THE INTRODUCTION OF THE ALIEN AMPHIPOD *GAMMARUS TIGRINUS* SEXTON, 1939 (CRUSTACEA, AMPHIPODA) IN THE NETHERLANDS AND ITS COMPETITION WITH INDIGENOUS SPECIES

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GAMMARUS TIGRINUS IN THE NETHERLANDS

The first records on *Gammarus tigrinus* in the Netherlands date from 1964. A survey, carried out in 1965 proved that the species had already occupied the whole Yssellake (the former Zuydersea) and many waters in the adjacent province of North-Holland (NIJSSEN and STOCK, 1966). Surveys carried out in subsequent years revealed that *G.tigrinus* was rapidly invading the oligohaline waters in the western and northern parts of the Netherlands.

In 1973 (SMIT, 1974) a more or less stable situation seemed to have been established in which the range of *G.tigrinus* is bounded by (running) fresh waters in the eastern and southern parts of the country and by meso- to polyhaline waters in the coastal area (see Fig. 1).

THE POSITION OF THE INDIGENOUS SPECIES BEFORE THE INTRODUCTION OF *G.TIGRINUS*

Before the introduction of *G.tigrinus*, the area now occupied by *G. tigrinus* was inhabited by three local (sub)species viz. *G.d.duebeni* Lilljeborg, *G.zaddachi* Sexton and *G.p.pulex* (Linnaeus).

G.d.duebeni was the most common inhabitant of the oligo- to mesohaline waters in the Netherlands. It was found in the Yssellake, the lakes in the provinces of North- and South-Holland, Friesland and in most of the brackish waters behind the dikes in the provinces of Friesland and Groningen, the Frisian Isles and many inland waters in the Deltaic region (DEN HARTOG, 1964; DEN HARTOG and TULP, 1960; DE VOS, 1941, 1954-a, b).

G.zaddachi used to be a common inhabitant of meso- to polyhaline waters behind the sea-dikes along the Dutch coast, the many water bodies in the province of North-Holland (Waterland), the Northsea-canal (connecting the Amsterdam harbour with the sea) and the Deltaic region (DEN HARTOG, 1964; DE VOS, 1941, 1954-a, b).

G.p.pulex used to be the most common freshwater species. In the provinces of Friesland and South-Holland it also inhabited some of the shallow oligohaline lakes (DEN HARTOG and TULP, 1960; own data).

THE POSITION OF THE INDIGENOUS SPECIES AFTER THE INTRODUCTION OF *G.TIGRINUS*

In 1973 a survey was carried out (SMIT, 1974) with special emphasis to the position of the indigenous species. The results of this survey were astonishing: it appeared that the original species had almost com-

