Hydrobiologia (2005) 542:203–220
H. Segers & K. Martens (eds), Aquatic Biodiversity II
DOI 10.1007/s10750-004-8930-9

# Native and exotic Amphipoda and other Peracarida in the River Meuse: new assemblages emerge from a fast changing fauna

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*Key words:* aquatic biodiversity, alien species, invasive species, invasibility, community dynamics, *Dikerogammarus villosus*, *Chelicorophium curvispinum*

## Abstract

Samples issued from intensive sampling in the Netherlands (1992–2001) and from extensive sampling carried out in the context of international campaigns (1998, 2000 and 2001) were revisited. Additional samples from artificial substrates (1992–2003) and other techniques (various periods) were analysed. The combined data provide a global and dynamic view on the Peracarida community of the River Meuse, with the focus on the Amphipoda. Among the recent exotic species found, *Crangonyx pseudogracilis* is regressing, *Dikerogammarus haemobaphes* is restricted to the Condroz course of the river, *Gammarus tigrinus* is restricted to the lowlands and seems to regress, *Jaera istri* is restricted to the 'tidal' Meuse, *Chelicorophium curvispinum* is still migrating upstream into the Lorraine course without any strong impact on the other amphipod species. After a rapid expansion *Dikerogammarus villosus* has continued its upstream invasion between 1998 and 2002 at a rate of 30–40 km per year, but no further progression was noticed in 2003. Locally and temporarily the native species (*Gammarus fossarum* and *G. pulex*) and naturalized species (*G. roeseli* and *Echinogammarus berilloni*) *may* have been excluded by the most recent invaders (mainly *D. villosus*), but none of the native and naturalized species has disappeared completely. Therefore, the number of amphipod species found in the River Meuse has increased. Moreover, the native and naturalized species keep on dominating the tributaries from which the recent invaders seem to be excluded. A changing Peracarida community structure is observed along the course of the River Meuse: four native or naturalized species inhabit the upstream (Lorraine) course, three invasive species dominate in the middle reach (Ardenne-Condroz zone), one exotic species is housed in the Border Meuse and three or four invasive species dominate the assemblages in the lowlands.

## Introduction

Introductions of exotic species dramatically increased in the past decades. Rivers and canals are considered among the most invadable systems, especially if they have been subjected to anthropogenic deterioration followed by environmental rehabilitation (Van der Velde et al., 2002). In the case of the macro-crustaceans it is supposed that the assemblages in the Western European rivers were rather stable until the mid 1960s (Pinkster et al., 1992) and that most introductions occurred after 1993 (Van der Velde et al., 2002, Wouters, 2002).

One of the most puzzling questions about the introduction of exotic species is the unpredictable character of any particular invasion (Kornberg & Williamson, 1987) as well as the unpredictable invasibility of any particular community (Levine & D'Antonio, 1999). Some statistical predictions, however, can be made when numerous introductions occur, e.g. the so-called tens rule. This rule holds that one of 10 imported species appears in the wild, one of 10 of such introduced species becomes established and one of 10 of the established species becomes a pest, but this rule suffers many exceptions as pointed out by its authors (Williamson & Fitter, 1996). For some aquatic groups this rule is indeed confirmed (Van der Velde et al., 2002).

Many papers on invasions deal with rather restricted ecosystems regardless of what is going on elsewhere. In this paper, as in Usseglio-Polatera & Beisel (2002b), we intend to analyse the situation for the whole course of the River Meuse, taking profit from the results of national and international surveys. The River Meuse flows through three countries: France (km 0–489), Belgium (km 489–633) and the Netherlands (km 685–943). From km 633–685 the Border Meuse marks the frontier between Belgium and the Netherlands. As most large European rivers, it has been changed strongly by human activities. The alterations (dams, weirs, locks,…) to improve navigation in the river started in the Netherlands in 1825 and in Belgium in 1850 (Vereerstraeten, 1971).

For geo-morphological reasons it is convenient to divide the River Meuse into four main zones: the Lorraine course (km 0–405), the Ardenne-Condroz course (km 405–632), the Border Meuse course (km 633–685) and the lowland course (sand Meuse and tidal Meuse) (km 685–943). In this study on the peracarid communities, however, the Meuse was subdivided into six sections that are defined further in the paper.

From Pagny-sur-Meuse (km 127) to Sedan (km 350) some navigation occurs in the canal de l'Est, running parallel to the river, with some short common reaches. From Sedan to Borgharen (km 632) the river has been deepened and the current speed is slowed down by 58 weirs and locks in France, nine in Belgium and one in the Netherlands. From Namur to Liège, the river is heavily navigated and the banks were petrified in order to withstand the heavy ship's backwash. From Borgharen (km 632) to Maasbracht (km 685) navigation takes place in the parallel Juliana Canal and not in the river itself, the so-called Border Meuse. From Maasbracht to the sea six weirs and locks make the river again commercially and intensively navigated. Its banks were strengthened with blocks.

The nowadays quality of the water can be inferred from regular surveys made on request of the 'Commission Internationale de la Meuse/Internationale Maascommissie', formerly the 'Commission Internationale pour la Protection de la Meuse/Internationale Commissie voor de Bescherming van de Maas' (C.I.M.-I.M.C., 2003, C.I.P.M.-I.C.B.M., 2001, 2002a, b).

The headwaters of the river, surveyed at Goncourt (km 46) and Brixey (km 87) are eutrophicated and contain high level of organic matter; dissolved oxygen can be in deficit. Downstream, from Saint Mihiel (km 177) until Tailfer (km 526), the chemical indicators show a noticeable reduction of the organic load but eutrophication does not decrease much. A local mercury contamination is detected at Ham-sur-Meuse (km 472). From Liège (km 599) to Eijsden (km 620) various indicators (oxygen deficit, organic matter, eutrophication, several heavy metals and anthropogenic bacteria) show multipollution. In the subsequent Border Meuse, surveyed at Lanaken (km 633) and Kinrooi (km 679) the water still contains relatively high levels of various heavy metals, organic mater and is eutrophicated. The load of organic matter decreases at Belfeld (km 716) but it increases again at Keizersveer (km 884). The eutrophication remains rather high. However, it is no longer the case at the mouth (Haringvlietdam, km 943) where the waters from the rivers Rhine and Meuse have mixed. Other quality indicators (pH, temperature, chloride and sodium concentrations) fluctuate in favourable ranges. The calcium concentration is naturally high in the headwaters and decreases downstream.

## Materials and methods

### *Sampling methods*

The present paper presents a meta-analysis and a synthesis of data from various sources: 459 samples ('historical' samples and samples from the tributaries not included) were taken into consideration. No selection on unity in the sampling methods was made. Responding to different objectives, the following methods were used.

(a) Handnet sampling (25 samples): bank sampling of various substrates with a 500 μm mesh size handnet. This method was performed for the Direction générale des Ressources naturelles et de l'Environnement (Ministère de la Région wallonne) in Wallonia in 1991, 1995 and 1998 (Vanden Bossche et al., 1999, Vanden Bossche, 2002, this paper).

(b) Artificial substrates of the C.I.P.M.-I.C.B.M. sampling campaign (117 samples), of the I.B.G.A. type: strong 10-mm mesh nylon netbags are filled with 5 l of 4- to 8-cm stones and a rope about 1.2 m long and left submerged for 28 days (Gay-environnement, 1997). This method was applied in 1998, 2000 and 2001 in France, Belgium and the Netherlands.

(c) Larger artificial substrates used by the R.I.Z.A. (256 samples): stainless steel cages of eight litres are filled with 2-cm glass marbles (De Pauw et al., 1994, Ketelaars & Frantzen, 1995, R.I.Z.A., 1998). This method was applied 12 or 14 times per year from 1992 to 2001 at Borgharen and Grave, the Netherlands.

(d) Small artificial substrates (61 samples) specifically designed for sampling Amphipods in this study: polypropylene nets with 1-cm mesh size are filled with 1 l of calcareous gravel (size: 5.2 ± 3.4 cm$^3$: av. ± st. dev.). The substrates were left in the water for 2–3 weeks and were used in 2002 in France and Wallonia and in 2003 all along the river.

