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Ecological aspects, explosive range extension and impact of a mass invader, *Corophium curvispinum* Sars, 1895 (Crustacea: Amphipoda), in the Lower Rhine (The Netherlands)

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Abstract. A few years after it invaded, the amphipod *Corophium curvispinum* Sars appeared to be the most numerous macroinvertebrate species in the River Rhine. From 1987 to 1991 the densities of this species on the stones of groins in the Lower Rhine at a depth of 0.5 m increased from 2 to 200000 specimens per m^2. In the Lower Rhine and its branches the densities of *C. curvispinum* increased with increasing current velocities and with increasing water depths. So far, a maximum population density of 750000 specimens per m^2 has been found in the Lower Rhine, which is many times the densities recorded elsewhere. Population parameters, densities and distribution of *C. curvispinum* were studied in the Lower Rhine and its branches, using artificial substrates and sampling stones from groins. The success of this immigrant is related to its competitive strategy, which shows several aspects of a *r*-strategy. In addition, the heavily eutrophicated Lower Rhine provides abundant food (phytoplankton, suspended organic matter) for this opportunistic filter-feeder. The increased salinity and water temperatures in the Lower Rhine resulting from industrial discharges have contributed to the current success of this southern species originating in brackish waters. The very high densities of *C. curvispinum* might have an enormous impact on the river ecosystem by changing food webs.

Key words: *Corophium curvispinum* – Mass invasion – Lower Rhine – Ecological aspects – Range extension

The ecosystem of the River Rhine has been changed dramatically under human influence, as have many other large river systems in the world (Petts 1989). River engineering and the discharge of industrial, agricultural and domestic sewage, as well as industrial cooling-water effluents, have resulted in an impoverishment of ecological values, especially in the lower reaches (Van Urk 1984; Van den Brink et al. 1990).

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Faunal diversity was lowest in the late 1960s, when levels of toxicants were highest and oxygen levels were extremely low. After improvement of the oxygen and ammonium levels and a reduction in the levels of some heavy metals and organic pesticides, faunal diversity increased again (Van Urk and Bij de Vaate 1990; Van der Velde et al. 1991; Admiraal et al. 1993). However, the species composition had changed remarkably. Instead of characteristic riverine species, large numbers of euryoecious and exotic species invaded the river system to fill the empty niches (Van den Brink and Van der Velde 1986a, b; Den Hartog et al. 1989; Den Hartog and Van der Velde 1987; Van den Brink et al. 1988, 1989, 1990; Bij de Vaate and Greijdanus-Klaas 1990a). Most of these invaders are oligohalinous species, thermophilous species and *r*-strategists.

The amphipod *Corophium curvispinum* Sars is one of the most recent immigrants in the River Rhine. Originating from the Ponto-Caspic area the species has expanded its distributional range since 1900 from the rivers entering the Caspic and Black Seas via connected canals and rivers to western Europe, probably aided by shipping traffic (Jazdzkewski 1980). Despite intensive earlier investigations of the Rhine fauna (Van Urk 1978; 1984; Klink and Moller Pillot 1982; Van den Brink and Van der Velde 1986a, b; Van den Brink et al. 1988, 1990; Schiller 1990; Tittizer et al. 1990; Van der Velde et al. 1990 and references therein), the species was first observed in the Lower and Middle Rhine in 1987 (Van den Brink et al. 1989; Schöll 1990). A few years after its introduction, *C. curvispinum* was found to be by far the most numerous macroinvertebrate species in the Rhine system (Schöll 1990; Van den Brink et al. 1991a, b). The question arises of why this species appears to be more successful than any other invader in this system.

Knowledge of the biology and ecophysiology of invader species is necessary in order to understand the functioning of stressed ecosystems and to evaluate the impact of immigrants on the system. Some invaders may enter the system and remain at low densities for many years or disappear gradually, whereas others might have a dramatic impact on the existing ecosystem by changing food webs and energy fluxes. *Corophium curvispinum* seems to belong to the latter category (Van den Brink et al. 1991a).

Apart from information on its geographical distribution (Jazdzewski 1980 and references therein; Wouters 1985; D'Udekem d'Acoz and Stroot 1988; Van den Brink et al. 1989; Pygott and Douglas 1989; Schöll 1990; Van den Brink and Van der Velde 1992), and information on the salt physiology of the species (Taylor and Harris 1986a, b; Bayliss and Harris 1988; Harris and Bayliss 1990), very little is known about the ecology of *C. curvispinum* (Bortkewitch 1987; Van den Brink et al. 1991a, b).

We therefore decided to study, in addition to the range extension of *C. curvispinum* in the Netherlands, some important ecological aspects, such as population densities, life cycle and fecundity, as well as changes in densities of the most common macroinvertebrates in the Lower Rhine due to the presence of this mass invader.

