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The distribution of Asellus aquaticus (L.) and Proasellus meridianus (Rac.) in the southwestern part of the Netherlands

by

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Abstract

The distribution of *Asellus aquaticus* and *Proasellus meridianus* in the southwestern part of the Netherlands is described. Differences cannot be ascribed to different salinity tolerances, but a different pollution tolerance seems probable.

Introduction

The freshwater isopods *Asellus aquaticus* and *Proasellus meridianus** are common in the Netherlands Holthuis, 1956). According to Holthuis "*Asellus meridianus* occupies the same habitat as *A. aquaticus*; in most cases the two species are found together" (translated from the Dutch). This observation is recorded many times in the literature, recently by Gruner (1965).

The co-occurrence of these taxonomically closely allied species seems to exhibit an exception to Gause's principle or the principle of competitive exclusion (Hardin, 1960). For this reason these species were studied intensively in Britain. Papers were published by Moon (1957, 1957a, 1964, 1968), by Edwards & Learner (1960), by Williams (1960, 1962, 1962a, 1962b, 1963), by Reynoldson (1961), by Steel (1961), and by Hynes & Williams (1965).

Their conclusions may be summarized as follows. Experimentally as well as in field investigations any sign of interbreeding between *A.*

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*Henry & Magniez (1970) consider *Asellus meridianus* Rac. to belong to the independent genus *Proasellus*.

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aquaticus and *P. meridianus* was not found. Therefore they have to be considered taxonomically as well as ecologically as valid species (WILLIAMS, 1962a). *P. meridianus* is the earlier inhabitant of western Europe. *A. aquaticus* only colonized this area from the East after the Pleistocene ice-cover had retreated, thus checking the further extension of *P. meridianus* in the northeastern part of the Netherlands (WILLIAMS, 1962). The life cycles of both species are nearly identical apart from small differences in timing (WILLIAMS, 1960; STEEL, 1961). The same is true for their reproductive capacity (WILLIAMS, 1960).

Ecologically, the two species are also very similar. EDWARDS & LEARNER (1960) stated; "the oxygen consumption of *A. meridianus* and *A. aquaticus* are very similar at 20°C and both species behave similarly in low oxygen concentrations." WILLIAMS (1960, 1962b) found no important differences between these species with regard to food, micro-habitat, vertical distribution, tolerance for high temperatures, tolerance for low oxygen concentrations, and tolerance for desiccation.

WILLIAMS (1960, 1963) also investigated the possibility of competition between these species. He studied 115 localities in an area where the two species occurred and found most localities occupied by only one species. A statistical analysis revealed that it is extremely unlikely that the observed pattern had arisen by chance, and it must be concluded, therefore, that somehow, populations of the two species interact. From this and other field investigations and from experiments, WILLIAMS assumed that *A. aquaticus* and *P. meridianus* compete and that the latter species is gradually being replaced by the former, which is in accordance with GAUSE's principle. On this matter HYNES & WILLIAMS reproted again in 1965, stating: "it is shown that under conditions in which both species survive and reproduce satisfactorily, *A. aquaticus* replaces *A. meridianus*, and that the, as yet unexplained, reaction between the two species is a violent one." The authors suggest that this reaction may be caused by *P. meridianus* being eaten by the "carnivorous" *A. aquaticus*.

Indications for the same phenomenon of replacement of *P. meridianus* by *A. aquaticus* may be found in the papers by MOON (1957, 1957a, 1968).

Only in polluted waters a difference between the two species exists. Williams (1960) found that *P. meridianus* is absent from polluted waters, where *A. aquaticus* may occur.

The distribution of both species in the southwestern part of the Netherlands seems to indicate that small ecological differences between both species exist. This paper reports on these differences and discusses them in relation to the results of previous authors.

