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Composition and abundance of oligochaetes in large Scandinavian lakes in a morpho-edaphic index framework—in the 1970s and 50+ years later

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Abstract

Bottom-living oligochaetes and chironomid larvae, thanks to their supposedly integrative power, could provide more robust measures of the water quality of lakes than separate chemical data. The oligochaete fauna of the large lakes of southern Scandinavia has been studied in detail over many years—often 100 years or more (Milbrink, 2020). Characteristic species associations and the ecological preferences of each oligochaete species are thus relatively well-known. In Milbrink (2020) it was shown that the precision could be greatly improved if the relationship between oligochaete species and chemical data could be instead demonstrated within a morpho-edaphic index framework (Ryder *et al.* 1974). The percentage composition and total abundance of oligochaetes per sample in a number of large lakes or selected basins of large lakes in southern Sweden and Norway were thus tested against this index in the 1970s (Milbrink, 1978). The trophic change which had taken place in the oligotrophic Lake Vättern—first with eutrophication and later with oligotrophication—was illustrated graphically and discussed in this work (Milbrink, 2020).

A very similar trophic change could also be seen in the oligotrophic Lake Vänern (the basin of Värmlandssjön), as well as in the more eutrophic Lakes Mälaren and Hjälmaren. All these large lakes, once eutrophied in the 1950s and 1960s, are today undergoing oligotrophication. We simply have a melioration thanks to advanced sewage treatment since the 1960s. With our new knowledge, it is informative studying changes in species composition after trophic change. In a time when efforts to save the environment often fail, this new development is a real success story.

Introduction

Early studies in England demonstrated very clearly the indicative value of freshwater oligochaetes in the evaluation of the quality of running waters (Brinkhurst & Kennedy, 1965; Kennedy, 1965; Aston, 1973). Indicator communities of oligochaetes have proven to be also indicative in lakes (Milbrink 1978, 1980, 2020; Lang, 1984). However, this relationship between the oligochaete composition in the bottom fauna and the water chemistry (for instance total phosphorus concentrations) in surficial water strata has been found to be rather unprecise. It was then suggested (Milbrink, 1978) that precision could increase dramatically if the oligochaete composition was instead put in relation to the so-called morpho-edaphic index (Ryder *et al.* 1974), i.e., the average total phosphorus content (in µg/l) in surficial water strata divided by the mean depth (in meters) of the lake or a particular basin of a lake.

Accordingly, in 1977 a comprehensive diagram (then in black and white) was presented showing the actual relationships between profundal oligochaetes in the large lakes of southern Scandinavia and a few additional lakes and the morpho-edaphic index (Milbrink, 1978). Forty years later (Milbrink, 2020), this diagram was replaced by a similar diagram (Figure 1) with a colour scale in accordance with the scale in the original "Saprobien System"—well-known from the continent and designed by Liebmann (1962), and Zelinka and Marvan (1961). In that system blue stands for sensitive species and favourable conditions, and red stands for the opposite, i.e. tolerant species and bad conditions. Accordingly, shades of blue dominate the left part of the diagram—in oligotrophy, whereas striking red colours dominate the right part—in eutrophy (see below for further explanations). Each lake locality is marked in the diagram in the form of a histogram positioned along the abscissa which stands for the actual morpho-edaphic index value (in a logarithmic scale). Low index values indicate oligotrophic localities and high values eutrophic

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localities. Each histogram shows the average percentage composition of oligochaete species with reference to their recognized sensitivity to eutrophication (cf. Table I). The ordinate—also in a logarithmic scale—shows the mean abundance of oligochaetes in each locality and at each moment. In each histogram, abundance is marked with a short horizontal line. In a double-logarithmic scale, abundances from the different localities roughly fall along a straight line (Milbrink, 1978). With reference to the morpho-edaphic index, oligochaetes thereby would have an indicator value both qualitatively and quantitatively—an advantage both from a scientific, as well as from a practical point of view.

TABLE 1. Mean occurrence of freshwater oligochaetes in Scandinavian lake-types (redrawn from Milbrink 1978). The mean percentual occurrence of each species in the oligotrophic, mesotrophic and eutrophic environments, respectively, as estimated by the senior author. Full names of the species in the table are, *Limnodrilus hoffmeisteri* Claparède, *Potamothrix hammoniensis* (Michaelsen), *Limnodrilus claparedianus* (Ratzel), *Aulodrilus pluriseta* (Piguet), *Potamothrix heuscheri* (Bretscher), *Ilyodrilus templetoni* (Southern), *Potamothrix vejdovskyi* (Hrabě), *Potamothrix bedoti* (Piguet), *Limnodrilus udekemianus* Claparède, *Potamothrix moldaviensis* (Vejdovský & Mrázek), *Lophochaeta ignota* (Štolc), *Aulodrilus limnobius* Bretscher, *Bothrioneurum vejdovskyanum* Štolc, *Aulodrilus pigueti* Kowalewski, *Psammoryctides albicola* (Michaelsen), *Rhyacodrilus coccineus* Vejdovský, *Rhyacodrilus falciformis* Bretscher, *Psammoryctides barbatus* (Grube), *Limnodrilus profundicola* (Verrill), *Spirosperma ferox* (Eisen), *Rhynchelmis tetratheca* Michaelsen, *Stylodrilus heringianus* Claparède, *Eiseniella tetraedra* (Savigny). In the absence of more data, *Tasserkidrilus acapillatus* (Finogenova, 1972), so far only identified from Lake Vättern, has not yet been included in the table. A score of 10 points in oligotrophy would be expected.

