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FURTHER OBSERVATIONS ON THE DISTRIBUTION AND BIOLOGY OF TWO ALIEN AMPHIPODS, *GAMMARUS TIGRINUS* SEXTON, 1939, AND *CRANGONYX PSEUDOGRACILIS* BOUSFIELD, 1958, IN THE NETHERLANDS (CRUSTACEA, AMPHIPODA)

Sjouk PINKSTER & Dirk PLATVOET

ABSTRACT

Like in many previous years, the distribution pattern of *G. tigrinus* was followed. *G. tigrinus* proves to have recovered from its decline after the severe winter of 1978/1979.
Likewise the distribution of *C. pseudogracilis* was checked, three year after its first discovery in the Netherlands. Some minor range extensions were found. In a monthly sampling program and in laboratory experiments information was collected on the biology so far unknown for this species. Its possible future interaction with local amphipod species is discussed.

INTRODUCTION

After its introduction (probably in 1964) *Gammarus tigrinus* successfully invaded most of the oligohaline waters in the Netherlands (see Dieleman & Pinkster, 1977). In every sampling survey up to 1978 the area inhabited by this species was larger than before. In 1979 it became apparent that, apart from some minor range extensions in the southwestern part of the country, *G. tigrinus* had disappeared from a great number of formerly inhabited waters, especially in the northeastern part of the country. On the other hand, local species like *G. d. duebeni* Liljeborg, 1852, and *G. zaddachi* Sexton, 1912, which had almost disappeared from the area previously invaded by *G. tigrinus* showed a remarkable recovery. The severe and long winter of 1978/1979 is considered to be the main cause of the sudden decline of *G.*

