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Climate change impacts on structure and diversity of fish communities in rivers

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Abstract

It is widely accepted that climate change constrains biota. Yet, because of the lack of consistent multisite and multitaxon surveys, few studies have addressed general rules about how climate change impacts on structure and diversity of animal communities. Especially, the relative influence of nonclimatic anthropogenic disturbances on this impact is fairly unknown. Here, we present for the first time a meta-analysis assessing the effect of global warming on stream organisms. Fish communities of large rivers in France undergoing various anthropogenic pressures showed significant increase in proportions of warm-water species and of specific richness during the last 15–25 years. Conversely, the equitability decreased, indicating a gradual decrease of the number of dominant species. Finally, the total abundance increased, coupled with rejuvenation and changes in size-structure of the communities. Interestingly, most of these effects were not depressed by the strength of nonclimatic anthropogenic disturbances. Conversely, geographical location of communities and especially closeness of natural barriers to migration could influence their response to climate change. Indeed, increase in the proportion of southern species seemed hindered at sites located close to the southern limit of the European species' geographical ranges. This work provides new evidence that climate change have deep impacts on communities which, by overtaking the effects of nonclimatic anthropogenic disturbances, could be more substantial than previously thought. Overall, our results stress the importance of considering climate change impacts in studies addressing community dynamics, even in disturbed sites.

Keywords: anthropogenic disturbances, climate change, community, diversity, fish, France, large rivers, long-term studies, meta-analysis, time series

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Introduction

Understanding the effects of climate change on plant and animal population, community structure and ecosystem functioning is one of the main challenges of modern ecology. Since the beginning of the 1990s, the literature concerning climate change has noticeably increased. The first studies were mostly predictive (Pastor & Post, 1988; Melillo *et al.*, 1993; Vitousek, 1994) and stimulated the emergence of long-term surveys which, in turn, allowed for a new generation of descriptive studies (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Harley *et al.*, 2006). However, the majority of the latest studies were performed at single study sites, making the results sensitive to site-specific confounding factors, and hindering the quest for general rules in the ecological impacts of global warming. To tackle this problem, some authors have put efforts on publishing reviews combining the results of different studies (Walther *et al.*, 2002; Harley *et al.*, 2006) and/or performed meta-analyses of data sets collected in the literature (Parmesan & Yohe, 2003; Root *et al.*, 2003). Their results have strengthened the case that climate warming is a cause for biological changes, highlighting the trend of spring biological events to occur earlier and showing clear spatial shifts in species geographical ranges

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towards higher altitudes or latitudes. However, these studies have focused on single species, and have not attempted to assess the relative importance of climate change and anthropogenic habitat alterations as causes of biological change (Jensen, 2003; Parmesan & Yohe, 2003). Hence, it is still difficult to evaluate the relative effects of climate changes vs. nonclimatic disturbances on ecosystems, and to estimate how climate change might affect community structure and biodiversity.

In an attempt to fill these gaps and tackle these technical difficulties, we present here a meta-analysis on a multisite and multifish species data set. Stream fish are poikilotherms whose movements are significantly constrained by the spatial structure of their environment. This makes them suitable biological models for studying the impact of climate change on biota (Daufresne *et al*., 2004). Surprisingly, as far as we know, few studies based on actual data have assessed the influence of climate warming on large river communities (Daufresne *et al*., 2004; Mouthon & Daufresne, 2006), probably because available data sets are scarce. However, we showed in a previous study that southern and warm-water species have gradually come to dominate the fish community of the upper Rhône River (France) over the last 20 years (Daufresne *et al*., 2004). As observed for many organisms (Walther *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003), these patterns were correlated with thermal constraints during spring. This period coincides for most of the cyprinids (dominating fish communities in large European rivers) with the reproduction, a key period for fish population dynamics (Mills & Mann, 1985; Cushing, 1995; Daufresne *et al*., 2004).

We propose, here, to evaluate the effect of climate change, especially spring warming, on global abundance, structure (proportion of southern and warm-water species to the total abundance) and diversity [specific richness, Shannon equitability index (or evenness; Begon *et al*., 1990)] of fish communities in large rivers. We used data collected each year on seven different study areas located along large French rivers (the Rhône, the Loire and the Seine rivers) on periods ranging from 15 to 25 years (Fig. 1, Table 1), making up a set of 24 study area $\times$ sampling site combinations to our knowledge unique in stream ecology. Using meta-analysis technique, we first analyse the common patterns shared by all communities. Then, we examine whether the strength of the local nonclimatic disturbances can weighted the responses of the different communities to the global warming. Our study stresses the impacts of climate change on fish communities.

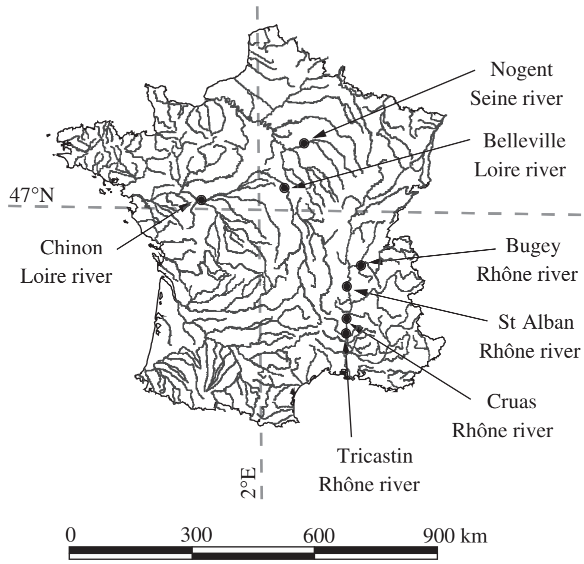

Fig. 1 Location of the study areas.

