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Ecological functioning of a eutrophic, high-altitude shallow lake in Ecuador, Laguna Yahuarcocha

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Preface / Dankwoord

After 5 years of university, this is it. This thesis is my final touch of my academic carrier at the university. With this preface I would like to express my gratitude to all the people who supported me in the writing of this thesis. First of all I want to thank Professor Koenraad Muylaert for coaching me and offering me the opportunity to go to Ecuador. Thank you for guiding us in Ecuador, for helping us with the start-up of the experiments and providing feedback. Thank you Willem Van Colen for reading and reviewing this thesis over and over again, giving feedback and hints. This experience has a great value for me and I can’t thank you both enough for this. Also thank you to Pieter Lemmens, who shared his knowledge on the fish community. Thank you UTN (Universidad Técnica Del Norte) for the co-operation and assistance during the sampling in Yahuarcocha. Agradezco mucho a la Universidad Técnica del Norte por la cooperación y el acompañamiento durante los muestreos en Yahuarcocha! Particularly, I want to thank Karen Portilla and Francisco Caicedo for organizing and the support and help when things didn’t proceed as planned. Thank you for the very warm hospitality and friendship in Ecuador! Tim Tytgat, I also want to thank you for the great company during the long and sometimes tough days in Ecuador. To Anita and her husband, to Lily and Rommel, the best host family of Ecuador. I want to thank you all for letting me into your family, for making empanadas together, for showing the city. Thank you! I also want to thank my family and my colleagues from biology for the support. And last but not least: Thank you mom, dad and Jasper for the support, not only for this thesis but for the support during my time in university. This would never be possible without you guys!

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Pauline Saelens
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Abbreviations

Chl *a*	chlorophyll *a*
DN	dissolved nitrogen
DP	dissolved phosporus
DnRN	dissolved non-reactive nitrogen
DnRP	dissolved non-reactive phosphorus
DRN	dissolved reactive nitrogen
DRP	dissolved reactive phosphorus
N	nitrogen
P	phosphorus
PAR	photosynthetic available radiation
PC	phycocyanin
TN	total nitrogen
TP	total phosphorus
Stdv	standard deviation

Contents

1. Introduction

1.1 Shallow lakes around the world

1.1.1 Defining shallow lakes

There is some discussion about which criteria make a lake ‘shallow’. Some authors define shallow lakes as lakes with an average depth of less than three meter (Scheffer, 2004; Cooke *et al.*, 2005), others propose a depth of five meter as a transition from shallow to deep lakes (e.g. Padisák & Reynolds, 2003). Scheffer (2004) also defines shallow lakes as lakes where there is no stratification for long periods in the summer. Thermal stratification is the separation of the water column into different layers caused by the differences in water temperature induced by solar irradiance. The warm water (epilimnion) then rests on top of the cold and denser water layer (hypolimnion) and these two layers can be regarded as two physically isolated layers. The water column of a shallow lake however mixes frequently from top to bottom (Scheffer, 2004), mainly as a result of the wind (Wetzel, 2001). This mixing has an important influence on the limnology by allowing a more intense interaction between the sediment and the water column. Furthermore, the limnology of shallow lakes also differs from deeper lakes by the higher degree of colonization by macrophytes. Being primary producers and being at the base of the food web, these macrophytes have an important influence on higher trophic levels and hence the functioning of the whole lake (Carpenter & Lodge, 1986). It should be concluded that defining shallow lakes by an absolute depth is often topic of discussion, and that it is more appropriate to define a shallow lake based on the limnology of the lake.

1.1.2 Distribution

Shallow lakes are very abundant in many regions of the world and are more numerous than deep lakes (Dokulil & Teubner, 2003; Scheffer, 2004). A lot of them originate from human activities such as digging for gravel, sand, clay or peat (Scheffer, 2001). Shallow lakes are often located close to densely populated areas making them more susceptible to human disturbance. Over the last century the quality as well as the quantity of wetlands has decreased dramatically. Drainage for agricultural purposes has reduced the amount of wetlands worldwide, while eutrophication (see ‘1.4.1 Eutrophication’) has dramatically modified the ecological condition of many wetland communities (Carpenter *et al.*, 1998; Smith, 2003; Scheffer, 2004). Between 2004 and 2009, an estimated 25.200 hectare of wetlands were lost in the United States (Dahl, 2011).

1.1.3 Ecosystem services

Shallow lakes are of great ecological, social and economic importance especially in densely populated areas. They form often habitats that are rich in wildlife and hence support biodiversity (Dudgeon *et al.*, 2006; Strayer & Dudgeon, 2010). Shallow lakes can maintain a lot of macrophytes, which are important for providing habitat. Due to macrophytes habitat complexity, shallow lakes can support a high biodiversity (Carpenter & Lodge, 1986; St. Pierre & Kovalenko, 2014). Moreover, shallow lakes can be very important from a recreational point of view. Fishing, boating, bird watching and swimming can attract a large public (Scheffer, 2004). Also these lakes provide mankind with many services such as water for drinking, irrigation, food production, transportation and aesthetic enjoyment (Costanza *et al.*, 1997; Peterson *et al.*, 2003).

1.2 Functioning of shallow lakes

1.2.1 Light condition

Light is the driving factor for photosynthesis and hence determines how much plant growth there is in the water column and which growth forms of plants are dominant (Scheffer, 2004). Lack of clarity caused by algal blooms and suspended sediment strongly affects the general functioning of a lake by reducing the abundance of submerged vegetation, sometimes leaving only floating-leaved plants (Havens *et al.*, 2004). The intensity of light diminishes with depth in an approximately exponential way. When the photon enters the water two things can happen: it can be scattered into a different direction or it can be absorbed by particulate matter such as sediment particles, biota and detritus. Usually light intensities are measured only over the range of wavelengths that can be used by plants for photosynthesis. This portion of the light is called the Photosynthetic Active Radiation (PAR). Green light usually penetrates the water column deeper than other colors that can be used for photosynthesis (Scheffer, 2004).

1.2.2 Sedimentation and resuspension

Resuspension of sediments is defined as the redistribution of sediment particles, which had been settled on the lake bottom before, back into the water column. Depending on the lake depth and morphometry and the wave base, the whole water body or only deeper layers are affected by resuspension (Bloesh, 1994). The sensitivity of sediment to resuspension depends strongly on the state of the sediment surface layer (Scheffer, 2004). The current and waves are the major factors driving resuspension (Scheffer *et al.*, 2003), but also feeding behavior by benthivorous fish can stir up the sediment (Meijer *et al.*, 1990; Scheffer, 2004; Roozen *et al.,* 2007). Resuspension of the sediment can also indirectly increase the turbidity of the water column by enhancing nutrient recycling, eventually leading to an increasing algal biomass (Kirstensen *et al.*, 1992; Schallenberg & Burns, 2004).

1.2.3 Nutrient dynamics

Algal cells require elements in a relatively fixed proportion in order to reproduce. The elemental composition of the ash-free dry material is dominated by carbon (C), hydrogen (H), oxygen (O) and nitrogen (N), together with smaller amounts of phosphorus (P) and sulphur (S). At least 14 other elements (Ca, Mg, Na, Cl, K, Si, Fe, Mn, Mo, Cu, Co, Zn, B, V) are consistently recoverable if sufficient analytical accuracy is applied (Reynolds, 2006). Nutrients are important for phytoplankton to secure development and functioning. Nitrogen and phosphorus are respectively the fourth and sixteenth most abundant elements in our solar system (Downing & McCauley, 1992). Nevertheless, these two elements are considered as limiting growth in most aquatic ecosystems (Holland *et al.*, 2004; Klausmeier *et al.*, 2004; Hall *et al.*, 2005).

Phosphorus (P) is an essential element for all life forms. It is a component of nucleic acids and many intermediary metabolites (Correll, 1998). P in the water column occurs in many different forms. In comparison to other macronutrients required by biota, P is the least abundant and is often the first element to limit biological productivity. The range of total P in fresh waters is large, from < 5 µg L^{-1} in very unproductive waters to > 100 g L^{-1} in highly eutrophic waters (Wetzel, 2001). As P is often considered to be the biomass-limiting constraint in pelagic ecosystems, P enrichment can provide a significant stimulus to the sustainable biomass of phytoplankton. Many species can take up freely available P at very rapid rates, sufficient to sustain a doubling of cell mass in a matter of a few (≤ 7) minutes (Reynolds, 2006). P is chemically reactive, technically easier to remove from water than N, and does not have major reservoirs in the atmosphere (Wetzel, 2001). Iron is very important in immobilizing P in sediments, but this binding only works under aerobic conditions. In deep stratified lakes, sediments are most of the time anoxic. In shallow lakes, however, mixing usually supplies enough oxygen to the sediment surface to maintain a superficial aerobic layer. Also, high pH values reduce the capacity of iron to bind P (Søndergaard *et al.*, 2003; Scheffer, 2004).

Nitrogen (N) is a constituent of amino acids and thus all the proteins from which they are synthesized. N constitutes more than three percent of the ash-free dry mass of living cells (about 0.05 mol N $(\text{mol C})^{-1}$) (Reynolds, 2006). N is less often reported as a limiting nutrient in lakes than P. Three major features set N aside from P; (1) it does not accumulate in the sediment that strongly; (2) it can disappear as gas into the atmosphere under certain conditions; and (3) some cyanobacteria can use atmospheric N as a nutrient (Scheffer, 2004).

Aquatic primary productivity, especially in surface waters, is frequently limited by the availability of nutrients. Principally this involves limitations in the supply of N and P

(Schindler, 1977; Lean & Pick, 1981; Elser *et al*., 2007). The identification of nutrient limitation of phytoplankton growth and identifying of the limiting factor(s) in a water body is of considerable importance to the understanding of the ecology of aquatic systems and to water management practices. It enables managers to define an appropriate nutrient loading budget for the catchment and respond to possible perturbations (Beardall *et al.*, 2001). It is generally considered that marine ecosystems tend to be nitrogen limited (N), while freshwater were to be phosphorus (P) limited (Vitousek & Howard, 1991; Holland *et al.*, 2004). However, there are exceptions such as the North Pacific Sub-tropical Gyre and regions of the Mediterranean Sea (Karl, 1999; Krom *et al.*, 1991; Elser *et al.*, 1990). Using absolute concentrations to identify the limiting nutrient, can be problematic. Despite the fact that nutrients like N and P might be present in aquatic systems, they are not necessarily available to the primary producers. It seems that anthropogenic nutrient sources can be more readily bioavailable than organic nutrient sources coming from a natural catchment (Bowman *et al.*, 2005; North *et al.*, 2013). A more commonly used, and scientifically approved method to identify the limiting nutrient is monitoring the growth response of phytoplankton to nutrient additions. A reference condition, without added nutrients allows to interpret the manipulated conditions (Holland *et al.*, 2004), in which a specific nutrient was added (ammonium, nitrate, phosphate, silicate, …) (Fisher *et al.*, 1999). It needs to be taken into account that it is just an indication, other factors than nutrient limitation may be minimized or magnified (Holland *et al.*, 2004). The experiment can be influenced by phytoplankton species composition and the fact that adding a macronutrient can induce the limitation of another (Beardall *et al.*, 2001).

1.2.4 Trophic levels

The food web of shallow lakes contains different trophic levels in a simple representation: piscivorous fish (top-predators), planktivorous fish (meso-predators), benthivorous fish, zooplankton (herbivores), phytoplankton (primary producers) and macrophytes (primary producers) (Fig. 1).

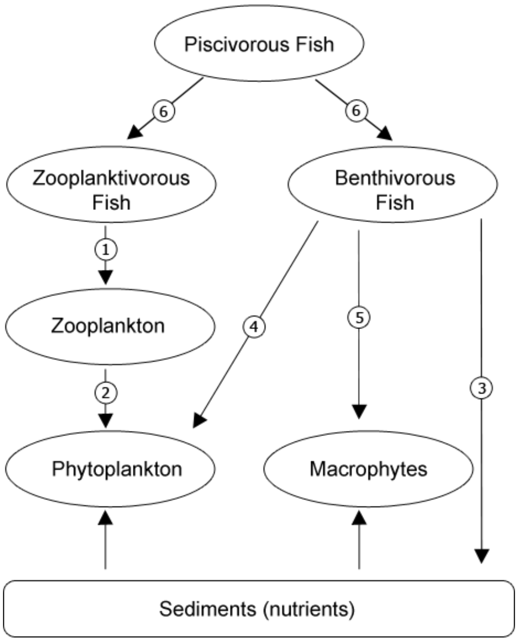

Fig. 1: A simplified food web showing the major interactions (modified from Lemmens, 2014).

Primary producers, being phytoplankton and macrophytes, form the base of the aquatic food web. They obtain their energy through the process of photosynthesis and therefore they live in the euphotic zone (i.e. the layer of water starting from the surface until the depth where 1% of the initial PAR radiation is left) of the water column (Häder *et al.*, 1998). Nutrients for growth are provided by the sediment and by the dissolved inorganic fraction in the water column. Macrophytes can be emergent, floating or submerged and grow in the littoral region of most lakes (Gasith & Hoyer, 1998). Submerged macrophytes are defined as plants that are rooted in the bottom soil with the vegetative parts predominantly submerged, while emergent macrophytes are also rooted but rising above the water surface. Dense macrophytes in shallow lakes help stabilize shoreline and bottom sediments. Because plants themselves provide micro-habitats, biodiversity in shallow lakes can be high (Jeppesen *et al.*, 2000; Cooke *et al.*, 2001). Macrophytes rooted in the sediment mainly use nutrients from the sediment (Barko *et al.*, 1988) and depending on a number of factors, they can act as a source or a sink for nutrients (Pieczynska, 1993; Sachse *et al.*, 2014). They are also capable of absorbing large quantities of nitrogen from the sediments (Wetzel, 2001). Zooplankton can seek refuge from predation by vertical migration into the metalimnion and hypolimnion during the day (Gliwicz, 1986; Leech & Williamson, 2000) and migrate back to the upper water column (Gliwicz, 1986) during the night to feed on the phytoplankton. Zooplankton can also migrate horizontal into macrophytes for refuge (Schriver *et al.*, 1995; Stansfield *et al.*, 1997; Burks *et al.*, 2001b) in shallow lakes (Jeppesen *et al.*, 1997a; Lauridsen & Lodge, 1996; Sachse *et al.*, 2014).

The next trophic level in the aquatic food web is composed of the primary consumers, mainly zooplankton, which feed on phytoplankton. Zooplankton grazing pressure on phytoplankton is low in eutrophic lakes in which the phytoplankton is dominated by grazing-resistant species, such as cyanobacteria (Zhang *et al.*, 2007). Cyanobacteria are known to be poor food for zooplankton because they cause mechanical interference with feeding (Bednarska *et al.*, 2014), contain hepatotoxins and neurotoxins (Carmichael, 2001) that markedly reduce survival (Ferraõ-Filho *et al.,* 2000; Hairston *et al.,* 2001) and have low nutritional value (Ferraõ-Filho *et al.,* 2000). Grazing efficiency of zooplankton is variable among taxa. For example copepods are less efficient grazers than cladocerans like *Daphnia* spp. (Elser & Goldman, 1991; Zhang *et al.*, 2007).

Fish plays a central role on the structure and dynamics of food webs in shallow lakes. This dominant role can largely be attributed to their efficient predator behavior (Carpenter & Kitchel, 1996; Scheffer, 2004), which exerts strong top-down effects on prey communities (Hansson *et al.*, 2007b). Some planktivorous fishes are obligate planktivores feeding exclusively on plankton; others are facultative planktivores feeding on plankton as well as on other items. Planktonic fish larvae consume zooplankton and sometimes phytoplankton (Lazzaro, 1987). The zooplankton and phytoplankton communities can be affected by the feeding selectivity of planktivorous fishes. High densities of planktivorous fish lead to a zooplankton community dominated by small, relatively inefficient grazers (Carpenter *et al*., 2001). Not only does selective predation of fish remove the larger individuals, some *Daphnia* clones also change their behavior and life history strategy in response to chemical cues released by fish (De Meester *et al.,* 1995), leading amongst other things to a smaller average size of individuals (Feniova *et al*., 2015). The effects of piscivory on shallow lake food webs have been studied less intensively than the effects of planktivory and benthivory. Nonetheless, it had become clear that predation is an important structuring force in fish communities. In the presence of piscivorous fish, potential prey fish often change their behavior in order to reduce predation risk, and this can lead to crowding and increased food competition in safe vegetated areas (Scheffer, 2004). Benthivorous fish on the other hand also have a big impact on the functioning of shallow lakes. They resuspend solids from the bottom while searching for food by sucking up sediment and rejecting the non-food particles to the water and by causing small waves during this behavior (Lammens & Hoogenboezem, 1991; Zambrano *et al.*, 2001).

Changes in one trophic level can have consequences for the higher or lower trophic level. These changes can be the start of a chain-like effect throughout the whole trophic structure of an ecosystem and this effect can go from the top down or from the bottom up. In reality it is often a combination of a top-down and bottom-up effect that will characterize the trophic structure of the ecosystem. A trophic cascade is a form of top-down control. In its simplest form, the trophic cascade addresses changes in a four-level food chain of piscivorous fishes, planktivorous fishes, zooplankton and phytoplankton: a large increase (decrease) in piscivores causes a decrease (increase) in planktivores, an increase (decrease) in zooplankton, and a decrease (increase) in phytoplankton. Trophic cascades have been applied successfully in lakes before (Carpenter *et al*., 1985; Potthoff *et al.*, 2008). However, the previous representation of trophic cascades is oversimplified. Cascades depended on complex processes such as ontogenetic changes in diet and habitat use of fishes, behavioral shifts related to foraging opportunity and predation risk, size-selective predation, body size shifts among zooplankton, nutrient recycling by zooplankton, stoichiometry of zooplankton, and others (Romare & Hansson, 2003; Carpenter *et al.*, 2010). Beyond the direct impacts of predator-prey interactions, trophic cascades can be either weakened or intensified by behavioral responses of both prey and predators. Animals at intermediate trophic levels may avoid top predators with consequences for lower trophic levels and ecosystem processes. Behaviors of top predators that affect choice of foraging sites or prey preferences may also alter trophic cascades (Carpenter *et al.*, 2010). It is also important to notice that top-down control doesn't only affect the population size of the underlying trophic level but also the community composition, due to selective predation (based on size, digestibility, …) (Carpenter & Kitchell, 1996; Declerck *et al.*, 1997; Jeppesen *et al.* 1997b; Carpenter *et al.* 2001; 2010).

1.2.5 Differences between deep and shallow lakes

Shallow lakes differ in their ecology from deep lakes in many ways. First of all it is typical for shallow lakes that they are fully mixed throughout the year, whereas most deep lakes are summer-stratified (Jeppesen *et al.*, 1997a). Stratification isolates the upper water layer (epilimnion) from the colder, deeper water (hypolimnion) and thus there is no interaction with the sediment during the summer (Scheffer, 2001). In stratified deep lakes the nutrients stay in the hypolimnion or sediment and cannot be used for growth anymore (Jeppesen *et al.*, 1997a). In the mixed water column of shallow lakes however, nutrients from the sediment can leak back into the water (=internal loading) and can reach the euphotic water layer to stimulate growth. This internal loading in shallow lakes can be as significant as the external loading of nutrients into the water column and could easily induce harmful algal blooms (Cooke *et al.*, 2001). The increased photosynthetic activity during algal blooms will elevate the pH (9 or higher), which in turn promotes phosphorus release from iron complexes and sediments, increasing the algal biomass even further. Many shallow lakes do not have the chemical buffering capacity of deep lakes allowing pH changes to occur faster, hence making them more susceptible to the process of internal loading (Cooke *et al.*, 2001).

A second important difference between shallow and deep lakes is the role of macrophytes in the ecosystem functioning. In deep lakes, submerged plant growth is limited to a small zone near the shore where sufficient light can penetrate the water column. Lakes in which most of the basin is deeper than 10-15 meter are not expected to have abundant submerged aquatic macrophytes (Gasith & Hoyer, 1998). In contrast, shallow lakes can be colonized by these macrophytes in almost all of the lake area (Cooke *et al.*, 2001).

Thirdly, the impact of fish on the ecosystem functioning will be different in shallow lakes compared with deep lakes. While searching for food in the sediment, fish tend to resuspend a lot of sediment. This can have a huge impact on the turbidity of the water. In deep lakes fish disturbance of shallow water sediments is limited to the near shore area (Cooke *et al.,* 2001; Cooke *et al.*, 2005), whereas in shallow lakes this effect can be present in the whole lake area. A change in the turbidity of the water can have important consequences on the ecosystem functioning and ecological condition of the lake (see ‘ 1.3 Alternative stable states’) (Scheffer *et al.*, 1993).

Table 1: Characteristics of shallow and deep lakes (Cooke *et al.,* 2005).

Characteristic	**Shallow**	**Deep**
Likely size of drainage area to lake area	Large	Smaller
Responsiveness to diversion of external P loading	Less	More
Polymictic	Often	Rarely
Benthic-pelagic coupling	High	Low
Internal loading impact on photic zone	High	Lower
Impact of benthivorous fish on nutrients/turbidity	High	Lower
Fish biomass per unit volume	Higher	Lower
Fish predation on zooplankton	Higher	Lower
Nutrient control of algal biomass	Lower	Higher
Responsiveness to strong biomanipulation	More	Lesser
Chance of turbid state with plant removal	Higher	Lower
Probability of fish winterkill	Higher	Lower
% Area/volume available for rooted plants	High	Low
Impact of birds/snails on lake metabolism	Higher	Lower
Chance of macrophyte-free clear water	Low	Higher

1.3 Theory of alternative stable states

1.3.1 Turbid versus clear water state

Shallow lakes can have two alternative equilibria: a clear state dominated by aquatic vegetation and a turbid state characterized by high algal biomass (Scheffer *et al.*, 1993; Scheffer, 2004). The clear-water state with well-established submerged vegetation is stabilized by high zooplankton grazing rates, low phytoplankton density, and relatively high densities of piscivorous fish. The turbid state without vegetation is stabilized by low light availability, high phytoplankton densities, relatively low zooplankton grazing rates and high abundances of planktivorous and benthivorous fish. It is clear that many ecological mechanisms are involved in the existence of alternative equilibria in shallow lake ecosystems (Fig. 2), but the whole feedback system is thought to center around the interaction between submerged vegetation and turbidity (Scheffer *et al.*, 1993; Jeppesen *et al.*, 1997a; Scheffer, 2004).

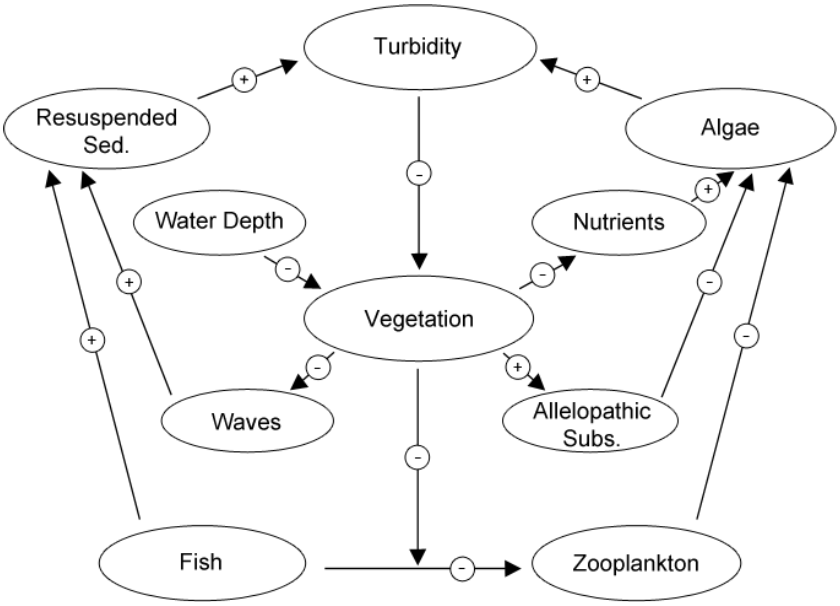

Fig. 2: Major positive and negative feedback mechanisms in a shallow lake (modified from Scheffer *et al.*, 1993).

Vegetation is an important factor that has an overall positive effect on water transparency in freshwater lakes. The positive effect of vegetation on water clarity is the result of a number of different mechanisms.

Firstly resuspension of bottom material is reduced by vegetation. Resuspension of sedimented particles in lakes is mainly the result of wave action or feeding activity of benthivorous fish. Dense macrophytes in shallow lakes help stabilize shoreline and bottom sediments. Charophyte vegetation for example can reach a high biomass and most species concentrate this biomass close to the sediment, covering it like a dense mat. Obviously, this strongly reduces the water movement at the sediment surface. Resuspension by waves within such vegetation will occur rarely if at all. Also, access of benthivorous fish to the sediment is hindered (Scheffer, 2004).

Secondly, aquatic plants provide a refuge for phytoplankton-grazing zooplankton against planktivorous fish. When submerged aquatic vegetation is lost from a lake, so is the refuge they provide for *Daphnia* and other large zooplankton against plankton-eating fish (Jeppesen *et al.*, 1997b). The refuge effect for cladocerans, particularly for *Daphnia*, varies with the composition of the potential predators (Jeppesen *et al.*, 1997a), as the plants can also host juvenile fish (Persson & Eklöv, 1995), and multiple predatory invertebrates (Burks *et al.*, 2001a). Submerged vegetation is often abundant in warm (sub)tropical waters but is less effective as zooplankton refuge because large numbers of small fish also find refuge there from their own predators (Meerhoff, 2006; Meerhoff *et al.*, 2007; Moss *et al.*, 2011). The refuge effect also seems to depend on the plant bed size or density (Lauridsen *et al.*, 1996; Burks *et al.*, 2001b), and percent of the lake volume inhabited by the plants (Schriver *et al.*, 1995), as well as the trophic state of the lake (Lauridsen *et al.*, 1999; Meerhoff, 2006).

Thirdly, vegetation suppresses algal growth due to competition for nutrients (Scheffer, 2004). By taking up nutrients form the sediment and water column, they reduce the amount of nutrients available for phytoplankton growth (Van Donk & van de Bund, 2002).

And fourthly, plants can suppress phytoplankton through the release of chemical substances that inhibit phytoplankton growth (Wium-Andersen *et al.*, 1982; Gross *et al.*, 2003). Such chemical suppression, called allelopathy, is known to play an important role in some cases. Chemical compounds isolated from Chara (Wium-Andersen *et al.*, 1982) and from some other plants have been shown to inhibit the photosynthesis of natural phytoplankton assemblages (Scheffer, 2004).

Overall, it's clear that vegetation tends to stabilize or even enhance water clarity. But there are also factors stabilizing the turbid state. High turbidity of the water prevents the establishment of macrophytes population due to light limitation. Submerged plants can only grow down to a certain turbidity-dependent depth beyond which the light availability becomes too low (Scheffer, 1993).

Fish also play a stabilizing role in the occurrence of the turbid, algae-rich water state (Cooke *et al.*, 2001), such as benthivorous fish (due to their feeding behavior) (Miller & Crowl, 2006). Clear water is maintained by piscivores in an indirect way by keeping zooplanktivorous fish density low leading to higher zooplankton biomass and less suspended algae. Benthivorous fish increase turbidity in the water column in a direct way by stirring up sediment particles while searching for food. Plants support abundant piscivores which control planktivore and benthivore abundance, and zooplankton thrive keeping suspended algae low. High fish densities has been shown to be important on the effect of turbidity in waters (Breukelaar *et al.*, 1994; Cooke *et al.*, 2001). Meijer *et al.* (1994) showed that a reduction of the benthivorous fish stock in the shallow Lake Bleiswijkse Zoom (The Netherlands) resulted in an almost instant increase in transparency which appeared to be due to a drop in the concentration of resuspended bottom material.

1.3.2 The crucial role of nutrient concentration

As shown in Fig. 2, turbidity is determined by a lot of different feedback mechanisms stabilizing either the turbid or the clear water state. Nutrient concentrations play a crucial role these mechanisms (Fig. 3). At very low nutrient concentrations submerged vegetation is present and the water is in a clear state. When increasing the nutrient concentrations, at first the turbidity will slightly increase but vegetation will remain present and control the turbidity to a certain extent. But when a critical threshold for the turbidity is reached, vegetation will disappear very quickly and the system will switch to an even more turbid water state. It is important to notice that at intermediate nutrient concentrations, both alternative stable states are theoretically possible. Presence of vegetation will determine the actual state of the water. Vegetation can stabilize a clear-water state in shallow lakes up to relatively high nutrient loadings. Once the system has switched to a turbid state, it takes a nutrient reduction to very low nutrient concentrations in order to reduce turbidity and enable recolonization by plants, leading to a switch back to the clear water state equilibrium (Scheffer *et al.*, 1993; Scheffer, 2001). This strong reduction in nutrient concentration can be very difficult and costly to realize implying serious consequences for the management of the lake.

