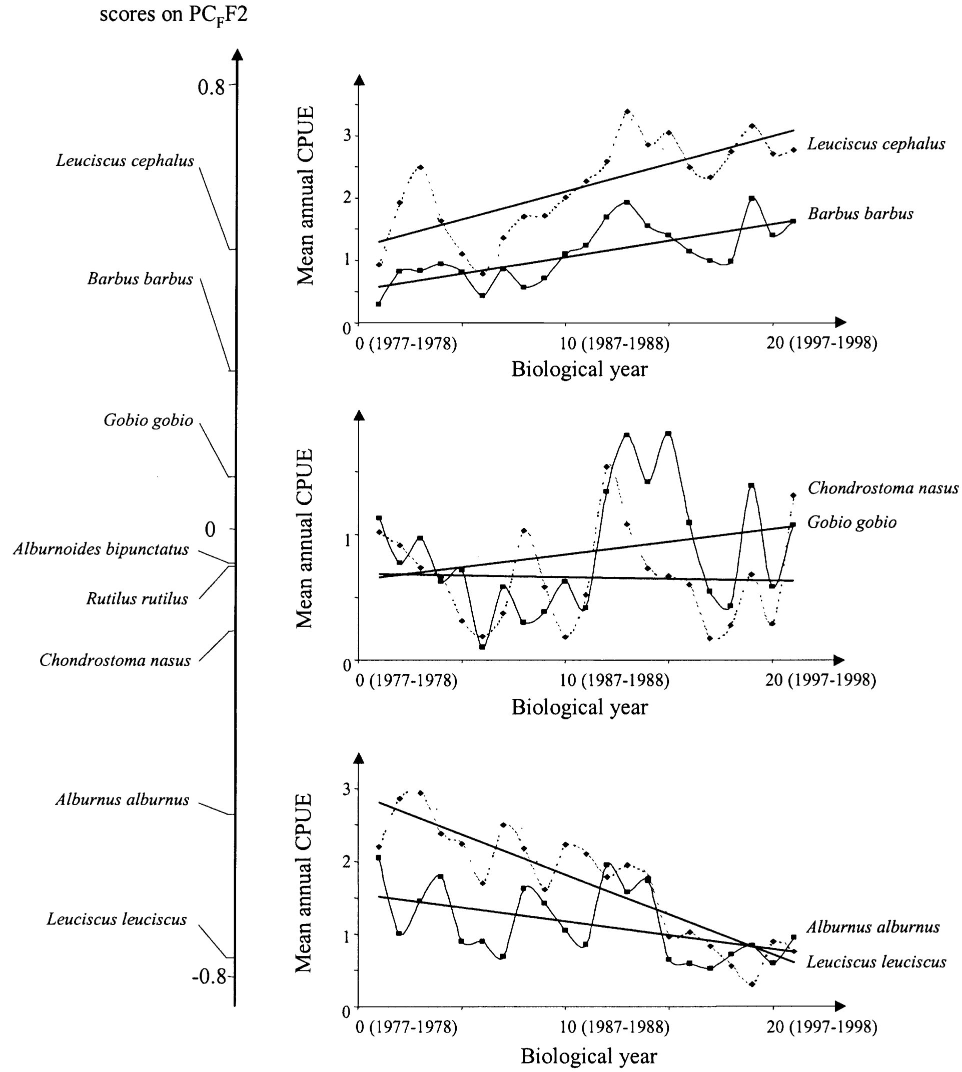

Fig. 4 Examples of mean annual catch per unit effort (CPUE) time series of species discriminated by the second axis of the principal component analysis realized on fish abundance data (PC_FF2). Trends are shown ($Y(t) = at + b$).

exhibited positive trends ($P < 0.001$ for sites b and c and $P < 0.05$ for site a) (Table 3). In all sites, the abundance of taxa such as *Athricops*, *Potamopyrgus* and *Lepidostoma* gradually increased, whereas the abundance of taxa such as *Protonemura*, *Chloroperla* and *Nemoura* decreased (Fig. 5b).

