Novel ecosystems in urbanized areas under multiple stressors: Using ecological history to detect and understand ecological processes of an engineered ecosystem (lake Markermeer).

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1 Summary

Estuaries, which can be considered as the most resource rich, biodiverse, and increasingly densely populated areas in the world, have often been dammed and are partly or fully reconstructed. Many of these artificially compartmentalized and constructed areas suffer from reduced natural dynamics and anthropogenic induced stressors. Whereas damming for safety and water security were the main focus in the first half of the 20th century, ecology, biodiversity and natural values have recently become increasingly important. An example of such a novel ecosystem created by damming a previous estuary with a history of changing focus on its ecosystem services, is lake Markermeer in the Netherlands. This resulted in many studies commissioned by governmental organizations on the ecology of lake Markermeer over the last decades. Since only a minor part of these studies have been published in peer reviewed journals, valuable abiotic and biotic data on lake Markermeer is scattered.

In this report, we first aim to combine the knowledge from all these studies on lake Markermeer and the larger IJsselmeer area with monitoring data to provide a historical overview of the ecological developments of lake Markermeer during its forty years of existence and derive the main hypotheses and suppositions on the causes of its ecological deterioration. Secondly, we elaborate on their likelihood of impeding the ecology of lake Markermeer based on retrieved data support, perform a multivariate analysis and provide a synthesis on the ecological functioning and future of the lake.

To obtain better insight into the ecological functioning of lake Markermeer, seven hypotheses were generated from the literature, related to: 1) Silt dynamics, 2) Lack of nutrient availability, 3) Disturbances of nitrification processes, 4) Toxic compounds, 5) Switch of phytoplankton species, 6) Decline of bulk prey species (*Dreissena polymorpha* and *Osmerus eperlanus*), and 7) Lack of natural land-water gradients. We provide a description for each of the hypotheses and analyses of available data. From the multivariate analysis, it became clear that combinations of hypotheses could have contributed to the ecological problems in the lake during the last four decades.

The review shows that amount of silt in lake Markermeer did not increase over time, while the only relevant change in silt load would have been caused by translocation, changes in top layer characteristics, or increased resuspension. Resuspension processes driven by wind activity and waves determine turbidity, nutrient availability and ecological developments in lake Markermeer. Since the separation by the Houtrib dike, roughly five characteristic phases can be distinguished for lake Markermeer: 1976-1981, 1982-1991, 1992-1998, 1999-2008, and 2009-2014. The environmental conditions in lake Markermeer gradually changed over the years in these time periods, with severe changes in environmental conditions in the transition years. This clustering pattern was explained by several parameters attributing to the perceived environmental developments.

However, even after reaching the defined nutrient goals in the last period, recovery was still poor for many of the ecological components of the lake ecosystem in this strongly compartmentalized delta. New initiatives, e.g. development of the islands of the Marker Wadden, can potentially improve the ecosystem since gradual land-water gradients could locally provide habitat and alternative food source for consumers. However, as many nature development projects in the lake IJsselmeer area proved, erosion, sedimentation, a fixed unnatural water regime, and the dominance of steep artificial shores will remain an obstacle for natural development and ecology in lake Markermeer.

2 Introduction

Many nature areas are being adjusted to human needs and safety. Increasing urbanization, expected climate change effects, and considering ecosystems in terms of ecosystem services justify the modification of dynamic natural systems to rigid water basins. Especially estuaries, which can be considered as the most resource rich, biodiverse, and increasingly densely populated areas in the world, have been dammed and fully reconstructed. Many of these artificially constructed areas suffer from ecological stressors. Innovation and technical capabilities have led to a wide range of options to tame natural dynamics. Whereas damming for safety and water security were the main focus in the first half of the 20th century, ecology, biodiversity and natural values have recently become increasingly important. Innovation is now exploring the possibilities for fine-tuning their engineering techniques and using natural processes in constructing novel ecosystems.

An example of such a novel ecosystem created by damming a previous estuary with a history of changing focus on its ecosystem services, is lake Markermeer in the Netherlands. This artificial freshwater lake on marine sediment was until the construction of the Afsluitdike in 1932, the south-western part of the former Zuiderzee (Southern Sea). After losing connection with the marine environment, the lake was even further isolated to a 70,000 ha freshwater compartment in 1976 for impoldering purposes. In 1990, the plan to impolder lake Markermeer was abandoned, it was decided that the lake would remain open water. Water managers then started a process to recover the lake since it suffered severe ecological problems. Changes in nutrient availability and silt dynamics were mentioned amongst others to be responsible for the declining population of *D. polymorpha*, fish and birds. The initial perception of water managers was that the accumulation of fluffy silt caused a bottleneck for the ecology in lake Markermeer. The upper layer of the originally marine sediment erodes into fluffy silt. Wind and water dynamics distribute this fluffy silt throughout the lake, causing high turbidity in the water column. Due to a dominant south-western wind direction, especially the middle and eastern part of the lake can become turbid. In these turbid regions, macrophytes do not develop and fauna remains scarce. Recovery of the ecological functions of the lake became especially relevant since the lake Markermeer became a Natura 2000 area.

As an attempt to improve the ecological quality of lake Markermeer and create additional nature value, the Marker Wadden project was initiated to create a bird paradise by constructing wetland islands from local sludge and using local dynamic processes to further develop these wetlands. Especially during first years of initial biological development, the organisms on the newly created islands will depend on the ecological processes and food availability of the surrounding lake. It is therefore utterly important to understand the ecological mechanisms leading to the current situation of lake Markermeer to predict how wetlands constructed with local sludge might develop and whether these wetland islands can improve the ecological value for this lake.

Framework conditions imposed by the construction of the lake (Figure 1) have a huge impact on the ecology of the lake. Wind induces waves that erode the bottom sediment, rigid shores fixed by dikes that limit natural dynamics, dispersal and the development of ecologic buffer zones, and the fixed unnatural water regime that prevents natural colonisation on seasonal banks. These conditions impede ecological development and the resilience of the ecosystem. However, since the removal or adjustment of these modifications are not an option for the government, these engineering structures are merely regarded as the framework within which applied research on ecological constraints could operate. It is therefore that most research in this lake focused on aquatic abiotic processes and species occurrences.

Over the last decades, many studies have been performed on the ecology of lake Markermeer, ranging from quick scans to historical reviews and experimental studies. Most of these studies were commissioned by governmental organizations. Although many projects have been carried out in lake Markermeer, only a minor part of these studies have been published in peer reviewed journals. As a consequence, valuable abiotic and biotic data measured in these projects are difficult to access and knowledge on lake Markermeer is scattered. In this report, we aim to combine the knowledge from all these studies and monitoring efforts into a historical overview of the ecological developments of lake Markermeer during its forty years of existence and derive the main hypotheses and suppositions on the causes of its ecological deterioration. Some of these hypotheses are not mutually exclusive, and combine into interesting scenarios. Multivariate techniques are used to analyse the biological developments of the lake in relation to observed and plausibly altering environmental conditions. After shortly presenting the hypotheses constructed from literature, this report will elaborate their likelihood of impeding the ecology of lake Markermeer based on retrieved data support and provides a synthesis on the ecological functioning and future of the lake.

3 Materials and methods

3.1 Description of lake Markermeer

Lake Markermeer is an artificial freshwater lake on marine sediment, with a surface estimated at 68,000 hectares (including lakes IJmeer and Gouwzee) and an average depth of 3.6 m (Van Duin 1992). It used to be a part of a bay-shaped estuary of the former Zuiderzee. In 1932, this estuary was closed by a dike and divided into several compartments, together referred to as 'IJsselmeer' area. Some of those compartments were reclaimed, while others evolved into freshwater lakes. Lake Markermeer is one of these compartments. Its artificial shores are fixed by large dikes made of groyne stones. Gradual land-water transitions, shallows, and natural shores are lacking. Lake Markermeer is now characterized in the Water Framework Directive as a oligotrophic, shallow freshwater lake (WFD water type M21, Ministry of Infrastructure and Environment (2012)) and is preserved as Natura 2000 area because of its value for migrating birds and waterfowl.

The water bottom composition (i.e. the upper 5 cm) ranges from more sandy components in the northwest to more lutum containing deposits in the south (>35% lutum). Clay and sandy clay form 75% of the bottom surface. Peat remnants from Hollandveen occur locally. With an average calcium content of 15.6%, lake Markermeer can be regarded as calcium rich lake (Winkels 1995). The bottom sediment offers little possibilities for seepage. The upward pressure of the deeper groundwater is low and the 10 meters thick Holocene clay layers prevent seepage water to enter the lake (Schultz 1975). No major rivers discharge into the lake, and the residence time of the water is estimated at 1.5 year. Erosion of the Zuiderzee bottom had locally created deep gullies (Zuiderzee-Vereeniging 1920) and scattered the peat layers that locally used to be upper sediment, uncovering the Holocene clay sediment underneath. This Holocene clay sediment is currently the sediment surface at most places in the lake.

3.2 Natura 2000 protected area

Lake Markermeer is assigned as Natura 2000 protected area. Natura 2000 is a network of nature protection areas in the territory of the European Union, and is the key instrument to protect biodiversity in the European Union. This network of protected areas is set up to ensure the survival of Europe's most valuable species and habitats. These habitats and species are defined in the Natura 2000 legislation. The habitats directive and birds directive qualified lake Markermeer because of its benthic *Chara* spp. vegetation in the southern part of the lake (Gouwzee and Muiderkust) and for nineteen bird species that occur on the lake. Lake Markermeer needs to fulfil conservation objectives for these selected target species (Ministry of LNV 2009). For birds, these objectives are formulated either as a certain number of individuals that the lake needs to be capable of supporting, or as conservation targets for their current habitat. Lake Markermeer has difficulties to meet the conservation objectives for five bird species (Ministry of LNV 2009): smew (*Mergus albellus*), great crested grebe (*Podiceps cristatus*), common pochard (*Aythya ferina*), common merganser (*Mergus merganser*), and little gull (*Larus minutus*). Most of these species use lake Markermeer for foraging and resting. The decreases of the piscivorous species (smew, great crested grebe, little gull, and common merganser) are probably determined by the decline of European smelt in lake Markermeer during the 1990s. Recovery of the smelt population in lake Markermeer is not yet expected and therefore the conservation objectives for these species will not likely be realised in the near future. Common pochards mainly feeds on *Dreissena* species in the lake. During the huge decline of *D. polymorpha* in lake Markermeer in the 1990s, the numbers of common pochard decreased simulateously. At the same time, common pochard densities increased in neighbouring lakes (Veluwerandmeren) where vegetation and *Dreissena* populations improved after de-eutrophication measures were carried out (Noordhuis 2010, Ministry of LNV 2009).

3.3 Development of natural land-water gradients

Currently, there are two large initiatives to enhance natural land-water gradients in lake Markermeer. The first initiative is to build islands in the lake, the Marker Wadden, using the building with nature principle. The second initiative is to reconnect the shallow wetlands of the Oostvaardersplassen and the Lepelaarplas to the Markermeer. The latter initiative provides also a range of technical challenges, since the water levels in the lake are a few meter higher compared to the wetlands in the embanked areas. Currently, the feasibility of the reconnection is studied.

To improve the ecological quality of lake Markermeer and create additional nature value, Natuurmonumenten (Dutch Nature Conservation foundation) initiated the Marker Wadden project. The aim of the Marker Wadden project is to create a bird paradise by constructing wetland islands from local sludge, and by making use of local dynamic processes to develop these wetlands. In this concept, an autonomous development is expected in which benthic and wetland biodiversity interacts with physical and biogeochemical processes during the consolidation of sludge. Besides its ecological goal, the project provides an opportunity for innovation. A growing interest in the management of fine sediments is foreseen in the use of soft sediment as building material. Building with soft sediments is, however, surrounded with big uncertainties from both the construction point of view and ecological expectations. The constitution of the sediment has consequences for the environmental conditions and suitability of the newly constructed habitats for biological development. To estimate the potentials of the sediment as building material, its characteristics should be understood. Furthermore, to predict the perspectives for biologic development on these soft substrate wetlands, the ecology of the lake in which the islands are embed should be well understood.

3.4 Literature study

This review is based on studies on ecological aspects of lake Markermeer. Most of these studies were carried out by order of the Dutch Ministry of Infrastructure and the Environment. A literature survey on publications about lake Markermeer resulted in 21 peer reviewed papers, and 1320 publications that can be referred to as “grey literature” (reports, dissertations, isolated data, (incidental) monitoring, presentations, symposia and so forth). All peer reviewed papers about ecology and sediment dynamics have been included in this literature study. Subjects of the non-peer reviewed publications included ecology (n=593), sediment (n=506), policy (n=426), and spatial planning (n=252). Subsequently, relevant studies available at the Ministry of Infrastructure and the Environment were selected from their database. Among these are studies focusing on the feasibility and pros and cons of the impoldering of lake Markermeer, which contain historical data on sediment characteristics, development, and ecology of lake Markermeer that have not been published internationally. Grey literature publications were included in this study according to the following selection criteria: the publication should be based on measured data from lake Markermeer and contain ecological or morphological observations.

3.5 Data bases and analyses

Step one was to identify hypotheses for ecological mechanisms that determine the current state of lake Markermeer. Subsequently, the plausibility of these hypothetical scenarios was studied by checking whether references and measured historical data could confirm the plausibility of those hypotheses. Physical-chemical data and biological data were obtained from the gathered literature and from existing and accessible databases (most of the data were monitoring data measured by the water authority and accessible via their open data source DONAR). The main source of lake Markermeer data was the national Dutch water authority (Rijkswaterstaat), and included both long term monitoring sequences (MWTL-data) and occasional measurements. A difficulty was to standardize the information in terms of methodology and measured units. Also the locations where parameters were measured varied among the years and replications were scarce. Spatial patterns were difficult to detect as most physical chemical monitoring was limited to a few locations (n=2). Whenever possible, retrieved data was consolidated into one main data base that contains environmental and biological information for nearly forty years of lake Markermeer (1976-2014). Whenever data could not be traced, the lacking information was searched for in text references to provide qualitative indication on how the parameter had behaved (low, high, alterations). The consolidated data set was analysed by principle component analysis (PCA) and correspondence analysis (CA) on log-transformed biological and environmental data in order to detect trends and patterns over the years using Canoco for Windows v5.0 (Ter Braak and Šmilauer 2012).

4 Results and Discussion

4.1 Overview of hypotheses ecological functioning lake Markermeer

To obtain better insight into the ecological functioning of lake Markermeer, seven hypotheses were generated from the literature, related to physical, chemical and biological components of the lake and their interactions. These hypotheses were grouped into aspects associated with the silty sediment, nutrient availability, contaminants, biological changes and morphology of the lake. Eventually, each of these hypotheses affected the fishes and birds of the lake (main species of concern for conservation) through different paths and processes (Figure 1). This overview of the various processes mentioned in the literature showed the changes in biological components (White text boxes) and the framework conditions (Grey text boxes). The processes were also numbered corresponding to the hypothesis they referred to.

Integration of the various hypotheses (indicated by the numbers in the textboxes) on ecological processes shaping the ecological development in lake Markermeer within the framework conditions imposed by the construction of the lake (light grey boxes).

