Global Change Biology (2006) **12**, 441–449, doi: 10.1111/j.1365-2486.2006.01095.x

Effects of the 2003 heatwave and climatic warming on mollusc communities of the Saône: a large lowland river and of its two main tributaries (France)

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Abstract

The study of the dynamics of mollusc populations of the Saône and its two main tributaries, the Doubs and Ognon, over several years has provided us with the opportunity of highlighting the consequences of climatic warming and especially of the heatwave of 2003 on these organisms. From 1987 to 2003, the mean temperature of the waters of the Saône upstream of Lyon (Couzon) increased by 1.5 °C. In addition, the summer of 2003 was the hottest since 1500 at least. We used correspondence analysis to identify structure change in mollusc data dating from September 1996 to December 2004. The results revealed: (1) during the period from September 1996 to July 2003, a significant progressive change in the mollusc community structure of the Saône upstream of Lyon, probably linked to the increase of temperature; (2) from July to August 2003 during the heatwave, a sudden change in the structure of mollusc communities and a significant decrease of species richness and density of gastropods and bivalves. During 2004, mollusc density and particularly that of *Pisidium* remained dramatically low. Similar observations were performed at four other sites along the Saône and in the lower reaches of its two main tributaries. This suggests that the resilience of the mollusc populations (i.e., the speed with which they return to a predisturbance state) to the heatwave is low. In this way, as different climatic models have predicted an increase in the frequency of summers as hot as that of 2003 during this century, more than half the mollusc species currently inhabiting the potamic area of the Saône, Doubs and Ognon, and probably other large rivers, are probably directly threatened with extinction.

Keywords: climatic warming, freshwater, heatwave, molluscs, Saône river

Received 19 May 2005; revised version received 2 November 2005; accepted 7 October 2005

Introduction

Since the second half of the 19th century, global mean temperature has increased by 0.7 °C (IPCC, 2001). In Europe, the number of cold and frost days has decreased, whereas the number of days with temperatures above 25 °C and of heatwaves has increased. This augmentation has been higher than the mean with an increase of 0.95 °C (EEA, 2004). In addition, the summer of 2003 has probably been the hottest since the year 1500 (Black *et al*., 2004; Luterbacher *et al*., 2004), at least. According to Stott *et al*. (2004), a significant share in the causes of this extreme climatic event can be attributed to anthropogenic origins and the heatwave of 2003 is a manifestation of global warming.

There is now no doubt about the effect of global change on ecosystems (Walther *et al*., 2002). In particular, its effects are already apparent in running water ecosystems, despite the fact that studies bearing on current data in these environments are rare (Elliot *et al*., 2000; Bradley & Ormerod, 2001; Daufresne *et al*., 2004). However, most studies concerning the ecological consequences of climatic change have only taken into account a gradual increase of temperatures. To our knowledge, no study based on actual data has evaluated the ecological consequences of the European 2003 heatwave.

The molluscs of the Saône and its two main tributaries, the Doubs and Ognon have been collected for several years in order to study the population dynamics

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and the biological cycles of different species. These data sets have given us the opportunity to show the effects of the abnormally high temperatures of summer 2003 on the malacocenoses of these rivers.

Materials and methods

Study area

The Saône draws its source from the Vosges mountains at an altitude of 405 m. Channelled from Corre, 70 km from its source, this nonregulated river flows into the Rhône at Lyon (altitude 160 m), reaching a length of 482 km (Fig. 1). Its catchment area is approximately 29 900 km^2. Its mean slope is 0.5 m km^{-1} but only 0.08 m km^{-1} in its latter 300 km. The Saône receives about 20 tributaries of which the Doubs and the Ognon (both nonregulated) are the largest. The river is linked to the basins of the Moselle, Seine and Loire by different canals.

Environmental variables

The mean daily temperatures of the Saône at lock of Couzon located about 10 km from the confluence with the Rhône, were obtained from automatic readings. These data were supplied by Electricité De France (EDF). Discharge rates at Mâcon, situated 78 km upstream from the confluence with the Rhône and downstream of the Saône's main tributaries, were extracted from the HYDRO database (web site: http://www.mde.tm.fr).

