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Dispersal of invasive species by drifting

M.C. VAN RIEL[1,2], G. VAN DER VELDE[1,3*], A. BIJ DE VAATE[4]

[1] Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Animal Ecology and Ecophysiology, Section Aquatic Animal Ecology, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
[2] Team Freshwater Ecology, DLO-Alterra, P.O. Box 47, 6700 AA Wageningen, The Netherlands
[3] Netherlands Centre for Biodiversity Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands
[4] Waterfauna Hydrobiologisch Adviesbureau, Oostrandpark 30, 8212 AP Lelystad, The Netherlands

Abstract Drifting can be an effective way for aquatic organisms to disperse and colonise new areas. Increasing connectivity between European large rivers facilitates invasion by drifting aquatic macroinvertebrates. The present study shows that high abundances of invasive species drift in the headstream of the river Rhine. *Dikerogammarus villosus* and *Chelicorophium curvispinum* represented up to 90% of the total of drifting macroinvertebrates. Drift activity shows seasonal and diel patterns. Most species started drifting in spring and were most abundant in the water column during the summer period. Drift activity was very low during the winter period. Diel patterns were apparent; most species, including *D. villosus*, drifted during the night. Drifting macroinvertebrates colonised stony substrate directly from the water column. *D. villosus* generally colonised the substrate at night, while higher numbers of *C. curvispinum* colonised the substrate during the day. It is very likely that drifting functions as a dispersal mechanism for crustacean invaders. Once waterways are connected, these species are no longer necessarily dependent on dispersal vectors other than drift for extending their distribution range [*Current Zoology* 57 (6): 818–827, 2011].

Keywords Amphipods, Invaders, Colonization, Drift, Daily rhythms, Seasonal variation

Drifting downstream can be an effective way for aquatic organisms to disperse and colonise new areas (Williams and Hynes, 1976; DeLucchi, 1989; Mackay, 1992; Quinn et al., 1998; Elliot, 2002b; Principe and Corigliano, 2006; Van Riel et al., 2006a). Whether macroinvertebrates accidentally or deliberately enter the water column in order to start drifting remains speculative. Some studies suggest that by drifting, macroinvertebrates escape macroinvertebrate predators, or unsuitable or changed abiotic conditions (Koetsier and Bryan, 1995; Wooster and Sih, 1995). Other studies suggest that drift results from competition between benthic macroinvertebrates for resources and space, since macroinvertebrates often start migrating when competition or crowding increases (Minshall and Winger, 1968; Waters, 1972; Müller, 1974). Macroinvertebrates may also passively set off to drift after being dislodged from the substrate, by for instance physical disturbances such as velocity fluctuations and discharge (Elliot, 2002a).

In large rivers, macroinvertebrate drift and colonization of stone substratum fluctuate strongly, show diel and seasonal dynamics, and reflect life cycle characteristics (Cellot, 1996; Quinn et al., 1998). Diel periodicity has been observed for drift in various streams (Allan, 1978; Koetsier and Bryan, 1995), especially for amphipods (Elliot, 2002a). It has been suggested that predation activity of predators hunting by sight may be responsible for the tendency to avoid drifting during the daytime (Allan, 1978), but this would not explain the occurrence of diel periodicity in drift observed in large, turbid rivers (Koetsier and Bryan, 1992), nor would it explain increased drift at night in streams where fish are absent (Elliot, 2002a).

Triggers that cause macroinvertebrates to actively start drifting are therefore probably related to the composition, densities and dynamics of the benthic macroinvertebrate community. Populations of invasive species usually grow fast, which leads to crowding and increasing competition for resources (Van der Velde et al., 2000; Van Riel et al., 2006a). This process would likely cause macroinvertebrates to drift. Invaders may use drift as a dispersal mechanism to enter and colonise connected water bodies and establish their populations, which could then be continuously supplemented with new individuals from the drift (Van Riel et al., 2006a). In this way, drifting animals could even be the most important source of new colonists (Townsend and Hildrew, 1976;

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* Corresponding author. E-mail: G.vandervelde@science.ru.nl

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Matthaei et al., 1997; Fenoglio et al., 2002; Van Riel et al., 2006a).

Drift may play an important role in the invasion process going on in the large European rivers, as connectivity between these rivers has considerably increased (Bij de Vaate et al., 2002) and invasive macroinvertebrates have been found to colonise new areas rapidly (Van der Velde et al., 2002; Jazdzewski et al., 2004). Since the Main-Danube canal has connected the river Rhine with the river Danube in 1992, the Rhine has been successfully invaded by mostly Ponto-Caspian macroinvertebrates (Table 1) (Van der Velde et al., 2002; Leuven et al., 2009).