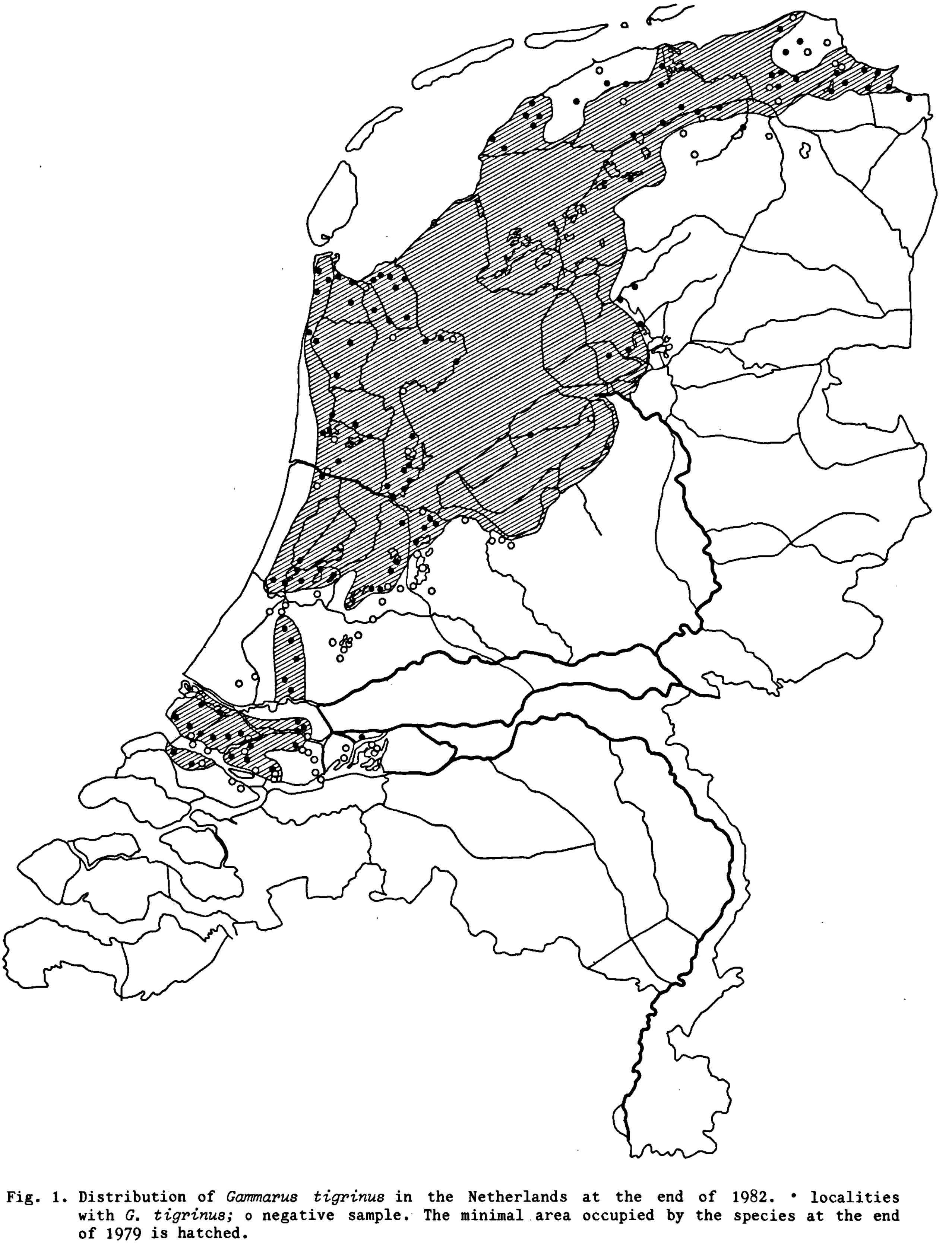

Fig. 1. Distribution of *Gammarus tigrinus* in the Netherlands at the end of 1982. • localities with *G. tigrinus*; o negative sample. The minimal area occupied by the species at the end of 1979 is hatched.

tigrinus, an opinion which is in accordance with the results of Pinkster et al., 1977.

During the 1979 survey, another amphipod, *Crangonyx pseudogracilis*, was found, a species so far unknown to the Dutch fauna.

Since 1979 a survey is made each year throughout the former distribution area of *G. tigrinus* and the adjacent areas to follow its interesting and sudden decline. The same was done for *C. pseudogracilis*, together with a monthly sampling program and a series of laboratory experiments in order to obtain information on the biology of this species.

THE POSITION OF *GAMMARUS TIGRINUS* AT THE END OF 1981

During our survey in the summer and autumn of 1981, old and abandoned localities of *G. tigrinus* have been revisited, as well as the areas adjacent to the known distribution area. It appeared that in most parts of the country *G. tigrinus* had reoccupied the formerly abandoned positions. It again is the dominant species in the province of North-Holland and in the oligohaline waters in Friesland and Groningen. In the IJsselmeer, the former Zuiderzee, it is the only species found. In a few localities only, especially in the northeastern part of the country, it has not yet returned; in these localities the position of *G. tigrinus* is taken over by *G. zaddachi* and *G. duebeni*. In the southwestern part of the Netherlands, the Deltaic region of the Rhine, which was recently invaded (Pinkster et al., 1980) the range extension of *tigrinus* seems to have come to a standstill. Apart from two new localities on the island of Voorne-Putten, no new localities have been found (Fig. 1).

THE POSITION OF THE INDIGENOUS SPECIES IN THE INVESTIGATED AREA

Gammarus p. pulex (Linnaeus, 1758).

The position of *G. p. pulex* did not change much since our last survey. It is still the dominant species in the central part of the province of South-Holland. In the provinces of North-Holland, Friesland and Groningen *G. p. pulex* still maintains its position in the fresh and oligohaline waters on sandy bottoms. It is the dominant gammarid species in the running fresh waters in the eastern and southern parts of the country.

Gammarus d. duebeni Liljeborg, 1852.

After the collapse of *G. tigrinus* in 1979 *G. d. duebeni* was more frequently found than in the previous years, sometimes in rather dense populations, but it never did benefit on a large scale (Pinkster et al., 1980). During the present survey it became clear that this revival had only a limited and temporary character. Most probably the reproductive capacity of this species is too low to profit on a large scale of the (temporary) disappearance of *G. tigrinus*. It can only maintain its position when *G. tigrinus* is absent as is the case in some mesohaline waters behind the dikes, on the isles of the Deltaic region and on the Frisian isles.

Gammarus zaddachi Sexton, 1912

The position of *G. zaddachi* did not change since the last survey in 1979. It is still the dominant species in the meso- and polyhaline waters behind the dikes, on the isles of the Deltaic region and on the Frisian isles, where it coexists with *G. d. duebeni*.