Samples provided by artificial substrates can be considered as reproducible (De Pauw et al., 1986) and thus provide semi-quantitative results. However, artificial substrates of different sizes should not be compared with each other. Unless otherwise stated, the data used in the figures are restricted to those provided by one kind of artificial substrate at a time.

Extra samples were collected in some tributaries, acting as possible reservoirs of species, in the last few kilometres before their confluence with the River Meuse: mainly in the Rivers Semois, Viroin, Lesse and Berwinne. Other extra, 'historical', samples from the collection of the Natural Science Institute of Belgium are mentioned (Wouters, personal communication).

For the sake of clarity the zone or section limits and the sampling points are mentioned with a kilometric reference counted from the source at Pouilly-en-Bassigny (km 0) to the mouth, closed by the Haringvlietdam (km 943). These distances refer to old national systems that were combined, but since the river has been straightened at many places, the actual distances are probably shorter (Fig. 1).

### *Peracarid species found in the River Meuse*

*Amphipoda*
Corophiidae
  *Chelicorophium curvispinum* (Sars, 1895)
Crangonyctidae
  *Crangonyx pseudogracilis,* Bousfield, 1958
Gammaridae
  *Echinogammarus berilloni* (Catta, 1878),
  *Dikerogammarus villosus* (Sowinsky, 1874),
  *Dikerogammarus haemobaphes* (Eichwald, 1841)
  *Gammarus fossarum,* Koch, 1835
  *Gammarus pulex* (L., 1758)
  *Gammarus roeseli* (Gervais, 1835)
  *Gammarus tigrinus*, Sexton, 1939
Talitridae
  *Orchestia cavimana,* Heller, 1865

*Isopoda*
Asellidae
  *Asellus aquaticus,* L., 1758
  *Proasellus meridianus* (Racovitza, 1919)
  *Proasellus coxalis* (Dollfus, 1892)
Janiridae
  *Jaera istri,* Veuille, 1979

*Mysidacea*
Mysidae
  *Hemimysis anomala,* Sars, 1907
  *Limnomysis benedeni*, Czerniavsky, 1882

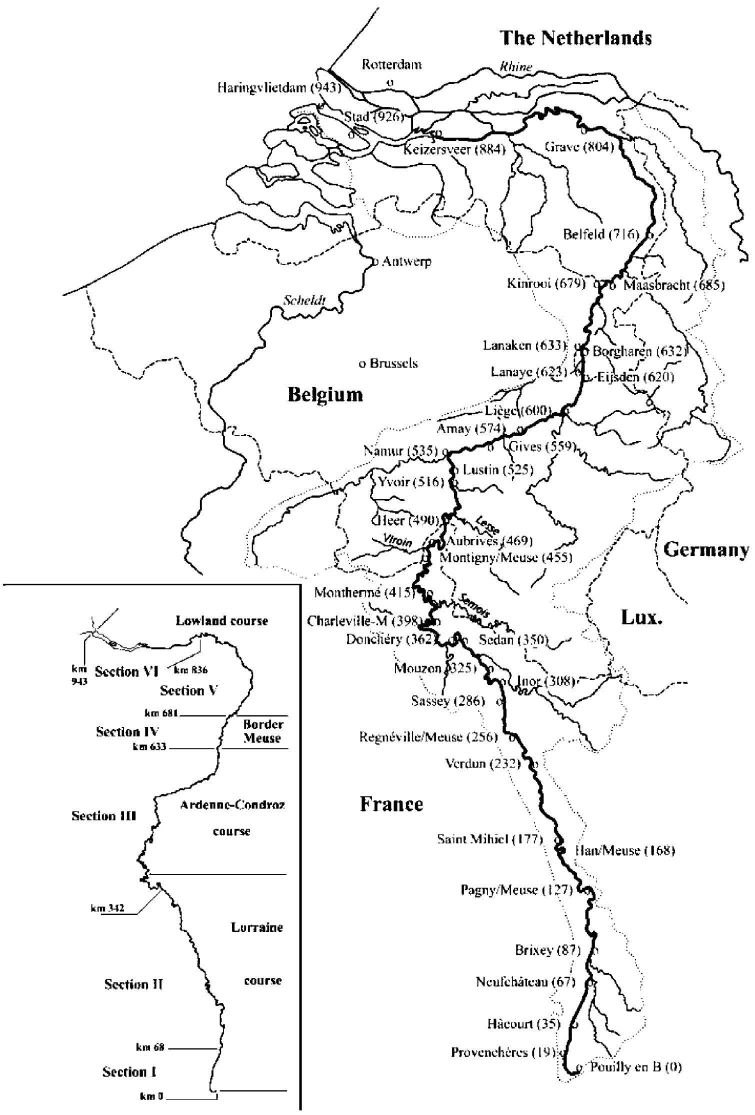

*Figure 1.* Map of the River Meuse with most of the locations mentioned in text. The numbers in brackets refer to the kilometric distances from the source. The zones and sections are figured in the insert.

### *Multivariate analysis*

Prior to perform a correspondence analysis (CA) the data set was worked out. Two locations (Borgharen and Grave), with 12 or 14 samples per year during ten years, contributed for 55% to the whole data set. In order to avoid an imbalance with the other locations, these data were reduced to annual averages. Twelve samples, which did not contain any amphipods or isopods (and would be positioned at the origin of the axes of the factorial planes), have been discarded. The four geo-morphological zones of the Meuse previously defined were reorganized in six sections based on their peracarid community (see further in the text). Finally the log transformed data of the remaining matrix (215 samples × 11 taxa) were processed by correspondence analysis with the software ADE 4.0 (Thioulouse et al., 1997).

Other statistical analyses were made on log transformed numbers of individuals per substrate (or ind. subs.$^{-1}$) with the software STATISTICA 6.

## Results

*Analytical results*

### Amphipoda

*Gammarus fossarum*

*G. fossarum* was present in the artificial substrates at Brixey (km 87) where this species was rather abundant in 1998 and 2000 (29 and 16 ind. subs.$^{-1}$, respectively) but absent in 2001. It was again present at Hâcourt (km 35) in 2002 and at Savigny (km 91) in 2003 (Fig. 2).

*G. fossarum* was mentioned at several places in 1980–84 between Aubrives (km 469) and Rivière (km 522), always just downstream the old weirs, in turbulent water (Meurisse-Genin et al., 1987), at Tailfer and Hastière in 1989 (Frantzen, 1991) and at Hastière (km 494) in 1991 (Ketelaars, 1993). Some individuals were caught at Grave (km 804) in 1996.

It was present in samples from the River Viroin and was the dominant gammarid in 2001 in the River Semois (tributaries of the Meuse at km 465 and 415, respectively).

*Gammarus pulex*

*G. pulex* was present in the artificial substrates from Brixey (km 87) or Hâcourt (km 35) in 2002, to various places from Heer (km 490) in 2000, to Kinrooi (km 679) in 1998 (Fig. 2). In 2001 one isolated specimen was also collected at Lanaken (km 633). In the Dutch Meuse it was found in small numbers at Borgharen (km 632) in 1994 and 1995 and in larger numbers at Grave (km 804) from 1992 to 1996. It vanished there after the arrival of *D. villosus*, but some isolated specimens were caught again in 1999 and 2001 (Fig. 6).

In the Belgian Meuse historical samples showed the presence of *G. pulex* in 1934 at Namèche (km 545) and in 1943–1945 at Hastière (km 494), Hermeton (km 492) and Chertal (km 609) (Wouters, personal communication). In 1980–1984 it was collected at 13 places from Aubrives (km 469) to Amay (km 574) (Meurisse-Genin et al., 1987). It is mentioned at Hastière (km 494) in 1984–1993 by Ketelaars & Frantzen (1995). In our samples the species was dominant in 1991 (80–100% of the gammarids) at four localities from Heer (km 490) to Lustin (km 525). In 1995 it was still dominant at 10 localities sampled between Heer (km 490) and Petit Lanaye (km 624). In 1998 it was still present at eight localities and dominant at two of them (Heer, km 490 and Lustin, km 525). However, in 2000 it had vanished from the Belgian Meuse except from Heer (Vanden Bossche, 2002, this paper). In 2001 and 2002 it was locally present again in small numbers.

