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The amphipod, *Gammarus tigrinus* Sexton, 1939, introduced in the Netherlands (Crustacea)

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Gammarus tigrinus is an euryhaline brackish water species, originally endemic to the east coast of North America from the St. Lawrence estuary to Florida (BOUSFIELD, 1958). It is common now in certain coastal brackish waters, and in fresh waters where pollution has raised the ion content, in the English Midlands and in the northern part of Ireland (HYNES, MACAN & WILLIAMS, 1960). HYNES (1955) supposes that the English population of *G. tigrinus* is recently introduced, possibly through bilge water or ballast tanks of ships.

SCHMITZ (1960) reports that *G. tigrinus* has been introduced purposely in 1957 in the rivers Weser and Werra in Germany, where it succesfully spread since 1959. The spreading and increase in number of the about 1000 specimens originally set in the Weser-system were so enormous, that TESCH & FRIES (1963) speak of the "Eindruck einer Masseninvasion" in summer 1962. These authors report on certain damage caused by the amphipod to bow-nets and fish caught in it: "Den zahlreichen Meldungen sowie Anfragen beim Niedersächsischen Institut für Binnenfischerei ist zu entnehmen, dass der Neubürger sich bisher anscheinend eher schädlich als nützlich bemerkbar gemacht hat."

Similar records and alarmist rumours came from Dutch fishermen during summer 1964. The mass occurrence of amphipods seemed to be concentrated in the northern part of the Yssellake ("IJsselmeer", the former Zuydersea). A sample collected near De Ven, north of Enkhuizen, in May 1964, and sent for identification to the Zoological Museum of Amsterdam, proved to consist entirely of *Gammarus tigrinus*.

A survey carried out in the northern part of the Netherlands in October, November and December 1965, showed that *G. tigrinus* actually is the most common, if not the only amphipod in great parts of the Yssellake. It occurs virtually everywhere in the lake, except in the freshest part of it, i.e. around

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the mouth of the river Yssel. In the Veluwelake, a part of the Yssellake, where the salinity is also low by the inflow of several streams, it lives together with *Gammarus pulex* (Linnaeus, 1758). It often outnumbers *G. pulex* in a ratio of 1 to 10, except in the very mouth of the streams, where *G. pulex* tends to be more numerous. *G. tigrinus* has not been observed penetrating into these fresh water streams. HYNES (1955) never observed the joint occurrence of *G. tigrinus* and *G. pulex* and concludes that the latter can succesfully compete with the former. Our observations seem to point in a slightly different direction : *G. tigrinus* can successfully compete with *G. pulex*, and eventually can replace it entirely, in standing, oligohaline or somewhat polluted waters, where *G. pulex* may live at the boundery of its possibilities. *G. tigrinus* fails to penetrate into the chief *pulex* biotope, the middle and undercourse of streams. If this failure is due to competition pressure (as Hynes supposes), or to the fact that *G. tigrinus* is not well enough adapted to running waters, we are unable to decide at this moment. At any rate, *G. tigrinus* can live and reproduce quite well in purely fresh waters, as is proved by its fresh water occurrence in Ireland. On the other hand, *G. tigrinus* penetrates into the moderately polluted waters of the harbour of Amsterdam (more specifically, it has been found in the Buiten-Y), but not, or not yet, in the extremely polluted Amsterdam-Rijnkanaal, which connects with the Buiten-Y.

The slightly more brackish western shores of the Yssellake are co-inhabited by *G. tigrinus* and *G. duebeni* Lilljeborg, 1851. The latter was the most common amphipod after the closing of the Zuydersea (SCHIJFSMA, 1954; DE VOS, 1941, 1954), but now seems clearly outnumbered or in some localities replaced entirely by *G. tigrinus*.

G. tigrinus is not restricted to the Yssellake. In the 1965 survey, it was found in a great number of localities inside the dikes in the central and northern part of the province of North-Holland and in one locality near Muiderberg, in the south-east of this province. It was not found penetrating into inland waters in the provinces of Utrecht, Gelderland, and Overijssel (fig. 1). The province of Friesland was not sampled during this study, so data for 1965 concerning the inland occurrence of gammarids in this province are lacking. The only two *Gammarus* species found in the northern provinces in 1963 were *G. pulex* and *G. duebeni* (WICHERS, 1964; see also DEN HARTOG & TULP, 1960).