Table 1 Main properties of the study areas

Study area	River	Sampling period	Latitude (°N)	Catchment area (km^2)	No. of sampling sites: Upstream from NPS	No. of sampling sites: Downstream from NPS	No. of samples per year
Belleville	Loire	1989–2003	47.5	34 883	1	1	1
Bugey	Rhône	1979–2003	45.8	15 830	3	4	4
Chinon	Loire	1988–2003	47.2	60 024	1	1	1
Cruas	Rhône	1983–2003	44.6	68 878	1*	2*	4
Nogent	Seine	1987–2003	48.5	8939	1	2	1
Saint-Alban	Rhône	1985–2003	45.4	50 736	1	3*	4
Tricastin	Rhône	1982–2003	44.3	74 256	1*	2*	4

*Sampling sites located along (i.e. $<$5 km from) hydropower schemes.
NPS, nuclear power station.

Materials and methods

Data

We used data that were collected each year on seven different study areas located along large French rivers (the Rhône, the Loire and the Seine rivers; Fig. 1) over periods ranging from 15 to 25 years (Table 1). These data were collected in the vicinity of nuclear power stations (NPS) operated by Electricité de France. At each study area, fish sampling sites were located either upstream from the NPS (control sampling sites) or downstream from the NPS (sampling sites potentially disturbed by thermal discharges). Nine sampling sites were located along (i.e. <5 km from) hydropower schemes. Hydropower schemes include a bypassed section, closed by an upstream diversion dam, and a diversion canal ended by a hydropower dam. Finally, this represented a set of 24 study area $\times$ sampling site combinations. Fish were sampled one to four times per year (Table 1), from a boat, along banks and using electrofishing techniques. Fish data were obtained by point abundance sampling (Persat & Copp, 1990) at Saint-Alban and continuous sampling at the other study areas. Size of the sampling sites depended on sampling duration but was ca. 300–400 m long and 2–4 m wide for a 30 min continuous sampling period (Daufresne *et al*., 2004). For each sample, the species abundance was expressed as catch per unit effort (CPUE), (i.e. the number of fish of a given species captured in a 20 min fishing period; Cattanéo *et al*., 2001; Grenouillet *et al*., 2001; Daufresne *et al*., 2004). According to Grenouillet *et al*. (2001), we used the equivalence found between point abundance and continuous sampling (Pont *et al*., 1993) to evaluate CPUEs at Saint-Alban. For each species, CPUEs were then averaged by biological year $\times$ sampling site (called site-years afterwards). Biological year (from 1 July to 30 June of the next calendar year) was defined according to the 'average' hatching date of most of the cyprinid species present in large rivers (Daufresne *et al*., 2004). This allowed comparing similar year classes across the different study areas. Because part of its life cycle is completed in the sea, the eel (*Anguilla anguilla*, L.) was not included in the study. The fish abundance data set finally contained 47 columns (species) and 503 rows (study area $\times$ sampling site $\times$ biological year combinations).

We defined a set of five biological variables to study changes in total abundance, structure, and diversity of fish communities. For each site-year, we first calculated the total abundance (as the sum of the average CPUE of the different species), the specific richness (i.e. the number of species with a non-null average CPUE) and the Shannon equitability index (Begon *et al*., 1990). These first three variables were calculated using all the species sampled each site-year. Then, we calculated the proportions (to the total abundance) of southern and warm-water species. We calculated both variables to determine if changes in proportions of southern species could be linked to thermal preferences. For a given study area, we only considered the most common species, excluding those accounting for $<5\%$ of the total number of fish sampled. We focused on dominant species because affinities for temperature and geographical ranges were not available for all the less-abundant species. We first calculated the relative position of the study area in the geographical range of the most common species (x values; Daufresne *et al*., 2004; Fig. 2). Species with the upper 25% x values were considered as southern species. The proportion of southern species time series was calculated by dividing the CPUE of southern species by the total CPUE for each site-year. Then, we calculated the proportion of warm-water species time series. To do so, we first coded affinities for high temperatures of all the most common species sampled in the different study areas (18 species). We defined a group of six species with the highest affinity for high temperature: tench (*Tinca tinca* L.), bream (*Abramis brama* L.), white bream (*Blicca bjoerkna* L.), rudd (*Scardinius erythrophthalmus* L.), wels catfish (*Silurus glanis* L.) and black bullhead (*Ameiurus melas* R.).

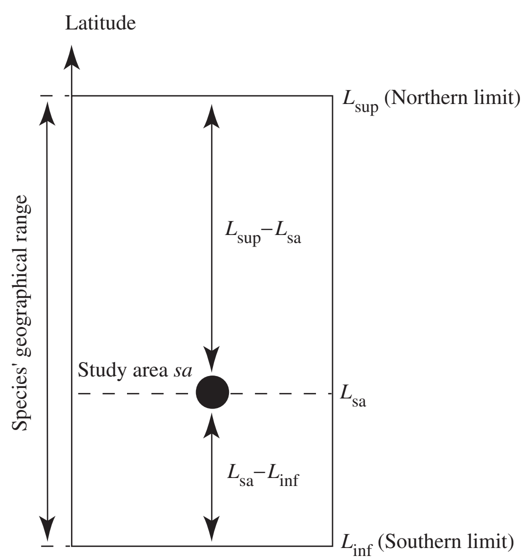

Fig. 2 Relative position (x) of a study area sa in the geographical range of a species. x is coded on the basis of the geographical range of European fish species (Bruslé & Quignard, 2001; Keith & Allardi, 2001) as a function of: $x = (L_{sa}-L_{inf})/(L_{sup}-L_{sa})$, where L_{sa}, L_{sup} and L_{inf} are the latitudes (°N) of the study area, the northern limit of the species' geographical range and the southern limit of the species' geographical range, respectively (Daufresne *et al*., 2004).

