



Long-term changes in mollusc communities of the Ognon river (France) over a 30-year period

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With 7 figures and 2 tables

Abstract: The mollusc fauna of the Ognon river, one of the main tributaries of the Saône, surveyed for the first time in 1977, was re-sampled in 2007 to assess long-term changes. Overall, the total number of collected individuals increased by 33.6 % (55.2 % for gastropods and 23.7 % for bivalves) but total species richness remained stable during the period (40 vs. 39 species) although there was considerable species turnover: 8 disappearances offset by 7 appearances including that of the invasive *Corbicula fluminea* which accounted for 30.4 % of the total number of individuals in 2007. The use of trend test, similarity index and principal component analyses (PCA) revealed radical changes in mollusc communities between years particularly in the upstream-downstream gradients of species richness, total number of molluscs, and gastropods, bivalves, pulmonates, sphaeriid and unionid mussel densities. The upstream colonisation of several species was observed in the upper part of the river but in the lower part divergences in terms of species richness, density and structure increased in a downstream direction. The chronology of the changes observed strongly suggest that competition for food following the proliferation of *C. fluminea* and the 2003 heatwave may be, responsible for the dramatic decline of native bivalves (Unionidae and Sphaeriidae, respectively). Given the magnitude of these changes, a return to a state prior to the disturbance of the malacological structure is hardly conceivable. However, the evolution towards a new relatively stable state is an alternative hypothesis.

Key words: mollusc decline, heatwave, *Corbicula*, competition, global warming.

Introduction

Long term data sets are continuous (samples collected every month, every year) or discontinuous (data missing for most or all years between the first and the last year sampled) and are of great interest for evaluating changes in communities. However it is rare to have comparable data for periods exceeding 20 years (Jackson & Füreder 2006).

Habitat destruction (channelization), hydrologic regime alteration (hydropower dams), point and non point pollution, global warming and biological invasions have become the most significant causes of shifts in the composition and structure of communities over

recent decades (Riccardi 2006, Daufresne & Boët 2007). Climatic change (a ramp disturbance, i.e. a perturbation steadily increasing over time, Lake 2000) as well as the extreme climatic events that accompany it such as heatwaves (a pulse disturbance i.e. a short-term perturbation, Bender 1986) have a significant impact on the distribution, density, phenology, morphology and genetic frequencies of organisms (Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003). One of the most remarkable effects of climatic warming is a shift in areas of distribution to higher latitudes and altitudes. This type of phenomenon has already been identified locally in flowing water environments from studies of existing temporal series (e.g. Daufresne et

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al. 2004, Daufresne & Boët 2007). However, studies of the spatial variability of the response of communities to climatic warming along upstream-downstream gradients remain rare and are mainly based on modelling areas of species distribution as a function of different climatic scenarios (e.g. Buisson & Grenouillet 2009).

Biological invasions have reached unprecedented levels in recent years, as can be seen in the number of non native aquatic species identified in both North America and Europe (Ricciardi & MacIsaac 2000, Ricciardi 2001, Bij de Vaate et al. 2002, Devin et al. 2005). Regarding *C. fluminea*, recorded in France and Portugal at the end of the 1970s (Mouthon 1981), and which is now present in the main watersheds of European countries, its impact on benthos remains relatively poorly known (Hakenkamp et al. 2001, Werner & Rothhaupt 2007) and its negative effects on native bivalves controversial (Strayer 1999, McMahon 2000, Vaughn & Spooner 2006, Sousa et al. 2007).

The survey of mollusc communities of the Ognon along an upstream-downstream gradient in 1977 revealed the presence of abundant populations rich in species particularly regarding unionid and sphaeriid bivalves (Mouthon 1980). However, during the years 1999–2000, this lowland river was massively colonised by the alien bivalve *C. fluminea* (Mouthon 2000). A later study of the dynamics of mollusc communities in the Saône and in the lower reaches of its two main tributaries, the Doubs and the Ognon, showed a dramatic decline of these animals after the 2003 heat-wave (Mouthon & Daufresne 2006). We hypothesize that these two events have radically modified the composition and structure of mollusc communities along the entire length of the Ognon. This river was then re-surveyed in 2007 following 30 years of warming in order to examine the impact of climatic change and biological invasion on the spatial distribution of mollusc communities.

Material and methods

Study area

The source of the Ognon is located in the Vosges massif (altitude 903 m) and this river flows into the Saône 215 km downstream (altitude 190 m) (Fig 1). Its very elongated watershed has a surface area of 2,285 km². Its mean slope is 5.4‰ (46.9‰ from the source to Servance, 4.8‰ from Servance to Montbozon, 0.45‰, from Montbozon to its confluence). It has a large number of relatively small tributaries in the impermeable crystalline ground of the Vosges and the sub-Vosges region though there are fewer tributaries in the limestone part of the

middle and lower valley. At this point its bed has been modified by the construction of run-of-the-river dams and extraction of alluvial deposits.

Environmental variables

Discharge (Q) rates at Pesmes (st. 14), situated 14 km upstream from the confluence with the Saône and downstream of most of its tributaries, were extracted from the Hydro data base (data available at <http://www.mde.tm.fr>).

Water temperature was recorded hourly at Avilley (downstream from st. 8, Fig. 1) from March to August 2002 and in 2004. Similar measurements were carried out at Brussey (downstream from St. 12) from February to August 2002 and from January to September 2003. Finally, temperatures were recorded hourly at Thervay (upstream from st. 14) from February to December 2001, February to September 2002, December 2003 to December 2004, March to December 2005, in 2006, and in January, February and from August to December 2007.

Monthly mean water temperatures correlate strongly with the monthly mean air temperatures recorded at Besançon (Fig. 1) by Météo France (Pearson correlation coefficient = 0.98, 0.96 and 0.98 for Avilley, Brussey and Thervay, respectively). Therefore we used linear regression models to predict water temperature from air temperature data during the period 1975–2009.

Water and sediment quality of the Ognon river was examined at three sites using data from 1997 to 2007, located along the river: Servance (st. 3, bimonthly analyses), Les Aynants and Pesmes (st. 6 and 14, monthly analyses). Chlorophyll-*a* data (st. 4 and 14) were also examined. Sampling was performed by the Agence de l'Eau Méditerranée Corse (data available at <http://www.sierm.eaurmc.fr>).