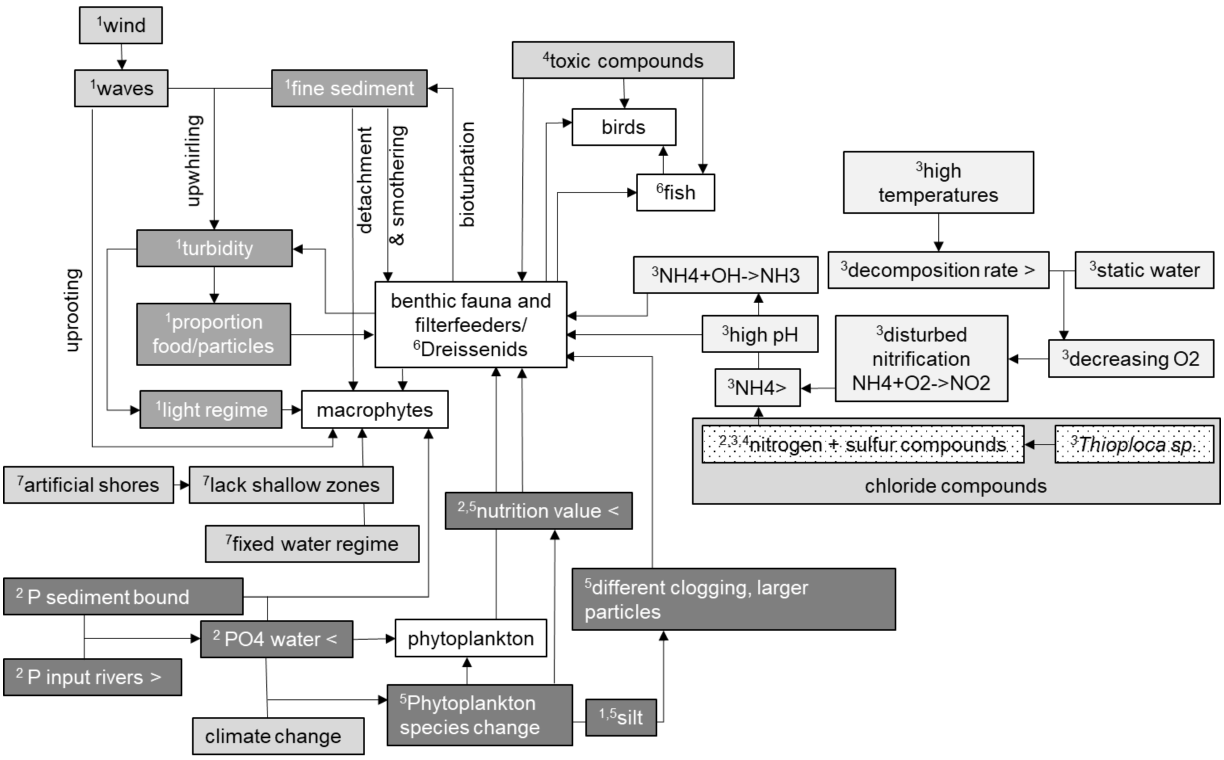


Figure 1: Integration of the various hypotheses (indicated by the numbers in the textboxes) on ecological processes shaping the ecological development in lake Markermeer within the framework conditions imposed by the construction of the lake (light grey boxes).

In this section (3.1), we describe the different hypotheses and the relevant questions related to each of the hypotheses. The analyses of the hypotheses are provided in section 3.2 divided into an extensive description followed by the analysis of available (monitoring) data from the lake to provide answers on the questions and hypotheses. In a way, the posed hypotheses are focused on an explanation for the sudden decrease of *D. polymorpha* in the 1990s and eventually leading to declined numbers of bulk prey species for the Natura 2000 target bird species. Therefore, we performed a multivariable analyses to explore and discuss in what way combinations of hypotheses could have contributed to the ecological problems in the lake (section 3.3).

4.1.1. Hypothesis 1: Silt dynamics

There exist several pathways through which silt increases in lake Markermeer. Strong south-western winds have a long fetch over the lake which promotes wave development. The wind-induced waves together with shipping and dredging activities whirl-up the fine sediment. The marine-clay sediment erodes into a fine silt layer that easily re-suspends into the water column. The up-whirling of fine sediment increases turbidity and inhibits under-water light climate and the development of submerged macrophytes. Wind and wind induced waves further distribute the eroded fine sediment throughout the lake. Silt may smother clumps of *Dreissena* mussels, resulting in a decreasing food availability for benthic feeding birds and increasing turbidity even more as the capacity of filter-feeders to filter particles from the surface water declines. The following research questions should be answered to assess the probability of this hypothesis: did the concentration total suspended matter increase in lake Markermeer during the last decades? Do turbidity and visibility correlate to silt concentrations? What is the contribution of chlorophyll a (Chl a) on the visibility and turbidity of the lake?

4.1.2. Hypothesis 2: Lack of nutrient availability

Phosphates in lake Markermeer bind to iron and to a lesser extent to calcium (Van den Berg *et al.* 2014), and are therefore not easily available for organisms. Since the nutrient input by rivers and canals into lake Markermeer decreased as a result of de-eutrophication measures, the lake food-web now strongly depends on the internal nutrient availability in the lake. A decrease of dissolved phosphates in the lake may have caused a decline of filter-feeders and their nutrition value through a decrease in their food quantity (i.e. algal biomass) and/or food quality. Subsequently, the decline of *D. polymorpha* in lake Markermeer resulted in a lower filtration rate of the surface water in the lake, which further increases turbidity and inhibits macrophyte development. Research questions that should be addressed for this hypothesis are: what is the availability of nutrients in the water and sediment of the lake? Do research results support phosphate binding processes in the sediment? Did the lake food-web respond to decline in nutrients over time?

4.1.3. Hypothesis 3: Disturbances of nitrification processes

The process of nitrification by bacteria is sensitive to low concentrations of oxygen. During summer periods with high temperatures and low water dynamics, stratification can cause a decrease of oxygen concentrations just above the sediment when the oxygen rich surface water does not mix into this benthic layer. This disturbs the nitrification processes and will result in accumulation of ammonium in the benthic layer. In case this co-occurs with high pH levels (>9), ammonia is formed and could reach concentrations lethal to benthic organisms (Noordhuis 2010). The water in lake Markermeer is usually well mixed because of constant movement induced by wind and waves. The presence of sulphur bacteria (e.g. *Thioploca* species) in lake Markermeer (Bij de Vaate 2011) could additionally increase ammonium concentrations in the benthic layer. For this hypothesis to be valid, the following questions should be confirmed: Did the circumstances that trigger disturbances of nitrification processes occur? If so, were declines in benthic organisms reported for these periods?

4.1.4. Hypothesis 4: Toxic compounds

The sediment in lake Markermeer may contain chemical compounds that are harmful to flora and fauna. Historic pollution of the river Rhine catchment and untreated waste water effluent contained metals and other compounds potentially harmful for the environment. Although pollution levels have been strongly reduced since the 1960s, some compounds have a long half-life and together with various metals can have accumulated in the sediment of the lake. For testing the validity of this hypothesis, the following questions should be confirmed: What are the levels of toxic components in the lake surface water and sediment? How do these level relate to the requirements the Water Framework Directive has set for toxic compounds in surface water bodies?

4.1.5. Hypothesis 5: Switch of phytoplankton species

the Since 2006, changes in plankton species dominances have been observed (Noordhuis 2010). The currently dominant phytoplankton species may clog in a different way to silt particles in the water than the previously dominant species (Noordhuis *et al.* 2014, Brinkmann *et al.* 2019). If their aggregates with silt result in larger flocs (De Lucas Pardo 2014), these could lower uptake by filter-feeding *Dreissena* and negatively affect the mussel banks in lake Markermeer and turbidity of the water column. Research questions for this hypothesis include: Did the composition of phytoplankton change in lake Markermeer? Did these changes in phytoplankton co-occur with declines in *D. polymorpha* populations? Were changes observed for grazing rates of mussels or zooplankton? Did zooplankton abundances and composition change as well?

4.1.6. Hypothesis 6: Decline of bulk prey species (Dreissena polymorpha and Osmerus eperlanus)

Populations of smelt, which has long been considered the main food source for bird populations on lake Markermeer, have significantly declined to a level that is not sufficient anymore to maintain the fish eating bird populations on lake Markermeer as set by the Natura 2000 standards. The sudden decline of *D. polymorpha* in the early 1990s, is thought to have affected benthic feeding birds. Research on population dynamics of these two species can give insight on the probability of this hypothesis to be the bottle neck for the food availability in the lake. Research questions that address this hypothesis are: Does the population dynamics of these two bulk prey species coincide with the overall food availability for target species in lake Markermeer?

4.1.7. Hypothesis 7: Lack of natural land-water gradients

The highly artificial morphology of lake Markermeer lacks natural land-water gradients and shallows that are important for developing diverse, inundated, natural shore vegetation or wetlands with a diverse macroinvertebrate assemblage. The current groyne stone shores do not provide conditions for germination and colonisation on a large scale in the lake. Currently, fixed shores and a controlled, unnatural water level regime with low variations could limit ecological development in the lake. The recovery of natural land-water gradients could provide a stimulus for the ecology of the lake. Research questions related to this hypothesis are: What is the importance of natural land-water gradients in shallow lakes? How can natural land-water gradients be successfully restored within the morphological constraints of lake Markermeer?

4.2 Analysis of the proposed hypotheses

4.2.1. Silt dynamics hypothesis

4.2.1.1. Description silt hypothesis

Resuspension processes are very prominent in shallow and large lakes, like lake Markermeer, and the organic matter source of the benthic zone mostly derives from these processes (De Rozari 2009). Ever since its isolation from lake IJsselmeer in 1976, blocking direct influence of the river IJssel and outflow to the Wadden Sea, silt has been abundant in lake Markermeer (De Temmerman and Van Meurs 2012, Winkels 1995). Even before lake Markermeer existed, silt was abundant in this area of the former Zuiderzee (Zuiderzee-Vereeniging 1920) and was considered, together with an unequal mixture of saline and freshwater, to hinder the development of vegetation (Zuiderzee-Vereeniging 1905). It was assumed that the silt supply (estimated at 400,000 m3 per year; Beekman 1917) derived from the river IJssel and was distributed towards the southern part of the Zuiderzee by wind and wave activity (Zuiderzee-Vereeniging 1920, Schultz 1975). Wind speed combined with large wind fetches (up to 30 km) and shallow depth (<5 m) locally impacted the sedimentation fluxes (Van Duin 1992, De Rozari 2009).

Since the construction of the lake, wind induced waves and currents directly erode the bottom and whirl up fine sediment particles from the benthic zone that easily suspend in the water column and are subsequently transported along the lake. Driven by strong south-western winds, the silty deposits accumulate in the deeper eastern parts of the lake to a maximum height of 45 cm (Winkels 1995) and in deep gullies and excavation pits (Brongers 2001), but remain absent in the north-western part. This silt allocation process towards the Oostvaardersdike presumably started after lake Markermeer was isolated and still continues. Several studies stated that the total amount of silty lake IJsselmeer deposits have not changed since isolation of the lake (Schultz 1975, De Temmerman and Van Meurs 2012, Winkels 1995), while others reasoned that the transition from an estuarine to a freshwater system combined with erosion have increased the silt concentration in lake Markermeer (Noordhuis 2010). If the silt is formed by continuous erosion of the Holocene clay sediment layer, turbidity may still increase and affect ecology in a negative way (Noordhuis and Houwing 2003). With the closure of the Houtrib dike, silt transport out of lake Markermeer was largely restricted. It is thus extremely difficult, if not impossible, to get rid of the silt while the bottom remains susceptive to erosion by waves and silt transportation from the lake to other areas is limited.

The Water Framework Directive regards sludge as one of the main inhibitors for ecology in lake Markermeer (Van Luijn and Rijsdijk 2004). Turbidity inhibits photosynthesis within the water body that according to Winkels (1995) contains sufficient nutrients (total P around 0.1 mg P/l; total N around 1.5 mg N/l). Assumed consequences are a low primary production, absence of rooting water plants, and disturbance of predators that prey on sight. Furthermore, nutrient absorption by silt will probably affect filter-feeding and phytoplankton (Ibelings 1997). Experiences from neighboring shallow lakes illustrate how turbid water can block the development of benthic flora and fauna. Here, an increase of transparency was followed by an increased plant growth and abundances of zebra mussels (Noordhuis *et al.* 2016). During the 1980s visibility had improved artificially in these lakes after removal of bream, but this clear water period did not lead to ecological recovery of those lakes.

4.2.1.2. Data analysis silt hypothesis

Strong fluctuating values for suspended matter and Chl a have been measured in monitoring programs of lake Markermeer, indicating fluctuating intensities of resuspension processes. Maxima in suspended matter, up to 300 mg dry matter/l, always co-occurred during severe wind activity. Strong winds frequently occur at lake Markermeer especially during autumn (Figure 2d). Noordhuis and Houwing (2003) found strong correlations between higher amounts of particulate matter and wind speed. The effect of wind speed on the water level is huge, water height differences during storm surge can exceed to one meter water level difference between (Noordhuis 2010), while lake water level differences under average weather conditions differ less than 5 cm. As monitoring is not carried out during strong winds, average amounts of suspended matter are probably underestimated. The western and southern part of the lake seem less turbid (Figure 2b). These are the areas where the majority of the zebra mussel populations occurred (Bij de Vaate 1991, Bij de Vaate and Jansen 2011, 2012). Local differences in water depth, sediment composition and exposition to wind determine the susceptibility to resuspension processes and create a diverse pattern of suspended matter and visibility in the lake (Houwing *et al.* 1997, Noordhuis and Houwing 2003).

High concentrations of suspended matter (1978, 1986 and 2000) do not necessarily coincide with low visibility (Figure 2). The conditions in the western part during 1989-1990 and 2010-2012 seem extraordinary; very high visibility coincided with both minimal suspended matter and Chl a concentrations. In the central part such patterns were not observed, and visibility seemed in general lower than in the other parts. Periods of relatively lower visibility occurred around 1985 and 1994-2004. Peaks in mean suspended matter were observed during these periods (1986, 1995, 1998 and 2000), but only in 1995 led to instant worsening of visibility. Visibility was relatively low during the winters of 1996-2007. This presumable turbid period does, however, not coincide with significantly higher amounts of suspended matter. Suspended matter concentrations vary a lot and merely show peaks within mediocre fluctuations than periods of consequently high or low values. Examples of such peak are observed in the years 1978, 1986 and 2000. In 2010, visibility values had increased back to historical mean values. The suspended matter increase in 1995 and 2000 coincided with a strong increased algae appearance in winter. From 2000 onwards, winter Chl a concentrations became systematically higher than those during summer. Since most of the monitored parameters do show large standard deviations, these can be regarded as an indication for the huge spatial and temporal variation induced by the dynamic environment of the lake.