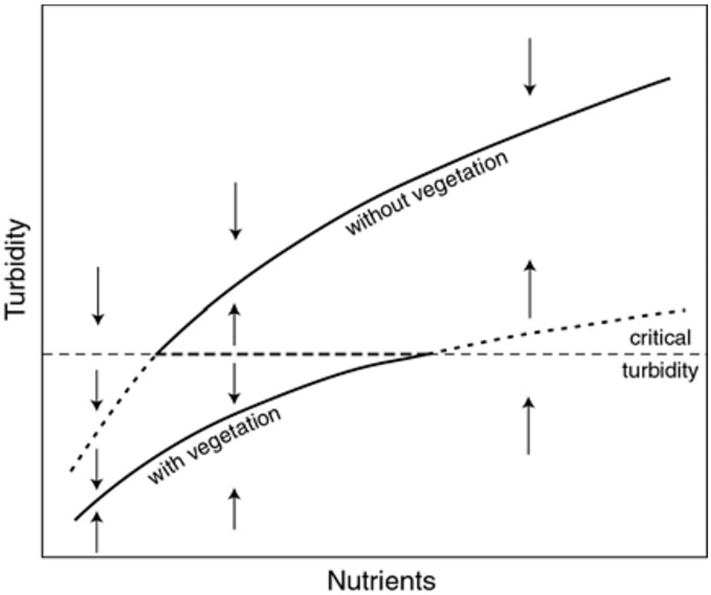

Fig. 3: Graph showing the relation between nutrient concentrations, vegetation presence and the turbidity of the water column. Two alternative stable states can occur: turbid without vegetation or clear water with vegetation. The arrows indicate the direction of change when the system is not in one of the two alternatives (Scheffer, 2001).

1.4 Shallow lakes under pressure

Due to a change from a clear state to a turbid state the ecosystem can collapse; the biodiversity can hereby be lost (Dudgeon *et al.*, 2006; McKinnon & Taylor, 2012) and the services provided by the ecosystem decrease, resulting in a large cost to society

(Dodds *et al.*, 2009). This sudden change is also called a ‘regime shift’ (Scheffer & Carpenter, 2003). The process of eutrophication, invasive species, climate warming, urbanization, habitat degradation and overexploitation exert pressure on the lake ecosystems. Lakes under pressure may develop a very poor water quality condition, characterized by nuisance blooms of toxic cyanobacteria (Carey *et al.*, 2012).

1.4.1 Eutrophication

Eutrophication is the response of the ecosystem to the addition of artificial or natural nutrients, mainly phosphorus and nitrogen. The high concentration of nutrients as a result stimulates the primary production. Lakes enriched by human activities are said to be culturally eutrophic. Humans now have a very strong influence on almost every major aquatic ecosystem (Smith, 2003). Thousands of lakes around the world have been impacted by extreme inputs of nutrients from human-related uses of the land (Ansari & Gill, 2013). This excessive nutrient enrichment of waters has severe effects upon the quality of receiving waters (Carpenter *et al.*, 1998; Correll, 1998; Conley, 2009) resulting in change from oligotrophic (poorly nourished) water bodies to mesotrophic (moderately nourished), eutrophic (well nourished) and finally to hypertrophic (over nourished) systems.

Over the past few decades massive increases in nitrogen have been established in the water bodies. In agricultural lands, the use of nitrogen fertilizers has grown more than 10 times since 1950, and continues to increase (Peñuelas *et al.*, 2013). Elevated emissions of nitrogen oxides (NO_x) from fossil fuel combustion (25–33 Tg N per year), biomass burning, and nitrogen-based fertilizer (118 Tg N per year) contribute to high atmospheric levels and increasing deposition, especially around densely populated areas (Peñuelas *et al*., 2012). Only 22% of these total human inputs of nitrogen ends up accumulating in soils and biomass, whereas 35% enters the oceans via atmospheric deposition (17%) and leaching via river runoff (18%). Although atmospheric nitrogen deposition from anthropogenic activities mostly impacts northern ecosystems, it will likely extend to the tropics during this century (Peñuelas *et al.*, 2013).

Phosphorus levels in the water bodies have also significantly increased since the last decades. The worldwide application of mineral phosphorus fertilizers to croplands is 17 Tg P per year (Peñuelas *et al.*, 2013). When the use of livestock slurry and manure is included, the total phosphorus application in agriculture amounts to 22–26 Tg P per year (Peñuelas *et al.*, 2012). In contrast to the massive additions of reactive nitrogen, the only source of atmospheric phosphorus deposition is through mineral aerosols (dust and fly ash from wildfires). This source is small, with a total global flux estimated at 3–4 Tg P per year (Mahowald *et al.*, 2008) and it is not clear whether it will increase or decrease in the future in response to human activities and climate change. Other human sources of phosphate can be in the out flows from municipal and industrial wastewater (Conley *et al.*, 2009). However, during the past decades the phosphorus concentrations in the out flows are significantly reduced due to several measurements that have been applied such as the ban on use of phosphates in detergents and P removal in wastewater treatment plants.

The most common effect of increased N and P to aquatic ecosystems is an increase in the biomass of algae and aquatic plants (Smith, 2003; Conley *et al.*, 2009), but the decay of algal blooms also results in a high concentration of dead organic matter. The decay process consumes dissolved oxygen in the water, resulting in hypoxic conditions, which can also have a bad smell. Phytoplankton blooms in eutrophic lakes often consist mainly of cyanobacteria or blue-green algae (Scheffer *et al.*, 1997; Dokulil & Teubner, 2000). These cyanobacteria can form surface scums (Chorus & Bartram, 1999) and can cause fish kills (Landsberg, 2010). It seems that cyanobacterial toxins can cause a shift in zooplankton size and community composition (Hansson *et al.*, 2007a). Moreover, they can reduce the drinking water quality (Smith, 2003; Reynolds, 2010) because many cyanobacteria can produce toxic compounds that are dangerous to animals (Landsberg, 2010), but also to humans (Codd *et al.*, 1999; Codd, 2000; Chorus & Bartram, 1999; Funari & Testai, 2008; Pitois *et al.*, 2010). In some instances, the severe growth of blue-green algae may lead to the closure of the lake facilities, as happened at many reservoirs in England during the summer of 1989 (NRA, 1990; Pitois *et al.*, 2010). Eutrophication might also influence the abundance, composition, virulence and survival of pathogens that are already resident in aquatic ecosystems (Townsend *et al.*, 2003; Smith & Schindler, 2009).

The global economic impacts of harmful algal blooms have not been fully calculated, but the cost of eutrophication on fisheries, drinking water treatment and the health of humans and livestock is likely to be billions of dollars per year (Smith & Schindler, 2009). Anderson *et al.* (*2000)* estimated the annual economic impacts from harmful algal blooms in the U.S. of the 1987-1992 period to be $500 million. More recently, Dodds *et al*. (2009) estimated that the combined costs of losses in recreational water usage, waterfront real estate, spending on recovery of threatened and endangered species and drinking water, were approximately $2,2 billion annually as a result of eutrophication in the U.S. freshwaters.

1.4.2 Biodiversity loss

Freshwaters are experiencing declines in biodiversity far greater than those in the most affected terrestrial ecosystems (Sala *et al.*, 2000). Over 10 000 fish species live in fresh water (Lundberg *et al.*, 2000). This is approximately 40% of global fish diversity and one quarter of global vertebrate diversity. When amphibians, aquatic reptiles and mammals are added to the freshwater fish total, it becomes clear that as much as one third of all vertebrate species are confined to fresh water (Dudgeon *et al.*, 2006). Population trends indicate declines averaging 54% among freshwater vertebrates (mainly waterfowl), with a tendency toward higher values in tropical latitudes. Furthermore, 32% of the world's amphibian species are now threatened with extinction, a much higher proportion than mammals (23%) or threatened birds (12%) and 168 species may already be extinct (Dudgeon *et al.*, 2006; AmphibiaWeb, 2015) and many freshwater fish stocks are over-fished to the point of population collapse (e.g. FAO, 2000). Rates of species loss from fresh waters in non-temperate latitudes are not known with any degree of certainty. They are likely to be high because species richness of many freshwater taxa increases toward the tropics (Dudgeon *et al.*, 2006).

1.4.3 Climate change

Recent evidence suggests that symptoms of eutrophication may be exacerbated by climate change, because of the rising nutrients input and increasing temperatures (Jeppesen *et al.*, 2010; Moss *et al.*, 2011). Climate change could increase the nutrient loading for example by aggravated storms, warming soils, rainfall patterns or melting glaciers (Jeppesen *et al.*, 2011). This will make the rehabilitation of culturally eutrophic lakes even an greater challenge in the future (Ansari & Gill, 2013).

Warming temperatures may cause increased evaporation in lakes, this reduces the habitat area and leads to potential changes in water quality (e.g., temperature, salinity). Some shallow lakes and ponds might even dry out (Meerhoff, 2006). Also, higher temperatures and lower water levels will likely enhance the sediment resuspension and release of nutrients, especially of phosphorus (Meerhoff, 2006). Because of the optima for growth of many cyanobacteria and their resistance to grazing by small zooplankters, the relative proportion of this sometimes toxic group may increase (Jöhnk *et al.*, 2008; Paerl & Huisman, 2008; Moss *et al.*, 2011; Kosten *et al.*, 2012a). Also, the number of fish species, and definitely also the potentially zooplanktivorous ones, increases from cold to warm lakes (Fernando, 1994). Because climate change leads to warmer water this will most likely increase the predation pressure on zooplankton (Jeppesen, 2003). The biomass of large *Daphnia* will decline, and with it the ability to control phytoplankton (Moss *et al.*, 2011). Increased chance of eutrophication, decreased oxygen, and increased salinity in lakes will result in a decline in species diversity and abundance, especially among endemics (Anderson *et al.*, 2009). Finally, the synergistic, interactive effects of climate change with other stressors to ecosystems such as habitat modification, exotic species and water pollution, may be severe and unexpected (Anderson *et al.*, 2009).

1.4.4 Overexploitation

Water may be extracted from a standing water body to use for a potable supply or in industry and irrigation applications. Removing water from the system in an unsustainable way will decrease water levels. Overexploitation occurs if a water resource is extracted at a rate that exceeds the recharge rate. This may exacerbate nutrient enrichment, cause deterioration of marginal vegetation through drawdown and cause shallow lakes to dry out (Ansari & Gill, 2013). Also the overexploitation of fish and other organisms are a main threat in water ecosystems (Grafton *et al*., 2007).

1.5 Restoration efforts

1.5.1 Restoration goal

The general assumption is that the more desirable state of a shallow lake is to be a clear water plant-dominated state, because this state is associated with the highest biodiversity and economic value and the least problems of smell, fish kills, toxicity of algal blooms and water supply (Moss, 2007; Poikane, 2014). There are various techniques for lake restoration of which the main used techniques will be discussed below.

1.5.2 Restoration techniques

Nutrient management

The first step in lake management is the reduction of external nutrient loading to lower the concentration of nutrients (phosphorus, nitrogen, etc.) in the water column (Jeppesen *et al.*, 2003; Cooke *et al.,* 2005). The primary cause of excess algae is high nutrient levels hence when nutrient concentrations are lower, a switch to a stable clear water state is more likely (Scheffer *et al.*, 2001). Since the turbid, phytoplankton-dominated state in freshwater lakes is often caused by excessive total phosphorus (TP) concentrations, an external TP load reduction is in the majority of cases the essential prerequisite for turbidity to fall below a threshold value specific for the lake (Hilt *et al.*, 2006). But there is no certainty that the water quality of the lake will improve even after nutrient load reductions (Van Liere & Gulati, 1992). Lake recovery is invariably afflicted by two factors: (1) internal P loading from the sediments (van der Molen & Boers, 1994) and (2) foraging and metabolic activities of the abundant benthivorous and planktivorous fish in these shallow lakes (Gulati & Van Donk, 2002). In shallow lakes the intense sediment-water contact gives an extra dimension to the eutrophication problem. Much of the phosphorus that has been absorbed by the sediment during eutrophication can be released back to the water column later. This internal loading can cause a delay of many years in the response of lake water concentrations to a reduction of external loading. For nitrogen the sediment-buffer effect is less relevant. Instead, it has been shown that substantial amounts of nitrogen can disappear from shallow lakes as a result of denitrification (Scheffer, 2004). The internal loading can be reduced significantly by various restoration methods, such as removal of phosphorus-rich surface layers (dredging) or by the addition of iron or alum to increase the sediment's sorption capacity (Søndergaard *et al.*, 2003). For example

Bootsma *et al*. (1999) described the eutrophication abatement for Lake Naardemeer. The restoration project was aimed at reducing the external P load using P-poor inlet water and dredging of the lake-bed sediment was confined to certain areas. Even though sediment P release appeared to retard lake recovery, turbidity decreased and the vegetation had re-established itself. But control of nutrient loading from lake sediments has proven to be an even trickier task than controlling external nutrient loading (Gulati & Van Donk, 2002). Additional lake restoration measures may therefore be needed to switch back to a clear stable state.

Biomanipulation

Biomanipulation is a form of ecological management in which top-down control is used as a way to manipulate the food web. Lake biomanipulation principally involves reducing the existing planktivore population and introducing piscivores (Gulati & Van Donk, 2002). Two mechanisms seem to be predominantly responsible for the initial increase of clarity after fish stock reduction in shallow lakes. Reduction of the pressure by planktivorous fish allows populations of large-bodied zooplankters to peak and graze down the algal biomass causing clear water. Planktivorous fish can be eliminated by poisoning, removal or increased piscivory (by planting piscivores). This technique is relatively inexpensive, and has been successful, but usually for a limited time and in combination with P reduction (Cooke *et al.*, 2005). Secondly when the fish community is dominated by species that feed at the bottom, resuspended bottom material is often the main cause of turbidity and consequently removal of fish leads to an almost instantaneous increase of transparency. In shallow lakes the increase of transparency after biomanipulation is typically followed by a strong development of submerged vegetation in following years (Scheffer *et al.*, 1993).

The record of biomanipulation as a management tool often has been positive, but the actual responses to deliberate fish manipulations have been variable (Gulati *et al.*, 1990, Søndergaard *et al.*, 2000). The failures are generally linked not only to insufficient or no decrease at all in the autochthonous or in-lake nutrient loadings, but also to rapid increase of the planktivorous fish in the years following their reduction (Gulati & Van Donk, 2002).

Hydrology management

There are several hydrology management techniques, for example water level manipulation. The water level of shallow lakes can sometimes be manipulated with little effort. Such manipulations are not always feasible in practice as they may interfere with recreational or agricultural interests. However, the potential impact of water level manipulation can be large. The basic explanation is that shallow water promotes submerged vegetation as it allows more light to penetrate to the plants (Scheffer, 2004). Complete draw-down is an extreme form of water level management. It is applied frequently to fish-ponds and reservoirs but there is less experience with applying this approach to natural lakes. In vegetated lakes, prolonged draw-down is used as a way to control aquatic plants as it usually results in the loss of most submerged species. Another management technique is flushing. Flushing a lake with relatively clean water can reduce its nutrient level, but may also help to get rid of colonial cyanobacteria in a more direct way (Scheffer, 2004). For example the responses of nutrient concentrations were studied in the flushed, shallow Lake Müggelsee (Köhler *et al*., 2005). Müggelsee had a drastic reduction in external nutrient loading and a strong reduction in the percentage of cyanobacteria.

Others
There are also many other techniques for example the addition of barley-straw to ponds can lead to a remarkable reduction in phytoplankton biomass. Another technique is dredging and it is the most common procedure for sediment removal. There are many more techniques such as: lake protection from urban runoff, artificial circulation, hypolimnetic withdrawal, hypolimnetic aeration, herbicides and algicides o.a. copper sulfate treatment (e.g. Cooke *et al.*, 2005).

1.6 Tropical shallow lakes

1.6.1 Basic limnology of tropical lakes

While temperate lakes are much better studied and understood, limnology studies in the tropics have mainly been performed the last two decades (Lewis 1996; Sperling, 1997; Lewis, 2000; Reddy, 2005). Because of differences in functioning between cold temperature versus warm tropical lakes, the management of lakes must be approached somewhat differently in the tropics from how it is approached at temperate latitudes (Lewis, 2000). Since many warm lakes suffer from eutrophication there is a need for insights into trophic interactions and potential lake restoration methods for tropical lakes. The expected increase in eutrophication in the near future underlines the importance of this field of study (Jeppesen *et al.*, 2007). Moreover, the knowledge about lake functioning in the tropical ecosystems may be useful when evaluating the effects of climate warming on temperate lakes (Meerhoff, 2006).

Tropical lakes are far less numerous than temperate lakes because lakes of glacial origin are rare in the tropics. Also, the mixture of lake types differs from tropical to temperate latitudes; lakes of riverine origin are probably more common than any other type in the tropics (Fig. 4). 10% of the world's lakes are tropical (Lewis, 1996). Most tropical lakes are shallow and show circulation patterns that are different from those in temperate lakes. These patterns, coupled with the higher temperatures, result in a unique metabolism in tropical lakes (Ansari & Gill, 2013). Nevertheless abrupt switches from a clear to a turbid state, just as their temperate counterparts, have also been described for tropical lakes (Loverde-Oliviera *et al.*, 2009).

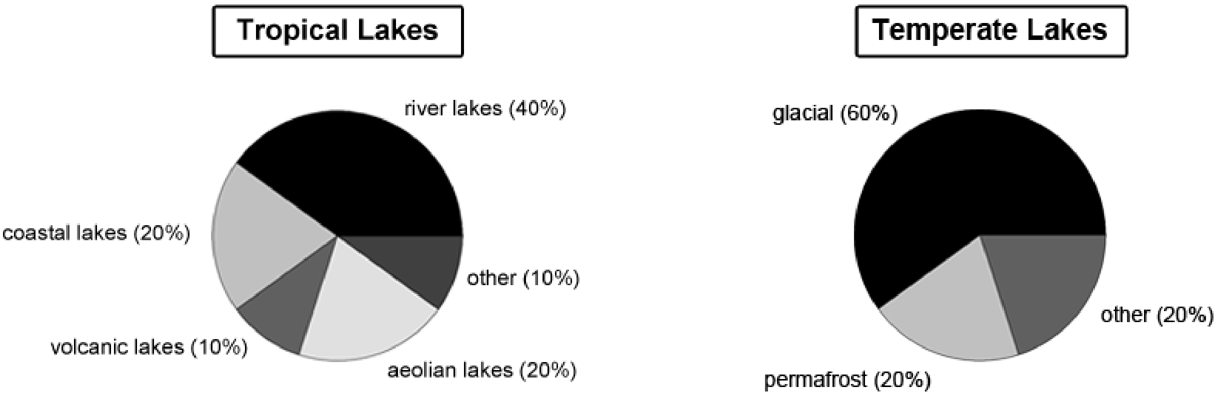

Fig. 4: Approximate proportions of lake types found at temperate and tropical latitudes, as determined by random sampling from maps (modified from Lewis, 1996).

Tropical lakes differ from their temperate counterparts in several important aspects. Very important is the differences in solar irradiance. The higher annual irradiance at low latitudes is responsible for higher minimum water temperatures and mean water temperatures, and a smaller thermal differentiation between upper and lower water column. The deep water of a tropical lake is only as cool as the annual minimum temperature for the coolest months, which is generally about 24°C at sea level (the minimum is also affected in a predictable way by elevation) (Lewis, 1996). Discounting diurnal heat gain, the top and bottom of the water column are separated by only a small temperature difference, which ranges around 1.5°C for equatorial lakes. Seasonality is suppressed in the tropics (but is not absent), hence stratification is less stable than at higher latitudes. Another factor that may affect the thickness of the mixed layer is the Coriolis effect (Lewis, 1996). The Coriolis effect is defined as the apparent deflection of objects (such as airplanes, wind and ocean currents) moving in a straight path relative to the earth's surface. The Coriolis effect is a function of latitude; it is negligible at the equator and highest at high latitude. The low Coriolis effect in the tropics will make wind more effective in establishing a mixed layer, thus reinforcing the effect of low stability in tropical warm water columns. As a consequence nutrients that have moved from the mixed layer to deeper water are more likely to return and for this reason tropical lakes are likely to cycle nutrients more efficiently than temperate lakes. As would be expected from higher nutrient cycling efficiencies, tropical lakes appear to show greater primary production for a given nutrient load (Lewis, 1996).

Water temperature affects the metabolic processes of lakes. In general, the relationship between temperature and metabolism can be described by a Q10 of approximately 2.0, that is, metabolic rates are likely to double with a 10°C increase in temperature, provided that some other factor is not strongly suppressing the rate (Toerien & Cavari 1982; Lewis, 2000). The high temperatures in tropical lakes sustain high rates of microbial metabolism. Nutrients are likely to be regenerated more rapidly and completely, and oxygen is removed much more rapidly than would be the case at the lower temperatures that are characteristic of temperate lakes. Therefore, undesirable effects associated with anoxia caused by eutrophication will be more serious and more quickly realized in tropical lakes than temperate lakes (Lewis, 2000). The maximum rate of photosynthesis per biomass and time (photosynthetic capacity) is a function of temperature, hence primary production in warm tropical lakes is about two to three times higher than in temperate lakes (Melack, 1979; Lemoalle, 1981). Higher incident irradiance and enhanced mixing are additional factors promoting primary production in tropical lakes (Erikson *et al.*, 1998). The prolonged growth season in low latitudes (Melack 1979), can explain the annual average biomass among lakes with a higher risk of long-lasting algal blooms and dense floating plant communities (Jeppesen *et al.,* 2007).

1.6.2 Nutrient dynamics in tropical lakes

Phosphorus is widely considered to be the dominant limiting nutrient for lakes in temperate latitudes (Welch & Lindell, 1992). Nitrogen is more often a limiting element in tropical than in temperate lakes (Lewis, 2000) possibly due to greater phosphorus supply by chemical weathering of rocks and higher nitrogen losses because high denitrification rates (Lewis 2000; 2002; Huszar *et al.*, 2006). Denitrification is stimulated by anoxia and by high temperatures in sediments. Anoxia is more likely to occur and be more persistent in tropical lakes than in temperate ones (Lewis, 2000). Abundance of nitrogen fixers is high in many tropical waters and element ratios in biomass are often suggestive of nitrogen deficiency (Lewis & Levine, 1984; Lewis, 1996). This is not to say that phosphorus limitation is impossible in the tropics (Sarnelle *et al.* 1998; Elser *et al*., 2007).

1.6.3 Food web characteristics of tropical lakes

In contrary to the terrestrial environments of the tropics with impressive biodiversity, the phytoplankton communities are probably no more diverse than temperate ones (Lewis, 2000). Phytoplankton communities show broad overlap in species composition with temperate communities and have little endemism (Lewis, 1996; Figueredo & Giani, 2009). However, the higher temperature in tropic regions has a positive effect on the growth of cyanobacteria so there is more chance for cyanobacterial dominance (Kosten, 2012a).

Zooplankton community composition also shows overlap with temperate lakes but has a higher degree of endemism, contains more taxa that are typically tropical, and is composed of smaller species than temperate communities (Lewis, 1996). For example *Daphnids* are responsible for high biomass in temperate lakes, but are seldom abundant in tropical aquatic ecosystems. Whenever present in tropical lakes, they are generally characterized by a relative small body size (Lewis, 1996). Zooplankton communities in tropical and subtropical lakes are often dominated by small cladocerans (i.e. *Diaphanosoma, CerioDaphnia* and *Bosmina*), rotifers and copepod juveniles and nauplii (Lewis, 1996; Branco *et al.*, 2002; Jeppesen *et al.*, 2007). In contrast to what is observed in vegetated temperate lakes, top-down control of phytoplankton appears to be unimportant in tropical and subtropical lakes (Jeppesen *et al.,* 2007; Meerhoff *et al.*, 2007b; Loverde-Oliveira, 2009). Discussion about this still exists as others state that zooplankton grazing is an important form of top-down control in tropical lakes after all (Hubble & Harper, 2000). The zooplanktivorous phantom midge *Chaoborus* also seems to be more abundant in tropical lakes (Lewis, 1996). Tropical lakes develop anoxia in the bottom water more quickly than temperate lakes, which may provide *Chaoborus* with a fish predation refuge and hereby allow strong predation pressure on zooplankton (Jeppesen *et al.*, 2000).

In the tropics and subtropics, the effects of macrophytes on trophic interactions are more complex, as all life forms (emergent, submerged, floating-leaved and large free-floating species) can be extremely prominent. Winters are very mild so plants usually remain present throughout the year as they can simply keep growing, while in temperate regions wintergreen vegetation occurs especially on sheltered sites or under ice cover where wave action is minor (Scheffer, 2004). In warm waters submerged plants are often replaced by floating plants (Feuchtmayr *et al.,* 2009, Netten *et al.,* 2010), which are less effective as refuges (Meerhoff *et al.,* 2007a; Moss *et al.*, 2011). Also in tropical and subtropical lakes, the smallest fish species and individuals aggregate in all vegetation forms (Meschiatti *et al.*, 2000; Meerhoff *et al.*, 2003; Jeppesen *et al.,* 2007). Small-sized fish species were found in submerged plant beds in a subtropical lake. Therefore, submerged vegetation in warm lakes may be a poor refuge for large-bodied zooplankton, particularly cladocerans (Meerhoff *et al.,* 2003; Jeppesen *et al.*, 2007).

The fish species richness is often higher in tropical and subtropical lakes (Teixeira de Mello *et al*., 2009). South America and Africa have an extraordinarily rich freshwater fish fauna (Sunaga & Verani, 1991). The fish stock in tropical and subtropical lakes is often dominated by omnivorous species that feed on zooplankton but also consume phytoplankton, periphyton, benthic invertebrates, and detritus (Branco *et al.*, 1997; Blanco *et al.*, 2003). Compared to temperate fish communities, only few piscivorous fish are present (Quirós, 1998) so top-down control by piscivores is most likely weaker in (sub)tropical lakes than in temperate lakes. Fish reproduction occurs throughout the year (Fernando, 1994) and many species are viviparous and/or show parental care (Scasso *et al.*, 2001), assuring higher juvenile survival rates. Since small fish are more zooplanktivorous and have higher energy demand per unit biomass, this leads to higher predation pressure on zooplankton (Jeppesen *et al.*, 2005). It is debatable whether fish manipulation methods used in cold temperate lakes can be employed in warm temperate, subtropical and tropical lakes. Several factors indicate that fish stock manipulation may not have the same positive effects in warm lakes (Jeppesen *et al.*, 2005; Jeppesen *et al.*, 2007). Yet, only few studies have investigated the applicability of the biomanipulation theory to tropical and subtropical freshwater ecosystems (Northcote *et al.,* 1990; Saha & Jana, 1998).

1.7 Andean lakes of Ecuador

1.7.1 Importance of water-related services

The Andes region of South America encompasses Bolivia, Colombia, Ecuador, Peru and Venezuela. The Andes region provides many ecosystem services that are under serious anthropogenic threats such as mining, logging, constructing and agriculture. One of the important ecosystem services that human populations in the Andes rely on (40 million people in 2009; data from Josse *et al.*, 2009) are water-related services (Bradley *et al.*, 2006; Buytaert *et al.*, 2006; Vuille *et al.*, 2008; Anderson *et al.*, 2009) which encompass hydropower, irrigated agriculture, water for domestic and industrial uses, and ecoservices (Célleri & Feyen, 2009). Ecuador’s capital city for instance, depends for more than 80% (7400 L s^{-1}) of its water supply on the surrounding páramo ecosystem. Water retained in the Andean watersheds is of principal importance for agriculture as it is used for irrigation of downstream cropland to supplement rainfall. Currently agriculture accounts for 82% of all freshwater withdrawal in Ecuador. The percentage of total cropland that is irrigated represents 28.8% in 1999 (Worldbank, 2009). Furthermore, approximately half of Ecuador’s demand for electrical energy is met by hydroelectric resources. However, Ecuador’s hydropower potential can still be developed further, as it harbours the possibility of producing approximately ten times its current hydropower use (Célleri & Feyen, 2009). But the ability of Andean ecosystems to provide these services in the future is of great concern (Anderson *et al.*, 2009) due to climate change, the rapid growing population and the rising living standards. Ecuador’s human population is amongst the most rapidly growing of Latin America. Álvarez-Berríos *et al.* (2013) estimated a doubling of the population within the next 25 years. Temperatures will rise more in the high mountains than at lower elevations (Thompson *et al.*, 2000; Foster, 2001; Messerli *et al.*, 2004; Buytaert *et al.*, 2006). Temperature in the Andes has increased by approximately 0.1 °C/ decade (Vuille *et al.*, 2008). The rising temperatures will induce glacier melt, an upward shift of the snowline, erosion and runoff. These processes will affect the hydrological cycle and may have severe consequences because ice and glaciers of mountains sustain important water supplies (Buytaert *et al.*, 2006). As these water resource buffers shrink and some watersheds disappear completely, alternative water supplies may become very expensive and/or impractical in the face of increased demand as population and consumption rise (Bradley *et al.*, 2006).

