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Where have all the ”vejdovskies” gone (*Potamothrix vejdovskyi* Hrabe)? Ponto-Caspian tubificid oligochaete species in Lake Mälaren, south-central Sweden, in a 100 year perspective

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Abstract

Potamothrix vejdovskyi is one of several alien Ponto-Caspian species presently invading Europe and the New World. Its invasive success has been suggested to be dependent upon the trophic degree of the water, and this species is considered to be particularly indicative of mesotrophy (Lang & Reymond 1996). Bottom fauna surveys performed by the Swedish Fisheries Board in 1915 and 1916 and in 1933–1935 did not reveal the existence of *P. vejdovskyi* in Lake Mälaren, whereas extensive bottom fauna programs in the lake in 1967–1976 demonstrated a wide distribution of the species in the central, least polluted basins. Strict quantifications of the distribution of oligochaetes in those basins in 1974 showed that *P. vejdovskyi* then made up on average 28 % of the total abundance of oligochaetes. However, in later bottom fauna surveys in Lake Mälaren, performed by the Swedish Environment Protection Agency in 1981 and in 2009–2011), *P. vejdovskyi* could not be found at all. Sewage treatment around Lake Mälaren accelerated in the late 60’s and the phosphorus load is nowadays considerably lower than before treatment (about 30 % less in terms of total-P concentrations in the water). The question of why this species seems to have more or less disappeared from the lake remains unsolved.

Key words: Ponto-Caspian species, alien species, invasions, *Potamothrix vejdovskyi*, Lake Mälaren, distribution

Introduction

The present European distribution of several alien Ponto-Caspian oligochaete species of the genus *Potamothrix* originating in the Black Sea-Caspian Sea areas is today fairly well-known (Milbrink 1999, Milbrink & Timm 2001). Modes of dispersal are also discussed in these works. In most cases the world distribution of the same species is more uncertain, due to the fact that the oligochaete fauna in great parts of the world is on the whole little known. Most characteristically, however, several *Potamothrix* species have managed to cross the Atlantic Ocean and reached the Great Lakes of North America. It is only natural to think of such east-west dispersal via the ballast water of ships. In other cases there is a most typical north-south gradient in the dispersal of the same species. Some Ponto-Caspian *Potamothrix* species have actually reached localities in South-America and other species places on the African continent. In those cases birds (see below) are likely to be the vectors of dispersal (Milbrink, 1999).

Most of these Ponto-Caspian oligochaetes are known to be particularly invasive once natural physical obstacles like mountain ridges and oceans have been crossed. The massive construction of canals for transportation in the 19th century, the regulation of lakes and major rivers for energy production, and, in the 20th century, the use of ballast water tanks in large vessels, has greatly facilitated dispersal (Bij de Vaate *et al.* 2002).

Whereas the world distribution and modes of dispersal of *Potamothrix heuscheri* and *Potamothrix moldaviensis* over the world have previously been described, not much, however, has been said about *Potamothrix vejdovskyi* in that respect although briefly commented upon in Milbrink & Timm, 2001. This paper is devoted to the known presence of *P. vejdovskyi* in Lake Mälaren in southern Sweden between 1966 and 1980. After that period there are no records at all from Sweden of this species. Why is that so?

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Results

World distribution of *P. vejdovskyi* and other alien species of the genus *Potamothrix*

All available world distribution data on alien species of the genus *Potamothrix* have been compiled by Dr. Tarmo Timm, Tartu University, Estonia, and transformed into world maps, such as for *P. hammoniensis* (Fig. 1) and *P. vejdovskyi* (Fig.2). Similar distribution maps for *P. heuscheri* and *P. moldaviensis* have previously been published in Milbrink 1999 and Milbrink & Timm 2001, respectively. The distribution pattern covering Europe (and parts of Western Asia) is rather similar for several *Potamothrix* species, whereas the world distribution of the different species vary considerably.