*G. pulex* was fairly common in 2002 in the samples from the Rivers Semois, Viroin and Lesse (tributaries of the Meuse at km 415, 465 and 505, respectively).

*Gammarus roeseli*

*G. roeseli*, originating from the Balkan area (Jazdzewski, 1980), can be considered as a naturalized species (it is a former exotic species, well established since a long period and in balance with its environment). It was present in the artificial substrates from Brixey (km 87) to Heer (km 490) (Fig. 2). In the Dutch Meuse it was consistently present at Grave (km 804) in small numbers from 1992 to 2001 (Fig. 6).

In the Belgian Meuse, historical samples (1943–1945) showed the presence of G. *roeseli* at Hastière (km 494) and Hermeton (km 492) (Wouters, personal communication). In 1980–1984 it was mentioned at four places from Chooz (km 480) to Bas-Oha (km 562) (Meurisse-Genin et al., 1987) and at Hastière (km 494) in 1987 (Frantzen (1991). From 1991 to 1998 the species was sporadically found at Heer (km 490) and Yvoir (km 516) and more regularly at Anseremme (km 504). After the invasion by *D. villosus*, it seemed to have vanished from the Ardenne-Condroz part of the river, but some specimens were caught again at Anseremme (km 504) in 2002.

It occurs in the River Sambre and in some canals connected with the River Meuse.

*Gammarus tigrinus*

*G. tigrinus* originates from North America. It was introduced in the Netherlands via Great Britain, probably in 1960 (Pinkster et al., 1992), it invaded the River Meuse at the latest in 1983 and became very abundant in 1991 at Keizersveer (Ketelaars, 1993, Ketelaars & Frantzen, 1995). It is still present from Belfeld (km 716) to Keizersveer (km 884) (Fig. 2).

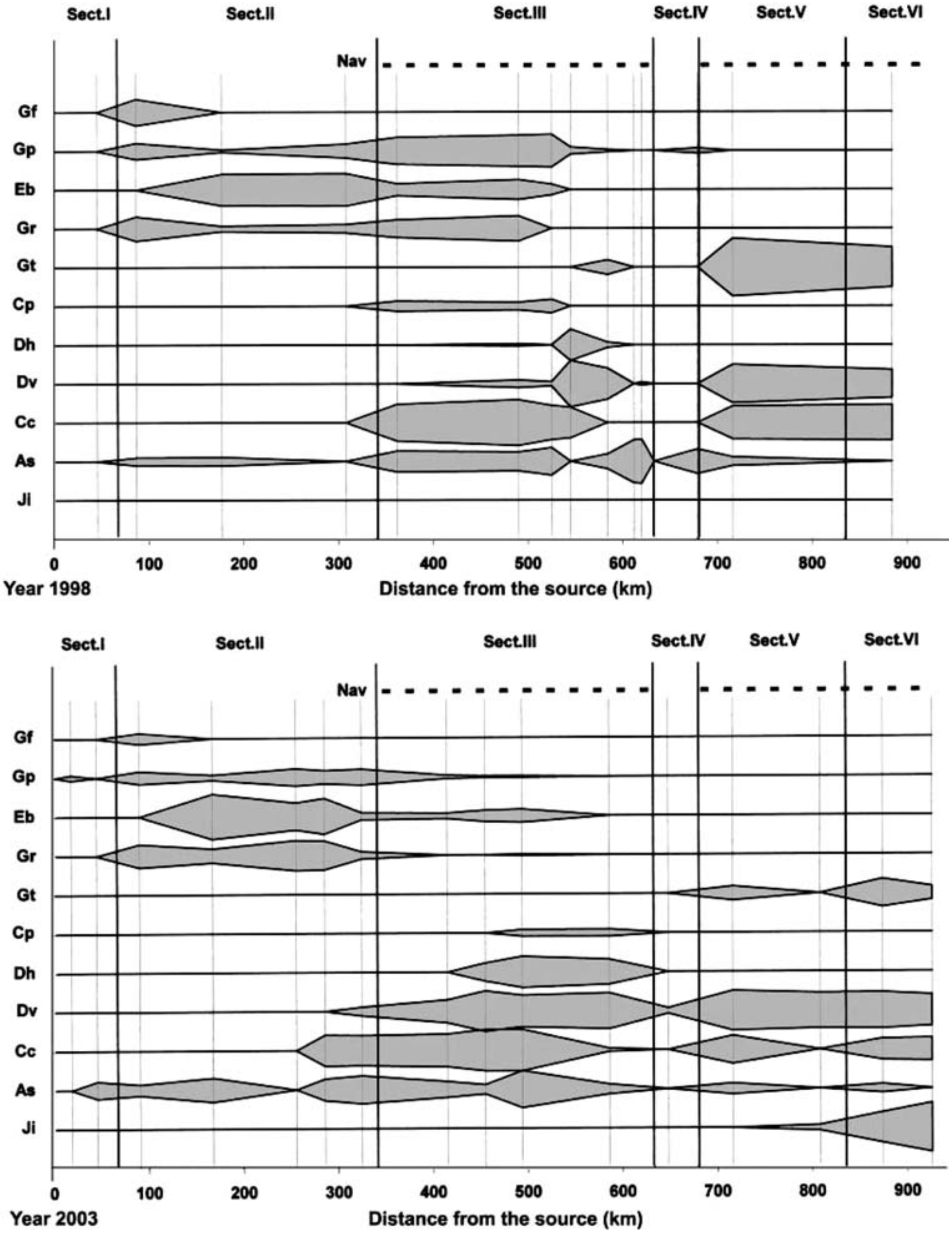

*Figure 2.* Longitudinal distribution of the Amphipoda and Isopoda in the River Meuse, above: in 1998 (C.I.P.M.-I.C.B.M. substrates, but at km 632 and 804: larger substrates) and below: in 2003 (small artificial substrates). Vertical solid lines = section limits, vertical dotted lines = sampling points. Horizontal dotted line (nav) = navigated zone. Other horizontal figures = species densities, the height at each sampling point is proportional to the log of the mean number of individuals per artificial substrate. As = Asellidae (*Asellus aquaticus* + *Proasellus meridianus* + *Proasellus coxalis*), Cc = *Chelicorophium curvispinum*, Cp = *Crangonyx pseudogracilis*, Dh = *Dikerogammarus haemobaphes*, Dv = *Dikerogammarus villosus*, Eb = *Echinogammarus berilloni*, Gf = *Gammarus fossarum*, Gp = *Gammarus pulex*, Gr = *Gammarus roeseli*, Gt = *Gammarus tigrinus* and Ji = *Jaera istri*.

At Grave (km 804) it was the dominant gammarid species from 1992 to 1996 and declined, but did not vanish, after the arrival of *D. villosus* (Fig. 6).

It was collected at Borgharen (km 632) in small numbers in 1992 and from 1994 to 1996, at Petit Lanaye (km 624) in 1995 and at Chokier (km 584) in 1998.

*Echinogammarus berilloni*

*E. berilloni*, originating from South-West France, can be considered as a naturalized species. It was present in the artificial substrates depending on years from Saint-Mihiel (km 177) or Han-sur-Meuse (km 168) to various places from Heer (km 490) to Anseremme (km 504). In 2001 some isolated specimens were also collected at Gives (km 559). It builds up densities that seem to complement those of *G. pulex* and *G. roeseli* (Fig. 2).

*E. berilloni* is present in large proportions (between 15 and 75% of the gammarids) in the Lorraine Meuse. However, it is absent from the headwaters of the river.

In the Belgian Meuse, historical samples showed the presence of *E. berilloni* in 1933 at Dave (km 529) and in 1943–1945 at Hastière (km 494) and Hermeton (km 492) (Wouters, 2002). In 1980–1984 it was common from Aubrives (km 469) to Amay (km 574) (Meurisse-Genin et al., 1987), it was also common in 1989 at Tailfer (km 526) and occurred at Hastière (km 494) in the period 1984–1993 (Ketelaars & Frantzen, 1995). This species was absent from our samples collected in 1991 from Heer (km 490) to Lustin (km 525) but present in the same localities in 1995 and 1998. In the Border Meuse, it was reported until the mid sixties (Pinkster et al., 1992).

