



Open Archive Toulouse Archive Ouverte (OATAO)

OATAO is an open access repository that collects the work of Toulouse researchers and makes it freely available over the web where possible.

This is an author-deposited version published in: <http://oatao.univ-toulouse.fr/>
Eprints ID: 6225

To link to this article : DOI:10.1007/s10530-009-9506-4
<http://dx.doi.org/10.1007/s10530-009-9506-4>

To cite this version : Piscart, Christophe and Bergerot, Benjamin and Laffaille, Pascal and Marmonier, Pierre *Are Amphipod invaders a threat to the regional biodiversity? Conservation prospects for the Loire River.* (2010) *Biological Invasions*, vol. 12 (n° 4). pp. 856-863. ISSN 1387-3547

Any correspondence concerning this service should be sent to the repository administrator: staff-oatao@inp-toulouse.fr

Are amphipod invaders a threat to regional biodiversity?

Christophe Piscart · Benjamin Bergerot ·
Pascal Laffaille · Pierre Marmonier

Abstract The impact of invasions on local biodiversity is well established, but their impact on regional biodiversity has so far been only sketchily documented. To address this question, we studied the impact at various observation scales (ranging from the microhabitat to the whole catchment) of successive arrivals of non-native amphipods on the amphipod assemblage of the Loire River basin in France. Amphipod assemblages were studied at 225 sites

covering the whole Loire catchment. Non-native species were dominant at all sites in the main channel of the Loire River, but native species were still present at most of the sites. We found that the invaders have failed to colonize most of tributaries of the Loire River. At the regional scale, we found that since the invaders first arrived 25 years ago, the global amphipod diversity has increased by 33% (from 8 to 12 species) due to the arrival of non-native species. We discuss the possibility that the lack of any loss of biodiversity may be directly linked to the presence of refuges at the microhabitat scale in the Loire channel and in the tributaries, which invasive species have been unable to colonize. The restoration of river quality could increase the number of refuges for native species, thus reducing the impact of invaders.

C. Piscart (✉) · P. Marmonier
UMR CNRS 6553 Ecologie, Biodiversité et Evolution,
Université de Rennes1, Campus Beaulieu, 263 Av. du
Général Leclerc, 35042 Rennes cedex, France
e-mail: christophe.piscart@univ-lyon1.fr

B. Bergerot
UMR CNRS 5173 Conservation des Espèces,
Restauration et Suivi des Populations, Museum National
d'Histoire Naturelle, 55 rue Buffon CP 51, 75005 Paris,
France

P. Laffaille
URU 420 Biodiversité Fonctionnelle et Gestion des
Territoires, Service du Patrimoine Naturel, Université de
Rennes1 & Museum National d'Histoire Naturelle,
Campus Beaulieu, 263 Av. du Général Leclerc, 35042
Rennes cedex, France

Present Address:
C. Piscart · P. Marmonier
UMR CNRS 5023 Laboratoire Ecologie des
Hydrosystèmes Fluviaux, Université de Lyon 1, Campus
de La Doua, 43 Bd du 11 Novembre 1918, 69622
Villeurbanne, France

Keywords Species distributions · Crustacean
invasion · Habitat · Native and invasive species ·
Refuge · Colonization process

Introduction

The introduction of non-native species is one of the most important factors endangering native biodiversity in aquatic ecosystems (Rahel and Olden 2008), and is now considered to be the third biggest cause of biodiversity decline in aquatic ecosystems (Sala et al. 2000). The arrival of invasive species is also viewed

as an unprecedented form of global change (Ricciardi 2007). Even in cases where biodiversity does not decrease, aquatic fauna can suffer from homogenization due to the arrival of non-indigenous species, the elimination of native species, and habitat alteration, which can facilitate both these processes (Rahel 2002; Piscart et al. 2005, 2007). Consequently, studies of the extension of invasive species have become commonplace, especially in the freshwater ecosystem literature, and numerous studies illustrating the extent of the phenomenon have recently been published (Richardson and Pysek 2008). Most of these studies have focused either on the interaction between native and non-native species, or on the spread of invasive species throughout different geographical areas and along the main channels of rivers. As a result, although the impact of invasions on local biodiversity had been well established, their consequences for regional biodiversity were still poorly documented, and this is certainly because it has proved difficult to disentangle the respective roles of environment and interspecies interactions in the success of invasive species over native ones (Lepäköski et al. 2002; Piscart et al. 2009).

Among freshwater invertebrates, amphipods provide very good models for investigating the relationship between ecosystems, human disturbances and invasive species (Piscart et al. 2007, 2009). This group of species is widely distributed worldwide throughout freshwater ecosystems, and is highly diversified. Moreover, in Western Europe, non-native amphipods have met with more success than most other taxa (Devin and Beisel 2007; Grabowski et al. 2007). The ecology of European amphipod species is well documented, and several recent studies have been devoted to the dispersal of invasive species in various European catchments (Jazdzewski 1980; bij de Vaate et al. 2002; van der Velde et al. 2002; Jazdzewski et al. 2004; Devin and Beisel 2008). For example, the Loire River basin corresponds to the largest catchment in France, and constitutes one of the most diversified large river systems for amphipods, with 12 species currently reported (Goedmakers 1974; Chovet and Lécureuil 1994; Bollache et al. 2004; Piscart et al. 2007). Because of its central position in France, the Loire River has suffered several successive arrivals that began with *Gammarus roeselii* (Gervais 1835), a species that is now considered to have been naturalized in France since it

arrived during the 19th century (Jazdzewski and Roux 1988), and continued with the American species *Crangonyx pseudogracilis* Bousfield, 1958, which arrived in 1980s (Lécureuil and Chovet 2003), and which has locally colonized several canals connected to the Loire River. These species were followed in 1999 by the Ponto-caspian *Chelicorophium curvispinum* (G.O. Sars 1895) (Lécureuil and Chovet 2003), and in 2001 by the killer shrimp *Dikerogammarus villosus* (Sowinskyi 1894), which has colonized most of the main channel of the Loire River (Lécureuil and Chovet 2003; Bollache et al. 2004). Finally, another American invasive species, *Gammarus tigrinus* Sexton, 1939, has recently arrived in the Loire River estuary, where it was first recorded in 2005 (Piscart et al. 2007), and is currently expanding into the Lower Loire and adjacent canals (Piscart et al. 2008).