Study area

Population parameters of *Corophium curvispinum* were studied in the Lower Rhine at Lobith, the Netherlands, close to the Dutch-German border (Fig. 1). Distribution and population densities were studied in the Lower Rhine and its branches: the River Waal, which is the main branch, receiving 65% of the water, and the Rivers IJssel and Nederrijn/Lek (Fig. 1). In the R. Nederrijn/Lek three weirs have been constructed for regulation of the water level and the water discharge in this branch and in the R. IJssel. Because of differences in the water discharge, the annual flow rates and current velocities vary between the Lower Rhine branches (Table 1). In general, they are highest in the upper parts of the branches, and lowest in the wider lower parts. The river beds of the Lower Rhine and its branches have been fixed by groins, breakwaters which consist of large stones (grauwacke). The river bed largely consists of heavily disturbed shifting sands, except in the R. Nederrijn/Lek during low discharges. Vegetation is only present in the calmer downstream reaches, in small quantities. The river banks are sandy (R. Lower Rhine, R. Waal, R. Nederrijn/Lek) or covered by stones (R. IJssel) in order to prevent erosion. Water levels vary annually, but are generally lowest in September–October.

Table 1. Average flow rate and current velocity of the Dutch Rhine branches

River branch	Flow rate ($m^3\ s^{-1}$)	Current velocity ($m\ s^{-1}$)
R. Lower Rhine	780–10,300	0.7–2.0
R. Waal	470– 6,700	0.7–2.0
R. IJssel	285– 2,160	0.3–1.1
R. Nederrijn/Lek	25– 1,440	<0.1–1.1

Methods

Distribution and population densities

In order to study the range extension of *C. curvispinum,* and the relative densities of the most common macroinvertebrates, stones of groins in the main Rhine branches Waal, Nederrijn/Lek and IJssel were sampled by carefully brushing them in the period September–October of 1988, 1989, 1990 and 1991. This period was chosen for sampling because water levels of the Lower Rhine are lowest, so that it was possible to collect by hand stones which are always below the water surface. Unless otherwise stated the stones were collected from the end of the groins, at a water depth of 0.5 m. The surface area of these stones was estimated as described by Bij de Vaate and Greijdanus-Klaas (1991). Additional data on the distribution of *C. curvispinum* in the Netherlands were obtained from S. Pinkster, R.F.M. Buskens, H.P.J.J. Cuppen and A.G. Klink.

The densities of *C. curvispinum, Dreissena polymorpha* (Pallas), *Gammarus tigrinus* Sexton and Chironomidae were studied at 13 sites on three groins in a transverse transect perpendicular to the river axis of the R. Waal near Nijmegen (km 875) in relation to the water velocity at these sites at the time of sampling. The water velocity was measured with a portable flow meter (Hontzsch, type TAD-micro). Sampling took place at the end of August 1990, at very low water levels.

In order to study the densities of *C. curvispinum* on groin stones in relation to the water depth, stones from groins at six locations in the Lower Rhine and its branches were sampled in October 1991 at depths ranging from 0.5 to 5 m.

The relationships between population density and abiotic parameters (current velocity and water depth) were tested for significance by the Spearman rank correlation test (Sokal and Rohlf 1981).

Population dynamical aspects

In 1990 the seasonal development of *C. curvispinum* in the Lower Rhine at Lobith (Fig. 1) was studied by at least monthly sampling from artificial substrates. This study was carried out as part of a long-term biomonitoring programme (Bij de Vaate and Greijdanus-Klaas 1990b). The sampling device was a stainless steel frame (20 × 20 × 20 cm) with a closed top and bottom, and with sides of wire netting made of steel thread (1.8 mm thickness). The mesh openings were 11 mm. To prevent loss of animals when pulling the cage out of the water, the bottom was covered with wire netting with 2-mm mesh openings. The cage was filled to the brim with glass marbles (diameter 20 mm). The effective colonization surface per cage was 7000 cm^2. After 1 month the cages were carefully and slowly lifted out of the water and the marbles thoroughly washed over a 0.5-mm sieve. All material was preserved in 70% ethanol. In the laboratory all specimens were identified to species level or as far as possible. *C. curvispinum* was separated from the other material in order to study its life cycle and fecundity. Within each sample all specimens of *C. curvispinum* were counted, sexed [using the presence (males) or absence (females) of genital apophyses on the ventral face of peraeon segment VII as the criterion], and their rostrum-telson length was measured to the nearest 0.05 mm using a binocular microscope. The presence of males, pre-ovigerous females, ovigerous females and juveniles was recorded. Animals with a rostrum-telson length below 2.5 mm were considered as juveniles, as it was impossible to determine their sex. When samples were very large (> 500 specimens), a subsample of about 100 specimens was taken. In order to compare the size distributions of *C. curvispinum* specimens sampled with artificial substrates (at Lobith, km 860) with those of populations living on groin stones, and in order to compare populations of this species from different localities, three locations along the Lower Rhine were sampled. At Rheden (km 886), Tiel (km 915) and Werkendam (km 961) stones from one groin per location were sampled for *Corophium* by careful brushing.