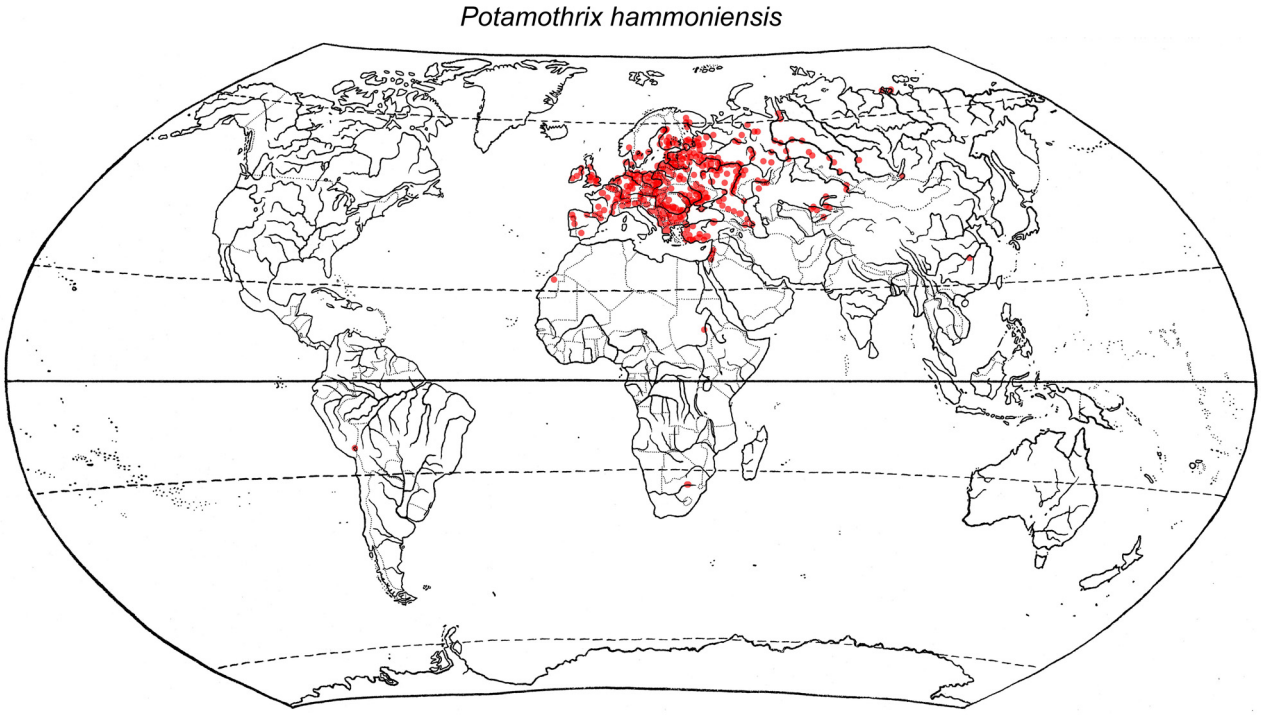

FIGURE 1. World distribution of *Potamothrix hammoniensis* (courtesy Dr. Tarmo Timm).

The world distribution of *P. hammoniensis,* by far the most frequently occurring *Potamothrix* species in Europe, covers most of Europe with extensions far into Asia (Fig 1). This species is steadily on the move to the north and north-west but has not reached north-western Scandinavia (Milbrink, 1999) and obviously not yet crossed the Atlantic Ocean. There is, however, one slightly mysterious record from the New World—Lake Titicaca in Bolivia—Peru (Juget & Lafont 1994) and there are also records from the Middle East and from three localities in Africa. In that respect its distribution pattern reminds of that of *P. heuscheri* which has also been found in Lake Titicaca (Juget & Lafont 1994) and in a few localities in Africa (Milbrink, 1999). *Potamothrix vejdovskyi* (Fig. 2), the target species for this study, seems to be fairly much bound to Europe. Though not shown in Fig. 2 there is, however, one record of this species from Ethiopia (Dr. Tarmo Timm, personal information). *Potamothrix moldaviensis, P. vejdovskyi, P. bedoti* and *P. bavaricus* have all also reached the Great Lakes of North-America. *P bavaricus* has an even wider distribution in the U.S.A.than the other species mentioned, and there are also records from Australia and surrounding islands.