Mollusc sampling

The 15 sites sampled in 1977 were re-sampled in September 2007 using the same technique (Mouthon 1980); however Emagny (st. 12), which has become difficult to reach, was replaced by Vregille located about 1 km upstream. Molluscs inhabiting fine sediments and the macrophytes growing on the latter were collected by rectangular hand-net (25 × 18 cm, 500 µm mesh size) dragged along the bottom. The samples, 0.25 m² each, were taken at several places at each site. The total surface areas sampled were from 0.5 to 1 m² (upper reach sites) and from 1 to 3 m² (lower reach sites), depending on the surface area of mollusc habitats. In addition lithophilic species (*Ancylus fluviatilis*, *T. fluviatilis*...) were collected using a Surber net sampler (S = 1/10 m², 500 µm mesh size). Samples were fixed on-site in 12 % neutralised formaldehyde and sieved at 500 µm in the laboratory, where the molluscs were separated, identified and counted. The densities of molluscs collected at each site were expressed per m².

Statistical analysis

To detect trends in time series (Q, T) and in upstream-downstream gradients of molluscs, we used a modified Mann-Kendall trend test developed by Hamed & Rao (1998). This nonparametric test (based on ranks) looks for trends once autocorrelation effects are removed. Tests were performed using R (R Development Core Team 2006). In addition, we used the Jaccard Index based on presence-absence data (Koleff et al. 2003), a principal

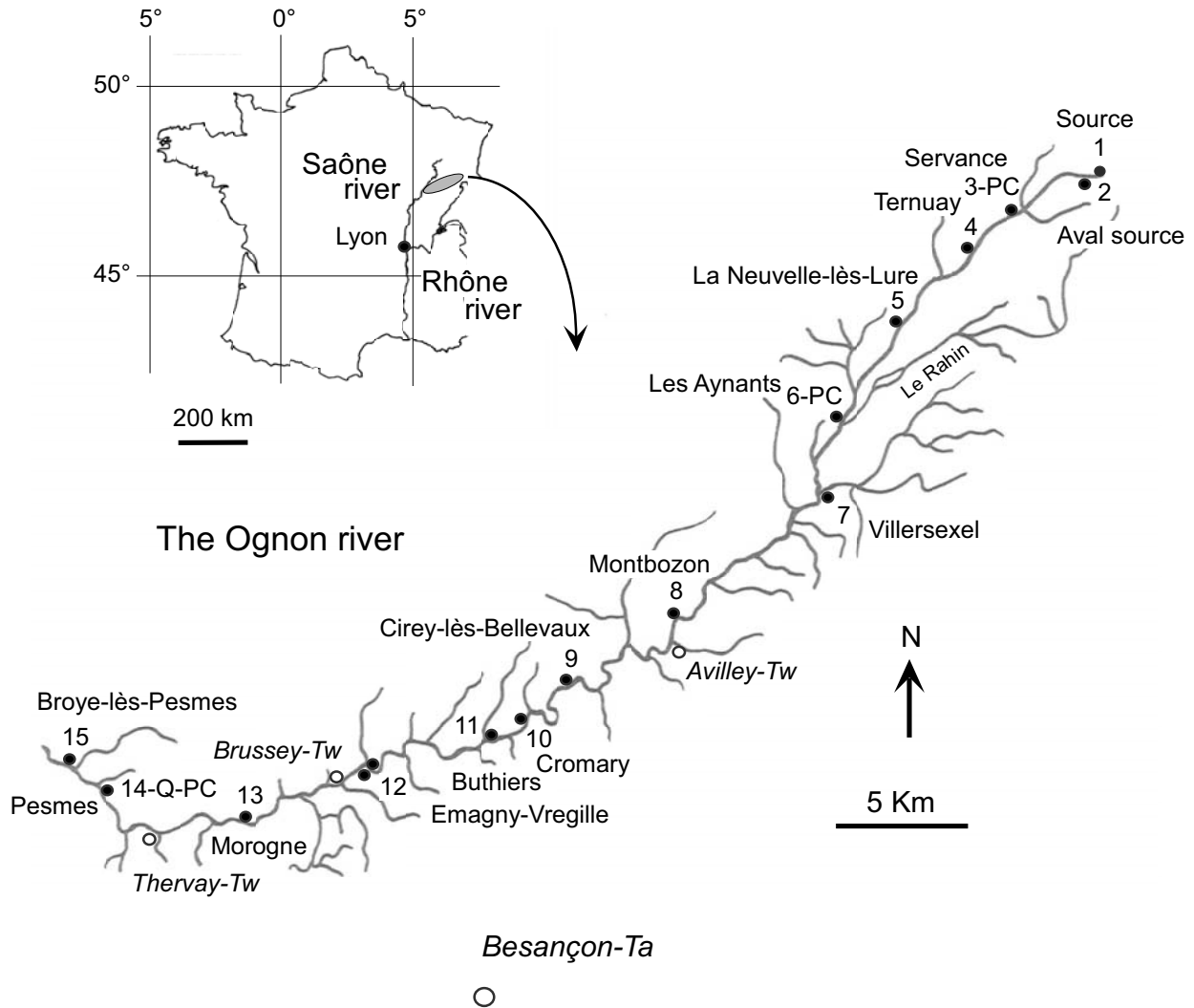


Fig. 1. Study area and location of the mollusc sampling sites (solid circles), Q= discharge recording site, PC = physico-chemical sampling sites, Ta, Tw = air, water temperature sampling sites (in italics, open circles).

component analysis (PCA) performed on mollusc density data ($\ln(x+1)$ transformed to normalize their distributions) and an hierarchical ascending classification (HAC) to define site groups (inertia ellipses) in order to evaluate changes in community composition and structure. The Tukey HSD post-hoc test was used to compare mean annual concentrations of chlorophyll-*a* and the Wilcoxon non parametric test when testing differences of species richness and mollusc density between years. These statistical analyses were extracted from the Statistica package library (version 9.0).