Sampling sites

We sampled seven sites (Fig. 1 and Table 1). The first is situated on the Saône at the river's entry into the conurbation of Lyon. At this point the river is approximately 150 m wide, two-thirds of this width being taken up by a navigable channel. The site, located on the right bank, was approximately 150 m in length. From May to October, more than half its surface area was covered

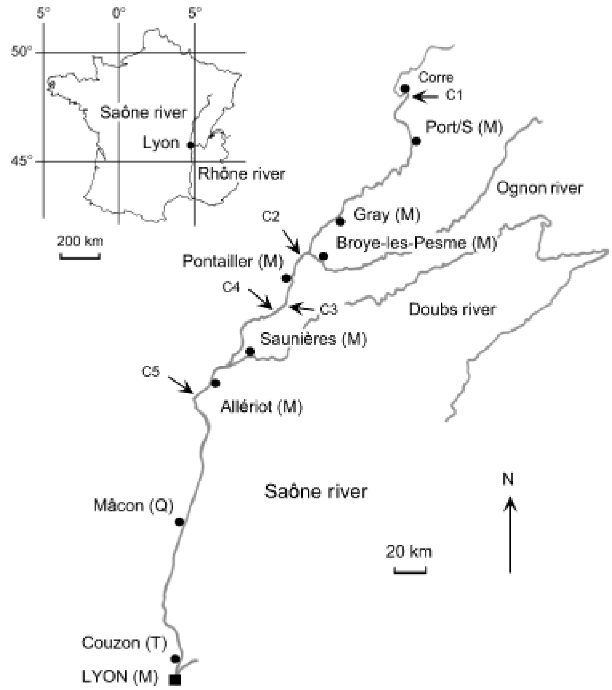

Fig. 1 Study area and location of the mollusc sampling sites (M) and the temperature (T) and discharge (Q) recording sites. C1–C5 (Canals): C1, East canal; C2, Marne to Saône canal; C3, Rhône to Rhine canal; C4, Burgundy canal; C5, Centre canal.

with different species of macrophytes: *Nuphar*, *Ceratophyllum*, *Potamogeton* and filamentous algae. Additional samples were collected at different times before and after the heatwave at six other sites. The sites of Port/Saône, Gray and Pontailler were located in by-passed sections (old channel nonnavigable). The site of Allériot is situated downstream of the confluence of the Doubs. Broye-les-Pesmes and Saunières were, respectively, located in the lower reaches of the Ognon and the Doubs just before their confluences with the Saône.

At each site, the samples, 0.25 m^2 each, were taken at four stations at a depth from 0.50 (depth at which wake effects lessen) to 1.5 m, using a rectangular hand-net

Table 1 Distance from Rhône confluence and sampling frequency and periods of each site

Site (River)	Distance from Rhône confluence (km)	Sampling frequency	Periods
Lyon (Saône)	10	Monthly	From September 1996 to December 2004
Port/Saône	366	Annually	Autumns 1997 To 2000 And 2004
Gray (Saône)	288	Annually	Autumns 1997 To 1999 And 2004
Pontailler (Saône)	257	Annually	Autumns 1997 to 1999 and 2004
Allériot (Saône)	150	Annually	Autumns 1997 to 2000 and 2004
Broye-les-Pesmes (Ognon)	260	Annually	Autumns 1997, 1997, 2003 and 2004
Saunières (Doubs)	170	Annually	Summers 1997, 1998, 2004 and autumn 2003

($25 \times 18\,cm^2$); the total surface area sampled was $1\,m^2$. These samples were kept separately and fixed on site in 12% neutralized formaldehyde and sieved at 315 μm in the laboratory, where the molluscs were separated from the sediment and identified. Only live specimens were used.

Statistical analysis

Temporal community changes were assessed using species richness and density of gastropods and bivalves. In addition, a correspondence analysis (Lebart *et al.*, 1995) was performed on mollusc density data ($\ln(x+1)$ transformed to normalize their distributions) in order to evaluate changes in community structure.

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

A Mann–Whitney test was used to test significant differences of factorial site scores, species richness and density of gastropods and bivalves between the periods of September 1996 and July 2003 (before the heatwave) and August 2003 and December 2004 (after the heatwave). These statistical analyses were extracted from the STATISTICA package library.

