

To conquer and persist: colonization and population development of the Ponto-Caspian amphipods *Dikerogammarus villosus* and *Chelicorophium curvispinum* on bare stone substrate in the main channel of the River Rhine

M. C. van Riel^{1, 3}, G. van der Velde^{1, 3} and A. bij de Vaate^{2, 3}

With 7 figures and 2 tables

Abstract: Macroinvertebrate communities on the stones in the Rhine are dominated by the Ponto-Caspian amphipods *Chelicorophium curvispinum* (since 1987) and *Dikerogammarus villosus* (since 1995), which have invaded the Rhine through canals connecting the large rivers of Europe. Colonization of bare stones suspended in the water of the Rhine main channel was studied. At the same time the macroinvertebrates drifting in the water layer were sampled. Macroinvertebrate populations on the newly colonized stones were followed for two months (June – August 2002). Bare stones were colonized from the water layer, with *D. villosus* and *C. curvispinum* most numerous from the start. Species richness was highest after one month. *D. villosus* and *C. curvispinum* continued to dominate the macroinvertebrate community on the stones throughout the experiment, representing 70–95 % of the total number of macroinvertebrates. In the first period week of colonization, especially juveniles of both amphipod species settled on the bare stones. After one week, the number of adults of *D. villosus* increased. After one month, ovigerous females of *D. villosus* became abundant on the newly colonized substrate. The numbers of adult *C. curvispinum* increased after one month and ovigerous females were present after two months. Newly settled populations resembled the amphipod populations present in the water layer, but started to deviate as colonization time increased, indicating that development of populations on stones became increasingly autonomous and less dependent on new colonization by

¹ **Authors' addresses:** Department of Animal Ecology and Ecophysiology, Section Aquatic Animal Ecology, Institute for Wetland and Water Research, Radboud University Nijmegen, Toernooiveld 1, NL-6525 ED Nijmegen, The Netherlands; E-mail: gvandervelde@science.ru.nl

² Ministry of Transport and Public Works, Institute for Inland Water Management and Waste Water Treatment, P.O. Box 17, NL-8200 AA Lelystad, The Netherlands

³ Member of Netherlands Centre for River Studies, P.O. Box 177, 2600 MH Delft, The Netherlands.

amphipods from the water layer. Ovigerous females of both amphipods were much more abundant on the stones than in the water layer. Juvenile *C. curvispinum* were smaller on the stones than in the water layer, indicating that the stone substrate is important for reproduction of at least *C. curvispinum*. Most juveniles of this species first grow to a certain body length on the stones before they start drifting off and swimming in the water layer. *C. curvispinum* and *D. villosus* densities were positively correlated in the early stages of colonization, but showed an inverse relationship after longer colonisation time. As both dominant amphipods colonize new stone substrate from the water layer where they drift or swim, they may not depend on extra vectors, such as shipping, for dispersal through the connecting canals and within the river.

Key words: Amphipods, invaders, colonization, drift, population development.

Introduction

The increased connectivity between rivers that is created as canal systems removing former geographic barriers, combined with extensive shipping traffic, expose lotic freshwater ecosystems to invasions by non-indigenous species, allowing species from different watersheds to mix. The River Rhine is a good example of a heavily invaded river, which is being colonized mostly by Ponto-Caspian species reaching the Rhine through the canal network connecting the large rivers of Europe. BIJ DE VAATE et al. (2002) distinguished three main pathways by which Ponto-Caspian species have reached Western Europe, viz., a northern, a central and a southern corridor. When the River Rhine became connected to the River Danube by the Main-Danube canal (southern corridor), which was opened in 1992, this led to a major increase in the invasion rate of Ponto-Caspian species colonizing the Rhine (BIJ DE VAATE et al. 2002, VAN DER VELDE et al. 2000, VAN DER VELDE et al. 2002).

Most successful Ponto-Caspian invaders are amphipods that prefer a hard stone substrate. *Chelicorophium curvispinum* entered the Rhine via the Mittel-land Canal (central corridor) in 1987 (VAN DEN BRINK et al. 1989), followed by *Echinogammarus ischnus* in 1989 (VAN DEN BRINK et al. 1993). *Dikergammarus villosus* reached the Rhine via the Main-Danube canal in 1995 (BIJ DE VAATE & Klink 1995). After colonization, *C. curvispinum* reached densities of hundreds of thousands of individuals per m² in 1990 (RAJAGOPAL et al. 1999, VAN DEN BRINK et al. 1991, VAN DER VELDE et al. 1994). This tube building, filter-feeding amphipod covered the stone substrate with mud tubes, making colonization and development difficult for other hard substrate species. Since 1995, the omnivorous, predatory gammarid *D. villosus* (DICK et al. 2002, VAN DER VELDE et al. 2000) has increased in numbers, reaching densities of ten thousand individuals per m², while populations of *C. curvispinum* decreased to densities of several tens of thousands of individuals per m² (VAN

DER VELDE et al. 2000). Nowadays, *D. villosus* and *C. curvispinum* both dominate the hard substrates in the River Rhine.

