

## The impact of climate change on lakes in the Netherlands: a review

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### Abstract

Climate change will alter freshwater ecosystems but specific effects will vary among regions and the type of water body. Here, we give an integrative review of the observed and predicted impacts of climate change on shallow lakes in the Netherlands and put these impacts in an international perspective. Most of these lakes are man-made and have preset water levels and poorly developed littoral zones. Relevant climatic factors for these ecosystems are temperature, ice-cover and wind. Secondary factors affected by climate include nutrient loading, residence time and water levels. We reviewed the relevant literature in order to assess the impact of climate change on these lakes. We focussed on six management objectives as bioindicators for the functioning of these ecosystems: target species, nuisance species, invading species, transparency, carrying capacity and biodiversity. We conclude that climate change will likely (i) reduce the numbers of several target species of birds; (ii) favour and stabilize cyanobacterial dominance in phytoplankton communities; (iii) cause more serious incidents of botulism among waterfowl and enhance the spreading of mosquito borne diseases; (iv) benefit invaders originating from the Ponto-Caspian region; (v) stabilize turbid, phytoplankton-dominated systems, thus counteracting restoration measures; (vi) destabilize macrophyte-dominated clear-water lakes; (vii) increase the carrying capacity of primary producers, especially phytoplankton, thus mimicking eutrophication; (viii) affect higher trophic levels as a result of enhanced primary production; (ix) have a negative impact on biodiversity which is linked to the clear water state; (x) affect biodiversity by changing the disturbance regime. Water managers can counteract these developments by reduction of nutrient loading, development of the littoral zone, compartmentalization of lakes and fisheries management.

### Introduction

Global average surface temperatures on earth have increased by approximately 0.6 °C over the last century. The past two decades were the warmest

since 1861 (Houghton et al. 2001). Without proper action against anthropogenic greenhouse effects the Intergovernmental Panel on Climate Change (IPCC) predicts increases in global average surface temperature of 1.4 to 5.8 °C for the year 2100

(Houghton et al. 2001). Northern Europe will experience an increase in the frequency and intensity of precipitation. However, regional climate changes are harder to predict as small spatial fluctuations in climate patterns have far-reaching consequences for regional climate.

Ecological responses to recent climate change have been demonstrated across different natural systems (Walther et al. 2002; Parmesan and Yohe 2003). Long time series analyses of physical and biological characteristics of fresh water ecosystems in Northern Europe have shown that climate change affects the winter concentration of nitrate nitrogen (George et al. 2004), the concentration of dissolved reactive phosphorus (George et al. 2004), and the timing of seasonal succession events of phytoplankton and zooplankton (Müller-Navarra et al. 1997; Weyhenmeyer et al. 1999; George 2000; Gerten and Adrian 2000; Straile 2000; Straile and Adrian 2000; Straile 2002; Carvalho and Kirika 2003; George et al. 2004). However, differences in lake morphometry and site specificity result in differences in the relative effect of climate change on ecosystem variables (Gerten and Adrian 2001; George et al. 2004).

Because of their smaller volume and absence of stratification in summer, shallow water bodies are less influenced by meteorological conditions in the preceding winter than deeper waterbodies, and respond more directly to the prevailing weather conditions (Gerten and Adrian 2000, 2001). The importance of morphometry and site specificity, added to the strong deviations of local climate from global climate, imply that specific predictions on the effects of climate change can only be made with a specific type of ecosystem and a specific region in mind.

Here, we focus specifically on large, shallow lake ecosystems in the Netherlands. Several parameters of climate change are relevant to these ecosystems: changes in temperature, ice-cover, wind and precipitation. Secondary effects of climate change may include changes in nutrient loading, residence time and water level. In contrast to other large, shallow European lakes, the Dutch shallow lakes have a poorly developed littoral zone partly due to their non-natural origin and partly due to continuous mixing and high turbidity. Furthermore, the highly controlled hydrology of Dutch lakes results in their water level to be unnaturally stable. The combined effect of the absence of a true littoral

zone, and the non-natural stable water levels might render the Dutch lakes less resilient to external stress factors (Scheffer et al. 2001a, 2001b) – such as climate change – than other lakes in Europe.

In this paper, we will give a state-of-the-art review of the observed, predicted and potential effects of climate change on shallow lakes in the Netherlands, using proven bioindicators for the functioning of these freshwater ecosystems. The potential deleterious effects of climate change will be judged by indicators at the species level, i.e. target species, nuisance species and invading species, and by indicators at the ecosystem level, i.e. transparency (in principle a physical parameter but used here as an indicator of the associated ecosystem state), carrying capacity and biodiversity. First, we describe the general characteristics of shallow lakes in the Netherlands as compared to shallow lakes in other parts of Europe. Next, we discuss the projected climate change scenarios for the Netherlands and how each of the indicators of the functioning of shallow lakes in the Netherlands is affected by climate change. In the discussion we integrate these findings into an impact assessment, put them into an international perspective, and evaluate their implications for management.

### Shallow lakes

The main Dutch freshwater lakes (Table 1) are shallow, varying in depth from 1 to 5 m (Gulati and Van Donk 2002). They are located in the lower catchment area of the river Rhine and range in size from a few hectares to more than 100,000 ha. Sand, clay and peat are the main substrate types and the water residence time in lakes varies from 1 to 14 months. Most of the Dutch lakes are man-made and lack a well-developed littoral zone. Water levels are regulated such that water tables are kept relatively low in winter to facilitate run off of surplus water and relatively high in summer to facilitate drainage of water to agricultural land, i.e. the regulation leads to reversal of the natural regime. Due to their controlled hydrology and poorly developed littoral zone, the Dutch lakes are rather difficult to compare with many other shallow lakes in Europe. In a more natural situation, most of these lakes would be comparable with: Lake Peipsi (Russia/Estonia), Lake Võrtsjärv (Estonia), Lake Uluabat (Turkey),

Table 1. Some general characteristics of the major shallow lakes in the lower catchment of the river Rhine.

	Water level	Transparency (cm)	Transparency ( $\mu\text{g l}^{-1}$ )	PVI (%)	Residence time (year)	Bottom substrate	Depth (m)	Surface area (ha)	References
Lake Volkerak	Constant	80–120	20–50	10	0.16	Sand	5.2	4500	Breukers et al. (1997), Lammens et al. (2002)
Lake IJssel	Constant	40–60	40–80	2.1	0.33	Sand	4.5	120,000	Lammens (1999), Lammens and Van den Berg (2001), Ibelings et al. (2003)
Lake Veluwe	Constant	50–120	10–40	89	0.15	Sand	1.5	3400	Lammens et al. (2002), Portielje and Rijdsdijk (2003)
Lake Wolderwijd	Constant	50–90	10–40	70	0.35	Sand	1.9	2500	Portielje and Rijdsdijk (2003)
Lake Marken	Constant	30–50	40–60	4.8	1.2	Clay	3.5	67,000	Lammens (1999)
Lake Loosdrecht	Constant	30–40	50–100	5	1	Peat	1.8	1500	Moss et al. (2003b), Pel et al. (2004)
Lake Tjeukemeer	Constant	30–40	50–100	1	0.35	Sand/peat	1.5	2200	Lammens et al. (2002)
Lake Eem	Constant	25	100	1	0.08	Clay/sand	1.7	1500	Portielje et al. (2001)

All lakes given are located in the Netherlands and man-made by closure of sea-arms and peat excavation. They lack a natural hydrological regime. Most of the lakes are in the turbid phytoplankton-dominated state. Data on transparency, chlorophyll and PVI (Percentage Volume Infested by macrophytes) represent annual averages over the past decade.