Results

Environmental variables

The Ognon has a pluvial-oceanic type hydrological regime with high flows in winter (from Decem-

ber to March, maximum in January) and low flows in summer (minimum in August). Regarding the period 1964–2008 (45 years), the monthly mean flows at Pesmes ranged from $57 \text{ m}^3 \text{ s}^{-1}$ in January to $9.6 \text{ m}^3 \text{ s}^{-1}$ in August (annual mean $33.9 \text{ m}^3 \text{ s}^{-1}$). During this time an alternation of dry and wet years occurred, but without any obvious trend (Fig. 2). The year 2003 was characterised by a considerable water shortage with an mean annual flow of only $20.3 \text{ m}^3 \text{ s}^{-1}$. However, mean flows lower than those of 2003 had been recorded in 1964, 1971, 1972 and 1976 (16.5 , 14.1 , 18.4 and $19.4 \text{ m}^3 \text{ s}^{-1}$, respectively). Contrary to discharge conditions, the annual mean temperature of the Ognon at Avilley, Brussey and Thervay showed a significant positive trend during the 1975–2009 period due to atmospheric

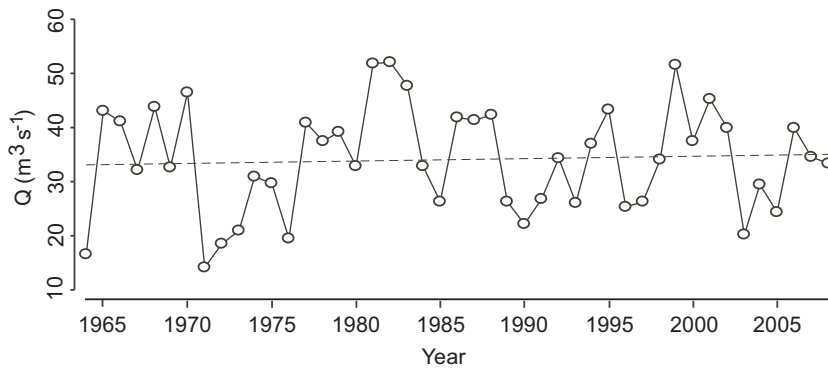


Fig. 2. Mean annual daily discharge at Pesmes (st. 14) from 1964 to 2008. Linear trend is shown (dotted line).

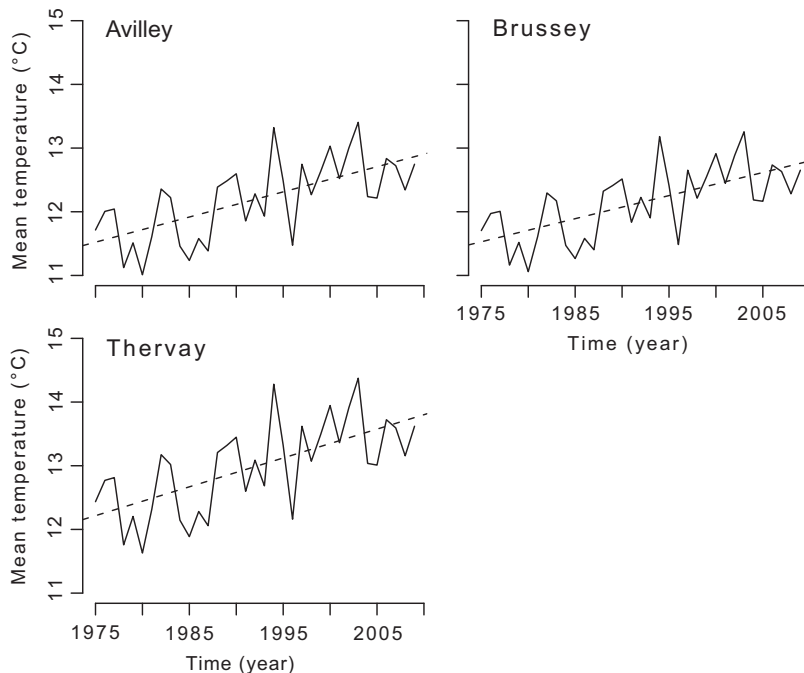


Fig. 3. Mean annual temperature at Avilley, Brussey, Therway from 1975 to 2009. Linear trend is shown (dotted line).

warming (Mann-Kendall trend tests, p values < 0.001) and had increased by about 1.3, 1.1 and 1.6 °C, respectively (Fig. 3). 1994 was almost as warm as 2003 due to a very mild winter.

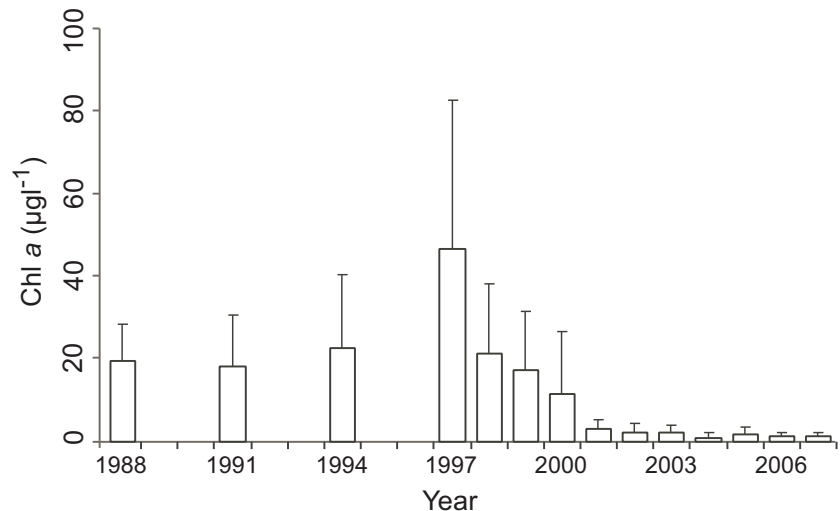
The waters of the upper reach of the Ognon are sometimes acidic, slightly mineralised and poor in calcium. However, when the river leaves the crystalline soils of the Vosges massif and enters the limestone, its waters quickly become richer in minerals (Table 1). According to the French water quality standard (SEQ-Eau, available on <http://sierm.eaurmc.fr/eaux-superficielles/fichiers-telechargeables/grilles-seq-eau-v2.pdf>) the waters of the Ognon are of good quality regarding organic and oxidizable materials, and phosphated and nitrated materials except for excess nitrates in its lower reach in 1999 and from 2003, and of average

quality regarding pesticides (st. 14). Overall, when taking into account the main physicochemical parameters of the water, these three sites are in good ecological state. Sediment quality is good for organic micropollutants and pesticides, average for PAH (polycyclic aromatic hydrocarbons), poor for arsenic in 2001 and 2003 (st. 3), 1999, 2003 and 2004 (st. 6) and average for the other heavy metals (st. 3, 6 and 14).