As amphipods show a very active migration pattern, migrating both upstream and downstream (BRITAIN & EIKELAND 1988, RAWER-JOST et al. 1999), but mainly disperse by drifting downstream (BRITAIN & EIKELAND 1988, ELLIOT 2002), the increased connectivity between large European rivers and the intensive shipping on these rivers can be assumed to facilitate Ponto-Caspian amphipods entering the main channel of the Rhine by swimming in the water layer or attaching to floating pieces of substrate or ship hulls. Earlier studies found that 41–82 % of the colonizing macroinvertebrate species in streams entered new habitats by drift (TOWNSEND & HILDREW 1976, WILLIAMS & HYNES 1976) and that gammarids are capable of deliberately swimming down to a substrate from the water column (CIBOROWSKI & CORKUM 1980). Drifting macroinvertebrates are known to be the earliest arrivals on bare substrates. Most of them merely inspect the substrate, but the more sedentary macroinvertebrates are true colonizers, characterized by frequent, asynchronous reproduction, high growth rates, high, often age-restricted, dispersal, and long activity periods. Early colonizers profit from an initial period of enemy-free space. Filter feeders tend to be successful early immigrants, as they collect their food from the water layer rather than from the substrate itself. Whether newly colonized individuals are able to successfully build up stable populations depends not only on the colonization rate but also on resources, life cycles and interspecific interactions (MACKAY 1992).

The present study focused on the colonization of a bare stone substrate by *D. villosus* and *C. curvispinum* from the water layer in the River Rhine, and the development of their populations after settlement, answering the following questions:

- A) Do Ponto-Caspian amphipod species colonize bare substrate from the water layer?
- B) How do newly colonized species develop populations?
- C) How important are the developed amphipod populations on the stones for further dispersal of the species?
- D) Are amphipod populations determined by both colonization from the water layer and reproduction on the newly colonized substrate?
- E) Is there an interaction between the dominant amphipods that influences the process of colonization by these species?

Material and methods

Study site

The River Rhine is a large river fed by glaciers and rainfall, and has been highly regulated by anthropogenic changes to its geomorphology and hydrology. In the Nether-

Table 1. Physico-chemical characteristics of the River Rhine during sampling.

Month	June	July	August
Chloride (mg/l)	98.0	96.0	92.0
Conductivity (mS/m)	62.7	62.1	61.4
Temperature (°C)	20.0	20.5	22.8
Turbidity (FTU)	34.7	29.2	27.9
pH	8.0	7.6	7.5
Oxygen content (mg/l)	10.7	7.8	7.6
Current velocity (m/s)	1.0	1.0	0.99
Water depth (m)	5.7	5.4	5.1

lands, the Rhine becomes a delta river in which groynes, made of basalt stones, have been constructed to consolidate the sandy riverbed, and the riverbanks are protected against erosion by stones. These stones and groynes are continuously being colonized by macroinvertebrates. Colonization of stones in the River Rhine was studied near Lobith, The Netherlands (5° 75' E, 52° 33' N). For physico-chemical habitat characteristics of the Rhine during this study, see Table 1.

Field methods and analysis

Nets (0.45 m × 0.70 m, mesh size 0.8 cm) were filled with 15 lava stones each (to a total stony surface of 0.23 m²). A series of 10 nets with stones were tied to a pontoon and suspended at a depth of approx. 2–3 m in the main channel of the river Rhine at 6 June 2002, approx. 4–3 m above the sediment, to make sure that the stones were only colonized by macroinvertebrates from the water layer. Macroinvertebrates were collected during the daytime after a colonization period of one night (8 hours, 6 June 2002), one day (24 hours), one week (168 hours), one month (720 hours, 7 July 2002) and two months (1464 hours, 7 August 2002). Two nets with stones were collected per time interval. During this colonization experiment, drifting macroinvertebrates were collected monthly from the water layer in the main channel of the Rhine by suspending a net (0.5 m × 0.5 m aluminium frame, mesh size 0.5 mm) in the main channel for 30 minutes at night at different depths: bottom (5.7–5.1 m), intermediate depth (3–2.5 m) and surface (0–0.5 m). A weight of 20 kg was attached to the net to keep it drifting steadily in the main channel. An extra pair of nets with stones was added to the experiment at 12 June 2002 and sampled after three weeks. As these nets with stones were put into the water one week later, results from these nets are used only in density dependant research (Fig. 6) and not in the figures describing the colonization process and population development.

Macroinvertebrates sampled from both the water layer and the stone substrate in the nets were preserved in 70 % ethanol immediately after collection. The collected fauna was sorted, identified and counted. For amphipods, body length (rostrum to telson), life stage and sex (juvenile, male, female and ovigerous female) were determined. If a sample of amphipods contained more than 200 adults and/or juveniles, body length was determined for a sub-sample of 200 juveniles and/or 200 adults. Ash-free dry weight (AFDW) was calculated from body length (BL) using the following

formulas: for *C. curvispinum* $AFDW(\mu\text{g}) = 11.99 \cdot BL(\text{mm}) + 48.4$ (RAJAGOPAL et al. 1999) and for *D. villosus* $AFDW(\text{g}) = 0.0035 \cdot BL(\text{mm}) - 0.0331$ (BRUIJS et al. 2001).