As stated above, the localities, except for one, in North-Holland are all situated in the central and northern part of the province. The species has not been found in inland waters south of the line Edam-Monnikendam-Alkmaardermeer. Other local species of *Gammarus* (*G. duebeni*, *G. pulex*, *G. zaddachi* Sexton, 1912) abound south of this line. It is to be expected that *G. tigrinus* will penetrate in due time also in these waters.

The western limit of *G. tigrinus* in the province of North-Holland is formed by the Noordhollands Kanaal. West of this canal, only *G. pulex* was found in the 1965 survey.

The map (fig. 2) shows the minimal area that *G. tigrinus* occupied in

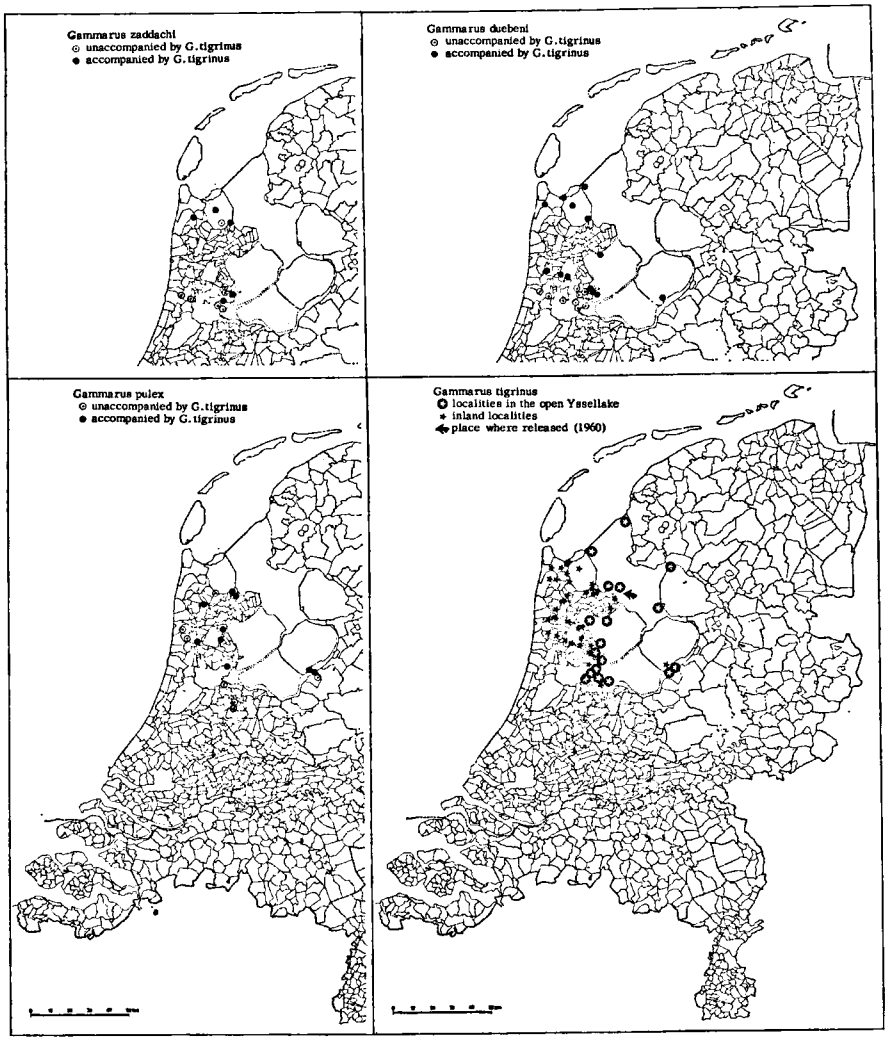

FIG. 1. Distribution of four *Gammarus* species in and around the Yssellake in October, November, and December 1965.

autumn 1965. All details concerning the localities wherein *G. tigrinus* was found, are summarized in table I. In many cases a water analysis was made; the chlorinities are incorporated in the table. It appears that *G. tigrinus* abounds in oligohaline waters; in some localities situated in the municipality Wieringermeer, *G. tigrinus* inhabits α-mesohaline waters. In one case (Oud-Naarden) the water was entirely fresh.