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Tench, bream and rudd, were assigned to this group according to Philippart & Vranken (1983) (i.e. lethal temperature: >34 °C; optimal growing temperature: 20–28 °C; reproduction temperature: 20 °C). White bream, was added to this group according to Küttel *et al*. (2002) (e.g. critical thermal maximum for larvae, juveniles and adults = 28, 34 and 36 °C, respectively, maximum reproduction temperature = 23 °C), as well as black bullhead (e.g. critical thermal maximum for adults = 38 °C, maximum reproduction temperature = 20 °C). Wels catfish was included because this species is known to grow faster at high temperature (>20 °C; Proteau *et al*., 1996) and to reproduce at temperatures above 20 °C (Bruslé & Quignard, 2001). According to Philippart & Vranken (1983) we then define a group of six species with medium affinity for high-temperature (lethal temperature, 28–34 °C; optimal growing temperature, 14–23 °C; reproduction temperature, 7–15 °C): Bleak (*Alburnus alburnus* L.), stream bleak (*Alburnoides bipunctatus* B.), barbel (*Barbus barbus* L.), chub (*Leuciscus cephalus* L.), roach (*Rutilus rutilus* L.) and bitterling (*Rhodeus sericeus* P.). Stream bleak and barbel were considered as slightly stenothermic by Philippart & Vranken (1983). However, stream bleak was assessed to this group because of its abilities to grow at high temperature (optimal range: 18–27 °C for adults; Küttel *et al*., 2002) and to reproduce in warm water (optimal range: 12–24 °C; Küttel *et al*., 2002). Similarly, barbel has some affinities for warm water (Kraiem, 1979; Bruslé & Quignard, 2001) and can reproduce at high temperature (maximum: 29 °C; Küttel *et al*., 2002). Finally, we defined a group of six species with the lowest affinity for high temperature: pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.), pumpkinseed (*Lepomis gibbosus* L.), gudgeon (*Gobio gobio* L.), nase (*Chondrostoma nasus* L.) and dace (*Leuciscus leuciscus* L.). According to Philippart & Vranken (1983) pike, nase and dace have the same affinities for temperature than the species of the previous group but are defined has slightly stenothermic. Indeed, reproduction and larval growth of pike are optimal at low temperature (optimal range: 5–10 and 8–15 °C, respectively; Küttel *et al*., 2002). Perch presents similar properties (optimal range: 6–15 and 12–18 °C for reproduction and larval growth, respectively; Küttel *et al*., 2002) and eggs are sensitive to high temperature (lethal temperature: 16 °C; Elliott, 1981). Larvae of nase and dace have also affinities for cold water (lethal temperature: 19 and 18 °C, respectively; Küttel *et al*., 2002) and both species reproduce at low temperature (maximum: 16 and 14 °C for nase and dace, respectively; Küttel *et al*., 2002). Gudgeon was assessed to this group because of its optimal temperature for reproduction (optimal range: 12–17 °C; Küttel *et al*., 2002), lower than those of the species of the second group (Küttel *et al*., 2002). Finally, despite the ability of the adults of pumpkinseed to face high temperatures (lethal temperature: 35 °C; Küttel *et al*., 2002), this species was conservatively assessed to this group because of its thermal optimum for growth (ca. 20 °C, Scott & Crossman, 1973) and the sensitivity of the juveniles to warm water [lethal temperature: 25 °C (Küttel *et al*., 2002); high mortality rate in warm environment (Dembski *et al*., 2006)]. Heterogeneity of data available for the different species did not allow computing affinities for high temperature using mathematical procedures. Thus, we assigned an affinity of 0.75, 0.5 and 0.25 for the species of the three different groups, respectively. For each site-year, the proportion of warm-water species was calculated by first summing the products of species abundance with species affinity. Then this sum was divided by the total CPUE.

Water temperatures were recorded right upstream from the NPS by Electricité de France. To evaluate the potential effect of temperature on fish communities (biological year n), we calculated the average temperature during reproduction (April–June, biological year n–1) for each study area (Daufresne *et al*., 2004).

Statistical analysis

We performed a weighted meta-analysis on data using Mann–Kendall trend statistics (S) and the slope of the linear regression of biological variables on reproduction temperature (b) as 'effect sizes' (Gurevitch & Hedges, 1993). S provides information on long-term changes of biological variables, whereas b provides information on the interannual relationship between the biological and temperature variables. Variances of S and b were corrected for temporal autocorrelations before the analysis (Hamed & Rao, 1998; Pyper & Peterman, 1998). For each biological variable, we first evaluated the overall magnitude of S and b (called grand mean effect sizes) and calculated their 95% confidence intervals using the bootstrap procedure. To test whether effect sizes depended on nonclimatic anthropogenic constraints (NPS and hydropower schemes), we defined two categorical variables. The first one discriminated whether or not sampling sites were located downstream from a NPS. The second one discriminated whether or not they were located along hydropower schemes. We used a mixed effect model (Gurevitch & Hedges, 1993) to test whether grouping variables explained significant heterogeneity in the effect size, whereby the overall heterogeneity was divided into within-group heterogeneity and between-group heterogeneity (Q_b). The effects of categorical variables on effect sizes were evaluated using 10 000 randomizations and Bonferroni's corrections (Sokal & Rohlf, 1995). Because such corrections are known to be conservative (Sokal & Rohlf, 1995), significant results at the 0.1 (and lower) level were discussed (Hillebrand, 2004). All statistical analyses were performed using *R* (R Development Core Team, 2006).