Species	Oligo	Meso	Eut	Species	Oligo	Meso	Eut
Limnodrilus hoffmeisteri	1	2	7	*Lophochaeta ignota*	2	4	4
Potamothrix hammoniensis	1	3	6	*Aulodrilus limnobius*	2	5	3
Limnodrilus claparedianus	1	3	6	*Bothrioneurum vejdovskyanum*	2	5	3
Aulodrilus pluriseta		4	6	*Aulodrilus pigueti*	3	5	2
Potamothrix heuscheri		4	6	*Psammoryctides albicola*	4	5	1
Tubifex tubifex	5		5	*Rhyacodrilus coccineus*	4	6	
Eiseniella tetraedra	5		5	*Rhyacodrilus falciformis*	(5)	(5)	
Ilyodrilus templetoni		5	5	*Psammoryctides barbatus*	5	5	
Potamothrix vejdovskyi		5	5	*Limnodrilus profundicola*	7	3	
Potamothrix bedoti		5	5	*Spirosperma ferox*	8	2	
Limnodrilus udekemianus	1	4	5	*Rhynchelmis tetratheca*	8	2	
Potamothrix moldaviensis	2	4	4	*Stylodrilus heringianus*	9	1	

In the diagram in Figure 1 we thus have a colour pattern from the left to the right changing from blue to red, and abundance values constantly rising. To the left we have the deep and fairly large Lakes Mjösa (368 km^2, max depth 450 m) and Tyrifjorn (136 km^2, max depth 154 m), central Lake Vättern (1893 km^2, max depth 128 m) and central Lake Vänern (5650 km^2, max depth about 106 m)—oligotrophic lakes with a considerable share of species recognized from oligotrophic environments, i.e., *Spirosperma ferox* and *Stylodrilus heringianus.* Further to the right in Figure 1 are the central basins of Lake Mälaren (1072 km^2, max. depth 106 m) and eutrophied bays and fjords of Lake Vänern, and the pink colour stands for a considerable share of species usually dominating in more eutrophic environments, i.e., *Potamothrix hammoniensis* and allied species. Even further to the right are western Lake Hjälmaren (483 km^2, max. depth 25 m) and various eutrophic basins of Lake Mälaren with increasing shares of a deep red colour standing for the very tolerant species *Limnodrilus hoffmeisteri*.

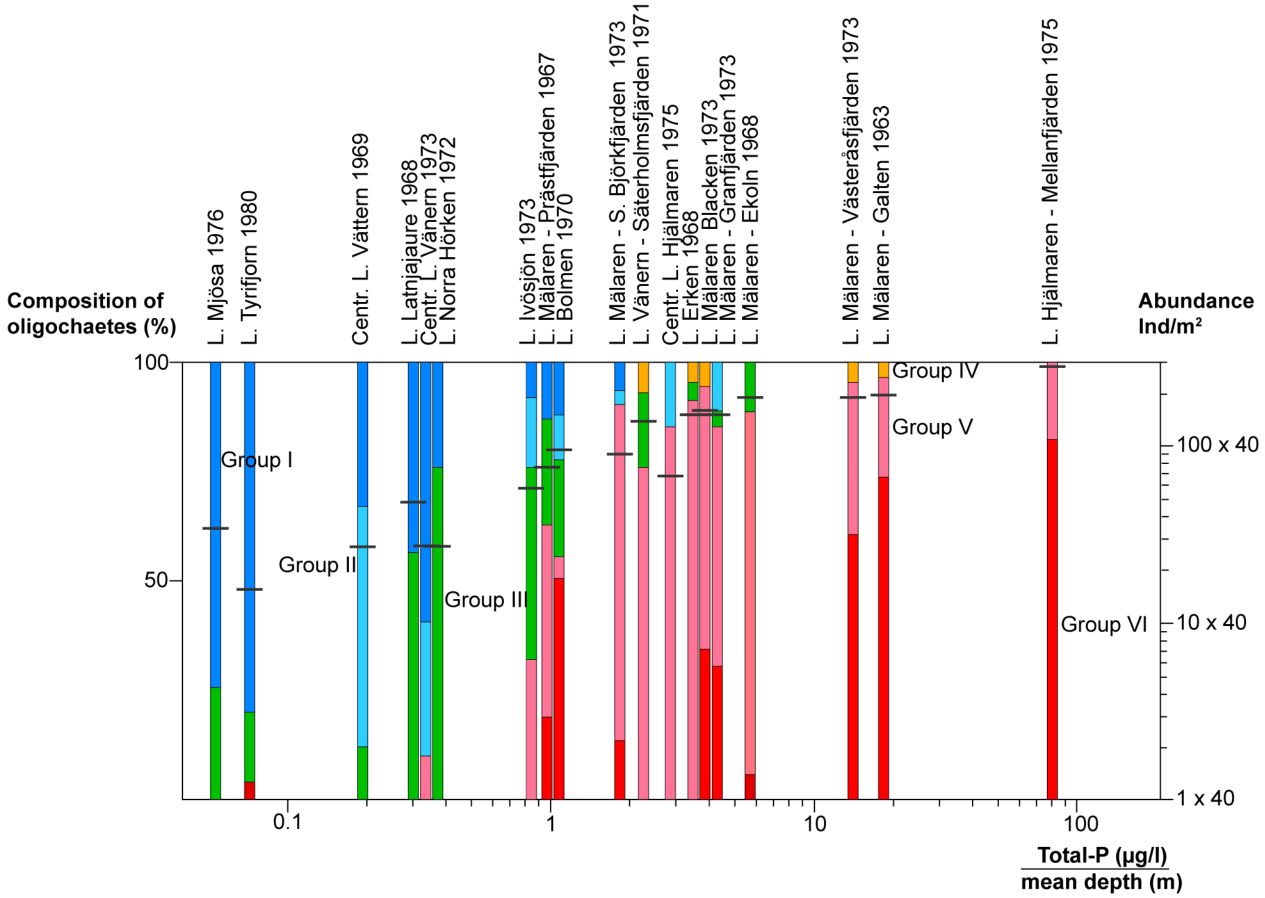

FIGURE 1 Percentage composition of profundal oligochaetes in lakes of different nutrient standard and size in Scandinavia (redrawn from Milbrink, 1978). Each histogram in the diagram shows the percentage composition of oligochaetes in a particular site at a particular time in accordance with the continental colour scale (Liebmann, 1962; Zelinka & Marvan, 1961), thus forming characteristic species groups with known specific sensitivity to oxygen deficiency (see explanation in text). Each histogram is positioned along the abscissa with reference to the morpho-edaphic index value. Oligochaete abundance is also given on the ordinate. Both axes are logarithmic. The abundances form an approximate straight line (see text below).