Results

Temperature and discharge data

The mean temperature had increased by about 1.2 °C from 1977 to 2002 ($P<0.05$) and by 1.5 °C from 1996 to 2004 ($P<0.01$) (Fig. 2a). From 1996 to 2002 the maximum water temperatures generally occurring in August ranged from 24.3 °C in 1996 to 26.4 °C in 2002 and the number of days during which temperatures were higher than 25 °C ranged from 0 (1996, 1998, 1999) to 17 (2001). In 2003, the temperature reached 29.5 °C and exceeded 25 °C for 75 days.

The Saône has a pluvial-oceanic-type hydrological regime (Pardé, 1925) with high flows in winter and spring and low flows in summer. From 1977 to 2004 we observed an alternation of wet and dry years, but without any obvious trend (Fig. 2b). The year 2003 was characterized by a considerable water shortage with a mean annual flow of only $261\,m^3\,s^{-1}$. However, mean flows lower than those of 2003 had been recorded in 1972 and 1973 (245.6 and $245.7\,m^3\,s^{-1}$, respectively).

Mollusc data

From September 1996 to December 2004, 123 241 individuals were collected 53.2% of which were bivalves.

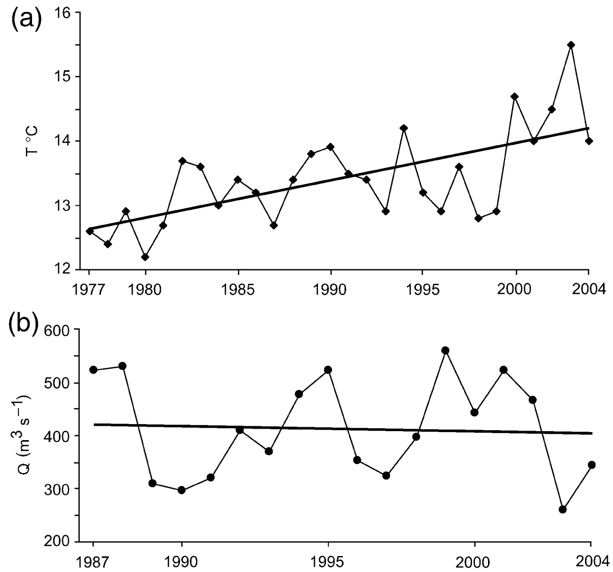

Fig. 2 (a) Mean annual daily water temperature at Couzon (EDF data) and (b) mean annual daily discharge at Macon from 1977 to 2004. Trends are shown ($Y(t) = at + b$).

These molluscs belonged to 24 species (14 gastropods + 10 bivalves) (Table 2). Three of them, namely *Valvata piscinalis*, *Pisidium subtruncatum* and *Corbicula fluminea* represented nearly 60% of total density (28.4%, 16.4% and 15.1%, respectively). Regarding the other molluscs, only eight species account for more than 1% of the total density: *Potamopyrgus antipodarum*, *Gyraulus albus* and *Bithynia tentaculata* in the gastropods (8.3%, 2.2% and 2.1%, respectively), and *Musculium lacustre*, *Pisidium nitidum*, *P. casertanum*, *P. amnicum* and *P. moitessierianum* in the bivalves Sphaeriidae (5.5%, 4.2%, 3.3%, 3.2% and 2.2%, respectively).

Temporal changes in mollusc community structure

The two first axis of the correspondence analysis (F1 and F2) accounted for 43.8% of total mollusc data inertia (Fig. 3a). Each year is situated at the barycentre of the factorial scores of its monthly samples. The years 1997–2004 succeed each other from left to right along axis 1. The tests performed on the monthly factorial scores on F1 reveal a significant positive trend from September 1996 to 2004 but also from September 1996 to July 2003 (P-values <0.01) (Fig. 3b). Nonetheless, during this latter period the species richness and total density of gastropod and bivalve populations did not show any trend. From September 1996 to July 2003, species such as *M. lacustre, B. tentaculata, V. cristata, V. piscinalis*, *H. complanata* and *C. fluminea* tended to increase (Fig. 3b). All of them except *C. fluminea* had reached their maximum densities during the summers of 2002 and 2003.

