Impacts of climate change and nutrients on phytoplankton, especially on cyanobacteria

by

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Abstract

Eutrophication is a global problem experienced by many water bodies that can lead to excessive growth of phytoplankton, especially cyanobacteria that create numerous water quality issues. Cyanobacterial species are known to produce toxins that pose threats to animal health and can produce large scale surface scums that degrade aesthetics and reduce oxygen in aquatic systems. It is hypothesised that increasing temperatures with climate change would further intensify the effects of eutrophication on phytoplankton dynamics. It is likely that both varying temperatures and nutrients interact to change the growth environment of phytoplankton, although, the relative influence of each factor may vary depending on nutrient availability. Rising temperature and nutrients can affect phytoplankton community directly by changing the metabolic rates and indirectly by altering the thermal structure of lakes.

The main aim of this study was to understand the changes in the phytoplankton growth, succession and composition as a result of climate change and nutrients. One main focus was to determine whether the negative impacts of rising temperatures could be alleviated by nutrient reduction. Three primary approaches were taken to address the above aims. First, the response of phytoplankton to varying nutrients under a warming climate was assessed in two lakes with different trophic status. Second, the oligotrophic lake was used as model system to explore the changes experienced by the water column stability as a result of changes in nutrients and temperature. Finally, the effects of water column stability on phytoplankton abundance and functional diversity were assessed by analysing small scale changes in mixing and stratification during the transition period from spring to summer.

The importance of trophic status in driving phytoplankton dynamics was determined using two lakes with opposing nutrient status (Chapter 2). The responses and interactions of three main phytoplankton functional groups consisting of cyanobacteria, chlorophytes and diatoms under rising temperatures and modified nutrient availabilities were analysed. A calibrated and validated open-source, 1-dimensional hydrodynamic model, General Lake Model (GLM) coupled with the Framework for Aquatic Biogeochemical Model (FABM) was used to simulate the hydrodynamics, nutrients and phytoplankton in the oligotrophic and eutrophic lake. A combination of 25 scenarios, including changes in nutrient availability and rising temperatures, were used to evaluate and compare the responses of the phytoplankton in the

two lakes. Nutrients were decreased and increased by 10-20 folds to cause a shift in the trophic status and temperatures were increased by 1-4 °C based on the future climate projections in the IPCC 4th Assessment Report.

Nutrients and temperatures, individually and interactively, were found to cause substantial changes in the phytoplankton growth and composition. A 3-fold increase in the phytoplankton biomass relative to the base conditions was observed in the oligotrophic lake as the nutrient status changed from meso-oligotrophic to hyper-eutrophic. The effects of rising temperatures were disguised by the profound impacts of nutrient enrichment in the oligotrophic lake. The eutrophic lake also experienced a 2-fold increase in phytoplankton growth under high nutrients, but rising temperature had a higher influence on phytoplankton abundance. Reduced nutrients had a minor influence on the total phytoplankton biomass in the oligotrophic lakes but, in the eutrophic lake, it prevented the boosted phytoplankton growth which would have otherwise occurred under high temperatures. Nuisance phytoplankton growth expected under high temperatures can be alleviated by nutrient reduction. Phytoplankton composition also changed as the nutrient status changed under a warming climate. Chlorophytes were observed to dominate under high nutrients and cyanobacteria thrived under low nutrient and high temperatures in both lakes. Although cyanobacteria species are normally observed under eutrophic, warm conditions, the physiological adaptations of chlorophytes and cyanobacteria that promote their functionality, such as their high surface area to volume ratios, presence of mucilaginous sheath and resistance to predation, could explain the above observations. A simple sensitivity analysis indicated that trait specific parameters related to growth and nutrient uptake rates have a considerable influence on the interactions simulated between chlorophytes and cyanobacteria.

The thermal structure of lakes is an important physical feature that exerts control over the ecosystem structure and function. The changes in the mixing and stability of the water column in the oligotrophic lake as a consequence of varying nutrients and rising temperatures were then assessed in detail in Chapter 3. Similar scenarios were adopted and the resulting thermal profiles were used to calculate the thermal stability and thermocline depth for each scenario. Lake Tarawera experienced atypical variations in the seasonal heat fluxes under nutrient rich, warm scenarios. The highest evaporative losses occurred in spring-summer period and an increase in net heat occurred during winter-autumn period. The latter caused an advancement in the onset of stratification as the trophic status changed from oligotrophic to hyper-eutrophic under rising temperatures. The onset and duration of stratification were assessed and the relative contribution of surface temperature, nutrients and mixing in determining thermal stability under each scenario was evaluated using linear regression models. A rise in temperature by 1-4 °C under eutrophic conditions led to an increase in average thermal stability of the water column with the onset of stratification events advancing and persisting for a longer period of time relative to base conditions. Under similar circumstances, the average thermocline depth was also reduced, and persistent, incomplete mixing was observed, even during winter. Temperature, thermocline depth and total chlorophyll were the main factors that influenced thermal stability but the influence of each factor varied depending on the nutrient status of the lake. Nutrient driven total phytoplankton concentrations had the highest influence on stability under intermediate temperature rises of 1-2 °C. Beyond a temperature rise of 2 °C, temperature had the greatest impact on stability of the water column. Nutrient reduction was found to improve winter mixing by increasing thermocline depth under a temperature increase of 2 °C, which was absent during nutrient enriched conditions under the same temperature rise. Hence, nutrient reduction can increase mixing and improve water quality in deep lakes under temperature increases between 1 and 2 °C, but may not be effective if the temperatures are to rise beyond 2 °C.

Changes in mixing, stratification and subsequent modifications in light and nutrient distribution can be considered as disturbances in the ecosystem that have an impact on the phytoplankton abundance and composition. Intensive, twice a week sampling was carried out in Mt Bold Reservoir (largest storage reservoir in South Australia) to determine the changes in the phytoplankton community and the functional diversity as environmental factors vary during the seasonal shift from spring to summer (Chapter 4). Functional diversity of the phytoplankton community was assessed using characteristic morphological adaptations that determine their competitive abilities and survival opportunities. Long term seasonal trends in increasing surface water temperatures and thermal stability emerged as the most significant factors that affect phytoplankton taxonomic and functional diversity.

While the taxonomic diversity indicated a progressive declination as spring extends, the functional diversity showed the highest diversity during early spring and then declined steadily. Relating the functional diversity trend to the intensity and the frequency at which the disturbances occurred in the system suggested that the functional diversity fitted the Intermediate Disturbance Hypothesis (IDH) (Grime 1973, Cornell 1978). The highest functional diversity was observed when the magnitude of the forcing event (change in mixing) was of medium intensity when comparing to the minimum and maximum intensities observed in the reservoir, during the period of study. Low intensity fluctuations and gradual increase in stability resulted in the selection of a few genera consisting of *Microcystis* (cyanobacteria) and *Sphaerocystis* (chlorophyte) that possessed physiological adaptations to dominate under such conditions. High intensity oscillations in other physical attributes, such as in Lake Number and surface mixed layer created an unstable environment with non-equilibrium conditions that prevented competition exclusion of species and facilitated co-existence amongst species.

Overall, this study assessed the direct and indirect impacts of long term changes in the environment in relation to varying nutrient dynamics and climate change and evaluated in detail the effects of short term changes in the abiotic and biotic factors on phytoplankton biomass and diversity. The results from this study highlighted that improved water quality (e.g., reduced nuisance algal growth and cyanobacterial dominance, increased water clarity) in a future climate with increased air temperatures can only be achieved if external nutrient loadings to lakes are reduced considerably. While it is true that climate change demands a global response, local managers have the opportunity to offset some of the impacts through catchment management and reducing nutrients at the local and catchment scale. Nutrient concentrations may have to be reduced substantially from present day values in many lakes if lake resilience to the detrimental impacts of climate change is to be promoted.

Thesis Declaration

I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the University of Adelaide and where applicable, any partner institution responsible for the joint-award of this degree.

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Chaturangi Wickramaratne

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Date

Foreword

This thesis has been prepared as a series of chapters in a format that will be suitable for future publication in scientific journals, as specified below. Maintaining the sense of individual chapters has inevitably led to some repetition between chapters.

Chapter 2:

Vulnerability of oligotrophic lakes to the synergistic impacts of nutrients and temperature

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Chapter 3:

Effects of warming and nutrients on the thermal structure of a deep, oligotrophic lake

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Chapter 4:

Species diversity and functional diversity are determined by disturbance intensity during spring to summer in an eutrophic reservoir

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Statement of Authorship – Chapter 2

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Principal Author

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Contribution to the Paper	Calibration and validation of the model, ran simulations for scenarios, data analysis and interpretation, wrote manuscript		
Overall percentage (%)	85%		
Certification:	This paper reports on original research I conducted during the period of my Higher Degree by Research candidature and is not subject to any obligations or contractual agreements with a third party that would constrain its inclusion in this thesis. I am the primary author of this paper.		
Signature		Date	24.02.2016

Co-Author Contributions

By signing the Statement of Authorship, each author certifies that:

i. the candidate's stated contribution to the publication is accurate (as detailed above);

ii. permission is granted for the candidate in include the publication in the thesis; and

iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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iii. the sum of all co-author contributions is equal to 100% less the candidate's stated contribution.

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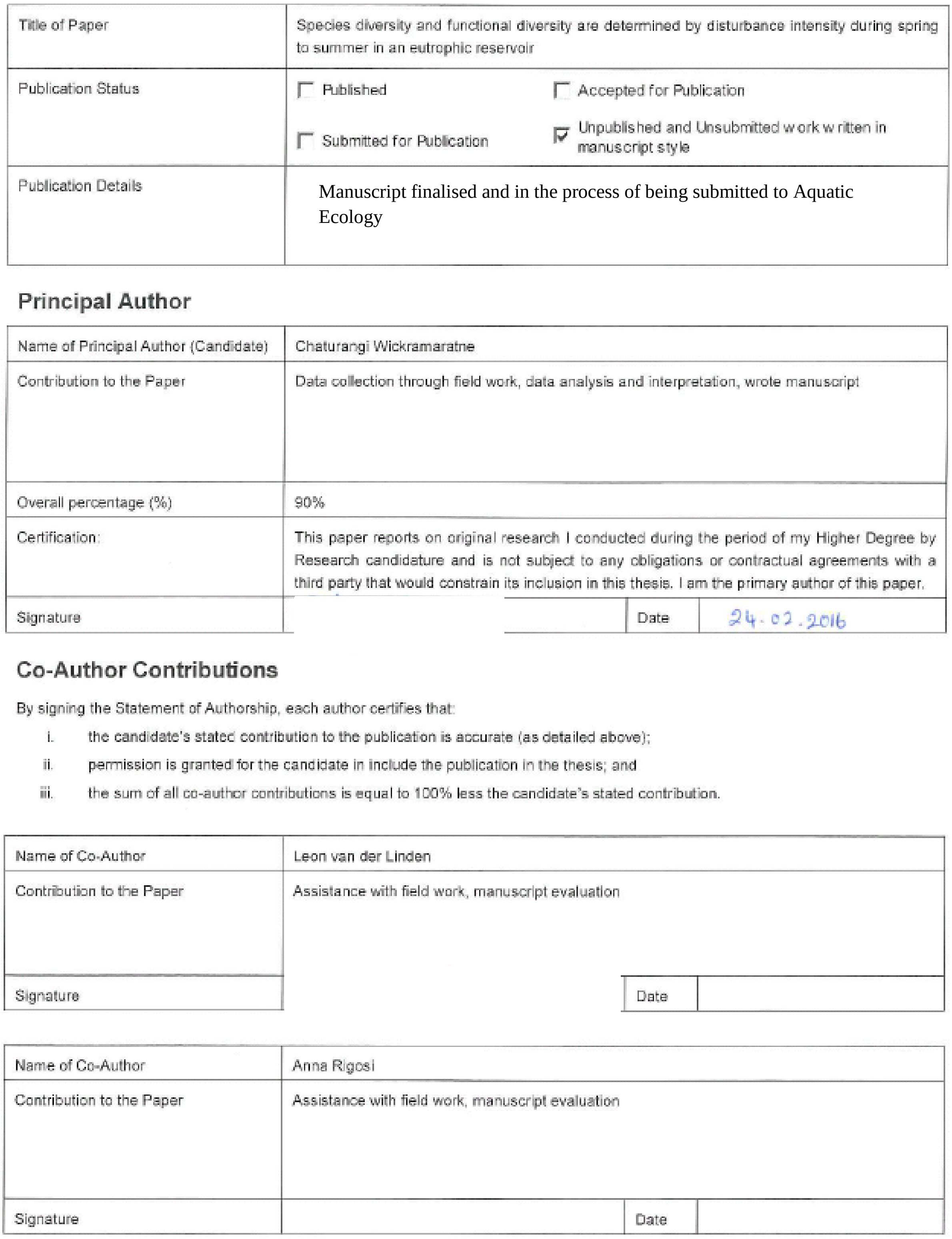
Contribution to the Paper	Project supervision, manuscript evaluation		
Signature		Date	24 Feb 2016

Statement of Authorship – Chapter 4



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Name of Co-Author	Leon van der Linden		
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Chapter 1 General Introduction

Nutrients and temperature

Global water resources are under threat (Vörösmarty et al. 2000). Anthropogenic influences, such as increased land use changes and growing population, together with altered hydrological cycles can degrade surface water quality. Poor surface water quality impairs its use for drinking, agricultural and recreational activities and affects the health of aquatic organisms. Nutrients and temperature are two main drivers responsible for changes in water quality. Nitrogen (N) and Phosphorus (P) are key nutrients required to maintain the productivity of aquatic ecosystems, but excessive amounts of these nutrients can have detrimental impacts leading to algal blooms, increased turbidity and associated loss of ecosystem functions (Drewry 2006). Quality and quantity of nutrient entering waterways are determined, not only by the chemical composition of the inflows, but also the frequency, magnitude and duration of the inflows. In-lake processes such as sedimentation, re-suspension and biogeochemical cycles that regulate internal nutrient cycling can also affect the overall nutrient concentrations of the water column. It is observed and predicted that physical, chemical, and biological properties of lake are affected by continuing global warming and increasing anthropogenic activities (Carpenter et al. 2011, Tilman et al. 2002, Vörösmarty et al. 2000).

Climate change

Fossil fuel combustion and related anthropogenic activities have increased the concentrations of greenhouse gases (carbon dioxide, methane, ozone, nitrous oxide, and chlorofluorocarbons) in the atmosphere that absorb and emit radiation in the thermal infrared range. It is widely shown that increased warming related to climate change will have significant impacts on hydrologic regimes and freshwater ecosystems (Aldous et al. 2011, Adrian et al. 2009, Sahoo and Schladow 2008, IPCC 2013). Under increasing air temperatures, surface waters are warming, with global lakes having warmed at an average of 0.34 °C decade^{-1} (Sharma et al. 2015) and large lakes warmed at an average rate of 0.045 ± 0.011 °C yr^{-1} during the period of 1985-2009 (Schneider and Hook 2010).