Today we have much more information on oligochaete associations from lakes of all kinds in Scandinavia and elsewhere. We could ask ourselves: do these relationships which were based upon preliminary data from the 1960s and 1970s, hold 40–50 years later? In a study from 2018 it was shown that so was the case for Lake Vättern—a basically oligotrophic lake affected by first eutrophication and later oligotrophication strongly affecting the position of its representative histogram in Figure 1 (Milbrink, 2020).

Sewage treatment had been proclaimed all over Sweden in the 1960s and we could therefore hypothesize that a similar sequence of events had taken place concomitantly in the other large lakes of south Sweden, i.e., Lakes Vänern, Hjälmaren and Mälaren, likewise affecting their positions in the diagram.

Material and Methods

The large lakes and individual basins referred to in this work have been characterized by oligochaete communities found in deep-water sediment samples from those lakes. At each locality an average of 3 to 5 parallel Ekman samples (aperture 225 cm^2) has been selected to represent the lake. This is the method empirically used to get representative bottom samples from deep lakes in Scandinavia, cf. Milbrink *et al.* (1974). The sieving nets have had a mesh-size of 0.5 mm. Animal residues have been preserved in 70% alcohol and thereafter identified to species in the microscope. All oligochaetes in the residues have, with no exceptions, been identified to species by the senior author and so has all oligochaete material in this work except the early material from Lake Vättern (1911–1914), some from contemporary samples and some from old collections. Strangely enough, oligochaete collections from Lake Vänern from the early 1920s had not until recently been identified to species.

Figure 1 is the result of analyses made on oligochaete material obtained from station nets on profundal deposits in the large lakes of southern Scandinavia. Figure 2 is a map showing the geographical positions of those lakes. The capitals Stockholm and Oslo are also indicated on the map.

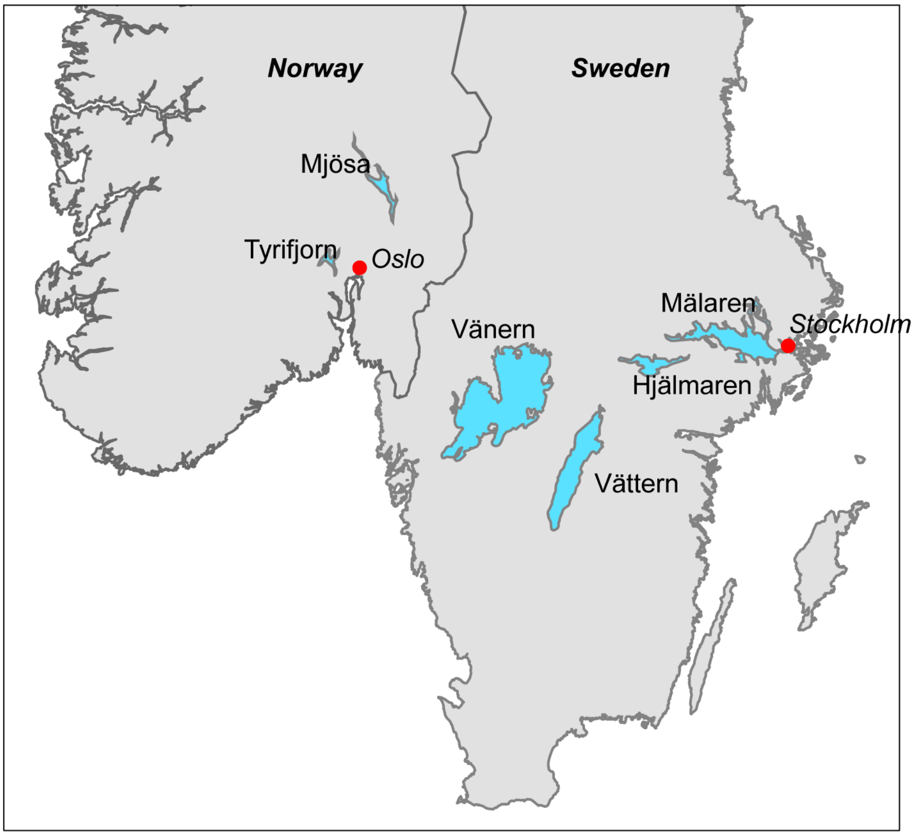

FIGURE 2 Map of southern Scandinavia showing the large lakes in south Sweden—Vänern, Vättern, Mälaren and Hjälmaren—and in south Norway—Mjösa and Tyrifjorn. The capitals of Sweden and Norway—Stockholm and Oslo, are also indicated on the map.

Oligochaete analyses on complementary material from a number of other reasonably large lakes in Scandinavia have been added to Figure 1.

In the diagram in Figure 1, logarithmic scales were chosen to minimize large differences in values, be that abundance values or positions on the morpho-edaphic index scale. Double-logarithmic scales would certainly facilitate the existence of linear relationships in the diagram.

Methodological tests of the Ekman sampler

Beginning in 1911, the Ekman bottom sampler had been used for taking representative profundal samples on deposition bottoms in lakes in Scandinavia and elsewhere. The question is, of course, how accurate are those samples? On this point the authors would rely upon statistical test-results obtained with an Ekman sampler (aperture 225 cm^2) and a core sampler (aperture 39 cm^2; Milbrink, 1971) in the basin of Hovgårdsfjärden in southern Lake Mälaren adjacent to the basin of Södra Björkfjärden (cf. Figure 7), one of the central mesotrophic basins of the lake (Milbrink *et al.* 1974). This study was carried out from the ice in February 1971. The bottom is a typical depositional sediment, quite flat and relatively large (about 8 x 2 km^2) with soft texture. The depth is between 30 and 32 m and conditions would seem to be ideal for the purpose. A grid system, 100 x 50 m, i.e., comprising 5000 square meter units, was marked in the thin snow cover on the ice. Each sample was taken at random in the grid system and each sample was sieved on the spot. The conclusions from these statistical test-series are given below.