This study addresses the following questions on the role of drift in the dispersal of macroinvertebrates in the Rhine: a) What is the composition and relative abundance of invasive species in the drift? b) Which diel and seasonal patterns can be observed? c) Do macroinvertebrates settle on substrate from drifting in the water column? d) Are densities of drifting macroinvertebrates related to the densities of macroinvertebrates on the stony substratum? e) To what degree could dispersal by drifting explain the success of crustacean invaders?

1 Materials and Methods

1.1 Study site

The Rhine is a large river ecosystem under various forms of anthropogenic stress, such as normalisation, water pollution and salination (Van der Velde et al., 1990, 2006; Bij de Vaate et al., 2006). The floodplain is embanked with dikes and the main channel has been canalised, reducing its heterogeneity to two main biotopes, i.e., sandy streambeds and stony riverbanks and groynes (Admiraal et al., 1993; Van Riel et al., 2006b). Water quality has improved lately by sanitation, but rehabilitation of the native fauna seems to be inhibited by the large numbers of invasive species present in the Rhine (Van der Velde et al. 2000, 2002). The river Rhine in the Netherlands is a regulated river with a heavily modified geomorphology and hydrology (Leuven et al., 2009). Groynes stabilize the riverbed and the riverbanks are protected against erosion by groyne-stones and riprap. These stones are continuously colonised by macroinvertebrates (Van Riel et al., 2006a).

1.2 Field methods and analysis

Drift of macroinvertebrates in the headstream of the river Rhine was studied near Lobith (5°75′E, 52°33′N) by placing a nylon net (0.5 m × 0.5 m aluminium frame, length 2 metre mesh size 500 μm) in the headstream for 30 minutes at three different depths: bottom (8.5–9.5 m) middle depth (4–5 m) and surface (0–0.5 m). A weight (20 kg) was attached to the frame to keep it upright in the water. During the sampling period of 30 minutes per sample, the net did not clog. Drift was standardized to numbers per hundred cubic metres. Drift was studied once a month during both day and night over one annual cycle (April 2002–April 2003). Physical and chemical water characteristics (water velocity, chloride, conductivity, temperature, discharge, turbidity, pH, nitrate, oxygen, ammonium, phosphate, and water level) measured in the Rhine during this study were obtained from the Institute for Inland Water Management and Waste Water Treatment (RIZA, www.waterstat.nl), measured at the RIZA field station where we performed our experiment.

Macroinvertebrates caught in the net and attached to the outer side of the net were collected and immediately preserved in 70% ethanol. The macroinvertebrate fauna

Table 1 Drifting invaders of the river Rhine arranged according to appearance (first record)

Invader	Preferred substrate	first record	Reference
Chelicorophium curvispinum	stone	1987	Van der Velde et al., 2002
Corbicula fluminea	sand	1988	Van der Velde et al., 2002
Echinogammarus ischnus	stone	1991	Van den Brink et al., 1993b
Dikerogammarus villosus	stone	1995	Bij de Vaate and Klink, 1995
Hypania invalida	sand and stone	1996	Klink and bij de Vaate, 1996
Jaera istri	stone	1997	Kelleher et al., 2000
Hemimysis anomala	water, shelter between stones or vegetation	1997	Ketelaars et al., 1999
Limnomysis benedeni	water, shelter between stones or vegetation	1997	Kelleher et al., 1999
Dendrocoelum romanodanubiale	stone	1999	Bij de Vaate and Swarte, 2001; Van der Velde et al., 2002
Caspihalacarus hyrcanus	stone	2000	Bij de Vaate et al., 2002
Echinogammarus trichiatus	stone	2002	Cristescu et al., 2004

was sorted, counted, and identified to species level for amphipods and other macroinvertebrates to family level. Body length (anterior head margin to hind tip telson) and sex were determined for the amphipods.

While collecting drift samples, we also studied the initial settlement on stony substratum of drifting macroinvertebrates. Nets (0.45 m × 0.70 m, mesh size 0.8 cm) were filled with 15 porous lava stones with a mean diameter of 5.3 cm each (total area 0.232 m^2), and suspended at a depth of 4–6 m in the headstream of the river Rhine at Lobith, 2–4 m above the bottom. Macroinvertebrate fauna was collected from four nets with lava stones after eight hours of exposure during the day and eight hours during the night. Settlement on the stones was studied in summer (July), winter (January) and spring (April) during 2002–2003.