To understand the local and regional effects of the arrival of non-native species on the biodiversity of a large watershed, the following two questions must be addressed: (1) What is the threat to native biodiversity along the longitudinal (upstream-downstream) and lateral (from the main channel to tributaries) gradients? Or, in other terms, can native species find refuges in the Loire River or in its tributaries? (2) Does the arrival of non-native species modify the biodiversity at the regional scale? To answer these questions, we studied the amphipod assemblage of the Loire River, and the consequences of the successive arrivals of non-native amphipods at various scales of observation: from microhabitats in the main channel to the regional scale.

Materials and methods

The Loire River is the longest river in France, with a total length of 1,020 km from multiple sources in the Mont Jerbier de Jonc area (44°50'38" N, 4°13'12" E) to the estuary at St Nazaire, on the Atlantic coast (47°16'50" N, 2°12'31" W). The Loire River catchment is localized in central France. It is composed of more than 20,000 tributaries, and spreads over one fifth of the French territory (around 117,000 km²). Its maximum altitude is 1,500 m, and it has a very patchy geology and landscape, consisting of woodlands, pastures, agricultural plots, and large cities downstream. The main axis of the catchment (i.e. the Loire

River and its main tributary, the Allier River) is less regulated and has better longitudinal connectivity than the other tributaries (including large rivers), some of which are now substantially impounded (Lasne et al. 2007a). The Loire basin as a whole is hence usually considered to have suffered less impact than other large river systems in Europe (Pont et al. 2005).

We studied the micro-distributions of native and non-native species in three tributaries (the Beuvron River, the Cisse River and the Thouet River—Table 1). For each tributary, one site was located at the confluence with the Loire River, one site between 100 and 150 m upstream from the confluence, and one site in the Loire River channel opposite the confluence. In these nine sites, amphipods were collected separately from four microhabitats (litter, macrophyte, roots, and pebbles). Triplicate samples of 0.25 m² were collected at each site using a quantitative Surber net sampler (500 µm mesh size). Differences in species density with respect to the microhabitat were tested using variance nested analysis with ‘microhabitat’ as the fixed-effect factor, and a two-level nested analysis (microhabitat nested in position according to the confluence nested in tributaries). Tukey’s HSD tests were used for multiple comparisons within the sites.

The large scale distribution of amphipods was examined at 225 sites covering the whole Loire catchment (Fig. 3). Amphipods were sampled in 2006 and 2007 using a hand net (500-µm mesh size). We used presence–absence data for each site. A total of 180 sites that harbored amphipods were used in this analysis. Environmental parameters, such as land-use type (urban, cultivated land, meadow and

forest), habitat (riffles, pools, fast running channels, and slow running channels), substratum type (pebble, gravel, leaf litter, vegetation and root), mean flow velocity (m s⁻¹), and river channel width (m) were measured at each sampling site. Amphipod assemblage classification was performed using self-organizing maps (SOM) according the Lasne et al. (2007a) protocol. This unsupervised artificial neural network method is used to analyze complex data sets with non-linear relationships (Kohonen 2001; Lek et al. 2005). In this study, the SOM procedure was used to organize the 180 sample sites into 64 neural network cells. Samples with similar species composition were classified as belonging to the same cell. By using weight vectors of trained SOMs, clustering techniques (Ward’s method) were used to subdivide the SOM cells into three clusters, i.e., subgroups of amphipod assemblages. The probability that each species would be present and the diversity (number of species per sampling site) in the different clusters identified were compared using Kruskal–Wallis tests and Dunn’s post test. In order to characterize clusters by testing whether they could be characterized by one or more indicator species, we used the indicator value (IndVal) according to the method developed by Dufrêne and Legendre (1997). The IndVal, expressed as a percentage, is based on both the fidelity and the specificity of the species for each cluster. Fidelity is highest when the species is present in all the sites in a cluster. Specificity is highest when all the individuals of a species are found in the same cluster. A Stepwise discriminant analysis was used to determine which environmental variables discriminated between the three clusters obtained with the SOM procedures.

Table 1 Environmental parameters of sites used in the microdistribution study according to their location along the waterways (100–150 m upstream from the confluence with the Loire River, at the confluence with the Loire River and in the Loire River itself)

River	Position	Channel width (m)	Mean flow velocity (in m s ⁻¹)
Beuvron River	Upstream	16	0.040
	Confluence	18	0.025
	In the Loire River	100	0.125
Cisse River	Upstream	18	0.040
	Confluence	18	0.092
	In the Loire River	150	0.092
Thouet River	Upstream	40	0.030
	Confluence	40	0.020
	In the Loire River	100	0.114

Results

The same microdistribution pattern of the native and non-native species was observed in the three sites in relation to the distance from confluence (upstream in the tributary, confluence between the tributary and the Loire River, and downstream from the confluence in the Loire River; Fig. 1). The invader *D. villosus* was never found in the upstream zones in the tributary, whereas its densities had increased markedly further downstream, and it was dominant in the Loire River ($F_{3,8} = 5.62$, $P < 0.0001$). In the main channel of the Loire River, *D. villosus* was widely distributed in all the microhabitats without showing any clear substratum preference ($F_{3,8} = 2.1$,

$P = 0.107$). At the confluence, this species was mainly found in pebbles (Fig. 1; $P = 0.005$).