Results

During the whole study periods a total number of 362 692 fish of 47 species were captured, representing an average of 51 813 ± 14 111 (average ± 95% confidence interval) fish and 32 ± 3 (average ± 95% confidence interval) species for each study area. The upstream water temperature of our study areas during reproduction has gradually increased over the last 25 years [modified Mann – Kendal trend test (Hamed & Rao, 1998), $P < 0.01$, $n = 25$, Fig. 3]. We observed a good synchronism of water temperature time series at large spatial scale (narrow 95% confidence intervals of mean water temperature; see Fig. 3). In addition, the water temperature and the maximum air temperature measured by Météo France at the closest sampling sites from the study areas (i.e. 60, 36, 170, 8, 14, 83 and 26 km from Belleville, Bugey, Chinon, Cruas, Nogent, Saint-Alban and Tricastin, respectively) were significantly correlated [modified Pearson's correlation test (Pyper & Peterman, 1998), P-values < 0.01].

Analysis of grand mean effect sizes revealed significant increasing temporal trends (S) in total abundance and proportion of warm-water species at all the sampling sites and a significant decreasing trend in equitability (Figs 4a and 5). Body size measurements at Bugey highlighted that the increase in abundance could be coupled with a drastic increase in the proportion of small individuals (Fig. 6a and b). The specific richness also significantly increased at all the sampling sites but this pattern was more pronounced at the sites located along hydropower schemes ($Q_b = 10.7$, Bonferroni corrected $P < 0.1$). This increase was partially due to appearance of some species, including non native species (*Carassius gibelio* B., *Pseudorasbora parva* T. & S., *Silurus glanis* L.), but was mainly due to a global increase in occurrence of local species (Table 2). Finally, the proportion of southern species significantly increased at the sampling sites which were not located along hydropower schemes but did not show any significant trend

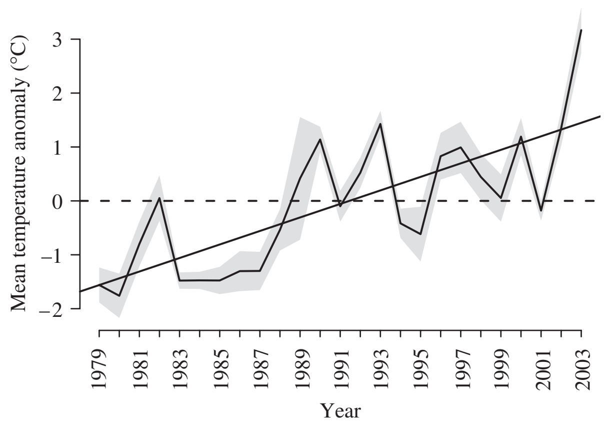

Fig. 3 Annual mean anomalies (±95% confidence intervals) of temperature during reproduction (April–June). Temperatures were recorded upstream from the study areas. The trend is shown ($Y(t) = 0.12t - 1.56$).

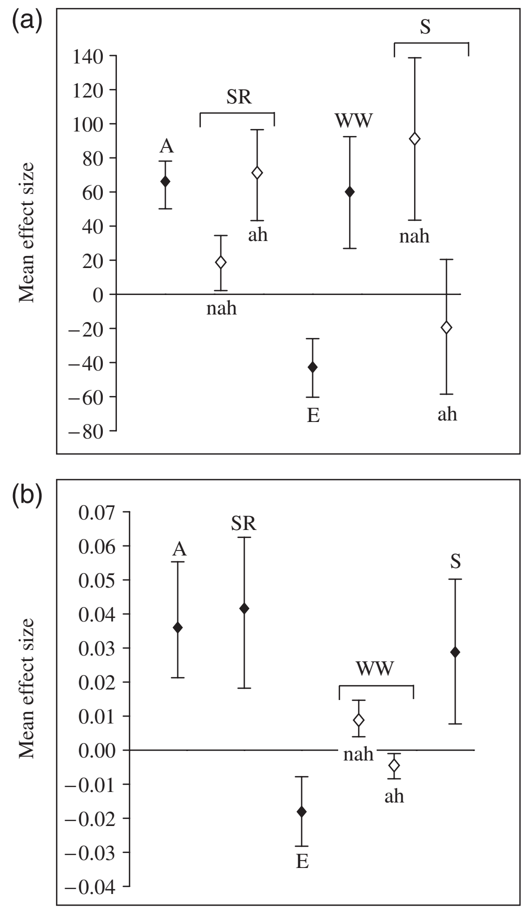

Fig. 4 Mean effect sizes (±95% confidence intervals). (a) Mean for the trend S of the total abundance of fish (A), the specific richness (SR), the Shannon equitability index (E), the proportion of southern species to the total abundance (S) and the proportion of warm-water species to the total abundance (WW) at the different sampling sites. Significantly different means at sampling sites located along hydropower schemes (ah) or not (nah) are represented (open diamonds). (b) Mean for the slope of the linear regression with temperature during reproduction b of A, SR, E, S and WW at the different sampling sites. Significantly different means at sampling sites located along hydropower schemes (ah) or not (nah) are represented (open diamonds). To increase readability, b values (and confidence intervals) of A and SR were divided by 1000 and 10, respectively. Nonoverlapping of confidence intervals with 0 indicates significant effects.