Loch Leven (Scotland) and Lake Balaton (Hungary) (Table 2).

Being shallow, all of these lakes are permanently mixed (polymictic) and the sediments are regularly disturbed by wind action. Consequently, there is no stratification of temperature or oxygen. In the Netherlands, water temperature shows annual maximum of 20–22 °C at the beginning of August and a minimum of 2–4 °C at the end of January (Mooij and Van Tongeren 1990). Most of the Dutch lakes indirectly receive eutrophic water (total P, 150–300  $\mu\text{g l}^{-1}$ ; total N, 4–9  $\text{mg l}^{-1}$ ) from the river Rhine. The chlorophyll-*a* levels in the lakes range between 25 and 90  $\mu\text{g l}^{-1}$ , total P between 100 and 300  $\mu\text{g l}^{-1}$  and total N between 2 and 3.5  $\text{mg l}^{-1}$  (Portielje and Van der Molen 1998). The biomass of the phytoplankton in these mesotrophic to eutrophic systems may often be limited by underwater light rather than P or N.

Temperate shallow lakes have been considered to be in one of two alternative stable states, a clear macrophyte-dominated state or a turbid phytoplankton-dominated state (Scheffer et al. 1993). Due to eutrophication, the majority of the Dutch shallow lakes have become turbid, with transparencies ranging from 0.25 to 0.5 m, so that macrophytes are suppressed by light limitation. Similar trends can be observed in large shallow lakes in other parts of Europe (Table 2). Biomanipulation can cause a switch from the turbid to the clear state and thus enhance macrophyte growth (Van Donk et al. 1990; Meijer 2000). When Secchi-disc transparency depth exceeds about 1 m, enough light reaches the bottom in large areas of most lakes and macrophytes have the potential to develop as they did in the 1990s in ca. 70–90% of the area in lakes Veluwemeer and Wolderwijd (Lovvorn and Gillingham 1996; Portielje and Rijdsdijk 2003).

The food webs in these eutrophic lakes in the turbid state are relatively simple as the species diversity in the lakes is low. Phytoplankton is dominated during the largest part of the summer (or even year round) by cyanobacteria with concentrations of chlorophyll-*a* ranging between 50 and 150  $\mu\text{g l}^{-1}$  (Van der Molen and Portielje 1999). Zooplankton is represented by a few cladoceran species (mainly *Bosmina longirostris*, *Daphnia galeata* and *Chydorus sphaericus*) and cyclopoid copepods, usually with spring peaks of several hundred ind.  $\text{l}^{-1}$  and low concentrations during the summer (Vijverberg and Boersma 1997).

Table 2. General characteristics of and observed ecological response on climate change of large shallow lakes in Northern Europe.

	Water level	Transparency (cm)	Transparency ( $\mu\text{g l}^{-1}$ )	Chlorophyll PVI (%)	Residence time (year)	Bottom substrate	Depth (m)	Surface area (ha)	Ecological response to climate change	Source
Lake Peipis (sensu lato), Estonia/Russia	Unregulated	200	20	1	1.1	Peat	7.1	355,500	Decrease of vendace ( <i>Coregonus albus</i> )	Noges et al. (1996), Van Eerden and Lammens (2001)
Lake Balaton, Hungary	Regulated	40–70	10–30	1–3	3–8	Silt	3.25	59,300	Cyanobacteria blooms	Specziar and Biro (1998), Kovacs et al. (2003)
Lake Võrtsjärv, Estonia	Unregulated	110	22	1	1	Sand Gravel	2.8	27,000	Change in water levels, Cyanobacteria blooms	Haberman and Laugaste (2003), Moss et al. (2003b), Noges et al. (2003), Kisand and Noges (2004)
Lake Uluabat, Turkey	Regulated	40–160	20–80	30–50		Clay Peat	2.5	19,900	Water level changes	Lammens et al. (2001)
Loch Leven, Scotland	Unregulated		20–40	0.43		Sandstone	3.9	1330	Shifts in plankton phenology	Carvalho and Kirika (2003)

All lakes given are located outside the Netherlands. Data on transparency, chlorophyll and Percentage Volume Infested (PVI by macrophytes) represent annual averages over the past decade.

In some lakes the zooplankton community is dominated by rotifers (Gulati and Van Donk 2002). Zoobenthos is dominated by chironomids and oligochaetes with biomasses of 1–10 g fresh weight  $\text{m}^{-2}$  (Lammens et al. 1985). The fish are mainly represented by cyprinids, particularly bream *Abramis brama* and the fish standing crop amounts from 100 to 200  $\text{kg ha}^{-1}$  (Lammens et al. 2002). This low diversity occurs in the turbid state. At total-P levels of 50–150  $\mu\text{g l}^{-1}$  a switch can occur to a clear vegetation-rich state with a high diversity (Scheffer 1998) as was observed in Veluwemeer and Wolderwijd after a drastic reduction of the bream population amongst other restoration measures. Also, an increase of the zebra mussel population may have contributed to the return of the clear-water phase in some lakes (Lovvorn and Gillingham 1996; Portielje and Rijdsdijk 2003).

### Climate change

In the Netherlands, in the past century an increase of 0.8 °C can be noted in yearly averages of air temperature (Klein Tank 2004). This increase is correlated with an increase in world average temperature of 0.6 °C. Further analysis of the historical data showed that the strongest temperature increases could be observed during late winter and early spring (Oldenborgh and Van Ulden 2003). Since 1901, an increase in average winter precipitation has been observed (Oldenborgh and Van Ulden 2003). Based on the findings of the third IPCC report (Houghton et al. 2001) the KNMI (the Royal Netherlands Meteorological Institute) developed three climate scenarios for the Netherlands for the 21st century (Table 3). There is considerable uncertainty in these climate projections concerning the changes in the amount of precipitation, the influence of cloud cover, the influence of ocean circulation on the regional climate and the changes in climate variability (e.g. the frequency of events such as storms, extreme warm winters or extreme wet years).