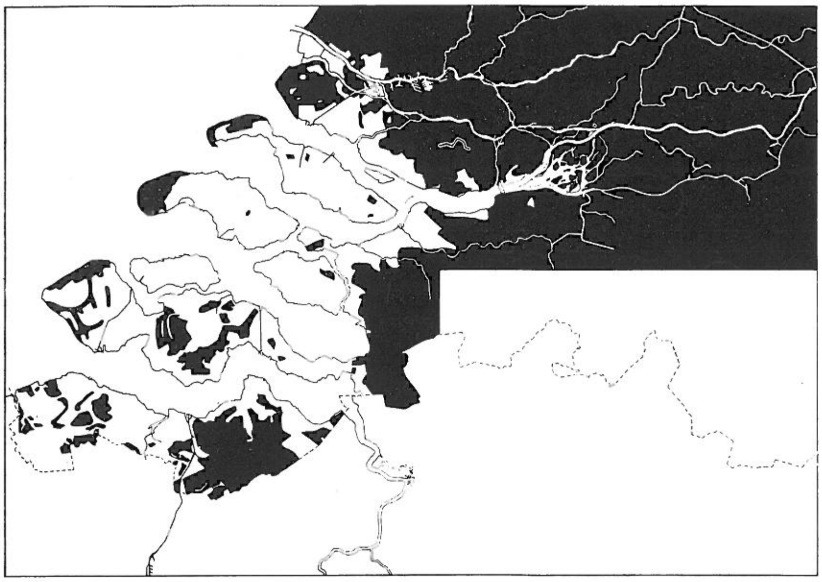

Fig. 1. Distribution of fresh water in the polder areas of the southwestern part of The Netherlands. In the black areas salinity does never rise above $1^0/_{00}$ Cl′. Salinity in the large estuaries and rivers is not shown in this figure.

Investigations in the Delta area

The estuarine area of the rivers Rhine, Meuse, and Scheldt in the southwestern part of the Netherlands is usually called the Delta area (fig. 2). The topography and hydrography of this area were described by DEN HARTOG (1963), PEELEN (1967), PARMA (1968) and for the brackish and fresh inland waters by WOLFF (1968). The distribution of fresh, brackish, and salt water in this area is shown in fig. 1.

Asellus was looked for all over the area in the years 1959—1968, but especially in the period 1965—1967. Collecting was generally done by hand and by hand-operated nets, but in some cases by dredges and a 0.1 m² Van Veen-grab. All material was identified in the laboratory on the shape of the sexual pleopods. All specimens identified are stored in the collections of the Delta Institute and the State Museum of Natural History at Leiden.

Distribution of Asellus in the Delta area

Both *A. aquaticus* and *P. meridianus* live in the tidal freshwater zone of the river Meuse and in that part of the Biesbosch area dominated by the water of the Meuse (figs. 2 and 3). In the waters fed by the Rhine only *A. aquaticus* occurs. The recorded distribution of the two species is given in table I. From these data may be concluded that

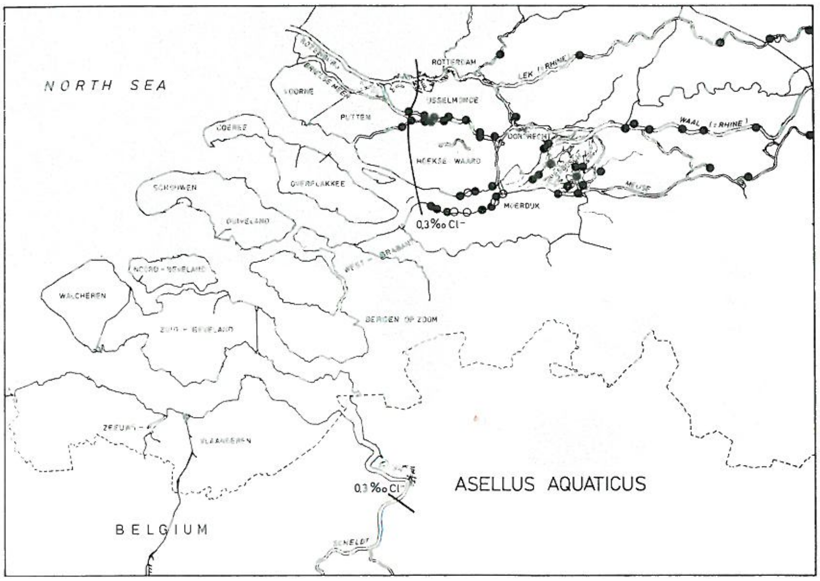

Fig. 2. Distribution of *Asellus aquaticus* in rivers and tidal waters. Dots denote records of *A. aquaticus*; circles of not specifically identified *Asellus*. Shown is the isohaline of $0.3^0/_{00}$ Cl′ for the estuarine waters during average river discharge and mid-tide.