Gammarus pulex (Linnaeus 1758) was the most abundant native species found in the tributaries. This species was not randomly distributed among the microhabitats but displayed a significant substratum effect ($F_{9,90} = 7.57$, $P < 0.0001$). The microdistribution of *G. pulex* was considerably modified when *D. villosus* was present. Upstream from the confluence, the abundance of *G. pulex* had increased considerably from pebble to vegetation roots (Fig. 1; $P < 0.0015$), whereas it had disappeared from the pebble habitat in the area of the confluence, and was restricted to the leaf litter and roots in the Loire River.

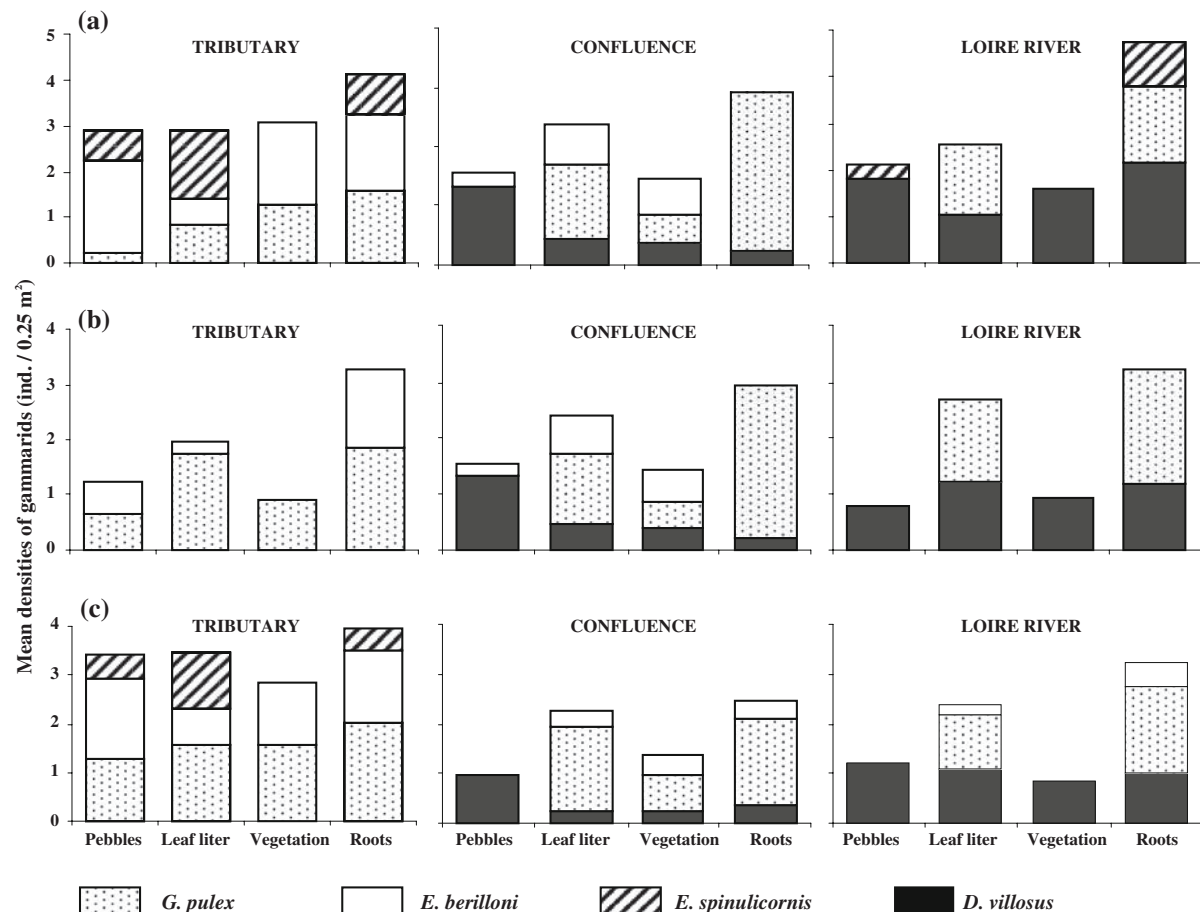


Fig. 1 Mean cumulative amphipod densities (individuals per 0.25 m^2) at the microhabitat scale in **a** the Beuvron River, **b** the Cisse River and **c** the Thouet River. The first column represents sites in the tributary upstream from the confluence with the

Loire River; the second represents confluence sites between the tributary and the Loire River, and the third, sites in the Loire River downstream from the confluence

We also observed that the microhabitat had a major impact on the distribution of both *Echinogammarus berilloni* Catta, 1878 and *Echinogammarus spinulicornis* Pinkster and Stock 1971 ($F_{9,90} = 4.33$, $P = 0.0001$ and $F_{9,57} = 15.51$, respectively, $P < 0.0001$). Upstream of the confluence, *E. berilloni* was found in all microhabitats, but at a lower density in the leaf litter ($P < 0.013$). In contrast, *E. spinulicornis* was more abundant in the leaf litter ($P \leq 0.0001$), but absent from the vegetation in the tributaries. The microdistributions of the *Echinogammarus* species were also considerably disrupted when *D. villosus* was present. The densities of *E. berilloni* were significantly lower at the confluence with the Beuvron River (Fig. 1a; $P = 0.0001$), and at that with the Thouet River (Fig. 1c; $P = 0.011$). In the Loire River where *D. villosus* was very abundant, the *Echinogammarus* species had disappeared near the Rivers Beuvron and Cisse, and only a few individuals were found in the leaf litter and in the roots near the Thouet River. *E. spinulicornis* seemed to be severely impacted by *D. villosus*, because had it disappeared from the confluence sites, and only few individuals remained in the pebbles and roots in the Loire River close to the Beuvron River.