It may be of some importance to stress that *G. tigrinus* demands a less specialized habitat than most of the other *Gammarus* species. So, it can penetrate into the biotopes of euryhaline brackish water species as *G. duebeni* and *G. zaddachi*, but also in the fresh water biotope of *G. pulex*.

TABEL I. Occurrence of *Gammarus tigrinus* Sexton, 1939, in the Nederlands

Locality	municipality	accompanying species	1965 date	‰ Cl.
Yssellake near sluices between Den Oever and the Dike-monument	Wieringen	——	Oct. 15	0.20
Amstellake near Houkessluis	Wieringermeer	*G. duebeni*	Nov. 15	1.21
Amstellake near Ulkesluis	Wieringermeer	——	Nov. 15	0.82
Boezem van de Zijpe near Anna-Paulowna	Anna-Paulowna	——	Nov. 15	0.92
Noordhollands kanaal, 5 km west of Anna-Paulowna	Anna-Paulowna	*G. duebeni*	Nov. 15	0.78
Den Oeverse vaart, 2½ km west of Wieringerwerf	Wieringermeer	*G. duebeni* *G. zaddachi*	Nov. 15	1.74
Waardkanaal near Oostwaard	Barsingerhorn	——	Nov. 15	0.60
Schagen-Kolhorn kanaal near Stolpen	Zijpe	——	Nov. 15	0.53
Schagen-Kolhorn kanaal near railroad	Schagen	——	Nov. 15	0.57
Kolhorner Diep near Kolhorn	Winkel	——	Nov. 15	——
Westfriese Vaart, 200 m west of pumping-engine Lely	Wieringermeer	*G. zaddachi*	Oct. 15	——
Kogger near Opperdoes	Opperdoes	*G. pulex*	Oct. 15	0.74
Cavesloot, 2 km south of Opperdoes	Medemblik	——	Dec. 6	0.12
Missloot, 1½ km south of Medemblik	Medemblik	*G. pulex*	Dec. 6	0.19
Veersloot, near Lambertschaag	Abbekerk	——	Dec. 6	0.14
Yssellake near Andijk	Andijk	——	Nov. 22	——
Hogesluissloot, 3 km south of Andijk	Bovenkarspel	——	Dec. 6	0.28
De Rijd	Nieuwe Niedorp	——	Dec. 6	0.21
Canal near Oudkarspel	Heerhugowaard	*G. pulex*	Dec. 6	0.36
Ringsloot near Broek op Langedijk	Langedijk	——	Dec. 6	0.15
Lakemansloot, 1 km east of Venhuizen	Venhuizen	——	Dec. 6	0.14
Yssellake near Wijdenes	Wijdenes	*G. duebeni*	Nov. 22	——
Yssellake near Hoorn	Hoorn	——	Nov. 22	——
Hoornse Vaart, west of Huigendijk	Oudorp	——	Dec. 6	——
Ursemmervaart near Rustenburg	Ursem	——	Nov. 15	0.74
Noordhollands kanaal east of Alkmaar	Alkmaar	*G.* species	Nov. 5	——
Beemster uitwatering, 2 km west of Oudendijk, east of pumping-engine	Oudendijk	*G. pulex*	Oct. 15	0.21
do., west of pumping-engine	Oudendijk	——	Oct. 15	0.21
Beemster Ringvaart near Oosthuizen	Oosthuizen	*G. pulex*	Nov. 3	0.44
Noordhollands kanaal near Akersloot	Akersloot	*G. duebeni*	Nov. 5	0.25