1.3 Statistics

The equipment used in this study to sample macroinvertebrates from the river Rhine's main stream, did not allow true replicates. However, samples which were taken during the same daytime (day or night) in the same season varied very little in numbers and species composition. Samples taken at different depths were highly similar. Although the practical setup of the experiment did not allow statistical analysis, trends in abundances and compositions of drifting macroinvertebrates were clearly visible in this study. Correlations between abiotic factors and drifting activity were analysed by Pearson's Rank correlation (SPSS 14.0).

2 Results

Exotic macroinvertebrates represented 91% of the total drifting individuals. Fish larvae were found in drift samples from April to August, and contributed 2% to the total of drifting individuals. Most of the macroinvertebrates found were of Ponto-Caspian origin (Table 1). Of the physico-chemical parameters measured, temperature (P=0.001, Pearson's Rank correlation=0.63, df = 23) and nitrate (P=0.037, Pearson's Rank correlation coefficient= -0.42, df = 23) correlated significantly with numbers of drifting macroinvertebrates. Although significant, correlations between abiotic factors and the numbers of drifting macroinvertebrates were not strong. Macroinvertebrates were observed drifting mainly during spring and summer. From October to February, macroinvertebrates were present in the water column in small numbers only (Fig. 1). Drifting macroinvertebrates were equally abundant at the bottom, middle, and surface in the course of the year. Macroinvertebrates drifted mostly at night and included 70%–90% invasive Ponto-Caspian amphipods (Fig. 1, 2). *Dikerogammarus villosus* represented the largest percentage of the macroinvertebrates drifting during spring (February–May). *Chelicorophium curvispinum* subsequently dominated the water column samples from July to December, whereas only low numbers of *Gammarus tigrinus*, *Echinogammarus ischnus*, and *Echinogammarus trichiatus* were found drifting. Furthermore, the Ponto-Caspian invaders *Jaera istri*, *Limnomysis benedeni*, *Hemimysis anomala*, *Caspihalacarus hyrcanus*, *Dendrocoelum romanodanubiale* and *Hypania invalida* were fairly abundant in the drift samples. Other macroinvertebrates such as triclads, annelids, molluscs, crustaceans and insects were found in low numbers only (Fig. 1, 2).

The dominant amphipods *D. villosus* and *C. curvispinum* drifted mainly during the night (Fig. 1, 2) and were mostly abundant as juveniles (Fig. 3). Adult amphipods were mainly observed during the night. Adult *D. villosus* were found drifting from May till October. Adult *C. curvispinum* were most abundant in the drift in September (Fig. 2, 3). Higher numbers of males than females were found drifting during reproductive periods (August–September for *C. curvispinum*, June–July for *D. villosus*). Adult *D. villosus* were observed also to attach their claws to the outer surface of the sampling net during the peak drift activity in May and June. These individuals were not included in the quantification of drifting individuals per m^3.

Expressed as total numbers during the whole study, 584 juveniles of *C. curvispinum* were sampled drifting during the daytime, while 1,785 juvenile *C. curvispinum* were caught drifting at night. Total numbers of juvenile *D. villosus* sampled while drifting were 991 during the daytime and 2,262 during the night. In total, 18 male and 14 female *D. villosus* were caught in the drift samples during the daytime, whereas a total of 264 male and 150 female *D. villosus* were caught drifting during the night. During the daytime, a total of 102 male and 101 female *C. curvispinum* were caught in drift, whereas the total number of drifting males (n=960) exceeded the number of drifting females (n=741) during the night.

Settlement on bare stones, which was studied simultaneously with the monitoring of drifting macroinvertebrates, showed that the species composition of the new colonists on stones matched that of the water column samples (Fig. 2). The timing of settlement also matched drifting activity: drifting and colonisation of substrate were both observed less during the day than during the