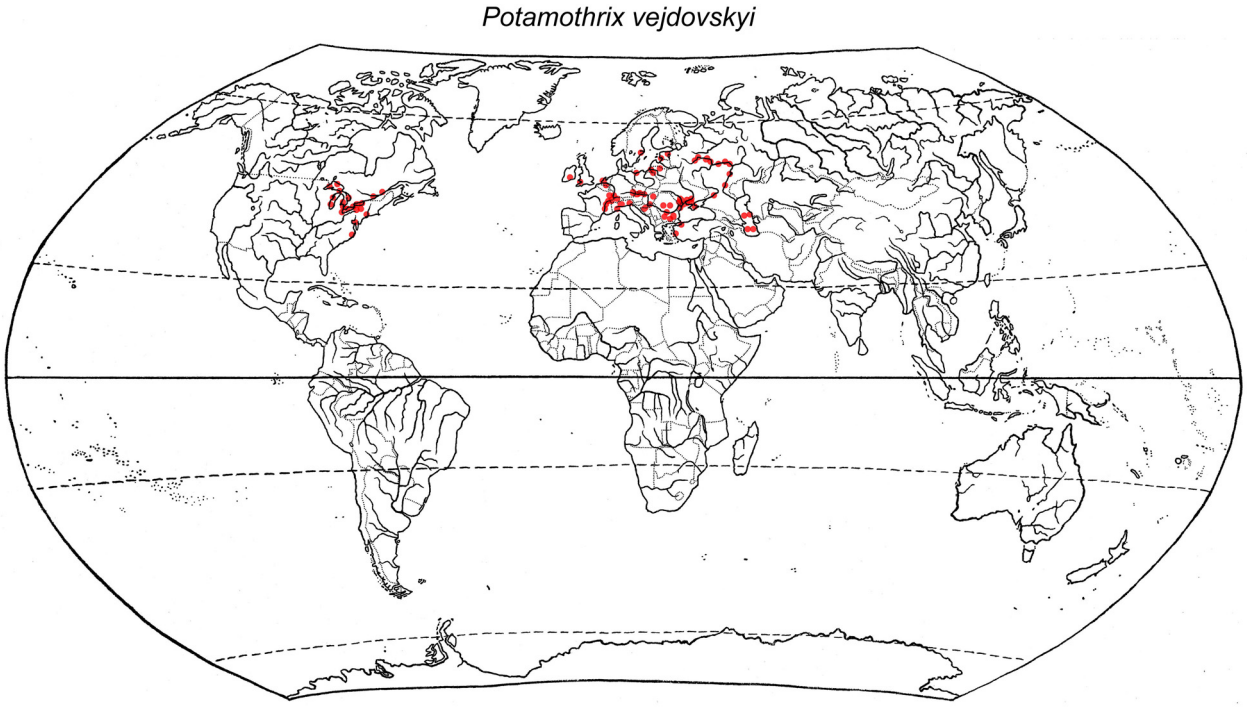

FIGURE 2. World distribution of *Potamothrix vejdovskyi* (courtesy Dr. Tarmo Timm).