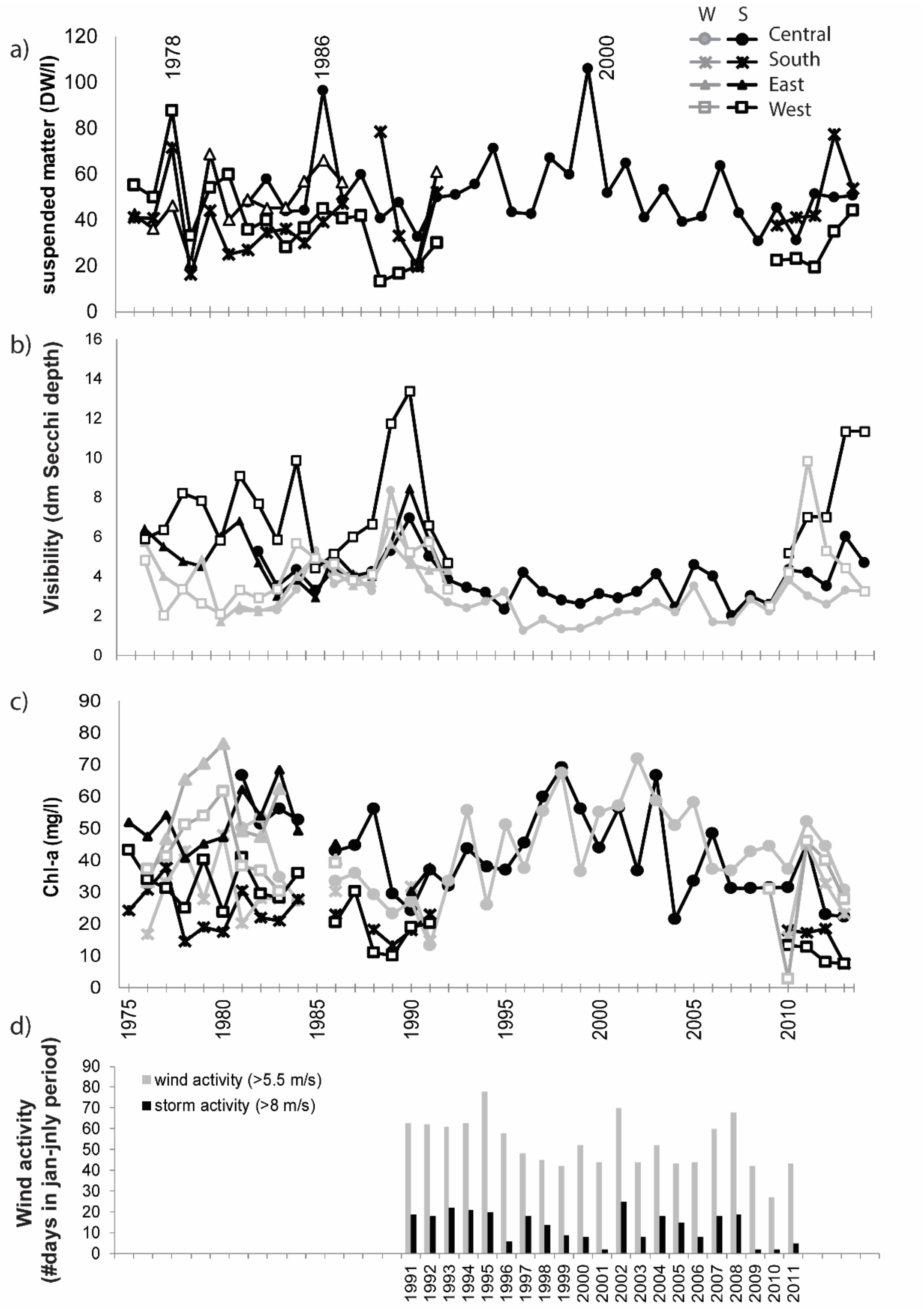


Figure 2: Overview of environmental conditions in the surface water expressed as yearly means for a) dissolved matter content; winter (grey line) and summer (black line) water b) visibility (Secchi depth) and c) concentrations of Chl a; and d) days with strong (>5.5 m/s) or stormy (>8 m/s) winds capable of inducing resuspension during the Jan-Jul period. Environmental conditions were measured at different sampling locations (symbols) in lake Markermeer between 1975 and 2014. Data sources: RWS monitoring data, and the Royal Netherlands Meteorological Institute (KNMI).

Visibility seems inverse to the proportion suspended particulate matter (Figure 2) as well as with residue on ignition (Mur *et al.* 1990, Van Nes 2005) indicating that resuspension determines both turbidity and phytoplankton distribution and in lake Markermeer. Noordhuis (2010) stated that the correlation between total suspended matter and visibility changed after 1990-1992; for comparable concentrations of suspended matter, visibility became less. Initially it was assumed that silt and a poor light regime hampered phytoplankton development. Nonetheless, Chl a has gradually increased whereas silt and nutrient conditions have not altered. Theoretically, this increase of Chl a could have contributed to the declining visibility since the early 1990s (Lammens 2001, Noordhuis 2001a). In the last decade, changes in flocculation are observed. These are ascribed mainly to alterations in phytoplankton composition (Lucas de Pardo 2014, Noordhuis *et al.* 2014) with microalgae species adapted to live on aggregates (Brinkmann *et al.* 2019).

Because of the fixed water level with summer and winter target levels of respectively -0.2 m +NAP and -0.4 m +NAP (Oude Essink *et al.* 2010), waves always hit the shores at the same height, causing severe erosion to the shores. The fixed water regime result in a more or less constant water level at these two heights. Deviations in average lake water levels are mainly caused by temporal high water peaks, increased wind activity, or sluice management: the water inlet via the Houtrib dike was for instance periodically higher during the period 1992-1998 (Landschap 2014). The water supply was higher during the 1980s and early 1990s, whereas during the last decade water supply was more or less stable (Van der Geest *et al.* 2018). The late 1990s to early 2000s was a period with low ice coverage, while 2010 and 2011 had relatively cold winters, but periods with ice occurring late in the winter (Feb-April) and only for short periods (frost period max 14 days). Re-suspended silt particles in the water layer can decrease the availability of nutrients, as these organic particles adsorb and aggregate dissolved nutrients (RIJP 1975). De Rozari (2009) found comparable nutrient contents in silt from the water column and silt in the benthic zone of lake Markermeer.

4.2.2. Nutrient availability hypotheses

4.2.2.1. Description nutrient availability hypotheses

Waters from brackish origin contain higher phosphorous concentrations than freshwater systems (Krebs *et al.* 1995), but could be limited in nitrogen. The inlet of more eutrophic freshwater in originally brackish lakes may have had a positive effect on their productivity. The input of nitrogen-based nutrients increase the total primary production, enabling population growth of invertebrates that are potential prey species for birds (Coops 2002). Originally brackish systems become very susceptible to eutrophication (Ross 1998) when nitrogen-rich freshwater is added, as adding N-based nutrients will decrease their high P/N ratio. In this situation, neither nitrogen nor phosphorous are limited and this excess of nutrients may result in algae blooms.

Table 1: Mean yearly input of nutrients and chloride in lake Markermeer in the first years after separation from lake IJsselmeer (periods 1976-1978 and 1981). Data source: RARO (1981).

	water (10^6 m^3)	P (10^3 kg)	N (10^3 kg)	Cl (10^6 kg)
Discharges provinces	710	950	5657	340
Adjacent lakes	1740	705	7810	310
total 1976-1978	2320	1525	12820	625
total 1981	2280	895	10725	585

After lake Markermeer was cut off from its marine nutrient supply, the input of nutrients, water and chloride mainly came from surrounding lakes and municipalities (Table 1, RARO 1981). Influence of seepage water is minimal, as seepage water is unlikely to rise through the sediment because of the huge resistance of the thick bottom layer of clay (Oude Essink *et al.* 2010). Chloride input from the sediment of lake Markermeer, i.e. formerly Zuiderzee marine deposits, was not considered an important input (e.g. Schultz

1975, RARO 1981,). During the first years after the formation of lake Markermeer, the most significant effects were reductions in concentrations of chloride (270 to 150 mg/l) and nitrate (from 3 mg/l to 1 mg/l), while orthophosphate-concentrations reduced little in lake Markermeer during these years (Van Acht and De Jong 1983). By 1981, nutrient input had decreased mainly because of a reduced input linked to the waste water effluent of the city of Amsterdam and Noord-Holland (Van der Geest *et al.* 2018). The discharges of nutrient rich waste-water and water from agricultural areas (Van Acht and De Jong 1983), occasionally induced a persistent bloom of cyanobacteria in inlet areas were effects on vegetation and birds were reported during the first years after completing the polder-dikes.

Parallel to the orthophosphates decrease in the rivers, total phosphorous contents in lake Markermeer reduced drastically (Table 2); orthophosphate decreased from 0.07 mg/l in 1976 to 0.005-0.02 mg/l from 1980 onwards. Summer averages of total phosphate in the water column in 1998-2007 ranged from 0.1 to 0.15 mg/l. Summer values of total phosphorous content in lake Markermeer water ranged between 0.25-0.20 mg/l in the first years after formation of the lake, but decreased to 0.07-0.01 mg/l during the period 1976-2002, and to values <0.1 mg/l after 2002. Nitrogen concentrations in the water (summer means) of lake Markermeer decreased from 3 mg/l during the 1970s to 2 mg/l during the 1990s, and 1.5 mg/l after 2000 (Noordhuis 2010). However, lake Markermeer showed a different pattern to other lakes in close vicinity within the IJsselmeer region. These other smaller and shallower lakes recovered after the decreased river nutrient inflow and switched to a clear state with high abundances of *Dreissena* mussels and submerged macrophytes including charophytes (Noordhuis *et al.* 2016). The submerged macrophytes can obtain nutrients from the sediment and maintain high productivity in areas with low nutrients in the water column. Due to the larger size of lake Markermeer, wind induced resuspension events occur more frequent compared to the smaller lakes in the IJsselmeer region. These conditions are less suitable for macrophyte development. The decrease of dissolved phosphates in the surface water of lake Markermeer (Figure 3) may have had a profound effect on nutrient availability for the food web of the lake. It could have caused a decline of numbers and nutrition value of bulk prey species, such as filter-feeders and small fish. Subsequently, the decline of *D. polymorpha* in lake Markermeer resulted in a lower filtration rate of the Markermeer water column, which further increases turbidity. Nitrogen concentrations continue to decrease as well, but less radically than phosphorous concentrations (Noordhuis 2010).

Beltman and Van der Krift (1997) found that increasing sulphate and chloride concentrations in a peat lake with long term bound phosphates could transform these phosphates towards forms that plants could uptake more easily. It is not sure if the opposite of this process can also occur. Which could imply that phosphate availability would drop when sulphate and chloride concentrations in the lake decrease due to increased phosphate binding. The decrease of chloride in lake Markermeer (Figure 4) could than gradually have decreased the internal nutrient availability over time.

Table 2: Nutrient concentrations (PO4 and total N) in the river IJssel, and the lakes IJsselmeer and Markermeer before (1960-1970) and after (1990s) de-eutrophication measures were carried out. Concentrations of PO4 have always been lower in lake Markermeer compared to the other two water bodies. Data source: Noordhuis (2010).

	PO_4 (mg/l)		Nt (mg/l)	
	1960-1970	1990s	1960-1970	1990s
River IJssel	0.2 to >0.4	<0.1	5-6.5	3
Lake IJsselmeer	0.15-0.2	<0.05	3.5-4.5	3
Lake Markermeer	0.07	0.005-0.02	3	2

4.2.2.2. Data analysis nutrient availability hypotheses

Nutrient detections have been performed by the monitoring network of the water authority during the entire history of lake Markermeer (Figure 3). In forty years, methods and detection limits have altered. For instance, the detection limit for orthophosphates was lowered in 1982 and in 2010 (Noordhuis and

Houweling 2003, Noordhuis pers. comm), meaning that sudden drops in the trend graph are partial the effects of monitoring method agreements instead of actual phosphate decreases. Phosphorous contents in lake Markermeer sediment vary from 0.3 to 2 g P/kg DW sediment with 1.2 g P/kg DW sediment on average, with sandy sediments containing less P than silty sediments (Schulz 1975).

The average nitrogen content is 2 g N/kg DW sediment (Schulz 1975). These values are comparable to those of surrounding lakes (Vink and Winkels 1991). Ammonium (NH4) concentrations strongly decreased from 2002 onward. From that year on, mean concentrations of NH4 were equal to average nitrate (NO3) concentrations. The high NH4 peak in 1986 could be a sign of disturbances in the nitrification process if the environmental circumstances comprised high pH values beyond 9.

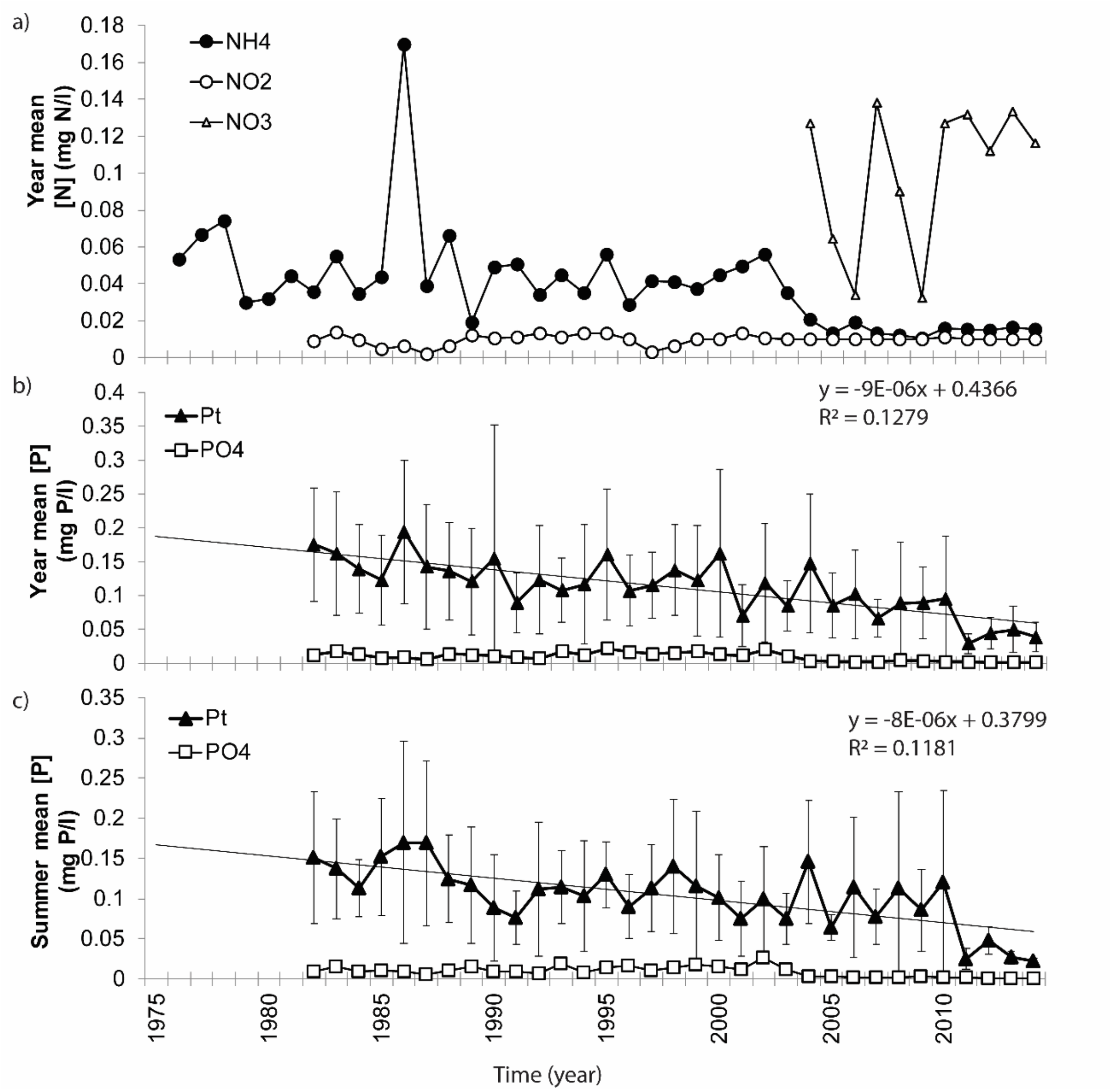


Figure 3: Nutrients in the surface water of lake Markermeer: a) year mean concentrations for dissolved inorganic nitrogen (DIN) compounds; and b) year and c) summer mean total (Pt) and dissolved inorganic (PO4) phosphorus concentrations including long-term trends over the period 1975-2014 for Pt. Source: RWS monitoring dataset.