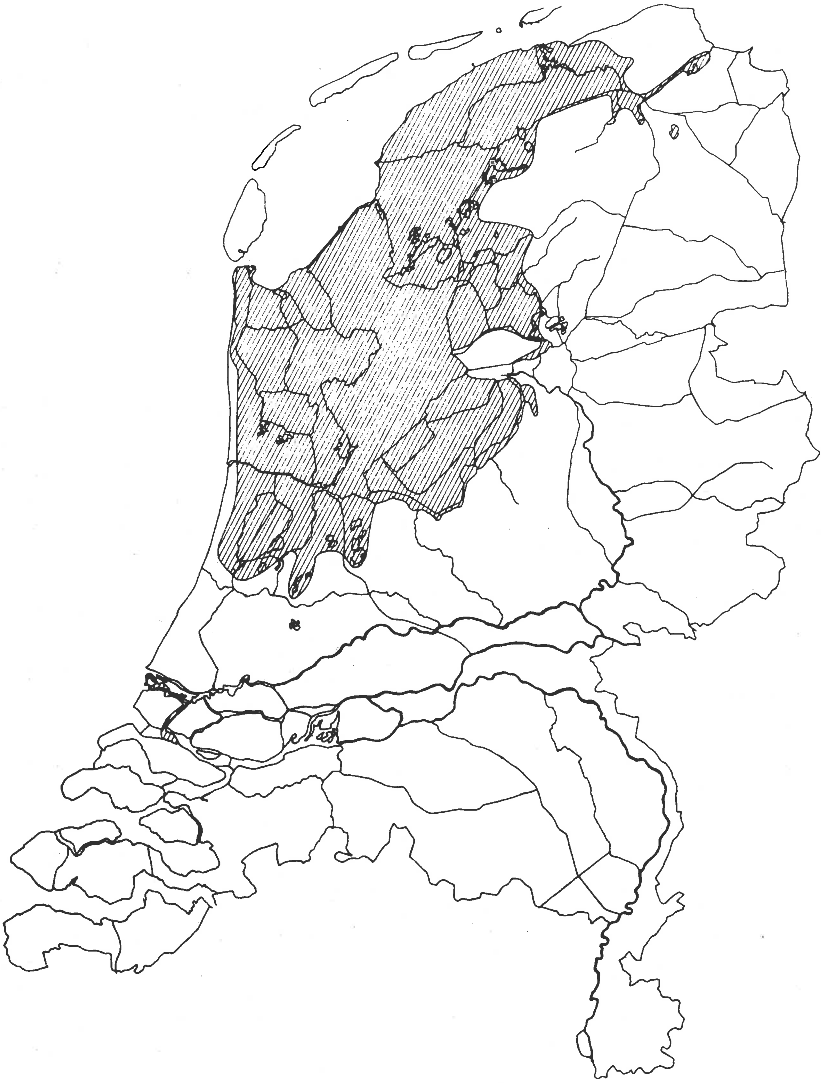

Fig. 1. The approximate distribution area of *Gammarus tigrinus* in the Netherlands in 1973.

pletely disappeared from the area now occupied by *G.tigrinus*.

G.d.duebeni could hardly been found. It had almost completely disappeared from the localities where it was common before except from some localities in which conditions are extremely variable because of changes in water levels or salinity.

G.zaddachi had also disappeared from many localities. However, the species is still very common in waters with higher salinities like the Northsea-canal, pools and ditches behind the sea-dikes and in the Deltaic Region. In many of these localities it coexists with *G.tigrinus*.

G.p.pulex had disappeared from most of the shallow lakes in the provinces of Friesland and South-Holland. It could however easily thrive in the fresh and soft waters in the eastern and southern parts of the country in which *G.tigrinus* has not yet penetrated.

COMPETITION OF *GAMMARUS TIGRINUS* WITH THE INDIGENOUS SPECIES

Having seen the rapid replacement of the local gammarid fauna by *G. tigrinus* the question arises how it can compete so successfully with these original habitants. Possible answers to this question have been sought in differences in a) salinity tolerance, b) salinity preference, c) reproduction cycle, d) egg incubation period, and e) time needed to reach sexual maturity.

a) Salinity tolerance.

RUOFF (1968) and DORGELO (1974) discussed the salinity tolerance of *G. tigrinus* based on survival rates at different temperature/salinity combinations. They both concluded that *G. tigrinus* can survive in waters, varying in salinity from almost fresh to above sea-water concentrations. However, to maintain itself in a certain habitat a population has not only to survive but also has to reproduce.

In a series of laboratory experiments the possibility to reproduce was tested at different salinity and temperature combinations. The results of these experiments, as summarized in Table I, give a good indication of the possibility of a certain species to reproduce at a given salinity/temperature combination.

	18,000	1800	900	360	180	mg Cl'/1
5°C	--	--	--	--	--	(diluted seawater)
10°C	+	++	++	+	--	
15°C	+	++	++	++	--	
20°C	-	++	++	++	--	

Table I. Possibilities of *Gammarus tigrinus* to reproduce at various temperature/salinity combinations.

-- no eggs or juveniles observed
- eggs observed; eggs died during development
+ eggs and offspring observed in a few cases only
++ mass production of eggs and offspring

From Table I we can read that *G. tigrinus* does not reproduce when temperatures are too low and/or salinities are too low. Thus it can reproduce in sea-water on condition that temperatures are favourable.

From literature (HYNES, 1954, 1955; KINNE, 1953, 1959, 1961; DENNERT et al. 1969; DENNERT and VAN MAREN, 1974) and from our own field observations we know that both *G. zaddachi* and *G. d. duebeni* can reproduce in waters with salinities varying from almost fresh to sea-water concentrations. However, it is important to know that at lower salinities reproduction stops when temperatures become too high (DENNERT et al., 1969; DENNERT and VAN MAREN, 1974; KINNE, 1953; HYNES, 1955).

Gammarus p. pulex usually only reproduces in fresh or slightly oligohaline waters. When temperature become too low (ROUX, 1970; HYNES, 1955; own observations) the reproduction stops at all salinities.

b) Salt preference.

