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First records, pathways and distributions of four new Ponto-Caspian amphipods in France

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ABSTRACT

In Europe, the number of establishment of non-native species, especially from Ponto-Caspian area, has dramatically increased over the past decades and induced important changes in macroinvertebrate assemblages, mainly in large rivers. However, although many Ponto-Caspian species were established in adjacent countries, only two Ponto-Caspian amphipods were formally observed in French hydrosystems since 1996. To update our knowledge on the present distribution of the Ponto-Caspian species in France, we collected amphipods from 203 sites in the Rhine, Meuse and Seine River basins in 2008 and again in 2009. Thirteen amphipod species were found in the study area. Among them, four were first formally recorded in France (*Dikerogammarus haemobaphes*, *Dikerogammarus bispinosus*, *Echinogammarus ischnus*, and *Echinogammarus trichiatus*). Our study revealed three different corridors used by these species to arrive in France. We also observed a different pattern of colonization for each species, which might indicate some between-species differences in their preferences for environmental conditions. The snapshot of the early distributions of these recently established species may hence be used to study the invasion pattern in France in order to manage their potential impact in and outside France.

Introduction

Establishments of non-native species dramatically increased in the past decades. In Europe, the construction of canals, connecting previously separated biogeographic regions, is considered to be one of the most important sources of unintentional introductions of non-native species (Bij de Vaate et al. 2002). The interconnection of river basins has facilitated the range expansions of many species (Jazdzewski 1980). This process may also be facilitated by the extirpation of native species and habitat alteration (Van der Velde et al. 2002; Piscart et al. 2007, 2009, 2010; MacNeil et al. 2009).

In the case of the macro-crustaceans in the Western European rivers were rather stable until the mid 1960s (Pinkster et al. 1992) and most establishments occurred after 1993 and the opening of the Main–Danube-Canal (Van der Velde et al. 2002). This is especially true for Ponto-Caspian species, which recently colonized many hydrosystems in Western Europe. Bij de Vaate et al. (2002) identified three important canal corridors for the range extension of Ponto-Caspian species in Europe. The northern corridor covers the route Volga River–Baltic Sea used by *Dreissena polymorpha* (Pallas, 1771) for its range extension in the 18th century. The central corridor covers the route Dnieper River–Elbe River–Rhine River used by the amphipod *Chelicorophium curvispinum* (G.O. Sars, 1895), observed near Berlin in 1912 (Wundsch 1912) and it was followed by *Echinogammarus ischnus* in 1928 (Stebbing, 1899). Finally, the southern corridor covers the route Danube River–Rhine River. These river basins were linked by the Main–Danube Canal in Germany and it has already been successfully traversed by *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinskyi, 1894), and *Echinogammarus trichiatus* (Martynov, 1932), and also by many other macro-crustaceans (see review in Bij de Vaate et al. 2002; Leuven et al. 2009). Many invasive species arrived in France through this southern corridor, either via the Rhine River (Bij de Vaate et al. 2002) or via its tributaries the Meuse and Moselle (Dhur and Massard 1995; Devin et al. 2001; Josens et al. 2005).

In France, Ponto-Caspian species represent around 40% of all non-native macro-crustacean (Devin et al. 2005). The first observation of a Ponto-Caspian species, *C. curvispinum* was realized in the Moselle River in 1993 (Dhur and Massard 1995). Since this observation, *D. villosus* was observed between 1995 and 1997 in the Rhine, the Meuse and the Moselle rivers (Devin et al. 2001; Bollache et al. 2004) and the Isopoda *Jaera sarsi* Valkanov, 1938 observed in 1999 in the Moselle River (i.e. *Jaera istri* in Devin et al. 2005). Two other species *D. haemobaphes* and *E. ischnus* were supposed

