A blooming business

Identifying limits to Lake Taihu's nutrient input

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Chapter 1

Introduction

"September 2015 - Amidst the honking traffic, the endless neighborhoods of monotonous tower-blocks and the huge crowd of people on their way to work, we try to navigate to the subway. We are in the north of this megalopolis near our final destination. Still, our trip takes considerable time due to the incredible dimensions of this city. Fortunately, the public transport system is highly efficient. The population of the city has grown exponentially up to several millions only during recent decades, so the infrastructure is built according to the latest standards. It all seems so well-organized, or isn't it? This city has many more streams to channel; food flows, water flows, energy flows, waste flows, etc. These are streams that are not necessarily visible to the citizens. Would they be aware of what it takes to make their city run?" – Annette Janssen

Last century, the world population grew immensely to a level never seen before (United Nations, 2015). Currently, earth inhabits over 7 billion people, and during the time it takes you to read this paragraph, the global population will increase by about 70 people (Gerland et al., 2014). This tremendous population growth is facilitated by important discoveries in health care, the green revolution that increased food production, and the construction of good sanitation (Ponting, 1991). Cities have grown to an unprecedented large scale and, currently, more than half of the human population lives in urban areas (Chen et al., 2014). In China, booming cities even tripled in size between 1987-2010 (Schneider et al., 2014).

To successfully manage these booming cities, it is crucial that resources meet demands and that waste is adequately removed to prevent disease outbreaks. Ancient Romans understood this concept well and built aqueducts for water supply and a complex sanitation system to remove their waste (Lofrano et al., 2010). In fact, even ants create sophisticated networks to prevent disease outbreaks in their 'megacities' (Hart et al., 2002).

Yet, constructing a functional and sustainable network for resources and wastes is far from trivial. Many advanced civilizations have collapsed in history due to resource crises (Diamond, 2005). A well-known examples is the Maya culture, whose collapse is believed to be connected to severe environmental degradation (Diamond, 2005). When demand exceeds available resources, overexploitation looms. Additionally, wastes need a destination without negatively affecting future resources. At present, cities increasingly grow beyond these borders leading to extreme anthropogenic pressure on the earth's ecosystems (Rockström et al., 2009a). For instance, the downside of China's booming cities are the serious problems with air pollution forcing people to wear facemasks at a daily basis (Wang et al., 2012) and the deteriorated water quality in over 80% of China's main lakes (Le et al., 2010).

An important consequence of anthropogenic pressure is the distortion of global nutrient cycles (Kroeze et al., 2013; Beusen et al., 2016). In the pristine situation, nutrient availability was limited and depended on slow processes such as weathering of rocks (Seitzinger et al., 2005; Beusen et al., 2016). Excess of nutrients was therefore an exception rather than a rule, although historical cases of local eutrophication exist. For instance, in Mauritius a severe drought around 4200 years before present triggered a drastic change in nutrient flows (De Boer et al., 2015). Driven by thirst, large vertebrates including giant tortoises and dodos migrated massively to the only freshwater source left. While drinking the last bits of water, these animals dropped their excrements causing toxic hypertrophic conditions in which cyanobacterial blooms prevailed. Finally, these toxic conditions became fatal to the large vertebrates leading to a mass extinction close to the water source, which triggered an even higher nutrient load from the animal remains (De Boer et al., 2015). More of these early eutrophication cases took place; however, these occurred at a much smaller scale than today. At present, human activities accelerate the release of nutrients e.g. by phosphorus mining, industrial nitrogen fixation and fossil fuel combustion (Seitzinger et al., 2005; Beusen et al., 2016). The transport of both nitrogen and phosphorus to the ocean has nearly doubled in the 20th century (Beusen et al 2016).

As result of the distortion of global nutrient cycles, ecosystems at various locations around the world deteriorate. A well-known example of deterioration of ecosystems is the increasing number of lakes with toxic algal blooms (Glibert et al., 2005; Paerl et al., 2009; Janse et al., 2015). More and more, previously clear lakes with flourishing macrophytes turned into a turbid state with blooming algae (see for instance Watson et al. (2016), Glibert (2014) and Paerl et al. (2013)). The shift from a clear to a turbid state is the result of increased nutrient loads that these lakes need to process (Smith, 2003). In conditions of high nutrient load, algae outcompete macrophytes by impairing favorable light conditions which are essential for macrophyte growth (Scheffer et al., 1993). High algal abundance has the risk to become toxic to all kinds of life forms, including humans (Codd et al., 1999). Consequently, these lakes become unsuitable for drinking water and food supply and form a health risk to the human population (Codd et al., 1999; Paerl et al., 2013).

Lake Taihu (East China) is notoriously famous in this respect (Figure 1.1). In the 1970s this lake was still renowned for its flourishing fish swirling in the lake, the mysterious underwater life and the green reeds along its shore (Song: Taihu Mei (Beautiful Taihu), Long-Fei). Within a decade after the song was published, though, the first algal blooms emerged in the lake (Duan et al., 2009). Although these blooms were the first signs of a regime shift in Taihu's ecosystem, the change was initiated roughly a century earlier when human population started to grow exponentially (Ellis et al., 1997). It was this exponential growth, combined with the associated increase of food production, industrial growth and economic prosperity that eventually accelerated nutrient input to Lake Taihu (Ellis et al., 1997; Gao et al., 2010). The first appearance of algae at the end of the 1980s was only a prelude of what had yet to come. In 2007, eutrophication and the resulting toxic algal blooms reached disastrous proportions (Qin et al., 2010; Zhang et al., 2010). As a result of toxic algal blooms, a drinking water station near Wuxi had to shut down and millions of people were forced to switch to an alternative source of drinking water (Zhang et al., 2010).

Figure 1.1. Map of Lake Taihu and it geographical location in China. Lake Taihu's surface area is about 2250 km^2 and the lake has an average depth of 1.9 m.

The question that arises is whether such problems can be avoided. For a long time we have known that an excess of nutrients may result in deterioration of lake ecosystems (Schindler, 2006). Yet, whilst the cause of these events are known, it appears a challenge to quantify the 'safe operating space' of these ecosystems (Rockström et al., 2009a). The 'safe operating space' specifies the bounds for sustainable use of ecosystems. In limnology, the safe operating space of lakes is primarily confined by the concept of critical nutrient load (e.g. Scheffer et al., 1993; Scheffer et al., 2007). The critical nutrient load is the maximum nutrient load ecosystems can absorb, while remaining in a good ecological state. As long as the actual nutrient load is kept below the critical nutrient load, the ecosystem is within the ‘safe operation space’. Crossing the critical nutrient load has, however, negative consequences.

Defining the critical nutrient load of specific lakes is scientifically challenging. First, each lake is uniquely characterized by its specific depth, shape, sediment type, and climate. The response to eutrophication of each lake is, therefore, unique as well (Janse et al., 2008), leaving no ‘one-size-fits-all’ solution. Besides, the critical nutrient load depends on local environmental factors which are subject to changes. For example, in case of wet years the critical nutrient load may be lower (Kong et al., 2016). Finally, in particular large lakes may be spatially heterogeneous and may therefore have a range of critical nutrient loads for different parts of the lake.

The title of this thesis, ‘A blooming business’ has a dual meaning. First, it refers to China’s b(l)ooming economy that resulted in better living standards for the Chinese population. Second, it refers to algal blooms that started due to the increasing anthropogenic pressure; a ‘blooming business’ for water quality managers. The desired situation, in which economic growth is maintained while algae blooms are absent, sets limits to the nutrient input. In this thesis I aim to determine the limit to Lake Taihu’s nutrient input. Defining these critical nutrient loads is a quantification of the ’safe operating space’ (Rockström et al., 2009a). Critical nutrient loads help managers to define policies that combat eutrophication of their lakes. I will approach the search for critical nutrient loads of Lake Taihu by solving a quadripartite puzzle (Figure 1.2) where each piece reveals a part of the answer.

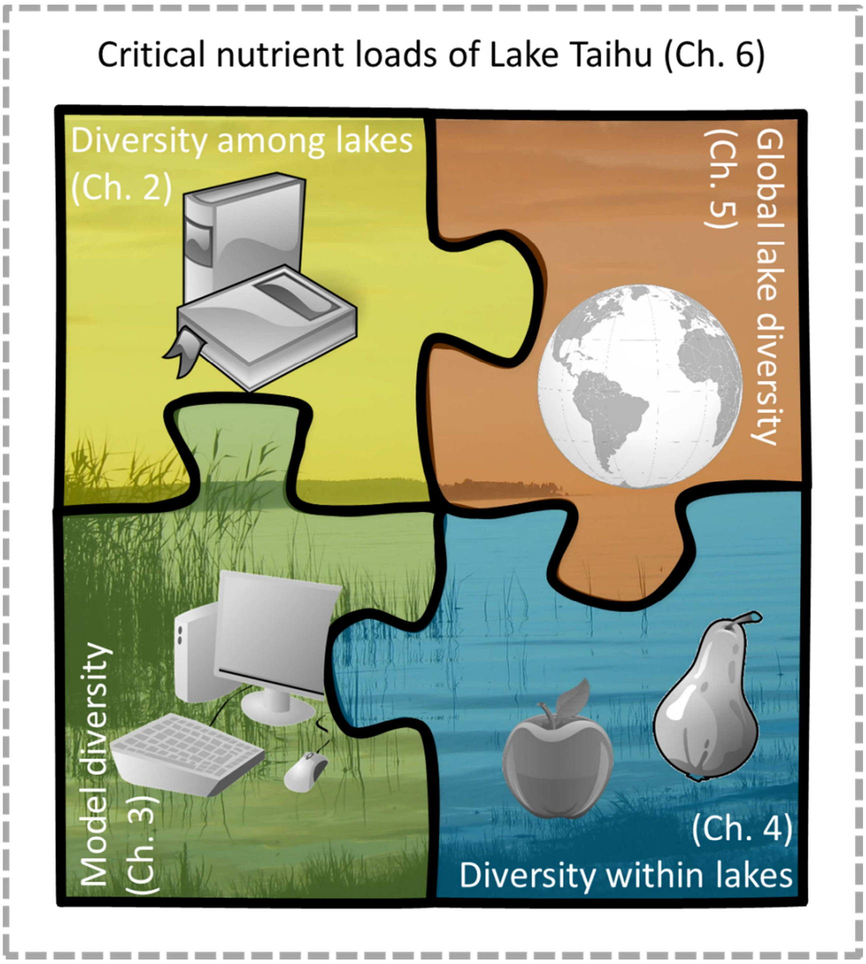

Figure 1.2. The quadripartite puzzle showing the pieces that make up this thesis. Together these pieces reveal the final picture.

The first piece covers the diversity among large shallow lakes with respect to the presence of macrophytes and algae (chapter 2). I study what kind of lakes could exhibit alternative stable states, a phenomenon which emerges when the lake's response to eutrophication differs from its response to oligotrophication. For the second piece of the puzzle I will explore, exploit and evolve models that are available to answer limnological questions such as the identification of a lake-specific critical nutrient load (chapter 3). This step is essential to get grip on the diverse set of available modelling tools available for further research on the critical nutrient loads of Lake Taihu. For the third piece of the puzzle I dive into the spatial heterogeneity within lakes. I look at the effect of spatial heterogeneity of especially nutrient load and nutrient redistribution on lake restoration (chapter 4). This knowledge is of great importance to understand the response to restoration of large shallow lakes which are not fully-mixed. In the remaining piece of the puzzle, I put algal blooms in a global context and look at future projections of water quality in lakes around the world (chapter 5). The full quadripartite puzzle combines knowledge on alternative stable states in large shallow lakes, the available modelling tools, effects of spatial heterogeneity and lake diversity in a global context. With this knowledge in hand, I determine the critical nutrient load of Lake Taihu (chapter 6). I finally put the findings in perspective in the general discussion (chapter 7).

Chapter 2

Alternative stable states in large shallow lakes?

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Abstract

Many lakes worldwide are experiencing great change due to eutrophication. Consequently, species composition changes, toxic algal blooms proliferate, and drinking water supplies dwindle. The transition to the deteriorated state can be catastrophic with an abrupt change from macrophyte to phytoplankton domination. This has been shown repeatedly in small lakes. Whether such alternative stable states also exist in large shallow lakes is less clear, however. Here we discuss the characteristics that give rise to alternative stable states in large shallow lakes either in the lake as whole or restricted to specific regions of the lake. We include the effect of *lake size*, *spatial heterogeneity* and *internal connectivity* on a lake's response along the eutrophication axis. As a case study, we outline the eutrophication history of Lake Taihu (China) and illustrate how *lake size*, *spatial heterogeneity* and *internal connectivity* can explain the observed spatial presence of different states. We discuss whether these states can be alternatively stable by comparing the data with model output (PCLake). These findings are generalized for other large, shallow lakes. We conclude that locations with prevailing *size effects* generally lack macrophytes; and, therefore, alternative stable states are unlikely to occur there. However, most large shallow lakes have macrophytes whose presence remains unexplained when only *size effect* is taken into account. By including *spatial heterogeneity* in the analysis, the presence of macrophytes and alternative stable states in large shallow lakes is better understood. Finally, *internal connectivity* is important because a high internal connectivity reduces the stability of alternative states.

Introduction

Eutrophication drives numerous lakes worldwide to a deteriorated state where phytoplankton dominate over macrophytes (Smith et al., 1999). As a result, species composition changes (Smith et al., 1999; Jeppesen et al., 2000), toxic algal blooms proliferate (Paerl et al., 2011a) and drinking water supplies dwindle (Smith et al., 1999; Falconer et al., 2005). The transition to a phytoplankton dominated state is often nonlinear and in many cases catastrophic (Scheffer et al., 2000). In case of a catastrophic transition, a change from the macrophyte dominating state to the alternative phytoplankton state will be rapid and recovery may show hysteresis (alternative stable states) when positive feedbacks between macrophytes and phytoplankton are strong (Scheffer et al., 1993).

Small lakes are more likely to appear in a macrophyte rich state than large lakes (Van Geest et al., 2003) primarily because these lakes are less prone to destructive wind forces (Janse et al., 2008) and fish are less abundant (Scheffer et al., 2007). Examples of small lakes that shifted between the macrophyte and phytoplankton dominated state are the gravel pit lakes in England (<1 km^2, <2 m depth) (Wright et al., 1992; Scheffer et al., 1993) and Lake Veluwe in the Netherlands (30 km^2, 1.5 m depth) (Meijer, 2000). But there are also larger lakes with macrophytes and where alternative stable states are presumed. For example, Lake Apopka (125 km^2) in the USA became susceptible to disturbances due to increasing nutrient loading; the large macrophyte stands finally disappeared after a disruptive hurricane event (Bachmann et al., 1999; Lowe et al., 2001).

It is an intriguing question as to under which conditions large shallow lakes show alternative stable states. The impression is often that these alternative states appear lake wide (Scheffer, 1990; Scheffer et al., 1993), though it is conceivable that in some cases these may be restricted to certain areas within a lake as well. This information is crucial because the type of transition (catastrophic or not) will determine the lake's response to restoration measures

(Scheffer et al., 2001). It has been shown that it is difficult to restore large shallow lakes (Gulati et al., 2008). For instance Lake Okeechobee (USA, 1900 km^2, 2.7 m depth) (Beaver et al., 2013), Chaohu (China, 760 km^2, 2.5 m depth) (Shang et al., 2005) and Lake Markermeer (the Netherlands, 700 km^2, 3.2 m depth) (Lammens et al., 2008; Kelderman et al., 2012b) still suffer from water quality problems after restoration. This affects large populations that depend on the services provided by these large lake ecosystems (Carpenter et al., 2011).

Here, we discuss the response of large shallow lakes to eutrophication. We aim to characterize conditions that promote alternative stable states within large shallow lakes (>100 km^2). First, we describe the effect of different lake characteristics on the lake response to eutrophication. We focus on *lake size*, *spatial heterogeneity* (spatial variation in patterns and processes within a lake) and *internal connectivity* (horizontal exchange between lake compartments; here defined as spatially distinct regions that are relatively homogeneous in characteristics and processes). These characteristics are all recognized as key factors in understanding ecological systems (Cadenasso et al., 2006). Second, we will present the eutrophication history of Lake Taihu, China's third largest freshwater lake. Next, the effects of *lake size*, *spatial heterogeneity* and *internal connectivity* on the observed spatial development of this lake will be addressed in a model output supported discussion. Finally, we discuss how we may generalize the effects of *lake size*, *spatial heterogeneity* and *internal connectivity* for other large shallow lakes.

Theory: size, spatial heterogeneity and internal connectivity

Alternative stable states are the result of strong reinforcing feedback loops that strengthen the competitiveness of the ruling state with other states (May, 1977; Scheffer et al., 2001). The dominant state is therefore not only dependent on the present conditions, but also on the prevalent state of the past (Scheffer et al., 2003a). As a result of strong reinforcing feedback, multiple states are possible given the same conditions (Scheffer et al., 2007). Two important states distinguished in shallow lakes are the clear macrophyte state and the turbid phytoplankton state (Scheffer et al., 1993). These states are alternatively stable if the reinforcing feedback between algae and macrophytes is sufficiently strong to facilitate potential dominance of either of both (Phillips et al., 1978; Hosper, 1989; Scheffer et al., 1993).

PCLake is an ecosystem model that can be used as a tool to predict the state of lakes (e.g. macrophyte dominated or turbid) and indicate whether these states are alternative stable or not (Janse, 1997). Previous studies showed that the presence of alternative stable states strongly depends on depth and fetch ('distance between any point in a lake and the shore in the wind direction') (Janse et al., 2008; Janse et al., 2010). Results of a bifurcation analysis using the general settings of PCLake illustrate that too great a depth or fetch prevents macrophyte dominance (Figure 2.1, white area, 'Macrophyte-lacking state') while very shallow lakes are likely to have unconditionally sufficient light conditions impeding algae domination (Figure 2.1, white area, 'Macrophyte dominating state'). Only lakes that meet the requirements for both states to dominate under the same conditions will show alternative stable states (Figure 2.1, grey area, 'Hysteresis'). These requirements for alternative stable states can be fulfilled in a lake as a whole but also fragmentally, showing different states side by side. For details on these general settings see Janse (2005) and for details on the bifurcation analysis see Appendix 1.

Size effect

Lake size is a very important factor in shaping the response of lakes to eutrophication, here further referred to as the *size effect*. As a result of the *size effect*, large shallow lakes are often presumed to lack alternative stable states (Janse et al., 2008). First, with larger lake *size*, fetch is increased (Figure 2.2a, process 1) (Jeppesen et al., 2007; Janse et al., 2008). A longer fetch leads to larger wind-driven waves resulting in a higher shear stress on the sediment (Carper et al., 1984). Therefore, large shallow lakes are more prone to wind forces than small shallow lakes. As a result of high *size effect*, macrophytes are damaged by wave forces and sediment resuspension is more severe, which inhibits macrophyte growth by light attenuation (Scheffer et al., 1993; Scheffer, 2004). A second example of a *size effect* is the depth, which tends to be deeper when lake *size* increases (Bohacs et al., 2003; Søndergaard et al., 2005). Macrophytes have difficulties to sustain in deep lakes because of low light availability. A third example of the *size effect* is the relatively small littoral zone in larger lakes due to a low perimeter to surface area ratio (Figure 2.2a, process 2). Macrophytes growing in the littoral zone therefore have less impact on the limnetic zone of the lake ecosystem (Janse et al., 2001; Sollie et al., 2008b).

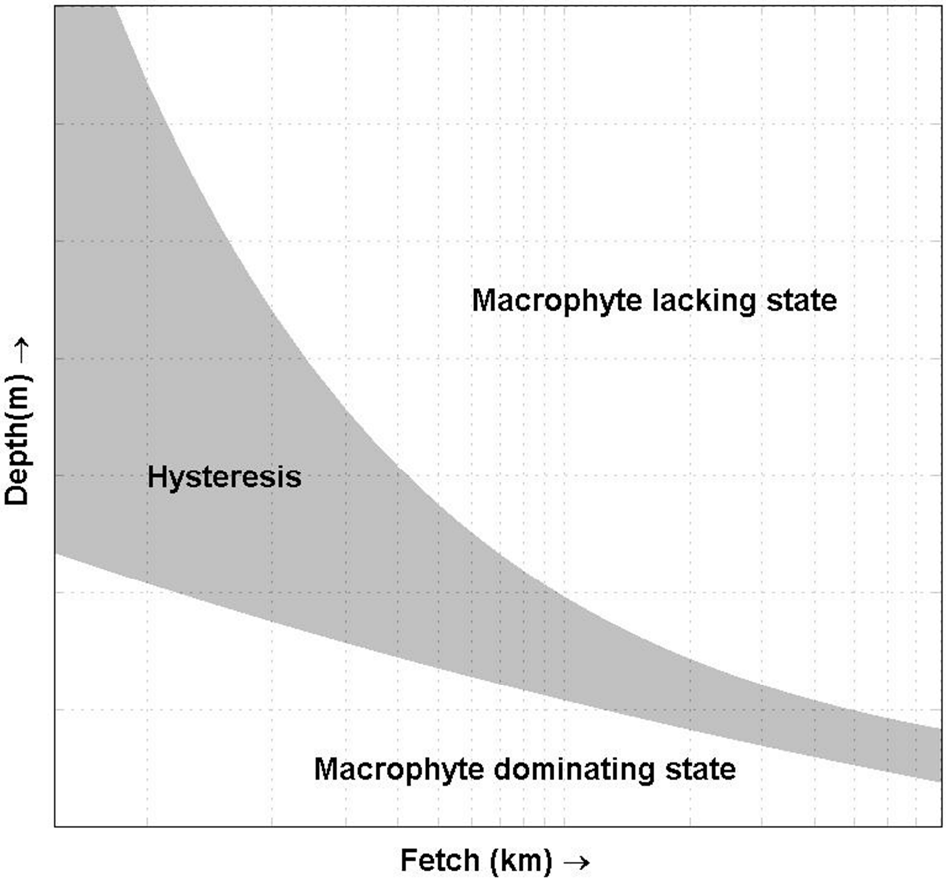

Figure 2.1. Model output indicating the presence of alternative stable states depending on lake fetch and depth (PCLake, Janse et al., 2010). Alternative stable states are predicted in the grey area ('Hysteresis').

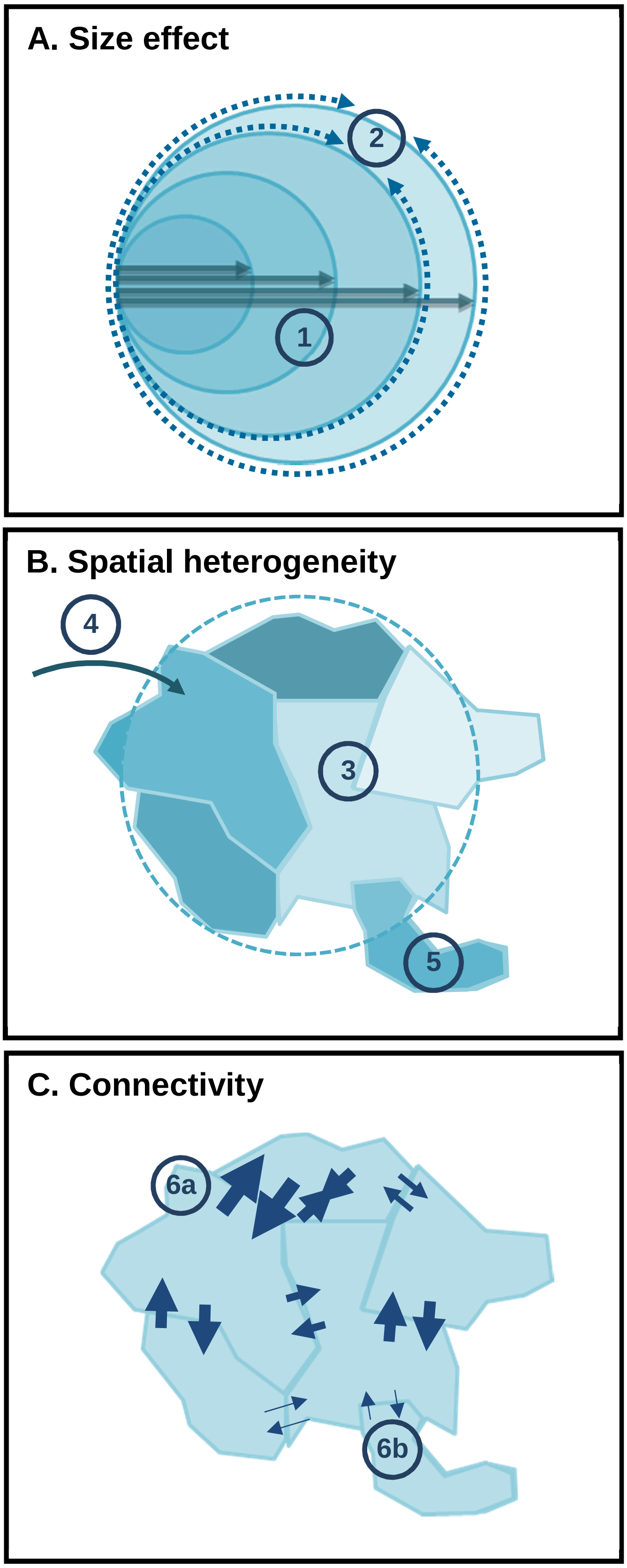

Figure 2.2. Schematization of the a) size effect, b) spatial heterogeneity and c) internal connectivity of lakes. Numbers denote the different processes including (1) fetch, (2) perimeter to surface area ratio, (3) heterogeneous distribution of input, (4) heterogeneity within the lake like depth, sediment etc. (5) heterogeneous shape or fetch and (6a) high and (6b) low connectivity.

Spatial heterogeneity

According to Tobler's 'first law of geography' "everything is related to everything else, but near things are more related than distant things" (Tobler, 1970). This implies that the chance of *spatial heterogeneity* within a lake increases with *lake size*, a phenomenon known in spatial ecology as well (Wiens, 1989). With *spatial heterogeneity* is meant here the horizontal spatial variation in structure and biochemical processes within a lake. Examples of *spatial heterogeneity* are variation in depth and sediment type related nutrient storage (Figure 2.2b, process 3), both influencing the potential for macrophyte growth (Stefan et al., 1983; Canfield et al., 1985; Chambers et al., 1985; Jeppesen et al., 1990; Middelboe et al., 1997).

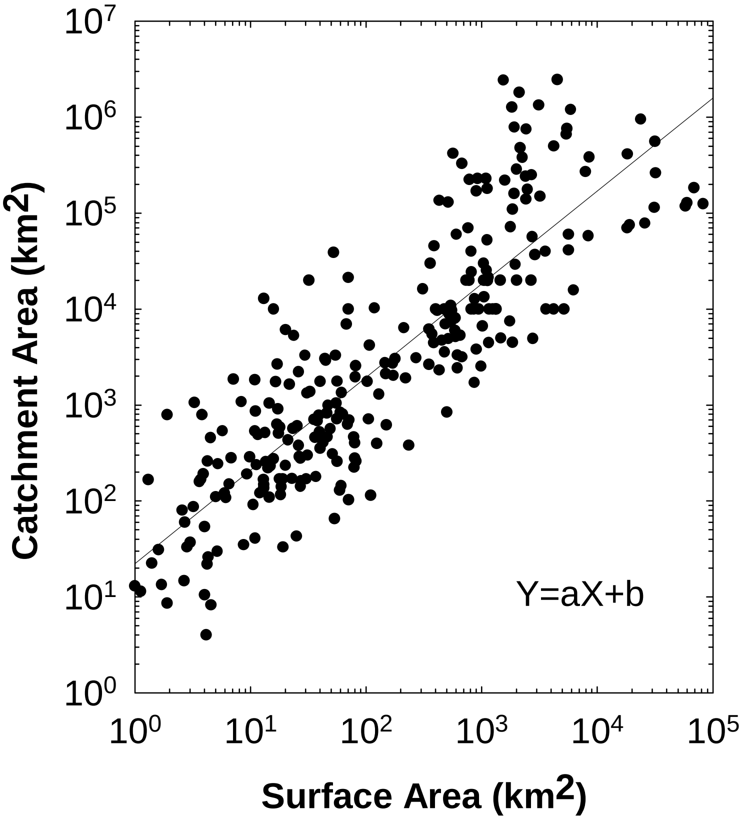

Figure 2.3. Relationship between lake surface area and catchment area (Y=aX+b, a =0.965±0.07, b=1.397±0.11). With a≈1 on the log-log scale, the relationship is close to linear on normal scale as well ($y=10^b x^a \approx 10^{1.4} x^{0.97} \approx 24x$), leading to a constant lake area to catchment area ratio. Data from ILEC (1999).

Additionally, external drivers can be *spatially heterogeneous* such as allochthonous nutrient input. Data imply that eutrophication stress per unit of area experienced by lakes with similar land use is independent of lake size (Figure 2.3). However, particularly in large lakes, the distribution of the nutrient input is often *spatially heterogeneous*. Allochthonous nutrient input enters the lake mostly via tributaries and overland flow (Figure 2.2b, process 4) which exerts a higher eutrophic stress in the vicinity of inlets and lake shores, than further away. When eutrophication stress becomes excessive, the macrophytes that often grow luxuriously in the vicinity of the inlet and lake shores will retreat to only very shallow parts of the lake where light is not limited (Figure 2.1, lower white region). Subsequently, these littoral macrophytes lose their capacity to reduce the impact of inflowing nutrients (Fisher et al., 1999).

A last example of *spatial heterogeneity* is the irregular shape of the lake's shoreline or presence of islands which can result in unequal distribution of wind stress. The hypothetical lake in Figure 2.2b for example, has a large fetch indicated by the dashed circle. At the same time the bay in the lower right corner forms a compartment with a shorter fetch and is thus more protected from strong wind forces (Figure 2.2b, process 5). In this way the size of different lake compartments matters for macrophyte growth potential (Andersson, 2001).

Internal connectivity

The *internal connectivity* is defined here as horizontal exchange between different compartments ('*connectivity*') within a lake ('*internal*'). With respect to the earlier mentioned 'first law of geography' (Tobler, 1970), *internal connectivity* concerns the degree of relatedness of the different compartments and processes in a lake. A higher *internal connectivity* provides a higher relatedness and thus tends to minimize variability (Van Nes et al., 2005; Hilt et al., 2011). High *connectivity* (Figure 2.2c, process 6a) leads therefore to a well-mixed lake in which transport processes (e.g. water flow, diffusion, wind driven transport) are dominant. On the other hand, with low connectivity (Figure 2.2c , process 6b) the lake processes are biochemically driven and heterogeneity is maintained in different lake compartments (Van Nes et al., 2005). Intuitively, *internal connectivity* decreases though narrowing of the lake or dams in the lake, since they obstruct water flow between different lake compartments. Additionally, with increasing lake size, opposing shores become less connected because a longer distance needs to be spanned which requires increasing time for exchange. Depending on the connectivity of a lake, local regime shifts can be obstructed or, on the contrary, promoted by water quality states elsewhere within a lake (Scheffer et al., 2007; Hilt et al., 2011). In this way, events like state shifts can propagate as a domino effect throughout a lake (Van Nes et al., 2005; Hilt et al., 2011).

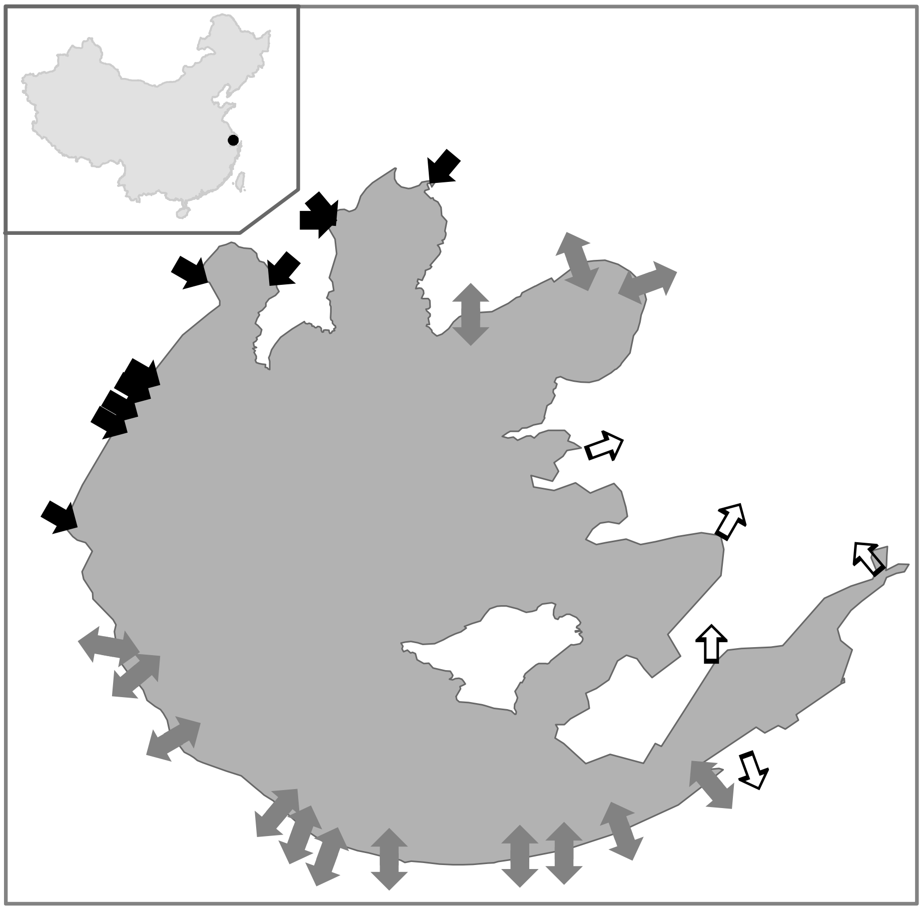

Figure 2.4. Inflow (black arrows), outflow (white arrows) and bi-directional flow (grey arrows) of Taihu. Bi-directional flow of rivers means seasonally depended alternating in- and outflow of river water (after Li et al., 2011a).

The combination of *size effect*, *spatial heterogeneity* and *internal connectivity* of large shallow lakes leads to a unique spatial response of these lakes to eutrophication. Given the relatively low number of large shallow lakes (ILEC, 1999; Bohacs et al., 2003; Downing et al., 2006) and the large differences between these lakes (e.g. in precipitation, altitude or latitude) it is difficult to make generalizations. Here, we will focus on a large shallow lake, Lake Taihu, located in eastern China (Figure 2.4). Measured in terms of its depth to surface ratio, Taihu is among the shallowest of large lakes, only surpassed by Lake Eyre (Australia, ephemeral), Lake Chilwa (Malawi, temporarily dried out in 1968), Lake Taimyr (Russia, riverine and frozen for most of the year), Lake Hungtze (China, riverine) and during the dry season by Lake Tonlé Sap (Cambodia, riverine) (ILEC, 1999). Taihu is therefore a good model system to study the contribution of *size effect*, *spatial heterogeneity* and *internal connectivity* to the spatial variability and development of large shallow lakes.

Development in the Taihu Basin

Taihu is China's third largest freshwater lake (2338 km^2) situated in the Yangtze River delta, approximately 100 km west of Shanghai (Qin et al., 2007). The lake is very shallow compared to its size with only 1.9 m average depth to a maximum of 2.6 m and is polymictic (Shen et al., 2011). More than 200 tributaries form a complex network that connects the lake with its own catchment. In the north, the catchment borders the Yangtze River. Since the 1980s, the lake has been plagued by algal blooms. The seriousness of the situation became particularly clear at the end of May to early June 2007, when more than 1 million people in the nearby city of Wuxi were without drinking water for up to a month due to large cyanobacterial scums at the water plant inlet (Guo, 2007; Qin et al., 2010). The current lake water quality with its cyanobacterial toxins is a direct health risk for the 40 million people that live in the Taihu Basin and depend on the lake ecosystem (Qin et al., 2010). The problem is of national significance since 10.3% of China's GDP (2000) is produced in the watershed of Taihu (Duan et al., 2009). Up until now, measures to reduce the algal blooms in Taihu have had little effect (Hu et al., 2008; Chen et al., 2009; Chen et al., 2012a; Li et al., 2013).

Pristine situation

Prior to 6500BC, farming societies established in the region of Lake Taihu (Smith, 1995). The fertile soils and the regular supply of nutrients and water by the Yangtze River were important conditions for the early agricultural development (Ellis et al., 1997). Anthropogenic pressures seem to have been low at that time (An et al., 2008). Information on the pristine state of the lake is sparse, however a Chinese song "Beautiful Taihu" (太湖美, Long-Fei) written in 1978 tells that the water was beautiful with flourishing fish swirling in the lake, with a mysterious water and green reeds along the shore. According to macrophyte records taken in the 1960s (Figure 2.5), macrophytes were indeed present at the shores and bays with the east of the lake being most vegetated (Qin et al., 2007). However, it is likely that the lake has never been totally vegetated as a result of strong winds that act as a destructive force on the lake's center. Remnants of long-term wind forcing can also be seen in the absence of fine sediments in the lake (Shen et al., 2011). Therefore it is arguable that the lake center has always lacked macrophytes and appeared turbid on days of strong wind. Phytoplankton concentrations were thought to be low during this time (Zheng et al., 2009).

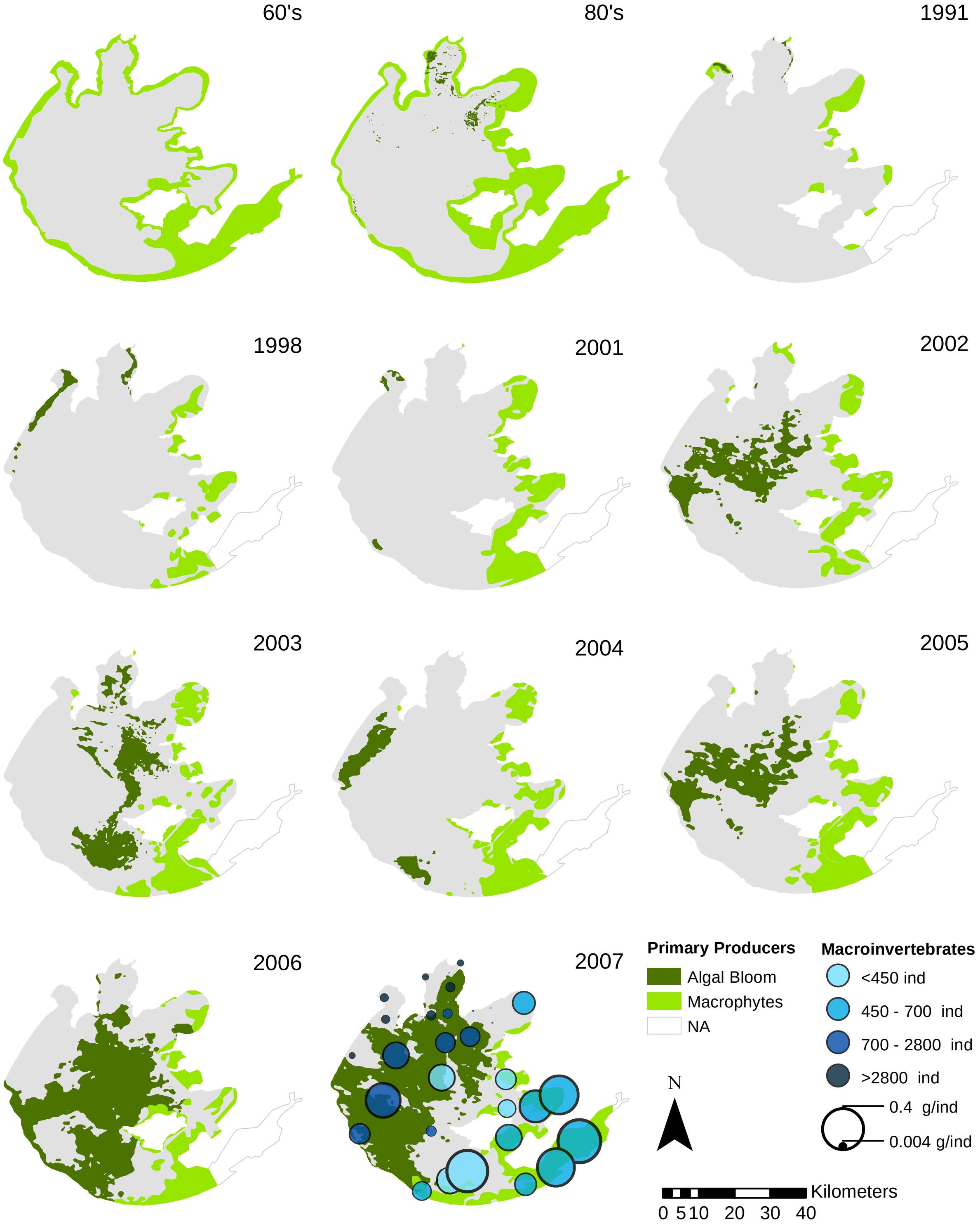

Figure 2.5. Development of the ecosystem in Lake Taihu. Compilation of different maps with phytoplankton, macrophytes and macroinvertebrates data. Source macrophytes data 1960s and 1980s from Qin et al. (2007) and 2002-2007 from Zhao et al. (2012a). Phytoplankton data originates from Ma et al. (2008) and Duan et al. (2009). Macroinvertebrates data of 2007 originates from Cai et al. (2012).

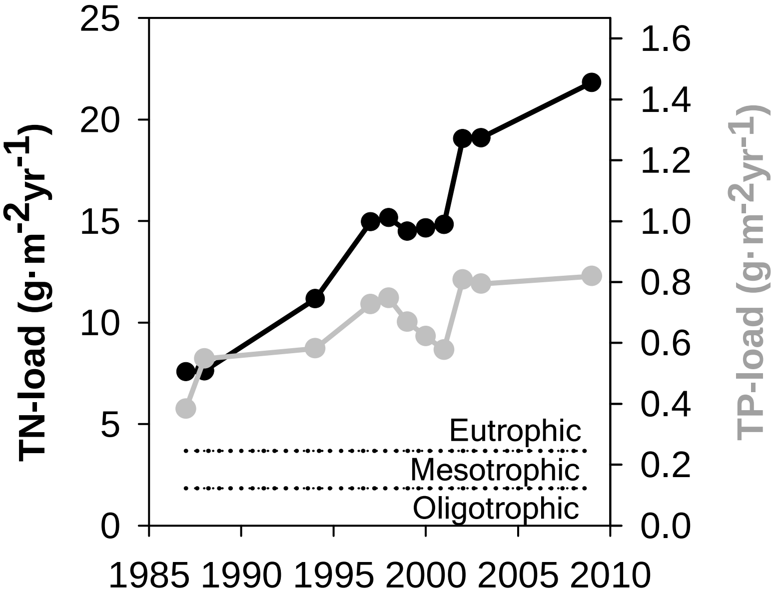

Figure 2.6. Total nitrogen (black) and total phosphorus (grey) load from tributaries in Taihu. The dashed lines show the limits for different trophic states which are based on the input-output model of Vollenweider (1975) for phosphorus: $L_p=P/(10+q_s)$ with L_p the areal nutrient load, P the lake water phosphorus concentration (with upper limits for oligotrophic and mesotrophic respectively P = 0.01 mg.L^{-1} and P = 0.02 mg.L^{-1}) and q_s the hydraulic loading rate (average depth z divided by the residence time τ_w) which is 2.24 m.yr^{-1} for Taihu. The limits for nitrogen are set with the ratio of Vollenweider (1975) using limit TP concentrations and the nitrogen to phosphorus ratio N:P = 15:1 to obtain the limit TN concentrations. Data 1987-2003 from Zhang (2007) and 2009 from Yan et al. (2011).

Anthropogenic pressure

Increasing anthropogenic pressure caused a change to this pristine situation. After the end of the Taiping rebellion (1850-1864) population grew exponentially, demanding a higher food production (Ellis et al., 1997). However, agricultural land in the Taihu Basin became limited, requiring a means to increase productivity (e.g. fertilizers, pesticides and higher irrigation efficiency) to meet the food demand (Ellis et al., 1997). In the end, agricultural innovation allowed for more than a tripling of population in 150 years to more than 40 million people at the start of the 21st century (An et al., 1996; Ellis et al., 1997; Zhang et al., 2008; Tian et al., 2011). Small villages and cities in the Taihu basin grew rapidly and merged into one of the world's largest "megalopolitan regions" (based on population) (Tian et al., 2011). Due to this urbanization, waste water production has locally intensified and exceeded the increment of wastewater treatment capacity (Gao et al., 2010). Cesspits that used to be emptied on the fields for fertilization were replaced by flush toilets, resulting in better hygiene, but negatively impacting the nutrient cycle (Ellis et al., 1997; Gao et al., 2010). In 2009, domestic wastes contributed more than 40% of the total waste input (Liu et al., 2013). Eutrophication has been further amplified by industries and the world's largest aquacultural fish production residing in China (Liu et al., 2005; Guo, 2007; Qin et al., 2007). The construction of concrete embankment around most of the lake in 1991 as a response to flood events, destroyed the connection between the lake and its surrounding wetlands (Yang et al., 2010). Sluices are now regulating water levels within the lake which means a loss of the natural water level fluctuations (Yang et al., 2010).

Nutrients

Increasing amounts of nutrients have been discharged to the lake as a result of the anthropogenic pressure (Figure 2.6). Fortunately, strict regulations for industrial waste loads ("zero-point-action") starting from 1998 seemed to pay off, as could be seen from a decline in both nitrogen and phosphorus load between 1999 and 2001 in Figure 2.6 (Li et al., 2011a; Liu et al., 2013). However, these regulations could not prevent the nutrient load from increasing any further after 2001. Most allochthonous nutrient input comes from the north and west of the Taihu Basin where most cities and the major inflow rivers are situated (Yu et al., 2007; Li et al., 2011a) (Figure 2.4, black arrows). As a result, high nutrient concentrations in the lake water can be found at the north and west side of Taihu. These nutrient concentrations decrease in a south-easterly direction from the input sources, through the lake center towards the outlet rivers in the east (Figure 2.4, white arrows) (Chen et al., 2003a; Kelderman et al., 2005; Li et al., 2011a; Paerl et al., 2011b; Otten et al., 2012). The spatial decline in nutrient concentrations can be mainly explained by a loss of nutrients to the sediments and atmosphere. Nitrogen is removed mainly during summer by the large phytoplankton bloom populations and by denitrification (Xu et al., 2010; Paerl et al., 2011b). Phosphorus is immobilized in the sediments mainly during winter when pH levels are low (Xu et al., 2010). As a result, nitrogen and phosphorus are alternately limiting phytoplankton production in Lake Taihu (Paerl et al., 2011b). The removal of nutrients 'en route' is important to prevent algal blooms in the east of the lake, but has a drawback as well. Years of intensive nutrient input have led to accumulation of mainly phosphorus in the lake sediments, forming a potential for internal nutrient loading once the external nutrient load has been reduced (Qin et al., 2006; Zhu et al., 2013).

Macrophytes

Until the 1980s, macrophyte coverage was around 25% of the lake surface (Figure 2.5, excluding East Taihu Bay) but that decreased tremendously to approximately 5% at the end of the 1980s (Figure 2.7). The disappearance of macrophytes can be mainly assigned to the massive mortality along the western shores and northern bays (Figure 2.5). Meanwhile, macrophytes in the eastern part of the lake changed little, which could be explained by the low nutrient concentrations, wind-shading and the shallowness providing more light for macrophytes (Li et al., 2011a; Zhao et al., 2012a). Despite the increasing eutrophication, the vegetated area in Taihu seems to have slowly increased since its minimum coverage in the late 1980s (Figure 2.7), mainly due to increased macrophyte coverage in East Taihu (Zhao et al., 2013). Instead of being a sign of recovery, the increase of macrophyte coverage has been interpreted as a sign of an upcoming shift to the phytoplankton dominated state (Zhao et al., 2012a). This interpretation is based on the theory of alternative stable states that assumes macrophytes to respond nonlinearly to eutrophication, showing first an increase due to higher fertility, prior to the collapse of the macrophyte stands (Timms et al., 1984; Janse et al., 2008). Another indication of an upcoming shift in this region can be found in the increasing dominance of floating macrophytes at the expense of the submerged macrophytes (Scheffer et al., 2003b; Zhao et al., 2012a).

Floating macrophytes are able to better cope with lower light conditions than submerged macrophytes since they grow at the water surface. When light conditions deteriorate close to the shifting point, floating macrophytes will therefore predominate submerged macrophytes (Scheffer et al., 2003b).

Phytoplankton

While macrophytes disappeared, the total primary production of Taihu increased more than twofold from 1960 (5.46 $t.km^{-2}.yr^{-1}$) to 1990 (11.66 $t.km^{-2}.yr^{-1}$) owing to the increasing phytoplankton biomass that bloomed due to the excessive nutrient input (Li et al., 2010). The first algal blooms occurred in 1987 in Meiliang Bay (Figure 2.5, 1980s). Subsequently, algal blooms dominated by non-N_2-fixing cyanobacteria (*Microcystis*) increased in coverage and frequency, and appeared earlier in the season (Chen et al., 2003b; Duan et al., 2009; Paerl et al., 2011b). The presence of mainly non-N_2 fixing cyanobacteria indicates that external and internally-supplied nitrogen are sufficient to maintain proliferation over N_2-fixers (Paerl et al., 2011b). The early blooms in the northern bays and western shores occurred right where enrichment was most severe and easterly winds drove algae to form thick scums (Chen et al., 2003b; Li et al., 2011a). At that time, high concentrations of suspended solids in the lake center due to wind action (Figure 2.8) might have prevented algal growth by light limitation (Sun et al., 2010; Li et al., 2011a). Despite this mechanism, blooms also emerged in the lake center from 2002 onwards (Duan et al., 2009). Finally, in 2007 the problems with drinking water became so severe that it was not possible to ignore the blooms anymore (Qin et al., 2010).

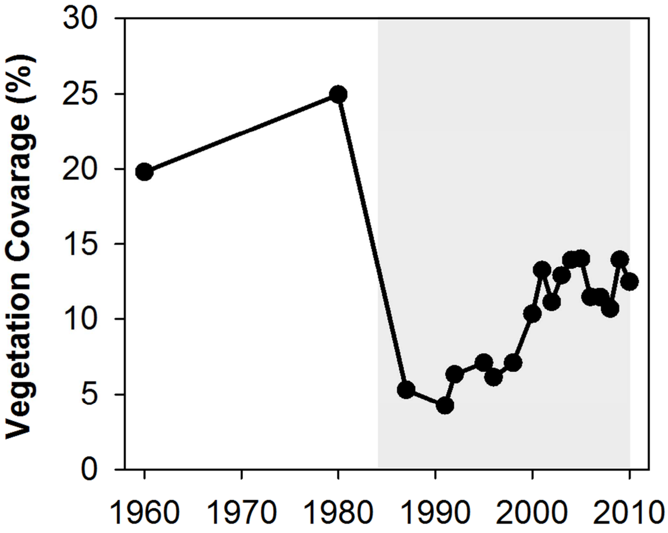

Figure 2.7. Macrophyte coverage in Lake Taihu. East Taihu Bay is not included in the calculation since data was not available for all years, see Figure 2.5. Grey area corresponds with the timespan of the increasing loads in Figure 2.6.

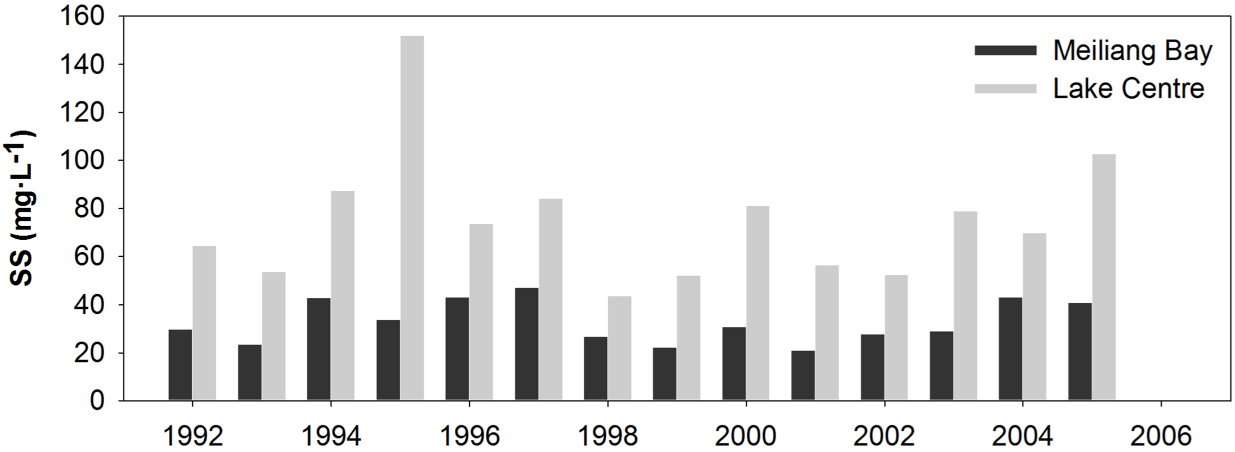

Figure 2.8. Yearly average suspended solids concentration at Meiliang Bay and the lake centre for 1992-2006 (Sun et al., 2010).

Food web

The effects of excessive nutrient loads go beyond the shift in primary producers alone and appear also higher in the food web. As the biomass of primary producers and zooplankton grew over time, the biomass of higher trophic levels shrank and several species disappeared (Li et al., 2010; Guan et al., 2011). There are indications that in the presence of *Microcystis*, the zooplankton shifted their diet to the detritus-bacteria pathway rather than grazing on living phytoplankton (De Kluijver et al., 2012). A macroinvertebrate survey in 2007 by Cai et al. (2012) showed that small individuals (e.g. Tubificidae) appear in large numbers in the algal blooming zone (Figure 2.5, 2007). The appearance of mainly small macroinvertebrate species might be related to the absence of refuges to prevent predation (e.g. macrophytes) (Cai et al., 2012) and the relatively low food quality due to the presence of toxic *Microcystis* (De Bernardi et al., 1990; Chen et al., 2003b; Otten et al., 2012). In contrast, in East Taihu, where water quality is still relatively good, large individuals (e.g. Gastropoda) live in relatively low numbers as these species can hide from predators between macrophytes and have access to a relatively high food quality (e.g. periphyton and high-quality detritus) (Cai et al., 2012). Also fish are affected by the anthropogenic pressures. Large fish species almost disappeared from Taihu mainly due to overexploitation by fisheries, which is amplified by construction of flood protection dams and the destruction of spawning grounds by land reclamation (Li, 1999; Li et al., 2010; Guan et al., 2011). Also the exposure to different pollutants (e.g. DDT, POP and heavy metals) and the resulting bioaccumulation could have forced a decline in fish stocks (Feng et al., 2003; Wang et al., 2003; Rose et al., 2004).