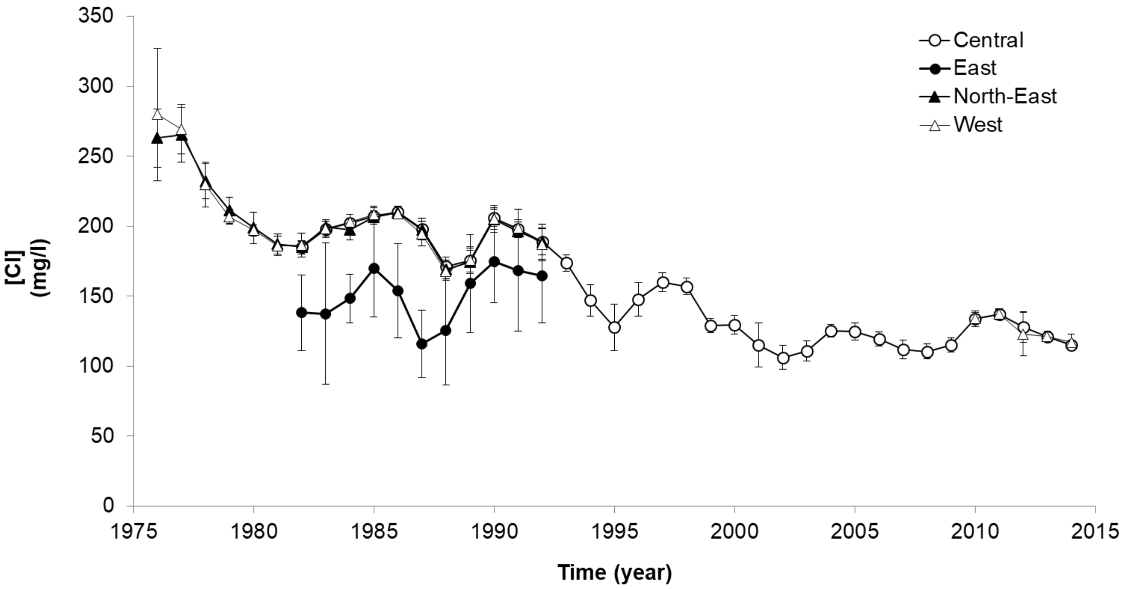


Figure 4: Development of year mean (± SE) chloride concentrations in the surface water of lake Markermeer, measured at four locations in the lake. Data source: RWS monitoring dataset.

4.2.3. Disturbed nitrification hypothesis

4.2.3.1. Description disturbed nitrification hypothesis

Because of the poor water quality of the river water during the 1960s and 1970s, oxygen concentrations remained low and inhibited the nitrification process in the Dutch rivers (Noordhuis 2010). As a result, the large amounts of dissolved inorganic nitrogen (DIN) which entered lake IJsselmeer from the river IJssel contained a lot of ammonium (38% of DIN). Noordhuis (2010) assumed low oxygen concentrations and a poor water quality near the bottom of the lakes in the lake IJsselmeer area during the 1970s, as a result of river water eutrophication by N-based nutrients predominantly containing ammonium. Ammonia toxicity probably has occurred in lake IJsselmeer and lake Ketelmeer during the 1970s and 1980s. The nitrogen excess during that time (with ammonium presenting 38% of DIN in river IJssel) in combination with low oxygen values (<10%) and the high pH values at that time, possibly has led to ammonia poisoning of benthic fauna in the neighbouring lakes IJsselmeer and Ketelmeer and have decreased the *D. polymorpha* populations of the river IJssel and lake Ketelmeer (Van Urk and Marquenie 1989). Accumulation of organic matter and high water temperatures near the bottom of lake IJsselmeer could have increased the risk of ammonia formation, but data on sediment chemistry are scarce (Noordhuis 2010).

During the late 1970s and 1980s, the ammonium content in the river Ijssel and the lakes Ketelmeer and IJsselmeer decreased to values <10% DIN because of an increased oxygen availability in the water. Until 1981, *D. polymorpha* populations were scarce in river IJssel and lake Ketelmeer, but eventually these population increased. Van Nes (2005) detected a seasonal pattern in nitrogen concentrations in lake Markermeer with lower NO3 and N-total values during summer, which could indicate increased denitrification during higher temperatures. However, nitrogen concentrations in the water of lake Markermeer (1970s: 3 mg/l, 1990s: 2 mg/l, 2000s: 1.5 mg/l) have always been less than in lakes IJsselmeer and Ketelmeer (1970s; 6 mg/l, 1990s: 4 mg/l, 2000s: 3 mg/l) since the separation of the lakes (Noordhuis 2010).

Surface water pH levels can increase rapidly during development of plants and phytoplankton in summer. High photosynthesis activity consumes large amounts of bicarbonate and CO2, which reduces the buffer capacity of lakes. Buffering capacity of lake Markermeer, analysed during 2007, showed that the concentration of bicarbonate in the water column remains at 140 mg/l during summer with a small decrease to 120 mg/l during spring (Noordhuis 2010). Nitrate-storing sulphur bacteria, such as *Thioploca sp.*, detected in lake Markermeer by Bij de Vaate in 2008 (Noordhuis 2010), could also add to an accumulation of ammonium. These large vacuolated bacteria oxidize sulphide by reducing their internally stored nitrate, thereby producing ammonium. However, besides the observation of Bij de Vaate, no additional observations of such bacteria in lake Markermeer could be found.

4.2.3.2. Data analysis disturbed nitrification hypothesis

Although it is difficult to measure ammonia, data on concentrations of ammonium, nitrite, and nitrate can be indicative for disturbances of the nitrification process. Mostly, these circumstances occur during warm summers. Combining ammonium concentrations with pH levels and water temperatures (Figure 5) should indicate how likely the circumstances for nitrification process disturbances occurred in lake Markermeer.

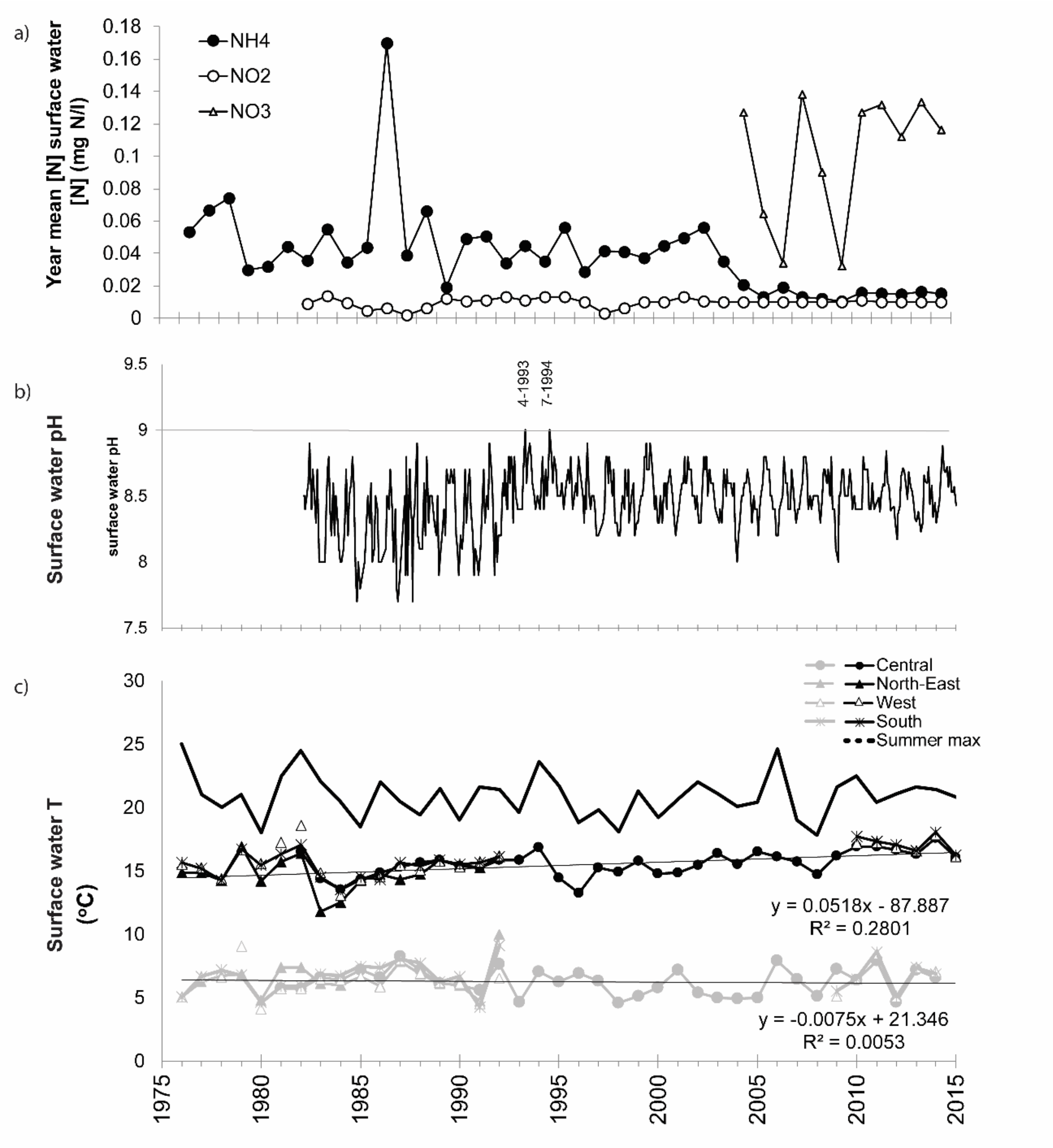


Figure 5: Identifying periods of potential nitrification disturbance in lake Markermeer during the last decades, identifying two critical months (April 1993 and July 1994). Analyses based on a) year mean DIN concentrations, b) monthly variation in surface water pH, and c) year mean surface water temperature in summer (black symbols) and winter (grey symbols). Yearly maximum surface water temperature is plotted as dotted line. Data source: RWS monitoring dataset.

Yet, because the MWTL-monitoring network only includes limited locations, which are near the surface and with monitoring intervals of once a month, the data cannot be more than indicative. Water temperatures were high during the summers of 1981, 1994 and 2006. Lake Markermeer water is classified as moderately to strongly alkaline with pH levels varying between 7.7 and 9.1. Although pH levels were generally high during summers, pH levels reached critical values (>9) only during the summers of 1993 and 1994. Besides the stress of high pH levels during a longer period of time in 1993 and 1994 which in itself is harmful for *D. polymorpha*, benthic populations may have suffered from ammonia production as well. However, according to MWTL-data the ammonium concentrations measured during 1993 to 1994 were not that high. There was an ammonium peek observed in 1986, but at that time pH values remained rather moderate (Figure 5).

Van den Berg *et al.* (2014) observed high concentrations of ammonium in combination with high temperatures and pH values >9 in their mesocosm experiment studying ecological development on lake Markermeer sediment. This could indicate that the conditions for nitrification process disturbance could still occur in still water zones during warmer summer periods with and may influence ecology in sheltered wetland areas that will be constructed in the lake. Although the data prove that accumulation of ammonia may take place in lake Markermeer, the influence of ammonia most likely remains locally and temporary. The remarkable decrease in NH4 since 2002, makes ammonia toxicity less likely to determine the ecology in lake Markermeer in the recent decade. Low oxygen levels near the sediment could also induce development of other reduced elements, especially sulphides. However, monitoring reports and the research of Van den Berg *et al.* (2014) concluded that although concentrations of sulphur in the sediment are locally high, the current sulphide concentrations in the sediment of the lake did not limit plant development.

4.2.4 Toxic compounds hypothesis

The level of contaminants in the top layer of the sediment of lakes Markermeer and IJmeer, tested against the Evaluatienota Water, was generally quite low (Schultz 1975). Toxicity was more apparent during the 1980s and temporally, concentrations of copper (in 85-1987 and 1991-1993) and nickel (in 1985) in lake Markermeer water exceeded the maximum allowed level (RIZA-RIKZ (2002). Based on the sediment sampling over depth in the Oude Hoornse Gat it appeared that the quality of the silt in the Markermeer has improved over the last decennia for all substances of concern. When toxicity in lake Markermeer decreased in the late 1980s, Chironomids increased in numbers and individuals and abnormalities occurred less (Van Urk and Kerkum 1986). Various studies that were carried out during the 1990s concluded that the toxic components in lake Markermeer sediment remained within the range required for sufficient water quality nowadays (Prins *et al.*1992, RIZA-RIKZ 2002, Noordhuis 2001a). Noordhuis (2010) concluded that the surface water of lake Markermeer posed no risks for organisms based on bio-essay experiments carried out in 1996. The uptake of toxic components of lake Markermeer water by organisms was analysed in 1992 and 1997 with no indications for toxicity observed. Toxic components (Hg, Pb, Cd, PCBs, pesticides, PAKs PAHs) in the water, sediment, and organisms of lake Markermeer were found to be rather low in comparison to other Dutch lakes (Noordhuis 2010). Nonetheless, the Water Framework Directive qualified the surface water of lake Markermeer as 'at risk' because PCB and chlorpyrifos concentrations exceeded their maximum permitted levels (Van Luijn and Rijsdijk 2004).

4.2.5. Phytoplankton species dominance hypothesis

4.2.5.1. Description phytoplankton species dominance hypothesis

During the Zuiderzee period, the plankton at lake Markermeer location contained relatively few species, but with extremely high densities (Van Breemen 1905). The most abundant species that occurred year round were *Coscinodiscus sp., Synchaeta spp., Acartia bijilosa* and *Temorella hirundoides*. The low biodiversity of both phytoplankton and zooplankton is striking compared to adjacent marine ecosystems (North Sea or Wadden Sea). Freshwater species that could enter the Zuiderzee via the river IJssel did not disperse into the Zuiderzee estuary although *Scenedesmus* and *Merismopedia* species could cope with the brackish water. During the first decade of lake IJsselmeer (1932-1942), in which the area transformed from a saline inland sea to a freshwater lake, phytoplankton comprised of a community typical for eutrophic freshwater systems (RWS-RIJP 1984) with diatoms developing in spring, followed by increasing abundances of green algae and cyanobacteria development late summer with a risk of cyanobacteria blooms in the late summer period. The most dominant cyanobacteria were *Microcystis aeruginosa*, *Aphanuzomenon flos-aquae* and *Oscillatoria spp.* (including *O. agardhii*). After 1971, cyanobacteria blooms were observed almost yearly in the IJsselmeer area lakes. Most blooms were caused by *Microcystis aeruginosa* and *Aphanizomenon flos-aquae* (RWS-RIJP 1984).

Phytoplankton density and composition were relatively favourable before lake Markermeer was isolated from lake IJsselmeer in 1976 (Dixhoorn 1983). The separation of the lakes immediately resulted in differences in phytoplankton, which in lake Markermeer became dominated by cyanobacteria and green algae with low concentrations of chlorophyll compared to lake IJsselmeer. Algae blooms seldom occurred (Berger *et al.* 1986). Seasonal phytoplankton patterns in lake Markermeer were in the early 1980s characterized as follows: diatoms start to develop in November and peak in spring, followed by an increase of green algae in summer periods, and occasionally a bloom of cyanobacteria. With Chl a concentrations fluctuating between 20 and 100 mg/m3 (Van Acht and De Jong 1983). Until the early 1980s, nutrients were not the limiting factor for phytoplankton growth (Dixhoorn 1983, Van Acht and De Jong 1983).
During the 1990s, phytoplankton counting methods changed several times (Bijkerk 2005). Data from this period were mainly reported in aggregated form (main groups of phytoplankton) and was difficult to include in trend analyses. The phytoplankton composition in the early 1990s was dominated by green algae. Blooms of cyanobacteria occur, mainly of *Aphanizomenon flos-aqua*. Growth of *Oscillatoria agardhii* was observed regularly, but abundant blooms did not occur (Van Duin 1992). Compared to 1994-1998, the share of dominant green algae *Coelastrum*, *Pediastrum* and *Scenedesmus* declined in 2002-2006, whereas the share of undefined small algae (<5 µm) increased. This shift could indicate a declining phosphate availability or decreased predatory pressure by zooplankton, since increase in biomass of small sized algae indicate a decline in grazing pressure (Noordhuis 2010). However, this could also reflect the earlier mentioned changes in monitoring counting methods. During the last decades, *Aphanizomonenon flos-aquae* was observed more regularly during August-November (Noordhuis 2010), while *Tetrastrum komarekii* is an upcoming green algae in lake Markermeer.