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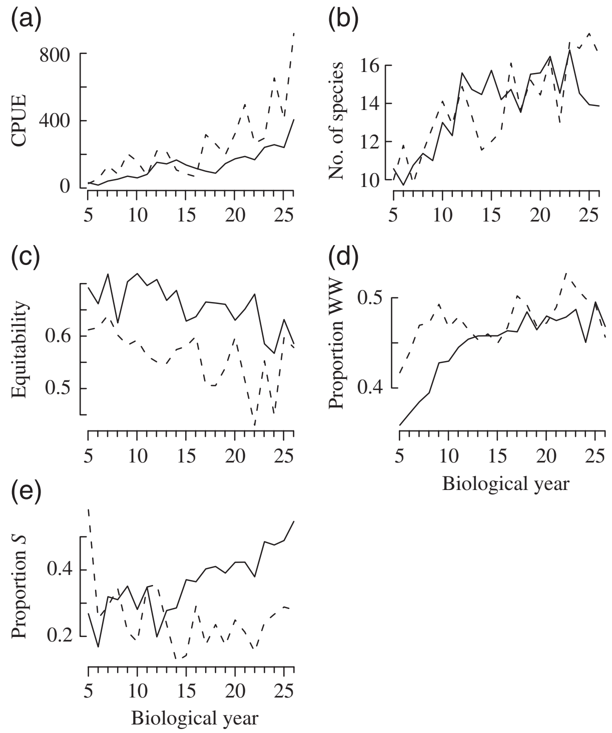

Fig. 5 Temporal changes (annual means) in total abundance, community structure and diversity at the sampling sites located along hydropower schemes (dotted lines) or not (continuous lines). (a) Total abundance (expresses as CPUE). (b) Specific richness (expresses as number of species). (c) Shannon equitability index. (d) Proportion of warm-water species (WW) to the total abundance. (e) Proportion of southern species (S) to the total abundance. CPUE, catch per unit effort.

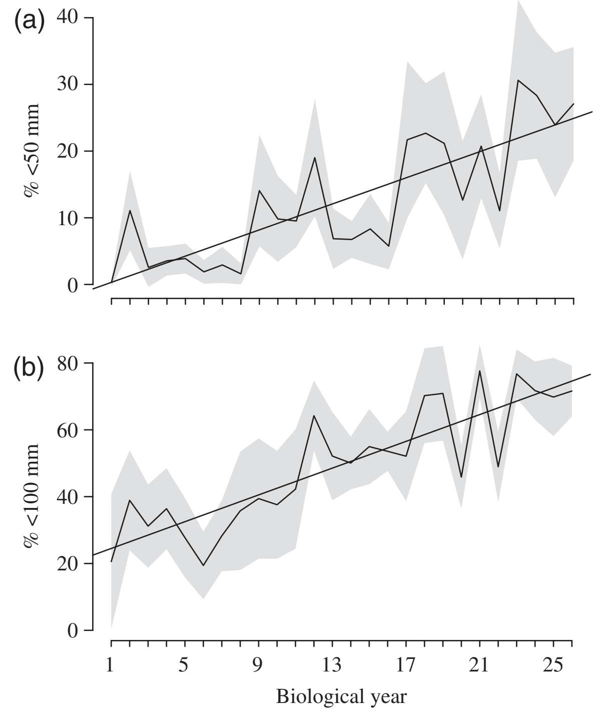

Fig. 6 Annual mean percentages (±95% confidence intervals) of small fish sampled at Bugey. (a) Fish smaller than 50 mm. (b) Fish smaller than 100 mm. Biological year (from 1 July to 30 June of the next calendar year) was defined according to the 'average' hatching date of most of the cyprinid species present in large rivers (Daufresne *et al.*, 2004). The trend are shown ($Y(t) = 0.98t - 0.66$ for fish smaller than 50 mm and $Y(t) = 2.00t + 22.49$ for fish smaller than 100 mm).

at the other sampling sites ($Q_b = 13.04$, Bonferroni corrected $P < 0.1$).

Total abundance, species richness and the proportion of southern species were all positively related to temperature during reproduction (b), whereas equitability was negatively related (Fig. 4b). Proportion of warm-water species was positively related to temperature at sites without hydropower influences, but negatively related at sites located along hydropower schemes (Fig. 4b; $Q_b = 13.4$, Bonferroni corrected $P < 0.05$).

All patterns were highly consistent among sampling sites located either upstream or downstream from a NPS (Q_b ranging from 4.8×10^{-4} to 0.9). Beside temporal aspect, ANOVAS performed on total abundance, equitability, specific richness and proportions of warm water and southern species did not neither highlighted any significant overall differences among sampling sites located upstream or downstream from a NPS (Bonferroni corrected $P > 0.1$ in all cases). Conversely, ANOVAS highlighted an overall detrimental effect of hydropower schemes on equitability (lower at sites located along schemes; Bonferroni corrected $P < 0.01$; Fig. 5c) and proportion of warm-water species (higher at sites located along schemes; Bonferroni corrected $P < 0.01$; Fig. 5d).

Discussion

General long-term changes

The consistent increase in water temperature at large spatial scale, correlated with air temperature, confirmed the results of former studies about the impact of climate change on temperature of European rivers (Webb, 1996; Daufresne *et al.*, 2004; Mouthon & Daufresne, 2006). Concomitantly, we observed important changes in total abundance, structures and diversity of fish communities, significantly linked to the temperature during reproduction (Fig. 4). These changes, mostly consistent across communities that were submitted to similar climate warming but to different kind and strength of

Table 2 Comparison of species occurrences between the first 5 biological years vs. the last 5 biological years of study periods at each study area

	Belleville	Bugey	Chinon	Cruas	Nogent	St Alban	Tricastin
Appearing (number of species)	–	2 (Barbt, Silg)	–	3 (Cotg, Carg, Psep)	–	3 (Gymc, Psep, Rhos)	2 (Psep, Rhos)
Disappearing (number of species)	–	–	1 (Amem)	–	–	–	1 (Chot)
Increasing occurrence (number of species)	7	13	7	15	11	11	14
Decreasing occurrence (number of species)	4	6	7	4	6	5	8

Species occurrence was calculated as the total number of biological year when the species has been sampled at the study area. Amem, *Ameiurus melas*; Barbt, *Barbatula barbatula*; Carg, *Carassius gibelio*; Chot, *Chondrostoma toxostoma*; Cotg, *Cottus gobio*; Gymc, *Gymnocephalus cernuus*; Psep, *Pseudorasborra parva*; Rhos, *Rhodeus sericeus*; Silg, *Silurus glanis*.

nonclimatic constraints, highlight the specific impacts of climate change on communities.