Obviously, the safe operating space (cf. Rockström et al., 2009b) with respect to e.g. nutrient cycles, land use and freshwater use needed for a healthy ecosystem in Taihu has been transgressed. While at first water quality was negatively affected by the anthropogenic pressures, now human development is hampered by low water quality (Guo, 2007). According to the Chinese standards, which are based on physical and chemical parameters, acceptable drinking water has a total phosphorus concentration lower than 0.1 mg.L^{-1} and total nitrogen concentration lower than 0.5 mg.L^{-1}. Standards for biological parameters are not included in the Chinese classification but according to the European Water Framework Directive, the chlorophyll-a concentration (depending on the lake type) should not exceed ~30 µg.L^{-1} in order to ensure acceptable drinking water quality (Altenburg et al., 2007). At present, all these standards are exceeded at least some months during the year (TBA, 2014).

Insights from Taihu

Today, Taihu can be roughly divided into three zones: the wind-shaded phytoplankton blooming zone (north and west of the lake), the wind-disturbed phytoplankton blooming zone (lake center), and the shallow wind-shaded macrophyte dominated zone (south-eastern part of the lake) (Cai et al., 2012; Zhao et al., 2012a). The development of Taihu revealed how the *size effect*, *spatial heterogeneity* and *internal connectivity* had its effect upon this spatial zonation.

The water quality model PCLake (Janse et al., 2010) is used for a multifold of bifurcation analyses for different values depth and fetch, to illustrate the possibility of alternative stable states in lakes (see Appendix 1). The derived grey domain (Figure 2.9) indicates the possible existence of alternative stable states for a hypothetical set of lakes using the general PCLake settings (omitting horizontal exchange between lake compartments). Of course these model results depend on more factors than fetch and depth alone, but a full sensitivity analysis of the model for the setting of Taihu is beyond the scope of this study. However, a sensitivity analysis of the model for the default settings is available in Janse et al. (2008). In this study the output should be seen as an indication of what is possible rather than an exact prediction.

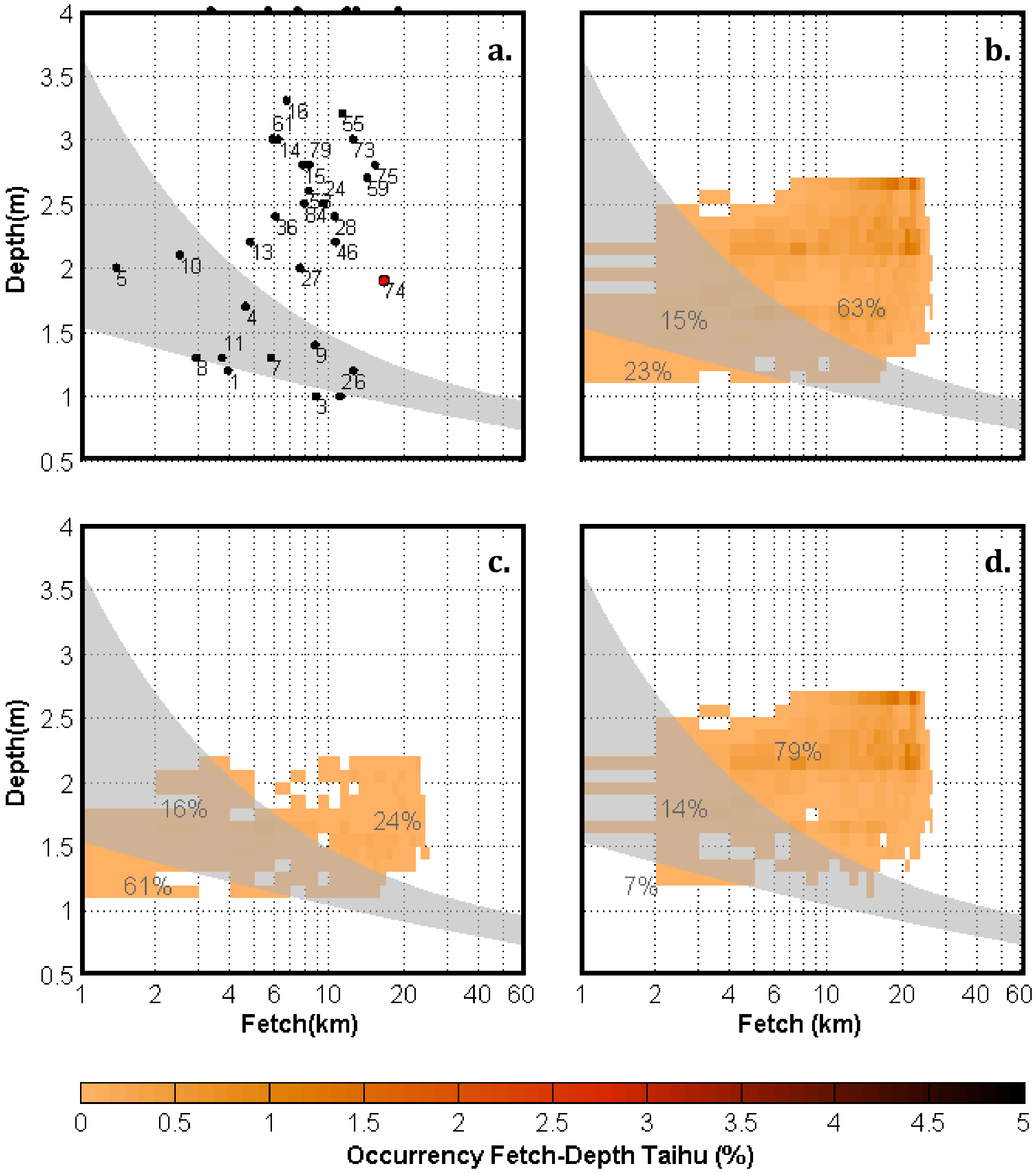

Figure 2.9. A first estimation of alternative stable states (grey area) using a bifurcation analysis with PCLake, depending on fetch and depth (Janse et al., 2010). a) expectation based on mean depth and fetch of different shallow lakes (black dots, with numbered items referring to Table 2.1) and for Taihu specific (red dot, number 74). b) frequency distribution of the combination fetch-depth of areas within Taihu. c) frequency distribution of fetch-depth restricted to only the macrophyte dominated areas in Taihu (according to the 1980s). d) frequency distribution restricted to only the macrophyte-lacking areas in Taihu (according to the 1980s). The percentages denote the relative surface area that belongs to either the domain with possibility of alternative stable states or to the domain where only one of the two states are possible. Depth data from Liu (2013).

Table 2.1. Large Shallow lakes

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
1	Istokpoga	USA	27°22'N , 81°17'W	113	1.2	3.0	3.9	15.3	YES	Although the lake is eutrophic, water level stabilization caused excessive dense macrophyte stands in the large shallow littoral zone (O'Dell et al., 1995; Bunch et al., 2010). Herbicide treatments led the macrophytes only temporally decline (O'Dell et al., 1995).
2	Tathlina	Canada	63° 32'N, 117° 35'W	573	1.0		11.0	83.8	YES	-
3	Upemba	Congo	8°37'S , 26°23'E	530	1.0	4.0	9.3	38.3	YES	Swampy-lake. Floating-mats of emergent macrophytes generally dominated by papyrus (Thompson et al., 1979; Azza et al., 2006).
4	Apopka	USA	28°37'N, 81°37'W	125	1.7		4.6	15.7	ASS	The entire lake shifted from macrophyte to phytoplankton dominance triggered by a hurricane, after long-term eutrophication (Bachmann et al., 1999; Lowe et al., 1999; Bachmann et al., 2001; Lowe et al., 2001).
5	Boraphed	Thailand	15°42'N, 100°14'E	106	2.0	5.8	1.4	9.5	ASS	Southeast part of the lake is macrophyte rich. Here the lake is shallow. The rest of the lake is turbid (Mizuno et al., 1970).
6	Claire	Canada	58°35'N, 112°04'W	1410	1.2	2.0	12.5	86.6	ASS	-
7	Cross	Canada	54°59'N, 97°48'W	591	1.3	12.0	5.8	78.7	ASS	-
8	Guiers	Senegal	16°10'N, 15°52'W	228	1.3	2.5	2.9	43.3	ASS	Macrophytes have overgrown the shallow zone in the south completely after the construction of a dam causing problems for boating (Cogels et al., 1997; Hellsten et al., 1999; Thiam et al., 2013).
9	Hongze	China	33°20'N, 118°40'E	1960	1.8		8.7	60.6	ASS	Phytoplankton dominated lake (Hu et al., 2014)

Table 2.1 continued…

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
10	Loktak	India	24°33'N, 93°47'E	289	2.1	4.6	2.5	13.1	ASS	Over 50% of the lake is overgrown by macrophytes, which proliferate after the construction of a dam (Singh et al., 2011).
11	Tisza (Kisköre)	Hungary	47°36'N , 20°40'E	127	1.3	17.0	3.7	24.1	ASS	Reservoir is covered with macrophytes (Kiss et al., 2003).
12	Abaya	Ethiopia	6°07'N, 37°38'E	1160	7.0	13.0	9.4	60.2	-	-
13	Abert	USA	42°37'N, 120°14'W	148	2.2	3.4	4.8	20.0	-	-
14	Abitibi	Canada	48°38'N, 79°48'W	904	3.0	10.0	6.2	66.3	-	-
15	Alexandrina	Australia	35°25'S , 139°07'E	570	2.8	5.0	7.8	45.7	-	Macrophytes where present before 2008, but a severe drought that went along with increasing salinity resulted in the disappearance of macrophytes (Skinner et al., 2014).
16	Balaton	Hungary	46°50'N, 17°42'E	593	3.3	12.2	6.7	72.2	-	Waves limit the distribution of macrophytes in the offshore and southern part of the lake. At the lee side in the north vegetation is present (Istvánovics et al., 2008).
17	Bangweulu	Zambia	11°05'S, 29°45'E	1510	4.0	10.0	12.8	72.2	-	-
18	Beloye Ozero	Russia	60°10'N , 37°38'E	1120	4.0	20.0	18.8	85.5	-	-
19	Beyşehir	Turkey	37°47'N , 31°33′E	650	5.0	9.0	8.5	48.6	-	<10% coverage when water level was high (before 1982) to 35% when water table had dropped in 1997 (Beklioglu et al., 2006).
20	Bositeng	China	42°0'N, 87°03'E	1010	7.7	16.0	10.2	67.0	-	Reeds present (Jun et al., 2001).
21	Buir	China	47°48'N , 117°40'E	610	8.0	11.0	12.1	42.6	-	-
22	Cedar	Canada	53°10'N, 99°60'W	1320	4.2	10.0	13.7	99.5	-	-
23	Chad	Cameroon	13°20'N, 14°10'E	1540	4.1	10.5	12.1	64.1	-	Chad is sensitive to water fluctuations. When water table is low, almost the entire lake is covered with macrophytes (Leblanc et al., 2011).

Table 2.1 continued…

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
24	Chao Hu	China	31°30'N, 117°34'E	760	2.5	5.0	9.4	49.3	-	Around 30% of the lake has been covered by macrophytes in 1950 but after dam construction and increasing nutrient loading, there is less than 1% left (Kong et al., 2013; Zhang et al., 2014a)
25	Chapala	Mexico	20°15'N, 103°0'W	1100	4.5	10.5	11.0	80.5	-	Submerged macrophytes are suppressed by high turbidity, however floating macrophyte species survive (Villamagna et al., 2010).
26	Churchill	Canada	55°58'N, 108°20'W	559	9.0	24.0	11.0	45.5	-	-
27	Colhué Huapi	Argentina	45°30'S, 68°45'W	810	2.0	5.5	7.6	43.0	-	-
28	Dauphin	Canada	51°16'N, 99°45'W	521	2.4	3.4	10.5	50.5	-	-
29	Derg	Ireland	53°00'N, 8°20'W	118	7.6	36.0	2.2	22.1	-	-
30	Deschambault	Canada	54°40'N, 103°33'W	542	6.2	22.4	5.0	37.1	-	-
31	Dongting	China	29°13'N, 112°55'E	2740	6.7	30.8	6.5	56.1	-	Inundation frequency determines macrophyte abundance (Deng et al., 2014).
32	Eğirdir	Turkey	38°01'N, 30°51'E	590	9.0	14.0	6.9	39.5	-	Marsh and reeds at the shores (Arslan, 2006).
33	Evans	Canada	50°51'N, 77°02'W	474	5.0	13.0	3.9	33.0	-	-
34	Frobisher	Canada	56°22'N, 108°14'W	516	5.5	19.0	2.6	25.9	-	-
35	Gaoyou	China	32°50'N, 119°15'E	663	7.9		8.0	57.7	-	'Transitional', macrophytes and phytoplankton present (Hu et al., 2014).
36	George	Uganda	0°00'N, 30°10'E	250	2.4	4.5	6.1	22.9	-	Surrounded by swamp macrophytes. Floating macrophytes are abundant but submerged macrophytes are absent in the center of the lake where phytoplankton dominate (Lock, 1973).

Table 2.1 continued…

	Lake	**Country**	**Coordinates**	**A**	**Z_{mean}**	**Z_{max}**	**F_{mean}**	**F_{max}**	**M**	
37	Hjälmaren	Sweden	59°13'N, 15°46'E	478	6.1	22.0	6.4	76.0	-	Before lowering the water surface, macrophytes where rare. After lowering the water table, macrophytes became more abundant. The northern shores and western basins have nowadays extensive macrophyte growth (Andersson, 2001).
38	Hulun	China	48°55'N, 117°22'E	1731	5.0	7.0	18.3	95.0	-	Macrophytes absent, phytoplankton dominates (Chen et al., 2012b).
39	IJsselmeer	the Netherlands	52°49'N , 5°15'E	1100	5.5	8.0	11.2	73.1	-	Diking with steep slopes and managed water levels reduced macrophyte growth (Sollie et al., 2008a).
40	Ilmen	Russia	58°16'N , 31°17'E	982	5.7	11.0	12.9	88.2	-	-
41	Kairakkumskoye	Tajikistan	40°17'N, 70°00'E	513	6.2	25.0	7.5	50.0	-	-
42	Kakhovskoye	Ukraine	47°30'N, 34°20'E	2150	8.5	24.0	10.4	121.9	-	-
43	Kasumigaura	Japan	36°00'N, 140°25'E	220	4.0	7.0	3.4	29.6	-	Construction of concrete levees has harmed littoral macrophytes with totally disappearance of submerged macrophytes (Nishihiro et al., 2009).
44	Khanka	China	44°55'N, 132°25'E	4190	4.5	6.5	28.3	92.5	-	-
45	Khar	China	48°04'N , 93°11'E	575	4.2	7.0	11.3	49.8	-	Macrophyte stands in the littoral zone (Krylov, 2012)
46	Khar us	China	48°02'N , 92°17'E	1578	2.2	4.5	10.5	62.9	-	-
47	Koka	Ethiopia	8°23'N, 39°05'E	250	9.1	13.0	4.1	23.0	-	-
48	Krementchugskoye	Ukraine	49°20'N, 32°35'E	2250	6.0	20.0	14.3	146.4	-	-
49	Kujbyshevskoe	Russia	54°30'N, 48°40'E	5900	9.8	41.0	10.0	123.3	-	-
50	Kyoga	Uganda	1°30'N , 33°0'E	1720	5.7	8.0	6.6	100.5	-	Macrophyte rich, except for the deeper areas. (Ogutu-Ohwayo et al., 2013).
51	Leopold II (Mai-Ndombe)	Congo	2°00'S, 18°20'E	2070	5.0	12.0	7.9	86.2	-	-

Table 2.1 continued…

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
52	Lough Neagh	UK	54°36'N, 6°25'W	385	8.9	34.0	8.4	45.1	-	Due to depth, turbidity and exposure, macrophytes are restricted small sheltered areas close to the shore (Winfield et al., 1994).
53	Louch Ree	Ireland	53°30'N, 7°57'W	105	6.2	35.0	2.6	22.1	-	-
54	Mangueira	Brazil	33°5'S , 52°45'W	817	2.6		6.7	82.3	-	Macrophytes mainly in the Taim wetland in the north northeast (Fragoso et al., 2008).
55	Manitoba	Canada	51°00'N , 98°50'W	4625	7.0	28.0	17.3	114.3	-	-
56	Markermeer	the Netherlands	52°34'N , 5°13'E	700	3.2	5.0	11.2	52.9	-	Almost no vegetation due to turbidity and depth (Kelderman et al., 2012a; Kelderman et al., 2012b).
57	Moose	Canada	53°57'N, 100°09'W	1340	4.1	19.8	13.0	45.1	-	-
58	Mweru	Congo	9°00'S, 28°45'E	4350	7.0	37.0	26.1	124.3	-	-
59	Nipissing	Canada	46°14'N, 79°49'W	855	4.5	69.0	8.4	80.5	-	-
60	Okeechobee	USA	26°56'N , 80°48'W	1900	2.7	6.0	14.1	53.3	-	Vegetation mainly at the south and eastern shore. Water levels as well as sheltering are important for the macrophyte distribution (Carrick et al., 1994; Havens et al., 2005; Rodusky et al., 2013).
61	Oulujärvi	Finland	64°20'N , 027°15'E	900	7.0	38.0	7.2	83.4	-	-
62	Ozero Evoron	Russia	51°27′N, 136°30′E	590	3.0		5.9	22.8	-	-
63	Pátzcuaro	Mexico	19°38'N, 101°38'W	130	4.9	15.0	2.5	16.3	-	Around 42% of the lake used to be covered by macrophytes, mainly in the south of the lake growing at sheltered and shallow conditions (Torres A et al., 1989; Torres, 1993).

Table 2.1 continued…

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
64	Peipsi	Estonia Russia	58°41'N , 27°29'E	3555	7.1	15.3	27.3	105.9	-	The water table of Lake Peipsi is unregulated with, despite the eutrophication, still macrophytes at the shores, mainly where till is present instead of sandstone. Lake center is dominated by algae (Mäemets et al., 2010).
65	Pielinen	Finland	63°13'N, 29°40'E	867	9.9	60.0	6.6	101.1	-	-
66	Playgreen	Canada	54°0'N, 97°55'W	653	4.0	18.0	5.7	51.3	-	-
67	Poyang	China	29°05'N, 116°17'E	3210	8.4	25.0	9.6	81.1	-	Rich in vegetation especially the shallow parts (Hui et al., 2008; Liao et al., 2013).
68	Pyasino	Russia	69°50'N, 87°40'E	735	4.0	10.0	11.7	78.5	-	-
69	Rio Hondo	Argentina	27°32'S, 64°57'W	330	5.3		4.2	24.1	-	-
70	Rybinsk	Russia	58°20'N, 38°40'E	4550	5.6	28.0	21.4	156.8	-	-
71	Tonlé Sap	Cambodia	12°53'N , 104°04'E	13000	-	12.0	15.8	115.6	-	Submerged macrophytes are uncommon due to turbidity and large water level fluctuations. The shallow shoreline of the lake consist of dense emergent and floating mat macrophytes (Campbell et al., 2006).
72	Skadar	Albania	42°10'N, 19°20'E	372	5.0	8.3	6.2	45.3	-	-
73	Saint Clair	USA Canada	42°28'N , 82°40'W	1113	3.0	6.0	12.4	58.4	-	Macrophytes dominate over phytoplankton except for the lake center (Schloesser et al., 1985; Schloesser et al., 1986).
74	Taihu	China	31°15'N, 120°15'E	2428	1.9	2.6	16.5	68.3	-	Macrophyte growth at the shores (in the past) and in the southeast (Zhao et al., 2012a; Zhao et al., 2012b; Zhao et al., 2013).

Table 2.1 continued…

	Lake	Country	Coordinates	A	Z_{mean}	Z_{max}	F_{mean}	F_{max}	M	
75	Taimyr	Russia	74°35'N, 103°00'E	4560	2.8	26.0	15.2	326.5	-	No vegetation (Timm, 1996).
76	Tana	Ethiopia	11°59'N, 37°20'E	3600	9.0	14.0	20.4	76.5	-	-
77	Tsimlyanskoye	Russia	48°15'N, 43°05'E	2702	8.8	35.0	10.2	108.5	-	-
78	Tumba	Congo	0°50'S, 18°0'E	500	4.0	6.0	7.5	48.1	-	-
79	Uluabat	Turkey	40°10′N, 28°35E	240	2.5	3.0	3.7	25.7		Submerged macrophytes where sparse during high water level but expanded to 55% of the lake's surface area during low water level (Beklioglu et al., 2006).
80	Võrtsjärv	Estonia	58°15'N, 26°3'E	271	2.8	6.0	8.3	34.0	-	In the south macrophytes grow in a sheltered condition (Feldmann et al., 2007)
81	Vygozero	Russia	63°37'N , 34°38'E	1250	6.2	18.0	9.7	110.1	-	-
82	Winnebago	USA	44°01'N , 88°25'W	557	4.7	7.0	10.5	45.2	-	-
83	Winnipegosis	Canada	52°36'N, 99°50'W	5150	4.2	18.3	16.3	146.8	-	-
84	Yuqiao R.	China	40°2'N, 117°32'E	250	4.6	12.0	3.2	19.2	-	-
85	Ziway	Ethiopia	7°58'N, 38°50'E	485	2.5	9.0	7.9	31.4	-	Extensive vegetated shoreline (mainly emergent). Around 12% of the lake area is covered by macrophytes (Tamire et al., 2013).

A = surface area of the lake, Z_{mean}= average depth, Z_{max}=max depth, F_{mean}= average depth, F_{max}= max depth, M = Model outcomes on presence of macrophytes (YES) and alternative stable states (ASS).

Combining the model output with Taihu's average depth and fetch (for details on fetch determination see Appendix 2), the *size effect* seems to be too excessive for any macrophyte growth (Figure 2.9a, red dot). However, this contradicts the observations showing macrophytes growth in parts of the lake. By using average values for fetch and depth and thereby ignoring the *spatial heterogeneity*, important explanatory information for macrophyte presence is neglected. Indeed, large parts of the lake do not behave according to the average. The frequency distribution shown on Figure 2.9b accounts for the *spatial heterogeneity* considering the presence of shallow and wind shaded versus relative deeper windy regions. By including *spatial heterogeneity,* the presence of macrophytes in the bays in the north and east can be better understood since regions that are less prone to wind forces as result of a shorter fetch (Figure 2.9b, process 5) or are relatively shallow (Figure 2.9b, process 3) are accounted for. A comparison between the model simulations and the frequency distribution that depicts the *spatial heterogeneity* in depth and fetch of Taihu, suggests that nearly 40% of the lake has the potential for macrophyte growth and 15% may potentially have alternative stable states (Figure 2.9b).

To examine whether the macrophyte-suitable area has indeed been macrophyte-dominated in the past, the frequency distribution is split (according to the distribution data of the 1980s) into frequency distributions for macrophyte-dominated (Figure 2.9c) and macrophyte-lacking (Figure 2.9d) areas. Although the model results are only meant as indicative, this analysis imply that more than 75% of the vegetated area coincides with the potential suitable areas for macrophyte growth as indicated by the model output, of which more than 15% has the possibility of alternative stable states (Figure 2.9c). The latter areas can be mainly found in near-shore areas around the lake, in Ghonghu Bay and southeast Taihu. Most northeasterly macrophyte stands have nowadays disappeared as result of *spatially heterogeneous* nutrient input (Figure 2.2b, process 4). In contrast, macrophyte sites far away from the inlets were only moderately affected. The areas that lack macrophytes (Figure 2.9d) are usually deeper and have a longer fetch. The areas where *size effects* prevail, are mainly restricted to the lake's center where fetch length exceeds more than 20 km (Cai et al., 2012). This long fetch prohibits macrophyte growth due to the wind-driven waves that cause high concentrations of suspended solids and that would damage any macrophyte (Figure 2.2a, process 1) (Pang et al., 2006; Cai et al., 2012; Zhao et al., 2012a). Additionally, the lake center is deeper than other parts of the lake and has a mineral soil due to the ongoing resuspension (Figure 2.8) which prevented an organic lacustrine sediment layer to develop (Shen et al., 2011). Due to unsuitability of the lake center for macrophyte growth, alternative stable states are most likely not present here.

The large variation in nutrients and suspended solids indicate a low *internal connectivity* in Taihu, especially between the east and the rest of the lake (Li et al., 2011a). Likely, the variation in concentrations is the result of the long residence time of 300 days, the effect which is enhanced by the prevailing winds that blows floating algae away from the east, preventing them to deteriorate East Taihu (Qin et al., 2010; Li et al., 2011b). If the flushing rate in the lake would be higher, nutrient concentrations would most likely be more equally distributed and macrophytes in the east would be more affected by eutrophication (Figure 2.2c, process 6). A whole-lake flushing measure to reduce water age in Taihu (Li et al., 2011a) revealed the effect of *internal connectivity* on Taihu's water quality. The water age reduction was meant to flush out nuisance algae. However, the water age could not be shortened enough to overcome cyanobacterial growth (Qin et al., 2010). At the same time the most eutrophic bay (Meiliang) did not significantly improve in water quality as a result of flushing because local prevailing currents prevented inflow of the water into the bay (Qin et al., 2010; Li et al., 2013). In the past, the *internal connectivity* of this bay has been decreased by land reclamation; some islands became peninsula and thereby separated bays that where connected before (Li, 1999; Hu et al., 2004). Hence, the low *internal connectivity* prevents exchange between bays and restricts propagation of the phytoplankton towards the east where at present macrophytes still prevail.

Consequently, Taihu has a modular response to eutrophication leading to different states side by side, some states conceivably alternatively stable, others probably not.

Other large shallow lakes

It is interesting to know whether *lake size*, *spatial heterogeneity* and *internal connectivity* acting in Taihu are exemplary for the existence and patterning of alternative stable states in other large shallow lakes. Based on a number of large shallow lakes listed in Table 2.1, the generality of these mechanisms will be discussed.

The estimated probability of other large shallow lakes to have macrophyte domination, and, if so, whether these have a potentially alternative stable state is shown in Figure 2.9a. A comparison with the model outcomes indicate that 8 lakes might have alternative stable states (Table 2.1) including Lake Apopka (USA) where literature previously presumed alternative stable states as well (Bachmann et al., 1999; Lowe et al., 2001). The majority of the other lakes that are indicated by the model to potentially have alternative stable states are reported to support macrophytes, which in some lakes became too excessive, resulting in problems with boating access and flooding as in Lake Guiers (Senegal) (Cogels et al., 1997; Hellsten et al., 1999) and Loktak (India) (Singh et al., 2011). Other lakes are largely turbid such as the Boraphed Reservoir in Thailand (Mizuno et al., 1970). Whether these lakes indeed show alternative stable states has not been proven by this analysis and would require further research.

Model results also indicated 3 lakes to have habitats that are particularly suitable for macrophyte growth mainly because of their shallowness. These are Lake Upemba (Congo), Lake Istokpoga (USA) and Lake Tathlina (Canada). Indeed, macrophytes are abundantly present in Lake Upemba. Also in Lake Istokpoga macrophytes are flourishing. Despite great effort, removal of excess of macrophytes had only a temporal effect (O'Dell et al., 1995) indicating that Lake

Istokpoga has conceivably only one stable state which is macrophyte dominated. Whether Lake Tathlina (Canada) is also macrophyte dominated is not clear since data are not available.

The majority of the lakes fall outside the suggested domain with the possibility of having macrophytes. These large shallow lakes are expected to be prone to the *size effect*. This is not surprising, since they have a large fetch or depth making the window of opportunity for macrophytes confined (Figure 2.2a, process 1). However, this contrasts to observations in the literature showing that in most of the lakes macrophytes had a chance to grow at least some time of history (Table 2.1). In some of the lakes this can be explained by natural water fluctuations. A drop in water level restricts the surface area where *size effects* prevail. For example, the water fluctuations in Lake Chad make the lake switch from a great large inland 'sea' in wet periods to a marshy macrophyte rich area in dry periods (Leblanc et al., 2011). Additionally, in Lake Beyşehir and Lake Uluabat (both in Turkey) receding water levels reveal large areas suitable for macrophyte growth, whereas high water levels go along with high turbidity (Beklioglu et al., 2006). Water level fluctuations can thus lead to alternating behavior of lakes to eutrophication, which will be showing a turbid state during high water levels, a macrophyte dominated state during extreme low water levels and possibly alternative stable states in between (Blindow et al., 1993; Van Geest et al., 2005). However, fluctuating water levels are not the sole explanation of macrophyte presence in all lakes.

So far, the effects of *spatial heterogeneity* have been ignored. If *spatial heterogeneity* is accounted for, as with the data of Taihu, there may well be compartments within large shallow lakes that are more sheltered or shallower and thereby being suitable for macrophyte growth. The *size effect* is then often restricted to the lake center as has been reported for many lakes including Lake George (Uganda) (Lock, 1973) and Saint Clair (USA and Canada) (Schloesser et al., 1985; Schloesser et al., 1986). Lake shores are excellent examples of sheltered and often shallow areas that support macrophyte growth like in Lake Eğirdir

(Turkey), Lough Neagh (UK) Tonlé Sap (Cambodia), Peipsi (Estonia, Russia) and Ziway (Ethiopia). However, not all shores are suitable for macrophyte growth. For example, in Lake Balaton (Hungary) prevailing northern winds cause high waves in the south, preventing macrophyte growth in this part of the lake while macrophytes are growing at the sheltered northern shores (Istvánovics et al., 2008). The same holds for Okeechobee (USA) where vegetation is restricted to the lee side in the south and west (Carrick et al., 1994; Havens et al., 2005; Rodusky et al., 2013) and Lake Võrtsjärv (Estonia) where most macrophytes grow at the lee side in the south of the lake. The sheltered conditions in Lake Võrtsjärv are enhanced by the natural narrowing of the lake's shores in the south (Feldmann et al., 2007). Other lakes have unsuitable littoral regions for macrophyte growth due to the construction of firm dikes around the lake such as in Lake IJsselmeer (the Netherlands) and Lake Kasumigaura (Japan). Some lakes lack macrophytes because the general conditions are too harsh, as in Lake Alexandrina where a severe drought caused too high salinity for macrophytes (Skinner et al., 2014), Lake Taimyr that is frozen most of the year (Timm, 1996) or the artificially created Lake Markermeer (the Netherlands) where the *size effect* is presumably too high, resulting in continuous resuspension of the soft sediment (Vijverberg et al., 2011; Kelderman et al., 2012a; Kelderman et al., 2012b).

The question remains whether the macrophyte rich areas in large shallow lakes could be alternatively stable showing hysteresis between the processes of eutrophication and oligotrophication. As Figure 2.9a illustrates, locations having the right characteristics for alternative stable states may exist. Of course, the model sensitivity to other factors than fetch and depth has been omitted causing uncertainty in the exact positioning of the domain of alternative stable states. These uncertainties may lead to either extension (e.g. presence of a marsh zone) or reduction (e.g. more resuspension sensitive sediment) of the alternative stable state's domain (Janse et al., 2008). Additionally, the *internal connectivity* has been neglected so far. The *internal connectivity* is ignored in the analysis of Figure 2.9, though its effect can be logically deduced. Take, for example, those lake compartments within the domain of alternative stable states of Figure 2.1. If these compartments are part of a homogeneous lake, *connectivity* will lead to local resistance to perturbations since other compartments will continuously supply inputs corresponding to the prevalent state, which leads to rehabilitation of the perturbed areas. Only when the entire lake has lost its resilience to perturbations, will a shift abruptly propagate through the lake like a 'domino effect' (Scheffer et al., 2012). This might be the case for Apopka (Florida), a lake that is rather homogeneous with respect to its depth; several perturbations did not lead to a lake wide shift. However after persistent eutrophication a single hurricane event led to a whole lake shift from macrophyte to phytoplankton domination (Schelske et al., 2010).

Heterogeneous lakes, however, have most likely regions that only appear in a single stable state besides these potentially alternative stable compartments. These single stable state compartments will destabilize the alternatively stable compartments that appear in a contrasting state, but stabilize those that have the same state. Therefore, the regions that could potentially show alternative stable states tend to appear in the same state as their neighboring compartments that only have a single state. As a consequence, high *internal connectivity* will enhance synchrony throughout the lake, through which edges of the grey domain in Figure 2.9a will move towards each other, making the domain of alternative stable states more confined. In Lake Markermeer for example, the high turbidity in most of the lake can easily affect the more shallow parts and thereby prevent macrophyte growth (Kelderman et al., 2012b). In Lake Pátzcuaro (Mexico) however, which is highly heterogeneous with respect to depth, main water flow direction to the north prevents the turbid water of the north from affecting the macrophytes in the south (Torres, 1993). This *low connectivity* between the lake compartments leads to asynchronous response within the lake to eutrophication. Conforming, *low connectivity* may allow for alternative stable states to occur within certain lake compartments. Since shifts in such a lake will occur at different times, the lake as a whole will probably show a gradual response to eutrophication stresses (Scheffer et al., 2012). In Lake Balaton, for example, a natural narrowing in the lake prevents *connectivity* between the west and east side of the lake. Though alternative stable states are unlikely to occur in this lake, this narrowing leads to different eutrophic levels in different compartments of the lake (Pálffy et al., 2013).

Conclusion

The unique combination of *lake size, spatial heterogeneity* and *internal connectivity* determines the spatial extent of stable states in large shallow lakes. At locations where *size effects* prevail, macrophytes are generally absent and alternative stable states are unlikely to occur. However, the occurrence of macrophytes is inexplicable when only size effect is taken into account. By including *spatial heterogeneity* in the analysis, the presence of macrophytes and alternative stable states in large shallow lakes is better understood. Taking into account the *internal connectivity* is important in the evaluation whether the effect of *spatial heterogeneity* is either offset (high *internal connectivity*) or promoted (low *internal connectivity*).

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Chapter 3

Exploring, exploiting and evolving diversity of aquatic ecosystem models: a community perspective

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Abstract

Here we present a community perspective on how to explore, exploit and evolve the diversity in aquatic ecosystem models. These models play an important role in understanding the functioning of aquatic ecosystems, filling in observation gaps and developing effective strategies for water quality management. In this spirit, numerous models have been developed since the 1970s. We set off to explore model diversity by making an inventory among 42 aquatic ecosystem modelers, by categorizing the resulting set of models and by analyzing them for diversity. We then focus on how to exploit model diversity by comparing and combining different aspects of existing models. Finally we discuss how model diversity came about in the past and could evolve in the future. Throughout our study we use analogies from biodiversity research to analyze and interpret model diversity. We recommend making models publicly available through open source policies, to standardize documentation and technical implementation of models, and to compare models through ensemble modelling and interdisciplinary approaches. We end with our perspective on how the field of aquatic ecosystem modelling might develop in the next 5-10 years. To strive for clarity and to improve readability for non-modelers we include a glossary.

Introduction

The societal niche for aquatic ecosystem models: developing short-term and long-term management strategies

Aquatic ecosystems provide a range of ecosystem services (MEA, 2005), in particular by being sources and sinks for natural resources and anthropogenic substances. For example, as a source they provide water for drinking, irrigation, hydropower and industrial processes. Moreover, they provide many food products. More recently, their aesthetic and recreational value has been recognized with associated health benefits. Aquatic ecosystems also act as a sink for various substances, including sewage, agricultural runoff, discharge from impoundments, industrial waste and thermally polluted water. Equally important, they provide a critical habitat for organisms that form an important part of the biodiversity. Each of the anthropogenic and natural source functions puts specific requirements on the quality of the aquatic ecosystem (Postel et al., 2003; Keeler et al., 2012). At the same time, these quality requirements can be hampered by both the source (through overexploitation) and the sink (through pollution) function of the aquatic ecosystem. Aquatic Ecosystem Models (hereafter referred to as AEMs) frequently play a role in quantifying ecosystem services and developing strategies for water quality management (Jørgensen, 2010; Mooij et al., 2010). The AEMs used for this purpose are often engineering-oriented based on accepted theory and methodology for routine applications. Engineering models may be complex and linked to one another, but components are always tested. Using projections and scenario analyses, engineering-oriented AEMs can assess the various source and sink functions to help optimize and understand aquatic ecosystem function in terms of human and conservation needs. For example, AEMs have been applied as management tools to evaluate the efficiency of eutrophication mitigation strategies, to understand oceanic dynamics (e.g., the global carbon cycle), and to predict biotic responses to climate change (Arhonditsis et al., 2004). AEMs can also be used for near real-time modelling and forecasting to facilitate immediate management decisions on, for instance, the shutdown of drinking water intakes (Huang et al., 2012; Silva et al., 2014) or the suitability of water for swimming (Ibelings et al., 2003).

The scientific niche for AEMs: advancement of theory

A strong scientific motivation for the development of AEMs is to encapsulate and improve our understanding of aquatic ecosystems. For instance, scientific AEMs can help to close mass balances of essential elements such as carbon, nitrogen and phosphorus and thereby allow quantifying the role of aquatic systems in national and global carbon and nutrient budgets (Robson et al., 2008; Harrison et al., 2012). Keeping track of mass balances can also provide help in answering stoichiometric questions (Giordani et al., 2008; Li et al., 2014). Additionally, scientific AEMs can help untangle the feedbacks between aquatic biodiversity and aquatic ecosystem functioning (Bruggeman et al., 2007), and also achieve an integrated ecosystem health assessment (Xu et al., 2001). Yet another timely research topic studied with models is assessing the resilience of ecosystems to changes in external forcing arising from nonlinear functional relationships between ecosystem components (Ludwig et al., 1997; Scheffer et al., 2001). This has been done by analyzing the strength of various positive and negative feedback loops in the socio-ecological system (Van der Heide et al., 2007; Downing et al., 2014). Such studies generate new hypotheses that can then be tested in laboratories or in the field. Models are therefore effective scientific tools because they allow undertaking “virtual experiments” that would be too expensive or impractical to carry out in real world systems (Meyer et al., 2009).

The methodological niche for AEMs: filling data gaps and inverse modelling

Another motivation to develop AEMs is to fill gaps in observations. For instance, some quantities (e.g. primary production) are measured at high spatial resolution, but at a low temporal resolution and vice versa. Modelling then allows for interpolation in space and time such as seen in climatology (Jeffrey et al., 2001). Other examples include interpolating through time between satellite images or across space to fill gaps caused by cloud cover (Hossain et al., 2015). Inverse modelling is another application within the methodological niche for AEMs, in which specific system parameters or process rates that are difficult to measure are estimated. In contrast with forward modelling, inverse modelling uses observations to estimate the processes or factors that created these observations (Tarantola, 2005). Since inverse modelling in general lacks a unique solution it is important to include all a priori information on model parameters and processes to reduce the uncertainty on the results (Tarantola, 2005; Jacob, 2007). Methods used for inverse modelling include Bayesian inference, often used with the Markov Chain Monte Carlo technique (Press, 2012; Gelman et al., 2014) and Frequentist inference (Press, 2012). Different software packages for implementation of these methods exist (Vézina et al., 1988; Reichert, 1994; Lunn et al., 2000; Soetaert et al., 2010a; Van Oevelen et al., 2010; Doherty, 2015).

Existing diversity in AEMs

Due to numerous potential AEM applications (in an analogy to biodiversity we refer to these as 'model niches'), scientists began to develop these models in the 1960s, in tact with the availability of the necessary computing infrastructure to implement them (e.g. King et al., 1967). Since then, an array of AEMs has been developed around the world, with each development directed by a specific set of questions and hypotheses. In many cases, investigators and engineers implemented their own models rather than starting with an existing model. While this practice of creating one's 'own model' can be criticized because it bears the inefficiency of 'reinventing the wheel' (Mooij et al., 2010), it has produced a great diversity in approaches, formulations, complexity and applications, which can be seen as an advantage. In addition, the extra investment is often compensated by a more efficient model application for the issue at hand and a better model understanding. Furthermore, the availability of modelling resources through the internet provides new opportunities to explore and exploit this diversity and will most likely affect the evolution of model diversity in the near future.

A working definition of what constitutes an AEM

This paper aims to present a current perspective on how we can explore, exploit and evolve the existing diversity in AEMs as seen by a diverse and international community of aquatic scientists (the authors). We try to reach out to both the skilled modelers, but also to aquatic ecologists that are inexperienced in modelling. To make this study feasible, we need a definition of what constitutes an AEM. Here we define an AEM as *"a formal procedure by which the impact of external or internal forcing on aquatic ecosystem state(s) can be estimated".* In most cases, AEMs cover many processes and are spatially explicit, but both are not a prerequisite. According to our definition, a minimal model that qualitatively describes the ecosystem response to external forcing also qualifies as an AEM (Figure 3.1). We exclude models that focus on one single component of an ecosystem (e.g. models that only deal with the population dynamics of a given species), but include models that zoom in on one part of the ecosystem (e.g. the fish or macrophyte community) while treating the remainder of the ecosystem in an aggregated way (typically through the use of carrying capacities or mortality rates). Two distinct classes of AEMs exist: those that formulate a direct mathematical relation between forcing and state (statistical models) and those that are formulated in terms of the processes underlying this relation (process-based models). Statistical models directly link forcing and state that can be derived from data with standard statistical techniques. Linking process-based models to data involves less standardized calibration and validation techniques. The advantage of process-based models is that they provide insight in the mechanisms underlying change and recovery. This study is primarily focused on the diversity in process-based models, although we acknowledge the diversity and usefulness of statistical models that directly link forcing and state. AEMs, as defined here, combine elements from a number of scientific modelling disciplines (Figure 3.2). In addition to defining what constitutes an AEM, we developed a glossary of terminology used in the field of aquatic ecosystem modelling (given in Box 3.1). The purpose of this glossary is to strive for clarity within the context of this study. This glossary may also be of help to newcomers in the modelling field. While working on the glossary we noted that it is impossible to make a clear distinction between models (the mathematical description of a system), their implementation (e.g. software packages) and their applications (where model inputs/parameters are adapted to a specific ecosystem and confronted with data) because there is great diversity in how these components are perceived and combined by different modelers.

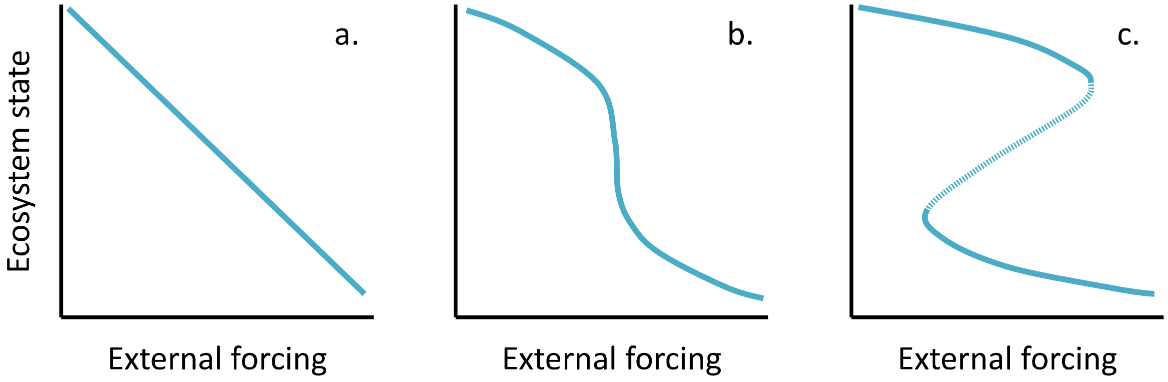

Figure 3.1. Example of output of a conceptual AEM showing a linear (a), catastrophic (b) and hysteretic (c) response of ecosystem state to external forcing. Modified after Scheffer et al. (2001).

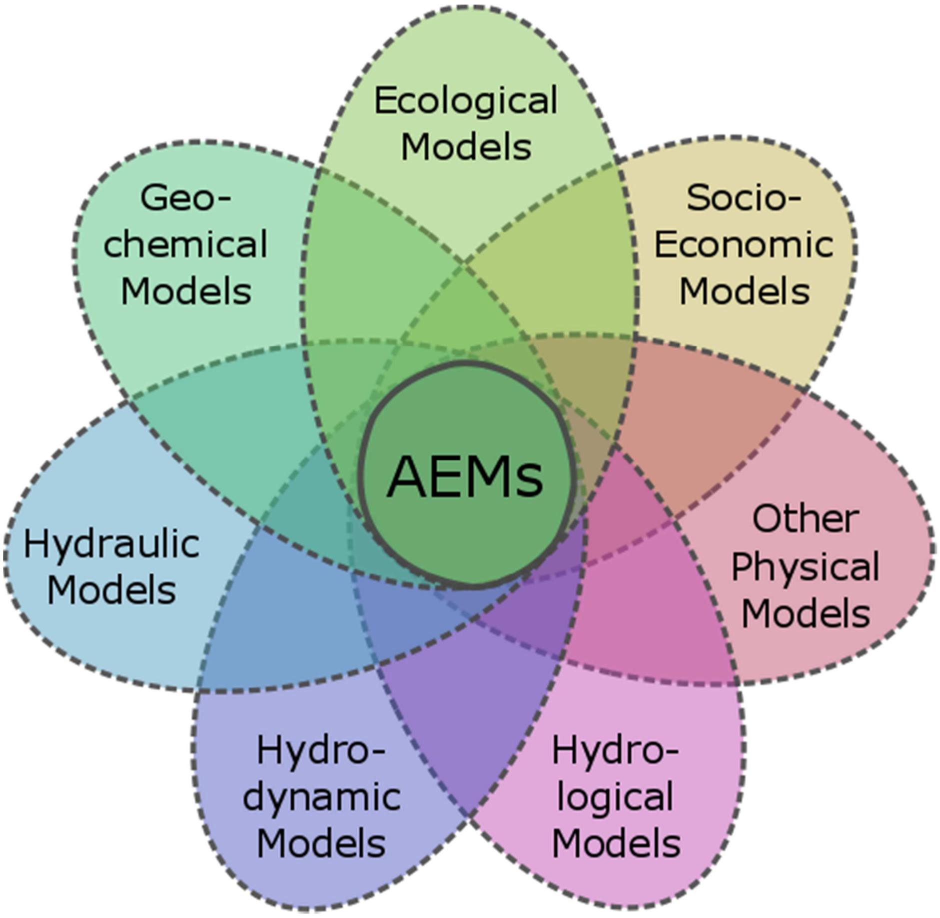

Figure 3.2. A diagram showing the major modelling disciplines that can contribute to Aquatic Ecosystem Models (AEMs). There is a great diversity among AEMs in the weight given to each component: each modeler should select the most appropriate combination and size of the petals to fit the research question.

Table 3.1. An overview of the number of AEMs, hydrological and hydrodynamic drivers, supportive software and relevant modelling approaches considered in this and other studies.

Explorative and exploitative activity	Number considered in this study	Number considered in other studies
Glossary of AEMs, hydrological and hydrodynamic drivers, supportive software and relevant modelling approaches (Box 3.1)	277	14[a] 66[b] > 100[c] 1360[d] 33[e]
Survey of knowledge and expertise level of AEMs, hydrological and hydrodynamic drivers, supportive software and relevant modelling approaches (Appendix 4)	133	
Categorization of AEMs Appendix 5)	42	15[f] 27[g] 6[h]
Comparison of state variables of AEMs (Appendix 6)	24	
Comparison of process formulations of AEMs	0	13[i] 4[j]
Ensemble modelling with multiple AEMs	0	3[k]

[a] Refsgaard et al. (2004), [b] http://www.mossco.de/doc/acronyms.html, [c] http://en.wikipedia.org/wiki (NB: no overview page of AEMs), [d] Benz et al. (2001) http://www.ecobas.org (NB: ecological models in general, only 18 overlap with the terms in Box 3.1),
[e] https://wiki.csiro.au/display/C2CCOP/Inventory+of+C2C+models [f] Mooij et al. (2010), [g] Weijerman et al. (2015), h Lenhart et al. (2010) [i] Tian (2006), [j] Recknagel et al. (2008) [k] Trolle et al. (2014).

How this study is structured

We first focus on exploring AEM diversity by discussing approaches to inventorize, categorize and document these models and finally present a more formal analysis of model diversity. To support our discussion we compare a number of AEMs, hydrological and hydrodynamic drivers, relevant modelling approaches and supportive software for model implementation and model analyses that came about in a survey among modelers participating the third AEMON (Aquatic Ecosystem MOdelling Network) workshop held in February 2015. To put our analysis in perspective, we compare the number of AEMs, hydrological and hydrodynamic drivers, relevant modelling approaches and supportive software for model implementation and model analyses with published lists (Table 3.1). We cover both marine and freshwater AEMs, with a bias towards the latter group. All data can be found in Appendix 3. It is remarkable that earlier attempts by e.g. Benz et al. (2001) have little overlap with our overview, which shows that there is an greater diversity than presented here. We then focus on exploiting diversity and ask several questions. How can we make use of the full breadth of expertise captured in existing AEMs, and how can we easily switch between spatial configurations or software packages to run and analyze the models using package-specific tools? We continue with stressing the potential of ensemble modelling, and we end this section with a discussion on how to exploit the full range of approaches used in aquatic ecosystem modelling. In the section on evolving diversity, we describe the origins of the current diversity in AEMs and discuss how model diversity could evolve in the future and how standardization can facilitate this process. In the final section, we discuss how we can learn from concepts and techniques in biodiversity research in our study on model diversity. Finally, we provide a list of practical recommendations and a perspective for the field of aquatic ecosystem modelling in the next decade.

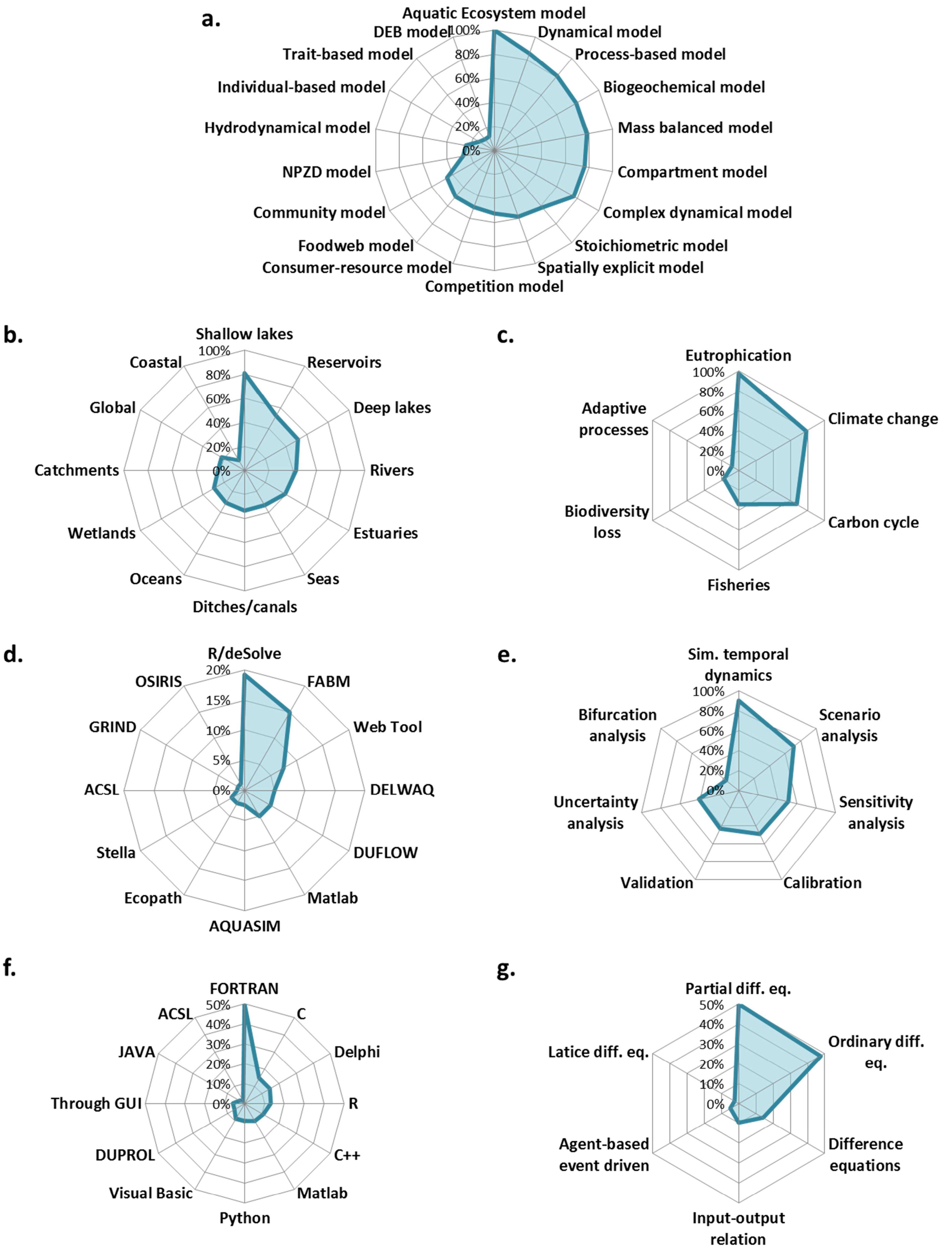

Figure 3.3. Outcome of a categorization of 42 AEMs on six types of categorizations: (a) modelling approach (for all levels see Appendix 4), (b) environmental domain of the model, (c) model application domain, (d) modelling framework, (e) type of analysis available within the model's framework, (f) programming language and (g) mathematical equation type. See text for explanation.

Exploring diversity in AEMs

AEMs have been and are being developed independently in many places around the world. In this section we explore model diversity.

Making an inventory of the diversity in AEMs

An exploratory survey among 42 modelers participating in the third AEMON workshop 2015 resulted in 133 different models, packages or programming languages in use in the field of aquatic ecosystem modelling (data presented in Appendix 3, Datasheet 2). We performed a Redundancy Analysis (RDA, using the methods of Oksanen et al. (2014)) on 39 AEMs from this list (results in Appendix 4). This analysis demonstrates that the professional affiliation and country of origin played an important role in determining knowledge and usage of models. The driver behind this could be the research group's background, but also the diverging needs that motivated the development of models, such as whether there are mainly shallow lakes or deep reservoirs in a specific country. Three approaches seem suited for developing a more formal and ongoing inventory of model diversity: (1) lists, (2) wikis, and (3) code repositories. We are not aware of an up-to-date list of AEMs with a good coverage of the field. Laudable attempts to list ecological models are UFIS (Knorrenschild et al., 1996) and the ECOBAS initiative by Joachim Benz (http://www.ecobas.org, Benz et al., 2001). ECOBAS provides meta-data on a wide range of models, including hydrological, hydrodynamic, meteorological and ecological models. However, the website has only rarely been updated since 2009; updating is a challenge for any top-down initiatives. An alternative could be an open community-based approach, such as wikis, where multiple editors independently contribute information. The obvious and overwhelmingly successful example of this approach is Wikipedia (http://www.wikipedia.org) which maintains many lists, for instance of programming languages (http://en.wikipedia.org/wiki/List of programming languages). The potential lack of consistency of such community-based lists seems to be compensated by the scope and immediacy of the information provided and the commitment resulting from the community-based approach. The third option is code repositories, such as SourceForge (http://sf.net) and GitHub (http://github.com), which are increasingly popular platforms enabling open source communities to develop software and distribute code.

