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FURTHER OBSERVATIONS ON THE RANGE EXTENSION OF THE ALIEN AMPHIPOD *GAMMARUS TIGRINUS* SEXTON, 1939, IN THE NETHERLANDS DURING THE YEARS 1974 TO 1976

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ABSTRACT

In the autumn of 1975 and in the spring of 1976 a new survey of the range of *Gammarus tigrinus* Sexton, 1939, was carried out, especially at the borders of the 1973 range. Considerable range extensions were found in the north-eastern parts of the province of Groningen, the Kampereiland (province of Overijssel), in the Deltaic Region and in some more or less isolated areas in the province of Zuid-Holland. In most of the newly invaded areas *G. tigrinus* has replaced the indigenous *Gammarus* species. Sampling along the Dutch-German border revealed that no invasion has taken place from any of the German populations. A fungus was found which appeared to be pathogenic for *G. tigrinus*.

INTRODUCTION

After the introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands (probably in 1964) a series of sampling surveys showed a rapid range extension of this species (Nijssen & Stock, 1966, Pinkster & Stock, 1967, Dennert et al., 1968, Gras, 1971, and Lourens, 1972). In 1973, a new survey was made with special emphasis on the position of the local gammarid fauna in the area now inhabited by *G. tigrinus* (cf. Smit, 1974). During this survey only minor range extensions were found. Notable new localities were the Kralingse Plassen at Rotterdam, where an isolated population was found, and the Haringvliet near Middelharnis, the southernmost record of *G. tigrinus* in the Netherlands and the first record for the Deltaic region. The most striking result of this survey was the disappearance of the indigenous species *G. p. pulex* (Linnaeus, 1758), *G. duebeni* Liljeborg, 1852, and *G. zaddachi* Sexton, 1912, from extensive areas, now

inhabited by *G. tigrinus* alone.

In autumn 1975 and in 1976 a new sampling survey was carried out along the boundaries of the distribution area of *G. tigrinus* as determined in 1973. Moreover, intensive sampling was done along the eastern border of the Netherlands, to check a possible invasion of *G. tigrinus* from West Germany, where this species was purposely introduced in the rivers Weser and Werra (Schmitz, 1960, Tesch & Fries, 1963, and Ruoff, 1968), while recently new localities were found in the Schlei (Bulnheim, 1976). The total area, investigated during the present survey, is indicated in fig. 2.

RANGE EXTENSION OF *G. TIGRINUS* IN THE AREAS INVESTIGATED IN 1975 AND 1976

During the present survey considerable range extensions have been found especially in the northeastern and southwestern parts of the country. The new localities, together with the distribution area found by Smit (1974) are illustrated in fig. 1. Table I summarizes the exact localities, dates and chlorinities of the samples containing *G. tigrinus*.

Notable is the range extension in the southwest on the islands of Voorne, Putten and Beijerland, an area almost without any gammarid fauna at all before the introduction of *G. tigrinus* (Den Hartog, 1964, Smit, 1974).

In the Haringvliet, where it was found only once in 1973, *G. tigrinus* has become a common inhabitant and even inside the dikes on the island of Goeree-Overflakkee the species was found in one single locality. In stony and exposed places along the border of the Haringvliet *G. tigrinus* was often found together with *G. duebeni*. More to the east, in the Hollands Diep and the Biesbosch (a former freshwater tidal area) there is still no gammarid fauna at all.

The isolated population in the Kralingse Plassen in Rotterdam (cf. Smit, 1974) has succesfully invaded the Bergscne Plassen and the Schiebroeksche Polder, further to the north at the city boundary.

In the central part of the province of Zuid-Holland some formerly inhabited localities, found abandoned during the 1973 survey, were again occupied by *G. tigrinus* (Vliet, Geer, Noord A). In the same area several new localities were discovered (Benthuizer Vaart, Stompwijkse Vaart, Langeraarse Plas, Kromme Mijdrecht).

In the province of Groningen (northeastern Netherlands) the species has successfully invaded nearly all inland waters north of the line Groningen-Winschoten-Nieuweschans, except for some pools and ditches behind the dikes of the Waddenzee. South of this line no gammarid fauna was found at all, in spite of intensive sampling. Most probably this is caused by the heavy organic pollution and the complete absence of oxygen during the summer months.