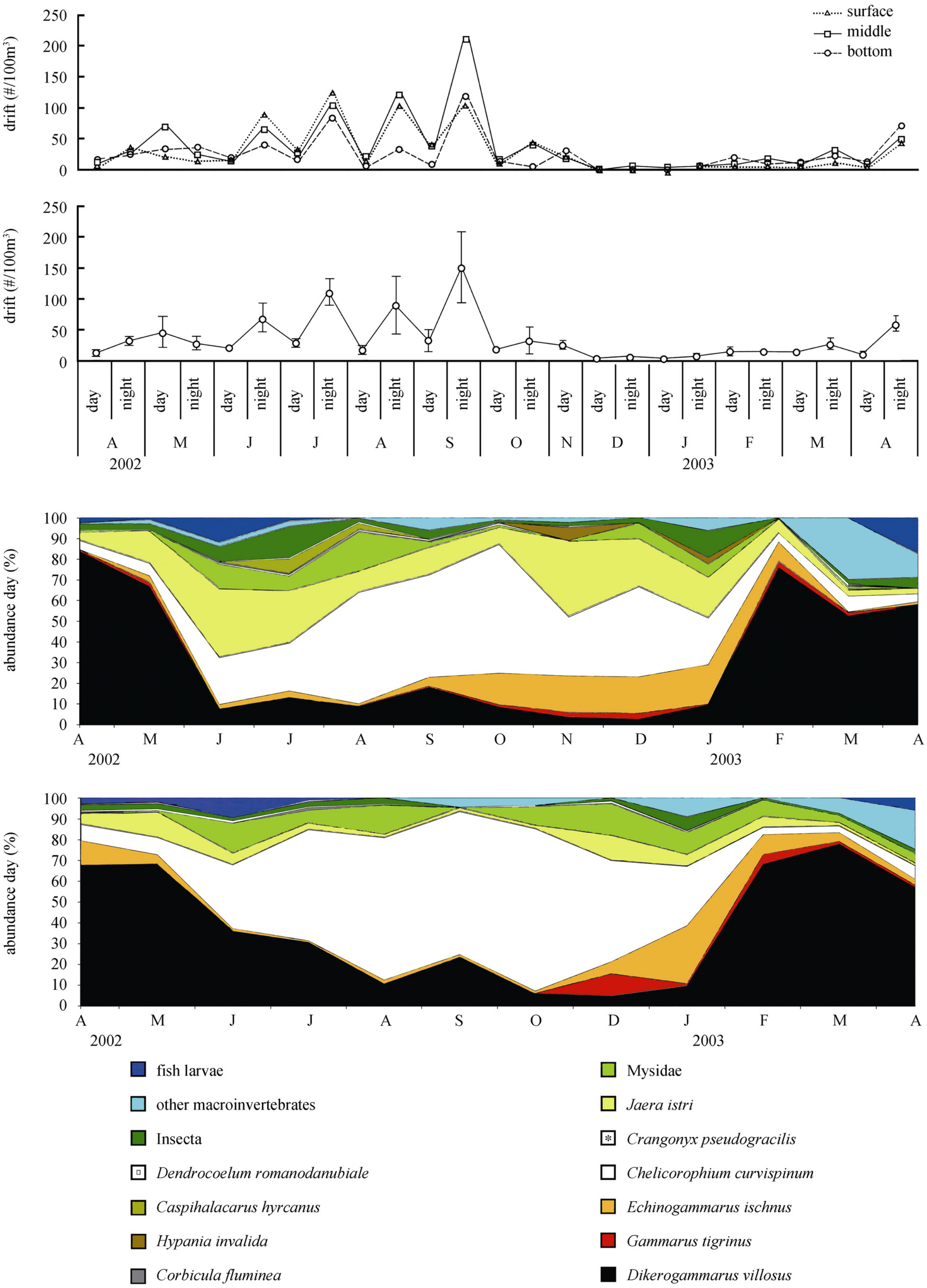

Fig. 1 **Total drift at different depths, mean drift (± *SEM*), and species composition (percentages) during the day and night**