#### Temperature and ice cover

The KNMI scenarios predict temperature increases varying from 1 to 6 °C (Table 3). Water temperature in shallow lakes, which are polymictic, is tightly coupled to air temperature: any dif-

Table 3. KNMI climate change scenarios for the Netherlands in the year 2100 based on the 3rd IPCC report.

	Low estimation	Medium estimation	High estimation
Temperature	+1 °C	+2 °C	+4-6 °C
Average summer precipitation	+1%	+2%	+4%
Summer evaporation	+4%	+8%	+16%
Average winter precipitation	+6%	+12%	+25%
Intensity of extreme rainfall events	+10%	+20%	+40%
Frequency of extreme rainfall events	47 yrs	25 yrs	9 yrs
Sea level rise	+ 20 cm	+ 60 cm	+ 110 cm

The sea level rise is corrected for lag and subsidence (source KNMI/IPCC).

ference between air temperature and water temperature is reduced by 50% within three days (Mooij and Van Tongeren 1990; Gerten and Adrian 2001). Given the tight relationship between air temperature and water temperature, any change in the former will mostly result in a corresponding change in the latter. In about 50% of the winters, the Dutch lakes have a partial or complete ice cover for a few days to a few weeks. A climate-related rise in temperature would cause a drop in the frequency, extent and duration of periods with ice cover.

#### *Precipitation*

The projected increase in precipitation will be augmented by periods with extreme precipitation resulting in an increased frequency of so-called 'wet years' (Table 3). The predicted changes in precipitation and evaporation in Europe (Houghton et al. 2001) will increase discharges of the river Rhine during winter and spring (Middelkoop 2000), whereas extended periods with low water discharge may be expected in summer and autumn (Loaiciga et al. 1996). As a result, winter water levels would increase whereas lower levels are likely in summer, potentially leading to drying of the shallowest parts of the lakes. Also, water residence time of shallow lakes is expected to decrease in winter and to increase in summer.

#### *Wind/waves*

The extent of changes in wind and changes the frequency of storm events due to climate change is still highly uncertain. In the past 41 years, the

frequency of storms has decreased in the Netherlands (Klein Tank et al. 2002). Wind speeds in the Netherlands are sufficient to homogenize the water in lakes up to some 10 km<sup>2</sup> in surface area. Significant wind resuspension of sediment occurs about every second day in a medium-sized 'peat lake' in summer, and resuspension of > 50% of the lake area is not exceptional. Wind-induced resuspension markedly increases vertical light attenuation, and thus directly limits primary production (Gons et al. 1991). Despite the observed decrease in the number of storms, climate scenarios predict only a 2% increase in the maximum wind speed in 25 yrs (Dorland et al. 1999).

#### *Consequences for nutrient loading*

Climate change will affect nutrient loading of lakes in the Netherlands in different ways. Changes in water supply may have an effect on the water chemistry of lakes, as the increased water supply of riverine origin (carrying high loads of nitrogen compounds, chloride and sulphate) will affect local water quality. Furthermore, an increase of net precipitation in winter, and especially an increase in extreme rainfall events, will tend to increase the P-loading of lakes. The P-loading from smaller streams is to a large extent determined by peak discharges following heavy rainfalls. In stream catchments with agricultural land-use and a history of fertilization, P-saturation is higher in the top soil layer. Thus, higher groundwater levels will result in higher concentrations in the water that is discharged to surface water (Van der Molen et al. 1998). In their study on four lakes in the English Lake district, George et al. (2004) recorded higher soluble reactive phosphorus concentrations after

heavy rainfall in the lakes with a short retention time. Nitrogen concentrations in streams depend less on stream discharge, and losses of nitrogen during transport in a catchment mainly occur by denitrification, which is largely governed by water temperature. Increasing temperatures will thus cause higher denitrification rates and higher N-losses in soil and surface waters, and thus to lower N-loading of downstream situated lakes. In conformity with this explanation, George et al. (2004) observed lower concentrations of nitrate during mild winters in their study on four lakes in the English Lake district. As these effects appeared to be relatively independent of the nature of these lakes, the findings of George and co-workers may be applicable to the Dutch situation.

### Ecosystem management objectives

The primary goal of water management in the Netherlands is to protect the country against

flooding and to provide good conditions for agriculture. The second goal is to obtain a good water quality and ecological conditions according to the European Water Framework Directive and the Birds and Habitats Directives. In practice, this means a stimulation of target species, mainly birds, and attempts to reduce nuisance and invasive species. Of course, the occurrence of these species depends to a large extent on ecosystem processes and states. Of these, we selected water transparency as the most relevant ecosystem state variable of shallow lakes (Scheffer 1998). It is also the prime goal in management of shallow lakes (Figure 1). In addition, we discuss the more general factors of carrying capacity and biodiversity. Carrying capacity is defined as the biomass of a population that can be supported by an ecosystem; whereas biodiversity is mostly simply measured as the number of species or genera in a certain group (e.g. fish, macrofauna, phytoplankton, etc.) at a certain site, but more complex indices are also applied widely (Purvis and Hector 2000).