Statistical analysis

The species richness of macroinvertebrate populations on the stones in the nets sampled after more than one month of colonization was compared to that of populations sampled after a shorter colonization time using a Mann-Whitney test (Fig. 1). Differences within the groups were tested using a Kruskal-Wallis test as homogeneity of variances was significant ($p < 0.000$, Levene's test). Differences in biomass between the dominant amphipods were tested using a repeated measures ANOVA (RM-ANOVA) considering colonization time the between subject factor and species the within subject factor. Differences in mean body length between the populations present on the stones and in the water layer in June, July and August were tested using a t-test comparing the body length of each life stage on the substrate to that of the comparable life stage in the water layer for each species (Table 2). Linear regression analysis was used to test the relation between the densities of the dominant amphipods at low densities on substrate, whereas the relation between dominant amphipods at high densities was analysed using power regression. Mentioned statistical tests were carried out using SPSS 11.5 for Windows. Principal Component Analysis (PCA) was carried out on square-root transformed macroinvertebrate densities in the water layer and on the stones, using the ordination program CANOCO 4.0 (TER BRAAK & SMILAUER

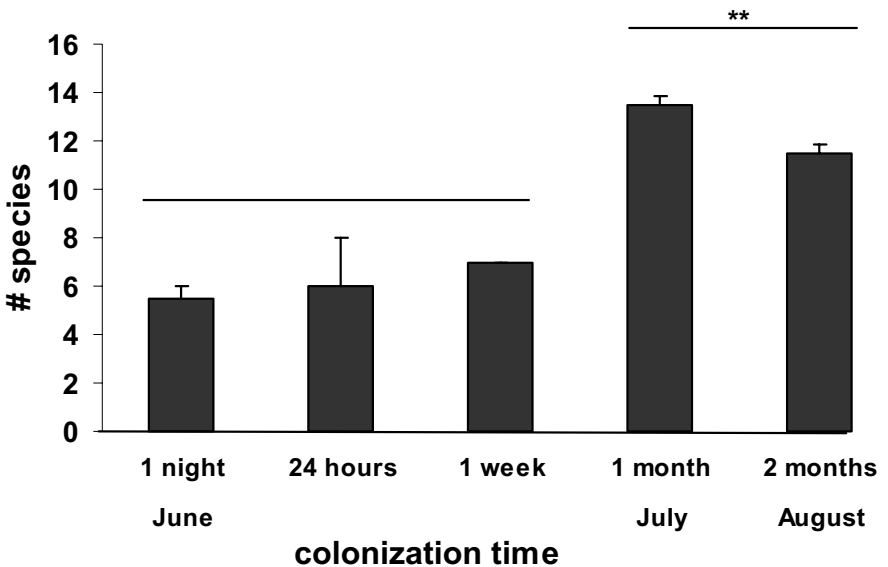


Fig. 1. Species richness (mean number of species \pm SD) in relation to colonization time on the colonized bare stone substrate. Horizontal lines above the bars indicate clusters of short colonization periods and longer colonization periods. Species richness of the clusters is tested using a Kruskal-Wallis test. Significance levels: ** $p \leq 0.01$

Table 2. Mean body length (mm) per life stage and sex of *D. villosus* and *C. curvispinum* on the colonized substrate and in the water layer. – means not found. Significance levels: *** p<0.001, ** p<0.01, * p<0.05

	June			July			August						
	substrate	n	water layer	n	substrate	n	water layer	n	substrate	n	water layer	n	signifi- cances
<i>D. villosus</i>													
males	10.54 ± 1.50	34	9.28 ± 1.59	104	11.08 ± 1.64	413	8.95 ± 1.79	71	11.70 ± 2.47	200	9.29 ± 1.36	14	***
all females	10.38 ± 0.86	18	9.43 ± 1.46	31	10.30 ± 1.31	614	9.97 ± 1.42	73	10.71 ± 1.32	386	9.72 ± 1.50	12	*
non-ovigerous females	10.32 ± 0.77	17	9.33 ± 1.39	30	9.91 ± 1.31	427	9.67 ± 1.36	315	10.42 ± 1.36	260	9.26 ± 1.07	10	*
ovigerous females	12.00	1	12.20	1	11.19 ± 0.75	187	11.34 ± 0.72	13	11.31 ± 0.97	126	12.00 ± 1.41	2	NS
juveniles	5.11 ± 2.47	76	4.28 ± 1.91	195	2.37 ± 1.89	1111	3.63 ± 1.89	302	3.78 ± 2.41	129	2.85 ± 1.73	99	***
<i>C. curvispinum</i>													
males	3.08 ± 0.61	5	3.55 ± 5.70	42	3.66 ± 0.55	635	3.54 ± 5.02	138	3.54 ± 0.58	3785	3.37 ± 4.73	106	*
all females	2.77 ± 0.70	7	4.29 ± 1.11	56	4.21 ± 0.91	844	3.84 ± 0.86	150	3.80 ± 0.70	6220	3.66 ± 0.66	125	*
non-ovigerous females	2.77 ± 0.70	7	3.92 ± 9.60	41	3.89 ± 0.64	595	3.59 ± 7.79	104	3.69 ± 0.68	2691	3.39 ± 4.95	74	**
ovigerous females	–	0	5.31 ± 8.45	15	4.96 ± 1.02	249	4.40 ± 7.58	46	4.49 ± 0.67	3529	4.04 ± 6.80	51	***
juveniles	1.34 ± 0.29	47	2.19 ± 5.75	179	1.77 ± 0.64	4034	2.28 ± 4.56	490	1.83 ± 0.60	25229	2.22 ± 4.99	575	***

1998). Scaling was focused on inter-species distances, species scores were divided by standard deviation, and the data were centred by species.