At the regional scale, 11 aquatic species and one terrestrial species (*Orchestia cavimana* Heller 1865) were found in the study area (Table 2). Among them only 7 are considered to be native (*Echinogammarus berilloni*, *E. spinulicornis*, *Gammarus fossarum* (Koch 1835), *G. lacustris* (G.O. Sars 1863), *G. orinos* Pinkster and Scholl 1984, *G. pulex*, and *Orchestia cavimana*), four non-native and invasive (*C. pseudogracilis*, *C. curvispinum*, *D. villosus*, and *G. tigrinus*), and one a naturalized non-native species (*G. roeselii*). We also observed a lack of amphipods in the upstream part of the Loire catchment basin, which is mainly composed of temporary or poorly mineralized streams (Fig. 2).

Based on the similarity of the cells in the SOM procedure, the clustering procedure identified three main clusters that were composed of 67, 92 and 21 sites, respectively. Most species varied significantly between the different clusters, except for four very scarce species *G. orinos*, *O. cavimana*, *G. lacustris* and *C. pseudogracilis* (Table 2). *G. pulex* was very common (mean probability of occurrence $\approx 75\%$), but was not present in any of the cluster-3 sites. Only

D. villosus was present in all the clusters. The diversity was higher in the sites sampled in the first cluster than in those of the other two. *E. berilloni* was present in all the cluster-1 sites, and can be considered to be the most indicative species of this cluster (Table 2), with *E. spinulicornis* as the second most characteristic species of cluster 1 (Table 2). *G. pulex* was present in most of the cluster-2 sites, and can be considered to be indicative of the second cluster together, with *G. fossarum* and secondarily *G. roeselii* (Table 2). Finally, all the invasive species (*D. villosus*, *C. curvispinum*, *G. tigrinus*, and *C. pseudogracilis*) were found in the pooled cluster-3 sites (Table 2) and, except for *C. pseudogracilis*, these were the species indicative of this cluster.

The results of the stepwise discriminant analysis including all environmental variables highlighted the fact that all three clusters were significantly distinguished by river width ($F_{2, 172} = 32.29$, $P < 0.0001$) and habitat (i.e., riffles, pools, fast running channels, and slow running channels; $F_{2, 172} = 5.0$, $P = 0.0077$). Sites in cluster 1 were characterized by being in small and medium size lowland rivers (mean width = 11.6 ± 11.5 m), which were all located in the north-western part of the Loire catchment and dominated by chalky geology (Fig. 2). This cluster was mainly constituted by fast running habitats (riffles, fast running channels). Cluster 2 included most of the sites also characterized by small and medium size rivers (mean width = 16.0 ± 27.0 m), but was widely distributed throughout the Loire Catchment (Fig. 2), and in most habitats (riffles, fast and slow running channels or pools). The regional-scale distribution of non-native species, corresponding mainly to the cluster 3, was characterized by large river size (mean width = 89.0 ± 103 m) with pools and slow running channels (Figs. 2, 3), and was restricted to the main channel of the Loire River except for that of the naturalized *G. roeselii*, which has colonized some tributaries in the eastern part of the Loire catchment (Fig. 3).

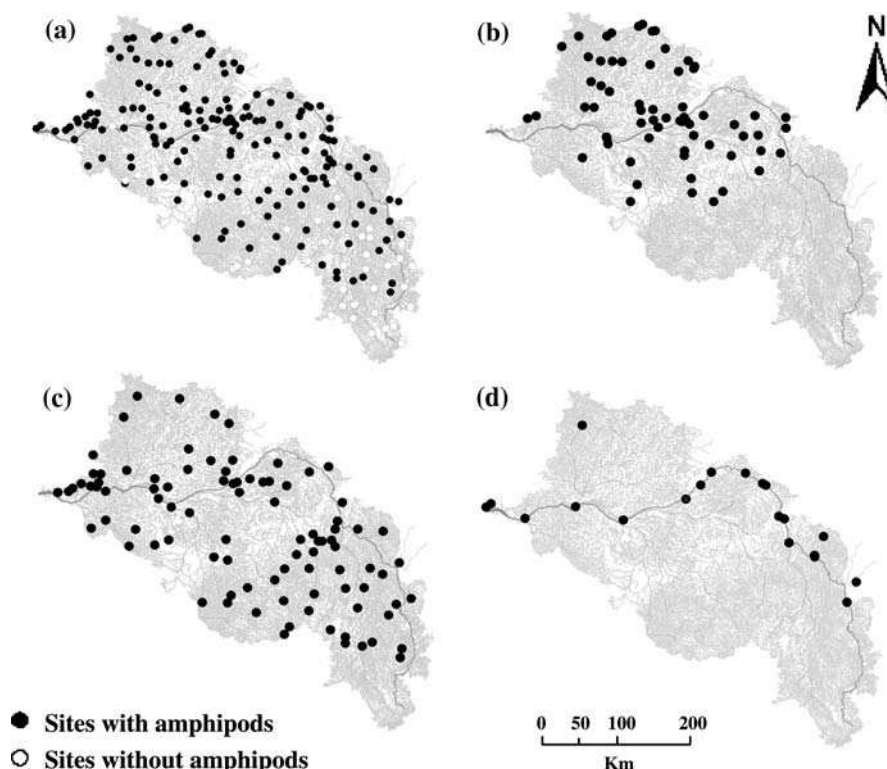
An upstream-downstream pattern of alien species was found along the Loire channel, with only native species in the upstream sector, a combination of *D. villosus* and *C. curvispinum* in the first half of the river, *D. villosus* alone in the second half of the river and, finally, *G. tigrinus* in the more salty downstream area (Fig. 3).