Documenting diversity in AEMs

To preserve and communicate model diversity, proper documentation of models is crucial. There is no standard way of documenting AEMs, and different model developers have different methods to obtain and save their information. The existing ODD protocol (Overview, Design concepts, and Details) for individual-based models (Grimm et al., 2006), the Earth System documentation project (http://es-doc.org) or the TRACE approach (TRAnsparent and Comprehensive Ecological modelling documentation) might be adopted by aquatic ecosystem modelers in the future (Grimm et al., 2014). Models can be documented through model homepages, scientific publications or grey-literature reports. Wikipedia is not an option because it has a strict policy of not being a primary source of documentation but instead only providing referenced information. To be useful in the current practice of scientific research, any type of documentation should be accessible through the internet, preferably with open access. The majority (71%) of the AEMs analyzed in Appendix 5 has a website that provides model documentation. Furthermore, for 86% of the models we could identify a primary publication, however only 3 out of 42 AEMs analyzed in Appendix 5 have a page on Wikipedia (Ecopath, PCLake and PCDitch).

Categorizing diversity in AEMs

To cope with the diversity in models, some form of categorization is useful. 'Bining' models in clearly defined categories provide an overview for newcomers and experts, and helps to identify what is missing. From the list of models in Appendix 3, Datasheet 2, we selected those models that can be classified as an

AEM according to our definition. This resulted in a list of 42 AEMs (see for data Appendix 3, Datasheet 3). For these models we were able to obtain metadata from experts to categorize them (see Appendix 5 for all the details and see Box 3.1 for an explanation of all the technical terms used below). For the modelling approach it was found that over 75% of the models were qualified as being dynamic, process-based, biogeochemical, mass-balanced, compartmental or complex dynamical (Figure 3.3a). Over 45% of them were qualified as being stoichiometric or spatially explicit as well as being a competition, a consumer-resource, a food web or a community model. About 25% of them were qualified as being of the NPZD type of model (Nutrients, Phytoplankton, Zooplankton, Detritus) as well as being a hydrodynamic model. One out of seven of these models contained individual-based approaches, more specifically being an individual-based community model, a trait-based model or a dynamic energy budget model. The 42 AEMs cover every aquatic habitat, with 22% of models claiming global applicability (Figure 3.3b). Eutrophication is an application domain of no less than 98% of the analysed models (Figure 3.3c). Next, in decreasing order of importance are climate change, carbon cycle, fisheries, biodiversity loss and adaptive processes. 90% of the 42 models allow for dynamic simulations (Figure 3.3e). The remaining models are based on statistical relations. About half of the models are implemented in frameworks that have tools for sensitivity analysis, calibration, validation and uncertainty analysis. Here we define a framework as a software package that can be combined with user-written code to create a software application (for a more extensive definition see Box 3.1). Tools for bifurcation analysis are less common. Over two third of the models is implemented within an existing modelling framework, with the R/deSolve package (Soetaert et al., 2010b) and the Framework for Aquatic Biogeochemical Models (FABM) (Bruggeman et al., 2014) being the most used of the 12 modelling frameworks that we encountered (Figure 3.3d). One can rightfully say that the field of aquatic ecosystem modelling is quite scattered when it comes to the use of modelling frameworks. This notion was one of the incentives for developing Delft3D-Delwaq (Deltares, 2014), FABM (Bruggeman et al., 2014) and the Database Approach to Modelling (DATM) (Mooij et al., 2014). With 50%, FORTRAN is the dominant programming language for coding AEMs (Figure 3.3f). Next comes C or C++ (together 26%), Delphi (15%) and R (15%). The majority of AEMs are implemented as ordinary or partial differential equations (Figure 3.3g).

Analyzing diversity in AEMs

Analyzing model diversity goes beyond the more descriptive approach mentioned above. Here the aim is to identify whether we are dealing with true diversity or ‘pseudo-diversity’. Models are often related to each other. The MyLake model (Saloranta et al., 2007), for example, has characteristics that are also found in other lake models like DYRESM-CAEDYM (Hamilton et al., 1997), MINLAKE (Riley et al., 1988), PROBE (Blenckner et al., 2002), and BELAMO (Omlin et al., 2001; Mieleitner et al., 2006). We aim for a more objective and in-depth analysis of a list of AEMs using a similarity index (for details on the analysis see Appendix 6 and for the data Appendix 3, Datasheet 4). One approach is to compare state variables between models. We analyzed 24 AEMs for which sufficient information was provided, which gave in total almost 550 unique state variables. The minimum number of state variables found in a model is 2 and the maximum is 118 (Figure 3.4). It should be noted that in some (especially the larger and general) models not all state variables are included simultaneously in each model application but rather subsets of variables are being used. Additionally, some models have state variables that can be duplicated by changing their parameters (e.g. cohorts of a species). A Sørensen similarity analysis (Sørensen, 1948) using the state variables of 24 models (Appendix 6) shows that models become more similar as their complexity increases. This is an expected result as the chance of similarities increases with increasing sampling size of a given pool. However, overall the dissimilarity is higher than the similarity since more than 80% of the models have a similarity index of less than

0.25. Hence, many models benefit from predecessor models even though they are still unique with individual features not found in predecessor models. Most overlap can be found in general state variables such as phosphorus, ammonia and a generic group of phytoplankton or zooplankton. Three groups of models can be distinguished: general-purpose models with a relative high overlap, specialized models with low overlap and intermediate models with an intermediate level of overlap (see dendrogram in Appendix 6). Interestingly, some models are significantly more dissimilar than would be statistically expected based on their number of state variables (red downward arrow, Figure 3.4). This is because these models capture only a specific non-overlapping part of the aquatic ecosystem (e.g. the Guam Atlantis Coral Reef Ecosystem Model versus PCLake or CAEDYM). Other models are more similar than would be expected based on the number of state variables (upward green arrow); these models simulate the aquatic ecosystem in a more general way, such as CCHE and Mylake. A following step could be to compare the models for their mathematical process formulations, though this is beyond the scope of this paper. An educated guess is that this will reveal an even higher diversity, as endless combinations can be made with the available process formulations. For example, Tian (2006) counted 13 functions used to describe the effect of light forcing on phytoplankton growth. Using these light functions in combination with other functional relations, for instance, temperature forcing (10 different relations), zooplankton feeding (20 different relations), prey feeding (15 different relations) and mortality (8 different relations) lead to hundreds of thousands of combinations that give different results and are all 'the best', depending on the aim of the model (Gao et al., 2000).

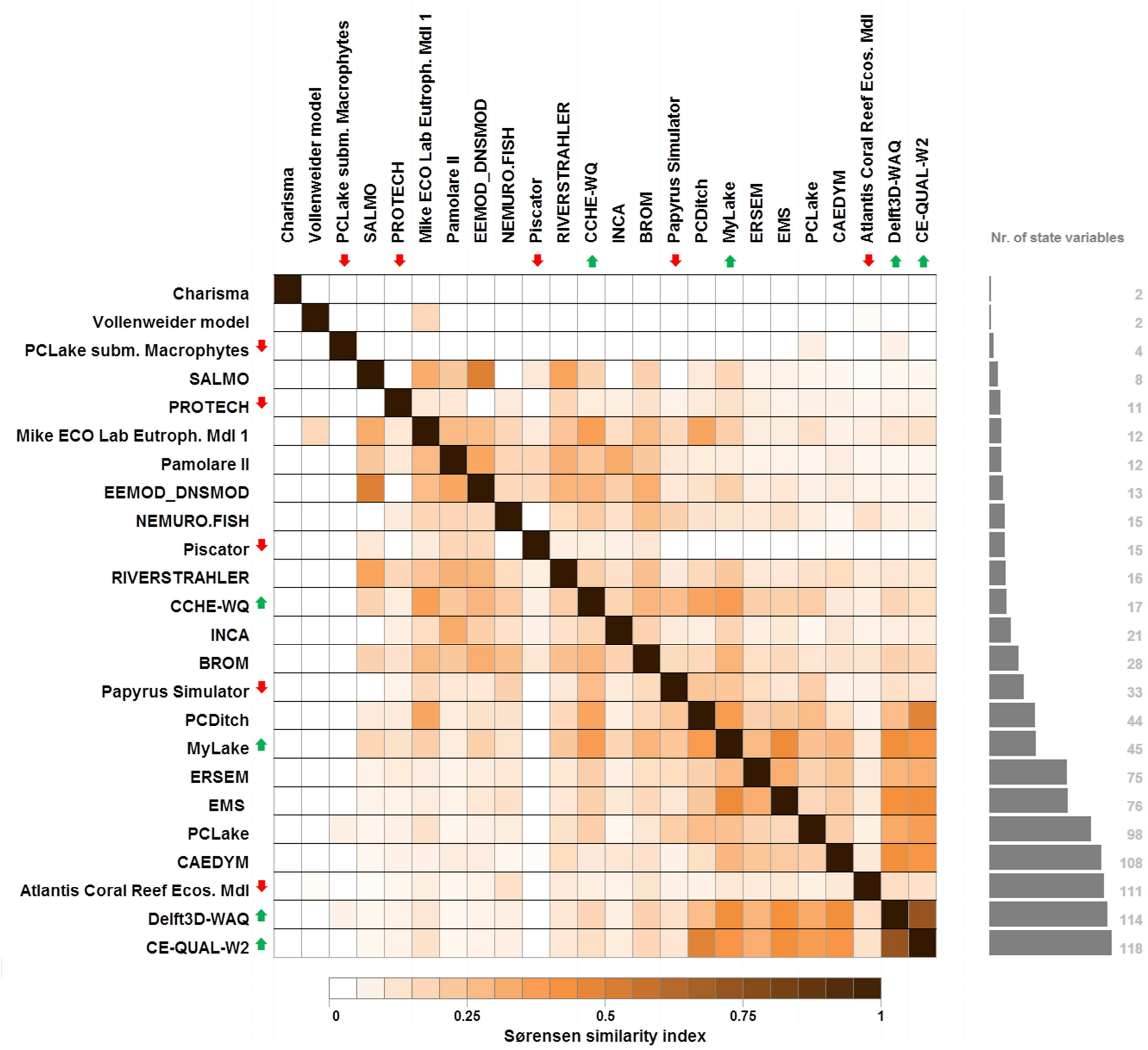

Figure 3.4. Similarity matrix based on the Sørensen similarity index between the state variables considered in the models. Darker colors mean higher similarity. Models with a green upward arrow are significantly more similar to other models corrected for the maximum number of state variables (p<0.05). Models with a red downward arrow are significantly more dissimilar to other models corrected for the number of state variables (p<0.05). Grey bars on the right show the maximum number of state variables within a model. For detailed information on methods and results see Appendix 6.

Exploiting diversity in AEMs

The inventory of the AEMs reveals a great diversity in model approaches, formulations and applications. Here we ask whether and how this diversity could be exploited.

Exploiting the diversity in disciplines

One of the options is to exploit the diversity in contributing disciplines (see Figure 3.2) and work in teams consisting of not only aquatic ecologists, but also social scientists, economists, climatologists, hydrologists, statisticians, mathematicians, et cetera. Working in an interdisciplinary setting helps one to look beyond the personal expert field and provides a more holistic view upon both models as well as aquatic ecosystems (Hamilton et al., 2015). Resulting interdisciplinary models have an increased complexity with the disadvantage that full understanding of the model by the individual modeller is lost (Scholten et al., 2007; Robson, 2014a). The problem of inappropriate usage of complex models can be overcome by again working in interdisciplinary teams. In this way team members are able to focus on their own area of expertise while the team as a whole is able to understand the full model. Statisticians and mathematicians can support interdisciplinary teams with their knowledge on mathematical formulations and their insight in model uncertainty. Especially within the scientific niche, understanding of the model is important since novel ideas need to be tested and understood. Within the engineering niche, there is less need to understand each model component in detail. Indeed, many people drive a car safely without having a detailed technical background on the engine's functionality.

Exploiting the diversity in spatial explicitness of AEMs

Another way to exploit the diversity in AEMs is by using the full width of spatial explicitness, which varies from spatially homogeneous (0D) and vertically or horizontally structured (1D) to fully 3D. Within these dimensions, a modeller can additionally choose between different structured grids (e.g. Cartesian grid, regular grid and curvilinear grid) and unstructured grids (e.g. finite elements). Following Occam's razor, model complexity should be minimized and only increased if this increases the predictive performance of the model or its generality/universality (please note that, while mentioned here in the context of spatial explicitness, Occam’s razor applies to all aspects of complexity in AEMs). Therefore, to understand the basics of ecological processes in a well-mixed system one should use a 0D model as its dynamics are often easier to understand. Additionally, 0D models are well-suited for checking the internal consistency of the model functions. Spatially explicit models, however, are more realistic, as they account for the spatial heterogeneity of ecosystems, with the risk of getting lost in complexity when explaining model behavior. Nonetheless, some research questions cannot be solved without taking spatial resolution into account (e.g. population dynamics of fish in Jackson et al. (2001), and spatial distribution of macrophytes and algae in Janssen et al. (2014)). Recent advances facilitate the implementation of a model in different spatial settings. For example, with Delft3D-Delwaq, FABM and DATM it is possible to switch between a 0D, 1D, 2D to 3D implementation of, for instance, PCLake (Van Gerven et al., 2015). However, these frameworks are currently implemented without accounting for feedbacks between ecology and hydrodynamics. Interfaces like OpenMI (Gregersen et al., 2007) and FABM (Bruggeman et al., 2014) allow for such coupling and are designed to overcome the issues that emerge when integrating ecology and hydrodynamics. Examples of these issues are the different time scales and spatial schematization for ecology and hydrodynamics (e.g. Sachse et al., 2014) and feedbacks between ecology and hydrodynamics, such as the effects of water plants on the water flow (e.g. Berger et al., 2008).

Exploiting diversity by having a given AEM implemented in multiple frameworks

Recent approaches like DATM (Mooij et al., 2014), FABM (Bruggeman et al., 2014) and the open process library in Delft3D-Delwaq (Deltares, 2014) make it possible to exploit model implementations in multiple frameworks without much overhead. Therefore, a myriad of tools for model analysis (e.g. sensitivity analysis, calibration, validation, uncertainty analysis, bifurcation analysis) become easily available. The redundancy in tools among frameworks insists modelers to stick to the framework they are familiar with for most analyses, whereas the complementarity in tools is tempting to switch to other frameworks for alternative analyses (Van Gerven et al., 2015), including the switch between 0D and 3D. In this way, the strengths of frameworks (including runtime) can be exploited and the underlying ecological question can be approached from different perspectives.

Exploiting diversity in dealing with uncertainty in AEMs

As a simplification of nature, AEMs suffer from uncertainty in their outcomes (Beck, 1987; Chatfield, 1995; Draper, 1995). Sources of uncertainty are structural uncertainty, i.e., incomplete or imperfect process formulations, parameter uncertainty, uncertainty in forcing functions and initial values, uncertainty in validation data and uncertainty due to the numerical methods used. A full coverage of the topic of uncertainty in AEMs is beyond the scope of this paper. For more information on this topic we refer to the extensive literature available on this topic including Beck (1987), Chatfield (2006) and Doherty (2015). Below we limit ourselves to presenting three different views on how to deal with uncertainty in parameters. First, a modeler measures the parameters' magnitudes directly. The parameter values are then purely based on biologically, chemically or physically knowledge. Due to errors in the measurements (experimental uncertainty, Moffat (1988)) and limited transferability (e.g. between lab and field conditions), these a priori parameter values have an uncertainty as well (Draper, 1995). By repeating the measurements over and over, the experimental uncertainty can be reduced, thereby minimizing the parameter uncertainty but this is often a costly measure (Chatfield, 1995). A second option is to estimate the parameters using calibration data and statistics without the use of a priori knowledge. This method leads in many cases to multiple possible parameterizations of the model with equal fit (e.g. Beven, 2006) and bears the risk of overfitting (Hawkins, 2004). For this reason, a modeller may choose for the third option where the parameters are estimated based on calibration data, statistics and a priori knowledge (e.g. Janse et al., 2010). In this case, a realistic range of parameter values is defined, prior to the parameter estimation by statistics. Thereafter, using Bayesian statistics, the parameters can be estimated within the range of realism (Gelman et al., 2014).

Exploiting diversity by ensemble modelling with AEMs

One way to deal with the uncertainty is using the diversity of models in ensemble techniques (e.g. Ramin et al. (2012) or Trolle et al. (2014), see Figure 3.5 for an example from the latter study). A variety of ensemble techniques exists, each duplicating a certain aspect of the modelling process. In multi-model ensembles (MME), multiple models are applied to a given problem. Single-model ensembles use different model inputs (parameters, initial values, boundary conditions) to exploit the model's sensitivity (e.g. Couture et al. (2014), Gal et al. (2014) or Nielsen et al. (2014)). More ensemble techniques or combinations of techniques exist including multi-scheme ensembling (use of different numerical schemes) and hyper-ensembling (use of multiple physical processes). Ensemble modelling has become a standard in meteorological forecasting (e.g. Molteni et al., 1996) and climatic forecasting (e.g. IPCC, 2014). There is an increasing number of applications in hydrology and hydrodynamics as well (e.g. Stepanenko et al. (2014) or Thiery et al. (2014)). In aquatic ecosystem modelling, the use of ensemble techniques is still rare (but see examples in, for instance, Lenhart et al. (2010), Ramin et al. (2012), Gal et al. (2014), Nielsen et al. (2014) or Trolle et al.

(2014)). However, the relevance of MME for ecological modelling is large, as a strictly physically-based description is not practically feasible and a unified, transferable set of equations is, therefore, not available. Additionally, we foresee that ensemble modelling will become common practice because of (i) the emergence of active communities of aquatic ecosystem modellers such as AEMON, (ii) the increase of freely available papers, data and model code, and (iii) the development of approaches such as Delft3D-Delwaq, FABM and DATM. Hence, the results of decades of individual model niche development can now be better utilized (Mooij et al., 2010; Trolle et al., 2012). The comparative list provided in Appendix 3 (Datasheet 4) is a useful starting point of ensemble modelling with AEMs. When using a model to provide forecasts, MME have two major advantages over single-model approaches. First, the ensemble mean may be a better predictor than any of the sole ensemble members (Trolle et al., 2014). This is especially true when an aggregated performance measure over many diagnostics variables is considered (Hagedorn et al., 2005; Trolle et al., 2014). Second, the ensemble spread can serve as a convenient measure of predictive uncertainty if a spread-skill correlation exists. Although MME are attractive, their limitations need to be recognized. First, despite ever increasing computer power, they are time-consuming to put in place. More importantly, MME-based estimates of structural uncertainty can only be meaningful if the models involved differ substantially. Another more general limitation of ensembles is that the attainable estimate of uncertainty is inevitably incomplete, for example due to a limited number of suitable models and the requirement of each model to have its own set of - ideally standardized - parameters and initial values. Ensemble techniques therefore only quantify part of the total uncertainty in predictions (Krzysztofowicz, 1999). In the context of ecological process-based modelling though, the integration of multiple models should not be viewed solely as an approach to improve our predictive devices, but also as an opportunity to compare alternative ecological structures, to challenge existing ecosystem conceptualizations, and to integrate across different (and often conflicting) paradigms (Ramin et al., 2012). Future research should also focus on the refinement of the weighting schemes and other performance standards to impartially synthesize the predictions of different models. Several interesting statistical post-processing methods presented in the field of ensemble weather forecasting will greatly benefit our attempts to develop weighting schemes suitable for the synthesis of multiple ecosystem models (Wilks, 2002). Other outstanding challenges involve the development of ground rules for the features of the calibration and validation domain, the inclusion of penalties for model complexity that will allow building forecasts upon parsimonious models, and performance assessment that does not exclusively consider model endpoints but also examines the plausibility of the underlying ecosystem structures, i.e., biological rates, ecological processes or derived quantities (Arhonditsis et al., 2004).

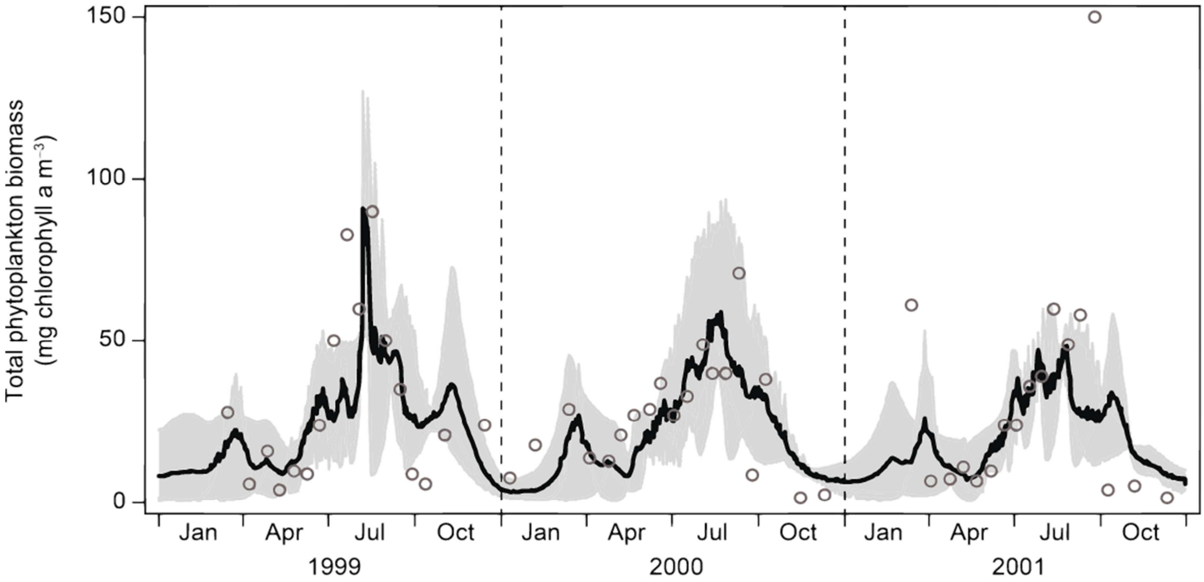

Figure 3.5. Example of a multi-model ensemble (MME). The shaded area shows the full width of predicting outcomes made by different models, the black line shows the mean of all models and the circles are the observations. Figure modified after Trolle et al. (2014) where the authors show that the prediction by the average model outcome is better than the prediction by individual models.

Exploiting the diversity in fundamentally different approaches in aquatic ecosystem modelling

Finally, we could exploit the diversity in more fundamentally different model approaches, for example, statistical- versus process-based models. The diversity in model approaches is the product of the numerous choices that can be made during model development, pursuing a certain trade-off between effort, model simplicity, realism, process details, boundary conditions, forcings and accuracy along various dimensions such as time and space (e.g. Weijerman et al., 2015). For example, minimal models aim to understand the response curve of ecosystems to disturbances, but they are generally too simple to allow for upscaling and process quantification. Complex models on the other hand can describe the cycling of nutrients through many compartments of an ecosystem as well as the flow of energy through the system. Therefore, they often allow for quantitative scenario evaluations, but their output is difficult to interpret as it is demanding to decipher the numerous interactions and feedback loops. More complexity also can be introduced by individual-based and trait-based models, which allow the inclusion of evolutionary processes. Thus, a higher diversity of model approaches permits addressing a higher number of different purposes, provided that they are sufficiently complementary. There is a great value in combining different modelling approaches, as insights gained by one model can be useful for the application of another, and we benefit from the strengths of different model types (Mooij et al., 2009). Combining modelling approaches helps to develop an integrative view on the functioning of aquatic systems and seems almost essential for the adaptive management of the source and sink functions of lake ecosystems, which require integrated thinking and decision support.

Evolving diversity in AEMs

We have explored and exploited diversity in AEMs. Before reflecting on possible future evolution of model diversity, it is interesting first to look back and see how the existing diversity came about.

A historical perspective on evolving diversity in AEMs

The field of AEMs started with great expectations when the first mainframe computers were installed at universities in the 1960s (Lavington, 1975). But because of the adaptive nature of living systems, making predictive AEMs proved to be more difficult than predicting the trajectory of a rocket to the moon. This sparked the emergence of individual-based models *sensu lato*, including dynamic energy budget models (Kooijman, 1993), structured population models (De Roos et al., 1992) and individual-based models *sensu stricto* (Mooij et al., 1996), that zoom in on a particular (group of) species in the ecosystem. In an opposite direction, minimal dynamical models of ecosystems zoomed out to detect dominant nonlinearities in ecosystem responses to external forcing (Scheffer et al., 2001). Renewed interest in large ecosystem models occurred in the past decades, not the least as a result of the increased and distributed computational power, but this time with the tendency to link the models with individual-based and trait-based approaches (DeAngelis et al., 2005) and compare their behavior with minimal dynamical models (Mooij et al., 2009). In the past, region-specific questions have led to region-specific models, however, as a result of current globalization, the need for widely applicable models and models covering regional or continental aspects is rapidly increasing. The growing recognition of the importance anthropogenic stressors on ecosystems and the services provided by ecosystems, asks for coupling of ecological models with socio-economics models (e.g. Downing et al., 2014). This can be realized by using output of one model as input for the other model, or run-time exchange of input and output between such models. The latter method is more complicated and only becomes necessary when there are strong feedbacks between ecology and socio-economics.

Arguments for reducing diversity

There are valid arguments why aquatic ecology as a whole could benefit from streamlining the diversity in AEMs. First, some formulations have been shown to be both less accurate and more complex than alternatives (Tian, 2006). Second, some models are developed to answer one specific question and thus lose their functionality once this question has been addressed. It is likely that this kind of models has a high turnover-rate, but such models could also be incorporated in large models as the results prove to be relevant. Finally, the presence of pseudo-diversity is an argument to reduce the number of models. For example, in climate studies it has been shown that the performance of ensemble models significantly improved when pseudo-diversity was reduced (Knutti et al., 2013). Ideally, groups that work in parallel on similar models should have the incentives to join efforts, but these incentives are often not in place. Also at the level of the individual scientists there seem to be few, if any, incentives to give up one's own model, whereas there are many incentives to maintain it or even start yet another one. Only when the incentives that lead to fragmentation are overcome, or are outweighed by incentives to join forces, can we expect a healthy consolidation of the field to take place. Frameworks like Delft3D-Delwaq (Deltares, 2014), FABM (Bruggeman et al., 2014) and DATM (Mooij et al., 2014) facilitate this process, but also these frameworks have the risk to be duplicated, leading to yet another layer of fragmentation. The turnover rate of AEMs is hard to measure since publications on dropped models are rare, if they even exist. At the same time, the absence of publications on a specific model does not necessarily mean that a model became unused, as engineers, for example, might use the specific model on a daily basis without publishing the results. Furthermore, unlike extinct species that reduce biodiversity, 'dead' models can become 'alive' when a need for their existence emerges, thereby contributing again to model diversity.

Arguments for enlarging diversity

Because the field of aquatic ecosystem modelling can appear quite fragmented, arguments for enlarging diversity in AEMs are easily overlooked. Nevertheless, there should always be room for good ideas and new avenues. An interesting example is provided by minimal dynamical models. When these became prominent in the shallow lake literature about 25 years ago, they were met with considerable reservation and hardly perceived as a step forward. Nowadays, their ability to illustrate and communicate essential nonlinearity in the response of ecosystem (and many other dynamical systems) is broadly recognized (Scheffer et al., 2001). Another emerging approach with many applications in the aquatic domain are Dynamic Energy Budgets (DEB) (Kooijman, 1993). The scope of current DEB models, however, is too limited to be qualified as ecosystem models as defined in this study.

Arguments for conserving diversity

With the first generation of aquatic ecosystem modellers about to retire, there can be serious concern about a loss of useful models and approaches, requiring active conservation effort by the community at large. Proper implementation of conservation schemes will help to prevent the proverbial ‘reinvention of the wheel’ (Mooij et al., 2010). Additionally, it can help future model developers to anticipate what models and formulations worked well and which did not. Obviously, this learning process is hampered at the lack of documentation of failures in the scientific literature. Conserving diversity would thus have a great educational value, and would help understand the “genealogy” of the existing models. Conservation of model diversity is important for science as well, as science builds on repetition which only can be complied with when code is conserved. However, model diversity conservation has to overcome ‘code rot’, which is the deterioration of software as a result of the ever evolving modelling environment, making the software invalid or unusable (Scherlis, 1996). To prevent code rot, the code should be maintained. Another option is to conserve models in their purest mathematical form (e.g. like in the concept behind DATM, Mooij et al. (2010)).

How to facilitate evolving diversity

One would like to have tools available and mechanisms in place that would allow diversity to evolve through a 'natural selection' of models. Natural selection is an emergent property of a system in which there is variation among agents, this variation is transferred to the offspring of the agents and has an impact on the survival of the agents. We have shown that there is ample diversity among AEMs and there seems to be a healthy cross-fertilization of ideas leading to continued development of new versions and models. What may be hampering 'natural selection' among AEMs, however, are standardized methods to compare model 'fitness' within their niche and given the research question they address. Here we point specifically to the research question since models might have a different purpose and it only makes sense to compare the fitness of those models that are able to answer the same research question. To enhance selection and "gene transfer", easy model accessibility is necessary in the first place. Easy accessibility not only includes freely available model software but also low time costs of, for instance, learning new modelling code or approaches. Additionally, data availability is very important for the improvement of models (Hipsey et al., 2015). As long as models are inaccessible, due to, for example, license restrictions or inappropriate manuals, modellers will most likely choose the models in use by their colleagues (see Appendix 4). These easily accessible models may not be the best suitable to answer their questions. Secondly, standard objective assessment criteria to calibrate and validate models are important (Refsgaard et al., 2005; Robson, 2014b). These criteria are different for each modelling niche, as models that are suitable, for example, for forecasting of algal blooms require other criteria than models suitable for biodiversity assessments. It also implies providing a freely accessible set of data used as calibration or validation data (meteorology, hydrology, hydrodynamics, nutrient fluxes etc.) of the models to be benchmarked. The application of the models to these common test data enables a direct comparison without interfering effects from differences in basin morphometry, hydrology, meteorology and so on. The main idea behind this benchmarking is not to classify models into 'good' and 'bad' ones, but instead to characterize the dynamic behavior and specific abilities of the separate models. Finally, we would like to point to the importance of the conservation and maintenance of expertise and experience for model evolution. Currently, project life cycles are generally short and while mobility of people can help to spread models, the same mobility could lead to a local loss of expertise (Herrera et al., 2010; Parise et al., 2012).

Discussion

How can biodiversity research help us to interpret model diversity?

One could see the myriad of model purposes as niches that shape model diversity. Like biodiversity, model diversity can be organized in taxonomic structures to classify models. Using Wikipedia as a reference, such a taxonomic study has been done already for programming languages and showed a phylogenetic tree with new programming languages emerging from different elements of earlier programming languages (Valverde et al., 2015). A similar study for AEMs is intriguing, but is beyond this study. Our analysis revealed a large diversity in the models. We argue that to fully exploit the niche, the tools for analysis provided in each modelling framework should be used. If we divide the AEMs in specialists or generalists, the majority of the AEMs seem to be specialists that address the research question that led to their development but with little application beyond. This can be attributed to the fact that models are often locked within frameworks which obstruct communication and cross-fertilization between the models (Mooij et al., 2014). For the same reason we could question whether there is enough competition between the models to enable survival of the fittest and thus competitive exclusion. At present, most models seem to have the fingerprints of the resource group it is developed in, as if they were species that evolved in their island-specific supported niche. This has the disadvantage of reinventing the wheel, but surely has its advantage as well since the independently evolved models can be used for comparison as in ensemble modelling.

Recommendations

Our analysis of exploring, exploiting and evolving diversity in AEMs leads us to three types of recommendations related to 1) availability, 2) standardization and 3) coupling of AEMs.

Availability of AEMs

With respect to the availability of AEMs, it is important to continue the current trend of open source policies for AEM models, tools for analysis and data. This will increase the transparency of model structure, assumptions and approaches. Besides that, there is an urgent need for a public overview of existing AEMs. This could be a Wikipedia list, with links to relevant (online) documentation or similar initiatives. Such a list could be complemented with an overview of the forces and niches that created the existing diversity in AEMs. Once there is an overview of the niches in which models are designed, the suitability of models for other applications is better assessed. Documentation of the available AEM's will create awareness of the full width of approaches in AEMs to avoid tunnel vision. We should also actively preserve AEMs to learn from the past and thereby avoid reinventing the wheel but also to identify and prevent pseudo-diversity in AEMs.

Standardization of AEM practices

We recommend developing standardization in the documentation of AEMs (comparable with e.g. ODD for IBMs, Grimm et al. (2006)), terminology to categorize AEMs and the methods to analyze AEMs. Standardization of documentation and terminology is desirable for the communication on the different available models. Standardization of methods for parametrization, comparison, calibration, testing, structuring, conversion and interpolation in AEMs will lead to a common practice in model analysis.

Linking AEMs

In our analysis we compared models by their state variables, while additional diversity is hidden in the process formulations. Here we recommend fulfilling the next step by comparing models by their process formulations. Currently this step is a time consuming and difficult task as a result of lack in the availability of model definitions. Perhaps this step will be possible in the future due to the emerging linking approaches such as DATM. And linking has more benefits. We advocate linking AEMs with models from other disciplines to answer questions that require a holistic approach. We recommend running AEMs in more than one spatial setting to gain more insight in the effects within the spatial context and suggest running a given AEM in multiple frameworks to use the full set of tools for analysis and advice of the user community. Finally, we recommend ensemble modelling with AEMs in order to use the best out of multiple models. For example, statistical- and process-based AEMs should be used side-by-side because they have complementary strengths.

We anticipate that increasing model availability, standardization of, e.g., model documentation, and various forms of linking will lead to an evolving diversity of AEMs in which the better performing models out-compete the poorer performing models. Given the large number of model niches, however, there will always remain a great diversity in AEMs.

Perspectives

We can only speculate where the field of aquatic ecosystem modelling will be heading in the coming five to ten years. We expect that many new developments will be triggered and enabled by general trends in science, technology and society. Here we list ten of these possible trends. (1) We expect that wikis (e.g. Wikipedia), where users can either retrieve information or contribute information through standardized web interfaces, will gain in importance for the documentation and distribution of AEMs. While we recognize the inherent lack of quality control, we highly value the ease of access, the community effort and dynamic nature of this approach (the name 'wiki' is derived from the Hawaiian word for 'quick'). (2) We recognize initiatives to develop e-infrastructures for the implementation of AEMs and other environmental models where users of different levels of experience share easy and secure access to models and data according to their needs. (3) We envision that current trends in the mandatory storage of scientific data in repositories will be extended to model code. (4) We envision that online databases of model parameters will be developed and become an important resource for the development and improvement of AEMs. (5) We see a change from the way consultancy companies earn money with AEMs. Formerly, their business model was based on copyrights of model code. Now we see a switch to a business model emerging that is based on expertise in applying open-source models. (6) We hope for a further integration of the development, analysis and application of AEMs in fundamental research and applied science. It will be a challenge to develop models of intermediate complexity that are simple enough to be thoroughly analyzed, yet complex enough to be applicable in real life cases. (7) We hope for a better coverage of the mutual interaction of ecosystem dynamics and biodiversity in AEMs. (8) We expect that the domain of model application (e.g. type of water, climate zone and stress factors) of AEMs will increase. In the end, this will allow for global analysis of aquatic ecosystems exposed to multiple stressors. (9) We envision the implementation of AEMs in apps that run in a local context (e.g. using GPS information) on a smartphone or tablet computer. (10) Finally, we expect that various forms of ensemble modelling will gain importance. Through a comparative evaluation of model performance, ensemble modelling can contribute to a 'natural selection' of AEMs within their niches that are defined by questions from society and science.

Box 3.1. Glossary of terms related to aquatic ecosystem modelling. This glossary can also be found in database format in Appendix 3, Datasheet 1. For each term an acronym and a description, followed by, in so far known to us, a Wikipedia page, a homepage or other relevant web pages and one or more key publications is given, using the following style: Term (Acronym): Definition of term (Wikipedia | Web page | Publication).

ACSL (Advanced Continuous Simulation Language): A computer language with user interface and analysis tools for the implementation of sets of ordinary differential equations. (http://en.wikipedia.org/wiki/Advanced_Continuous_Simulation_Language | http://www.acslx.com |).

ADCIRC (ADvanced CIRCulation Model): A model for storm surge, flooding and larvae drift. (| http://adcirc.org |).

AED in FABM (Aquatic EcoDynamics modelling library): A configurable library of biogeochemical model components including oxygen, nutrients, phytoplankton, zooplankton and sediment implemented in FABM. (| http://aed.see.uwa.edu.au/research/models/AED, http://sf.net/p/fabm | Bruce et al., 2014).

AEM (Aquatic Ecosystem Model): A formal procedure by which the impact of external or internal forcing on aquatic ecosystem states can be estimated. In sometimes used as a synonym for water quality model. (http://en.wikipedia.org/wiki/Aquatic_ecosystem, http://en.wikipedia.org/wiki/Ecosystem_model, http://en.wikipedia.org/wiki/Water_quality_modelling | | Mooij et al., 2010).

AEMON (Aquatic Ecosystem MOdelling Network): A grassroots network of aquatic ecosystem modellers that aims for sharing knowledge, accelerating progress and improving models. (| https://sites.google.com/site/aquaticmodelling |).

Agent-based model (): A modelling format used in individual-based models. (http://en.wikipedia.org/wiki/Agent-based_model | | DeAngelis et al., 2005).

Algorithmic uncertainty (): A misestimate of the data by the model's output as result of errors made by the numerical integration method that is used. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).

AQUASIM (): A modelling framework for the implementation of AEMs in pre-defined compartment types. (| http://www.eawag.ch/en/department/siam/software | Reichert, 1994).

AQUATOX (): An AEM that predicts the fate of various pollutants. (| http://www.epa.gov/athens/wwqtsc/html/aquatox.html | Park et al., 2008).

ASM2d (Activated Sludge Model no. 2D): A model for biological phosphorus removal with simultaneous nitrification-denitrification in activated sludge systems. (| https://build.openmodelica.org/Documentation/WasteWater.ASM2d.html | Henze et al., 1999).

Aster2000 (modified *ASTERionella formosa* model): An AEM for reservoirs. (| | Thébault, 2004).

ATLANTIS (): A flexible, modular modelling framework for developing AEMs that aims to consider all aspects of a marine ecosystem, including biophysical, economic and social aspects. (| http://atlantis.cmar.csiro.au | Fulton et al., 2007; Fulton et al., 2011).

BaltWeb (): An application of the model LakeWeb to the Baltic Sea. (| | Håkanson et al., 2005).

BELAMO in AQUASIM (Biogeochemical Ecological LAke MOdel in AQUASIM): A biogeochemical and ecological lake model implemented in Aquasim which allows flexible modifications of the differential equations. (| | Reichert, 1994; Omlin et al., 2001).

BELAMO in R (Biogeochemical Ecological LAke MOdel in R): A biogeochemical and ecological lake model implemented in R which allows flexible modifications of the differential equations. (| | Reichert, 1994; Omlin et al., 2001).

Bifurcation analysis (): A mathematical analysis technique that aims for identifying qualitative shift in model behavior, e.g. stable versus unstable, in response to internal or external forcing to the model. Extensively used in theoretical ecology, but much less so in the analysis of AEMs, despite its potential to reveal general response curves of the model such as those depicted in Figure 3.1. (http://en.wikipedia.org/wiki/Catastrophe_theory | | Scheffer et al., 2001).

Biogeochemical model (): A model of the chemical, physical, geological and biological processes in an ecosystem. (http://en.wikipedia.org/wiki/Biogeochemistry | |).

BLOOM II (): A phytoplankton community model that uses linear programming, an optimization technique, to calculate the maximum biomass that can be obtained given the available amount of nutrients and constraints on growth and mortality. (| | Los, 1991).

BNN-EQR (Bayesian Belief Network model for Ecological Quality Ratio): A statistical model relating Ecological Quality Ratio as defined in the Water Framework Directive in lakes and rivers to abiotic and management factors. (| | Gobeyn, 2012).

Box model (): A representation of a complex system in the form of boxes or reservoirs linked by fluxes. (http://en.wikipedia.org/wiki/Climate_model#Box_models | |).

BRNS (Biogeochemical Reaction Network Simulator): A simulation environment in which transport processes are interfaced with relevant biogeochemical reactions for sediment diagenesis. (| http://www.geo.uu.nl/Research/Geochemistry/RTM_web/project1.htm | Aguilera et al., 2005).

BROM (Bottom RedOx Model): A water-sediment column model of elemental cycles, redox chemistry and plankton dynamics. (| | Yakushev et al., 2014).

C (): A general purpose procedural programming language. (http://en.wikipedia.org/wiki/C_(programming_language) | |).

C++ (): A general purpose object-oriented programming language. (http://en.wikipedia.org/wiki/C%2B%2B | |).

CAEDYM (Computational Aquatic Ecosystem DYnamics Model): A complex ecological and biogeochemical model that can be coupled with the hydrodynamic drivers DYRESM or ELCOM. (| http://www.cwr.uwa.edu.au/software1/models1.php?mdid=3 | Hipsey et al., 2006).

Calibration (): - (| | See Model calibration).

Cartesian grid (): - (| | See Cubic grid).

Catastrophic shift (): - (| | See Regime shift).

CCHE1D-WQ, CCHE2D-WQ, CCHE3D-WQ (Center for Computational Hydroscience and Engineering 1D/2D/3D Water Quality model): A model that simulates water quality processes in river channels, streams, lakes and coastal waters in an 1, 2 or 3D setting. (| http://www.ncche.olemiss.edu/research/basic/water |).

CE-QUAL-W2 (Corps of Engineers water QUALity model Width averaged 2d): A two-dimensional longitudinal/vertical hydrodynamic and water quality model for reservoirs/lakes, rivers, and estuaries that includes full eutrophication modelling state variables including sediment diagenesis, algae, zooplankton, and macrophytes. (| http://www.ce.pdx.edu/w2, http://www.cequalw2wiki.com/Main_Page | Cole et al., 2003).

Charisma (): An individual-based macrophyte community model. (| http://www.projectenaew.wur.nl/charisma | Van Nes et al., 2002b).

CLI (Command Line Interface): A way of controlling a computer or program by entering text messages at a command line. The computer or program responds with text but also with graphical output. (http://en.wikipedia.org/wiki/Command-line_interface | |).

COASTMAB (COASTal MAss Balance model): A dynamic model for coastal water quality based on LakeMab. (| | Håkanson et al., 2007).

Code rot (): A deterioration of software as a result of the ever evolving environment, making the software invalid or unusable. (http://en.wikipedia.org/wiki/Software_rot | | Scherlis, 1996).

Code verification (): A substantiation that a model code is in some sense a true representation of a conceptual model within certain specified limits or ranges of application and corresponding ranges of accuracy. (| | Refsgaard et al., 2004).

COHERENS (COupled Hydrodynamical-Ecological model for REgioNal and Shelf seas): A hydrodynamic driver available in FABM. (| http://odnature.naturalsciences.be/coherens/about |).

Community model (): A model of closely interacting species within an ecosystem. (http://en.wikipedia.org/wiki/Community_%28ecology%29 | |).

Compartment model (): - (| | See Multi-compartment model).

Competition model (): A model of competing species within an ecosystem. (http://en.wikipedia.org/wiki/Competition | |).

Complex dynamic model (): A dynamic model with many components. One way to further define this concept would be as those dynamical models that are too complex to be analysed with analytical techniques. See also Minimal dynamic model. (| http://en.wikipedia.org/wiki/Mathematical_model#Complexity |).

Conceptual model (): A description of reality in terms of verbal descriptions, equations, governing relationships or natural laws' that purport to describe reality. (http://en.wikipedia.org/wiki/Conceptual_model | | Refsgaard et al., 2004).

Consumer-resource model (): A model of two or more species that interact with each other through predation, competition, parasitism, mutualism, etc. (http://en.wikipedia.org/wiki/Consumer-resource_systems | |).
Cubic grid (): A n-dimensional regular grid consisting of unit squares or cubes. (http://en.wikipedia.org/wiki/Regular_grid | |).
Curvilinear grid (): A n-dimensional regular grid with cuboidal cell structure. (http://en.wikipedia.org/wiki/Regular_grid | |).
DATM (Database Approach to Modelling): An approach in which a model is specified in mathematical terms in a database. To create a running instance of a model, framework-specific code is generated with automated code generators. (| | Mooij et al., 2014).
DEB (Dynamic Energy Budgets): An approach that captures the elementary energy allocation within an organism and the consequences thereof for growth and reproduction. (http://en.wikipedia.org/wiki/Dynamic_energy_budget | http://www.bio.vu.nl/thb/deb | Kooijman, 1993; Kooijman et al., 2014).
Delft3D (): A modelling suite for 1D, 2D and 3D hydrologic, hydrodynamic, hydraulic and water quality models. (| http://www.deltaressystems.com/hydro/product/621497/delft3d-suite, http://oss.deltares.nl/web/delft3d |).
Delft3D-DELWAQ (): An interface between various components of the Delft3D suite, in particular between hydrodynamic, water quality and sediment modules. (| http://oss.deltares.nl/web/delft3d/delwaq |).
Delft3D-Flexible Mesh (): A 1D/2D/3D open source modelling suite to investigate hydrology, hydrodynamics, sediment transport and morphology, water quality for fluvial, estuarine, coastal, rural and urban environments. (| http://oss.deltares.nl/web/delft3dfm |).
Delft3D-FLOW (): A 2D/3D hydrodynamic program of the Delft3D 4 Suite to simulate non-steady flows in relatively shallow water. It incorporates the effects of tides, winds, air pressure, density differences, waves, turbulence and drying and flooding. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delft3D-MOR (): A component of the Delft3D 4 Suite that computes sediment transport and morphological changes for an arbitrary number of cohesive and non-cohesive fractions. Both currents and waves act as driving forces and a wide variety of transport formulae have been incorporated. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delft3D-PART (): A component of the Delft3D 4 Suite that estimates the dynamic spatial concentration distribution of individual particles by following their tracks in time. The waste substances may be conservative or subject to a process of simple, first order decay; a typical application is oil spill modelling. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delft3D-SED (): A subset of the DELWAQ process library for short- or medium term - days, weeks, months - cohesive and non-cohesive sediment transport. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delft3D-WAQ (incl GEM/BLOOM/ECO): A component of the Delft3D 4 Suite that simulates the far and mid-field water and sediment quality due to a variety of transport and water quality processes. To accommodate these, it includes several advection diffusion solvers and an extensive library of process formulations for user-selected substances. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delft3D-WAVE (): A component of the Delft3D 4 Suite that computes the non-steady propagation of short-crested waves over an uneven bottom, considering wind action, energy dissipation due to bottom friction, wave breaking, refraction, shoaling and directional spreading. The programme is based on the spectral model SWAN. (| http://oss.deltares.nl/web/delft3d/manuals |).
Delphi (): An object oriented programming language based on pascal. (http://en.wikipedia.org/wiki/Delphi_(programming_language) | |).
Delta Shell (): A modelling framework for developing and analysing environmental models to simulate water, soil and the subsurface processes. (| http://oss.deltares.nl/web/delta-shell |).
deSolve (R package): A set of general solvers for initial value problems of Ordinary Differential Equations, Partial Differential Equations, Differential Algebraic Equations, and Delay Differential Equations. (| https://cran.r-project.org/web/packages/deSolve | Soetaert et al., 2010b).
DIECAST (DIEtrich Center for Air Sea Technology): A hydrodynamic model. (| http://efdl.as.ntu.edu.tw/research/diecast |).
Domain of applicability of conceptual model (): A prescribed set of conditions for which the conceptual model has been tested, i.e. compared with reality to the extent possible and judged

suitable for use by model confirmation. (| | Refsgaard et al., 2004).
Domain of applicability of model (): A prescribed set of conditions for which the site-specific model has been tested, i.e. compared with reality to the extent possible and judged suitable for use by model validation. (| | Refsgaard et al., 2004).
Domain of applicability of model code (): A prescribed set of conditions for which the model code has been tested, i.e. compared with analytical solutions, other model codes or similar to the extent possible and judged suitable for use by code verification. (| | Refsgaard et al., 2004).
DUFLOW (DUtch FLOW model): A modelling suite for the simulation of non-stationary 1D hydrodynamics and water quality processes. (| http://www.mx-groep.nl/duflow |).
DUPROL (DUtch PROgramming Language): A computer language for the implementation of the water quality processes in DUFLOW. (| http://www.mx-groep.nl/duflow |).
Dynamic model (): A mathematical model that captures the development of the system through time as opposed to a static model. (http://en.wikipedia.org/wiki/Mathematical_model | |).
DYRESM (DYnamic REservoir Simulation Model): A 1D hydrodynamic model for predicting the vertical distribution of temperature, salinity and density in lakes and reservoirs. DYRESM coupled with CAEDYM. (| http://www.cwr.uwa.edu.au/software1/models1.php?mdid=2 | Hamilton et al., 1997).
Ecopath with Ecosim (): A software package for balancing food-web interactions, calculating network characteristics and assessing the impact of fishing on the food-web. (http://en.wikipedia.org/wiki/Ecopath | http://www.ecopath.org | Christensen et al., 1992).
Ecosystem model (): An abstract, usually mathematical, model of an ecological system which is developed and analysed to understand and predict the dynamics of the real system. (http://en.wikipedia.org/wiki/Ecosystem_model | |).
ECOWASP (ECOsystemmodel for WAdden Sea Project): A dynamic model for the integrated simulation of biological, chemical, and physical processes in shallow tidal water systems. (| | Brinkman et al., 2001).
EEMOD_DNSMOD (Detailed Nitrogen Sediment MODel inside of an Essential Ecological MODel): An aquatic nitrogen cycle model including a layered sediment compartment. (| http://sourceforge.net/projects/eemoddnsmod |).
EFDC (Environmental Fluid Dynamics Code): A hydrodynamic model that can be used to simulate aquatic systems in one, two, or three dimensions and that can be coupled with WASP. (http://en.wikipedia.org/wiki/EFDC_Explorer | http://www.epa.gov/athens/wwqtsc/html/efdc.html | Hamrick et al., 1997; Wu et al., 1997).
ELCOM (Estuary, Lake and Coastal Ocean Model): A 3D finite-difference baroclinic hydrodynamic model to simulate stratified waters bodies with environmental forcing. ELCOM can be coupled with CAEDYM. (| http://www.cwr.uwa.edu.au/software1/models1.php?mdid=5 | Robson et al., 2004).
ELISE (): A software interface to couple results of a hydrodynamic model with biological equations in a box-model representation. (| | Ménesguen, 1991).
EMS (Environmental Modelling Suite): A modelling suite consisting of a hydrodynamic model SHOC, a sediment dynamic model MECOSED and an ecological/biogeochemical model. EMS is optimised for coastal systems. (| http://www.emg.cmar.csiro.au/www/en/emg/software/EMS.html | Skerratt et al., 2013).
Ensemble technique (): A forecasting technique where certain aspects of modelling processes are duplicated. Examples of ensemble techniques are the use of multiple models, multiple model inputs or multiple integration schemes. (http://en.wikipedia.org/wiki/Ensemble_forecasting | |).
Environmental niche model (): A model that predicts the distribution of a species in its geographic space on the basis of the distribution of its environmental requirements. (http://en.wikipedia.org/wiki/Environmental_niche_modelling | |).
ERGOM (Ecological ReGional Ocean Model): A semi complex NPZD type of model with cyanobacteria. (| http://www.ergom.net | Neumann, 2000; Neumann et al., 2002).
ERSEM (European Regional Seas Ecosystem Model): A marine AEM. (| http://www.meece.eu/library/ersem.html | Baretta et al., 1995).
ESMF (Earth System Modelling Framework): An interface between various hydrodynamic and water quality process formulations. (| http://www.earthsystemmodeling.org/about_us, http://sourceforge.net/p/esmf/esmf/ci/master/tree |).
Euler integration (): A simple way to integrate ordinary differential equations that bears similarity with difference equations but is fundamentally different because it aims for describing a continuous

process. (http://en.wikipedia.org/wiki/Euler_method | |).
eWater Source (): A model that is designed to simulate all aspects of water resource systems to support integrated planning, operations and governance from urban, catchment to river basin scales including human and ecological influences. (http://en.wikipedia.org/wiki/EWater | http://ewater.com.au/products/ewater-source, http://www.toolkit.net.au/tools/Source%20%28public%20version%29 | Argent et al., 2009).
Experimental uncertainty (): A measure of errors in observational data. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).
FABM (Framework for Aquatic Biogeochemical Models): An interface between various hydrodynamic and water quality process formulations. (| http://fabm.sourceforge.net |).
FEMME (Flexible Environment for Mathematically Modelling the Environment): A modelling framework for the implementation of AEMs. (| | Soetaert et al., 2002).
Finite Element (): A numerical technique to solve boundary problems by subdividing the domain in simpler subdomains - finite elements - in order to approximate the exact solution. (http://en.wikipedia.org/wiki/Finite_element_method | | Hrennikoff, 1941).
FLAKE (Freshwater LAKE model): A freshwater lake model for predicting vertical temperature distribution and mixing conditions. (| http://www.flake.igb-berlin.de | Mironov, 2005).
Flexible Mesh (): An unstructured grid in 1D, 2D or 3D consisting of different geometric shapes within one mesh. (| http://oss.deltares.nl/web/delft3dfm |).
FME (Flexible Modelling Environment, R implementation of FEMME): A flexible modelling framework for inverse modelling, sensitivity, identifiability, Monte Carlo analysis. (| http://cran.r-project.org/package=FME | Soetaert et al., 2010a).
Foodweb model (): A model of species within an ecosystem that are linked by trophic interactions. (http://en.wikipedia.org/wiki/Food_web | |).
FORTRAN (FORmula TRANslation system): A general purpose procedural programming language with object-oriented extensions. (http://en.wikipedia.org/wiki/Fortran | |).
Framework (): - (| | See Modelling framework).
Functional programming (): A programming paradigm that treats computation as the evaluation of mathematical functions. Functional programming is focused on describing what should be calculated rather than how it should be calculated. (http://en.wikipedia.org/wiki/Functional_programming | |).
FVCOM (Finite Volume Community Ocean Model): An unstructured grid, finite-volume, 3D primitive equation, turbulent closure coastal ocean model. (http://en.wikipedia.org/wiki/Finite_Volume_Community_Ocean_Model | | Chen et al., 2006).
GEMSS (Generalized Environmental Modeling System for Surfacewaters): An integrated system of 3D hydrodynamic and transport modules embedded in a geographic information and environmental data system. (http://en.wikipedia.org/wiki/Generalized_Environmental_Modeling_System_for_Surfacewaters | http://www.gemss.com |).
Generalized Lotka-Volterra model (): A multi-dimensional implementation of the Lotka-Volterra competition and predation equations, typically with linear interaction terms.. (http://en.wikipedia.org/wiki/Generalized_Lotka%E2%80%93Volterra_equation | |).
GETM (General Estuarine Transport Model): A structured grid 3D hydrodynamic model that can be coupled with FABM. (| http://www.getm.eu |).
GLEON (Global Lake Ecological Observatory Network): A transdisciplinary network that aims at sharing and interpreting high resolution sensor data from different lakes worldwide. (| http://www.gleon.org |).
GLM (General Lake Model): A 1D Lake and Wetland hydrodynamic model that simulates the balance of water, salt and heat, including vertical stratification. (| http://aed.see.uwa.edu.au/research/models/GLM | Hipsey et al., 2014).
GLOBIO-AQUATIC (): An empirically-based model of biodiversity intactness and species richness as a function of main abiotic drivers. (| http://www.globio.info | Stehfest et al., 2014; Janse et al., 2015).
GLUES (Global Land Use and technological Evolution Simulator): A model used for land use and socio-technological evolution simulations. (| http://sf.net/p/glues |Lemmen et al., 2011; Lemmen et al., 2014).
GOTM (General Ocean Turbulence Model): A 1D water column model with focus on vertical mixing that can be coupled with FABM. (| http://www.gotm.net |).
GPL (GNU General Public Licence): An open source software licence.