Global mean surface temperature is projected to rise by 0.3-4.8 °C till the end of 2100 (IPCC 2013) (Fig 1.1) and the geographic distribution of the projected temperature change is non-uniform (IPCC 2013) (Fig 1.2). Africa, Europe, Poles, Northern and Central Asia are likely to warm more than the global average. The projected warming is also likely to differ according to the season, with high winter warming in northern parts of Europe and North America, and high summer warming in the southern parts of Europe and North America (Christensen et al. 2007). Australia has warmed 0.9 °C over the last century (1910-2011) and the number of record-breaking hot days per decade has increased every decade since the 1950s (Cleugh et al. 2011, Head et al. 2014). Increased frequency of warmer weather is expected with annual average temperatures of Australia expected to rise by 1-4 °C by 2100 (IPCC 2013).

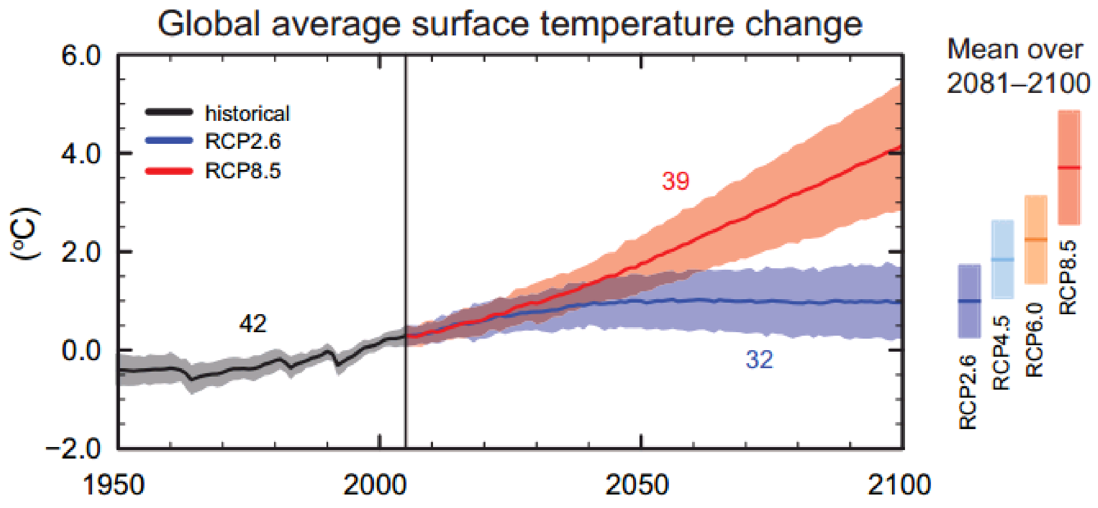

Figure 1.1 Projected global average surface temperature change till 2100 based on the lowest and highest Representative Concentration Pathways (RCP) (source: IPCC 2013, pg. 21)

Climate change directly affects freshwaters through the variability caused to precipitation and runoff and indirectly affects the thermal properties of water, leading to changes in the hydrodynamics. Climate change will alter the characteristics of precipitation, including their amount, frequency, intensity, duration and type (Trenberth et al. 2007). Similar to temperature, changes in precipitation will not be uniform. Mediterranean areas are anticipated to experience a decrease in precipitation, which can lead to longer residence times and highly stagnant water columns (de Senerpont Domis et al. 2013). On the contrary, increased precipitation is expected at mid and high latitudes and in regions with monsoon regimes (IPCC 2013). Increasing temperatures have been observed to increase heavy precipitation events over the mid-latitudes in the last half century (Trenberth et al. 2007).

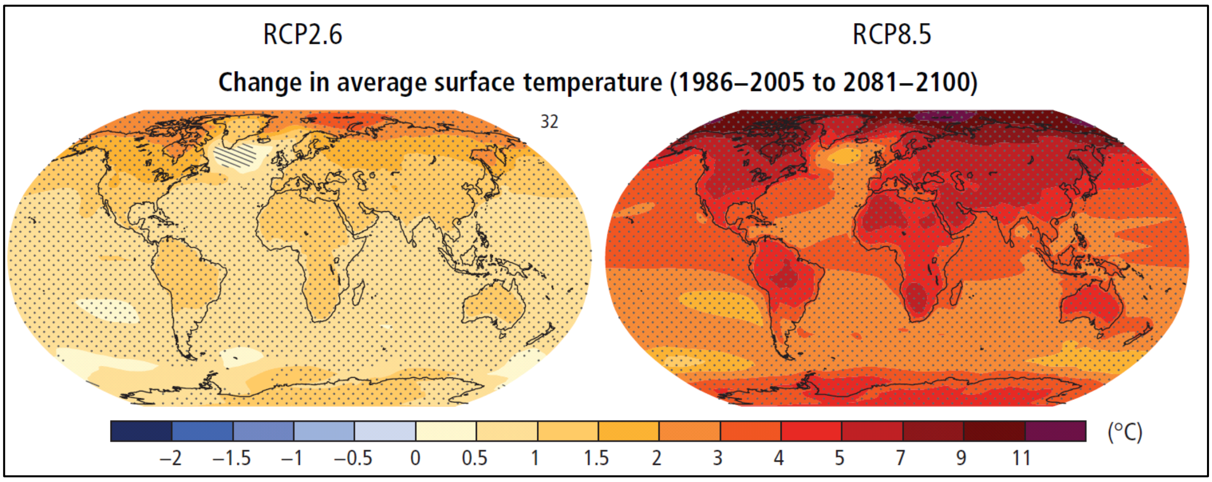

Figure 1.2 Projected surface temperature for different geographic regions based on the lowest (RCP2.6) and highest (RCP8.5) Representative Concentration Pathways (source: IPCC 2013, pg. 22)

As the driest inhabited continent on Earth, Australia is particularly susceptible to relatively minor changes in rainfall. Southwest Western Australia has recorded a steady decline in rainfall over the past 30 years, with a 15% decrease in winter rainfall since the mid-1970s (Cleugh et al. 2011). The southeast and east of Australia have experienced drying since the mid-1990s with a 61% decrease in winter rainfall (Murphy and Timbal 2008). A change in the heavy rainfalls is also observed, with a decrease in heavy rainfall in eastern Australia and an increase in Western Australia (Head et al. 2014). The regional increases and decreases in rainfall are likely to continue with the projected average changes in precipitation (IPCC 2013). In summary, Australia can experience temperature extremes with increased warm nights and heatwaves, and longer dry spells with intermittent extreme precipitation (Head et al. 2014).

Changes in precipitation are often reflected in runoff (Chiew and McMahon 2002). Alterations made to the runoff in return would affect the lake water budgets, nutrient transport, primary productivity and transparency (Stefan et al. 1993). Extreme rainfall events, especially in winter, can increase runoff generation which mobilize nutrients on land and increase the amounts of nutrients received by waters (Mooij et al. 2007, Paerl and Paul 2012, Deelstra et al. 2011). Similarly reduced rainfall and increased evaporation could lead to low runoff volumes. It is predicted that the runoff in the regions of sub-Saharan Africa, southern Europe, South America, southern Australia and western mid-latitude North America will reduce by 10-30% by 2040–60 (Milly et al. 2005). The projections for Australia show an increase in the runoff by 25% for the catchments near the north east coast and up to 35% decrease in the runoff for the catchments located in the South Australian Gulf (Chiew and McMahon 2002).

Eutrophication

Between one-third to one-half of the land's surface has been transformed by land clearing, agriculture, forestry, animal husbandry and urbanization (Smith et al. 1999). There has been a net reduction of 66.4 million ha in the global forest area during the period between 1990 and 2005 (FAO & JRC 2012). Loss of vegetation cover and the subsequent increase in impervious surface area has increased runoff into freshwaters (Chiew and McMahon 2002). Agricultural and farming practices consisting of application of fertilizers and manures, or livestock grazing have contributed additional amounts of reactive N and P, which are poorly utilized, to soils. Excess nutrients are either lost to the atmosphere (NH_3 and NOx) and/or temporarily (N), or more permanently (P), immobilized as surplus nutrient in the soil (Withers et al. 2014). These excess nutrients are transported to groundwater in percolating leachate (nitrate) and to surface waters in runoff (ammonium N, dissolved and particulate P) generated by precipitation.

Between 1960 and 1995, worldwide use of nitrogen fertilizer increased 7-fold, and phosphorus use increased 3.5-fold and both are expected to increase another 3-fold by 2050 unless there is a substantial increase in fertilizer efficiency (Tilman et al. 2002). In the United States, a reported 10 billion kg of N and 3.6 billion kg of phosphate were applied as fertilizer in 2010 (Smith et al. 2014), and significant quantities of this agricultural N and P ultimately find their way into surface waters (McDowell et al. 2004). The process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs, is termed as eutrophication (Nixon 1995). Eutrophication creates numerous problems such as increased algal blooms, reduced water quality, odour and taste changes in local freshwater systems (Kling et al. 2014, Jöhnk et al. 2008, Paerl and Huisman 2008). Above problems induce loss of a range of ecosystem functions including degradation of recreational opportunities and contaminated drinking water (Chislock et al. 2013). Dodds et al. 2009 estimated an annual cost of approximately $2.2 billion associated with damages caused by eutrophication in the U.S.

Land use changes in Australia took place during European settlement where 1.2 million km^2 or 13% of the continent was cleared for horticulture, farming and urban development (McAlpine et al. 2007, Brodie and Mitchell 2005). Clearing native vegetation for grassland and cropland has decreased the water vapour flow in the continent by 10%, which corresponds to an annual freshwater flow of almost 340 km^3 (Gordon et al. 2003). Especially in south-east and south-west Australia, groundwater tables have risen, creating large scale dryland salinity problems as a result of clearing native vegetation (McAlpine et al. 2007, Gordon et al. 2003). Export from the catchments with modified land uses resulted in altered chemical ratio of N:P, with agricultural land leading to increased P concentrations and farmlands contributing elevated N. Large scale algal blooms, such as the 1000 km long blooms of cyanobacteria on the Murray Darling river in December 1991 and 2009, were observed in Australia as a result of increased eutrophication resulting from land use changes, modified hydrologic regime and extreme precipitation events (Young et al. 1996, Ryan et al. 2009) (Fig 1.3). Phytoplankton blooms in Australian freshwaters result in economic costs between AUD 180 and 240 million every year (Atech 2000). Research following the above major event in 1991 has identified stratification and light availability, in addition to nutrients, to be major triggers of algal blooms in Australian freshwater bodies (Davis and Koop 2006).

Figure 1.3 Aerial photograph of the widespread extent of the algal bloom in the Murray Darling River in 2009 (source: Ryan et al. 2009, pg. 12)

Globally, since early 1960’s, it is been well recognised that anthropogenic activities cause substantial changes in the fluxes of N and P entering waterways from both point and non-point sources (Vollenweider 1976, Lee et al. 1978, Smith et al. 2002, Schindler 2006). With growing population and increasing demands, the severity of eutrophication in lakes, reservoirs, estuaries and rivers is increasing, especially in the developing countries like China. For instance, Lake Taihu, which is one of the largest drinking water sources in China, has been experiencing nuisance, toxic cyanobacterial blooms as a result of increased nutrient input to the lake from the surrounding watersheds consisting of urbanised and agricultural land (Xu et al. 2010). As a result, the lake has lost its ability to provide key ecosystem functions supporting fisheries, potable water and tourism, all of which have contributed to loss of economic growth.

Lakes in developed countries too have experienced similar degradation in water quality associated with cultural eutrophication. Lake Erie, the shallowest, most productive of the Great Lakes, experienced its largest harmful algal bloom in its recorded history in 2011. It was observed that severe spring precipitation events, together with long-term increasing trends in agricultural land use and practices, produced a pulse of extremely high loading of dissolved reactive phosphorus that stimulated and intensified the bloom (Michalak et al. 2013). Therefore, nutrient reduction at catchment scale maybe required to counteract the negative impacts on aquatic systems caused by the changes in the hydrologic regime and meteorological conditions resulting from climate change.

First attempts of nutrient load reduction was carried out in the early 1970s following the establishment of the Vollenweider (1976) model, which linked eutrophication to P loads and lake mean depth. Main focus was on the management of external P loading and control measures included changes to the laundry detergent formula (which contained up to 50% of P) and management of human and industrial waste (Schindler 2006). The best method for the restoration of the ecological state in small to large lakes is observed to be the drastic reduction of external nutrient loading (Jeppesen et al. 2007). Reduction in P loads has been observed to result in lowered summer mean chlorophyll concentrations in selected Danish lakes, with reduced contribution by cyanobacteria to overall algal biomass (Jeppesen et al. 2002). Re-oligotrophication of some deep lakes have also been successful, showing reduced summer chlorophyll (Jeppesen et al. 2005) and increased coexistence and higher phytoplankton diversity caused by increased heterogeneity in the water column (Pomati et al. 2012). However, nutrient reduction in some shallow eutrophic Mediterranean and sub-tropical lakes have showed decreased phytoplankton biomass but continued dominance of cyanobacteria, with changes in the slow growing filamentous cyanobacterial forms to smaller chlorococcal cyanobacteria (Romo et al. 2005, Scasso et al. 2001). Hence the success of re-oligotrophication efforts is likely to vary depending on the regional climate, retention time and depth of the lake.

In addition to cultural eutrophication, other anthropogenic activities such as construction of dams and selective water withdrawal from reservoirs can have implications for the physical structure of reservoirs and thereby, regulating the successional dynamics of biota. Changes in the outflow regime, including withdrawal rate, duration and frequency and depth at which water is extracted from a reservoir are found to result in changes in phytoplankton assemblage (Rigosi and Rueda 2012).

Direct impacts of nutrients and temperature

P and N are the most important macronutrients driving phytoplankton growth as they are required for the synthesis of cellular proteins and provide source of energy for cellular reactions (Reynolds 2006, Wetzel 2001). There is a well-established positive correlation between nutrient loading and productivity in water bodies (Vollenweider 1976, Carlson 1977, Reynolds 1984). The phytoplankton growth can be limited by one of few important nutrients, such as P, N, carbon, or silica in relation to its cellular stoichiometric ratios, but annual productivity in freshwaters is most frequently limited by P (Watson et al. 1997, Anderson et al. 2002). Optimal N:P stoichiometry for phytoplankton growth is considered to be 16:1 (atoms) following Redfield (1958), who observed the similarity between the average N:P ratio in plankton and in deep oceanic waters. However, recent studies by Klausmeier et al. 2004, have observed the optimal stoichiometry for phytoplankton growth to be species specific and to be dependent on the ecological conditions such as light and nutrient limitation.