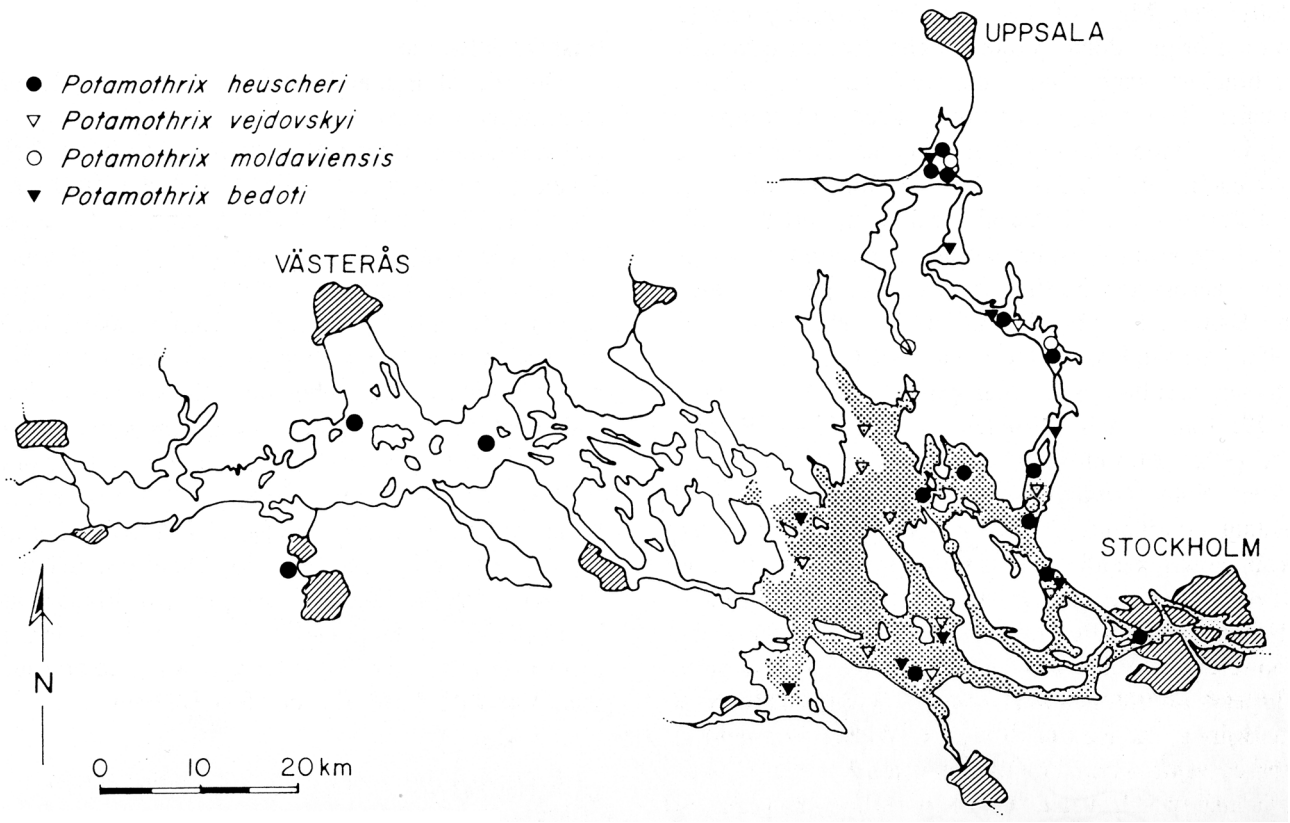

FIGURE 3. Distribution of all Ponto-Caspian species of the genus *Potamothrix,* except *P. hammoniensis* (species frequently occurring nearly everywhere in the lake) found in Lake Mälaren in the early 1970's. The full extension of brackish water in the profundal in the 1930's is indicated in grey (Dr. Sten Vallin, personal information; from Milbrink, 1980).

The Swedish distribution of *P. vejdovskyi*

In several early faunistic surveys over Lake Mälaren, i.e. the first ones in 1915 and 1916 and later in 1933–1935, *P. vejdovskyi* was not present (Milbrink, unpublished). In 1966, however, this species was suddenly present all over the central, northern and eastern basins (Milbrink 1999). *Potamothrix vejdovskyi* is likely to have reached Lake Mälaren in the 1950ies. The known distribution of all species of the genus *Potamothrix* in Lake Mälaren in the early 1970's (except *P. hammoniensis* which is abundantly present everywhere in the lake) is shown in Fig. 3. As an illustrative example of the fairly dense populations of *P. vejdovskyi* in the central basins of Lake Mälaren around 1970 the following study in the basin of Hovgårdsfjärden may be mentioned (Milbrink *et al.* 1974). It was primarily a study on the horizontal distribution of the oligochaete fauna. Accordingly, in February 1970 a grid measuring 100 m x 50 m was marked on the ice over a mudflat at a depth of 30 meters, and tube bottom and Ekman grab samples were randomly taken within the grid (Fig. 4). Thus in all 38 tube bottom samples (aperture about 38cm^2) and 6 Ekman grab samples (aperture about 225 cm^2) were obtained. Here *P. vejdovskyi* made up about 28% of all oligochaetes, *P. hammoniensis* about 34%, *Limnodrilus hoffmeisteri* about 8%, *Spirosperma ferox* and *Psammoryctides barbatus* about 2–3% each, etc. (Fig. 5). In total, no less than 19 different oligochaete species were recorded. *P. vejdovskyi* was actually present in all samples obtained except one. The specific horizontal distribution of oligochaetes was in accordance with the negative binomial, i.e. a slightly aggregated distribution, whereas chironomids showed a random (Poisson) distribution (Milbrink *et al.* 1974). High species diversity and presence of the sensitive species *S. ferox* and *P. barbatus* reveal mesotrophic conditions so characteristic of the central basins of Lake Mälaren.