(http://en.wikipedia.org/wiki/GNU_General_Public_License | http://www.gnu.org/licenses |).

GRIND for MATLAB (): A modelling framework based on MatLab. (| http://www.sparcs-center.org/grind |).

Guam Atlantis Coral Reef Ecosystem Model (): An evaluation and management strategy tool used particularly for simulating management policies and methods for coral reef conservation and assessment. (| http://www.pifsc.noaa.gov/cred/guam_atlantis_ecosystem_model.php |).

GUI (Graphical User Interface): A communication tool with graphical icons to enable interaction between the electronic device and the user. (http://en.wikipedia.org/wiki/Graphical_user_interface | |).

HABITAT (): A spatial analysis tool to analyse the availability and quality of habitats for individual or groups of species. (| https://publicwiki.deltares.nl/display/HBTHOME/Home | Haasnoot et al., 2009).

HBV (Hydrologiska Byråns Vattenbalansavdelning model): A catchment hydrological model simulating river discharges and solute transport in the rivers and catchments. (http://en.wikipedia.org/wiki/HBV_hydrology_model | http://www.smhi.se/forskning/forskningsomraden/hydrologi/hbv-1.1566 | Bergström, 1976).

HEC-RAS (Hydrologic Engineering Center River Analysis System): A hydraulic model for engineering of pipes and canals and rivers, which has also modules for basic water quality. (| http://en.wikipedia.org/wiki/HEC-RAS, http://www.hec.usace.army.mil/software/hec-ras | Brunner, 2001).

Hydraulic model (): A model describing fluid mechanics including power generation and distribution. (http://en.wikipedia.org/wiki/Hydraulics | |).

Hydrodynamic model (): A model describing motion of water. (http://en.wikipedia.org/wiki/Fluid_dynamics | |).

Hydrological model (): A model describing the water cycle. (http://en.wikipedia.org/wiki/Hydrology, http://en.wikipedia.org/wiki/Hydrological_transport_model | |).

IBM (Individual-based model): An ecological model, build on basis of traits, physiology and behavior of interacting individuals. (http://en.wikipedia.org/wiki/Agent-based_model | | DeAngelis et al., 2005).

IDE (Integrated development environment): A software application that provides comprehensive facilities to computer programmers for software development. (http://en.wikipedia.org/wiki/Integrated_development_environment | |).

Identifiability (): A property of a model pointing at identical distribution of the data and the values of the model. Non-identifiable models can lead differences in conclusions drawn based on the model values and observed data. (http://en.wikipedia.org/wiki/Identifiability | | Huang, 2005).

IMAGE (Integrated Model to Assess the Global Environment): A global catchment nutrient model. (| http://themasites.pbl.nl/models/image | Morée et al., 2013).

Imperative programming (): A programming paradigm that describes computation in terms of statements that change a program state. Imperative programming is focused on describing how a program operates. (http://en.wikipedia.org/wiki/Imperative_programming | |).

INCA (INtegrated CAtchment model): A process-based dynamic model for plant-soil system dynamics and in-stream biogeochemical and hydrological processes. (| http://www.reading.ac.uk/geographyandenvironmentalscience/research/INCA | Wade et al., 2002).

Interpolation uncertainty (): An unknown difference between model and reality as result of calibration on different spatial or temporal data than the validation of the model. Whenever the validation falls out of the calibrated range an interpolation uncertainty is introduced. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).

Inverse Modelling (): A technique used to infer from observations the causal factors that produced them. (http://en.wikipedia.org/wiki/Inverse_problem | |).

InVitro (): An agent-based ecosystem-level management strategy evaluation modelling framework. (| http://www.cmar.csiro.au/research/mse/invitro.htm | Fulton et al., 2011).

JAVA (): A general purpose object-oriented computer programming language that allows to run software applications under various operating systems without the need for recompilation. (http://en.wikipedia.org/wiki/Java_%28programming_language%29 | |).

JPJS (named after Jensen-Pedersen-Jeppesen-Søndergaard): A model for describing the recovery process after nutrient abatement. (| | Jensen et al., 2006).

LAKE (from H. Baumert): A 1D hydrodynamic k-epsilon turbulence model that considers internal waves. (| | Baumert et al., 2004).
LAKE (from V. Stepanenko): A 1D hydrodynamic k-epsilon turbulence model capable of simulating methane. (| | Stepanenko et al., 2011; Stepanenko et al., 2013).
LAKEMAB (LAKE MAss Balance model): A dynamic model for lake water quality. (| | Bryhn et al., 2007).
LAKEoneD (): A 1D hydrodynamic k-epsilon turbulence model with submodules for dissolved oxygen and a simple competition model for three functional phytoplankton groups. (| | Jöhnk et al., 2001; Jöhnk et al., 2008).
LakeWeb (): A model to quantitatively describe characteristic lake food web interactions so that production and biomasses can be determined for the nine functional groups of organisms included in the model. (| | Håkanson et al., 2003).
Lanier (): A network model based on EcoPATH, but using P as the currency. (| | Borrett et al., 2007).
LDE (Lattice differential equations): A set of spatially discrete ordinary differential equations. (| | Chow et al., 1996).
LGPL (GNU Lesser General Public Licence): An open source software licence that is less strict then GPL. (http://en.wikipedia.org/wiki/GNU_Lesser_General_Public_License | http://www.gnu.org/licenses/lgpl.html |).
MARVL (MARine Virtual Lab): A suite of complex models, e.g. ocean circulation, waves, water quality, and marine biogeochemistry, a network of observing sensors, and a host of value-adding tools. (| http://www.marvl.org.au |).
Mass balanced model (): A model that checks for the conservation of mass. (http://en.wikipedia.org/wiki/Mass_balance, http://en.wikipedia.org/wiki/Conservation_of_mass | |).
Mathematica (): A computational software program. (http://en.wikipedia.org/wiki/Mathematic | http://www.wolfram.com/mathematica |).
MATLAB (): A numerical computation environment. (http://en.wikipedia.org/wiki/MATLAB | http://nl.mathworks.com/products/matlab |).
MATSEDLAB (): A Matlab module for sediment diagenesis, carbon burial, and bio-mixing. (| https://uwaterloo.ca/ecohydrology/software | Couture et al., 2010).
MECOSED (Model for Estuarine and COastal SEDiment transport): A model for estuarine and coastal transport. (| https://wiki.csiro.au/display/C2CCOP/EMS+-+MECOSED |).
Medawar zone (): A conceptual zone depicting the area of problems which are most likely to produce fruitful results. Problems that are too simple are unlikely to produce novel or significant results. Problems that are too ambitious may not succeed at all or may be rejected by the research community at large. (http://en.wikipedia.org/wiki/Medawar_zone | |).
Meta model (): An abstraction of another model. (http://en.wikipedia.org/wiki/Metamodeling | |).
Mike11 (after developer Mike Abbot): A 1D hydrodynamic and hydrological model for simulation of rivers and channels. (http://en.wikipedia.org/wiki/MIKE_11 | http://www.mikepoweredbydhi.com/products/mike-11 | Nishat et al., 2009; Wijesekara et al., 2014).
Mike21 (after developer Mike Abbot): A 2D hydrodynamic model with flexible mesh for coastal and marine engineering and water quality applications. (http://en.wikipedia.org/wiki/MIKE_21 | http://www.mikepoweredbydhi.com/products/mike-21 | Appendini et al., 2013; Kaergaard et al., 2013).
Mike3 (after developer Mike Abbot): A 3D hydrodynamic model with flexible mesh for coastal and marine engineering and water quality applications. (http://en.wikipedia.org/wiki/MIKE_3 | http://www.mikepoweredbydhi.com/products/mike-3 | Passenko et al., 2008; Bolaños et al., 2014).
Mike-ECO Lab Eutrophication Model 1 (after developer Mike Abbot): An aquatic ecosystem modelling tool for use with Mike hydrodynamic drivers that includes several built-in ecosystem configurations and the ability to implement own equations. (| | Rasmussen et al., 2000; Hammrich et al., 2014).
Mike-FLOOD (): A toolbox for flood modelling. (http://en.wikipedia.org/wiki/MIKE_FLOOD | http://www.mikepoweredbydhi.com/products/mike-flood |).
Mike-SHE (after developer Mike Abbot - System Hydrologique European): A system for integrated catchment modelling, including groundwater, surface water, recharge and evapotranspiration. (http://en.wikipedia.org/wiki/MIKE_SHE |

http://www.mikepoweredbydhi.com/products/mike-she | Refsgaard et al., 2010).
Mike-URBAN (): A toolbox for urban water modelling. (http://en.wikipedia.org/wiki/MIKE_URBAN | http://www.mikepoweredbydhi.com/products/mike-urban |).
Minimal dynamic model (): A dynamic model with few components. One way to further define this concept would be as those dynamical models that are simple enough to be analysed with analytical techniques. See also Complex dynamic model. (http://en.wikipedia.org/wiki/Mathematical_model#Complexity | |).
MINLAKE (): A 1D hydrodynamic model that includes dissolved oxygen. (| | Fang et al., 1996b; a; Stepanenko et al., 2013).
MIP (Model Intercomparison Project): A project to intercompare the output of multiple models using the same input data, i.e. an ensemble technique. Often used in climate and hydrologic research, sparse in aquatic ecosystem modelling. (| http://www.unige.ch/climate/lakemip |).
MME (Multi-Model Ensembles): A type of ensemble modelling in which a given problem is addressed concurrently with multiple models. (http://en.wikipedia.org/wiki/Ensemble_averaging | |).
Model (): A knowledge domain-specific mathematical description of a study object, including input data and parameter values. An example of a knowledge-domain is aquatic ecology. (http://en.wikipedia.org/wiki/Mathematical_model | | Refsgaard et al., 2004).
Model application (): A usage of a specific model for a specific case study. (| |).
Model application domain (): A set of model applications that belong to a specific collection of model usages. An example of a model application domain is 'eutrophication'. (| |).
Model approach (): A modelling technique or method used to access a question. Examples of model approaches are mechanistic - e.g. trait-based, process-based - versus statistical - e.g. regression, neural network. (| |).
Model calibration (): A procedure of adjustment of parameter values of a model to reproduce the response of reality within the range of accuracy specified in the performance criteria. (| | Refsgaard et al., 2004).
Model code (): A mathematical formulation in the form of a computer program that is so generic that it, without program changes, can be used to establish a model with the same basic type of equations - but allowing different input variables and parameter values - for different study areas. (http://en.wikipedia.org/wiki/Source_code | | Refsgaard et al., 2004).
Model confirmation (): A determination of adequacy of the conceptual model to provide an acceptable level of agreement for the domain of intended application. This is in other words the scientific confirmation of the theories/hypotheses included in the conceptual model. (| | Refsgaard et al., 2004).
Model set-up (): An establishment of a site-specific model using a model code. This requires, among other things, the definition of boundary and initial conditions and parameter assessment from field and laboratory data. (| | Refsgaard et al., 2004).
Model uncertainty (): A misestimate of the data by the model's output. Model uncertainty has different origins as for example parameter uncertainty, structural uncertainty or algorithmic uncertainty. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).
Model validation (): An approval that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model. (| | Refsgaard et al., 2004).
Modelling environment (): A term that can refer to a modelling framework, an integrated development environment or a combination of both. (| | See IDE and Modelling framework).
Modelling framework (): A software package that can be combined with user-written code to create a software application. A key characteristic of a modelling framework, also referred to a software framework is that the framework calls the user-defined code. This distinguishes a modelling framework from a software library. Mostly, the framework itself cannot be modified by the user. (http://en.wikipedia.org/wiki/Software_framework | | Mooij et al., 1996).
Modelling suite (): A set of interconnected models, mostly implemented in a common modelling framework. (| https://www.deltares.nl/nl/software/delft3d-suite, http://www.mx-groep.nl/duflow, http://www.emg.cmar.csiro.au/www/en/emg/software/EMS.html, http://www.deltares.nl/en/software/sobek |).
MOM (Modular Ocean Model): A 3D numerical ocean model based on the hydrostatic primitive equations. (http://en.wikipedia.org/wiki/Modular_ocean_model | http://mom-ocean.org/web |

Griffies et al., 2005).
MONERIS (MOdelling Nutrient Emissions in RIver Systems): A catchment nutrient model. (| http://www.icpdr.org/main/activities-projects/moneris-modelling-nutrient-emissions-river-systems |).
MOSSCO (MOdular coupling System for Shelves and COasts): An interface between various hydrodynamical and water quality process formulations. (| http://www.mossco.de |).
Multi-compartment model (): A type of mathematical model used for describing the way materials or energies are transmitted among the compartments of a system. (http://en.wikipedia.org/wiki/Multi-compartment_model | |).
MUSIC (Model for Urban Stormwater Improvement Conceptualisation): A decision support system for storm-water quality management. (| http://www.ewater.com.au/products/music |).
Mylake (): A 1D model for lake physics and biogeochemistry suitable for uncertainty estimation and sensitivity analysis. (| https://github.com/biogeochemistry/MyLake_public | Saloranta et al., 2007).
MyM (): An integrated environment for the development, visualization and application of simulations of dynamic systems. (| http://www.my-m.eu | Beusen et al., 2011).
NEMO (Nucleus for European Modelling of the Ocean): A 3D modelling framework for oceanographic research, operational oceanography seasonal forecast and climate studies. (| http://www.nemo-ocean.eu | Madec, 2012).
NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography): A model to simulate the dynamics of nutrient-phytoplankton-zooplankton food web in the ocean. (| https://www.myroms.org/wiki/index.php/nemuro.in | Kishi et al., 2007).
NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography with FISH module): An NEMURO model version extended with a fish module. (| | Megrey et al., 2007).
NETLOGO (): A programmable modelling framework based on the LOGO programming language for developing agent-based models of natural and social phenomena with agent-based models. NET refers to the decentralized, interconnected nature of the phenomena that can be modelled. LOGO refers to the LOGO language of which a dialect is used. (http://en.wikipedia.org/wiki/NetLogo | http://ccl.northwestern.edu/netlogo |).
Neural network model (): A family of statistical learning models inspired by biological neural networks. (http://en.wikipedia.org/wiki/Artificial_neural_network | |).
NPZD model (Nutrient-Phytoplankton-Zooplankton-Detritus model): An AEM that focusses on the dynamics of nutrients, phytoplankton, zooplankton and detritus, thereby ignoring higher trophic levels. (| http://fvcom.smast.umassd.edu/2014/01/17/2-research-npzd-model | Heinle et al., 2013).
Numerical integration method (): A computational method to solve differential equations by approximating the integral. (http://en.wikipedia.org/wiki/Numerical_integration | | Press et al., 1986).
Numerical recipes (): A book series and an extensive set of algorithms to perform various mathematical techniques, available in FORTRAN 77, FORTRAN 90, Pascal, C and C++. (http://en.wikipedia.org/wiki/Numerical_Recipes | http://www.nr.com | Press et al., 1986).
Object-oriented programming (): A programming paradigm based on the concept of objects, which are data structures that contain data, in the form of fields, often known as attributes and code, in the form of procedures, often known as methods. (http://en.wikipedia.org/wiki/Object-oriented_programming | |).
ODD (Overview, Design concepts and Details): A format to document individual-based models. (| | Grimm et al., 2006).
ODE (Ordinary differential equations): A function or a set of functions of one independent variable and its derivatives. (http://en.wikipedia.org/wiki/Ordinary_differential_equation | |).
OMEXDIA in FABM (Ocean Margin EXchange and early DIAgenesis model): A model describing the dynamics of carbon, nitrogen and oxygen in marine sediments. (| http://www.rforscience.com/modelling/omexdia | Soetaert et al., 1996).
Optimization model (): A model in which - part of the - parameters are chosen such as to maximize or minimize a certain function, for instance the total amount of biomass. (http://en.wikipedia.org/wiki/Mathematical_optimization | |).
OSIRIS (Object-oriented SImulation fRamework for Individual-based Simulations): A set of C++ routines that assist the development of ecological simulation models, including individual-based models. (| | Mooij et al., 1996).
Pamolare I (): A model for deep lakes with thermocline development by incorporating three lake

models: a one-layer model, a structurally dynamic model and a drainage area model. (| | Gurkan et al., 2006; Jørgensen, 2009; Jørgensen, 2010; Xu et al., 2013).
Pamolare II (): A structurally dynamic model for shallow lakes. (| http://unep.org/ietc/pamolare/tabid/79376/default.aspx | Gurkan et al., 2006; Jørgensen, 2009; Jørgensen, 2010; Xu et al., 2013).
Papyrus Simulator (): An ecosystem model for rooted papyrus Cyperus papyrus vegetation in seasonally or permanently inundated wetlands in Africa implemented in Stella. (| | Van Dam et al., 2007; Hes et al., 2014).
Parameter uncertainty (): A misestimate of the data by the model's output as result of errors in the parameter estimation. Parameter uncertainty can be the result of experimental uncertainty in the data used to estimate the parameter values as well as due to the estimation method used. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).
PCDitch in ACSL/GRIND for MATLAB/OSIRIS/R (): A box model implementation of an AEM for linear waters with a focus on competition between various growth forms of macrophytes and the transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCDitch | | Van Liere et al., 2007).
PCDitch in DUFLOW (): A network implementation of an AEM for linear water structures with a focus on competition between various growth forms of macrophytes and the transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCDitch | | Van Liere et al., 2007).
PCDitch metamodel (): A metamodel of the outcomes of the box model implementation of PCDitch for a range of management relevant settings of the model. (http://en.wikipedia.org/wiki/PCDitch | http://themasites.pbl.nl/modellen/pcditch | Van Liere et al., 2007).
PCLake in ACSL/GRIND for MATLAB/OSIRIS/R (): A box model implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | | Janse et al., 2008; Janse et al., 2010).
PCLake in DELWAQ (): A 2D horizontal model implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | | Janse et al., 2008; Janse et al., 2010).
PCLake in DUFLOW (): A network implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | | Janse et al., 2008; Janse et al., 2010).
PCLake in FABM (): A 1D vertical implementation of an AEM for shallow lakes with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | | Janse et al., 2008; Janse et al., 2010).
PCLake metamodel (): A metamodel of the outcomes of the box model implementation of PCLake for a range of management relevant settings of the model. (http://en.wikipedia.org/wiki/PCLake | http://themasites.pbl.nl/modellen/pclake | Janse et al., 2008; Janse et al., 2010).
PCLake submersed macrophyte equations (): A sub-model containing PCLAKE submerged macrophyte equations for stratified lakes that can be coupled to SALMO and GOTM in R. (| http://r-forge.r-project.org/projects/rlimnolab, http://rlimnolab.r-forge.r-project.org | Sachse et al., 2014).
PCR-GLOBWB (PCRaster Global Water Balance): A large-scale hydrological model intended for global to regional studies. (| http://pcraster.geo.uu.nl/projects/applications/pcrglobwb | Van Beek et al., 2011; Sutanudjaja et al., 2014).
PDE (Partial differential equations): A function or a set of functions of multiple independent variables and its derivatives, in contrast to ODE. (http://en.wikipedia.org/wiki/Partial_differential_equation | |).
PELETS-2D (Program for the Evaluation of Lagrangian Ensemble Transport Simulations): A program for the evaluation of Lagrangian ensemble transport simulations. (| http://www.coastdat.de/applications/pelets_2d | Callies et al., 2011; Neumann et al., 2014).
Performance criteria (): A level of acceptable agreement between model and reality. The performance criteria apply both for model calibration and model validation. (| | Refsgaard et al., 2004).
PERSIST (Pan-European Runoff SImulator for Solute Transport): A semi-distributed rainfall-runoff modelling toolkit for use with the INCA family of models. (|

http://www.slu.se/en/collaborative-centres-and-projects/slu-water-hub/models/persist, http://www.hydrol-earth-syst-sci.net/18/855/2014/hess-18-855-2014.html |).

PEST (model independent Parameter Estimation & Uncertainty Analysis): A standard software package for parameter estimation and uncertainty analysis of complex computer models. (| http://www.pesthomepage.org | Doherty, 2015).

PHOSMOD (PHOSphate MODel): A model to simulate the effects of fertilizers on plant growth and plant P concentration. (| | Greenwood et al., 2001).

PHREEQC (PH REdox EQuilibrium in C): A computer program for speciation, batch-reaction, one-dimensional transport, and inverse geochemical calculations. (| http://wwwbrr.cr.usgs.gov/projects/GWC_coupled/phreeqc | Appelo et al., 2005).

Physiologically structured population models (): An individual-based model approach in which growth, reproduction, mortality and interactions with other organisms are linked with individual traits in general and with size in particular. (| | De Roos et al., 2001).

Piscator (): An individual-based model of fish communities. (| http://www.projectenaew.wur.nl/piscator | Van Nes et al., 2002a).

Polar coordinates (): A two-dimensional coordinate system in which each point on a plane is determined by a distance from a reference point and an angle from a reference direction. (http://en.wikipedia.org/wiki/Polar_coordinate_system | |).

POM (Pattern-Oriented Modelling): A bottom up approach to the analysis of complex systems through a focus on only the relevant patterns in the real system, instead of trying to approximate the real system as closely as possible in all aspects. (http://en.wikipedia.org/wiki/Pattern-oriented_modeling | | Grimm et al., 2005).

POM (Princeton Ocean Model): A 3D finite-difference open source hydrodynamic model. (http://en.wikipedia.org/wiki/Princeton_ocean_model | http://www.ccpo.odu.edu/POMWEB, http://www.aos.princeton.edu/WWWPUBLIC/PROFS/NewPOMPage.html |).

Procedural programming (): A programming paradigm, derived from structured programming, based upon the concept of the procedure call to routines, subroutines, methods, or functions. (http://en.wikipedia.org/wiki/Procedural_programming | |).

Process-based model (): A model that models the dynamics of the states of the system on basis of the processes acting on these states. (| http://www.coastalwiki.org/wiki/Process-based_modelling |).

PROTECH (Phytoplankton RespOnses To Environmental CHange): A phytoplankton community model. (| http://www.ceh.ac.uk/services/lake-ecosystem-models-assessing-phytoplankton | Reynolds et al., 2001; Elliott et al., 2010).

Python (): A general purpose object-oriented high-level programming language. (http://en.wikipedia.org/wiki/Python_(programming_language) | https://www.python.org |).

QUAL2E (stream water QUALity Model, 2nd Enhanced version): A river and stream water quality model for 1D diurnal dynamics. (| | Brown et al., 1987).

QUAL2K (stream water QUALity Model): A river and stream water quality model for 1D diurnal dynamics. Updated version of QUAL2E. (| http://www.epa.gov/athens/wwqtsc/html/qual2k.html | Chapra et al., 2008).

QUAL2KW (stream water QUALity Model): A river and stream water quality model that is intended to represent a modernized version of the QUAL2E model and includes more processes than QUAL2K. (| http://www.ecy.wa.gov/programs/eap/models.html | Pelletier et al., 2006).

R (): A programming language and software environment for statistical computing and graphics. The package R/deSolve allows for numerical simulation of systems of differential equations. (http://en.wikipedia.org/wiki/R_(programming_language) | http://www.r-project.org , http://desolve.r-forge.r-project.org |).

Reality (): A natural system that is the object of a particular scientific study. (http://en.wikipedia.org/wiki/Reality | | Refsgaard et al., 2004).

Rectilinear grid (): A n-dimensional grid consisting of rectangles. (http://en.wikipedia.org/wiki/Regular_grid | |).

Regime shift (): A relatively abrupt change from one regime to a contrasting one, where a regime is a dynamic 'state' of a system with its characteristics stochastic fluctuations and/or cycles. (http://en.wikipedia.org/wiki/Regime_shift | | Scheffer et al., 2009).

Regression model (): A statistical technique for estimating the relationship between a dependent variable and one or more independent variables. (http://en.wikipedia.org/wiki/Regression_analysis

| |).
Regular grid (): A n-dimensional grid of parallelotopes such as rectangles, parallelograms or cuboids. (http://en.wikipedia.org/wiki/Regular_grid | |).
RIVERSTRAHLER (): A nutrient and phytoplankton model for rivers. (| | Billen et al., 1994).
RIVPACS (River InVertebrate Prediction And Classification System): A statistical model relating species composition in rivers to abiotic factors. (| http://www.ceh.ac.uk/products/software/rivpacs.html |).
ROMS (Regional Ocean Modeling System): A free-surface, terrain-following, primitive equations ocean model. (http://en.wikipedia.org/wiki/Regional_Ocean_Modeling_System | https://www.myroms.org | Shchepetkin et al., 2005).
ROMS-BGC (Regional Ocean Modeling System BioGeoChemical model): An ocean biogeochemical model with various configuration options. (| http://www.myroms.org | Xiao et al., 2014).
rSALMO (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food-web of lakes and reservoirs implemented in R. It can link to a sub-model for PCLake's submerged macrophytes and can be driven by hydrophysics provided by external models. 0D to 1D model grids can be set up. (| https://r-forge.r-project.org/projects/rlimnolab |).
Runge Kutta integration (): An important family of implicit and explicit iterative methods to numerically solve ordinary differential equations. (http://en.wikipedia.org/wiki/Runge%E2%80%93Kutta_methods | |).
Runoff model (): A mathematical model describing the rainfall–runoff relations of a rainfall catchment area, drainage basin or watershed. (http://en.wikipedia.org/wiki/Runoff_model_(reservoir) | |).
SALMO 1D/HR (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food-web of lakes and reservoirs implemented in Delphi and C. (| http://www.simecol.de/salmo | Benndorf et al., 1982; Baumert et al., 2005).
SALMO 2 (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food-web of lakes and reservoirs implemented in Java. (| http://www.simecol.de/salmo | Benndorf et al., 1982; Petzoldt et al., 2002).
Scenario analysis (): A process of analysing possible future events by considering alternative possible outcomes. In contrast to prognoses, scenario analysis does not aim at extrapolation of the past. Instead, it tries to consider a whole suite of possible developments and turning points for the future. (http://en.wikipedia.org/wiki/Scenario_analysis | |).
SCOBI (Swedish Coastal and Ocean BIogeochemical model): A functional-group-based phytoplankton and water quality model. (| http://www.smhi.se/en/research/research-departments/oceanography/scobi-1.8680 | Eilola et al., 2009).
Scripting language (): A programming language that supports interpreted - rather than compiled - scripts that automate the execution of tasks that could alternatively be executed one-by-one by a human operator. (http://en.wikipedia.org/wiki/Scripting_language | |).
SENECA (Simulation ENvironment for ECological Application): A modelling framework for the implementation of AEMs. (| | De Hoop et al., 1992).
Sensitivity analysis (): A quantification of the change in model output as a function of the change in model input. (http://en.wikipedia.org/wiki/Sensitivity_analysis | |).
SHOC (Sparse Hydrodynamic Ocean Code): A sparse coordinate hydrodynamic model optimized for coastal systems. (| http://www.emg.cmar.csiro.au/www/en/emg/software/EMS/hydrodynamics.html | Wild-Allen et al., 2010; Oke et al., 2013; Herzfeld et al., 2014).
SIMCAT (SIMulation of CATchments): A very simple water quality model for lakes. (| | Comber et al., 2013).
SIMSTRAT (): A 1D-model for simulating mixing, stratification and temperature in lakes, based on k-epsilon approach, including effects of internal waves. (| | Goudsmit et al., 2002).
Simulation (): - (| | See Temporal simulation).
SMART (Simulation and Modelling Assistance for Research and Training): A tutorial modelling framework for the implementation of dynamical models that is structured in database fashion and therefore bears resemblance with DATM. Next to implementation SMART enables running of models in a structured way, i.e. in model experiments, that contain the model version and input used and the resulting output. (| http://harmoniqua.wur.nl/smart | Kramer et al., 2001).
SOBEK (after SOBEK, the ancient Egyptian god of the nile): A 1D/2D modelling suite for flood

forecasting, optimization of drainage systems, control of irrigation systems, sewer overflow design, river morphology, salt intrusion and surface water quality. (| http://www.deltares.nl/en/software/sobek |).
Software application (): A set of user-written code within a modelling framework that is designed to execute certain functions or tasks. (| |).
Software framework (): **-** (| | See Modelling framework).
Software library (): A set of functions or routines that can be called from a software application to perform a specific task, e.g. numerical integration. (http://en.wikipedia.org/wiki/Library_(computing) | |).
Spatially explicit model (): A model that explicitly takes space into account. This can be done with vector- or grid-based approaches. (| | Minor et al., 2008).
SPM in FABM (Suspended Particulate Matter model): A suspended particulate matter pelagic model with multiple size classes. (| http://sf.net/p/fabm | Burchard et al., 2004).
Statistical model (): A set of assumptions concerning the generation of the observed data, and similar data from a larger population. (http://en.wikipedia.org/wiki/Statistical_model | |).
STELLA (): A modelling framework that allows for drag and drop modelling in a graphical user interface. (| http://www.iseesystems.com/softwares/Education/StellaSoftware.aspx |).
Stoichiometric model (): A modelling approach that considers how the balance of energy and elements affects and is affected by organisms and their interactions in ecosystems. (http://en.wikipedia.org/wiki/Ecological_stoichiometry | |).
Structural equation model (): A statistical model based on the combination of two components: a measurement model that defines latent variables using one or more observed variables, and a structural regression model that links latent variables together. (http://en.wikipedia.org/wiki/Structural_equation_modeling | |).
Structural uncertainty (): A misestimate of the data by the model's output due to missing or imperfect process formulations within the model. (http://en.wikipedia.org/wiki/Uncertainty_quantification | |).
Structured grid (): - (| | See Curvilinear grid).
SWAN (Simulating WAves Nearshore): A wave model for wind generated waves in coastal regions and inland waters. (| http://www.swan.tudelft.nl, http://swanmodel.sourceforge.net | Booij et al., 1996).
SWAT (Soil and Water Assessment Tool): A semi-distribution eco-hydrological model. (http://en.wikipedia.org/wiki/SWAT_model | http://swat.tamu.edu | Arnold et al., 1998).
SWATCUP (Soil and Water Assessment Tool Calibration and Uncertainty Procedure): A calibration utility for the SWAT model. (http://en.wikipedia.org/wiki/Swat-CUP | | Abbaspour, 2007; Abbaspour et al., 2007).
SWMM (Storm Water Management Model): A dynamic rainfall–runoff–subsurface runoff simulation model primarily for urban and suburban areas. (http://en.wikipedia.org/wiki/Storm_Water_Management_Model | |).
TDT (Typed Data Transfer library): An interface for the transmission of data between programs in a platform- and programming language-independent way. (| https://www.pik-potsdam.de/research/transdisciplinary-concepts-and-methods/archiv/projects/modsimenv/modenv/tdt |).
Telemac (): An integrated suite of solvers for use in the field of free-surface flow. (http://en.wikipedia.org/wiki/TELEMAC | http://www.opentelemac.org |).
Temporal simulation (): A basic model analysis technique in which time series of output data are produced, mostly by numerical integration of process formulations in the form of ordinary, partial, or lattice differential equations. (http://en.wikipedia.org/wiki/Computer_simulation | | Refsgaard et al., 2004).
Trait-based model (): An individual-based model approach in which growth, reproduction, mortality and interactions with other organisms are linked with individual traits. (| http://bio.uib.no/te/research/traits.php |).
Triangular mesh (): A mesh grid consisting of triangles in one, two or three dimensions. (http://en.wikipedia.org/wiki/Triangle_mesh | |).
TRIM (Tidal, Residual and Inter-tidal Mutflat model): A hydrodynamic model optimized for coastal systems. (| http://sfbay.wr.usgs.gov/watershed/hydro_model.html | Cheng et al., 1993; Cugier et al., 2002).

TUFLOW-FV (Two-dimensional Unsteady FLOW Finite-Volume): A 3D flexible mesh finite volume hydrodynamic model. (| http://www.tuflow.com/Tuflow%20FV.aspx | Jamieson et al., 2012; Bruce et al., 2014).
Uncertainty analysis (): A quantification of the uncertainty in model output as a function of the uncertainty in model input. (http://en.wikipedia.org/wiki/Uncertainty_analysis | |).
Validation (): - (| | See Model validation).
VisSim (VISual language for SIMulating nonlinear dynamic systems): A visual block diagram language for simulation nonlinear dynamic systems. (http://en.wikipedia.org/wiki/VisSim | http://www.vissim.com |).
Visual Basic (): An object-oriented programming language and integrated development environment. (http://en.wikipedia.org/wiki/Visual_basic | https://msdn.microsoft.com/en-us/vstudio/ms788229.aspx |).
Vollenweider model (): An empirical and statistical lake eutrophication. (http://en.wikipedia.org/wiki/Richard_Vollenweider | | Vollenweider, 1975).
WAFLEX (): A spreadsheet-based model. It can be used to analyse upstream-downstream interactions, dam management options and water allocation and development options. (http://en.wikipedia.org/wiki/WAFLEX | |).
WASP (Water quality Analysis Simulation model): A dynamic water quality model used to investigate pollutants in aquatic systems in 1D, 2D, and 3D. (| http://www.epa.gov/athens/wwqtsc/html/wasp.html |).
Water Framework Explorer (): An analysis tool to calculate the effect of restoration and mitigation measures on the ecological and chemical quality of surface waters. (| https://www.deltares.nl/en/projects/water-framework-directive-explorer, https://publicwiki.deltares.nl/display/KRWV/KRW-Verkenner |).
Water quality model (): A formal procedure by which the impact of external or internal forcing on water quality parameters can be estimated. Water quality model is sometimes used as a synonym for AEM. (http://en.wikipedia.org/wiki/Water_quality_modelling | |).
Water quantity model (): - (| | See Hydraulic model, Hydrodynamic model and Hydrological model).
WATERRAT (WATER quality Risk Analysis Tool): A spreadsheet-based modelling package used to make decisions in the management of surface water quality. (| | McIntyre et al., 2003; McIntyre et al., 2004).
WMS (Watershed Modeling System): A model for water quantity and quality in watersheds. (http://en.wikipedia.org/wiki/WMS_(hydrology_software) | http://www.xmswiki.com/wiki/WMS:WMS |).
WWQM (Wetlands Water Quality Model): A model of constructed wetland dynamics. (| | Chavan et al., 2008; Huang et al., 2014).

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Chapter 4

Spatial distribution of water and nutrient sources determines success of lake management

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Abstract

All ecosystem productivity on earth crucially depends on nutrients. Human activity greatly impacts the pathways of allochthonous nutrient input to ecosystems as well as the way nutrients are dispersed within ecosystems. Due to the human impact, many ecosystems have deteriorated. We propose that the success of restoration of these ecosystems depends on hitherto neglected effects of the type of allochthonous nutrient sources in combination with the internal dispersal of nutrients. To this end, we study lakes as a model system, and broaden our findings by referring to other ecosystems as well. We compare the effect of three common types of restoration measures (stress release, adjusting resilience or perturbation treatment) to four types of lakes with contrasting allochthonous nutrient input (point or diffuse nutrient loading) and distribution patterns (seepage or drainage lakes). We show that restoration effectiveness depends on spatial dissimilarities that result from different water and nutrient source types. These spatial dissimilarities are particularly evident in the spatial eutrophication level, which we define here as the sum of the allochthonous and autochthonous nutrient load at a given location. It appears that the allochthonous nutrient load type determines the spatial position of the highest eutrophication levels, while the dispersal of nutrients by water skews the spatial patterns of eutrophication levels. We found that due to the spatial dissimilarities, a perturbation measure only works in seepage lakes with a diffuse nutrient source. Adjusting the resilience by flushing is counterproductive in lakes with a point nutrient source. Results show that stress release is effective in all cases. Our results provide guidance for decision making to achieve successful recovery of ecosystems.

Introduction

Ecosystem productivity depends on the mineralization of nutrients within the system (autochthonous input) as well as the input of nutrients from elsewhere (allochthonous input). The sources of allochthonous nutrient input are numerous and include atmospheric wet and dry deposition, transport via water flows such as groundwater, rivers and tide (e.g. Burford et al., 2008), and erosion of hill slopes (Reiners et al., 2003). Additionally, an often overlooked source of nutrients originates from animal motility (Doughty et al., 2016). The various sources of allochthonous nutrient input are commonly categorized into two main source types: point and diffuse nutrient sources (Carpenter et al., 1998; Rissman et al., 2015). Point sources of nutrients are local foci of nutrient input while diffuse sources are broadly dispersed, resulting in spatially more homogeneous nutrient input.

Human activity has greatly impacted the global nutrient cycle (e.g. Rockström et al., 2009b; Kroeze et al., 2013; Doughty et al., 2016). As a result, pathways of allochthonous nutrient input to ecosystems are altered and nutrient distribution within ecosystems is adjusted. First, the alteration of pathways for allochthonous nutrient input is visible in the increased input from point as well as diffuse sources. Point sources, such as sewage water, nowadays strongly enrich ecosystems with both phosphorus and nitrogen (Beusen et al., 2016). Likewise, the higher nutrient losses from agriculture have greatly enhanced diffuse nutrient sources (Beusen et al., 2016). As a result of these intensified nutrient input, the transport of both nitrogen and phosphorus to the ocean has nearly doubled during the last century (Beusen et al., 2016).

Second, the spatial nutrient distribution within ecosystems has changed. Examples of nutrient distribution within ecosystems are wind redistributing dust in deserts (Westrich et al., 2016), water flow mixing dissolved matter in tidal mudflats (Burford et al., 2008) and megafauna transporting organics within forests (Bakker et al., 2016). Due to human activities, these means of nutrient dispersal within ecosystems now increasingly differ from the past. Dust distribution alters due to climate change (Tegen et al., 2004), water flow is modified for instance due to the construction of dams (Kong et al., 2016) and megafauna have nearly gone extinct (Bakker et al., 2016; Doughty et al., 2016).

As result of human activities, the altered pathways of allochthonous nutrient input and adjusted spatial nutrient distribution within ecosystems have led to ecosystem degradation. Examples are peatland degradation due to increased atmospheric nitrogen deposition and adjusted hydrology (Bragazza et al., 2006; Buytaert et al., 2006); the deterioration of coral reefs due to raised coastal runoff of water, sediments and nutrients (D'Angelo et al., 2014); and the emergence of harmful algal blooms due to higher nutrient enrichment of lakes (Paerl et al., 2013). Ample attempts are made to restore the deteriorated ecosystem by controlling the allochthonous nutrient input as well as by addressing the dynamics that determine the spatial nutrient distribution within ecosystems. Unfortunately, restoration of deteriorated ecosystems has been only partly successful while restoration measures are often costly to apply (Elliott et al., 2007; Søndergaard et al., 2007; Suding, 2011).

We hypothesize that the effectiveness of ecosystem restoration measures depends on hitherto neglected combination of type of allochthonous nutrient sources in combination with the spatial distribution of nutrients in ecosystems. We test this hypothesis using lakes as a model ecosystem and subsequently identify similar phenomena in other ecosystems. Using a modelling approach, we first explore how the allochthonous nutrient source types and the spatial distribution of nutrients within ecosystems affect the spatial arrangement of biota. Next, we determine the consequences of the different types of allochthonous nutrient sources and the spatial distribution of nutrients for the success of three different ecosystem restoration methods.

Materials and methods

We use a full factorial design to explore the effect of type of allochthonous nutrient sources in combination with the spatial distribution of nutrients in ecosystems. For the allochthonous nutrient source type we apply the distinction of point and diffuse nutrient sources. With respect to the internal distribution of nutrients within the ecosystem we link this to lake hydrology. The lake hydrology is associated with the water input of lakes. Accordingly, lakes that receive water primarily from surface inlets have a spatially nearly uniform flow-through of water and are defined as drainage lakes. In contrast, lakes that receive water mainly from groundwater and precipitation have a build-up of water flow towards the lake's outlet and are defined as seepage lakes (Driscoll et al., 1985).

Combining the two allochthonous nutrient load types with the two types by which nutrients are dispersed by water movement within the ecosystem, we categorize lakes into four different lake types (Figure 4.1). The first lake type represents drainage lakes that receive nutrients primarily from autochthonous point sources from an inflowing river, stream or ditch (Figure 4.1a, 'point-loaded drainage lakes'). The second type of lakes also comprises drainage lakes (Figure 4.1b, 'diffuse-loaded drainage lakes') but differs fundamentally from the first type, because these lakes receive nutrients from diffuse allochtounous sources like dry atmospheric nutrient deposition or agricultural leaching. The third type of lakes (Figure 4.1c, 'point-loaded seepage lakes') represents seepage lakes, receiving water mainly via groundwater and precipitation, whereas the majority of nutrient loading originates from a point source, such as industrial waste water or untreated sewage water. Like the third, the fourth type of lake comprises seepage lakes (Figure 4.1d, 'diffuse-loaded seepage lakes'), but these lakes receive nutrients from diffuse sources like wet atmospheric deposition or nutrient rich groundwater.

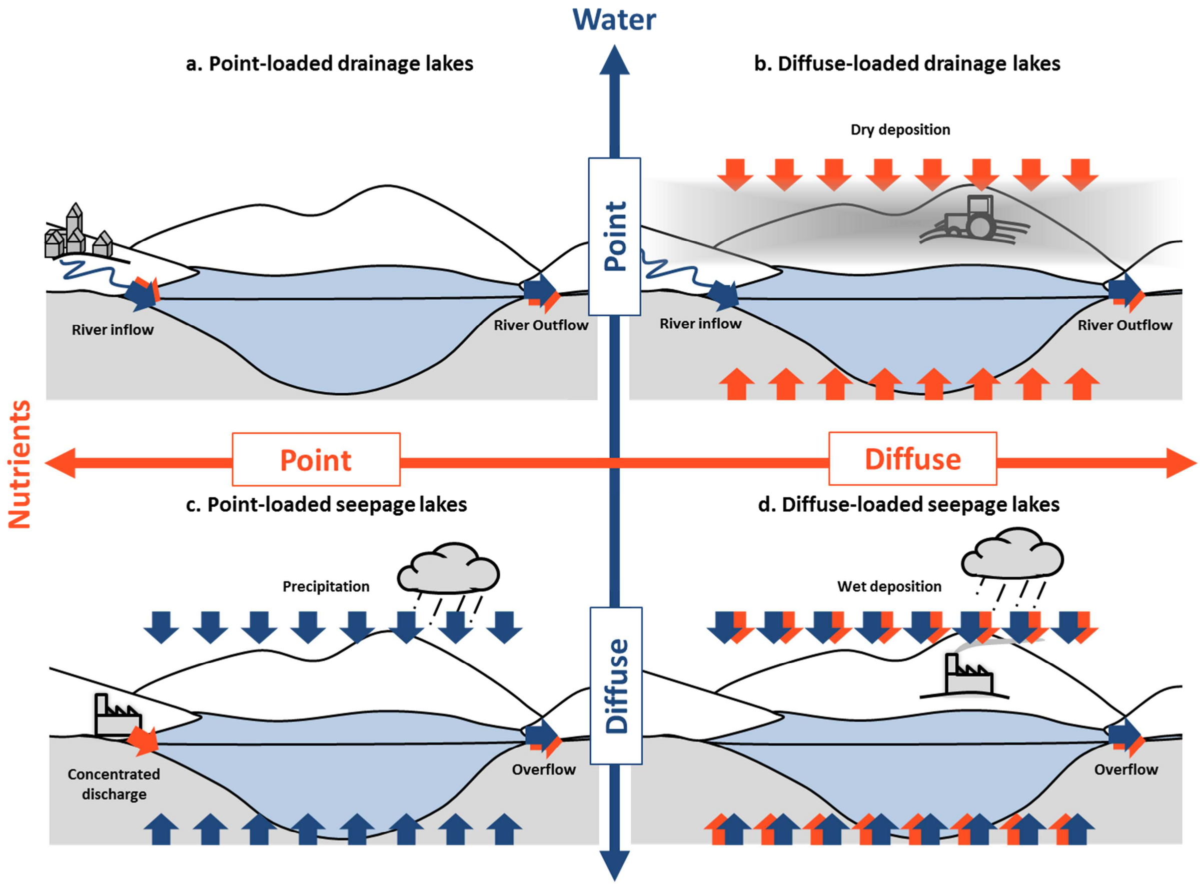


Figure 4.1. Four different lake types characterized by the nutrient load (horizontal axis; red arrows) and the hydrological dispersal of nutrients following the water input (vertical axis; blue arrows).

To study the success of lake restoration measures we use a modelling approach. For this purpose, we selected the ecosystem model PCLake, since the model is broadly used for different types of shallow lakes (Janse et al., 2010; Nielsen et al., 2014), and is, as one of a few, well-suited to estimate critical nutrient loadings at which a lake in an undesired turbid state can be restored to a preferred clear state (Janse et al., 2010; Janssen et al., 2015). We translated the model code of PCLake to R by using the recently developed Database Approach To Modelling (DATM) (Mooij et al., 2014; Van Gerven et al., 2015). The aquatic ecosystem model PCLake includes both water column and sediment layer food webs, with functional groups ranging from three phytoplankton types, zooplankton, zoobenthos, planktivorous and piscivorous fish (Janse, 2005; Janse et al., 2008; Janse et al., 2010).

We schematized each hypothetical lake into a one-dimensional chain of grid cells. In each grid cell, biogeochemical processes take place as defined by PCLake. A simple hydrodynamic model takes care of the movement of transportable substances, such as nutrients, phytoplankton and inorganic matter (see Appendix 7). To guarantee a fair comparison between the hypothetical lakes, each of the lakes receives an equal total amount of allochthonous nutrients and water, yet the distribution over the segments depends on the source type. In the case of drainage lakes or lakes with a point nutrient source, the total amount of water respectively nutrients is received by the first segment. The first segment passes the water with its substances on to the next segment as an internal loading after biogeochemical processes have taken place. In the case of seepage lakes or lakes with a diffuse nutrient source, each segment receives an N^{th} part of the total amount of water respectively nutrients as allochthonous load. Furthermore, each segment receives a certain level of internally transferred load from previous segments. The last segment of all lakes discharges the water via an out- or overflow.

We perform a bifurcation analysis to identify the spatial effects of the different loading types on lake resilience. To this end, we repeatedly ran the model to equilibrium, each time selecting a constant nutrient load from a range of loading levels that varies between 0.002 and 0.05 $gP.m^{-2}.d^{-1}$ with a constant N:P ratio of 10, following earlier studies (Janse et al., 2010). To establish the presence of alternative stable states (i.e. hysteresis) we repeated this procedure twice, once starting with a clear oligotrophic lake and the other with a turbid eutrophic lake. For the entire bifurcation analysis we evaluate the eutrophication level at different locations within the lake as well as for the average of the lake. Here we define eutrophication level as the total nutrient load, which comprises the allochthonous and autochthonous nutrient loads at a given location.

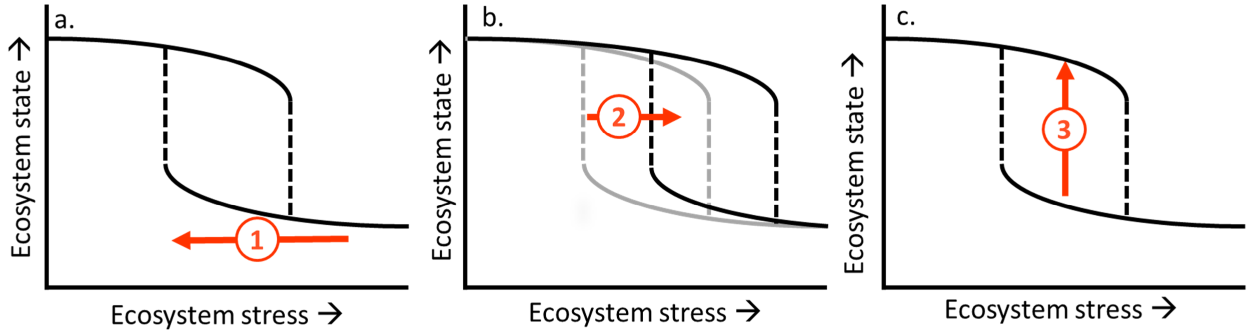


Figure 4.2. Options for ecosystem restoration: a) stress release b) increase resilience of ecosystem c) perturbation. Modified after Janse et al. (2008).

Finally, we analyzed the effect of the three types of general restoration measures, each of which could be used to restore degraded ecosystems (e.g. Scheffer et al., 2001; Beisner et al., 2003; Janse et al., 2008). Each type of general restoration measure aims to restore ecosystems in a specific way (Figure 4.2). First, the stress release method reduces the stress that acts upon an ecosystem. The second type of restoration measure alters the resilience of the ecosystem such that the preferred state becomes the most resilient. The last type of restoration measure perturbs the ecosystem, allowing the ecosystem to shift to the preferred state. In our case, we aim at restoration measures that reduce the biomass of algae such that the entire lake shifts from the undesirable turbid to the preferred clear state. To this end, we model nutrient load reduction over the full range from eutrophic to oligotrophic as a stress-release measure. Second, retention time reduction with 50% more water input via a simulated clear water pipeline is applied as measure that alters the resilience. Lastly, biomanipulation by catching 90% of all planktivorous fish, and thus allowing zooplankton to increase in density and suppress phytoplankton, is modeled as a substantial perturbation to push the lake ecosystem to another state.

Results

To understand the effect of the different nutrient and water source types on lake restoration, it is important first to interpret the results of these effects for different locations within the lake.

Effect of nutrient loading

Nutrient load types affected the spatial distribution of eutrophication levels within lakes in different ways (Figure 4.3). Lakes with a diffuse allochthonous nutrient source exhibit the highest eutrophication levels close to the outlet (Figure 4.3b and Figure 4.3d). This pattern is in contrast to the spatial response of lakes with an allochthonous nutrient point source, where eutrophication levels are lowest at the outlet (Figure 4.3a and Figure 4.3c). Hence, the highest levels of eutrophication occur at opposing lakesides for the two distinct nutrient load types. Internal nutrient balances explain these differences in the position of highest eutrophication levels. Where there is an allochthonous point source, nutrients enter in bulk form at the inlet, promoting luxurious growth of either macrophytes (low allochthonous nutrient load) or phytoplankton (high allochthonous nutrient load) close to the inlet. Towards the outlet of the lake, nutrient depletion leads to a decrease in primary production and internal load. In contrast, lakes with a diffuse allochthonous nutrient load receive a spatially homogeneous nutrient load. Since only a fraction of the nutrients are retained at any location along the course of water movement, the diffuse nutrient loading leads to spatial accumulation of nutrients towards the outlet. In the diffuse-loaded drainage lakes this mechanism leads to increasing eutrophication levels towards the outlet (Figure 4.3b), which approaches a relatively constant eutrophication level. The constant eutrophication level results from equilibrium between biochemical processes: water retention time and incoming allochthonous nutrients. Therefore, the nutrient concentration, macrophyte biomass and the chlorophyll-a levels all tend to reach a constant level. Interestingly, diffuse nutrient loading in seepage lakes leads to completely homogeneous nutrient, phytoplankton and macrophyte distributions (Figure 4.3d). The homogeneity follows from a constant ratio between the incoming water and the autochthonous nutrient load, which keeps the nutrient concentrations at a constant level.

Effect of internal dispersal of nutrients

The effect of the two types of dispersion of nutrients by water within the on the spatial pattern of eutrophication levels is subtler than the effect of the nutrient load type. It skews the spatial pattern of eutrophication levels rather than determining the position of the highest eutrophication levels. A comparison between lakes with a similar nutrient load type reveals that the spatial variation in eutrophication levels is more extreme in seepage lakes than in drainage lakes, a pattern most visible in point-loaded lakes (Figure 4.3a and Figure 4.3c). This interesting difference emerges from the low water retention time, which limits the nutrient retention in drainage lakes. In contrast, seepage lakes experience higher retention times at locations especially away from the overflow, resulting in a high degree of nutrient retention and therefore lower internal nutrient transport within the lake.