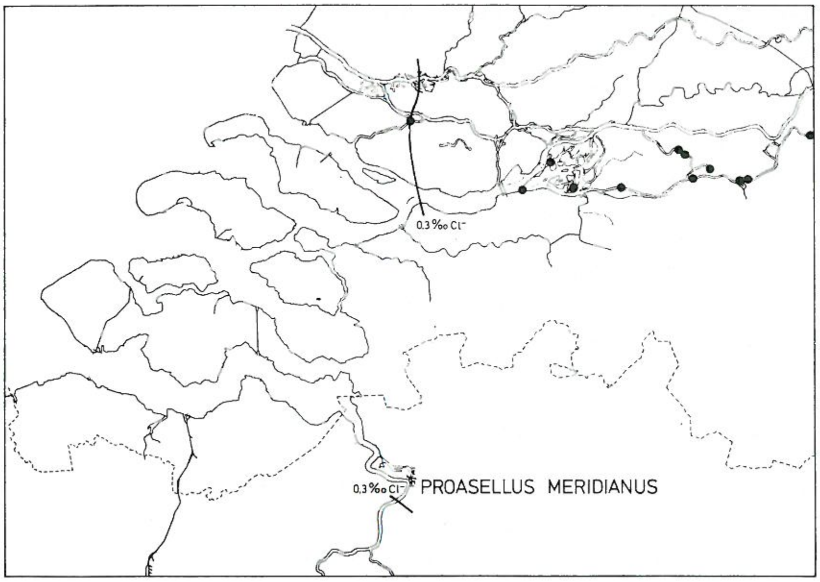

Fig. 3. Distribution of *Proasellus meridianus* in rivers and tidal waters. Shown is the isohaline of $0.3^0/_{00}$ Cl′ for the estuarine waters during average river discharge and mid-tide.

TABLE I

Occurrence of Asellus aquaticus *and* Proasellus meridianus *in the water of the large rivers reaching the Delta area.*

	Rhine water	Meuse water
Asellus aquaticus	40 observations	12 observations
Proasellus meridianus	1 observation	11 observations

the distributions of the two species differ significantly (χ^2-test; $P < 0.005$).

Some characteristics of the water of these two rivers in the years of our investigation are enumerated in table II. The low oxygen values as well as the relatively high contents of inorganic salts indicate that the river Rhine is much more polluted than the river Meuse. *A. aquaticus* apparently is able to withstand these conditions, contrary to *P. meridianus* which is lacking from the former river. The absence of *P. meridianus* from heavily polluted waters was also noted by WILLIAMS (1960), who remarked that it is likely not due to different tolerances to low oxygen values. The observations of EDWARDS & LEARNER (1960) confirm this. The difference in the contents of the above mentioned electrolytes, therefore, may be important for Asellus.

However, both species do not only occur in the rivers, but also in the stagnant inland waters of the Delta area (figs. 4 and 5). In the polder area studied intensively by us (west of a line connecting Rotterdam, Dordrecht, Moerdijk, Bergen op Zoom and the place where the river Scheldt crosses the frontier of the Netherlands), *P. meridianus* (fig. 5) is only found in the polders between the branches of the Rhine and the Meuse and in Zeeuws-Vlaanderen situated at the margin of the more elevated sandy Pleistocene soils in Belgium.

Asellus aquaticus (fig. 4) also occurs abundantly in these areas, and on several of the islands in between. On the islands of Voorne,

TABLE II

Mean values of some parameters for the quality of the water of the rivers Rhine and Meuse over the years 1965—1968. Data supplied by the State Institute for the Purification of Sewage.

Percentage of oxygen saturation	Meuse 81%	Rhine 58%
biological oxygen demand after 5 days (BOD 5)	6.2 mg 0/1	5.1 ml 0/1
NH^+_4	1.5 mg/l	1.6 mg/l
NO^-_3	13.0 mg/l	11.0 mg/l
Cl'	44.5 mg/l	128.0 mg/l
SO^{2-}_3	58.5 mg/l	70.5 mg/l
phenoles	8.75 μg/l	14.25 μg/l