Some of the observed changes were quantitatively extremely important. For instance, the mean change in total abundance (±95% confidence interval) was of +232% (±103%) when comparing average values for the first 5 years vs. the last 5 years of the study periods. We can propose two hypotheses to explain such increase. First, since recruitment of cyprinids is favoured by warm water (Mills & Mann, 1985; Mann, 1996), we can hypothesize that the increase in abundance was mostly the fact of small young fish of the year. For instance, the percentage of fish smaller than 50 mm at Bugey (a study area for which fish size was available) presented a drastic increase (Fig. 6a). At these sizes, fish are considered as young of the year for most of European cyprinids (Bruslé & Quignard, 2001; Keith & Allardi, 2001; Daufresne *et al.*, 2004; Froese & Pauly, 2006). Second, we can hypothesize that this increase in abundance may underline a global increase in abundance of small size species such as stream bleak (maximum size = 160 mm; Froese & Pauly, 2006) and bitterling (maximum size = 100 mm; Froese & Pauly, 2006) as it has already been suggested in large French rivers (Daufresne *et al.*, 2004; Daufresne & Boët, 2005). Hence, the increase in total abundance may be mostly due to rejuvenation and/or an increase in the abundance of small size species. For instance, fish smaller than 100 mm actually came to dominate the fish community at Bugey (Fig. 6b). Interestingly, this fits the ecogeographical rule highlighted by Knouft (2004), which states that the average body size within fish communities tends to increase with decreasing latitude (i.e. increasing temperature).

Beside the trend of the total abundance, we observed a general significant increase in specific richness and decrease in equitability. According to Connell (1978) and Wilson (1990) the increase in specific richness is not surprising because gradual climate change would be one of the most convincing explanations for Hutchinson's 'paradox of the plankton' (1961; i.e. 'How [it is] possible for a number of species to coexist in a relatively isotropic or unstructured environment, all competing for the same sorts of materials?'). The initial hypothesis is based on the assumption that communities seldom reach an equilibrium state. Under gradual climate change no species would have time to eliminate (by the way of competitive exclusion) the others before being itself constrained by the environment. As a consequence, the communities always include a mixture of species favoured by the current vs. previous climate. The latter species do not necessarily disappear suddenly but can be eliminate only after several generations (Wilson, 1990). Regarding the current global warming this would explain why species seem to invade faster from lower latitudes than resident species recede pole ward, ultimately leading to an increase of the specific richness (Sagarin *et al.*, 1999). However, this phenomenon could be only transitional (Walther *et al.*, 2002). Actually, Connell (1978) suggested that too quick environment changes will not allow communities to change and, thus will not promote diversity. From this view point, the fact that we observe very few new comers within the communities (Table 2), as well as the decrease in equitability, matches the hypothesis of a detrimental effect of climate change on biodiversity (Sala *et al.*, 2000). Indeed, if we observe a gradual increase of specific richness, very few species seem to take advantage of the warming. For instance, over the last 2 biological years, the communities were dominated by bleak and stream bleak at Belleville (accounting for 26.4% and 22.0% of the total abundance, respectively), stream bleak and chub at Bugey (accounting for 50.8% and 18.7% of the total abundance, respectively), bleak

Table 3 Median (25–75% percentiles) of chemicals in the vicinity of six of the seven study areas during the 1985–2005 period

	O_2 *(6)*	pH	BOD_5 *(6)*	NH_4 *(0.5)*	NO_2 *(0.3)*	NO_3 *(50)*	P *(0.5; 0.2*)*
Chinon	10.1	8.3	4.4	0.1	0.08	11.1	0.22*
	(9.4–10.7)	(8.2–8.5)	(3.8–5.0)	(0.1–0.2)	(0.07–0.09)	(10.0–13.0)	(0.15–0.29)
Cruas	9.8	8.0	1.5	0.2	0.09	6.4	0.19
	(9.7–10.0)	(8.0–8.1)	(1.1–1.6)	(0.2–0.3)	(0.09–0.11)	(6.1–6.6)	(0.18–0.41)
Bugey	10.1	8.1	1.2	0.1	0.06	3.9	0.10
	(10.0–10.3)	(8.0–8.1)	(1.0–1.4)	(0.1–0.1)	(0.06–0.07)	(3.7–4.2)	(0.08–0.15)
Nogent	10	8.0	1.9	0.1	0.07	19.7	0.10*
	(9.1–10.3)	(8.0–8.1)	(1.7–2.9)	(0.1–0.1)	(0.06–0.09)	(17.8–21.2)	(0.07–0.14)
St. Alban	10.0	8.0	1.6	0.2	0.08	6.2	0.20
	(9.7–10.2)	(8.0–8.1)	(1.4–2.0)	(0.2–0.3)	(0.07–0.09)	(5.8–6.5)	(0.17–0.23)
Tricastin	9.8	8.0	1.5	0.1	0.10	6.5	0.16
	(9.5–10.0)	(8.0–8.0)	(1.3–1.8)	(0.1–0.2)	(0.09–0.12)	(6.2–6.9)	(0.15–0.38)

Values in italics represent the upper or lower (for O_2) limits currently defining the good ecological state for French rivers according to the European Water Framework Directive (Direction de l'eau 2005).
O_2, oxygen; BOD_5, 5-day biological oxygen demand; NH_4, ammonium; NO_2, nitrite; NO_3, nitrate; P, phosphate (or total phosphorus*). All values but pH are expressed as $mg\,L^{-1}$. Statistics are derived from data collected by the Agences de l'eau (http://www.lesagencesdeleau.fr) at Chinon, 27 km upstream from Cruas, 11 km downstream from Bugey, at Nogent, 27 km upstream from St Alban and 33 km downstream from Tricastin. No data were available at the vicinity of Belleville for the 1985–2005 period.

and stream bleak at Chinon (accounting for 24.0% and 23.1% of the total abundance, respectively), roach and bleak at Cruas (accounting for 34.0% and 25.2% of the total abundance, respectively), roach and bleak at Nogent (accounting for 22.8% and 16.6% of the total abundance, respectively), roach and bleak at Saint Alban (accounting for 49.9% and 17.5% of the total abundance, respectively) and chub and roach at Tricastin (accounting for 45.5% and 15.8% of the total abundance, respectively). Note that these results tend to confirm the gradual domination of communities by small size species (e.g. bleak and stream bleak).