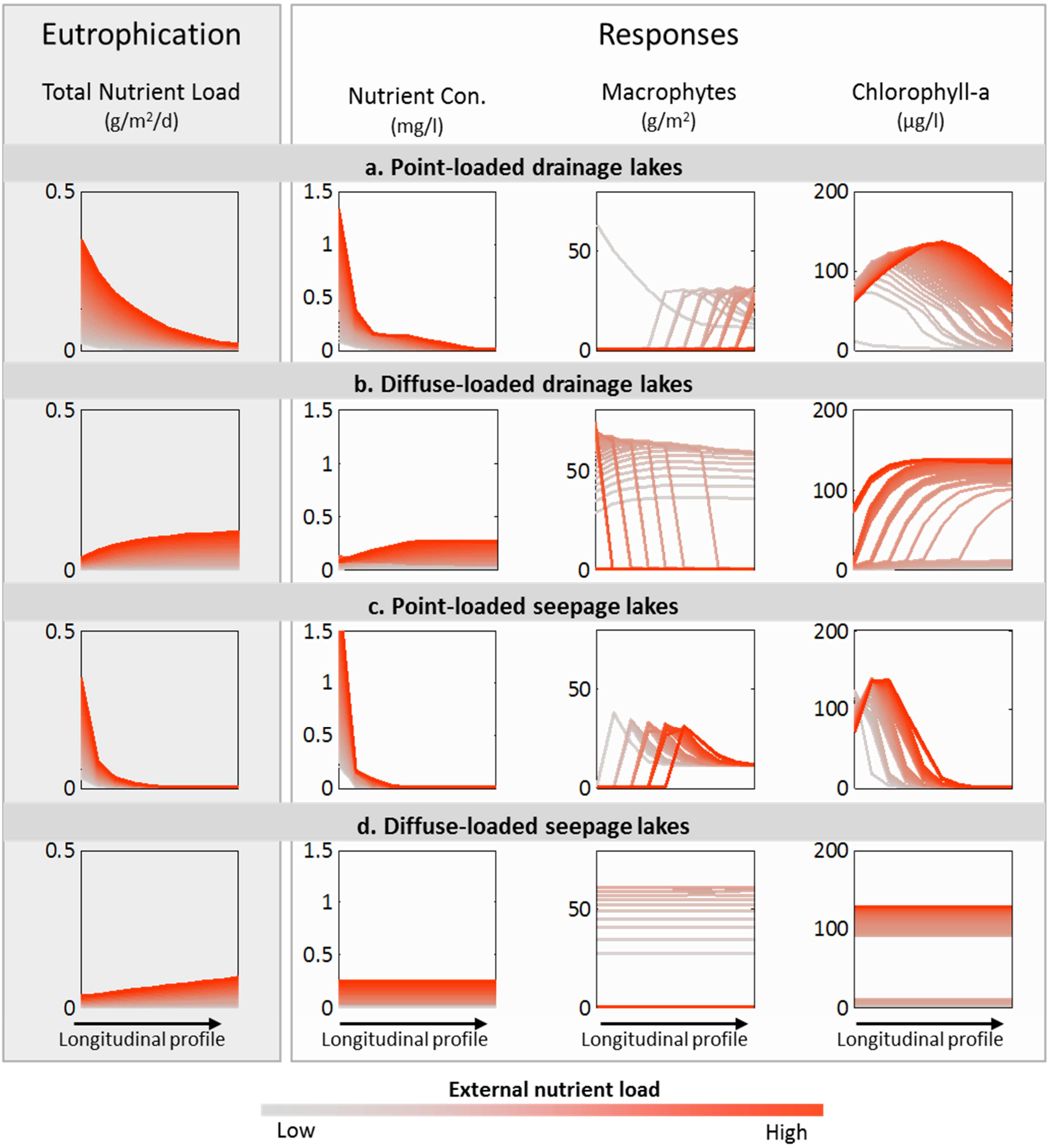


Figure 4.3. Model results showing the response of nutrients and biota in lakes over the longitudinal axis to different autochthonous nutrient load scenarios, starting with low nutrient load in grey to high nutrient load in red. The variables from left to right are the total nutrient load (eutrophication level) defined as the local sum of autochthonous and internal nitrogen load per segment ($gN.m^{-2}.d^{-1}$) (graphs for total P-loading are similar), surface water nutrient concentrations of NH_4 ($mg.L^{-1}$) (graphs for other nutrients are similar), biomass of macrophytes ($g.m^{-2}$) and chlorophyll-a concentration as proxy for phytoplankton biomass ($\mu g.L^{-1}$).

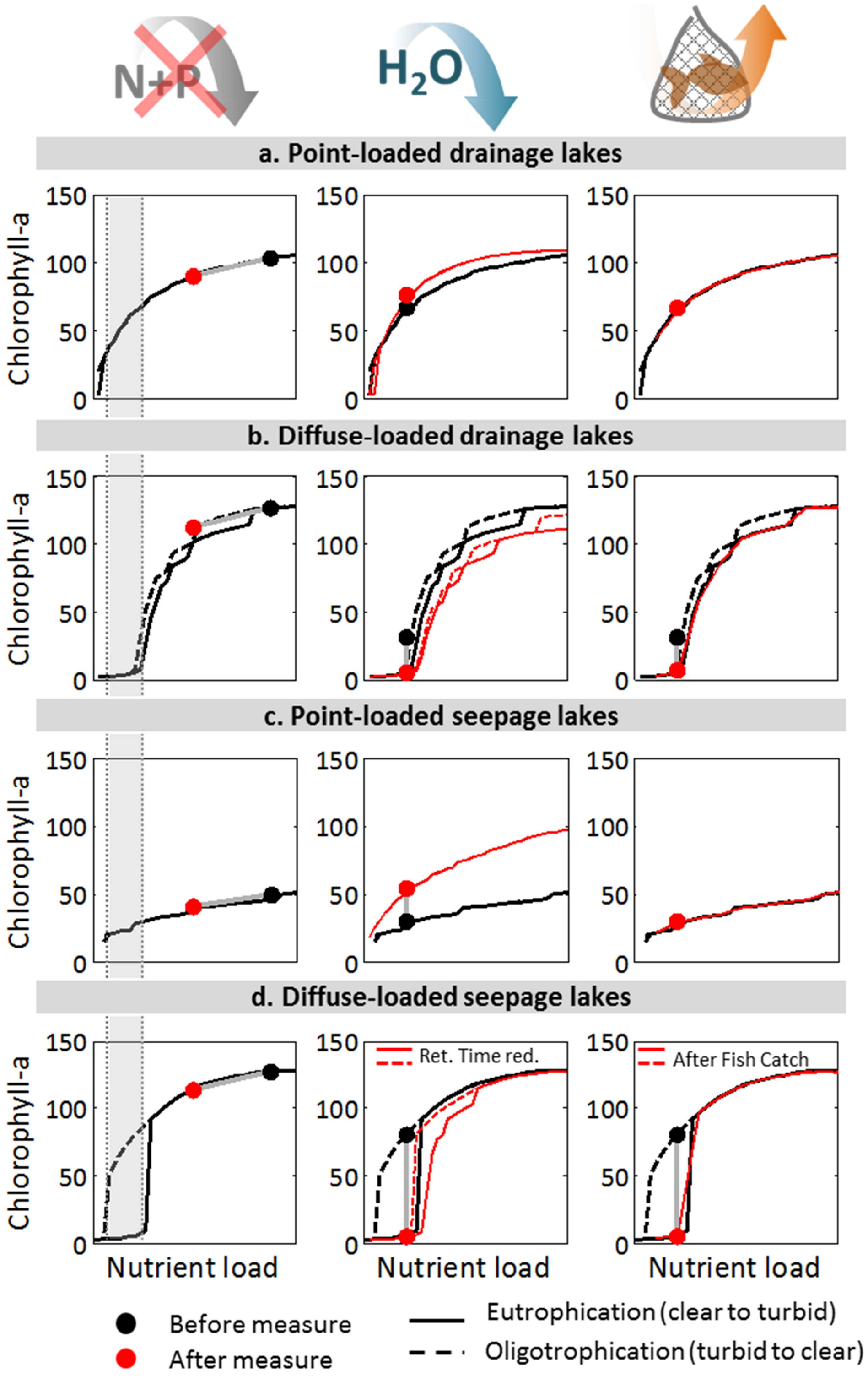


Figure 4.4. Spatially-averaged load-response curves resulting from bifurcation analysis showing the total autochthonous nutrient load for each lake type on the horizontal axis and the lake average chlorophyll-a (mg.m^{-2}), as proxy for phytoplankton biomass, on the vertical axis. These are, from left to right, nutrient load reduction, retention time reduction (+ 50% more water input from a clear water pipeline) (red line) and biomanipulation (90% catch of planktivorous fish biomass). The grey bar shows the area of alternative stable states for the diffuse-loaded seepage lakes.

Lake-wide effects

The spatially explicit processes of water and nutrient inflow (Figure 4.3) have a clear effect on the eutrophication status of the lake as a ‘generalized’ whole, when the chlorophyll-a values are spatially averaged for each lake type (Figure 4.4, left column). In this regard, it is worth noting that the occurrence of alternative stable states (i.e., phytoplankton versus macrophyte dominance at the same nutrient loading) are prominent in the modelled diffuse-loaded seepage lakes (Figure 4.4d, left column), are present in the diffuse-loaded drainage lakes (Figure 4.4b, left column), but are absent in the point-loaded lakes (Figure 4.4a and Figure 4.4c, left column). This results from the fundamental differences between rooted macrophytes and free-flowing phytoplankton and their spatial distribution within the lakes. Once phytoplankton is growing at high densities at the inlet in the point-loaded lakes, it disperses by water movement across the lake. This transport of phytoplankton into initially macrophyte-dominated areas negatively affects the competitive strength of macrophytes. Thereby, the strong positive feedbacks that otherwise would maintain the macrophyte-dominated state are weakened. In lakes with diffuse nutrient load, however, the positive feedbacks that maintain macrophytes are less affected by transport of phytoplankton, since significant chlorophyll-a levels appear first mainly concentrated close to the lake outlet (diffuse-loaded drainage lakes) or at a homogeneous constant level throughout the entire lake (diffuse-loaded seepage lakes). Consequently, the feedbacks that allow alternative stable states to exist are unaffected by phytoplankton transport in the diffuse-loaded lakes. Still, there are differences between the diffuse-loaded lakes. In diffuse-loaded drainage lakes (Figure 4.4b, left column), alternative stable states are weaker and are based on successive local events, rather than on a shift occurring at the same time across the whole lake, which is predicted in the diffuse-loaded seepage lakes (Figure 4.4d, left column). Finally, note that the load-response curve in point-loaded drainage lakes (Figure 4.4a, left column, black solid line) resembles the oligotrophication curve of diffuse-loaded seepage lakes (Figure 4.4d, left column, black dashed line). Additionally, the load-response curve of diffuse-loaded drainage lakes (Figure 4.4b, left column, black dashed and solid line) is similar to that of the load-response curve for eutrophication of diffuse-loaded seepage lakes (Figure 4.4d, left column, black solid line). Thus, in drainage lakes, nutrient load type determines the position of the dominating curve, both during eutrophication and oligotrophication.

Effect on success of restoration measures

We analyzed the potential success of three commonly applied restoration measures: (A) nutrient reduction, (B) retention time reduction and (C) biomanipulation.

A) Stress release measure: nutrient reduction

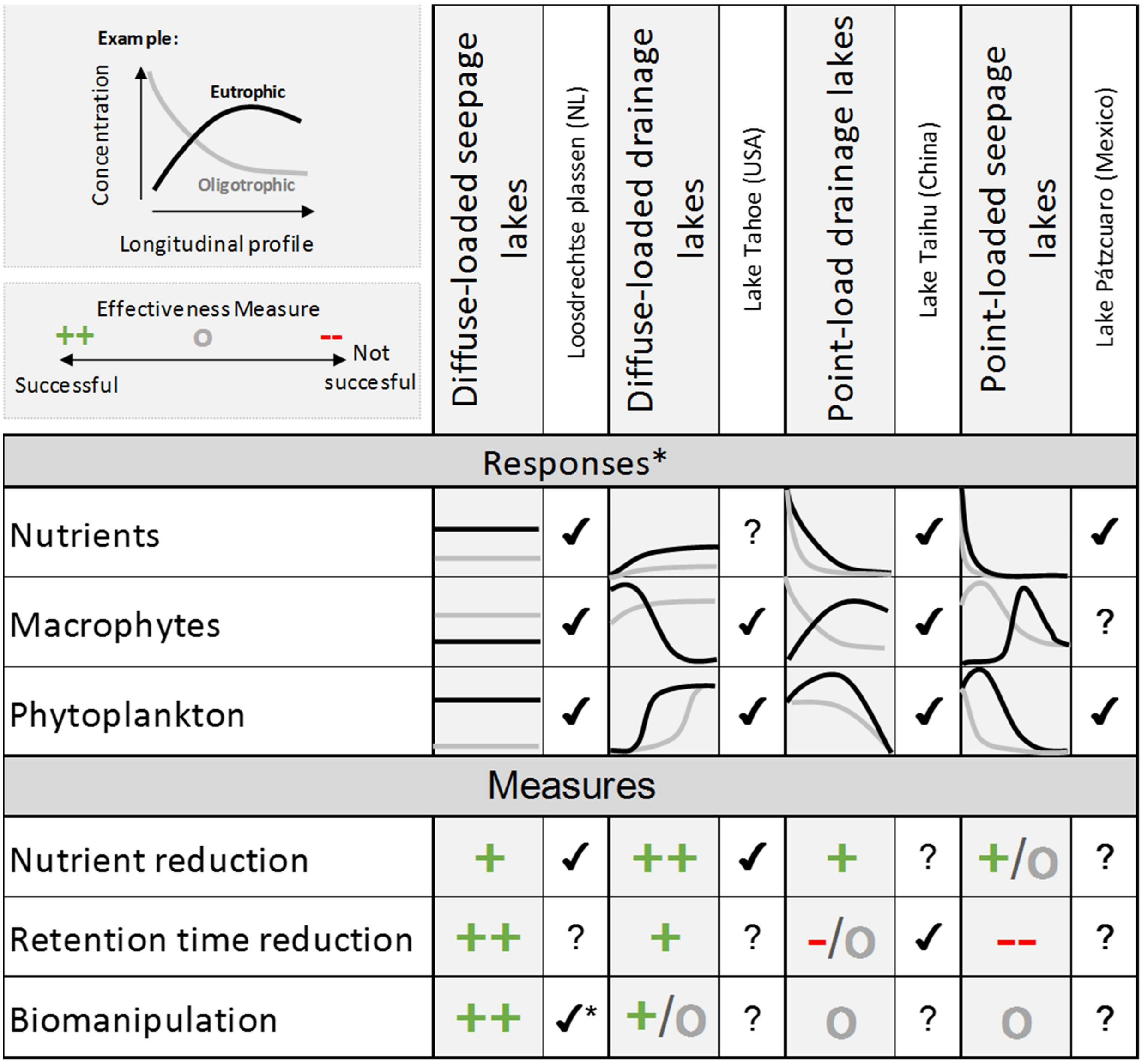
The success of using nutrient input reduction to sufficiently reduce phytoplankton chlorophyll-a concentrations critically depends on 1) the current stress induced by the allochthonous nutrient load 2) the effort to reduce nutrient load and 3) whether or not alternative stable states are present (Figure 4.4, left column). Alternative stable states occur in the diffuse-loaded seepage lakes, and if the state is initially eutrophic, a strong reduction in allochthonous nutrient load, to below the lower of the two critical nutrient loads, is required to achieve good water quality (Figure 4.4d, left column, dashed line). Initially eutrophic point-loaded drainage lakes need an equal amount of nutrient load reduction as diffuse-loaded seepage lakes for a similar achievement in water quality. In contrast to diffuse-loaded seepage lakes, however, this amount of nutrient load reduction is also similar to the amount of increased load that transformed them from the desirable quality to the undesirable state is required in the first place (Figure 4.4a, left column). On the contrary, the diffuse-loaded drainage lakes demand a considerably lower nutrient reduction to return to the oligotrophic state (Figure 4.4b, left column). In contrast to these three types of lakes, point-loaded seepage lakes respond much more gradually to nutrient load reduction (Figure 4.4c, left column). While such limited response to nutrient load reduction may be perceived as inefficient, it should be noted that point-loaded seepage lakes are least affected in the first place by the nutrient load compared to all other lake types, as most of the total nutrient load concentrate at the outlet.

B) Measure to alter resilience: retention time reduction

Surprisingly, our analysis highlights that retention time reduction through increased water flow is not necessarily beneficial to restore the lake to a clear state. Indeed, a further deterioration of the lake ecosystem is even possible in the case where the lake is point-loaded (Figure 4.4a and Figure 4.4c, middle column). For these lake types, nutrients at the inlet are dispersed farther through the lake instead of being retained close to the inlet. The dispersal of nutrients causes higher biomass levels away from the inlet. This paradox does not apply to lakes with a diffuse nutrient load (Figure 4.4b and Figure 4.4d). Due to retention time reduction, chlorophyll-a drops to lower levels because of the negative effects on phytoplankton growth. Additionally, retention time reduction could result in an abrupt shift to the clear state in lakes with a diffuse nutrient load. This happens in case the amount of allochthonous nutrient load is lower than the, by retention time reduction increased, critical nutrient load (Figure 4.4b and Figure 4.4d, middle column, red dashed line).

C) Perturbation measure: biomanipulation

Being a temporary perturbation only, a long lasting impact of biomanipulation requires the existence of alternative stable states (i.e. hysteresis), because otherwise the lake will eventually return to its initial state given that nutrient load is the same. Therefore, a long-term effect of biomanipulation can only be observed in the diffuse-loaded seepage lakes and to a lesser extent in the diffuse-loaded drainage lakes, provided that the autochthonous nutrient load lies between the lower and higher critical levels (Figure 4.4, right column).



	Diffuse-loaded seepage lakes	Loosdrechtse plassen (NL)	Diffuse-loaded drainage lakes	Lake Tahoe (USA)	Point-load drainage lakes	Lake Taihu (China)	Point-loaded seepage lakes	Lake Pátzcuaro (Mexico)
Responses*								
Nutrients		✓		?		✓		✓
Macrophytes		✓		✓		✓		?
Phytoplankton		✓		✓		✓		✓
Measures								
Nutrient reduction	+	✓	++	✓	+	?	+/o	?
Retention time reduction	++	?	+	?	-/o	✓	--	?
Biomanipulation	++	✓*	+/o	?	o	?	o	?

Figure 4.5. Comparison between model results and empirical data. The graphs depicted under the title 'responses' show the spatial pattern deduced from Figure 4.3 (outlet on the right). The pluses, zeros and minuses depicted under the title 'measures' indicate the effectiveness of restoration measures according to the model simulations. With a ✓-sign it is indicated that the pattern is confirmed by empirical observations. A question mark indicates missing values since the restoration measure is not carried out or information on the results are lacking. * In Lake Loosdrecht biomanipulation has not been applied, however in a nearby, smaller, diffuse-loaded seepage lake (Lake Zwemlust), biomanipulation has been applied successfully.

Discussion

We have shown that nutrient load types determine the spatial position of the highest eutrophication levels, while internal dispersion of nutrients skews the spatial pattern of eutrophication levels (Figure 4.3). These spatial differences in eutrophication levels determine the spatial distributions of biota (Figure 4.3), and are crucial to the success of restoration measures (Figure 4.4). To summarize our main findings (Figure 4.5), in going from diffuse-loaded drainage lakes through point-loaded drainage lakes, to point-loaded seepage lakes, the peaks of nutrients and phytoplankton move away from the outlet, while the peak of macrophytes moves towards the outlet. A similar pattern has been discussed before for a chain of lakes in USA (Carpenter et al., 2014) and a chain of drainage ditches (Van Gerven et al., 2016). With this knowledge in mind we now check for empirical evidence for the predicted patterns and the effectiveness of measures in four lakes around the world that are characteristic for each of the four lake types used in our model study.

Real lakes

Diffuse-loaded seepage lakes

Historically, Lake Loosdrecht (the Netherlands) has received groundwater from an elevated sand ridge and input from rainwater (Van Liere, 1986; Van Liere et al., 1991) and can be characterized as a diffuse-loaded seepage lake. Nutrients and phytoplankton were relative homogeneous in Lake Loosdrecht, as expected for a diffuse-loaded seepage lake. To prevent too low water levels resulting from reduced seepage in this lake, a river water inlet was constructed. However, the high nutrient content of the river water pushed the lake temporarily towards a point-loaded seepage lake (Van Liere et al., 1991). To improve water quality, the autochthonous nutrient loading has been drastically reduced (Van Liere, 1986; Van Liere et al., 1991; Engelen et al., 1992), which, unfortunately, did not lead to lower phytoplankton concentrations and the reestablishment of macrophytes (Janse et al., 1992). Possibly, this limited success resulted from the existence of alternative stable states, as predicted for diffuse-loaded seepage lakes. Although potentially effective according to our analysis, the option of retention time reduction is not recommended in Lake Loosdrecht for practical reasons (Janse et al., 1992). Experience with another diffuse-loaded seepage, Lake Zwemlust, confirmed the potential of biomanipulation in this type of lake (Ozimek et al., 1990); however, in Lake Loosdrecht this measure is conceived to be infeasible due to the challenge to capturing a sufficient amount of fish and due to the low potential for macrophyte reestablishment owing to the high concentration fine particles that are susceptible to wind-caused resuspension (Janse et al., 1992; Penning et al., 2013). This leaves a further reduction of autochthonous phosphorus and a restoration of the original low-nutrient groundwater flow as the most promising measures (Engelen et al., 1992; Janse et al., 1992).

Diffuse-loaded drainage lakes

The alpine Lake Tahoe (USA) receives water that mainly originates from watershed runoff, whereas the major nutrient load is atmospheric deposition from combustion emissions, agricultural fertilizers and industrial wastes (Jassby et al., 1994; Schuster et al., 2004). Accordingly, Lake Tahoe is classified as a diffuse-loaded drainage lake. Historically, highest eutrophication levels are found near the outlet of the lake (Abrahamsson et al., 1970) and recent reports show that macrophytes only resist turbidity away from the outlet (Caires et al., 2013). These spatial patterns are consistent with our model results. Eutrophication control focusses on the reduction in atmospheric deposition as well as on reduction of point loading (Schuster et al., 2004). Most restoration projects focusing on nutrient reductions have been successful in reducing the nutrient concentrations (Schuster et al., 2004), yet macrophytes have not recovered to the undisturbed level as measured in the 1960s (Caires et al., 2013).

Point-loaded drainage lakes

Lake Taihu (China) can be characterized as a point-loaded drainage lake, since the majority of nutrients originate from point sources (90%) and water input is mainly from rivers (75%) (Kelderman et al., 2005). In accordance with our predictions, highest concentrations of algal biomass appear in the northern and central parts of the lake, while algal biomass and nutrient levels are lower closer to the outflow (Wang et al., 2005; Janssen et al., 2014). Nutrient reduction was attempted as a restoration measure but could not keep up with the rapid socio-economic development in the region (Janssen et al., 2014). In an attempt to reduce the nuisance of increasing occurrence of algal blooms, the retention time of the most eutrophic part of the lake has been reduced using Yangtze River water (Qin et al., 2010). While this measure temporarily reduced algal biomass at the inlet, movement of phytoplankton resulted in higher chlorophyll-a levels elsewhere in the lake (Qin et al., 2010). Our model results show that this is indeed a plausible negative impact of retention time reduction in this type of lake.

Point-loaded seepage lakes

The main water source of Lake Pátzcuaro (Mexico) is rainwater, while point loadings from wastewater at the south of the lake have become the main nutrient load (Chacón-Torres et al., 1997; Bernal-Brooks et al., 2003). Decreasing nutrient concentrations, macrophyte biomass and chlorophyll-a away from the main input at the south and towards the northern regions have been observed (Rosas et al., 1993; Bernal-Brooks et al., 2003). This pattern fits well with our predictions for point-loaded seepage lakes. We are not aware of restoration plans to reduce the impact of eutrophication on the ecology of Lake Pátzcuaro.

The four real lakes described above are textbook examples of the lake types, yet plenty of lakes do not fit into these discrete, unchanging categories. Indeed, ongoing anthropogenic pressures cause changes in nutrient sources and the way nutrients are mixed within the lake. These changes could force shifts from one lake type to another. Hence, the classification in the field should be looked on as a continuum of types rather than the discontinuous categories described here so far. Endless options exist to partition the nutrient source types and to mix them within the ecosystem. Besides, due to temporal and spatial differences in nutrient sources, the varying nutrient dispersal processes, and spatial heterogeneity in other lake characteristics, the resulting spatial eutrophication pattern can be hybrid as well, as discussed below.

Temporal changes

Firstly, due to socio-economic developments, the major nutrient load type may change over time. As discussed, such change occurred in Lake Loosdrecht, but also in the wetland ecosystem of The Everglades (USA). Conservation Area 2A within The Everglades has undergone a transition from a diffuse-loaded seepage wetland dominated by atmospheric nutrient load to a point-loaded wetland with nutrient rich canal inflow, as the result of the construction of the Everglades Agricultural Area (Davis, 1994; Chimney et al., 2006). Due to the changes in nutrient sources and hydrology, the eutrophication pattern changed. An exponential decrease in nutrient concentrations as function of distance from the artificially created inflow became visible (Reddy et al., 1993). Close to the inflow of autochthonous point sources, sawgrass has been succeeded by cattail (Typha), a species associated with high nutrient concentrations (Hagerthey et al., 2008).

Spatial differences

Spatial differences may lead to 'subtypes' within one ecosystem. For instance, Lake Victoria (East Africa) best resembles a diffuse-loaded seepage lake since the majority of both the water and nutrients originate from atmospheric sources (Scheren et al., 2000; Tamatamah et al., 2005). However, point loading has a local high impact inshore and in the Victoria's Nyanza Gulf (Scheren et al., 2000; Hecky et al., 2010; Guya, 2013). Therefore, despite the general classification as diffuse-loaded seepage lake, locally this lake is classified as a point-loaded discharge lake. Clearly, this shows the challenge of differentiating between large and small scale, especially in large ecosystems such as Lake Victoria (Downing et al., 2014). Another important note is that incoming nitrogen and phosphorus are not necessarily similarly distributed across the lake. For instance, while atmospheric deposition might be the main source of nitrogen, the same lake could receive phosphorus primarily from a point wastewater source. Indeed, the case of Lake Victoria illustrates how the assumption of spatial homogeneity can be particularly misleading. How this will affect the spatial eutrophication pattern and the success of lake ecosystem restoration is beyond the scope of this paper but is certainly interesting for further research.

Other causes of spatial heterogeneity in response to eutrophication

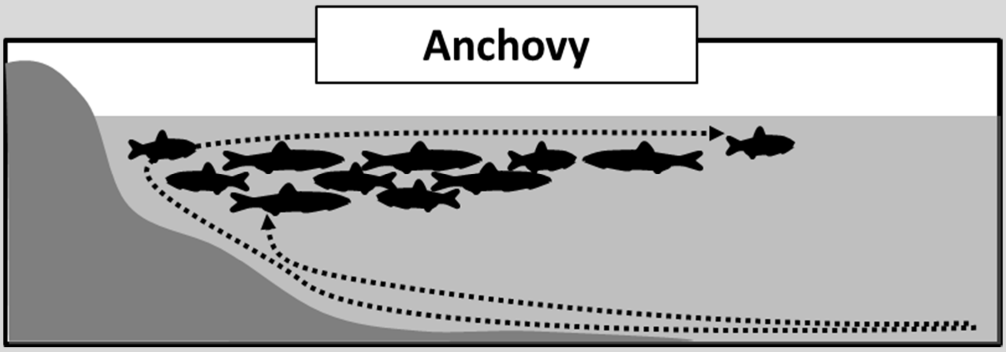
It is evident that spatial heterogeneity in lake biota is not only the result of different types of nutrient sources and internal mechanisms of dispersal. Also differences in depth, sediment type and, importantly, the distribution of grazers, affect the spatial heterogeneity (Dionisio Pires et al., 2002; Kratz et al., 2005). For example, Lake IJsselmeer is a point-loaded drainage lake, which is reflected by the high nutrient concentrations near the inlets, yet most algae grow at the outlet due to high grazing pressure imposed by zebra mussels that grow best on the substrate near the inlet (Bij de Vaate, 1991).

Implications for theory and management

In the scientific literature, lake eutrophication is linked inextricably to the theory of alternative stable states. The validity of this theory, however, is still part of a lively debate (Scheffer et al., 2007; Janssen et al., 2014; Capon et al., 2015). The discussion often focuses on the applicability of the theory for shallow lakes; however, deep lakes are thought to have alternative stable states as well, through a different mechanism with positive feedbacks in the phosphorus cycle and oxygen control by algae (Carpenter et al., 1999; Genkai-Kato et al., 2005). Our study complements this debate by showing that alternative stable states are restricted to lakes that can be classified as diffuse-loaded seepage lakes. This adds to previous studies showing that spatial heterogeneity in internal characteristics, such as depth or sediment types in lakes, prevent the existence of alternative stable states (Van de Leemput et al., 2015). Consequently, we suggest that alternative stable states are limited to lakes that are homogeneous in autochthonous nutrient load and in their internal characteristics. It is therefore not surprising that, as far as we know, most cases of alternative stable states are only suspected in relatively homogeneous ecosystems that have a diffuse source of nutrients such as the deserts, heathlands and woodlands (Scheffer et al., 2003a). Another interesting aspect for lake restoration, which likely applies to ecosystems in general, is the temporal and spatial change in types, as, for instance, seen in The Everglades wetland as well as in Lake Loosdrecht. Since any modification of the relative contributions of autochthonous nutrient sources and internal dispersion may result in a transition in type, this principle can be used to the benefit of ecosystem restoration. For instance, if a drainage lake is point-loaded, the restoration of its ecosystem can be facilitated by pushing the lake to a diffuse-loaded drainage lake type through minimizing the relative contribution of the nutrient point sources.

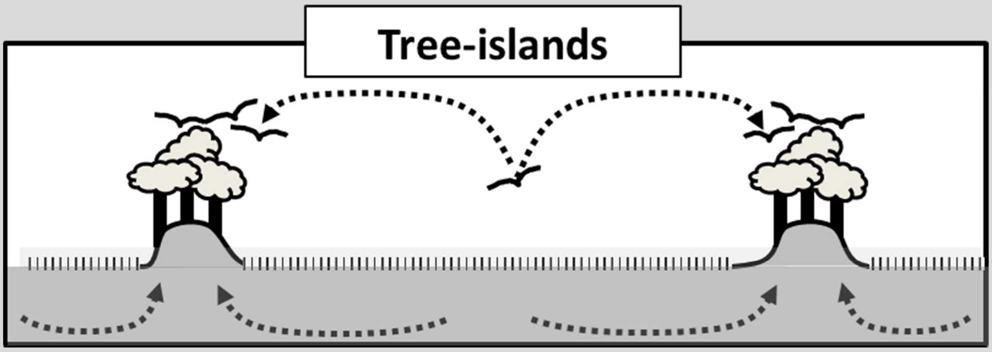
Our findings show the importance of nutrient source types and the nutrient dispersal processes for the effectiveness of lake management. Similar to that of lakes, the distribution of biota in any other ecosystem is inevitably linked with the type of nutrient sources as well as the way the nutrients are mixed within the ecosystem (see Box 4.1). The unique distribution of biota that emerges from these ecosystem's specific characteristics are continually altered by anthropogenic impact. Attempts to restore these affected ecosystems potentially lead to unintended negative consequences, when underlying processes for nutrient sources and nutrient dispersal processes are neglected. Therefore, the assessment of the type nutrient sources and dispersal processes is essential to ecosystem restoration.

Box 4.1. Four examples of ecosystems showing patterns comparable to the four lake types.



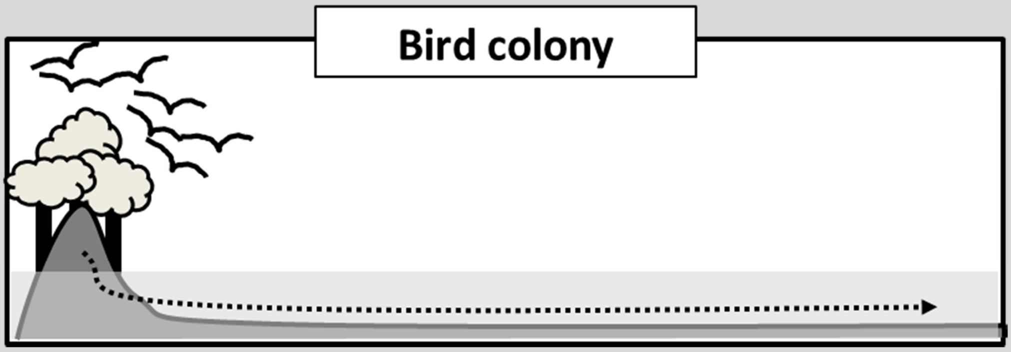
Anchovy

Deep sea upwelling at the continental coast asserts a **point source** of nutrients which locally supports the growth of large anchovy populations (Ward et al., 2006). The anchovy system is comparable to the high productivity at the inflow of **point-loaded drainage** lakes.



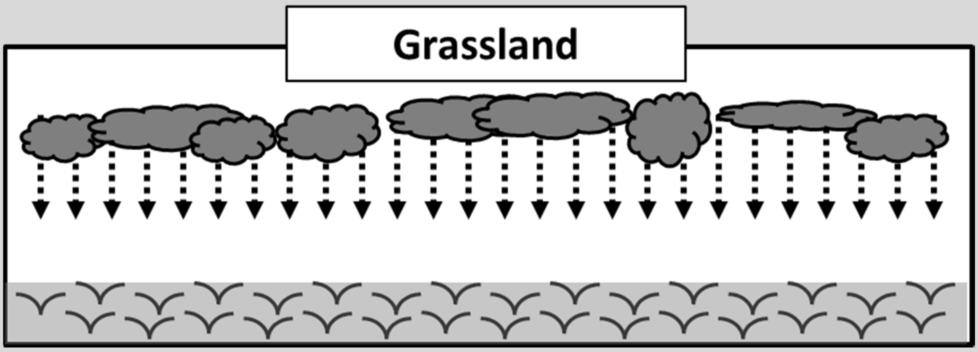
Tree-islands

Tree-islands are nutrient-rich isolated patches of forest in nutrient-poor marshes (e.g. Everglades). Tree-islands are effective accumulation points of **diffusely dispersed nutrients**. The accumulation is due to transpiration (D'Odorico et al., 2011), nesting places of colonial wading birds (Oliver et al., 1988) and the capture of airborne nutrients as dry deposition (Lowman et al., 2004). Tree-islands are similar to the nutrient-rich vegetation at the outflow of **diffuse-loaded drainage** lakes.



Bird colonies

Bird colonies that nest at a confined area such as a cliff or small island cause a local **point source** to the surrounding sea. Within the area of the colony, nutrient accumulate leads to local increase of eutrophication (Klimaszyk et al., 2015) The bird colonial system is comparable to the steep gradient in productivity from the inflow of **point-loaded seepage** lakes.



Grassland

Grasslands are ecosystems that receive nutrients by **diffuse atmospheric deposition.** If grasslands are relatively homogeneous, it has been shown that they exhibit alternative stable states with forests and deserts (Holmgren et al., 2001; Staver et al., 2011). Accordingly, grasslands are comparable to **diffuse-loaded seepage** lakes.

Acknowledgements

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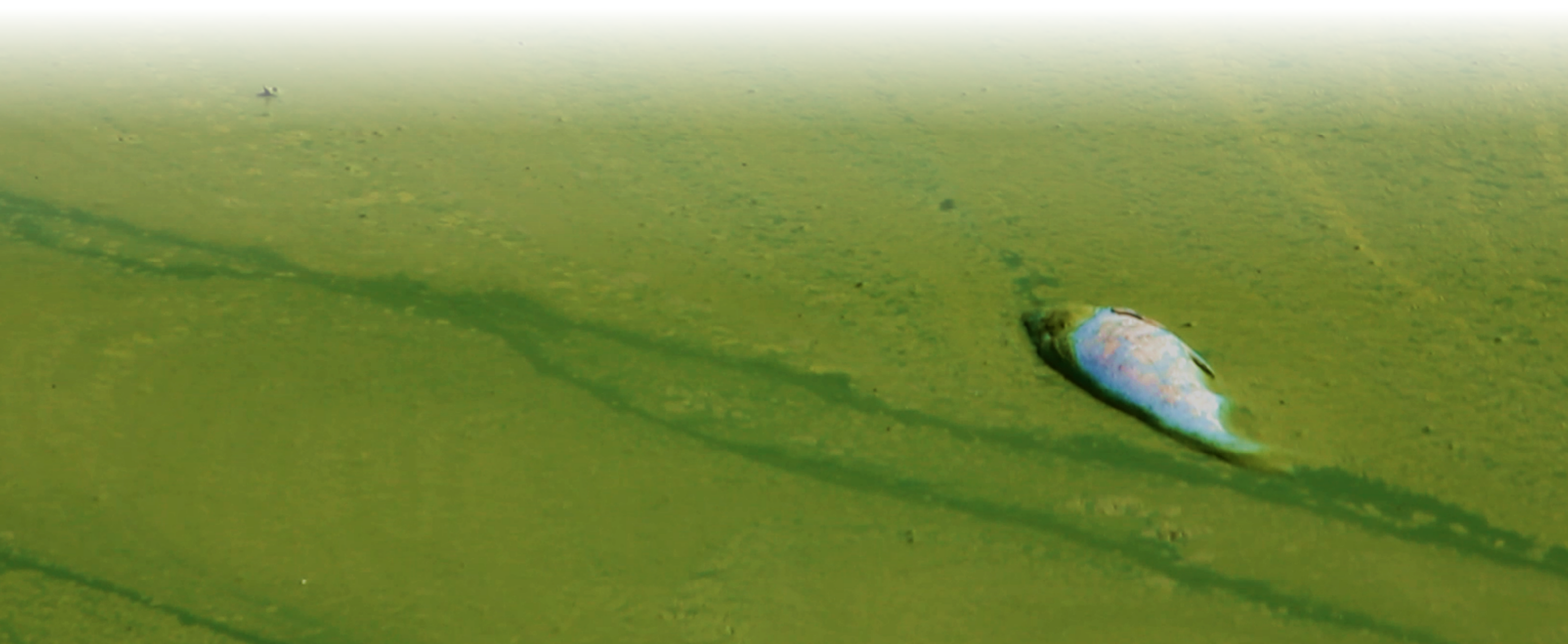
Chapter 5

How to model algal blooms in any lake on earth?

Annette B.G. Janssen, Jasmijn Rost, Arthur H.W. Beusen, Wolf M. Mooij, Jan H. Janse.



Abstract

On a geologically recent time scale, human impact marks a new epoch: the Anthropocene. Prognoses for the Anthropocene suggest many upcoming changes in the global environment. To anticipate these global changes, projections of future developments are crucial. Based on socio-economic scenario runs, mathematical models could project these possible future global developments. In this respect, developing models for future projections of freshwater ecosystems is particularly urgent because of their importance to humanity. Such model could hindcast how algal blooms in freshwater lakes have globally changed and forecast algal blooms for different socio-economic scenarios. The resulting projections will help to guide mitigation and adaptation to ecological changes that are ahead of us. Here we first define the requirements for the ideal global model to evaluate socio-economic scenarios for global freshwater lake water quality. Subsequently, we show how we can work towards a global model using existing components. Such a model should at least be composed of (i) an aquatic ecosystem component with global applicability (ii) a transport component that connects the lakes within the global network, and (iii) an environmental component that accounts for major anthropogenic impacts on a global scale. As a first step towards such a model, we selected the existing aquatic ecosystem model PCLake as the aquatic ecosystem component, with the global water flow model PCR-GLOBWB and the nutrient flow model GNM as transport components and the integrated model to assess the global environment IMAGE as the environmental component. We conclude that with these components as building blocks we can start to hindcast and make future projections of algal blooms in lakes. Major challenges for future applications are improving the formulations for deep lakes, adding small lakes to the simulation set, expanding the dataset of water quality variables, continuing of the multidisciplinary working approach and including the carbon cycle.

Introduction

On a geologically infinitesimal moment of time, human activities have become a major factor governing the earth's environment (Crutzen, 2002; Rockström et al., 2009a; Rockström et al., 2009b). Human activities have caused considerable changes in the climate, land use and biodiversity (MEA, 2005; Rockström et al., 2009a; Rockström et al., 2009b). This geologically recent rise of human impact marks a new epoch: the Anthropocene (Crutzen, 2002). As a consequence of human impacts, the resilience of natural systems is decreasing and on top of that more extremes in, for instance, weather conditions, disease outbreaks and algal blooms may be expected (Paerl et al., 2008; Scheffer et al., 2009).

To anticipate these global changes, projections of future developments are crucial. Projections will help to guide mitigation of, and adaptation to ecological changes that are ahead of us (Purves et al., 2013). Mathematical models are able to make these projections for possible future global developments based on socio-economic scenario runs. For instance, well-developed climate models for best and worst case socio-economic scenarios show the projections for future climate change (e.g. IPCC, 2014). Additionally, projections from the millennium ecosystem assessment (MEA) indicate possible global ecosystem loss for the coming half century (MEA, 2005). Finally, ample models exist that project pollution flows from land to sea (Kroeze et al., 2016). Projections through all these kind of models have put the potential impacts of global change at the top of many political, societal and economic agendas. For this reason we conceive that such models will play a prominent role in the future.

The development of mathematical models for future projections is particularly urgent for aquatic ecosystems because of their importance to humanity (Dudgeon et al., 2006). First, freshwater is one of the essential sources of life. Lakes are among the most important sources of drinking water and act as water buffers for irrigation (Shiklomanov, 1993; Jeppesen et al., 2015). Furthermore, lakes provide food for many people around the world (e.g. Li, 1999;

Welcomme et al., 2010; Downing et al., 2014; McIntyre et al., 2016). Finally, lakes are hotspots for recreation and tourism whose values are reduced when toxic algae dominate the water column (McIntyre et al., 2016). All these services provided by lakes are threatened by severe anthropogenic pressure. Water quality problems started with faecal and organic pollution in the 19th century and more recently eutrophication was added to the long list of water quality threats (Meybeck et al., 1989). As a result, harmful algal blooms are frequently occurring around the world (Glibert et al., 2005; Paerl et al., 2009; Janse et al., 2015).

For several reasons, it seems the right time for global modelling of lake ecosystems (Purves et al., 2013). Important discoveries that mark the century of biology help to unravel the molecular laws in biology and open new ways of assessing biodiversity (Venter et al., 2004; Dwyer, 2008). The increasing willingness to share information extricates data that were previously locked within organizations and therefore were unavailable to global assessment studies (Janssen et al., 2015). Moreover, remote sensing makes new data available at a global scale (Teixeira et al., 2015). Last, important breakthroughs in computational power and modelling techniques fill the observation gaps that emerged because observing water quality variables and quantifying nutrient loads of millions of lakes is practically infeasible (Mooij et al., 2014; Read et al., 2014; Janssen et al., 2015).

In this chapter, we propose a globally applicable freshwater lake ecosystem model to evaluate the impact of socio-economic scenarios of anthropogenic stress on water quality. We envision a model that could answer the question (i) how algal blooms in freshwater lakes have globally intensified over the past century and for what reasons, and (ii) how algal blooms could possibly develop in freshwater lakes in the future under various socio-economic scenarios. First we explore the requirements of an ideal global model for freshwater lake ecosystems. Thereafter we propose suitable components of a global model for freshwater lake ecosystems based on existing models and present a way to couple these components. Then, we discuss the challenges and opportunities to further improve our proposed global model for freshwater lake ecosystems towards our vision on the ideal model. We end with a list of recommendations.

Requirements of an optimal global model for freshwater lake ecosystems

The envisioned model for freshwater lake ecosystems should have global applicability and is able to (i) hindcast the development of historical algal blooms in freshwater lakes and (ii) project future algal blooms based on socio-economic scenarios. The interest in global algal blooms arises from their threat to lake ecosystem services such as the provisioning of drinking and irrigation water, fish and the opportunities for recreation (Finlayson et al., 2005). In order to indicate the severity of algal blooms, chlorophyll-a is often used as proxy. The optimal global model for freshwater lake ecosystems is able to produce algal bloom output for nearly all freshwater lakes on earth. We restrict ourselves to freshwater lakes defined as water bodies of variable size with standing or slow-moving water with a low salt content. In our definition, reservoirs and ponds are included.

Estimations suggest that earth counts over 117 million lakes with a surface area larger than 2000 m^2 (of which 0.3 million larger than 1 km^2) (Verpoorter et al., 2014). These lakes show a great diversity of site-specific characteristics (Messager et al., 2016). To understand algal blooms in lakes around the world, it is important to couple these site-specific lake characteristics with broad-scale environmental drivers and processes (Read et al., 2014). Additionally, lakes are part of a global transport network in which water and nutrients flow from mountains to oceans, often passing human settlements. Rivers, groundwater and aerial influences such as rain and wind connect the lake with the network (Beusen et al., 2016). Due to their connection with a network, lakes are affected by environmental drivers that not necessarily have their origin near the lake. An ideal global model for freshwater lake ecosystems would, therefore, comprise such networks that link environmental drivers of change with the specific characteristics of lakes. An optimal global model for freshwater lake ecosystems should thus consist of (i) a generic aquatic ecosystem component, (ii) a transport component which connects the lakes with the network, and (iii) an environmental component that accounts for major anthropogenic and natural impacts (Figure 5.1).

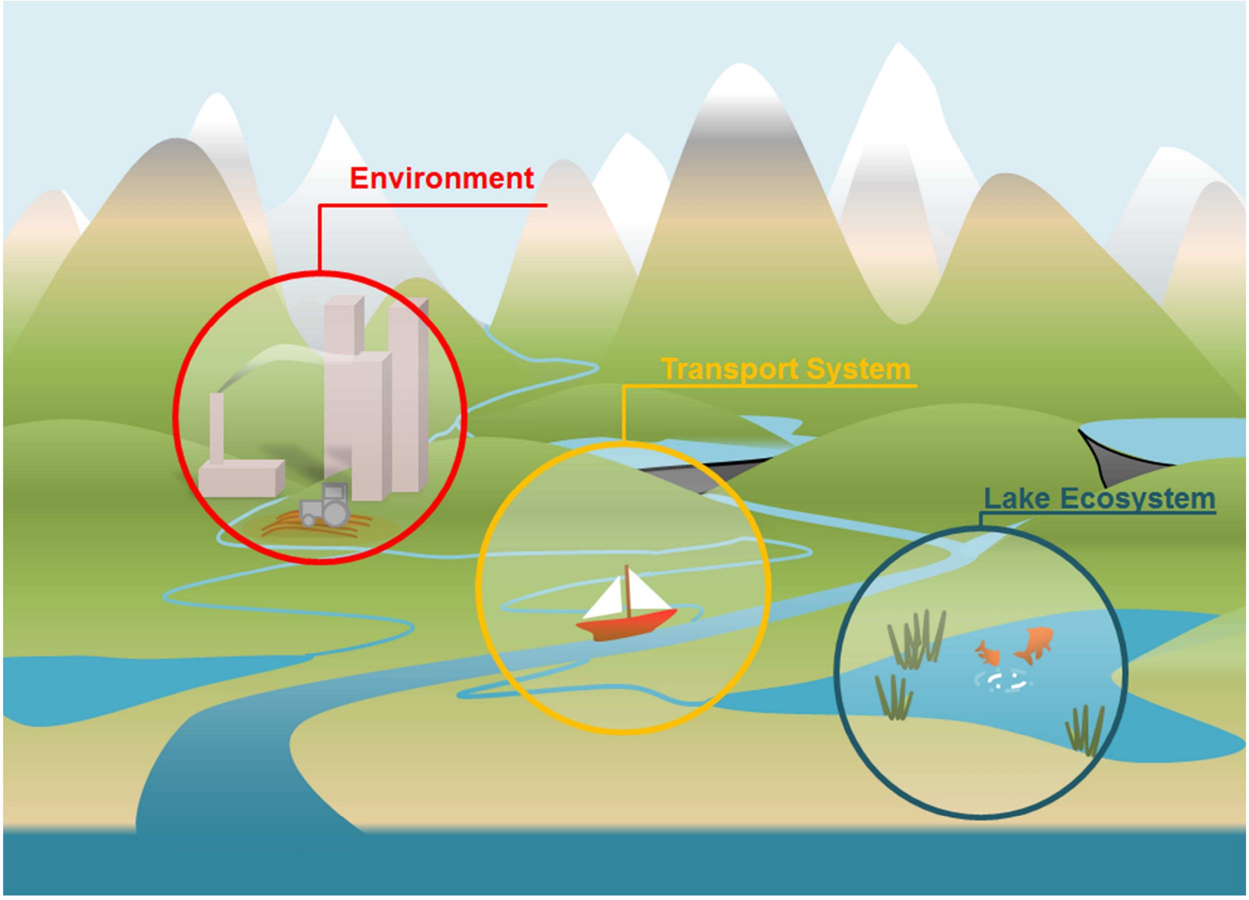


Figure 5.1. Three components of an ideal global model for freshwater lake ecosystems: (i) a well-described aquatic ecosystem component, (ii) a transport component which connects the lakes within the network, and (iii) an environmental component that accounts for major anthropogenic and natural impacts.

Aquatic ecosystem component

The aquatic ecosystem component should be able to translate local lake characteristics to local lake responses, using generic biological, physical and chemical process descriptions. In this way the full variety of freshwater lakes existing on earth could be simulated. Examples of local characteristics are the climate, lake depth, lake surface area, sediment type and spatial heterogeneity (see Box 5.1 and Figure 5.2). Other local characteristics are the water and nutrient input. Quantification of the water and nutrient input should be estimated by the transport component whereas the other local lake characteristics can be obtained from global maps, global databases and satellite images. The generic process descriptions should account for the most important feedbacks in aquatic ecosystems that determine algal blooms in lakes, such as grazing and competition. Simulation of an aquatic food web is thus desirable. The output of the aquatic ecosystem component could be used as proxy for the severity of algal blooms.

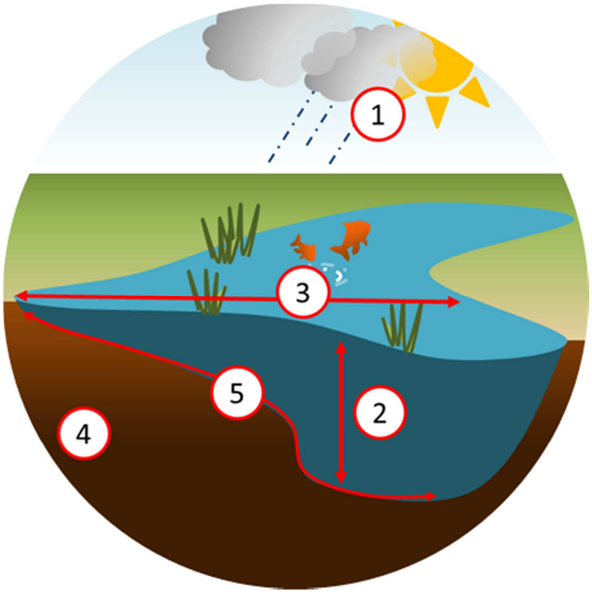


Figure 5.2. Local lake characteristics determining local lake responses: 1) climate, 2) depth, 3) lake shape, 4) sediment type and 5) spatial heterogeneity.

Box 5.1. The effect of local lake characteristics on lake processes.

Local lake characteristics are important to lake responses. Examples of local characteristics are the 1) local climate, 2) lake depth, 3) lake shape, 4) sediment type and 5) spatial heterogeneity (Figure 5.2). The optimal aquatic ecosystem component should be able to capture these local lake characteristics.

(1) The local climate is an important factor that determines lake processes. Light, temperature, wind, precipitation and evaporation are among the main factors that determine the local climate. The seasonal pattern differs from poles to the equator. At the poles, light determines the season whereas at the equator light is more or less equally distributed over the year, and precipitation pattern dictates the season. Climate determines the length of the growing season of the lakes' biota. Near the equator species grow and reproduce all year round, while in temperate regions growth and reproduction are bounded by seasonal pattern (Jeppesen et al., 2010; Kosten et al., 2012). This difference is particularly important for the growth of primary producers such as phytoplankton and macrophytes. For instance, cyanobacterial abundance increases vastly with higher temperatures at the expense of other phytoplankton species (Kosten et al., 2012). The tropical climate also selects for large floating macrophytes (Scheffer et al., 2003b). Finally, the difference in seasonality affects the top-down control of piscivorous fish to planktivorous and benthivorous fish which is lower in higher temperatures (Scheffer et al., 2003b; Kosten et al., 2012). As a result, in tropical regions there are more small-sized omnivorous and herbivorous fish, which suppress zooplankton abundance at lower latitudes (Jeppesen et al., 2010).

(2) Second, the ideal aquatic ecosystem component should be applicable to both shallow and deep lakes. Shallow lakes are considered well-mixed throughout the water column (Scheffer, 2004). Macrophytes are often an important determinant of the dynamics in shallow lakes (Scheffer et al., 2007). In contrast to shallow lakes, deep lakes stratify seasonally or all year round. In case of stratification, mixing of water and substances between the surface water

(epilimnion) and the deep layer (hypolimnion) is hampered (Håkanson et al., 2003). As a result, primary production processes are decoupled from decomposition processes leading to nutrient depletion in the epilimnion and deoxygenation in the hypolimnion (Woolway et al., 2014). Stratification depends on factors including water temperature, lake morphometry, wind speed and water clarity (Woolway et al., 2014). The critical depth (sometimes referred to as mixing depth) marks the border between the epilimnion and the hypolimnion.

(3) Third, lake shape is an important local character of a lake (Janssen et al., 2014). The shape of the lake can be measured in different parameters. First, lakes differ in perimeter. The perimeter is among the factors determining the potential surface area suitable for macrophytes growth (Janssen et al., 2014). Additionally, the distinction can be made between small or large lakes. Larger lakes experience stronger wind forces resulting in a higher resuspension than seen in small lakes of the same depth (Evans, 1994). To express the effect of wind, usually 'fetch' is used. Fetch is the distance along which wind blows over a lake surface.

(4) Fourth, sediment type is an important characteristic of lakes (Scheffer et al., 1993). The sediment type is, among others, important for the concentration of resuspended material in the lake water and thereby influences the underwater light climate of lakes (Søndergaard et al., 2003). In case of high concentration of resuspended material, there will be little light left for primary producers such as phytoplankton and macrophytes (Scheffer et al., 1993). Additionally, the type of sediment determines the soil chemistry thereby influencing the binding capacity of e.g. phosphorus by the lacustrine sediments (Søndergaard et al., 2003).

(5) Finally, heterogeneity is a local character which makes lakes unique (Janssen et al., 2014). Due to heterogeneity in morphometry, bathymetry, sediment type or wind forces, parts of a lake may develop in a different way. As a result, some parts of a lake might become turbid while other parts keep clear, as is for example the case in Lake Taihu (Janssen et al., 2014).

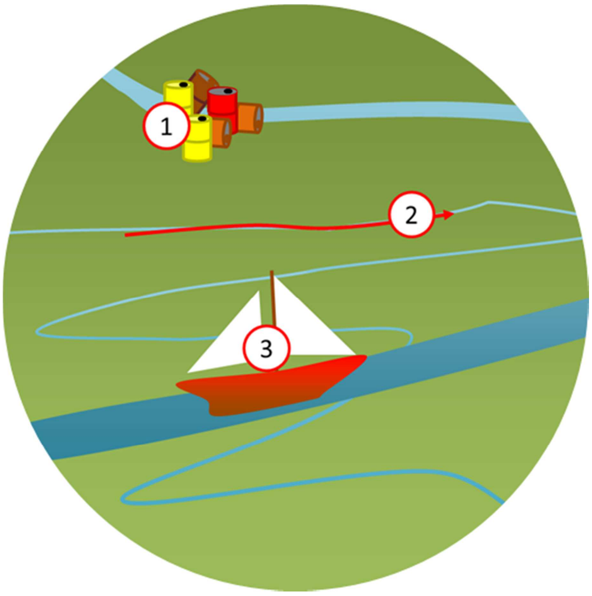


Figure 5.3. Important factors for the transport component: 1) the type of substances (e.g. nitrogen, phosphorus or carbon) transported, 2) the roadmap of the network and 3) the amount of water and substances transported by the network.