Concentrations of Chl a (Nes 2005) and algal biomass (Van Duin 1992) in lake Markermeer fluctuated largely and were much lower than in adjacent waters and mainly light-limited due to wind-induced sediment resuspension. Sedimentation and resuspension processes determined phytoplankton occurrence and made phytoplankton switch from benthic to pelagic environments for shorter of longer periods (Jagtman and Urk 1988, Mur *et al.* 1990, Van Duin 1992) as both resuspended silt and phytoplankton sediment in equal proportions (Mur *et al.* 1990). This mechanism of co-sedimentation may determine the behaviour, composition, and development of phytoplankton in lake Markermeer (Brinkmann *et al.* 2019), suppresses the development of cyanobacteria (Mur *et al.* 1990, Ibelings 1997), and probably determines the differences between lake Markermeer and lake IJsselmeer phytoplankton assemblages (Jagtman and Van Urk 1988). During their stay in the sediment, light conditions are very unfavourable for phytoplankton, especially for species like the cyanobacteria *Microcystis* that have much more difficulties coping with rapidly changing light conditions and longer periods in darkness than the green algae *Scenedesmus* (Mur *et al.* 1990). Resuspension provides settled phytoplankton light again. A high amount of vivid phytoplankton cells (17% of the total phytoplankton concentration according to Mur *et al.*1990) is present in the benthic layer (Jagtman and Van Urk 1988, Mur *et al.*1990). This supports the assumption that in lake Markermeer, the benthic zone is a very important source for phytoplankton (Mur *et al.* 1990). De Lucas Pardo (2014) tested the effects of colonial algae and filamentous algae on flocculation, in particular floc size and structure, and found that with the changes in species composition, flocculation has changed towards the formation of larger aggregated flocks. In a detailed study of individual aggregates, Brinkmann *et al.* (2019) showed that micro-algae could obtain phosphorus from the aggregates.

During longer periods of calm weather, silt concentrations in the water column decrease, but remain turbid because of phytoplankton growth. Remnants of death algae are relatively scarce. Although these conditions are favourable for cyanobacteria development, the rapidly fluctuating light conditions with larger periods of poor light availability (Mur *et al.* 1990) combined with a depth *below* 2.5 m (Berger 1987) prevent algae blooms in lake Markermeer. For *Aphanizomenon flos-aquae*, nitrogen and light conditions are unfavourable for blooming (Noordhuis 2010) and cyanobacteria do not develop in the lake until late summer (Lammens 1993).

When characterizing zooplankton in lake Markermeer, roughly three periods can be distinguished: Zuiderzee, eutrophic water during the 1970s and early 1980s, and the period after 1990. Two species of *Copepoda* were characteristic for zooplankton in the Zuiderzee: *Acartia bifilosa* and *Temorella hirundoides* (Van Breemen 1905). From the late 1970s till early 1980s, lake Markermeer had a zooplankton assemblage that was characteristic for eutrophic waters, consisting of Cladocera species *Bosmina coregoni*, *B. longirostris*, *Chydorus sphaericus*, *Daphnia hyaline*, and the Copepoda *Eurytemora affinis*. In the early 1980s, zooplankton assemblages contained Protozoa (Rhizopoda, Ciliata), Rotifera, Copepoda, and a high abundance of several Cladocera species (Dixhoorn 1983, RWS-RIJP 1984). Cladocera seemed more abundant than Copepoda, but both groups could locally reach large abundances, with densities generally higher close to the shores than in the middle of the lake (RWS-RIJP 1984).

After nutrients in the lake had decreased, zooplankton densities and species richness remained relatively low. Zooplankton is currently dominated by *Daphnia galeata/cucullata*, *Bosmina coregoni*, and cyclopoid Copepoda. Whereas Daphnia populations tend to peak in spring in freshwater lakes, densities in lake Markermeer remain low at 5 to 40 individuals/l (Lammens 1993). The small sizes of Daphnia (0.55-0.95 mm on average), Copepoda and *Bosmina coregoni*, indicate that their growth is constrained. Predation pressure or unfavourable nutrient conditions are mentioned as possible constraints (Lammens 1993, Noordhuis 2010). The zooplankton patterns of 1990-1999 did not significantly differ from those in 1980-1990. The monitoring results of the year 2000 report found mainly Rotifera (200-1000 per µl) and a small share of Cladocera and Copepoda (each <100 per µl) in the zooplankton assemblage of lake Markermeer (Noordhuis 2001a). As a consequence of this type of zooplankton population, consumption of algae beyond 50 µm diameter relies on adult Copepoda. Filter-feeders can only consume the smaller fraction of algae in the community. Other observations are decreasing average sizes, and a gradually increasing biomass during early spring combined with a decreasing biomass during summer (Noordhuis 2001a).

4.2.5.2. Data analysis phytoplankton species dominance hypothesis

Phytoplankton monitoring in lake Markermeer was performed irregularly and locally over the years. A standardized monitoring dataset is therefore not available. Different sampling methods were used and during the 1990s phytoplankton counting methods even changed several times (Bijkerk 2005). Counting results switched from number of individuals to number of cells, and not all size classes were counted (e.g. phytoplankton <5 µm was not counted during 1993-1999).

Chl a concentrations were high during the first decade of lake Markermeer, followed by a decrease throughout the 1980s (Figure 2). Concentrations increased again in the 1990s with a small decrease observed from 2004 to 2014. From 2000 onwards, Chl a patterns during the winter half-year (October-May) altered and winter year mean Chl a became higher than summer mean Chl a (Figure 2). Comparing seasonal Chl a developments before and after 1996, Noordhuis (2010) showed a tendency towards higher Chl a concentrations during the winter in the latter period, while Chl a concentrations during summer remained comparable. Based on Chl a monitoring trends (Figure 2c), it is possible that the alterations observed in the early 1980s, 1990 and 2000, and 2004 could have induced ecological effects. The water authority reported higher fluctuations of Chl a concentrations (higher peaks and lower minima, particularly in 1994 and 1999) and increased Chl a concentrations during winter/early spring (January-April) compared to previous periods (Noordhuis 2001a). Noordhuis (2010) also observed an increase of Chl a during early spring, but added that developments in phytoplankton during the 1990s were more evident in terms of species composition and size than Chl a concentration changes.

4.2.6. Decline of bulk prey species (Dreissena polymorpha and Osmerus eperlanus)

4.2.6.1. Description decline of bulk prey species hypothesis

Originally, the Zuiderzee estuary was inhabited by salt water species, with *Mytilus edulis* being the most abundant macroinvertebrate (Van Benthem Jutting 1954). As the southern part of the Zuiderzee, lake Markermeer used to be the least dynamic and brackish part. Mussel beds did not occur in this part and the benthic fauna consisted of brackish water species such as *Cerastoderma glaucum*, *Balanus improvisus*, and *Rhithropanopeus harrisii* (Noordhuis 2001b). Within four years, the isolated estuary became a freshwater lake. During the first two years, marine species rapidly disappeared from this area as they could not adjust to the decreasing salinity. The bivalve community was however not displaced by any brackish water species and a brackish interphase never developed (Van Benthem Jutting 1954, Wibaut Isebree Moens 1954). The only benthic invertebrate species that remained in the lake after closure had wide salinity tolerances such as *Corophium lacustre, Praunus flexuosus*, and *Cordylophora caspia* (Noordhuis 2001b). As a consequence, instead of developing into a brackish system, a mollusc vacuum occurred during the transition from saline estuary to freshwater lake from 1934 to 1936 (Van Benthem Jutting 1954, Wibaut Isebree Moens 1954).

Freshwater species started to colonise the newly created lake, with *Dreissena polymorpha* larvae observed in lake IJsselmeer plankton since 1938 (Wibaut Isebree Moens 1954). Most likely, a small population of adult *D. polymorpha* already occurred in the relatively less saline southern part of the Zuiderzee estuary before it became lake Markermeer (Van Benthem Jutting 1954, Wibaut Isebree Moens 1954, Bij de Vaate and Kerkum 1978). This population increased soon after the area lost its marine connection in 1932 (Van Benthem Jutting 1954), facilitated by a strong decrease of chloride concentrations in the lake to values below 5‰ in 1936 (Havinga 1941). This can be regarded as the upper limit of chloride concentration at which a *Dreissena* population can develop (Janssen and Janssen-Kruit 1967; Wolff 1969). Densities of *D. polymorpha* increased tremendously and colonised almost every piece of sediment other than silt (Van Benthem Jutting 1954). *Dreissena* invasions are generally followed by a decrease in Chl a concentrations, zooplankton abundance and pelagic productivity, and could induce a shift in lakes from a turbid to a clear state (Noordhuis *et al.* 2016).

The distribution of *D. polymorpha* strongly related to the amount of attachable materials on the bottom, which in lake Markermeer were mostly remnants of shells of the Zuiderzee species *Mya arenaria* that were present in the top layer of lake Markermeer sediment and emprise 28% of the total benthic surface of the lake (Bij de Vaate 1991). As a result, *D. polymorpha* occurred in a non-evenly distribution, mainly present as clumps on solid substrates. The probability of finding such a clump while monitoring largely influenced population estimation (Noordhuis 2009). Until the early 1990s, all solid substrates in the lake were overgrown with *D. polymorpha*, and substrate became the limiting factor for further expansion (Bij de Vaate 1991). Only areas prone to sedimentation and resuspension processes were free of *D. polymorpha*. Although wind and waves facilitate fast distribution of veliger larvae (June-August), resuspension and sedimentation processes cover solid substrates with newly settled post-veliger larvae on it. Veliger larvae cannot find substrate to attach themselves to and attached post-veligers will die if the coverage lead to anaerobic conditions for longer than one week (Walz 1973). Younger, smaller mussels are especially susceptive to coverage, since relative oxygen consumption by *D. polymorpha* decreases as size increases (Mikheyev 1964). With a maximum shell length of 27 mm, *D. polymorpha* remained smaller in lake Markermeer than in adjacent lakes. Slower shell growth and a shorter life span of the mussels in lake Markermeer could be explanations for this limited adult size (Bij de Vaate 1991). After a fast colonization of the dammed lake Markermeer, a decreasing trend was observed for *Dreissena polymorpha* in the lake in terms of abundancies, biovolumes, and sizes since the mid-1980s, since the discharge of waste water loads from Amsterdam in lake Markermeer had stopped.

The species became an important food source for cyprinid fish and diving ducks (*Aythya fuligula, A. marila,* and *A. ferina*) in lake Markermeer (Havinga 1941, Lammens 1993, Suter 1982, Van Eerden and Bij de Vaate 1984, Van Eerden 1997, De Leeuw 1997) and crustaceans (Bij de Vaate pers. comm.). *Dreissena* predators in lake Markermeer consisted mainly of *A. fuligula* and *A. ferina* (Noordhuis and Houwing 2003). *Dreissena* predation is influenced by water depth, prey density, mussel size and attachment (clumps or loose mussel beds). Generally, small mussels were preferred because they had a better flesh content, while clumps of mussels were consumed without size selection (Van Eerden 1997).
Despite of its fast colonization and population growth, *Dreissena* densities declined rapidly during the early 1990s. Both population densities and vitality declined simultaneously in this period. It is assumed that several parameters are related to this decline. Storm events frequently occurred (Figure 2d), phosphates depleted (Figure 3), water temperatures were relatively high (Figure 5), Chl a concentrations were low (Figure 2c), but visibility was poor because of the high concentrations of resuspended silt (Figure 2). Not the total suspended matter, but the resuspension and allocation processes were mainly threatening *D. polymorpha*. Besides the increased risk of smothering due to more frequently resuspension and sedimentation processes, these factors mentioned also worsened nutrient conditions for *D. polymorpha* (Penning *et al.* 2013). Mussel banks may accumulate sediment and the excretion of pseudo-faeces as a consequence of filter-feeding result even in more sticky particles. The expectation of Noordhuis and Houwing (2003) is that this decline in *Dreissena* densities resulted in a vicious circle towards more turbidity, eventually also affecting macrophytes and fish feeding birds. Other studies, however, mention that *Dreissena* mussels in lake Markermeer were only found on hard substrata and did not occur in silty areas (Van Bethem Jutting 1954, Bij de Vaate 1991, Brongers 2001). *Dreissena* was not expected to colonise the deeper silty central part of the lake, due to their negative correlation with silty sediment and dependence on Zuiderzee shell remnants as substrate (Brongers 2001).

The filter-feeder *Dreissena* consumes algae and can process algae of a certain size category depending on the size of the mussel (Berg *et al.* 1996), which varies with seasonal phytoplankton dynamics and composition. *Dreissena* are selective filter-feeders that adjust their feeding behaviour depending on phytoplankton composition, to capture and ingest high quality phytoplankton, while also avoiding consumption of certain species such as cyanobacteria (Berg *et al.* 1996). Large phytoplankton (diameter >50 µm (Naddafi *et al.* 2007) or >70 µm (Sprung and Rose 1988)), or very small phytoplankton cannot be digested by *D. polymorpha*. A retention plateau is formed at 5 µm particle diameter and maximum retention efficiency is attained within a range of 5-35 µm particle diameter (Sprung and Rose 1988). Cotner *et al.* (1995) found that *D. polymorpha* removed large bacteria (> 0.9 µm diameter) more effectively than small bacteria with a lower limit for particle size removal of less than 0.4 µm diamter. Flexibility of feeding behaviour combined with differences in susceptibility among phytoplankton groups to mussel ingestion indicates that *D. polymorpha* could alter phytoplankton community composition. Hardenbicher *et al.* (2015)

found that filter-feeding by *Dreissena* led to pronounced shifts in the phytoplankton community composition. These authors proved that water temperatures influence consumer effects on phytoplankton biomass and species composition as well as potential feedback effects of phytoplankton food quality on its consumer. However, their observations were done by water temperatures shifts (15-20-30°C) that have not occurred in lake Markermeer (Figure 5).

Noordhuis *et al.* (2010) stated that food conditions for *Dreissena* in lake Markermeer were poor since the late 1980s because the high silt content of suspended matter combined with the low nutrient availability that limit algal growth. Still, the mussels seemed to have endured these nutrient poor conditions for 15 years. Although Chl a concentrations have increased again after the decline of the filter-feeder population, and despite of the large amounts of brood observed every year, *D. polymorpha* populations have not recovered. First, it was assumed that predation by roach and diving ducks was responsible for the zebra mussel decline (Lammens 1993). Roach preyed on *D. polymorpha* in summer (mainly mussels <1 cm) whereas diving ducks fed mainly on *D. polymorpha* during winter. The ducks were estimated capable of removing up till 50% of the total *D. polymorpha* biomass yearly. Lammens (1993) therefore argued that recovery of *D. polymorpha* mussel banks could not be expected unless areas were excluded from predation. However, the large decline of diving ducks in the 1990s did not result in a recovery of the mussel population even though the amount of brood remained high. The decline of diving duck populations has been contributed to the low nutritional quality of *D. polymorpha* in lake Markermeer compared to the surrounding lakes (Noordhuis 2010). Fast colonisation, exponential population growth and strongly fluctuation populations characterize this successful invader. Sudden population declines after a phase of exponential growth are typical for mass invasive species and dramatic decreases of *D. polymorpha* have been reported for other lakes (Stańczykowska 1975, 1978, Walz 1974). Explanations such as low water levels and predation by diving ducks and freshwater fish have been mentioned (Walz 1974), but crashes with no obvious reasons have been observed as well (Stańczykowska 1975, Bij de Vaate 1991).