DISCUSSION

It is clear that *G. tigrinus* has rapidly recovered from its severe decline in the winter of 1978/1979. This was to be expected because its reproductive capacity is much higher than that of the local brackish water species (Pinkster et al., 1977). Only in regions with a relatively high salinity *G. zaddachi* and *G. d. duebeni* can maintain their positions. It will be very interesting to follow the future developments and the long term effects of the variations in the climatic conditions on the position of *G. tigrinus* and the other brackish water species. Likewise it is clear that *G. tigrinus* is not able to invade the fresh (and often running) waters in the eastern and south-

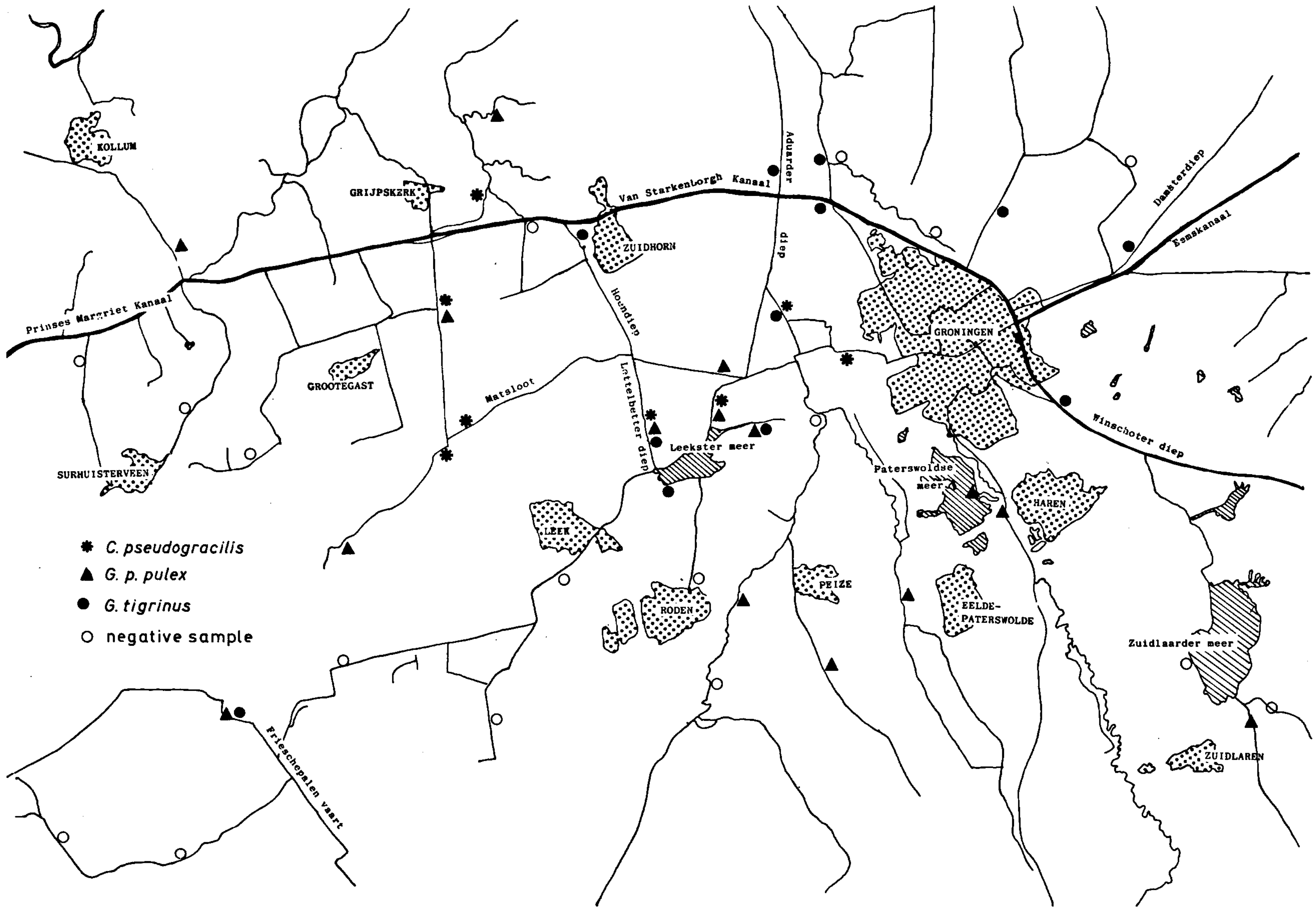

Fig. 2. Distribution of *Crangonyx pseudogracilis* and other aquatic amphipod species by the end of 1982.

ern part of the country. Here *G. p. pulex* is still the dominant species and this situation does not seem to alter. In contact zones between *G. tigrinus* and *G. p. pulex*, e.g. in the Hierdense Beek (Province of Gelderland), the division between the two species did not move upstream (or downstream) during the 15 years of the present investigations.