Transport component

The transport component should be able to estimate both the water and nutrient fluxes to lakes. The input of water determines the residence time of lakes. A high residence time allows biological processes to drive the lake ecosystem dynamics, a low residence time serves hydrodynamic processes to flush the lake together with the solubles and suspended biotic and abiotic materials (Baranyi et al., 2002; Janssen et al., 2014). The input of nutrients forms an important food source for all organisms living in the lake but also determines the lake ecosystem's state. Whereas with low nutrient input lakes appear often in a clear water state, with high nutrient input lakes often turn turbid and show algal blooms (e.g. Scheffer et al., 2003a). In order to estimate water and nutrient fluxes, there are three major requirements (Figure 5.3). The first requirement is the determination of the type of substances that should be included. Phosphorus and nitrogen are generally seen as the most important nutrients for algal growth. Additionally, micronutrients determine the growth potential of algae. For instance, silica is important to the growth of especially the algal group of diatoms.

The second requirement is a schematization, a definition of the network of water and nutrient pathways connected to lakes, comparable to a map of available roads to enter a city. The network should account for water and nutrient pathways via rivers, groundwater and air. The last requirement is the quantitative estimation of water and nutrient fluxes via each pathway of the transport component.

Environmental component

The environmental component should optimally be able to qualify and quantify the various nutrient emissions by the coupled human and natural system. In the human system nutrient emissions are driven by anthropogenic activities such as industrial production of goods, fertilizer use in agriculture and the generation of energy for instance by combustion of fossil fuels (Gruber et al., 2008; O'Neill et al., 2015). These anthropogenic activities are affected by the local population, economy, policies, technology, lifestyle and resources (O'Neill et al., 2015). In the natural system, nutrient emissions are connected to biogeochemical nutrient cycles that include conversion processes (e.g. denitrification), mineralization processes (e.g. organic matter decomposition), fixation processes (e.g. N_2-fixation) and release processes (e.g. weathering) (Gruber et al., 2008). Nutrients emitted by both the human and natural systems depend on climate (Gruber et al., 2008). As climate in turn is affected by carbon emissions due to human activities (energy generation, agriculture) (IPCC, 2014), these links should be included in the model framework. Finally, the environmental component should quantify the emitted nutrients to each pathway (e.g. ground, river or air) of the transport network (Figure 5.4).

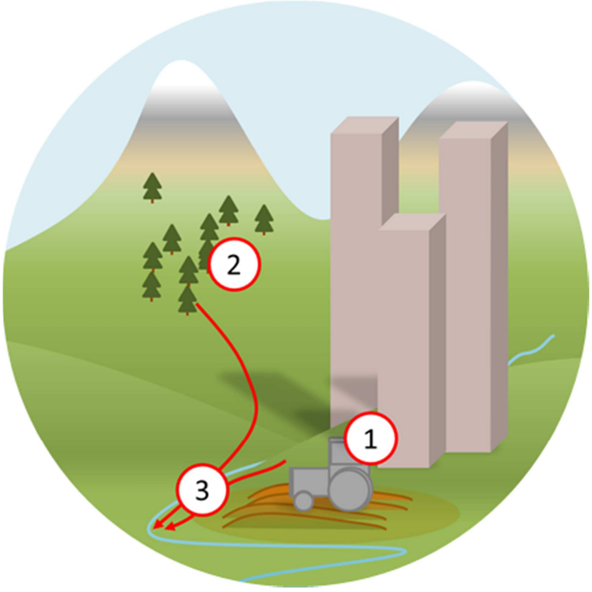


Figure 5.4. Factors important for the environmental component: 1) nutrient emissions due to human activities, 2) nutrient emissions from the natural system and 3) amount of substances released to the transport network.

Coupling of the three components

An ideal global model for freshwater lake ecosystems will connect the environmental system via the transport network to the lakes. Additionally, there should be feedback from lakes to the transport network and even to the environmental system. Indeed, lakes affect the concentrations of substances within the network by nutrient retention and carbon sequestration, and have impact on the local economy (Harrison et al., 2009; Tranvik et al., 2009; Downing et al., 2014). The optimal global model for freshwater lake ecosystems will account for all these relationships and feedbacks.

Model input

The proposed global model for freshwater lake ecosystems will be used for hindcasting to validate the simulation outputs against data and for future projections on algal bloom formation to anticipate global changes under different socio-economic scenarios. For both steps, specific input is needed. For hindcasting, historical information on human activities, biogeochemical cycles, climate patterns and network structure is required. Ideally, the hindcasting simulations will run from the pre-industrial period, when lake ecosystems are presumed to be in their pristine, little-disturbed state, until the present state with high human impact. Hence, we aim to cover the full time frame of ecological development from low to high impact. For future projections, the input to the model should be based on different socio-economic scenarios with expectations for climate change, land use change and changes in the network (for example including new reservoirs or the construction canals). The contemplated future projections will run simulations until 2100, in line with previous projections by e.g. the IPCC.

Validation methods

The hindcasting step is used for validation. In this step, model output can be correlated to historical measurement data. In this validation process, measurement data are a prerequisite. Data are often scattered over many datasets. Merging these various datasets not only helps to increase data available to the validation process, but also increases the quality of data (see examples in Box 5.2). With a merged database at hand, we suggest to first validate the boundary conditions of the aquatic ecosystem component, as produced by the transport component. This step should prevent the accumulation of errors further down in the calculation process. Boundary conditions of the aquatic ecosystem component are the lake water temperature, the light climate and inflow of water and nutrients. Next to the boundary conditions, also the output of the aquatic ecosystem component should be validated. Most common variables to validate are phosphorus (TP, PO_4), nitrogen (TN, NH_4, NO_3) and chlorophyll-a. Data on other variables such as macrophyte abundance, zooplankton biomass and fish are desirable but often unavailable at a global scale. Multiple statistical methods exist to validate models (Sargent, 2013). With our simulation goal in mind, we aim for a statistical test that is able to test the historical trend in algal bloom development as well as the severity of the algal blooms.

Box 5.2. Database quality improvements.

Merging datasets helps to improve the quality of the data. For example inconsistencies such as differences in lake surface areas for the same lake appear when merging datasets. In addition, errors in e.g. units have a higher chance to be detected because they appear as outliers.

In addition, there are more options to increase the quality of datasets, which are based on 'ecological laws'. Since lakes are in most cases retaining nutrients (Harrison et al., 2009), it is expected that the inflowing concentration of nutrients is larger than the concentration within lakes ($C_{in}>C_{lake}$). The opposite case ($C_{in}<C_{lake}$) is less common unless in case of a recent load reduction, and could point at an error in the data. Such an error may result from missing an important input of nutrients to the lake or a unit error in either the lake concentration or the lake input. Merging a nutrient load dataset with a nutrient concentration dataset, thus helps to improve the database quality.

According to another 'ecological law', the total nitrogen concentration is usually considerably larger than the total phosphorus concentration in both the lake water as well as inflowing water. The opposite is possible, however, less common. Therefore, in case the phosphorus concentration exceeds the nitrogen concentration it is wise to check the data for errors.

Last, merging datasets has the risk of duplicating measurements in the combined dataset in case a measurement is reported in two different databases. A check on duplicates is thus wise before using the merged dataset.

But even after this quality control, merged datasets include data with a different level of quality. Some datasets are well-annotated and mention, beside the measured value, time and location also the method, detection limits, number of samples and origin of the measurement. Other datasets are rather limited, e.g. due to a small number of samples, inaccurate methods or incomplete reporting of metadata. We therefore think it is important to categorize the data based on the quality while merging datasets.

Proposed global model for freshwater lake ecosystems

Now that we have defined key-components of an ideal global model for freshwater lake ecosystems, the next step is to find model components based on existing models, so as to avoid 'reinventing the wheel' (Mooij et al., 2010). As model components we propose an aquatic ecosystem model based on PCLake (Janse et al., 2008). For the transport component we propose to use PCR-GLOBWB (Van Beek et al., 2011) to model the global water flow and GNM (Beusen et al., 2015; Beusen et al., 2016) to model the global nutrient flow. The global environmental assessment model IMAGE (Stehfest et al., 2014) will simulate environmental change (Figure 5.5). IMAGE will thus provide information to PCR-GLOBWB and GNM and, in turn, PCR-GLOBWB and GNM will provide input to PCLake. Furthermore, there is a possible feedback of outflowing nutrients from PCLake into the transport component existing of PCR-GLOBWB and GNM. Below we will explain each specific component with special focus on the aquatic ecosystem component. The other components are adopted without adjustments and are well-described in literature (Van Beek et al., 2011; Stehfest et al., 2014; Beusen et al., 2015; Beusen et al., 2016). For more details on these components we thus refer to detailed descriptions in literature.

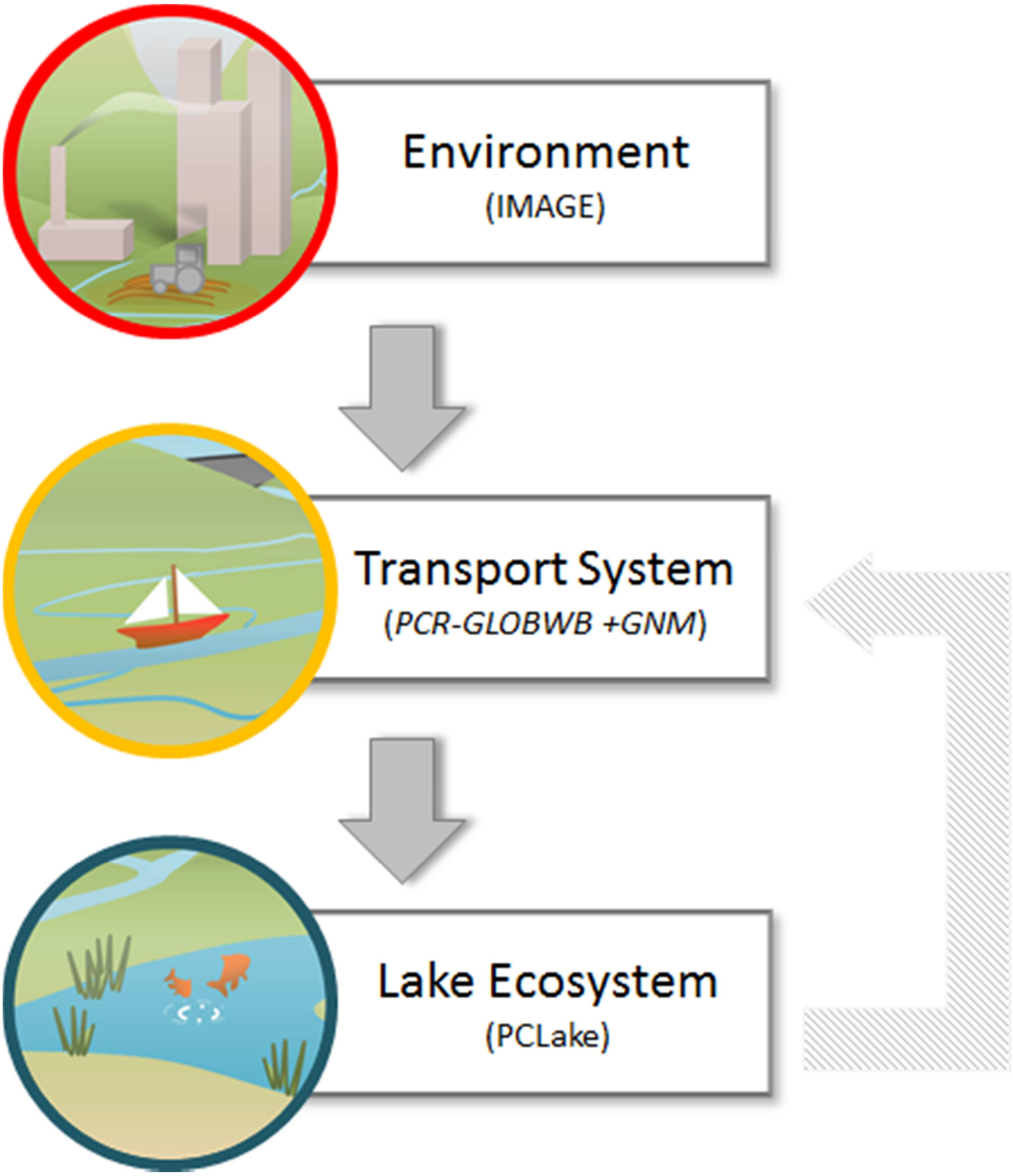


Figure 5.5. Schematic overview of component coupling for the global model for freshwater lake ecosystems. Between brackets the name of each model component is given.

Proposed aquatic ecosystem component

As aquatic ecosystem component we propose to use an adjusted version of the aquatic food web model PCLake. The model is able to predict algal biomass with a minimal set of equations while including the most important interactions. This setup keeps the runtime relatively low while producing adequate output.

The original version of PCLake is calibrated based on 43 lakes in Western Europe (Janse et al., 2010), however, there are many successful applications for different locations around the world (e.g. Fragoso et al., 2011; Janssen et al., 2014; Nielsen et al., 2014; Mellios et al., 2015; Kong et al., 2016; Rolighed et al., 2016) and also theoretical applications showing its potential to model climate change effects (Mooij et al., 2007). PCLake simulates an aquatic food web consisting of algae (three types), macrophytes, zooplankton and planktivorous, benthivorous and predatory fish and keeps track of the stoichiometry of all functional groups in dry weight, nitrogen and phosphorus (Figure 5.6). Additionally, PCLake covers geochemical dynamics in the sediment based on the sediment type and a benthic food web. The full set of state variables, parameters, equations of the original PCLake can be found in the DATM-file of the model (Appendix 8). Since PCLake was originally developed for shallow lake ecosystems, the model requires adjustments to capture both shallow and deep lakes in one set of equations. Our proposed version of PCLake therefore includes the possibility for stratification (see Box 5.3). We plan to run PCLake for all lakes and reservoirs for which output is provided by the transport system. At present, a selection of large lakes (≥500 km^2) from the GLWD-1 database is incorporated in the routing scheme. This selection was replenished with smaller lakes, taken from the GLWD-3 database, to provide evaporative surfaces in arid basins. Reservoirs are only included in the transport system if their collective volume within a grid cell is larger than the collective volume of rivers within the same grid cell. Information on the reservoirs comes from the GRanD database. The total selection of reservoirs and lakes in the routing scheme accounts for 80% of the global lake area, with a focus on mainly large lakes. The local lake characteristics are obtained from, or calculated as indicated in Table 5.1.

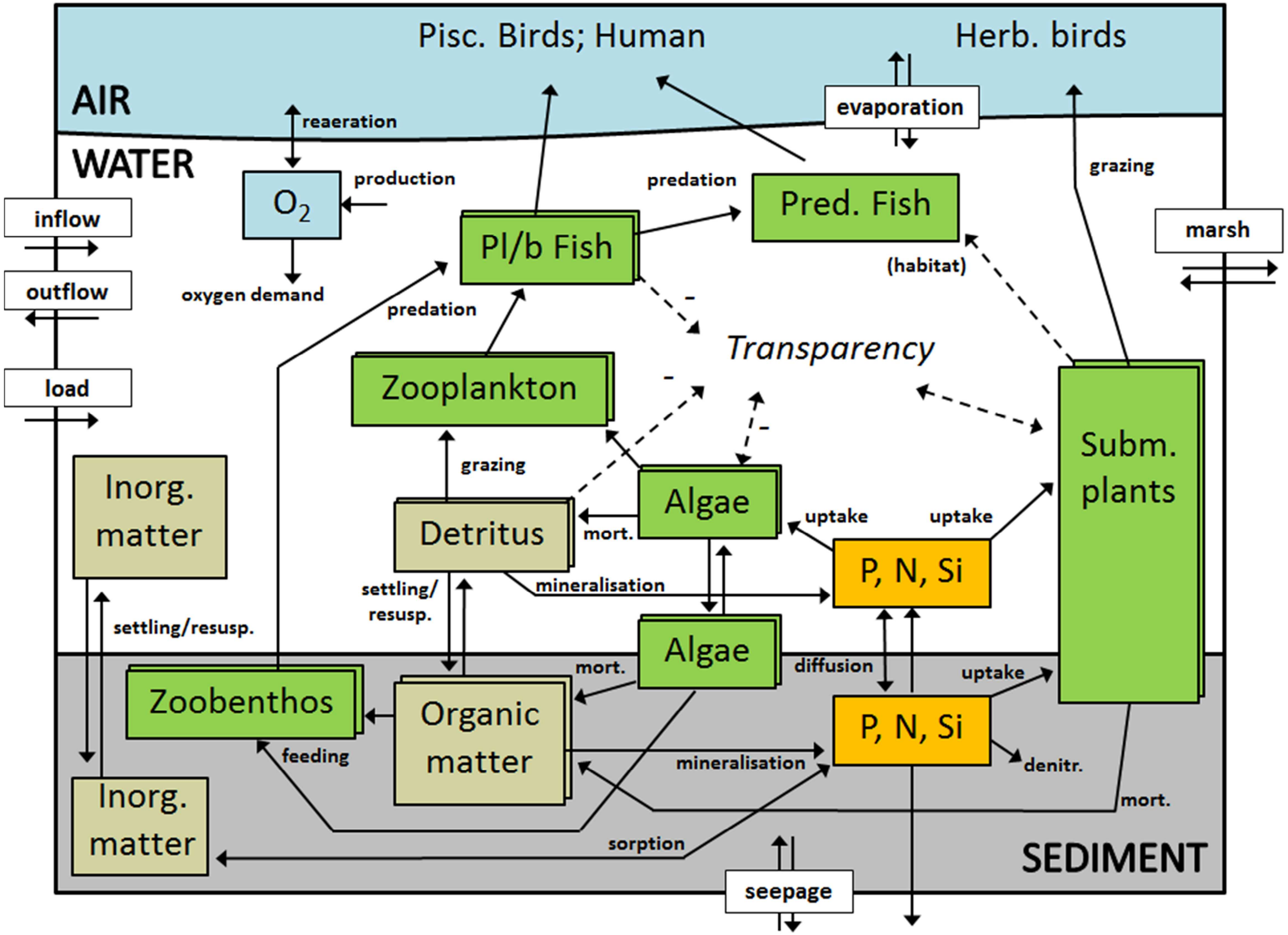


Figure 5.6. Schematic overview of the original version of PCLake. Modified after Janse (2005).

Table 5.1. Input for PCLake.

Lake Characteristics	Source or calculation method
Lake Area	Data on surface area originates from the GRanD database for reservoirs (Lehner et al., 2011) and the GLWD database for lakes (Lehner et al., 2004).
Lake Depth	Average lake depth from Flake (Kourzeneva, 2010; Kourzeneva et al., 2012; Choulga et al., 2014) or calculated in case of missing or inaccurate data with an empirical relationship based on a lake surface area and volume relationship. We assume water depth to be constant over the years.
Water input	Calculated by transport component as total discharge per time.
Nutrient load (TN and TP)	Calculated by transport component as total nitrogen (TN) and total phosphorus input (TP) to the lake. PCLake accounts for the speciation processes to estimate the input of the different kind of nutrients (e.g. PO_4, NO_3 or NH_4). As for the input of silica (Si), PCLake uses a default estimate if this input is not provided b y the transport system.
Water temperature	Calculated by transport component as surface water temperature.
Fetch	Calculated based on shapefiles from GLWD-1 and GLWD-2 (Lehner et al., 2004) and methods presented in Janssen et al. (2014). See also Appendix 2
Light input	Meteorological equation (Stull, 2000) based on the latitudinal position of the lake, the solar angle at the location and the transmissivity of the atmosphere (Appendix 9).
Evaporation	Estimated based on Thornthwaite equation (Thornthwaite, 1948) using the surface water temperature (Appendix 10)

Box 5.3. Adjustments for PCLake

PCLake was originally developed for shallow lake ecosystems. To adequately simulate deep lakes, the model needs some adjustments. Our proposed new version of PCLake includes a rule to decide on using the existing version for shallow lakes or an adjusted version for deep lakes. The decision is based on the critical depth. The critical depth of a specific lake is empirically estimated with Equation 5.1 (Hanna, 1990).

$$C_{depth} = a * F^b \qquad \text{Equation 5.1.}$$

with a=0.569 and b=0.336, and F the fetch (m) measured as maximum effective length (MEL), which is defined as the maximum length along which wind can blow over the lake surface in the dominant wind direction. According to Hanna (1990), this formulation is applicable to many lakes with a broad range of sizes, shapes and geographical location.

With Equation 5.1 at hand, we next use the first decision rule as defined below:

Option 1 (Grey zone in Figure 5.7) :

If (mixing depth >= depth of lake) → lake is unlikely to stratify, use original PCLake for shallow lake as shown in Figure 5.6.

Option 2 (White zone in Figure 5.7):

If (mixing depth < depth of lake) → lake is likely to stratify, use adjusted PCLake for deep lakes as shown in Figure 5.8.

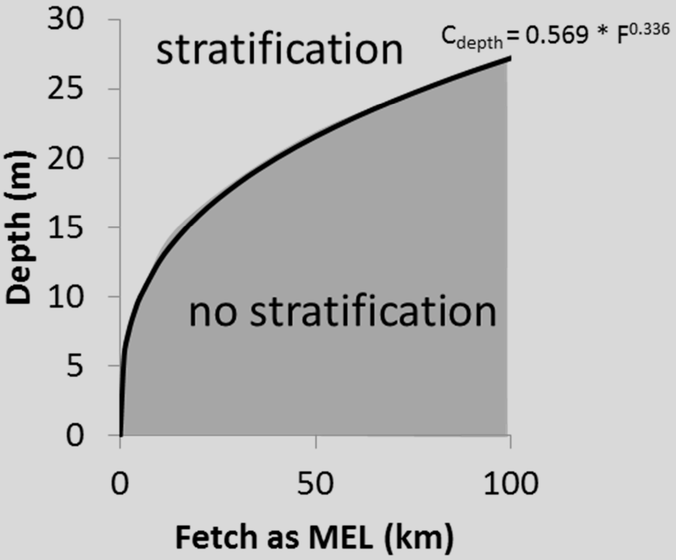


Figure 5.7. Empirical relation to determine the critical depth (black line) for stratification. Lakes with a depth in the grey zone will most likely lack stratification; lakes in the white zone have the possibility to stratify.

The adjusted version of PCLake distinguishes between the epilimnion and hypolimnion (Figure 5.8). Both the epilimnion and hypolimnion have their own state variables for nutrients, oxygen, three groups of algae, detritus, inorganic matter and zooplankton. The planktivorous fish, benthivorous fish, predatory fish and macrophytes are physically not restricted by the mixing depth and are each captured in a single state variable that counts for biomasses in the entire water column. The river inflow and outflow of water is connected to the epilimnion as well as to the marsh zone. Infiltration and seepage is connected with the hypolimnion.

A second decision rule will be included that estimates the period of stratification. Ideally, such function will estimate the water density gradient over depth based on the thermal gradient, however, this approach is not feasible with the input information we have at hand. Therefore, we adopt an empirical rule from Ostë et al. (2010) assuming that stratification occurs in case the water temperature is <4 °C (winter stratification) or >10 °C (summer stratification):

Option 1

If [(surface water temperature < 4 °C) OR (surface water temperature > 10 °C)] → lake is stratified, no mixing between epilimnion and hypolimnion

Option 2

If [(surface water temperature >= 4 °C) AND (surface water temperature <= 10 °C)] → lake is not stratified, mixing between epilimnion and hypolimnion

So, in case of stratification, mixing between the epilimnion and hypolimnion is switched off. In case of absence of stratification a simple mixing formula similar to the exchange of water and substances between the marsh zone and the water column (Janse, 2005) will account for mixing between both water layers.

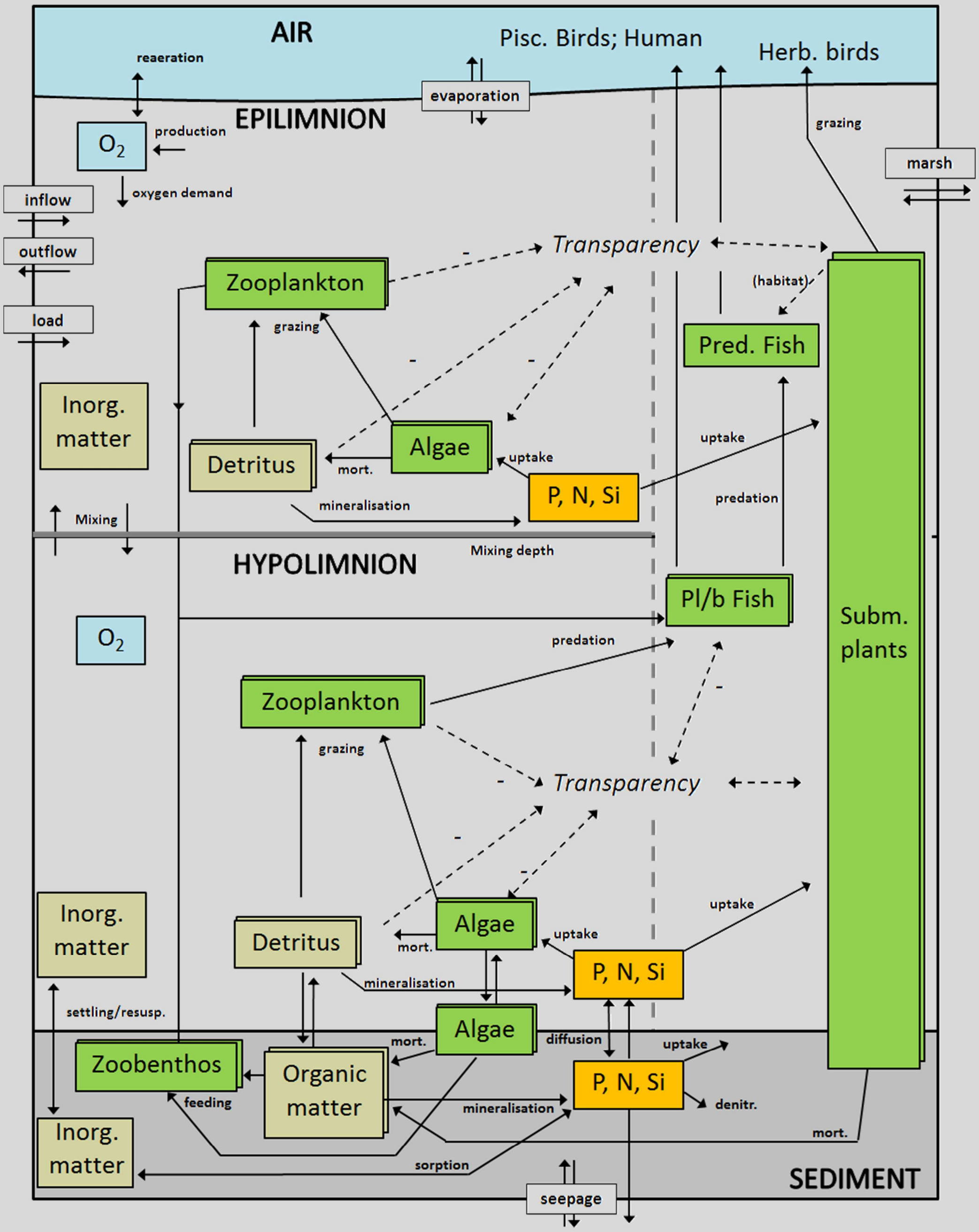


Figure 5.8. Schematic overview of the proposed version of PCLake for stratifying lakes. At the left side of the grey dotted line the state variables are shown that are connected to either the hypolimnion or the epilimnion. At the right side of the grey dotted line the state variables are shown that are physically not restricted by stratification and are thus each captured in a single state variable that count for biomasses in the entire water column.

Proposed transport component

We propose PCR-GLOBWB (PCRaster Global Water Balance) in combination with GNM (Global Nutrient Model) as models used for the transport component. Based on climate forcing such as precipitation and temperature, PCR-GLOBWB quantifies water storage in the soil column and canopy layer, and determines fluxes through direct flow and subsurface flow to a river network (Van Beek et al., 2011). The model simulates a water balance for a 30 arc-minutes global grid. GNM simulates total nutrient load to surface water based on soil nutrient budgets, emissions from point sources and direct atmospheric deposition (Beusen et al., 2015). For more information on PCR-GLOBWB please refer to Van Beek et al. (2011) or check the project website of PCR-GLOBWB: http://pcraster.geo.uu.nl/projects/applications/pcrglobwb/. For more information on GNM, see Beusen et al. (2015) and Beusen et al. (2016).

Proposed environmental component

As environmental component we propose IMAGE (Integrated Model to Assess the Global Environment). IMAGE includes the human system to simulate anthropogenic activities and an earth system simulating the impact of the natural environment (Stehfest et al., 2014). The human system is based on agricultural land use, energy supply and demand. The earth system is based on land use and climatological and oceanographic forcing. Together with the drivers (population, economy, policy, technology, lifestyle and resources) these two systems determine the nutrient input to the transport component (Beusen et al., 2015). For more information on IMAGE, see Stehfest et al. (2014), Beusen et al. (2015), Beusen et al. (2016), or check the project website: http://themasites.pbl.nl/models/image.

Coupling of proposed model

The proposed model components can be coupled both offline as well as online. In our specific case, offline coupling means that the transport component influences the lake dynamics, while the feedback of the aquatic ecosystem component back to the transport component is not incorporated. The advantage of offline coupling is the possibility to run the model in parallel with relatively short run times. In contrast, online coupling takes into account both the effect of the transport component to the lake dynamics as well as the opposite effect. This addition results in a more realistic model, however, due to the interdependent relationships, runtimes will be significantly longer. We propose to start with offline coupling to get a first glimpse of potential patterns in algal blooms around the world. As a future step we suggest online coupling for a more complete understanding.

Input for proposed model

We envision to run the coupled model both for hindcasting and for projections of future algal blooms. For hindcasting, input based on historical data on global climate, land use and the network structure will be used (Beusen et al., 2016). For future projections on algal blooms, we will follow the Shared Socio-economic Pathways (SSPs) approach (O'Neill et al., 2014) in combination with climate objectives that are described in the Representative Concentration Pathways (RCPs) (Van Vuuren et al., 2012). SSP is a scenario framework based on socio-economic challenges for mitigation and adaptation to a changing world (Figure 5.9). There are 5 SSPs for which narratives are proposed that include important elements such as development of demographics, economy, welfare and technology (O'Neill et al., 2015). RCPs describe possible future greenhouse gas trajectories. The 4 RCPs describe the increase of future radiative forcing in W.m^{-2} (Van Vuuren et al., 2012). We envision to run simulations based on the SSPs in combination with RCPs to make future projections of global freshwater lake ecosystem development.

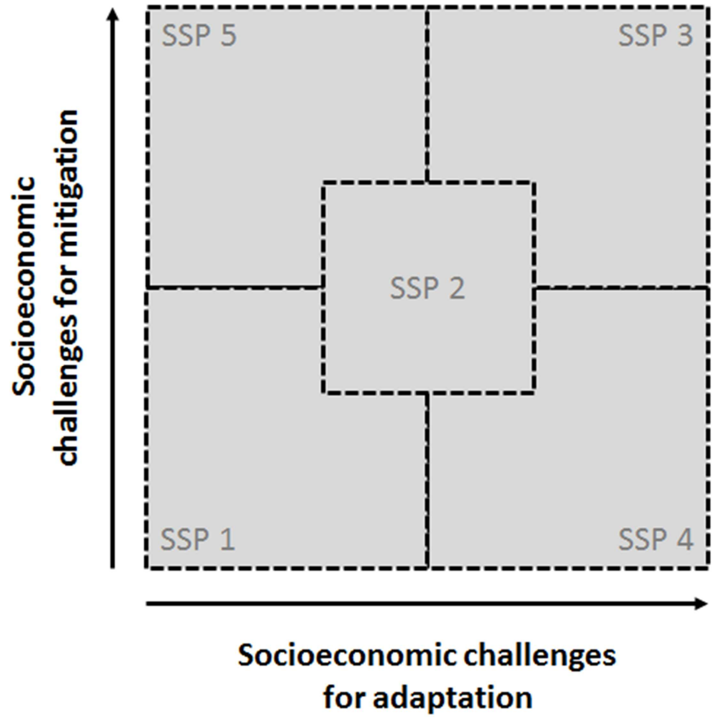


Figure 5.9. The scenario framework based on socio-economic challenges for mitigation and adaptation to a changing world. SSP 1: Low challenges, SSP 2: Intermediate challenges, SSP 3: High challenges, SSP 4: Adaptation challenges dominate, SSP 5: Mitigation challenges dominate (O'Neill et al., 2014).

Validation of proposed model

To validate the proposed global model for freshwater lake ecosystems, we have merged different databases (Figure 5.10), including GEMS, ILEC, Limnodata Neerlandica, Netherlands Eutrophication Survey, Waterbase EEA and several literature articles (see for more information on the metadata: Appendix 11). The USGS database has not yet been included. After merging the USGS database, the merged database will contain nearly 14000 unique lakes with qualitative data of at least one water quality variable of interest. These variable of interests include total nitrogen load (TN-load), total phosphorus load (TP-load) and water discharge to validate the transport component (PCR-GLOBWB and GNM) and lake concentrations of TN, TP and chlorophyll-a and lake water Secchi depth to validate the aquatic ecosystem component (the adjusted PCLake) (an overview of data points per state variable can be found in Appendix 11). We checked the consistency and plausibility of the entries in the merged database following the procedure described in Box 5.2. The data have a strong bias towards Europe and USA, possibly as result of open data policies in combination with sampling biases. For other continents data are likely to exist, but at this point are unavailable to us. Despite this limitation, the dataset covers the full variation in latitude, elevation, lake water depth, discharges and residence time seen on earth (Figure 5.10). The database is somewhat biased towards lakes with a larger volume and lake area. Expanding the merged dataset is an ongoing process as more data become available.

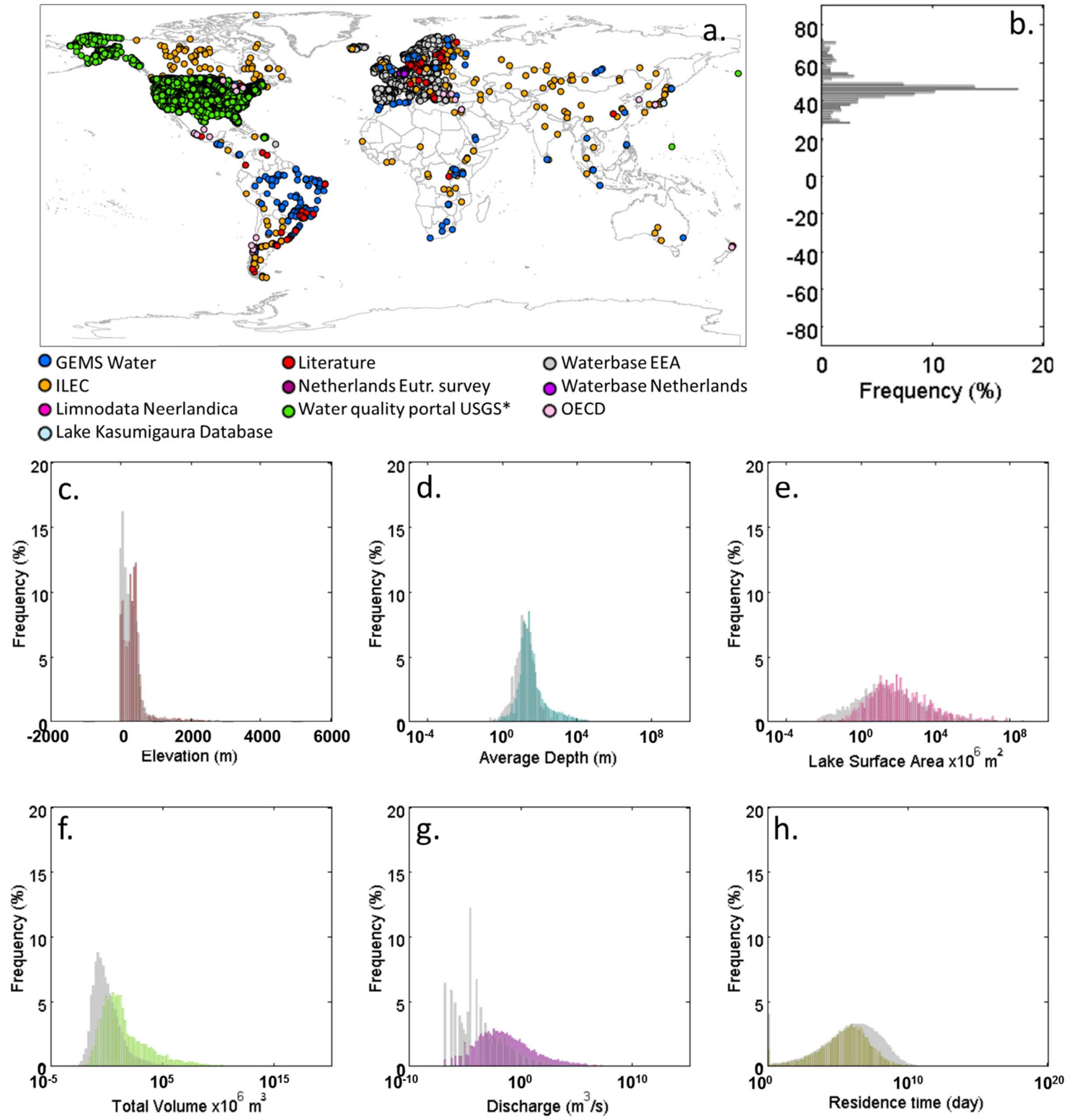


Figure 5.10. Summary of the lakes included in the merged database: a) overview of locations, b) latitudinal distribution, c) elevation, d) average depth of the lakes, e) lake surface area, f) lake volume, g) lake discharge (with an overestimation of lakes with low discharge, see for more information Messenger et al. (2017)) and h) lake residence time. Grey area shows the distribution of all lakes in hydroLAKES which we consider as a good representation of the world (Messager et al., 2016). Coloured area shows the distribution of our database. Database with * is not yet merged.

Preliminary Results

The original version of PCLake was run until equilibrium for a selection of 50 unique lakes for which nutrient load data (TN or TP) and discharge data were available in the database. Since for some lakes data were available for multiple years, the total number of runs was 2712. We assumed that the model reached equilibrium after 30 years. Observation data were compared with the last year model output. Results are promising for shallow lakes, however, as expected, deep lakes were not represented well by the model's formulations as shown by the significant lower slope for the best fit of the deep lakes subset (Figure 5.11). Especially the deep lakes Borup Sø (depth 17 m), Engelsholm Sø (depth 20 m) and Viborg Nørresø (depth 25 m) have low predicted chlorophyll-a (<10 μg.L^{-1}) compared to the observed chlorophyll-a concentration (20-165 μg.L^{-1}). The adjustment to PCLake for deep lakes has not yet been tested. Additionally, the shallow Lake Finjasjön (depth 3 m) shows relatively low predicted chlorophyll-a concentrations compared to observations, especially for data measured in the 1980s. This is due to phosphorus release from sediments due to anaerobic conditions in the lake (Annadotter et al., 1999). Therefore, algal growth increased even after phosphorus load had been reduced (Annadotter et al., 1999). This mismatch between model predictions and observations will probably diminish if the equilibrium runs will be replaced by runs that simulate continuously from preindustrial to present. The subset of shallow lakes without Lake Finjasjön approaches the 1:1-line.

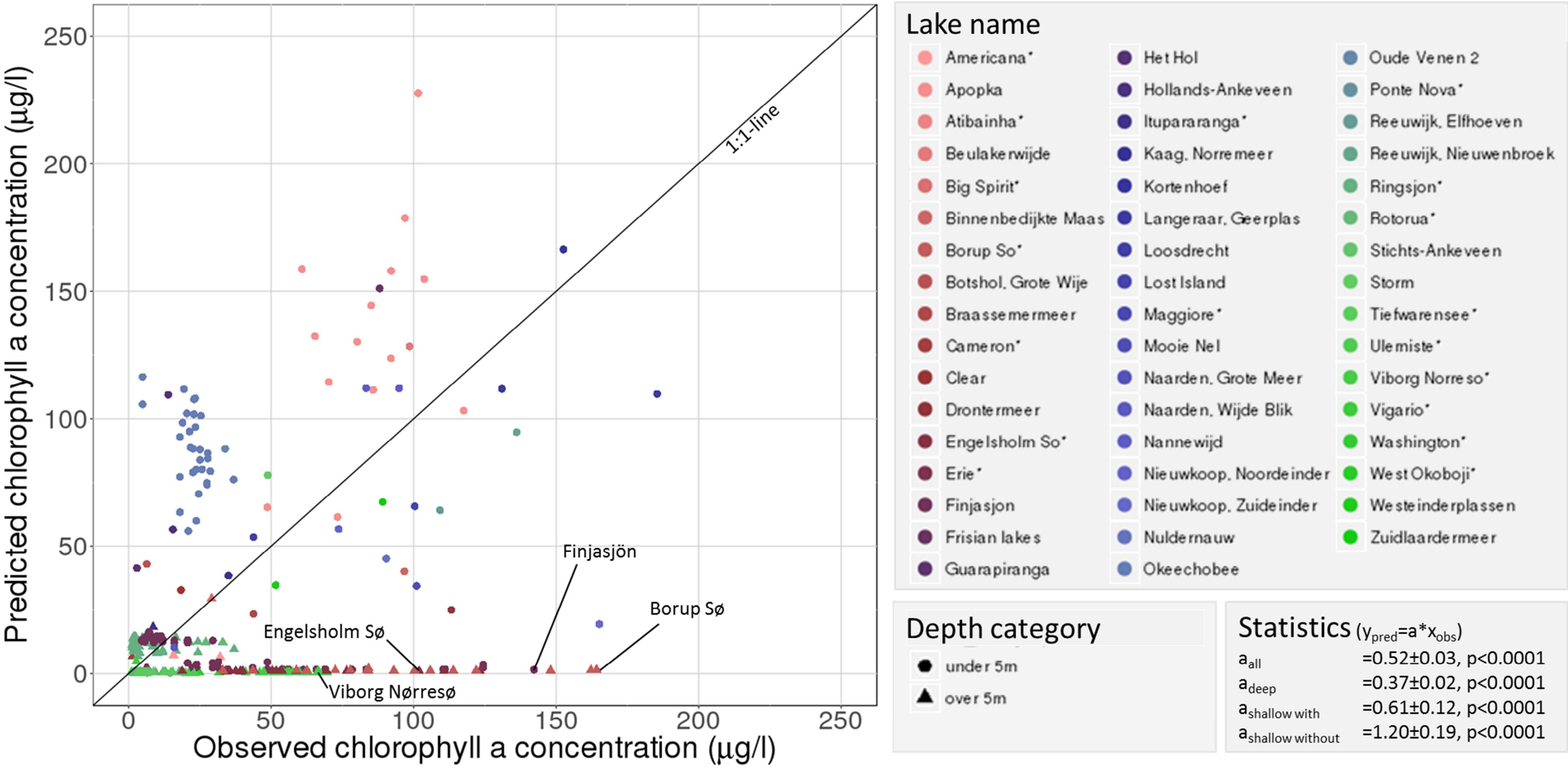


Figure 5.11. Preliminary results for simulations using the original version of PCLake in combination with loading data from the database for a selection of lakes. Results show chlorophyll-a based on the observations from the database (x-axis) and predicted by PCLake (y-axis). Different colours represent different lakes. Lakes with a depth equal to or shallower than 5 m are indicated with a circle in the graph. Lakes deeper than 5 m are indicated with triangles in the graph and a '*' in the legend. With regression analysis for a linear line (y=ax), the slope and its significance for the entire dataset (a_{all}), a subset of deep lakes (a_{deep}), a subset of shallow lakes ($a_{shallow}$) and a subset of shallow lakes without Finjasjön ($a_{shallow\ without}$) is defined (see statistics).

Discussion

Now that we proposed the model components, we will evaluate whether these model components approach our ideal model. Thereafter, we will discuss what we could learn from previous attempts to make projections of global environmental change due to human activities.

Ecosystem component

The ecosystem component should translate local lake characteristics (e.g. climates, depth, shape and sediment type) to local lake responses, using generic process descriptions. PCLake has already been applied for shallow lakes in a broad range of climates, lake sizes and sediment types. Mooij et al. (2007) have shown that the relative abundance of cyanobacteria increases and the zooplankton decreases if temperatures are higher, which is in line with recent findings (e.g. Kosten et al., 2012). With respect to lake depth, the original PCLake is well able to simulate shallow lakes, however, preliminary results showed that deep lakes were, as expected, not represented well by the model's formulations. We expect that including the process of stratification will improve the output for deep lakes using PCLake. In the implementation of stratification, there is a trade-off between model complexity and feasibility to run the model at global scale. Although the calculation of the critical depth is promising, the formulation of the period of stratification probably needs validation. To see if our implementation functions well, we first plan to validate the adjusted model using a deep lake dataset (i.e. lakes with mean depth larger than their critical depth), before applying it at a global scale.

Transport component

The use of PCR-GLOBWB in combination with GNM, enables estimation of the water and nutrient balances of mainly large lakes around the world. The calculation of the water and nutrient balances is currently limited to large lakes. Smaller lakes are not included since PCR-GLOBWB runs at a 30 arc-minutes global grid. Simulations for smaller lakes will therefore result in scaling errors. In the future we envision including smaller lakes in our projections as well, either by running the transport component at a finer grid or by translating the nutrient fluxes from the transport component into loadings to these smaller lakes by additional GIS-based estimates. Despite this limitation, the current set of lakes includes the majority of the total lake surface area as well as lake volume found on earth (Messager et al., 2016).

Environmental component

IMAGE has a focus on the two most important nutrients for eutrophication of lakes, nitrogen and phosphorus. Other substances are currently missing in this model (Kroeze et al., 2016). For instance, carbon inflow is currently not explicitly included in PCLake, although it would certainly be interesting to include its direct effect in our model setup. Additionally, silica concentrations are, in the current model version, estimated by a default function in PCLake. Estimations by the environmental component could replace this crude estimation and thereby improve the simulation of the diatoms, the algal group that depends most on this micronutrient. Finally, the refinement of the grid of IMAGE would be a requirement if we would choose to run the transport component at a finer grid in order to estimate loadings to smaller lakes.

What to learn from previous attempts to make projections?

For interpreting the output of our proposed global model for freshwater lake ecosystems, we can learn from previous attempts to make projections of global environmental change due to human activities. While a full overview of earlier attempts would be a review on its own, we here touch upon some common grounds.

First, we look for a few key parameters that represent the state of lakes in general. Yet, we also have to deal with spatial heterogeneity between as well as within lakes. This is a challenge that other developers of global projections face too. The IPCC, for instance, makes projections of future global temperature (IPCC, 2014). Yet, temperature differs between as well as within regions. Therefore, the IPCC reports relative values instead of absolute numbers. We plan to adopt this principle as well during the further development of the global lake modelling.

Besides spatial heterogeneity there are temporal differences. For the purpose of projections on global algal development we consider yearly minima, average and maxima of chlorophyll-a per lake as a sufficient temporal level of detail. However, chlorophyll-a is known for its daily variations (Yentsch et al., 1957). These temporal variations are comparable to daily weather conditions that are variations in the prevailing climate. These variations can be communicated to the general public using a bandwidth of the expected temporal variation. The proposed model will produce enough data to show this bandwidth.

In addition to temporal and spatial variation, there is uncertainty in the predictive value of the output. There will always be uncertainty about future developments and thus we are limited in our capacity to make projections. These projections can be written in narratives that will form the basis of the scenario runs. Defining the uncertainty of model output is a challenge, because model output uncertainty is not equal to model uncertainty. Model uncertainty follows from ambiguity in the choice of model parameters, model structure, model boundaries and numerical integration methods (Janssen et al., 2015). Uncertainty in the model output depends on uncertainties in input, measurements, adaptive responses and innumerous other factors that drive global change. There are several methods to produce probabilistic output to quantify the degree in uncertainty of model output (Janssen et al., 2015).

For the best approximation of global patterns, the optimal level of model complexity has to be found (Grimm et al., 2005). Too simple models will neglect essential processes, while too complex models will have too long computational time and the analysis of its results will drown in details. In between simple and complex models there is an optimal level of model complexity, the so called "Medawar zone" (Grimm et al., 2005). Accordingly, modelling any lake on earth, while taking into account its spatial heterogeneity, would be too complex for our purpose. Instead, we chose PCLake because the model is constructed in a way that it produces average output that approaches the average of lakes.

Recommendations

Comparing our list of characteristics of an ideal global model for freshwater lake ecosystems with our proposed model reveals challenges and opportunities for further improvements. In addition, we see that we can learn from previous attempts to make global projections. Based on experiences with developing the model, we formulate the following recommendations to improve global models for freshwater lake ecosystems:

1) *Improve the formulation of stratification for the expanded version of PCLake* - The critical depth is well-described in literature, however, as far as we know, approaches to define the period of stratification based on simple rules are still limited. We proposed to define the stratification period based on water temperature. We suggest testing this crude formulation of stratification and improving it in case new insights for improvements arise. Preferably, the required refinement will not add too much complexity in order to keep the runtime low.
2) *Include other nutrient cycles* - Lakes are influenced by other nutrient cycles beside phosphorus and nitrogen. For example the global carbon and silica cycle are currently missing. These cycles are important to lakes. It seems therefore logical to include these cycles in the aquatic ecosystem component, and to model its feedback to the environment.
3) *Refine the calculation grid of drivers to lakes* - Currently the calculations of water and nutrient input are based on a relatively coarse grid of 30 arc-minutes. This limits the projections to only large lakes. By refining the grid we could expand the projections to small lakes. An alternative would be to find a way to modify the coarse gridded water and nutrient input with empirical or GIS-based relations to make it applicable to small lakes.

4) *Expand the list of lakes to which the model is applied with small lakes* - At the moment, our conclusions will be limited to large lakes. To increase the understanding of algal blooms in lakes in general we recommend incorporating small lakes as well in our analysis. Characteristics of these lakes can, for instance, be obtained from the dataset of HydroLAKES (Messager et al., 2016).
5) *Improve the geographic coverage of the validation database* - The current database is biased to European and USA lakes. We recommend expanding the database with lakes on other continents.
6) *Make the expansion of the database an ongoing process* - New data are gathered every day and existing data become available by new sharing policies. The merged database is therefore never finished and should continue to grow.
7) *Unify global data storage* - There are various ways to store data, with different quality levels. This lack of standardization hampers merging the datasets. An important challenge is thus to unify datasets according to common standards. A good start could already be to define unique lake identities besides latitude and longitude.
8) *Advocate open data policies* - It seems already the trend to share data, however, there is still room for improvement. By sharing data, global assessment studies in general will have easier access to data for model input, model calibration and model validation.
9) *Collaborate with different disciplines* - Projecting global freshwater quality is by definition a multidisciplinary task, requiring strong collaboration. The quality of projections depends not only on aquatic ecologists but also on hydrologists, sociologists, economists, mathematicians, etc.
10) *Learn from earlier projections* - In the past, others have already paved the way of making projections. We could learn from their collective experiences. Their creative solutions could be an answer to our challenges.

Learning from earlier attempts to make projections will prevent "reinventing the wheel".

Conclusion

We have proposed a lake ecosystem model with global applicability based on PCLake, with a global water flow component (PCR-GLOBWB), a nutrient flow component (GNM) and a global environmental component (IMAGE). With the proposed model we plan to make projections of global algal blooms, first for large lakes. Subsequently, we want to increase the applicability of the proposed model, including simulations for smaller lakes. We envision that global projections of freshwater ecosystems will increasingly gain importance and provide a valuable contribution to general projections of the impact of global change.

Acknowledgments

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Chapter 6

Spatial identification of critical nutrient loads of large shallow lakes: implications for Lake Taihu (China)

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Abstract

Ongoing eutrophication frequently causes toxic phytoplankton blooms. This induces huge worldwide challenges for drinking water quality, food security and public health. Of crucial importance in avoiding and reducing blooms is to determine the maximum nutrient load ecosystems can absorb, while remaining in a good ecological state. These so called critical nutrient loads for lakes depend on the shape of the load-response curve. Due to spatial variation within lakes, load-response curves and therefore critical nutrient loads could vary throughout the lake. In this study we determine spatial patterns in critical nutrient loads for Lake Taihu (China) with a novel modelling approach called *Spatial Ecosystem Bifurcation Analysis* (SEBA). SEBA evaluates the impact of the lake's total external nutrient load on the local lake dynamics, resulting in a map of critical nutrient loads for different locations throughout the lake. Our analysis shows that the largest part of Lake Taihu follows a nonlinear load-response curve without hysteresis. The corresponding critical nutrient loads vary within the lake. They also depend on management goals*, i.e.* the maximum allowable chlorophyll concentration. According to our model, total nutrient loads need to be more than halved to reach chlorophyll-a concentrations of 30-40 $\mu g.L^{-1}$ in most sections of the lake. To prevent phytoplankton blooms with 20 $\mu g.L^{-1}$ chlorophyll-a throughout Lake Taihu, both phosphorus and nitrogen loads need a nearly 90% reduction. We conclude that our approach is of great value to determine critical nutrient loads of lake ecosystems such as Taihu and likely of spatially heterogeneous ecosystems in general.

Introduction

Extensive eutrophication threatens numerous lakes worldwide, leading to major challenges for drinking water supply, food security and public health (Brooks et al., 2016). To minimize negative consequences, water quality managers look for successful and efficient measures. In this process, they need to carefully walk on the thin line between the desired water quality and the available financial resources (Groffman et al., 2006).

Importantly, success of management actions depends on the identification of ecological thresholds (Kelly et al., 2015). These thresholds set limits to sustainable use of resources within the safe operating space (Rockström et al., 2009b) and exceedance leads to undesired ecological consequences such as toxic phytoplankton blooms (Groffman et al., 2006). Currently, there is a great interest in ecological thresholds (Kelly et al., 2015). In the first place, ecological thresholds support adaptive management by defining limits to maximum stress, and, secondly, ecological thresholds support recovery by setting a restoration goal (Kelly et al., 2015). A common threshold used in limnology is the concept of critical nutrient loads. We define critical nutrient load as a maximum nutrient load an ecosystems can absorb, while remaining in a good ecological state. This definition of the critical nutrient load includes both gradual and sudden changes in water quality.