In order to study the ingested food, the contents of the intestinal tracts of 20 specimens of *C. curvispinum* collected from the stones of the groins during the summer of 1990 were investigated. Food particles were identified using a normal light microscope and a scanning electron microscope.

The biomass was calculated from a correlation between rostrum-telson length (*L*) and ash-free dry weight (AFDW). The weights were obtained from unpreserved animals, dried to constant weight at 105° C for 12 h and ashed at 550° C for 3 h.

Data on physico-chemical parameters of the Lower Rhine at Lobith, and average current velocities of the Lower Rhine and its branches, were obtained from Rijkswaterstaat/RIZA, Lelystad and from RIWA, Amsterdam, The Netherlands.

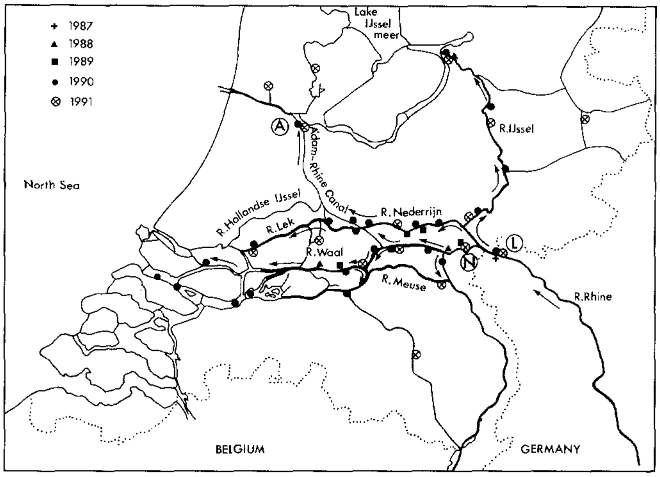

Fig. 1. Distribution map of *Corophium curvispinum* in the Netherlands

Results

Distribution and range extension

Figure 1 shows the distribution of *C. curvispinum* in the Netherlands since its introduction in 1987. The map clearly illustrates the westward downstream dispersal of the species in the Lower Rhine branches as well as its northward dispersal to the stagnant Lake IJsselmeer via the Amsterdam-Rhine Canal and via the R. IJssel (Fig. 1). In the freshwater range of the Lower Rhine and its branches *C. curvispinum* was the only *Corophium* species. In the oligohaline parts of the Lower Rhine estuary, the species co-occurred with the related brackish-water species *C. lacustre* Vanhöffen and *C. multisetosum* Stock. In the Amsterdam-Rhine Canal near Amsterdam the species was found together with *C. multisetosum*. Here niche segregation between the two species was observed, as *C. curvispinum* was found on the stones in the littoral zone, whereas *C. multisetosum* inhabited the sandy sediment in the deeper parts of this canal. In 1991 the species was found in the freshwater Lake IJsselmeer, co-occurring with *C. lacustre*. In the same year it was also the only *Corophium* species found in several canals connected to the Rhine branches via sluices. In these canals the species was found both on stones in the littoral zone and in the sandy sediments at the bottom.

Population densities and biomass

A few years after its introduction, *C. curvispinum* numbers have increased explosively in the Lower Rhine (Table 2). From 1987 to 1991 the densities of this species on stones increased from 2 to 220000 specimens per m^2. These stones were collected from groins near Lobith (km 860) at a depth of 0.5 m. Selected physico-chemical parameters of the Lower Rhine at Lobith, measured during 1986–1991 (Table 2), show that relatively high water temperatures, oxygen concentrations and concentrations of sodium and chloride occur in this river at present. However, the amounts of total organic carbon (TOC) and suspended matter show a decline over the years 1989–1991, which might be related to the increase in the population density of *C. curvispinum* (Table 2).

The densities of *C. curvispinum* in the Lower Rhine were found to decrease in a downstream direction (Figs. 1, 2). Densities were lower in the R. Nederrijn-Lek branch, which is dammed by weirs, than in the weir-free R. Waal and R. IJssel branches (Fig. 2). The densities of *C. curvispinum* in the Lower Rhine branches showed a positive correlation with the average river flow and current velocities (Fig. 2, Table 1). The highest densities of *C. curvispinum* were recorded in the upstream parts of the Lower Rhine and the R. Waal and R. IJssel branches, which have higher annual current velocities than the wider lower parts and the weired R. Nederrijn/Lek branch (Table 1).