DORGELO (in press) in his laboratory experiments found that *G.tigrinus* prefers oligohaline waters to waters with higher or lower salinities. An increase in temperature influences the salt-preferendum making the preferred range smaller.

After having compared the results of DORGELO with the distribution pattern of *G.tigrinus* in the Netherlands we see that *G.tigrinus* is confined to oligohaline waters (its own salt-preferendum). Data on other species are not available.

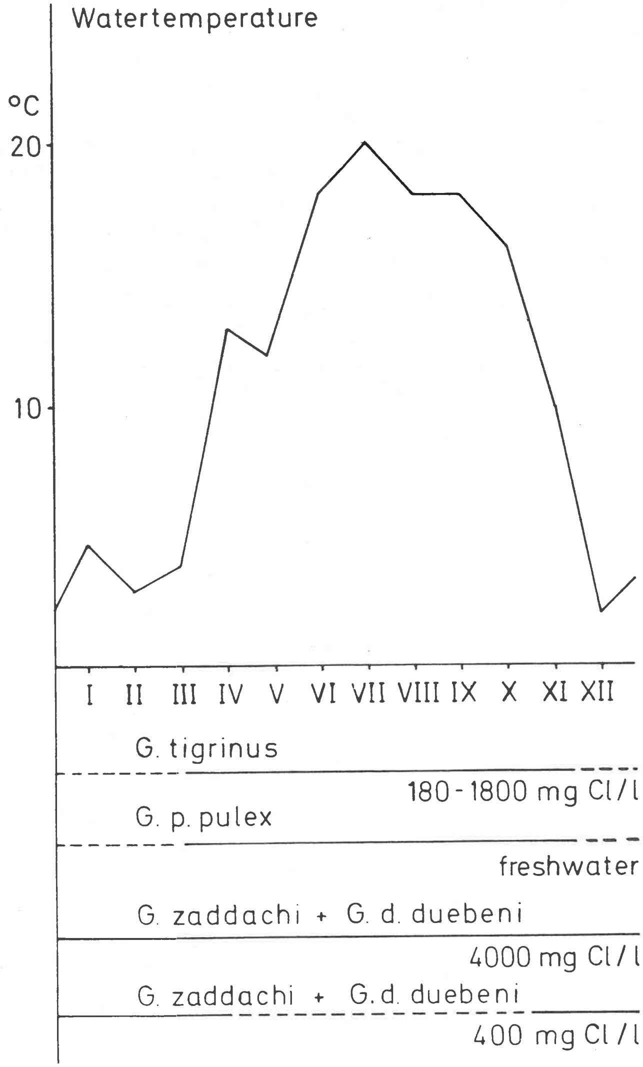

Fig. 2. Schematical view of the monthly watertemperature and the length of the reproductive period of *G.tigrinus* and the three indigenous (sub)species at various conditions.
(broken line = resting period; uninterrupted line = reproductive period).

c) Reproductive cycle.

During the years 1971 and 1974 the reproductive cycles of some po-populations of *G.tigrinus*, *G.zaddachi* and *G.d.duebeni* have been studied. Every month the composition of the various populations was determined by measuring the cephalic length. The presence of ovigerous females was used as an indication that a population was reproducing. It appeared that the length of the reproductive period was influenced by both salinity and temperature. The lengths of the reproductive period of the various (sub)species is schematically illustrated in Fig. 2.

From Fig. 1 it can be learned that *G.tigrinus* reproduces during the summer months when water temperatures are high. The same holds true for *G.p.pulex* in freshwater or oligohaline waters (own data; HEINZE, 1932; ROUX, 1970).

G.d.duebeni and *G.zaddachi* can reproduce throughout the year when salinities are high enough. However, when salinities become too low (viz. a situation that is found in the area now inhabited by *G.tigrinus*) these species can only reproduce during the winter months when water-temperatures are low.

d) Egg incubation period.

The data on the reproductive cycle give little information on the total offspring and the number of generations that can be produced in one year. Therefore the duration of the egg incubation period and the time that is needed to reach sexual maturity have to be known. From field observations, laboratory experiments at various conditions and from literature (CHAMBERS, 1971; KINNE, 1953, 1959, 1961; HYNES, 1954, 1955; HEINZE, 1932) the approximate duration of the incubation period at different temperatures was calculated for the various (sub)species and summarized in Table II.