To estimate the critical nutrient load of a specific lake, it is important to know the type of load-response curve. The load-response curve of lakes is generally defined as the response of phytoplankton (i.e. chlorophyll-a) to a range of nutrient loads. Literature distinguishes three types of load-response curves which differ in linearity and the presence of hysteresis (Figure 6.1) (e.g. Scheffer et al., 2001). The first type is a linear load-response curve for which a reduction in nutrient load results in a proportional decrease in chlorophyll-a, irrespective of the nutrient load (Figure 6.1a). The critical nutrient load for lakes with a linear load-response curve is quite sensitive to the human-defined maximum allowable chlorophyll-a concentration. These human-defined maxima closely relate to the lake's societal functions (e.g. recreation or drinking water). Depending on the maximum allowable chlorophyll-a concentration, the critical nutrient load varies between a relatively high (Figure 6.1a blue line (1)) and low value (Figure 6.1a red line (2)). The second type of load-response curve is nonlinear (Figure 6.1b). The critical nutrient load for lakes with a nonlinear load-response curve depends on the positioning and slope of the fold. Therefore, the critical nutrient load only slightly depends on human-defined limits to the maximum allowable chlorophyll-a concentration. This can be seen from the relative small difference between the critical nutrient loads for the two hypothetical maximum allowable chlorophyll-a concentrations (Figure 6.1b blue (1) and red line (2)). Finally, the third load-response curve is nonlinear as well, but includes hysteresis that emerges from strong positive feedbacks leading to two alternative stable states (Figure 6.1c). Lakes exhibiting a nonlinear load-response curve with hysteresis have two critical nutrient loads, one for eutrophication and one for oligotrophication (Figure 6.1c denoted by CL_a and CL_b). In this case, the critical nutrient load is nearly independent of human-defined chlorophyll-a limits, due to the abrupt character of the shift (Figure 6.1c blue and red line, with no differences between the critical nutrient loads).

Multiple methods exist to estimate load-response curves and the corresponding critical nutrient loads of lakes. First, field data can be used for hindcasting. For instance, hindcasting has been applied for Lake Veluwe, the Netherlands (Ibelings et al., 2007) and a couple of US Lakes (Baron et al., 2011). While this method gives good results for specific cases, it requires a large dataset to cover the full range of load-responses for both eutrophication and oligotrophication. Such load-response data are scarce in many cases (Baron et al., 2011; Capon et al., 2015). Additionally, hindcasting always lags behind as both eutrophication and oligotrophication need to have occurred to prove the presence of hysteresis. Hence, this method is unsuitable to estimate critical nutrient loads for lakes that are yet to be restored.

Another option is to determine load-response curves and critical nutrient loads through laboratory or field experiments as has been done for Hickling Broad (UK) using mesocosms (Barker et al., 2008). In this method, the critical nutrient load is determined in small containers or cattle tanks in which each batch of replicates receives a certain amount of nutrients. These experiments are relatively easy to perform and have the advantage of replication, however, they may not represent the field situation (Stewart et al., 2013). Indeed, essential feedbacks like the interaction between phytoplankton and macrophytes, or the effect of wind fetch could be easily missed.

Finally, a modelling approach can be used. Modelling has the advantage that most important feedbacks can be incorporated and that scenario simulations can be run nearly 'unlimited' times without affecting the real lake ecosystem. Studies using a modelling approach to determine load-response curves of lakes are numerous (e.g. Janse et al. (2010) and Kong et al. (2016)). However, in these cases only a single load-response curve is identified that should hold for entire lakes. While single load-response curves may be valid for small and homogeneous lakes, in case of large shallow lakes they critically ignore spatial variation in lake characteristics and connectivity (Janssen et al., 2014).

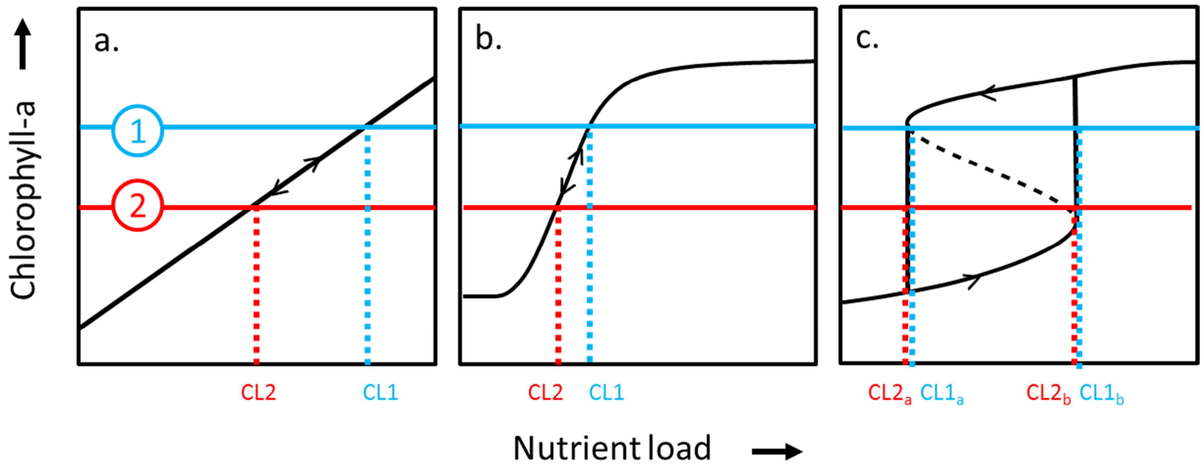

Figure 6.1. Three types of load-response curves: a) Linear; b) Nonlinear without hysteresis; c) nonlinear with hysteresis (alternative stable states). The horizontal solid lines depict two human-defined restrictions for the maximum allowable chlorophyll-a that are strict (blue, number 1) and less strict (red, number 2). The blue and red dotted line show the corresponding critical nutrient load (CL) (e.g. Scheffer et al., 2001).

Lake Taihu (Southeast China) is a good example a large shallow lake with high spatial variation (Figure 6.2) (Janssen et al., 2014). In its pristine state, nutrient loads per unit area of lake surface were below 0.4 $gP.m^{-2}.yr^{-1}$ and 8 $gN.m^{-2}.yr^{-1}$ (Yan et al., 2011). Macrophytes were established at the shores and in the bays, whereas they were absent in the lake's center due to strong wind forces (Janssen et al., 2014). In recent decades, the nutrient load rose above 0.93 $gP.m^{-2}.yr^{-1}$ and 19 $gN.m^{-2}.yr^{-1}$ (2012) resulting in excessive phytoplankton blooms that threaten millions of people depending on Taihu (Xu et al., 2015b). These blooms concentrate primarily in the north and center of the lake, while macrophytes still flourish in the east (Zhao et al., 2013). Clearly, assuming spatial homogeneity is invalid for Lake Taihu. Instead, high spatial heterogeneity in the abundance of macrophytes and phytoplankton suggest variation in the responses to eutrophication within the lake. This variation results in a spatial patterning of critical nutrient loads in Lake Taihu.

In this study, we aim to determine the spatial pattern of critical nutrient loads of Lake Taihu, using a novel and comprehensive modelling approach that accounts for connectivity and spatial variation in lake characteristics. We consider determining critical nutrient loads in a spatial context an important scientific innovation. This implies that the message presented here goes beyond the specific application of our method to Lake Taihu. Our proposed method includes two steps. First, we spatially determine load-response curves by applying bifurcation theory for different locations within the lake. Second, for each location the critical nutrient load is defined. Together, these steps result in a map of Lake Taihu, showing critical nutrient loads in a spatial context. This is an important result for lake restoration management of poorly mixed, spatially heterogeneous lakes such as Taihu.

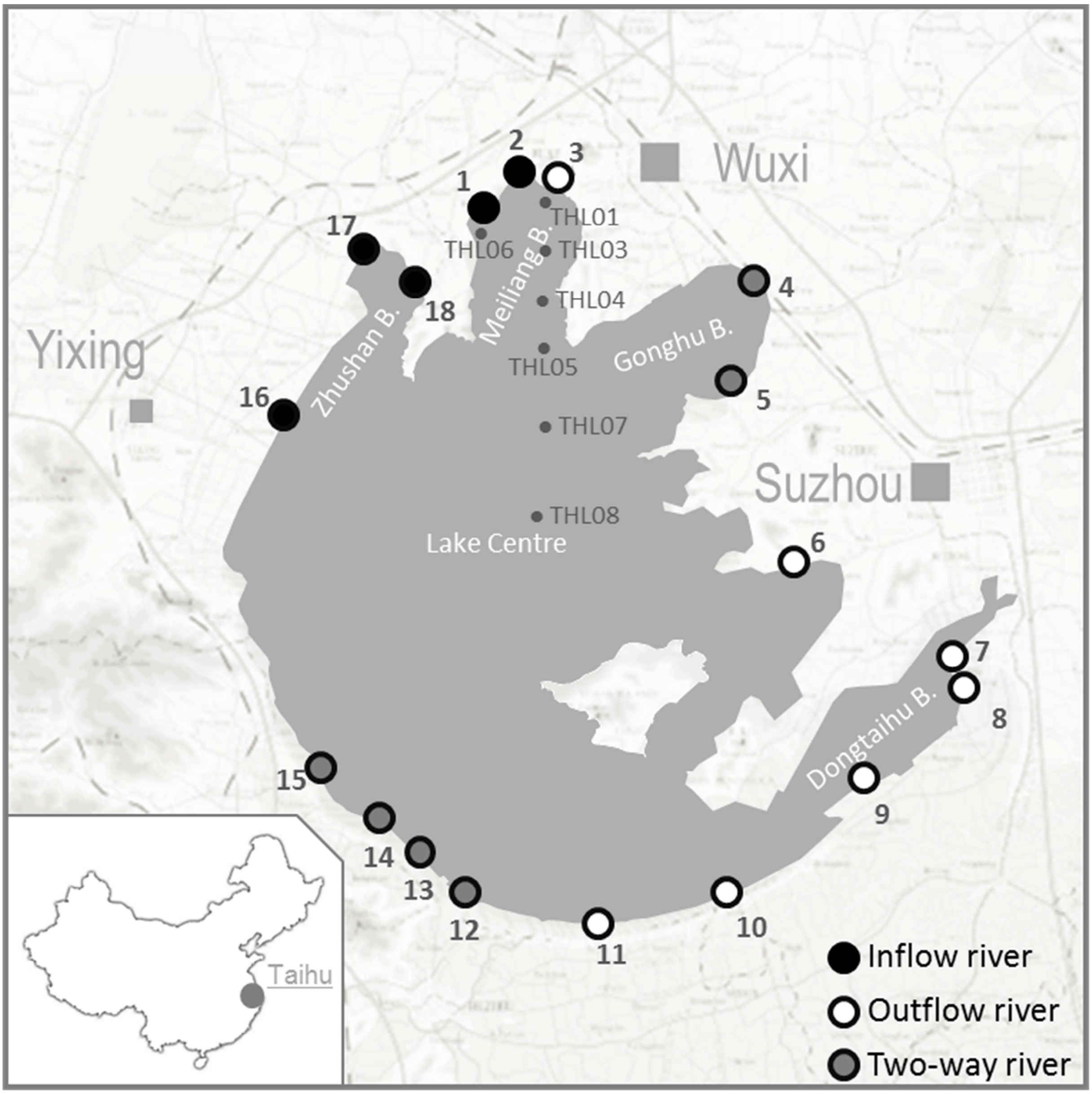

Figure 6.2. Map of Lake Taihu with the main inflow (black dots) and outflow (white dots) rivers. Grey dots show rivers that contribute to both in- and outflow, depending on the season. Numbers refer to 1. Zhihugang River, 2. Yugang, 3. Liangxi River, 4. Wangyu River, 5. Longtanggang River, 6. Xujiang River, 7. Guanjin Kou, 8. Lianhu Bridge, 9. Taipu River, 10. Tuanjie Bridge, 11. Tiaoxi River, 12. Sainli Bridge, 13. Hangchang Bridge, 14. Yangjiapugang River, 15. Changxinggang River, 16. Chendonggang River, 17. Caoqiao River, 18. Yapu Bridge. THL01-THL08 are monitoring stations.

Methods

To determine the different load-response curves and the corresponding critical nutrient loads for different locations throughout Lake Taihu we developed *Spatial Ecosystem Bifurcation Analysis* (SEBA) using model simulations. Like classical ecosystem bifurcation analysis, SEBA evaluates the equilibrium response of lake dynamics along the axis of external nutrient load (Scheffer et al., 2001). SEBA differs, however, from classical ecosystem bifurcation analysis by accounting for spatial heterogeneity in lake characteristics such as wind dynamics and depth. Technically, this comes down to substituting of ordinary differential equations for each substance concentration C used in classical ecosystem bifurcation analysis ($dC/dt=f(t)$) by partial differential equations ($dC/dt=f(x,y,t)$). Substitution leads to equations that not only account for bio-physicochemical processes, but also include diffusion and advection processes. Additionally, lake characteristics such as wind and depth will differ spatially. Subsequently, SEBA results in load-responses and critical nutrient loads for different locations throughout the lake.

Applying bifurcation analysis within a spatial context has implications for the definition of the external nutrient load. There are two options to define the external nutrient load: i) as the nutrient supply to a specific part of the lake or ii) as the total external load to the whole lake. The first definition might appear attractive because of its local character. However, this definition has several drawbacks which specially hamper the comparability of the different load-response curves and critical nutrient loads within one lake (see Appendix 12 for details). The second definition is identical to the definition used in classical ecosystem bifurcation analysis with simplifies the comparison between both approaches. This definition is also more useful for lake managers because their data and targets relate to the total external nutrient load to the whole lake rather than the local load. Therefore, we consider it most informative to put the lake wide external nutrient load on the x-axis of the load-response curve while putting the local response on the y-axis.

To perform SEBA, we selected the ecosystem model PCLake because it is, as far as we know, the most extensively used food web model for aquatic ecosystems applied for bifurcation analysis. The advantage of PCLake over other eutrophication models is its focus on the competition between three types of phytoplankton (diatoms, green algae and cyanobacteria) and macrophytes (Janssen et al., 2015). Additionally, zooplankton, fish and benthic organisms are included in PCLake as well as the bio-physicochemical interactions between water and sediment (Appendix 13.1). By using such a comprehensive model, we account for a wide variety of essential processes that, besides nutrient load, indirectly influence the shape of load-response curves of shallow lakes. Since spatial heterogeneity is key to our research, the modelling setup requires a spatial approach. Therefore we couple PCLake with the interface Delft3D-DELWAQ using the Database Approach To Modeling (DATM) (Mooij et al., 2014; Van Gerven et al., 2015). The advantage of Delft3D-DELWAQ is the connection with the hydrodynamic modules Delft3D-FLOW and Delft3D-WAVE. We use the hydrodynamics as previously defined and simulated for Lake Taihu on a 3D-grid (500 x 500 m grid) (Liu et al. (2013) and Appendix 13.2). In this hydrodynamic simulation, Lake Taihu is connected with the 18 most important rivers for in- and outflow (Figure 6.2 and Appendix 13.3).

We coupled PCLake at an aggregated horizontal 2D-grid (~1500 x 1500 m grid) using the default parameter settings as given by (Janse et al., 2010). Lake specific settings such as sediment and wind characteristics are defined using information from literature (see Appendix 13.4 for references and calculations). The full set of state variables, parameters and equations can be found in Appendix 14 as a DATM-file. We used nutrient load data and mass balances of Taihu (Yan et al., 2011; Janssen et al., 2014) in combination with watershed data to estimate the load contribution by each river (Yu et al. (2007) and Appendix 13.5). Since the original resuspension equation of PCLake lost its meaning within a spatial setting, we substituted it by a dynamic equation based on shear stress and wind (Appendix 13.6).

Next, the model is validated in two ways. First, in an earlier study we have shown that PCLake predicts the spatial distribution of macrophytes in the oligotrophic situation of Lake Taihu well with only 7-24% discrepancy between data and model (Figure 2.9 of chapter 2). Second, in the present study we validate the model based on a dataset of 8 variables for the period 1996-2006 from Sun et al. (2010) (see Figure 6.2 for measurement stations). Like Trolle et al. (2014), we use R^2 and the mean relative absolute error (RE) for model validation (Appendix 13.7). High R^2-values indicates good resemblance of the seasonal pattern in the data by the model. Low RE-scores show that the model output falls well within the range of the measurement data. To put our results in perspective, we compared them with the results obtained by Trolle et al. (2014) (Figure 6.3). The best fit of chlorophyll-a is found for the field stations located in Meiliang Bay (THL01, THL03, THL04, THL06). In the lake center the model has a poorer fit to the field data (THL07 and THL08). There are two methodological explanations for this mismatch. First the floating phytoplankton could be missed in the sampling procedure resulting in an underestimation of the occurring phytoplankton blooms in the lake center (Janssen et al., 2014). A second explanation is a shortcoming in the model. While the model covers the effect of wind on the water movement, the effect on floating biomasses is not included. It is known that floating phytoplankton biomass are produced in the lake center, but are driven by the wind against water flow in north-western direction (Wu et al., 2015). In the bays this effect is much smaller due to lower fetch. This shortcoming creates the risk to underestimate the critical nutrient load in the lake center and overestimate it in at the north-western shores.

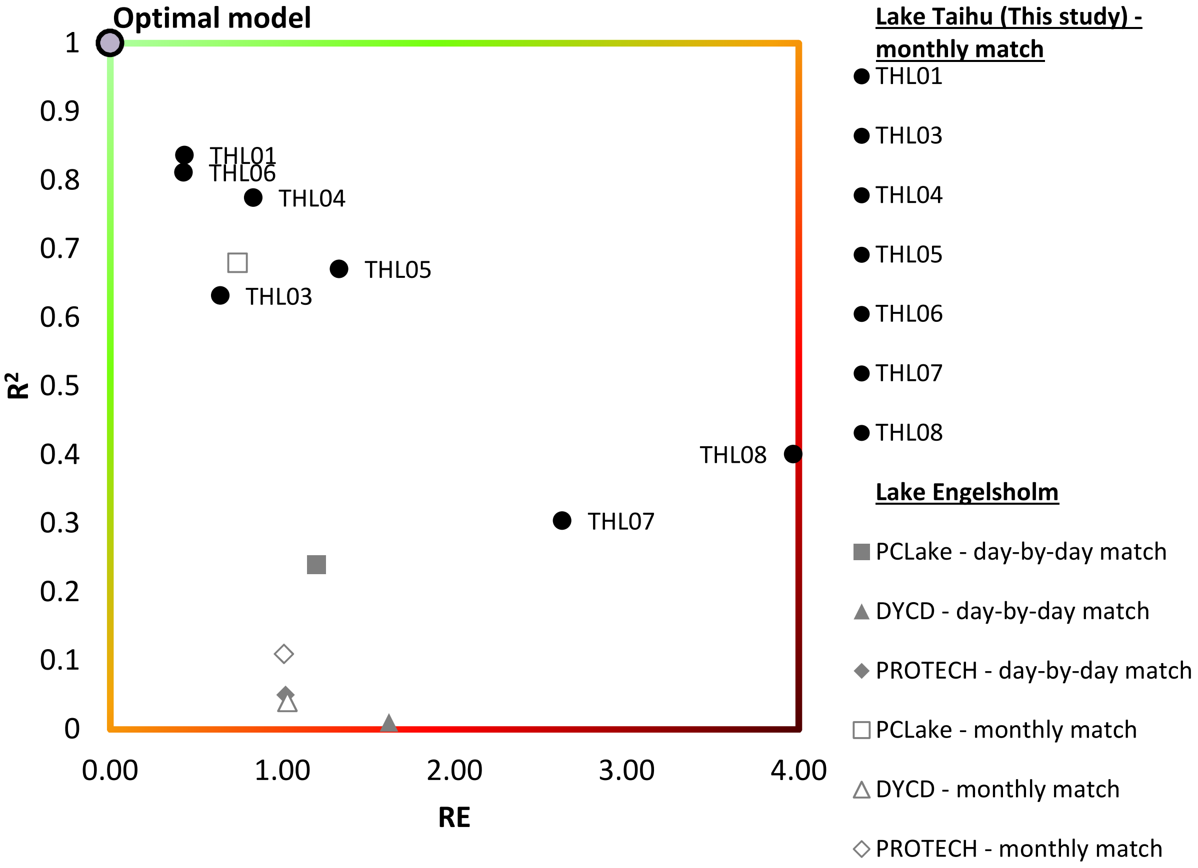

Figure 6.3. Validation of model outcomes for chlorophyll-a concentrations at 7 different stations in Lake Taihu. Ideally, a model has R^2 values of 1 and an RE of 0: "optimal model". To put our results in perspective, we compared them with the results obtained by Trolle et al. (2014) for Lake Engelsholm with the three lake ecosystem models PCLake, DYCD and PROTECH.

With the validated model, we performed SEBA. Similarly to classical ecosystem bifurcation analysis, both load-response curves for eutrophication and oligotrophication are determined in order to ascertain the presence of hysteresis. Hysteresis would mean a dissimilarity in shapes between the load-response curves for eutrophication and oligotrophication. First, we construct the eutrophication load-response curve starting with initial settings of an oligotrophic lake (see Appendix 13.8 for settings). We impose a yearly constant, but seasonally and spatially variable nutrient load. We run the model to equilibrium, which we define here as a recurring identical yearly pattern while preserving the seasonal variability. We assume equilibrium been reached if 99% of the grid cells have a deviation between the chlorophyll-a output of the last five years of no more than 5%. We repeat the run 50 times with the same initial conditions, though each time with a higher nutrient load than the previous run. In all repeated runs the relative contribution of nutrient load by each river and the ratio between the various kinds of nutrients are kept invariant. For each run, we calculate the yearly average chlorophyll-a concentrations per individual grid cell. Load-response curves for eutrophication per grid cell follow from the total nutrient load of each of the 50 runs and the 50 corresponding calculated yearly averaged chlorophyll-a concentrations. Next, in order to construct load-response curves for oligotrophication we repeat the same procedure with 50 runs, though starting with initial settings of a eutrophic lake and imposing decreasing nutrient loads. The imposed nutrient load per unit area of lake surface ranges between 0.12-3.00 gP.m^{-2}.yr^{-1} with a corresponding N-load of 2.40-60.0 gN.m^{-2}.yr^{-1} (N-load:P-load=20). The highest nutrient load in our simulations, 3.00 gP.m^{-2}.yr^{-1} and 60.0 gN.m^{-2}.yr^{-1} is nearly a threefold of the current nutrient load (Xu et al., 2015b). Nutrient loads for individual rivers are calculated using the proportional contribution as calculated in table V in Appendix 13.4. The nutrient load of each river is based on concentrations in order to account for seasonality in loads. To speed up runtime performance we run the model in parallel using the High Performance Computing cloud IAAS infrastructure offered by SURFsara (https://www.surf.nl).

The results of SEBA are highly data-rich and therefore a simple representation of the load-response curve for each grid cell as seen in Figure 6.1 is inconvenient. Instead, we use two objective, though exclusive indicators that respectively assess the linearity and the presence of hysteresis that distinguish the three types of load-response curves. First, we determine the linearity of the load-response curve of each grid cell which enables us to distinguish the linear (Figure 6.1a) from the nonlinear types of load-response curves (Figure 6.1b and Figure 6.1c). A test for linearity might seem superfluous because of the use of the nonlinear model PCLake, however, a linear output would still be possible in case the positive feedbacks are significantly weakened. To determine the linearity we calculate the predictive power of a linear model to resemble the load-response curve. We use the adjusted coefficient of determination $\left(R_{adj}^2 = 1 - \frac{\mathrm{n-1}}{\mathrm{n-p}} * \frac{[\mathrm{SSE}]}{[\mathrm{SST}]}\right)$ as an objective indicator for linearity (Figure 6.4a). Essentially, the load-response curves calculated by PCLake depend on a set of mathematical equations that lack stochasticity and are low in computational errors. Therefore, the value of R^2_{adj} purely results from the deviation of the load-response curve from the linear model. The load-response curve can be regarded as linear in case R^2_{adj} approaches one, while lower values indicate a nonlinear load-response curve.

Second, we assess the presence of hysteresis to distinguish the load-response curve of Figure 6.1c from the load-response curves in Figure 6.1a and Figure 6.1b. Therefore, we look for major differences between the surface area (integral) below the load-response curves for eutrophication and oligotrophication (Figure 6.4b). In case of hysteresis, the surface area below the load-response curve of oligotrophication should be substantially larger than the surface area below the load-response curve of eutrophication. From earlier studies we know that such differences are at least 10 $\mu g.L^{-1}(gP.m^{-2}.yr^{-1})^{-1}$ (Janse et al., 2008).

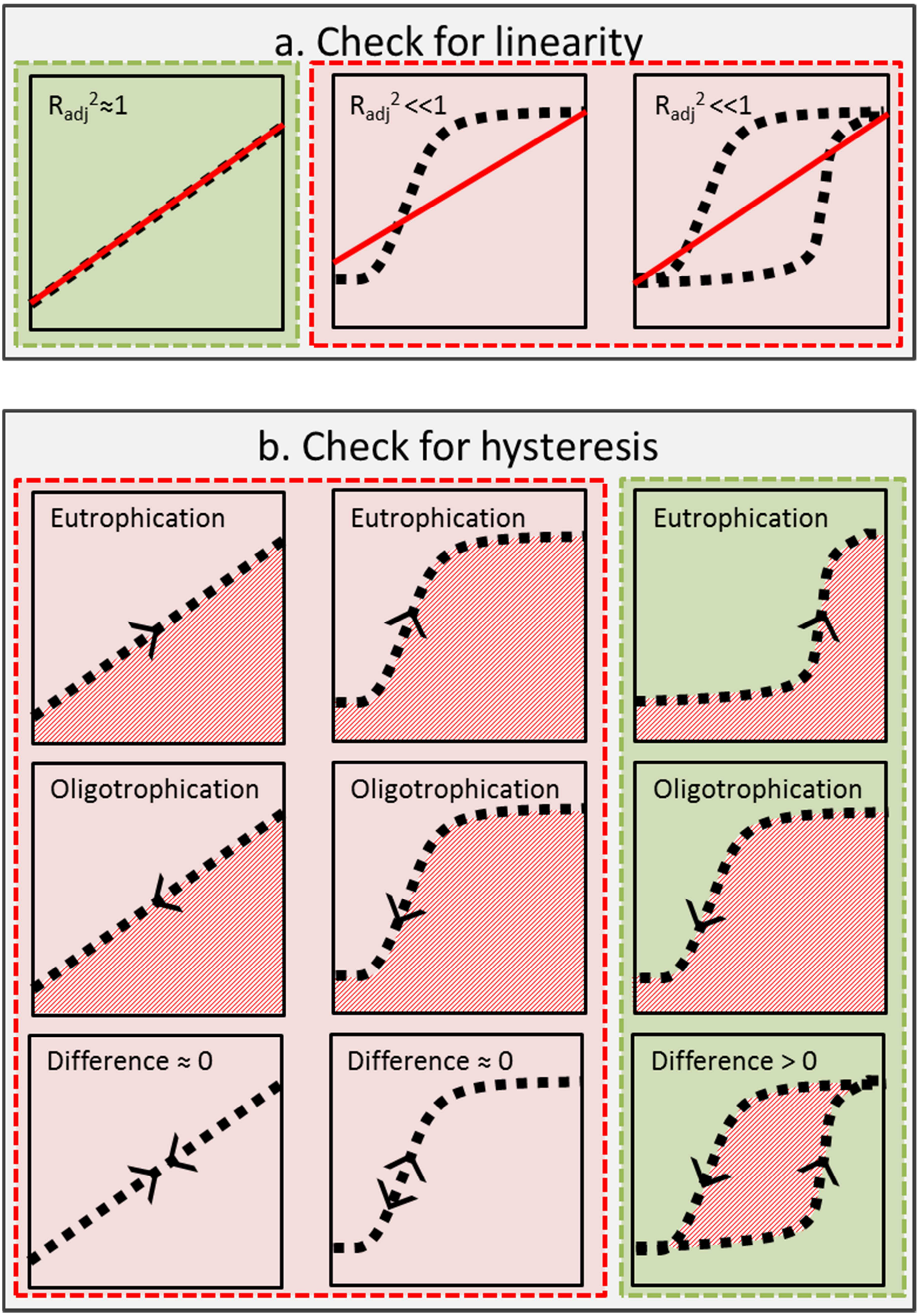

Figure 6.4. Methods to distinguish between load-response curves: a) check for linearity and b) check for hysteresis.

In case load-response curves are linear to moderately nonlinear, maximum allowable chlorophyll-a concentration needs to be defined according to the societal functions of the lake (Figure 6.1). Lake Taihu serves different societal functions, including drinking water, fisheries, irrigation, shipping and flood control. It is inevitable that each societal function has different requirements with respect to chlorophyll-a concentrations. Drinking water requires low chlorophyll-a concentrations whereas higher chlorophyll-a concentrations are allowed for fisheries or irrigation. From earlier studies we know that at 20 $\mu g.L^{-1}$ chlorophyll-a, bloom formation starts in Lake Taihu which becomes especially harmful if concentrations exceed 40 $\mu g.L^{-1}$ chlorophyll-a (Xu et al., 2015b). We focus on a range of maximum allowable chlorophyll-a concentrations between 20 and 50 $\mu g.L^{-1}$ chlorophyll-a, to cover the full width of bloom formation and beyond. The critical nutrient load of a specific grid cell is calculated as the maximum nutrient supply to the entire lake, for which chlorophyll-a concentrations in this specific grid cell remains below the maximum allowable chlorophyll-a concentration.

Results

We found that the indicator for linearity, R^2_{adj}, keeps largely below 0.4, suggesting that largest parts of Lake Taihu react nonlinearly to eutrophication and oligotrophication (Figure 6.5, histogram and load-response curves for location 3 and 4). Yet, there are exceptions to this pattern as for example in Dong Taihu Bay where the indicator for linearity is high (Figure 6.5, location 1). Dong Taihu Bay is an isolated area that shows no response at all. Additionally, close to the water inlet at the south-western shore the R^2_{adj} is higher, corresponding with a slightly nonlinear load-response curve (Figure 6.5, location 2).

In our search for hysteresis we compared the surface areas below the two load-response curves for eutrophication and oligotrophication where a large difference would indicate hysteresis. We found a maximum difference between the surface areas of less than 1.3 $\mu g.L^{-1}(gP.m^{-2}.yr^{-1})^{-1}$. In most cases we found even less than 1% deviation between the surface areas below the two load-response curves. These values are considerably lower than 10 μg.L^{-1}(gP.m^{-2}.yr^{-1})$^{-1}$ (Janse et al., 2008). Therefore, it is more likely that this deviation results from small computational errors rather than from hysteresis.

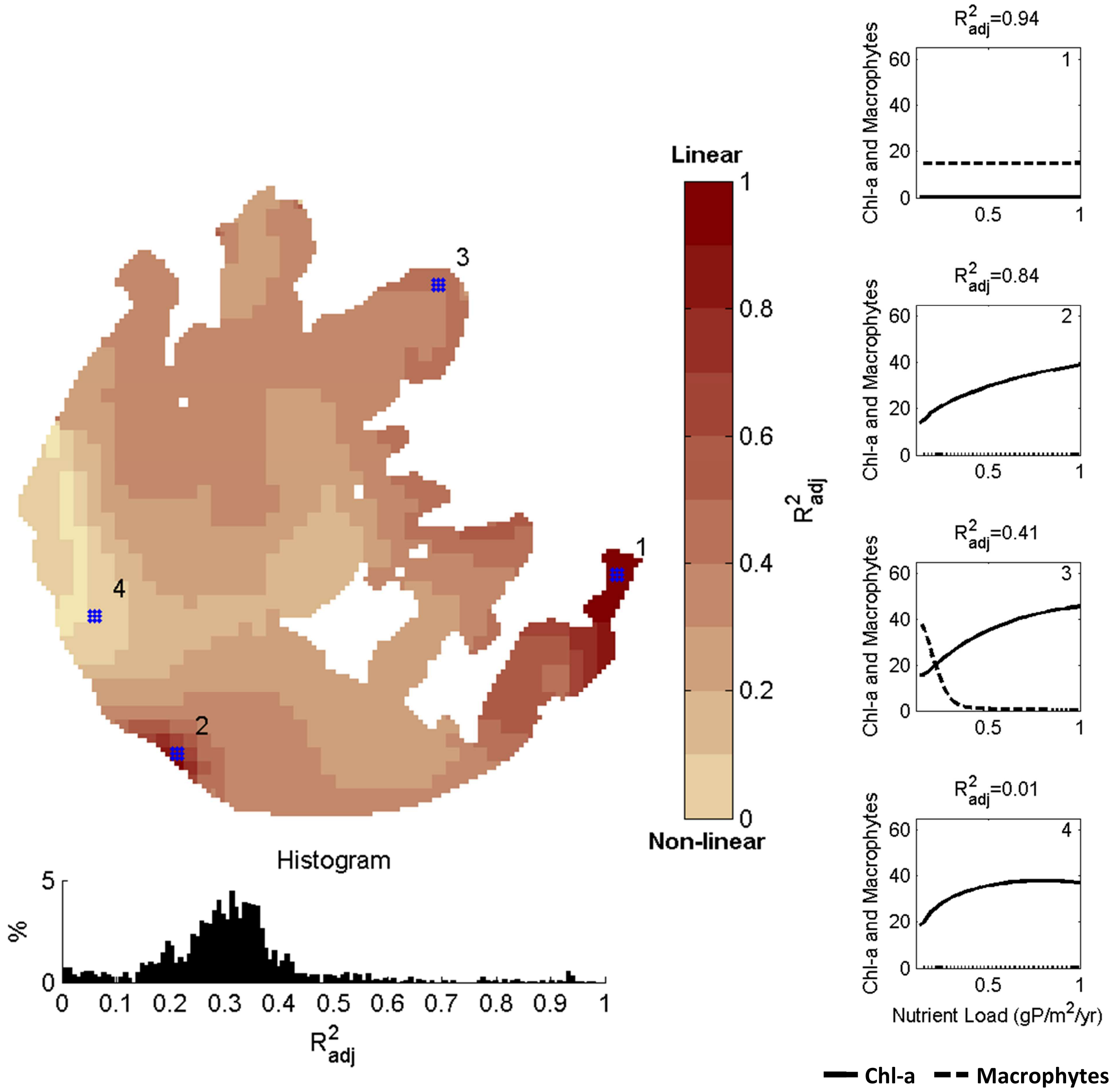

Figure 6.5. Test for linearity based on modelled chlorophyll-a concentrations. High R^2_{adj} -values suggest high linearity. The load-response curves are exemplified for four locations that differ in linearity. The nutrient load is expressed as mass per unit area of lake surface per year.

In summary, these analyses indicate a nonlinear load-response curve without hysteresis for major parts of Lake Taihu (Figure 6.1b) with a few regions that show a linear load-response curve (Figure 6.1a). In both cases, critical nutrient loads will partly depend on human-defined limits to the maximum allowable chlorophyll-a concentration. We calculated the critical nutrient load for Lake Taihu using a range of possible human-defined maxima for yearly average chlorophyll-a, varying from 20 μg.L^{-1} chlorophyll-a to 50 μg.L^{-1} chlorophyll-a. Results show large spatial variation in critical nutrient loads (Figure 6.6). Intriguingly, the pattern of spatial variation depends on the chosen maximum allowable chlorophyll-a concentration. In case of 20 μg.L^{-1} chlorophyll-a as maximum allowable chlorophyll-a concentration, 84% (the area under a normal distribution minus a one-side tail of one standard deviation) of the critical nutrient loads of Lake Taihu are below 0.19 gP.m^{-2}.yr^{-1} (3.8 gN.m^{-2}.yr^{-1}) (Figure 6.6a). The lake center shows lowest critical nutrient loads indicating that this area is most likely to reach the maximum allowable chlorophyll-a concentration of 20 μg.L^{-1} chlorophyll-a first. Contrarily, Dong Taihu Bay has a higher critical nutrient load indicating that this isolated region is least vulnerable to increased nutrient load. The shores also show higher critical nutrient load especially in the west of the lake. Even at extremely high nutrient loads, a 20 μg.L^{-1} chlorophyll-a threshold is unreachable for about 10% of the regions within Lake Taihu. These regions are indicated in gray in Figure 6.6.

Next, we look at the critical nutrient loads for the maximum allowable chlorophyll-a concentration of 30 μg.L^{-1} (Figure 6.6b). Model simulations show that 84% of the critical nutrient loads are below 0.27 gP.m^{-2}.yr^{-1} (5.4 gN.m^{-2}.yr^{-1}). The spatial pattern is similar to the 20 μg.L^{-1} chlorophyll-a with most vulnerable areas in the lake center. At extremely high nutrient loads, about 15% of the lake will not reach the maximum allowable chlorophyll-a concentration of μg.L^{-1} chlorophyll-a.

With a maximum allowable chlorophyll-a concentration of 40 μg.L^{-1} chlorophyll-a the most vulnerable areas moves towards Gonghu bay and to a lesser extent to Zhushan Bay and Meiliang Bay (Figure 6.6c). Less than 80% of the lake area reaches this maximum allowable chlorophyll-a concentration and of these regions the critical nutrient loads are between 0.25 and 0.47 gP. .m^{-2}.yr^{-1} (5 gN.m^{-2}.yr^{-1} - 9.4 gN.m^{-2}.yr^{-1}).

In case of a maximum allowable chlorophyll-a concentration of 50 μg.L^{-1} chlorophyll-a an interesting pattern emerges (Figure 6.6d). In our simulations, the lake center is unable to reach this maximum allowable chlorophyll-a concentration. Instead, critical nutrient loads are reached first at the outer edges of the northern bays including Zhushan Bay, Mailiang Bay and Gonghu Bay. Additionally, the southeast shore reaches the maximum allowable chlorophyll-a concentration of 50 μg.L^{-1}. The critical nutrient loads within the regions that reach the maximum allowable chlorophyll-a concentration of 50 μg.L^{-1} is between 0.32 and 0.78 gP.m^{-2}.yr^{-1} (6.4 gN.m^{-2}.yr^{-1} - 15.6 gN.m^{-2}.yr^{-1}). Only 25% of the lake area reaches the maximum allowable chlorophyll-a concentration of 50 μg.L^{-1} chlorophyll-a.

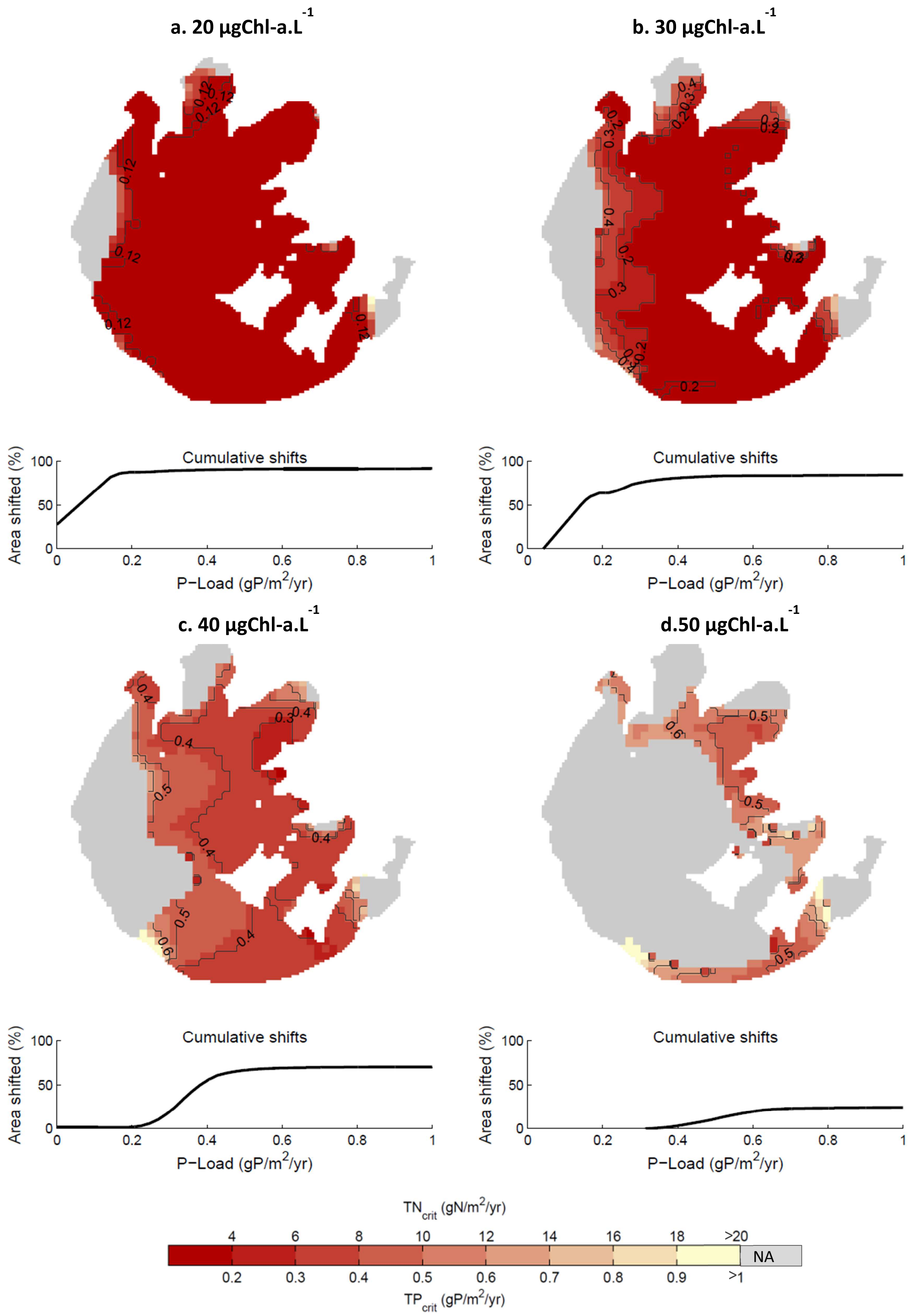

Figure 6.6. Critical nutrient load per grid cell for TN and TP ($g.m^{-2}.yr^{-1}$) for four maximum allowable chlorophyll-a concentration between 20 to 50 $\mu g.L^{-1}$. The gray colors indicate the areas that that never reached the maximum allowable chlorophyll-a concentration within our simulations. The cumulative graphs below the maps show the area of the lake that reached the maximum allowable chlorophyll-a concentration at a specific critical P-load (TN:TP=20).

Discussion

In the first step of our analysis we identified variation in the shapes of load-response curves. Hysteresis as assumed in, for instance, large shallow Lake Apopka (USA) (Bachmann et al., 1999), is not detected within Lake Taihu. Apparently, the lake's surface area is too large, allowing wind forces to dominate and preventing vegetation growth in most part of the lake (Zhao et al., 2013). Additionally, Taihu has heterogeneous lake characteristics which are believed to weaken large-scale hysteresis as well (Van Nes et al., 2005; Van de Leemput et al., 2015). Local hysteresis in isolated areas is also absent, possibly due to sufficient interaction between isolated regions and the lake center (Janssen et al., 2014). Accordingly, Taihu joins the long list of large lakes without hysteresis (Janssen et al., 2014; Capon et al., 2015; Bunting et al., 2016). Please note, however, that we found nonlinear load-response curves in largest part of the lake (Figure 6.1b).

Nonlinearity within load-response curves results from nonlinear interactions (e.g. Scheffer et al., 2001). Indeed, phytoplankton growth is limited at extreme low and high nutrient load due to nutrient respectively light limitation. In contrast, phytoplankton growth is highest at medium loads (Reynolds, 2006). Apparently, these nonlinear interactions are strong enough for nonlinear load-response curves to occur, but too weak for hysteresis. At some locations in Lake Taihu, however, the load-response curves are nearly linear. These are regions where positive feedbacks are suppressed e.g. due to strong hydrological influences by rivers that dominate over biological processes (e.g. southwest Taihu), or due to the great distance from the actual nutrient source leading to limited impact of external nutrient loads (e.g. Dong Taihu Bay).

Beside the differences between load-response curve types (Figure 6.1), also differences within types can be seen. An important difference is expressed in the maximum chlorophyll-a concentrations reached by the nonlinear load-response curves. Indeed, the maximum allowable yearly averaged chlorophyll-a concentrations of 50 $\mu g.L^{-1}$ is only feasible in a limited area of the lake. These are regions where nutrient concentrations rise to unprecedented levels while light availability is sufficient for phytoplankton growth as for example in the northern bays. In the middle of the lake it seems that these high averages for chlorophyll-a concentrations cannot be reached due to high suspended matter concentrations (Zhang et al., 2014b).

In the second step of our analysis we determined the critical nutrient loads for different locations in the lake. The differences between and within load-response types, result in a range of critical nutrient loads for Lake Taihu. Besides, critical nutrient loads depend on the maximum allowable chlorophyll-a concentrations because of the gradual slope in Taihu's nonlinear load-response curves. Therefore, for multiple maximum allowable chlorophyll-a concentrations, a range of critical nutrient loads have been defined.

The low critical nutrient loads in the lake center are noteworthy in this respect. As mentioned in the validation process, the critical nutrient load has the risk to be underestimated in the lake center due the absence of wind-driven floating phytoplankton movement within the model. Adding floating phytoplankton to the model is far from trivial, thus we restrict ourselves to a thought experiment to elucidate the effect of this shortcoming. Intuitively, addition of wind-driven floating phytoplankton movement could improve the critical nutrient load prediction. Likely, this addition will lead to lower predicted phytoplankton biomass in the lake center where they are skimmed and to higher predicted phytoplankton biomass at the northwestern shores where they accumulate. Hence, the extended model will show higher critical nutrient loads at the lake center and will show lower critical nutrient loads at the northwestern shores. This difference between the potential extended and the present model, points us at interesting aspects in the theory of critical nutrient loading within a spatial context. Indeed, the extended model probably approximates better where the problems become apparent. However, the present model might better in indicating where the problems arise. While good localizations of problems are important for symptom treatment, they will not help to localize the problem's origin. It is like mopping the floor, without checking whether the tap still runs.

To check if the critical nutrient loads from our study still make sense, we compared our results with other studies (Table 6.1). First we made a comparison with historical measurement data. From these data we know that blooms have occurred at nutrient loads of around 0.4 $gP.m^{-2}.yr^{-1}$ and 8 $gN.m^{-2}.yr^{-1}$ (Yan et al., 2011). Furthermore, previous regime shift analysis with data of Lake Taihu suggest a regime shift between late 1980s and early 1990s when nutrient loads were between 0.38-0.58 $gP.m^{-2}.yr^{-1}$ and 7.6-15 $gN.m^{-2}.yr^{-1}$ (Xu et al., 2015a; Yan et al., 2011). These load values just exceeded our predicted critical nutrient loads for the minimum allowable chlorophyll-a concentration of 20 $\mu g.L^{-1}$. Our results are thus well in line with historical data.

Next we make a comparison with lab experiments. In the bioassay study by Xu et al. (2015b), nutrient thresholds were defined based on the maximum allowable chlorophyll-a concentration of 20 $\mu g.L^{-1}$. It appears that our model simulations predict lower critical nutrient loads than found by Xu et al. (2015b). This is especially true for the phosphorus threshold. An explanation for this discrepancy could be neglected lake-size-related processes in the bioassay such as wind forces that act on the sediment. Bioassays could therefore be regarded as "small lakes" of which earlier studies found that critical values are lower (Van Geest et al., 2003; Janse et al., 2008). Estimating critical nutrient load using bioassays have thus the risk of overestimation. The deviation is unlikely caused by the lacking floating phytoplankton transport in the model because higher chlorophyll-a at one location is probably compensated by lower concentrations elsewhere. Additionally the chlorophyll-a estimations for Meiliang Bay in the validation step were reliable.

Finally, we compare our results with the empirical model of Vollenweider, 1975. The phosphorus thresholds found by Vollenweider fall well in the range of what is found in our analysis (20 $\mu g.L^{-1}$ - 30 $\mu g.L^{-1}$). Vollenweider's thresholds for the nitrogen are slightly lower than what have been found in our study (20 $\mu g.L^{-1}$ - 30 $\mu g.L^{-1}$).

These comparisons give us confidence in our results, and allow us to discuss the aspects of SEBA with respect to methodology, scientific insight and societal applicability.

Methodological aspects of SEBA

In this study, we introduced the novel technique of *Spatial Ecosystem Bifurcation Analysis* (SEBA). In contrast to conventional methods such as Vollenweider's models and bioassays, SEBA indicates spatial variation in the critical nutrient loads. Spatial variation is, together with temporal variation and methodological anomalies, a major factor in the uncertainty of the critical nutrient loads (Janse et al., 2010). Therefore, SEBA elucidates an important part of critical nutrient load uncertainty. The spatial patterns in critical nutrient loads give important insights in the most vulnerable regions of Lake Taihu. Interestingly, we found that vulnerability of regions to nutrient load depends on the maximum allowable chlorophyll-a concentration. With increasing maximum allowable chlorophyll-a concentrations, the most vulnerable region moves from the center of Lake Taihu towards the borders of the northern bays. Indeed, the 2007's water crisis started at a drinking water station in one of these northern bays (Qin et al., 2010; Zhang et al., 2010). This is important information for drinking water companies.

Compared to 0D-models used in classical ecosystem bifurcation analysis, SEBA requires longer computational time due to the spatial grid, as well as due to the threefold increase to reach equilibrium due to advection and diffusion. With the present increase in computational power, calculation time is less of an issue.

Scientific aspects of SEBA

SEBA allows for unique insights in local responses of large lake ecosystems such as Taihu and should be applicable to spatially heterogeneous ecosystems suffering from eutrophication in general. First, the wide range of load-response curves and critical nutrient loads shows that simple theory (e.g. Scheffer et al., 2001) breaks down in heterogeneous lakes. Critical nutrient load as estimated by conventional methods such as Vollenweider and bioassays will result in one single value which is not always representative for the whole lake (Janssen et al., 2014). Indeed one may question the meaning of this value, if the variation in critical nutrient loads is huge. SEBA leads to a range of critical nutrient loads that apply to different locations. The highest critical nutrient load within the range marks the load at which the first improvements appear. The lowest critical nutrient load marks the load at which the risks on blooms in the entire lake are diminished.

Second, dynamics of Lake Taihu can only be understood when connectivity is taken into account. Within Taihu we found relatively isolated regions such as Dong Taihu Bay. In these regions, prevailing processes such as eutrophication and wind forces that govern major part of the lake are locally unimportant. This can explain why macrophytes still prevail in Dong Taihu Bay, notwithstanding the high eutrophication (Zhao et al., 2013). A simple 0D-model simulation based on average values of Lake Taihu likely leads to wrong conclusions for Dong Taihu Bay. Critical nutrient loads can thus only be understood if connectivity is accounted for.

An important next step would be to identify the dependence of critical nutrient loads on the TN:TP ratio of the nutrient load. For simplicity, here we assumed a fixed TN:TP ratio. Xu et al. (2015b), however, assumed P-limitation while defining the critical N-load and vice versa assuming N-limitation to establish the critical P-load. The best solution probably lies in the middle since in nature the TN:TP ratio changes due to natural variability and human activities (Beusen et al., 2016). Information on the dependency of critical nutrient loads on the TN:TP ratio will contribute to the ongoing debate on nutrient control for lakes. In a previous study on Lake Taihu the need for dual nutrient management is expressed (Paerl et al., 2011b). In a dual management approach, the TN:TP load ratio is kept constant. Others suggest that the ratio in loads could be used to promote specific desired species as each species has its optimal TN:TP ratio (Anderson et al., 2002).

Finally, SEBA can be applied to other stressors as well. For instance, heavy metals pesticides or pharmaceuticals are major threats to aquatic ecosystems. Like we have done here for chlorophyll-a, critical thresholds for these stressors can be determined spatially as well. Another interesting future step is to look after the effect of climate change to critical nutrient loads as this might be a major factor changing the hydrodynamics of lakes and thereby the spatial patterns.

Societal aspects of SEBA

The information on the spatial pattern of critical nutrient loads in Taihu will help managers to develop restoration strategies more effectively. Managers have two options. First, in order to prevent any exceedance of the maximum allowable chlorophyll-a concentrations, managers could aim to reduce the present nutrient load below the lowest critical nutrient load found within the entire lake (law of the minimum). For Taihu this will mean a reduction of at least 15% of the present phosphorus load and over 20% of the nitrogen load to meet the standards of the 50 $\mu g.L^{-1}$ chlorophyll-a. To reduce structural emergence of blooms of 20 $\mu g.L^{-1}$ chlorophyll-a, nutrient loads need a more drastic reduction of nearly 90% of both nitrogen and phosphorus. However, if little exceedance of chlorophyll-a concentrations is allowed in certain areas of the lake, managers could select for the second option for which the reduction may be less strong. In that case managers could assign specific societal functions to certain parts of a lake. Societal functions with strict requirements to chlorophyll-a concentration can then be assigned to the least vulnerable regions.

Conclusion

SEBA (*Spatial Ecosystem Bifurcation Analysis*) provides detailed insights in the critical nutrient loads of large shallow lakes. These insights help lake managers in realizing spatially explicit management goals. Indeed it gives a better understanding of the critical nutrient loads throughout the lake, the local vulnerability to harmful phytoplankton blooms and the local recovery trajectories. We conclude that nutrient loads of Taihu have to be more than halved to reach chlorophyll-a concentrations of 30-40 $\mu g.L^{-1}$ in most sections of the lake. Preventing structural emergence of phytoplankton blooms containing 20 $\mu g.L^{-1}$ chlorophyll-a throughout Lake Taihu requires a more drastic nutrient load reduction of nearly 90% of both phosphorus and nitrogen. We feel that our approach contributes to the growing societal interest in critical nutrient loads of lakes such as Taihu and of spatially heterogeneous ecosystems in general.

Table 6.1. Overview of critical loads per unit area of lake surface for Lake Taihu, calculated by our study and others.

Method	Critical P-load		Critical N-load		N:P	Reference
	Lower	Upper	Lower	Upper	N:P	
	gP.m^{-2}.yr^{-1}	gP.m^{-2}.yr^{-1}	gN.m^{-2}.yr^{-1}	gN.m^{-2}.yr^{-1}	(-)	
Spatial Ecosystem Bifurcation Analysis (2D model)						
20 μg.L^{-1} chlorophyll-a threshold *	<0.12	0.19	<2.4	3.8	20	This study
30 μg.L^{-1} chlorophyll-a threshold *	<0.12	0.27	<2.4	5.4	20	This study
40 μg.L^{-1} chlorophyll-a threshold *	0.25	0.47	5	9.4	20	This study
50 μg.L^{-1} chlorophyll-a threshold *	0.32	0.78	6.4	15.6	20	This study
Field data						
Measurement data	<0.4		<8		20	Yan et al., 2011
Lab experiment						
Bioassay	0.70**		6.71**		-	Xu et al., 2015b
0D model						
Vollenweider (oligotroph->mesotroph)	0.12		1.84		15	Vollenweider, 1975; Janssen et al., 2014
Vollenweider (mesotroph->eutrotroph)	0.24		3.67		15	Janssen et al., 2014; Zhang et al., 2014b

* Variation defined as mean (μ) plus or minus the standard deviation (σ).

** At a threshold of 20 μg.L-1 chlorophyll-a, the concentration at which bloom formation is expected in Taihu according to Xu et al. (2015b).