Species specific traits together with the availability of nutrients and their distribution gradients can drive the changes in the phytoplankton composition and dominance due to resource based competition (Tilman 1982). There are noticeable interspecific differences in the cell specific rates of nutrient-uptake and in the concentrations needed to saturate them. Rate-adapted phytoplankton species are able to take up nutrients faster than others while affinity-adapted species are able to satisfy their requirements at lower external concentrations (Reynolds 1998). For instance, chlorophytes have higher nutrient requirements in comparison to cyanobacteria which influence their mutual competition along N:P gradients (Reynolds 1984). For diatoms, availability of silica (Si) and the ratios of Si:P will determine the growth and competition amongst species. Cyanobacteria can benefit from high nutrients, especially under high P concentrations, as they have luxury P storages and some species (e.g. *Anabaena*, *Aphanizomenon*) are able to fix N under N-limiting environments due to the possession of specialized cells called heterocysts. On the other hand, cyanobacteria can also dominate in low nutrient conditions due to their low nutrient requirements and high affinity for P (Reynolds 1984, Posselt et al. 2009). In general, increased nutrients in surface waters provide the required resources to support cell growth and replication of phytoplankton. This increases the capacity to increase production and maintain larger standing crops of phytoplankton, leading to the formation of blooms.

Temperature is a known major control which influences phytoplankton growth rates, nutrient stoichiometry, and spatial and temporal distribution in aquatic systems. Phytoplankton metabolic rates are controlled primarily by temperature, irradiance and carbon supply (Reynolds 1984). Additionally, temperature can also influence the interactions among phytoplankton species (Ibelings et al. 2011, Carey et al. 2012). Many cellular processes are regulated by temperature and their rates accelerate in a non-linear, exponential manner with rising temperatures, until the optimum temperatures are reached. The maximum rates of metabolic processes, including enzyme activity and nutrient uptake, increase towards the temperature optima but for the increased potential rate to be beneficial, sufficient substrate need to be present (Rhee and Gotham 1981, Staehr and Sand-Jensen 2005). Most phytoplankton species express highest metabolic rates under optimum temperatures between 25 ºC and 40 ºC, above which the rates will decline (Reynolds 1984, Robarts and Zohary 1987). Historical studies have observed cyanobacterial species such as *Microcystis* sp. to have higher optimum temperatures greater than 25 ºC (Krüger and Eloff 1978, Reynolds 1984, 2006). Therefore, it is believed that warming can selectively promote cyanobacterial growth as their growth rates may be optimized at relatively high temperatures (Paerl and Paul 2012).

However, a recent study by Lürling et al. 2013 on the temperature effects on the growth rates of eight species of cyanobacteria and eight species of chlorophytes identified that the optimum growth temperature of cyanobacteria did not vary greatly from that of chlorophytes. The mean optimum growth temperature for both of the phytoplankton groups was 29.2 ºC. A literature survey was also carried out by Lürling et al. 2013 to support their findings, which revealed the same; the optimum growth temperatures for cyanobacteria (27.2 ºC, n = 62) and chlorophytes (26.3 ºC, n = 67) are similar. Hence, it is argued that the bloom forming cyanobacterial species are likely to be benefited more from the indirect effects than from the direct impacts of warming. Alternatively, the direct impacts of temperature are likely to be synergistic with the indirect changes in other factors such as light, nutrients and wind activity (Robarts and Zohary 1987, Carey et al. 2012, Lürling et al. 2013).

Indirect effects of temperature and nutrients

The indirect effects of increasing temperatures and nutrients can lead to modifications in the thermal stability that alter the distribution of light and nutrients which impinge upon the relative competitive status of the different species. Solar radiation induces strong degree of density dependent stratification in lakes as the surface waters are heated. The density gradient is further confined by the changes in other meteorological conditions such as the air temperature and wind speed. Magnitude of stratification is dependent upon the balance between surface energy heat budget, driven by evaporation, conduction and radiation and momentum fluxes driven by wind, inflows and outflows (Fischer et al. 1979, Socolfsky and Jirka 2004, Rigosi and Rueda 2012) (Fig 1.4). An essential parameter that regulates heat distribution in lakes is water clarity, which determines how the radiation is distributed in the water column. Water clarity affects the proportion of the radiation absorbed or backscattered by suspended particles and this subsequently influences the lake-atmosphere heat fluxes (Jones et al. 2005, Heiskanen et al. 2015). Abundance and phytoplankton diversity greatly regulate the absorption and scattering of irradiance that lead to changes in the heat storage, thermal stratification and surface temperature (Jones et al. 2005, Rinke et al. 2010).

High epilimnetic heat storage contributes to strong thermal stratification in lakes, with warm surface waters overlaying the colder hypolimnion separated by the thermocline. The upper epilimnion which is well illuminated and is exposed to surface winds retain the mixed nature under stratified conditions. Hence, the phytoplankton growth results in epilimnetic nutrient depletion and high light attenuation (Reynolds 1984). The hypolimnion, on the contrary, will be stagnant and the reduced oxygen concentrations create anaerobic conditions that can lead to decomposition of organic matter and re-mineralization of inorganic matter (Hupfer and

Lewandowski 2008). Low redox potential can have severe impacts on water quality by inducing reduction of carbon dioxide to methane, sulphate to sulphide, nitrate to ammonia and Fe^{3+} to Fe^{2+}. Consequently, other nutrients such as reactive P will be immobilized and released from sediments to the water column causing increased internal nutrient loading (Nürnberg 1984, Hupfer and Lewandowski 2008).

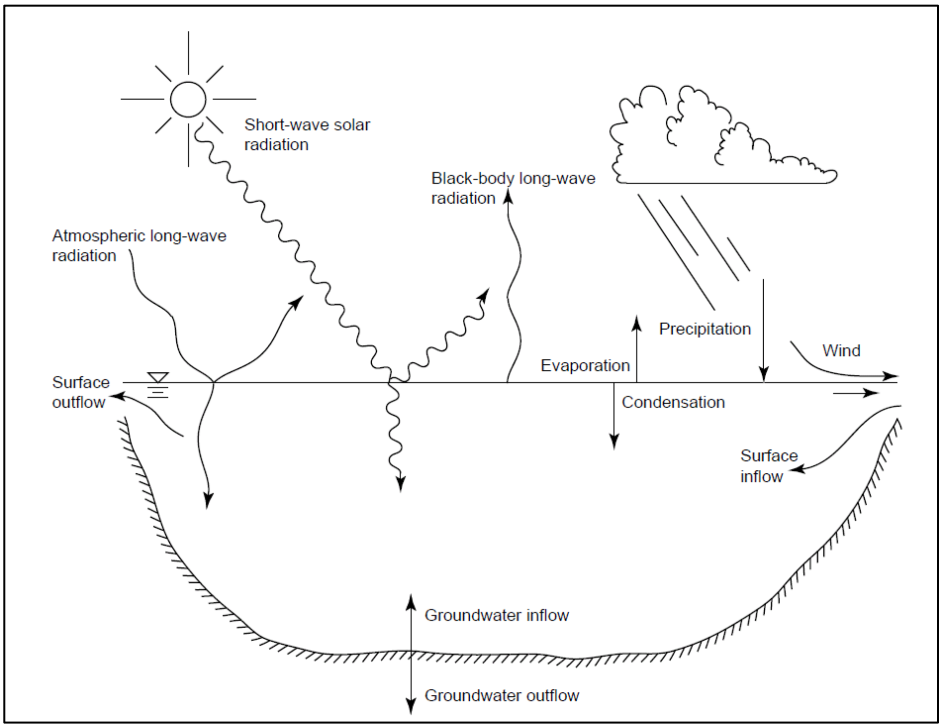

Figure 1.4 Energy input and output within a lake (extracted from Socolofsky and Jirka 2004)

Nutrient enrichment and the subsequent excessive growth of phytoplankton can increase turbidity in waters and thereby, causing light attenuation, heat entrapment and self-shading (Mazumder et al. 1990, Kumagai et al. 2000, Rinke et al. 2010). Consequently cyanobacterial blooms can modify the local environment to promote their growth by increasing water temperatures and stratification. High turbidity can also result in a shift between the macrophyte dominated state to phytoplankton dominate state due to high attenuation of light by the dissolved and particulate matter (Scheffer 1998). Cyanobacterial species possessing gas vacuoles can regulate their buoyancy, which provides them with the ability to access nutrient rich hypolimnion and illuminated surface waters (Walsby 1972, Ganf and Oliver 2000). Increasing temperatures with climate change and resulting increases in strengthened and prolonged stratification events (Adrian et al. 2009, Winder and Schindler 2004, Sahoo and Schladow 2008) are likely to favour the growth of cyanobacterial species that can migrate within the water column to gain access to primary resources (Paerl and Paul 2012, Cayelan et al. 2012).

Interactions between nutrients and temperature

The effects of temperature and nutrients individually on water quality and freshwater phytoplankton have been studied in greater extent. However, except for a few studies (e.g. Rigosi et al. 2014, Scheffer 2001, Elliott et al. 2006, Carvalho and Kirika 2003), the interactions between the two, and their effects on phytoplankton communities, remain relatively under-studied due to the difficulty in disentangling and quantifying the effects. This is challenging as implications of climate change and eutrohication are multifaceted as presented in Figure 1.5. High water temperatures result in more stable and prolonged stratification that can separate the epilimentic and hypolimnetic waters resulting in anoxic bottom waters. Low oxygen levels will not only affect the living biota, especially fish, but can also change the redox potential of P release from the sediments leading to excessive nutrient loading. Increased nutrients and warm and stratified waters can lead to excessive growth of phytoplankton which can increase turbidity, cause self-shading and modify the local environment (Mazumder et al. 2009, Kumagai et al. 2000). High turbidity can also result in a shift between the macrophyte dominated state to phytoplankton dominate state due to high attenuation of light by the dissolved and particulate matter (Scheffer 1998).

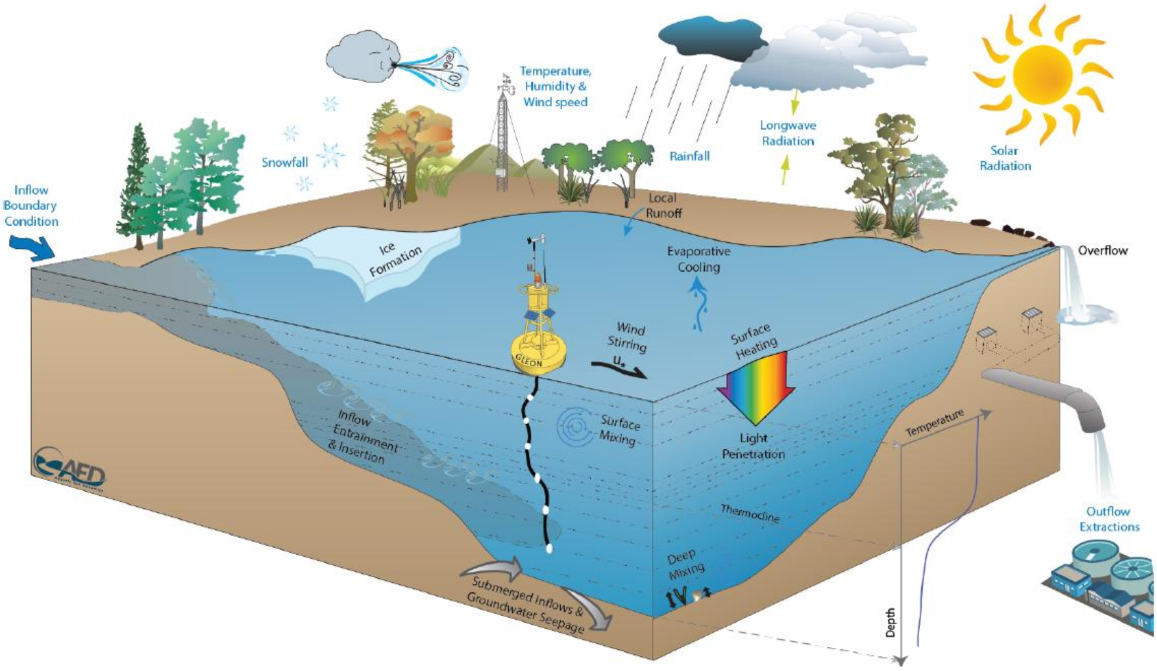

Figure 1.5 Schematic representation of the main processes in lakes and reservoirs that could be impacted by climate change and eutrophication (source: Hipsey et al. 2014)

Importance of trophic status

Trophic status is used to classify aquatic systems in relation to their nutrient concentrations, which is governed by numerous factors including lake morphometry, water residence time, local climate and the catchment characteristics (Paul et al. 2008, Carlson 1977, Nurnberg 1984). The trophic state index of a lake can be defined using turbidity (Secchi disk depth), Chlorophyll a (phytoplankton productivity or biomass) and/or using total phosphorus (TP) as proxies (Carlson 1977, Nürnberg 1984). Trophic status is divided broadly into four main classes consisting of oligotrophic (<10 µg/L), mesotrophic (10≤TP≤30 µg/L), eutrophic (30<TP≥100 µg/L) and hyper-eutrophic (TP>100 µg/L) (Nürnberg 1984). In general, shallow lakes with frequent or continuous mixing tend to be eutrophic while deep stratifying lakes tend to be more oligotrophic (Tilzer 1990). Nutrient status of the lake can affect the abiotic components such as water chemistry and transparency (light climate) and biotic components such as the phytoplankton abundance and composition. Phytoplankton species can rapidly respond to a wide range of environmental perturbations due to their fast growth rates and therefore, are often used to infer lake trophic state (Reynolds 1998). For instance, cyanobacteria are frequently found in higher abundance in eutrophic lakes than other phytoplankton (Oliver & Ganf 2000) while diatom assemblages are commonly found in oligotrophoic lakes (Reynolds 1998). Trophic status can therefore be a useful indicator of the relationships between abiotic and biotic components of aquatic systems (Reynolds 1998, Ryan et al. 2006, Paul et al. 2008).

Drivers of cyanobacterial blooms

Freshwater cyanobacterial blooms are hazardous as they not only degrade aesthetic, recreational and ecological values, but many cyanobacterial species can also produce toxins that affect animal health and produce other bioactive compounds that can change the odour and taste of drinking water. The World Health Organization (WHO) has issued an advisory limit for drinking water of 1 μg/L for toxins (e.g. microcystin) and the bioactive compounds such as geosmin can alter the taste and odour at concentrations as low as 5 μg/L. It is presumed and observed in many cases, cyanobacteria to be favoured by eutrophication and rising temperatures as they possess physiological, morphological and ecological adaptations that enable them to thrive under such environments, as discussed in the previous sections.

While water temperature is considered as one of the main drivers of phytoplankton succession, it is coincided with other variables such as thermal stability of water column, light environment and nutrient availability in (Anneville et al. 2005, Elliott et al. 2006). Variation in both temperature and nutrients place stresses on the bias selection in favour of species known for their tolerance or adaptability to these conditions, such as cyanobacteria (Reynolds 1998). However, the interactions between temperature and nutrients or the relative importance of warming climate against nutrient loading in driving cyanobacterial dynamics is still under investigation (Lürling et al. 2013, Elliott et al. 2006).