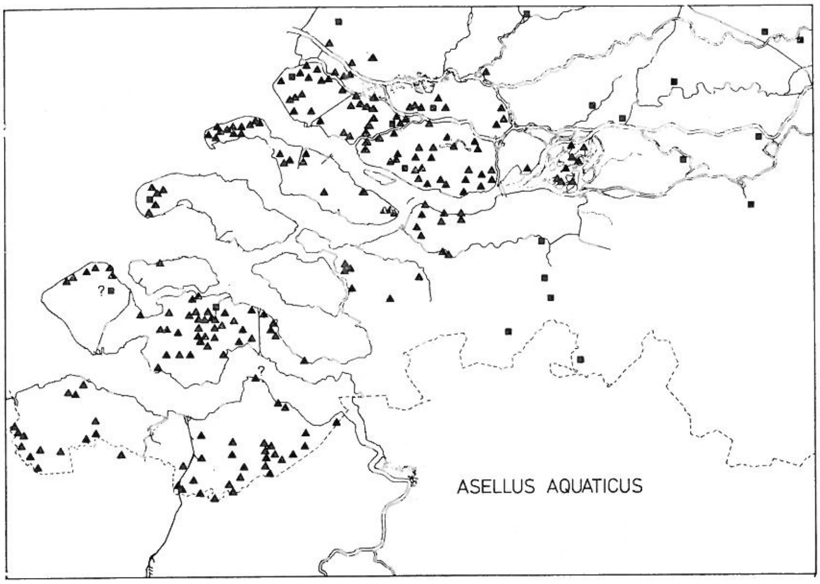

Fig. 4. Distribution of *Asellus aquaticus* in stagnant or slow-running inland waters. Triangles denote our observations; squares literature data.

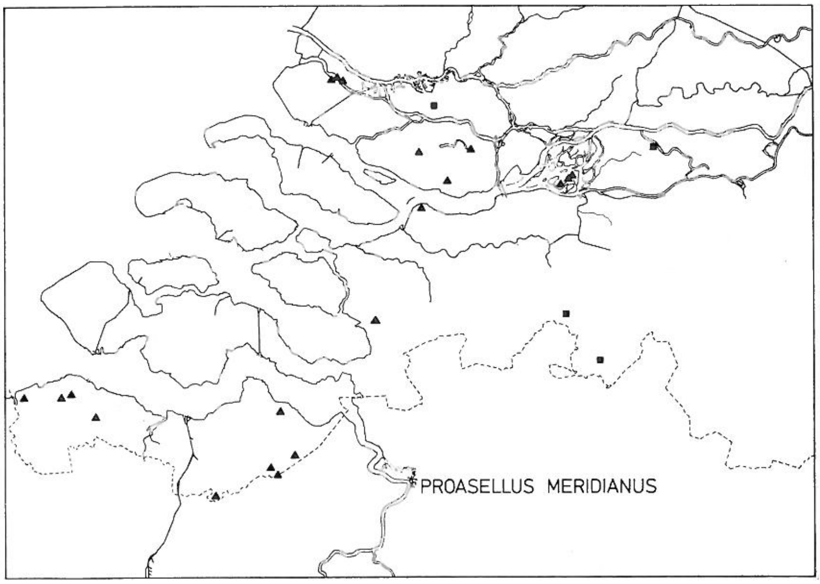

Fig. 5. Distribution of *Proasellus meridianus* in stagnant or slow-running inland waters. Triangles denote our observations; squares literature data.

Goeree, Schouwen and Walcheren it occurs abundantly in the dune areas along the coast of the North Sea. Moreover this species is also found in the polder areas of the islands of Overflakkee, of Noord-Beveland and of Zuid-Beveland. In an earlier paper (WOLFF, 1968) it was explained that it is very improbable that these polder areas continually have formed a suitable habitat for fresh water animals, owing to inundations with salt and brackish water. Moreover the island of Overflakkee, for instance, only came into being in the 14th century. Therefore it is very probable that the populations of *Asellus aquaticus* inhabiting these areas now, have originated by immigration during the last five centuries.

The question arises why only *A. aquaticus* was able to do so. MOON (1957, 1957a) supposes that *A. aquaticus* was introduced in the English lake district with weeds for ornamental ponds. Such introductions are not very probable in the Dutch Delta area, because most finds were made in ditches and drinking pools for cattle, where ornamental weeds and similar objects were never introduced.

It seems more probable that the present distribution has arisen merely by chance, for instance by incidental transport by man and by birds. This hypothesis is difficult to test, but to do so, I have made the following assumptions. First, it is assumed that the frequencies of the two species in the area where they occur together, has been the same in the course of time. As a measure of frequency the number of inland localities of each species on the islands of Rozenburg, Voorne-Putten, IJsselmonde and Hoekse Waard and the areas West-Brabant and Zeeuws-Vlaanderen has been adopted. *A. aquaticus* was found in 131 localities in this area and *P. meridianus* in 18 localities. Secondly it has been assumed that the remaining islands have been colonized by individuals (gravid females, for instance) originating from this area. Thirdly, it was assumed that one succesful transport was sufficient to start the further colonization of an island. Owing to the engineering works of the last century it is a little difficult to point out the limits of an island. I have considered as such Goeree-Overflakkee, Schouwen-Duiveland, Noord-Beveland, Zuid-Beveland, and Walcheren.