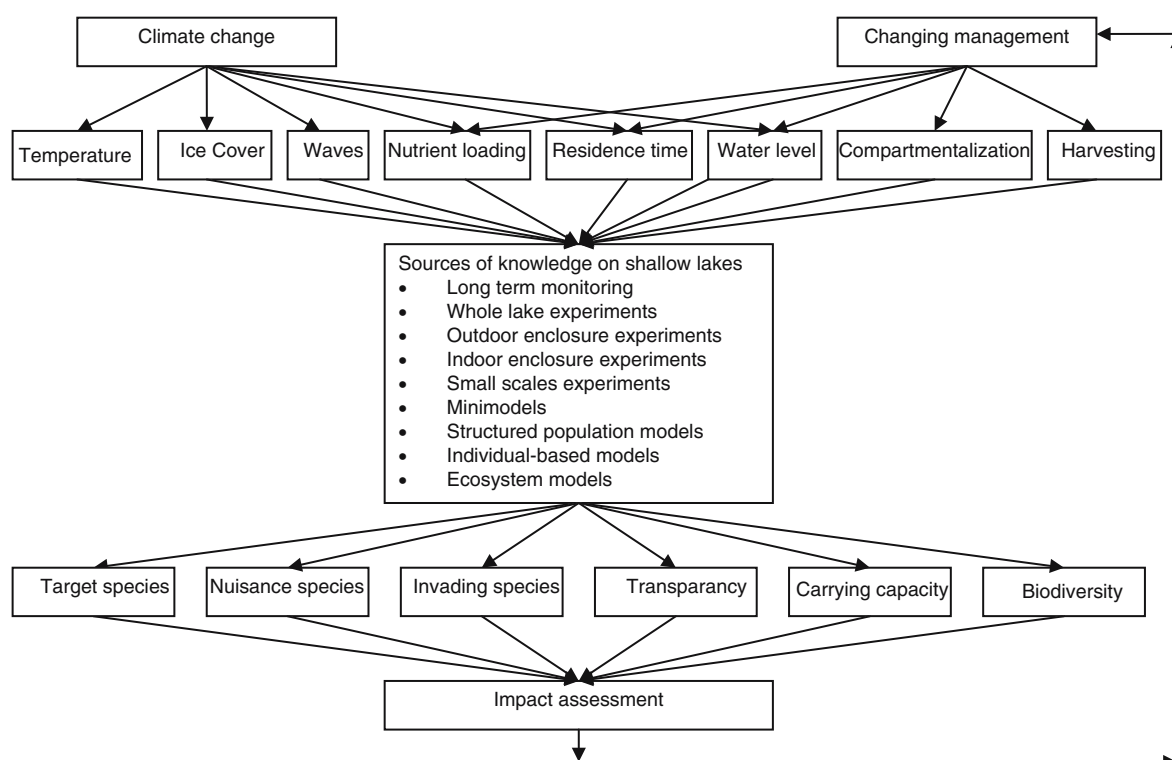


Figure 1. Aspects of climate change and management objectives relevant to an impact assessment of the effect of climate change on shallow lakes in the Netherlands. Also listed are the various empirical and theoretical approaches from which knowledge on the structure and functioning of shallow lake ecosystems was obtained. Note that several factors are both affected by climate change and changing management and that there is a feedback loop from impact assessment to changing management.

### Target species

Target species are defined as species that are valued positively in nature management, as opposed to the nuisance species and invasive species that are valued negatively. Target species can be of several types:

- Rare species, that always occur in small numbers;
- Endangered species, that have seriously declined in densities;
- Vulnerable species, that have a limited distribution;
- Susceptible species, that potentially respond strongly to habitat changes;
- Typical species, which are characteristic for a given habitat type;
- Core species, that occur in disproportionately large numbers in a certain region;
- Keystone species, with a profound effect on ecosystem functioning.

The first three types typically feature in so-called red lists, whereas in the Netherlands core species are listed in a so-called blue list (Osieck and Hustings 1994). *Daphnia* and *Dreissena* are important keystone species in Dutch shallow lakes due to their profound effects on algal biomass and hence the transparency of lakes. They are discussed separately in relation to the management objectives transparency and invading species, respectively.

Shallow lakes in the Netherlands contain a large number of core water bird species (Scott and Rose 1996). Of these, tundra swan (*Cygnus columbianus*), scaup (*Aythya marila*), and smew (*Mergellus albellus*) occur in such internationally significantly high numbers that they have been included on the blue list (Osieck and Hustings 1994). The concentration of water birds in the Netherlands is due to the presence of the many nutrient-rich and shallow lakes, located along the main East Atlantic flyway and positioned just south-west of the 0 °C January isotherm, which prevents long-term ice cover during most winters (De Leeuw 1997).

The forecasted increase in winter temperatures, which is predicted to be especially pronounced in northeastern Europe (Parry 2000), will shift the 0 °C January isotherm in northeastern direction.

As a result, the shallow lakes of the Netherlands are expected to lose their importance for core species like whooper swan (*Cygnus cygnus*) and goosander (*Mergus merganser*) that nowadays show influxes during severe winters. Many other water bird species like gadwall (*Mareca strepera*), teal (*Anas crecca*), pochard (*Aythya ferina*), tufted duck (*Aythya fuligula*), and scaup (*Aythya marila*) that often overwinter in large numbers in the Netherlands, can be expected to do so further north-east, for instance in the Baltic region. Such shifts in non-breeding distribution in response to climate change have been observed in wader bird species (Austin and Rehfish 2005). Many northern waterfowl species, particularly males and older individuals, tend to overwinter as close as possible to the breeding grounds in order to return there early (Sayler and Afton 1981; Suter and Van Eerden 1992). It is unknown, however, if food limitation will preclude this option for this latter group of birds. At present, it seems unlikely that the birds already deplete the food resources in the Baltic region during the autumn; it is, however, unknown if the resources would last the whole winter.

Water depth is a critical habitat factor in water bird feeding by diving and up-ending (Lovvorn and Gillingham 1996; De Leeuw 1997; Nolet et al. 2001). The predicted, moderate increase in the average, as well as the variation in, rainfall in winter in Northern Europe (Parry 2000), will lead to years with exceptionally high water levels in some regions. Because short periods of water level increase are sufficient to trigger the departure of diving and up-ending birds, climate change is thought to increase the incidence of rainfall-related mass movements of water birds. With respect to fish, pike (*Esox lucius*) is a target species (typical species), which is tending to recover and rehabilitate in Dutch lakes. Under more natural conditions the fish community of Lake IJssel would closely resemble that of Lake Peipsi (Estonia), where a broad littoral shoreline with large stands of emergent vegetation creates excellent conditions for pike (Van Eerden and Lammens 2001). Only if climate change leads to higher water levels in spring would the pike population be stimulated by enhanced spawning possibilities.

We conclude that climate change might reduce the numbers of several target species of wintering

birds, mainly because of wintering further north. Effects on other target species such as pike are considered to be of minor importance.

#### *Nuisance species*

Various species of bacteria, phytoplankton, insects and macrophytes may be broadly referred to as nuisance and harmful species due to problems they cause in water management. Nuisance may be of various types, e.g., clogging of filters in drinking-water plants or reducing the water transparency required for swimming, whilst harmful species are the ones that can pose threats to human and animal health.

Temperature rise as one of the driving forces for internal eutrophication causes enhanced development of nuisance cyanobacteria (Robarts and Zohary 1987; Blenckner 2001). Adrian et al. (1995) described a change in phytoplankton community structure from one dominated by diatoms and cryptophytes to that by cyanobacteria related to mild winters. Conditions during winter may also affect the 'inoculum' of species in spring and thus the succession pattern of the whole year (Adrian et al. 1999). Studies on Tjeukemeer (Moed and Hoogveld 1982) and Veluwemeer (Reeders et al. 1998) indicated that filamentous cyanobacteria, mainly *Planktothrix agardhii* (previously called *Oscillatoria agardhii*), were more abundant after ice-free winters than following periods of prolonged ice cover. Wind resuspension of deposited trichomes with associated detritus particles stabilizes the cyanobacterial population (Gons and Rijkeboer 1990; Rijkeboer et al. 1991).