From 1988 to 2000 at Pesmes, the annual mean concentrations of Chl-*a* ranged from 11.5 to 46.6 $\mu\text{g l}^{-1}$, whereas from 2001 to 2007 they remained $< 3.0 \mu\text{g l}^{-1}$ and were significantly different from those of the period 1988–2000 (Tukey HSD test, after Bonferroni correction $p < 0.001$ including and excluding 1997) (Fig. 4).

Table 1. Mean \pm SD values of physico-chemical variables at three sampling sites over the 1997–2007 period. Units are % for saturation, $\mu\text{S cm}^{-1}$ for conductivity and mg l^{-1} for the other variables. DOC: dissolved organic carbon.

	Servance (st. 3) mean \pm SD	Les Aynans (st. 6) mean \pm SD	Pesmes (st. 14) mean \pm SD
pH	7.1 \pm 0.39	7.7 \pm 0.40	8.0 \pm 0.29
DO	10.5 \pm 1.2	10.7 \pm 1.47	10.1 \pm 1.90
Saturation	95.8 \pm 7.75	98.0 \pm 12.52	97.1 \pm 11.74
Conductivity	49.1 \pm 11.42	161.9 \pm 50.00	345.7 \pm 46.28
BOD ₅	1.1 \pm 0.42	1.62 \pm 0.85	1.51 \pm 1.18
DOC	1.9 \pm 0.67	2.0 \pm 0.84	2.7 \pm 1.08
NH ₄ ⁺	0.03 \pm 0.01	0.07 \pm 0.10	0.06 \pm 0.04
NO ₂ ⁻	0.01 \pm 0.01	0.04 \pm 0.03	0.04 \pm 0.02
NO ₃ ⁺	2.5 \pm 1.2	4.8 \pm 1.40	8.3 \pm 4.03
PO ₄ ⁻⁻⁻	0.04 \pm 0.05	0.11 \pm 0.07	0.12 \pm 0.06
P total	0.01 \pm 0.01	0.05 \pm 0.03	0.08 \pm 0.05
Cl ⁻	4.4 \pm 1.82	6.2 \pm 2.41	10.7 \pm 3.74
Ca ⁺⁺	5.1 \pm 1.76	19.0 \pm 6.38	55.2 \pm 9.84
Mg ⁺⁺	0.7 \pm 0.24	4.5 \pm 1.65	5.8 \pm 4.07
Na ⁺	2.9 \pm 0.69	3.9 \pm 1.31	5.7 \pm 2.31
K ⁺	0.4 \pm 0.19	1.4 \pm 0.62	2.2 \pm 0.80
SO ₄ ⁻	3.7 \pm 1.53	14.4 \pm 4.45	19.4 \pm 6.87
HCO ₃ ⁻	13.8 \pm 5.64	60.0 \pm 18.92	159.3 \pm 24.04

**Fig. 4.** Variations in mean annual chlorophyll-*a* concentrations ($\mu\text{g l}^{-1}$) from 1988 to 2007 at Pesmes (st. 14). Vertical bars are standard deviations.

Mollusc fauna

A total number of 20,533 molluscs from 47 species were collected in 1977 and 2007, 8790 and 11,743, respectively (Table 2). The total number increased from 33.6 % (55.2 % for gastropods, 23.7 % for bivalves) between years. Species with a density > 10 % made up 41 % of the population in 1977 and 58.2 % in 2007 (30.4 % for *C. fluminea*). The apparent stability of species richness (40 vs. 39 sp.) hides considerable species turnover: the disappearance of 3 gastropods and 5 bivalves vs. the appearance of 5 gastropods and 2 bi-

valves. The frequency of occurrence of several gastropods (*Ancylus fluviatilis*, *Lymnaea stagnalis*, *Gyraulus albus*) and most of the bivalves decreased. However, that of *Ferrissia clessiniana* and *Physella acuta* increased considerably.

The upstream-downstream gradient of species richness was significantly more apparent in 1977 than in 2007 (Mann Kendall test $p < 0.0001$ vs. $p < 0.05$) and the Kendall tau was lower during this year (0.43 vs. 0.88); species richness fell at Villersexel (st. 7), then from Cromary (st. 10) (Fig. 5a). Furthermore, the Jaccard Index used to measure similarity between

Table 2. Frequency of occurrence and total number of individuals of mollusc species collected in the Ognon river in 1977 and 2007. Species which appear + or disappear – between years are indicated.