Results

After one night in the water layer, macroinvertebrates had already colonized the bare stones. Species richness on the newly colonized substrate increased in the first month after settlement (Fig. 1), leading to a higher number of species for longer periods of colonization than that in macroinvertebrate populations after shorter colonization periods. Although differences in species richness within the various colonization periods were not found to be significant ($p = 0.11$, Kruskal-Wallis test), comparing pooled data of species richness after longer colonization periods (1 month to 2 months) to those after short colonization periods (1 night – 1 week) showed significantly higher species richness for the longer periods of colonization ($p = 0.01$, Mann-Whitney test). After the first month, the number of species did not increase any further, and most populations of macroinvertebrates, except *C. curvispinum*, had reached their maximum densities. *D. villosus* and *C. curvispinum* dominated the macrofauna population on the colonized substrate from the start, representing 75–95% of the total number of specimens (Fig. 2). *Echinogammarus ischnus* was less abundant in the samples than the other two Ponto-Caspian amphipods: only 56 individuals were caught in the water layer and 3 juveniles actually colonized the stone substrate. During the first period of colonization, *D. villosus* dominated the system in both numbers and biomass. In July, numbers of *C. curvispinum* increased quickly, representing 95% of the macrofauna population on the colonized stones in August. *D. villosus*, however, continued to dominate the colonized substrate in terms of biomass ($p = 0.001$, within subject effect RM-ANOVA). Colonization time affected the differences in biomass between the species ($p = 0.027$, interaction RM-ANOVA) and total biomass ($p = 0.022$, between subject effect RM-ANOVA) (Fig. 3).

During the first hours of colonization, it was mainly juvenile amphipods that settled on the stone substrate. After one week for *D. villosus* and one month for *C. curvispinum*, adult amphipods became numerous, and ovigerous females increased in number (Fig. 4). Mean body length altered with colonization time: males and females of *D. villosus* were significantly larger in August ($p < 0.0001$, t-test) than in July, while the numbers of adults on the substrate in June were too small to test for significant differences. Juvenile *D. villosus* were smallest during the reproduction peak in July ($p < 0.0001$, t-test). Adults of *C. curvispinum* on the substrate in July were larger ($p < 0.008$, t-test) than adults in August. In June, adults were only present in small numbers and appeared to be smaller than adults in July. Juveniles grew significantly (p