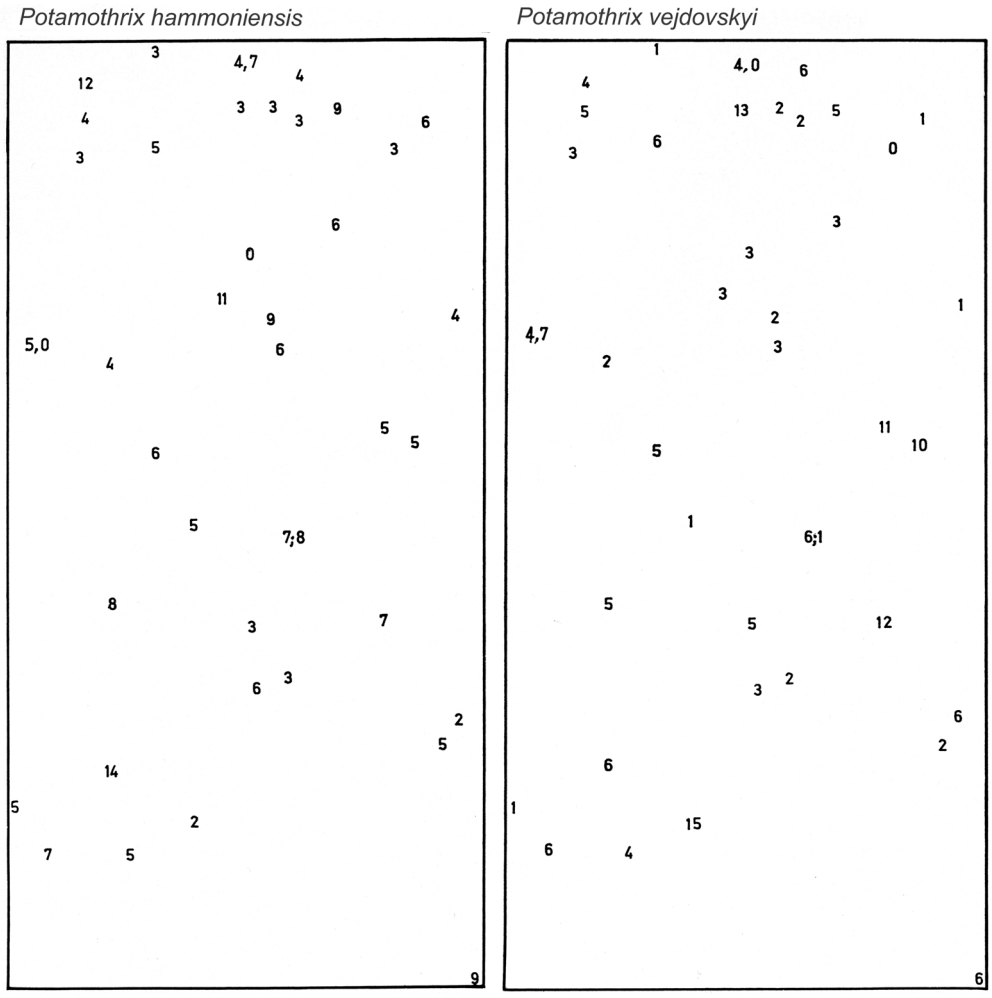

FIGURE 4. Horizontal distribution of the Ponto-Caspian oligochaete species *Potamothrix vejdovskyi* and *Potamothrix hammoniensis* in a grid measuring 100 x 50 m^2 in the basin of Hovgårdsfjärden in central Lake Mälaren. Samples obtained with a core sampler (38 samples) and the larger Ekman grab sampler (6 samples) at a depth of 30 meters. The total numbers of oligochaetes in the same samples are also given in this figure. For strict comparisons abundance values obtained with the Ekman grab sampler are divided by a factor of 6 (from Milbrink *et al.* 1974).

Potamothrix vejdovskyi had its strongholds in the central basins, such as in Prästfjärden and Södra Björkfjärden. Abundance in the profundal was generally high and steadily around 30% of all oligochaetes (see below). Even in 1980 abundance was constantly high, but thereafter no specimens of *P. vejdovskyi* have been observed in the lake or elsewhere in Scandinavia. Other species of the genus *Potamothrix*, however, are still present in Lake Mälaren after 1980 (Milbrink, unpublished).

Potamothrix vejdovskyi has been found to be rather erratic in its appearance in Sweden, Switzerland and France and has mostly been associated with mesotrophic conditions (Lang & Reymond 1996). Modes of dispersal of the Ponto-Caspian oligochaete fauna are further discussed below.