Compared with other plankton species, the coccoid toxin-producing *Microcystis* spp. show a very high  $Q_{10}$  value for the growth rate (Reynolds 1997) and thus may catch up with competitors as the water gets warmer. It has also been proposed (Shapiro 1997) that elevated water temperatures promote the benthic recruitment of *Microcystis* cells or colonies, which may partly explain sudden blooms of *Microcystis* during spells of warm weather. Elevated temperature and a stability of water column favour large-sized cyanobacteria exhibiting vertical migration by buoyancy derived from intracellular gas vacuoles (Humphries and Lyne 1988; Ibelings et al. 1991). However,

increases in cloud cover and wind speed as predicted for north-west Europe would weaken thermal gradients and offset the competitive advantage derived by cyanobacteria from their buoyancy regulation. Analysis of surface blooms in Lake IJssel showed that scums are absent at wind speeds  $> 2\text{--}3 \text{ m s}^{-1}$  (Ibelings et al. 2003) and should become less frequent if the winter is slightly more windy as predicted (Howard and Easthope 2002).

The heterotrophic bacterium *Clostridium botulinum* type C, the major cause of botulism outbreaks in wild waterfowl, has an ubiquitous distribution in lake and marsh sediments (Williamson et al. 1999). These bacteria grow under anaerobic conditions and can persist there for long periods of time (Davies et al. 1995); the risk of their outbreak in freshwater bodies has been reported to be enhanced by climate related factors such as warmer water temperature ( $> 20 \text{ }^\circ\text{C}$ ) at alkaline pH (7.5–9.0), a negative redox potential, decreasing water transparency and high precipitation levels (Rocke et al. 1999; Barras and Kadlec 2000). Temperature seems to be the key factor stimulating the production of the toxins, the optimum in this regard being  $> 30 \text{ }^\circ\text{C}$ . Increased frequency of storms will add to the abundance of these bacteria in the water layer due to enhanced resuspension of sediment (Stenstrom and Carlander 2001). Blooms of toxic cyanobacteria may co-occur with botulism, potentially resulting in interacting, effects on wild life (Murphy et al. 2000), some of which are apparently deleterious: the outbreaks of botulism in waterfowl in the Netherlands have occurred mostly in exceptionally warm summers (Haagsma 1974).

Higher temperatures and higher humidity may also promote insects pests. Some of the pest species may carry diseases and endanger human populations that were previously 'safe' from infection. For instance, encephalitis caused by the West Nile Virus has been recently observed in North America (New York) and has spread over a great part of the continent (Martens 1999). The virus is transmitted by *Culex pipiens*, a cosmopolitan mosquito species. However, the virus is highly temperature-sensitive and so the distribution of the West Nile Virus is more limited than the distribution of the mosquito that carries it.

Summarizing, climate change will generally favour and stabilize the dominance of cyanobacteria in phytoplankton communities. Relationships



between the occurrence of cyanobacterial toxins and botulism merit more attention. Climate change may cause an increase in vector borne diseases.

### *Invasive species*

Invasive species are species that arrive at locations where they were never recorded before (Crooks 2002). Although this is in principle a natural process, human activities and the resulting process of global change have led to an accelerated invasion of ecosystems by alien species, also known as the 'invasional meltdown' (Ricciardi and Maclsaac 2000). Freshwater lakes are considered to belong to the most vulnerable among different ecosystems to invasions by exotics (Ricciardi and Maclsaac 2000).

In the Netherlands, most invasions have their origin in the Ponto-Caspian region. The rate of invasions has been accelerated by the interconnection of river basins in the central corridor (Dnjepr, Vistula, Oder, Elbe, Rhine), which has played a key role for invasion into the freshwater systems of the Netherlands (Bij De Vaate et al. 2002). Climate warming is expected to support biological invasions into shallow lakes in the Netherlands because most of the Ponto-Caspian species originate from warmer regions (Bij De Vaate et al. 2002).

A large number of invading species are macro-invertebrates. In the Dutch part of the river Rhine, ca. 35 macro-invertebrate species (over 15%) are non-indigenous. Depending on their areas of origin, over half of these may be considered thermophilic (Bij De Vaate et al. 2002). In river branches of the Rhine their success is likely due to a 3 °C temperature rise over the past century, mainly due to cooling water discharges (Dr Bij De Vaate unpubl.). In lakes, the success of thermophilic invaders depends on winter survival, which may increase with climate change.

The zebra mussel *Dreissena polymorpha* invaded the Netherlands almost 200 years ago (Bij de Vaate et al. 2002) but is a recent invader in North America (Ahlstedt 1994). This mussel thus provides an excellent case for assessing the impact of an invading species on biodiversity and ecosystem functioning (Dukes and Mooney 1999). In the Netherlands, where virtually all lakes are man-made and of relatively recent origin, most of them

being eutrophied, the invasion of *Dreissena* is not considered to be a nuisance but is welcomed by lake managers since it provides a potent filter feeder that may help to increase water transparency (Dionisio Pires et al. 2005). This is in sharp contrast to the situation in the USA where *Dreissena* invaded only recently, mostly into natural lakes which were much less degraded by man than most Dutch lakes. Zebra mussels changed phytoplankton and zooplankton composition due to their high filtration rate (Strayer et al. 1999). Nutrients are consequently not exploited by phytoplankton and macrophytes benefit from increased availability of nutrients and also from increased light intensity (Lake et al. 2000). The readily available food biomass of zebra mussels is of advantage to the omnivorous ducks (Petrie and Knapton 1999).

Exotic bird and mammal species (e.g. Chilean Flamingo *phoenicopterus chilensis*, Black Swan, *Cygnus atratus*, Egyptian Goose, *Alopochen aegyptiacus* and Mandarin Duck, *Aix galericulata*, (Lensink 1996); Coypu/Nutria, *Myocastor coypus*, (Broekhuizen et al. 1992) – descendants of escaped domestic animals – have increased dramatically in the Netherlands in the last century: their numbers are mostly negatively affected by severe winters. A reduction in the occurrence of severe winters will conceivably further contribute to their successful establishment.

There are only a few documented examples of invasive freshwater algal species. The subtropical filamentous cyanobacterium *Cylindrospermopsis raciborskii* is a notable exception. It thrives in waters that have high temperatures, a stable water column and high nutrient concentrations: it has recently spread rapidly in temperate regions and is now commonly encountered throughout the USA and Europe (Dyble et al. 2002). It was first recorded in the Netherlands in 2001. The widespread proliferation of *C. raciborskii* in drinking and recreational water supplies has caused international, public health concerns due to the potential production by this cyanobacterium of the alkaloid hepatotoxin cylindrospermopsin (Ohtani et al. 1992) and saxitoxin, the toxin responsible for paralytic shellfish poisoning (Lagos et al. 1999).

We conclude that climate change will favour invasive species (Dukes and Mooney 1999), mainly due to increased temperatures, especially during winter. For the Netherlands, the warmer Ponto-

Caspian region is a major source of invasive species.