Table 2 List, occurrence (number of sites where species were caught), origin (*N* native, *NN* non-native and *NNN* naturalized non-native) and mean (\pm SD) occurrence of each of the species found in the Loire river catchment, and the species diversity (\pm SD) in all the sites where amphipods were present (180 sites vs. 225 sampled sites) and by cluster

Family	Species	Occurrence	Origin	All sites	Cluster 1 sites	Cluster 2 sites	Cluster 3 sites	KW
Crangonyctidae	<i>Crangonyx pseudogracilis</i>	6	NN	0.01 \pm 0.07	–	–	0.05 \pm 0.22	ns
Corophiidae	<i>Chelicorophium curvispinum</i>	1	NN	0.03 \pm 0.18	–	–	0.29 \pm 0.46 ^a	***
Gammaridae	<i>Dikrogammarus villosus</i>	17	NN	0.11 \pm 0.31	0.03 \pm 0.17	0.05 \pm 0.23	0.57 \pm 0.51 ^a	***
	<i>Echinogammarus berilloni</i>	67	N	0.38 \pm 0.47	1.0 \pm 0.0 ^a	0.01 \pm 0.10	–	***
	<i>Echinogammarus spinulicornis</i>	12	N	0.08 \pm 0.27	0.18 \pm 0.39 ^a	0.02 \pm 0.15	–	***
	<i>Gammarus fossarum</i>	29	N	0.16 \pm 0.37	0.12 \pm 0.33	0.23 \pm 0.42 ^a	–	*
	<i>Gammarus lacustris</i>	1	N	0.01 \pm 0.07	–	–	0.05 \pm 0.22	ns
	<i>Gammarus orinos</i>	2	N	0.01 \pm 0.11	–	0.02 \pm 0.15	–	ns
Talitridae	<i>Gammarus pulex pulex</i>	128	N	0.73 \pm 0.44	0.75 \pm 0.44	0.89 \pm 0.31 ^a	–	***
	<i>Gammarus roeseli</i>	7	NNN	0.03 \pm 0.18	–	0.07 \pm 0.25 ^a	–	*
	<i>Gammarus tigrinus</i>	3	NN	0.02 \pm 0.13	–	–	0.14 \pm 0.36 ^a	***
	<i>Orchestia cavimana</i>	2	N	0.01 \pm 0.11	0.01 \pm 0.12	0.01 \pm 0.10	–	ns
	<i>Diversity</i>			1.57 \pm 0.72	2.09 \pm 0.73 ^a	1.30 \pm 0.53	1.10 \pm 0.44	***

^a Highest values ($\alpha = 0.05$) according to Dunn's post test when Kruskal–Wallis tests are significant (*** <0.001, ** <0.01, * <0.05, ns not significant)

Fig. 2 Map showing the locations of the 225 sites (with or without amphipods) sampled in 2006 and 2007 (a), sites constituting cluster 1 (b), cluster 2 (c) and cluster 3 (d) of the SOM procedure



Discussion

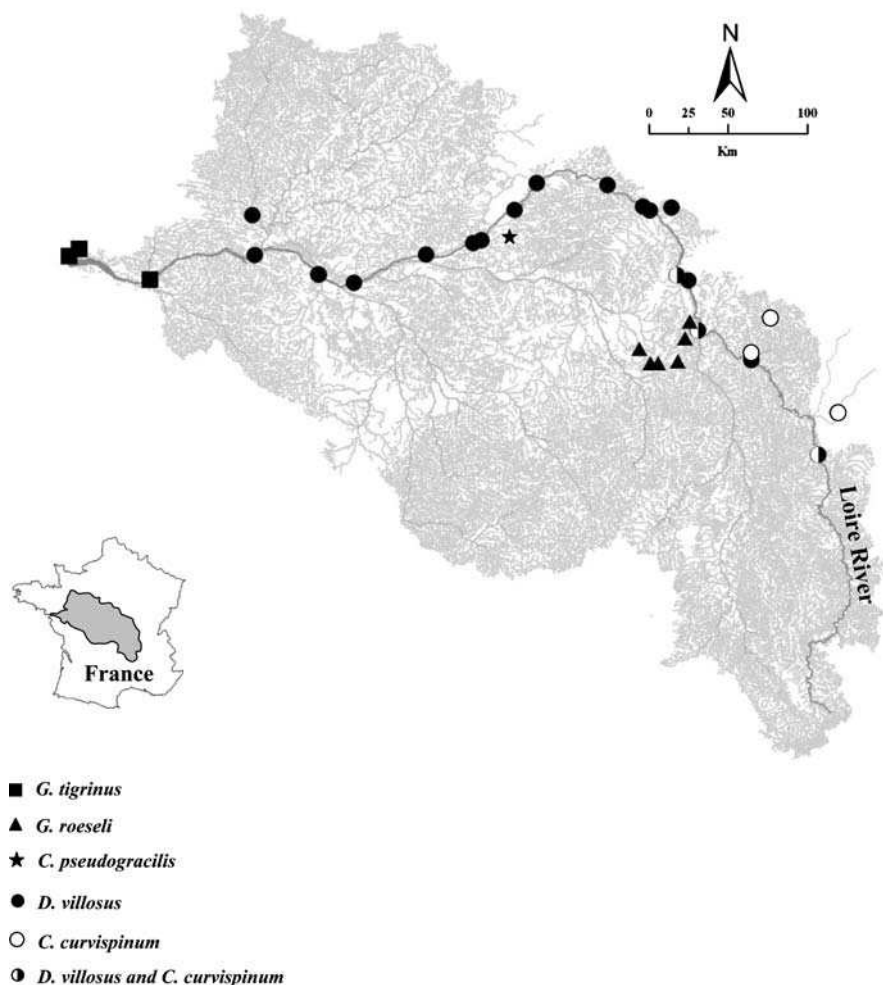
Threats to biodiversity in the Loire River and in its tributaries