Osmerus eperlanus (European smelt) used to be the main prey species for fish eating birds in lake Markermeer (RWS-RIJP 1984), but the species has severely declined (Van Eerden 1997, RIZA-RIKZ 2002). The population dynamics of *O. eperlanus*, reproducing already after one year, resulted in strongly fluctuating densities. Although initial decline in adult *O. eperlanus* coincided with high fishery activities in the lake in the 1980s (Mous *et al.* 2003), no clear recovery has been recorded after these activities stopped. A reduction in the availability of zooplankton during the same period, induced by changes in phytoplankton densities, species composition and overall phytoplankton food quality in the lake, could also have influenced recovery of *O. eperlanus* populations (Noordhuis 2010). The natural habitat of *O. eperlanus* (estuaries) is characterised by turbid conditions, so the decline of this bulk prey species is not expected to be related to increased turbidity of the lake. More likely is the influence of increased water temperature on the populations of *O. eperlanus*. This salmonid species prefers cool and oxygen-rich water, with spawning temperatures between 4 and 12 °C and optimum growth conditions between 10 and 20 °C (Noordhuis 2010). Earlier spawning of *O. eperlanus* induced by higher spring temperatures could also result in a mismatch with their zooplankton food source (Noordhuis 2010). The lack of deeper areas in lake Markermeer can limit the presence of cooler water during warm summers. Earlier development of phytoplankton and zooplankton in spring induced by global change could also result in a mismatch between availability and requirement of resources for *O. eperlanus*. Finally, also predation of *O. eperlanus* by perch and pikeperch can influence population dynamics of this species (Noordhuis 2010). Other fish species such as carp, ide, pike, white bream, flounder, sea trout, gudgeon, and the three spined stickleback occur in the lake, but form a relatively low share of the fish biomass, which was estimated at 300 kg/ha during the early 1980s (RWS-RIJP 1984). A steep decline was observed in fish density during the first half of the 1980s (Figure 9) Despite of their relatively low share, these non-target fish species do influence macroinvertebrate density. Noordhuis (2001a) showed a tree times higher density of worms and chironomids in exclosures in lake Markermeer that were isolated from fish and birds compared to open exclosures.

4.2.6.2. Data analysis decline of bulk prey species hypothesis

The first records of adult *Dreissena* in lake Markermeer region date from 1939 (Havinga 1941). There is no data on *Dreissena* populations in lake IJsselmeer between 1943 and 1967. In 1968, the total *Dreissena* population in lake IJsselmeer region was estimated to be 700 billion individuals (Van Soest 1970) and 350 to 400 billion in 1976 (Van der Wal 1979). Colonisation of juveniles during the late 1970s ranged from 2700 to 19000 per m2 hard substrate (Bij de Vaate and Kerkum 1978). Mussel monitoring data for lake Markermeer is available from 1969 (Figure 6). The first monitoring in 1969, carried out for the upper half of the lake, shows that mussels occurred in the north-eastern part. These populations could not maintain after the Houtrib dike was closed (Noordhuis 2010).

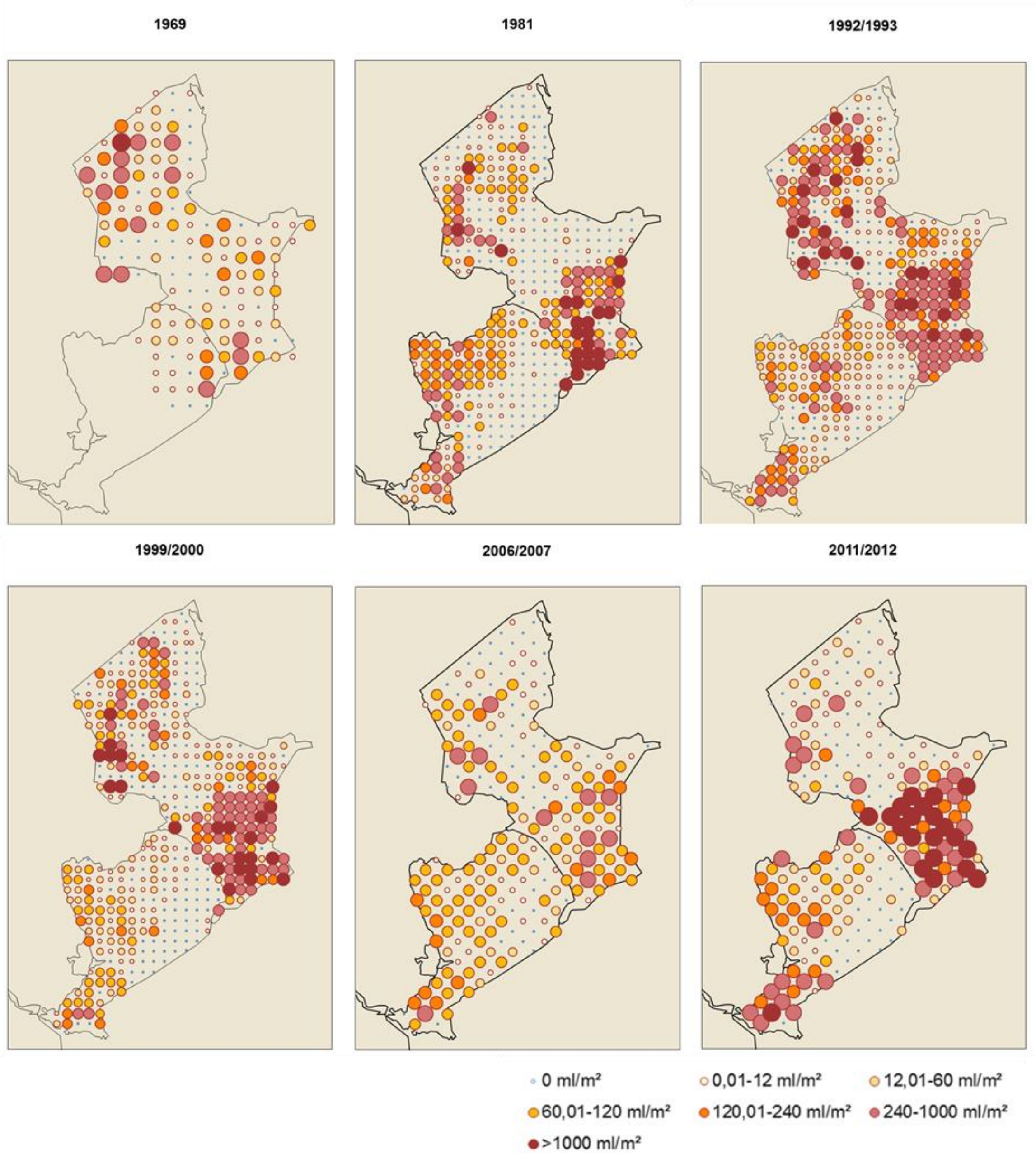


Figure 6: Population development of *Dreissena* species in lake Markermeer and lake IJsselmeer (expressed in bio-volume; ml shell/m2) over the period 1969 to 2012 shows large fluctuations in occurrence and hotspots. Data sources: Van Soest (1970), Bij de Vaate (1991), Brongers (2001), Noordhuis and Houwing (2003), Noordhuis (2009, 2010), Bij de Vaate and Jansen (2011, 2012).

Dreissena populations are characterized by highly fluctuating population dynamics (Brongers 2001, Bij de Vaate 1991, Noordhuis and Houwing 2003, Noordhuis 2010) with both rapid growth and strong declines observed without clear explanations for all fluctuations. Whereas the decline in lake IJsselmeer and lake Ketelmeer during the late 1970s was most likely due to ammonia poisoning of benthic fauna (Van Urk and Marquenie 1989), while another decline in 1982 occurred for no obvious reason. Bij de Vaate (1991) reported thousands of diving ducks which were seen near the sampling site that winter, and he concluded that predation could have led to this decline. More recently, decreasing dispersal patterns became evident in the period 1993-2000, when *D. polymorpha* showed a 53% decline in biovolume (Brongers 2001) with an average density of 400 individuals per m2 calculated for the entire lake area and 1000 per m2 for the suitable areas where *D. polymorpha* occurred (Bij de Vaate 1991) with local bio-volumes ranging from 12 to 60 ml/m2 (Noordhuis 2010). This decline in *D. polymorpha* co-occurred with decreases in numbers of benthivorous birds and visibility and initiated extensive research as the *D. polymorpha* crash was held responsible for a decline of water birds in the area (Van Eerden 1997, Brongers 2001, Noordhuis 2010, Van Eerden 2011, Noordhuis *et al.* 2014, 2016). A simultaneous decline of bird numbers was also observed in the river Ijssel (Noordhuis 2010). A strong decrease in fresh weight of mussels could already be observed during the period 1981-1993, although dispersal patterns did not show declines (Van Eerden 1997). This indicates that the zebra mussels were already under stress before the 1990s and that their 'crash' would rather result from longer term processes than from instant stressors. Monitoring results from 2000 showed a decline in mean *Dreissena* bio-volume of more than 50% compared to 1993 (Brongers 2001). This observation led to the negative trend theory for the ecology of lake Markermeer (ANT, Noordhuis *et al.* 2014), which initiated an extensive research program on the cause of this crash.

The monitoring in 2010 however showed a substantial increase of another *Dreissena* species in parts of lake Markermeer: *Dreissena rostriformis bugensis* or the quagga mussel (Bij de Vaate and Jansen 2010). The colonization by *D. r. bugensis* meant an increase of total *Dreissena* density, and a factor 4.9 total bio-volume increase in 2011 compared to 2006 (Bij de Vaate and Jansen 2011, 2012). By 2012, the share of *D. polymorpha* in the mussel population was half of what it used to be, whereas increasing total dry weight of *D. r. bugensis* in lake Markermeer (Bij de Vaate and Jansen 2012) suggests that, in contravention of the hypothesis that *D. polymorpha* could no longer filter sufficient food to maintain in lake Markermeer, this other *Dreissena* species was indeed capable to obtain sufficient nutrients from the lake.
Spatial patterns of *Dreissena* densities in lake Markermeer were consistent, but showed fluctuating densities. Based on spatial differences in *Dreissena* densities, lake Markermeer can roughly be divided into the following areas: the western part (Hoornsche Hop), the southern part (lake IJ), and the central part and the eastern shores. The first monitoring reported *Dreissena* populations in the northeast (Figure 6). These populations disappeared after the Houtrib dike had closed, while populations in the western part (Hoorsche Hop, most populations bio-volume 60-120 ml/m2) and southern part (IJmeer, several hotspots of >250 ml/m2) rapidly increased. *D. polymorpha* crashes in the early 1990s were reported more than once (60% according to Van Eerden 1997, De Leeuw 1997, Noordhuis 2010). These crashes mentioned in ecological studies have mostly affected the populations in the western part (Hoornsche Hop: -57%). Although total bio-volume of *Dreissena* in lake Markermeer in 1993 had declined with 18-30% compared to estimated bio-volumes in 1981, their spatial pattern was expanded in 1993 compared to 1981, albeit in small populations (bio-volumes <12 ml/m2).

Dreissena hotspots developed again in the southern part (IJmeer) and central-western part of lake Markermeer in 2011. This development was not a sign of *D. polymorpha* recovery, but should be ascribed to the colonisation by *D. r. bugensis* (Bij de Vaate and Jansen 2011). This *Dreissena* species shows a lot of similarity to *D. polymorpha*, but *D. r. bugensis* has i) a lower respiration rate and therefore needs less energy to maintain, ii) grows in bunches instead of clumps, and iii) is less sensitive to disturbances (Bij de Vaate 2008). Quagga mussels tolerate lower temperatures and reproduce at lower temperatures than zebra mussels, while the latter are more tolerant to temperatures above 25 °C. This means that the circumstances in lake Markermeer favour *D. r. bugensis* as competitor over *D. polymorpha*. Monitoring results from 2011 showed that the *Dreissena* population in lake Markermeer consisted for 80% (numbers) to 90% (bio-volume) of *D. r. bugensis*, a pattern which has remained over the last years.

Although a decrease in *Dreissena* bio-volume from 87 ml/m2 in 1987 to 71 ml/m2 in 1993 (Figure 7) does not seem alarming, a loss in *Dreissena* total biomass for the lake from 218x106 g to 86x106 g was reported for the same period (Van Eerden 1997). Over the next decade (1993-2000), total bio-volumes of *Dreissena* in lake Markermeer declined on average by 50-55% (ranging from 69% in the central part to very low declines in the south; Noordhuis and Houwing 2003, Brongers 2001), which were in turn 18-30% lower (due to a concentrated decline in the west) compared to 1981. The filtration capacity per biovolume unit, however, had increased since the 1980s because of a higher share of smaller sized *Dreissena* (Noordhuis and Houwing 2003). Mean total biovolume was low for lake Markermeer (20 ml/m2) compared to the adjacent lakes (120 and 500 ml/m2) during 2000-2008 (Noordhuis 2010). Because *Dreissena* are an important bulk food species and are valuable for modelling nutrition paths in the lake, their total biomass was closely monitored since 2011 (Bij de Vaate and Jansen 2012). The crash during the 1990s mainly affected the development rate of the mussels resulting in a strong decline of larger mussels. In 2001 and 2002, the conditions proved especially hard for mussels above 12 mm, and populations that time consisted for the majority of juveniles younger than one year. In 2012, both *D. polymorpha* and *D. r. bugensis* in lake Markermeer were mainly juveniles and relatively small (13 mm and 18 mm, respectively) compared to mussels in adjacent lakes (in lake IJsselmeer 20 mm and 25 mm, respectively; Bij de Vaate and Jansen 2012)

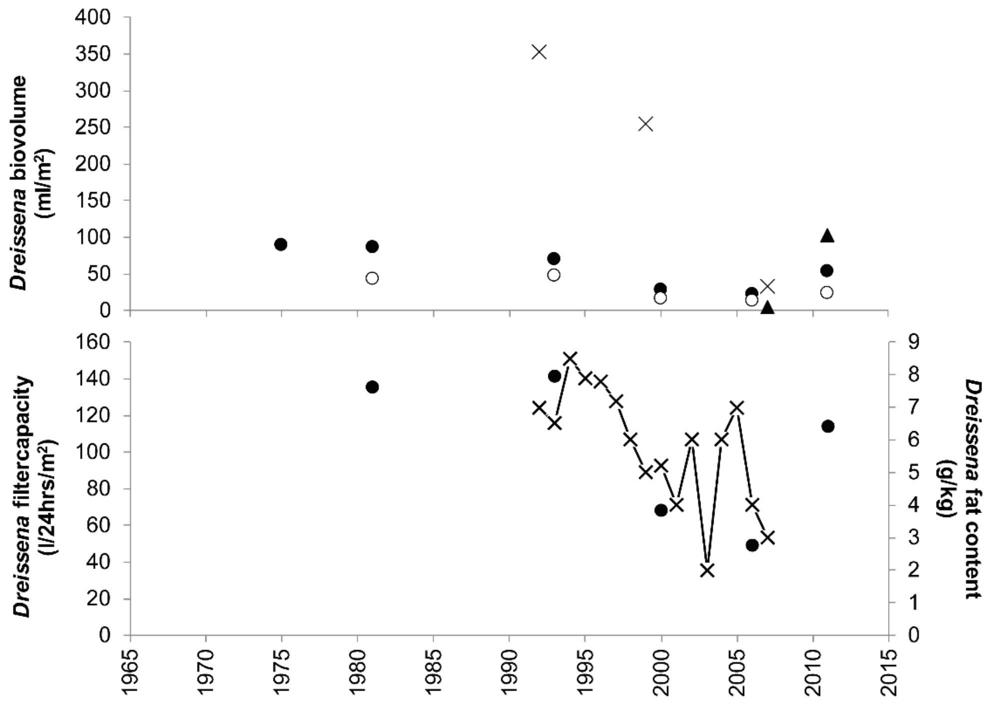
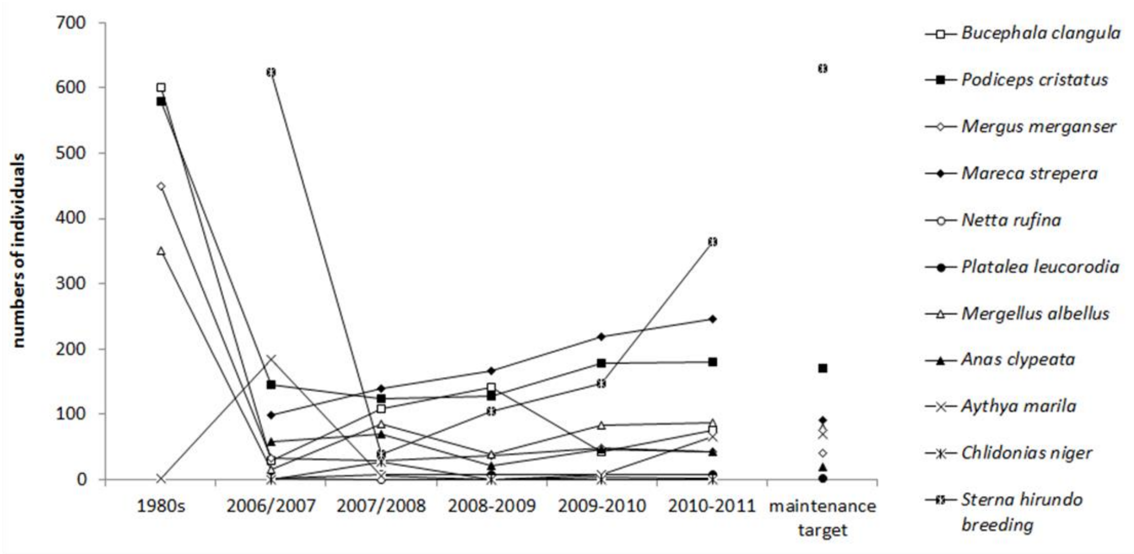


Figure 7: *Dreissena* characteristics in lake Markermeer (circles) and the adjacent lake IJsselmeer (crosses) with some information specifically for *D. r. bugensis* in lake Markermeer (triangles): a) total mean bio-volume of *Dreissena* declined in both lakes until the introduction *D. r. bugensis* around 2007 with the same pattern in b) *Dreissena* filtercapacity in lake Markermeer, while *Dreissena* fat content in lake IJsselmeer showed yearly fluctuations with an overall decline in the period 1991-2007. Data sources: Bij de Vaate (1991), Brongers (2001), Noordhuis and Houwing (2003), Noordhuis (2009, 2010), Bij de Vaate and Jansen (2011).