Recent studies have observed the importance of temperature in driving cyanobacterial development to be dependent upon trophic status and to vary among different cyanobacterial taxa (Rigosi et al. 2014). Oligotrophic lakes are suggested to be more sensitive to nutrient loadings while nutrient rich lakes are sensitive to temperature increases in relation to cyanobacterial dominance (Brookes and Carey 2011, Rigosi et al. 2011). However, the interactions between warming temperatures and changing nutrients are not straightforward and can differ from one lake to another depending on morphometry, regional climate and catchment characteristics (Adrian et al. 2009). For instance, in the polymictic, eutrophic Lake Müggelsee total phosphorus (TP) concentration was observed to be the principal force driving cyanobacteria contribution to total algal mass with climate-induced changes in the thermal regime, than direct temperature effects, positively influencing cyanobacteria dominance (Wagner and Adrian 2009). De Senerpont et al. (2007) carried out field mesocosm experiments and mechanistic modelling to determine the effects of different climate scenarios (warm, average, cold spring seasons) on cyanobacteria, chlorophytes and diatoms. It was observed that contribution by cyanobacteria to total biomass to be higher during warm springs, with chlorophytes being the most abundant in all three scenarios. Gallina et al. 2011 found no effect of extreme air temperatures on cyanobacterial dominance over other phytoplankton in five peri-Alpine lakes with varying trophic status extending from oligotrophic to eutrophic and mean depths of 40 m-100 m. Above studies indicate that, in addition to lake specific characteristics, interactions between different phytoplankton functional groups are important in driving the responses of aquatic systems under changing nutrients and a warming climate.

Aims and objectives

Degradation of water quality under a changing climate and rapid economic development will cause water scarcity in most regions of the world, by reducing the quality and quantity of water available for consumption (Vörösmarty, et al. 2000). The present work is an attempt to understand in detail the influence of the predicted increase in eutrophication and increasing temperatures on water quality, especially in relation to nuisance and harmful phytoplankton blooms. The study aims to disentangle individual and combined effects of changing nutrients and climate change to help determine the best management options and nutrient reduction targets that can be implemented to offset the undesirable effects of continuing climate change.

To satisfy the above aim, an open source hydrodynamic model was used to test different scenarios with varying nutrient regimes and increasing temperatures to simulate the phytoplankton dynamics in two lakes with opposing nutrient status. Additionally, field work was carried out to investigate the effects of changing environmental factors on phytoplankton development and functional trait diversity as the mixing changes from strong to weak in an eutrophic reservoir.

Three main aims that were addressed in this study are,

Chapter 2:

The effects of warmer climates and nutrient loadings on lake physical and biogeochemical processes are certainly inter-wound. This study quantified the relative impacts of nutrients and temperature on two lakes with opposing nutrient statuses (oligotrophic and eutrophic) in relation to phytoplankton dynamics of three main phytoplankton functional groups consisting of cyanobacteria, chlorophytes and diatoms. An array of scenarios with both increasing and decreasing nutrient status together with rising temperature would be modelled to gain an understanding of responses of the two lakes under changing environmental conditions.

Chapter 3:

Many studies that have looked at the impacts of climate change have only sparsely focused on the combined impacts of rising temperature and altering nutrient status on lake thermal structure. Temperature and wind driven stratification and mixing result in the vertical partitioning of dissolved oxygen, nutrients and light which influence the seasonal dynamics and vertical distribution of plankton. Especially in deep lakes, the phytoplankton growth is more or less determined by the time and the extent of stratification. In return, as part of the feedback processes, lake clarity determined by planktonic content could influence the lake thermal dynamics. This study evaluated in detail the changes in the lake heat content in relation to the onset and duration of stratification and mixing under future climate change and nutrient scenarios in a deep, oligotrophic lake. The results are assessed to determine whether nutrient management can offset the negative effects a warming climate have on the physical structure of lakes.

Chapter 4:

Changes in the thermal stability and nutrient content in lakes can be considered as potential disturbances to the system that induce changes in the biotic community. Disturbances provide intermittent fluctuations in the resources, light and nutrients, allowing an array of phytoplankton with different resource requirements to grow (Hutchinson 1957, Salmaso 2003). This study focused on the impact of short term or long term disturbances consisting of both biotic and abiotic factors on phytoplankton development and composition. It assessed in depth the changes that may occur in aquatic systems in relation to phytoplankton growth and functional diversity when transitioning from well-mixed to stratified conditions.

Approach

In light of above discussion and aims, a combination of methods consisting of modelling and field work was used in this study to evaluate the impacts of a changing climate and nutrients on phytoplankton dynamics. In Chapter 2 and 3, a 1-dimensional hydrodynamic model, General Lake Model (GLM), was used to simulate the physical processes in the two lakes. The model is composed of a layer structure which expands and contract according to the density changes occurring from heat fluxes and inflows and outflows (Hipsey et al. 2014). The hydrodynamic model is coupled with the biogeochemical code, Framework for Aquatic Biogeochemical Modelling (FABM), used for the simulation of nutrients and phytoplankton (Hipsey et al. 2013, Bruggeman and Bolding 2014). Model process equations of GLM-FABM are provided in the Appendix at the end of the thesis (pg. 145-pg. 153).

A matrix of 25 different scenarios including nutrient alterations and future temperature projections are tested for the two lakes with different nutrient scenarios. The responses relating to phytoplankton growth and composition between the two lakes are then compared and analysed to determine the relative impact of temperature and nutrients in driving the changes in the phytoplankton dynamics. Furthermore, the changes in heat budget and the subsequent impact on the thermal structure of the oligotrophic lake are also analysed in detail and the relative influence of nutrients and temperature on thermal stability is assessed using statistical measures.

Additionally, intensive, periodic water sampling twice every week was carried out in an eutrophic reservoir during the transition period between spring to summer to assess the implications of water column stability and mixing on phytoplankton dynamics. The seasonal transition period is characterised by changes that occur over varying temporal scales and intensities. The influence of the nature, frequency and intensity of disturbance on overall phytoplankton succession and selection was assessed in Chapter 4. Further to the assessment of changes in the taxonomic composition of phytoplankton, especial attention was paid to the variation in functional diversity and the influence of external disturbance on regulating the coexistence amongst phytoplankton species with different functional traits.

Chapter 2 Vulnerability of oligotrophic lakes to impacts of nutrients and temperature

Phytoplankton growth, abundance and succession in freshwater lakes are strongly influenced by temperature and nutrients (Reynolds 2006). Increasing temperatures associated with climate change will therefore influence phytoplankton diversity, competition and total biomass (Anneville et al. 2002, Elliott et al. 2006, Gerten and Adrian 2002). Nutrients and temperature strongly interact to influence phytoplankton growth (Rigosi et al. 2014), and the strength of this interaction varies with lake trophic status and is specific to lake morphometry, local geology and climate (Adrian et al. 2009, Anneville et al. 2005). Due to the impact of phytoplankton on water quality, it remains imperative to understand the interactions between temperature and nutrients in driving phytoplankton dynamics under future plausible conditions.

Global mean air temperatures are projected to increase between 2.5 and 4 °C by 2100 (IPPC 2013). Lakes have warmed as atmospheric temperatures have increased (O'Reilly et al. 2015, Sharma et al. 2015, Schneider and Hook 2010). Temperature directly affects phytoplankton metabolic processes related to growth and photosynthesis (Robarts and Zohary 1987) and elevated temperatures favour certain phytoplankton taxa, such as cyanobacteria, which have optimum growth rates at higher temperatures than other species (Paerl and Paul 2012). Higher temperatures can also affect phytoplankton indirectly by changing thermal stratification, which can alter the mixing and underwater light climate that cells experience (Straile et al. 2003, Tirok and Gaedke 2007, Winder and Sommer 2012). The nutrient status of a lake not only directly affects algal growth through resource dependence but also indirectly influences the availability of other resources such as light (Reynolds 1998, Smith 1986, Tilman et al. 1982, Vollenweider 1976). Nutrient inputs support growth of algae which then modify the light climate through absorption and scattering, while increasing heat trapping in surface waters and intensifying stratification (Brookes and Carey 2011, Kumagai et al. 2000). Increased stratification can then restrict upward flux of nutrients (Livingstone 2003, O'Neil et al. 2012) whilst simultaneously increasing duration of anoxic conditions in the hypolimnion and increasing internal nutrient loading (Jensen and Andersen 1992, Søndergaard et al. 2003).

Different phytoplankton groups possess eco-physiological adaptations that enable them to thrive in certain habitats (Reynolds et al. 2002). For example, surface-blooming cyanobacteria gain a competitive advantage over other species under stratified conditions, facilitated by gas vesicles, which enable them to regulate their buoyancy and access favourable light and nutrient environments (Brookes and Ganf 2001, Ganf and Oliver 1982, Walsby 1972). High densities of cyanobacteria pose a health risk as they may produce toxins (Carmichael 2001) and also incur high economic costs associated with the production of tastes and odours and the disruption of recreational access to water bodies (Brookes and Carey 2011, Dodds et al. 2009). Taxa that have higher nutrient requirements (e.g., chlorophytes) have the ability to exploit nutrient-enriched conditions, allowing them to dominate under eutrophic conditions (Reynolds 1998). Certain other taxa (e.g., bacillariophytes) require turbulence for re-suspension and tend to have lower temperatures for optimal growth. Thus relationships amongst phytoplankton taxa and environmental drivers are complex, multi-faceted and require more understanding how they are impacted by global change. Disentangling the interactions amongst climate, nutrients and phytoplankton in lakes of different trophic status would allow implementation of effective nutrient reduction targets that could counteract the effects of rising temperatures, including the development of cyanobacterial blooms.

The aim of this study is to examine the dynamic responses and interactions of different phytoplankton groups (cyanobacteria, chlorophytes and diatoms) to temperature and nutrients in two lakes of different trophic status. Mt Bold (South Australia) is a hyper-eutrophic, highly turbid reservoir supporting high mean phytoplankton biomass, while Lake Tarawera (New Zealand) is a meso-oligotrophic, clear lake that has low phytoplankton biomass. We hypothesised that competition between phytoplankton groups under a warming climate would be influenced by differences in the trophic status of the two lakes. To evaluate this hypothesis, a coupled one-dimensional (1D) biogeochemical hydrological model (GLM-FABM) was used to explore how the phytoplankton community might respond to changes in nutrient loading and air temperature. A matrix of 20 scenarios was generated with air temperature increased by 1, 2, 3, 4 °C from a 'base' case (i.e., current climate), as guided by IPCC predictions, and nutrient loads increased and decreased by 10 or 20 times from the base case (current nutrient loading) in order to explore the impacts on phytoplankton dynamics and lake trophic status. The modelled results were used to assess the individual and interactive roles of nutrients and temperature in influencing phytoplankton dynamics in two lakes of different trophic state.

Methods

Modelling approach

Lake hydrodynamics were simulated using the General Lake Model (GLM) (Hipsey et al. 2014), which is a dynamic (time-varying), open source, 1D-hydrodynamic model that simulates water transport and vertical stratification. GLM has been used to accurately predict surface temperatures and capture mixing and stratification events in a large number of temperate lakes (Read et al. 2014). GLM was coupled with the Aquatic Ecodynamics (AED) modules within the Framework for Aquatic Biogeochemical Model (FABM; Hipsey et al. 2013, Bruggeman and Bolding, 2014) to simulate the biogeochemical and ecological dynamics of the ecosystem. The GLM-FABM-AED model approach and parameters are similar to DYRESM-CAEDYM (Hamilton and Schladow 1997, Imberger and Patterson 1981, Romero et al. 2004a) which has been applied to lakes across the globe (Gal et al. 2009, Kara et al. 2012, Rigosi et al. 2011). The algorithms used to model the hydrodynamic components in GLM are similar to the ones used in other commonly used 1D models that have been successfully applied to lakes across the world (Hamilton and Schladow 1997, Gal et al. 2009, Kara et al. 2012, Rigosi et al. 2011).

Phytoplankton model

Phytoplankton productivity is simulated for each of the phytoplankton group and is dependent upon maximum potential growth at 20 °C and limitation by light, phosphorus, nitrogen and silica (Hipsey et al. 2013).

$$f_{uptake}^{PHY_{ca}} = R_{growth}^{PHY_a} \quad \left(1 - k_{pr}^{PHY_a}\right) \quad \phi_{tem}^{PHY_a}(T) \quad \phi_{str}^{PHY_a}(T)\ldots$$

$$\ldots \min\left\{\phi_{light}^{PHY_a}(I),\ \phi_{N}^{PHY_a}\left(NO_3, NH_4, PHY_{N_a}\right),\ \phi_{P}^{PHY_a}\left(PO_{4,}PHY_{P_a}\right),\ \phi_{Si}^{PHY_a}(R_{Si})\right\} \qquad \text{Equation 1}$$

Where $R_{growth}^{PHY_a}$ is the maximum growth rate at 20 °C, $\left(1 - k_{pr}^{PHY_a}\right)$ is the photorespiratory loss, $\phi_{tem}^{PHY_a}(T)$ is the temperature scaling, $\phi_{str}^{PHY_a}(T)$ is the metabolic stress and 'min' expressions represent limitation by light, nitrogen, phosphorus and silica respectively.

A temperature function as described below is used to account for the reduced growth at non-optimal temperatures, with maximum productivity occurring at the optimum temperature T_{opt}, productivity decreasing to zero at the maximum temperature T_{max} and productivity following a simple Arrhenius scaling formulation below standard temperature T_{std}.

$$\Phi_{tem}^{PHY_a}(T) = \vartheta_a^{T-20} - \vartheta_a^{k[T-c1_a]} + c0_a \qquad \text{Equation 2}$$

where $c1_a$ and $c0_a$ are solved numerically given input values of T_{std}, T_{opt} and T_{max}.