In the microhabitat of stones on groins in the Lower Rhine between Lobith and Nijmegen *C. curvispinum* numbers showed a clear positive correlation with river

Table 2. Maximum population densities of *Corophium curvispinum* on stones from the groins at a depth of 0.5 m during the months of September-October and yearly median water quality parameters of the Lower Rhine at Lobith (km 860) of a number of consecutive years

Year	Population density (N m^{-2})	Temperature (°C)	Oxygen (mg l^{-1})	Na^+ (mg l^{-1})	Cl^- (mg l^{-1})	TOC (mg l^{-1})	Suspended matter (mg l^{-1})
1986	0	12.4	8.7	94	183	6.5	40
1987	2	13.2	8.8	83	179	5.4	37
1988	8	13.6	9.3	79	146	5.9	40
1989	1400	11.9	9.6	92	175	5.1	34
1990	100000	16.1	10.1	100	191	5.5	29
1991	220000	13.6	9.5	101	192	5.2	32

TOC = total organic carbon

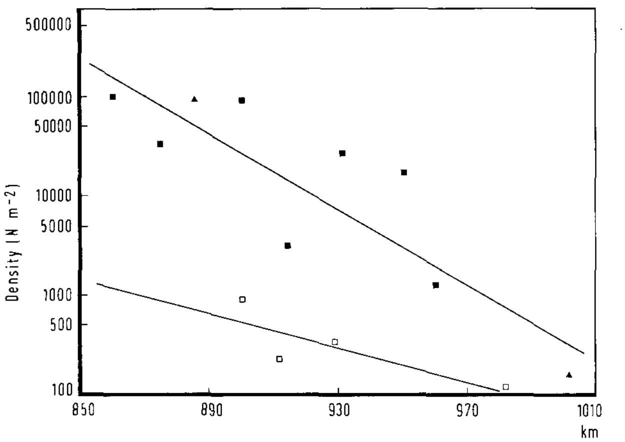

Fig. 2. Population densities of *Corophium curvispinum* along the three major branches of the Lower Rhine during the autumn of 1990. *Above:* densities in the non-dammed R. Waal *(solid squares)* and R. IJssel *(solid triangles)* branches; *below:* densities in the dammed R. Nederrijn/Lek branch *(open squares)*. *Km* = international river distance in km. *Lines* were fitted by eye

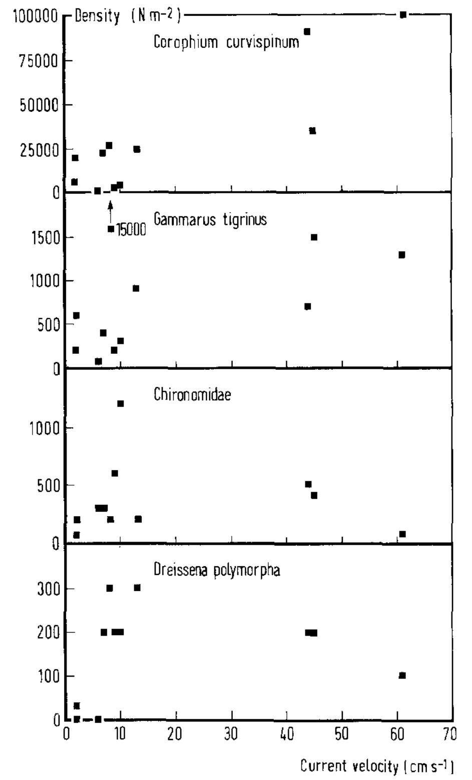

Fig. 3. Densities of *Corophium curvispinum, Gammarus tigrinus,* Chironomidae and *Dreissena polymorpha* on stones from groins in the Lower Rhine (km 870) plotted against flow velocity at the sites in August 1990

current velocities (which ranged from 0 to 60 cm s^{-1} at the time of sampling) ($P = 0.02$) in contrast with subdominant taxa such as *Gammarus tigrinus* ($P = 0.06$), *Dreissena polymorpha* ($P = 0.51$) and Chironomidae ($P = 0.16$) (Spearman rank correlation test) (Fig. 3).

The densities of *C. curvispinum* on the groin stones in relation to water depth are shown in Table 3. Highest densities were found at depths of more than 1 m (range 0.5–5 m). The highest density of *C. curvispinum* observed during our study was 750000 specimens per m^2, at a depth of 2–3 m in the R. Waal at Tiel in October 1991 (km 915).

In order to estimate the biomass of *C. curvispinum,* a length-biomass correlation was calculated by regression analysis. The correlation between length (mm) and AFDW (g) is given by the equation: $\log(\mathrm{AFDW}) = 2.83 \log(L) - 5.36$ ($r^2 = 0.97$; $P < 0.001$; $n = 550$). The *C. curvispinum* density of 220000 specimens per m^2 observed in the Lower Rhine in September 1991 corresponded to a biomass of 21.4 g AFDW (Table 4).

Population structure

Size-frequency distributions of the populations from Lobith and Rheden, which were sampled by different methods showed no major differences (Fig. 4), indicating that the artificial substrate method provided a useful tool for studying population dynamic aspects. The size-frequency distributions of populations of *C. curvispinum* sampled from different stations (river km 860 downstream to river km 961) also showed great similarity.