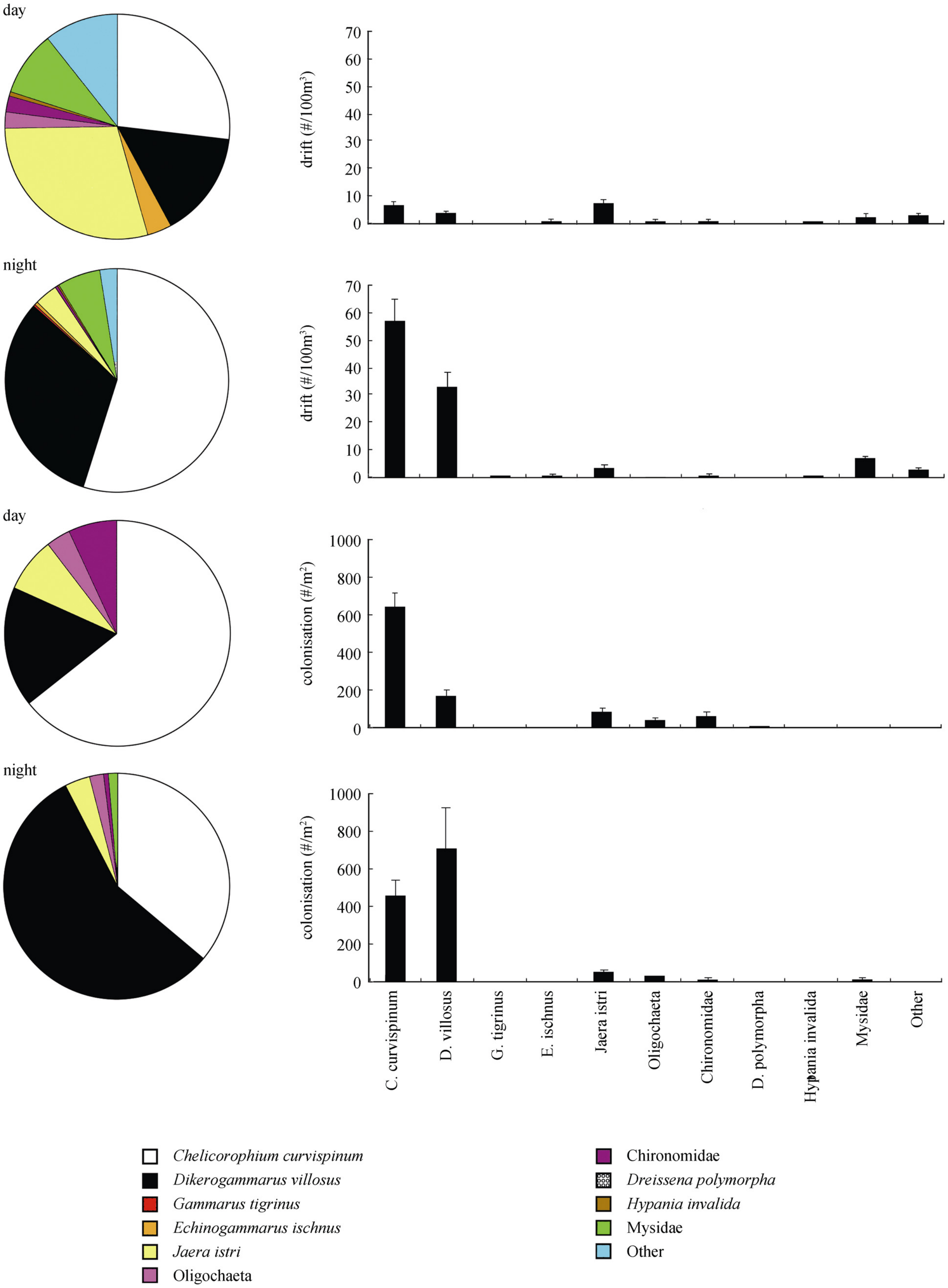

Fig. 2 Macroinvertebrates in the water column (mean ± SEM) and in substrate nets during the day and night in summer (June–August 2002)

night. *C. curvispinum* was an exception with high numbers drifting during the night, but showing a higher settlement rate during the day than during the night (Fig. 2).

Seasonal peaks in the drift of *D. villosus* generally reflected the densities of this species on the stones (Fig. 4), except during September and October. During these