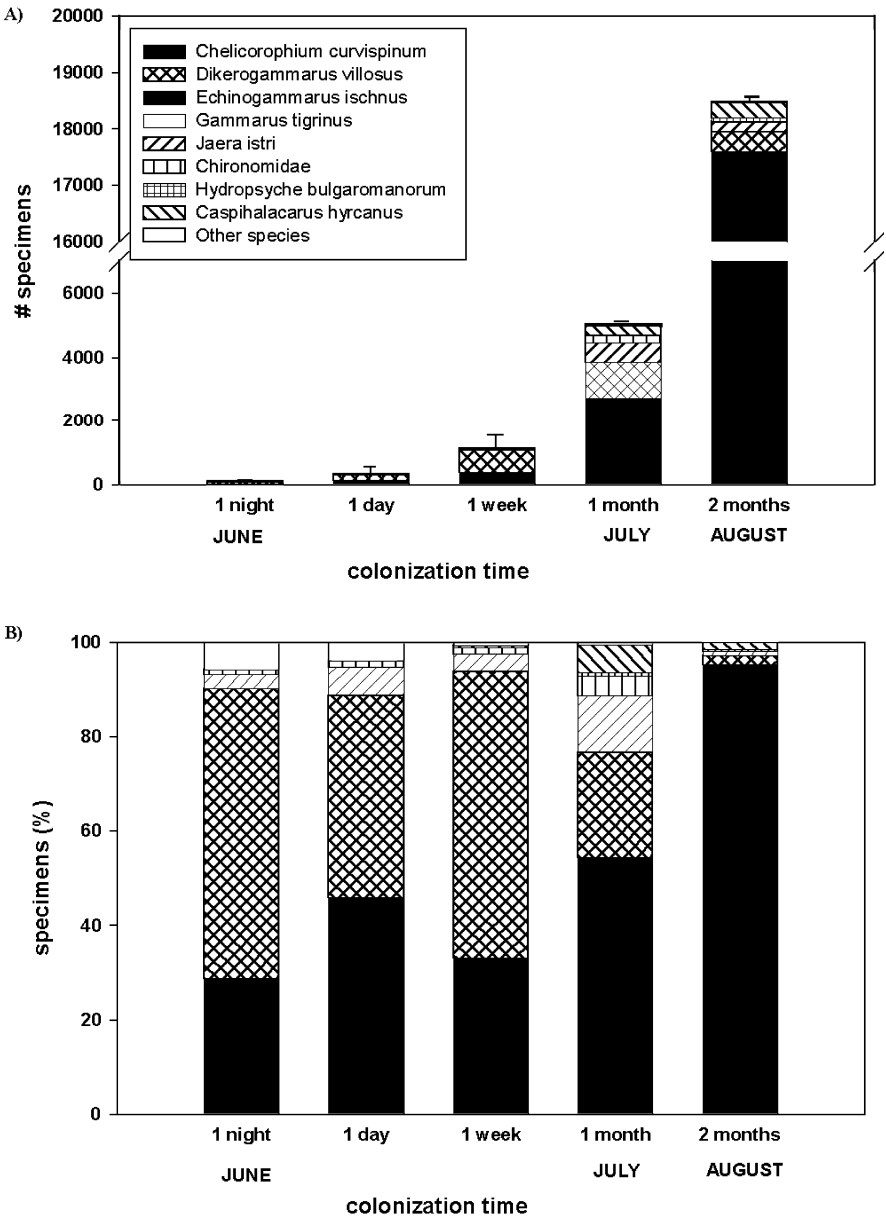


Fig. 2. Numbers (A) and percentages (B) of macroinvertebrate species on the colonized substrate.

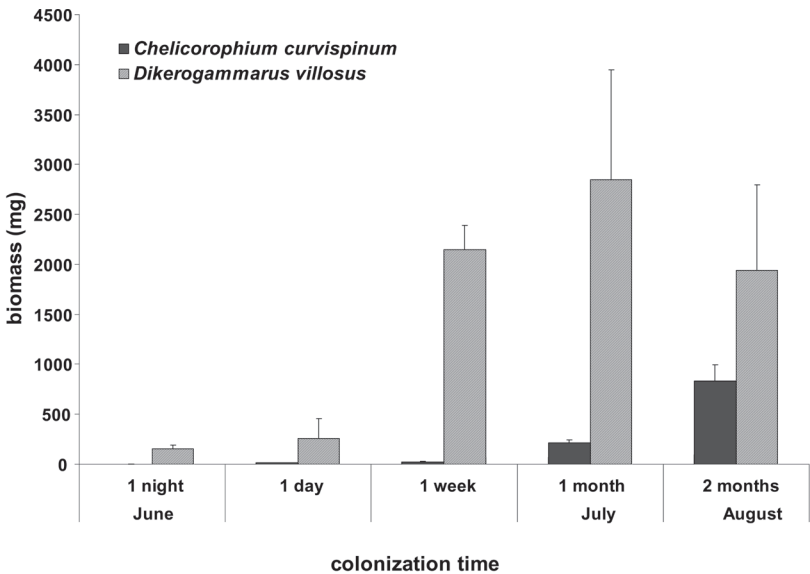


Fig. 3. Biomass of *C. curvispinum* and *D. villosus* on the colonized substrate.

<0.0001, t-test) larger with every month (Table 2). In the first week after settlement, the composition of the amphipod populations (in terms of life stage and sex) on the newly colonized stones resembled that of the amphipods in the water layer, with juveniles dominating the populations in both habitats (Fig. 5). From this stage, populations on the stones showed a more independent development, less similar to that of the amphipod populations in the water layer (Fig. 5), and mean body length per life stage differed significantly between the amphipods on the substrate and those in the water layer (Table 2). Amphipods drifting in the water layer did not develop into populations with large numbers of adults (Fig. 5). After one week of colonization, adult *D. villosus* became more abundant on the substrate than in the water layer, whereas *C. curvispinum* showed a much greater increase in the numbers of juveniles on the substrate after one month of colonization (Fig. 5).

In the first weeks of colonization, the numbers of *D. villosus* and *C. curvispinum* on the substrate increased simultaneously, and showed a positive relationship (Fig. 6 a, $R^2 = 0.63$). After three weeks, however, when the densities of *D. villosus* had risen above 4,000 individuals per square metre, or the densities of *C. curvispinum* had risen above 20,000 individuals per square metre, the two species showed a strong inverse relationship (Fig. 6 b, $R^2 = 0.92$).

The PCA ordination diagram in Fig. 7 showed a clear difference in community structure considering *D. villosus* and *C. curvispinum* populations in the water layer and on the stones, based on different life stages and sexes of both