The overwintering population consisted of animals with a total body length of 2.4–4.5 mm, belonging to two size classes (Fig. 5). Very large adults (5.5–7.0 mm size class) appeared in the samples in March, and disappeared at the end of May, after the first peak of juveniles (April–May). After the second peak of juveniles, in July, the second peak of very large adults became extinct. Finally, in October a third peak of juveniles was found, showing that three generations per year are produced. The period

Table 3. Population densities of *C. curvispinum* along depth gradients on groins in the Lower Rhine and its branches in the Netherlands during October 1991

Depth (m)	R. Lower Rhine/Waal		R. IJssel		R. Nederrijn/Lek	
	Lobith km 860 (n m^{-2})	Tiel km 915 (n m^{-2})	Velp km 885 (n m^{-2})	Olst km 965 (n m^{-2})	Rhenen km 912 (n m^{-2})	Lekkerkerk km 982 (n m^{-2})
0–1	220000	200000	30000	900	11000	80
1–2	120000	300000	140000	1100	8000	5100
2–3	160000	750000	80000	600	11000	1500
3–4	270000	580000	400000	1200	110000	1300
4–5	360000	630000	120000	200	74000	1400

Table 4. Population densities and biomasses of *C. curvispinum*

Density (N m^{-2})	Biomass (g m^{-2})	Location	Country	Reference
3000	3.0 (a)	R. Ingulez	USSR	Bortkewitch (1987)
7700		R. Warthe	Germany	Schellenberg (1942)
8600	0.8 (b)	L. Balaton	Hungary	Muskó (1989)
10000		R. Don	USSR	Harris and Bayliss (1990)
50000		R. Mosel	Germany	Schöll (1990)
100000		R. Middle Rhine	Germany	Schöll (1990)
220000	21.4 (b)	R. Lower Rhine	The Netherlands	this study
750000		R. Waal	The Netherlands	this study

a = dry weight, b = ash-free dry weight

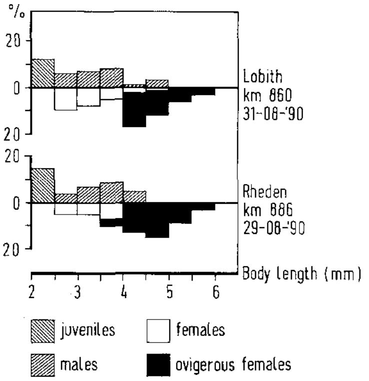

Fig. 4. Size frequency distributions of populations of *Corophium curvispinum* as sampled with artificial substrates (Lobith) and by sampling stones from groins (Rheden)

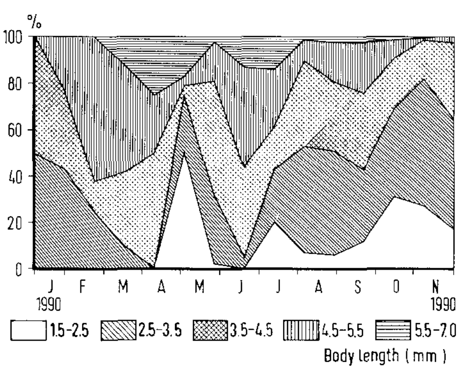

Fig. 5. Size frequency distribution of *Corophium curvispinum* during 1990, as sampled with artificial substrates in the Lower Rhine at Lobith

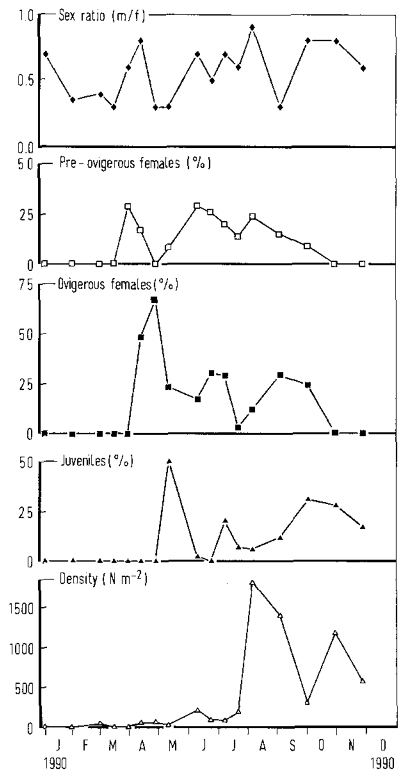

Fig. 6. Sex ratio, relative occurrence of pre-ovigerous females, ovigerous females and juveniles, and population density of *Corophium curvispinum*, during 1990, as sampled with artificial substrates in the Lower Rhine at Lobith

May–August saw the largest shifts in size, indicating that growth rate was highest in that period. This period also has the highest water temperatures (15–20° C).

