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NOTES ON THE GAMMARID FAUNA OF THE FRISIAN LAKE DISTRICT FOLLOWING THE INVASION OF THE ALIEN AMPHIPOD *GAMMARUS TIGRINUS* SEXTON

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ABSTRACT

Gammarus tigrinus was first recorded in the Netherlands in 1960 and has spread rapidly since. In 16 of 18 lakes sampled in the Frisian lake district, *G. tigrinus* was the dominant gammarid. *G. pulex* was found in 6 lakes, and *G. duebeni* in 1 lake. *G. tigrinus* has now largely replaced the former gammarid faunas of the Frisian lake district.

INTRODUCTION

Since the recording of *Gammarus tigrinus* Sexton in the Netherlands in 1960, the species has spread rapidly through large areas of the country. This spread has been well documented (Nijssen & Stock, 1966; Pinkster & Stock, 1967; Dennert et al., 1968; Gras, 1971; Lourens, 1972). The data given in these papers record accurately the boundaries of *G. tigrinus*. The effects of this new species on

the gammarid faunas of newly colonized lakes however are not known.

The ecology of *G. tigrinus* has been under intensive study in the Tjeukemeer since 1968 (Chambers, unpubl. and in prep.). *G. tigrinus* was first recorded in the Tjeukemeer in 1966 (Pinkster & Stock, 1967), and in collections taken in 1967 and 1968 by Dr. E. White of the University of Liverpool it was the only gammarid present. In a short time *G. tigrinus* had become the dominant species in this lake. There is no information on the abundance or effects of *G. tigrinus* on the previous gammarid faunas of other colonized lakes of the Frisian lake district. The success of *G. tigrinus* in colonizing and reaching new areas is well established, but its subsequent fate is not so well known.

The results described in this paper are based

on an attempt to assess the extent to which *G. tigrinus* has now established itself in the Frisian lake district, and its effect on the previous gammarid fauna. Before the invasion of this species, *G. pulex* and *G. duebeni* were the only two species recorded (den Hartog & Tulp, 1960; Wichers, 1964). *G. pulex* was found by the former in the Tjeukemeer, Sneekermeer, and Langweerder Wielen; *G. duebeni* was the only species found in the Heegermeer, Fluessen, and Oudegaaster Brekken, and co-existed with *G. pulex* in the Tjeukemeer and Sneekermeer. In 1963, Wichers (1964) found *G. duebeni* and *G. pulex* co-existing in the Langweerder Wielen, and *G. pulex* in the Tjeukemeer.

METHODS

In the last week of November and the first week of December 1970, 18 lakes in the Frisian lake district were sampled for their gammarid faunas. The lakes sampled were from the Bergumermeer in the north-west to the Morra in the south-east (fig. 1). Samples were taken with 1 mm mesh hand net and preserved in 5% formalin. The gammarids in each sample were identified and counted. Samples were taken from as great a variety of habitats as possible, although in no one lake was it possible to sample all the habitats occupied by gammarids. The Cl-content of the open water in most of the lakes was also recorded.

RESULTS AND DISCUSSION

The results of the sampling programme are given in table I.

G. tigrinus was present in 16 of the 18 lakes sampled. The two exceptions were the Palse Poel and the Schuttel Poel, in both of which *G. pulex* was the only species found. Only one point in each of these two lakes was sampled, but it is probable that *G. tigrinus* was not present. There is no apparent reason for this. The Cl-content in the Schuttel Poel was 109 mg/l, which is well within the limits that *G. tigrinus* can tolerate, and the two lakes are connected to the Heegermeer in which *G. tigrinus* is abundant.

In the 16 lakes in which *G. tigrinus* was found, *G. pulex* was found in 4 - Bergumermeer, Langweerder Wielen, Koevorde and Brandemeer. In each of these 4 lakes *G. pulex* was scarce and found only in marginal habitats - thick beds of rotting vegetation or muddy sediments where the O₂ content

was probably low. The records from these 4 lakes are therefore parallel with the findings from the Tjeukemeer, where *G. pulex* has only been found in such habitats during three years of study (Chambers, unpubl.). If more intensive sampling had been possible in the other lakes, *G. pulex* would probably have been found in many of them.

The absence of *G. pulex* from the most westerly lakes may be a valid indication of its absence from them. The observed Cl-levels in these lakes are within the limits which *G. pulex* can survive and breed (den Hartog, 1964). However, the higher Cl-level in these lakes, combined with high concentrations of other ions, may make these lakes unsuitable for *G. pulex* when in competition with *G. duebeni* and/or *G. tigrinus*. Den Hartog & Tulp (1960) found only *G. duebeni* in the western lakes, whilst in 1970 *G. tigrinus* was the dominant species in all of them and possible the only gammarid in some of them.