1.7.2. Conducted research so far

It's clear that the Northern Ecuadorian lakes are of significant importance. They have a historical and ecological value, they are an important source of drinking water and have high valued tourist attraction, especially the lakes of the Imbabura province. Despite of their importance, little is known about the ecology of tropical lakes. Due to the fact that the Andes extends over a high longitude and altitude there is also great variation among Andean lakes. This makes it even more complicated but also emphasizes the necessity to investigate tropical lakes in different regions. Limnological investigations performed in Ecuador are few, and consequently, knowledge on its aquatic systems are scarce. Steinitz-Kannan *et al.* (1983) refers to the first investigations carried out in Ecuador on the limnology of lakes. There have also been performed a few investigations on phyto- and zooplankton species and macrophytes. For an overview of the most important research on Ecuadorian lakes see Table 2. To secure the social ecosystem services of Andean lakes a good and sustainable management is required.

Table 2: Overview of the most important research on Ecuadorian lakes. '-': data was not present in the paper.

Name of the lake	Distribution	Basin	Province	Altitude (m)	Trophic state	Reference
Limpiopungo	Paramo lake	Possibly behind morraine	Cotopaxi	3970	-	(Steinitz-Kannan *et al.* 1983)
Laguna de San Marcos	Paramo lake	Fjord lake	Pichincha	3414	-	(Steinitz- Kannan *et al.*, 1983)
Cuicocha	Below paramo	Caldera	Imbabura	3380	Oligotrophic	(Steinitz-Kannan *et al.*, 1983) (Gunkel & Beulker, 2009) (Gunkel *et al.*, 2008) (Kiersch *et al.*, 2004)
Mojanda Grande	Paramo lake	Caldera	Imbabura	3714	Oligotrophic	(Steinitz-Kannan *et al.*, 1983)
Mojanda Chica	Paramo lake	Maar	Imbabura	3696	-	(Steinitz-Kannan *et al.*, 1983)
Mojanda Negra	Paramo lake	Volcanic	Imbabura	3700	-	(Steinitz-Kannan *et al.*, 1983)
Laguna de San Pablo	Below paramo	Volcanic land-form	Imbabura	2660	Eutrophic	(Steinitz-Kannan *et al,*. 1983) (Gunkel & Casallas, 2002) (Casallas, 2005) (Cassallas & Gunkel, 2001) (Kiersch *et al.,* 2004) (Gunkel, 2000)
Yahuarcocha	Below paramo	Volcanic land-form	Imbabura	2380	Eutrophic	(Steinitz-Kannan *et al.*, 1983)
Quilotoa	Paramo lake	Caldera	Cotopaxi	3914	-	(Steinitz-Kannan *et al.*, 1983) (Gunkel *et al.*, 2008) (Aguilera *et al.*, 2000)
Laguna de Limoncocha	-	Riverine lake	Sucumbíos	-	-	(Colinvaux *et al.,* 1985) (Durañona, 2005)

Gunkel (2000) did research on a high altitude tropical lake in Ecuador: Lake San Pablo is located at an altitude of 2 660 m near Otavalo, which also is situated in Imbabura. Water temperature varies between 17°C and 19°C and lake conditions are meso-eutrophic. Phytoplankton is dominated by green algae and some diatoms and the abundance of the zooplankton is low, amounting to < 20 ind. L^{-1} *Daphnia pulex* and < 6 ind. L^{-1} *Metacyclops mendocinus.* There also have been some investigations on lakes located in the Andes, apart from Ecuador. For example Aguilera *et al.* (2013) has performed some investigation in high altitude lakes (> 4000 m a.s.l.) in Bolivia. There has also been research in Colombia (lake Guatavita e.g. Zapata-Anzola *et al.*, 2006), Argentina (Queimaliños *et al.*, 1998; Balseiro *et al.*, 2001; Arribére *et al.*, 2010) and Chile (Mühlhauser *et al.*, 1995). It's clear the majority of research in tropical lakes has only been performed during the last two decades. The theory of alternative stable states has barely been studied on South-American lakes. Kosten *et al.* (2012b) is one of the few who investigated this subject in South-America, but not in the Andean part of the continent.

1.7.3 Need for sustainable management

Ecuador established in 1981 the Sistema Nacional de Áreas Protegidas (Steinitz-Kannan, 1997). Nowadays, approximately 20 % of Ecuador contains protected areas. Ecuador has a large number of wildlife. However, many species are endangered and even extinction for different reasons. Direct causes are the destruction and fragmentation of natural habitats, overexploitation, illegal trafficking of species and the introduction of exotic species. 1252 vertebrate species are within threat categories, of which 217 are mammals, 328 birds species, 276 reptiles and 521 species amphibians (Ministerio del Ambiente, 2014). Hereby, the Ministery of Environment proposed the "Protect Ecuador, the responsibility belongs to everyone" campaign, that informs the public about the endangered species and encourage their protection. In Ecuador there are some conflicts over water rights (Hermann, 2002). Recently in 2014 the government fast-tracked a new water law, endorsing the privatization of water and permitting extractive activities in sources of freshwater. On 21 June 2014, social sectors reacted with a cross-country walk of protest. Part of the problem is the large inequality in access to water. Indigenous leader Perez Guartambel has claimed that Ecuador's wealthiest one percent controls 64 percent of freshwater.

1.8 Research project

A special type of tropical lakes are the mountain lakes in the equatorial zone. They are located in the tropics, but due to the high altitude the temperature is lower than in tropical lakes. Lakes in the tropical Andes fulfil a huge variety in ecosystem services such as providing drinking water, water for irrigation, hydroelectricity, tourism, ecological value and recreation. Despite of their importance, little is known about the limnology of tropical lakes in Ecuador. A few limited studies has been performed by Steinitz-Kannan in 1984 and Günkel in 2000 on these unique ecosystems. The northern region of Ecuador is also known as 'the province of the lakes'. Here our investigation took place on one of these lakes, Yahuarcocha. This lake in northern Ecuador is situated at a relatively high altitude, and close to urban areas. It is exposed to human impacts (see 2.1 Studied site) and these impacts on the lake are exacerbated by climate change. To secure the ecosystem services of Andean lakes, a sustainable management needs to be developed. A better understanding of the functioning of a tropical lake ecosystem is crucial in the development of this management. This research is framed within a VLIR-UOS collaboration between KU Leuven, UGent and Universidad Técnica del Norte (UTN) (South Initiative project "Sustainable management of lakes in Northern Ecuador under growing economic activities and a changing climate", ZEIN2013 Z140). The aim of this study is to evaluate some important limnological parameters of lake Yahuarcocha, including physico-chemical parameters (e.g. oxygen, nutrients, hydrology), biological parameters (phyto- and zooplankton, macrophytes) and interaction between sediment and water column. Important goals of this study also include the identification of the main nutrient limiting phytoplankton biomass and determining the trophic state of the lake at this time of research. This knowledge will be used to develop a monitoring system to evaluate and monitor the ecological status of Yahuarcocha. Before developing a management strategy one more important question needs to be answered: do we need to approach lake Yahuarcocha as a temperate lake or as a tropical lake? This approach will be a decisive factor in terms of failure or success regarding management of the lake. Previous research indicated that the ecology of Yahuarcocha has similarities with temperate lakes (lower temperatures due to the high altitude), but their equatorial position on the other hand results in fundamental differences in the functioning of these lakes.

2 Methods

2.1 Studied site

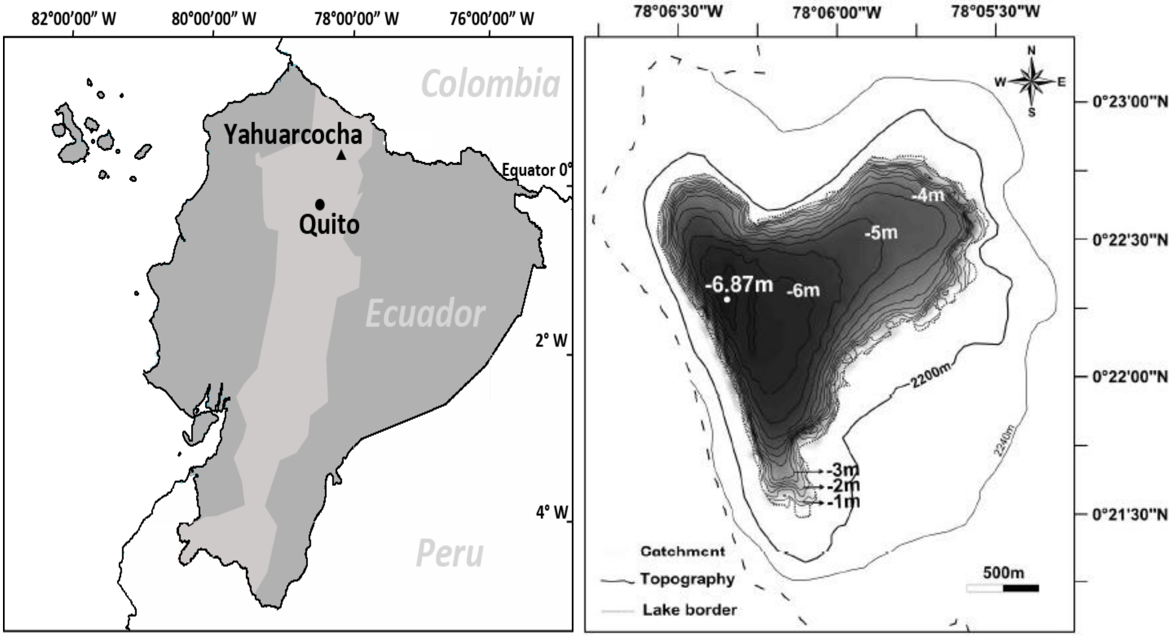

Fig. 5: Lake Yahuarcocha is situated in the Andean region in Ecuador (left). (right) Bathymetric map of Yahuarcocha, contour lines of depth are spaced with a 0.5 m interval, contour lines of elevation are spaced with a 40 m interval. Yahuarcocha is a shallow lake. It's deepest point reaches a depth of 6.87 which is denoted by the white dot (Blomme, 2014).

Yahuarcocha (0°22'N 78°06'W) is an Andean shallow lake situated in the North of Ecuador (Fig. 5) in the province Imbabura. Yahuarcocha is located at an altitude of 2192 m near the city center of Ibarra (Fig. 6) and the dormant volcano Imbabura. Due to a mild air temperature (20-25°C), various touristic activities and a good accessibility, Yahuarcocha became one of the most visited lakes of this province (Trijillo *et al.*, 2011). An investigation of the Universidad Tecnica del Norte (UTN) in 2010 stated that 20 000 tourists weekly visit Yahuarcocha of which 85% passes during the weekend (data from UTN University). Not only tourists are attracted to this lake, also a relative high amount of farmers settled in the Yahuarcocha catchment area. About 25% of the catchment is used for agriculture. Urban zones, consisting of villages and roads, accounts for 6.1% of the catchment area and some páramo vegetation (1.6%) is present on the highest slopes, that reach up to 3820 m (Table 2) (Blomme, 2014). Lake Yahuarcocha has a surface area of about 2.61 km^2 and contains 12.7 million m^3 of water (Table 3) (Trijillo *et al.*, 2011). The mean annual precipitation varies between 500 and 750 L m^2 (Blomme, 2014).

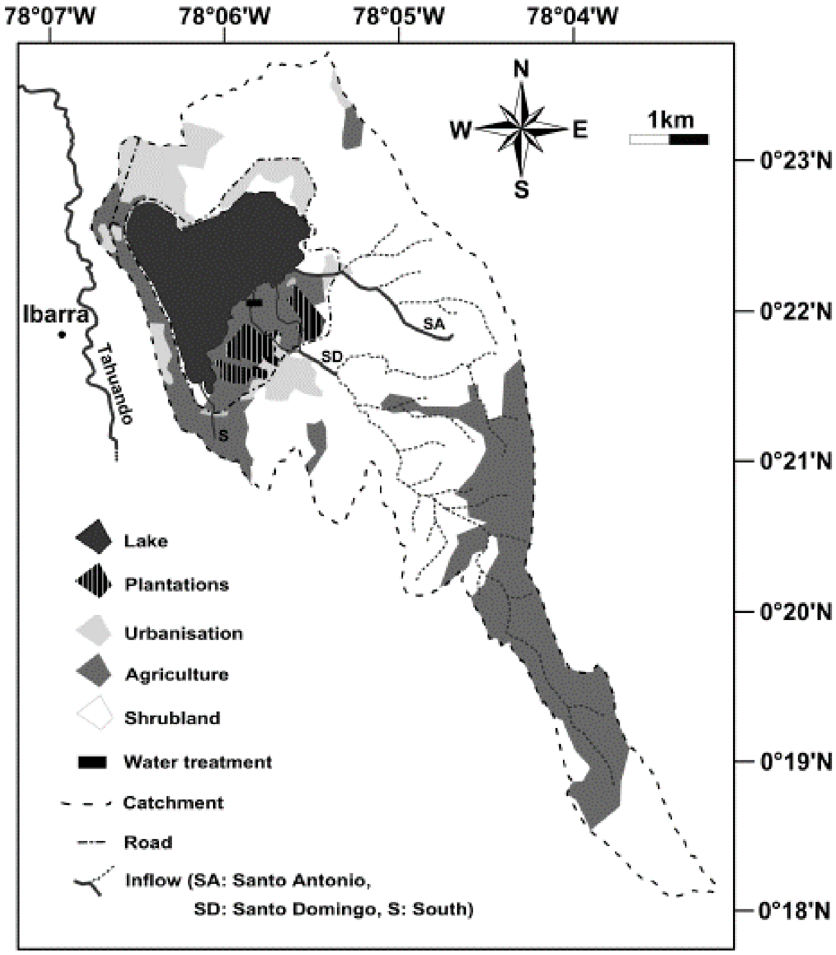

Fig. 6: Lake Yahuarcocha is situated east of Ibarra. Its catchment area is detached from this city and consists mainly of shrub land and agriculture. There are three streams that reach the lake at its south-eastern border. The water treatment station and the ring road are depicted too (modified from Blomme, 2014).

Table 3: General characteristics of lake Yahuarcocha.

Parameter	Yahuarcocha
Latitude (N)	00°22'32,2"
Longitude (W)	078°06'6,5"
Altitude (m)	2192
Surficial area (km²)	2.6
Maximum depth (m)	6.9
Mean depth (m)	4.9
Volume (m³)	$12.7*10^6$
Annual precipitation (mm)	750
Catchment area (km²)	23.71
Urban area (%)	6.07
Plantations (%)	1.86
Agricultural area (%)	25.64
Páramo (%)	1.64

Yahuarcocha is situated close to the city Ibarra, but domestic wastewater of its 139.721 inhabitants (data from 2014) and runoff water of this city does not enter the lake but is discharged into a river close to Yahuarcocha; the Tahuando river. Years ago, farmers settled around Yahuarcocha and used water from this lake to irrigate their crops. Water levels of Yahuarcocha were dropping and to solve this problem they made a channel that connects Yahuarcocha with the Tahuando river. This channel was made upstream where wastewater is not yet discharged into the river. This channel passes through residential areas and their wastewater does flow into it. The Santo Domingo and Santo Antonio are the two other main inflows in Yahuarcocha. Rainfall in the mountains of the catchment forms two main rivers. Their branches are used as a source to fill irrigation channels. When Yahuarcocha started to have problems with the water from these channels, that was probably enriched by wastewater and/or fertilizers, they build a wastewater treatment plant. The wastewater treatment plant did not work properly and two years ago they closed it and it has been out of order ever since.

2.2 Monitoring

Samples were collected and measurements were performed every month during a period of one year (March 2014 – March 2015) by the UTN at 12 different sampling points in lake Yahuarcocha. Some sampling points were randomly chosen, others were chosen for a certain characteristic: point 5 was chosen because it is situated close to the inflow of Santo Domingo and Santo Antonio, point 6 is situated close by the water treatment, point 7 is close to some agriculture, point 8 is close to the inflow of the Tahuando channel and point 9 is the deepest point (Fig. 7).

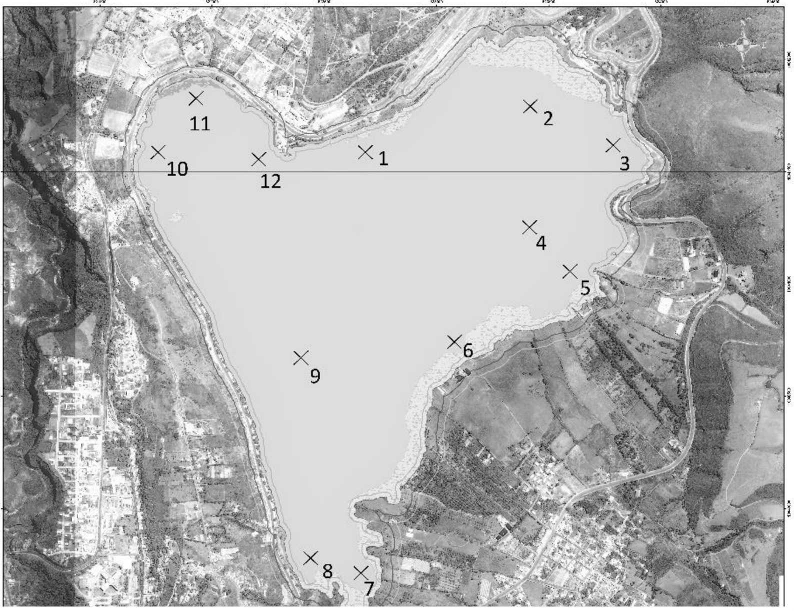

Fig. 7: The sampling points in lake Yahuarcocha.

2.2.1 Physico-chemical parameters

Temperature, pH, conductivity and dissolved oxygen (% and mg L^{-1}) of the surface water (0 -1 m) of each sampling point was measured by using a multimeter (*Horiba U-50*), containing sensors for all of those parameters. The deepest point (9) was used to determine whether there was stratification or not. Therefore a vertical profile of the physico-chemical parameters was determined using measurements at 1, 2, 3, 4, 5 and 6 meter of depth. Water transparency was also determined each month by using a Secchi disk at every sample point.

2.2.2 Nutrients

Each month, an integrated surface water sample (all the sample points together) was collected using the Van Dorn sampler. This water sample was used for measurements of nutrient concentrations. Nutrients N and P were fractionated in a total (TN and TP, analyzed on unfiltered water samples) and dissolved (DN and DP, analyzed on Whatmann GF/F filtered water samples) fraction. For the dissolved fraction, a further fractionation was made between dissolved reactive (DNR and DRP) and dissolved non-reactive (DnRN and DnRP) nutrients. For analysis of TN and TP as well as for the analysis of DnRN and DnRP, the water samples were digested prior to analysis using alkaline persulphate digestion. The two subsamples per month (unfiltered for total nutrients and filtered for dissolved nutrients) of the integrated water sample were stored in the freezer at -20°C until analysis in Belgium. Nutrients were analyzed using a microflow Technicon segmented flow nutrient analyzer (QuAAtro; Seal Analytical) equipped with standard manifolds for the analysis of NH_4, NO_2, NO_3 and PO_4. This system has a detection limit of 0.4 µg L^{-1} for NH_4, 0.3 µg L^{-1} for the sum of NO_2 and NO_3 and 0.2 µg L^{-1} for PO_4.

2.2.3 Phytoplankton

Species composition

For the phytoplankton species composition an integrated surface water sample was taken every month. The sample was filtered over a 64 µm filter in order to remove zooplankton. A 250 ml bottle was filled with this integrated sample and formol was added until a total concentration of 4% formol was reached. The fixed samples were stored in the dark at room temperature until analysis. For analysis of the phytoplankton species composition, a 10 ml plankton chamber was filled with the sample and left to sediment for four hours. Then the phytoplankton could be identified and counted by using an inverted microscope. All the individuals were counted per subsample and identification of the phytoplankton was done up to the level of genus.

Biomass

Chlorophyll *a* (Chl *a*), an indicator for total algae biomass, and phycocyanin, an indicator of cyanobacteria biomass, were measured using a fluorometer based on in vivo fluorecence (*Turners designs Aquauor*). A 2 mL water sample was placed in the dark for 30 min. Before chlorophyll *a* and phycocyanin were measured. Chl *a* was also measured with the fluorometer after methanol extraction. For the extracted Chl *a* measurements an integrated surface water sample was taken using the van Dorn sampler every month. The water was filtered over a 64 µm filter to remove the zooplankton. After this, the water was filtered over a (Whatman GF/F grade, pore size 0.7 µm) filter until the filter was saturated with algae. The volume filtered was noted. This filter was cut into small pieces and 10 ml of 100% methanol was added to extract the Chl *a*. The tubes were put in the dark at 4°C for 24 hours and homogenized once after 23 hours to prevent Chl *a* gradient inside the tubes. The tubes were centrifuged and the supernatans was analyzed with the fluorometer.

Pigment analysis

Other pigments were identified and quantified with a high performance liquid chromatography (HPLC) in the lab in Belgium. Through HPLC it is possible to get more precise and detailed information about chlorophyll concentrations and other pigments. Each month, phytoplankton was collected by filtering an integrated surface water sample over a glass fiber filter until saturation. All filters were stored at -20°C and transported to Belgium for analysis. For the analyses with HPLC, pigments were extracted from the GF/F filters in 90% methanol using ultrasonication. The carotenoid trans-β-apo-8'-carotenol was added during the extraction as an internal standard. Pigments were separated and quantified on a Waters Alliance HPLC system equipped with a Waters Spherisorb ODS2 column using a ternary gradient of 80:20 methanol : 0.5 M ammonium acetate, 90:10 acetonitrile: water and ethyl acetate. Carotenoids were identified using a PDA detector and the system was calibrated using pure standards (DHI, Denmark).

2.2.4 Zooplankton

A depth-integrated sample was collected for analysis of zooplankton community composition. A zooplankton net was lowered to 0.5 meter above the bottom. The net was slowly pulled up and this was repeated for every sample location every month. The samples were put together to make the integrated sample. Formol was added to this sample until a total concentration of 4% formol was reached. These fixed samples were stored in the dark at room temperatures until analysis. A 10 ml subsample was taken from the fixed sample after good homogenization and the species composition and densities were determined by using an inverted microscope. For the species composition 150 individuals were counted and identified up to genus level. For the density all the individuals were counted and identified up to group: cladocerans, copepods and rotifers.

2.2.5 Macrophytes

The littoral zone was divided into regions for which the macrophytes were assessed to be submerged, floating or emergent and for which the extent of coverage (patchy or total coverage) was estimated.

2.2.6 Fishing

To investigate the fish community we used a gillnet randomly in the lake. The gillnet was 25 meter long and 1.5 meter wide and had 12 mesh sizes varying between 6.25 and 55 mm. We laid it out at 4 p.m. and the next morning we got the net out of the water at 10 a.m. The gillnet had different mesh sizes, so we could catch fish of various sizes. The fish were counted and identified up to species level.

2.2.7 24-hour monitoring

In March, a 24 hour survey was performed every six hours. We started at midnight (12 p.m.), then at 6 a.m., 12 a.m. and ended at 6 p.m. At four different sample points (near the shore between the Totora reeds, between the submerged vegetation, 60 meter off shore and at the deepest point) zooplankton was sampled trap at one meter depth using the Schindler-Patalas. At the deepest point a sample close to the bottom was also collected for analysis. Each time three replicates were taken. Samples were fixed in 4% formol and kept in the dark at room temperature until microscopal analysis. Zooplankton was counted and identified up to species level under a stereo microscope. Vertical profiles of the physico-chemical parameters (pH, temperature, dissolved oxygen) were determined at the deepest point (point 9, Fig. 8).

2.2.8 Sediments

Sediment samples were taken in the 13 sampling points at a depth of about 50 cm. The 12 sampling points depicted in Fig. 8 were analyzed and the center of the lake was added as a sampling point. Dried sediment samples were stored at 4°C until they could be analyzed in Belgium for nutrients. Elemental analysis of the sediment (Na, Mg, Al, P, K, Ca, Mn, Fe, Co, Ni, Cu, Zn, As, Mo, Cd, Pb) was performed using Inductively Coupled Plasma - Mass Spectrometry (ICP-MS). For these analyses, 5 mg of dried sediment was acidified to a pH < 1 (1 ml of HNO3, 65%, Suprapur) and autoclaved after 24 hours. Before analysis, samples were diluted in milliQ water until the final concentration of HNO3 in the sample was < 5%.

2.3 *In situ* experiments

Between January and March 2015, a series of *in situ* experiments were performed on lake Yahuarcocha. The goals of these experiments were to investigate the nutrient limitation, the zooplankton grazing capacity, the influence of light intensity and UV radiation on phytoplankton growth. Each experiment was incubated for two days in lake Yahuarcocha. Blomme (2014) and Mandonx (2014) did some exploratory experiments on this lake and some of their results will be included in the results to compare with our results.

2.3.1 Nutrient limitation experiment

One way to detect nutrient limitation is to evaluate the response of phytoplankton to addition of nutrients. 12 bottles of 2 L were filled with lake water that was filtered over a 64 µm filter and divided in four different treatments: P enrichment (addition of 0.77 mg L^{-1} P as K_2HPO_4), N enrichment (7.01 mg L^{-1} N as $NaNO_3$), NP enrichment (addition of both P and N) and a control receiving no nutrient additions. For each treatment there were three replicates. The bottles were placed randomly on an aluminium frame horizontal in the surface water layer. A double shade netting was secured above the bottles to reduce the light intensity to about 10% of the direct solar irradiance. The treatments were incubated in the water for two days. Chl *a* and phycocyanin- content was measured directly after finishing the experiment using the fluorometer (*Turners designs Aquafluor*).

2.3.2 Zooplankton grazing experiment

Zooplankton grazing was evaluated by comparing growth of phytoplankton in treatment with and without zooplankton. Nutrients were added in order to avoid interference of nutrients excreted by zooplankton with phytoplankton growth. A frame was constructed with nine bottles of 0.5 L filled with zooplankton free lake water from Yahuarcocha attached to an aluminium frame placed in the surface water layer of the lake. A double shade netting was secured above the bottles to reduce the light intensity to about 10% of the direct solar irradiance. In three bottles no zooplankton was added (Controle), three bottles were each filled with 10 *Daphnia* individuals from Yahuarcocha (+D), and the other three bottles were each filled with 10 copepod individuals from Yahuarcocha (+C). After two days of incubation the Chl *a* and phycocyanin-content was measured directly after finishing the experiment using the fluorometer.

2.3.3 The influence of light intensity and UV radiation

For this experiment two sticks with 40 bottles of (0.5 L) were incubated in Yahuarcocha for two days. 20 bottles were carefully taped with UV filtering foil (-UV treatment) and the other 20 bottles were not taped with the filter (+UV treatment). The bottles were filled with zooplankton free water from Yahuarcocha. Nutrients were added to make sure that primary production was not limited by nutrient deficiency (addition of 0.77 mg L^{-1} P and 7.01 mg L^{-1} N). The bottles were placed at a certain depth for which the percentage of residual irradiance was calculated with the formula 100*exp(extinction coefficient*depth). The extinction coefficient could be measured with the Secchi depth. After calculation the bottles were placed respectively at 0.02 m, 0.06 m, 0.1 m, 0.18 m, 0.24 m, 0.3 m, 0.4 m, 0.52 m, 0.74 m and 1 m. There were two replicates for each depth. After two days incubation the Chl *a* and phycocyanin- content was measured using the fluorometer.

Table 4: Depth of the bottles on the UV-ladder with on the right the irradiance after calculation.

Depth (m)	**Irradiance (%)**
0.02	89.3
0.06	71.2
0.10	57.0
0.18	36.1
0.24	25.7
0.30	18.3
0.40	10.4
0.52	5.3
0.74	1.5
1	0.4

2.4 Statistics

All the data were processed using *Statistica 10, StatSoft, Inc* . Graphs were made with *Sigmaplot 11.0.* Data of the zooplankton grazing experiment was analyzed using Welsh two sample t-tests and data of the zooplankton migration was analyzed using Factorial Anova’s.

3 Results

3.1 Physico-chemical parameters

3.1.1 Monitoring

All the observations of the physico-chemical parameters each month is the average of 12 different sample points in Yahuarcocha. Table 5 includes an overview of the average limnological data of Yahuarcocha measured from March 2014 to March 2015. On average a temperature of 21.4°C was measured and a pH of 8.9 which indicates slightly alkaline conditions, a dissolved oxygen concentration of 6.8 mg L^{-1} and a conductivity of 498 µS cm^{-1}. The annual average Secchi depth was 0.47 meter (Fig. 11).