We have observed changes in the amphipod assemblages of the Loire River over the last 30 years as a result of the arrival of non-indigenous species (*C. pseudogracilis*, *G. roeselii*) and invasive species (*D. villosus*, *C. curvispinum*, and *G. tigrinus*), as well as of shifts in the distribution and density of some native (*G. pulex*, *E. berilloni*) and endemic (*E. spinulicornis*) species. The distributions found for regionally rare native species (*G. lacustris*, *G. orinos*, and the terrestrial landhopper *O. cavimana*) did not allow us to draw any conclusions about changes in their distribution.

Although interactions between native and invasive species tend to result in reductions in the population densities of native species, some of them are able to persist in the main channel. Moreover, our findings suggest that there are refuges in the tributaries where native species have been able to resist the invaders for at least 7 years, since Bollache et al. (2004) observed

the arrival of *D. villosus* in the Loire River near the Beuvron River between 2001 and 2002. In this sector, we observed the native species *E. spinulicornis* and *G. pulex* in 2007. However, the microdistribution of native species has been severely disrupted, and they are now mainly restricted to organic substrates (i.e. roots and leaf litter). The mechanism underlying the change in the microdistribution of native species remains unclear, but it is clearly a combination of two different processes (Dick 1996; Piscart et al. 2007; van Riel et al. 2007): a difference in microhabitat preferences that limits the overlap and interaction between native and invasive species, and competitive interaction in microhabitats that harbor both native and invasive species). This phenomenon has already been observed in Brittany and in Northern Ireland, where the microdistribution of the endemic *Gammarus duebeni celticus* has been disrupted by the arrival of *G. pulex*, which has replaced the endemic species in its optimum microhabitats (Dick 1996; Piscart et al. 2007). In this context, the endemic *G. duebeni celticus* was only able to persist in microhabitats ignored by *G. pulex* (Dick 1996). Our results suggest that a similar process is occurring in the Loire River, where the

Fig. 3 Map showing the distribution of non-native species in the Loire catchment



native species *E. spinulicornis* and *G. pulex* have both resisted *D. villosus* in leaf litter, which is not colonized by the predatory *D. villosus*, and in roots, which have mainly been colonized by juveniles (Devin et al. 2003). *D. villosus* juveniles probably compete with the native species less effectively than adults. The larger *D. villosus*, which constitute the main threat to native species (Dick 1996), are indeed known to have a clear preference for hard substrata (Devin et al. 2003; Platvoët 2007; MacNeil et al. 2008b), which reduces their encounters with predators, and the risk of being detected and caught by fish or invertebrate predators (Crowder and Cooper 1982; Power 1992).

Potential changes at the regional scale

We did not find any overall pattern of extension of non-native species in the Loire River catchment. The

distribution of the non-native *G. roeseli* had been considerably reduced since 1994 (Chovet and Lécureuil 1994), especially along the main channel of the Loire River, and was now restricted to a few tributaries in the middle section of the Loire catchment. The decline of *G. roeseli* in areas where it had been present since the 1980s (Jazdzewski and Roux 1988) may confidently be attributed to interactions with *D. villosus* (e.g. intraguild predation, competition), which has colonized the middle section of the Loire River since 2001 (Lécureuil and Chovet 2003). The invasive species *C. pseudogracilis* and *C. curvispinum* were restricted to few backwater pools and canals (Lécureuil and Chovet 2003; Bollache et al. 2004), and had failed to extend their distribution in the Loire catchment.

However, in this study we have confirmed an extension of the range of the invasive species *D. villosus* and *G. tigrinus* along the Loire River

(Bollache et al. 2004; Piscart et al. 2007). This was particularly true of *D. villosus*, which has colonized most of the Loire channel. However, the Ponto-Caspian *D. villosus* had failed to colonize the upstream part of the river characterized by poorly mineralized waters (Wijnhoven et al. 2003). Upstream extension of *D. villosus* in the future is therefore improbable due to the physico-chemical conditions (e.g. poorly mineralized waters, fast running flows), which in the Loire River are tolerated only by the native *G. fossarum*. Regarding the downstream extension of *D. villosus*, our findings suggest that this species is still extending its range beyond the distribution observed by Bollache et al. (2004) in the downstream sector and in two large tributaries (the Maine and the Mayenne Rivers), both of which are located close to the downstream limit and in the northern part of the Loire catchment. It is difficult to predict the future advance of this species. However, we can predict that the extension of *D. villosus* has probably not yet come to an end. This species may well progress further downstream, and could eliminate *G. tigrinus* from the freshwater section of the Loire River, as has already been observed in several European waterways (Dick and Platvoët 2000; bij de Vaate et al. 2002; Devin et al. 2003). The continued longitudinal extension of *D. villosus* in the Loire River looks certain, but we did not observe any lateral extension in the tributaries, except in the downstream part of the Maine and Mayenne Rivers. This species appeared to be unable to colonize tributaries, and it was restricted to just a few meters upstream of the confluence with the Loire River (Fig. 1). The reasons for this limited lateral extension of *D. villosus* in tributaries are probably related to the local physico-chemical parameters, but remain unclear. This phenomenon has commonly been observed (Jazdzewski et al. 2002; Füreder and Pöckl 2007; Piscart et al. 2007) along invasion corridors, but is surprisingly rarely discussed in the literature (Pinkster et al. 1977; Dick 1996; Piscart et al. 2007). Recently, Piscart et al. (2009) proposed an interesting hypothesis combining the effects of environmental conditions and intraguild predation of native species by non-native species. These authors have shown that *G. pulex*, an invader in Ireland, has failed to eliminate the native *G. duebeni celticus* as a result of intraguild predation in good quality water. This experimental finding confirmed the observation made by MacNeil et al. (2008a) in the Isle of Man that successive field