CRANGONYX PSEUDOGRACILIS Bousfield, 1958

Introduction.-

After the introduction of *Gammarus tigrinus* in the Netherlands and its subsequent rapid dispersal over great parts of the country, we were anxious to follow the distribution pattern of the recently discovered *Crangonyx pseudogracilis*, particularly since this species was already widely distributed in Great Britain and Ireland. We also were curious to see if this species would be as successful as *tigrinus* and what again the influence would be on the local gammarid species. Since, at the time of its first discovery almost no information was available on the biology of the species, we started to collect data on its life cycle, the incubation period of the eggs, the time needed to reach sexual maturity and the fecundity of the species. In a later stage these data have been compared with data on the local gammarid species (if available) in order to foretell eventual future developments and the impact on the local gammarid fauna.

Distribution.-

In 1979 *C. pseudogracilis* was first discovered in a rather limited area in the province of

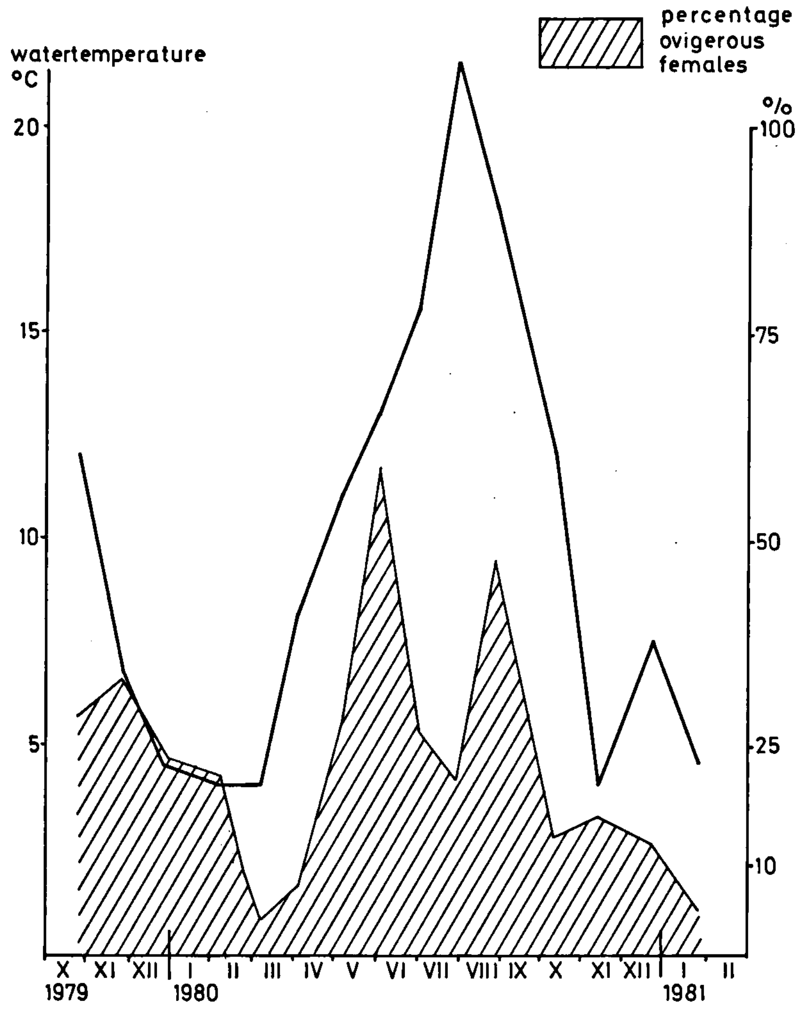

Fig. 3. Yearly temperature changes and percentage of ovigerous females in a population of *Crangonyx pseudogracilis*.