Locality	municipality	accompanying species	1965 date	‰ Cl.
Beemster Ringvaart near Westgraftdijk	Graft	*G. pulex*	Nov. 5	0.44
Schermer Ringvaart near Spijkerboor	Beemster	*G. duebeni*	Nov. 5	0.41
Beemster Ringvaart near Kwadijk	Beemster	——	Nov. 3	0.41
Noordhollands kanaal near fort Jisperweg	Beemster	*G. duebeni*	Nov. 5	0.64
Edam, inside the lock	Edam	——	Oct. 5	——
Yssellake near lock at Edam	Edam	——	Oct. 5	0.28
Trekvaart of Edam at Zedde	Katwoude	*G. zaddachi* *G. pulex*	Nov. 3	0.37
Molentocht near Monnikendam	Monnikendam	——	Nov. 3	0.71
Yssellake, 2 km north of Monnikendam	Katwoude	*G. duebeni*	Oct. 5	0.41
Yssellake, near Poel, south of Monnikendam	Broek in Waterland	*G. duebeni* *G. zaddachi*	Oct. 5	0.52
Yssellake near the beginning of the dike to Marken	Broek in Waterland	*G. duebeni*	Oct. 5	0.58
Yssellake near Barnegat	Amsterdam	*G. duebeni*	Oct. 5	0.30
Buiten-Y at Amsterdam	Amsterdam	——	Oct. 12	——
Yssellake (harbour), at Durgerdam	Amsterdam	——	Oct. 12	——
Yssellake (harbour), at Muiden	Muiden	——	Oct. 7	0.20
Yssellake between Muiden and Muiderberg	Muiden	——	Oct. 7	0.18
Ditch at Muiderberg	Muiden	——	Nov. 2	——
Yssellake near Oud-Naarden	Naarden	——	Oct. 7	0.07
Veluwelake near Oostermeen	Harderwijk	——	Oct. 15	——
Mouth of Hierdense Beek	Ermelo	*G. pulex*	Oct. 15	0.12
Veluwelake near pumping-engine Lovink	Oostelijk Flevoland	*G. pulex*	Oct. 15	0.28
Near pumping-engine Lovink inside the dike	Oostelijk Flevoland	*G. duebeni*	Oct. 15	0.52
Yssellake, Harbour of Urk	Urk	——	Nov. 14	——
Yssellake at Lemmer	Lemsterland	——	Oct. 15	0.16
Yssellake, closingdam near the Frisian coast	Wonseradeel	——	Oct. 15	0.21

In particular, *G. tigrinus* seems able to occupy empty niches in these biotopes. On the shores of the Yssellake, e.g. those bordering Het Gooi (S.E. of Amsterdam), it lives in great abundance on the surface of very shallow (depth 10—30 cm), exposed sandy bottoms, a niche never inhabited by our local *Gammarus* species. Its abundant occurrence in the Buiten-Y, Amsterdam, shows that *G. tigrinus* can stand pollution better than other gammarids. No gammarids were observed in that area in surveys in 1950, 1951, 1952, 1953, 1957, and 1960.

It is also our impression that *G. tigrinus* prefers larger waterways; it has not been found in smaller, shallower ditches, either because the invasion took