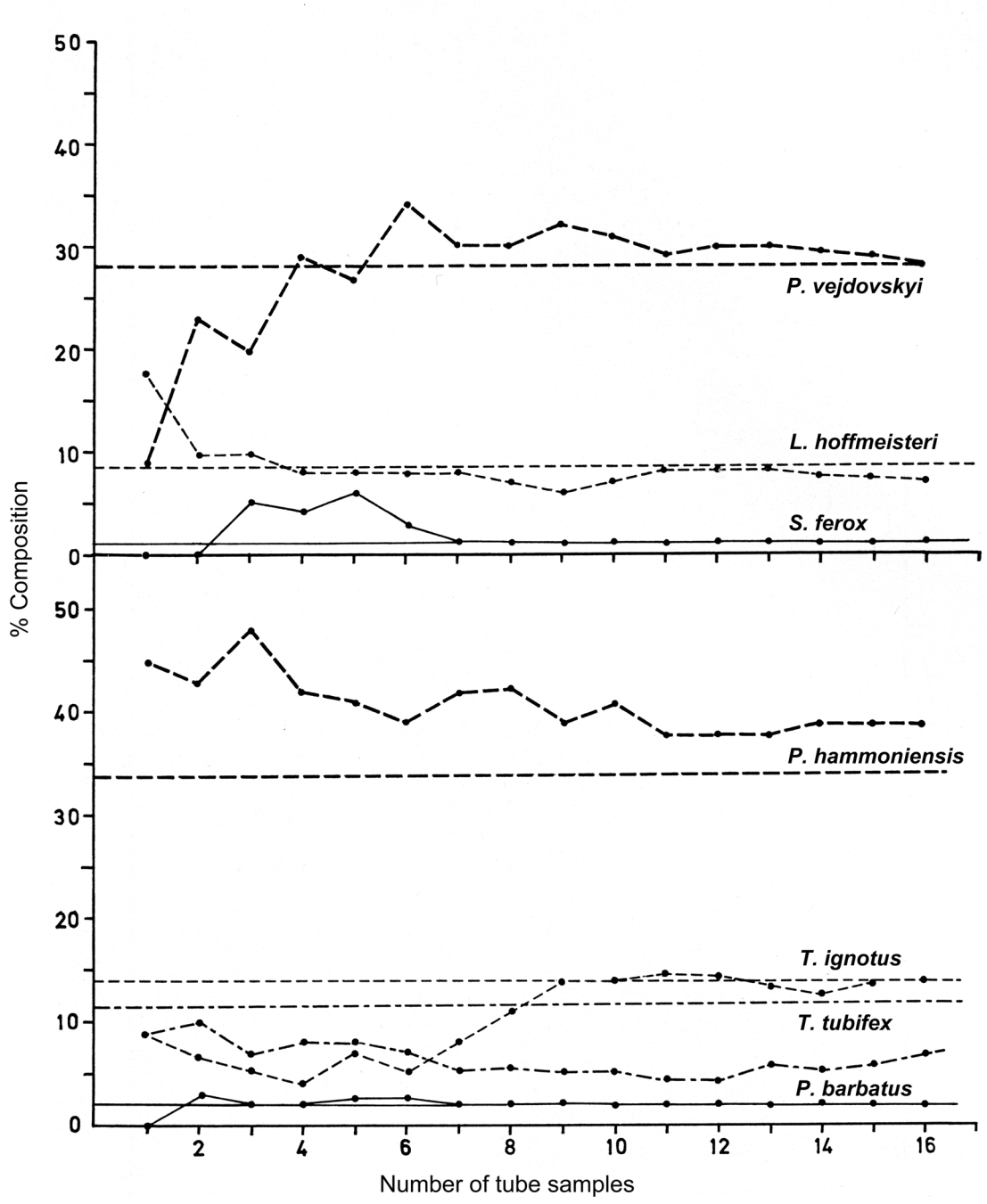

FIGURE 5. Percentage composition of oligochaete species inside the sampling net (Fig. 4) for different numbers of tube bottom samples (accumulative values). Horizontal lines are the percentages obtained after 38 samples (from Milbrink *et al.* 1974).

Discussion

Distributional pathways for species of the genus *Potamothrix* and modes of dispersal of the Ponto-Caspian tubificid oligochaete fauna

According to Timm (1980) and Milbrink & Timm (2001) *P. hammoniensis* was one of the first species to disperse from the Black Sea-Caspian Sea area over Eurasia in a first invasion wave. *Potamothrix heuscheri, P. moldaviensis, P. bavaricus,* and *P. bedoti* are supposed to have dispersed over the world in a second invasion wave. *P. vejdovskyi* is likely to be in the midst of a third wave rather than in the second wave (Milbrink & Timm 2001) presently having reached Lake Mälaren in Scandinavia and, for example, lakes in Switzerland and France (Lang 1994; Lang & Reymond 1996).

Most Ponto-Caspian species of the genus thus originated in the Black Sea-Caspian Sea area and have gradually dispersed over Europe along three main pathways described by, for instance, Bij de Vaate *et al.* (2002) primarily for amphipod species—the Northern, the Central and the Southern Pathways. The Northern Pathway goes to the north-west along Rivers Don and Volga, the Central mainly follows Rivers Dnjeper, Bug, Wistula, etc. and via canal systems reaches the River Rhine estuary in the Netherlands. The Southern Pathway stretches mainly to the west along Rivers Danube and Rhine. There are obviously also other pathways facing south over Turkey and Italy.

There is little doubt that the Ponto-Caspian fauna has spread over Europe via major rivers and canals mainly dug in the 19th century. Several species of amphipods—in all about 20—have thus spread in a ”Central corridor” and via a number of waterways connecting Rivers Dnjeper and Rhine reached Holland and there partly outcompeted the indigenous fauna (Bij de Vaate *et al.* 2002). The ballast water of ships trafficking these rivers and dense networks of connecting canals has, of course, greatly facilitated the dispersal of the Ponto-Caspian fauna. Carlton & Geller (1993) and Hallegraeff & Bolch (1991) have stated that the ballast water of ships is perhaps the overall most efficient agent of dispersal of aquatic invertebrates and planktonic algae. We are talking about ”conveyor belts” across, for instance, the Atlantic Ocean (Carlton & Geller, 1993). Centres of further dispersal of oligochaete species are harbours—often in estuaries, where ballast water is likely to be exchanged. Ballast water often containing stirred sediment and most likely live oligochaetes and cocoons is thus pumped into ships which after having reached distant harbours is again exchanged (Timm 1980). Timm has beautifully described the gradual dispersal of the oligochaete species *Tubifex (Isochaetides) newaensis* in Russia via Rivers Don and Volga eventually reaching the Finnish Bay in the Baltic Sea.