Various studies have elaborated on the causes of the *D. polymorpha* decrease during the 1990s. Mentioned are unfavourable feeding conditions, siltation, and (temporally) increased predation by birds and fish. However, none of the studies reviewed consider diseases or parasites as a potential cause. Unfavourable conditions and siltation seem to have less affected *D. r. bugensis* densities, as this species has continued to increase in the first years since initial colonisation in 2007. It is unlikely though that *D. r. bugensis* is more resistant to siltation than *D. polymorpha* since both species are generally smaller in lake Markermeer compared to lake IJsselmeer (Bij de Vaate & Jansen 2012). The increased colonisation of *D. r. bugensis* in lake Markermeer since 2007 makes the hypothesis that silt would be only responsible for the lack of *D. polymorpha* recovery less obvious. Increased suspended matter and resuspension activity in the early 1990s may have initiated the strong decline in *D. polymorpha* in the 1990s. The change in food quality resulting in of phytoplankton might have a more profound impact on *D. polymorpha* populations compared to *D. r. bugensis*. Predation by fish is supposed to have local effects mainly on *Dreissena* populations. The recruitment of roach, bream, and ruffe in 1992 could have increased fish predation, but could not be responsible for the huge decline in that period. Furthermore, eel biomass was very low during that time. If predation by ducks would be the cause of the *D. polymorpha* decrease, mussel biomass should thus be lowest during spring and increase during summer after spat settlement (Lammens 1993). Increased numbers of scaup (Aythya marila) during the winters of 1992 to 1994 could have attributed to predation, but tufted ducks (Aythya fuligula) present during summer barely eat mussels during this season. Compared to their abundances in the 1980s (Figure 8), the presence of birds at lake Markermeer had hugely decreased and after *D. polymorpha* declined over the period 1995-1998, the numbers of benthivorous birds at the lake dropped even more.



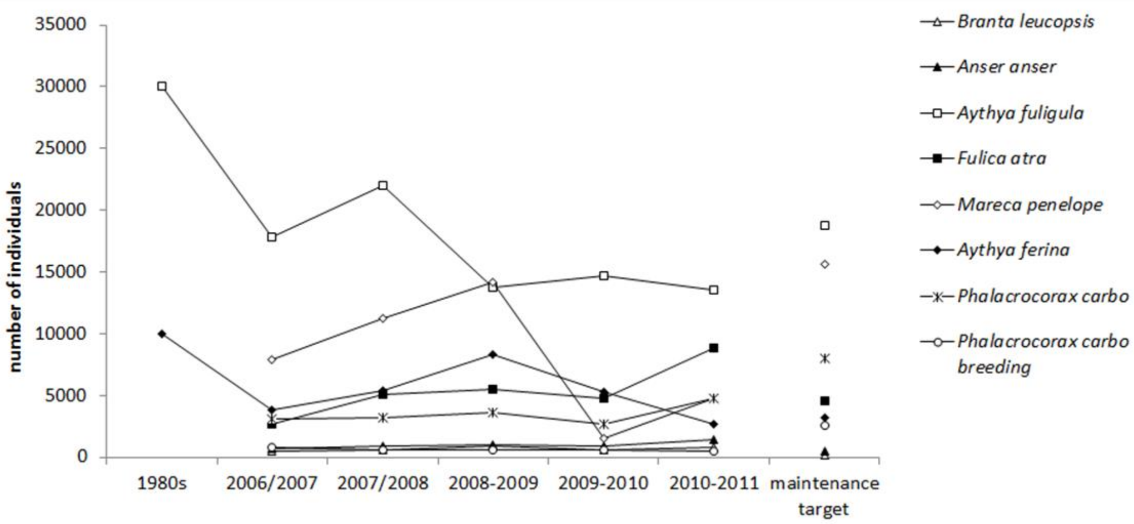


Figure 8: Bird densities derived from yearly countings at lake Markermeer for a) relative rare and b) common species. Natura 2000 conservation objectives for each bird species (presented at the right side of the graph) are not always reached, especially for piscivorous species. Data source: Ministry of LNV (2002, 2005, 2008, 2009).

A steep decline was observed in *O. eperlanus* density during the first half of the 1980s (Figure 9), eutrophication measures and significantly less water exchange with lake IJsselmeer after the closure of the Houtrib dike were suggested as causes for this decline. This decline during the 1980s was not specifically for European smelt, but affects all fish species in the lake. Since the 1990s, fish densities of all species in lake Markermeer remained low in general and did not increase anymore. Causes for the lack of recovery of O. are hard to establish. The monitoring of zooplankton species has been quite fragmented throughout the history of lake Markermeer (Noordhuis 2010). It is therefore not possible to determine direct relationships between population dynamics of *O. eperlanus* and their food source. However, a combination of several factors seems likely, among which the high pressure of commercial fishery and decrease of nutrient input. Negative effects of both P/C ratio of algae and of increased flocculation on cladocerans seem likely (Sarpe *et al.* 2014) and the response to increase of water temperatures by earlier spawning suggests the possibility of mismatching (Noordhuis 2010). More information is required to assess the bottlenecks for the recovery of this important bulk prey species in lake Markermeer

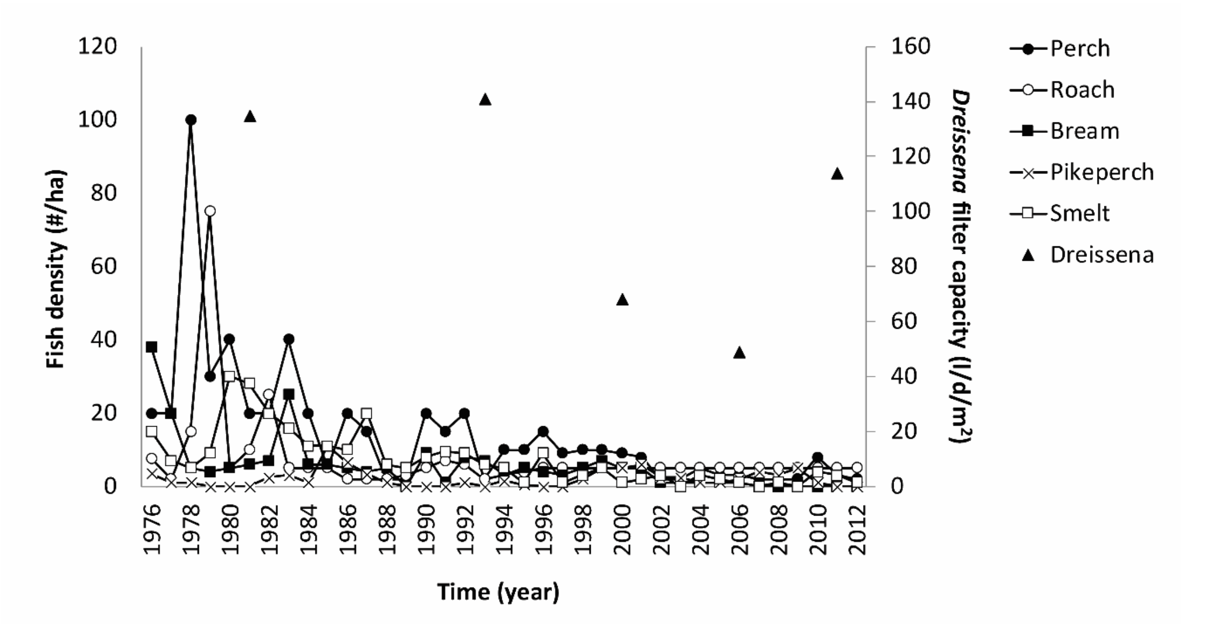


Figure 9: Fish populations in lake Markermeer remain at constant and low densities since strong declines for most species during the 1980s, even after recovery of the mussel filtration capacity around 2010. Data source: De Graaf *et al.* (2014), Noordhuis (2000), RIZA-RIKZ (2002).

4.2.7. Lack natural land-water gradients hypothesis

The highly artificial morphology of lake Markermeer could largely define the perspective for ecosystem development. The ecosystem has not enough buffering capacity to cope with temporary distortions and therefore immediately responds to changing conditions. In order to develop diverse and inundated shore vegetation or wetlands with natural vegetation, including a diverse macroinvertebrate assemblage, it is important that the banks provide suitable conditions for germination and colonisation on a large scale. Currently, fixed shores and a controlled, unnatural water level regime with low variations limit the occurrence of such areas (Tosserams *et al.* 1999). A natural water regime is characterized by low water levels during summer and higher water levels during winter, with big differences between years, providing opportunities for colonization, expansion and rejuvenation of wetland vegetation dry during periods of low water level in summer (Coops 2002). However, in lake Markermeer an unnatural water regime has been installed with higher water levels during the summer (-0.20m NAP) than during the winter (-0.40m NAP; Broderie *et al.* 2012).

The benefits that installing a natural water regime could provide, could in the case of lake Markermeer be offset by the steep diked shores and the absense of shallow areas. Even with a natural water level, the conditions for wetland and natural shores will not occur. Restoration of gradual land-water transitions are also necessary to develop gradients in environmental conditions from land to open water. These gradients are necessary for ecological development. For example, Noordhuis (2001a) found that the number of insect larvae correlated negatively with water depth, indicating that shallow water areas and land-water gradients could improve the conditions for these organisms. The question remains if newly created gradual shores and temporary islands will be stable enough to withstand erosion by the wind induced waves and currents in the lake. This erosion is severe in lake Markermeer as large wind fetch areas combined with the lack of shallow zones and gradual slopes allow waves to increase in strength as there are no (natural) structures in the lake to subside wave energy.

Many nature development projects carried out in lake IJsselmeer area since 1989 focused on creating natural shores with gradual slopes (Platteeuw *et al.* 2001), mainly by creating sandy or silty islets close to the shores. Valuable pioneer vegetation colonised the newly created nature areas, but reed (*Phragmites australis*) and club-rush (*Schoenoplectus lacustris*) hardy developed on the islets during the first decade after construction. Birds visited and foraged on the newly created land-water gradients, but breeding habitat for marshland birds failed to establish. Overall, erosion and sedimentation processes behaved differently than expected. Shores that were not protected against waves suffered severe erosion, and the assumption that sedimentation processes would add to islet growth was too expectant.

4.3 Environmental and ecological developments in lake Markermeer

After exploring the probabilities of the hypotheses suggested in literature individually by reviewing research references, we composed a dataset in order to combine available environmental and ecological data and analysed what developments have occurred in environmental conditions and species composition in the 40 years since the separation of lake Markermeer from lake IJsselmeer by the Houtrib dike. Multivariate analyses of this composed data set could detect trends and shifts in ecosystem conditions and ecology, even revealing sudden or more gradually occurring ecosystem developments over time and provide an indicate which combinations of parameters played a role in these developments. We explore whether those conditions match the range of hypothesized scenarios and which processes attributed to the ecological characteristics of lake Markermeer over time.

Principal component analysis (PCA) on lake Markermeer data showed developments in both environmental factors and biological factors (Figure 10 and 11). Parameters included in the PCA analysis included: Chloride concentrations, Chl a (summer and winter concentrations), water temperature, water level (seasonal means, minima and maxima), pH (mean and maxima), visibility (minima and maxima), concentrations of suspended matter (minima, maxima, and mean), dissolved oxygen (saturation % and mg/l), dissolved organic carbon (DOC; mean, minimal and maximum), and weather conditions such as yearly averages for wind, the number of warm days, tropical days and ice days per year. For the period of 1982 to 2014, surface water concentrations of nutrients (NH4, NO2, PO4, and P-total) were included as well. For most of the parameters, data were categorised into summer and winter mean values in order to distinguish processes that are linked to seasons.

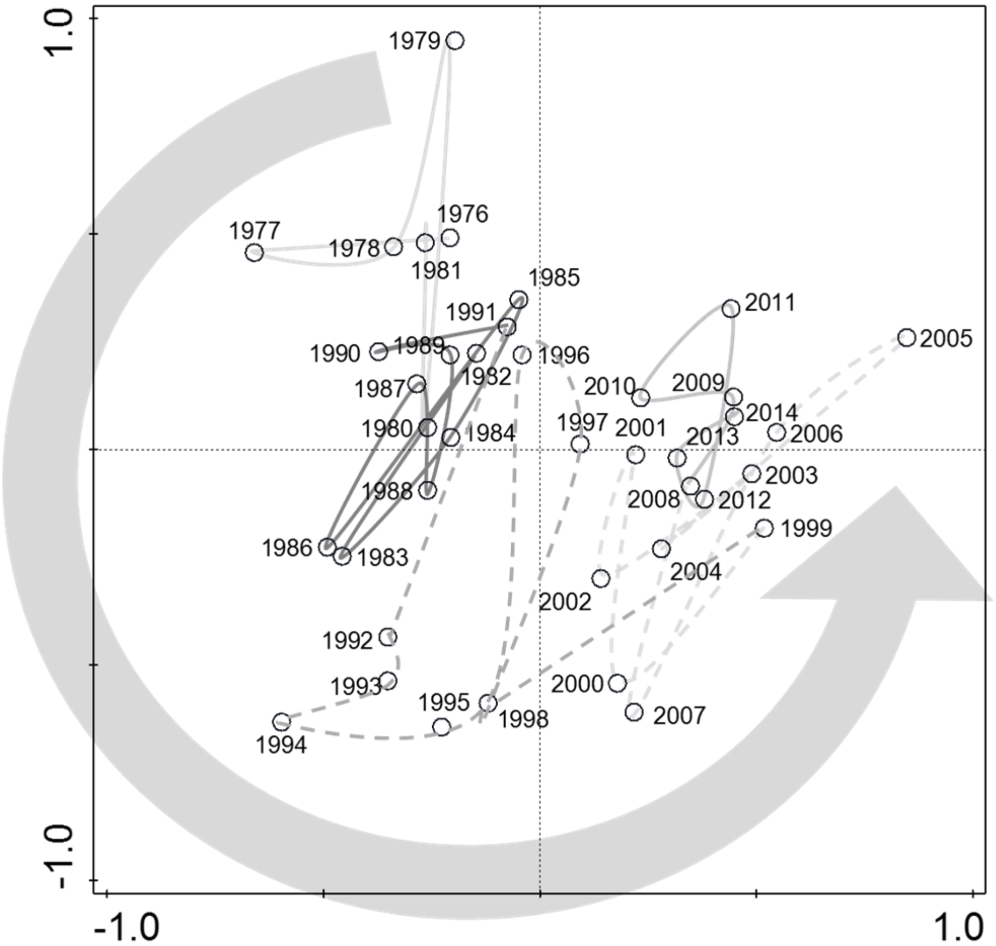


Figure 10: PCA ordination graph on historical environmental data of lake Markermeer (1976-2014) with explained variance 18.88% on first axis and 13.04% on second axis (see text for variables included in analysis). Only the years are plotted with the grey arrow pointing out the general direction of the development of environmental conditions in the lake through the years. Different types of connection lines refer to periods with dissimilar environmental conditions.