Table 2 Mean densities (m^{-2}) (± SE) of mollusc species before and after the 2003 heatwave

	Mean density (± SE)	
	September 1996–July 2003 period	August 2003–2004 period
Gastropods		
Valvata piscinalis (Müller, 1774)	430.9 ± 74.83	124.4 ± 43.58
Valvata cristata (Müller, 1774)	10.4 ± 2.2	0.9 ± 0.64
Potamopyrgus antipodarum (Gray, 1843)	155.7 ± 23.02	1.1 ± 0.37
Bithynia tentaculata (Linnaeus, 1758)	32.4 ± 6.49	7.9 ± 2.47
Lithoglyphus naticoides (Pfeiffer, 1828)	26.5 ± 6.86	0.5 ± 0.3
Theodoxus fluviatilis (Linnaeus, 1758)	1.8 ± 0.54	0
Physella acuta (Draparnaud, 1805)	24.5 ± 4.83	3.2 ± 1.1
Radix ovata (Draparnaud, 1805)	4.4 ± 2.4	0
Radix auricularia (Linnaeus, 1758)	1.8 ± 0.4	0.4 ± 0.19
Gyraulus albus (Müller, 1774)	35.8 ± 7.49	0.4 ± 0.21
Menetus dilatatus (Gould, 1841)	0.6 ± 0.14	0.9 ± 0.55
Hippeutis complanata (Linnaeus, 1758)	6.8 ± 1.23	0.6 ± 0.24
Ferrissia clessiniana (Mirolli, 1960)	13.8 ± 3.22	9.4 ± 3.56
Acroloxus lacustris (Linnaeus, 1758)	1.2 ± 0.33	0
Bivalves		
Dreissena polymorpha (Pallas, 1771)	2.9 ± 0.4	9.2 ± 2.37
Musculium lacustre (Müller, 1774)	81.9 ± 9.35	50.5 ± 13.92
Pisidium amnicum (Müller, 1774)	52.2 ± 6.9	1.8 ± 0.89
Pisidium casertanum (Poli, 1791)	54.3 ± 5.3	0.1 ± 0.08
Pisidium henslowanum (Sheppard, 1823)	18.5 ± 2.07	0.9 ± 0.3
Pisidium moitessierianum (Paladilhe, 1866)	36.3 ± 3.5	0.1 ± 0.06
Pisidium nitidum Jenyns, 1832	69.6 ± 8.08	0.2 ± 0.14
Pisidium subtruncatum Malm, 1855	258.7 ± 31.95	2.1 ± 0.58
Pisidium supinum Schmidt, 1851	23.7 ± 3.78	16.5 ± 3.45
Corbicula fluminea (Müller, 1774)	219.6 ± 13.83	83.6 ± 13.76

From July to August 2003, i.e. during the heatwave, an abrupt change was observed (dotted arrow): the malacocenoses, which up to then were close to those of 2001 and 2002, became closer to those of 2004. This change occurred with a fall in mollusc density and species richness (Fig. 4) and an increase in the relative density of *P. supinum*, *F. clessiniana*, *D. polymorpha* and *M. dilatatus*. After August 2003, the mean density of most of the other species fell considerably; some of them, including six of the seven *Pisidium* were represented by only a few individuals and showed no sign of recovery in 2004. These changes were confirmed by Mann–Whitney tests. Mean monthly factorial scores on F1, mean mollusc density and mean species richness were significantly different before vs. after the heatwave (P values <0.01).

Heatwave effects on mollusc communities in the middle part of the Saône catchment area

A fall in gastropod density was observed from 1999–2000 to 2004 in the by-passed sections de Port/Saône (2449 vs. 853 ind m^{-2}), Gray (368 vs. 165 ind m^{-2}) and Pontailler (520 vs. 98 ind m^{-2}) (Fig. 5). Among these sites, that of Gray had the sharpest fall in the number of species in comparison with the mean of previous years (6 vs. 10 sp.). A marked fall in density was also seen at Allériot from 1999–2000 to 2004, although variations of density can be naturally high at this site located immediately downstream of the confluence with the Doubs. Regarding the two tributaries, gastropod densities were very low in October 2003 though in 2004, they were comparable with those observed in July 1997 (Doubs) and September 1995 (Ognon).