Table 5: Limnological data of Yahuarcocha, measured from march 2014 till march 2015. Each month 12 different sample points were measured and the overall averages of these parameters are presented in this table.

Variables	**Yahuarcocha**
Temperature (°C)	21.4
pH	8.9
Dissolved oxygen (%)	76.2
Dissolved oxygen (mg L^{-1})	6.8
Conductivity (µS cm^{-1})	498
Secchi depth (m)	0.47

The average temperature of Yahuarcocha for the whole year is 21.4°C. In August the water was the coldest with an average temperature of 19.6°C and in April the water was the warmest with an average of 22.4°C (Fig. 8). There is a significant difference between the temperature of the warmest water and the coldest water with 1°C (p-value < 0.001).

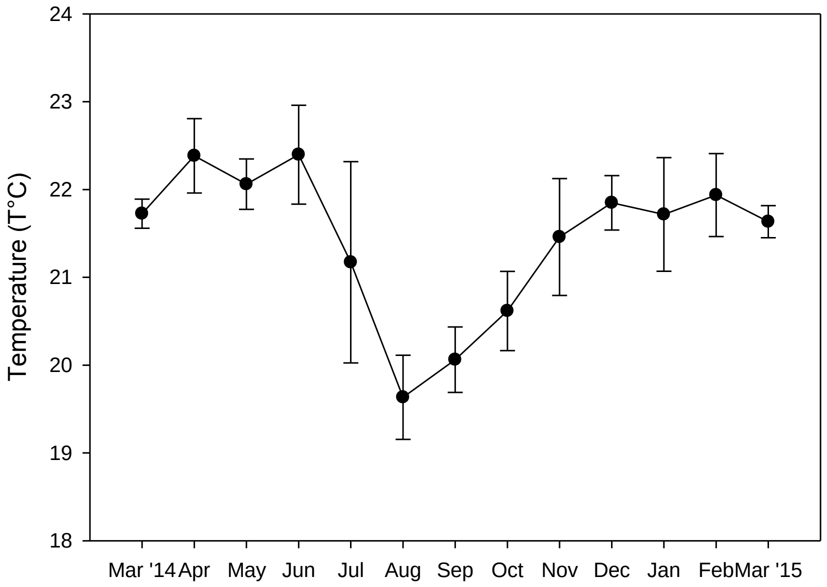

Fig. 8: Monthly temperature of Yahuarcocha. Measured from March 2014 till March 2015.

In each month small fluctuations in temperature could be observed in the surface water layer (0-1 m depth). These fluctuations were the highest in November with a difference of 2°C between 0 and 1 meter depth. Below 1 meter temperature always remained more or less constant (Fig. 9).

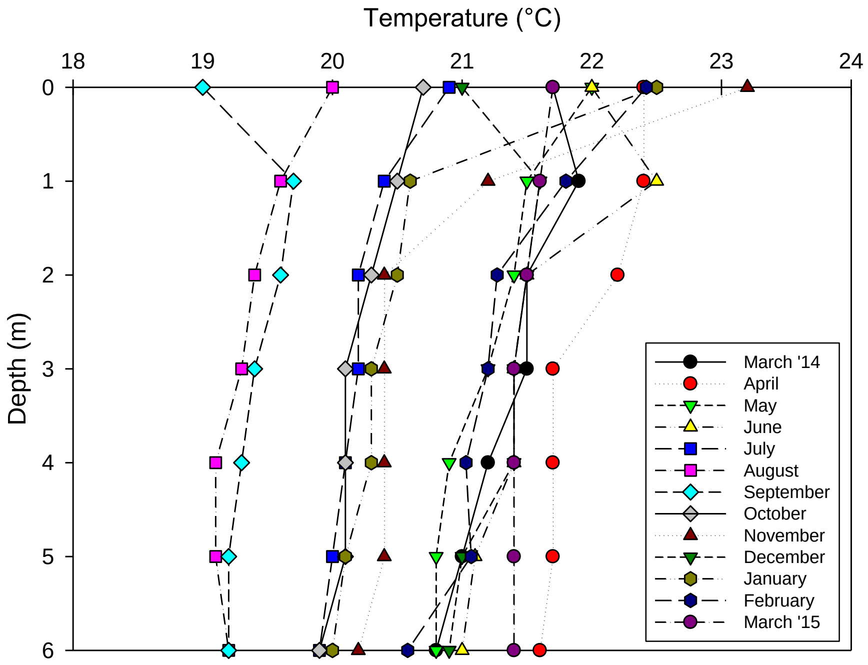

Fig. 9: Vertical profile of the temperature of the water in Yahuarcocha. Measured from March 2014 till March 2015.

Dissolved oxygen in the water surface layer fluctuated every month between an average of 5.5 mg L^{-1} and 8.3 mg L^{-1}. The highest monthly average of dissolved oxygen was measured in January 2015 with 8.3 mg L^{-1}. Looking at the measurements in the different sample points the highest value measured was 10.3 mg L^{-1} in November. In general dissolved oxygen levels slightly decreased with increasing depth. The highest fluctuations in the vertical profiles were measured in January and March 2015 with dissolved oxygen concentrations falling back to only 0.06 mg L^{-1} at a depth of six meters (Fig. 10).

pH fluctuated between 8.7 and 9.2 every month. Also pH slowly declined throughout the water column. The average conductivity over the whole year was 498 µS cm^{-1}. It fluctuated between 443 and 572 µS cm^{-1}.

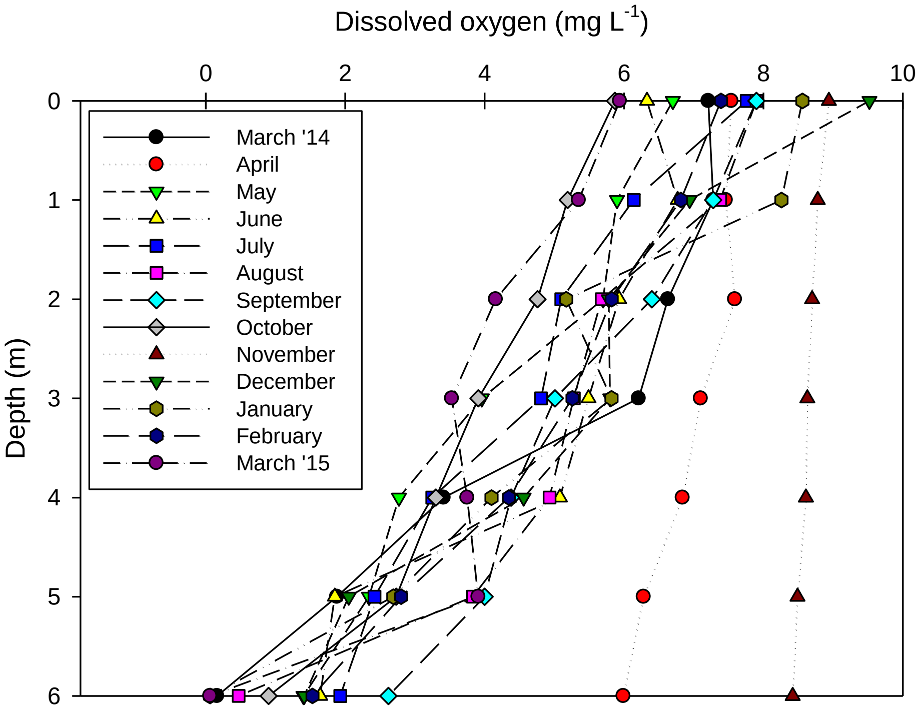

Fig. 10: Vertical profile of the oxygen dissolved each month from March 2014 till March 2015.

The Secchi depth in March 2014 was 0.63 meter and declined to 0.29 meter in March 2015. Water clarity was the highest in May 2014 with a Secchi depth of 0.76 meter (Fig. 11).

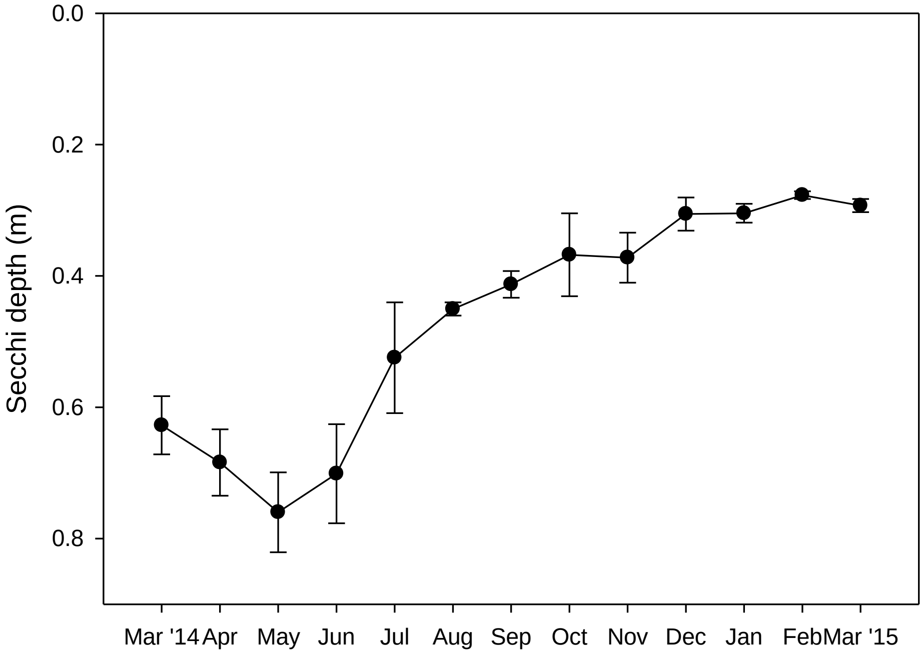

Fig. 11: Secchi depth every month in Yahuarcocha. Every month 12 sample points were measured in Yahuarcocha.

3.1.2 24-hour monitoring

During the 24-hour monitoring in February 2015, the temperature values showed only small variations in temperature near the water surface, being 21.7°C, at 6 a.m. and 22.34°C at mid-day. Vertical profiles (Fig. 12) show the presence of thermal stratification with the highest fluctuation in temperature occurring between three and four meters depth. The surface water had an average temperature of 22.06°C and the average bottom water was 21.48°C, showing a difference of 0.58°C The average temperature water was relatively constant: 22.01°C, 21.95°C, 21.78°C and 21.62°C at 12:00, 24:00, 18:00 and 6:00 respectively.

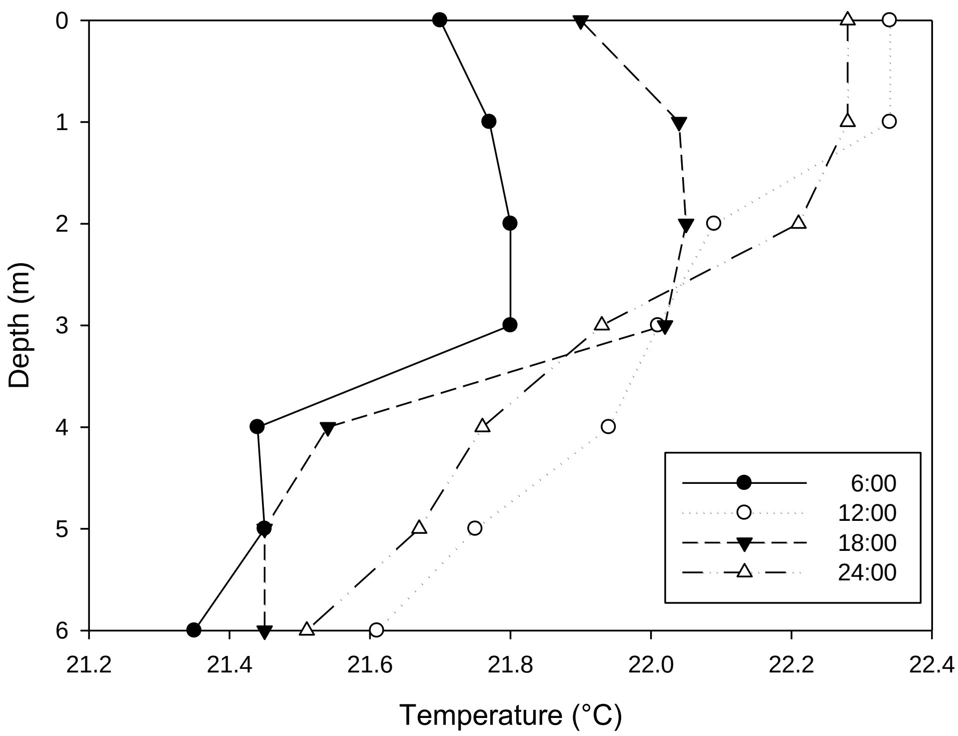

Fig. 12: Vertical profile of the temperature of the water. Measured at 6:00, 12:00, 18:00 and 24:00.

pH declined in a gradual way with increasing depth and no abrupt changes in pH were detected. At 6 a.m. there was a slightly lower pH with 8.51 and at 6 p.m. there was a slightly higher pH with 8.81, which is clearly only a very small difference. The average pH at the surface water was 8.65 and above the lake bed (at 6 meters) the average pH was 8.07. So there is a difference in pH between surface and bottom of 0.58.

In August 2013 a similar 24-hour monitoring was performed by Blomme (2014). The results concerning temperature are shown in Fig. 13.

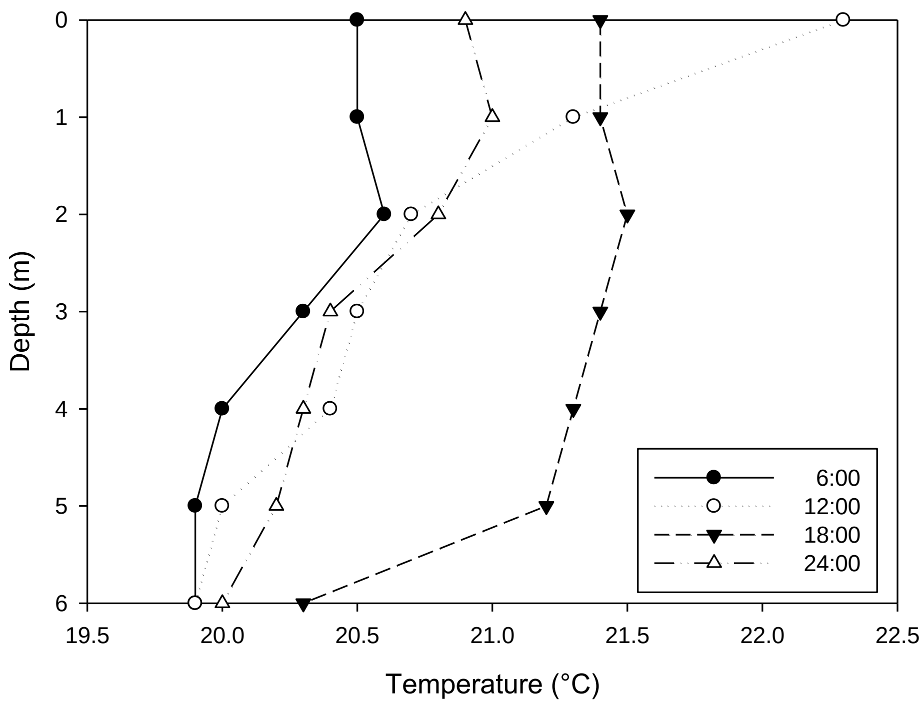

Fig. 13: Data received from Blomme (2014). vertical profile of the temperature of the water at the 24-hour monitoring. Sampling done in August 2013.

Water surface temperature equaled 21.5 °C to reach 19.4 °C just above the Yahuarcocha lake bed. At night, thermal difference between surface and bottom waters decreased, as surface water cooled down to 20.5 °C, according to their 24-hour sequence data. A maximum temperature of 22.3 °C was reached at mid-day, while water at a depth of 6 meter did not vary through time.

3.2 Nutrients

3.2.1 Nitrogen

For N the total concentration varied between 1.2 mg L^{-1} in June and 2.2 mg L^{-1} in November with an average of 1.6 mg L^{-1} through the whole year (Table 6). There was no clear increase or decrease during the study period. The majority of N was located in the dissolved non-reactive fraction (97%) and only 3% was located in the dissolved reactive fraction.

Table 6: overview of the mean, minimum and maximum of DRN (dissolved reactive nitrogen), DnRN (dissolved non-reactive nitrogen) and TN (total nitrogen).

Statistics	**DRN (µg.L^{-1})**	**DnRN (µg.L^{-1})**	**TN (µg.L^{-1})**
mean	31.9	909.0	1599.8
min	13.9	706.8	1222.0
max	65.8	1165.0	2233.7
stdv	24.0	657.7	820.1

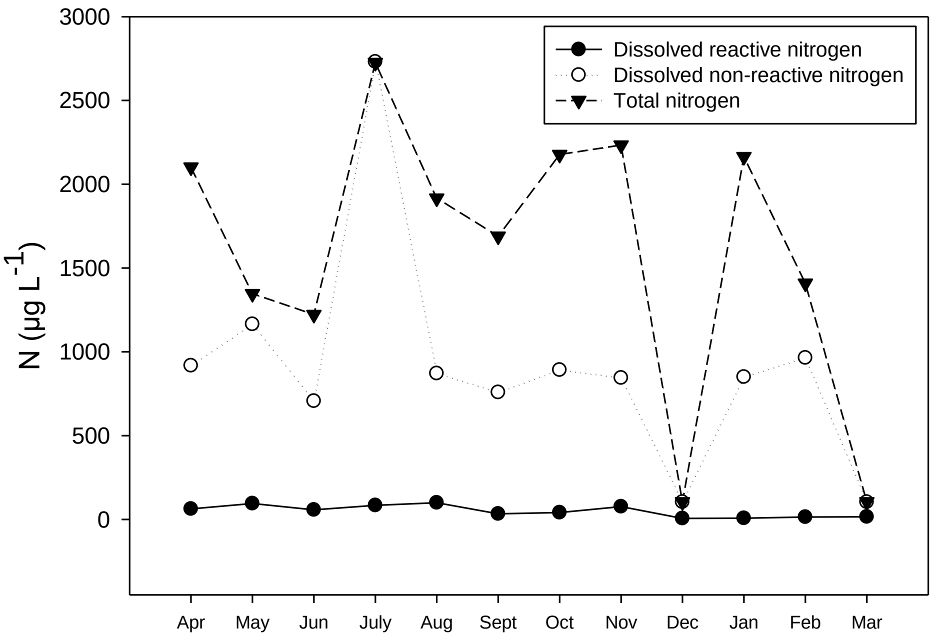

Fig. 14: Dissolved reactive, dissolved non-reactive and total nitrogen (µg L^{-1}) for Yahuarcocha each month.

The data of TN and DnRN in July, December and March are considered as outliners (Fig. 14). Probably something went wrong during collection of the samples, the preserving of the samples or the digestion of the samples.

3.2.2 Phosphorus

Phosphorus concentrations were 32 times lower than the nitrogen concentrations. The highest phosphorus concentration was 71 µg L^{-1}, measured in March (Table 7). The total phosphorus varied between 35.8 µg L^{-1} in June and 71 µg L^{-1} in March. The total phosphorus shows a clear increase during the study period (Fig. 15). June contained an outliner which we did not take into account.

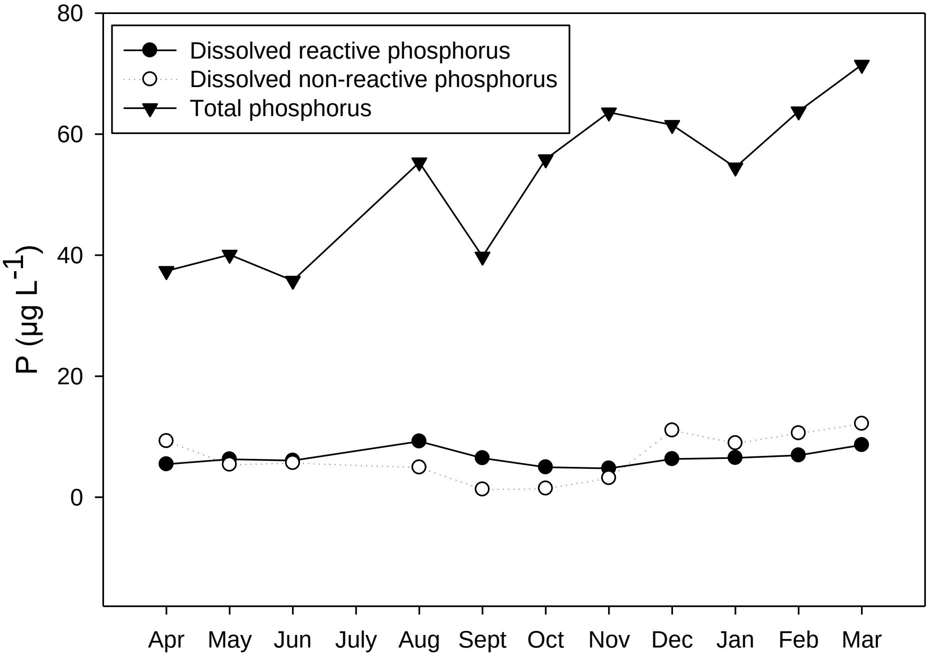

Fig. 15: Dissolved reactive, dissolved non-reactive and total phosphorus (µg L^{-1}) for Yahuarcocha each month.

Table 7: Overview of the mean, minimum and maximum of DRP (dissolved reactive phosphorus), DnRP (dissolved non-reactive phosphorus) and TP (total phosphorus).

Statistics	**DRP (µg/L)**	**DnRP (µg/L)**	**TP (µg/L)**
mean	7.9	14.8	56.42
min	4.8	1.3	35.8
max	23	12.2	71.5
stdv	4.93	28.5	17.6

3.2.3 NP-limitation experiment

For all experiments Chl *a* was used as indicator for phytoplankton biomass. Fig. 16 shows the results of the nutrient limitation experiment in terms of Chl *a* concentrations measured. *In vivo* Chl *a* measurements show a significant higher Chl *a* concentration where N and NP were added compared with the control (p-values < 0.002) and the P treatment (p-values < 0.003). There was also a difference observed between N and NP itself (p-value < 0.001), indicating that the algae biomass responded mainly to the addition of NP. When both nutrients (NP) were added the highest increase in biomass was observed.

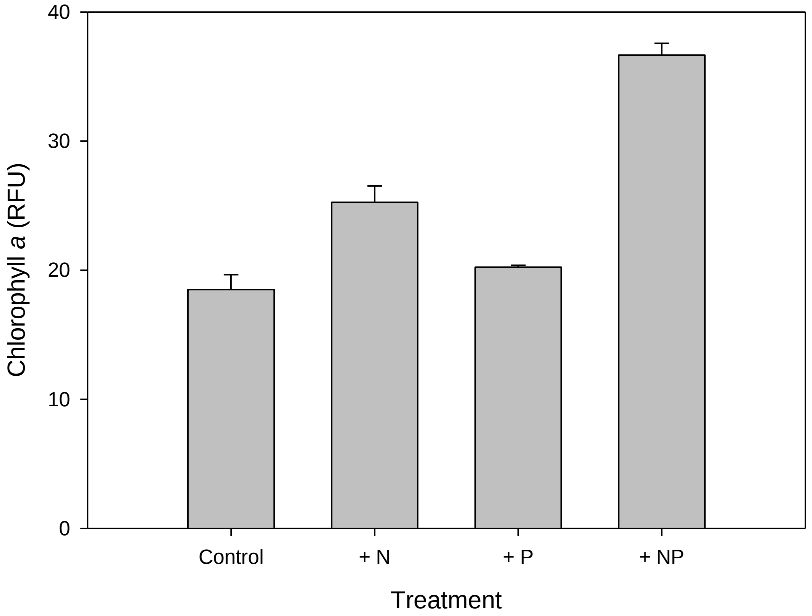

Fig.16: Chlorophyll *a* concentrations (RFU) for each treatment.

Besides Chl *a*, also phycocyanin was measured for each treatment. Fig. 17 illustrates the results. The same pattern can be observed as for Chl *a*. Adding N resulted in a significant increase of phytoplankton biomass (p-value < 0.001) and addition of only P did not have any effect (p-value = 0.05). Adding N and P again resulted in the highest increase in primary production (p-value < 0.001).

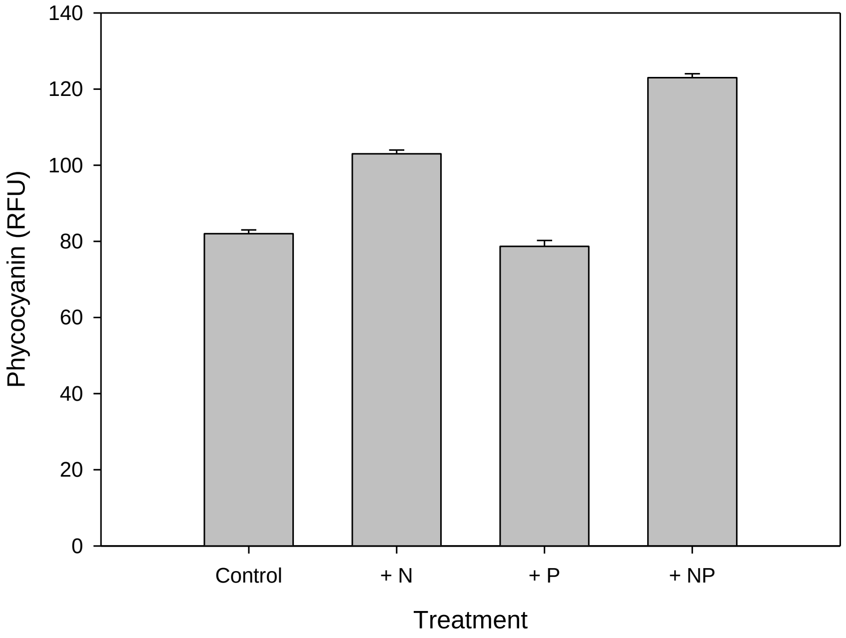

Fig. 17: Phycocyanin concentrations (RFU) for each experiment.

In August 2013 did Mandonx (2014) a similar experiment. Her data are shown in Fig. 18.

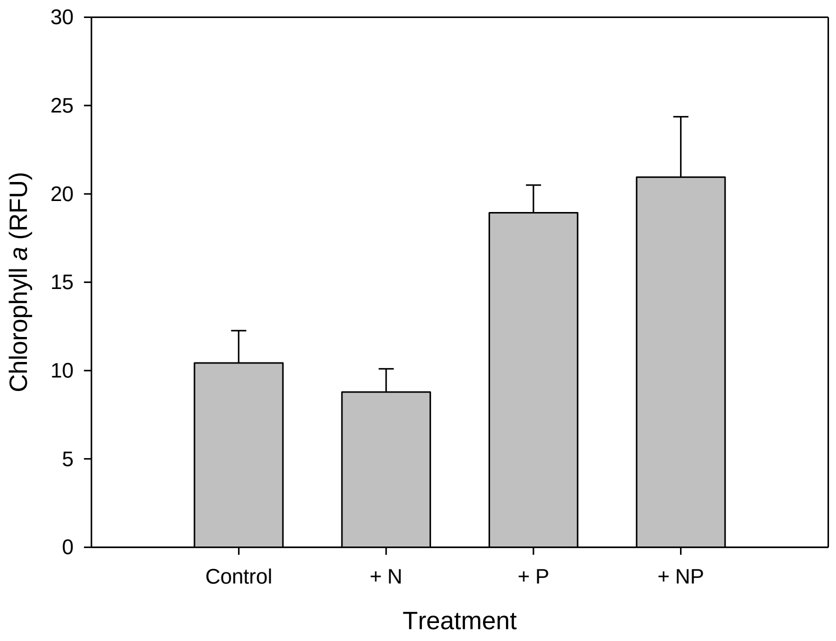

Fig. 18: Chlorophyll *a* concentrations (RFU) for each treatment data received from Mandonx (2014).

Their chlorophyll *a* measurements showed a significant higher chlorophyll *a* concentration in the treatments where P and NP were added compared with the control and N treatment. On the other hand no difference was observed between P and NP itself, indicating that the algae biomass responded mainly to the addition of P.

3.3 Phytoplankton

3.3.1 Species composition

In March 2014 the cyanobacterium *Anabaena* was the dominant species in terms of numbers with 40% of the total counted cells being *Anabaena* sp. In April *Monoraphidium,* a green alga, and *Microcystis,* a cyanobacterium, were the most abundant species with 18.3% and 16.7% respectively. In June, July and August, the diatom *Fragilaria* was the dominant species with densities reaching 65.4% of the total counted cells in July. In September a cyanobacterial species *Cylindrospermopsis* (27.7%), was the dominant species together with *Monoraphidium* (26.5%). Since September, *Cylindrospermopsis* stayed the dominant species with a peak in December (50.1%) (Fig. 21). When looking at the cell countings throughout the whole year, it was noted that *Cylindrospermopsis*, *Monoraphidium* and *Fragilaria* were the most counted species with respectively 27.53%, 19.18% and 14.15% (Table 8).