Light limitation on phytoplankton growth is computed as below and can be modelled as photoinhibited (Eqn. 3, used for chlorophytes) or non-photoinhibited (Eqn. 4, used for cyanobacteria and diatoms).

$$\Phi_{light}^{PHY_a}(I) = 1 - e^{\left(-\frac{I}{I_{k_a}}\right)} \qquad \text{Equation 3}$$

$$\Phi_{light}^{PHY_a}(I) = \frac{I}{I_{S_a}} e^{\left(1-\frac{I}{I_{S_a}}\right)} \qquad \text{Equation 4}$$

Phytoplankton productivity is limited by the availability of N and P and is based on the internal stoichiometry. Internal N and P stores related to the dynamic nutrient uptake (given below) are calculated using the Droop model (1974) (Eqn. 5 and Eqn. 6).

$$f_{uptake}^{PHY_{N_a}} = R_{NUptake}^{PHY_a} \Phi_{tem}^{PHY_a}(T) \left\{ \Phi_N^{PHY_a} \frac{\left(\frac{[PHY_{N_a}]}{[PHY_{C_a}]} - x_{NMIN}^{PHY_a}\right)}{\left(x_{NMAX}^{PHY_a} - x_{NMIN}^{PHY_a}\right)} \right\} \qquad \text{Equation 5}$$

$$f_{uptake}^{PHY_{P_a}} = R_{PUptake}^{PHY_a} \Phi_{tem}^{PHY_a}(T) \left\{ \Phi_P^{PHY_a} \frac{\left(\frac{[PHY_{P_a}]}{[PHY_{C_a}]} - x_{PMIN}^{PHY_a}\right)}{\left(x_{PMAX}^{PHY_a} - x_{PMIN}^{PHY_a}\right)} \right\} \qquad \text{Equation 6}$$

Site description, model set-up and data availability

Mt Bold (MB) - Mount Bold Reservoir is located in the Mount Lofty Ranges in South Australia. It is classified hyper-eutrophic reservoir according to the classification of (Carlson 1977, Nürnberg 1996) with high dissolved organic and particulate matter (Oliver 1981). It has a mean and maximum depth of 25.4 m and 47 m, respectively, a capacity of 0.046 km^3 and a surface area of 3.1 km^2 (Fig 2.1). Model simulations for Mt Bold were conducted with meteorological and hydrological inputs for the period 1 January 2003 to 5 May 2006. The daily meteorological data were collected from a station on the reservoir surface. The simulation included two inflows, Echunga Creek and Onkaparinga River, the latter being the major contributor. Outflows were either from overtopping at the crest level or at an outlet approximately 4 m above the reservoir bottom. Temperature and dissolved oxygen were monitored at least monthly and were used for model calibration and validation.

Nutrients (TP, TN, ammonium, nitrite and nitrate, filterable reactive phosphorus (FRP)), and chlorophyll *a* were measured monthly from surface samples collected at the deepest site of the reservoir, adjacent the dam wall. Phytoplankton cell abundance, measured as 5 m surface integrated samples, were converted to biomass using biovolumes and carbon content per cell, and carbon to volume relationship from the literature (Menden-Deuer and Lessard 2000). The three dominant phytoplankton groups (chlorophytes, diatoms, cyanobacteria) were simulated using group-specific parameters (Table 1).

Tarawera – Lake Tarawera is located in the Central Volcanic Plateau of North Island, New Zealand, occupying part of the Haroharo Caldera (Fig 2.1). It is a deep, monomictic, meso-oligotrophic lake, with a mean and maximum depth of 56 m and 88 m, respectively, a volume of 2.3 km^3 and a surface area of 41.4 km^2. Simulations were conducted for the period 1 January 2003 to 12 February 2006. Meteorological data for this period were obtained from Rotorua Airport meteorological station located approximately 9 km from the lake. A correction factor was applied for wind speed measurements based on meteorological data collected using a lake buoy for a limited time period between 2009 and 2012. Four inflows were included in the simulation, representing rain, cold-water streams, geothermal streams and ungauged inputs. For each inflow the daily volume, temperature, salinity and nutrient concentrations were estimated based on observations from 20 different monitoring sites located around the lake (Hamilton et al. 2006). A single outflow was simulated in order to represent the Tarawera River. No high frequency water temperature data were available for the model calibration and validation, hence discrete (monthly) temperature data at different depths of the water column (0 to 83 m at 1 m intervals) were used for this purpose.

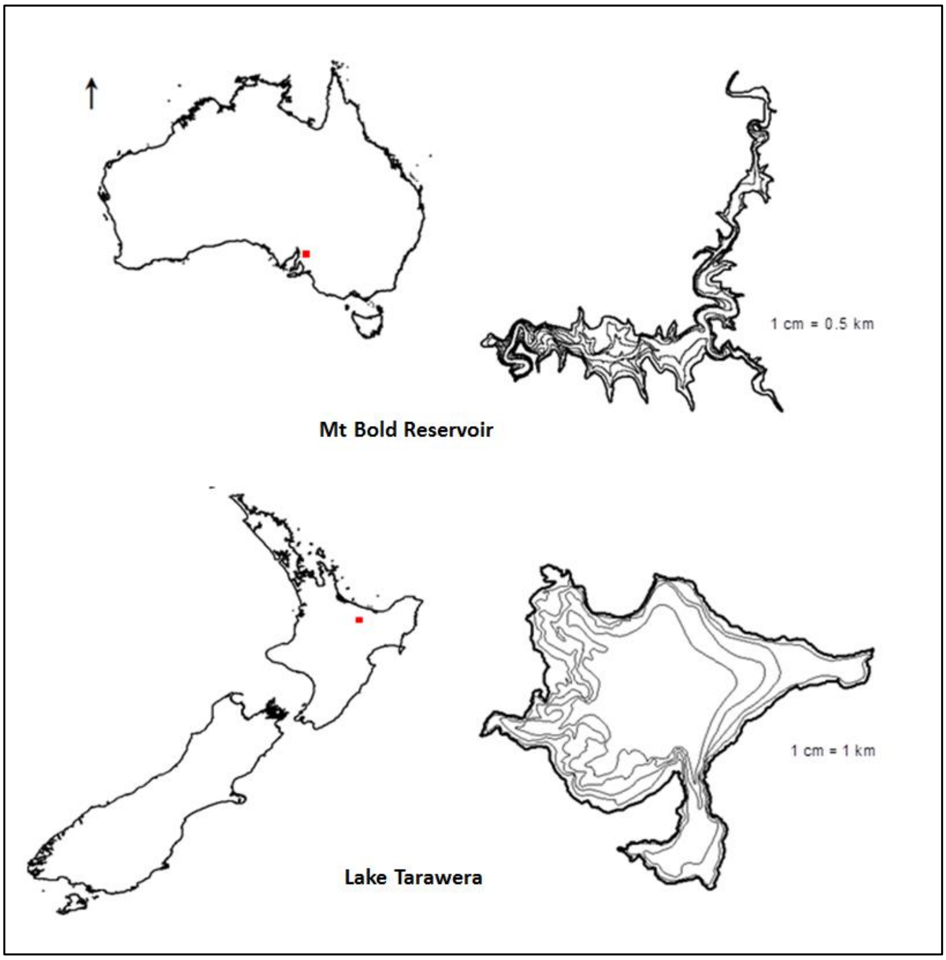

Figure 2.1 Location and bathymetry of Mt Bold Reservoir and Lake Tarawera with contour lines every 10 m and 20 m respectively

Other variables measured monthly and used for validation included: dissolved oxygen, measured from 0 to 83 m at 2 m intervals; nutrients sampled at three depths (0, 30 and 65 m); and chlorophyll-a integrated over a surface layer (0 to 17 m depth). Information about presence/absence of some phytoplankton groups at different depths was available from a previous study (Hamilton et al. 2010). Phytoplankton cell count data were sparse but when available, the carbon content per cell of the most abundant species observed in Tarawera was calculated as above, guided by Menden-Deuer and Lessard (2000). Similar to Mt Bold, three phytoplankton groups, consisting of chlorophytes, diatoms, cyanobacteria, were simulated.

Model calibration and validation

The calibration period for Mt Bold Reservoir was two years from 1 Jan 2003 to 31 Dec 2004, while the validation period was from 1 Jan 2005 to 31 May 2006. For Lake Tarawera, the calibration period was from 1 Jan 2003 to 31 Dec 2004 and the validation from 1 Jan 2005 to 12 Feb 2006.

Model calibration parameters related to surface heat exchange and mixing efficiency were adjusted within a range of plausible values (Imberger and Patterson 1981) to improve comparisons of simulated temperature to measured values. Parameters controlling nutrient dynamics were then adjusted within the range of literature values (Gal et al. 2009, Hamilton and Schladow 1997, Romero et al. 2004b). A set of parameters for the three phytoplankton groups was developed from literature values (Table 2.1), with manual calibration as specified below, which was used to fine-tune the fit of simulated biomass to observations. Higher growth rates, nutrient uptake rates and loss rates (mortality and respiration) were specified for chlorophytes relative to cyanobacteria as determined by both experimental (Lürling et al. 2013) and modelling studies (Burger et al. 2008, Gal et al. 2009, Trolle et al. 2011). Phytoplankton groups were calibrated manually one group at a time, starting with the most abundant. Zooplankton grazing was not represented explicitly in the model but a phytoplankton mortality parameter was increased to represent grazing effects. Model performance was assessed based on both (a) visual inspection, plotting each state variable against the observed data ('chi by eye') and (b) quantification of model goodness of fit, calculating the Root Mean Squared Error (RMSE) (Beven 2012, Rigosi et al. 2010) and estimating the coefficients of determination (r^2) (Trolle et al. 2011, Gal et al. 2009) for both calibration and validation periods. RMSE was calculated as

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}\left(X_{mod,i} - X_{obs,i}\right)^2}$$

where $X_{mod,i}$ and $X_{obs,i}$ are the ith modelled and observed values, respectively, and n is the number of observations. Iterative manual calibration was used to minimise RMSE and improve r^2 in a stepwise manner.

Scenarios

The calibrated model was used to run scenarios consisting of factorial combinations of temperature and nutrient changes (Table 2.2). Following IPCC projections, daily air temperatures were increased by +1 to +4 °C at 1 °C intervals. With similar increase in temperatures expected in surface waters generally (Schneider and Hook 2010), inflow temperatures (excluding those for groundwater and rainfall) were also increased as above. The filterable reactive phosphorus (FRP) concentrations of the inflows were increased or decreased by a factor of 10 or 20 times in order to ensure a change in TP great enough to shift the lake into a different trophic status. No changes were made to other components of TP. Trophic status classification was based on TP concentrations (Nürnberg 1996); oligotrophic (<10 µg/L), meso-oligotrophic ($10 \leq TP \leq 30$ µg/L), eutrophic ($30 < TP \geq 100$ µg/L) and hyper-eutrophic ($TP > 100$ µg/L). Nitrate (NO_3) concentrations were increased relative to the FRP concentrations using the Redfield molar ratio of 16:1 to guide the level of increased based on FRP. No changes were made to other components of TN as they constituted to be minor components of the total TN load.

Table 2.1 Group-specific phytoplankton parameters

					Chlorophytes		**Cyanobacteria**		**Diatom**	
Parameter	**Unit**	**Chlorophytes**	**Cyanobacteria**	**Diatom**	Literature Min	Literature Max	Literature Min	Literature Max	Literature Min	Literature Max
Growth Rate	/day	1.20	0.70	1.80	0.80[i]	2.70[ii]	0.60[iii]	0.70[ii]	1.80[v]	3.60[ii]
Temperature multiplier for growth	no units	1.08	1.10	1.06	1.06[iii]	1.14[iv]	1.05[iii]	1.14[iv]	1.06[v]	1.08[ii]
Standard temperature	˚C	20.00	22.00	14.00	12.00[v]	20.00[ii]	19.00[iii]	24.00[ii]	12.00[v]	14.00[vi]
Optimum temperature	˚C	25.00	28.00	17.00	23.00[v]	28.00[iii]	26.00[iii]	28.00[v]	15.00[ii]	23.00[v]
Maximum temperature	˚C	35.00	40.00	24.00	30.00[v]	35.00[ii]	34.00[iii]	40.00[vii]	22.00[ii]	30.00[v]
Saturating light intensity	μmol/m^2/s	40.00	150.00	5.00	10.00[v]	400.00[ii]	150.00[ii]	200.00[v]	10.00[v]	200.00 [v]
Phytoplankton respiration/metabolic loss rate	/day	0.05	0.03	0.08	0.05[iv]	0.12[v]	0.05[v]	0.06[ii]	0.05[iv]	0.12[v]
Temperature multiplier for respiration	no units	1.09	1.1	1.09	1.05[v]	1.14[iv]	1.05[iii]	1.14[iv]	1.06[v]	1.14[iv]
Half-saturation concentration of nitrogen	mg N/L	0.03	0.02	0.03	0.03[ii]	0.05[v]	0.02[iii]	0.08[ii]	0.02[iv]	0.05[ii]
Minimum internal nitrogen concentration	mg N/mg Chla	1.40	2.01	2.01	1.35[viii]	2.00[iii]	1.00[ii]	4.00[iii]	1.49[iv]	2.00[v]
Maximum internal nitrogen concentration	mg N/mg Chla	9.47	7.00	7.00	4.50[v]	9.00[iii]	2.40[ii]	9.00[iii]	4.50[v]	6.00[ii]
Maximum nitrogen uptake rate	mg N/mg Chla/day	4.81	2.33	4.67	2.00[iii]	5.20[vi]	1.50[v]	4.80[ii]	3.00[v]	6.00[ii]
Half-saturation concentration of phosphorus	mg P/L	0.003	0.002	0.005	0.003[iv]	0.025[iii]	0.002[ii]	0.006[v]	0.005[ii]	0.01[v]
Minimum internal phosphorus concentration	mg P/mg Chla	0.30	0.52	0.36	0.25[iii]	0.99[iv]	0.20[iii]	0.50[v]	0.25[v]	0.36[ii]
Maximum internal phosphorus concentration	mg P/mg Chla	0.98	1.99	1.03	0.99[iv]	2.00[iii]	2.00[ii]	4.00[iii]	1.30[v]	2.40[ii]
Maximum phosphorus uptake rate	mg P/mg Chla/day	0.50	0.35	1.03	0.25[iii]	1.00[v]	0.30[v]	0.50[iii]	1.00[v]	16.00[ii]
Settling rate	m/day	0.0	1.0	0.2	-	-	-	-	-	-

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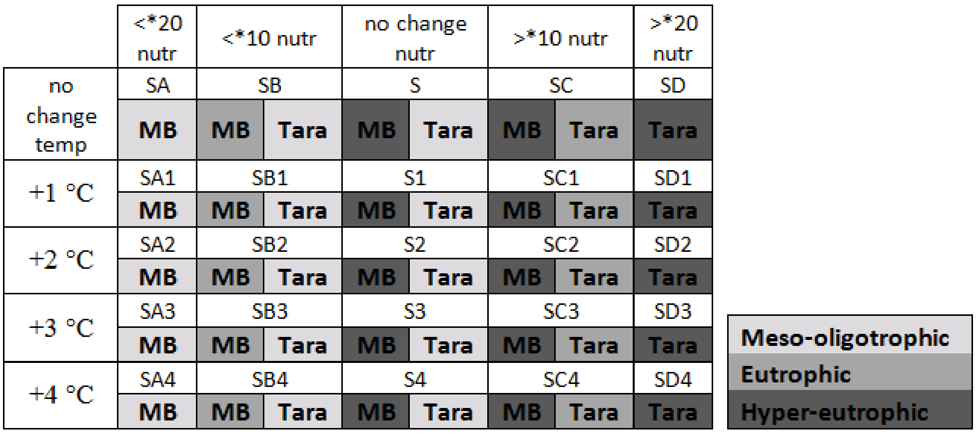
Table.2.2 Matrix of the temperature (temp) and nutrients (nutr) scenarios simulated with the GLM-FABM model for Mt Bold (MB) and Lake Tarawera (Tara). <*20 nutr and <*10 nutr refer to a decrease in nutrients by 20 and 10-fold, respectively while >*10 nutr and >*20 nutr refer to an increase in nutrients by 10 and 20 fold, respectively. Different shades of grey show the changes in the trophic status associated with the respective nutrient alterations. Scenario S (no change in nutrients and temperature) represents the base case



	<*20 nutr	<*10 nutr		no change nutr		>*10 nutr		>*20 nutr
no change temp	SA	SB		S		SC		SD
	MB	MB	Tara	MB	Tara	MB	Tara	Tara
+1 °C	SA1	SB1		S1		SC1		SD1
	MB	MB	Tara	MB	Tara	MB	Tara	Tara
+2 °C	SA2	SB2		S2		SC2		SD2
	MB	MB	Tara	MB	Tara	MB	Tara	Tara
+3 °C	SA3	SB3		S3		SC3		SD3
	MB	MB	Tara	MB	Tara	MB	Tara	Tara
+4 °C	SA4	SB4		S4		SC4		SD4
	MB	MB	Tara	MB	Tara	MB	Tara	Tara

Meso-oligotrophic
Eutrophic
Hyper-eutrophic

Model outputs considered for the assessment included: surface temperature (temp), nitrate (NO_3-N), FRP, chlorophyll *a* (TCHLA), chlorophytes (green), diatoms (diatom), cyanobacteria (cyano) represented by equivalent chlorophyll *a* concentration, euphotic depth (Zeu), TP and TN. The effects of the nutrient scenarios on the phytoplankton community were undertaken both with and without temperature change, focusing on total chlorophyll *a* and phytoplankton taxa represented by contributions to chlorophyll *a*.