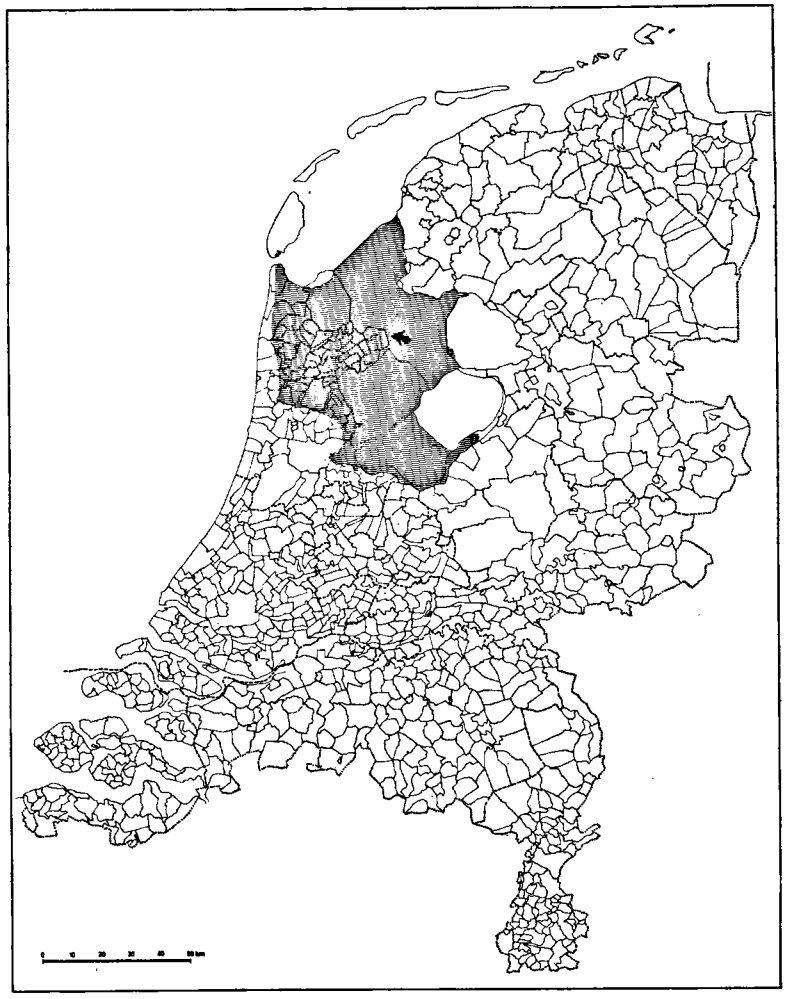

FIG. 2. Supposed minimum area occupied in autumn 1965 by *Gammarus tigrinus*. The arrow indicates the place where a small number of individuals were released in 1960.

place through the larger ship-canals, or because the biotope of the ditches is not appropriate for *G. tigrinus*.

The origin of the Dutch population of *G. tigrinus* is not quite clear. On the one hand, Dr. C. L. Deelder, of the Rijksinstituut voor Visserijonderzoek (Government Fisheries Research Institute), IJmuiden, kindly informed us that he released some dozens of specimens of *G. tigrinus* in a place called Kooizand, just north of Enkhuizen in the Yssellake. The animals originated from Lough Neagh, in northern Ireland, and were released on July 29, 1960, after a number of unsuccessful breeding experiments in the laboratory. Dr. Deelder gives as his opinion (in litt. Oct. 13, 1965) that the "numbers

released were so trifling, that I take it for out of the question that these animals were able to cause the actual population explosion" (translation is ours). In a discussion on the problem, Dr. Deelder expressed his belief that the "explosion" of *G. tigrinus* in the Netherlands must have been caused by members of the continental population, transported accidentally in ballast tanks of ships coming from Germany. He pointed out that ballast water is often discharged in the Yssellake, just north of Enkhuizen.

Indeed, it is significant in our eyes, that the centre of distribution of *G. tigrinus* seems to lie in the Yssellake near Enkhuizen, where the specimens were released in 1960, and not in other parts of the Yssellake, where ballast water is discharged as well. The only place where *G. tigrinus* is found in inland waters is in the province of North-Holland. Practically all inland localities in which *G. tigrinus* is found lie in a radius of less than 35 km around Enkhuizen. The migration wave stops (at least in autumn 1965) at the line Edam-Monnikendam-Alkmaardermeer, as mentioned above.

On the distinction of *Gammarus tigrinus*

Although Bousfield (1958 : 67) states that "In the British Isles the brackish water *tigrinus* is conspicuously unlike all other native species", we feel that his remark should be restricted to the summer phase of the "definitive adult stage" (in terminology of Sexton, 1924) of the male.

The conspicuous features of the male, in this phase and stage are (1) the curled setae on the 2nd antenna, peraeopods and 3rd uropods and (2) the first antenna, which is shorter than the second. Apart from the fact that the male of another British (and European) brackish water species, *Gammarus chevreuxi* Sexton, 1913, possesses a setation similar to that of *G. tigrinus*, we can confirm that younger, though mature, males and winter specimens of *G. tigrinus* tend to have straighter hairs. To make the confusion greater, certain definitive adult males of *G. zaddachi* Sexton, 1912, have curved setae on the 2nd antenna (this fact is not mentioned in literature, but has been observed by us both in French material, from the Slack estuary near Ambleteuse, department Pas-de-Calais, and in Dutch material, from a canal in the Wieringermeer, province of North-Holland).

The second outstanding character of *G. tigrinus*, the shortness of the 1st antenna, holds true for "definitive adult males" only. In younger mature males, in immature material, and in females, the 1st and 2nd antennae have about equal lengths.