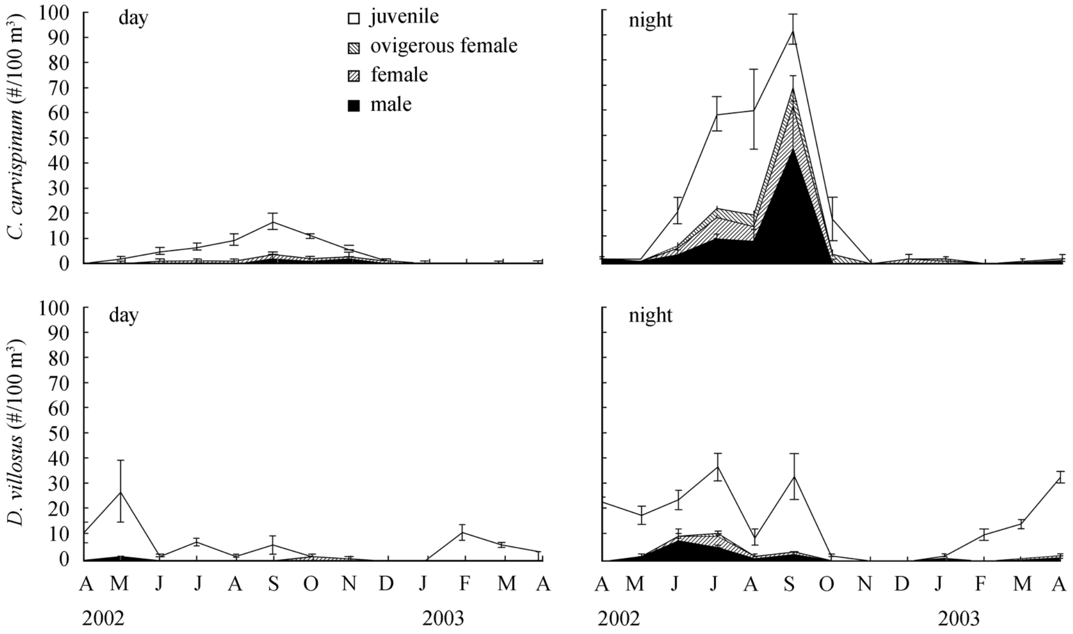

Fig. 3 Contributions of life stages (mean ± *SEM*) of *Dikerogammarus villosus* and *Chelicorophium curvispinum* found in drift samples during the day and night

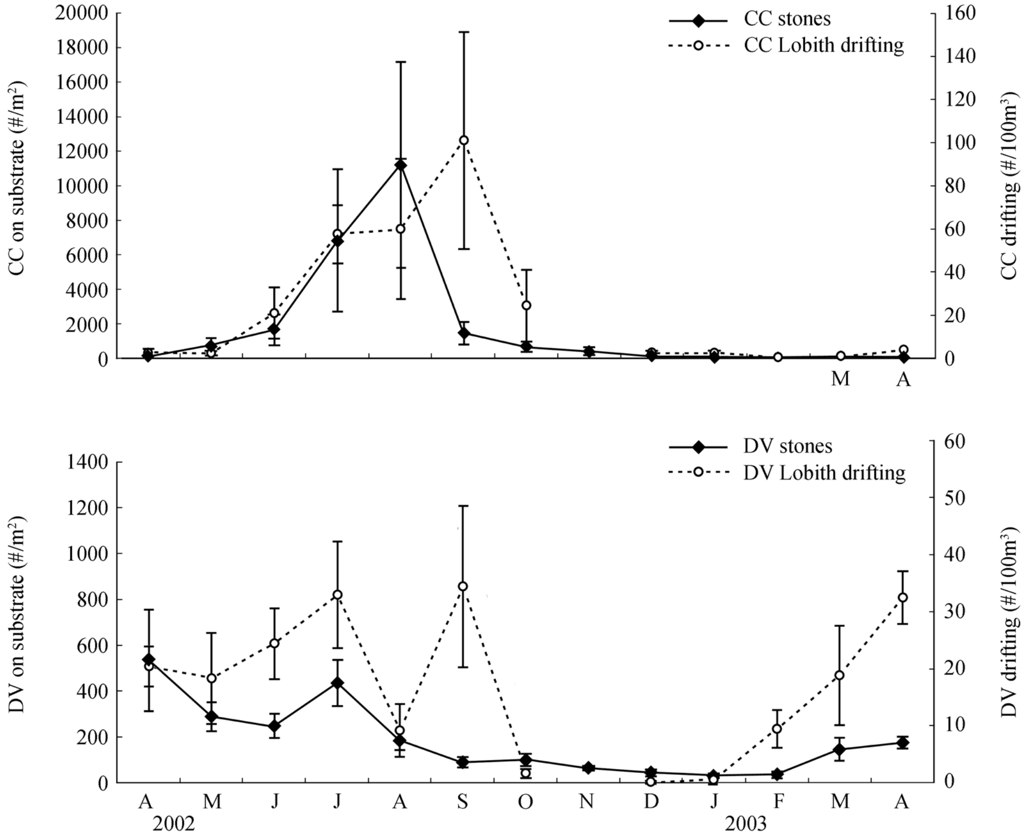

Fig. 4 Abundances of *Dikerogammarus villosus* (DV) and *Chelicorophium curvispinum* (CC) on the stones (mean of the values at the Lobith, Tiel, Lekkerkerk, Kampen and Wijhe locations ± *SEM*) and in the water column (mean ± *SEM*) during one year

months, high peaks of *D. villosus* were found drifting, but numbers of *D. villosus* on the stones were low. *C. curvispinum* peaked in drifting activity after a period of high densities on the stones (Fig. 4). Drift and settlement showed comparable seasonal fluctuations (Fig. 5). Both drift and colonization were highest during the summer and almost absent during the winter. Although *C. curvispinum* dominated the drift in the course of the year, the stones were mostly colonised by *D. villosus*. During the spring, drift and colonization mostly happened at night and both were dominated by *D. villosus*.