Scenario results were analysed using several methods; calculating percentage abundance of the three selected phytoplankton taxa and phytoplankton biomass (TCHLA) integrated over the depth of the surface mixed layer over the simulation period. Additionally, limitation by the primary resources, light, temperature and nutrients, on regulating the growth of the three phytoplankton groups were assessed using model diagnosed limitation functions. The resulting output is presented in two forms; as time series variation for selected scenarios and by using the averages of the two years to compute the half year means for summer-autumn (January-June) and winter-spring (July-December) periods for all scenarios.

Results

Model performance

Modelled surface water temperatures and water column temperatures agreed well with the observed records with r^2>0.90 (Table 3). GLM captured the timing and duration of thermal stratification and mixing events in both lakes (Appendix Fig 2.1 (Tarawera) and Fig 2.2 (Mt Bold)). Tarawera has higher winter temperatures and lower summer surface temperatures, ranging between 10-12 °C and 18-22 °C, respectively while Mt Bold ranged between 8-10 °C and 22-24 °C, respectively. The surface temperatures in both Tarawera and Mt Bold were on average slightly under-predicted by the model, with mean differences (± standard deviation) of -0.4 ± 0.5 °C and -0.2 ± 1.5 °C, respectively. Surface temperatures in both lakes increased in a linear manner with increasing air and inflowing water temperature (shown in Chapter 3). Mt Bold also experiences a shallower thermocline depth (<10m) compared to Tarawera, which has a deeper thermocline at ~20 m mostly due to its transparency and low temperatures. The thermocline depths were well predicted by the model with the variation between the simulated and observed temperature profiles being less than 1.5 °C (Table 2.3). Further details on the calibrated and validated results for temperature, nutrients and phytoplankton are presented in the Appendix (Chapter 2).

Table 2.3 Root Mean Square Error (RMSE) and coefficient of determination (r^2) values estimated for the comparison between model simulations and field measurements of surface (surf) (depth integrated 0-17m for Tarawera, 0-1.6m for Mt Bold) and of the water column (prof) for temperature, dissolved oxygen (DO), filterable reactive phosphorus (FRP), nitrate (NO_3), total phosphorus (TP), total nitrogen (TN), total chlorophyll-a (TCHLA) chlorophytes (chloro), diatoms (diatom), cyanobacteria (cyano). Field profile measurements of temperature and DO were only available for both lakes.

	RMSE				r^2			
	Tarawera		Mt Bold		Tarawera		Mt Bold	
	Calib.	Valid.	Calib.	Valid.	Calib.	Valid.	Calib.	Valid.
Temperature (surf) (°C)	0.651	0.703	1.499	1.244	0.989	0.990	0.930	0.957
Temperature (prof) (°C)	0.773	0.786	1.337	1.078	0.980	0.987	0.953	0.946
DO (surf) (mg/L)	0.905	0.899	1.844	2.083	0.652	0.923	0.469	0.422
DO (prof) (mg/L)	0.929	0.886	2.134	2.255	0.651	0.910	0.739	0.749
FRP (mg/L)	0.004	0.004	0.011	0.014	0.043	0.012	0.645	0.136
NO3 (mg/L)	0.002	0.002	0.120	0.292	0.047	0.148	0.688	0.089
TP (mg/L)	0.007	0.007	0.112	0.192	0.157	0.363	0.231	0.272
TN(mg/L)	0.017	0.040	0.296	0.286	0.423	0.477	0.698	0.666
TCHLA (µg/L)	1.247	0.929	3.417	2.188	0.306	0.304	0.006	0.003
Chloro (µg/L)	-	-	3.148	1.500	-	-	0.106	0.101
Diatom (µg/L)	-	-	1.446	1.300	-	-	0.205	0.100

Cyano (µg/L)	-	-	0.744	0.387	-	-	0.274	0.154

Scenario Analysis

Total chlorophyll-a (TCHLA) increased almost 3-fold in Lake Tarawera and 2-fold in Mt Bold, under the highest levels of nutrient enrichment and temperature increase (Fig 2.2). An increase in nutrients alone produced a notable rise in TCHLA relative to the base conditions in Lake Tarawera compared to Mt Bold. Under its original oligotrophic state, summer TCHLA in Lake Tarawera showed little or no change under warming temperatures in relation to the base case. However, as nutrients were increased from 10 to 20 folds, summer TCHLA approximately doubled. In hyper-eutrophic Mt Bold, increase in temperature without a change in nutrients (see S1-S4 scenarios) caused a notable increase in TCHLA. A decrease in nutrient inputs had little effect on the total algal biomass in Lake Tarawera but in Mt Bold, it prevented the increase in TCHLA which would otherwise have occurred under high temperatures. Under high nutrient scenarios, the effect of temperature increase of 1-2 °C on TCHLA is similar in both of the lakes, indicating that high nutrients had a stronger effect on phytoplankton under intermediate temperature rises of 1-2 °C. There was a noticeable advance in the summer TCHLA peak in both Lake Tarawera and Mt Bold under the 3 and 4 °C increase scenarios and is more pronounced under the highest nutrient scenario. The corresponding summer biomass peak, under a temperature rise of 4 °C, advanced by about 4.5 months (from March 2004 to mid-October 2003) in Lake Tarawera and by 2.5 months (from April 2004 to mid-Jan 2004) in Mt Bold.

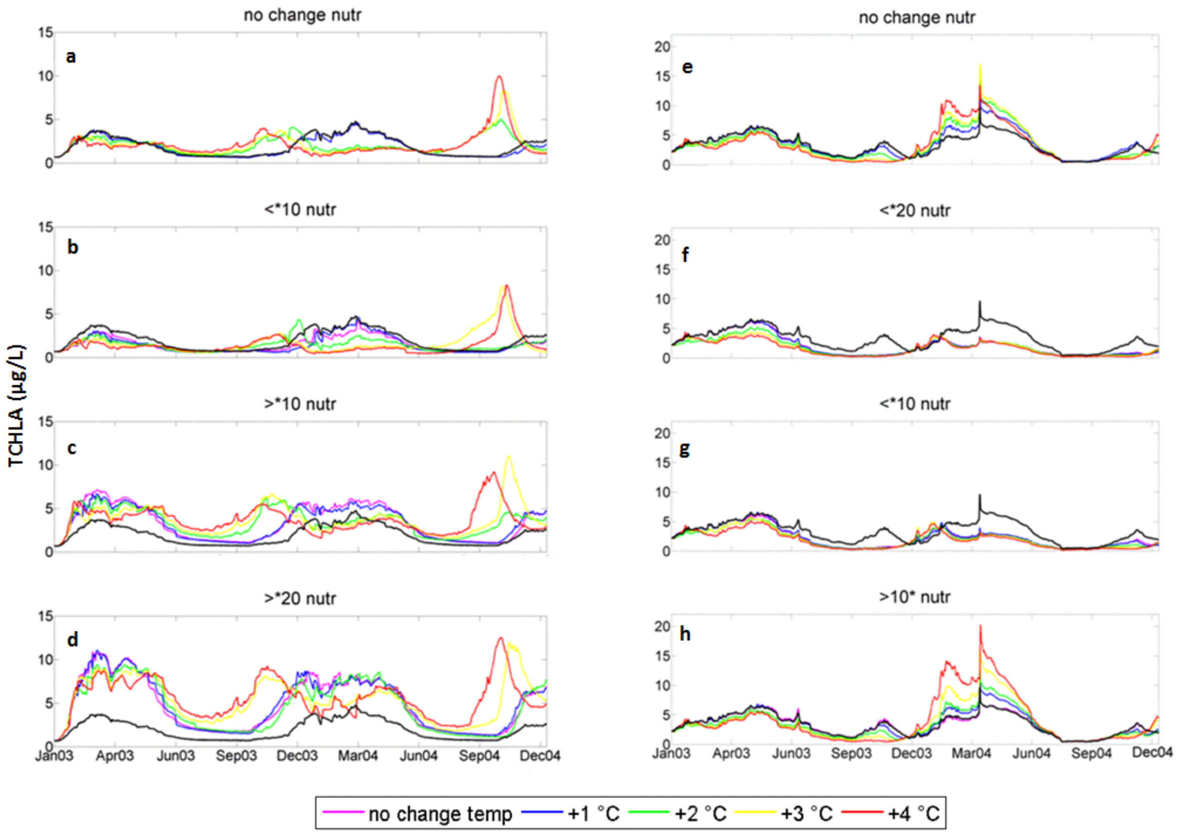


Figure 2.2 Total Chlorophyll-a (TCHLA, µg/L) under different scenarios of nutrient loading in Lake Tarawera (left, a-d) and Mt Bold (right, e-h). Black line refers to the base condition. >* refer to increase and <* decrease by 10 and 20 folds.

The observed phytoplankton community in Lake Tarawera is generally represented by chlorophytes and cyanobacteria (average 50-60%) in summer and by chlorophytes and diatoms (~40%) in winter-spring. Under the low-nutrient scenario, cyanobacteria thrived and became dominant in Lake Tarawera, as observed in scenarios SB - SB4 (Fig 2.3) but were outcompeted by chlorophytes when nutrients increased. Cyanobacteria also thrived under increase temperature scenarios under all tested nutrient loadings, with the most marked increase (both abundance and duration) being observed under decreased nutrients. However, the highest relative abundance of cyanobacteria was seen under intermediate rise in temperature (2-3 °C), for the low nutrient levels (10-fold reduction). A large diatom peak was observed in the second simulation year under scenarios of a temperature increase of 3 and 4 °C (Fig 2.3 and Fig 2.4).

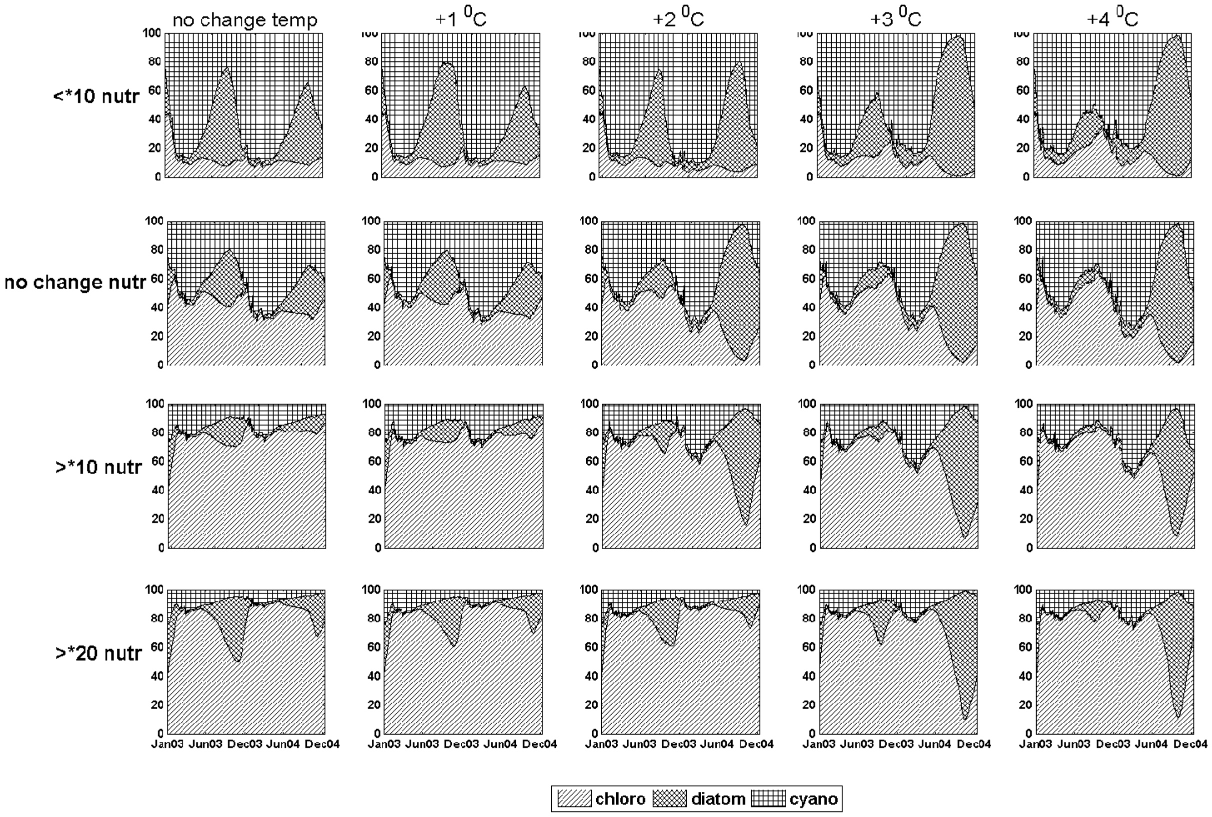


Figure 2.3 Percentage abundance of chlorophytes (chloro), diatom and cyanobacteria (cyano) under different nutrient loading and air temperature increase scenarios in Lake Tarawera

Phytoplankton in Mt Bold under base conditions consisted mostly (>80%) of chlorophytes during summer and diatoms during winter-spring (Fig 2.4). Chlorophytes were dominant in all the scenarios, under both nutrient enriched and depleted conditions. While chlorophyte and diatom compositions decreased under the reduced nutrients, cyanobacterial abundance rose to 3-10% when the nutrients were reduced by 20 fold. Diatom growth increased with increasing nutrients but decreased under the low nutrient and high temperature scenarios.