introductions of *G. pulex* into sites previously dominated by *Gammarus duebeni celticus* failed in good quality rivers, whereas increased river pollution could favor the replacement of native by introduced species.

More generally, these results provided in situ evidence that environmental parameters (current velocity, microhabitats or chemical parameters) can influence the competitive equilibrium between non-native invasive and native amphipods. This process can occur either to the detriment of the native species (which is usually what happens) or to that of non-native species by enhancing the ability of the native species to compete with the invader.

Finally, if we look at the consequences of successive arrivals of non-native species on the biodiversity at the scale of the Loire catchment, our results do not show that non-native species are having any strongly detrimental impact on amphipod diversity in the Loire River catchment. We only observed a major impact of invaders (i.e., *D. villosus* and *G. tigrinus*) in the main channel of the Loire River, which may have important consequences for amphipod diversity (Dick 1996; Dick and Platvoët 2000), for the macroinvertebrate community (Dick et al. 2002; Platvoët 2007), or for the fish community (Pinkster et al. 1977; Casellato et al. 2007; Platvoët 2007). In fact, at the regional scale, since the first arrival of non-native species 25 years ago, there has been an increase of 33% in amphipod diversity (from 8 to 12 species). This increase has been directly linked to the presence of refuges in the Loire channel at the microhabitat scale, and in the tributaries at the catchment scale. For example, the main changes in amphipod assemblages were caused by *D. villosus* but, even in the main channel of the river, our results have shown that the endemic *E. spinulicornis* and the native species *E. berilloni* and *G. pulex* have been able to maintain populations at least over the time scale of this study (7 years). This phenomenon has also been observed in several other European Rivers (Dick 1996; Jazdzewski et al. 2002; Devin et al. 2003; Piscart et al. 2007). The Loire River is considered to be less impacted than other large river systems in Europe (Pont et al. 2005), and the role of refuges has probably been amplified by the habitat quality and diversity, especially in the middle and downstream sections (Lasne et al. 2007b). The presence of refuges at both the microhabitat scale

and the regional scale justifies optimism with regard to the conservation of native amphipod species. The restoration of altered ecosystems should reduce the expansion of invaders, and may boost re-colonization by native species from refuges. However, a lack of knowledge about the long-term ecological and evolutionary feedback between native and invasive species makes it difficult to predict the long-term impact of this restoration. Future studies therefore appear to be essential for a better prediction of the long-term consequences of biological invasions for the biodiversity of rivers.

Acknowledgments We would like to thank Valérie Briand for her essential help with literature resources and the two anonymous referees for their valuable comments. This study was supported by the 2005 PAPIER project of the ECosphere COntinentale program, and the InBioProcess project (ANR-06-BDIV-007-InBioProcess (2007–2010) of the 2006 Biodiversity program of the National Research Agency (Agence Nationale de la Recherche, ANR).