The profundal of the central and eastern basins of Lake Mälaren was not long ago connected with the Baltic Sea (indicated in grey in Fig. 3), and there are still some brackish water invertebrate species of other phyla present in the bottom fauna (Milbrink, 1980). The Ponto-Caspian *Potamothrix* species are believed to have reached ports in Lake Mälaren via ocean-going ships from ports in the Baltic states.

Passive dispersal via harbours and the ballast water of ships has naturally made ”sudden leaps” across the Atlantic possible. Since the Great Lakes of North-America have since long been fully accessible for ocean-going ships, there have been no physical obstacles for the Ponto-Caspian fauna (four *Potamothrix* species so far) to reach these lakes (Ricciardi & MacIsaac, 2000). Other distant destinations like the Australian continent, Tasmania and New Zealand are also likely to have been reached by ships (*P. bavaricus)*.

Some destinations for Ponto-Caspian oligochaete species could not, however, be explained by ships as vectors of dispersal, since the physical obstacles for dispersal are so huge, for instance Lake Titicaca in South-America (*P. hammoniensis* and *P. heuscheri*; Juget & Lafont 1994*),* various inland sites in Africa—Kenya, Congo, Botswana (*P. heuscheri*) and Ethiopia (*P. vejdovskyi),* etc. (cf. Milbrink, 1999). The author feels inclined to suggest migratory birds, especially wading and swimming birds, as vectors of dispersal (Milbrink 1999). Here ”stepping-stone ” dispersal along north-south gradients is most likely. There could thus be a logical explanation for the presence of *P. heuscheri* in Lake Tiberias in Israel, which is a well-known resting spot for wading birds on their yearly migration to East Africa and further south. The same explanation may go for the dispersal of oligochaete species in inland South-America, such as in Lake Titicaca in Bolivia-Peru (*P. hammoniensis, P, heuscheri*; Juget & Lafont 1994). Based on laboratory experiments performed by the present author not only the cocoons of oligochaetes but also live young specimens could be carried in droplets of water contained in the plumage of migratory birds even over fairly long distances, provided temperatures are low enough (around +4° C) at cruising altitudes (Milbrink, unpublished).

Possible explanations to the sudden disappearance of *P. vejdovskyi* in Lake Mälaren

In the author´s opinion there are no risks for misidentifications involved, or this species having been overlooked at any time. The setal set-up is so very characteristic with all bifid setae having equally long broad prongs and dorsal hair seta being short and characteristically bent. The setal bundles are also organized in fan-like arrangements easy to observe (Fig.6).