*E. berilloni* is the dominant amphipod in the lower courses of the River Viroin (Schmit & Josens, 2004) and the Rivers Lesse and Berwinne (tributaries of the Meuse at km 465, 505 and 618, respectively), but seems to be absent from the lower course of the River Semois.

*Dikerogammarus haemobaphes*

The Ponto-Caspian *D. haemobaphes* invaded the Rhine River basin through the Main-Danube Canal after its opening in 1992 (Schleuter et al., 1994). From then, it expanded massively in Germany (Tittizer et al., 2000; Müller, 2001). Despite the intensive sampling in the Dutch Meuse it was collected only once, at Grave (km 804), in 2000.

This species is quoted here for the first time from Belgium. It appeared in the Meuse in 1998 (concurrently with *D. villosus*), in small numbers at four localities between Namèche (km 545) and Petit Lanaye (km 624). One isolated specimen was also caught the same year at Heer (km 490). In 2000 and the following years it became common in the whole Belgian Meuse, including the blind arms (Vieille Meuse and Nouvelle Gravière) at Lanaye (km 623), but in its upstream expansion it hardly crossed the French-Belgian border (in 2002 and 2003 it was found in small numbers at Montigny-sur-Meuse, km 455) and it remained absent from the Border Meuse (Fig. 2).

*Dikerogammarus villosus*

The Ponto-Caspian *D. villosus* invaded the Netherlands in 1994 (Bij de Vaate & Klink, 1995) through the Main-Danube Canal and the River Rhine (Tittizer et al., 2000) and was first caught in the River Meuse in 1996 at Grave (km 804) (Fig. 6). It reached Borgharen (km 632) in 1997 and in 1998 it was present at 12 localities between Heer (km 490) and Keizersveer (km 884), but it was absent from the Border Meuse (Usseglio-Polatera & Beisel, 2002a, Vanden Bossche, 2002). In the subsequent years, its invasion extended both into the Lorraine course and into the Border Meuse (Fig. 2).

The ongoing upstream invasion by *D. villosus* in the Meuse can be characterised by (a) a front of adults in small numbers (generally one or two individuals per artificial substrate) (b) about 30–60 km downstream a much higher density ( > 50 individuals per artificial substrate) including adults and juveniles and (c) an upstream progression at a speed of 30–40 km per year between 1998 and 2002. The front was at Heer (km 490) in 1998, at Ham-sur-Meuse (km 472) in 2000 and at Mouzon (km 325) in 2002. However, in 2003 it had not moved, it was still found at Mouzon but not upstream (Fig. 3).

*Crangonyx pseudogracilis*

*C. pseudogracilis* originates from North America. It appeared in northern Netherlands in 1979 (Pinkster & Platvoet, 1983), but it was never collected in the Dutch Meuse and was first caught in the Belgian Meuse at Heer (km 490) in 1991 (Vanden Bossche, this paper). In 1995 it was present from Anseremme (km 504) to Namur (km

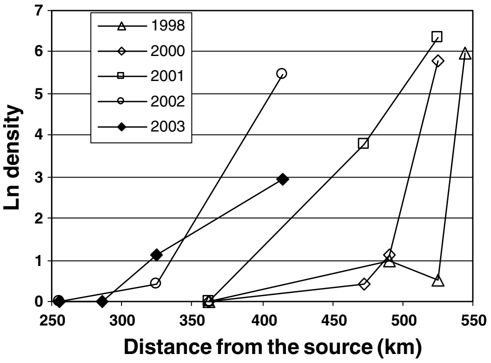

*Figure 3.* The ongoing upstream invasion *by Dikerogammarus villosus* (natural log of the mean number of individuals per artificial substrate) in the Meuse from 1998 to 2002. For the sake of clarity only the three or four most upstream locations where *D. villosus* was present have been figured. The data of 1998, 2000 and 2001 were acquired with C.I.P.M.-I.C.B.M. substrates, those of 2002 and 2003 with small artificial substrates.

535) and was common from Yvoir (km 516) to Loyers (km 541). In 1998 it was still present in small numbers from Donchéry (km 362) to Lustin (km 525) (Fig. 2) and had become abundant in a blind arm (Vieille Meuse) at Lanaye (km 623). In 2000 it seemed to be vanishing: few specimens were found at Donchéry (km 362) and Chokier (km 584) and one isolated specimen was caught in the Border Meuse at Kinrooi (km 679). In 2001 it was present again from Lustin (km 525) to Lanaye (km 621). In 2001 and 2002 it was no longer found in the French Meuse but continued to be abundant in the blind arms at Lanaye (km 623).

*C. pseudogracilis* was reported to be abundant in some gravel pits, liable to flooding, that were dug along the Border Meuse (Klink & de la Haye, 2000).

### *Chelicorophium curvispinum*

The Ponto-Caspian C. *curvispinum* was first recorded in the Belgian Meuse near Huy (km 566) in 1981 and had become a dominant species of the benthic fauna at Champalle (km 515) in 1986. In the same year it had extended its expansion until Montigny-sur-Meuse (km 455) (Wouters, 1985, d'Udekem d'Acoz & Stroot, 1988) and was abundant at Tailfer (km 526) in 1989 (Ketelaars & Frantzen, 1995) and at Hastière (km 494) in the period 1984–1993 (Ketelaars & Frantzen, 1995). In France it is still migrating upstream: it was present in the artificial substrates at Donchéry (km 362) in 1998, Inor (km 308) in 2000 and 2001 and Sassey (km 286) in 2003. Its average migration speed is therefore about 15 km per year. In 1987 the species invaded the Dutch part of the River Rhine from the German part of that river (Van den Brink et al., 1993) and subsequently the Dutch Meuse (Van der Velde et al., 1998). Presently it can be found from the lower Lorraine stretch until the mouth of the river with a gap in the Border Meuse (Fig. 2).

At Grave (km 804) the Dutch survey showed that its density increased rather steadily from 1992 to 2001 with a temporary decrease in 1997, at the onset of *D. villosus*. At Borgharen (km 632) some scattered individuals were collected from 1993 to 2001 (Fig. 6).

Some specimens were found in the River Lesse in 2002 at about 5 km from the confluence with the Meuse (km 505) and repeatedly caught, equally in small numbers, in the River Viroin in 2002 and 2003 at about 5 km from the confluence with the Meuse (km 465).

### *Orchestia cavimana*

*O. cavimana* lives along the river banks. It is therefore rarely sampled with artificial substrates and is not included into the figures. It is locally common along the river, under stones or dead plant debris. It was introduced in the early 20th century and was mentioned at Jambes (km 533) in 1983 and along the Zuid-Willemsvaart Canal in 1980 (Wouters, 2002). In 2002 and 2003 special attention was paid at this species and it was found at Montigny-sur-Meuse (km 455), Givet (km 489), Waulsort (km 498), Gives (km 559), Lanaye (km 621), Maasmechelen (km 648), Belfeld (km 716), Balgoij (km 808) and Stad aan 't Haringvliet (km 926).

## Isopoda

### *Asellus aquaticus*

*A. aquaticus* is present in small numbers in the Lorraine and Ardenne courses of the Meuse and becomes more common downstream the French-Belgian border. It reaches high densities downstream from Liège and is often the dominant peracarid at Eijsden (km 620), in the still water of the blind arms at Lanaye (km 623) and at Borgharen (km 632). It is present in the Border Meuse and in the lowlands: at Grave (km 804) its density decreased in 1997 when *D. villosus* became dominant (Fig. 6). It is thus the most ubiquitous peracarid in the Meuse (Fig. 2).

In 1980–1984 it was common at 17 locations from Aubrives (km 469) to Lixhe (km 618) (Meurisse-Genin et al., 1987) and in 1984–1993 at four locations from Hastière (km 494) to Borgharen (km 632) but rare at Keizersveer (km 884) (Ketelaars & Frantzen, 1995, Ketelaars, 1993).