In the central part of the Netherlands there is only a small number of new localities: in the Noordoost Polder, in the deltaic area of the river IJssel and in some places just inside the dikes along the former Zuyderzee (the parts now called Eemmeer and Veluwemeer).

Intensive sampling along the Dutch-German border revealed, that no invasion had taken place from any of the populations recently introduced in West Germany.

THE INDIGENOUS SPECIES IN THE INVESTIGATED AREA

Gammarus pulex pulex (Linnaeus, 1758)

In the central part of the province of Zuid-Holland there is still an extensive area in which *G. p. pulex* is the dominant species, with the exception of some lakes in which *G. tigrinus* is the only gammarid. This area is characterized by the presence of many oligohaline, relatively unpolluted ditches with a well-developed and diverse flora and fauna. In this type of habitat *G. p. pulex* can build up dense populations. The area is now almost completely surrounded by waters containing *G. tigrinus* and it will be quite interesting to investigate further developments there.

Den Hartog (1964) expected a dispersion of *G. p. pulex* from the existing localities in the Deltaic region and the small Brabantian rivers into the Haringvliet, the Hollands Diep and the Biesbosch after the closing of the sea arms and the subsequent refreshing of these waters. However, the reverse seems to happen: some localities in which formerly *G. p. pulex* was found are now occupied by *G. tigrinus* whereas the Brabantian rivers are so severely polluted that they act as an effective barrier rather than a way for dispersion. So it seems most likely that *G. tigrinus*

will soon occupy the Hollands Diep and the Biesbosch since it is already abundant in the Haringvliet.

In the provinces of Friesland and Groningen *G. p. pulex* is gradually loosing ground to *G. tigrinus* (see also Smit, 1974), and now has almost completely disappeared.

In the eastern part of the Netherlands, where *G. p. pulex* used to be a common species, it has almost completely disappeared. The reason for this cannot be found in the competition with *G. tigrinus* but more likely in the progressive pollution of the water systems in this region. In the northern part of the Veluwe area, where pollution is less severe until now, *G. p. pulex* is still common.

Gammarus duebeni duebeni Liljeborg, 1852

Smit (1974) already noticed the spatial separation of *G. d. duebeni* and *G. tigrinus* in the Buiten-IJ near Amsterdam. A comparable situation can be found in Waterland (the area north of Amsterdam with many ditches, canals and small lakes with chlorinities of 500 to 1000 mg/l) where *G. d. duebeni* lives on exposed, stony places, and *G. tigrinus* lives in all other microhabitats.

In the Haringvliet, where *G. tigrinus* has become a very common species, *G. d. duebeni* is still found but only on exposed and stony places and even in these habitats it is rather scarce. The salinity might have reached too low values to permit successful reproduction here except during the winter months (see Pinkster, 1975, for the combined influence of temperature and salinity on reproduction).

Compared with the situation found by Den Hartog (1964) *G. d. duebeni* now inhabits a more restricted area in the northern Deltaic region. Only on the island of Goeree-Overflakkee, where ditches and pools with a chlorinity of 3,000 up to 10,000 mg/l are still normal, abundant populations of *G. d. duebeni* were found.

In the province of Groningen where *G. d. duebeni* was still rather common in 1973, it now was found in one locality only, just behind the dike of the Waddenzee.

Gammarus zaddachi Sexton, 1912

This species, once a normal inhabitant of the head of estuaries and of saline inland waters, has now almost completely disappeared from the northern Deltaic region: it was found only on the island of Goeree-Overflakkee at chlorinities ranging from 3,000 to 10,000 mg/l. In the province of Groningen it has been replaced by *G. tigrinus* in many localities.

DISCUSSION

In his 1973 survey Smit (1974) only found some minor range extensions of *G. tigrinus*, giving the impression that the situation was stabilizing after the rapid expansion of *G. tigrinus* in the preceeding years. During the present survey, however, considerable range extensions were found again in the south-western as well as in the north-eastern part of the distribution area. In the middle of the country the only considerable range extension took place in the Deltaic area of the river IJssel.