Considering now the occurrence of *Asellus* on the "mainland" as a binomial distribution with *A. aquaticus* present in $\frac{131}{149}$ part of the cases and *P. meridianus* in $\frac{18}{149}$ part of them, we can calculate the probability of five transports of one gravid female of exclusively *A. aquaticus*. This chance is given by $\left(\frac{131}{149}\right)^5$ or about 49%. When one or more of the islands have been colonized from an island lodging already exclusively *A. aquaticus*, this value even will be higher. Hence, it may be concluded that the present exclusive occurrence of *A. aquaticus* on the islands of the Delta area might have arisen by chance very well.

On the other hand this calculation is based on so many questionable assumptions that it seems important to consider also another factor, which also extends its influence into the areas inhabited by both species, viz. the salinity of the water.

The inland waters of the Delta area often are brackish to some degree (fig. 1). Therefore, it seems important to investigate the hypothesis that *A. aquaticus* is able to tolerate brackish water, while *P. meridianus* is not able to do so.

The distribution of both species in the rivers Rhine and Meuse seems to be an argument of favour of this hypothesis. Also the exclu-

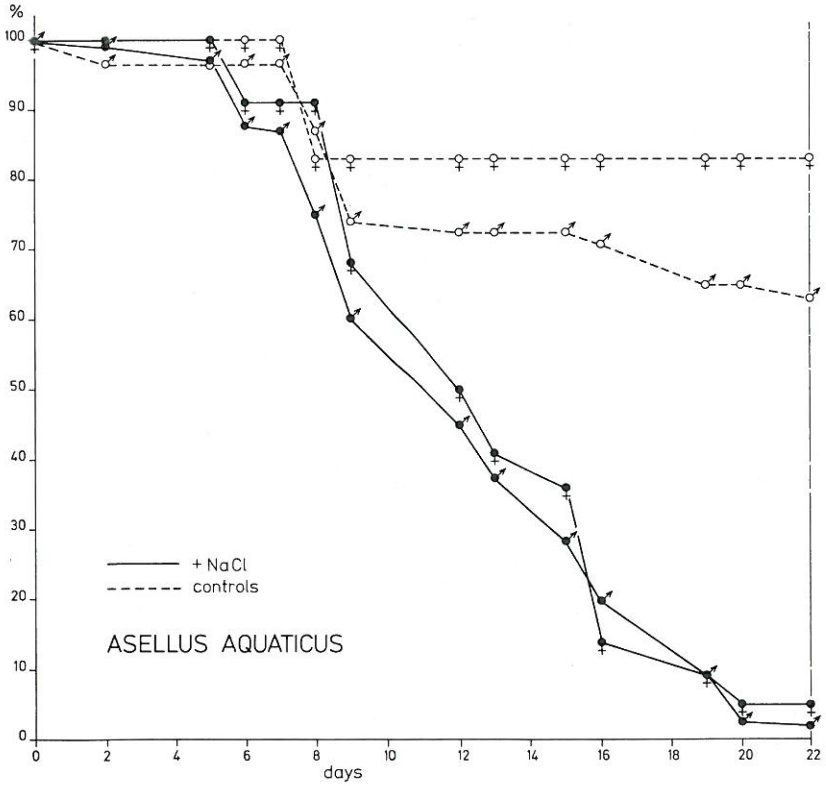

Fig. 6. Tolerance of *Asellus aquaticus* to raising salinity. Shown is the percentage of surviving specimens in water of raising salinity (n = 222) as well as in normal freshwater (controls; n = 58).