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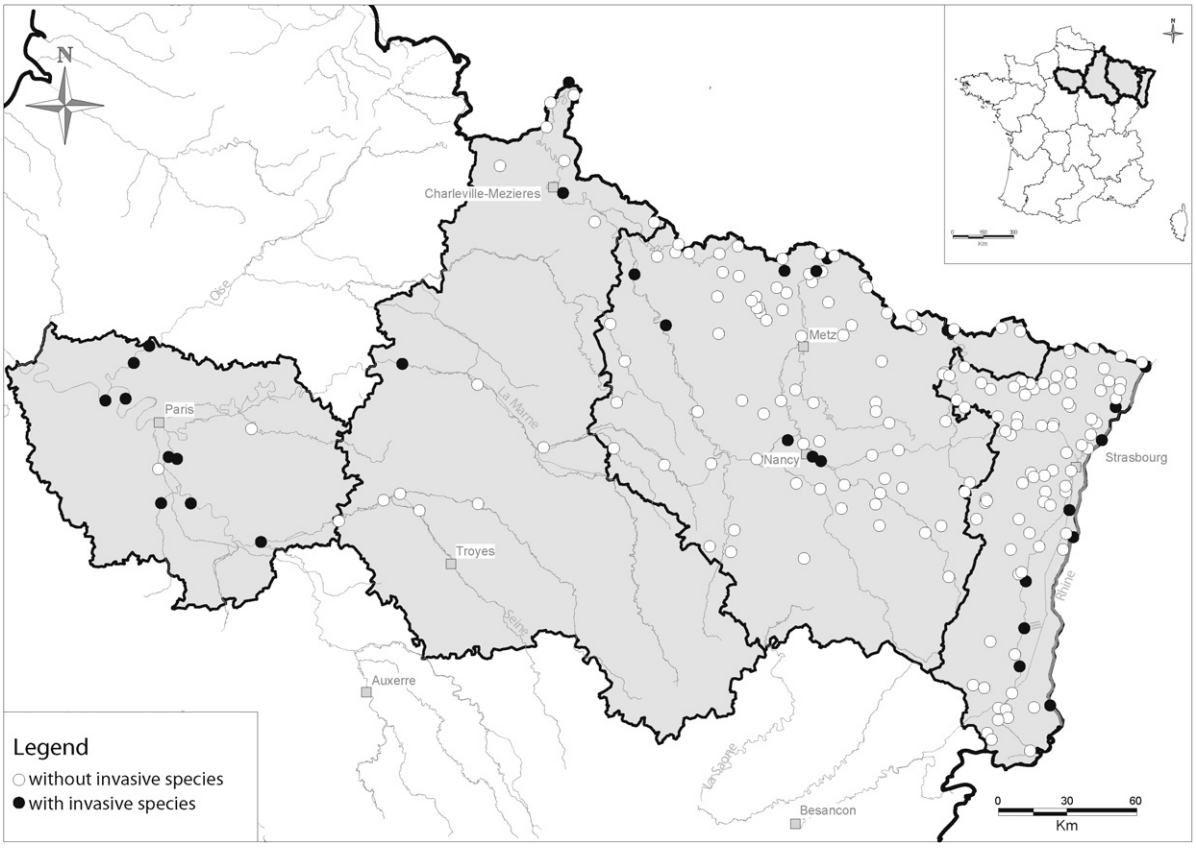

Fig. 1. Map showing the locations of the 203 sites with native species (open circles) or non-native species (black circles).

to be present (Devin et al. 2001, 2005) but not formally observed during this period and an extensive sampling of amphipods in the Moselle River between 2000 and 2001 did not reveal the presence of these two species in the Moselle River (Devin et al. 2003; Piscart et al. 2003). Another species *Chelicorophium robustum* (G.O. Sars, 1895) was observed in 2005 at the boundary between France and Germany at Lauterbourg (Martens et al. 2006). However, the lack of sampling intensity in the past decade to pick up new arrivals has restricted the observation of other Ponto-Caspian amphipods in French hydrosystems since 2005, whereas some other species (e.g. *E. trichiatus*, *Obesogammarus obesus* (G.O. Sars, 1894), and *Pontogammarus robustoides* (G.O. Sars, 1894)) are established in adjacent countries.

The first objective of this study is to update the distribution of non-native amphipods in the North-Eastern part of France, from where Ponto-Caspian species may colonize the French hydrosystems (Bollache et al. 2004). Secondly, the actual distribution and the range expansion of the Ponto-Caspian amphipods in this part of France is reviewed to identify their expansion routes in order to assess the expansion potential of these animals in and outside France.