Regarding the bivalves, low densities were observed both in October 1998 and after summer 2003. The former events correspond to the effect of an end-of-summer flood that had a greater impact on the density of these molluscs than on that of the gastropods. In the latter case (which corresponds to the heatwave), Sphaeriidae (*Pisidium* and *Sphaerium*) were more sensitive to high temperatures than other species such as in particular *C. fluminea*. They were only represented by a few individuals in the Saône and Ognon in 2004. On the contrary,

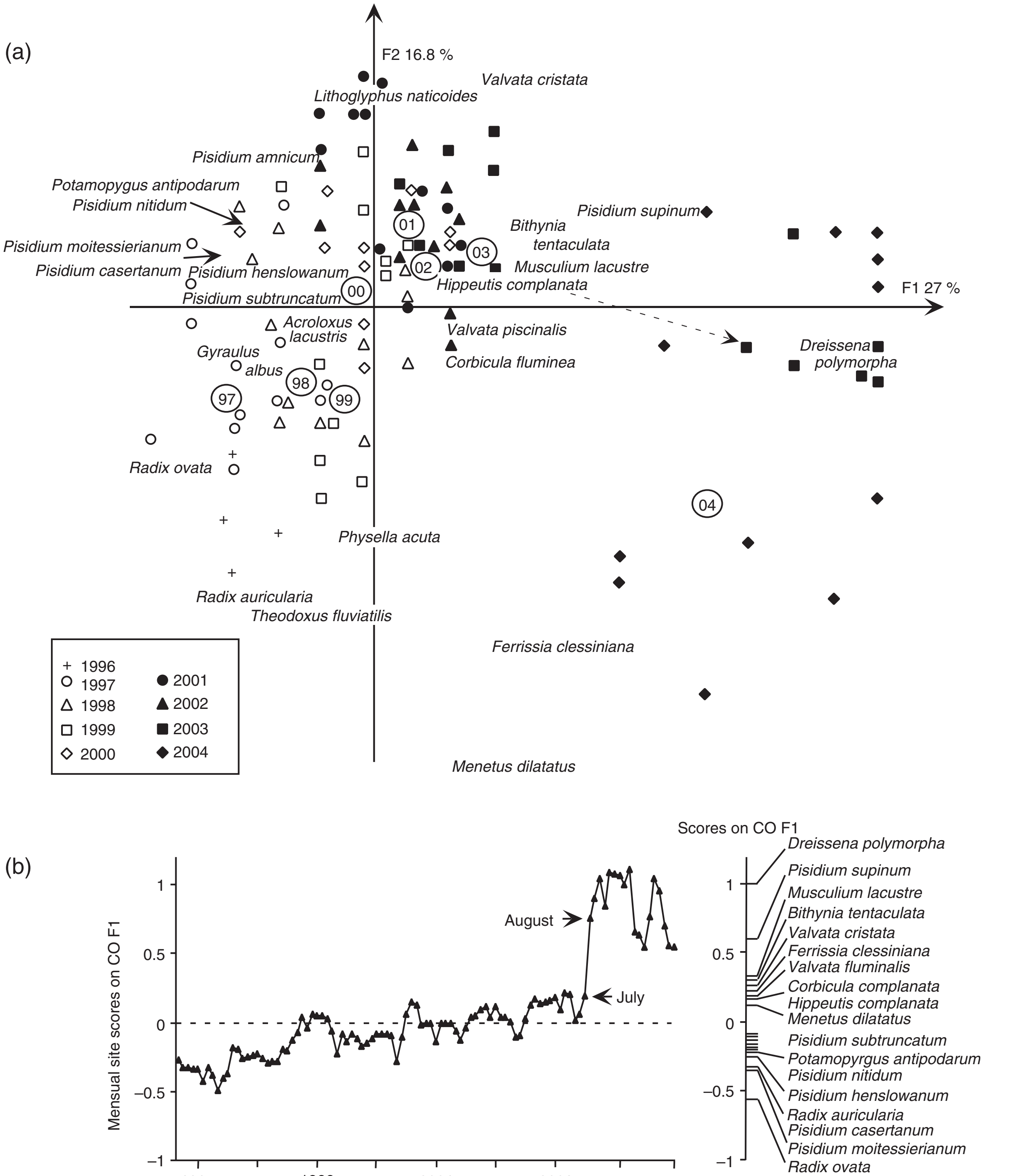

Fig. 3 (a) Results of the correspondence analysis of 24 mollusc species from the Saône river upstream of Lyon collected monthly from September 1996 to December 2004. Barycentres of the factorial scores of monthly samples of the different years are shown. Sudden change in the community structure between July and August 2003 is indicated by a dotted arrow. (b) Time series of site scores on the first axis of the correspondence analysis of mollusc data and contribution of 18 species (six molluscs with negative scores ranged from 0.08 to 0.2 are not indicated).