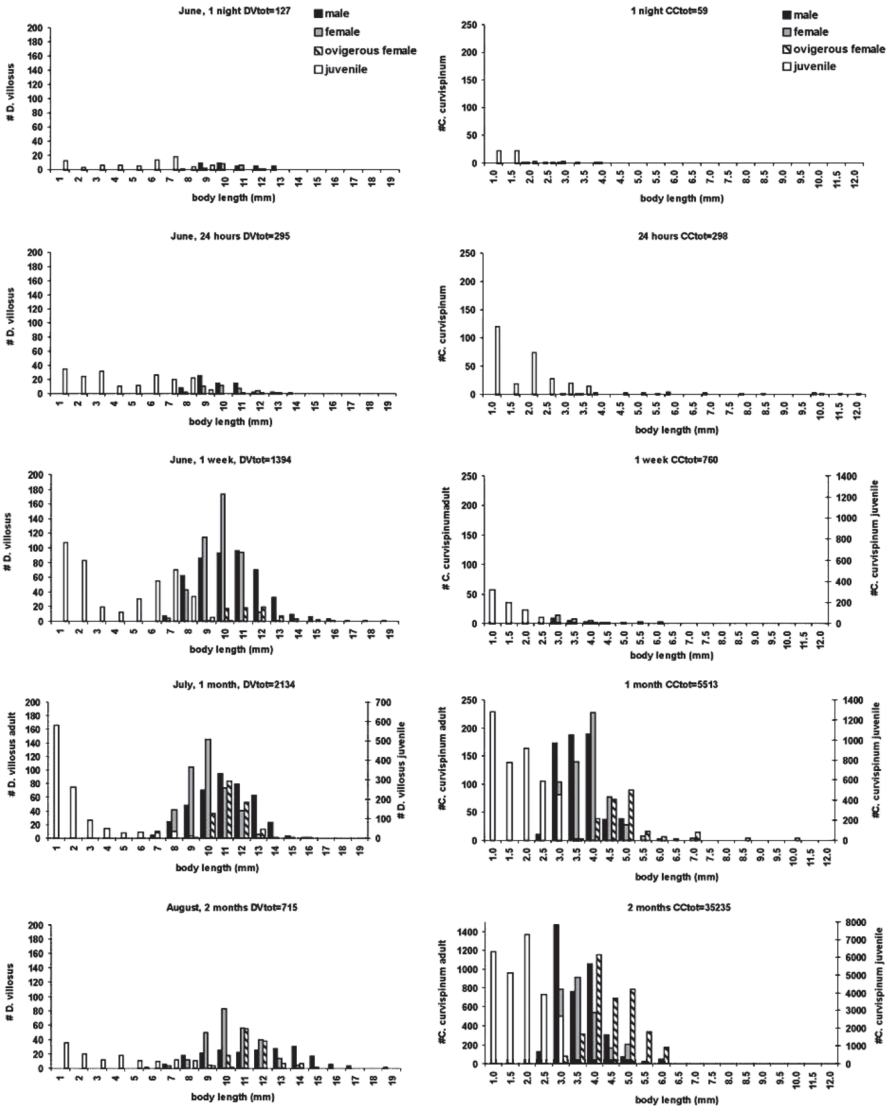


Fig. 4. Development of the populations of *D. villosus* (left panels) and *C. curvispinum* (right panels) on the colonized stones.

species on the stones and in the water layer during the same period. Communities in the water layer were more similar to each other than to communities on the colonized substrate, indicating a clear succession. Amphipod populations on newly colonized substrate resembled the populations in the water layer during the same period. *D. villosus* was most abundant on the substrate in July, whereas *C. curvispinum* peaked in August. Both amphipod popula-

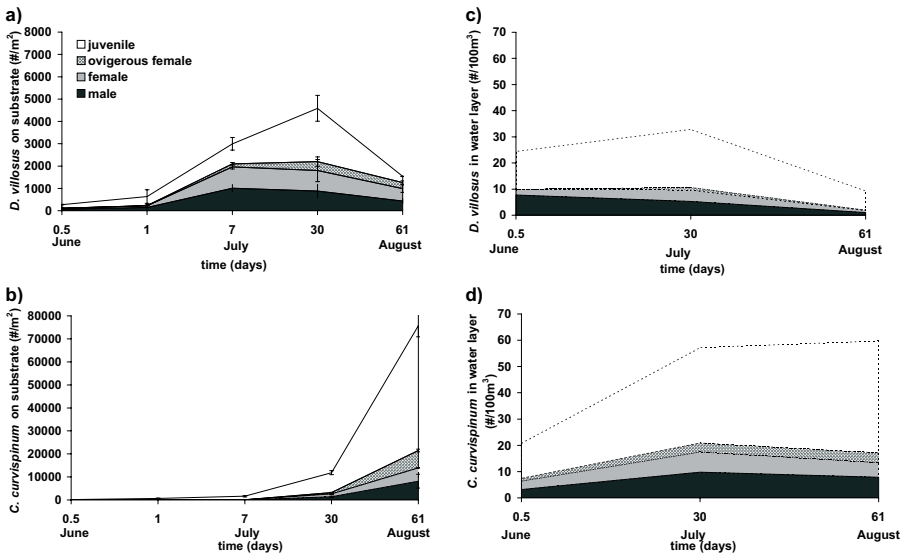


Fig. 5. Life stages of *D. villosus* (a, c) and *C. curvispinum* (b, d) on the colonized substrate (a, b) and in the water layer (c, d).

tions started developing mainly from the juveniles that first settled on the stones. Adults developed after some time and ovigerous females were observed last.

Discussion

The species richness of macroinvertebrate populations on stone substrate increased during the first month of colonization and stabilized afterwards, resembling the results found in studies on macroinvertebrates colonizing disturbed streams (e.g. FOWLER 2004, KORSU 2004, MATTAEI et al. 1997, QUINN 1998) and artificial substrate (e.g. MASON 1978, MEIER et al. 1979). Colonized macroinvertebrate populations were established and had developed within one month, after which macroinvertebrate species richness did not increase any further. This supports SHAW & MINSHALL'S (1980) finding that colonization much beyond two months does not greatly add to the community.