Correlation among the seasonal environmental variables (temperature, discharge)

The mean annual air and water temperatures were significantly correlated ($P < 0.01$). The mean annual air temperature was correlated with the mean water temperature during the fish reproduction period and the invertebrate biological year ($P < 0.01$ and $P < 0.05$, respectively). No relationship was found between the mean annual discharge and mean annual air or water temperature. The mean annual water temperatures during the reproduction period and discharge were significantly correlated ($P < 0.01$), as was the mean annual water temperature during the growth period and discharge ($P < 0.05$) (Table 4).

Link between community structure variability and environmental changes

For fish, site scores on the first axis of the principal component analysis were significantly correlated with the mean annual temperature and mean annual discharge during the reproduction period ($P < 0.05$ and $P < 0.001$, respectively). However, these two environmental variables were redundant (see above). On the

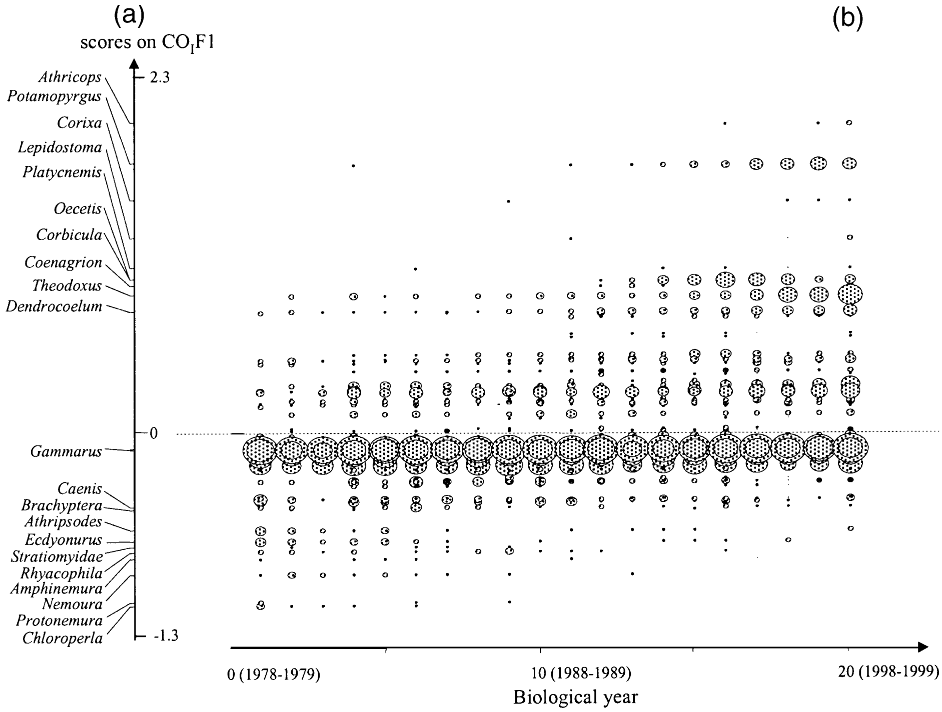

Fig. 5 Mean annual abundance per sample of invertebrate taxa (circle area and abundance are proportional) classified according to the first axis of the correspondence analysis of invertebrate data (CO_IF1) (b). Contribution of the 10 taxa with highest factorial scores, *Gammarus* and the 10 taxa with lowest factorial scores are given (a).