Breeding cycle and fecundity

Reproduction of *C. curvispinum* in the Lower Rhine takes place from April to September (Fig. 6), which is the warmest period of the year (12–20° C). The sex ratio was always below 1, which means that more females than males were collected. Ovigerous females were first present in mid-April at a water temperature of about 12° C. The first juveniles were collected at the beginning of May, so that embryonal development lasted about 2 weeks. In June an increase occurred in the 2.5–3.5 mm size group, which is the new generation of adults; hence larval development took approximately 4 weeks. At the onset of reproduction in April the largest females (5.00–6.30 mm) were ovigerous a few weeks earlier than the smaller ones (3.80–4.75 mm). Density fluctuations showed two peaks per year, during August–September and October–November (Fig. 6). This could not be attributed to fluctuations in flow velocity or fluctuations in water level, as river discharge was rather stable during that period.

A clear correlation was found between the female body length (L) and the number of eggs carried (N)

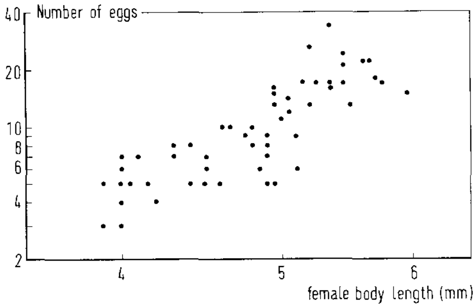

Fig. 7. Fecundity of *Corophium curvispinum* in the Lower Rhine in 1990

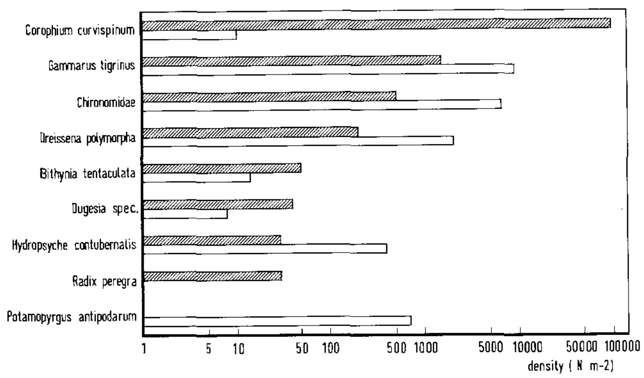

Fig. 8. Changes in densities of the nine most common macrozoobenthos taxa on the stones of groins in the Lower Rhine at Lobith (km 860) during October 1988 *(open columns)* and October 1990 *(shaded columns)*

(Fig. 7), according to the formula: $\log(N) = 4.13 \log(L) - 1.81$ ($r^2 = 0.70$; $P < 0.001$; $n = 54$ observations). The numbers of eggs carried ranged from 3 to 34 eggs per female. Egg sizes ranged from 360 × 280 μm (stage I) to 520 × 440 μm (stage IV).

Role in the food web

Examination of the intestinal tract of *C. curvispinum* showed planktonic diatoms (e.g. *Stephanodiscus hantzschii* Grün., *Melosira granulata* Ehr., *Diatoma elongatum* (Lyngb.) Ag. and *Asterionella formosa* Hass.), green algae (e.g. *Pediastrum boryanum* (Turp.) Menegh., *Ankistrodesmus falcatus* (Corda) Rahlfs and *Scenedesmus* spp.) as well as small mineral and organic particles. *C. curvispinum* uses these sediment particles to build muddy tubes in which it lives.

Apart from an enormous increase in density of *C. curvispinum* over the years 1988–1990, small increases were noted for *Bithynia tentaculata* (L.), *Dugesia* spec. [= *D. polychroa* (Schmidt) + *D. tigrina* (Girard)] and *Radix peregra* (Müll.), while serious declines were observed for *Gammarus tigrinus*, Chironomidae, *Dreissena polymorpha, Hydropsyche contubernalis* McL. and *Potamopyrgus antipodarum* (Gray) (Fig. 8).

C. curvispinum was collected from the gut of various fish species (Table 5).

Discussion

Distribution and range extension

During the few years since its first occurrence, *C. curvispinum* has increased explosively in the Lower River Rhine (Table 2). Observations on densities of this species from the Middle Rhine (Schöll 1990), showed that very high densities exceeding 100,000 specimens per m^2 occurred there as early as 1989, a year earlier than in the Lower Rhine. This makes it clear that the species entered the Netherlands via the upstream German part of the River Rhine. Consequently, densities in the Netherlands Rhine sections are highest near the Dutch-German border (Figs. 1, 2). Although the species was found in the Belgian part of the River Meuse in 1981 (D'Udekem d'Acoz