Although species richness on the colonized stones increased with colonization time, the Ponto-Caspian amphipods *D. villosus* and *C. curvispinum* remained dominant, contributing 70–95% of the total number of macroinvertebrates present. *D. villosus* proved to be a successful pioneer, as it quickly colonized the bare stones and became the dominant amphipod in both biomass and number during the first period of colonization. Although during a later stage of

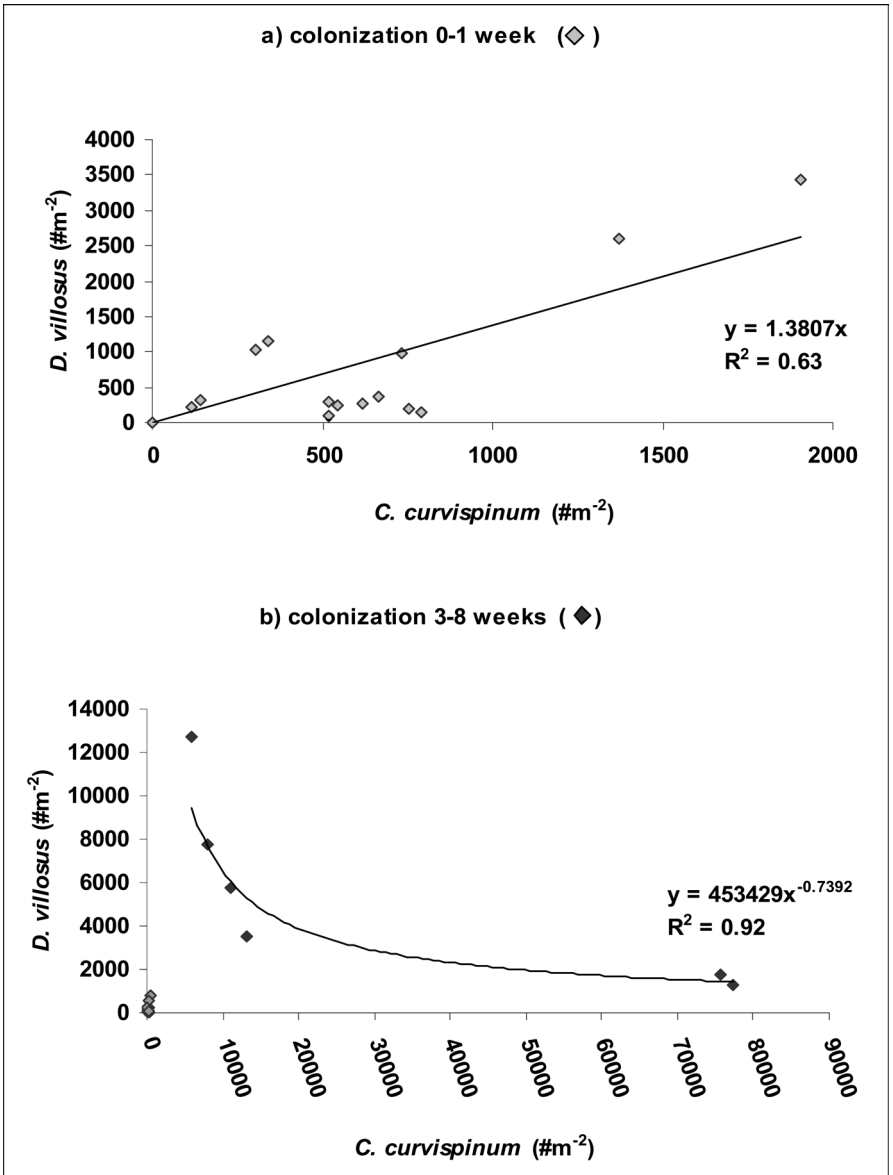


Fig. 6. Correlation between the numbers of *D. villosus* and *C. curvispinum* on the colonized substrate after a period of (a) 0–7 days of colonization and (b) 3–8 weeks of colonization.

colonization, viz. after one month, the numbers of *C. curvispinum* increased to a much higher level than those of *D. villosus*, *D. villosus* remained dominant on the stone substrate in terms of biomass.