*Proasellus meridianus*

*P. meridianus* is an exotic not invasive species originating from southern Europe (Tittizer et al., 2000). It was regularly collected, but always in small numbers, from Brixey (km 87) to Gives (km 559) and, in 2003, from Goncourt (km 46) to Flémalle (km 586). It was also sporadically collected at Eijsden (km 620) and Keizersveer (km 884). In the intensive surveys at Borgharen (km 632) it was caught sometimes from 1994 to 1997 and at Grave (km 804) from 1992 to 1995.

In 1980–1984 it was present at 11 locations from Aubrives (km 469) to Amay (km 574) (Meurisse-Genin et al., 1987) and in 1984–1993 occasionally at Hastière (km 494) and Keizersveer (km 884) (Ketelaars & Frantzen, 1995).

*Proasellus coxalis*

*A. coxalis* is another exotic not invasive species originating from southern Europe (Tittizer et al., 2000). It was collected once in the intensive surveys at Borgharen (km 632) in 1996 and several times at Grave (km 804) from 1992 to 1996.

*Jaera istri*

The Ponto-Caspian *J. istri* invaded the River Rhine through the Main-Danube Canal and reached the German-Dutch border in 1997 (Tittizer et al., 2000). It was first found in the River Meuse at Grave (km 804) in 1999 where it became abundant in 2001 (Fig. 6). In 2003 it was collected from Balgoij (km 808) to Stad aan 't Haringvliet (km 926). More upstream it was collected only once at Belfeld (km 716) in 2000 (Fig. 2).

## Mysidacea

*Hemimysis anomala*

*H. anomala* is not correctly sampled with artificial substrates. The species is therefore not included into the figures. This Ponto-Caspian species was first discovered in 1997, near Keizersveer, in a

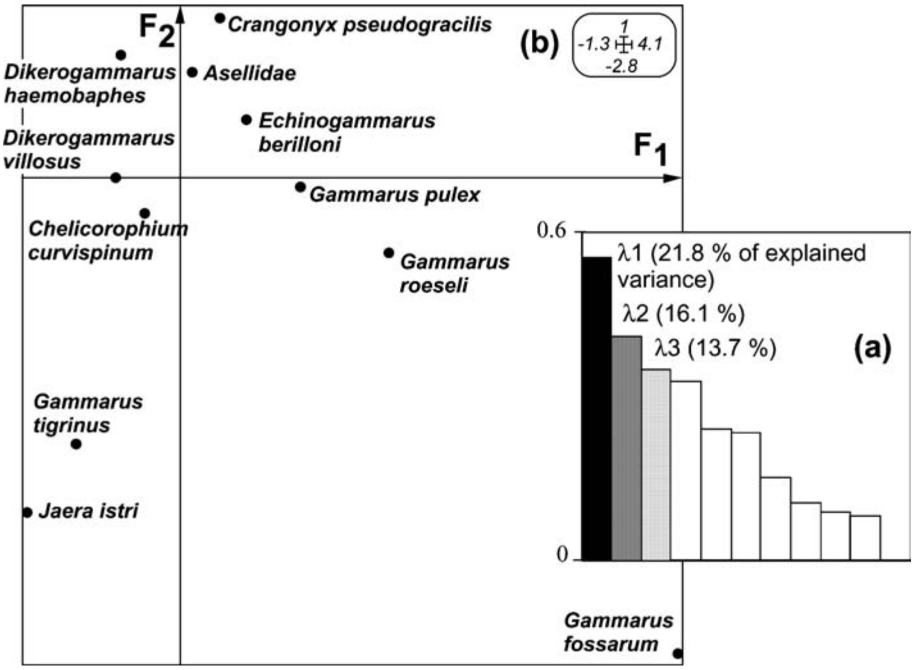

*Figure 4.* Ordination of species by Correspondence Analysis, (a). Histogram of eigenvalues, (b). Distribution of species ( = solid circles) on the F1–F2 factorial plane.

storage reservoir fed with Meuse water. The first record in the river Meuse itself (Keizersveer, km 884) dates from 1998 (Ketelaars et al., 1999). It was also collected at Grave (km 804) in 1999. In Belgium it was found at Gives (km 559), Lustin (km 525) and Heer (km 490) in 2000 and in the blind arms at Lanaye (km 623) in 2001 (Vanden Bossche, 2002). All these findings in the River Meuse are unique.

### *Limnomysis benedeni*

*L. benedeni* is not correctly sampled with artificial substrates and is therefore not included into the figures. This Ponto-Caspian species was first discovered in the Biesbosch, Dutch Meuse basin, in 1998 (Ketelaars et al., 1999). In 2000 and 2001 it was collected in the River Meuse itself at Keizersveer (km 884) and Belfeld (km 716).

### *Multivariate analysis*

Results of the correspondence analysis are shown in Figures 4 and 5. The two first factors explain 21.8% and 16.1% of the variance, respectively. They are both linked with the longitudinal gradient of the river and therefore generate an arch (Guttman effect). The factorial plane F1–F2 will be interpreted in terms of amphipod and isopod communities (see discussion).

The third factor (not shown) is linked with the temporal change of the fauna and explains 13.7% of the total variance.

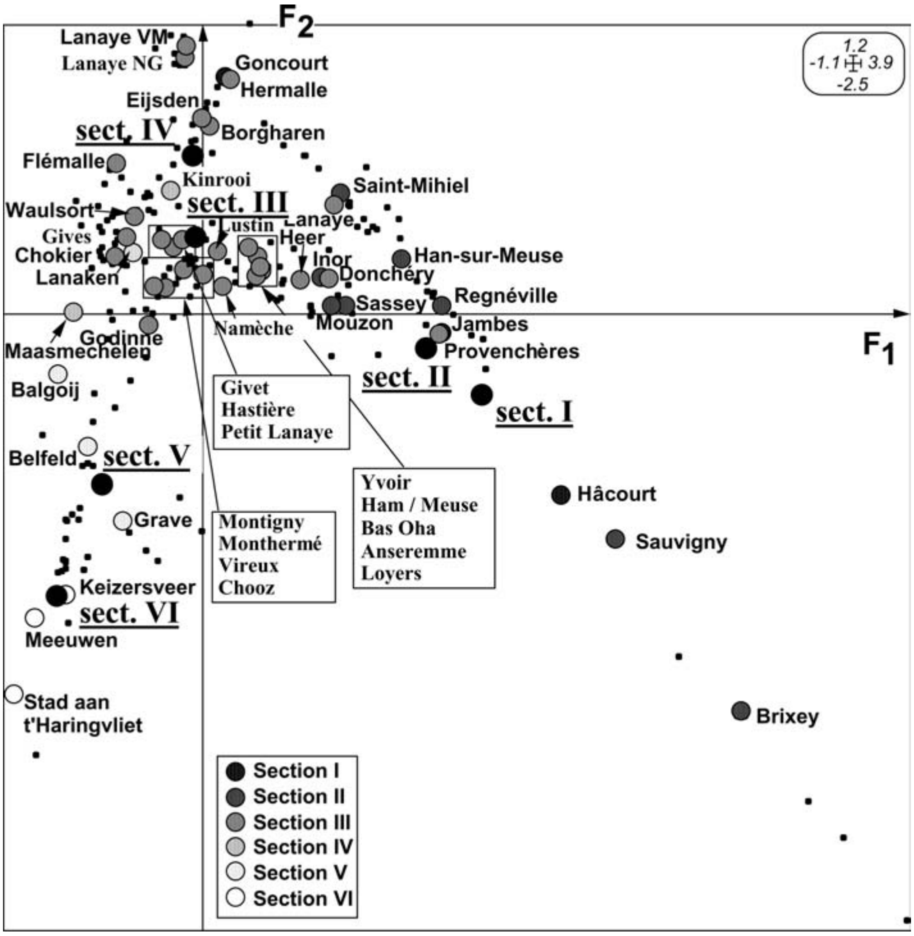

*Figure 5.* Ordination of samples, sites and sections by Correspondence Analysis. Distribution of samples (= small solid squares) on the F1–F2 factorial plane of the analysis. Each site (solid circle) was positioned at the weighted average of the sample positions representing this site. Each section (black solid circle) was positioned at the weighted average of the sample positions representing this section.