Table 5. Fish species recorded as predators of *C. curvispinum*

Species	Location	Reference
Acipenser stellatus Pallas	R. Volga	Behning (1914)
Acipenser ruthenus L.	R. Volga	Behning (1914)
Stizostedion lucioperca (L.)	R. Lower Rhine	Bergers (1991)
Gymnocephalus cernuus (L.)	R. Volga	Behning (1914)
	Shropshire Union Canal	Pygott and Douglas (1989)
	R. Lower Rhine	Bergers (1991)
Perca fluviatilis L.	L. Balaton	Sebestyén (1934)
	Shropshire Union Canal	Pygott and Douglas (1989)
Gobio gobio (L.)	R. Volga	Behning (1914)
	Shropshire Union Canal	Pygott and Douglas (1989)
Alburnus alburnus (L.)	L. Balaton	Sebestyén (1934)
Abramis brama (L.)	L. Balaton	Sebestyén (1938)
Noemacheilus barbatulus (L.)	R. Volga	Behning (1914)
Anguilla anguilla (L.)	L. Balaton	Muskó (1989)
	R. Lower Rhine	Bergers (1991)
Cottus gobio L.	R. Lower Rhine	Hanssen (1991)

and Stroot 1988), the Dutch part of the River Meuse has only very recently been colonized (Fig. 1). *C. curvispinum* most probably entered this river via its connections with the Lower Rhine and not via the upstream Belgian Meuse route. Despite intensive earlier investigations in the Dutch part of the R. Meuse (Peeters 1988; Klink 1990; Frantzen 1991), the species was first found in the lower reaches in 1990, close to the St. Andries Canal, which connects the rivers Waal and Meuse. In 1991 *C. curvispinum* was found in the R. Meuse near Grave, close to the Meuse-Waal Canal, but not higher upstream in the Dutch Meuse. The very high concentrations of cadmium in the R. Meuse downstream of the industrial area of Liège, close to the Dutch-Belgian border, have been correlated with a total absence of amphipods in this part of the river (Klink 1990).

In 1991 the species was found to have extended its distribution from the Lower Rhine area via connected waters to several canals and Lake IJsselmeer. Most of these stagnant or slow-flowing waters are fed with Rhine water, which has a relatively high ionic content (median: 4.4 mM Na^+, ranges: 2.5–7.0 mM Na^+; measured in the Lower Rhine at Lobith during 1991), favouring the occurrence of *C. curvispinum,* which needs a minimum [Na^+] of 0.5 mM (Taylor and Harris 1986b). The species was also observed in the oligohaline parts of the estuarine area of the Lower Rhine, concurring with the brackish water species *C. multisetosum* and *C. lacustre* (Van den Brink and Van der Velde 1992). A further penetration into brackish areas is to be expected, since *C. curvispinum* is originally a brackish-water species (<6‰ salinity) with a tolerance for very low salinities (Taylor and Harris 1986a, b; Bayliss and Harris 1988; Harris and Bayliss 1990).

Population densities and microhabitat selection

Maximum population densities of *C. curvispinum* found in the Lower Rhine branch the R. Waal during 1991 were 750000 specimens per m^2 stone surface, many times those recorded from other waters (Table 4). Even these densities are probably underestimated, as the smallest juveniles with a body length of 0–1 mm were not retained in our samples, due to the relatively large mesh size of the sieves (0.5 mm).

In the Netherlands *C. curvispinum* was most commonly found on stones in the Lower Rhine and its branches. In the sediment of the deepest part of the river bed at Lobith *C. curvispinum* was found at relatively low densities (2,550 individuals m^{-2}). It is likely that the shifting of the sandy sediments due to the very intensive shipping traffic provides an unsuitable habitat for settlement. Apart from stones and sandy sediments, the species also uses submerged vegetation (e.g. *Ceratophyllum demersum* L., *Myriophyllum spicatum* L., *Potamogeton pectinatus* L. and *P. perfoliatus* L.) (Sebestyén 1934, 1938; Pygott and Douglas 1989; Muskó 1989, 1990) and clayey sediments (Bortkewitch 1987) for settlement. In the Lower Rhine, vegetation and clayey sediments are scarcely present in the summer bed, so that these habitats can hardly be colonized. The stones of the groins in the Lower Rhine branches proved to be an excellent habitat for the species, since densities were high. Highest densities occurred at depths exceeding 1 m (Table 3), which must be related to the more stable conditions with regard to water level fluctuations and waves from passing ships. Besides a relation with water depth, the population densities of *C. curvispinum* in the stone habitat showed a clear positive correlation with the current velocity, since highest densities were found at sites with higher velocities ($P<0.05$), i.e. at the end of the groins (transverse to the river axis) and in the upstream parts (longitudinal direction) of the rivers Waal, IJssel and Lower Rhine (Figs. 1 to 3; Table 1). This correlation with current velocity might be related to the position of the animals with regard to the amount of food which can be collected with relative ease. For a filter-feeding species such as *C. curvispinum* food can be most easily collected at sites where the current is strong enough for a continuous supply of food, and weak enough to prevent erosion or drift of the population. It was found that the food of specimens from the Lower Rhine consisted of phytoplankton and other suspended matter. The phytoplankton species occurring in the intestinal tracts were the same species that dominate the Lower Rhine plankton (De Ruyter van Steveninck et al. 1989).