In total, 43 genera were present in Yahuarcocha. 23 belonged to the phylum Chlorophyta, 9 to Heterokontophyta, 2 to Dinoflagellata, 6 to Cyanobacteria and 3 belonged to Euglenozoa. The relative abundance of Cyanobacteria clearly increased since September and stayed the dominant phylum since then (Fig. 19 & Fig. 20).

Table 8: Genera present in Yahuarcocha with the average of the whole year.

Genus	Phylum	Average (%)
Amphora sp.	Heterokontophyta	(<1%)
Anabaena sp.	Cyanobacteria	4.1
Ankistrodermus sp.	Chlorophyta	(<1%)
Aulacoseira sp.	Heterokontophyta	(<1%)
Chlamydomonas sp.	Chlorophyta	2.390
Chlorella sp.	Chlorophyta	3.5
Chlorogonium sp.	Chlorophyta	(<1%)
Chroococcus sp.	Cyanobacteria	(<1%)
Coelastrum sp.	Chlorophyta	(<1%)
Cosmarium sp.	Chlorophyta	(<1%)
Crucigeniella sp.	Chlorophyta	(<1%)
Cyclotella sp.	Heterokontophyta	(<1%)
Cylindrospermopsis sp.	Cyanobacteria	27.5
Dictyosphaerium sp.	Chlorophyta	(<1%)
Eudorina sp.	Chlorophyta	(<1%)
Euglena sp.	Euglenozoa	(<1%)
Fragilaria sp.	Heterokontophyta	14.2
Golenkinia sp.	Chlorophyta	(<1%)
Gomphonema sp.	Heterokontophyta	(<1%)
Gonium sp.	Chlorophyta	(<1%)
Gymnodinium sp.	Dinoflagellata	(<1%)
Lagerheimia sp.	Chlorophyta	(<1%)
Melosira sp.	Heterokontophyta	(<1%)
Merismopedia sp.	Cyanobacteria	(<1%)
Micractinium sp.	Chlorophyta	(<1%)
Microcystis sp.	Cyanobacteria	6.5
Monoraphidium sp.	Chlorophyta	19.2
Oocystis sp.	Chlorophyta	(<1%)
Pediastrum sp.	Chlorophyta	(<1%)
Peridinium sp.	Dinoflagelata	1
Phacus sp.	Euglenozoa	(<1%)
Polyedriopsis sp.	Chlorophyta	(<1%)
Pseudanabaena sp.	Cyanobacteria	10.2
Scenedesmus sp.	Chlorophyta	3.3
Staurastrum sp.	Chlorophyta	(<1%)
Stauroneis sp.	Heterokontophyta	(<1%)
Synedra sp.	Heterokontophyta	(<1%)
Tetradesmus sp.	Chlorophyta	(<1%)
Tetraedron sp.	Chlorophyta	1.6
Tetrastrum sp.	Chlorophyta	(<1%)
Trachelomonas sp.	Euglenozoa	(<1%)
Trigonium sp.	Heterokontophyta	(<1%)
Westella sp.	Chlorophyta	(<1%)

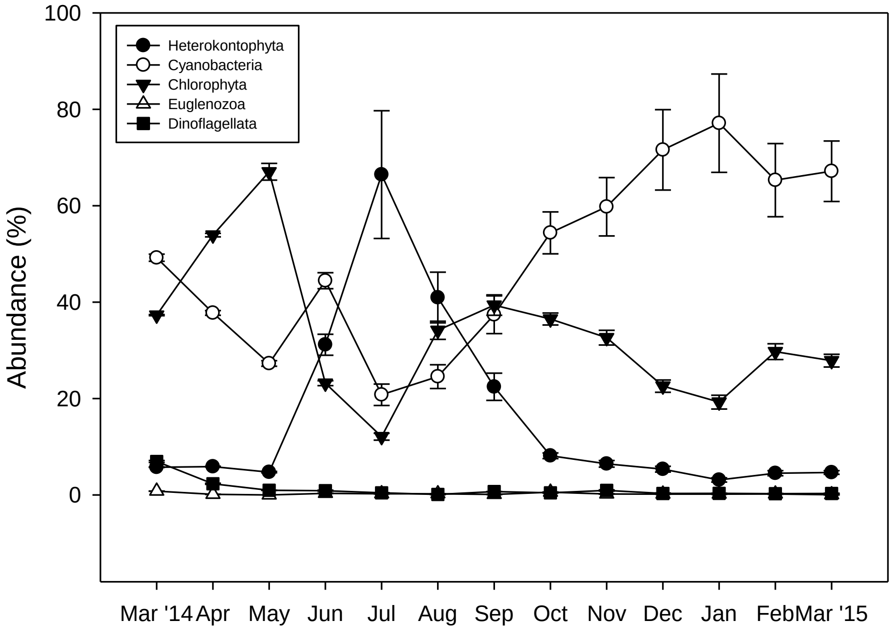

Fig. 19: Abundance of Euglenozoa, Heterokontophyta, Cyanobacteria, Chlorophyta and Dinoflagellata through the year.

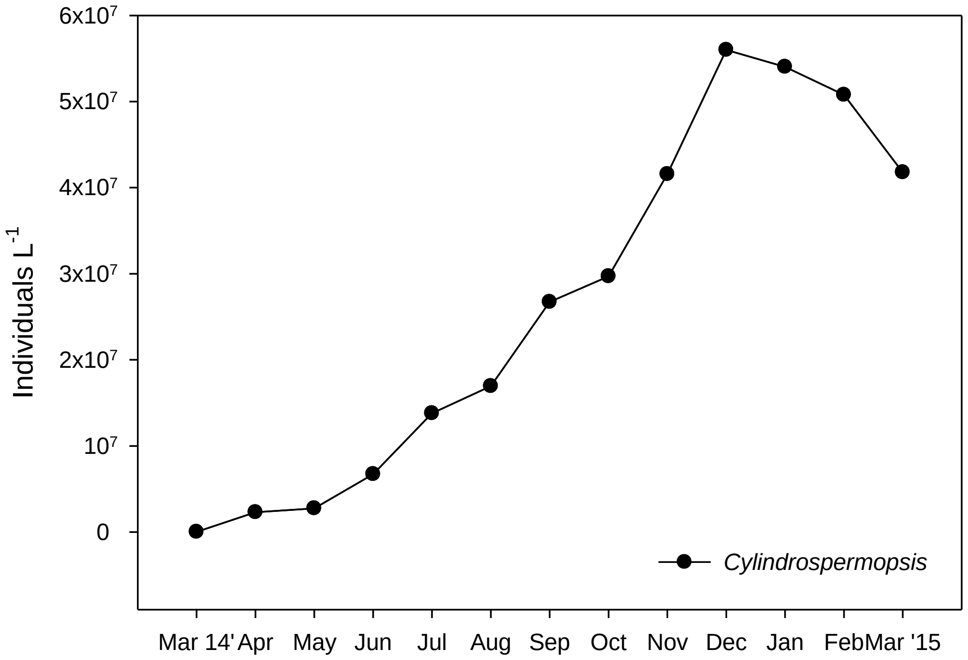

Fig. 20: Cylindrospermopsis sp. counted every month.

3.3.2 Pigments

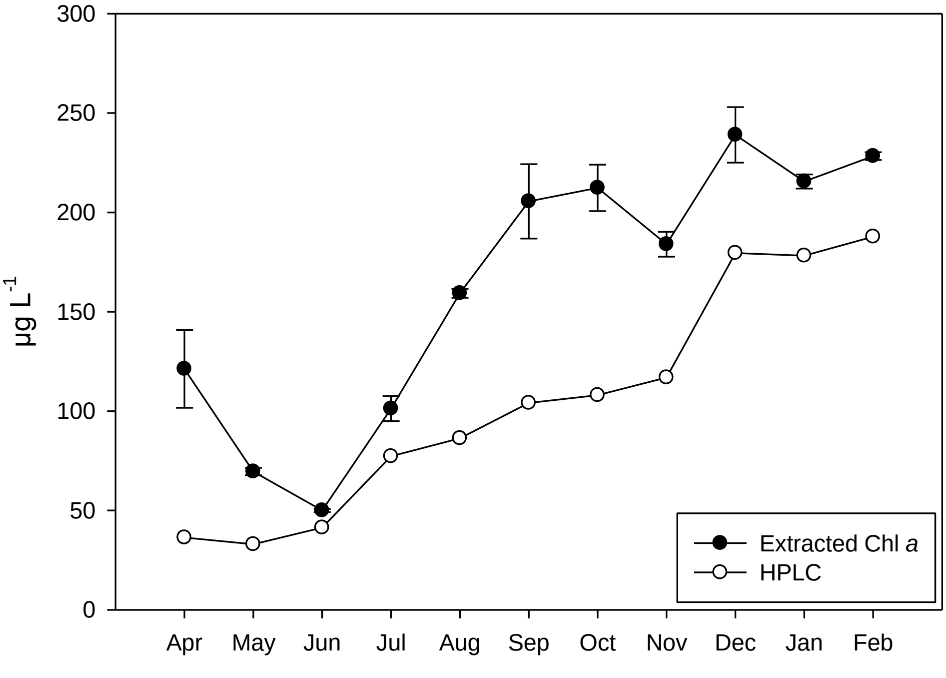

Fig. 21: Chlorophyll *a* concentrations (µg L^{-1}) analyzed as extracted Chl *a* and HPLC.

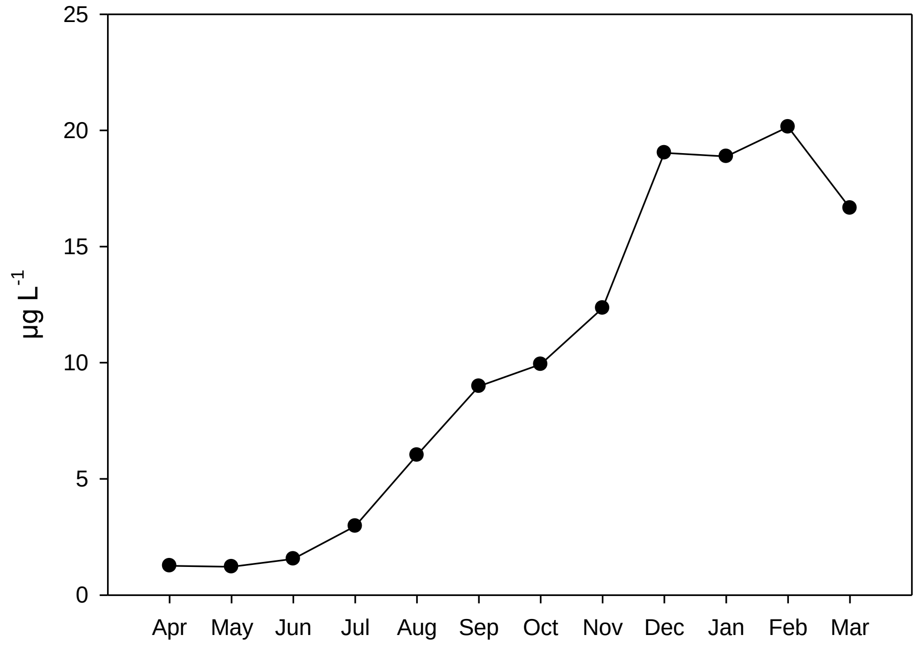

Fig. 22: Results of the HPLC analyze for the pigment echinenone.

Fig. 21 shows the results of Chl *a* concentrations. In the taxonomy most classes are characterized by a specific pigment. A high concentration of echinenone is characteristic for Cyanobacteria. In Fig. 22 are the results displayed of the HPLC analysis for echinenone. Echinenone shows a steep increase every month from 1.26 µg L^{-1} to 20.15 µg L^{-1} in February 2015.

3.3.3 Influence of light intensity and UV radiation on phytoplankton growth

Treatments were incubated at different depths in the water column to evaluate the influence of light intensity on phytoplankton growth rates. We measured a net increase in Chl *a* concentrations at all depths (Fig. 23). When looking at Chl *a* and PC (phycocyanin) concentration it appears that concentrations are the lowest in bottles incubated in the top layer of the water column. With increasing incubation depth, we saw that Chl *a* concentrations increase at first. At certain depth (0.3 m) primary production started to decrease again, in contrary to PC (Fig. 25). It's remarkable that there was still primary production of the phytoplankton including cyanobacteria at the deepest treatments where light intensities was estimated from Secchi depth to be only 1% of the surface light intensity (Table 4).

We also evaluated phytoplankton growth in function of light intensity (Fig 24. & Fig. 26) (as percentage of surface light intensity) by estimating the light intensity at different depths in the water column. We assumed that light intensity decreased exponentially with depth. The vertical light extinction coefficient was estimated from Secchi Depth (kD= 5.67).

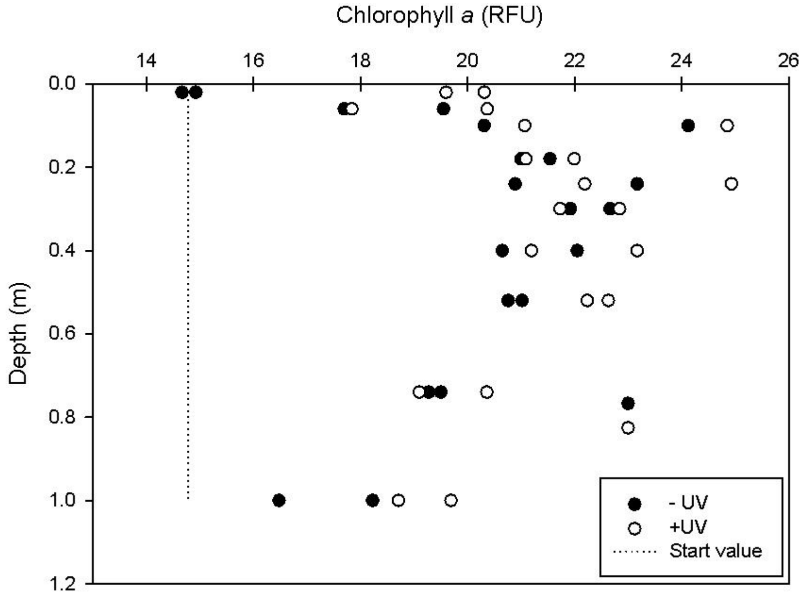

Fig. 23: The chlorophyll *a* content measured after the UV-ladder experiment with or without UV.

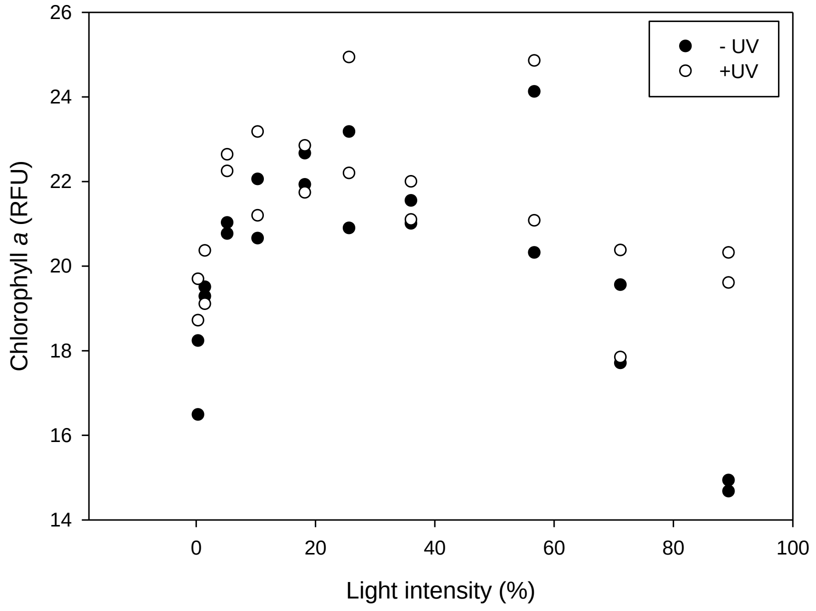

Fig. 24: Chlorophyll *a* in function of light intensity.

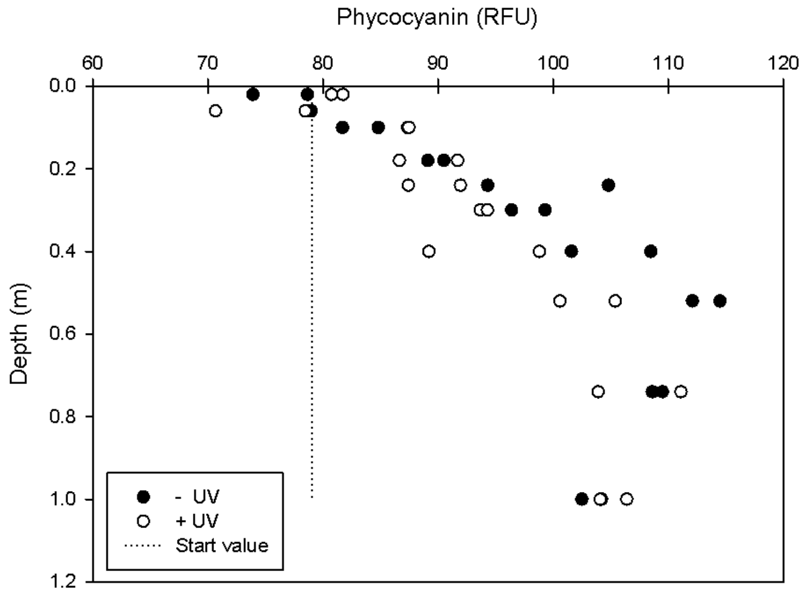

Fig. 25: Phycocyanin content measured after the UV experiment with or without UV.

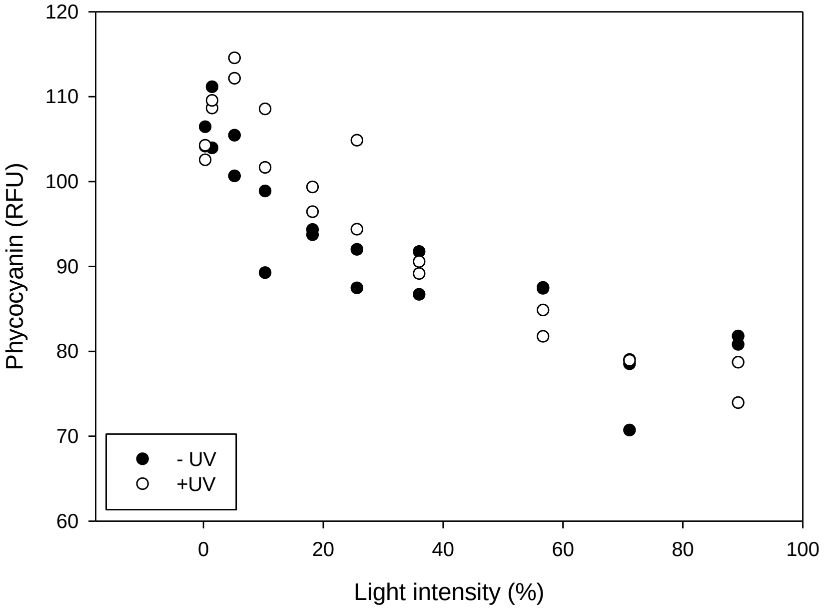

Fig 26: Phycocyanin in function of light intensity.

3.4 Zooplankton

3.4.1 Species

Table 9: Abundance of the zooplankton species in Yahuarcocha.

Group	**Species**	**Average (%)**
Cladocerans	*Daphnia* spp.	0.66
	Bosmina longirostris	0.66
Copepods	*Acanthocyclops* spp.	18.14
	Nauplius cyclopoide	6.60
	Dyaciclops ssp.	0.16
	Nauplius canaloid	3.66
	Tropocyclops spp.	0.16
Rotifers	*Brachionus bidentata*	1.75
	Brachionus calyciflorus	2.58
	Brachionus angularis	13.04
	Asplanchna spp.	2.09
	Ascomorpha spp.	2.10
	Collotheca spp.	1.47
	Keratella spp.	39.48
	Polyarthra vulgaris	5.40
	Filinia ssp.	1.97
	Monostyla spp.	0.08

Keratella ssp. (rotifer) was on average the most abundant (39.48%) in each month (Table 9). *Acanthocyclops* ssp. was the second most abundant (18.14%) (Table 9). *Bosmina longirostris* (0.66%) and *Daphnia* ssp*. (0.66%) w*ere only present in very low abundances (Fig. 27).

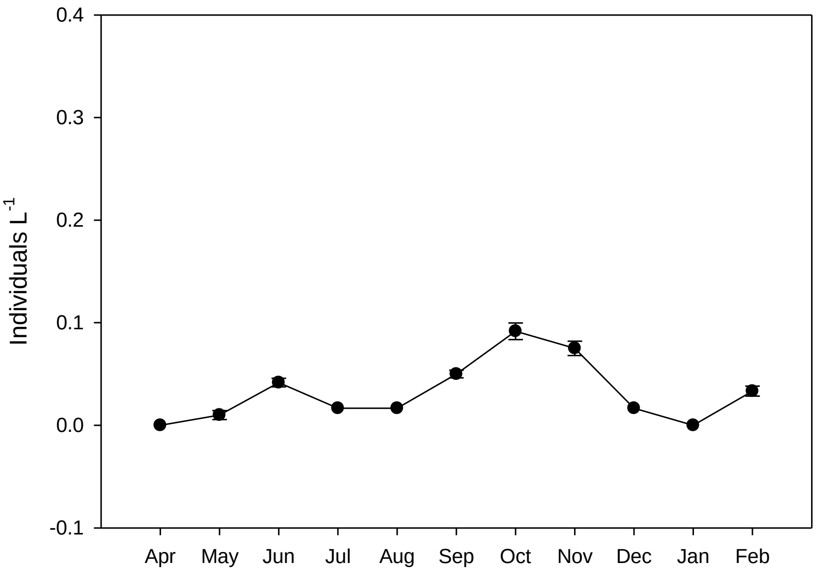

Fig. 27: *Daphnia* ssp. is present in very low abundances throughout the year.

3.4.2 Grazing-experiment

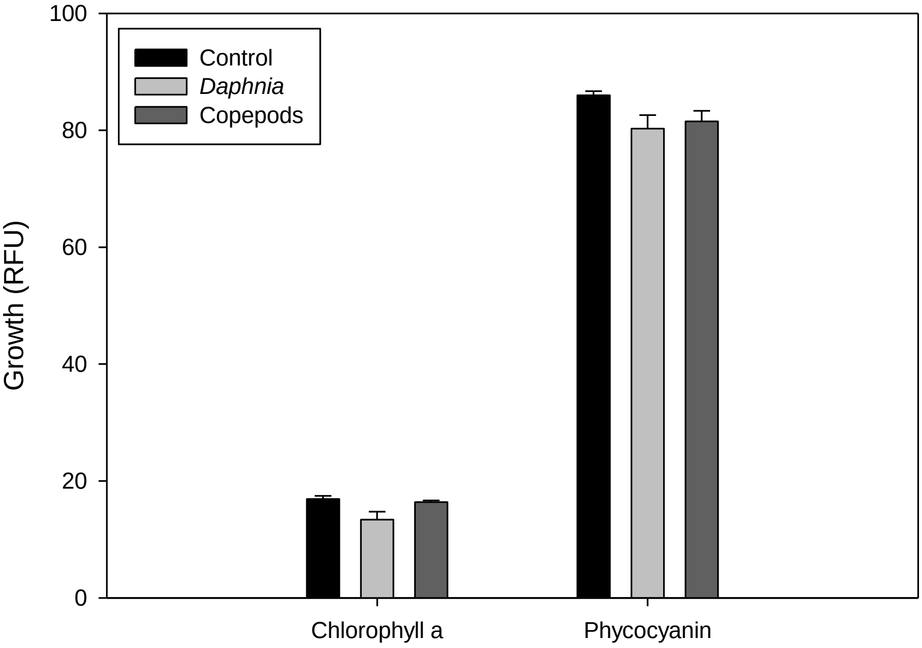

Fig. 28: Chlorophyll *a* content and phycocyanin after a grazing-experiment with *Daphnia*, Copepods and a control treatment.

Daphnia grazed significantly more than Copepods (p-value = 0.020) resulting in an average chlorophyll *a* concentration of 13.41 RFU. Phytoplankton biomass in the *Daphnia* treatment was significantly lower than the control (p-value = 0.013). For copepods, no effect like this was encountered. The chlorophyll *a* concentration in the copepod treatment did not differ significantly from the control treatment (16.923 RFU) (p-value = 0.197).

When we looked at the phycocyanin concentrations we saw that the treatments with *Daphnia* and copepods were significantly lower than the control (p-value = 0.015 and p-value = 0.016 respectively), but *Daphnia* did not differ significantly (p-value = 0.503) from the copepods treatments. Copepods had an average value of 81.53 RFU, *Daphnia* 80.28 RFU and the control 85.98 RFU (Fig. 28).

3.4.3 Vertical migration

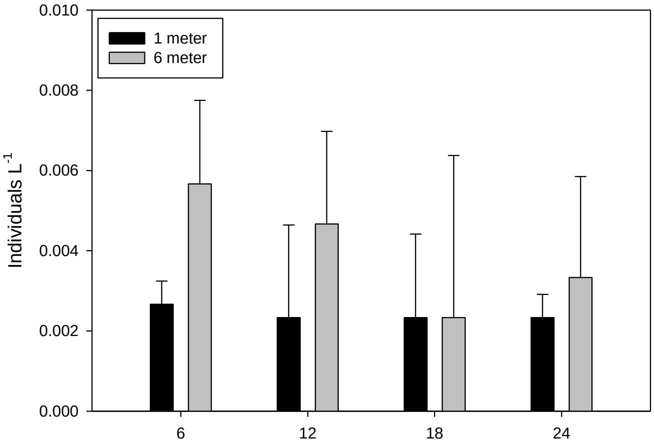

Fig. 29: Bosmina longirostris collected and counted at 1 meter deep and 6 meter deep (close to the bottom of the lake) at 6:00, 12:00, 18:00 and 24:00 hour.

Overall *Bosmina longirostris* was located closer to the bottom (6 meters deep), but this is not statistically proven (p-value = 0.113) (Fig. 29).

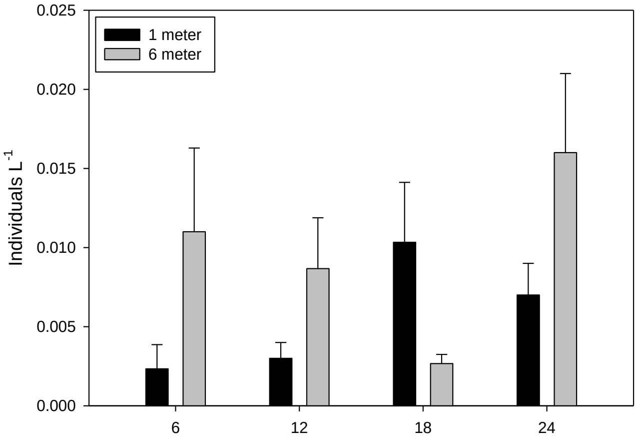

Fig. 30: Daphnia ssp. collected and counted at 1 meter deep and 6 meter deep (close to the bottom of the lake) at 6:00, 12:00, 18:00 and 24:00 hour.

Daphnia ssp. were encountered in a significantly higher abundance close to the bottom (p-value = 0.01). At 6 p.m. a significant difference was measured between the numbers of *Daphnia* counted near the lake bottom compared with number in the surface water layer with numbers being higher near the surface (p-value = 0.001) (Fig. 30).

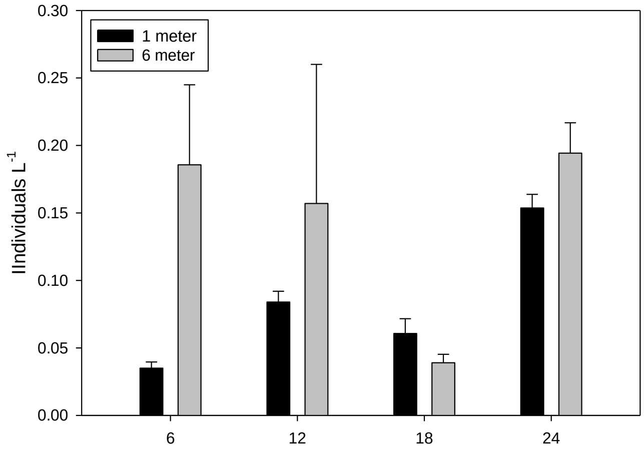

Fig. 31: Copepods collected and counted at 1 meter deep and 6 meter deep at 6:00, 12:00, 18:00 and 24:00 hour.