in the lower Doubs (whose waters are swifter than those of the Saône with a slope from 0.5 to 0.3 vs. 0.08 m km^{-1} for the latter), small populations remained. However, in the Ognon and the middle reach of the Saône, as with the Saône upstream of Lyon, no significant increase in the numbers of Sphaeriidae was observed in 2004.

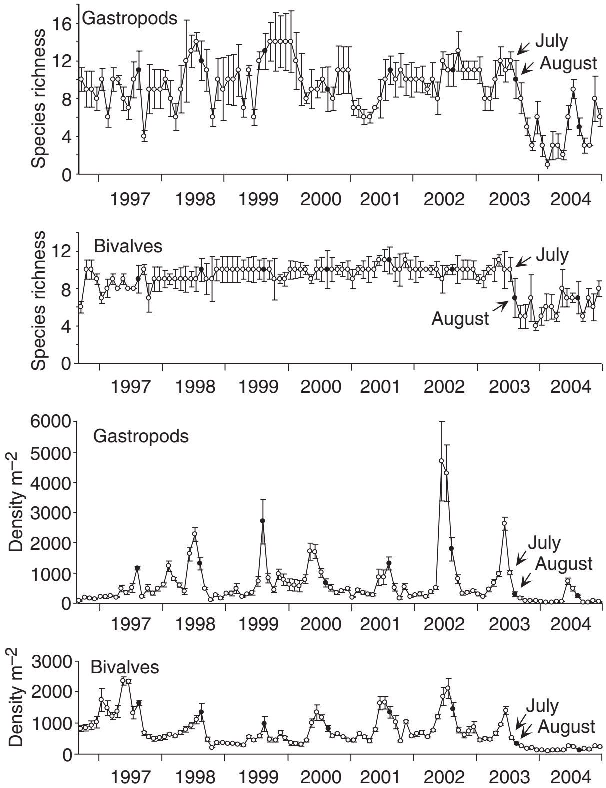

Fig. 4 Annual variations of species richness and density of mollusc communities in the Saône river upstream of Lyon. Vertical bars are standard deviation. Arrows indicate the time between July and August 2003 during which the community structure has changed. Species richness and density of molluscs in August is indicated by black circles.

Discussion

We observed that the heatwave of summer 2003 had caused a considerable and rapid change in the community's structure, as well as a drastic decrease of densities and species richness.

Causes of temporal changes in community structure from September 1996 to July 2003

Hydrological time series did not present any trends. In addition, at the interannual scale, the temporal succession of malacocenoses did not seem related to variations of annual mean flows. Community structures of years 1997 and 1999 are, for example, closed despite contrasted annual mean flows (325 and 560 $m^3 s^{-1}$ for 1997 and 1999, respectively). As a consequence, hydrological constraints could not explain observed changes.

Regarding water quality, interannual variations in physicochemical properties were weak during the whole study period (Mouthon, 2001 and data available at http://rdb.eaurmc.fr). In addition, the molluscs inhabiting the lower reaches of large rivers are generally euryoecious. The role of these variables in population structures is, therefore, probably limited and no study has highlighted major effects of such variations on the malacocenoses of large rivers.

From 1996 to 2003, the mean temperature of the Saône increased by 1.6 °C. The correspondence analysis separated the populations of the period from September 1996 to 1999 whose mean annual temperatures were less than or close to 13.5 °C, from those of the period 2000–2002 during which these temperatures were equal to or higher than 14 °C. Between these periods, i.e. between 1999 and 2000, the mean temperature increased by 1.8 °C. The influence of global warming on macroinvertebrates and fish communities was highlighted by Daufresne *et al*. (2004) at Bugey, on the Upper Rhône, less than 35 km from Lyon, where the mean water temperature increased by about 1.5 °C from 1979 to 1999. In addition, the longitudinal succession of molluscs species in rivers and their distribution in lake are known to be related to water temperature (Mouthon, 1990).