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Chapter 7

Discussion

"May 2013 – Silence. The roar of the city is far behind and leaves us alone with the wind that rustles the reeds along the shores. I see water, as far the horizon reaches. This huge lake has been praised, beloved and been sung for its great beauty. It is all history. Yet, I'm overwhelmed by the stench that can already be smelled from a far distance. At the shores I see accumulation of algae, as blue-green and syrupy as paint can be. Concrete embankments replace the riparian wetlands for flood control; huge vacuum cleaners suck algae from the lake water; and channels are dammed to prevent the further distribution of algae. This lake used to have great importance for food supply, drinking water and public health, but now it has turned into a toxic soup with only remnants of its former glory. How can this lake regain its health?" – Annette Janssen

Many ecosystems on earth have deteriorated. We have seen the deterioration of Lake Taihu due to increased anthropogenic pressure that finally led to the emergence of persisting toxic algal blooms (chapter 2). In the future, anthropogenic pressure will increase even more due to a growing world population (United Nations, 2015). Therefore, it is of great importance to find ways to keep the effect of the anthropogenic pressure within the margins of the safe operating space (cf. Rockström et al., 2009a). Critical nutrient loads mark these margins of the safe operating space of lakes with respect to eutrophication. The research objective of this thesis is *"to determine the critical nutrient load for Lake Taihu".* In this final chapter, I discuss Taihu's critical nutrient loads in five steps. First, I will reflect on the quadripartite puzzle of the research approach as introduced in chapter 1 (Figure 1.2). Next, I discuss the resulting critical nutrient loads that were found for Lake Taihu. Third, I will reflect on the limitations and uncertainties in the research approach and the results. Fourth, I will sketch possible restoration methods for Lake Taihu. Finally, I discuss the urgency of restoring Lake Taihu and come back to the concept of megacities that I started this thesis with.

Research approach: diversity as overarching topic

To solve the quadripartite puzzle introduced in chapter 1 (Figure 1.2), I used ‘diversity’ as the overarching theme: diversity in lakes, in models, in spatial patterns and in global features. Like biodiversity encompasses the variability of life covering the full width of niches, diversity in research provides variability in perspectives which contribute to the full understanding (Janssen et al., 2015). This thought is applied repeatedly throughout this thesis.

The first piece of the puzzle concerns the diversity in lakes. The great diversity in lakes on earth is an excellent opportunity to explore the generality within critical nutrient loads (chapter 2). To a certain extent, using the knowledge on a diverse set of lakes helps to overcome the ‘N=1 problem’. According to the N=1 problem, each lake is unique and therefore a ‘one-size-fits-all’ solution is impossible. However, lakes share similar limnological processes that govern their ecology. Looking at the generality between lakes, therefore, provides information on specific lakes. *The outcome of this chapter suggests that alternative stable states are unlikely to occur in Lake Taihu because of its large size. Although, if connectivity allows, there might be regions existing that show potential to exhibit local alternative stable states.*

The second piece of the puzzle concerns the diversity in models (chapter 3). Exploring the diversity in models provides an overview of available modelling tools. There is an ongoing development in aquatic ecosystem modelling, leading to diversity in modelling methods. A comparison of models reveals the complementarity as well as the redundancy between models. With an overview at hand, the diversity in models can be fully exploited. From the set of modelling methods that fit the aim of the research (in this case defining critical nutrient loads), the ‘fittest’ model can be chosen. The ‘fittest’ model suits the niche (i.e. is able to answer the research question) and is at the same time available at relatively low costs, including limited learning and time investments. Next, the diversity in models can be further evolved in order to better fit the purpose of this thesis: finding critical nutrient loads for Lake Taihu. *From the long list of* *available models I chose to use PCLake in further analysis because it appeared the most extensively used food web model for aquatic ecosystems applied for bifurcation analysis. The advantage of PCLake over other eutrophication models is its focus on the competition between three types of phytoplankton (diatoms, green algae and cyanobacteria) and macrophytes within a freshwater food web. To enable 2D-simulations, PCLake has been coupled to a simple hydrodynamic model from Van Gerven et al. (2016) and a more complex hydrodynamic model from Liu (2013).*

The third piece of the puzzle concerns the diversity in nutrient sources. I looked at the spatial heterogeneity in the distribution of nutrients and primary producers in lakes, emerging from a diverse range of nutrient sources to lakes (chapter 4). Nutrient loads of lakes are generally defined as nutrient masses putting pressure on a meter squared per time unit (i.e. surface area corrected load). Expressing nutrient load in this way results in a generic number that can be used for comparison of loads between lakes of different size. At the same time, a surface area corrected nutrient load doesn't necessarily preclude the effect of different nutrient source types. Nutrient loads to lakes can be supplied in diverse ways varying from atmospheric deposition and river input to groundwater flows. As noted in chapter 4, the diversity in nutrient loads is generally distinguished by point and diffuse sources. As a result, the spatial pattern of nutrients, macrophytes and algae in lakes depends on the type of nutrient source. Additionally, the dispersion of nutrients within the lake reinforces diversity in spatial patterns. The effect of restoration measures is shown to depend on the spatial patterns of lakes. Hence, equally sized lakes receiving an equal nutrient load, but from different nutrient source, may require different restoration methods. *Based on these results I show that spatial characteristics that are related to a point loaded drainage lake such as Taihu, will not allow for alternative stable states. Therefore, biomanipulation is not recommended as a successful measure for Lake Taihu. Additionally, residence time reduction by flushing will probably not be* *successful either. Nutrient reduction, on the other hand, is expected to be the most effective way to restore Lake Taihu.*

For the last piece of the puzzle, I place algal blooming in a global context. Lake size, depth, climate and sediment type are among the factors that differ between lakes. Due to varying local characteristics, their behavior to stressors like eutrophication is different as well. Yet, the processes which translate local characteristics to local behavior can be formulated in a generic way. In chapter 5 I propose a model with such generic formulation to describe algal blooming in freshwater lakes around the world. *The envisioned global projections of development of lake ecosystems around the world will help to understand local developments of lakes such as Taihu. Indeed, local changes of lake ecosystems are often related to global developments, for instance through their connection with rivers, soil and air but also through global climate change and global socio-economic developments.*

Finally, the overall picture which emerged from the quadripartite puzzle allows me to determine the critical nutrient load of Lake Taihu. In this final step I acknowledge spatial diversity within the lake characteristics which resulted in a better understanding of the spatial variation in critical nutrient loads within Lake Taihu (chapter 6). Accounting for spatial diversity of lake characteristics, reveals the most vulnerable regions of a lake to eutrophication. Besides, it gives insight in the boundaries of the 'safe operating space'. *It appears that there is not just one critical nutrient load for Taihu. Instead, the model output shows a range of critical nutrient loadings depending on the local characteristics at specific locations of the lake. This approach helps to reduce the uncertainties in the critical nutrient load of Lake Taihu. These insights would be missed using a method that ignores spatial heterogeneity in lake characteristics.*

Results: critical nutrient loads of Lake Taihu

The search for critical loads has enriched the understanding of the limits to Taihu's 'safe operating space'. This increased understanding emerges from the diversity in lakes are studied, the methods that are used, the load types that are analyzed, the global developments that considered as well as the characteristics of a specific lake that are accounted for. The result is more than a single value that indicates the critical nutrient load. It provides a range of values that mark a diffuse border of the safe operating space. But what is the meaning of these values?

First, the critical nutrient load values indicate the possible degree of recovery given a certain effort. The highest value of the range marks the onset of recovery. According to our results, reducing Taihu's risk of serious toxic algal blooms characterized by 40 $\mu g.l^{-1}$ chlorophyll-a (Xu et al., 2015b) starts if the present load is reduced to about 50% for both nitrogen and phosphorus. Note that, according to our findings, such a reduction will be just the start of recovery, and will not eliminate the risk of toxic algal blooms within the entire lake. To prevent structural emergence of algal blooms containing 20 $\mu g.L^{-1}$ chlorophyll-a in Lake Taihu, a drastic nutrient load reduction of nearly 90% of both nitrogen and phosphorus is required. Limited risk within this spatially heterogeneous large shallow lake is thus related to restoration of the weakest link. This weakest link is given by the lowest critical nutrient load of Lake Taihu. If nutrient load exceeds the Taihu's lowest critical nutrient load, risks of algal blooms will be substantial for parts of the lake.

Secondly, the range of critical nutrient load indicates the path of recovery. Each step in the load reduction leads to local improvements, which in turn contribute to a total recovery. This is in contrast to the recovery pattern seen in small shallow lakes where recovery is believed to be abrupt and simultaneous within the entire lake (Scheffer et al., 1993; Scheffer et al., 2007). The critical nutrient load of Lake Taihu thus marks a diffuse border of the safe operating space, rather than a specific point of change.

Although costs and efforts may be higher, it is worth taking a safe distance by reducing the nutrient load to Lake Taihu below the lower critical nutrient load. A reduction to the lowest critical nutrient load will prevent structural exceedance of the 'safe operating space', but there is always a possibility that extreme events will occur. Examples of these extreme events are periods of high lake water temperature or with water level rise (Mooij et al., 2007; Kong et al., 2016). In these cases the lake ecosystem needs a buffer to prevent the occurrence of occasional algal blooms (Mooij et al., 2007). A reduction below the lowest critical nutrient load will create such buffer.

Reflections on the research approach and the results

Identifying critical nutrient loads, the main topic of this thesis, has its limitations and is bound to uncertainties. I use diversity as an overarching topic in this thesis in an attempt to overcome these limitations and uncertainties. However, this approach does not cover all limits and uncertainties. Here I would like to discuss five major aspects of these limits and uncertainties. These are 1) adopting an equilibrium versus a transient approach, 2) balancing tradeoffs between generality and specialty, 3) handling data limitations, 4), dealing with heterogeneity and 5) ignoring important processes.

1) Adopting an equilibrium versus a transient approach

I used the equilibrium approach throughout this thesis, as opposed to focusing at transient dynamics. The equilibrium approach as used in this thesis refers to a reoccurring seasonal pattern instead of a constant value. In reality, however, this 'seasonal equilibrium' is unlikely to occur because external conditions keep changing, for instance due to local and global changes. As a result, ecosystems continuously aim for a moving equilibrium which is never reached. Moreover, all kind of stochastic processes keep ecosystems away from their equilibrium state, including weather variations. Despite this fact, the equilibrium approach is commonly used to determine critical nutrient loads of, for instance, lakes (e.g. Scheffer, 1990; Janse, 1997; Janssen et al., 2014). A major reason for this practice can be found in the difficulty to define the exact initial conditions of ecosystems on which the transient dynamics heavily depend.

2) *Balancing tradeoffs between generality and specialty*

When choosing or developing a model for a given purpose, there are tradeoffs between generality and specialty. One can argue whether it is feasible, or even desirable, to develop a 'one-size-fits-all' model of aquatic ecosystems. There may be tradeoffs between the necessary level of generality of such a model to be widely applicable and the necessary level of detail to produce insightful and useful projections for specific systems. For instance, one may argue that one of the strengths of PCLake is that it zooms in on shallow lakes, foodweb dynamics and alternative stable states, while ignoring spatial heterogeneity, stratification and hydrodynamics. This results in a focused model that can still be linked with theoretical ecology, has short run times and is recognized as a 'major' model within its own niche (Janssen et al., 2015). PCLake was originally developed for shallow lakes within the temperate zone (Janse et al., 2010). At this moment, however, the model has shown a wider applicability than was originally anticipated by its developers. Examples are studies on food web theory (Kuiper et al., 2015), on lakes in different climate zones (Kong et al., 2016) and on spatial aspects within lakes (chapters 4 and 6). In chapter 5, I propose to stretch the application of the model even further. Only future studies can prove whether this is a wise direction.

3) *Handling data limitations*

Data limitations are an often-heard complaint by researchers and this applies to this study as well. Restrictions on the availability of model input data required making assumptions on, for example, nutrient loads. Taihu is connected to many canals, ditches, streams and rivers which are not all sampled individually for their nutrient input contribution. Our findings are thus limited to the influx of nutrients from the most important river connections. Additionally, the limitations in the spatial coverage of the data restricted the spatial validation of the output to mainly the north part of Lake Taihu. Results on the south part of the lake can thus be considered as spatial extrapolations of validated processes in the north.

4) *Dealing with heterogeneity*

In this thesis, I showed several times how spatial heterogeneity affects the outcome of the analysis. The impact of different types of water and nutrient input on the distribution of biota and the effectiveness of recovery strategies in chapter 4 is a good example. Important spatial factors are included in this study such as spatial differences in fetch and depth. Some other spatial factors have been neglected, however, simply because information on these factors was unavailable to us. For instance, while identifying the critical nutrient load within Lake Taihu, we assumed a silty sediment type with unified grain coarseness. While silt is indeed the main sediment type within Lake Taihu, there are certainly spatial differences that could affect the findings for this lake. The estimation of the critical nutrient load in this thesis should therefore be taken as an approximation which has been improved by including some aspects of spatial heterogeneity but is still open for improvement. It also shows that we should not consider critical nutrient loads to be a single number.

5) *Ignoring important processes*

In the identification of critical nutrient loads I aimed to include the most important processes that affect these thresholds, while excluding processes that I considered to be of less importance in order to avoid over-complexity. This choice was made beforehand. After analyzing the results, however, the importance of processes can be re-evaluated, potentially leading to new research foci. In this study, this is the case with floating algal blooms. In contrast to algae in the water column, floating algae can be transported by wind against the prevailing water flow direction. This process could be an explanation for the overestimation of algal biomass in the lake center by the model. Therefore, critical nutrient loads at locations where these algae emerge are possibly underestimated and critical nutrient loads at locations where these algae end up are possibly overestimated. A major step forward in determining critical nutrient loads within a spatial context would be thus the inclusion of algal buoyancy and wind-driven horizontal transport of floating algae.

Possible pathways for restoration of Lake Taihu

Given the derived critical nutrient load, what does it take to reach good ecological status for Lake Taihu? There are multiple ideas on how to restore lakes. In this respect, three types of measures are generally mentioned; (i) stress release e.g. by nutrient input reduction, (ii) increasing the resilience e.g. by a decreased retention time and (iii) forcing a good state e.g. by biomanipulation (Janse et al., 2008). Stress release by nutrient reductions focuses directly on the causal pathway to achieve the clear water state, whereas the other two measures are indirect 'tricks' to manipulate the system. Applying biomanipulation for Taihu will be, most likely, fighting a losing battle, because of absence of the required alternative stable states (chapter 4 and 6). Additionally, due to the size of Lake Taihu, applying biomanipulation is unrealistic since it will be impossible to catch all fish. Retention time reduction will have little success (Qin et al., 2010), as Taihu is a drainage lake with mainly point sources (chapter 4). Beside retention time reduction, there are other options to increase the resilience of Lake Taihu such as allowing for water level fluctuations and restoration of wetlands. Allowing for natural water level fluctuations in Lake Taihu is, however, limited because of Lake Taihu's function for flood control (Qin et al., 2007; Yang et al., 2010). Wetland restoration, on the other hand, is suggested as a potential measure (An et al., 2007; Lu et al., 2007; Hu et al., 2010). Nutrient reduction, albeit costly and time consuming, may have the highest potential (Søndergaard et al., 2007; Conley et al., 2009). Internal loading delays the onset of recovery (Søndergaard et al., 2007), but the need for load reductions is widely recognized

(Conley et al., 2009). Until now, actions to reduce nutrient input to Lake Taihu included e.g. regulating waste from Chinese industries. The effect was, however, short-term as input of other wastes have concurrently increased (chapter 2). The current Chinese policy plans on “Zero Growth in Synthetic Fertilizers after 2020”, aiming to stop growth in synthetic fertilizers and to recycle 60% of manure, will neither be sufficient to avoid eutrophication (Strokal et al., 2017; Wang et al., 2017). Hence, more effort to reduce nutrient loading to Taihu is required for instance by increasing nutrient use efficiencies in food production (Paerl et al., 2011b; Wang et al., 2017).

Nutrient load reductions face two major challenges, the first being related to the societal attitude to load reductions and the other to the technical possibilities for efficient and sustainable methods. First, nutrient reductions will only be applied if the societal attitude allows for it. Stakeholders are only willing to reduce nutrient load if it does not affect their own economic interests. Nutrient reductions, though, are commonly believed to harm the stakeholders’ economic position while negative consequences of high nutrient load on the ecosystem are generally ignored. Negative effects on an ecosystem of an increase in nutrient load are initially low due to ecosystem resilience (Scheffer et al., 1993). This may lead to low urgency perceived by polluters to reduce their nutrient emissions. Nutrient load is thus an ‘externality’, which is defined in economics as costs affecting third parties that did not intend to make these costs (Crocker et al., 1992). This principle holds a major risk. Negative effects due to nutrient loading are initially low, though eventually these negative effects become notorious, when nutrient loadings reach the threshold (Scheffer et al., 2007). If there are no incentives to reduce the nutrient load, the economic interest of each stakeholder will be eventually affected; a ‘tragedy of the commons’ (Good et al., 2011). External pressures such as regulations will help to enforce the necessary nutrient reductions.

A second challenge is to find an efficient and sustainable method to reduce nutrient load. As mentioned before, nutrients originate from a large variety of sources including industry, agriculture and urban run-off. Hence, nutrient reductions are required at multiple sources. Methods to reduce nutrients from these sources are distinguished between 'end-of-pipe' and 'process-integrated' solutions (Zotter, 2004). End-of-pipe solutions aim to remove nutrients before wastewater is released into the environment. The resulting nutrient rich residue is economically uninteresting because it is costly to dispose or process (Zotter, 2004). In contrast, process-integrated solutions prevent wastewater production by the recycling of byproducts and by implementing efficiency improvements. The complexity of process-integrated solutions is, however, often a major problem (Zotter, 2004). The most far-reaching option within process-integrated solutions is to build a circular economy in which all waste is considered a renewable source (Andersen, 2007). In such an economic system, economic growth is decoupled from environmental impact (Andersen, 2007; Geng et al., 2013). First steps to build a circular economy have been taken in China, but, like in most places around the world, there is still a bumpy road ahead (Geng et al., 2013).

Reasons for restoration

Achieving a healthy environment for Lake Taihu takes much effort: required nutrient reductions are substantial and there are considerable challenges to overcome. The question may arise whether the effort to restore Taihu's ecosystem would perhaps take too much effort. Would it be an option to proceed with business as usual? There are several reasons why adopting this 'Ostrich policy' would be disastrous.

First, societies depend on ecosystems like Lake Taihu. By overexploiting the source functions and overusing the sink functions of Lake Taihu, the societal functions of the lake are lost (e.g. An et al., 1998; Xu et al., 2015a). Drinking water becomes undrinkable, fish becomes inedible or extinct, and residents that live in the catchment suffer from health problems. Numerous studies have shown that the total economic value of intact or restored ecosystems is generally higher than the value of overexploited or degraded ecosystems (e.g. Balmford et al., 2002; Russi et al., 2013).

Second, not everything can be supplied from elsewhere. Obviously, earth offers many ecosystems. In the case of Taihu, drinking water could be abstracted, after water purification, from the Yangtze River. There are many options to purify heavily polluted water for drinking water (Metcalf et al., 2004), though costs may rise out of control. In the end, however, it is infeasible to replace all ecosystem services by technical substitutes. For instance, there are fish species on the menu that are hard to cultivate.

Last, the deterioration of an ecosystem may trigger the collapse of another ecosystem leading to a chain reaction. This might happen if, for instance, goods are taken from other locations in case of local shortage. The side effect is a translocation of anthropogenic stress, which could lead to the collapse of other ecosystems. At 20 June 2016, UNHCR-chief Filippo Grandi stated that “if you don’t solve problems at the root, the problems will come to you”, which points exactly at this phenomon of chain reactions. Filippo Grandi’s quote is a reaction to the discontent in Europe about the expansion in numbers of refugees in 2016. The increase in refugees is due to conflicts in e.g. Syria. It is believed that the Syrian conflict is triggered by droughts which led to ecological collapse (Van Schaik et al., 2014; Kelley et al., 2015). In turn, the drought is aggravated by the increase of greenhouse gasses and the related global warming (Kelley et al., 2015). This example of refugees thus clearly exemplifies how a chain reaction of collapses may emerge and shows the importance to tackling the problems at the roots, in order to avoid escalation.

Closing remarks

I started the introduction by asking what it takes to make cities run and end here with the question how lake ecosystems can recover. It is no coincidence that I asked these two questions since they both lie at the heart of critical nutrient loads. Indeed, exceedance of critical nutrient loads will hamper cities to run and staying below critical nutrient loads will lead to the recovery of lake ecosystems. To see what keeps cities running and how to regain the ecosystem's health, I take one last excursion to the ants' 'megacities'. Ants can be considered sophisticated farmers that are known to cultivate fungi at industrial scale (Shik et al., 2016). To maximize growth, the ant tribe *Attini* optimizes the protein supply to their 'crops'. A surplus of proteins leads to the development of inedible mushrooms and a shortage of proteins to a failure of their harvest (Shik et al., 2016). The protein supply of ants is analogous to eutrophication, the mushrooms are a metaphor for toxic algae and the optimum protein supply is a similitude for the critical nutrient load. I believe that to reach a sustainable future for ecosystems such as Lake Taihu, we could learn important lessons from these ants' megacities that run by optimizing their nutrient cycle while keeping their supportive 'ecosystem' healthy.

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Appendices

All appendices for this PhD thesis are available on the ftp server: ftp://annette:V00rjaar2017@ftp.nioo.knaw.nl/. On this ftp-server you can find the following appendices:

Appendix 1.	Bifurcation analysis with PCLake (published as supplementary material in Janssen et al. (2014)).
Appendix 2.	Determination of fetch (published as supplementary material in Janssen et al. (2014)).
Appendix 3.	AEMON Database (Published as supplementary material in Janssen et al. (2015)).
Appendix 4.	Data and analysis of a list of models in use by the participants of the third AEMON workshop. (Published as supplementary material in Janssen et al. (2015)).
Appendix 5.	Data and analysis of list of AEMs and hydrodynamic drivers. (Published as supplementary material in Janssen et al. (2015)).
Appendix 6.	Data and analyses of list of state variables of selected AEMs. (Published as supplementary material in Janssen et al. (2015)).
Appendix 7.	Model details to model four lake types.
Appendix 8.	DATM-file of the original PCLake.
Appendix 9.	Estimation of light at the water surface.
Appendix 10.	Estimation of evaporation.
Appendix 11.	Metadata database.

Appendix 12. Defining external nutrient load in a spatial context of SEBA. (Published as supplementary material in a slightly different form in Janssen et al. (2017)).

Appendix 13. Modelling details for SEBA. (Published as supplementary material in a slightly different form in Janssen et al. (2017)).

Appendix 14. DATM-file used to run PCLake in DELWAQ. (Published as supplementary material in a slightly different form in Janssen et al. (2017)).

Summary (English)

Last century, human population grew to an unprecedented level, thereby distorting global nutrient cycles. As a result, many ecosystems now face serious eutrophication, i.e. an excessive supply of nutrients to ecosystems. In lakes, eutrophication ultimately leads to toxic algal blooms. Lake Taihu (China) is notoriously famous in this respect. During the 1980s, the first algal blooms emerged in the lake, reaching disastrous proportions in 2007. During that year, the intake of drinking water had to be shut down and millions of people had to look for an alternative source of drinking water. This raises the question whether such problems can be avoided. Of crucial importance in avoiding and reducing toxic algal blooms is the identification of the maximum nutrient load ecosystems can absorb, while remaining in a good ecological state. *In this thesis, I aim to determine the critical nutrient load for Lake Taihu* (chapter 1). I approach the search for critical nutrient loads of Lake Taihu by completing a quadripartite puzzle. Each piece of the puzzle reveals part of the answer.

The first piece of the puzzle (chapter 2) covers the characteristics of large shallow lakes that determine the presence of macrophytes and algae in large shallow lakes. For small lakes, it has been repeatedly shown that the transition from a macrophyte rich to the algae dominated state can be abrupt following theory on alternative stable states. In chapter 2, I discuss whether these alternative stable states could also be expected in large shallow lakes, such as Lake Taihu. On the basis of three lake characteristics, lake size, spatial heterogeneity and internal connectivity, I look upon the lake's response along the eutrophication axis. I conclude that locations with prevailing size effects, such as the center of Lake Taihu, generally lack macrophytes and thus likely lack alternative stable states. However, the presence of substantial macrophyte biomass in large shallow lakes remains unexplained when only size effect is accounted for. By accounting for spatial heterogeneity, the presence of macrophytes and alternative stable states in large shallow lakes is better understood. Finally, internal connectivity is important since a high internal connectivity reduces the stability of alternative states. *Despite the shallowness of Lake Taihu, the outcome of this chapter suggests that alternative stable states are unlikely to occur in Lake Taihu because of the lake's size. Although there might be parts of the lake with the potential to exhibit alternative stable states if connectivity is low enough.*

For the second piece of the puzzle (chapter 3), I present a perspective on how to explore, exploit and evolve aquatic ecosystem models. I set off to explore model diversity by making an inventory among 42 aquatic ecosystem modelers by asking which models they use. As part of the inventory, I categorized the resulting set of models and analyzed the models for their diversity. I then focus on how to exploit model diversity by comparing and combining different aspects of existing models. Finally, I discuss how model diversity came about in the past and could evolve in the future. Exploring, exploiting and evolving aquatic ecosystem models helps to get grip on the available modelling methods for further research on the critical nutrient loadings of Lake Taihu. *From the long list of available models, I chose PCLake to use in further analysis because it is the most extensively used food web model applied for bifurcation analysis of shallow aquatic ecosystems. The advantage of PCLake over other eutrophication models is its focus on the competition between three types of phytoplankton (diatoms, green algae and cyanobacteria) and macrophytes within a freshwater food web. To enable 2D-simulations, PCLake has been coupled to a simple and a more complex hydrodynamic model.*

For the third piece of the puzzle (chapter 4), I analyze the hitherto neglected effect of the type of nutrient source in combination with the internal distribution of nutrients on ecosystem recovery. I compared the effect of different restoration measures in four types of lakes with contrasting nutrient input (e.g. point or diffuse nutrient loading) and distribution patterns (e.g. seepage or drainage lakes). Point sources of nutrients are local foci of nutrient input while diffuse sources are broadly distributed, resulting in spatially more homogeneous nutrient input. Seepage lakes receive water input mainly from ground or atmosphere whereas drainage lakes receive water from rivers. I show that the spatial dissimilarities which result from different water and nutrient source types determine restoration effectiveness. These spatial dissimilarities are particularly evident in the spatial patterns of the eutrophication level, which is defined as the local nutrient concentration. It appears that the nutrient load type determines the spatial position of the highest eutrophication levels, while the distribution of nutrients by water skews the spatial patterns of eutrophication levels. *Based on these results, I show that spatial characteristics that are related to point loaded drainage lakes such as Taihu, will not allow for alternative stable states. Therefore, biomanipulation is not recommended as a successful measure for Lake Taihu. Additionally, residence time reduction by flushing will probably be not successful either. Nutrient reduction, on the other hand, will probably be the most effective way to restore Lake Taihu.*

In the last piece of the puzzle (chapter 5), I aim to place lake modelling in a global context. Like Taihu, many lake ecosystems are under pressure as a result of anthropogenic activities. To anticipate these global changes, projections of future developments are crucial. Based on socio-economic scenario runs, mathematical models could project these possible future global developments. First, the requirements for the ideal global model are defined, based on (i) an aquatic ecosystem component with global applicability, (ii) a transport component that connects the lakes within a global network, and (iii) an environmental component that accounts for major anthropogenic pressures. Subsequently, a proposal towards a global model using existing components is presented. As a starting point, I selected the existing aquatic ecosystem model PCLake as the aquatic ecosystem component, with the global water flow model PCR-GLOBWB and the nutrient flow model GNM as transport components and the integrated model to assess the global environment IMAGE as the environmental component. With these components as building blocks, I start making projections of algal blooms in lakes. Major challenges for future applications are improving the mathematical formulations for deep lakes, improving the transport estimates for small lakes, expanding the dataset of water quality variables, continuing the multidisciplinary working approach and including more nutrient cycles. *The envisioned global projections of development of lake ecosystems around the world will help to understand the dynamics of lakes such as Taihu. Indeed, changes of particular lake ecosystems are often affected by global developments, for instance through their connection with rivers, soil and air but also through global climate change and global socio-economic developments.*

The completed quadripartite puzzle (chapter 6) allowed me to determine the maximum nutrient load Lake Taihu can absorb, while remaining in a good ecological state (chapter 6). The critical nutrient loadings depend on the shape of the load-response curves. Due to spatial variation within Lake Taihu, its load-response curves and therefore critical nutrient loads vary throughout the lake. Furthermore, critical nutrient loads depend on management goals*, i.e.* the maximum allowable chlorophyll-a concentration. *According to the model results, total nutrient loads need to be more than halved to reach chlorophyll-a concentrations of 30-40 µg.L*$^{-1}$ *in most sections of the lake. To prevent phytoplankton blooms with 20 µg.L*$^{-1}$ *chlorophyll-a throughout Lake Taihu, both phosphorus and nitrogen loads need a nearly 90% reduction.*

The implications of these findings for Lake Taihu are discussed in chapter 7. Diversity emerges as an overarching topic throughout this thesis: diversity in lakes, diversity in models, diversity in spatial distribution of nutrient and water sources, diversity in the development of lakes around the earth and finally diversity within specific lakes. This approach has resulted in a range of critical nutrient loads for different parts of Lake Taihu. This range contrasts to the single point of recovery that is often found for small shallow lakes. The range in critical nutrient loads found for Lake Taihu can be interpreted as providing a path of recovery for which each step leads to water quality improvement in certain parts of the lake. To reach total recovery, nutrient reduction seems to be the most promising management option. The large effort needed for full recovery raises the question what would happen when we would continue business as usual. I argue that adopting this ‘Ostrich policy’ would be disastrous because of: (i) the dependency of societies on ecosystems like Lake Taihu, (ii) the difficulty to replace lost resources and (iii) the chance of triggering a chain reaction of other collapses in either nature or society. *This brings me to the conclusion that solving the eutrophication problems in Lake Taihu will take considerable effort. Nutrient load reduction is the most promising restoration measure. Along the path of recovery local improvements will become apparent. Finally, these local improvements will lead to total recovery.*

Summary (Nederlands)

De menselijke bevolking op aarde is de vorige eeuw uitgegroeid tot een ongekend niveau met de verstoring van de wereldwijde nutriëntenkringlopen als gevolg. Veel ecosystemen worden nu geconfronteerd met ernstige eutrofiëring, d.w.z. een te grote toevoer van voedingsstoffen naar de ecosystemen. In meren leidt eutrofiëring uiteindelijk tot toxische algengroei. Taihu (China) is berucht in dit opzicht. Tijdens de jaren 80 ontstond de eerste algenbloei in het meer welke uitgroeide tot rampzalige proporties in 2007. In dat jaar moest de inname van drinkwater worden stilgelegd en miljoenen mensen werden gedwongen op zoek te gaan naar een alternatieve bron van drinkwater. Dit roept de vraag op of dergelijke problemen kunnen worden vermeden. Van cruciaal belang bij het voorkomen en het verminderen van giftige algenbloei is de identificatie van de maximale nutriëntenbelasting die ecosystemen kunnen absorberen, terwijl een goede ecologische toestand gegarandeerd blijft. *In dit proefschrift bepaal ik de kritische nutriëntenbelasting van Taihu* (hoofdstuk 1). De zoektocht naar kritische nutriëntenbelasting van Taihu bestaat uit het oplossen van een vierdelige puzzel. Elk stukje van de puzzel onthult een deel van het antwoord.

Voor het eerste stuk van de puzzel (hoofdstuk 2) zoek ik naar de kenmerken van meren die de aanwezigheid van waterplanten (macrphyten) of algen bepalen. Voor kleine meren is meerdere malen aangetoond dat de overgang van een macrofytrijke staat naar een algen gedomineerde staat abrupt kan verlopen. Deze overgang is in detail beschreven in de theorie van alternatieve stabiele toestanden. In hoofdstuk 2 bespreek ik de vraag of deze alternatieve stabiele toestanden ook in grote, ondiepe meren, zoals Taihu verwacht kunnen worden. Aan de hand van drie kenmerken, meer grootte, ruimtelijke heterogeniteit en interne hydrologische connectiviteit, bekijk ik hoe het meer langs de eutrofiërings-as zich ontwikkelt. Ik concludeer dat op locaties waar de grootte van het meer van belang is, zoals het centrum van Taihu, er een algemeen gebrek aan waterplanten zal zijn. Deze locaties zullen dus waarschijnlijk geen alternatieve stabiele toestanden vertonen. Echter blijft de aanwezigheid van macrofyten in grote, ondiepe meren onverklaard, wanneer de analyse zich beperkt tot het effect van de grootte van het meer. Door ruimtelijke heterogeniteit mee te nemen in de analyse is de aanwezigheid van waterplanten en alternatieve stabiele toestanden in grote, ondiepe meren beter begrepen. Daarnaast is interne hydrologische connectiviteit belangrijk. Een grote interne connectiviteit vermindert de stabiliteit van alternatieve toestanden. *Ondanks dat Taihu een ondiep meer is, laten de uitkomsten van dit hoofdstuk zien dat alternatieve stabiele toestanden waarschijnlijk niet voorkomen in Taihu vanwege de grootte van het meer. Mogelijk zijn er wel delen van het meer met het potentieel om alternatieve stabiele toestanden te vertonen als de connectiviteit laag genoeg is.*

Voor het tweede stuk van de puzzel (hoofdstuk 3), presenteer ik een perspectief op hoe we ecosysteemmodellen kunnen exploreren, exploiteren en hoe ze in de toekomst kunnen evolueren. De diversiteit aan aquatische ecosysteemmodellen heb ik in kaart gebracht met behulp van een inventarisatie onder 42 aquatisch ecosysteemmodelleurs. Als onderdeel van de inventarisatie, heb ik de resultaten gecategoriseerd en de resulterende set modellen geanalyseerd op verschillen. Vervolgens heb ik gekeken naar hoe we modeldiversiteit kunnen benutten door het vergelijken en combineren van verschillende aspecten van bestaande modellen. Tot slot laat ik zien hoe modeldiversiteit tot stand is gekomen in het verleden en kan evolueren in de toekomst. *Onderzoeken van exploratie, exploitatie en evolutie van aquatisch ecosysteemmodellen helpt om grip te krijgen op de beschikbare modellen voor verder onderzoek naar de kritische nutriëntbelasting van Taihu. Van de lange lijst met beschikbare modellen, koos ik PCLake voor de verdere analyse, want het is het meest intensief gebruikt voedselweb-model bij bifurcatieanalyse van ondiepe aquatische ecosystemen. Het voordeel van PCLake ten opzichte van andere eutrofiëringsmodellen is de focus op de competitie tussen drie functionele groepen fytoplankton (diatomeeën, groenalgen en cyanobacteriën) en waterplanten binnen een zoetwater voedselweb. 2D-simulaties zijn mogelijk gemaakt door PCLake te koppelen aan een eenvoudig en complex hydrodynamisch model.*

Voor het derde puzzelstuk (hoofdstuk 4) analyseer ik het tot dusver verwaarloosde effect van het type voedingsbron in combinatie met de verdeling van nutriënten binnen het ecosystem op het herstel van ecosystemen. Ik vergelijk het effect van verschillende waterbeheersmaatregelen in vier meren met contrasterende nutriënteninput (punt of diffuse nutriënten) en nutriëntdistributiepatroon (bijvoorbeeld kwel- of drainagemeren). Puntbronnen van nutriënten zijn plaatselijke foci van nutriënten terwijl nutriënten uit diffuse bronnen ruimtelijk homogener worden verdeeld. Kwelmeren ontvangen waterinvoer hoofdzakelijk uit de grond of atmosfeer terwijl drainagemeren water ontvangen van rivieren. Het blijkt dat de ruimtelijke verschillen, die voortvloeien uit verschillen in water en voedingsstof brontypes, de effectiviteit bepalen van herstelmaatregelen. Deze ruimtelijke verschillen zijn vooral duidelijk in ruimtelijke patronen van het eutrofiëringsniveau, gedefinieerd als plaatselijke nutriëntenconcentratie. Het blijkt dat het type nutriëntbelasting bepaalt waar in het meer het hoogste eutrofiëringsniveau zich zal bevinden, terwijl het type waterbron de ruimtelijke gradiënt van het eutrofiëringniveau sterker of zwakker maakt. *Gebaseerd op deze resultaten, laat ik zien dat ruimtelijke kenmerken die gerelateerd zijn aan een punt belast drainage meer zoals Taihu, de aanwezigheid van alternatieve stabiele toestanden onwaarschijnlijk maakt. Daarom wordt biomanipulatie niet aangeraden als een herstelmaatregel voor Taihu. Daarnaast zal de reductie van de verblijftijd door het meer door te spoelen waarschijnlijk niet succesvol zijn. Vermindering van nutriënteninput zal waarschijnlijk de meest effectieve manier zijn om Taihu herstellen.*

In het laatste stukje van de puzzel (hoofdstuk 5), streef ik ernaar om meren te plaatsen in een mondiale context. Net als Taihu, staan ook andere meren onder druk als gevolg van menselijke activiteiten. Om te anticiperen op deze mondiale veranderingen zijn projecties van toekomstige ontwikkelingen cruciaal. Op basis van sociaaleconomische scenario's kunnen wiskundige modellen de mogelijke toekomstige ontwikkelingen van meren in de wereld projecteren. Ik heb allereerst de eisen voor een ideaal mondiaal model gedefinieerd, op basis van (i) een aquatisch ecosysteem component met de wereldwijde toepasbaarheid, (ii) een transport component die de meren verbindt binnen een wereldwijd netwerk, en (iii) een milieucomponent die belangrijke antropogene effecten simuleert. Vervolgens doe ik een voorstel voor een mondiaal model met behulp van bestaande componenten. Als uitgangspunt heb ik gekozen voor het bestaande aquatische ecosysteemmodel PCLake als de aquatische ecosysteemcomponent, het mondiale waterstromingsmodel PCR-GLOBWB en voedingsstoffen stromingsmodel GNM als componenten voor het transport van nutriënten en het geïntegreerde milieumodel IMAGE voor de milieucomponent. Met deze componenten als bouwstenen wil ik een begin maken voor projecties van algenbloei in meren. Belangrijke uitdagingen voor toekomstige toepassingen zijn het verbeteren van de wiskundige formuleringen voor diepe meren, de verbetering van de schatting van het nutriënttransport naar kleine meren, het uitbreiden van de dataset van de waterkwaliteit variabelen, de voortzetting van de multidisciplinaire manier van werken en de uitbreiding naar missende nutriëntencycli. *De beoogde wereldwijde prognoses voor de ontwikkeling van meren zal helpen om de dynamiek van meren, zoals Taihu, te begrijpen. Veranderingen in meren worden vaak beïnvloed door mondiale ontwikkelingen, bijvoorbeeld via de verbinding met rivieren, bodem en lucht, maar ook onder invloed van mondiale klimaatverandering en de sociaaleconomische ontwikkelingen.*

De voltooide vierledige puzzel (hoofdstuk 6) stelt me in staat om de maximale nutriëntenbelasting die Taihu kan absorberen te bepalen. De kritische nutriëntbelasting hangt af van de vorm van de curve die de response van het meer beschrijft als gevolg van de nutriëntenbelasting (belasting-response curve). Vanwege ruimtelijke variatie binnen Taihu, zijn belasting-response curven en dus de kritische nutriëntenbelasting heterogeen binnen het meer. Bovendien zijn de kritische nutriëntenbelastingen afhankelijk van managementdoelstellingen die de maximaal toelaatbare concentratie chlorofyl-a vaststellen. *Modelresultaten laten zien dat de totale nutriëntbelastingen naar Taihu meer dan gehalveerd moet* *worden om chlorofyl-a concentraties van lager dan 30-40 µg.L*$^{-1}$ *te bereiken in de meeste delen van het meer. Om fytoplanktonbloei van 20 µg.L*$^{-1}$ *chlorofyl-a te voorkomen in Taihu, moet de belasting van zowel fosfor als stikstof worden verminderd tot wel bijna 90%.*

In hoofdstuk 7 bediscussieer ik de bevindingen voor Taihu, met diversiteit als een overkoepelend thema in dit proefschrift: diversiteit in meren, diversiteit in modellen, diversiteit in de ruimtelijke verdeling van voedingsstoffen en waterbronnen, diversiteit onder de toekomstige ontwikkeling van meren op aarde en ten slotte diversiteit binnen meren. Deze aanpak heeft geresulteerd in een reeks van kritische nutriëntenbelasting voor verschillende delen van Taihu. Dit is in tegenstelling tot het vaste punt van herstel dat vaak wordt gevonden voor kleine ondiepe meren. De range aan kritische nutriëntenbelasting gevonden voor Taihu kan worden geïnterpreteerd als een pad van herstel, waarbij elke stap leidt tot verbetering van de waterkwaliteit in bepaalde delen van het meer. Om het totale herstel te bereiken, lijkt reductie van nutriënteninput de meest veelbelovende beheeroptie. De grote inspanning die nodig is voor volledig herstel roept de vraag op wat er zou gebeuren als er niets zou veranderen. Ik geef redenen waarom het aannemen van deze 'struisvogelpolitiek' rampzalig zou zijn vanwege: (i) de afhankelijkheid van samenlevingen van ecosystemen zoals Taihu, (ii) de moeilijkheid om verloren bronnen te vervangen en (iii) de kans op een kettingreactie in zowel de natuur als in de maatschappij. *Dit brengt mij tot de conclusie dat het oplossen van de problemen van eutrofiëring in Taihu aanzienlijke inspanning zal vragen. Nutriëntenbelastingreductie is een veelbelovende herstelmaatregel. Langs het pad van herstel zullen lokale verbeteringen plaatsvinden. Tot slot zullen deze lokale verbeteringen leiden tot een totaal herstel.*

Summary (中文)

二十世纪，全球人口增长已达到前所未有的水平，并导致了全球范围的营养物质循环失衡。由于过量营养物质排放等因素，众多生态系统面临着严重的富营养化问题。湖泊的富营养化最终会导致水华暴发，并在水体中产生大量有害的藻毒素。众所周知，中国太湖已长期被水华问题所困扰。20 世纪 80 年代初，太湖首次出现蓝藻水华；到 2007 年，水华在太湖灾难性地大规模暴发。这一自然灾害的发生直接导致了太湖水源地关闭，引发了无锡上百万人的用水危机，威胁到周边数千万人的用水安全，造成了严重的经济和社会后果。该事件也使得人们认识到水华问题是中国当前亟待解决的重大水环境问题之一。避免和治理水华的关键手段是控制湖泊营养盐浓度，使其低于产生水华暴发的营养盐阈值浓度，即营养盐负荷不应超过湖泊生态系统的自净能力。*本论文致力于探寻太湖水华暴发的营养盐负荷阈值（第一章），并分为五个步骤分别论述和解决上述问题：*

（1）探索了大型浅水湖泊中影响其水生植物占优或藻类占优的相关特性（第二章）。很多研究表明，根据多稳态理论小型浅水湖泊可从水生植物占优跃变到藻类占优的状态。在第二章中，对大型浅水湖泊（如太湖）是否也具有类似的多稳态进行了讨论，并基于湖泊的尺寸效应（size effect）、空间异质性（spatial heterogeneity）和水力内在连通性（internal connectivity）三个特性，研究了大型浅水湖泊在富营养化过程下稳态转换的响应机制。研究发现在现行尺寸效应下湖泊位置与稳态转换过程的关系，即尺寸效应较强的位置（如在太湖中心区域）几乎没有水生植物，因此没有明显的多稳态现象存在。然而，仅考虑湖泊尺寸效应又无法解释水生植物在大型湖泊中的大量分布（如东太湖区域）。在进一步考虑湖泊的空间异质性后，大型浅水湖泊中水生植物的分布与湖泊多稳态的关系可以得到更好的理解。最后，湖泊的水力内在连通性是衡量稳态转换过程的重要因素，较高的水力内在连通性将导致湖泊多稳态中不同状态的稳定性下降。

本章的研究结果表明，虽然太湖属于浅水湖泊，但由于太湖表面积极大，因此不具有明显的多稳态现象。但在太湖的某些特定区域，当水力内在连通性足够低时，可能能够观察到多稳态现象。

（2）对水生态系统模型的探索、利用及改进的研究（第三章）。本章通过咨询 42 位从事水生态系统模型的专家学者，统计其使用的模型，创建了专家数据库以探索水生态系统模型的多样性。作为数据库的一部分，本章对所有水生态系统模型的功能进行了分类，以利于分析其多样性。接下来，针对如何利用水生态系统模型的多样性，本章将现有模型不同方面的特征进行了对比和组合。最后，本章讨论了水生态系统模型多样性产生的原因，并展望了水生态系统模型在未来的发展和演化趋势。对水生态系统模型的探索、利用和改进，为进一步选取模型研究太湖营养盐负荷阈值提供了重要的线索和依据。*在本章讨论的所有水生态系统模型中， PCLake 模型由于在模拟浅水湖泊生态系统及其分岔分析（bifurcation analysis；即营养盐负荷阈值分析）中的广泛应用，被选为本课题的研究工具。PCLake 相较于其他模型的一大优势，是它重点关注了三种藻类（硅藻、绿藻和蓝藻）与水生植物在食物网中的竞争过程。为了实现在二维平面对太湖的空间异质性进行模拟，PCLake 已分别成功的与一个简化的水动力模型及三维水动力模型进行了耦合。*

（3）结合湖泊内部营养盐分布，分析了迄今为止仍被忽略的营养盐输入类型对生态系统修复的影响（第四章）。本章采用不同的营养盐输入形式（点源或面源输入）和流场类型（渗漏湖和径流湖），对比了四种类型的湖泊在不同的修复手段下的实施效果。点源营养盐负荷是指具有固定排放点的营养盐输入，而面源营养盐负荷输入的空间分布则更加广泛且均匀。渗漏湖的水量一般来源于地下水或大气降水，而径流湖的水量则主要来源于河流。研究结果表明，由不同的流场类型及营养盐来源类型导致的湖泊营养盐浓度、水生植物和叶绿素 a 浓度的空间分布差异，对湖泊修复的应用效果能起到决定性作用。在营养盐输入形式不同时，以营养盐浓度为衡量指标的富营养化程度的空间分布差异表现得尤其明显。结果还表明，

不同的营养盐输入类型可以决定富营养化峰值出现的空间位置，并且可以使湖泊富营养化程度的空间分布形状发生变化。*以上述研究成果为基础，本章说明了以径流补给为主且具有点源营养盐输入的大型浅水湖泊（如太湖），其空间特性将导致其生态系统不存在多稳态现象。因此，不建议采用生物操控手段对太湖进行生态修复。除此之外，采用冲刷稀释来减少水力滞留时间的效果也并不显著。对太湖来说，削减营养盐输入可能是最为有效的修复手段。*

（4）将湖泊生态系统模型模拟扩展到全球范围（第五章）。像太湖一样，众多湖泊生态系统正在遭受着人类活动带来的环境压力。为预测全球湖泊变化趋势，对未来发展趋势的模型模拟尤为重要。基于不同的社会-经济发展情境的模拟，数学模型可以对未来可能发生的全球变化进行预测。本章首先确立了理想的全球模型的具体要求：1）具有全球适用性的水生态系统模块；2）具有将湖泊与全球水循环连接起来的传输模块；3）具有模拟主要人类活动胁迫的环境模块。接下来，本章提出了采用现有模块构建全球模型的方案。作为起点，本章采用现有水生态模型 PCLake 作为全球模型的水生态系统模块；采用全球水文模型 PCR-GLOBWB 和全球营养盐循环模型 GNM 作为传输模块；采用全球环境集成化模型 IMAGE 作为环境模块。以上述模块构成的全球模型为基础，本章尝试对全球范围湖泊水华暴发进行预测。该课题在未来应用的主要挑战在于：改进模型并构建适用于深水湖泊的算法；提升小型湖泊营养盐输移评估的质量；扩展水质变量的数据集；保持多学科交叉的模式并加入更多种营养盐循环过程。*发展可模拟世界尺度的湖泊生态系统的全球模型，有利于加强对如太湖等湖泊的动态变化的理解。实际上，特定湖泊生态系统的变化常常受到全球变化趋势的影响，该影响既源于湖泊与河流、土壤及空气的相互作用关系，又源于全球气候及社会经济的发展和变化。*

（5）解答前四章的问题，为进一步确定保障太湖生态健康及满足其自净能力的营养盐负荷阈值最大值提供了基础（第六章）。湖泊营养盐负荷阈值取决于其对营养盐的负荷-响应曲线。由于太湖存在明显的空间差

异，其营养盐负荷-响应曲线在不同湖区有较大的不同。此外，营养盐负荷阈值还与水质管理目标，即允许的最大叶绿素 a 浓度值有关。*根据模型计算结果，湖泊总营养盐负荷至少需要减半才能达到湖泊大部分地区 30-40 μg.L-1 的叶绿素 a 浓度的治理目标。而为了防止水华暴发，即达到太湖全湖叶绿素 a 浓度低于 20 μg.L-1，湖内的磷、氮负荷都需要减少近 90%。*

最后，第七章讨论了上述在太湖的研究成果的对未来研究和管理的启示。通过本研究，多样性展现了其重要的讨论价值，这里所说的多样性包括：湖泊的多样性，模型的多样性，营养盐和水源空间分布的多样性，全球湖泊模拟的多样性及湖泊生态系统内部的多样性。该研究方法针对太湖不同区域，得到了不同的湖泊营养盐负荷阈值。大型浅水湖泊变化的营养盐负荷阈值与小型浅水湖泊唯一的营养盐负荷阈值形成了对比。在太湖的这一发现可以为其生态修复手段提供理论依据，即应分步骤针对特定湖区进行水质改善。为了达到全面的生态恢复，减少营养盐输入似乎是水质管理人员最为有效的选择。而全面的生态恢复所需付出的巨大牺牲对我们是否仍能进行正常的人类活动提出了质疑。本章认为采用带有逃避性质的“鸵鸟政策”（即盲目的实现全面生态恢复）导致的结果将是灾难性的，这是因为：1）社会发展对太湖等提供的生态服务的依赖；2）已失去的资源的不可替代性；3）在自然界或社会触发连锁反应可导致的系统崩溃。*因此本章得出结论，解决太湖富营养化问题将需要付出巨大的努力。而削减营养盐负荷是最有前景的修复手段。通过该修复方法，湖泊局部地区的水质提升会非常明显，而这些局部的水质提升将最终实现太湖生态系统的全面恢复。*

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Curriculum Vitae

Annette Janssen was born on 25 November 1986 in Gouda, the Netherlands. She moved soon thereafter to Monster, where she grew up between greenhouses in Netherlands' main horticultural area. After finishing here primary school at the "Eerste Westlandse Montessorischool" she continued her studies at the secondary school "Haags Montessori Lyceum" in The Hague. After finishing VWO (profile "Nature and Health") in 2006, Annette moved to Wageningen to start her bachelor study Soil, Water and Atmosphere. During her bachelor years, Annette was board member of both the study association "Pyrus" and the gymnastics club "WSTV SPLIT". Her studies sparked her broad interest in environmental sciences. Therefore, after finishing her bachelor in 2009, she continued her master in both hydrology and water quality. During this period she moved to Delft for her MSc-thesis at Deltares on algal blooms in IJsselmeer area and moved later to Silkeborg, Denmark, for her internship on the effects of extreme flooding and droughts on macrophyte composition in streams. In 2012 Annette obtained both an MSc-degree in Hydrology and Water Quality with distinction cum-laude. After her Masters, Annette started a PhD project at the Netherlands Institute of Ecology (NIOO-KNAW) on the water quality of Lake Taihu. Using models, Annette determined the maximum nutrient load the ecosystem of Lake Taihu can absorb, while remaining in a good ecological state. Furthermore she developed a model to simulate the behavior of lake ecosystems around the world under changing nutrient loads together with the Netherlands Environmental Assessment Agency (PBL). In 2015 Annette co-organized the AEMON workshop for around 40 participants from different places all over the world. Her work has been presented at various conferences and publications, and resulted in the thesis "A blooming business: identifying limits to Lake Taihu's nutrient input".

Publications

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Honors & Awards

- PE&RC Cover prize (2016) 3rd prize
- Aarde.nu Profielwerkstuk prijs (2006)

Certificate

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Environmental assessment of Lake Taihu

Writing of project proposal

- Identifying critical nutrient loadings for Lake Taihu, China, with a dynamic model for integrated water system research

Post-graduate courses (4 ECTS)

- Modelling critical transitions in nature and society; SENSE (2014)
- Consumer resource interactions; PE&RC (2014)

Laboratory training and working visits (11 ECTS)

- Project meeting PCLake; Nanjing University, China (2013)
- Modelling workshop; NERI, Aarhus University, Denmark (2014)
- Project meeting NWO; Beijing University, China (2015)
- Early warning signals workshop; CEH, Edinburgh (2015)
- Modelling workshop; University of Miami, Miami, FL, USA (2016)
- Lake meeting; IHB, Wuhan, China (2016)

Invited review of (unpublished) journal manuscript (8 ECTS)

- Environmental Modelling & Software: phytoplankton community description in water quality models (2013)
- Environmental Engineering Science: nitrate sources in Lake Chaohu, China (2014)
- Hydrobiologia: trophic state of a Greek lake (2014)
- Ecosystems: critical phosphorus loading in China (2015)
- Aquatic Ecology: water quality in Dutch lakes (2015)
- Hydrobiologia: bloom formation in Lake Taihu (2016)
- Hydrobiologia: long-term nutrient trends and algal blooms (2016)
- Water Research: food web modelling (2017)

Competence strengthening / skills courses (2.9 ECTS)

- Voice Matters – Voice and Presentation Skills Training (V&PT); WGS (2013)
- Effective behaviour in your professional surroundings; WGS (2015)
- PhD and Postdoc retreat; PCDI (2015)
- PhD Workshop carousel; WGS (2016)

PE&RC Annual meetings, seminars and the PE&RC weekend (7.2 ECTS)

- PE&RC Weekend start, end (2012, 2016)
- PE&RC Day (2013-2016)
- NERN Day (2013-2017)

Discussion groups / local seminars / other scientific meetings (6.1 ECTS)

- Food Web Ecology (2012-2016)
- Literature discussion NIOO (2012-2016)
- NIOO Seminars (2012-2016)
- NIOO Science days Heeze (2013, 2016)

International symposia, workshops and conferences (12.2 ECTS)

- SEFS 8th Symposium for European freshwater sciences (2013)
- 8th International shallow lakes conference (2014)
- AEMON Workshop (2015)
- ASLO Aquatic sciences meeting (2015)
- 10th INTECOL China (2016)

Lecturing / supervision of practicals / tutorials (3.3 ECTS)

- Models for ecological systems (2013-2015)
- Practical aquatic ecology and water quality (2014)
- Modelling course Nijmegen (2015)

Supervision of a MSc student (3 ECTS)

- Fish modelling using PCLake

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Colophon

The research presented in this thesis was conducted at the department of Aquatic Ecology at the Netherlands Institute of Ecology (NIOO-KNAW) and at the Aquatic Ecology and Water Quality Management Group at Wageningen University.

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