Like in the preceding years, mainly oligohaline waters were occupied (table I), and there are still no records of *G. tigrinus* from running freshwater or from its original environment, the tidal belt (Bousfield, 1958) (Holland, 1976, mentioned one locality from a salt marsh along the very polluted Mersey estuary in England). In some areas *G. tigrinus* does not penetrate into clean, oligohaline ditches, where *G. p. pulex* is abundant. The relatively low Cl-concentrations found in these areas (130 to 400 mg/l) cannot be the decisive factor in this respect, since *G. tigrinus* was often found at much lower chlorinities. Future observations as well as laboratory studies will be necessary to find an explanation for this phenomenon.

Pinkster (1975) already discussed, that in oligohaline waters *G. tigrinus* has a much greater reproductive capacity than *G. d. duebeni*, *G. zaddachi* and *G. p. pulex*. This is because of its favourable reproduction period compared with *G. d. duebeni* and *G. zaddachi*, its short egg-incubation period compared with *G. d. duebeni* and *G. p. pulex*, and its very short time to reach sexual maturity compared with all three species. In higher salinities, when *G. d. duebeni* and *G. zaddachi* extend their reproduction period to the summer months, this advantage of reproductive output of *G. tigrinus* diminishes.

Holland (1976) found the same pattern of dis-

tribution in England for the 4 species mentioned above: *G. zaddachi* only in higher chlorinities (2,000 mg/l and more), *G. d. duebeni* in chlorinities down to 500 mg/l, and *G. tigrinus* in chlorinities ranging from about 100 to several thousands of mg/l. *G. p. pulex* is very rare in waters influenced by the discharge of waste brine from the Cheshire Salt Field.

Dennert (1974) demonstrated that interspecific aggression as a component of interspecific competition could vary largely with temperature and salinity. At this moment a series of laboratory experiments are performed to determine the role of aggression and voracity in the relation between the four species mentioned above.

Finally a short note on a fungus found to kill *G. tigrinus* both in the field and the laboratory. In the field dead specimens covered with the fungus were found especially in August and September. In the laboratory this fungus rapidly killed all specimens of *G. tigrinus*, but *G. p. pulex* in the same basin was not influenced at all. The fungus was identified as *Saprolegnia* spec. Further identification was impossible as sexual reproduction stages were absent. So far no parasites or diseases have been reported for *G. tigrinus* from the Netherlands.

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TABLE I

FURTHER RECORDS OF *GAMMARUS TIGRINUS* IN THE NETHERLANDS (RANGE EXTENSIONS IN 1975 AND 1976)

Locality	Municipality	Accompanying *Gammarus* species	Date	mg Cl/l
Province of Zuid-Holland				
Vlietland	Voorschoten	-	16-X- 1975	190
Stompwijkse Vaart at Stompwijk	Leidschendam	-	16-X- 1975	330
Ditch, 2 km E of: (along road to Hellevoetsluis)	Rockanje	-	17-X- 1975	470
Moats of Hellevoetsluis	Hellevoetsluis	*duebeni*	17-X- 1975	400
Spui	Nieuw Beijerland	-	17-X- 1975	270
Old harbour in village	Piershil	-	17-X- 1975	360
Bergsche Achterplas	Rotterdam	-	28-X- 1975	180
Ditch in the Schiebroekse polder at city boundary	Rotterdam	-	28-X- 1975	160
Binnengedijkte Maas	Maasdam	-	30-X- 1975	130
Binnengedijkte Maas	Mijnsherenland	-	30-X- 1975	130
Welvliet near Biert	Geervliet	-	30-X- 1975	390
Ditch, 0.5 km SW of:	Oudenhoorn	-	30-X- 1975	790
Vierambachtenboezem	Geervliet	-	14-V- 1975*	-
Holle Mare	Zwartewaal	-	14-V- 1975*	-
Strijpsche Wetering	Rockanje	-	21-IV- 1976	430
Sluiswetering S of Tinte	Oostvoorne	-	21-IV- 1976	380
Hoofdwetering near Nieuwenhoorn	Hellevoetsluis	-	21-IV- 1976	1,160
Haringvliet	Stellendam	-	21-IV- 1976	320
Creek along Zuiderdiep	Stellendam	*duebeni*	21-IV- 1976	420
Haringvliet	Stad aan 't Haringvliet	*duebeni*	29-IV- 1976	280
Haringvliet	Den Bommel	-	29-IV- 1976	280
Ditch, 1.5 km ESE of:	Zuidland	-	29-IV- 1976	290
Creek along the Vuile Gat	Goudzwaard	-	29-IV- 1976	280