	1977		2007	
	Freq. oc./15	Total number	Freq. oc./15	Total number
Gastropods				
<i>Bythinella</i> sp.	3	284	3	361
<i>Bithynia tentaculata</i> (L.)	8	424	6	30
+ <i>Potamopyrgus antipodarum</i> (Smith)	–	–	9	702
<i>Theodoxus fluviatilis</i> (L.)	8	207	7	1523
+ <i>Valvata cristata</i> (Müller)	–	–	2	13
<i>Valvata piscinalis</i> (Müller)	5	81	4	94
– <i>Viviparus viviparus</i> (L.)	6	76	–	–
– <i>Acroloxus lacustris</i> (L.)	7	98	–	–
<i>Ancylus fluviatilis</i> (Müller)	14	517	8	237
<i>Ferrissia clessiniana</i> (Jickeli)	4	44	8	279
<i>Radix auricularia</i> (L.)	7	145	8	140
<i>Radix balthica</i> (L.)	4	57	3	54
<i>Lymnaea stagnalis</i> (L.)	9	46	1	12
<i>Galba truncatula</i> (Müller)	3	28	5	7
<i>Physa fontinalis</i> (L.)	2	77	1	3
<i>Physella acuta</i> (Draparnaud)	3	78	8	355
– <i>Anisus vortex</i> (L.)	1	80	–	–
<i>Armiger crista</i> (L.)	5	175	2	57
+ <i>Bathyomphalus contortus</i> (L.)	–	–	1	12
<i>Gyraulus albus</i> (Müller)	10	302	5	48
+ <i>Gyraulus laevis</i> (Alder)	–	–	2	21
<i>Hippeutis complanata</i> (L.)	4	32	4	9
+ <i>Menetus dilatatus</i> (Gould)	–	–	7	332
<i>Planorbis carinatus</i> (Müller)	2	13	1	1
Bivalves				
+ <i>Corbicula fluminea</i> (Müller)	–	–	9	3566
+ <i>Dreissena polymorpha</i> (Pallas)	–	–	3	30
<i>Anodonta anatina</i> (L.)	7	60	1	1
– <i>Anodonta cygnaea</i> (L.)	1	3	–	–
<i>Psilunio littoralis</i> (Cuvier)	6	71	4	4
<i>Pseudanodonta elongata</i> Holandre	5	24	1	1
<i>Unio crassus</i> Philipsson	6	81	2	4
<i>Unio pictorum</i> (L.)	7	54	1	2
– <i>Unio tumidus</i> Philipsson	2	20	–	–
– <i>Musculium lacustre</i> (Müller)	5	37	–	–
<i>Sphaerium comeum</i> (L.)	7	174	1	2
– <i>Sphaerium rivicola</i> (Lamarck)	2	13	–	–
– <i>Pisidium amnicum</i> (Müller)	2	1	–	–
<i>Pisidium casertanum</i> (Poli)	11	297	8	133
<i>P. casertanum</i> f. <i>ponderosa</i>	1	80	2	10
<i>Pisidium henslowanum</i> (Sheppard)	10	686	7	61
<i>Pisidium hibemicum</i> Westerlund	4	19	2	354
<i>Pisidium milium</i> Held	2	102	3	338
<i>Pisidium moitessierianum</i> Paladhilhe	9	1059	9	142
<i>Pisidium nitidum</i> Jenyns	10	520	4	631
<i>P. nitidum</i> f. <i>crassa</i>	1	56	3	25
<i>Pisidium personatum</i> Malm	5	15	1	5
<i>Pisidium subtruncatum</i> Malm	11	1465	8	1741
+ <i>P. subtruncatum</i> f. <i>incrassata</i>	–	–	1	2
<i>Pisidium supinum</i> Schmidt	7	1075	6	234
<i>Pisidium tenuilineatum</i> Stelfox	7	114	4	167
Gastropod species richness/total number	19	2764	21	4290
Bivalve species richness/total number	21	6026	18	7453
Total species richness/total number	40	8790	39	11743

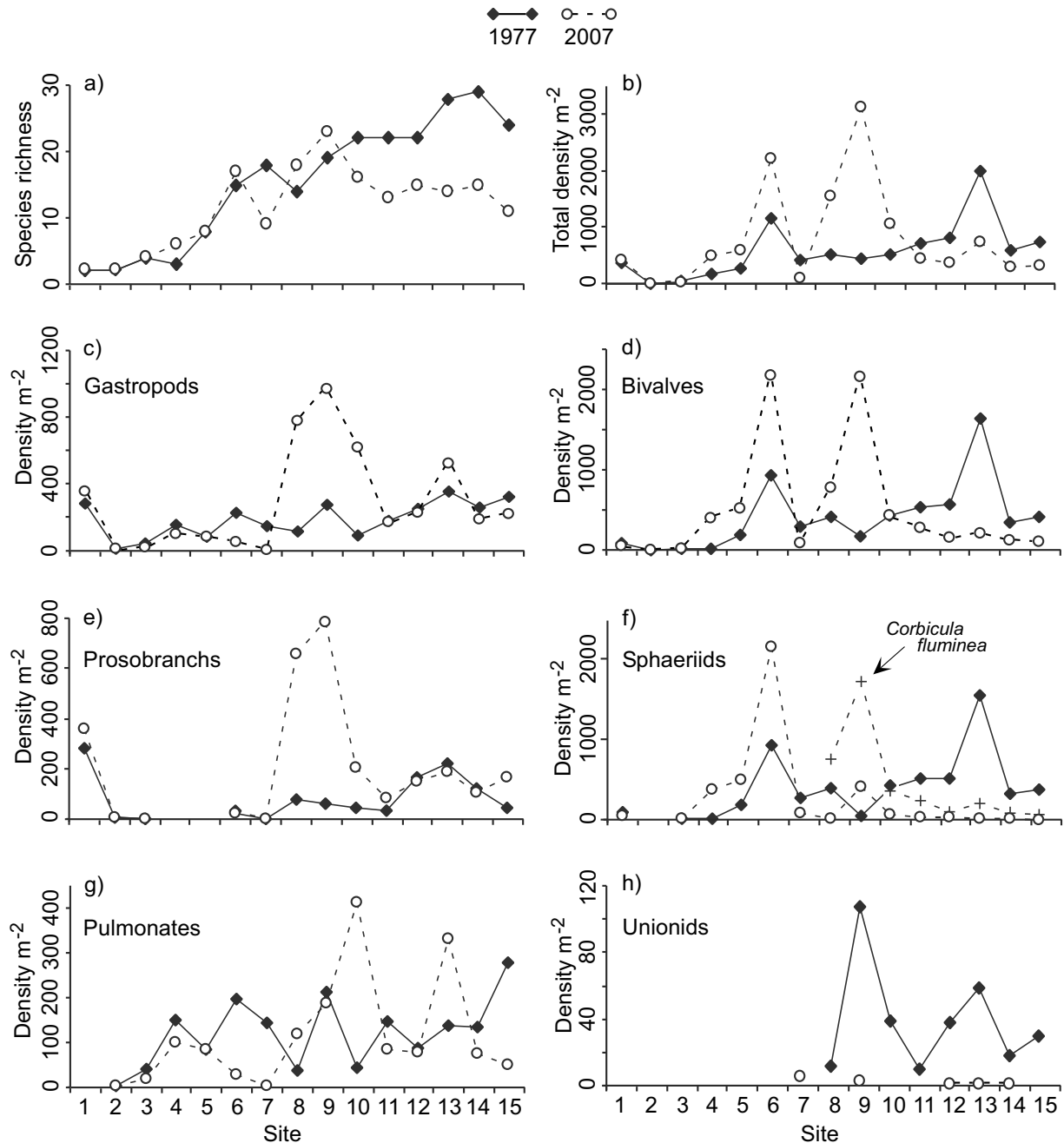


Fig. 5. Longitudinal variations of the species richness (a) and the density (m⁻²) of molluscs (b), gastropods (c), bivalves (d), prosobranchs (e), sphaeriids and *Corbicula fluminea* (f), pulmonates (g), and unionids (h) in the Ognon river between 1977 and 2007.