Presentation

Figure 1 is largely based upon Table I—originally from Milbrink (1978), but now slightly modified. In this table each oligochaete species has been given a t total of 10 points— equivalent to 100%. In essence, this table shows how frequently each species, on the average, is found in oligotrophic, mesotrophic and eutrophic environments, respectively, in Scandinavia. The species *S. ferox* and *S. heringianus* (Group I in the diagram), both recognized for being very sensitive to oxygen deficiency, have been given 8 and 9 points, respectively, in oligotrophic environments, 2 and 1 points in mesotrophic environments, and finally none in eutrophic environments. *Psammoryctides barbatus* (Group II), another fairly sensitive species, was given 5 points in the oligotrophic environment and 5 in mesotrophy, and has been given a light blue colour in the histograms. On the other side of the trophic spectrum, the very tolerant species *L. hoffmeisteri* and allied species (Group VI) were given 7 points in eutrophic environments, 2 in mesotrophy and 1 in oligotrophy. This species has been given a deep red colour in the histograms. The likewise very tolerant species *Potamothrix hammoniensis* (Group V) was given 6 points in eutrophic environments, 3 in mesotrophic and 1 in oligotrophic environments, etc. The latter species and some other species with rather similar ecological demands have been given a light red colour. In the original Table I in Milbrink, 1978, however, a few very characteristic oligochaete species had been omitted because of ecological ambivalence. One of these species, *Tubifex tubifex*, actually tends to occur on either side of the ecological spectrum (Milbrink, 1978) and would rather have obtained 5 points in both eutrophic and oligotrophic environments but none in mesotrophy (the present Table I). *Eiseniella tetraedra* is also a frequently occurring species but with little known preferences. This species is most often found in oligotrophy in Scandinavia but can also stand eutrophied environments. Also, this species would be given similar points in Table I as *T. tubifex*, i.e. 5 points in oligotrophy and 5 points in eutrophy. These two species have been given a green colour in Figure 1 (Group III in the original diagram). Finally, species with little shown preferences on geography and depth or those species with little known ecological demands have been given a yellow colour in Figure 1 (Group IV). Another species belonging to the latter group characteristically occurring in Lake Vättern, i.e., under oligotrophic conditions, is *Tasserkidrilus acapillatus* (Finogenova, 1972). In the absence of more data this species would be given 10 points in oligotrophy in the table.

Figure 3 is a diagram from Milbrink (2020) showing changes in the oligochaete fauna in Lake Vättern since the early 20th century, now modified also to encompass similar changes in Lakes Vänern, Mälaren and Hjälmaren. These transformations are marked with broad red arrows in the diagram. Lake Vättern had, in short, become markedly eutrophic due to outfalls of untreated sewage and rather intense agriculture in the drainage system in the 1950s and 1960s. In this diagram it was shown how the oligochaete communities at the end of the 1960s had changed to species associations indicating more eutrophic conditions. During this time of eutrophication, especially in the southern part of the lake, efficient general sewage treatment had been proclaimed in the country and soon a period of oligotrophication started in Lake Vättern. This evolution of events could be seen in the diagram (again with red arrows) where the histograms representing the oligochaete communities found in the deep parts of the lake first moved to the right and then again moved to the left on the morpho-edaphic index scale. According to this sequence of events conditions in the 21st century were now back to near the situation in 1911. At the same time abundance values (marked in the histograms as short horizontal lines) likewise slid along a more or less straight line from a minimum in 1911 to a maximum in 1967, and now back again to a minimum in 2016.

Water transparency in Lake Vättern has constantly improved in the last decades. At the beginning of the 20th century, as well as today, water transparency could reach Secchi depths of 15–16 m. In the 1960s, however, the Secchi depth was occasionally only 3.5 m or less, giving rise to much public concern (Figure 4).

Is this evolution of trophic events characteristic of Lake Vättern only, and of none of the other large lakes of southern Sweden? The authors would argue that oligotrophication is today a general force in these lakes, as well as in many other lakes in Scandinavia that had previously been under impact of eutrophication due to sewage outfalls and effects of other oxygen demanding products that had reached the recipient. This evolution of events in Lakes Vänern, Hjälmaren and Mälaren is likewise illustrated with broad red arrows in Figure 3, illustrating how the histograms are sliding to the left and abundance is sinking in pace with oligotrophication.