continued overleaf

*) Samples provided by Harry Smit

TABLE I, continued

Locality	Municipality	Accompanying *Gammarus* species	Date	mg Cl/l
Province of Zuid-Holland				
Langeraarse Plas	Ter Aar	*p. pulex*	20-V -1976	260
Benthuizer Vaart, 1.5 km W of:	Benthuizen	-	20-V -1976	830
Province of Utrecht				
Kromme Mijdrecht at Woerdense Verlaat	Wilnis	-	11-VIII-1976	160
Noordoostpolder				
Canal along Mammouthweg, 2.5 km S of Marknesse	Noordoostpolder	-	5-XI -1975	420
idem, 3 km N of Ens	Noordoostpolder	-	5-XI -1975	480
Province of Overijssel				
Canal from Ossenzijl to Steenwijk, S of Oldemarkt	Steenwijkerwold	-	5-XI -1975	190
Ganzediep near Grafhorst	IJsselmuiden	-	28-X -1976	202
Veneriete near Kamperzee-dijk-Oost	Zwollerkarspel	*p. pulex*	28-X -1976	198
Veneriete near Nieuwe Wetering	Zwollerkarspel	-	28-X -1976	150
Province of Friesland				
Palse Poel	Wijmbritseradeel	-	22-VI -1976	-
Het Wije, 3 km SE of:	Wolvega	*p. pulex*	5-XI -1975	220
Canal, 4 km NE of:	Heerenveen	*p. pulex*	5-XI -1975	170
Province of Groningen				
Canal at Schaapshok,	Slochteren	*p. pulex*	7-XI -1975	340
Termunterzijldiep at Scheemderzwaag	Scheemda	-	7-XI -1975	400
Termunterzijldiep at	Termunten	-	7-XI -1975	1,100
Brackish water basin near Oterdumerwarven	Delfzijl	-	7-XI -1975	1,430
Termunterzijldiep E of Wagenborgen	Termunten	-	7-XI -1975	370

continued overleaf

TABLE I, continued

Locality	Municipality	Accompanying *Gammarus* species	Date	mg Cl/l
Province of Groningen				
Ditch around Joh. Kerkhovenpolder, SE of Woldendorp	Termunten	-	7-XI -1975	1,110
Ditch around Carel Coenraadpolder	Finsterwolde	-	7-XI -1975	1,480
Buiskoopdiep between Beerta and Nw-Beerta	Beerta	-	7-XI -1975	540
Beersterdiep	Beerta	-	7-XI -1975	460
Buiten Nieuwediep 2 km E of:	Noordbroek	-	7-XI -1975	360
Nieuwe Ee, 1 km NE of:	Adorp	-	20-IV -1976	290
Boterdiep at Ellerhuizen	Bedum	*zaddachi*	20-IV -1976	220
Ditch at St. Annen	Ten Boer	-	20-IV -1976	280
Ditch at Rottum	Kantens	-	20-IV -1976	480
Ditch, 1 km N of	Warffum	-	20-IV -1976	760
Oude Maar, 1 km S of:	Uithuizen	-	20-IV -1976	530
Garsthuizer Maar, 1 km E of Garsthuizen	Kantens	-	20-IV -1976	270
Spijkstermaar at Losdorp	Bierum	-	20-IV -1976	330
Groote Heekt 2 km S of Holwierde	Bierum	-	20-IV -1976	280
Damsterdiep	Appingedam	-	20-IV -1976	360
Leermenstermaar 1 km S of Leermens	't Zandt	-	20-IV -1976	-
Province of Noord-Holland				
Ditch in polder Huizer en Naarder Aangerechten	Blaricum	-	8-XI -1976	186
Moats E of Naarden	Naarden	-	8-XI -1976	282
Province of Gelderland				
Ditch behind dike of Eemmeer, 1 km E of pumping-station in the Wiel	Nijkerk	-	8-XI -1976	124
Gelderse Gracht near Posthoorn	Oosterwolde	*p. pulex*	28-X -1976	62