## Discussion

Few information is available on the former composition of the Amphipoda and Isopoda communities of the River Meuse. However, from the samples collected during the second half of the 20th century until the early eighties, it can be inferred that the community of the Ardenne-Condroz course of the river consisted of four Amphipoda, *G.pulex*, *G. roeseli*, *G. fossarum* (the last species located just downstream the old weirs), *E. berilloni* and two Isopoda, *A. aquaticus* and *P. meridianus*, (Meurisse-Genin et al., 1987, Vanden Bossche, 2002, Wouters, 2002 and personal communication). In the lowland courses the Meuse housed mainly *G. pulex* and *E. berilloni* (Pinkster et al., 1992) and typical estuarine species as *Gammarus duebeni* Liljeborg, 1851 and *G. zaddachi* (Sexton, 1912) which were present in the Haringvliet (Den Hartog, 1964; Pinkster et al., 1992).

New communities have developed in the River Meuse as a consequence of successive introductions: *C. curvispinum* in 1981 (Wouters, 1985, d'Udekem d'Acoz & Stroot, 1988) and 1987 (Van der Velde et al., 1998), *O. cavimana* in 1983 or earlier (Wouters, personal communication), *G. tigrinus* in 1983 (Frantzen, 1991, Ketelaars & Frantzen, 1995), *C. pseudogracilis* in 1991 (Vanden Bossche, this paper), *D. villosus* in 1996 (this paper) and *D. haemobaphes* in 1998 (this paper).

### *The community of the head of the river (km 0–67) (section I)*

Section I (km 0–67, 12 samples) (Fl > 0 in the first factorial plane, Figs. 4 and 5) is characterized by an assemblage of three native species (*G. fossarum*, *G. pulex* and *A. aquaticus*) and one naturalized species (*G. roeseli*) with relatively low densities: some scattered individuals were caught at Provenchères (km 19), Hâcourt (km 35) and Goncourt (km 46). Six out of the 12 samples that did not contain any amphipods or isopods (discarded from the factorial analysis) came from this section. This rarity is thought to be linked with (a) a deepened riverbed and a very slow current, favouring the sedimentation of organic and locally anoxic mud, (b) the erosion of the surrounding clayey soils resulting in a clogged bottom substrate, (c) consequently the scarcity of suitable hiding places despite the presence of some aquatic vegetation (mainly helophytes) and (d) the fish abundance (Usseglio-Polatera, personal observations).

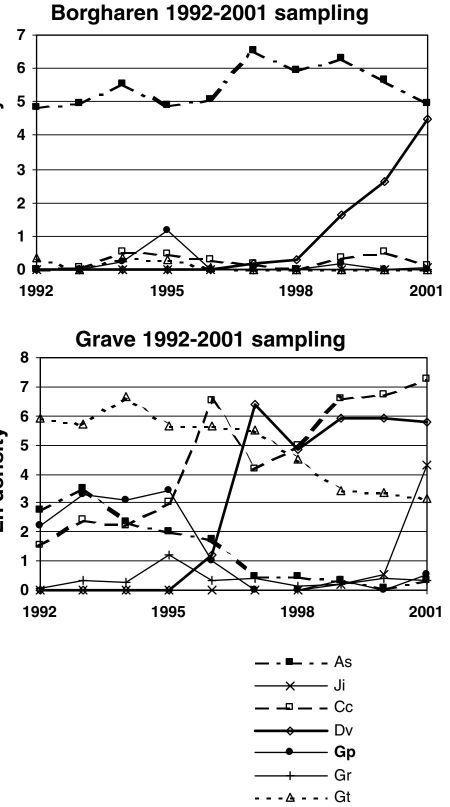

*Figure 6.* Temporal changes of the Amphipoda and Isopoda in the River Meuse, above: at Borgharen (km 632) and below: at Grave (km 804). Every annual point is the natural log of the average of 12 or 14 samples collected mostly from May to October with large artificial substrates. As = Asellidae (*Asellus aquaticus* + *Proasellus meridianus* + *Proasellus coxalis*), Cc = *Chelicorophium curvispinum*, Dv = *Dikerogammarus villosus*, Gp = *Gammarus pulex*, Gr = *Gammarus roeseli*, Gt = *Gammarus tigrinus* and Ji = *Jaera istri.*

### *The native-naturalized community in the upper Lorraine course (km 68–341) (section II)*

Section II (km 68–341, 35 samples) (Fl > 0 in the first factorial plane, Figs 4 and 5) is characterized by an assemblage of native and naturalized species: *G. fossarum*, *G. pulex*, *G. roeseli*, *E. berilloni*, *A. aquaticus* and *P. meridianus*, making a community that seems mature and rather stable: (a) from 1998 to 2001 every C.I.P.M.-I.C.B.M. artificial substrate (except one) retrieved between 50 and 120 individuals ($n = 21$ samples) and (b) in 2002 and 2003 every smaller artificial substrate (except three) retrieved between 70 and 270 individuals ($n = 14$ samples). In the community, as suggested by Figure 2, (a) a significant negative correlation exists between *E. berilloni* and *G. roeseli* and (b) a significant positive one exists between *G. pulex* and *G. roeseli*.

This section of the River Meuse has not been modified for navigation. We observed that it offers a variety of biotopes with locally shallow and fast flowing water and diverse aquatic vegetation. At Regnéville (km 256), for example, the algae *Enteromorpha intestinalis* and *Chara vulgaris* and the moss *Fontinalis antipyretica* coexist with a variety of spermaphytes: *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Elodea* sp., *Potamogeton pectinatus*, *P. perfoliatus*, *Lemna minor*, *L. trisulca*, *Nuphar lutea*, *Butomus umbellatus*, *Sagitaria sagittifolia* and *Sparganium demersum*.

The most downstream portion of this community was invaded by *C. curvispinum* without any apparent damage: the presence of 50 or more individuals per substrate at Sassey (km 286), Inor (km 308) or Mouzon (km 325) has not reduced the density of the native-naturalized community. *C. curvispinum* should not compete with the gammarids and asellids since it fills a totally different niche (Van der Velde et al., 1998). However, this community is downstream threatened by *D. villosus*, which reached Mouzon (km 325) in 2002. It is worth to notice that in 2003 *D. villosus* did not move further upstream (see section III). Perhaps the species has reached its uppermost extension in the River Meuse.

Despite the impression of a stable community it is worth to mention that significant variations (ANOVA, $p < 0.05$) between years were recorded for *G. fossarum* (from 0 to 29 ind. subs.$^{-1}$) and for *G. pulex* (from 8 to 24 ind. subs.$^{-1}$) in localities that were not subjected to any recent invasion. On the other hand in the same locations *E. berilloni* exhibited little variation between years (from 25 to 29 ind. subs.$^{-1}$).

### *The invasive community of the lower Lorraine and Ardenne-Condroz courses (km 342–632) (section III)*

Section III (km 342–632, 88 samples) (F2 > 0 in the first factorial plane, Figs. 4 and 5) associates native or naturalized species (*G. pulex*, *E. berilloni* and *A. aquaticus*) and recent dominating invaders (*C. pseudogracilis*, *D. haemobaphes*, *D. villosus* and *C. curvispinum*). Two of them (*C. pseudogracilis* and *D. haemobaphes*) that reach the most positive values on the axis F2 are thus restricted to this section.

The amphipod community in the Ardenne-Condroz course was in 2002–2003 dominated by recent invaders: (a) by *D. villosus* and *C. curvispinum* from Monthermé (km 415) until Givet (km 489), (b) by *D. villosus*, *D. haemobaphes* and *C. curvispinum* from Waulsort (km 498) to Gives (km 559) and (c) by *D. haemobaphes* and *C. pseudogracilis* in the blind arms of Lanaye (km 623). Those invaders were probably transported by ship in ballast water or among fouling organisms attached to the hull. Most of them may have been released near Liège which is the second European inland harbour and all along the section, which is submitted to an upstream decreasing gradient of navigation (Vanden Bossche et al., 1999).