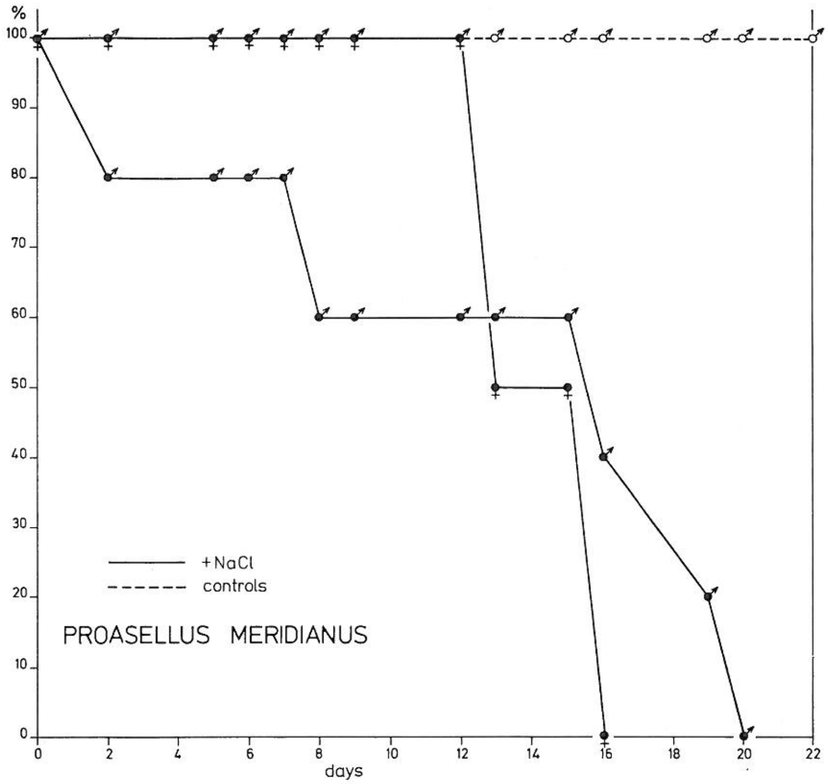

Fig. 7. Tolerance of *Proasellus meridianus* to raising salinity. Shown is the percentage of surviving specimens in water of raising salinity (n = 7) as well as in normal fresh water (controls: n = 3).

sive occurrence of *A. aquaticus* on the islands does not contradict it. GRUNER (1965) records that *A. aquaticus* is very euryhaline; the species is even able to live together with the brackish water isopods, *Cyathura carinata* and *Idotea chelipes*. In the Delta area *A. aquaticus* was found living in salinities up to 1.41$^0/_{00}$ Cl'. LOCKWOOD (1959) records that experimentally *A. aquaticus* was able to adapt to salinities of 400 mmol/l or about 14$^0/_{00}$ Cl'. Nothing, however, is known about the tolerance of *P. meridianus* to brackish water.

Experimental investigation of the tolerance of brackish water in Asellus

To carry out a preliminary test on the salinity tolerance of both species, a large number of specimens was collected in a locality where both species were known to occur. The sample then was divided into four subsamples of about 70—100 specimens and each subgroup was placed in a plastic container provided with some *Ceratophyllum submersum* as food. Every day a small quantity of sea water was added to three of the subgroups. This caused the salinity in the containers to rise about $0.5^0/_{00}$ Cl' daily. Every day before the sea water was added the animals having died during the preceding 24 hours were gathered from all four subgroups and identified, and a watersample was taken to determine the salinity. This procedure was only followed from Monday to Friday; on Saturday and Sunday the animals were not checked.

The results are given in figs. 6 and 7. Living specimens of *A. aquaticus* and of *P. meridianus* still occurred in salinities of $6.58^0/_{00}$ Cl' and $5.45^0/_{00}$ Cl', respectively. The results of this simple experiment do not show that *P. meridianus* is less tolerant to raised salinities than *A. aquaticus*. Thus, although the number of *P. meridianus* studied was rather low, it seems probable that the difference between the distributions of the two species cannot be attributed to differences in salinity tolerance.

Discussion

Williams (op. cit.) was forced to the conclusions that *A. aquaticus* and *P. meridianus* live in the same niche and microhabitat, and that both species are in competition. He also concluded that *P. meridianus* was yielding to *A. aquaticus*.

However, *P. meridianus* does not appear to be completely in the defense. For instance, the species occurs in several ditches in polders in the Biesbosch area which came into being not longer than one or two centuries ago. Also the species obtained recently an important stronghold in the Brielse Meer. This is a freshwater lake which originated when in 1950 the estuary Brielse Maas was dammed up. Apparently, *P. meridianus* is still able to colonize new biotopes. Of course, this does not exclude the conclusions mentioned above.

Moreover, my investigations did not alter the conclusions reached by Williams. The ecological similarity of the two species apparently may be extended to their tolerance to raised salinities. On the other hand it was possible to confirm that these species react differently to water pollution. This offers an important advantage to the most tolerant species, *A. aquaticus*, in our 20th century.

The main conclusion of this study is, however, that *A. aquaticus* and *P. meridianus* form an extremely interesting couple of species. A study of the way they colonize the future fresh Delta lakes therefore may result in valuable data on interaction of closely related species, and also has considerable theoretical interest. It is planned to undertake such a study.

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