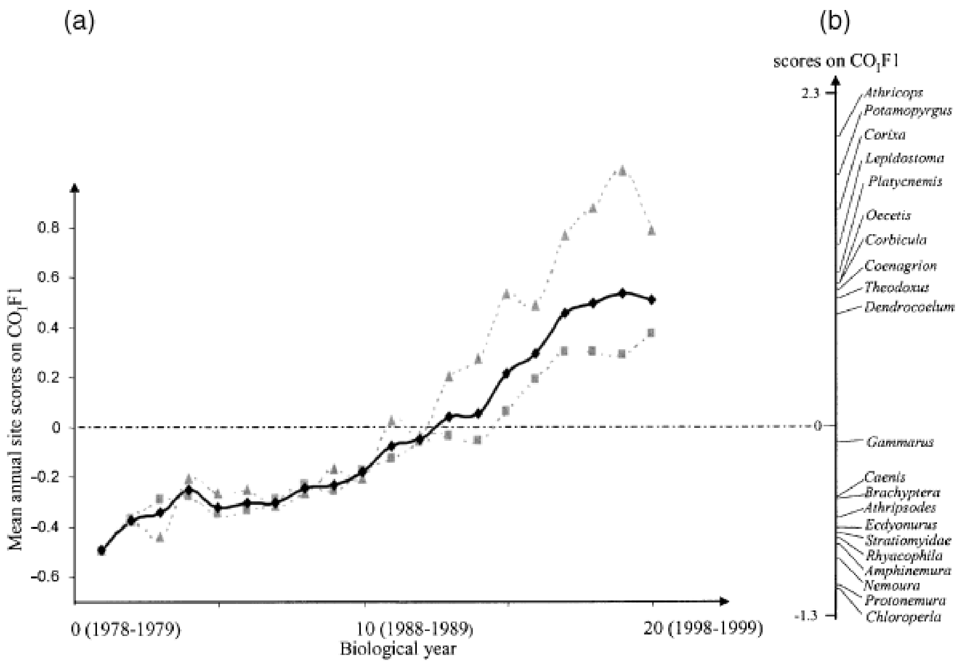

Fig. 6 Time series of site scores on the first axis of the correspondence analysis of invertebrate data (CO_IF1) (a). Scores are averaged across all sites (▲, continuous line), across sites downstream from the nuclear power plant (■ , dashed line) and across sites upstream from the nuclear power plant (▲, dashed line). Contribution of the 10 taxa with highest factorial scores, *Gammarus* and the 10 taxa with lowest factorial scores are given (b). Note that *Y*-axis scales of (a) and (b) are different.

Table 3 Trend probabilities (P) of factorial sites scores time series

Data set	Axis	Site	P
Fish data	First axis of the principal component analysis	1	**
		2	*
		3	*
		4	NS
		5	NS
		6	*
		7	**
	Second axis of the principal component analysis	1	***
		2	***
		3	***
		4	*
		5	***
		6	***
		7	**
Invertebrate data	First axis of the correspondence analysis	a	**
		b	***
		c	***

*$P<0.05$, **$P<0.01$, ***$P<0.001$, NS, non-significant.

first axis, these two variables explained, respectively, 20% and 46% of the variability in the mean annual site scores. No relationship was found between fish abundance in a sample and temperature or discharge on the day of sampling, indicating that this pattern was not a sampling protocol effect. Site scores on the second axis were significantly correlated with the mean annual temperature during the reproduction period ($P<0.05$). On the second axis, this variable explained 45% of the mean variability in annual site scores (Table 5).

For invertebrates, site scores on the first axis of the correspondence analysis were significantly correlated with the mean annual temperature calculated on the invertebrate biological year ($P<0.05$). On the first axis, this variable explained 29% of the mean variability in annual site scores.

Discussion

Since 1979, the Upper Rhône River has warmed up under the influence of climate warming. This pattern is consistent with the thermal change of many rivers in the northern hemisphere and especially in Europe (Webb, 1996). Punctual discordance between air and water temperature (e.g. 1996) are difficult to explain and could be due to the influence of factors such as snow melt. Water temperature was recorded continuously only upstream from the nuclear power plant. However, Ginot *et al.* (1996) have shown that the nuclear power plant discharges water 10 °C warmer on average than the input water. The warmed effluent stream cools of 1 °C on average per kilometer and only affects a narrow area (15–25 m wide) along the right bank, independent of the input water temperature (Ginot *et al.*, 1996). Therefore, we can reasonably assume that the relative increase of water temperature under climatic warming was the same in all sites since 1979. During the same period, we observed significant trends in both fish and invertebrate community structures.