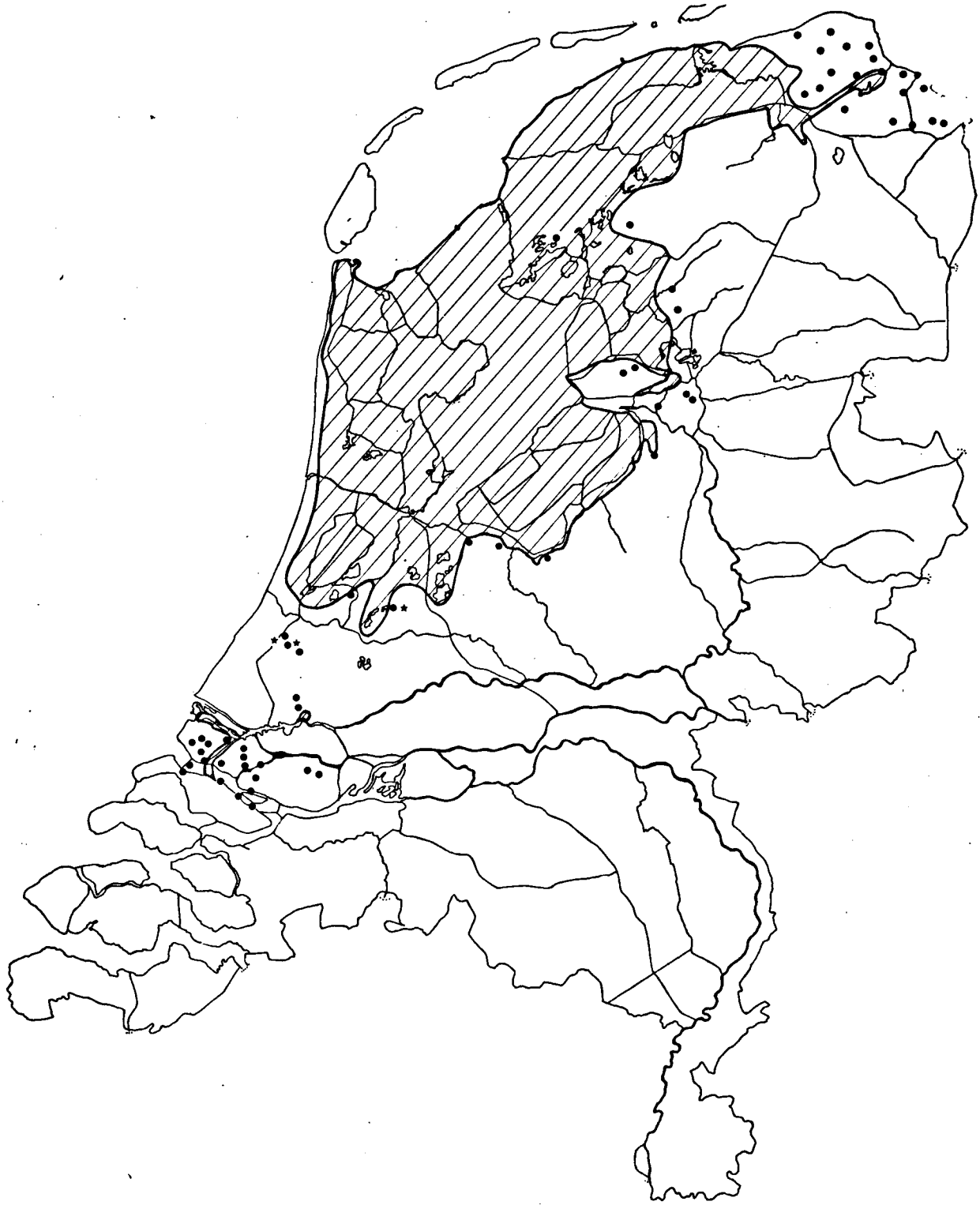

Fig. 1. New records in 1975 and 1976 of *Gammarus tigrinus* Sexton, in the Netherlands (each dot represents a new locality or a group of proximate localities). The minimal area occupied by the species at the end of 1973 is hatched. Asterisks indicate formerly inhabited areas, abandoned in 1973, but now again occupied.