each pair of sites for 1997 and 2007 decreased significantly from upstream to downstream ($p < 0.001$). Overall, changes of community structures were more marked in downstream areas than in upstream ones. Concerning the total density of molluscs, gastropods and bivalves, the upstream-downstream gradients were only significant in 1977 ($p < 0.001$, $p < 0.05$ and $p < 0.01$, respectively) (Fig. 5b to d) and were more marked for the bivalves than for the gastropods; the

trend was significant for Sphaeriidae ($p < 0.01$), Unionidae ($p < 0.01$) and pulmonates ($p < 0.05$), but not for prosobranchs (Fig. 5e to h). In 2007 the gradients were disturbed by the decline of native mussels and peaks in the densities of *C. fluminea* and the gastropods (*Theodoxus fluviatilis*, *Physella acuta*, *Menetus dilatatus*, *Ferrissia clessiniana*) in the lower part of the river. In addition, there were no significant differences between the means of species richness and densities

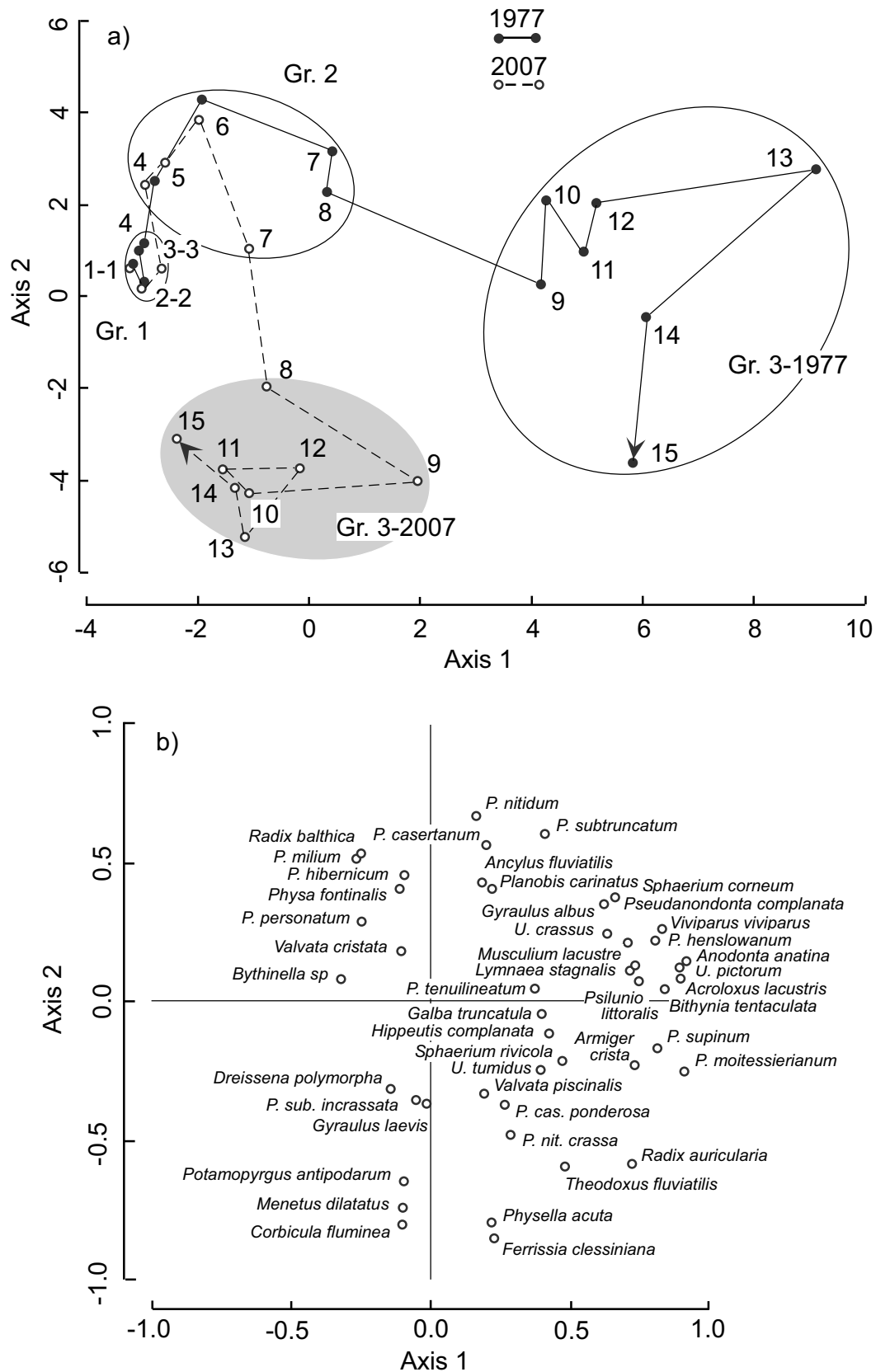


Fig. 6. Results of the principal component analysis (PCA) performed on mollusc data in the Ognon river: **a)** variations in the longitudinal structure between 1977 and 2007, **b)** species distribution in the plane F1F2. Site groups (ellipses) were defined by an ascendant hierarchical classification.

(molluscs, gastropods, bivalves, prosobranchs, pulmonates, Sphaeriidae and Unionidae) between years (Wilcoxon test $p > 0.05$).

Mollusc community analysis

Changes in the composition and structure of communities between 1977 and 2007 were studied using principal component analysis (PCA). The first two axes amounted to 43.4 % of total variance (26.43 and 16.96 % for axes 1 and 2, respectively).