With respect to fish, we observed an increase of chub and barbel abundance and a decrease of dace and bleak abundance. Considering the relative position of the study segment in the geographical range of fish species (Table 6), chub, barbel, stream bleak and gudgeon are southern species (Bugey is close to the center of the species latitudinal range). By contrast, Bugey is close to the southern limit of the geographical range of bleak, nase, roach and especially dace (Table 6). According to Ruslé & Quignard (2001), dace is the most northerly European cyprinid species. Therefore, the observed shift in fish community structure reflected the gradual displacement of northern species by southern species. Most of the eight studied species are eurytherme (Bruslé & Quignard, 2001; Keith & Allardi, 2001). However, barbel has a clear affinity for warm water (Kraiem, 1979; Bruslé & Quignard, 2001) and chub is attracted by warm water (Bruslé & Quignard, 2001). By contrast, dace prefers cold water (Bruslé & Quignard, 2001). With respect to invertebrates, we also observed a gradual disappearance of cold-water taxa as *Chloroperla*, *Protonemura*, *Nemoura* and *Amphinemura* (Tachet *et al.*, 2000) opposed to a gradual increase in abundance of warm-water taxa as *Corbicula* (Tachet *et al.*, 2000). However, developing taxa (*Athricops*, *Potamopyrgus*, *Corixa*, *Lepidostoma*, *Platycnemis*, *Oecetis*, *Corbicula*, *Coenagrion*, *Theodoxus*, *Dendrocoelum*) also prefer null or low current velocity and downstream zones (Tachet *et al.*, 2000). By contrast, decreasing taxa (*Chloroperla*, *Protonemura*, *Nemoura Amphinemura Rhyacophila*, *Stratiomyidae*, *Ecdyonurus*, *Athripodes*, *Brachyptera*, *Caemis*) prefer fast current velocity and upstream zones (Tachet *et al.*, 2000).

The overall increase of thermophilic and southern fish species and of thermophilic invertebrate taxa was consistent with the predictions or observations of the consequences of the global warming. Coutant (1990) and Carpenter *et al.* (1992) predicted a geographical shift of freshwater fish geographical range towards higher latitudes and higher altitudes. Hauer *et al.* (1997) and Mulholland *et al.* (1997) supposed that similar patterns could occur for freshwater invertebrates. Such patterns have already been observed in the marine environment. Attrill & Power (2002) and Sagarin *et al.* (1999) have locally observed an increase in the

Table 4 Air temperature (T_{air}) water temperature (T_{water}) and discharge (Q) seasonal variables correlation matrix