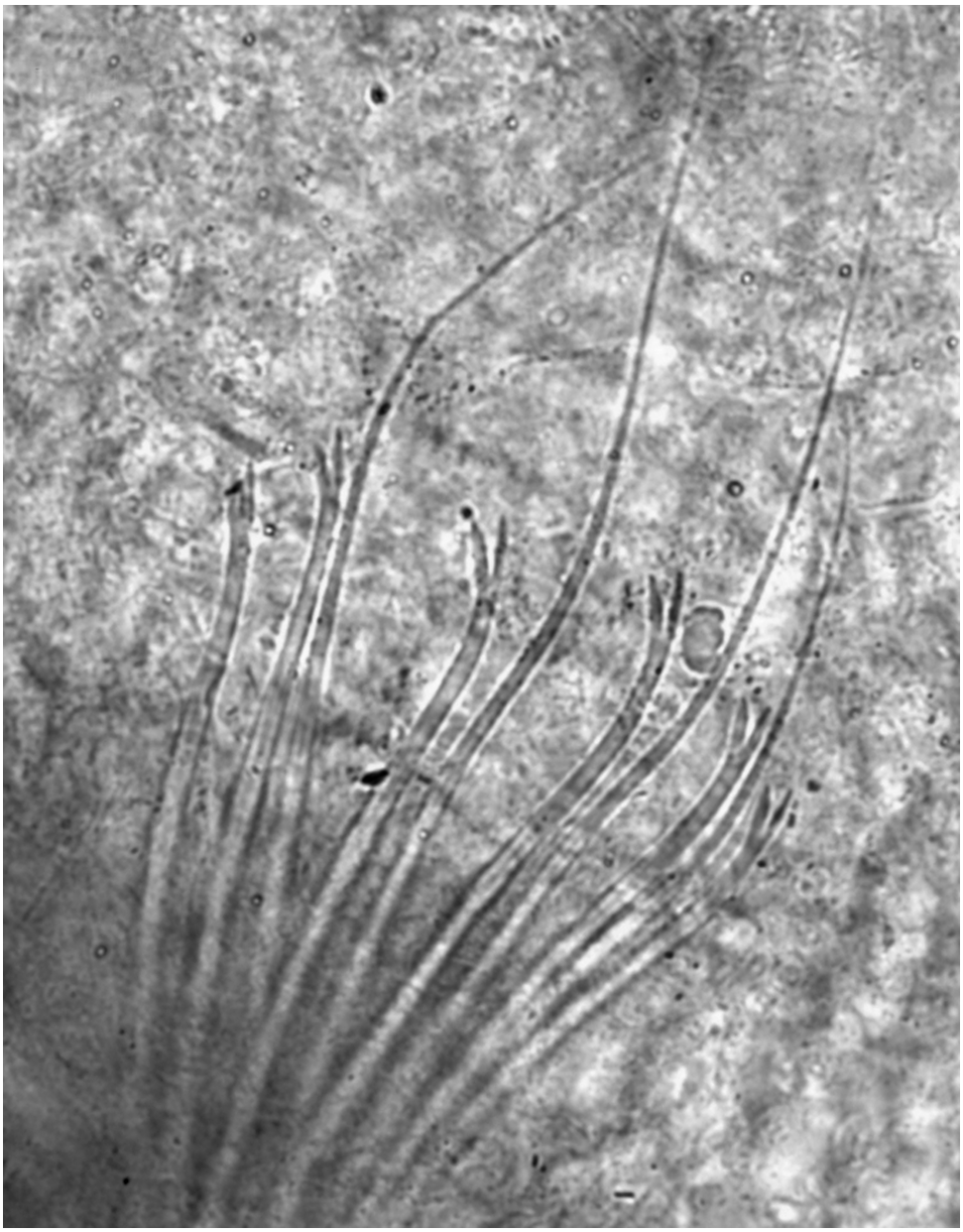

FIGURE 6. Dorsal setae of *Potamothrix vejdovskyi* from central Lake Mälaren in 1967 (photo G. Milbrink).

We know from the Lake of Geneva and Lake Neuchatel in Switzerland that *P. vejdovskyi* may be quite erratic in its appearance almost disappearing in localities affected by efficient sewage treatment (Lang & Reymond 1996). *P. vejdovskyi* may be particularly sensitive to changes in water quality over time such as has taken place in the large lakes in South Sweden. Eutrophication of Lakes Mälaren, Vänern and Vättern culminated in the 1960s and 1970s, after which conditions have improved fairly rapidly due to general sewage treatment. As said before *P. vejdovskyi* is mostly associated with mesotrophic conditions (Lang & Reymond 1996).

There are no indications from Lake Mälaren of Ponto-Caspian species excluding other indigenous species by species segregation for common nutrient resources. On the contrary there may actually be positive mutualistic interactions involved, because wherever *P. vejdovskyi* occurred in Lake Mälaren—often in great abundance—other species were mostly also abundant (Milbrink, unpublished). There are indications that

similar effects could locally be seen in the Lake of Geneva (Lang & Reymond, 1996). Laboratory experiments with *P. hammoniensis, L. hoffmeisteri* and *Tubifex tubifex* from the basin of Görväln in eastern Lake Mälaren have actually given results that suggested possible mutualistic interactions with references to bacterial resources involved (Milbrink 1993), similar to results obtained with species assemblages from Toronto Harbour in Ontario in Canada (Wavre & Brinkhurst 1971). Such mutual advantages would rather promote higher abundance than the opposite.

In the disappearance of *P. vejdovskyi* there might be viruses or pathogens involved. *Potamotrix hammoniensis* and *P. vejdovskyi* were both quite often parasitized by the cestode *Caryophyllaeus laticeps* in Lake Mälaren in the 1960s and 1970s (Milbrink 1975; Milbrink, unpublished), and other parasites we know little of may be involved and affect survival.

Could the fact that the number of stations visited each year by the Swedish Agricultural University for bottom fauna sampling has been reduced considerably during the last decades be of significance, and could therefore *P. vejdovskyi* still be present, but now in low abundance? Again in the author´s opinion this scenario is not very likely since at least one of those stations visited on a yearly basis is in Prästfjärden—one of the deep central basins of Lake Mälaren, where this species was always found between 1966-1980.

It may be a matter of sheer chance. Species may come and go. However, there are no indications that other alien Ponto-Caspian species have fluctuated in abundance that way in Lake Mälaren. Why only *P. vejdovskyi* in that case? A future comprehensive bottom sampling program carried out in the central basins of Lake Mälaren would certainly reveal whether there are still remaining populations of *P. vejdovskyi* in the lake.

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