In 1977, the malacological structure of the river was preferentially organised along axis 1 (Fig. 6a). Three groups of site were defined by an ascendant hierarchical classification (Ward criterion). The first (sites 1 to 4) included the area of the sources and the upper reach of the Ognon to which *Bythinella* sp. and *Pisidium casertanum* are directly associated (Fig. 6b). The second group (st. 5 to 8) represents the middle reach of the river characterised by *Radix balthica*, *Ancylus fluviatilis*, *Pisidium nitidum*, *P. subtruncatum*, *P. milium*. The confluence with outlets of ponds rich in nutrients explains the presence at Les Aynans (st. 6) of abundant populations of Sphaeriidae such as *Pisidium*

hibernicum, a more lacustrine species. The third group including the sites of the lower reaches of the river (st. 9 to 15) was inhabited by species located to the left of axis 2 and close to axis 1 such as the Unionidae, *Acroloxus lacustris*, *Viviparus viviparus*, *Bithynia tentaculata*, *Pisidium moitessierianum* and *P. supinum*.

In 2007 the malacological structure of the river was preferentially organised along axis 2. Sites 1 to 3 still belonged to group 1. On the other hand, this time Ternuay (st. 4), where three species (*P. subtruncatum*, *P. milium* and *R. balthica*) appeared, was linked to the stations of group 2 (Figs 6 & 7). For similar reasons Montbozon (st. 8) left group 2 and shifted towards the new group 3 (Gr. 3-2007), bringing together the stations of the lower reach of the Ognon whose malacological structure is much different from that of 1977: sphaeriid and unionid densities falling dramatically between years, whereas that of the prosobranchs increased substantially (Fig. 5). This latter group (st. 8 to 15) is associated with molluscs located below axis 1 and close to axis 2: *C. fluminea*, *M. dilatatus*, *Potamopyrgus antipodarum*, sampled only in 2007, *P. acuta* and *F. clessiniana* which had considerably increased their longitudinal distribution (Fig. 7) and *T. fluviatilis* whose total numbers had risen strongly (Table 2). It is interesting to note that the decrease in variability of the sites along axis F1 tends to show a homogenisation of the community's structure along the upstream-downstream gradient.

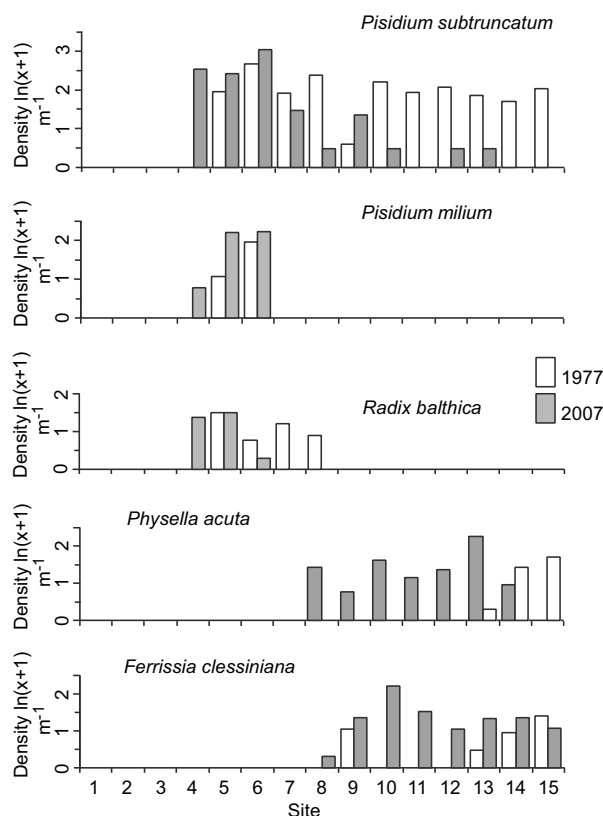


Fig. 7. Variations of the longitudinal distribution of five mollusc species in the Ognon river between 1977 and 2007.

Discussion

In 2007, the upstream-downstream gradient of the mollusc communities of the Ognon river was very different from that of 1977. The upstream colonisation of several species was observed in its upper reach but the changes were relatively slight. However, in its lower reach, divergences in species richness, density and structure were increasingly prominent. These divergences reflect species turnover, the proliferation of *C. fluminea*, the decline of bivalves (Sphaeriidae, Unionidae), and peaks in gastropod densities.

Causes of temporal changes in community structure and native filter-feeder decline

There were no obvious trends in the hydrological series between 1964 to 2008 and the water quality of the Ognon remained good between 1997 and 2007. It is therefore improbable that these two factors were responsible for the considerable changes in the structure of mollusc communities observed.

During the period 1999–2000 the invasive filter-feeder *C. fluminea* rapidly colonised the lower reaches of the Ognon (Mouthon 2000), while Chl-*a* concentrations fell sharply (Fig 3). According to Cohen et al. (1984), Leff et al. (1990), Beaver et al. (1991), dense populations of *Corbicula* can considerably reduce the production of phytoplankton. From this period onwards the numerous shells of native bivalves (*Anodonta*, *Psilunio*, *Unio*, *Sphaerium*) that were deposited every year on the gravel banks downstream of Morogne dam (st. 13) became rarer and were progressively replaced by those of *C. fluminea* (J. Mouthon, pers. obs.). The negative impact of *C. fluminea* on juvenile mussels was highlighted by Yeager et al. (2000) and a decline of native bivalves was observed following its introduction in several rivers in the United States (Gardner et al. 1976, Fuller & Richardson 1977, Clarke 1986, Clarke 1988, Sickel 1986). A sharp decline in densities of native mussels was also observed after the invasion by the filter-feeder *Dreissena polymorpha* of North American rivers and lakes (Strayer & Malcom 2007).

Laboratory experiments have shown that the degradation of sediment quality (increased concentrations of toxic NH₃-H and reduced dissolved O₂) that occurred following high mortality of *C. fluminea* could negatively affect unionid bivalves (Cherry et al. 2005, Cooper et al. 2005). However, high mortalities of *C. fluminea* in the Ognon have not occurred and following death soft parts undergoing decomposition are entrained in the flow and consumed by fish such as Siluridae or deposited on the river bank (J. Mouthon, pers. obs.).