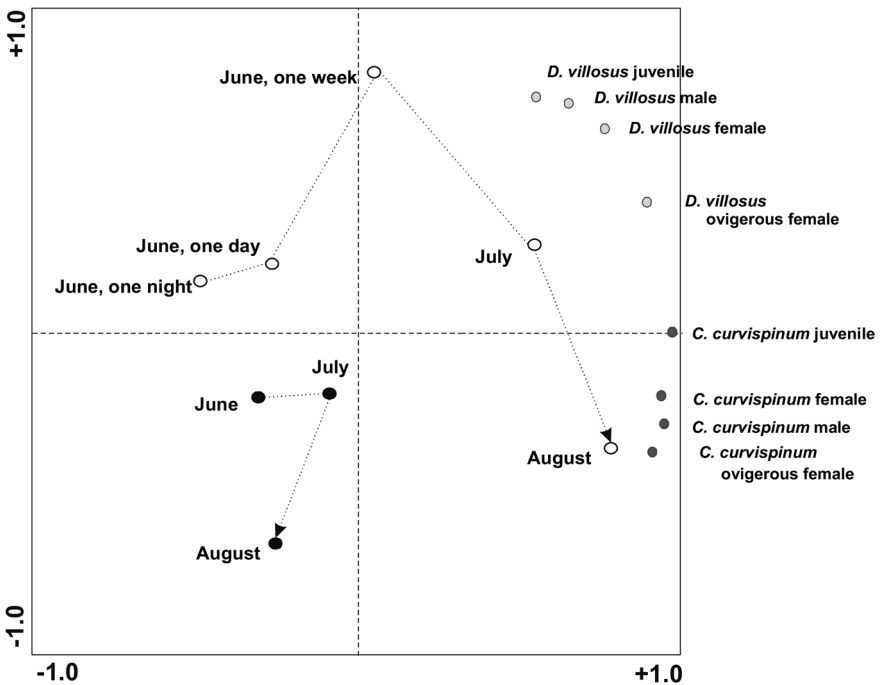


Fig. 7. Principal Component Analysis (PCA) of *D. villosus* and *C. curvispinum* communities showing population development based on abundances of life stages and sexes of *D. villosus* and *C. curvispinum* populations on colonized stone substrate (○) and in the water layer (●) of the River Rhine.

At low densities, the dominant amphipod species coexisted without limiting each other, but started to influence each other's densities when numbers of *D. villosus* rose above 4,000 or numbers of *C. curvispinum* rose above 20,000 individuals per square metre. A similar density-related competition has been found for the invasive Ponto-Caspian amphipod *Echinogammarus ischnus* and the native *Gammarus fasciatus* in the Canadian Great Lakes (VAN OVERDIJK et al. 2003). Competition for space between *D. villosus* and *C. curvispinum* is presumably influenced by life stage, population development and total abundance, factors which are determined by seasonal succession. The predation by *D. villosus* on *C. curvispinum* could also influence densities of *C. curvispinum* on the stones (VAN RIEL et al. 2006), while high densities of *C. curvispinum* could smother and narrow the spaces between stones as they build layers of muddy tubes (VAN DEN BRINK et al. 1991, 1993, VAN DER VELDE et al. 1994, 1998, 2002).

Populations of the two dominant amphipods developed in a similar process, but not equally fast. For both amphipod species, it was mainly juveniles

that colonized the bare stone substrate from the water layer. The data indicate that these juveniles grew into adults on the substrate. The adults reproduced as the number of ovigerous females on the substrate increased after some time, whereas ovigerous females of both species were not abundant in the water layer. The mean body length of juveniles of *C. curvispinum* on the substrate during the reproductive period was smaller for juveniles on the substrate than for those in the water layer. These observations indicate that stone substrate is essential for the reproduction of the amphipods studied, and that most juveniles of *C. curvispinum* first grow on stones to a length at which they start to drift off into the water layer.

Populations of *D. villosus* developed faster than those of *C. curvispinum*, as ovigerous females were present within one week, whereas ovigerous females of *C. curvispinum* were not abundant until one month after colonization. Populations of *D. villosus* decreased in numbers after two months, when populations of *C. curvispinum* were still increasing. These developmental differences in time could also be due to seasonal succession, as the same decline of *D. villosus* was also found in the water layer at the same time, while the numbers of *C. curvispinum* in the water layer remained more or less constant after a month.

Settlement of amphipod juveniles from the water layer seems to be the most decisive process for the colonization of the stones. The amphipod population structure on the colonized stones closely resembled the population structure in the water layer for only short periods of the colonization process (approximately a few days). For longer periods of time after colonization, the development of the amphipods on the stones themselves appeared to be more important to these populations than new input of amphipods from the water layer. Still, seasonal influences on the reproductive cycles of *D. villosus* and *C. curvispinum* have a major effect on populations in the water layer as well as those on stones, as densities of *D. villosus* on stones have been found to decline after their reproduction peak in June – July, whereas *C. curvispinum* populations do not increase until the reproduction peak in July – August (DEVIN et al. 2004, RAJAGOPAL et al. 1999).

From the present study the following conclusions can be drawn: (A) The Ponto-Caspian amphipod species *D. villosus* and *C. curvispinum* successfully colonize bare stone substrates in the Rhine from the water layer and dominate the macroinvertebrate community on stones. (B) Juveniles of these species are most abundant in the water layer, and are the first to colonize bare stones. These juvenile colonizers mature and reproduce on the stones. (C) New progeny is assumed to drift off into the water layer. Most juveniles of *C. curvispinum* first have to grow to a certain size on the stones before they start drifting off and swimming in the water layer. (D) For most of the time after colonization, the development of populations of *D. villosus* and *C. curvispinum* that

have settled on the stones is autonomous, rather than being influenced by new colonization from the water layer. Seasonal succession, however, does affect the populations on stones. (E) When amphipod populations on stones grow to high densities, competition for space and possibly predation by *D. villosus* on *C. curvispinum* determines the dominance of the colonists.

C. curvispinum and *D. villosus* successfully colonized the bare stone substrate from the water layer where they drifted or swam, indicating that connectivity of large rivers allows dispersal towards and colonization of the River Rhine by both species, and that these amphipods do not depend on vectors such as shipping. The presence of stones favours population development for both species, although species profit from and use the stones in different ways. Such stones could therefore function as stepping-stones for further colonization of the river and lakes.

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