Finally, the proportion of southern species significantly increased at the sampling sites that were not located along hydropower schemes and we also observed a general increase in the proportion of warm-water species for all sites. Such results are consistent with the general hypotheses about the ecological effects of climate change, as well as with results of previous single-site studies and meta-analysis (Walther *et al*., 2002; Parmesan & Yohe, 2003; Root *et al*., 2003). With regard to fish communities in large rivers, these results are to our knowledge the first to generalize the pattern that was highlighted by a single-site study performed on the Upper Rhône River (Daufresne *et al*., 2004).

Interestingly, according to the theory of ramp disturbance (i.e. disturbance with a steadily increasing strength in space and time; Lake, 2000), the observed trends were currently mostly continuous (van Nes & Scheffer, 2004). However, such trends may reduce the basin of attraction around the present community states (van Nes & Scheffer, 2004). This could result in sudden shifts in the community structures in the next few years, especially if the frequency of extreme climatic events tends to increase due to climate change. Actually, such pattern has already been observed in large rivers for invertebrate communities (Mouthon & Daufresne, 2006; Daufresne *et al*., 2007).

Thus, our results match the general hypothesis of an effect of climate warming on fish communities. In addition, such consistent changes across different ecosystems can only be due to a common disturbance, playing at large geographical scale. Nonetheless, besides climate warming, one may argue that large rivers in Europe also underwent a general improvement in water quality (Aarts *et al*., 2004). However, the water quality at the study areas during the study periods was globally good according to the European Water Framework Directive and did not presented major variations (Table 3). In addition, Daufresne *et al*. (2004) showed that changes in fish community structure at Bugey were not consistent with the potential effects of a water improvement. For instance, the dace, which is known to be highly sensitive to water quality (Verneaux, 1981; Bruslé & Quignard, 2001) tended to decrease in abundance whereas eury-tolerant species such as chub (Verneaux, 1981; Bruslé & Quignard, 2001) came to dominate the community. More generally, the species currently dominating the communities at the different study areas (e.g. bleak, chub and roach) are known to be not sensitive to water quality (Verneaux, 1981). In addition, even in rivers undergoing water-quality improvement the recovery of fish community seems low, probably because of a more important impact of other anthropogenic constraints (Aarts *et al*., 2004).

Impacts of climate change vs. nonclimatic anthropogenic disturbances

NPS and hydropower schemes could be defined as press disturbances (Bender *et al*., 1986) whereas climate warming mainly refers to a ramp disturbance (Lake, 2000). Press disturbances arise sharply and are maintained in time at a rather constant level. Many studies have clearly showed the influences of press disturbances on biota, especially on aquatic ecosystems (Bravard, 1987; Petts *et al*., 1989; Fruget, 1992; Kinsolving & Bain, 1993; Phillips & Johnston, 2004). Such disturbances typically rapidly modify the structure and diversity of communities, defining a new state until any other major changes occur. On the other hand, recent works highlighted that ramp disturbances generally induce gradual changes in community structures disrupted in times by rapid shifts (van Nes & Scheffer, 2004).

We did not find any significant impact of NPS neither on long-term trends (Fig. 4a) nor on grand means ($P > 0.1$) of total abundance, community structure and diversity. At the interannual scale NPS not either impacted the relationship between these variables and the reproduction temperature. These results are consistent with some previous studies highlighting marginal effects of NPS on fish at the community level (Kirchmann *et al*., 1985; Daufresne *et al*., 2004, 2005). In fact, the impacts of NPS on water temperature are rather punctual and fish can probably easily escape from this disturbance (Daufresne *et al*., 2004, 2005). Nonetheless, our results only refer to impacts of NPS on communities and do not imply that such disturbance has no effects at other biological scales (individual, population).