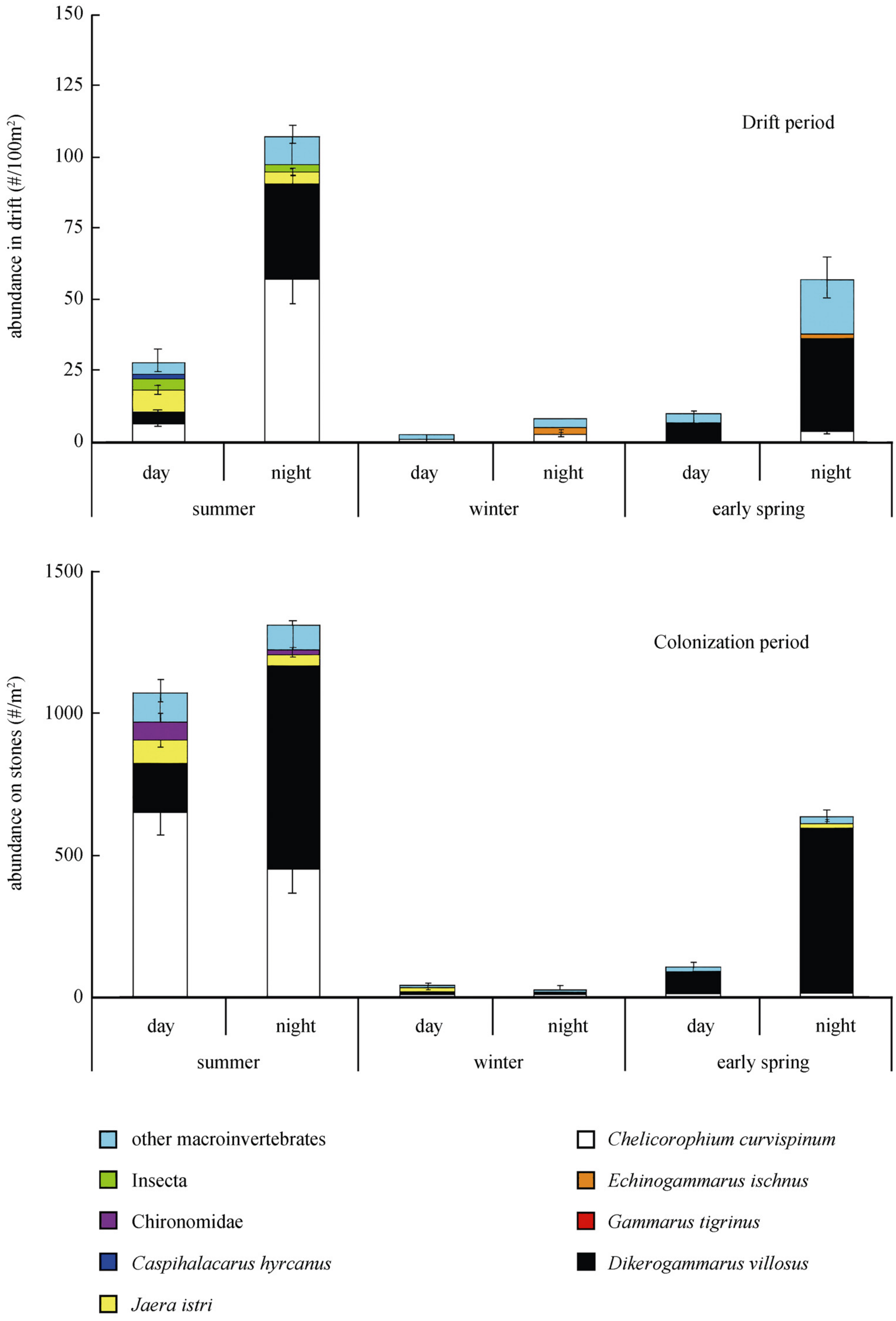

Fig. 5 Drift and colonization of stones by macroinvertebrates during different seasons

3 Discussion

The Main-Danube Canal forms the link between the Rhine and Danube river basins. Water levels in the upper part of the canal are maintained by pumping water from the Danube basin into the Rhine basin, which facilitates migration of mobile animals (e.g., crustaceans) from the Danube basin towards the Rhine basin. Tittizer (1997) estimated that 150 million m^3 of water from the Danube basin flows into the Rhine each year. Adult *D. villosus* were not only found drifting, but also attached to the outer side of our sampling nets. This may indicate that this species can also use floating substratum (floating wood, ship's hulls) for dispersal. *D. villosus* and the mud-tube building *C. curvispinum* may have been introduced in, or migrated to the Rhine using drift in combination with vectors like ship's hulls and floating substratum (Taylor and Harris, 1986a,b; Van den Brink et al., 1993a; Martens and Grabow, 2008).