A transition zone extends in the lower Lorraine and upper Ardenne-Condroz courses (approximately km 350–500) where native and exotic species are struggling. This unstable community reached its highest species richness with nine peracarid species (of which five introduced) in samples taken at Heer (km 490) in 2000 and at Hastière (km 494) in 2003. Most of the samples of the transition zone contained six or seven species versus the presence of three or four in the native-naturalized community.

The success of *C. curvispinum* in the River Rhine was claimed to be linked with relatively high chloride concentration (Van den Brink et al., 1993). However, Harris & Bayliss (1990) showed its acclimation capacity toward lower salt concentrations. This may have been achieved in the Meuse where the annual average chloride concentration, i.e. 0.41 mMol l$^{-1}$ from 1999 to 2002 at the French-Belgian border (C.I.M.-I.M.C., 2003, C.I.P.M.-I.C.B.M., 2001, 2002a, b), is lower than the threshold initially proposed for this species (Bayliss & Harris, 1990). It is even lower in the Rivers Viroin and Lesse where *C. curvispinum* is also present.

It was also claimed that *C. curvispinum* had filled an ‘empty niche’ (Den Hartog et al., 1992). Actually it was the first tubiculous amphipod that colonised the Rivers Rhine and Meuse (Van der Velde et al., 1998) and thus filled a niche that never existed there before. It is an active filter feeder (Hynes, 1970) that benefits from the high phytoplankton contents of large rivers (Van der Velde et al., 1998). Therefore the high phytoplankton content of the Lorraine Meuse should favour its continuing upstream migration in the Meuse, but the lesser phytoplankton content of the tributaries will probably hamper its invasion into those streams.

*C. curvispinum* is a rather fast migrant: d'Udekem d'Acoz & Stroot (1988) estimated its upstream migration speed at about 17 km per year. From those observations in 1986 to our first data, in 1998, this species migrated from Montigny-sur-Meuse (km 455) to Donchéry (km 362), i.e. at a speed of about 8 km per year. During the present study it reached Sassey (km 286) in 2003, its speed thus had again increased at about 15 km per year. Since upstream migration was regular we suggest that it moved upstream actively, i.e. in addition to ship transportation.

The behaviour of the most aggressive invader, *D. villosus*, can be characterized by (a) the high speed of upstream range extension: 30–40 km per year, i.e. about 100 m per day. As section III is entirely navigable, this high upstream speed may be favoured by ship transportation. However, migration occurs regularly and proceeds without 'gaps'. It might thus also be an active migration in addition to ship transport. The structure of the Meuse cut by weirs and locks into reaches of slow flowing water may obviously facilitate this migration, (b) Its high and fast conquering capacity: once the first adults have appeared in the samples the species becomes dominant already one year later. This invasive efficiency can be related with some of its biological traits such as its intra-guild predation behaviour (Dick & Platvoet, 2000) and its ability to colonize a wide range of substratum types (Devin et al., 2003). (c) Once established this invasive gammarid often builds up higher densities (200–500 ind. subs.$^{-1}$) than the previous native-naturalized community (50–120 ind. subs.$^{-1}$). The densities that *D. villosus* achieves are so high that they can hardly be supported by its predatory behaviour alone, therefore we suggest that it is also able to exploit the available food resources more efficiently than the native gammarid community.

The annual changes in the communities in section III suggest that *D. villosus* eliminates firstly *G. roeseli* and secondly *G. pulex*. *E. berilloni* seems to withstand this competition better at least at some locations. This is consistent with the dynamics observed in the annual cycle of the gammarids at Montigny-sur-Meuse (km 455) (Josens, unpublished).

Despite its migration dynamics, *D. villosus* has not yet been found in the Rivers Semois, Viroin and Lesse even at a short distance from their confluence with the Meuse. There does not seem to be any physical barrier preventing the upstream migration. Those tributaries are more natural, not navigated, flow faster, contain less dissolved salts, are cooler and poorer in phytoplankton than the Meuse, but it is too early to state which factor(s) could explain their non invasibility. Those tributaries therefore keep on sheltering the native species that could be able to reinvade the Meuse in case of a decreasing aggressiveness of *D. villosus*.

It is worth to mention the amazing extension of *D. haemobaphes* which is almost restricted to the Belgian Meuse. This invading species has found there favourable conditions that seem to be rather far from those occurring in Lake Balaton, where it lives among floating *Myriophyllum spicatum* (Musko, 1993). As it was pointed out by Usseglio-Polatera & Beisel (2002b) locations from km 362–525 display close physico-chemical characteristics but faunal organization vary deeply from the French to the Belgian Meuse, the frontier being located at km 490. The river is navigable for boats and barges of 300 and 1350 tons upstream and downstream from Givet (km 489), respectively. Indeed some relevant habitat parameters, such as the heterogeneity of current velocity, depth and substrates and the extent of impoundment and embankment for navigation change definitely at Givet and may be decisive in explaining *D. haemobaphes* upstream migration restriction.

### *The Border Meuse community (km 633–680) (section IV)*

Section IV (km 633–680, 149 samples) (Fl $< 0$ and F2 $> 0$ in the first factorial plane, Figs 4 and 5) is an impoverished stretch dominated by *A. aquaticus* and *D. villosus*. Five out of the 12 samples that did not contain any amphipods or isopods (discarded from the factorial analysis) came from this section. Between the Condroz and the lowland courses, the Border Meuse used to be a 'no-Amphipod stretch' in the period 1981–1990. According to Bij de Vaate (1995) a permanent high concentration of cadmium was responsible for this former amphipod absence. Although the cadmium concentration has been reduced substantially since 1992 (at $<0.5\ \mu g\ l^{-1}$: Volz et al., 2002), this section still suffers multipollution and its gammarid community is very slowly recovering. In 1998 some specimens of *G. pulex* were caught at Kinrooi (km 679). The first *D. villosus* were collected in the Border Meuse in 2000 at Lanaken (km 633) and Kinrooi (km 679) and catches were a little more abundant in 2001 at Lanaken. *D. villosus* was still the only gammarid present at Maasmechelen (km 648) in 2003 in small numbers.

Very nearby, at Borgharen (km 632) the intensive 1992–2001 sampling suggests that the conditions were getting better for the gammarids there than in the Border Meuse: *D. villosus* was collected first in 1997 and its density steadily increased (Fig. 6). However, it did not increase as fast as in the invaded locations of section III. Moreover a dramatic drop of asellid densities can be mentioned in 1998 from Borgharen (km 632) to the Border Meuse, one km downstream (Fig. 2).

Although the region of Liège (km 588–610) has been incriminated (Volz et al., 2002), it is worth to point out the complex situation downstream this industrial area. At this point the River Meuse undergoes a unique feature: it feeds three canals (Albert, Juliana and Zuid-Willemsvaart), leaving, when discharge is low, a minimal residual discharge of 10 $m^3\ s^{-1}$ through the dam of Borgharen in the Meuse itself (treaty of January 17, 1995, between Flanders and the Netherlands). There is no navigation on the Border Meuse. However, in the Border Meuse, the volume, current and depth fluctuate dramatically in short periods of time. In this area the amphipod communities show a complex pattern. On the one hand the samples taken in section III of the main channel of the river [at Hermalle-sous-Argenteau (km 612) in 1998, at Lixhe (km 618) in 2000 and at Eijsden (km 620) in 1998, 2000 and 2001] all contained either no amphipods or low densities (0–5 ind. subs.$^{-1}$). On the other hand the samples collected in the blind arms near Lanaye (km 623) in 1998, 2001 and 2002 did contain high densities (90–190 ind. subs.$^{-1}$) of *C. pseudogracilis* and both *Dikerogammarus* species (mainly *D. haemobaphes*). These blind arms, however, are widely connected to the main channel and thus similarly subjected to the same chemical characteristics. Moreover the samples collected at Borgharen (km 632) in still water contained only few amphipods in 1998 and 1999 but increasing densities in 2000 and 2001 (Fig. 6), whereas the densities stayed low at Lanaken (km 633) in the same years. Therefore a pollution effect alone cannot explain the absence or rarity of amphipods. It is striking that they are present in still waters and lacking in either strongly waved water (by navigation) or swiftly flowing water with huge level changes (in the Border Meuse).