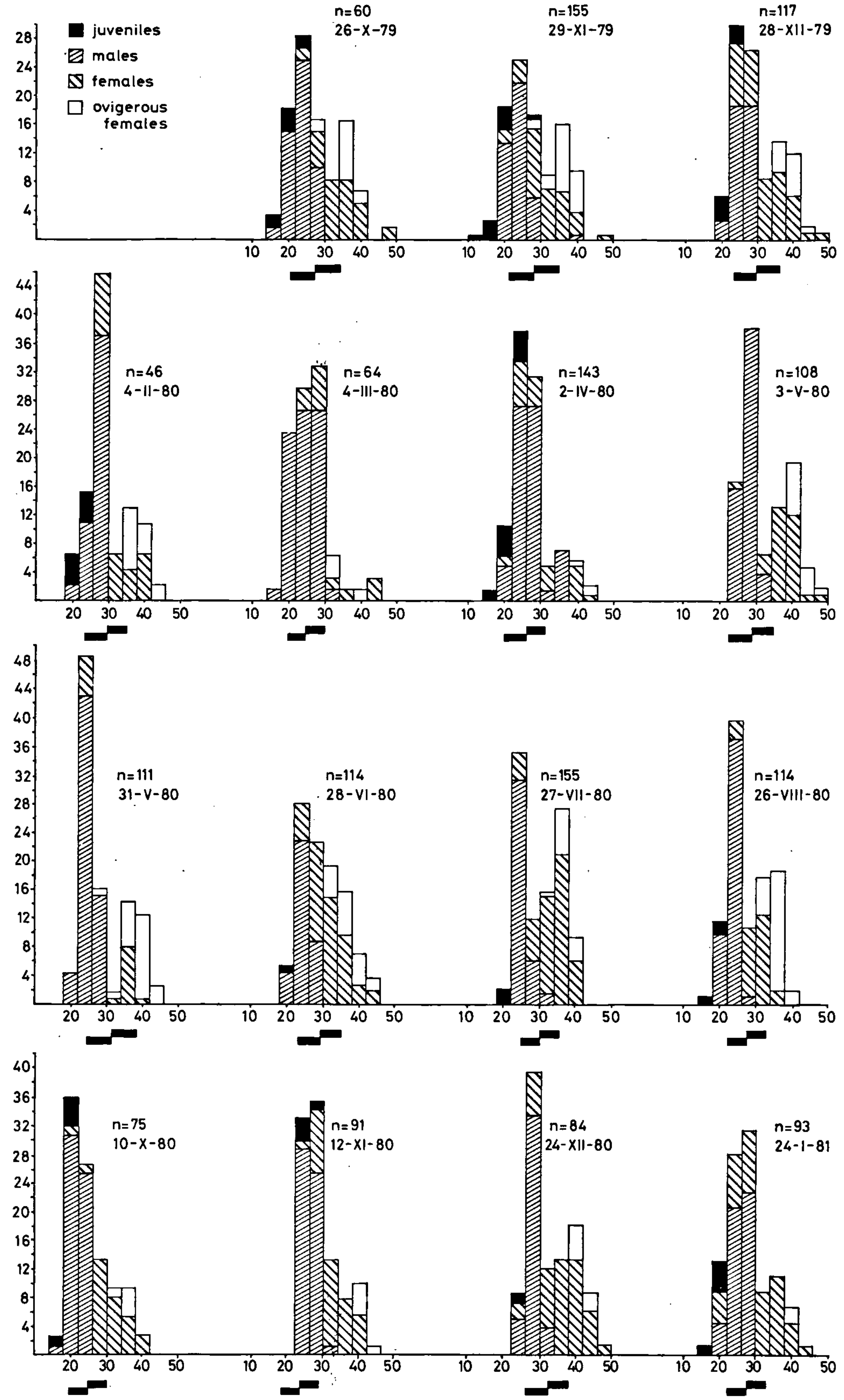

Fig. 4. The population composition in *Crangonyx pseudogracilis* from Boerakker. Lengths are expressed in mm. The mean length and standard deviation are indicated.

Groningen (see Fig. 3 in Pinkster et al., 1980). In the three consecutive years we followed the distribution of the species; in 1980 and 1981 no range extension was found and the species even disappeared from one locality. In the summer of 1982 however, some progress could be observed in nearly all directions. In one formerly inhabited locality it could not be retraced (see Fig. 2).

Life cycle.-

From October 1979 till January 1981, the reproductive cycle of one of the populations of *C. pseudogracilis* was followed. At this locality (near the village of Boerakker, province of Groningen) monthly samples were taken; we tried to collect at least 100 specimens, but this was not always possible, especially not in winter because of the low population density. At the same time some physico-chemical factors, such as temperature, chlorinity, pH and (sometimes) oxygen saturation, were measured. It was concluded that temperature was the most important and variable factor. All other factors (within a certain range) appeared to be more or less stable. In Fig. 3 the temperature changes during the period of investigation are illustrated.

Every month, the composition of the population was determined by measuring the cephalic length of every individual (for methods see Dennert et al., 1969) and population diagrams were made (see Fig. 4). The samples were divided in 4 categories: juveniles, males, non ovigerous females and ovigerous females. Likewise the percentage of ovigerous females (of all females) was calculated and illustrated in Fig. 3.

When comparing the yearly temperature changes and the percentage of ovigerous females, it becomes evident that *C. pseudogracilis* hardly reproduces during the winter months when temperatures are low.