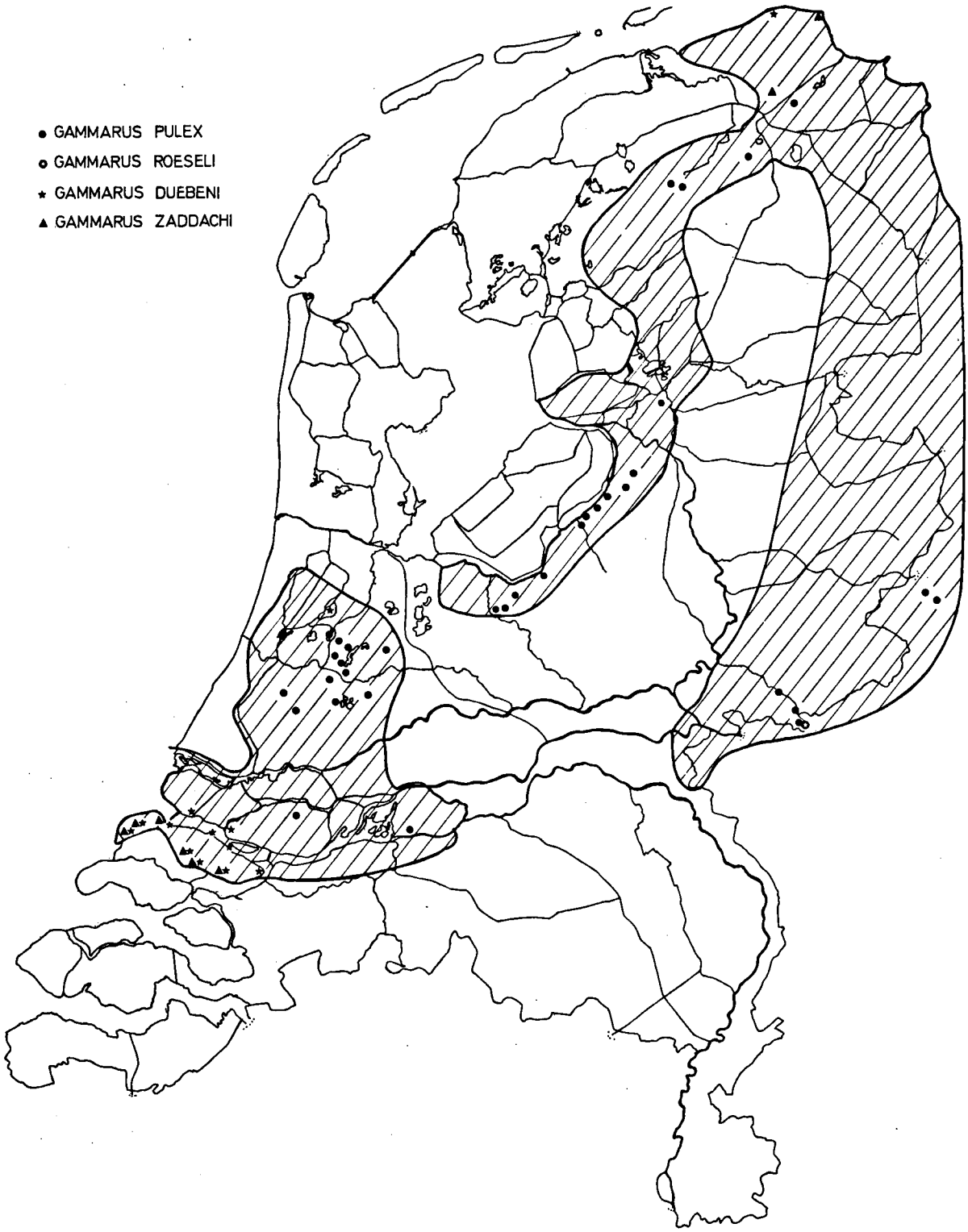

Fig. 2. Records of indigenous *Gammarus* species in the area investigated (hatched).