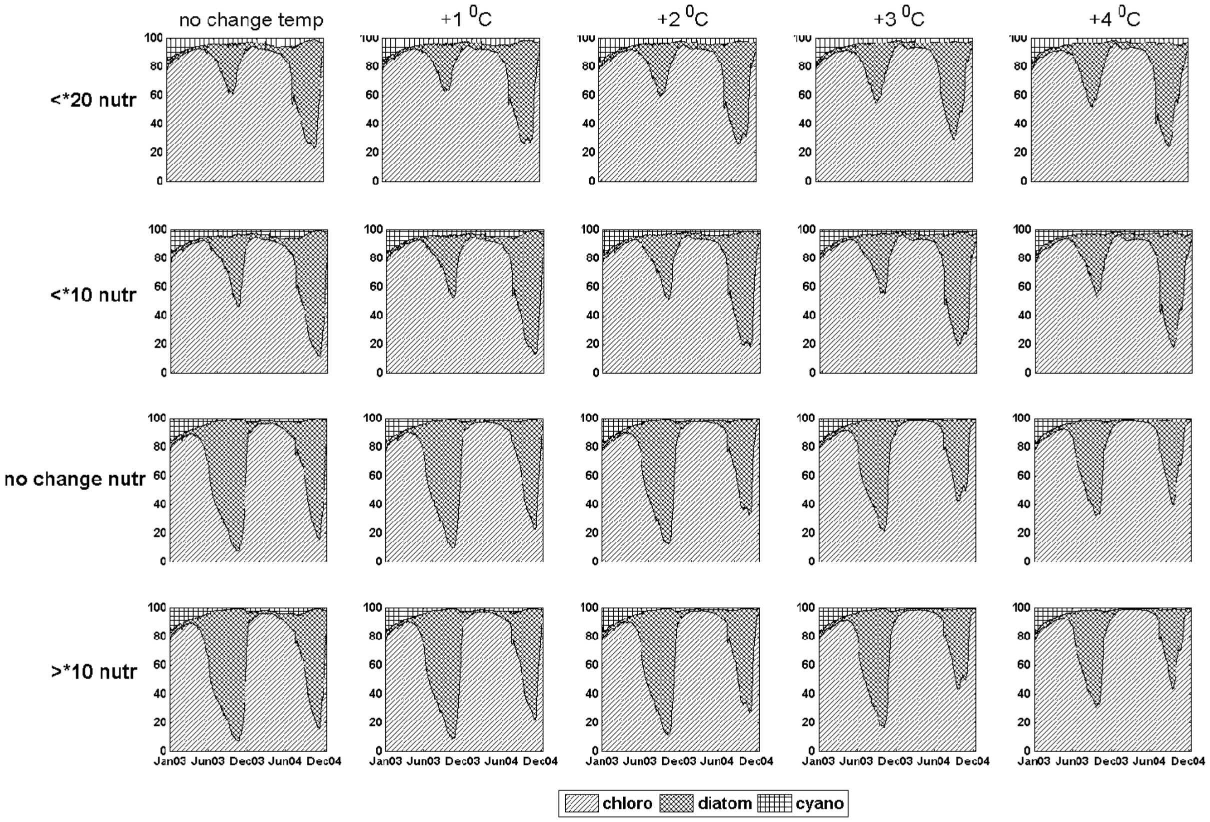


Figure 2.4 Percentage abundance of chlorophytes (green), diatom and cyanobacteria (cyano) under different nutrient loading and air temperature increase scenarios in Mt Bold

Resource limitation

The modelled temperature function (fT) indicated high temperature induced growth for both chlorophytes and cyanobacteria. Growth of both groups was favoured by the rising water temperature in winter-spring period and summer-autumn period. In Tarawera especially, fT values reached 1.2 in summer as water temperatures increased, indicating that the rising water temperatures reached the standard temperatures (T_{std}) for growth of chlorophytes (Fig 2.5) and cyanobacteria (not shown). On the contrary, for diatoms the increasing temperatures led to lower growth of this group in both lakes. The winter-spring diatom growth was less affected by the rising temperatures in Tarawera but was temperature limited during the summer-autumn period. Reduced diatom growth by elevated water temperature was severe for MB with the mean summer-autumn fT values decreasing from 0.47 (base) to 0.31 in MB as the temperatures increased by 4 °C, irrespective of the nutrient l (Table 2.4).

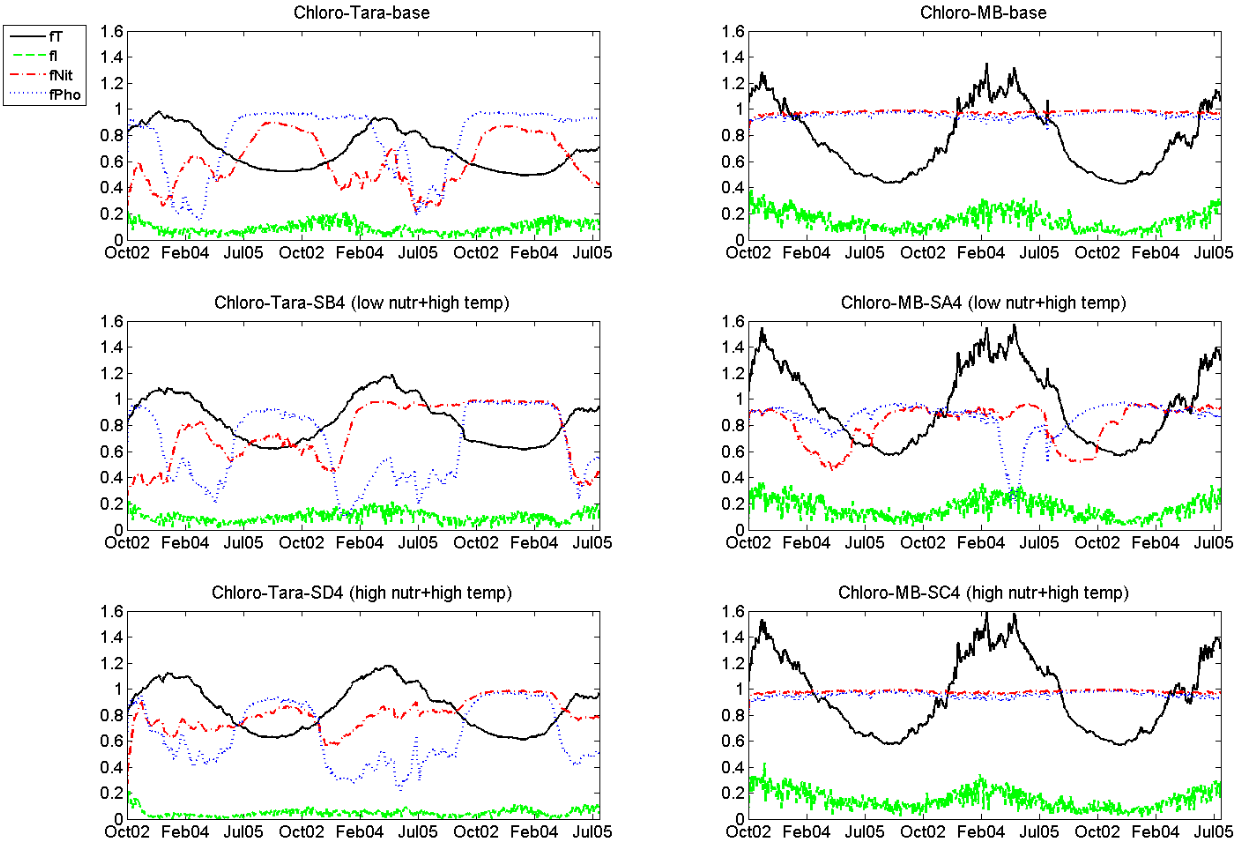


Figure 2.5 Variation of limitation functions over time for temperature (fT), light (fI), nitrogen (fN) and phosphorus (fPho) for chlorophytes for selected scenarios for Tarawera (left) and Mount Bold (right)

Light limitation (fI) was generally most severe for chlorophyte and cyanobacteria groups in both lakes. In Tarawera, the range in fI values for both chlorophytes and cyanobacteria in the base case scenario was 0.05-0.12 compared to the higher range of 0.17-0.25 for diatoms. Phytoplankton growth inhibition by light was most severe in Lake Tarawera where the surface layer represented an integrated value from 0 to 17 m. Light limitation increased as temperature increased and was further accentuated as nutrients increased, with a net reduction in fI by 0.02-0.12 under the high nutrient, high temperature scenario (SD4). Light limitation in cyanobacteria was least responsive in summer-autumn to the increasing nutrients and temperature of scenarios SC-SD4, with fI values of 0.03-0.04 (i.e., only slightly lower than the value of 0.05 in base case). The scenarios with reduced nutrients (SB) showed less limitation by light, indicating that water clarity was higher, but clarity decreased as the temperature increased in the warming scenarios (SB4), especially during the winter-spring period. In MB, scenarios with increasing nutrients and warming showed only a small net reduction in values of fI of 0-0.02 between the base and the nutrient rich, warm scenario (SC4).

Table 2.4 Limitation functions for temperature (fT), light (fI), nitrogen (fN) and phosphorus (fPho) for chlorophytes (CHLORO), cyanobacteria (CYANO) and diatoms (DIATOM). Cells coloured based on values, <0.1 (white), 0.1-0.4 (light grey), 0.4-0.7 (medium grey) and 0.7-1.1 (dark grey)

	TARAWERA																							
	CHLORO								CYANO								DIATOM							
	win-spr				sum-aut				win-spr				sum-aut				win-spr				sum-aut			
	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho
S(BASE)	0.58	0.12	0.73	0.95	0.80	0.08	0.48	0.61	0.51	0.08	1.00	0.95	0.76	0.05	1.00	0.58	0.69	0.25	0.45	0.95	0.66	0.17	0.18	0.44
S1	0.61	0.12	0.74	0.96	0.84	0.07	0.51	0.60	0.55	0.08	1.00	0.95	0.81	0.05	1.00	0.57	0.70	0.26	0.46	0.95	0.62	0.17	0.18	0.44
S2	0.66	0.10	0.72	0.83	0.88	0.09	0.75	0.52	0.60	0.06	1.00	0.86	0.86	0.05	1.00	0.51	0.70	0.21	0.47	0.84	0.57	0.19	0.39	0.34
S3	0.70	0.09	0.77	0.76	0.92	0.09	0.78	0.50	0.64	0.06	1.00	0.81	0.91	0.06	1.00	0.49	0.70	0.20	0.53	0.70	0.52	0.20	0.40	0.30
S4	0.75	0.06	0.82	0.77	0.98	0.04	0.74	0.56	0.71	0.04	1.00	0.82	0.98	0.03	1.00	0.54	0.67	0.14	0.56	0.68	0.43	0.10	0.24	0.27
SA																								
SA1																								
SA2																								
SA3																								
SA4																								
SB	0.58	0.12	0.74	0.95	0.79	0.08	0.57	0.63	0.51	0.08	1.00	0.95	0.75	0.05	1.00	0.58	0.69	0.26	0.46	0.95	0.66	0.18	0.21	0.49
SB1	0.62	0.12	0.73	0.96	0.83	0.09	0.55	0.63	0.55	0.08	1.00	0.95	0.81	0.06	1.00	0.58	0.70	0.26	0.46	0.95	0.62	0.19	0.19	0.49
SB2	0.66	0.11	0.71	0.94	0.88	0.09	0.67	0.55	0.60	0.07	1.00	0.93	0.85	0.06	1.00	0.52	0.70	0.24	0.44	0.92	0.57	0.19	0.23	0.34
SB3	0.70	0.10	0.78	0.74	0.92	0.10	0.76	0.54	0.64	0.06	1.00	0.80	0.90	0.07	1.00	0.51	0.70	0.21	0.52	0.69	0.52	0.22	0.39	0.31
SB4	0.74	0.10	0.74	0.75	0.96	0.11	0.77	0.54	0.70	0.07	1.00	0.80	0.95	0.07	1.00	0.51	0.68	0.23	0.47	0.75	0.46	0.23	0.39	0.31
SC	0.58	0.11	0.74	0.96	0.80	0.06	0.54	0.61	0.51	0.07	1.00	0.96	0.76	0.04	1.00	0.61	0.69	0.23	0.44	0.95	0.65	0.13	0.23	0.49
SC1	0.62	0.11	0.73	0.96	0.84	0.06	0.57	0.60	0.55	0.07	1.00	0.95	0.81	0.04	1.00	0.60	0.70	0.23	0.44	0.95	0.61	0.13	0.21	0.44
SC2	0.66	0.08	0.76	0.89	0.88	0.06	0.74	0.54	0.60	0.05	1.00	0.90	0.85	0.04	1.00	0.56	0.70	0.19	0.52	0.88	0.58	0.14	0.34	0.36
SC3	0.70	0.07	0.79	0.76	0.92	0.06	0.78	0.53	0.65	0.05	1.00	0.82	0.91	0.04	1.00	0.54	0.69	0.17	0.53	0.70	0.52	0.14	0.36	0.31
SC4	0.75	0.07	0.80	0.67	0.96	0.07	0.79	0.52	0.71	0.05	1.00	0.76	0.95	0.04	1.00	0.53	0.67	0.17	0.56	0.56	0.46	0.15	0.33	0.28
SD	0.59	0.09	0.83	0.96	0.81	0.04	0.64	0.66	0.52	0.06	1.00	0.96	0.77	0.03	1.00	0.68	0.69	0.20	0.56	0.95	0.65	0.10	0.34	0.59
SD1	0.62	0.09	0.81	0.96	0.85	0.04	0.65	0.64	0.56	0.06	1.00	0.96	0.82	0.03	1.00	0.66	0.70	0.20	0.54	0.95	0.60	0.10	0.30	0.50
SD2	0.60	0.09	0.82	0.96	0.82	0.05	0.60	0.65	0.53	0.06	1.00	0.96	0.79	0.03	1.00	0.65	0.70	0.20	0.55	0.95	0.63	0.11	0.30	0.52
SD3	0.71	0.06	0.84	0.81	0.94	0.05	0.77	0.57	0.65	0.04	1.00	0.87	0.93	0.03	1.00	0.59	0.69	0.15	0.61	0.75	0.49	0.10	0.33	0.34
SD4	0.76	0.06	0.84	0.74	0.97	0.04	0.78	0.57	0.71	0.03	1.00	0.82	0.97	0.03	1.00	0.58	0.67	0.13	0.59	0.64	0.45	0.10	0.29	0.30