From Figs. 3 and 4 it can be learned that a sharp increase in ovigerous females occurs in April and May, together with a steep rise in temperature. In the beginning of June almost 60% of the overwintering females is carrying eggs. In the next two months this percentage rapidly declines, due to the death of the overwintering population. Almost at the same time, the first juveniles can be found. The second peak in breeding is found in the end of August and beginning of September. Juveniles from this second peak first appear in our samples at the end of November, after about 3 months. Juveniles originating from the first peak most probably die in or just before the winter, as can be seen both from the low population density in the winter and the structure of the population. Juveniles originating from the second peak overwinter and produce new offspring as soon as water temperatures are high enough.

The life cycle of *C. pseudogracilis* as shown here resembles that of *G. tigrinus* and *G. p. pulex* in so far that it also has its main reproductive time during the warm summer months. It is in so far different that the reproductive cycle as a whole proceeds much slower than in the other two species.

Egg incubation period.-

Data on the reproductive cyle do not give information on the total offspring and the number of generations that can be produced in one year. To investigate these factors it is necessary to know the duration of the egg incubation period and the time that is needed for a female to reach sexual maturity. As we know, the duration of the development of eggs is temperature dependent. We, therefore, in August 1980 and January 1981 started two series of experiments in which we tried to determine the lapse of time in days between the apparance of eggs and the day when young were released from the brood pouch at three different temperatures. The values thus obtained are shown in Table I, together with other data on *C. pseudogracilis* and data on four *Gammarus* species (Sutcliffe & Carrick, 1981).

From this table it can be concluded that our results are in relatively good agreement with those from Sutcliffe & Carrick. When we compare these with known data on the four *Gammarus* species we may conclude that egg development in *C. pseudogracilis* is a little slower than in *G. zaddachi* and *G. tigrinus* but much faster than in *G. p. pulex*. At higher temperatures it is a little faster than in *G. d. duebeni*.

Time to reach sexual maturity.-

It is not just enough to know the egg incubation time of a certain species, but likewise it is important to know how long it takes to reach sexual maturity. We have no experimental data on this phenomenon but from our observations in the field we know that it takes nearly 3 months before the juveniles from the beginning of June start reproducing.

Sutcliffe & Carrick, 1981, calculated the interval between the subsequent moults and from these results we can roughly calculate the time needed to reach sexual maturity which is about 84 (80-106) days at 15°C, and 60-85 days at 25°C. In Table II these data are shown together with data on 4 *Gammarus* species from Pinkster et al., 1977.

Fecundity.-

The success of a newly introduced species in its competition with local species, not only depends on the length of the incubation time and the time to reach sexual maturity, but also on the number of eggs produced per batch per female. This fecundity depends on species, age, egg stage and environmental conditions like temperature and salinity (Goedmakers, 1981; Kinne, 1961). As females grow older, fecundity increases; the relation between (cephalic) length and fecundity is linear (Goedmakers, 1981).

From October 1979 till January 1981 all ovigerous females from our monthly samples were individually isolated in small tubes, and after being measured the number of eggs was counted. For the same purpose a great number of ovigerous females was collected in October 1981, August 1982 and September 1982. For the samples taken from October 1979 to January 1981 and during October 1981 we calculated the relation between the cephalic length and the number of eggs per female, as well as the mean number of eggs per female (for the total sample). The results are illustrated in Fig. 5 and Table III. In August 1982 and September 1982 we did