Material and methods

We collected amphipods from 203 sites sampled twice (2008 and 2009) in the Rhine, Meuse and Seine River basins (Fig. 1). Samples were collected for biological monitoring programs using three standardized protocols (Table 1): the French IBGN protocol (AFNOR 2004), the RCS protocol (Usseglio-Polatera et al. 2007) and the GCE protocol (Usseglio-Polatera and Wasson 2005). As several sampling methods have been used (handnet, kick sampling and dredges), no quantitative data can be accurately compared among sites and this survey can only be qualitative and semi-quantitative. However, all methods used in the study provided an extensive sampling of amphipods, which avoid the absence of species in certain rivers due to differences in sampling intensity. In all cases, samples were stored in 70% ethanol and analysed at the laboratory. Species were identified using a stereomicroscope following the taxonomic keys of Carausu (1943) and Eggers and Martens (2001, 2004).

Table 1
Details of the number of site, the sampling methods and the sampling periods.

Number of site	Sample methods	Region	Catchment area	Sampling dates
17	RCS/GCE	Champagne-Ardenne	Meuse and Seine Rivers	July–August 2008 July–August 2009
88	IBGN/RCS/GCE	Lorraine	Meuse, Meurthe and Moselle Rivers	July–September 2008 August 2009
87	IBGN/RCS/GCE	Alsace	Rhine River	July–September 2008 August 2009
11	GCE	Ile de France	Seine River	July–August 2008 August 2009

Table 2
Distribution of the freshwater amphipod species in the main rivers of the studied area.

	Rhine	Ill	Moselle	Meuse	Marne	Oise	Seine
French native species							
Gammarus pulex	X	X	X	X	X	X	X
Gammarus fossarum	X	X	X	X	X	X	X
Echinogammarus berilloni	X	X	X	X	X	X	X
North American species							
Gammarus tigrinus	X		X	X			
Crangonyx pseudogracilis		X					X
Balkan species							
Gammarus roeselii	X	X	X	X			
Ponto-Caspian species							
Chelicorophium curvispinum	X	X	X	X	X	X	X
Chelicorophium robustum	X		X	X			
Dikerogammarus bispinosus[a]	X						
Dikerogammarus haemobaphes[a]	X		X	X	X	X	X
Dikerogammarus villosus	X	X	X	X	X	X	X
Echinogammarus ischnus[a]	X						
Echinogammarus trichiatus[a]	X	X	X				

[a] New species for France.

Results

Thirteen species were found in the study area (Table 2). Among them only three are considered to be native in France (*Gammarus pulex* (Linneaus, 1758), *Gammarus fossarum* Koch, 1835, *Echinogammarus berilloni* (Catta, 1878)). We found seven Ponto-Caspian species (*Dikerogammarus bispinosus* Martynov, 1925, *D. villosus*, *D. haemobaphes*, *E. ischnus*, *E. trichiatus*, *C. curvispinum*, *C. robustum*), two North-American species (*Crangonyx pseudogracilis* Bousfield, 1958 and *Gammarus tigrinus* Sexton, 1939), and one naturalized non-native species *Gammarus roeselii* (Gervais, 1835).

Establishments of non-native species were confirmed in the three river basins (Fig. 2, Table 2). Previously established Ponto-Caspian species *D. villosus*, *C. curvispinum* and *C. robustum* have been sampled alone or in combination in all the three great basins studied. They have been found on the rivers Meuse, Moselle, and Marne until the downstream part of the Seine and Oise rivers located downstream the city of Paris (Fig. 2). Since its first observation in the Rhine River in 2005, the distribution of *C. robustum* had increased and the species colonized all sites of the Rhine River in 2009. *C. robustum* was also found in the downstream part of the Meuse River (at Givet and Lumes) in 2008 and 2009 (Fig. 3). In the Meuse River