Copepods were in significantly higher abundances close to the bottom (p-value = 0.006). At 6 p.m. there were no significant difference between the surface and bottom abundances (Fig. 31.) (p-value = 0.093).

3.4.4 Horizontal migration

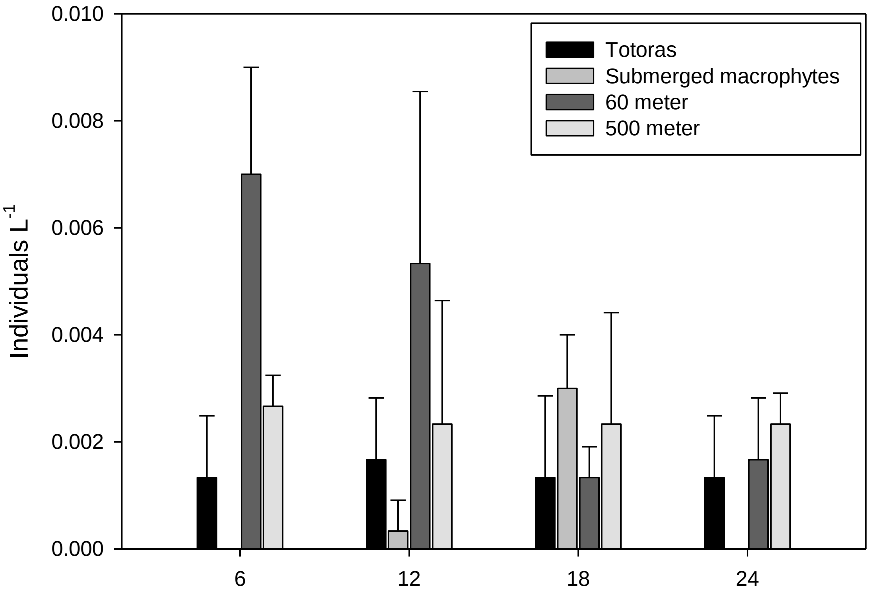

Fig. 32: Horizontal migration. Samples between the Totora reeds, submerged macrophytes, 60 meter far and 500 meter far were analyzed on *Bosmina longirostris* abundance.

Between time there was no significant difference observed (p-value = 0.12). *Bosmina* numbers were significantly higher 60 meter from shore (p-value < 0.001). There were no exceptional high abundances of *Bosmina longirostris* noticed between the submerged macrophytes. In the Totora vegetation and at 500 meter offshore were no significant differences depending on the time of the day (Fig. 32).

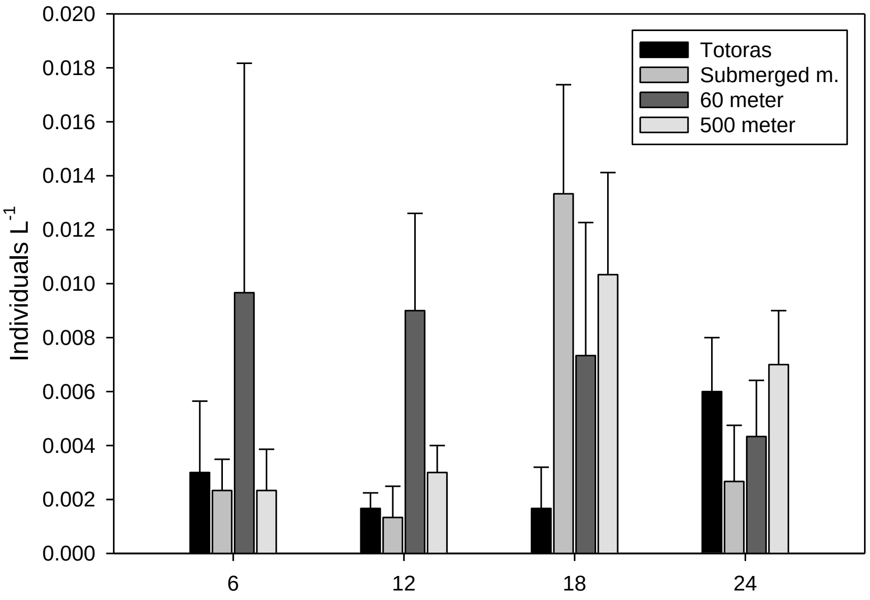

Fig. 33: Horizontal migration. Samples between the Totora, submerged macrophytes, 60 meter far and 500 meter far were analyzed on *Daphnia*.

At 6 a.m. and 12 a.m. (mid-day) was *Daphnia* in higher abundances 60 meter offshore (p-value = 0.018). At 6 p.m. there was a significant higher present of *Daphnia* compared to the other hours (Fig. 33) (p-value = 0.012).

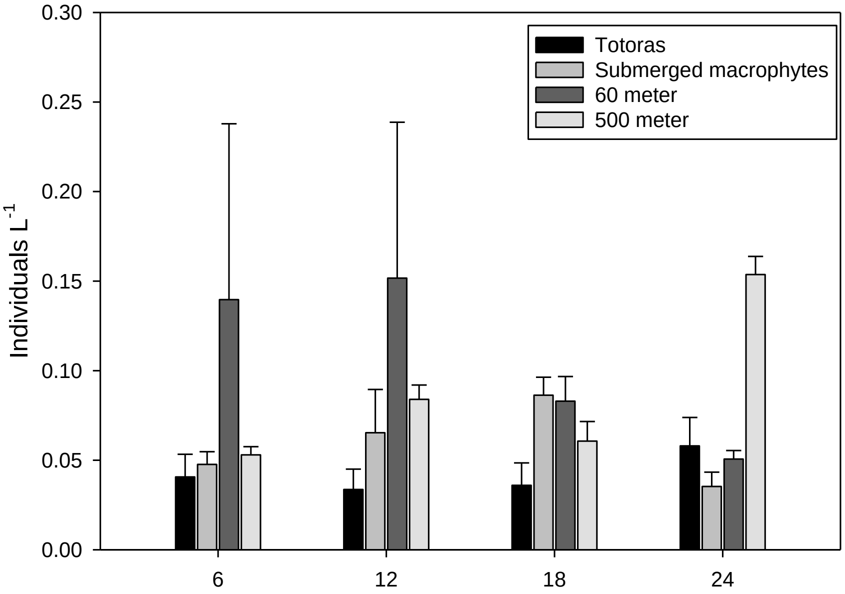

Fig. 34: Horizontal migration. Samples between the Totora, submerged macrophytes, 60 meter far and 500 meter far were analyzed on Copepods.

At 6 a.m. and 12 o'clock the copepods were significantly with a higher abundance 60 meter offshore (p-value < 0.001). At 24 o'clock they were in higher abundances further from shore (p-value = 0.001). There were no significant differences observed between hour (Fig. 33) (p-value = 0.656)

3.5 Macrophytes

Most of the macrophytes were emergent. Almost 7.4% of its surface area was covered with macrophytes (Fig. 34) (Blomme, 2014).

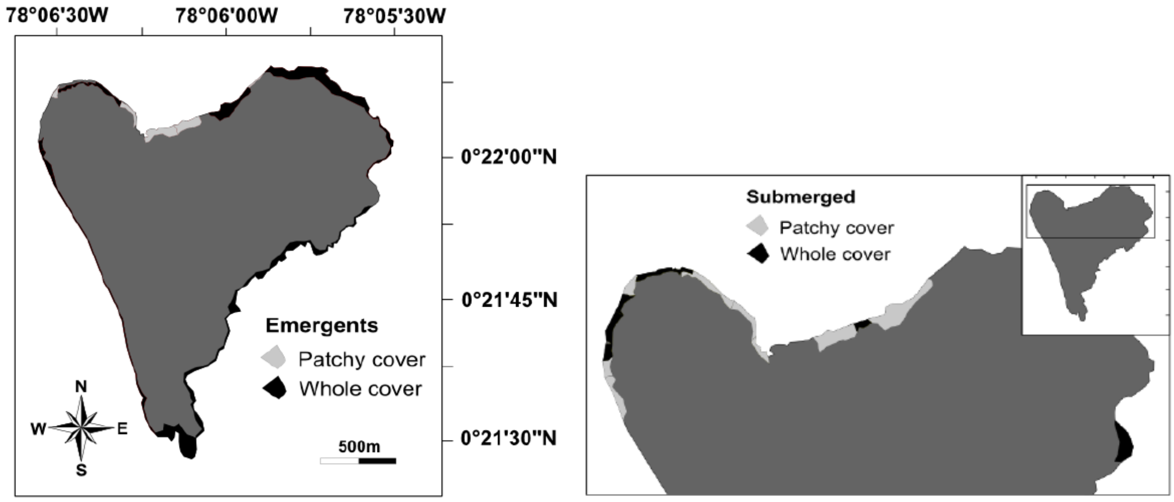

Fig. 35: Emergent and floating macrophyte distribution in Yahuarcocha. Emergent macrophytes are distributed all around the lake, whereas submerged is only found in the North (Blomme, 2014).

The most dominant species were water fern (*Azollla caroliniana*), termilfoil (*Myriphylum aquaticum*) and Totora (*Schoenoplectus californicus*) (Table 10). The most abundant species were in June *Myriphylum aquaticum* (57.12%), in July and August *Azolla caroliniana* with respectively 53.16% and 46.76%, in September *Myriphylum aquaticum* (76.88%) and in October *Azolla caroliniana* with 55.62%. Since then Totora was the most dominant species in November, December and January with respectively 28.19%, 35.18% and 28.46%. It's common that macrophytes are removed to avoid interferences with tourist boats for example from July till September the Totora reeds were partly cleared.

Table 10: A list of all the macrophytes present in lake Yahuarcocha with the average present of the macrophytes through the whole year.

Fylum	Family	Order	Genera	Species	Average (%)
Magnoliophyta	Alismatales	Lemnaceae	Lemna	*Lemna minor L.*	2.85
Magnoliophyta	Cyperales	Cyperaceae	Schoenoplectus	*Schoenoplectus californicus*	5.98
Magnoliophyta	Commelinales	Pontederiaceae	Eichhornia	*Eichhornia crassipes*	0.42
Magnoliophyta	Hydrocharitales	Hydrocharitaceae	Elodea	*Elodea canadensis*	1.26
Pteridophyta	Salviniales	Azollaceae	Azolla	*Azolla caroliniana*	39.4
Magnoliophyta	Poales	Typhaceae	Thypa	*Thypa domingensis*	0.05
Magnoliophyta	Apiales	Araliaceae	Hydrocotyle	*Hydrocotyle ranunculoides*	7.39
Magnoliophyta	Saxifragales	Crassulaceae	Umbilicus	*Umbilicus sp.*	0.10
Magnoliophyta	Saxifragales	Haloagaceae	Myriphylum	*Myriphylum aquaticum*	29.71
Pteridophyta	Polypoldiales	Dennstaedtiaceae	Pteridium	*Pteridium aquilinum*	0.002
Magnoliophyta	Asparagales	Iridaceae	Iris	*Iris pseudacorus*	0.10
Magnoliophyta	Asterales	Asteraceae	Tessaria	*Tessaria integrifolia*	0.45
Magnoliophyta	Cyperales	Poaceae	Arundo	*Arundo donax*	1.07
Magnoliophyta	Caryophyllales	Polygonaceae	Polygonum	*Polygonum punctatum*	8.13
Magnoliophyta	Lamiales	Calceolariaceae	Calceolaria	*Calceolaria crenata*	1.76
Magnoliophyta	Brassicales	Brassicaceae	Cardamine	*Cardamine nasturtioides*	0.02
Magnoliophyta	Brassicales	Brassicaceae	Moricandia	*Moricandia sp.*	0.36
Magnoliophyta	Commelinales	Commelinaceae	Commelina	*Commelina sp.*	0.92
Magnoliophyta	Cyperales	Cyperaceae	Cyperus	*Cyperus papyrus*	0.001

3.6 Sediments

Table 11: Analyze of the sediments of the different sample points in lake Yahuarcocha.

Nutrient	Average Concentration	Highest concentration	Point
Na mg g^{-1}	3.75	5.21	Point 1
Mg mg g^{-1}	8.99	24.33	Point 6
Al mg g^{-1}	19.74	27214.25	Point 7
P µg g^{-1}	412.04	613.51	Point 6
K µg g^{-1}	1.80	2.50	Point 6
Ca µg g^{-1}	14.73	27.90	Point 6
Mn µg g^{-1}	625.43	1153.14	Point 6
Fe mg g^{-1}	15.72	21219.34	Point 7
Co µg g^{-1}	6.48	9.15	Point 7
Ni µg g^{-1}	7.90	11.04	Point 7
Cu µg g^{-1}	51.85	132.11	Point 1
Zn µg g^{-1}	41.01	65.72	Point 12
As µg g^{-1}	8.88	12.32	Point 6
Mo µg g^{-1}	0.35	0.58	Point 6
Cd µg g^{-1}	0.08	0.12	Point 6
Pb µg g^{-1}	5.79	8.73	Point 7

The highest phosphorus concentration was measured at the water treatment station (613.51 µg g^{-1}) (Table 11) (Fig. 36).

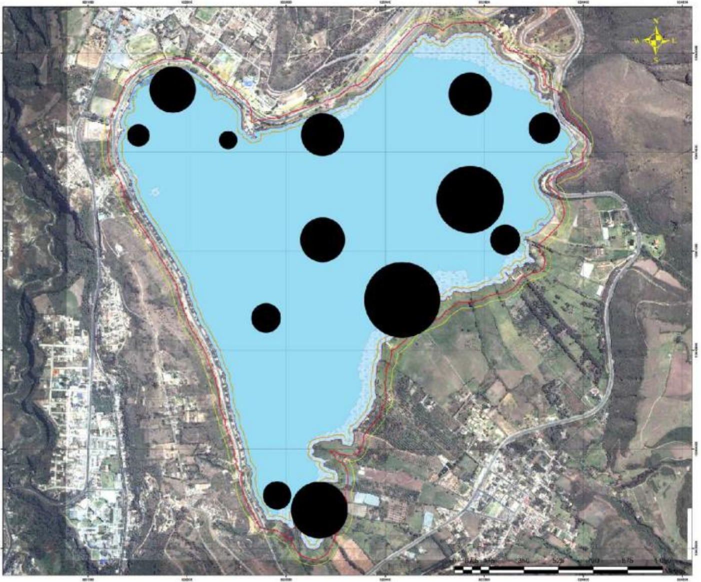

Fig. 36: Phosphorus concentration measured at 13 sampling points in Yahuarcocha. The highest phosphorus concentration was measured at the water treatment station (point 6).

3.7 Fish

In total 667 fish were caught in the gillnet (Table 12). A large amount of the fish were *Xiphophorus helleri.* The biggest part were females with 403 counted individuals and 252 males were counted (Table 13). The juveniles had an average length of 3.5 cm and the adults an average length of 8 cm for the males and 6 cm for the females. There were six *Tilapia*'s caught in the fishnet, with an average length of 14.5 cm. There were also six goldfish caught with an average length of 20 cm (Fig. 37).

Table 12: The fish that were present in the gillnet in lake Yahuarcocha.

Order	Family	Species	Common name	Total counted
Cyprinodontiformes	Poeciliidae	*Xiphophorus helleri*	Geen swordtail	655
Perciformes	Ciclidae	*Oreochromis niloticus*	Nile Tilapia	6
Cypriniformes	Cyprinidae	*Carassius auratus*	Goldfish	6

Table 13: Adults and juveniles from *Xiphophorus helleri*.

Gender	Age	Total counted
male	adult	196
female	adult	236
undetermined	juvenile	223

Fig. 37: Fishes of Yahuarcocha. Upper left: *Carassius auratus*. Upper right: juvenile *Xiphophorus helleri.* Bottom left: *Oreochromis niloticus*. Bottom right: male adult *Xiphophorus helleri*.

It was very remarkable that when sampling between macrophytes, a lot of guppy (*Poecilia reticulata*) were accidentally caught even though they were not present in the gillnet.

4 Discussion

4.1 The functioning of Yahuarcocha; a tropical shallow lake located at a high altitude

Yahuarcocha is a shallow lake situated at a high altitude (2192 m) on the equator (0°22’N 78°06’W). Due to the position on the equator, there is little seasonal variation in temperature. The high altitude, however, results in a relatively low temperature. We measured an annual average temperature of 21.4 °C, which is typical for temperate shallow lakes during summer. We observed that in July, August and September the temperature was slightly lower. The seasonal variation of the climate is not very significant and is mainly determined by seasonal changes in precipitation (Gunkel & Casallas, 2002). That is why the dry season (from June to September) is considered to be winter and the wet season is considered to be summer (from October to May). Seasonality is thus suppressed in the tropics but is not absent. It appears that the region follows the climate of the southern hemisphere despite the fact that the lake is situated just above the equator on the northern hemisphere.

Yahuarcocha is a shallow lake and therefore a stable thermal stratification is unlikely. Nevertheless, heating of the water surface by the intense tropical irradiance may result in a vertical temperature difference. The annual vertical gradient of the lake showed us that the surface water can be sometimes 2°C higher than the water at 1 m below the suface. The lake appears to be weakly stratified when there is little wind but this stratification disappears in windy conditions. In the dry summer period we observed no temperature gradient probably because the dry summer period contains strong winds (Gunkel & Casallas, 2002).

In addition to a temperature gradient, we also observed a vertical gradient in oxygen concentration and pH. Oxygen concentration and pH were high near the water surface and low near the bottom. The high oxygen and pH near the surface can be ascribed to a high photosynthetic productivity, resulting in high oxygen production and increase in pH due to consumption of CO_2. Vice versa, the low pH near the bottom results from high respiration that consumes oxygen and releases CO_2. Near the bottom, the oxygen concentration is close to 0, probably due to high consumption of O_2 by the sediment. It should be noted that oxygen concentrations are relatively low due to the low partial pressure of oxygen in the atmosphere, which is related to the high altitude. Oxygen concentrations in the atmosphere and in the water at 2200 m are 25% lower than at sea level. This result in a high risk of anoxia. However, low oxygen concentration during this study were restricted to the bottom water. Reports of fish kills in the past (e.g. in 2003, Maridueña *et al*. (2011) suggest that the lake may become at least partly anoxic occasionally. Because dense fish population occur in the lake, fish never appear to be eradicated completely by these anoxia.

4.2 Eutrophication and algal blooms.

Eutrophication is the response of the ecosystem to the addition of artificial or natural nutrients, mainly phosphorus and nitrogen. The high concentration of nutrients as a result stimulates the primary production. Humans now have a very strong influence on almost every major aquatic ecosystem (Smith, 2003). Thousands of lakes around the world have been impacted by extreme inputs of nutrients from human-related uses of the land (Ansari & Gill, 2013).

Lake Yahuarcocha is fed mainly by water from the Santo Domingo stream. This stream originates in the páramo highlands and is fed by the intense rainfall at this altitude. During the past years, the discharge of this stream has decreased because most water is used for irrigation in agriculture. This has resulted in a declining water level of the lake. To sustain the water level in the lake, other sources of water were diverted to the lake. These included wastewater from the tourism industry around the lake. Although the wastewater was treated before being discharged into the lake, this treatment was inefficient and was not capable of removing nutrients. Water from the nutrient-rich Tahuando river was also used to sustain the water level in the lake.

Based on total nutrients and chlorophyll *a* concentrations, lake Yahuarcocha can be considered to be a eutrophic lake. The concentration of total N is about 2233 µg L^{-1} and the concentration of total P is 71.5 µg L^{-1}. A large part of the total N consist of non-reactive N that is probably not bio-available to the phytoplankton. Most of the total P consist of particulate P that is probably mostly associated with the phytoplankton biomass. Concentrations of dissolved reactive N and P that are directly bio-available to phytoplankton were low, indicating that phytoplankton used most of the nutrients available for growth. Chlorophyll *a* concentrations varied between 173 and 220 µg L^{-1}. These high Chl *a* concentrations resulted in turbid conditions. Water transparency was low as evident from Secchi depths of only 0.29 m.

Although submerged macrophytes were present in the lake, their occurrence was restricted to the border of the lake where water depth was < 3 m. The high turbidity of the water probably restricts the growth of submerged macrophytes in the deeper parts of the lake. It is possible that frequent removal of macrophytes to avoid interference with tourist boats also play a role in the limited range of submerged macrophytes in the lake.

During the study period, starting in June 2014, a bloom of the cyanobacterium *Cylindrospermopsis* emerged. This bloom persisted until the end of the study period. Chlorophyll *a* concentrations increased from 39.5 to 196.7 µg L^{-1}, the Secchi depth decreased from 0.70 to 0.29 m, a rapid increase was observed in the pigment echinenone and a shift in the phytoplankton community occurred from a community dominated by chlorophytes or diatoms to a community dominated exclusively by *Cylindrospermopsis*. These observations are in contrast with observations by Blomme and Mandonx in August 2013, who observed a Secchi depth of 1.4 m, chlorophyll a concentrations of only 15 µg L^{-1} and virtually no cyanobacteria in the phytoplankton community.

Phytoplankton communities of eutrophic tropical lakes are often dominated by cyanobacteria that can form dense blooms (Gragnani *et al.*, 1999). In temperate lakes the algal blooms generally do not persist through the winter months due to low water temperatures. The permanently optimal water temperatures for *Cylindrospermopsis* in tropical regions may cause the algal-bloom to persist for a long time (Bouvy *et al.* 1999; McGreggor & Fabbro, 2000; Figueredo & Giani, 2009). *Cylindrospermopsis* is primarily a tropical genus (Komárek & Komárková, 2003), but recently they were also observed in several temperate lakes during the summer periods. These increased incidence of *Cylindrospermopsis* in temperate zones is ascribed to climate change (Briand *et al*., 2004; Paerl *&* Huisman, 2009; Sinha *et al*., 2012). The ecological success of *Cylindrospermopsis* in many lakes is attributed to many factors. Firstly, phosphorus is an important driver in the dominance of *Cylindrospermopsis.* This cyanobacterium has been found to dominate phytoplankton communities when dissolved inorganic phosphorus concentrations are below detectable limits. This is due to a higher phosphate uptake capacity and a higher phosphorus affinity compared to other cyanobacteria (Istvánovics *et al*., 2000). Secondly, there is low predation by zooplankton on *Cylindrospermopsis* (Panosso & Lürling, 2010). Thirdly, *Cylindrospermopsis* can tolerate low light, hence *Cylindrospermopsis* can persist in very dense populations without sudden collapses. Hereby, Secchi readings of 30 cm are characteristic during *Cylindrospermopsis* blooms (Padisak, 1997; Briand *et al*., 2002), which we also observed in Yahuarcocha. Fourthly, Cyanobacteria can migrate through the water column by regulating their buoyancy. Finally, other factors such as a high affinity for ammonium (while other heterocytic species must fix N_2) and allelopathic interference (Figueredo *et al*., 2007) also contribute to the ecological success of *Cylindrospermpopsis.* It's also common for many cyanobacteria, including *Cylindrospermopsis,* to produce toxins that can be harmful to humans. One of the toxins of *Cylindrospermopsis*, cylindrospermopsin, has the ability to effect the liver and kidneys in humans (Carmichael, 2001).

Due to the low latitude and the high altitude there is an intense irradiance and high UV intensity on Yahuarcocha. Both photoinhibition by high irradiance and UV stress can reduce phytoplankton productivity (Köhler *et al.*, 2001). But the treatment with UV seems to induce more phytoplankton growth, which was unexpected. A possible explanation is that the UV foil we used may hold back some light. This resulted in less photosynthesis production and less growth. Mandonx (2014) did a previous research on the UV radiation influence on the phytoplankton of Yahuarcocha. She observed that UV-A and UV-B extincted very fast, they could only penetrate into the water column for respectively 1 and 0.5 meter, resulting in only a limited-UV impact on the lake. We also tested the growth of cyanobacteria at different depths with decreasing light intensities. Cyanobacteria had clearly lower light requirements for its photosynthesis optimum which emphasis that they are still able to do photosynthesis at low light intensities. Laboratory studies have shown that *Cylindrospermopsis raciborskii* has low optimal light requirements for growth (Briand *et al*., 2004; Dyble *et al*., 2006; Kehoe *et al*., 2015).

4.3 Nutrients

Nitrogen and phosphorus are the main candidates for nutrient limitation of phytoplankton. Nitrogen limitation would be more important and widespread in the tropics than it seems to be in the temperate zone (Lewis, 2000). Abundance of nitrogen fixers is high in many tropical waters and element ratios in biomass are often suggestive of nitrogen deficit. Also chemical weathering of phosphorus from parent material is more efficient at high temperatures (Lewis 2000, Lewis, 2002; Huszar *et al.*, 2006). In addition evapoconcentration of phosphorus will be more pronounced at low latitudes than at high ones in general. Finally, nitrogen losses from tropical environments are certainly higher than from temperate latitudes due to the high water temperatures of tropical lakes, which increases denitrification (Lewis, 1996). Yahuarcocha is co-limited by both nutrients, nitrogen and phosphorus, but it used to be phosphorus limited before the bloom started (Mandonx, 2014). The total phosphorus concentrations in the lake increased since June, while total nitrogen stayed relatively the same. The occurrence of the bloom was associated with a slow increase in total P concentrations from 35.8 µg L^{-1} in June 2014 to 71.5 µg L^{-1} in March 2015. Phosphorus concentrations probably increased due to a phosphorus inflow from wastewater or agricultural irrigation water. However, another explanation is that *Cylindrospermopsis* sp. retained phosphorus out of the sediments due to his buoyancy. When sinking to lower water column, *Cylindrospermopsis* sp. can reach the phosphorus in the sediments and brings phosphorus back in the water column.

Due to co-limitation both nutrients are necessary in available form before the bloom can proliferate more. A possible supply can come from untreated wastewater and irrigation water that flows into Yahuarcocha. The most influential nutrient source (especially for nitrogen) of Yahuarcocha is agricultural runoff coming from the catchment and entering the lake through three streams. Most parts of the Yahuarcocha catchment are too steep to allow more agricultural land in the future (McConnell *et al.*, 2004), so it is unlikely that agriculture will become a higher trophic threat in the future

(Blomme, 2014), although there may be an increased use of N fertilizer due to increasing living standards. In contrast, wastewater discharges coming from the area around Yahuarcocha (between the ring road) release an important part of the phosphorus and nitrogen inputs of the lake. Houses and restaurants situated in this area discharge their effluents into the Santo Domingo stream and the Tahuando channel that enters the lake. Tourism has a large impact and is likely to grow in the future. The Santo Domingo stream is diverted to a water treatment station, but our sediment analysis indicates that the highest phosphorous concentrations in the sediments are close to the water treatment station. Blomme (2014) confirmed that this station was not an effective nutrient control: concentrations were higher downstream than upstream the station. Also the future perspectives, with probably a population expansion and a rise of the living standard, imply a higher threat by these domestic inputs too.

4.4 Potential for management: Biomanipulation

Biomanipulation can be used to improve water quality through trophic cascades. The goal of biomanipulation is to reduce the concentration of phytoplankton by increasing the grazing pressure on phytoplankton by zooplankton. This approach has been successful applied to many shallow lakes in European countries (Jeppesen *et al*., 1999). Some important prerequisites for management through biomanipulation are present in Yahuarcocha: submerged macrophytes and *Daphnia.* Unfortunately, other factors present in Yahuarcocha make restoration of the lake through biomanipulation problematic: Firstly, the *Daphnia* present in Yahuarcocha are not capable of grazing effectively on *Cylindrospermopsis* sp. Secondly, the macrophytes in Yahuarcocha host a lot of juvenile fish so that the submerged vegetation is ineffective as a zooplankton refuge (Meerhoff *et al.,* 2007b). Thirdly, there are no piscivorous fish species present in the lake that can control the dense populations of planktivorous fish.

A small part of the surface area of Yahuarcocha is covered with macrophytes (7.4%). Vegetation is an important factor that have an overall positive effect on water transparency in shallow lakes. Since Yahuarcocha is a shallow lake, it has the capability of harboring large vegetation of macrophytes. The dominant species found in Yahuarcocha are the emergent macrophytes *Azolla caroliana*, *Myriphylum aquaticum* and *Schoenoplectus californicus ssp. tatora.* They shade the water from sunlight and cause submerged plants to die due to light deficiency. Especially submerged macrophytes can counter trophic treats as they can extract nutrients from the lake water (Li *et al.*, 2010).