Life cycle and fecundity

In the Lower Rhine *C. curvispinum* breeds from April to September, producing three generations a year (Fig. 6), which is in good agreement with observations on the life cycle of a population of *C. curvispinum* from the Ponto-Caspic area (Bortkewitch 1987). Related species, such as *C. volutator* Pall., *C. bonnelli* M.-Edw., *C. arenarium* Crawford and *C. insidiosum* Crawford have only two generations each year (Sheader 1978; Fish and Mills 1979; Moore 1981; Möller and Rosenberg 1982). Ovigerous females of *C. curvispinum* were exclusively found in the warmest months of the year, in contrast to those of *C. bonnelli* and *C. insidiosum,* which also breed during the colder seasons (Sheader 1978; Moore 1981). The egg clutch size of *C. curvispinum* was found to increase as the fourth power of the total body size ($L^{4.1}$), showing a much higher increase with length than the number of eggs carried by *C. insidiosum* ($L^{3.1}$) (Sheader 1978) or by *C. arenarium, C. volutator* and *C. bonnelli* (L^1) (Fish and Mills 1979; Moore 1981). The numbers of eggs carried per female ranged from 3 to 34 (mean: 12) in our study (Fig. 7). Muskó (1989, 1990) found smaller numbers of eggs (range: 1–25, mean: 6) per female of *C. curvispinum* in Lake Balaton. These differences are not due to differences in female body length since the egg clutch size of large females of 5–6 mm was about 8–11 eggs in Lake Balaton (Muskó 1990), while in the Lower Rhine it was 12–25 eggs. The eggs of females from L. Balaton measured 478×369 μm (Muskó 1989), which is in the range of the sizes observed for eggs from specimens from the Lower Rhine (stage I: 360×280 μm, stage IV: 540×440 μm). The differences in egg clutch size might be related to differences in the amount of food available. In the Lower Rhine food conditions may be better because of a continuous supply of phytoplankton and suspended organic material by the flow of the river, which of course is absent in the stagnant L. Balaton.

Impact on the Rhine ecosystem

It may be questioned whether the successful invader constitutes a problem for the current attempts to restore the Rhine ecosystem. *C. curvispinum* outnumbers other inhabitants of the groins (Fig. 8). Among these are other invaders like *Gammarus tigrinus* and *Dreissena polymorpha,* but also autochthonous riverine species, such as the caddis fly *Hydropsyche contubernalis.* From 1988 to 1990 these species showed a decline in population densities in the Lower Rhine (Fig. 8). Because *Corophium curvispinum, Dreissena polymorpha* and *Hydropsyche contubernalis* are all filter-feeders, competition for food might be expected. The population explosion of *C. curvispinum* during 1989–1991 coincided with a decrease in the concentrations of total organic carbon (TOC) and total suspended matter in the Lower Rhine (Table 2), which might be related to the increase in filtration capacity in the river. Besides competition for food, there is probably also competition among macroinvertebrates for space, the groins form practically the only available solid substrate in the river. Bare solid substrates are indispensable for the attachment of *D. polymorpha* (Bij de Vaate 1991). Specimens of *D. polymorpha* were observed to be completely overgrown by the tubes of *C. curvispinum.* Moreover, in building its muddy tubes this species modifies the substrate, thereby preventing the settlement of young *Dreissena* larvae.

It is possible that within a few years densities of this amphipod will decrease, if predators or parasites start to take full advantage of this abundant food source. *C. curvispinum* has been found in the gut of various fish species (Table 5). In the Lower Rhine predators such as *Stizostedion lucioperca, Gymnocephalus cernuus, Perca fluviatilis, Gobio gobio, Abramis brama, Alburnus alburnus* and *Anguilla anguilla* are quite common (Van den Brink et al. 1990). Apart from fish species, predatory invertebrates such as flatworms and leeches can also consume *C. curvispinum.* Hence, it will be neccessary to follow the further development and range extension of this invader in order to evaluate its impact on the aquatic ecosystem of the Lower Rhine and its connected systems.

Conclusions

The following ecological aspects have contributed to the explosive dispersal of *C. curvispinum* in the Lower Rhine. Firstly, the species shows several characteristics of a *r*-strategist, with multiple (three) generations a year, a short developmental time (a few weeks in summer) and a short life span (about 1 year). Secondly, *C. curvispinum* is an opportunistic filter-feeder and the organically polluted and eutrophicated Lower Rhine provides an abundant food supply, resulting in a high fecundity. Thirdly, the species forms dense colonies of muddy tubes in which it lives, which might provide shelter against predators, and which make the substrate unsuitable for filter-feeding competitors like *Dreissena polymorpha* and *Hydropsyche contubernalis.* Finally, the current water chemistry (e.g. high ionic content), high water temperatures and morphology (e.g. the presence of stony substrates) of the Lower Rhine provide ideal circumstances for the development of this southern species of brackish origin.

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