#### *Water transparency*

High water transparency is the most important among the targets for water management and has often been used to evaluate the success of restoration measures (Drenner and Hambright 1999; Gulati and Van Donk 2002). According to the concept of alternative stable states (Scheffer et al. 1993), switches between a macrophyte-dominated clear-water state and a phytoplankton-dominated turbid state may occur abruptly with increasing nutrient loading. However, even phytoplankton-dominated, shallow lakes may have temporary clear-water phases, which are typically caused by enhanced grazing pressure on phytoplankton by zooplankton at the end of the spring (Gulati et al. 1982; Sommer et al. 1986). These periods of increased water transparency may initiate a switch to a macrophyte-dominated clear water state in shallow lakes after successful implementation of nutrient control measures (Hanson and Butler 1994; Scheffer 1998; Gulati and Van Donk 2002).

Temporary clear-water phases in temperate lakes usually correspond to high densities of *Daphnia*. Plankton phenology in spring was observed to be clearly related to elevated temperatures in winter and early spring in many lakes all over Western Europe (Reeders et al. 1998; Gerten and Adrian 2000; Scheffer et al. 2001b; Gerten and Adrian 2002a; Straile 2002). In Lake Constance, earlier clear-water phases after mild winters also tended to last longer but were negatively related to the biomass of *Daphnia* later in summer (Straile 2000). Phenologically similar results for a shallow, polymictic reservoir were attributed to temperature-mediated mortality patterns of *Daphnia*, which were, however, related to warming up in spring and early summer (Benndorf et al. 2001). Due to the low heat storage capacity in shallow lakes the effects of winter temperatures last only until early spring (Gerten and Adrian 2001). Consequently, an earlier clear-water phase in the shallow, polymictic Müggelsee (Germany) required a warming trend in April and was not related to the winter NAO index (Gerten and Adrian 2000) as found for deep lakes. Elevated temperatures, even later in the season (May–June),

were suggested to have a negative impact on daphnids because they favour growth of planktivorous young-of-the-year fish, which prey upon daphnids (Mehner 2000; Benndorf et al. 2001). Elevated temperatures may also cause a mismatch between a peak in phytoplankton density and the critical reproductive period for the crustacean zooplankton, which consequently will become food limited (George and Harris 1985; Winder and Schindler 2004a). The mismatch between phyto- and zooplankton development was strongly related to the timing of stratification in the large and deep Lake Windermere (George and Harris 1985) and probably also in Lake Washington (George and Harris 1985), but the significance of such a mismatch for shallow lakes is not clear. It is also uncertain how climate-related shifts in timing of the clear water-phase will affect the potential of macrophytes to develop.

Scheffer et al. (2001b) concluded from a recent time series analysis of shallow lakes in the Netherlands that climate warming may enhance the probability of clear-water phases. After re-analyzing both the empirical data and the model used by Scheffer et al. (2001b), Van Donk et al. (2003) concluded, however, that there is no link between temperature and the probability for a clear water phase. Jeppesen et al. (2003) even argued that climate warming will increase the probability of lakes to become locked in a turbid state. Several lines of evidence support this conclusion: (i) internal nutrient loading increases with temperature (Jensen and Andersen 1992; Liikanen et al. 2002) (see also section on carrying capacity), (ii) zooplanktivory by fish is likely to increase due to decreased winter mortality and higher recruitment (Mooij 1996; Mehner et al. 1998; Nyberg et al. 2001), and (iii) sediment resuspension by bioturbation and wind (Schelske et al. 1995) will probably increase. Because macrophytes that stabilize the clear-water phase are primarily light-limited in Dutch lakes (e.g. Van den Berg et al. 1999), these mechanisms maintaining (or even increasing) turbidity will prevent their establishment and, consequently, will stabilize the turbid state.

Studies using outdoor-microcosms (McKee et al. 2002a, 2002b, 2003; Moss et al. 2003a) have demonstrated that direct temperature effects on lakes in a clear state dominated by macrophytes are subtle and that warming does not significantly encourage phytoplankton blooms, even in combi-

nation with increased nutrients and fish. Nevertheless, warming produces trends in water chemistry that support the idea that even moderate warming has the potential to exacerbate existing eutrophication problems (Moss et al. 2003a). This will, at least in the long run, destabilize macrophyte-dominated clear-water states (e.g. Van De Bund and Van Donk 2002). Results of enclosure experiments in two subsequent years with different summer temperatures suggest that at critical nutrient levels a switch to the turbid state is more likely to occur in years with warmer summers (Van De Bund et al. 2004). Apart from these temperature-mediated nutrient effects, further climate-related factors like storms or changes in water levels may adversely affect the stability of macrophytes.

To sum up, we expect that climate change will negatively affect transparency in shallow lakes. First, climate change and climate variability will tend to destabilize macrophyte-dominated clear-water lakes, making a switch to a turbid phytoplankton-dominated state more likely and, second, will stabilize the turbid state and hamper the colonization of the lake by macrophytes under the current management regime. These negative effects of climate change may be counteracted by future measures in compliance with the European Water Framework Directive (see Discussion).

#### *Carrying capacity*

Carrying capacity is defined as the highest number or biomass of a certain species or functional group of organisms that can be supported by an ecosystem. Carrying capacity changes over time with the abundance of resources. When population density approaches carrying capacity, population growth rate approaches zero due to competition. Overall productivity – and thereby the potential for harvesting by grazers – is highest at intermediate biomass levels relative to the carrying capacity (Graham 1935).

The number of factors that can, and should, be considered when studying the effects of climate change on carrying capacity are seemingly countless. Harrington et al. (1999) remarked that most studies choose to ignore the plethora of possible ecological effects of climate change. For instance, climatic warming has the potential to induce shifts in the spatial and temporal coincidence of organ-

isms. Novel combinations may arise, driving the flux of organisms, and creating new temporal and spatial associations. One of the more striking consequences is the decoupling of the phenology of hosts and parasites or of predators and prey, with direct effects on carrying capacity for the populations involved (e.g. Visser et al. 1998). Patterns in fish recruitment and growth may show considerable temporal shifts with increasing temperatures (Mooij and Van Tongeren 1990; Mooij et al. 1994; Mooij 1996).

Higher temperatures will affect physiological processes such as photosynthesis and respiration, supposedly stimulating production of the phytoplankton (Kilham et al. 1996; Hughes 2000). The increased primary production leads one to anticipate that the carrying capacity of higher trophic levels will increase with increasing temperatures, assuming that the turnover rate of these higher levels remains unchanged. Conversely, if this assumption does not hold temperature will lead to a general increase in turnover rate of the system but not to shifts in the carrying capacity of higher trophic levels.

Elevated temperature may also favour cyanobacteria and in turn lead to a decoupling of phytoplankton and zooplankton growth because cyanobacteria are known to be relatively poorly edible food for zooplankton (Dawidowicz et al. 1988; Gliwicz and Lampert 1990). Cyanobacteria are also considered to be food of poor quality for zooplankton and zebra mussels due, among others, to the virtual lack of essential fatty acids (Ahlgren et al. 1992; Stoeckmann and Garton 2001; Wacker and von Elert 2001).