G. duebeni was recorded in only one lake - the Grote Gastmeer, and only one specimen, an ovigerous female, found. There was therefore still a breeding population left. Since the observations of den Hartog & Tulp (1960) and Wichers (1964), it is apparent that the species has become much less abundant. The absence of *G. duebeni* from the other lakes cannot be proved conclusively on the basis of the results presented here. *G. tigrinus* however was abundant in all of the lakes where *G. duebeni* was once the only species, and it must have very nearly replaced this species. *G. duebeni* is regarded as typically a brackish water species, though there are many records from fresh water (Hynes, 1954; Hynes, 1959). It has recently been shown that the freshwater form is a distinct subspecies (Pinkster et al., 1970; Stock & Pinkster, 1970). The water of the Frisian lake district was once brackish, but has been becoming fresher since the building of the Afsluitdyke. This may to some extent be responsible for the diminishing numbers of *G. duebeni*.

In the majority of lakes sampled, *G. tigrinus* was the dominant species. In most lakes it was abundant, and in lakes where only small numbers were recorded, this was because less favourable habitats were sampled. In the Tjeukemeer maximum *G. tigrinus* densities of over 20,000/m² were recorded (Chambers, unpubl.). In most lakes sampled, *G. tigrinus* was probably as abundant as in the Tjeukemeer.

It was not possible to sample all habitats in each lake, but over the lake district as a whole a great variety of habitats were sampled. It is therefore reasonable to assume that *G. tigrinus* is also abundant in habitats that could not be sampled in a particular lake. The only habitats in which it was not consistently abundant were thick mats of rotting detritus or muddy, anaerobic substrates. Though scarce in these places, it would

often be the only species found or the most numerous.

G. tigrinus is therefore adapted to occupy a great number of habitats, the variety of which are shown in table I. This may be one of the reasons for its success in colonizing lakes and replacing the former gammarid faunas. Other reasons such as its rapid growth rate and high fecundity may also assist in this replacement (Chambers, unpubl.).

Table I

RESULTS OF SAMPLING FOR *GAMMARUS* SPECIES IN LAKES OF THE FRISIAN LAKE DISTRICT,
NOVEMBER AND DECEMBER, 1970

Lake and Cl-content	Habitat	<i>G. tigrinus</i>	<i>G. pulex</i>	<i>G. duebeni</i>
Bergumermeer 119 mg/l	<i>Phragmites</i> bed, pebbly floor	A		
	<i>Phragmites</i> bed, deep detritus		S	
	<i>Phragmites</i> bed, inner edge, deep detritus	S	S	
	Same reeds bed, outer edge, no detritus	A		
	Stones in sand	A		
	<i>Phragmites</i> bed, inner edge, sand	A		
	Same bed, outer edge, sand	A		
Prinsenhof 76 mg/l	Peat substrate	C		
	<i>Phragmites</i> bed	C		
Pikmeer 90 mg/l	<i>Typha</i> bed, mud / sand	C		
Sneekermeer 97 mg/l	<i>Phragmites</i> bed, clay substrate	A		
	Floating mat of vegetation	A		
	<i>Phragmites</i> bed	A		
	Clay bottom	A		
	<i>Phragmites</i> bed, clay substrate	A		
Langweerder Wielen 84 mg/l	<i>Phragmites</i> bed	S	S	
	Stones on shore	A		
	<i>Phragmites</i> bed, centre, hard sand	A		
	Same bed, inner edge, deep detritus	C	S	
	Same bed, outer edge, hard sand	A		
Koevorde 100 mg/l	<i>Phragmites</i> bed, inner edge, deep detritus	C	S	
	Same bed, centre little detritus	C		
	Same bed, outer edge, little detritus	S		
	Sand / shell fragments	C		