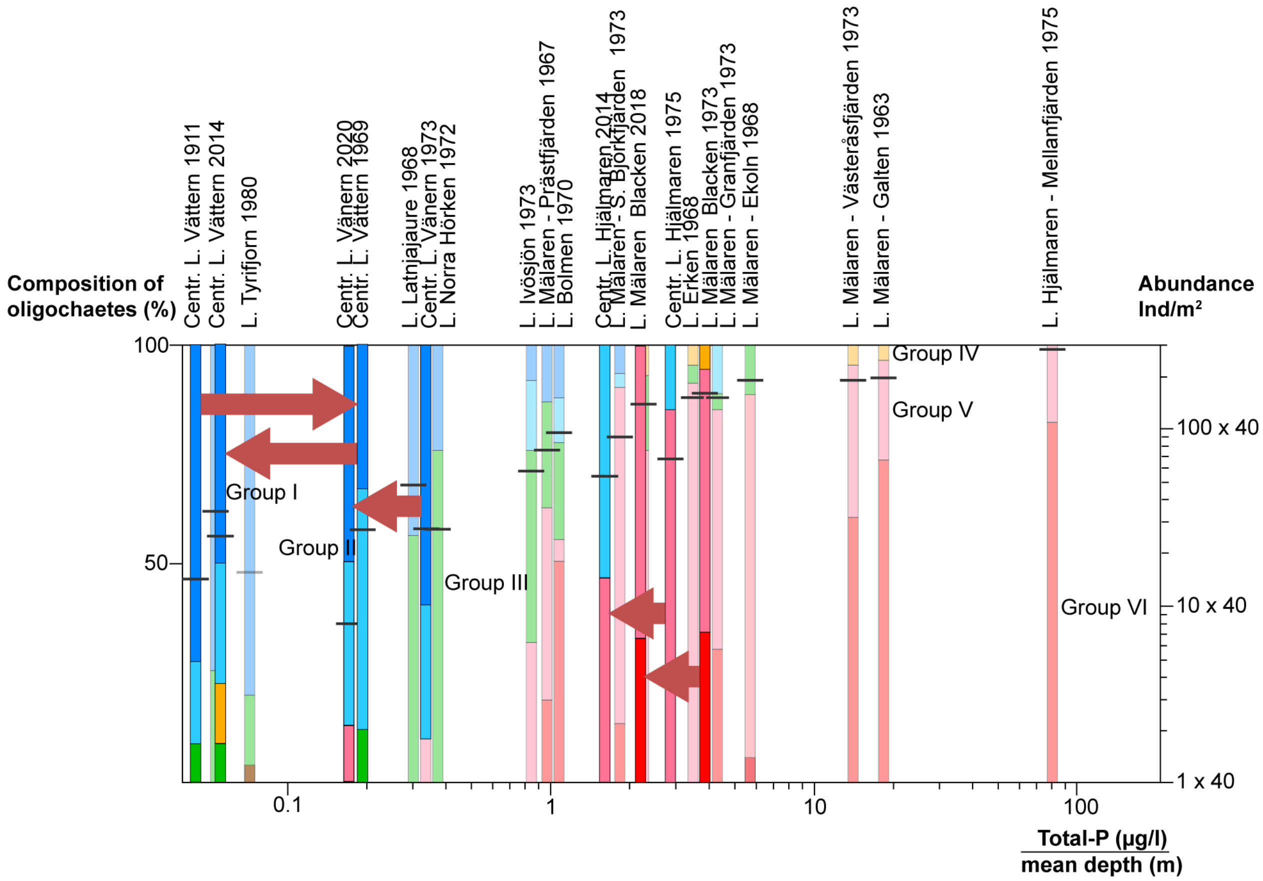

FIGURE 3 Modification of Figure 1 with particular reference to oligochaete communities from Lakes Vättern, Vänern, Hjälmaren and Mälaren. Oligochaete composition and abundance as in Figure 1. Arrows in red show the development from one time period to the next. Lake Vättern was specially treated this way in Milbrink (2020). Now Lakes Vänern, Mälaren and Hjälmaren are treated the same way. The histograms from samples discussed here in full colour while the background is slightly dimmed.

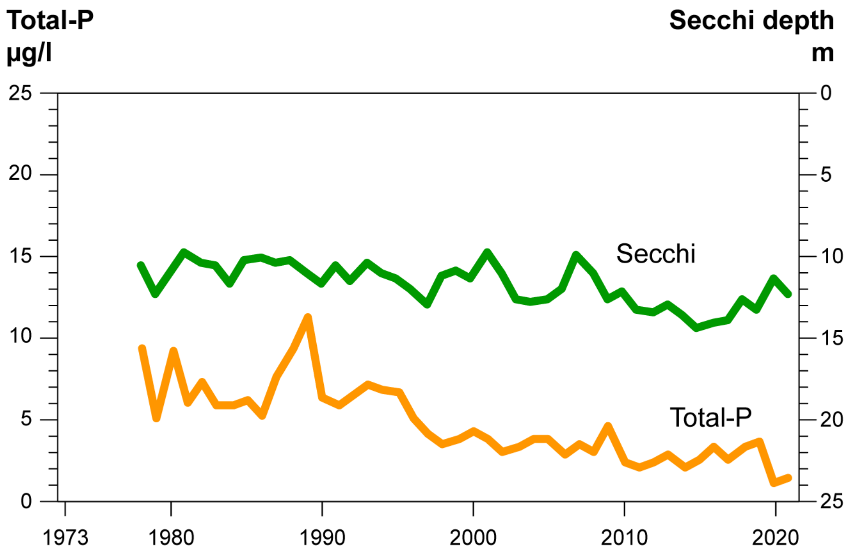

FIGURE 4. Annual mean total phosphorus concentrations (in µg/l) over time (1975–2021) in surficial water layers and Secchi disc readings (in m) in central Lake Vättern (station "Jungfrun", depth about 120 m). Total phosphorus levels have gradually decreased since the 1970s and the water transparency has increased at the same time.

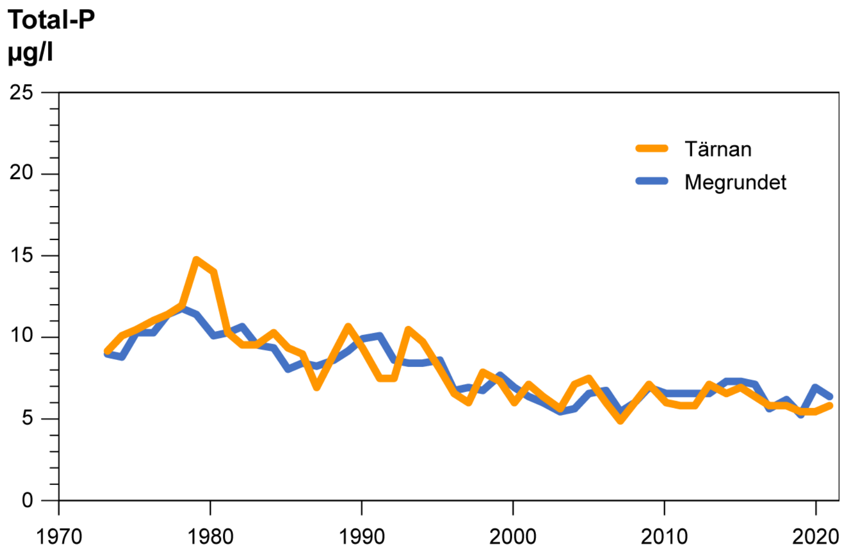

FIGURE 5 Annual mean total phosphorus concentrations (in µg/l) over time (1973–2021) in surficial water layers on two open-water reference stations in Lake Vänern.