			Annual			Summer			Winter			Reproduction		Growth		Invertebrate	
			Mean			Min.	Mean	Max.	Min.	Mean	Max.	Mean		Mean		Mean	
			T_{air}	T_{water}	Q	Q	Q	Q	Q	Q	Q	T_{water}	Q	T_{water}	Q	T_{water}	Q
Annual	Mean	T_{air}	1.00														
		T_{water}	0.71**	1.00													
		Q	0.17	−0.32	1.00												
Summer	Min.	Q	0.44	0.01	0.73**	1.00											
	Mean	Q	−0.05	−0.46*	0.81***	0.68***	1.00										
	Max.	Q	−0.17	−0.26	0.31	0.20	0.67**	1.00									
Winter	Min.	Q	0.22	0.06	0.47	0.55*	0.38	0.06	1.00								
	Mean	Q	0.12	−0.06	0.71**	0.49	0.43	−0.08	0.64**	1.00							
	Max.	Q	0.09	0.01	0.32	0.27	0.35	0.19	0.15	0.28	1.00						
Reproduction	Mean	T_{water}	0.65**	0.61*	−0.13	0.34	−0.08	0.04	−0.11	−0.19	0.23	1.00					
		Q	−0.42	−0.05	−0.09	−0.31	−0.06	0.03	0.21	0.18	−0.01	−0.61**	1.00				
Growth	Mean	T_{water}	0.07	0.39	−0.27	−0.15	−0.18	0.14	−0.37	−0.16	0.18	0.55*	−0.06	1.00			
		Q	0.29	0.20	0.21	0.21	−0.07	−0.27	0.50	0.35	−0.17	−0.24	0.20	−0.52*	1.00		
Invertebrate	Mean	T_{water}	0.57*	0.95***	−0.48*	−0.14	−0.60**	−0.29	−0.06	−0.13	−0.05	0.64*	−0.03	0.52*	0.00	1.00	
		Q	0.23	−0.19	0.84***	0.72**	0.75***	0.23	0.77**	0.79***	0.24	−0.10	-0.03	−0.40	0.41	−0.35	1.00

Annual, Summer, Winter, Reproduction, Growth and Invertebrate refer to, respectively, calendar year (January–December), summer (June–September), winter (December–May), fish reproduction period (April–June), growth period of young of the year fish (July–October) and invertebrate biological year (October–September). Min. and Max. designate minimum and maximum values, respectively.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 5 Correlation between site scores on factorial axes and seasonal environmental variables

	R		Site scores on PC_FF1	Site scores on PC_FF2	Site scores on CO_IF1
Reproduction	Mean	T_{water}	**0.45***	**0.67***	
		Q	**−0.68*****	−0.39	
Growth	Mean	T_{water}	0.06	0.36	
		Q	−0.30	0.01	
Invertebrate	Mean	T_{water}			**0.54***
		Q			−0.01

r, Pearson's correlation coefficient between mean annual site scores and environmental variables. PC_FF1 and PC_FF2 design, respectively, the first and second axis of the principal component analysis of fish data. CO_IF1 is the first axis of the correspondence analysis of invertebrate data. Reproduction, Growth and Invertebrate refer to fish reproduction period (April–June), growth period of young of the year fish (July–October) and invertebrate biological year (October–September), respectively. T_{air} and T_{water} design air and water temperature, respectively.
Bonferroni corrected global Fisher's test probability: *$P<0.05$, ***$P<0.001$.

Table 6 Relative position of the study segment in the geographical range of fish species

Fish species	Latitude of the nothern limit of the species' geographical range (°N)	Latitude of the southern limit of the species' geographical range (°N)	X
Alburnus alburnus	67.0	41.0	0.23
Alburnoides bipunctatus	62.0	36.0	0.61
Barbus barbus	57.0	42.0	0.34
Chondrostoma nasus	63.0	42.5	0.19
Gobio gobio	67.0	36.0	0.46
Leuciscus cephalus	63.5	36.5	0.52
Leuciscus leuciscus	70.0	41.5	0.18
Rutilus rutilus	66.0	41.0	0.24

This variable (x) is coded on the basis of the geographical range of the species (Keith & Allardi, 2001) as a function of: $x = L_{Bugey} - L_{inf}/L_{sup} - L_{Bugey}$ where L_{Bugey}, L_{sup} and L_{inf} are the latitudes (°N) of the study segment, of the northern limit of the species' geographical range and the southern limit of the species' geographical range, respectively.

abundance of southern taxa in invertebrate and fish marine communities. More generally, shifts of species range to upper latitude or altitude due to climate change have been observed in zooplankton, invertebrates, fish, plants, butterflies, birds and mammals (Hughes, 2000; Walther *et al.*, 2002).