continued overleaf

Table I, continued

Lake and Cl-content	Habitat	<i>G. tigrinus</i>	<i>G. pulex</i>	<i>G. duebeni</i>
Morra 157 mg/l	Large stones in muddy sand	A		
	Reed bed, sandy substrate	C		
Oorden 159 mg/l	Floating log	A		
	Floating mat of <i>Phragmites</i> stems	C		
Heegermeer 137 mg/l	Stones on shore	C		
	<i>Phragmites</i> bed, inner edge, stony floor	C		
	Same bed, outer edge	C		
	Stones with much epiphytic growth	C		
Fluessen 163 mg/l	Concrete blocks	A		
	<i>Phragmites</i> bed, sandy substrate	A		
Slootermeer 127 mg/l	<i>Phragmites</i> bed	A		
	<i>Phragmites</i> bed	A		
	Coarse sand	S		
Brandemeer 94 mg/l	<i>Phragmites</i> / <i>Typha</i> bed, mud, much detritus		S	
	Same bed, outer edge, gravelly mud	S		
Schuttel Poel 109 mg/l	<i>Phragmites</i> bed		C	
Palse Poel --	<i>Phragmites</i> bed		S	
Oudegaaster Brekken 223 mg/l	<i>Phragmites</i> bed, centre	C		
	Same bed, inner edge, deep detritus	S		
Ringwiël 230 mg/l	<i>Phragmites</i> bed	C		
Grote Gastmeer 273 mg/l	Submerged stones	C		
	<i>Phragmites</i> bed, hard sand, little detritus	A		S
Idsegaster Poel --	<i>Phragmites</i> bed, soft mud	S		

A - Abundant. Densities high and comparable to those in optimal habitats of the Tjeukemeer, where November / December density is around 4,000/m²

C - Common. Intermediate

S - Scarce. Few specimens found after much searching.

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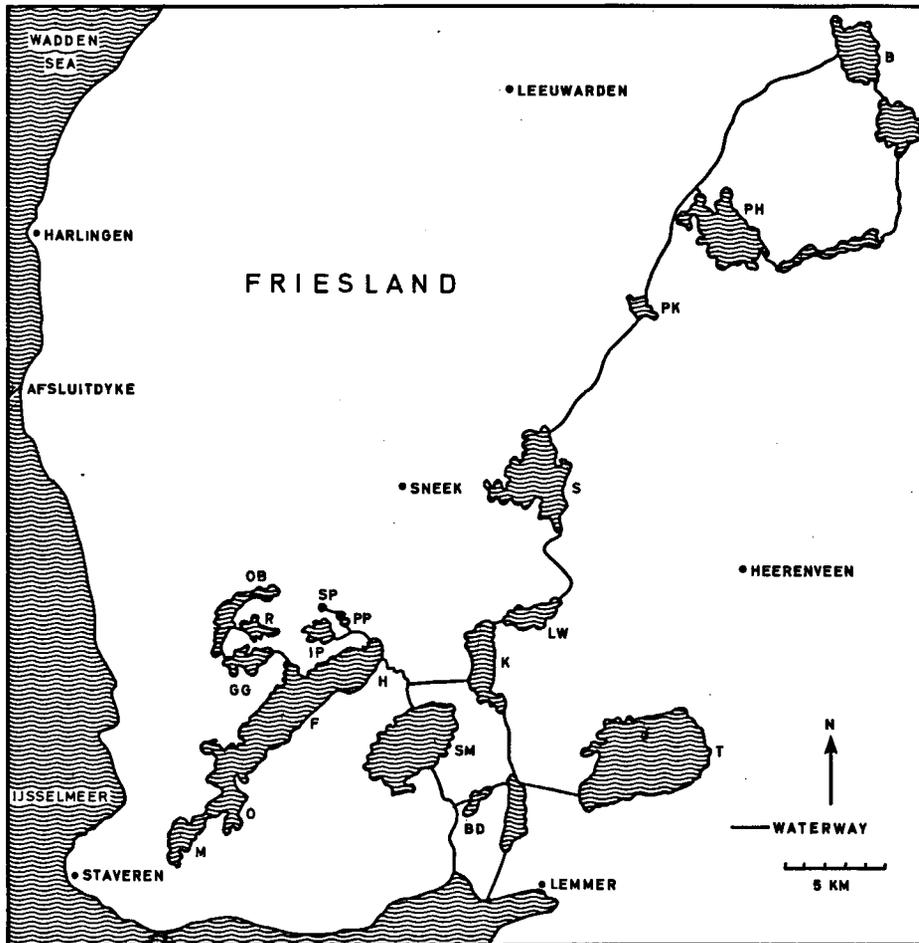


Fig 1. Lakes of the Frisian Lake District sampled for their Gammarid fauna.

B - Bergumermeer	K - Koevorde	PK - Pikmeer
BD - Brandemeer	L - Langweerder Wielen	PP - Palse Poel
F - Fluessen	M - Morra	R - Ringwieler
GG - Grote Gastmeer	O - Oorden	S - Sneekmeer
H - Heegermeer	OB - Oudegaster Brekken	SM - Sotermeer
IP - Idsegaster Poel	PH - Prinsenhof	SP - Schuttel Poel