Hynes (1954) established that water movement increases the osmoregulation capacity of gammarids through a better uptake of soluble ions: this could also be true for pollutants. It can be thought that animals that are undermined by multipollution can less easily withstand flowing or turbulent water and this should even be worse if the water level unpredictably changes as it is the case just downstream the dam of Borgharen (km 632).

Moreover, more downstream, in section V, the amphipods regain very high densities e.g. at Belfeld (km 716), Grave (km 804) and Keizersveer (km 884) despite the fact that cadmium bio-availability seems to stay high: the zebra mussel bioaccumulates as much Cd at Keizersveer as at Eijsden (km 620) (Maas, 2001).

### *The sand Meuse community (km 681–835) (section V)*

Section V (km 681–835, 140 samples) ($F1<0$ and $F2<0$ in the first factorial plane, Figs 4 and 5) houses only recent invaders (*D. villosus*, *C. curvispinum* and *G. tigrinus*).

This section is heavily navigated and the banks have been strengthened with blocks. The phytoplankton is less abundant than in the upstream sections and the vegetation is dominated by filamentous green algae (personal observations).

The 10-year intensive sampling at Grave (km 804) shows a contrasted situation before (1992–1995) and after (1997–2001) the establishment of *D. villosus* (Fig. 6). In 1992–1995 the community was dominated by *G. tigrinus* and *G. pulex* and the

Asellidae were moderately abundant. *G. roeseli* was present but rare and *C. curvispinum* increased slowly. *D. villosus* was collected first in May 1996 and became already dominant in 1997. From 1997 to 2001 the Asellidae and native gammarids almost vanished and *G. tigrinus* was reduced drastically. However, *C. curvispinum* kept on increasing and *J. istri* became moderately abundant in 2001.

The population dynamics followed a little different pattern at Belfeld (km 716): *D. villosus* became dominant in 2000 and *G. tigrinus* regressed. In contrast to Grave, *C. curvispinum* regressed and *J. istri* did not achieve its settlement. It is indeed known that *D. villosus* preys upon other macroinvertebrates such as *G. tigrinus* and *C. curvispinum* (Dick & Platvoet, 2000). The results from Belfeld could therefore be expected, but those from Grave show that another outcome is possible.

### *The 'tidal'Meuse community (km 836–943) (section VI)*

Section VI (km 836–943, 10 samples) (Fl < 0 and F2 < 0 in the first factorial plane, Figs 4 and 5) is rather similar to section V and also houses only recent invaders (*C. curvispinum*, *G. tigrinus* and *J. istri*). *D. villosus* here became dominant with some delay.

The 'tidal' Meuse, downstream the Lith dam, has no longer been subjected to tides since the closure of the Haringvliet in 1970. Therefore the typical estuarine species *Gammarus duebeni* and *Gammarus zaddachi* disappeared from the Haringvliet (Pinkster et al., 1992). Although few differences could be expected from section V, the 'tidal' Meuse is considered apart because it is directly and strongly influenced by the Waal, one of the major distributaries of the River Rhine.

Two species were very abundant in the 1996 samples from Keizersveer (km 884): *G. tigrinus* and *C. curvispinum*. *D. villosus* was first found in 1998, but it might have been present already in 1997. The subsequent increase of its density was rather slow and it became dominant only in 2001. Its aggressiveness towards the other species seems to be milder since *G. tigrinus* and *C. curvispinum* hardly regressed.

The samples collected in 2003 at Meeuwen (km 874) and Stad aan 't Haringvliet (km 926) are very similarly dominated by *D. villosus* and *C. curvispinum*. An extra species, *J. istri*, was the most abundant in one of the samples collected at Stad, in a muddy place, which contrasts with its reputation of a 'strictly rheophil' organism in the River Danube (Tittizer & Banning, 2000).

### *Invasibility of the River Meuse*

Obviously the different sections of the Meuse are neither equally likely to be invaded nor invadable by the same way. Sections VI and V can be invaded easily either by ship transportation, by active migration or simply by drifting from the River Rhine (via connecting canals in the case of section V). Section III can be invaded only by ship transportation as section IV, till now, does not offer favourable survival conditions for most peracarids and should constitute a barrier against active migration. Exotic species have indeed been introduced into Section III mostly between Namur and Liège where heavy navigation occurs. From Namur the upstream migration of exotic species progresses regularly, which suggests that, besides transport by ship, it may be due to active migration. Section II is not navigable, but navigation takes place in the canal de l'Est running parallel to the river with some short common reaches. Therefore if some ship transportation occurs then the invaders should easily reach Pagny-sur-Meuse (km 127), the uppermost navigable point of the Meuse. The non navigable section I, as well as the tributaries, can be invaded only through an active spread of the invaders and this has not yet occurred. However, in some cases canoeing activities might also facilitate the transportation of exotic species (e.g. in the River Lesse).

The invasibility of the River Meuse seems to be lower than of the River Elbe. In the latter, *D. villosus* was probably introduced near Magdeburg in 1998 (Tittizer et al., 2000) and spread in the same year over more than 200 km. In 1999 the species occurred over a stretch of 500 km and by 2001 it had invaded the whole German course of the Elbe, which is totally navigable, except the tidal section of the river (Krieg, 2002).

Among the predictions made for invasive fishes (Moyle & Light, 1996) some could apply to the peracarid fauna of the Meuse: (a) the most successful invaders are those adapted to the local hydrologic regime, (b) a much wider range of species can invade systems with higher levels of human disturbance and (c) a much wider range of species can invade systems with assemblages or organisms that have been temporarily disrupted or depleted. In its native region *E. berilloni* inhabits the middle reaches of streams (Pinkster, 1993), which predisposed this species to invade the tributaries of the Meuse and the Meuse itself but not its headwaters. On the other hand *D. villosus* and other recent invaders do not enter into the non navigable tributaries of the Meuse probably because the hydrologic regimes of their native water bodies are those of navigable or canalised streams, which are totally different from the shallow and rather fast flowing tributaries of the Meuse.

Moyle & Light (1996) and Tittizer (1996) pointed out the fact that extinctions following invasions in rivers and canals are rare. In case of the Meuse this applies only if the whole river is taken into consideration. At a more local scale, the native species have actually been driven to extinction.

## Conclusions

In general, the peracarid species richness of the River Meuse has increased because of the arrival of exotic species, but locally the native species have been driven to extinction. The success of the invasive species in each section of the river depends merely on the local hydrological conditions: most of the recent invaders originating from large water bodies have taken advantage of the impoundment of the river in its sections III, V and VI.

The Meuse basin shows a *gradient* of invasibility linked with the gradient of anthropogenic impacts. It exhibits a rather high level of resistance against invasions in its upper course as well as in its tributaries that have not been impounded and that act as reservoirs for the native species.

## Acknowledgements

We want to thank the A.E.R.M. (Agence de l'Eau Rhin-Meuse) and the research consultancy GREBE for the loaning of the C.I.P.M.-I.C.B.M. samples collected in France, the CRNFB-MRW (Centre de Recherche de la Nature, des Forêts et du Bois, DGRNE, Ministère de la Région wallonne) for the loaning of the C.I.P.M.-I.C.B.M. samples collected in Wallonia, the VMM (Vlaams Milieu Maatschappij) for the loaning of the C.I.P.M.-I.C.B.M. samples collected in Flanders, the R.I.Z.A. (Institute for Inland Water Management & Waste Water Treatment), that provided us the results of the C.I.P.M.-I.C.B.M. samples collected in the Netherlands and their ten-year surveys at Borgharen and Grave, the Netherlands.

We are grateful to Karel Wouters for the information he provided about the collections of the IRSNB-KBIN and to two anonymous referees whose comments contributed to improve the manuscript.

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