An important observation we found is that *Daphnia* is present in the lake. Without *Daphnia* ssp. in the lake, biomanipulation approach is not applicable (Gliwicz, 1990). Large-bodied cladocerans as *Daphnia* are effective in controlling the high phytoplankton abundance, including the algae bloom. We observed that the *Daphnia* in Yahuarcocha is not capable of grazing efficiently on the phytoplankton species that are present. We did find a significant but very weak impact on total phytoplankton, but not on the cyanobacteria that dominated the zooplankton community. This leads to an important conclusion that the *Daphnia* are not capable of grazing the cyanobacteria bloom that is present in Yahuarcocha. The densities of *Daphnia* ssp. were higher in the grazing experiment (20 ind. L^{-1}) than the densities in the lake. Thus, the grazing impact of *Daphnia* was no doubt overestimated. A previous investigation of Mandonx (2014) in Yahuarcocha also confirmed that the zooplankton grazing has no significant effect on the phytoplankton productivity.

We observed that the *Daphnia* in Yahuarcocha only consisted of relatively small species. *Daphnia* is seldom abundant in tropical ecosystems, but whenever they are present in tropical lakes, they are generally characterized by a relative small body size (Lewis, 1996). The large bodied zooplankters are more efficient at grazing down phytoplankton biomass than their smaller competitors. Small bodied animals results in lower grazing rates on phytoplankton (Carpenter & Kitchell, 1996; Declerck *et al.*, 1997) and increases the probability of algae blooms. An algal blooms can also cause the zooplankton to switch towards dominance of smaller cladocerans. The cyanobacteria including *Cylindrospermopsis* contain toxic metabolites that induce a higher mortality of *Daphnia* (Panosso & Lürling, 2009), but not only the present *Cylindrospermopsis* has an effect on the cladocerans, also *Pseudobanaena* has an effect on *Daphnia* ssp. Olvra-Ramírez *et al.* (2010) observed that *Pseudobanaena* had an negative effect on their survival, total progeny, average number of neonates per clutch and the number of clutches decreased. It is also known that high densities of planktivorous fish leads to a zooplankton community dominated by small grazers. The planktivorous fish *Poecilia reticulate* was in high abundancies observed between the macrophytes in the lake. The macrophytes host a lot of juvenile fish so that the submerged vegetation is in effective as a zooplankton refuge (Meerhoff *et al.,* 2007b), which is shown in other tropical shallow lakes before (Meerhoff, 2006; Meerhoff *et al.,* 2007). However, *Poecilia reticulate* was observed in the lake, they were not present in the gillnet. This could have different reasons: the guppy's are relative small and the mazes of the net could have been too big to effectively catch them. Another reason might be that they were not present on that location and depth were the gillnet was located.

In total 667 fishes were caught in the gillnet, of which *Xiphorphorus helleri* was the dominant species. Other fish that we observed were *Oreochromis niloticus* and *Carassius auratus*. All the fishes we caught in Yahuarcocha are exotic species, most of them are popular aquarium fish. It's possible that people released these aquarium fishes into the lake and as far as we know *Poecilia reticulata* was released into the lake for mosquito control and *Tilapia* was introduced for fishing. Exotic species are capable of contributing to the mechanisms that result in water quality decline in lakes. A meta-analysis for a wide range of northern New Zealand lakes revealed a strong correlation between the presence of exotic fish species and low water clarity. More importantly all of these species are invaders and they have the ability to change the food web structure (Auckland Regional Council, 2008). If the exotic fish can survive and reproduce very strong, it is sometimes very difficult to control or eradicate these fish and this can cost a lot of money. Exotic fish can also affect the native species by hybridizing, parasites of diseases. Also remarkable is that these fish are typically omnivores. They can have an effect by predation on zooplankton or cause resuspension of sediments which reduces water transparency and increases nutrients exchange from the sediments to the water (Cambray, 2003; Rowe, 2007). They can also disrupt the macrophytes or use the macrophytes for a spawning site and nursery. It is even shown that Tilapia for example feed directly on the macrophytes (Rao *et al.*, 2015).

No piscivorous fish were observed in lake Yahuarcocha. In subtropical and tropical lakes it is common that there is a higher degree of omnivorous feeding by fish and less piscivory (Jeppesen *et al.*, 2005). However, the same fish has been observed in lake Yahuarcocha in 2003 (Maridueña *et al.*, 2011) we have to be careful with our conclusions of the fish community. Our fish sampling by means of gillnets are rather qualitative than quantitative. We cannot determine the absolute fish densities based on this data, but we can examine the composition of the fish community. With some caution, because this method of sampling may have a species-specific catch efficiency. In this fish community it seems that *Xiphorphorus helleri* dominates numerically but we cannot determine precisely if the captured densities are high or low. We only used one fishnet on the lake with a surface of 2.6 km² so that the spatial variation in fish densities cannot be taken into account. The net was placed horizontally so it was only the upper 1 meter of the water column that was sampled. This could be a misperception if more or less fish swim in the upper or lower waters.

We can conclude biomanipulation will most likely have no impact on the restoration of the water quality. Herbivory of cladocerans and copepods can be enhanced with a decreased fish predation (Urrutia-Cordero *et al.,* 2015), but even a removal of all the fish will probably not induce the desired water quality. *Cylindrospermopsis* is not edible and this results in relative weak coupling between zooplankton and phytoplankton in the trophic cascade. The relatively weak coupling between primary producers and zooplankton grazers during blooms explains why attempts at biomanipulation by increasing the zooplankton have been relatively ineffective in controlling blooms (Boon *et al*., 1994; Rondel *et al*., 2008), even when zooplankton abundance is unrestricted by fish predation (Lacerot *et al*., 2013).

4.5 Nutrient management

As applying biomanipulation is highly impossible, the first step in restoring Yahuarcocha should be to remove direct inputs with high concentrations of nitrogen and phosphorus. This could be the untreated wastewater of irrigation water that flows into Yahuarcocha. Unless such external inputs are reduced, any long term benefits from in-lake treatments will usually not be realized. The second step in restoring is the reduction of external nutrient loading in the water column. The lake is at this moment in the turbid-state with an excess of algae due to the high nutrient levels. When control of external and/or internal loading is established, nutrient concentrations will be lower and a switch to a stable clear water state is more likely (Scheffer *et al.*, 2001). However, there is no certainty that the water quality of the lake will improve after nutrient load reductions (Van Liere & Gulati, 1992). Lake recovery is afflicted by the internal P loading from the sediments (van der Molen & Boers, 1994). The internal loading can be reduced significantly by removal of phosphorus-rich surface layers (dredging).

Another conflict that should be considered in the management of Yahuarcocha is the water shortage. Farmers settled around Yahuarcocha using its water to irrigate their crops. As the water level is lowering, a new inflow should be considered otherwise it’s possible Yahuarcocha will dry out completely in the future. There are two possibility’s (1) it’s possible to connect Yahuarcocha with other sources of water. This was applied before: a channel was made that connects Yahuarcocha with the Tahuando river. This channel was made upstream where wastewater is not yet discharged into the Tahuando river. This channel passes through residential areas and as a result their wastewater does flow into Yahuarcocha. (2) Another possible solution might be to limit the use of water for irrigation, so that Yahuarcocha does not completely dry out.

Summary

A special type of tropical lakes are the mountain lakes in the equatorial zone. Due to the position on the equator, there is little seasonal variation in temperature. The high altitude, however, results in a relatively low temperature. Yahuarcocha is a shallow tropical lake located on the equator at a high altitude (2192 meter). In June 2014 a large *Cylindrospermopsis*-bloom occurred. This algal bloom can persist all year round, in contrary to temperate lakes, and has a negative effect on the water quality. The primary cause of excess algae is high nutrient inputs and lake restoration is recommended. The lake was monitored during one year and a series of in situ experiments were carried out. We evaluate some important limnological parameters of lake Yahuarcocha, including physico-chemical parameters (e.g. oxygen, nutrients, hydrology), biological parameters (phyto- and zooplankton, macrophytes) and the possibility for biomanipulation as a restoration strategy. However, *Daphnia* and macrophytes are present in the lake, biomanipulation cannot be applied in Yahuarcocha. Three reasons why biomanipulation cannot be applied: Firstly, the macrophytes cannot serve as refugia because a lot of juvenile fish are between the macrophytes. Secondly, *Daphnia* cannot graze significantly and thirdly, there are no piscivorous fish present in the lake. The first step in the management of Yahuarcocha should be to reduce the inflow of nutrients coming from wastewater and agriculture run-off. The second step is to reduce the nutrients in the water column and prevent the release of phosphorus from the sediments by dredging.

Samenvatting

Tropische meren gelegen in de bergen vormen een aparte categorie van tropische meren. Door de positie op de evenaar is er een kleine variatie in de seizoensgebonden temperatuur. De grote hoogte resulteert echter in een relatief lage temperatuur. Yahuarcocha is een ondiep tropisch meer gelegen op een hoge hoogte (2192 m) op de evenaar. In Juni 2014 is er een grote *Cylindrospermopsis*-bloei opgetreden. Deze algenbloei kan het hele jaar aanhouden, in tegenstelling tot de gematigde meren, en heeft een negatief effect op de kwaliteit van het water. De primaire oorzaak van de algenbloei is de invloei van nutriënten en hierdoor is restauratie van het meer aanbevolen. Het meer werd gedurende één jaar bemonsterd en een reeks van in-situ experimenten werden uitgevoerd. Wij evalueerden enkele belangrijke limnologische parameters van Yahuarcocha, met inbegrip van fysisch-chemische parameters (bijvoorbeeld zuurstof, nutriënten, hydrologie), biologische parameters (fyto - en zoöplankton, macrofyten) en de evaluatie van biomanipulatie als mogelijke restauratie strategie. Wij kwamen tot de conclusie dat biomanipulatie niet kan worden toegepast in Yahuarcocha: in de eerste plaats omdat de macrofyten niet geschikt zijn als schuilplaats doordat er zich een groot aantal jonge vis bevindt tussen de macrofyten.

Ten tweede, *Daphnia* kan niet significant grazen en ten derde, er zijn geen piscivore vissoorten aanwezig in het meer. Voor de eerste stap in de management van Yahuarcocha zou de instroom van nutriënten, afkomstig van afvalwater en de landbouw run-off, moeten verlagen. De tweede stap is het verminderen van de nutriënten in de waterkolom en het voorkomen van het vrijkomen van fosfor uit de sedimenten met behulp van baggerwerk.

References

Aguilera, X., Lazzaro, X. & Coronel, J.S. 2013. Tropical high-altitude Andean lakes located above the tree line attenuate UV-A radiation more strongly than typical temperate alpine lakes. *Photochemical & Photobiological Science 12*:1649-1657.

Aguilera, E., Chiodini, G., Cioni, R., Guidi, M., Marini, L. & Raco, B. 2000. Water chemistry of Lake Quilotoa (Ecuador) and assessment of natural hazards. *Journal of Volcanology and Geothermal Research* 97:271-285.

Álvarez-Berríos, N.L., Parés-Ramos, I.K. & Aide, T.M. 2013. Contrasting patterns of urban expansion in Colombia, Ecuador, Peru and Bolivia between 1992 and 2009. *Ambio* 42: 29-40.

AmphibiaWeb. 2015. Worldwide Amphibian Declines: How big is the problem, what are the causes and what can be done? Information on Amphibian Biodiversity and Conservation. Berkeley, California, U.S.A. http://amphibiaweb.org/ (accessed 3 April, 2015).

Ansari , A.A. & Gill, S.S. 2013. *Eutrophication: Causes, Consequences and Control*. Springer: p264.

Anderson, E.P., Marengo, J., Villalba, R., Halloy, S., Young, B., Cordero, D., Gast, F., Jaimes, E. & Ruiz, D. 2009. Consequences of climate change for ecosystems and ecosystem services in the tropical Andes.

Anderson, D.M., Kaoru, Y. & White, A.W. 2000. *Estimated annual economic impacts from Harmful Algal Blooms (HABs) in the United States*. Economic Impacts of HABs in the U.S. p97.

Arribére, M.A., Campbell, L.M., Rizzo, A.P., Arcagni, M., Revenga, J. & Guevara, S.R. 2010. Trace elements in plankton, benthic organisms, and forage fish of lake Moreno, Northern Patagonia, Argentina. *Water Air Soil Pollution* 212:167-182.

Auckland regional council. 2008, report, 218p.

Balseiro, E.G., Modenutti, B.E. & Queimaliños, C.P. 2001. Feeding of Boeckella gracilipes (Copepoda, Calanoida) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake. *Journal of Plankton Research* 23(8): 849-857.

Barko, J.W., Smart, R.M., Mc Farland, D.G. & Chen, R.L. 1988. Interrelationships between the growth of *Hydrilla Verticillata* (L.f.) Royle and sediment nutrient availability. *Aquatic Botany* 32: 205-216.

Beardall, J., Young, E. & Roberts, S. 2001. Approaches for determining phytoplankton nutrient limitation. *Aquatic Sciences* 63:44-69

Bednarska, A., Pietrzak, B. & Pijanowska, J. 2014. Effect of poor manageability and low nutritional value of cyanobacteria on *Daphnia magna* life history performance. *Journal of Plankton Research*:1-10.

Blanco, S., Romo, S., Villena, M-J. & Martínez, S. 2003. Fish communities and food web interactions in some shallow Mediterranean lakes. *Hydrobiologia* 506-509: 473-480.

Bloesh, J. 1994. Editorial: Sediment resuspension in lakes. *Hydrobiologia* 284: 1-3.

Blomme, J. 2014. General limnology and zooplankton ecology of two tropical high altitude lakes in Northern Ecuador: Mojanda & Yahuarcocha. Dissertation, 80p.

Boon, P.I., Bunn, S.E., Green, J.D. & Shiel, R.J. 1994. Consumption of cyanobacteria by freshwater zooplankton: Implications for the success of ‘top-down’ control of cyanobacterial blooms in Australia. *Australian Journal of Marine & Freshwater Research* 45: 875-887.

Bootsma, M.C., Barendregt, A. & van Alphen, J.C.A. 1999. Effectiveness of reducing external nutrient load entering a eutrophicated shallow lake ecosystems in the Naardermeer nature reserve, The Netherlands. *Biological Conservation* 90: 193-201.

Bouvy, M., Molica, R., De Oliveira, S., Marinho, M. & Beker, B. 1999. Dynamics of a toxic cyanobacterial bloom (*Cylindrospermopsis raciborskii*) in a shallow reservoir in the semi-arid region of northeast Brazil. *Aquatic Microbial Ecology* 20: 285-297.

Bowman, M.F., Chambers, P.A. & Schindler, D.W. 2005. Epilithic algal abundance in relation to anthropogenic changes in phosphorus bioavailability and limitation in mountain rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 174-184.

Bradley, R.S., Vuille, M., Diaz, H.F. & Vergara, W. 2006. Threats to water supplies in the tropical Andes. *Science* 312: 1755-1756.

Branco, C.W., Rocha, M.I.A., Pint, G.F.S., Gômara, G.A. & De Filippo, R. 2002. Limnological features of Funil Reservoir (R.J., Brazil) and indicator properties of rotifers and cladocerans of the zooplankton community. *Lakes & Reservoirs: Research and Management* 7: 87-92.

Branco, C.W., Aguiaro, T., Esteves, F.A. & Carmaschi, E.P. 1997. Food sources of the teleost *Eucinostomus Argenteus* in two coastal lagoons of Brazil. *Studies on Neotropical Fauna and Environment Journal* 32:33-40.

Breukelaar, A.W., Lammens, E.H.R.R., Breteler, J.G.P.K. & Tátrai, I. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll a. *Freshwater Biology* 32: 113-121.

Briand, J.F., Robillot, C., Quiblier-Llobéras, C., Humbert, J.F., Couté, A. & Bernard, C. 2002. Environmental context of *Cylindrospermopsis raciborskii* (Cyanobacteria) blooms in a shallow pond in France. *Water Research* 36: 3183-3192.

Briand, J.F., Leboulanger, C. Humbert, J-F., Bernard, C. & Dufour, P. 2004. *Cylindrospermopsis raciborskii* (Cyanobacteria) invasion at mid-latitudes: Selection, wide physiological tolerance, of global warming? *Journal of Phycology* 40: 231-238.

Buytaert, W., Célleri, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J. & Hofstede, R. 2006. Human impact on the hydrology of the Andean páramos. *Earth-Science Reviews* 79: 53-72.

Burks, R.L., Jeppesen, E. & Lodge, D.M. 2001a. Pelagic prey and benthic predators: Impact of odonate predation on *Daphnia*. *Journal of the North American Benthological Society* 20(4): 615-628.

Burks, R.L., Jeppesen, E. & Lodge, D.M. 2001b. Littoral zone structures as *Daphnia* refugia against fish predators. *Limnology & Oceanography* 46(2): 230-237.

Cambray, J.A. Impact on indigenous species biodiversity caused by the globalisation of alien recreational freshwater fisheries. *Hydrobiologia* 500: 217-230.

Carmichael, W.W. 2001. Health effects of toxin-producing Cyanobacteria: “The CyanoHABs”. *Human and Ecological Risk Assessment* 7(5):1393-1407.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-639

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N. & Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559-568.

Carpenter, S.R. & Kitchell, J.F. 1996. *The trophic cascade in lakes*. Cambridge University Press. 397p.

Carpenter, S.R., Cole, J.J., Hodgson, J.R., Kitchell, J.F., Pace, M.L., Bade, D., Cottingham, K.L., Essington, T.E., Houser, F.N. & Schindler, D.E. 2001. Trophic cascades, nutrients and lake productivity: Whole lake experiments. *Ecological Monographs* 71(2):163-186.

Carpenter, S.R., Cole, J.J., Kitchell, J.F. & Pace, M.L. 2010. *Trophic cascades in lakes: Lessons and prospects*. Island Press, Washington D.C. p55-69.

Carpenter, S.R. & Lodge, D.M. 1986. Effects of submerged macrophytes on ecosystem processes. *Aquatic Botany* 26: 341-370.

Carey, C.C., Ibelings, B.W., Hoffmann, E.P., Hamilton, D.P. & Brookes, J.D. 2012. Eco-physiological adaptations that favour freshwater cyanobacteria in a changing climate. *Water Research* 46:1394-1407.

Cassallas, J.E. 2005. Limnological investigations in Lake San Pablo, a high mountain lake in Ecuador. Dissertation, p138.

Cassallas, J.E. & Gunkel, G. 2001. Algunos aspectos limnologicos de un lago altoandino: el lago San Pablo, Ecuador. *Limnetica* 20(2): 215-232.

Célleri, R. & Feyen, J. 2009. The hydrology of tropical Andean ecosystems: Importance, Knowledge status and perspectives. *Mountain Research and Development* 29(4): 350-355.

Costanza, R., d'Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruele, J., Raskin, R.G., Sutton, P. & van den Belt, M. 1997. – The value of the world's ecosystem services and natural capital. *Nature* 38: 253-260.

Chorus, I. & Batram, J. 1999. *Toxic cyanobacteria in water: A guide to their public health consequences, monitoring and management*. St Edmundsbury Press, Suffolk, p400.

Codd, G.A. 2000. Cyanobacterial toxins, the perception of water quality and the prioritization of eutrophication control. *Ecological Engineering* 16: 51-60.

Codd, G., Bell, S., Kaya, K., Ward, C., Beattie, K. & Metcalf, J. 1999. Cyanobacterial toxins, exposure routes and human health. *European Journal of Phycology* 34: 405-415.

Colinvaux, P.A., Miller, M.C., Liu, K.B., Steinitz-Kannan, M. & Frost, I. 1985. Discovery of permanent Amazon lakes and hydraulic disturbance in the upper Amazon Basin. *Nature* 13: 42-45.

Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C. & Likens, G.E. 2009. Controlling eutrophication: nitrogen and phosphorus. *Science* 323: 1014-1015.

Cooke, G.D., Lombardo, P. & Brant, C. 2001. Shallow and deep lakes determining successful management options. *Lakeline* 21: 42-46.

Cooke, G.D., Welch, E.B., Peterson, S. & Nichols, S.A. 2005. *Restoration and management of lakes and reservoirs, Third Edition*, CRC Press, 616p.

Correll, D. 1998. The role of phosphorus in the eutrophication of receiving waters: A review. *Journal of Environmental Quality* 27: 261-266.

Dahl, T.E. 2011. *Status and Trends of Wetlands in the Conterminous United States 2004 to 2009.* U.S. Department of the Interior, Fish and Wildlife Service, Washington D.C., 108 pp.

De Meester, L., Welder, L.J. & Tollrian, R. 1995. Alternative antipredator defences and genetic polymorphism in a pelagic predator-prey system. *Nature* 378: 483-485.

Declerck, S., De Meester, L., Podoor, N. & Conde-Porcuna, J.M. 1997. The relevance of size efficiency to biomanipulation theory: a field test under hypertrophic conditions. *Hydrobiologia* 360: 265-275.

Dodds, W.K., Bouska, W.W., Eitzmann, J.L., Pilger, T.J., Pitss, K.L., Riley, A.J., Schloesser, J.T. & Thornbrugh, D.J. 2009. Eutrophication of U.S. Freshwater: analysis of potential economic damages *Environmental Science & Technology* 43(1): 12-19.

Dokulil, M.T. & Teubner, K. 2000. Cyanobacterial dominance in lakes. *Hydrobiologia* 438: 1-12.

Dokulil, M.T. & Teubner, K. 2003. Eutrophication and restoration of shallow lakes – the concept of stable equilibria revisited. *Hydrobiologia* 506-509: 29-35.

Downing, J.A. & McCauley, E. 1992. The nitrogen: phosphorus relationship in lakes. *Limnology & Oceanography* 37(5): 936-945.

Dungeon, D., Arthington, A.H., Gessner, O.M., Kawabata, Z.I., Knowler, D.J., Lévêque, Naiman, R.J., Prieur-Richard A.H., Soto, D., Stiassny, L.J. & Sullivan, C. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163-182.

Duraõna, G.D.G. 2005. Estudio de los sedimentos de la laguna de Limoncocha. Dissertation. p112.

Dyble, J., Tester, P.A. & Litaker, R.W. 2006. Effects of light intensity on cylindrospermopsin production in the cyanobacterial HAB species *Cylindrospermopsis* raciborskii. *Afrikan Journal of Marine Science* 28(2): 309-312.

Elser, J.J., Marzolf, E.R. & Goldman, C.R. 1990. Phosphorus and Nitrogen limitation of phytoplankton growth in the freshwaters of North America: A review and critique of experimental enrichments. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1468-1477.

Elser, J.J., Matthews, E.S., Bracken, Cleland, E.E., Gruner, D.S., Harpole, S.W., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. and Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters* 10: 1135-1142.

Erikson, R., Hooker, E., Mejia, M., Zelaya, A. & Vammen, K. 1998. Optimal conditions for primary production in a polymictic tropical lake. *Hydrobiologia* 382:1-16.

FAO. 2000. *The State of World Fisheries and Aquaculture*. Fisheries Department, Food & Agriculture Organization (FAO) of the United Nations, Rome, Italy.

Funari, E. & Testai, E. 2008. Human healt risk assessment related to cyanotoxins exposure. *Critical Reviews in Toxicology* 38: 97-125.

Feniova, I., Dawidowicz, P., Gladyshev, M.I., Kostrezewska-Szlakowska, I., Rzepecki, M., Razlutskij, V., Sushchik, N.N., Majsak, N. & Dzialowski, A.R. 2015. Experimental effects of large-bodied *Daphnia*, fish and zebra mussels on cladoceran community and size structure. *Journal of Plankton Research* 0(0): 1-15.

Fernando, C.H. 1994. Zooplankton, fish and fisheries in tropical freshwater. *Hydrobiologia* 272: 105-123.

Ferrão-Filho, A.S., Azevedo, S.M.F.O. & DeMott, W.R. 2000. Effects of toxic and non-toxic cyanobacteria on the life history of tropical and temperate cladocerans. *Freshwater Biology* 45:1-19.

Feuchtmayr, H., Moran, R., Hatton, K., Connor, L., Heyes, T., Moss, B., Harvey, I. & Atkinson, D. 2009. Global warming and eutrophication: effects on water chemistry and autotrophic communities in experimental hypertrophic shallow lake mesocosms. *Journal of Applied Ecology* 46:713-723.

Figueredo, C.C., Giani, A. & Bird, D.F. 2007. Does allelopathy contribute to Cylindrospermpsis raciborskii (Cyanobacteria) bloom occurrence and geographic expansion? *Journal of Phycology* 43: 256-265.

Figueredo, C.C. & Giani, A. 2009. Phytoplankton community in the tropical lake of Lagoa Santa (Brazil): Conditions favoring a persistent bloom of *Cylindrospermopsis raciborskii. Limnologica* 39: 264-272.

Fisher, T.R., Gustafson, A.B., Sellner, K., Lacouture, R., Haas, L.W., Wetzel, R.L., Magnien, R., Everitt, D., Michaels, B. & Karrh, R. 1999. Spatial and temporal variation of resource limitation in Chesapeake Bay. *Marine Biology* 133:763-778.

Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55: 73-106.

Gasith, A. & Hoyer, M.V. 1998. Structuring role of macrophytes in lakes: Changing influence along lake size and depth gradients. *Ecological Studies: Analysis and Synsthesis* 13: 381-392.

Gliwicz, M.Z. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320:746-748.

Gliwicz, M.Z. 1990. Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 83-97.

Grafton, R.Q., Kompas, T. & Hilborn, R.W. 2007. Economics of Overexploitation Revisited. *Science* 318: 1601.

Gulati, R.D. & Van Donk, E. 2002. Lakes in the Netherlands, their origin, eutrophication, restoration. *Hydrobiologia* 478: 73-106.

Gulati, R.D., Lammens, E.H.R.R., Meijer, M.L. & van Donk, E. 1990. Biomanipulation – Tool for Water Management. Reprinted from *Hydrobiologia* 200/201, p612.

Gunkel, G. & Beulker, C. 2009. Limnology of the crater lake Cuicocha, Ecuador, a cold water tropical lake*. Internatial Review of Hydrobiology* 94:103-125.

Gunkel, G., Beulker, C. & Viteri, E. 2008. Hazards of volcanic lakes: analysis of Lakes Quilotoa and Cuicocha, Ecuador. *Advances in Geosciences* 14:29-33.

Gunkel, G. & Casallas, J. 2002. Limnology of an equatorial high mountain lake Lago San Pablo, Ecuador: The significance of deep diurnal mixing for lake productivity. *Limnologica* 32:33-43.

Gunkel, G. 2000. Limnology of an Equatorial high mountain lake in Ecuador, Lago San Pablo. *Limnologica* 30:113-120.

Gragnani, A., Scheffer, M. and Rinaldi, S. 1999. Top-down control of Cyanobacteria: a theoretical analysis. *The American naturalist* 153(1): 59-72.

Gross, E.M., Erhard, D. & Iványi, E. 2003. Allelopathic activity of *Ceratophyllum demersum L.* and *Najas marina ssp. Intermedia* (Wolfgang) Casper. *Hydrobiologia* 506/509: 583-589.

Häder, D.P., Kumar, H.D., Smith, R.C. & Worrest, R.C. 1998. Effects on aquatic ecosystems. *Journal of Photochemistry and Photobiology Biology* 46: 53-68.

Hall, S.R., Smith, V.H., Lytle, D.A. & Leibold, M.A. 2005. Constraints on primary producer N:P stoichiometry along N:P supply ratio gradients. *Ecology* 86(7):1894-1904

Hairston, N.G., Holtmeier, C.L., Lampert, W., Weider, L.J., Post, D.M., Fischer, J.M., Cáceres, C.E., Fox, J.A. & Gaedke, U. Natural selection for grazer resistance to toxic cyanobacteria: Evolution of phenotypic plasticity? *Evolution* 55(1):2203-2214.

Hansson, L.A., Gustafsson, S., Rengefors, K. & Bomark, L. 2007a. Cyanobacterial chemical warfare affects zooplankton community composition. *Freshwater Biology* 52: 1290-1301.

Hansson, L.A., Nicolle, A., Brodersen, J., Romare, P., Nilsson, P.A. & Brönmark, C. 2007b. Consequences of fish predation, migration, and juvenile ontogeny on zooplankton spring dynamics. *Limnology and Oceanography* 52(2):696-706.

Havens, K.E., Sharfstein, B., Brady, M.A., East, T.L., Harwell, M.C., Maki, R.P. & Rodusky, A.J. 2004. Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. *Aquatic Botany* 78: 67-82.

Herrmann, 2002. Management conflicts in the Ambato river watershed, Tungurahua Province, Ecuador. *Mountain Research and Development* 22(4): 338-340.

Hilt, S., Gross, E.M., Hupfer, M., Morscheid, H., Mählmann, J., Melzer, A., Poltz, J., Sandrock, S., Scharf, E-M. Schneider, S. & van der Weyer, K. 2006. *Limnologica* 36:155-171.

Holland, D., Roberts, S. & Beardall, J. 2004. Assessment of the nutrient status of phytoplankton: a comparison between conventional bioassays and nutrient-induced fluorescence transients (NIFTs). *Ecological Indicators* 4:149-159.