Hydrology and temperature widely influence the freshwater fauna (Magnuson *et al.*, 1979; Poff *et al.*, 1997). On the Upper Rhône River (45 km upstream from the study segment), Dolédec *et al.* (1996) found a gradual increase of lentic and thermophilic invertebrate taxa between 1980 and 1991, correlated with increasing water temperature. This pattern was continuous during the study period and was not an artifact due to the warm 1989 year. On the lower Rhône River, Fruget *et al.* (2001) showed that discharge and water temperature were the major factors controlling the long-term dynamics of invertebrate and fish communities. According to Fruget *et al.* (2001), low discharge and high temperature positively influenced the breeding success of fish. Such a positive influence has already been shown for many cyprinid species (Hellawell, 1974; Mann, 1974; Philippart, 1981, 1989; Mills & Mann, 1985; Araújo *et al.*, 1999), including in the Rhône River (Grenouillet *et al.*, 2001). Consistently, we found that low flow and high temperature during the reproduction period were associated with high total fish abundance and high proportions of YOY. In addition, water temperature during the reproduction period explained shifts in community structure. Generally, dace recruitment is positively influenced by high water temperatures (Philippart, 1981; Mann & Mills, 1985; Araújo *et al.*, 1999). However, Mann & Mills (1985) showed that a warm summer (especially a warm June; Mills & Mann, 1986) can result in a very low egg size and very low fecundity for the next spring. According to the authors, the energy investment in growth was at the expense of gonad development. The reproduction period that we defined included June. Thus, the dace population could have suffered from the increase in mean annual temperature in the reproduction period because of a gradual decrease in the species' breeding success. Moreover, Philippart (1981) has shown that dace has a high mortality rate after reproduction, from April to May. This mortality, due to the energy investment in gonad development and spawning, has probably been reinforced by the shift from thermal optima for cold-water and northern species.

Changes in invertebrate and fish communities could be complicated by interactions between the two trophic

Table 7 Evolution of the relative proportion of the eight species considered in our study

Fish species	During the study period at Bugey	Before completion vs. by-passed section (Persat, 1988)	Before completion vs. diversion canal (Persat, 1988)
Alburnus alburnus	–	–	–
Alburnoides bipunctatus	**+**	**–**	**–**
Barbus barbus	**+**	**~**	**–**
Chondrostoma nasus	**~**	**–**	**–**
Gobio gobio	**~**	**+**	**+**
Leuciscus cephalus	+	+	+
Leuciscus leuciscus	–	–	–
Rutilus rutilus	**~**	**+**	**+**

Comparison with the effects of hydropower schemes on fish structure of the Upper Rhône River (from Persat, 1988). An increase, a decrease and stability are indicated, respectively, by ' + ', '−'and ' ~ '. Rows in bold font highlight different variations in the two studies.

levels (Petchey *et al*., 1999; Hughes, 2000; Walther *et al*., 2002). Chub, dace, barbel and bleak are omnivorous (Bruslé & Quignard, 2001). These fish species eat invertebrate taxa that were either disappearing, appearing or stable in abundance during the study period. For example, chub and barbel do not preferentially eat invertebrates such as *Chloroperla* or *Protonemura*. Therefore, there was probably no cause and effect trophic relationship between fish and invertebrate community changes at Bugey.