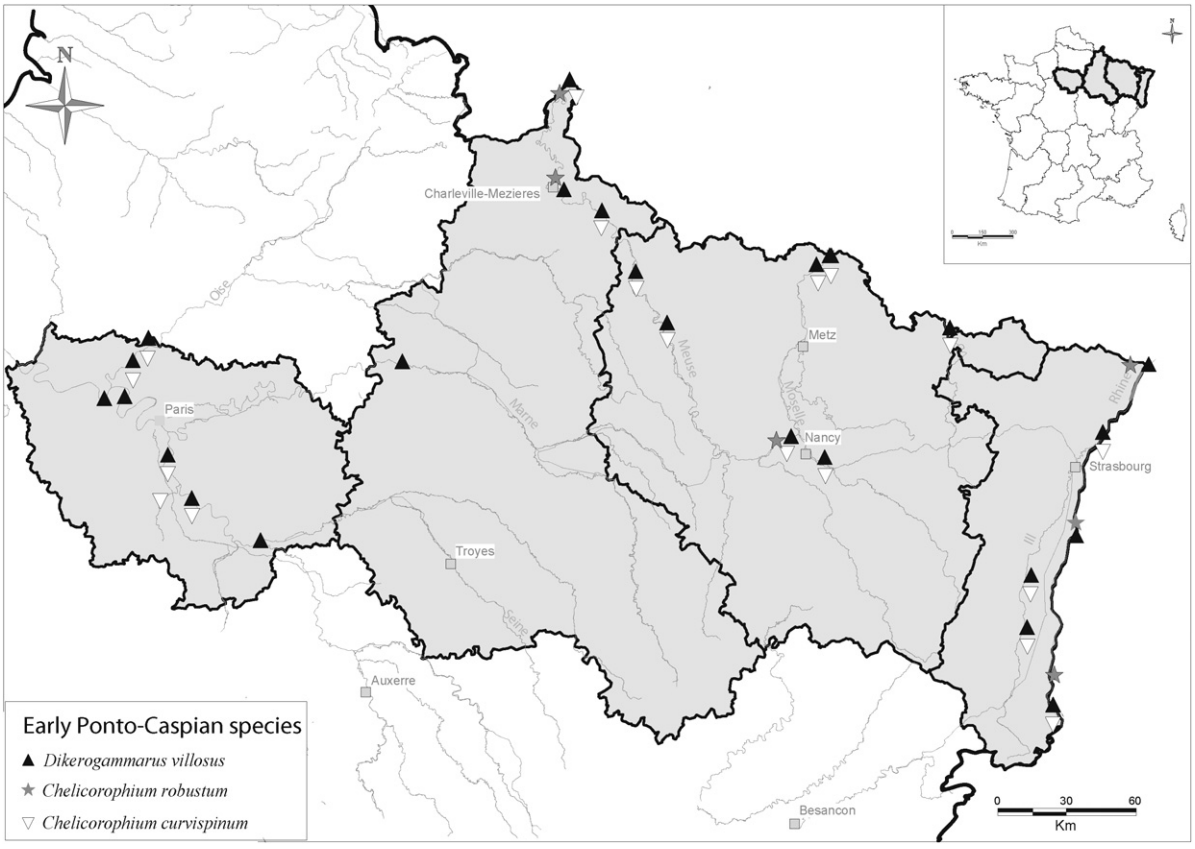

Fig. 2. Distribution map of the Ponto-Caspian species previously observed in France.