Hubble, D.S. & Harper, D.M. 2000. Top-down biological controls on tropical lake productivity. *Lakes & Reservoirs: Research and Management* 5:187-194.

Huszar, V.L.M., Caraco, N.F., Roland, F. & Cole, J. 2006. Nutrient-chlorophyll relationships in tropical-subtropical lakes: do temperate models fit? *Biogeochemistry* 79:239-250.

Isvánovics, V., Shafik, H.M., Présing, M. & Juhos, S.V. 2000. Growth and phosphate uptake kinetics of the cyanobacterium, *Cylindrospermopsis raciborskii* (Cyanophyceae) in throughflow cultures. *Freshwater Biology* 43: 257-275.

Jeppesen, E., Jensen, J.P., Søndergaard, M. & Lauridsen, T. 1997a. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342/343: 151-164.

Jeppesen, E., Søndergaard, M. & Christofferson, K. 1997b. *The structuring role of submerged macrophytes in lakes*, Springer. p427.

Jeppesen, E., Søndergaard, M., Kronvang, B., Jensen, J.P., Svenden, L.M. & Lauridsen, T.L. 1999. Lake and catchment management in Denmark. *Hydrobiologia* 395/396: 419-432.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., & Landkildehuis, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology* 45:201-218.

Jeppesen, E. 2003. Climatic warming and regime shifts in lake food webs – some comments. *Limnology and Oceanography* 48(3): 1346–1349

Jeppesen, E., Søndergaard, M., Mazzeo, N., Meerhoff, M., Branco, C., Huszar, V. & Scasso, F. 2005. Lake restoration and biomanipulation in temperate lakes: relevance for subtropical and tropical lakes. *Restoration and Management of Tropical Eutrophic lakes*: 341-359.

Jeppesen, E., Meerhoff, M., Jacobsen, B.A., Hansen, R.S., Søndergaard, M., Jensen, J.P., Lauridsen, T.L., Mazzeo, N. & Branco, C.W.C. 2007. Restoration of shallow lakes by nutrient control and biomanipulation – the successful strategy varies with lake size and climate. *Hydrobiologia* 581: 269-285.

Jeppesen, E., Moss, B., Bennion, H., Carvalho, L., DeMeester, L., Feuchtmayr, H., Friberg, N., Gessner, M.O., Hefting, M., Lauridsen, T.L., Liboriussen, L., Malmquist, H.J., May, L., Meerhoff, M., Olafsson, J.S., Soons, M.B. & Verhoeven, J.T.A. 2010. Interaction of climate change and eutrophication. *Climate Change Impacts on Freshwater Ecosystems.* p119 – 151.

Jeppesen, E., Kronvang, B., Olesen, J.E., Audet, J., Søndergaard, M., Hoffmann, C.C., Andersen, H.E., Lauridsen, T.L., Liboriussen, L., Larsen, S.E., Beklioglu, M., Meerhoff, M., Özen, A. & Özkan, K. 2011. Climate change effects on nitrogen loading from cultivated catchments in Europe: implications for nitrogen retention, ecological state of lakes and adaptation. *Hydrobiologia* 663: 1-21.

Josse, C., F. Cuesta, G. Navarro, V. Barrena, E. Cabrera, E. Chacón-Moreno, W. Ferreira, M. Peralvo, J. Saito and A. Tovar. 2009. Ecosistemas de los Andes del norte y centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Lima: Secretaría General de la Comunidad Andina, Programa Regional ECOBONA-Intercooperation, CONDESANProyecto Páramo Andino, Programa BioAndes, EcoCiencia, NatureServe, IAvH, LTAUNALM, ICAE-ULA, CDC-UNALM, and RUMBOL SRL.

Jöhnk, K.D, Huisman, J., Sharples, J., Sommeijer, B., Visser, P.M. & Stroom, J.M. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology* 14: 495-512.

Karl, D.M. 1999. A sea of change: Biogeochemical variability in the North Pacific Subtropical Gyre. *Ecosystems* 2:181-214.

Kehoe, M., O'Brien, K.R., Grinham, A. & Burford, M.A. 2015. Primary production of lake phytoplankton, dominated by the cyanobacterium *Cylindrospermopsis* raciborskii, in response to irradiance and temperature. *Inland Waters* 5: 93-100.

Kiersch, B., Mühleck, R. & Gunkel, G. 2004. Las macrófitas de algunos lagos alto-andinos del Ecuador y su bajo potential como bioindicatores de eutrofización. *Revista de Biología Tropical* 52(4)

Kirstensen, P., Søndergaard, M. & Jeppesen, E. 1992. Resuspension in a shallow eutrophic lake. *Hydrobiologia* 228: 101-109.

Klausmeier, C.A., Litchman, E., Daufresne, T. & Levin, S.A. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature* 429: 171-174.

Köhler, J., Schmitt, M., Krumbeck, H., Kapfer, M., Litchman, E. and Neale, P.J. 2001. Effects of UV on carbon assimilation of phytoplankton in a mixed water column. *Aquatic Sciences* 63: 294-309.

Köhler, J., Hilt, S., Adrian, R., Nicklisch, A., Kozerski, P. & Walz, N. 2005. Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshwater Biology* 20: 1639-1650.

Komárek, J. & J. Komárková, 2003. CyanoDB.cz – On–line database of cyanobacterial genera. Phenotype diversity of the cyanoprokaryotic genus *Cylindrospermopsis* (Nostocales); review 2002. *Czech Phycology* 3: 1–30

Kosten, S., Huszar, V.L.M., Bécares, E., Costa, L.S., van Donk, E., Hansson, L.A., Jeppesen, E., Kruk, C., Lacerot, G., Mazzeo, N., De Meester, L., Moss, B., Lürling, M., Nöges, T., Romo, S.A. & Scheffer, M. 2012a. Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology* 18: 118-126.

Kosten, S., Vernooij, M., Van Nes, E.H., Sagrario, M.D.L., Clevers, J.G.P.W. & Scheffer, M. 2012b. Bimodal transparency as an indicator for alternative states in South American lakes. *Freshwater Biology* 57:1191-1201.

Krom, M.D., Kress, N., Brenner, S. & Gordon, L.I. 1991. Phosphorus limitation of primary productivity in the eastern Mediterranean Sea. *Limnology & Oceanography* 36(3): 424-432.

Lacerot, G., Kruk, C., Lürling, M. & Scheffer, M. 2013. The role of subtropical zooplankton as grazers of phytoplankton under different predation levels. *Freshwater Biology* 58: 494-503.

Lammens, E.H.R.R. & Hoogenboezem, W. 1991. Diets and feeding behaviour. *Cyprinid fishes:systematics, biology and exploitation.* Chapman and Hall, pp. 353–376.

Lauridsen, T.L., Pedersen, L.J., Jeppesen, E. & Søndergaar, M. 1996. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *Journal of Plankton Research* 18(12): 2283-2294.

Lauridsen, T.L. & Lodge, D.M. 1996. Avoidance by *Daphnia magna* of fish and macrophytes: Chemical cues and predator-mediated use of macrophyte habitat. *Limnology and Oceanography* 41(4): 794-798.

Lauridsen, T.L., Jeppesen, E., Mitchell, S.F., Lodge, D.M. & Burks, R.L. 1999. Diel variation in horizontal distribution of *Daphnia* and Cerio*Daphnia* in oligotrophic and mesotrophic lakes with constrasting fish densities. *Hydrobiologia* 408/409: 241-250.

Landsberg, J.H. 2010. The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science* 10(2): 113-390.

Lazzaro, X. 1987. A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146:97-167.

Lean, D.R.S. & Pick, F.R. 1981. Photosynthetic response of lake plankton to nutrient enrichment: A test for nutrient limitation. *Limnology and Oceanography* 26(6):1001-1019.

Leech, D.M. & Williamson, C.E. 2000. Is tolerance to UV radiation in zooplankton related to body size, taxon or lake transparency? *Ecological society of America* 10(5):1530-1540.

Lemmens, P. 2014. Fish and the management of shallow lakes, Doctoral Dissertation, p200.

Lemoalle, J. 1981. Photosynthetic production and phytoplankton in the euphotic zone of some African and temperate lakes. *International Review of Hydrobiology* 14(1):31-37.

Lewis, W.M. 1996. Tropical lakes: How latitude makes a difference. *Perspectives in Tropical Limnology*: 43-64.

Lewis, W.M. 2000. Basis for the protection and management of tropical lakes. *Lakes & Reservoirs: Research and Management* 5:35-48.

Lewis, W.M. 2002. Causes for the high frequency of nitrogen limitation in tropical lakes. *Verhandlungen des Internationalen Verein Limnologie* 28: 210-213.

Lewis, W.M. & Levine, S.N. 1984. The light response of nitrogen fixation in Lake Valencia, Venezuela. *Limnology and Oceanography* 29(4): 894-900.

Li, E-H., Li, W., Wang, X-L., Xue, H-P. and Xiao, F. 2010. Experiment of emergent macrophytes growing in contaminated sludge: impact for sediment purification and lake restoration. *Ecological Engineering* 36: 427-434.

Loverde-Oliviera, S.M., Huszar, V.L.M., Mazzeo, N. & Scheffer, M. 2009. Hydrology-Driven Regime Shifts in a Shallow Tropical Lake. *Ecosystems* 12: 807-819.

Lundberg, G., Kottelat, M., Smith, G.R., Stiassny, M.L.J. & Gill, A.C. 2000. So many fishes, so little time: an overview of recent ichthyological discovery in continental waters. *Annals of the Missouri Botanical Gardens* 87: 26-62.

Mahowald, N., Jickells, T.D., Baker, A.R., Artaxo, P., Benitez-Nelson, C.R., Bergametti, G., Bond, T.C., Chen, Y., Cohen, D.D., Herut, B., Kubilay, N., Losno, R., Luo, C., Maenhaut, W., McGee, K.A., Okin, G.S., Siefert, R.L. & Tsukuda, S. 2008. Global distribution of atmospheric phosphorus sources, concentrations and deposition rates, and anthropogenic impacts. *Global Biogeochemical Cycles* 22: 1-19.

Mandonx, T. 2014. Trophic status and phytoplankton ecology of two lakes in northern Ecuador: Yahuarcocha & Mojanda. Dissertation, 86p.

Maridueña, A. Chalén, N., Coello, D., Cajas, J., Elías, E., Solís-Coello, P. and Aguilar, F. 2011. Mortandad de peces en la laguna de Yahuarcocha, Cantón Ibarra, Provincia de Imbabura. *Bolitín Especial* 02(1): 1-128.

McConnell W.J., Sweeney S.P. & Mulley B., 2004. Physical and social access to land: spatio-temporal patterns of agricultural expansion in Madagascar. *Agriculture Ecosystems & Environment* 101: 171-184.

McGregor, G.B. & Fabbro, L.D. 2000. Dominance of *Cylindrospermopsis* raciborksii (Nostocales, Cyanoprokaryota) in Queensland tropical and subtropical reservoirs: Implications for monitoring and management. *Lakes & Reservoirs: Research and Management* 5: 195-205.

McKinnon, J.S. & Taylor, E.B. 2012. Species chocked and blended. *Nature* 482: 313-314.

Meerhoff, M., Mazzeo, N., Moss, B. & Rodríguez-Gallego, L. 2003. The structuring role of free-floating versus submerged plants in a subtropical shallow lake. *Aquatic Ecology* 37: 377-391.

Meerhoff, M., Fosalba, C., Bruzzone, C., Mazzeo, N., Noordoven, W. & Jeppesen, E. 2006. An experimental study of habitat choice by *Daphnia*: Plants singal danger more than refuge in subtropical lakes. *Freshwater Biology* 51: 1320-1330.

Meerhoff, M. 2006. The structuring role of macrophytes on trophic dynamics in shallow lakes under a climate-warming scenario. p158.

Meerhoff, M., Iglesias, C., Teiceira De Mello, F., Clemente, J.M., Jensen, E., Lauridsen, T.L. & Jeppesen, E. 2007a. Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology* 52: 1009-1021.

Meerhoff, M., Clemente, J.M., Teixeira-de-Mello, F., Iglesias, C., Pedersen, A.R. & Jeppesen, E. 2007b. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? *Global Change Biology* 13:1888-1897.

Meschiatti, A.J., Arcifa, M.S. & Fenerich-Verani, N. 2000. Fish communities associated with macrophytes in Brazilian foodplain lakes. *Environmental Biology of Fishes* 58:133-143.

Meijer, M.L., Jeppesen, E., van Donk, E., Moss, B., Scheffer, M., Lammens, E., van Nes, E., van Berkum, J.A., de Jong, G.J., Faafeng, B.A. & Jensen, J.P. 1994. Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia* 275/276: 457-466.

Meijer, M.L., De Haan, M.W., Breukelaar, A.W. & Buiteveld, H. 1990. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? *Hydrobiologia* 200/201: 303-315.

Melack, J.M. 1979. Temporal variability of phytoplankton in tropical lakes. *Oecologia* 44:1-7.

Messerli, B. 2004. Mountains of the world – Water towers for the 21st century. *Ambio*: 29-34.

Netten, J.J.C., Arts, G.H.P., Gylstra, R., Van Nes, E.H., Scheffer, M. & Roijackers, R.M.M. 2010. Effect of temperature and nutrients on the competition between free-floating Salvinia natans and submerged Elodea nuttallii in mesocosms. *Fundamental and Applied Limnology* 177(2): 125-132.

Miller, S.A. & Crowl, T.A. 2006. Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. *Freshwater Biology* 51:85-94.

Ministerio del Ambiente. 2014. Protege Ecuador, La responsabilidad es de todos. http://www.ambiente.gob.ec/

Moss, B. 2007. The art and science of lake restoration. *Hydrobiologia* 581:15-24.

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K., Lacerot, G., Liu, Z., De Meester, L., Paerl, H. & Scheffer, M. 2011. Allied attack: climate change and eutrophication. *Inland Waters* 1: 101-105.

Mühlhauser, H.A., Hrepic, N., Mladinic, P. Montecino, V. & Cabrera, S. 1995. Water quality and limnological features of a high altitude Andean lake, Chungará, in northern Chile. *Revista Chilena de Historia Natural* 68:341-349.

North, R.L., Winter, J.G. & Dillon, P.J. 2013. Nutrient indicators of agricultural impacts in the tributaries of a large lake. *Inland waters* 3:221-234.

Northcote, T.G., Arcifa, M.S. & Munro, K.A. 1990. An experimental study of the effects of fish zooplanktivory on the phytoplankton of a Brazilian reservoir. *Hydrobiologia* 194:31-45.

NRA. 1990. *Toxic bue-green algae.* Water Quality Series No. 2. London: *National Rivers Authority*.

Olvera-Ramírez, R., Centeno-Ramos, C. and Martínez-Jerónimo, F. 2010. Toxic effects of *Pseudanabaena tenuis* (Cyanobacteria) on the cladocerans *Daphnia magna* and *CerioDaphnia dubia*. *Hidrobiológica* 20(3): 203-212.

Padisák, J. 1997. *Cylindrospermopsis raciborskii* (Woloszynska) Seenayya et Subba Raju, an expanding, highly adaptive cyanobacterium: worldwide distribution and review of its ecology. *Archiv für Hydrobiologie Supplement* 107(4): 563-593.

Padisák, J. & Reynolds, C. S. 2003. Shallow lakes: the absolute, the relative, the functional and the pragmatic. *Hydrobiologia* 506-509: 1-11.

Paerl, H.W. & Huisman, J. .2008. Blooms like it hot. *Science* 320: 57.

Paerl, H.W. & Huisman, J. 2009. Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environmental Microbiology Reports* 1(1): 27-37.

Panosso, R. and Lürling, M. 2010. *Daphnia* magna feeding on *Cylindrospermopsis raciborskii*: the role of food composition, filament length and body size. *Journal of Plankton Research* 32(10): 1393-1404.

Peñuelas, J., Sardans, J., Rivas-Ubach, A. & Janssens, I.A. 2012. The human-induced imbalance between C,N and P in Earth’s life system. *Global Change Biology* 18:3-6.

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M. & Janssens, I.A. 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature* 4: 1-10.

Peterson, G.D., Beard JR. T.D., Beisner, B.E., Bennett, E.M., Carpenter, S.R., Cumming, G.S., Dent, C.L. & Havlicek, T.D. 2003. Assessing future ecosystem services: a case study of the Northern Highlands Lake District, Wisconsin. *Conservation Ecology* 7(3): 1.

Persson, L. & Eklöv, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76(1): 70-81.

Pitois, S., Jackson M.H. & Wood, B.J.B. 2010. Problems associated with the presence of cyanobacteria in recreational and drinking waters. *International journal of environmental health research* 10: 203-218.

Pieczynska, E. 1993. Detritus and nutrient dynamics in the shore zone of lakes: a review. *Hydrobiologia* 251: 49-58.

Poikane, S., Portielje, R., van den Berg, M., Phillips, G., Brucet, S., Carvalho, L., Mischke, U., Ott, I., Soszka, H. & Van Wichelen, J. 2014. Defining ecologically relevant water quality targets for lakes in Europe. *Journal of Applied Ecology* 51:592-602.

Potthoff, A.J., Herwig, B.R., Hanson, M.A., Zimmer, K.D., Butler, M.G., Reed, J.R., Parsons, B.G. & Ward, M.C. 2008. Cascading food-web effects of piscivore introductions in shallow lakes. *Journal of Applied Ecology* 45:1170-1179.

Queimaliños, C.P., Modenutti, B.E. & Balseiro, E.G. 1998. Phytoplankton responses to experimental enhancement of grazing pressure and nutrient recycling in a small Andean lake. *Freshwater Biology* 40:41-49.

Quirós, R. 1998. Fish effects on trophic relationships in the pelagic zone of lakes. *Hydrobiologia* 361:101-111.

Rao, W., Ning, J., Zhong, P., Jeppesen, E. and Liu, Z. Size-dependent feeding of omnivorous Nile tilapia in a macrophytes-dominated lake: implications for lake management. *Hydrobiologia* 749: 125-134.

Reddy, M.V. 2005. Restoration and Management of Tropical Eutrophic Lakes. *Science* Publishers, Inc., USA. p31.

Reynolds C.S. 2006. *The Ecology of Phytoplankton.* Cambridge University Press, New York 552p.

Reynolds, C. 2010. Toxic blue-green algae: the problem in perspective. *Freshwater Forum* 1(1): 29-38.

Romare, P. & Hansson, L.A. 2003. A behavioral cascade: Top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceaography* 48(5): 1956 – 1964.

Rondel, C., Arfi, R., Corbin, D. Le Bihan, F., Ndour, E.H. & Lazzaro, A. 2008. A cyanobacterial bloom prevents fish trophic cascades. *Freshwater Biology* 53(4): 637-651.

Roozen, F.C.J.M., Lürling, M., Vlek, H., Van Der Pouw Kraan, E.A.J., Ibelings, B.W. & Scheffer, M. 2007. Resuspension of algal cells by benthivorous fish boosts phytoplankton biomassa and alters community structure in shallow lakes. *Freshwater Biology* 52:977-987.

Rowe, D.K. 2007. Exotic fish introductions and the decline of water clarity in small North Island, New Zealand lakes: a multi-species problem. *Hydrobiologia* 583: 345- 358.

Sachse, R., Petzoldt, T., Blumstock, M., Moreira, S., Pätzig, M., Rücker, J., Janse, J.H., Mooij, W.M. & Hilt, S. 2014. Extending one-dimensional models for deep lakes to stimulate the impact of submerged macrophytes on water quality. *Environmental Modelling & Software* 61: 410-423.

Saha, S. & Jana, B.B. 1998. Control of bloom in a tropical lake: grazing efficiency of some herbivorous fishes. *Journal of Fish Biology* 53: 12-24.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Sarnelle, O., Cooper, S.D., Wiseman, S. & Mavuti, K.M. 1998. The relationship between nutrients and trophic-level biomass in turbid tropical ponds. *Freshwater Biology* 40: 65-75.

Scasso, F., Mazzeo, N., Gorga, J., Kruk, C., Lacerot, G., Clemente, J., Fabián, D. & Bonilla, S. 2001. Limnological changes in a sub-tropical shallow hypertrophic lake during its restoration: two years of a whole-lake experiment. Aquatic Conservation: *Marine and Freshwater Ecosystems* 11: 31-44.

Schallenberg, M. & Burns, C.W. 2004. Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. *Freshwater Biology* 49: 143-159.

Scheffer, M. 2001. Alternative attractors of shallow lakes. *The scientific world* 1: 254-263.

Scheffer, M. 2004. *Ecology of shallow lakes*. Chapman and Hall, London, 377p.

Scheffer, M. & Carpenter, S.R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* 18(12):648-656.

Scheffer, M., Hosper S. H., Meijer M.L., Moss B. & Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution* 8: 275–279.

Scheffer, M., Rinaldi, S, Gragnani, A., Mur, R.L. and Van Nes, E.H. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. *Ecology* 78(1): 272-282.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591-596.

Scheffer, M., Portielje, R. & Zambrano, L. 2003. Fish facilitate wave resuspension of sediment. *Limnology & Oceanography* 48(5): 1920-1926.

Schindler, D.W. 1977. Evolution of Phosphorus Limitation in Lakes. *Science* 195:260- 262.

Schriver, P., Bøgestrand, J., Jeppesen, E. & Søndergaard, M. 1995. Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biology* 33: 255-270.

Sinha, R., Pearson, L.A., Davis, T.W., Burford, M.A., Orr, P.T. & Neilan, B.A. 2012. Increased incidence of *Cylindrospermopsis* raciborskii in temperate zones – Is climate change responsible? *Water Research* 46: 1408-1419.

Smith, V.H. 2003. Eutrophication of freshwater and coastal marine ecosystems. *Environmental Science & Pollution Research* 10 (2): 126-139.

Smith, V.H. & Schindler, D.W. 2009. Eutrophication science: where do we go from here? *Trends in Ecology and Evolution* 24(4): 201-207.

Søndergaard, M., Jeppesen, E., Jensen, J.P. & Lauridsen, T. 2000. Lake restoration in Denmark. Lakes & Reservoirs: *Research and management* 5: 151- 159.

Søndergaard, M., Jensen, J.P. & Jeppesen, E. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506-509: 135-145.

Sperling, E.V. 1997. The process of biomass formation as the key point in the restoration of tropical eutrophic lakes. *Hydrobiologia* 342/343: 351-354.

Stansfield, J.H., Perrow, M.R., Tench, L.D., Jowitt, A.J.D & Taylor, A.A.L. 1997. Submerged marcrophytes as refuge for grazing Cladocera against fish predation: observations on seasonal changes in relation to macrophyte cover and predation pressure. *Hydrobiologia* 342/343:229-240.

Steinitz-Kannan, M. 1997. The lakes in Andean protected areas of Ecuador. *The George Wright Forum* 14(3):33-43.

Steinitz-Kannan, M., Colinvaux, P.A. & Kannan, R. 1983. Limnological studies in Ecuador: A survey of chemica land physical properties of Ecuadorian Lakes. *Archiv für Hydrobiologie Supplement* 65(1): 61-105.

Strayer, D.L. & Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* 29(1): 344-358.

St. Pierre, J.I. & Kovalenko, K.E. 2014. Effect of habitat complexity attributes on species richness. *Ecosphere* 5(2): 1-10.

Sunaga, T. & Verani, J. 1991. The fish communities of the lakes in Rio Doce Valley, Northeast Brazil. *Verhandlungen des Internationalen Verein Limnologie* 24:2563-2566.

Teixeira de Mello, F., Meerhoff, M., Pekcan-Hekim, Z. & Jeppesen, E. 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. *Freshwater Biology* 54: 1202-1215.

Toerien, D.F. & Cavari, B. 1982. Effect of temperature on heterotrophic glucose uptake, mineralization and turnover rates in lake sediments. *Applied and Environmental Microbiology* 43(1):1-5.

Townsend, A.R., Howarth, R.W., Bazzaz, F.A., Booth, M.S., Cleveland, C.C., Collinge, S.K., Dobson, A.P., Epstein, P.R., Holland, E.A., Keeney, D.R., Mallin, M.A., Roger, C.A., Wayne, P. & Wolfe, A.H. 2003. Human health effects of changing N cycle. *Frontiers in Ecology and the Environment* 1(5): 240-246.

Thompson, L.G., Mosley-Thompson, E., & Henderson, K.A. 2000. Ice-core palaeoclimate records in tropical South America since the last glacial maximum. *Journal of Quaternary Science* 15 (4): 377-394.

Trijillo, C. A., Cruz Góngora, F. E., and Flores Valencia, D. B. 2011. Estudio del potencial ecoturistico e Historico-Cultural de la Laguna de Yahuarcocha, Canton Ibarra, Provincia de Imbabura. Dissertation, p141.

Urrutia-Cordero, P., Ekvall, M.K. & Hansson, L-A. 2015. Responses of cyanobacteria to herbivorous zooplankton across predator regimes: who mows the bloom? *Freshwater Biology* 60: 960-972.

Van Donk, E. & van de Bund, W.J. 2002. Impact of submerged macrophytes including charophytes on phyto- and zooplankton communities: allelopathy versus other mechanisms. *Aquatic Botany* 72: 261-274.

Van Liere, L. & Gulati, R.D. 1992. *Restoration and Recovery of Shallow Eutrophic Lake Ecosystems in The Netherlands.* Reprinted from *Hydrobiologia* 233, p293.

Van der Molen, D.T. & Boers, P.C.M. 1994. Influence of internal loading on phosphorus concentration in shallow lakes before and after reduction of the external loading. *Hydrobiologia* 275/276:379-389.

Vitrousek, P.M. & Howarth, R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* 13:87-115.

Vuille, M., Francou, B., Wagnon, P., Juen, I., Kaser, G., Mark, B.G. & Bradley, R.S. 2008. Climate change and tropical Andean glaciers: Past, present and future. *Earth-Science Reviews* 89: 79-95.

Welch, E.B. & Lindell, T. 1992. *Ecological effects of wastewater: applied limnology and pollution effects*. E & FN Spon, London, New York, p425.

Wetzel, R.G. 2001. *Limnology: Lake and river ecosystems, Third Edition*. Academic Press, 1006p.

Wium-Andersen, S., Anthoni, U., Christophersen, C. & Houen, G. 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). *OIKOS* 39: 187-190.

Worldbank. 2009. Ecuador: Country note on climate change aspects in agriculture. 11p.

Zambrano, L., Scheffer, M. & Martinez-Ramos, M. 2001. Catastrophic response of lakes to benthivorous fish introduction. *OIKOS* 94:344-350.

Zapata-Anzola, A.M. Rivera-Rondón, C.A. & Donato-Rondón, J.C. 2006. Dynamics of photosynthetic pigments in an Andean lake in Colombia. *Lakes & Reservoirs: Research & Management* 11(1): 29-38.

Zhang, X., Xie, P., Chen, F., Li, S. & Qin, J. Driving forces shaping phytoplankton assemblages in two subtropical plateau lakes with contrasting trophic status. *Freshwater Biology* 52:1463-1475.

Addendum

Risk Assessment

For the sampling we worked in Ecuador and this brought some extra health risks. We were vaccinated against yellow fever, hepatitis A, hepatitis B, typhus fever and tetanus. Most important risks related to the sample collection were high UV radiation, acute mountain sickness (AMS) and drowning risk. To protect against high UV radiation we put on sunscreen a few times a day with a high UV factor (≥ 50). AMS is caused by reduced air pressure and lower oxygen levels at high altitudes. Symptoms of mild to moderate acute mountain sickness may include: difficulty sleeping, dizziness, fatigue, headache, loss of appetite, nausea or vomiting, rapid heart rate and shortness of breath with exertion. To resolve this we acclimated a few days before starting the sampling in Yahuarcocha. Most of the experiments were acquired by navigating on a small boat. Drowning risk was reduced by wearing a life jacket, according to safety regulations. For the 24-hour monitoring, the sampling was also performed at night so sufficient light and navigation systems were present. Sampling in the field also embodied a lot of technical work with ergonomic dangers such as lifting heavy objects and danger associated with materials that had sharp edges or pointy objects. To minimize these dangers, a first aid kit was always available at the sampling sites.

During the sample analyzing in Ecuador and Belgium we used formaldehyde and methanol (Table A). Methanol is highly flammable and is toxic. It is important that this is kept away from heat sources. Methanol can cause eye damage, respiratory irritation and skin burns. Wash with soap and water if solutions comes in contact with skin. If swallowed, call immediately a physician. Same risks and precautions count for formaldehyde. To protect ourselves against the harmful effects we wore protective gloves and lab coats when handling the substance.

Table A: Potentially hazardous chemicals used for the analysis of the samples.

Substance	Formula	Safety classification
Methanol	CH_4O	Flammable, toxic,
Formaldehyde	CH_2O	Carcinogen, toxic, corrosive

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