The true effects of climatic change may be confounded by the effects of hydroelectric schemes built upstream of the study segment and by the nuclear power plant. The effects of flow regulation and urbanization on stream ecology has been well documented and includes a slower current, sedimentation, periodic releases and pollution (Bravard, 1987; Petts *et al*., 1989; Calow & Petts, 1992). In the study segment, no trend was detected for the mean annual discharge variables during the study. Since neither the width nor the depth of the study segment has been modified, no slowing in current has occurred since 1979. As far as the possible sedimentation of the study segment is concerned, visual observations did not indicate any gradual siltation since 1979. With respect to the potential influence of water releases from dams, the temporal changes in communities (represented by site factorial score time series) did not show any triennial cycles (the frequency of the releases on the Upper Rhône River). Similarly, Dolédec *et al.* (1996) has shown that such releases have no clear impact on the invertebrate community, probably because the substrate is cleaned after releases in a few months (Bournaud *et al*., 1987). Finally, water quality remained good at Bugey during the study (Table 1). Although the study segment was not regulated in terms of the river itself, an overall effect of the hydropower schemes could have influenced the local dynamics of communities. Distinguishing the effects of climatic factors and hydropower schemes on invertebrate data was complicated by the fact that taxa were only identified to the genus level. We observed an increase in both thermophile taxa and lentic taxa. In fact, at the generic level, taxa with warm water preferences always have preferences for lentic and downstream zones (Tachet *et al*., 2000). This could explain for example the paradoxical increase in eutrophic taxa (e.g. *Potamopyrgus*, *Drendrocoelum*) in an oligotrophic zone (chlorophyll *a* concentration $<10\,\mu g\,L^{-1}$; Table 1). In this way, the change in the invertebrate community observed at Bugey is consistent with the hypothesis of a combined effect of both climate change and hydropower scheme construction. But neither in our study nor in that of Dolédec *et al*. (1996) was the smooth change in the invertebrate community structure disrupted by a sudden switch at the completion of the schemes (1984, 1986). Moreover, the same community changes were observed in both studies under the same climatic influence but at different locations, with different numbers of upstream schemes and different distances between the study segment and upstream schemes. With respect to fish, Persat (1988) studied changes in fish community structure before and after the completion of schemes, in the by-passed section and in the diversion canal. These changes were quite different than those observed here (see Table 7). In particular, barbel, nase and stream bleak are sensitive to stream regulation (Lamouroux *et al*., 1999; Bruslé & Quignard, 2001), but their abundance increased or remained stable at Bugey.

Another factor that could have influenced changes in the communities was the presence of the nuclear power plant in the study segment. However, the temporal changes of communities in sites downstream and upstream from the nuclear power plant were very similar. The warmed effluent affected only a small area of our study segment and did not locally influence community trends. In addition, the consistency of the observed changes in the invertebrate community at Bugey and 45 km upstream (Dolédec *et al.*, 1996) suggests that the power plant did not play a central role in the temporal changes of the community structure. More generally, studies dealing with the influence of nuclear power plants on freshwater fauna have shown that qualitative differences between warmed and non-warmed sampling sites were small (Kirchmann *et al.*, 1985; Fruget *et al.*, 1999) and essentially due to velocity, substrate, deep or bank morphology differences (Ginot *et al.*, 1996).

To conclude, our results support that shifts in fish and invertebrate community structure towards thermophilic and southern taxa at Bugey were the consequence of global warming. The observed trends were significant, correlated with thermal variables and consistent with the predicted and observed consequences of climate change on many organisms (Walther *et al.*, 2002). However, the possibility that there was a cumulative effect of hydropower scheme construction on invertebrates could not be rejected. Our study is the first assessing the influence of the climate warming on fish and invertebrate communities in large streams. Most studies dealing with the influence of the climate change, including ours, have been conducted on a single site. To deal with the influence of confounding factors, there is nowadays a need for long-term studies on several sites. Identifying which species trait are impacted in comparative studies of multiple sites can improve our understanding of the effects of climate change on a wide range of organisms and environmental conditions. Such studies would be particularly helpful in large streams that have undergone many anthropogenic disturbances during the last century. This implies the production of new monitoring programs focusing on the consequences of global warming (Hughes, 2000), and the analyses of various existing data sets (Blenckner & Hillebrand, 2002). It is essential to take into account confounding factors in studies of the impacts of climate change. On the other hand, ecologists and other scientists working on temporal patterns must keep in mind that air temperature and atmospheric composition have been modified in the last century. Therefore, the possible effects of thermal and atmospheric changes have to be taken into account before making any conclusions on the causes of all kinds of temporal change.

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