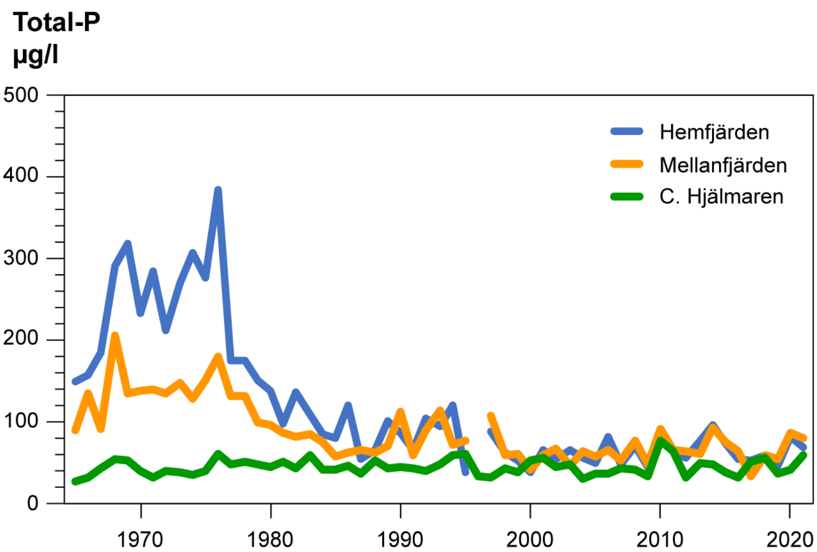

FIGURE 6 Annual mean total phosphorus concentrations (in µg/l) over time (1973–2021) on reference stations in surficial water layers in the three basins of Lake Hjälmaren, Hemfjärden, Mellanfjärden and Central Lake Hjälmaren.

It is obvious that the largest lake in Scandinavia, Vänern, since the 1980s has undergone a much similar development as Lake Vättern. Lake Vänern is principally oligotrophic, but many bays and fjords in the periphery have been under eutrophication since the 1950s. Industrial wastes containing mercury and other heavy metals have also affected several bays along the northern rim of the lake, resulting in severe deformities in the chaetal bundles of some oligochaete species, especially *P. hammoniensis* (Milbrink, 1983; Milbrink & Sonesten, 2014). On two stations in central Lake Vänern monitored by the Swedish Environmental Protection Agency (cf. Figure 7) and the Swedish University of Agricultural Sciences total phosphorus-values in the surface water have constantly fallen since the 1980s, indicating improved water quality (Figure 4). In Figure 3 the histogram representing the central basin of northern Lake Vänern has "moved" to the left the same way as for Lake Vättern. The sensitive oligochaete species *Spirosperma ferox* and *Stylodrilus heringianus* are, as before, dominant. The mean abundance of oligochaetes has likewise fallen along the "straight line". Like for Lake Vättern this change in water quality is marked with a broad red arrow facing to the left in the diagram (Figure 3).

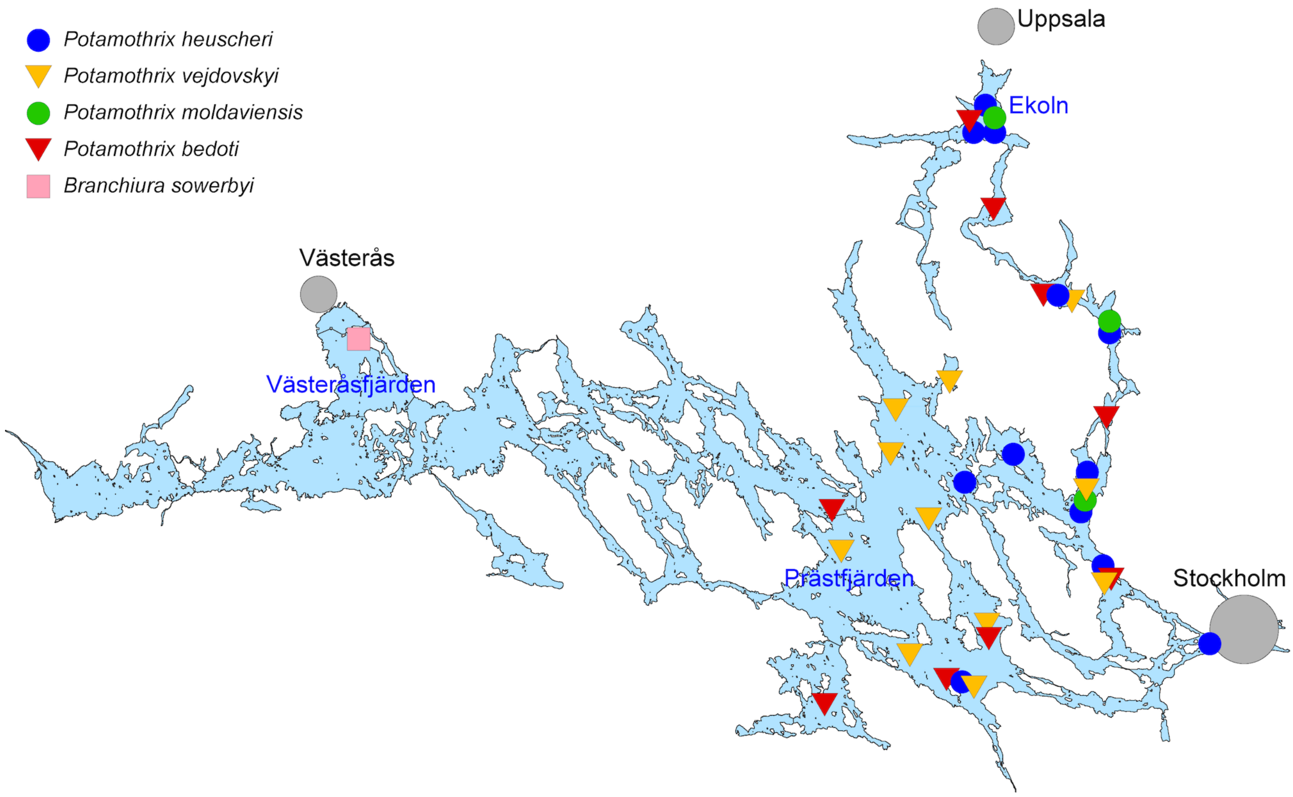

FIGURE 7 Map of Lake Mälaren with the names of some of the different basins referred to in text.