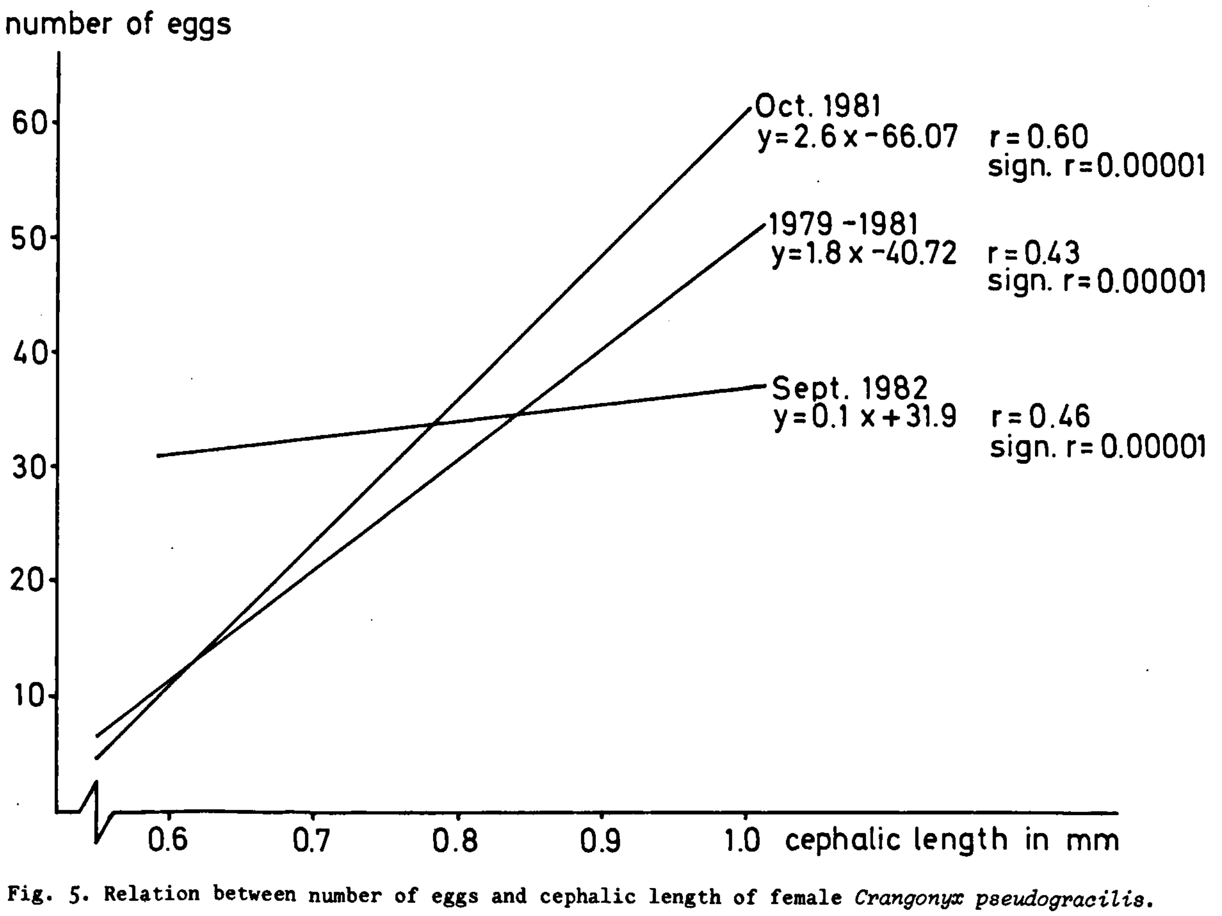

Fig. 5. Relation between number of eggs and cephalic length of female *Crangonyx pseudogracilis*.

not calculate this relation since all females belonged to the same length class. The calculated mean number of eggs per female for the two samples is indicated in Table III, together with data obtained from literature (Goedmakers, 1981; Chambers, 1971; Kinne, 1953, 1961). Although it is clear that our knowledge about other species is scarce and available data are not easily comparable with our own data, it nevertheless can be seen that the number of eggs produced by *C. pseudogracilis* is considerably higher than in the local species *G. p. pulex* and *G. tigrinus* and comparable to or lower than the numbers found in *G. zaddachi* and *G. d. duebeni*.

Seasonal and annual variation.-

Limited data on seasonal variation are available. In *C. pseudogracilis* there is nevertheless an indication of seasonal fluctuation in the mean fecundity/cephalic length ratio (compare data of October 1981, August 1982 and September 1982). In September 1982 the mean number of eggs was considerably lower than in August 1982 (19.85 versus 33.44). However, meanwhile the mean cephalic length decreased from 0.77 to 0.68 mm.

Discussion.-

Since its discovery in the Netherlands in 1979, *Crangonyx pseudogracilis* maintained its position and even slightly extended its range. However its dispersal was not as rapid as might be expected from its rapid distribution all over the British Isles (Gledhill et al., 1976).

In the area inhabited by *C. pseudogracilis*, with fresh and oligohaline waters on sandy bottom, only two other amphipod species, *G. p. pulex* and *G. tigrinus*, are found. The life cycles of these two species are roughly of the same type as in *C. pseudogracilis*, viz. a reproduction period during the warm summer months. Egg incubation time and the time to reach sexual maturity is longer in *C. pseudogracilis* than in *G. tigrinus* but shorter than in *G. p. pulex*. As a result it may be concluded that the reproductive capacity of *C. pseudogracilis* is much greater than that of *C. p. pulex* (and probably *G. tigrinus*). If *C. pseudogracilis* tends to occupy the same habitats as the local gammarid species and if it is subjected to the same controlling factors (which is unknown) then its greater reproductive capacity will finally result in a gradual replacement of *G. p. pulex* from these fresh and oligohaline waters (it must be emphasized here that *G. tigrinus* is not able to reproduce in fresh water and consequently is no competitor at all in this biotope).