	G.tigrinus	*G.d.duebeni*		*G.zaddachi*		*G.p.pulex*
	180 - 1800	6000	600	6000	600	freshw.
5°C	---	60-70	60-80	40-50	40-50	--
10°C	20 - 21	28-30	30-31	21	21-25	40
15°C	14 - 15	19-20	---	15	---	25-30
20°C	9 - 10	13-14	---	10	---	18-21

Table II. Egg incubation time of *G.tigrinus* and the three indigenous (sub)species at various temperature/salinity combinations. Salinity expressed in mg Cl'/1.

From the data presented in Table II and from the yearly temperature changes (not shown here) we can roughly calculate the average incubation time during the various months in which *G.tigrinus* reproduces. These values are shown in Table III.

March	22 - 25 days
April	18 days
May	14 days
June	10 days
July	8 - 9 days
August	10 days
September	13 - 15 days
October	18 - 20 days

Table III. Average egg incubation time of *G.tigrinus* during the reproductive period.

With the knowledge that the population reproduces constantly from March till November, theoretically 15 or 16 generations are possible during one year (viz. much more than any of the indigenous species could produce in the same conditions).

e) Time needed to reach sexual maturity.

Another factor that is important for the success of a species ia the time a female needs to reach sexual maturity. During the laboratory experiments and in the monthly samples females started to produce eggs at a total length of about 4 mm. The time required to reach this length depends on the temperature. The number of days to reach sexual maturity at the various temperatures is shown in Table IV, together with data for the three indigenous species as could be obtained from literature.

species	author	sexually mature at	10^oC	15^oC	20^oC
G.tigrinus	(own data)	4 mm	40-42	32-34	27- 29
G.d.duebeni	(Kinne, 1954)	11-12 mm			170-180
	(Hynes, 1955)	7-8 mm			150-210
G.zaddachi	(Kinne, 1961)	7-9 mm			40-50
G.p.pulex	(Hynes, 1955)	6 mm			± 90
G.p.pulex	(Heinze, 1932)	7.5 mm			90-120

Table IV. Body length at which females attain sexual maturity and the number of days required to reach this maturity at various temperatures.

DISCUSSION

The differences in time to reach sexual maturity together with the short incubation period and the favourable reproductive period can possibly explain the success of *Gammarus tigrinus* in its competition with indigenous species as shown by the following examples.

A female *G.tigrinus* born in April will be sexually mature in the middle of May. At the end of May she produces her first offspring and from that time on she produces every 10 to 15 days another generation until she dies. In the meantime, the females born in the end of May start to reproduce at the end of June and produce their first offspring in the first week of July etc.

Female *G.duebeni* likewise born in April will not be sexually mature until October. The eggs then produced develop slowly because of the low winter temperatures, and hatch in the first months of the next year. By that time, *G.tigrinus* has already produced an enormous mass of juveniles.

For *G.zaddachi* the situation is a little more complicated; when salinities are favourable, it can reproduce throughout the year. Although it needs some more time to reach sexual maturity, it can easily produce as great an offspring as *G.tigrinus*, since it can also use the wintermonths. This explains why it can withstand the competition of *G. tigrinus* in localities with an elevated salinity. When salinity is too low, as is the case in most of the waters now inhabited by *G.tigrinus*, it can only reproduce during the colder wintermonths when the incubation time of the eggs is much longer. Thus the reproductive output will then be much smaller.

For *G.p.pulex* in oligohaline waters, the situation is basically the same as discussed for *G.d.duebeni*. The result will be a much smaller reproductive output than *G.tigrinus*. In fresh water however, a situation as found in the eastern and southeastern parts of the Netherlands, it can easily compete with *G.tigrinus* since the latter species can not successfully reproduce in fresh water.

CONCLUSION

In oligohaline waters *Gammarus tigrinus* has a much greater reproductive capacity than any of the three indigenous (sub)species *G.d.duebeni*, *G.zaddachi* or *G.p.pulex*. The most important factors that enable this recently introduced species to compete the local species are: (a) its favourable reproductive period during the warm summer months, (b) its very short egg-incubation period, and (c) its very short time needed to reach sexual maturity.

So if (1) *G.tigrinus* tends to occupy the same habitats as the original *Gammarus* species and (2) it is subjected to the same density controlling factors then its greater reproductive capacity will enable this species to outnumber and gradually replace the three indigenous species.

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