Lake Hjälmaren is a eutrophic, polymictic lake, that has historically received much sewage from the relatively large city of Örebro via the River Svartån entering the lake in the west. Surrounding agricultural land has also contributed to eutrophication. Total phosphorus levels, however, especially in two western shallow basins, Hemfjärden and Mellanfjärden, have constantly fallen since the 1980s (Figure 5). In the central basin of Lake Hjälmaren total phosphorus levels in surficial water strata have since 1964 fallen from around 25 µg/l to around 20 µg/l, i.e., no large difference. The oligochaete composition, however, has clearly changed for the better indicating that oligotrophication has started also in Lake Hjälmaren. The fairly sensitive species *Psammoryctides barbatus* has continuously increased its share of the fauna since the 1970s. This species and *P. hammoniensis* are the totally dominant species in central Lake Hjälmaren. Total abundances would also seem to have dropped considerably over 40 years (Milbrink, unpubl. Material). The improvement in water quality is marked with a broad red arrow pointing to the left.

Lastly, Lake Mälaren is a more complicated lake in the respect that it is composed of a number of more or less separate basins, each with unique properties. Figure 7 is a map of Lake Mälaren on which the names of some of the basins referred to in this work are indicated. One of those is Västeråsfjärden in the western part, and another is Prästfjärden in central Lake Mälaren. Furthermost in the west we have the basin of Galten, heavily affected by organic wastes from industrial works and agriculture. The water quality is highly eutrophic. To the south of the Västeråsfjärden basin comes the basin of Blacken, long affected by effluents from the fairly large city of Västerås. These basins have today an improved water quality, and total-phosphorus levels have continuously dropped in the last decades in all three basins. The water quality of the Blacken basin, although still eutrophic, is today from time to time fairly close to conditions in the central basins of Lake Mälaren. In the basin of Prästfjärden, in central Lake Mälaren, total phosphorus levels have long remained between 15 and 20 µg/l or a bit more in surficial water strata (Figure 8). According to the water chemistry, the central basins have a clearly mesotrophic water quality.

In the basin of Blacken there are still no obvious changes in the oligochaete fauna dominated by *P. hammoniensis* and *L. hoffmeisteri.* Some profundal samples from this basin, however, have today contained some specimens of *P. barbatus* which is quite promising. Abundances would also seem to have dropped significantly over 40 years. This change in water quality is likewise marked with a broad red arrow pointing to the left in the diagram.

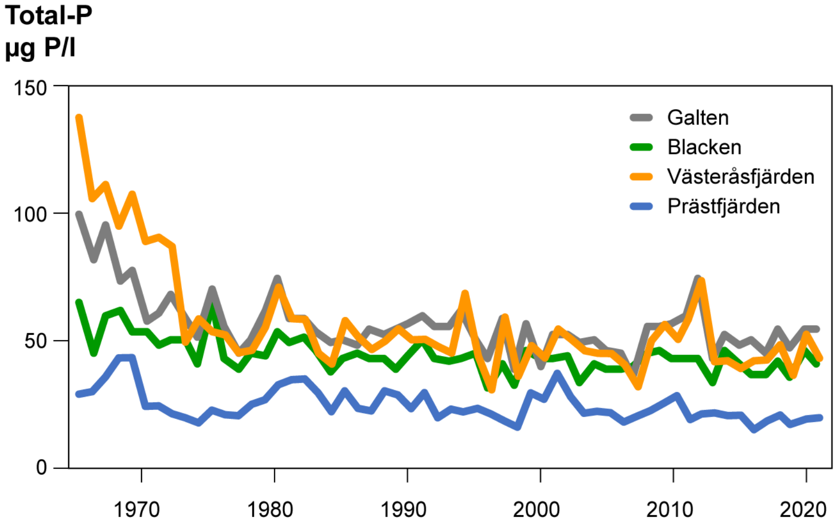

FIGURE 8 Annual mean total phosphorus concentrations (in µg/l) in the basins of Galten, Västeråsfjärden, Blacken and Prästfjärden in Lake Mälaren (see also Figure 7)—the first basin furthest to the west is heavily eutrophic, the second and third basins—also in the west—are less eutrophic.

The representativeness of profundal bottom samples obtained with the Ekman sampler

On the accuracy of the Ekman sampler, as said above, the authors would rely upon the statistical test-results from 1971 (Milbrink *et al.* 1974). The oligochaetes and chironomid larvae were supposed to be more or less randomly distributed and their distributions were thus tested against the Poisson distribution. Tested for the Goodness of Fit the chironomid larvae actually showed fairly good fit to the Poisson, whereas the oligochaetes showed relatively good fit to the Negative Binomial distribution. Most importantly, there were no indications of aggregated distributions of species. Whereas all oligochaetes were identified to species, the chironomid larvae were not. In the literature we know of no other comparable statistical tests on the horizontal distribution of the bottom fauna.

With reference to how representative the two samplers were in collecting the fauna, 1 to 2 Ekman samples and 6–8 core samples were found to be comparable in getting all species of oligochaetes in comparable percentages, i.e. in this case the percentages obtained after all 39 core samples and the 6 Ekman samples had been combined. The efficiency of different bottom samplers has also been treated in Milbrink and Wiederholm (1973) with rather similar results.

Several rounds of bottom sampling in the major basins of Lake Mälaren, as well as in other major and reasonably large lakes in Sweden over the years have given the senior author the experience that 3 to 5 parallel Ekman samples taken on profundal deposition bottoms generally give accurate information on the bottom fauna, and on the oligochaete fauna in particular.