Some authors (Kilham et al. 1996; Porter et al. 1996) predict that the effects of global warming on phytoplankton will mimic the effects of nutrient enrichment. With enrichment, the carrying capacity for phytoplankton increases, but paradoxically this works adversely for some zooplankton species and strengthens their risk of extinction (Rosenzweig 1971). Although Rosenzweig's concept has been severely criticized (e.g. McAllister et al. 1972; Arditì and Ginzburg 1989), seems at odds with observations of some others (McCauley and Murdoch 1990) and ignores various stabilizing mechanisms in ecosystems (Abrams and Walters 1996), it holds the important lesson that the effects of nutrients – and climate change – on consumer-food systems may be surprising (Scheffer 1998).

We conclude that one of the more striking consequences of climate change on carrying capacity is the decoupling of the phenology of hosts and parasites or of predators and prey, with direct effects on carrying capacity for the populations involved. Higher temperatures will affect physiological processes such as photosynthesis and respiration, potentially resulting in a larger carrying capacity of primary producers in shallow lakes. There is a general expectation that climate change will mimic some aspects of eutrophication.

### *Biodiversity*

Biodiversity is expected to decline in freshwater habitats in response to climate change at a far greater scale than is true for even the most affected terrestrial ecosystems (Ricciardi and Rasmussen 1999; Sala et al. 2000). Eutrophication, increased harvesting and habitat fragmentation have affected biodiversity of shallow lake ecosystems in the Netherlands in the past decades (Scheffer 1998; Gulati and Van Donk 2002). Given the current climate change projections, climate change might be one more driving forces (Sala et al. 2000), leading to a direct loss of species when the environmental variables reach levels that are beyond what an individual species can cope with through acclimation and adaptation (Thomas et al. 2004).

The effect of multiple stressors, e.g. eutrophication, climate change and biotic exploitation on biodiversity and ecosystem functioning, is assumed to be influenced by the sign of the relatedness of species co-tolerances (Vinebrooke et al. 2004). If species co-tolerances are positively related, i.e. a stress-induced community tolerance, initial exposure to a stressor should reduce the impact of other stressors. On the other hand, if species co-tolerances are negatively related, i.e. stress-induced community sensitivity, additional stressors will have a synergistic impact on biodiversity and ecosystem functioning. Results of mesocosm experiments carried out along a north-south, latitude gradient in Europe (Moss et al. 2004; Van De Bund et al. 2004) indicated that negative effects of eutrophication on ecosystem functioning will increase from north to south, i.e. by warmer temperatures. This implies that freshwater communities have stress-induced sensitivity to both eutrophication and climate warming. Therefore,

lake restoration measures targeting eutrophication, such as reduction of planktivorous fish mass and of nutrient concentrations, should be increased to counter the effect of climate warming.

Apart from the joint impact of climate change and other driving forces on biodiversity and ecosystem functioning, the initial biodiversity of the shallow Dutch lakes might influence the intensity of impact caused by climate change. Systems that have a high diversity might be less sensitive to climate change, as species richness is postulated to have a buffering effect on ecosystem productivity in a fluctuating environment by reducing the temporal variance in productivity (Insurance Hypothesis, Yachi and Loreau 1999). Furthermore, low diversity systems may be more subject to unstable population dynamics and thus more vulnerable to invasions (Elton 1958; McNaughton 1977; Naeem et al. 1994; Naeem and Li 1997; Kennedy et al. 2002). We conclude that the change from a clear-water state to a turbid-state, which occurred on a wide scale in the Dutch eutrophied lakes, was concomitant with a loss of biodiversity, due to the disappearance of submerged macrophytes, piscivorous fish and large bodied zooplankters (Scheffer 1998). Despite stringent restoration measures (Gulati and Van Donk 2002), most Dutch lakes seem to be incapable of compensating for the loss of biodiversity, so that they continue to be susceptible to environmental change (Naeem et al. 1994; Naeem and Li 1997; Yachi and Loreau 1999; Scheffer et al. 2001a; Kennedy et al. 2002).

### **Discussion**

Freshwaters are central to society and the environment and there is an increasing demand to assess the impacts of human-generated threats and to identify the possibilities to effectively address anticipated changes (Naiman and Turner 2000). A synthesis of reported climate-related effects is only possible by applying conceptual 'filters' (Blenckner 2005) and thus by concentrating on a specific region and a specific type of ecosystem. Here, we focus on possible effects of climate change on the shallow-lake ecosystems in the Netherlands. In search for the available sources of information we did not restrict ourselves to those dealing specifically with lakes in the Netherlands though.

Keeping the 'landscape filter' (Blenckner 2005) in mind, we will discuss our findings about the effects of climate changes in lakes in the Netherlands in a broader and more general perspective so as to cover shallow, freshwater lakes in Europe in general.

### *Approach*

For optimal use of existing knowledge we kept central the main ecosystem management objectives that have been formulated for shallow lakes in the Netherlands. By integrating the available knowledge concerning these management objectives, rather than applying a food-web perspective, we were able to develop an integrated, management-oriented view of the potential consequences of climate change for shallow lakes in the Netherlands. Although our review approach did not allow us to make quantitative predictions, we deliberately refrained from using models. Due to the large number of indirect pathways by which climate can affect ecosystems a reductionistic approach may easily result in misleading inferences (Harrington et al. 1999). Consequently, we consider the extrapolative power of current, integrated ecosystem models to be too low to make reliable predictions on the effects of climate change. Even more important, no single model is available that would allow us to consider all those management objectives we were interested in.

### *Impact assessment*

On the basis of our review we expect that all six management objectives (target species, nuisance species, invading species, transparency, carrying capacity and biodiversity) that we used as criteria for our assessment will be affected by climatic change. These six aspects of the ecological status of lakes are also linked to each other, water transparency being the key that provides a clue to the state of some essential biotic parameters. Specifically, high water transparency related to a macrophyte-dominated state is linked to high biodiversity, promotes several target species (birds, littoral macrofauna) and positively valued keystone species such as *Daphnia* and *Dreissena*. Macrophyte-dominated lakes are also less likely

to have nuisance-algal blooms. We conclude that climate change will negatively affect transparency, i.e. the lakes will have a higher probability of persisting in the turbid state with negative effects on target species (reducing their carrying capacity) and biodiversity, whereas nuisance species will be promoted. This strong link of several management objectives with transparency, however, also offers options to lake management to counteract the anticipated negative effects of climate change (see below). A management-oriented conclusion of our review is that lake restoration measures aimed at eutrophication mitigation, such as nutrient reduction and biomanipulation, should be stepped up to counteract the effect of climate warming.