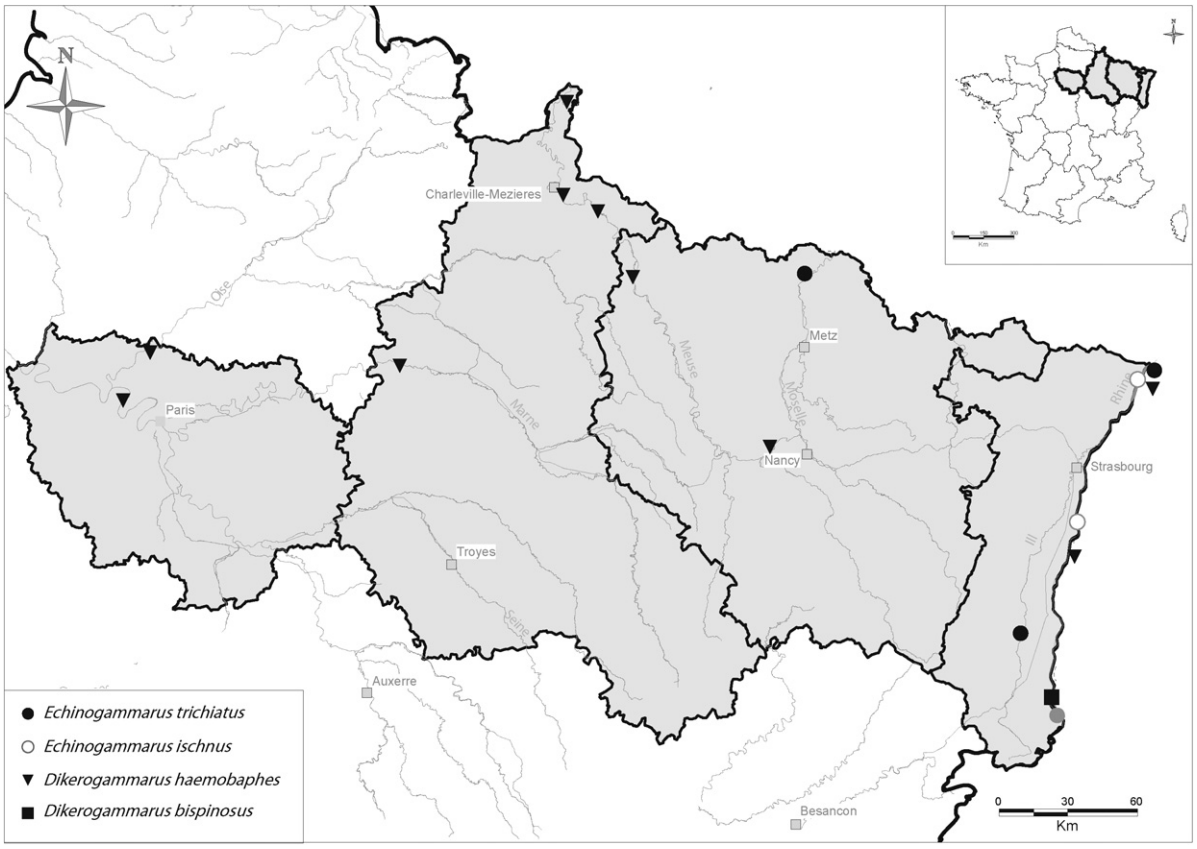

Fig. 3. Distribution map of the four Ponto-Caspian species newly observed in France.

the species often co-occurred with *D. villosus* and *D. haemobaphes*. Finally, *C. robustum* was also observed at all site of the Moselle River with increasing abundances downstream (Table 3) but was never observed in the Seine River basin (i.e. in the rivers Seine, Marne and Oise).

Newly established Ponto-Caspian species have been sampled alone or in combination at 14 sites in all the three main rivers (i.e. the Rhine, Meuse and Seine rivers) (Fig. 3). Abundances of species fluctuated between years (Table 3) making difficult the use of relative proportions of each species. This fluctuation was probably related to the sampling protocol, which allows picking up only a small part of the whole population of each species in 2008 whereas all specimens were removed in 2009.

The most wide-spread species, *D. haemobaphes*, has been found on seven sites located in all the three main basins studied (Fig. 3). In 2008 and 2009, we found significant populations of this species on the rivers Meuse, Oise, Seine and Marne, where it co-occurred at all sites with *D. villosus* (Table 3). It was not observed in the Rhine River in 2008 and a small population was observed in the lower reach of the river in 2009. In the Moselle River, only a small and fluctuating population of the species was observed in 2008 and 2009.

Only one individual of *D. bispinosus* was observed in the middle reach of the Rhine River at Kembs in 2008 (Fig. 3) and we did not find this species in 2009 (Table 3). At this site, it co-occurred with two Ponto-Caspian species *D. villosus* and *C. curvispinum*.

Table 3
Abundance of Ponto-Caspian amphipods observed in 2008 and 2009 in sites where new species occurred.