The abundance and composition of drifting macroinvertebrates varied strongly with the season and was influenced by water temperature and nitrate concentrations. As correlations were weak, however, drifting did not seem to be triggered by any abiotic factor in particular, except for light. Most of the abiotic factors tested also showed seasonal patterns. Environmental conditions during spring and summer facilitate survival and reproduction of macroinvertebrates and therefore generate an increase in biota (Winterbottom et al., 1997, Quinn et al., 1998). As seasonality incorporates multiple factors that directly affect macroinvertebrate life histories, community composition and food availability (Robinson and Burgherr, 1999), it is difficult to conclude what exactly determines seasonal fluctuations in macroinvertebrate abundances. Increased abundances of drifting macroinvertebrates during spring and summer could therefore be a result of seasonal changes in environmental conditions, but may also be triggered by higher overall macroinvertebrate abundances and reproduction.

In most large rivers, drifting appears to be strongly influenced by seasonal dynamics, and is thought to reflect life cycle characteristics of macroinvertebrates rather than flow regimes, if not too erratic (Cellot, 1996). Juveniles of the invasive Ponto-Caspian amphipods *Chelicorophium curvispinum* and *Dikerogammarus villosus* dominated the drift samples in the Rhine. For both *C. curvispinum* and *D. villosus*, peaks in drifting activity followed peaks in reproduction on the substrate. The composition of early colonisers of bare stones correlated with the composition observed in the drift samples, as densities, life stages and body length of drifting and colonizing specimens were comparable. The observed peaks in drifting juvenile invasive amphipods may function as an effective dispersal mechanism for these amphipods. Cellot (1996) stated already that drift is connected to life cycle dynamics.

The present study was part of a study on longer term population development on stones in the Rhine (Van Riel et al., 2006a), which showed high similarity between newly settled coloniser populations on stones and the abundance of drifting macroinvertebrates. From these colonisers, dense populations developed on stones within one month. During reproduction periods, juveniles started drifting into the water layer again. Drift, colonization and reproduction on the substrate may thus be regarded as interacting aspects of population development and dispersal processes. Invasive amphipods, drifting in large numbers, will profit from this dispersal mechanism and can spread over large distances within a short period of time. Besides seasonal patterns, diel periodicities in drift and subsequent colonisation were found for most species, including *D. villosus,* which drifted especially during the night in the summer period.

Whether macroinvertebrates start drifting actively or passively is still being discussed (Elliot 2002a). It is probable that both mechanisms occur in streams. Drifting could be an escape mechanism from predators, intraspecific competition, unfavourable environmental conditions or resource availability. On the other hand, benthic macroinvertebrates could dislodge from the substrate when they are highly active, when densities on the substrate are high, or in case of high water velocities or high discharge (Minshall and Winger, 1968; Elliot, 2002a). In the present study, no indication was found for an influence of water velocities or discharge on drift. Our results more likely indicate a population density dependent drift for *D. villosus* as well as for *C. curvispinum*. It is remarkable that in the present study, adult amphipods drifting during periods of reproduction peaks were mostly males. Similar patterns have been observed for marine amphipods and were thought to have a function in the reproduction process (Sudo and Azeta, 1992).

In conclusion: a) Invasive species were highly abundant in the drift in the river Rhine, with *D. villosus* and *C. curvispinum* representing up to 90% of total drift. b) Drifting activity showed diel and seasonal patterns. Seasonal patterns were observed as drift peaked during the summer and was lowest during the winter. Macroinvertebrates mostly drifted during the night. c) Macroinvertebrates colonised stony substrate from the water column. *D. villosus* colonised especially during the night, whereas higher numbers of *C. curvispinum* colonised during the day. d) Higher numbers of specimens were found drifting when population densities on the stony substratum were higher. e) Drifting may function as a dispersal mechanism for crustacean invaders. Once waterways become connected or a new river area is colonised, these species no longer need dispersal vectors other than drift to extend their distribution ranges.

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