### *A broader perspective*

There are no *a priori* reasons why the effect of climate change on plankton in Dutch lakes should differ from other shallow lakes in the temperate zone. Throughout north-western Europe, the observed higher water temperatures during winter and spring in the last decades were coupled to an earlier onset of the spring phytoplankton bloom (Weyhenmeyer et al. 1999) and the subsequent clear-water phase (Müller-Navarra et al. 1997; Straile and Adrian 2000; George et al. 2004) (Table 2). Such shifts may have unexpected consequences for the trophic interactions in freshwater ecosystems because many species show unique responses to changes in temperature (Gerten and Adrian 2002b; Winder and Schindler 2004b). With respect to plankton dynamics, a mismatch (Cushing 1990) occurs when a phytoplankton bloom either begins too early or does not last long enough. In deep lakes, different sensitivity to vernal warming was found to produce a growing divergence between the timing of zooplankton and their phytoplankton prey (Winder and Schindler 2004a). Although this specific phenomenon may not hold for non-stratifying shallow lakes there is certainly potential for climate-induced changes in species interactions and indirect food web effects in these systems, too, just as in marine systems (Edwards and Richardson 2004) or terrestrial systems (Visser et al. 1998). As a first indication, elevated temperatures in spring and early summer were found to have negative effects on *Daphnia*

densities later in summer in a shallow reservoir (Benndorf et al. 2001). The occurrence of a mid-summer decline of daphnids was related to temperature-dependent timing of several processes in the food web (Wagner et al. 2004). One important factor was temperature-related growth of young-of-the-year fish (Mehner 2000), influencing both the fish biomass (and thus their prey consumption rate) and ontogenetic changes in prey selection. Young-of-the-year fish are gape-limited when they start exogenous feeding. Temperature-related growth will determine from which time onwards they are able to feed on daphnids and whether intraguild predation will occur or not (Mehner et al. 1996). This has strong implications for year-class strength (Bremigan and Stein 1994; Mehner et al. 1998), ultimately affecting the whole food web. Fish predation on daphnids may further be mediated by temperature-dependent emergence of merolimnetic insects (Makino et al. 2001). For phytoplankton, increasing wind speed could cause shifts in the temporal distribution of species through modulation of the periodicity of, e.g. diatom species (Gons et al. 1991; Carrick et al. 1993).

More specific for the Dutch situation is the combination of many shallow lakes and the location near the current 0 °C January isotherm. This combination makes the Netherlands a prime wintering area for many migratory water birds. Other core areas for water birds along the 0 °C January isotherm are the shallow parts of deep lakes, river deltas or estuaries, for instance, the Swiss lakes and the Donau delta in Romania (De Leeuw 1997) and Chesapeake Bay in North America (Perry and Uhler 1988). Future shifts of the 0 °C January isotherm will mean that fewer water birds are expected to winter in these regions, provided that there are suitable wintering areas in the proximity of the new location of the isotherm.

Typical for the Dutch situation are the absence of a well-developed littoral zone and the highly managed water levels of most lakes in the Netherlands. This precludes effects such as those observed in the Estonian Lake Võrtsjärv (Table 2) where warmer winters bring about higher water levels (Noges et al. 2003). Due to the controlled hydrology of Dutch lakes, altered inputs of water into lake complexes may, in principle, be compensated, reduced, or accommodated. A cautious approach is needed: inflow of water into shallow

lakes during periods of drought from the main rivers may have serious repercussions for water quality. Rivers Rhine and Meuse are characterized by high levels of alkalinity and sulphate, resulting in internal eutrophication and a decline of macrophytes like *Stratiotes aloides* (Smolders et al. 2003). Technically, but only to a limited extent, existing water-level schemes can avoid shortages of water during dry summers and control excess water during wet periods, usually in winter. However, frequently excessive localized rainfall and extended periods of drought, would pose problems for managers that are difficult to cope with because the present hydraulic infrastructure may be insufficient. To solve this, a combination of technical solutions and larger areas for water retention and storage are currently being created (Anonymous 2000). Despite the measures taken, sea-level rise may enforce substantially increased base water levels in the future in low-lying lakes such as Lake IJssel.

#### *Options for management*

Of the three main aspects of climate change affecting lakes, management can counteract the impact of wind and waves and potentially residence time and water level but not of temperature. Potential measures largely comply with recent lake restoration plans which emphasise the integrity of lakes, other aquatic and semi-aquatic systems and the surrounding landscape, aiming at “nature development” (Nienhuis and Gulati 2002). The impact of wind and waves can be mitigated by making compartments or islands in order to reduce wind-fetch. Residence time and water levels can be adjusted somewhat by changing the hydrology within the constraints set by the many functions of lakes (transport, agriculture, drinking water, recreation, nature) in the Netherlands. Changes in hydrology will also affect the nutrient loading on the lakes. Related to both compartmentalization and hydrology is the development of the littoral. Littoral development will affect the connectivity between the lakes and their immediate catchment area and may also have its feedback on nutrient loading because the vegetation can act as a filter that absorbs nutrients and stimulates denitrification. Returning to somewhat more natural fluctuations in lake water levels (as opposed

to the current non-natural regime) is one promising measure to stimulate development of, e.g. the heliophyte community along the shore (Coops and Hoeser 2002; Coops et al. 2004). Finally, fisheries management can be implemented, or if already present, be attuned. Together with changes in the nutrient load, fisheries management, including biomanipulation, has proven to be a powerful tool to steer the biotic communities in shallow lakes (Meijer 2000).

To which management objectives will these potential measures contribute? Essentially all the measures listed above have been applied fairly successfully to improve water transparency in lakes. Over the past two decades this objective has received more attention from water managers than any of the other five objectives discussed in this paper. We concluded earlier in this paper that climate change may have a negative impact on water transparency, which conceivably can be counteracted employing the measures available to water managers to improve transparency. Moreover, this will most likely have a positive feedback on biodiversity as these two objectives are clearly linked in shallow lakes. Since it is yet unclear what the effects of climate change on the carrying capacity for higher trophic levels will be, it is early days to recommend on how to thwart these effects by changes in management.

The measures aimed at both stimulation of more natural water-level fluctuations and shoreline development for restoring a more 'natural' system are expected to increase resilience after perturbation and to promote resistance to permanent changes in external conditions. Fluctuating water levels and well-developed shorelines are a characteristic of many natural shallow lakes. The higher resilience and resistance imparted by fluctuating water levels and well-developed shorelines can be assumed to have a positive effect on target species and reduce the probability of the outbreaks of nuisance species, or the frequency of species invasions, or both. In general, if we identify climate change as a stress factor to which the lakes are exposed, measures that enhance the resilience and resistance of the system will help the lake ecosystems to withstand the additional stress resulting from climate change (Scheffer et al. 2001a). The potential negative effects of climate change thus should provide an extra stimulus to new and existing management strate-

gies to achieve a good ecological condition of the lakes as prescribed by the European Water Framework Directive.

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