These observations suggest that temperature is the main cause of the temporal variation in population structure observed from September 1996 to July 2003. Unfortunately, the mollusc-sampling period preceding the heatwave (6 years) was too short to permit making correlations between the trends observed on the basis of biological and environmental time series.

What are the possibilities of recovery for mollusc communities after the 2003 heatwave?

Drift and reproduction are the two main patterns by which species reconstitute their populations. Processes of recolonization in rivers are well documented in insects (Mackay, 1992). The passive hydrological transport of pediveligers and juveniles suspended in the water column plays a major role in the dispersion of this bivalve in rivers (Williams & McMahon, 1986; McMahon, 2000). Adults can also be transported downstream by the current by the secretion of a long mucus dragline allowing them to float between two water levels (Prezant & Chalermwat, 1984) or over the surface of the substratum during floods (Eng, 1979; Boltovskoy *et al*., 1997). In *D. polymorpha*, free-swimming planktonic larvae also constitute an efficient means of dispersion. In the rivers Saône and Rhône, the continuity of *Corbicula* populations is largely ensured by individuals recruited from upstream by drift (Mouthon, 2001, 2003). In *P. subtruncatum* the contribution of adults by successive winter floods 1996–1997 is at the origin of the exceptionally high-density peak of 1997 (Mouthon, 2005). Drift also plays an essential role in the recovery process of