Hynes et al., 1960, use only one not sex-bound character to discriminate between *G. tigrinus* and the closely related *G. zaddachi*, viz., the setation of the posterior walking legs. We have made numerous checks on this character and find it extremely variable and age dependant. Both in *G. tigrinus* and *G. zaddachi*, the inner surface of the basal segment of P_6 and P_7 bears fine setae; Hynes et al. claim these to be absent in *G. zaddachi*, but — although they are sometimes fewer in number and the groups of setae tend to be placed in a line — they are always available. These setae on the inner

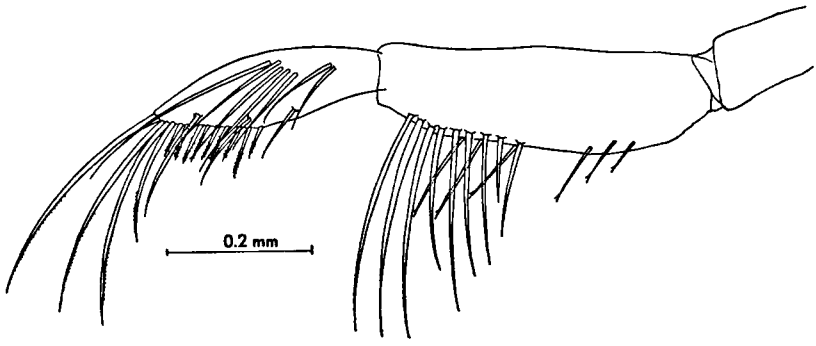

FIG. 3. Mandibular palp of *Gammarus tigrinus* (♂).

surface of the basal segment of P_6 and P_7 are often, but not always, rather numerous in *G. tigrinus* and the groups of setae tend to be more scattered over the entire hind lobe of the segment. However, so many intermediates occur between these typical patterns, that the character is totally unsuitable for an absolute distinction of *G. tigrinus* and *G. zaddachi.*

Since we have, during long years of fieldwork, always utilized the characteristics of the mandible palp, an extremely useful identification tool first put forward by KINNE, 1954, we have examined this palp of *G. tigrinus* and found that it presented, indeed, some distinguishing features. The palp has never been described or illustrated, as far as we know, so a figure of this appendage is inserted here. The terminal segment is armed on its ventral margin with the usual terminal group of long hairs and with a row of stiff, feathered setae. *The setae of this row, more particularly the proximal ones, are of mutually unequal length.* The *lateral* surface of the terminal palp segment bears *long setae, arranged into two groups,* with 3—6 and 0—3 setae in each group. *The first segment is unarmed.*

In *G. zaddachi* (see fig. 1 in KINNE, 1954), the *ventral setae* on the terminal palp segment are *very unequal in length*; there are *3 to 5 lateral groups of setae,* with 4—10, 4—10, 1—9, 0—5, 0—3 setae in each group; the *first palp segment bears 1 to 4 stiff setae.*

These palp characters are present in both sexes and those printed in italics are independant of the stage of maturity.

Another useful character, at least in older specimens (though not necessarily in the last molting stage) of both sexes, is the armature of the ventral margin of segment 1 of antenna 1.

In *G. zaddachi* this segment bears 4 to 6 groups of setae, the terminal group not included; in *G. tigrinus* 0 to 2 groups, very often with only 1 seta per group.

The only other Dutch species having irregular ventral setae on the terminal mandible palp segment is *Gammarus salinus* Spooner, 1947. Its palp and its antenna 1 resemble that of *G. zaddachi,* and thus are clearly different from the appendages of *G. tigrinus.*

Although this is not surprising, it may be stressed that the colour (used by HYNES et al., 1960, and by TESCH & FRIES, 1963, as distinguishing feature), varies so widely that — though in live state an indication — it never forms an absolute character.

It is certain that *G. tigrinus*, at least in our waters, does not reach the large size attained by *G. zaddachi*. The largest male of *G. tigrinus* found by us measures 14 mm, but they are usually much smaller, while *G. zaddachi* can attain a length of 23 mm.

SUMMARY

An alien amphipod, *Gammarus tigrinus* Sexton, has been observed in the Netherlands, mainly in oligohaline waters. It has had an "explosive" development in the Yssellake (the former Zuydersea) and occurs also in a great number of inland waterways in the province of North-Holland (fig. 1). It co-exists with, and often outnumbers, the local gammarids, *G. pulex*, *G. zaddachi* and *G. duebeni*. It is expected that the extension of its range will continue next years; fig. 2 illustrates the range of this introduced species in autumn 1965. Since Irish specimens of *G. tigrinus* were released in 1960 in the Yssellake, it is not clear whether the Dutch populations originate from the Irish stock, or whether that they were accidentally, e.g. in ballast tanks, carried to the Netherlands by ships coming from Germany, where a population explosion has taken place recently in the Weser-system.

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