In the same way, the hydropower schemes had an insignificant overall influence, but they clearly muted the effect of climate change on proportion of southern species and warm-water species while intensifying the effect on specific richness (Figs 4a and 5). The latter effect, significant at the 0.1 level, did not seem quantitatively important (Fig. 5b) and was probably due to a more gradual increase of the specific richness at the sites located along hydropower schemes. Regarding southern species, we can propose two nonexclusive hypotheses explaining why their proportion did not increase at sites located along hydropower schemes. First, these sites were the most southern sites and were located close to the Mediterranean Sea that can be considered as a natural southern barrier to migration. Second, these sites were located close to dams, which are barriers to migration as well. As a consequence, fish communities at these sites may have suffered from a reduced flow of southern individuals. Interestingly, we observed inconsistent long-term changes of southern vs. warm-water species at sites located along hydropower schemes (Figs 4a, 5d and e). This result is not surprising because we assigned thermal preferences at the species level. In this way, a given species had the same thermal preference at all the sites (e.g. tench was always considered as a warm-water species) but was not necessarily considered as southern at all sites. Thus, if warm-water species were favoured at all the sites, the most southern ones did not come to dominate the community at sites located along hydropower schemes because of natural and/or anthropogenic barriers to migration. Finally, we observed no correspondence between the long-term trend of warm-water species with increasing temperature and the increase in warm-water species with increasing within-year temperature at sites located along hydropower schemes (Fig. 4). Hydropower schemes actually reversed the relationship between temperature and proportion of warm-water species at long-term vs. interannual scale. This can be due to different processes. First, water temperature was negatively correlated [modified Pearson's correlation test (Pyper & Peterman, 1998), P-values < 0.001] to discharge measured at the vicinity of these sites [32, 17 and 18 km from the NPS (i.e. temperature-recording sites) of Saint Alban, Cruas and Tricastin, respectively]. Most of the warm-water species considered in the study deposit their eggs on aquatic macrophytes (tench, white bream, rudd and wels catfish) or either on macrophytes or on gravel (bream), often in the backwater areas of the river (Mann, 1995). As a consequence, the recruitment of such species is highly sensitive to environmental constraints (Mann, 1995) and particularly to dewatering. In this way, low proportion of warm-water species could be due to low recruitment the warm and dry years. Beside such negative effect of temperature at the interannual scale, the positive long term trend of proportion of warm-water species can be attributed to contradictory effects of an environmental factor on different development stages. Indeed, high temperatures may punctually decrease the recruitment but concomitantly increase the survival of juveniles and/or adults (knowing that these species have strong affinities for warm water) maintaining, at least transitionally, a positive growth rate of populations. Such processes could be of course enhanced by density dependent survivals. A similar process (but with opposite patterns) has already been observed for dace population at Bugey (Daufresne, 2004; Daufresne *et al*., 2004). Despite a positive effect of temperature on recruitment at the interannual scale, the population tended to collapse, probably because of an extra mortality rate of adults after reproduction.

These results do not question the influence of land use changes on community structures. Many studies have clearly showed the influences of such pressures, especially on aquatic ecosystems (Bravard, 1987; Petts *et al*., 1989; Fruget, 1992; Kinsolving & Bain, 1993; Phillips & Johnston, 2004). Actually, we highlighted an overall detrimental effect of hydropower schemes on equitability (Fig. 5c). Similarly, the proportion of warm-water species was significantly higher at the sampling sites located along hydropower schemes (Fig. 5d). The latter pattern is probably due to the general decrease in current velocity along the schemes, favouring eury-tolerant organisms and especially species with positive affinities with low current velocities and warm water (Fruget, 1992). Thus, our results do not exclude an effect of press disturbances but rather suggest that the effects of nonclimatic anthropogenic disturbances and climate change on communities are generally additives. Overall, these results have profound implications regarding management policy. Global change probably did not really undermine the progress in environmental management over the past 30 years. However, it sounds crucial not considering past conditions to evaluate the effect of such improvement. It is probably more accurate to consider, as a reference, sites submitted to climate change but not to the studied anthropogenic constraint, as it has been done in this study.

Limits of the study

First of all, patterns regarding the proportion of southern and warm-water species were only evaluated using a restricted number of species. We considered the most abundant species and we thus evaluated the most important quantitative effects. However, this study again underlines the crucial need of a better knowledge of the ecology of European freshwater fish, and especially of their thermal preferences (Elliott, 1981; Küttel *et al*., 2002).

Another potential caveat in our analysis is the use of several sampling sites within the different study areas. This may hinder the statistical independence of the different dynamics and in turn the meta-analysis itself. The mean distance between two consecutive sampling sites (along an upstream–downstream gradient) within a study area was of 5.1 km. In addition, the sampling of a study area was generally achieved within few hours. This should have ensured the independence of the samples between the different sampling sites. However, significant effects of the study areas were found for two of the 10 effect sizes: the b value of the proportion of warm-water species (ANOVA, Bonferroni corrected $P<0.05$) and the S value of the proportion of southern species (ANOVA, Bonferroni corrected $P<0.05$). The effects were mainly due to the homogeneity of the effect size at Bugey, where the mean distance between two consecutive sampling sites was only of 2.1 km. Indeed, effects of the study area were no longer significant when we only considered the most upstream and most downstream sampling sites at Bugey (18 km distant from each other). Rerunning the meta-analyses for these two effect sizes by only considering the most distant sampling sites for Bugey gave similar results than those found when considering all the sampling sites. Thus, our results did not strongly depend on the homogeneity of these two effect sizes among the different sampling sites at Bugey.

Finally, all the sites located along hydropower schemes were on the Rhône River. In this way, the characteristics of that river could have influenced the results. The increase in proportion of southern species, as well as the positive correlation between the proportion of warm-water species and temperature (i.e. the patterns observed in the most natural sites) were consistent with the patterns previously observed at Bugey (Daufresne, 2004; Daufresne *et al*., 2004), a site located on the Rhône River. This, together with the general independence of the effect sizes across study areas, underline that the river effect *stricto sensu* could be weak. However, sites submitted to the influence of hydropower schemes were also located close to the Mediterranean Sea, a natural southern barrier to migration. Thus, it is still difficult to disentangle the effects of geographical location vs. hydropower schemes on community changes. Nevertheless, (1) these effects appeared to be weak and (2) there was no significant effect of the distance to the sea on S values of proportion of southern species at these specific sites (Pearson' correlation test, $P>0.1$).

Conclusion

Our results show that species composition, diversity, global abundance and size structure of fish communities exhibited important trends related to water warming in large rivers. Most of the observed patterns did not seem strongly sensitive to the effects of hydropower schemes and NPS. Further studies, involving additional study areas and/or taxa, would be useful to quantify more clearly the relative influence of nonclimatic anthropogenic stressor and geographical location (e.g. closeness to natural southern barriers to migration) on the responses of communities to climate change. Nevertheless, our results suggest that it is crucial to more systematically include climate change as a potential confounding factor when studying long-term ecological patterns, even in sites undergoing non-climatic anthropogenic disturbances.

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