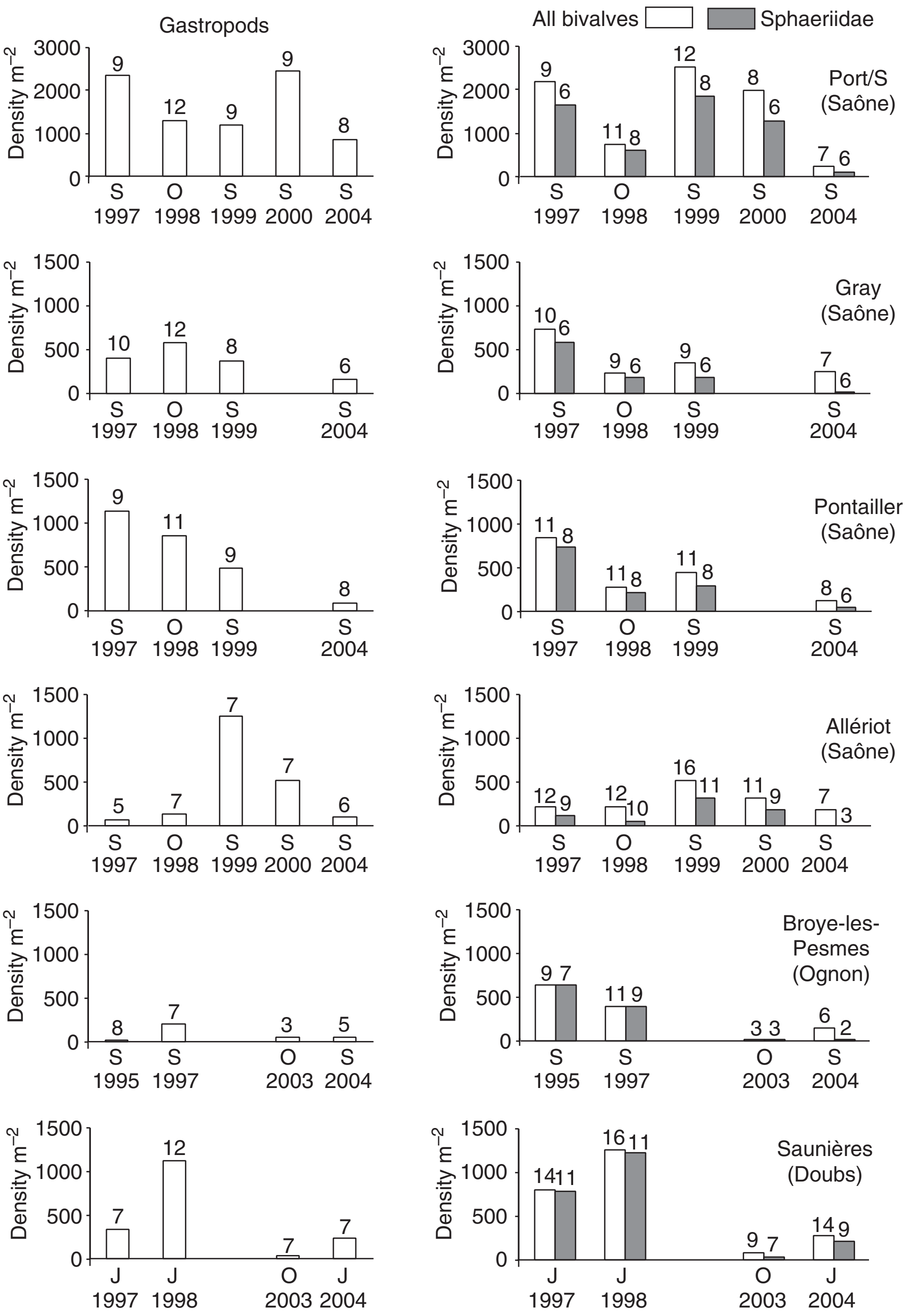

Fig. 5 Annual variations of density (histogram bars) and species richness (number above histogram bars) of mollusc communities in the Saône river (four sites) and in its two main tributaries (The Ognon and Doubs rivers) (J, July; S, September; and O, October).

mollusc populations. However, the low density of molluscs observed in the Saône and the lower reaches of its main tributaries after the summer 2003 has not favoured the recovery of these populations, except those of *C. fluminea* locally abundant upstream of the sectors studied and at the confluences of small tributaries.

In order to reconstitute its population following a disturbance a species can modify its reproduction strategy (i.e.), increase its reproductive effort and produce more generations during the year. In a general way, the fertility rate of gastropods is higher than that of *Pisidium*. *V. piscinalis* and *B. tentaculata*, for example, lay about 150 eggs per year and per capita (Frömming, 1956; Heywood in Fretter & Graham, 1978). By contrast, in *Pisidium* that incubate young in the inner demibranchs the number of embryos is generally from one to 42 (Holopainen & Hanski, 1986). In the *P. subtruncatum* of the Saône a maximum of 65 embryos has been observed, but the annual mean litter size (number of embryos per parent) only varied from 7.4 to 9.9 from 1997 to 2000 (Mouthon, 2005). The reproductive potential of *Pisidium* is therefore relatively low when compared with that of gastropods (Russel-Hunter, 1978). However, that of bivalves such as *D. polymorpha* and *C. fluminalis*, which produce a large number of larvae, is very high.

The resilience of macroinvertebrate communities to a disturbance (i.e. the speed with which they return to the predisturbance state) depends on the latter's nature and intensity. However, except in the case of a lasting change in the habitat, this resilience is generally high, with a first recovery of density levels before species number (Niemi *et al*., 1990; Wallace, 1990; Lake, 2000). In the Saône upstream of Lyon, the resilience of molluscs to the heatwave was essentially limited in 2004 to a partial increase of their species richness and an increase of the density of *D. polymorpha* and *M. dilatatus* and the relative density of *V. piscinalis, C. fluminea, M. lacustre, P. supinum*, *F. clessiniana* and *B. tentaculata*. In addition, this observation also applies to the populations of the middle Saône valley and the lower reaches of its main tributaries, the Doubs and the Ognon. This major decrease of donor patches suggests that the recovery of mollusc metapopulations will need several years and that, globally, that of gastropods should be faster than that of *Pisidium*. Simulations predict that the frequency of summers as hot as that of 2003 will progressively increase to become the norm in the second half of the 21st century (Nakicenovic & Swart, 2000; Beniston & Diaz, 2004; EEA, 2004; Schär *et al*., 2004). In this hypothesis, it sounds likely that more than half the mollusc species inhabiting the potamic zone of the Saône, the Doubs, the Ognon and probably other major rivers, whose waters are directly exposed to climatic warming (Webb, 1996), are directly threatened with extinction.

To conclude, we have shown that extreme climatic events could have strong impacts on mollusc communities. In addition, the resilience of communities to such events seemed low, maybe because they are already affected by a gradual long-term increase of temperature. Consequently, the effect of climate change on biota could be more pronounced than previously thought.

Acknowledgements

We thank A. Poirel (EDF, Grenoble) for water temperature data and P. Breil (Cemagref, Lyon) for discharge data.

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