When regarding the ordination by PCA of years based on the environmental dataset for the entire history of lake Markermeer, various clusters of time periods could be distinguished: 1976-1981, 1982-1991, 1992-1998, 1999-2008, and 2009-2014 (indicated with different line styles in Figure 10). The line connecting the years followed an anticlockwise direction in the graph. This indicated that the environmental conditions in lake Markermeer gradually changed over the years in these time periods. The transition years that deviated from the gradual pattern (i.e. 1980-1982, 1991-1992, 1996-1997, 1999, and 2005; Figure 10) could indicate periods of severe changes in environmental conditions. The distinguished year clusters can be characterised by environmental conditions (Figure 11). The explained variation (axes cumulative accounting for 18.88% (axis 1); 31.92% (+axis 2); 42.86% (+axis 3); 51.81% (+axis 4)) indicated that there was not one axis explaining the clustering pattern but several parameters attributed to the perceived environmental developments. The analyses showed that there was a strong seasonal effect. The second strongest influence was turbidity (influenced by the parameters visibility, suspended matter, and Chl a). Chl a was more related to suspended matter than to visibility, meaning that phytoplankton added to the turbidity of the lake, but that the effect of suspended matter was stronger.

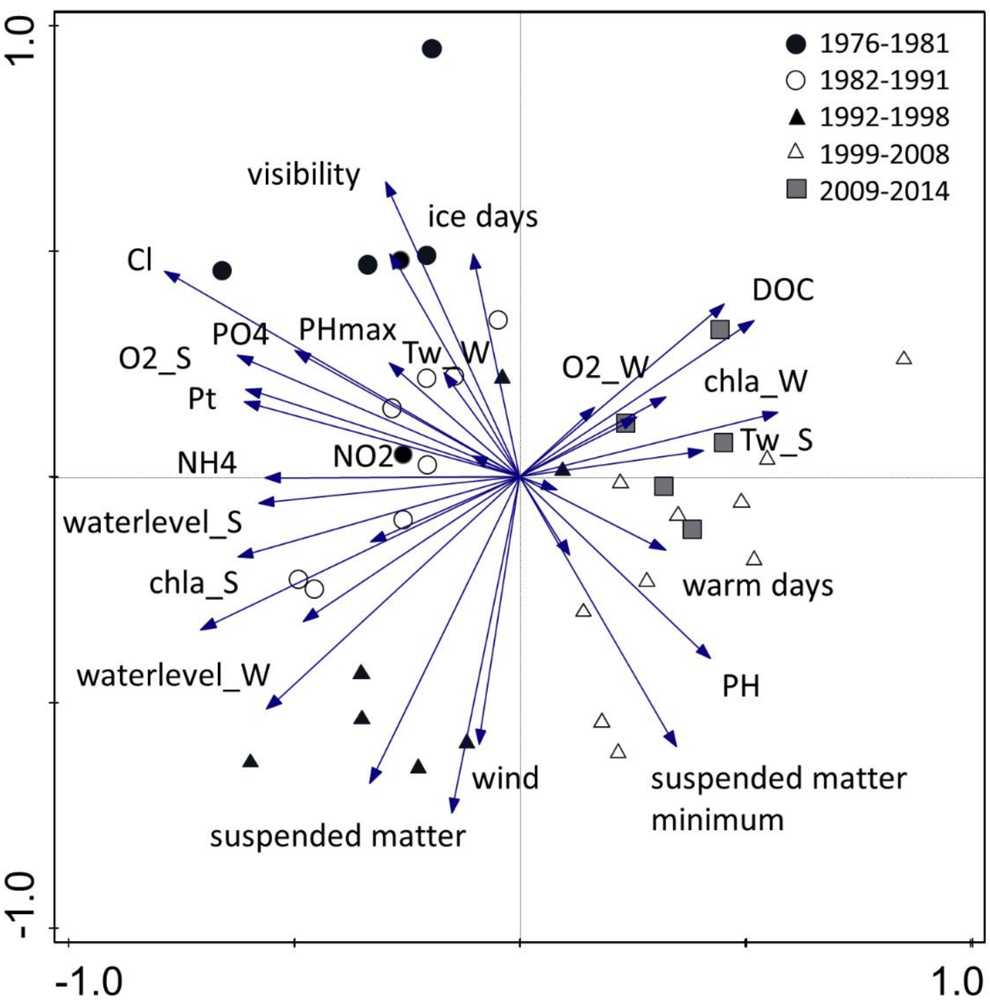


Figure 11: PCA ordination biplot graph on historical environmental data of lake Markermeer (1976-2014). Variables are mentioned in Materials & Methods section, years are referred to by symbols, with different symbols for each decade. The arrows refer to environmental variables. Eigenvalues for the four axes are respectively 0.1888; 0.1304; 0.1094 and 0.0895.

When characterising the development of environmental conditions in lake Markermeer, the first years after the closure of the Houtrib dike were characterised by decreasing chloride concentrations, cold winters, low water temperatures and good clarity. Conditions in the 1980s were influenced by high nutrient concentrations and high pH values. The late 1980s to early 1990s was a less characteristic period during which water levels played a pronounced role. The mid 1990s was a dynamic period in which drastic fluctuations occurred, for example 1995 and 1998 were turbid years with high levels of suspended matter and severe wind activity. From the year 2000, siltation processes became less decisive, but higher temperatures, increased Chl a concentrations during the winter, and DOC became more significant parameters.

In summary, our analyses showed no indication of a trend towards more suspended matter in lake Markermeer. The visibility decrease in the early 1990s was not related directly to the amount of suspended matter, but the correlation with wind activity suggested that silt concentrations were relatively high during the mid-1990s because of an increased resuspension process driven by wind. After 2009, suspended matter, Chl a concentrations and visibility were comparable to the situation before 1989. From ecological perspective, changes induced by the parameters broadly influencing turbidity occurred in the mid-1980s, the early 1990s, the early 2000s, and 2010. Direct effects on the ecological functioning of the lake due to sudden decreases or increases in environmental conditions could have played a prominent role in 1979, 1987, 1990, and 2000.

5 Synthesis

5.1 Silt dynamics trapped in artificial morphology

The review shows that amount of silt in lake Markermeer did not increase over time. If the amount of silt did not increase over time, the only relevant change in silt load would be caused by translocation, changes in top layer characteristics, or increased resuspension of silt. So not the amount of silt but complex co-resuspension processes driven by wind activity and waves determine turbidity, nutrient availability and ecological developments in lake Markermeer. Resuspension, turbidity, silt and phytoplankton cannot be regarded as separate factors in the complex co-resuspension dynamics (e.g. Brinkmann *et al.* 2019). Silt and phytoplankton are most directly subjected to these processes with turbidity and light regime restrictions as output which in turn limit the possibilities for ecology and nutrient availability.

The effects of dynamic wind induced processes are enhanced by the highly artificial morphology. This highly artificial morphology even largely defines the perspective for ecosystem development in Lake Markermeer. The combination of the physical aspects such as steep bank zones, the lack of low dynamic zones and the limited shallow areas, forms a huge obstacle for ecological development in the lake since these conditions limit the prospects for the development of essential habitats, biodiversity, and heterogeneous communities. As a result, macroinvertebrate assemblages remain very poor and aquatic and riparian vegetation cannot not fully develop and reed vegetation on the banks remains weak and under constant attack of erosion (Coops 2002, Van den Berg 2014). The current artificial morphology does not meet the conditions needed for essential settlement, nursery and succession for aquatic and riparian species, and limits the potentials of the ecosystem to cope with (temporal) changes in environmental conditions. Not only the lack of land-water gradients, but also the fixed water level and continuous erosion are important aspects of the artificial morphology that severely limit the prospects of the ecosystem lake Markermeer. Overall, the ecosystem has not enough buffering capacity to cope with temporary distortions and therefore immediately responds to changing conditions.

The historical trend analyses of this review show that lake Markermeer has a unique ecosystem that can be characterised as a shallow freshwater lake with a marine history and sediment as it originates from a brackish estuary of the Zuiderzee (period before 1932). From 1932 to 1976 lake Markermeer was part of lake IJsselmeer, which was then a closed inner sea that lost its salinity within a few years. Even after becoming freshwater, the lake underwent several developments in environmental conditions and ecology and it seems that the developments are still ongoing. The separation of lake IJsselmeer by closing the Houtrib dike hugely influenced nutrient availability and turbidity, as water exchange with the larger lake IJsselmeer system became significantly less and export of resuspended silt to lake IJsselmeer area was strongly restricted and the silt was retained within lake Markermeer.

5.2 Five phases in ecological history of lake Markermeer

Since the separation by the Houtrib dike, roughly five characteristic phases can be distinguished for lake Markermeer. This clustering pattern was explained by several parameters attributing to the perceived environmental developments. The first period after separation (1976-1981) was characterized by poor water quality (amongst others high chloride concentrations) with high nutrient inputs deriving from rivers in the catchment and direct sewage water inflow. Fish densities were relatively high and *D. polymorpha* had colonized every bit of hard substrate in this period. After installation of the waste water treatment plant in the city of Amsterdam and reductions in nutrients in the main rivers, phosphorus loads into lake Markermeer dropped quickly in the early 1980s (Van der Geest *et al.* 2018). Realization of the measures to reduce eutrophication of surface waters ended the hyper-eutrophic conditions in the water of the lake.
During the second period from 1982 to 1990, surface waters were characterized by eutrophic conditions and high pH values. The phytoplankton population mainly consisted of green algae, which forms a good quality food source for *D. polymorpha* and their population remained abundant. After more than 50 years presence in the area, *D. polymorpha* could be considered to be integrated into their allochthonous environment with other species adjusted to feed on the abundant available species (e.g. Strayer and Malcom 2006). However, in the 1980s fish biomass dropped, coinciding with fishery activities in the lake (Mous *et al.* 2003). At the end of this period, the population of *D. polymorpha* started to declined. This decline in population density and vitality was not likely induced acute adverse environmental conditions,

e.g. conditions indicating disturbance of nitrification and accumulation of toxic ammonia near the sediment were not detected (Van Nes 2005).

A third dynamic period followed (1991-1998), in which drastic fluctuations occurred, for example 1995 and 1998 were very turbid years while during the summers of 1993 and 1994 high surface water pH levels (>9) were measured. The visibility in the lake decreased in the early 1990swhich correlated strongly with wind activity. This suggests that silt concentrations were relatively high during the mid-1990s because of an increased resuspension process driven by wind. High silt content reduce the food uptake of adult *D. polymorpha*, however, at concentrations >0.5 g L-1 juveniles cannot acquire food anymore (Penning *et al.* 2013). Furthermore, the decline of *D. polymorpha* in lake Markermeer resulted in a lower filtration rate of the water column elongating periods with turbid conditions. Under these turbid conditions, only limited macrophyte development occurred on the western shore of the lake. Over this period, phosphorus and Chl a concentrations slowly dropped and resulted in shifts in the phytoplankton community composition observed after 1992-1993 (Noordhuis 2010).

In the fourth period (1998-2010), the alterations in phytoplankton community resulted in an increase in winter blooms and a shift in phytoplankton size classes. From the year 2000, siltation processes became less decisive and macrophyte communities extended along the western coast of the lake. Lake water reached higher temperatures during the warm summers in this period, approach values critical for the smelt population. Less waterfowl visited lake Markermeer, especially benthivorous and piscivorous species, and *D. polymorpha* populations remained small. At the end of this period, *D. r. bugensis* appeared as new benthic filter-feeder and started to replace the functions of *D. polymorpha*. This resulted in increased the benthic-pelagic coupling in the lake.

In the latter years (analysed from 2010 to 2014), the efforts to decline the nutrient flux in rivers and their adjacent, had paid off, resulting in low available phosphorus concentrations in the growing season. In this fifth period, suspended matter, Chl a concentrations and visibility were comparable to the situation before 1989. Macrophyte meadows slowly extended in this period, providing some seasonal habitat diversity in the lake. Still, macroinvertebrates and fish occurred only in low densities. All fish species were still present, but their densities and biomass did not increase. Diversity of macroinvertebrates remained low, with a few species dominating the benthic fauna community. Although contaminants could have accumulated in sediments of river deltas, no indications for potential ecotoxicological effect on benthic organisms have been measured in lake Markermeer. Apparently, reaching the defined nutrient goals does not guarantee recovery of all component of the lake ecosystem in this strongly compartmentalized delta.

5.3 Predicting future ecological development in multi-stressed environment

For a multi-stressed system, it may imply that when the assumed stress of eutrophication is solved, another stress factor prevents the ecosystem from developing into a productive and resilient ecosystem. Studies performed during the different phases mentioned for lake Markermeer, focus on different stress factors that are thought to limit ecology. Factors mentioned are in subsequent order: salinity, the lack of substrate, nutrients, isolation of the lake by the Houtrib dike, altered water levels, predation rates, wind- and water dynamics, silt, and flocculation between phytoplankton and silt particles. This makes clear that there may be more factors affecting this ecosystem. During the period of severe eutrophication, we could understand how the ecosystem reacted due to eutrophication, but it is more complex to predict how the ecosystem will react once this stressor is relieved. Especially in an constructed ecosystem such as lake Markermeer, which has always been a turbulent water system with soft sediment under influence of erosion and resuspension dynamics, it seems that processes are complex and are difficult to compare to those in a clear water lake with abundant water plant vegetation. It is therefore questionable if clear water systems should be a reference for lake Markermeer, and whether clear water is necessary to reach a resilient ecosystem. Lake Markermeer has functioned as a food source for fish and birds before, when it already was a turbulent lake with a food web that relied on the pelagic zone. This importance of benthic filter-feeders stimulating bentho-pelagic coupling has been observed as a key process in many aquatic ecosystems such as rivers, shallow lakes and littoral zones.

Finally, what can be expected from the construction of the Marker Wadden in terms of improving the ecosystem and nutrient availability of the lake? Creating gradual land-water gradients could locally provide nutrient input to improve especially the benthic primary production and the quality and availability of organic matter as food source for consumers. These constructed islands could add to the amount of shallow zones, provide low dynamic shelter areas, and act as nursery grounds. However, as many nature development projects in the lake IJsselmeer area proved, erosion, sedimentation, a fixed unnatural water regime and steep artificial shores will remain an obstacle for natural development and ecology. Reconnecting the shallow wetlands of the Oostvaardersplassen and the Lepelaarplassen to the lake would largely enhance the amount of shallow areas and natural water-land gradients. Since these areas are located behind the dikes of the embankment, the risk of wind-induced erosion of these gradients is negligible. However, the large difference in water tables (few meter) between these wetlands and the lake, makes the construction of the connection challenging. Given the restrictions in morphology of the constructed region as a whole, makes building with nature a challenge and it may require continuous management to maintain these land-water gradients. Birds will certainly visit the islands, but it will be more a challenge to maintain the (pioneer)habitats essential for birds breeding on the islands and to meet the food requirements . The latter are restricted to a small area from their nests (often within few kilometer) for gathering sufficient food to raise their offspring. Previous studies have shown that an increase of habitat, which the islands will provide, and even an increase in prey species, not necessarily guarantee an increase of nutrition value of these prey (Bij de Vaate 2008, Bij de Vaate and Jansen 2012, Ibelings 1997). With the current nutrient situation and aquatic food web as reference, food availability might form an issue and needs to be well reflected on.

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