It is difficult to predict the future development in the oligo- and mesohaline parts of the country since so far nothing is known about the salinity tolerance and/or preference of *C. pseudogracilis*. However when comparing the date on the life cycle, egg incubation time, time to reach sexual maturity and fecundity of *C. pseudogracilis* with those of the brackish water species *G. tigrinus*, *G. zaddachi* and *G. d. duebeni*, there is no reason to assume that these species will be easily outnumbered by *C. pseudogracilis* (except may be *G. d. duebeni*).

Summarizing, the best opportunity for a future range extension of *C. pseudogracilis* will be in southern and southeastern direction into the provinces of Drente and Friesland with dominantly stagnant and slowly flowing fresh waters on sandy bottom, in which *G. p. pulex* is the only gammarid species.

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Dr. S. Pinkster,
D. Platvoet,
Instituut voor Taxonomische Zoölogie,
(Zoölogisch Museum),
Postbus 20125,
1000 HC Amsterdam
The Netherlands.

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Table I. Egg incubation time (days) of *Crangonyx pseudogracilis* and four *Gammarus* (sub)species at various temperatures.

T (°C)	*C. pseudogracilis*[@]	*C. pseudogracilis*[@@]	*G. p. pulex*[@]	*G. tigrinus*[@]	*G. zaddachi*[@]	*G. d. duebeni*[@]
5	65.5 ± 3.0				40 - 50	60 - 70
10	(26.6)	A 32.4 ± 1.8 (9)	36 - 40	20 - 21	21	28 - 30
		B 29.9 ± 2.7 (23)				
15	14.8 ± 1.5	A 17.4 ± 0.9 (13)	21 - 30	14 - 15	15	19 - 20
		B 17.2 ± 2.1 (41)				
20	10.5 ± 1.7	A 11.7 ± 1.1 (19)	18 - 21	9 - 10	10	13 - 14
		B 10.1 ± 2.1 (23)				
25	7.0 ± 0.7		(14.2)			

@) data from Sutcliffe & Carrick, 1981; @@) own data; A from experiments started in January 1981; B from experiments started in August 1980. The number in parentheses indicate the number of females that produced offspring in the various experiments.

Table II. Number of days required to reach sexual maturity at various temperatures for *Crangonyx pseudogracilis* and four *Gammarus* species.

species	no. of days to reach maturity at				
	10°C	15°C	20°C	25°C	
Crangonyx pseudogracilis		84 (80-106)		60-85	Sutcliffe & Carrick, 1981
Gammarus tigrinus	40-42	32-34	27-29		Pinkster et al., 1977
Gammarus d. duebeni			170-180 150-210		(Kinne, 1954) (Hynes, 1955)
Gammarus zaddachi			40-50		(Kinne, 1961)
Gammarus p. pulex			c.90 90-120		(Hynes, 1955) (Heinze, 1932)

Although these data are far from complete it is clear that *C. pseudogracilis* is much faster in attaining sexual maturity than *G. d. duebeni* or *G. p. pulex*. *Gammarus zaddachi* seems to be a little bit faster, *G. tigrinus* is much faster than *C. pseudogracilis*.

Table III. Data on fecundity of *Crangonyx pseudogracilis* and 6 *Gammarus* species based on own research and literature.

species	mean number of eggs per female	n	source	other data/remarks
G. p. pulex	14.9	45	Goedmakers, 1981	
G. fossarum	11.1	1513	Goedmakers, 1981	
E. berilloni	28.8	703	Goedmakers, 1981	
G. tigrinus	21.59 7.44 9.05	? ? 5986	Chambers, 1971 Chambers, 1971 Chambers, 1971	on 12 May 1969 on 12 September 1969 whole year 1969
G. zaddachi	9.08 51.1	? ?	Kinne, 1961 Kinne, 1961	♀♀ of 8 mm ♀♀ of 13 mm
G. d. duebeni	52	?	Kinne, 1954	♀♀ of 13-14 mm
C. pseudogracilis	25.23 25.94 33.44 19.85	79 99 61 160	own data own data own data own data	October 1918 October 1979-January 1981 Augustus 1982 September 1982