References

- Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrates species in Europe. *Can J Fish Aquat Sci* 59:1159–1174
- Bollache L, Devin S, Wattier R, Chovet M, Beisel JN, Moreteau JC, Rigaud T (2004) Rapid range extension of the Ponto-Caspian amphipod *Dikerogammarus villosus* in France: potential consequences. *Arch Hydrobiol* 160:57–66
- Casellato S, Visentin A, La Piana G (2007) The predatory impact of *Dikerogammarus villosus* on fish. In: Gherardi F (ed) *Biological invaders in inland waters: profiles, distribution, and threats*. Springer, Berlin, pp 495–506
- Chovet M, Lécureuil JY (1994) Répartition des Gammaridae épigés (Crustacés, Amphipodes) dans la Loire et les rivières de la Région Centre (France). *Ann Limnol* 30:11–23
- Crowder LB, Cooper CE (1982) Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* 63:1802–1813
- Devin S, Beisel JN (2007) Biological and ecological characteristics of invasive species: a gammarid study. *Biol Inv* 9: 13–24
- Devin S, Beisel JN (2008) Geographic patterns in freshwater gammarid invasions: an analysis at the pan-European scale. *Aquat Sci* 70:100–106
- Devin S, Piscart C, Beisel JN, Moreteau JC (2003) Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. *Arch Hydrobiol* 158:43–56
- Dick JTA (1996) Post-invasion amphipod communities of Lough Neagh, Northern Ireland: influences of habitat selection and mutual predation. *J Anim Ecol* 65:756–767
- Dick JTA, Platvoët D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *P R Soc London B Biol Sci* 267:977–983
- Dick JTA, Platvoët D, Kelly DW (2002) Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Can J Fish Aquat Sci* 59:1078–1084
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Füreder L, Pöckl M (2007) Ecological traits of aquatic NIS invading Austrian fresh waters. In: Gherardi F (ed) *Biological invaders in inland waters: profiles, distribution, and threats*. Springer, Berlin, pp 233–257
- Goedmakers A (1974) Les Gammaridea (Crustacés, Amphipodes) du Massif Central. *Bull Zool Mus Univ Amsterdam* 3:211–219
- Grabowski M, Bacela K, Konopacka A (2007) How to be an invasive gammarid (Amphipoda: Gammaroidea)—comparison of life history traits. *Hydrobiologia* 590:75–84
- Jazdzewski K (1980) Range extensions of some gammaridean species in European inland waters caused by human activity. *Crustaceana Suppl* 6:84–107
- Jazdzewski K, Roux AL (1988) Biogéographie de *Gammarus roeselii* Gervais en Europe, en particulier en France et en Pologne. *Crustaceana suppl* 13:272–277
- Jazdzewski K, Konopacka A, Grabowski M (2002) Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) recently invading Polish water. *Contrib Zool* 71:115–122
- Jazdzewski K, Konopacka A, Grabowski M (2004) Recent drastic changes in the gammarid fauna (Crustacea, Amphipoda) of the Vistula River deltaic system in Poland caused by alien invaders. *Divers Distrib* 10:81–87
- Kohonen T (2001) Self-organizing map. Springer, Heidelberg
- Lasne E, Bergerot B, Lek S, Laffaille P (2007a) Fish zonation and indicator species for the evaluation of the ecological status of rivers: example of the Loire basin (France). *River Res Appl* 23:877–890
- Lasne E, Lek S, Laffaille P (2007b) Patterns in fish assemblages in the Loire floodplain: the role of hydrological connectivity and implications for conservation. *Biol Conserv* 139: 258–268
- Lécureuil JY, Chovet M (2003) Connexion entre les bassins hydrographiques européens et dissémination des espèces aquatiques: le cas de la Loire moyenne. *Symbioses* 9:25–31
- Lek S, Scardi M, Verdonschot PFM, Descy JP, Park YS (2005) Modelling community structure in freshwater ecosystems. Springer, Berlin
- Leppäkoski E, Gollasch S, Olenin S (2002) Invasive aquatic species of Europe: distribution, impacts and management. Kluwer, Dordrecht
- MacNeil C, Dick JTA, Gell FR, Selman R, Lenartowicz P, Hynes HBN (2008a) A long-term study (1949–2005) of experimental introductions to an island; freshwater amphipods (Crustacea) in the Isle of Man (British Isles). *Divers Distrib* 15:232–241
- MacNeil C, Platvoët D, Dick JTA (2008b) Potential roles for differential body size and microhabitat complexity in mediating biotic interactions within invasive freshwater amphipod assemblages. *Fund Appl Limnol* 172:175–182

- Pinkster S, Smit H, Brandse de Jong N (1977) The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. *Crustaceana Suppl* 4:91–105
- Piscart C, Moreteau JC, Beisel JN (2005) Biodiversity and structure of macroinvertebrate communities along a small permanent salinity gradient (Meurthe River, France). *Hydrobiologia* 551:227–236
- Piscart C, Manach A, Copp GH, Marmonier P (2007) Distribution and microhabitats of native and non-native gammarids (Amphipoda, Crustacea) in Brittany, with particular reference to the endangered endemic sub-species *Gammarus duebeni celticus*. *J Biogeogr* 34:524–533
- Piscart C, Maazouzi C, Marmonier P (2008) Range expansion of the North American alien amphipod *Gammarus tigrinus* Sexton, 1939 (Crustacea: Gammaridae) in Brittany, France. *Aquat Inv* 3:449–453
- Piscart C, Dick JTA, McCrisken D, MacNeil C (2009) Environmental mediation of intraguild predation between the freshwater invader *Gammarus pulex* and the native *G. duebeni celticus*. *Biol Inv*. doi:10.1007/s10530-009-9497-1
- Platvoët D (2007) *Dikerogammarus villosus* (Sowinsky, 1894), an amphipod with bite. The relationship between morphology, behaviour, micro-distribution and impact of this invading crustacean. Ph. D thesis, University of Amsterdam, Amsterdam
- Pont D, Hugueny B, Oberdorff T (2005) Modelling habitat requirement of European fishes: do species have similar responses to local and regional environmental constraints? *Can J Fish Aquat Sci* 62:163–175
- Power M (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* 73:1675–1688
- Rahel FJ (2002) Homogenisation of freshwater faunas. *Annu Rev Ecol Syst* 33:291–315
- Rahel FJ, Olden JD (2008) Assessing the effects of climate change on aquatic invasive species. *Conserv Biol* 22:521–533
- Ricciardi A (2007) Are modern biological invasions an unprecedented form of global change? *Conserv Biol* 21:329–336
- Richardson DM, Pysek P (2008) Fifty years of invasion ecology—the legacy of Charles Elton. *Divers Distrib* 14:161–168
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- van der Velde G, Nagelkerken I, Rajagopal S, bij de Vaate A (2002) Invasions by alien species in inland freshwater bodies in western Europe: the Rhine Delta. In: Leppäkoski E, Golash S, Olenin S (eds) *Invasive aquatic species of Europe: distribution, impacts and management*. Kluwer, Dordrecht, pp 360–372
- van Riel MC, Healy EP, van der Velde G, bij de Vaate A (2007) Interference competition among native and invader amphipods. *Acta Oecol* 31:282–289
- Wijnhoven S, van Riel MC, van der Velde G (2003) Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. *Aquat Ecol* 37:151–158