Discussion

Oligotrophication of previously eutrophied waters is a fact in Scandinavia (Milbrink, 2020), as well as in Switzerland (Lang, 1984; Lang & Reymond, 1996), due to improved sewage treatment. Oligochaetes have rapidly responded quite positively to the new situation in the large lakes of southern Sweden and in other lakes of reasonable size, as well. The transition to more sensitive species is gradual, but we could see that this is an ongoing process. Oligochaete species sensitive to oxygen deficiency are thus today replacing more tolerant species.

There are similar series of events described from Switzerland and from Sweden. In the early 1980s, Lang (1984) showed that the eutrophication of the large Swiss lakes, Geneva and Neuchatel, caused tolerant oligochaete species like *L. hoffmeisteri* and several Ponto-Caspian *Potamothrix* species such as *P. vejdovskyi* and *P. moldaviensis* to take over more and more. However, Lang and Reymond (1996) could later document that after large-scale sewage treatment these lakes had slowly recovered, implying that sensitive oligochaete species such as *S. heringianus* had come back, and more tolerant species like *Potamothrix* species had decreased in proportion.

In central Lake Mälaren, in the basins of Prästfjärden (cf. Figure 7), and Södra Björkfjärden to the south of the former basin there are obvious signs of oligotrophication with increased oligochaete species diversity (Milbrink, 1980, 2020). Lake Mälaren is surrounded by cities and industrial agglomeration in the west and in the north. This is also the case in the east; however, the treated wastewater from the city of Stockholm is nowadays diverted to the Baltic Sea rather than to Lake Mälaren. The whole of Lake Mälaren is also surrounded by agricultural land with diffuse leakage of nutrients into the lake. It is believed, however, that this leakage has successively decreased in recent decades due to improved agricultural techniques. With time, Lake Mälaren will no doubt undergo oligotrophication the same way as the other large lakes of south Sweden. The water chemistry also reveals that this is the case. In typically eutrophic basins adjacent to the central mesotrophic basins, sensitive oligochaete species such as *P. barbatus*, and rarely *S. ferox* and *S. heringianus*, turn up in occasional bottom samples, and this is, of course, a good sign. It should be added that in Sweden, as well as in Switzerland, major efforts have at the same time been made to decrease the use of agricultural fertilizers—and thereby the leakage of nutrients into the lake recipients.

There are several oligochaete species occurring in Scandinavia with rather unspecific or unknown ecological demands (Table 1, see above). Several Ponto-Caspian species of the genus *Potamothrix* are frequently found in central, northern and eastern Lake Mälaren, i.e. *P. vejdovskyi, P. moldaviensis, P. heuscheri* and *P. bedoti* (Figure 7). Their habitats are all found in eutrophic or mesotrophic basins. Those species have most likely arrived in different waves from eastern Europe, probably from the Black Sea area, in the ballast water of commercial ships (Milbrink, 1980, 1999). *Potamothrix heuscheri* is often found in highly eutrophic environments, together with *T. tubifex, P. hammoniensis* and *L. hoffmeisteri.* Until we know more about the specific ecological demands of the invading *Potamothrix* species it is difficult to say anything decisively about their indicative value. While most *Potamothrix* species are generally encountered in eutrophic environments, *P. moldaviensis* is sometimes found also in oligotrophic situations.

Some species are more or less confined to oligotrophy, such as *S. heringianus, S. ferox, Rhynchelmis tetratheca, Limnodrilus profundicola* and *T. acapillatus*. In Sweden, the two last mentioned species have only been found in Lake Vättern. It is also very difficult to say anything decisively about some species of the genus *Rhyacodrilus. Rhyacodrilus falciformis* has so far only been found in Lake Vättern in early collections, whereas *R. coccineus* has been identified also elsewhere in Sweden often in mesotrophic environments (Milbrink, unpublished).

Oligotrophication in Lake Vättern has had a great impact on the oligochaete communities since the 1970s, especially in its southern part. Since that time, oligotrophication has been recognized also in the fish populations and changes in fisheries in the lake (Milbrink, 2020). In the southern parts of Lake Vättern in the 1960s and 1970s the roach *Leuciscus rutilus*, a cyprinid fish species commonly found in eutrophic lakes and rivers all over Europe, and another cyprinid, the common bream *Abramis brama* also commonly occurring in eutrophic environments, became abundant in the littoral. Populations of roach could then even be found pelagically (Olof Filipsson, Swedish Fisheries, pers. com.). During the years of eutrophication, pelagic coregonids such as vendace, *Coregonus alba*, and white-fish, *Coregonus lavaretus*, increased dramatically and gave rise to an intense fishery. In recent decades under the influence of oligotrophication this fishery has more or less collapsed (Inst. Freshw. Res. at Drottningholm, professor Svärdson, pers. com.). Eutrophication had without doubt favoured pelagically occurring coregonids, as well as populations of the roach and the common bream. At the same time Lake Vättern as a major drinking water resource for southern Sweden had been under threat.

Likewise, in the northern bays and fjords of Lake Vänern, human consumption of fish except salmon was forbidden in the 1970s mainly due to the risk of contamination by heavy metals (Milbrink, 1983). Cyprinid fish were also much favoured by local eutrophication. Today, however, conditions have improved, and fish consumption is again allowed—although with certain restrictions concerning salmon and brown trout (high dioxin levels) and further concerns with the consumption of perch (*Perca fluviatilis)* and pike (*Esox lucius*) (heavy metal contamination). Swimming and water recreation is once again recommended (Milbrink & Sonesten, 2014).

Furthermore, the fishery of central Lake Hjälmaren is of great regional importance, and the catches of pike-perch (*Sander lucioperca*), perch (*P. fluviatilis*) and crayfish (*Pacifastacus leniusculus*) are of great magnitude and has without doubt been much favoured by long-time eutrophication. In the near future, however, it is unlikely that the present oligotrophication of Lake Hjälmaren will have much effect on the fishery.

Conditions have continuously improved in Lakes Vättern, Vänern, Mälaren and Hjälmaren over the last 40 years and have most positively affected the fauna. In a time when efforts to save the environment often fail, this is a real success story.

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