Since dense populations of *C. fluminea* co-occur with unionid species in many lotic systems, interspecific competition is already controversial (Strayer 1999, McMahon 2000, Vaughn & Spooner 2006). However, in the Ognon river our observations suggest that competition for food, i.e. Unionidae and *C. fluminea* filter-feeding on phytoplankton, is the most probable cause for the decline in native bivalves. The hot summers of the beginning of the century and particularly that of 2003 have undoubtedly accelerated the decline of Unionidae, already affected by competition for food with *C. fluminea*.

A previous study has shown that the dramatic fall in densities of Sphaeriidae in the Saône and the lower reaches of the Doubs and the Ognon (st. 15) was a consequence of the 2003 heatwave (Mouthon & Daufresne 2006). Like the Saône, the Ognon is a plains river with low minimum flows (~9.7 m³s⁻¹). Therefore, its waters are particularly vulnerable to climatic warm-

ing (Webb 1996). In its lower reaches the mean annual temperature had increased by about 1.6 °C from 1975 to 2009 vs 1.5 °C in the Saône between 1996 and 2004 (Mouthon & Daufresne 2006). Thus it is reasonable to assume that the negative impact of the heatwave on sphaeriid populations was similar in the two rivers. Competition with *C. fluminea* for food is another possible explanation for the observed decline in sphaeriid densities. However, field experiments performed in Lake Constance have shown that high densities of *C. fluminea* had no effect on those of *Pisidium* (Sphaeriidae), *P. antipodarum* or *B. tentaculata*, a non exclusive filter feeder (Werner & Rothhaupt 2007) and so this seems unlikely. These observations strongly suggest that this extreme climatic event is also responsible for the decline of these bivalves along the entire lower reach from Cromary (st. 10).

Temporal changes in community structure and climate warming

Extension of species distribution is one the most frequently observed consequences of climate warming (Parmesan & Yohe 2003, Root et al. 2003, Daufresne et al. 2004). At the river scale, the upstream colonisation of three species (*P. subtruncatum*, *P. milium* and *R. balthica*) into the upper reaches of the Ognon and the downstream colonisation of two warm-water gastropods (*P. acuta* and *F. clessiniana*) into its lower reaches are probably a sign of this phenomenon (Fig. 7). *F. clessiniana* and *A. lacustris* inhabit the same habitats (macrophyte stems and large leaves) the extension of the former, more potamic and thermophilic, probably occurred to the detriment of the latter (Table 2). Overall changes between years (distribution and density of species, invasion of opportunistic and warm-water molluscs, community shifts) are consistent with the consequences of climatic warming observed (Daufresne et al. 2004, Daufresne et al. 2007, Burgmer et al. 2007, Durance & Ormerod 2007), although other stressors (metals, pesticides, PAH...) may also be partly responsible for changes.

The spatial variability of the responses observed only partially agree with the predictions of Buisson & Grenouillet (2009) for European stream fish species. As predicted by these authors, we clearly observed the homogenisation of community structure. By contrast, and contrary to their predictions, the modifications of this structure mainly occurred in downstream areas. There are several potential explanations for this observation. Firstly, molluscs are not as able as fish to migrate upstream. Furthermore, the climatic warming

observed between 1977 and 2007 was not as great as the future warming predicted by the climatic models used by Buisson & Grenouillet (2009). Lastly, it is possible that these thermal models fail to accurately reflect the spatial heterogeneity of the impact of climatic warming. The area upstream should be relatively less exposed to climatic warming than the downstream areas due to plant cover and inflows of groundwater. Metal contamination (upstream sites) and the negative impact of *C. fluminea* on Unionidae (downstream sites) are also possible explanations.

Recovery possibilities

Community recovery (i.e. return to the pre-disturbance level of 1977) mainly depends on organism dispersal capabilities (drift, swimming, crawling, flight), reproduction characteristics, degree of isolation from potential recolonizing sources and persistence of stressors (Niemi et al. 1990). The fecundity of Sphaeriidae is quite low (Way & Wissing 1982). Unionidae produce large numbers of glochidia but between parental release and detachment from fish hosts after the parasitic phase, their mortality rate is very high: very few of them (<0.002%) reach the free living juvenile stage (Jensen et al. 2001). They are slow-growing, do not reach reproductive maturity until three years (Aldridge et al. 2007) and attain a life span of more than 40 years (Bauer 2001). The life history traits of native bivalves are therefore rather unfavourable to their rapid recovery.

Species preferentially inhabiting the lower rhithron or potamon (*A. lacustris*, *V. viviparus*, *Pisidium henslowianum*, *P. moitessierianum*, *P. supinum*, *Musculium lacustre*, *Sphaerium corneum*, *S. rivicola* and Unionidae) are seldom or not at all represented in the upper part of the Ognon river and its different small tributaries. Consequently, the scarcity of donor sites in the watershed makes the recolonisation of the lower reaches of the river by this species difficult. Nonetheless, recolonisation is possible. We discovered *Unio crassus* and *U. pictorum* (juveniles and adults) at Villersexel (st. 7), attested by additional samplings in October 2008, whereas in 1977 mussels appeared only from Montbozon (st. 8). But the latter, already impeded by dams that restrict the migration of fish hosting the mussel larvae, could be affected by the pollution of the river downstream of Lure (excessive maximal concentrations of NH_4^+ , NO_2^- and PO_4^{3-} at Les Aynans st. 6), and then by the confluence of its main tributary, the Rahin, which is contaminated by metals. The fall in

the species richness and density of molluscs observed at Villersexel (st. 7) attested to the negative impact of degraded water quality (Fig. 5a, b). *U. crassus*, which is protected under French law, is listed on the IUCN Red List of Threatened Species in the lower risk/near threatened category (available on <http://www.iucnredlist.org>).

Given the low resilience of filter-feeders, the turnover of species observed between years and the increase of the frequency of extreme climatic events forecast by models (Beniston et al. 2007, IPCC 2007, Planton et al. 2008), a return to the pre-disturbance situation of the malacological structure in the River Ognon is unlikely. The evolution to a new relatively stable state following a shift of mollusc community structure triggered by ramp and pulse disturbances (climatic warming, 2003 heatwave, proliferation of invasive species) is an alternative hypothesis (Scheffer et al. 2001, Scheffer & Carpenter 2003, van Nes & Scheffer 2004).

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