River	City	*C. curvispinum*		*C. robustum*		*D. bispinosus*		*D. haemobaphes*		*D. villosus*		*E ischnus*		*E. trichiatus*	
		2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
Meuse	Givet			4	1200			5	40	9	160				
	Lumes				5			8		8	8				
	Remilly		448						10		18				
	Sassey		3260					2	100	6	100				
Moselle	Sierck	1			1550					14	180				
	Cattenom		2484		187				20	28	380			3	
	Liverdun	1	19	1	8			6		3	40				3
Seine	Maisons							2	17	15	153				
Oise	bernes		1300					15	22	1	292				
Marne	Reuil							20	20	8	20				
Rhine	Lauterbourg				80				20	12	380		531		40
	Rhinau	1	68048		6730				1	10	359		2		
	Kembs		19		8	1				12	401		6		
Ill	Oberhergheim		45							7	477				2

E. ischnus was present at all three sites in the Rhine River in 2009 (Fig. 3) where it co-occurred with *E. trichiatus*, *D. villosus*, *D. haemobaphes*, *C. curvispinum*, and *C. robustum* (Table 3). However it was not observed in the other rivers.

E. trichiatus was observed in 2009 in the Rhine River at Lauterbourg (Fig. 3) where it co-occurred with *E. ischnus*, *D. villosus*, *D. haemobaphes*, and *C. robustum* (Table 3). It has been also found in a tributary, the Ill River at Oberhergheim (Fig. 3) where it co-occurred only with *D. villosus* (Table 3).

Discussion

Even if we did not highlighted the disappearance of native species, we have observed important changes in the amphipod assemblages of the North-eastern France over the last 10 years as a result of the arrival of two new Ponto-Caspian species (*D. bispinosus* and *E. trichiatus*) and the confirmation that *C. robustum*, *D. haemobaphes* and *E. ischnus* are established in French hydrosystems.

C. robustum likely entered the Rhine River drainage basin through the Main-Danube canal (southern corridor) and was first reported in 2002 from the Main River at Frankfurt (Bernerth and Stein 2003). The species was observed in the Rhine River in 2004 near the French boundary (Bernaurer and Jansen 2006) and in France in 2005 (Martens et al. 2006). In France, large populations of the species have been found in the rivers Meuse, Moselle and Rhine in 2009. The wide distribution of this species in French North-eastern Rivers suggests a relatively old establishment of this species. Possibly the species was not identified earlier due to confusion with the widespread *C. curvispinum* in earlier studies. The absence of the species in the upper reach of the Meuse River (i.e. the area were the Meuse River is linked to the rivers Rhine and Moselle via the Marne to the Rhine canal) is contradictory with a first establishment in France from the Meuse River. The pattern of establishment of *C. robustum* was likely a simultaneous establishment into France via the rivers Rhine and Moselle and a colonisation of the Meuse River using the Marne to the Rhine canal which links the Meuse River to the Moselle River at Toul located around 20 km upstream Liverdun.

D. haemobaphes is mainly present in the Meuse and Seine River basins. The low number of individuals found in the Rhine and Moselle rivers suggests a colonisation via the Meuse River, where it was observed in the Belgian part of the river already in 1998 (Josens et al. 2005). The presence of the species in the Moselle River at Liverdun in 2006 and Cattenom in 2009 is probably due to the Marne to the Rhine canal. The lack of *D. haemobaphes* in the downstream part of the Moselle River in 2000 and 2001 (Devin et al. 2003) and at Sierck in 2008 and 2009 are not congruent with an arrival by the Moselle River. The fact that *D. haemobaphes* has been observed only in 2009 in the downstream part of the Rhine River is also in disagreement with the hypothesis of a colonization from the French part of the Rhine River. The Marne–Rhine canal, which also links the Meuse River to the Marne River, has probably been used by *D. haemobaphes* to colonize the Seine River basin. The canal is hence considered as the corridor used by *D. villosus* to colonize the Seine River basin in 1997 (Bollache et al. 2004).

D. bispinosus is the last species of the genus *Dikerogammarus* that colonized Western Europe via the southern corridor (Bij de Vaate et al. 2002). It was observed for the first time in the German Danube near the Isar mouth in 1998 (Eggers and Martens 2001) but has not been found since that time (Bij de Vaate et al. 2002; Kinzler et al. 2009). Our first observation in the western part of Europe confirms a wider distribution of this species, not restricted to Germany and Netherlands (pers. obs., 2008). This lack of information is probably due to confusion between this species and *D. villosus,* which is morphologically close and widely distributed throughout Europe (Bij de Vaate et al. 2002; Bollache et al. 2004). In France, only one specimen *D. bispinosus* has been found in the upper French section of the Rhine River at Kembs, indicating a recent arrival of the species.

E. ischnus was found only in the Rhine River near Lauterbourg in 2009, the absence of this species in the Meuse River since 1998 (Josens et al. 2005) and in the Moselle River (Devin et al. 2003) confirms the use of the Rhine River to colonize the French hydrosystems. This species is indeed well-established in the lower part of the river in Germany since 1989 (Schöll 1990) and in the Netherlands since 1991 (Van den Brink et al. 1993). The observation of a large population of this species in the Rhine River is congruent with a previous colonization of the river since at least 2003 (Bollache, pers. com.).

E. trichiatus colonized the lower part of the Rhine River in 2000 and 2001 using the southern corridor (Bij de Vaate et al. 2002). Since this first observation, little information has become available concerning the distribution of this species between the delta of the Rhine River and France. This lack of information is probably due to confusion between this species and *E. ischnus* which is morphologically close. Only some individuals of the species were observed at the same time in the Moselle and Rhine rivers since 2008. The species likely used simultaneously these rivers to arrive very recently in France.

The geographical invasion patterns described above are based on the historical invasion record combined with the knowledge of the connection between river basins. Future range expansion of these species in France may follow the pattern observed for other Ponto-Caspian species, like *D. villosus* and *C. curvispinum*. Both species are now well-established in France (Bollache et al. 2004). Since the arrival in France in the late 1990s, Ponto-Caspian species have colonized most of French hydrosystems in less than 10 years. Bollache et al. (2004) described three colonization routes from the Rhine River. The first may be through the Rhône–Rhine canal, the second corridor corresponds to the Moselle River and through the Marne–Rhine and Moselle–Saône canals and the third corridor from the Meuse River, through canals joining the Meuse and Seine drainages. Despite the fluctuation of the amphipod abundance due to sampling method, the distributions of newly established species highlight the same three corridors. However, contrary to the multiple and recurrent arrival of *D. villosus* in the three corridors, our study highlights different patterns of establishment for the new immigrants. Some species (i.e. *E. ischnus* and *D. bispinosus*) have probably used only the Rhine River to arrive in France whereas two others species (i.e. *E. trichiatus* and *C. robustum*) have also used the Moselle River drainage. Finally, *D. haemobaphes* was the only species to use only the Meuse River.

The survey of the future distribution of these new Ponto-Caspian species may hence be very informative to highlight and manage the pattern of colonization from the different corridors. For these species, the use of different corridors might also reflect the difference of environmental conditions explaining the success of these species. For example, several studies have revealed that conductivity may promote the establishment of salt-tolerant species (Piscart et al. 2005; Kestrup and Ricciardi 2009; Grabowski et al. 2009) and other studies highlighted the role of environmental conditions in the success of amphipod invasions (Josens et al. 2005; Piscart et al. 2007, 2009, 2011; MacNeil et al. 2009). The three French corridors (i.e. the rivers Meuse, Moselle and Rhine) represent different environmental conditions, which may differently affect the success of the non-native species. For example, *D. haemobaphes* is known to have a strong preference for running waters in the Ponto-Caspian area (Carausu 1943) and this species used the Meuse River, which is the most running river among the three French corridors, to colonize the French hydrosystems. However, this remains to be verified

in future studies because another hypothesis may be an arrival from another corridor without a long-term establishment if the environmental conditions are not favourable. In this case, contrary to *D. villosus* and *C. curvispinum*, which were able to colonize all corridors, the range expansion of the new species may be constrained by the environmental preferences of these species.

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