	MOUNT BOLD																							
	CHLORO								CYANO								DIATOM							
	win-spr				sum-aut				win-spr				sum-aut				win-spr				sum-aut			
	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho	fT	fI	fNit	fPho
S(BASE)	0.68	0.13	0.99	0.96	0.87	0.18	0.98	0.95	0.63	0.07	1.00	0.84	0.86	0.11	1.00	0.76	0.58	0.33	0.93	0.93	0.47	0.41	0.88	0.90
S1	0.72	0.13	0.98	0.96	0.92	0.17	0.98	0.94	0.67	0.08	1.00	0.81	0.91	0.10	1.00	0.76	0.57	0.34	0.93	0.93	0.43	0.41	0.87	0.86
S2	0.76	0.13	0.98	0.96	0.97	0.18	0.98	0.93	0.73	0.08	1.00	0.83	0.96	0.11	1.00	0.75	0.55	0.35	0.93	0.92	0.39	0.42	0.87	0.79
S3	0.81	0.14	0.98	0.96	1.02	0.18	0.98	0.92	0.78	0.08	1.00	0.83	1.02	0.11	1.00	0.74	0.54	0.35	0.93	0.92	0.35	0.42	0.86	0.75
S4	0.86	0.14	0.98	0.96	1.07	0.18	0.98	0.90	0.84	0.08	1.00	0.84	1.08	0.11	1.00	0.72	0.52	0.36	0.93	0.91	0.31	0.42	0.86	0.71
SA	0.67	0.14	0.90	0.92	0.87	0.18	0.84	0.81	0.62	0.08	1.00	0.81	0.85	0.11	1.00	0.67	0.59	0.35	0.58	0.76	0.47	0.43	0.33	0.40
SA1	0.72	0.14	0.89	0.92	0.92	0.19	0.80	0.77	0.67	0.08	1.00	0.81	0.91	0.11	1.00	0.66	0.57	0.36	0.56	0.74	0.43	0.44	0.23	0.30
SA2	0.76	0.14	0.89	0.93	0.97	0.19	0.81	0.80	0.73	0.08	1.00	0.81	0.96	0.12	1.00	0.67	0.55	0.36	0.54	0.71	0.39	0.45	0.19	0.27
SA3	0.81	0.14	0.90	0.93	1.02	0.20	0.78	0.79	0.78	0.08	1.00	0.82	1.02	0.12	1.00	0.67	0.54	0.37	0.54	0.71	0.35	0.45	0.18	0.26
SA4	0.86	0.14	0.90	0.93	1.07	0.20	0.74	0.80	0.84	0.08	1.00	0.81	1.08	0.12	1.00	0.67	0.52	0.36	0.55	0.71	0.32	0.46	0.15	0.25
SB	0.68	0.14	0.96	0.94	0.87	0.18	0.91	0.81	0.63	0.08	1.00	0.81	0.85	0.11	1.00	0.67	0.58	0.35	0.81	0.85	0.47	0.43	0.47	0.51
SB1	0.72	0.14	0.96	0.93	0.92	0.18	0.90	0.79	0.68	0.08	1.00	0.82	0.91	0.11	1.00	0.66	0.57	0.35	0.80	0.84	0.43	0.43	0.39	0.40
SB2	0.76	0.14	0.96	0.94	0.97	0.19	0.89	0.79	0.73	0.08	1.00	0.82	0.96	0.12	1.00	0.67	0.55	0.36	0.78	0.83	0.39	0.44	0.33	0.35
SB3	0.81	0.14	0.96	0.94	1.02	0.19	0.87	0.76	0.78	0.08	1.00	0.82	1.02	0.12	1.00	0.65	0.54	0.36	0.77	0.81	0.35	0.45	0.29	0.29
SB4	0.86	0.14	0.96	0.94	1.07	0.19	0.88	0.79	0.84	0.08	1.00	0.80	1.08	0.12	1.00	0.66	0.52	0.36	0.76	0.80	0.32	0.45	0.31	0.31
SC	0.68	0.13	0.99	0.97	0.87	0.17	0.98	0.96	0.63	0.07	1.00	0.81	0.86	0.10	1.00	0.76	0.59	0.34	0.93	0.94	0.47	0.41	0.92	0.93
SC1	0.72	0.13	0.99	0.97	0.92	0.17	0.98	0.96	0.68	0.07	1.00	0.83	0.91	0.10	1.00	0.76	0.57	0.34	0.93	0.94	0.43	0.41	0.92	0.93
SC2	0.77	0.13	0.99	0.96	0.97	0.18	0.98	0.96	0.73	0.08	1.00	0.84	0.96	0.11	1.00	0.76	0.55	0.34	0.93	0.94	0.39	0.42	0.93	0.94
SC3	0.81	0.13	0.99	0.96	1.02	0.17	0.98	0.96	0.78	0.08	1.00	0.85	1.02	0.11	1.00	0.76	0.54	0.35	0.94	0.94	0.35	0.41	0.93	0.94
SC4	0.86	0.14	0.98	0.96	1.08	0.17	0.98	0.96	0.84	0.08	1.00	0.85	1.09	0.10	1.00	0.76	0.52	0.35	0.94	0.95	0.31	0.41	0.94	0.95
SD																								
SD1																								
SD2																								
SD3																								
SD4																								

<0.1	0.1-0.4	0.4-0.7	0.7-1.1

Increasing nutrients in the already hyper-eutrophic Mount Bold scenarios did not reveal major changes to the P limitation for phytoplankton growth (Fig 2.5). In Tarawera, diatoms initially benefited from the increased nutrients, especially P, in scenarios with temperature increased by 1-2 ºC but not when temperature increased by 3-4 ºC (Table 3). In MB, diatoms were favoured in scenarios that had an increase of both P and temperature. In scenarios with increased nutrients, increasing temperature resulted in greater phosphorus limitation in all phytoplankton groups at most times in both lakes. For instance, the initial fPho in the scenarios with the highest increase in nutrients and no change in temperature (SD) were 0.66 and 0.68 for chlorophytes and cyanobacteria, respectively, and these values decreased to 0.57 and 0.6 as the temperatures increased by 4 ºC (SD4) during the summer-autumn period in Tarawera (Table 2.4).

Nitrogen limitation under nutrient poor conditions (SA-SB) in MB increased for both diatoms and chlorophytes during the summer-autumn period (Table 2.4, Fig 2.5). Scenarios with reduced nutrients (state scenarios) increased N limitation across all phytoplankton groups and in both lakes as expected, but the relative increase was more severe in MB and was reinforced by higher temperature. Cyanobacteria were less inhibited by nutrient reduction and diatoms experienced the highest nutrient limitation as a result of nutrient reduction. Phosphorus and nitrogen inhibition of phytoplankton for the scenarios of reduced nutrients showed different trends in Tarawera; P limitation was more pronounced when the temperatures were higher relative to N limitation (Table 2.4). For example, fPho values decreased by 0.07-0.2 from 0.44-0.95 (summer average minimum and maximum) in the base conditions and fN values increased by 0.01-0.29 from 0.18-0.73 (summer average minimum and maximum) in the base case scenario as the nutrients reduced and the temperatures increased (Table 2.4).

Discussion

Impacts of nutrients and temperature on phytoplankton growth

An increase in phytoplankton biomass was observed in both lakes under eutrophic and hyper-eutrophic conditions with rising temperatures. Studies that have evaluated the effects of temperature and nutrients on phytoplankton composition have shown that nutrients, particularly phosphorus, have a greater effect on the species diversity and algal biomass than temperature (Moss et al. 2003, Elliott and May 2008). Mooij et al. (2007) observed an increase in TCHLA in shallow lakes at intermediate nutrient loads (within a range of 0.1-20 mg P/m^2/day) when the temperature was increased by 3 °C all year round. In the current study, a change from oligo-mesotrophic to hyper-eutrophic status was observed in Lake Tarawera when the loading rates were increased from 0.6 to 12 mg P/m^2/day. In our study the magnitude of the relative impact of temperature and nutrients on phytoplankton differs depending on the trophic status of the lake. The greatest increase in chlorophyll a in the oligotrophic lake occurred when nutrients were increased, whereas in the eutrophic lake, the most prominent increase was observed when the temperature was increased. Our findings support the hypothesis that phytoplankton dynamics in nutrient-poor lakes are more sensitive to nutrient enrichment than temperature rises as suggested by Brookes and Carey (2011).

Existing trophic status plays an important role in governing the phytoplankton responses to nutrients and temperature. In the current study, altering the major dissolved nutrients (FRP and NO_3) by 10 and 20 fold led to a change in the trophic status in Lake Tarawera and Mt Bold. The nutrient loadings in the scenarios used in this study are used as they drive a change in the trophic status in the studied lakes. Most studies that have assessed the effects of nutrients on water quality have simulated nutrient loading scenarios that vary by 10-100% of the original nutrient inputs. The modelling study by Elliott et al. (2006), examining the effects of increased nutrient loading and temperature on a eutrophic lake, noted a decrease in chlorophyll *a* during the scenario where there was simultaneous increase in nutrients by 50% and an increase in temperature of 4 °C. It was noted that although increased nutrients does in fact favour the growth of most species, high temperatures induced competition between the simulated phytoplankton species (cool water favouring *Plagioselmis* vs warm water favouring *Anabena*) lead to the overall decrease in algal biomass. Trolle et al. (2011) assessed the impacts of increase in loads (by 10%, 25% and 50%) and increase in temperatures (by 2.5-2.7 °C) on three lake ecosystems, and observed an increase in annual average biomass in the oligo-mestrophic and eutrophic lakes, but a decrease in annual average TCHLA in the hyper-eutrophic lake. In the current study, both lakes experienced increased phytoplankton biomass but the greatest increase was observed in the oligo-mesotrophic Lake Tarawera, compared to the eutrophic Mt Bold. While it is possible that a nutrient load increase by 50% in the other studies was not adequate to cause significant algal development under the respective temperatures, the overall phytoplankton growth is affected by the interactions between the different lake-specific phytoplankton groups and therefore each lake may respond differently to effects of nutrients and temperature.

Resource limitation driven phytoplankton growth

Rapid growth induced by increasing temperatures was most evident for chlorophytes and cyanobacteria while diatoms tended to be more restricted by temperature. Phytoplankton production is strongly regulated by physical and chemical factors (i.e. temperature, light, nutrients) which regulate photosynthesis and growth (Vollenweider 1976, Jones et al. 1996). Under optimum environmental conditions, minimum energy is required to acquire resources and the ability to convert resources into growth and reproduction is maximised (Finkel et al. 2004). Given that metabolic rates are regulated by temperature, phytoplankton can take up nutrients efficiently if the nutrients are abundant and the temperature is optimal (Klausmeier et al. 2004). Under nutrient replete conditions this was expressed by increased phytoplankton biomass but under the nutrient reduction scenarios it was evident that there were extended periods of strong nutrient limitation of phytoplankton productivity.

The relationship between increasing nutrients and light on regulating phytoplankton growth is complex, as feedbacks occur between resource availability and productivity. Increased resources can result in high productivity but the subsequent increase in light extinction can reduce the overall productivity as light levels decrease (Ganf and Oliver 1982, Rigosi et al. 2014). While light limitation of phytoplankton in oligotrophic Tarawera increased with high nutrient loading due to increases in phytoplankton biomass under increasing temperatures, light attenuation in MB was more resistant to changes in the nutrients. Many Australian inland waters are coloured and turbid and the initial conditions of MB are such that it already has high background extinction coefficients arising from absorption by the dissolved colour and scattering by suspended particulate matter (Oliver 1981). It should also be noted that the light input to the model is a daily average that is surface integrated (17 m for Tarawera and 2 m for MB); significant variability occurs within the day.

Model performance

Calculated goodness-of-fit measures consisting of root mean square error (RMSE) and coefficient of determination (r^2) provided insight into the performance of the model and the primary lake processes. The model reproduced the observed temperature generally well in both calibration and validation periods for the two lakes. However, surface temperature was at times slightly underestimated by ~0.5 °C on average. The r^2 values estimated for modelled nutrients in Lake Tarawera are similar to those reported by Trolle et al. (2011) for oligo-mesotrophic lakes from the same geographic region. A proportion of the error associated with nutrient simulations in oligo-mesotrophic lakes, such as Lake Tarawera, is the product of comparing simulated nutrient concentrations against observations that are below analytical detection limits (0.005 mg/L for FRP in Tarawera). The seasonal variability of nutrients in Mt Bold was generally simulated well by the model but TP concentrations were slightly overestimated. Due to the lack of observed measurements for bottom water nutrients for Mt Bold, parameters related to sediment nutrient fluxes could only be set at default values or guided by literature.

The low chlorophyll *a* values observed in Lake Tarawera are challenging for the model to capture, however the errors calculated between the modelled and observed TCHLA concentrations were within the values of previous literature (Arhonditsis and Brett 2004, Trolle et al. 2008, Burger et al. 2011). Low and high frequency temporal variability within the chlorophyll observations from Mount Bold indicated significant uncertainty generated by inter-annual variability and spatial heterogeneity and advection. The TCHLA measurements during the calibration and validation periods varied substantially. However, the model predicted TCHLA values were within the observed ranges. Use of two very different subsets of data for validation and calibration is useful for testing the model's ability to predict new conditions and therefore, provide confidence in carrying out scenario analysis (Arhonditsis and Brett 2004). Furthermore, the scale of the scenario changes are greater than the model vs observed error, which further instigates the validity of the scenarios. In both lakes, a lag can be observed between the observed and simulated TCHLA and the simulated TCHLA peak is observed ahead of time (57 ± 29 days). This unexplained variability in the timing of the primary productivity indicates higher growth of phytoplankton that is likely to be unbalanced by the rates of losses. Mortality due to grazing was included in the model as part of the loss term, as zooplankton dynamics could not be modelled explicitly due to the absence of relevant data. Additionally, inclusion of another biological component can increase the model complexity and may lead to lower model predictability.

Physiological basis for the observations

Chlorophytes became the dominant functional group in the present study under high nutrient and warming conditions in both lakes. Cyanobacteria and chlorophytes are well adapted to a wide range of environmental variables (Salmaso 2000) and can be abundant in lakes across a range of trophic levels. Many chlorophyte species have high growth rates and thus, a higher demand for nutrients (C-strategist, Reynolds 1988). Hence chlorophytes were defined to have maximum nutrient uptake rates higher than that of cyanobacteria, with N uptake rates almost twice than that of cyanobacteria. Diatoms generally have the highest nutrient requirements due to large cellular volume but their growth is promoted by cooler waters, as specified by the low optimum temperature of 17 ˚C. Thus their dominance growth was limited under high temperatures. This led to chlorophytes dominating (>80% of relative abundance) under simulated nutrient enriched and warm conditions. Although cyanobacteria are often considered symptomatic of eutrophic conditions (Smith 1986, Paerl et al. 2011) , in our model study, cyanobacteria thrived best in nutrient-poor environments due to their low growth rates and low demand for nutrients (S-strategist; Reynolds 1988).

Several field and lab based experiments have also shown similar phytoplankton dynamics that are in consistent with the current modelled results. Some lakes have experienced a shift from cyanobacteria to chlorophyte dominance under hypertrophic conditions (Jensen et al. 1994, Deng et al. 2014), implying that cyanobacteria may not always dominate when the nutrient load is high but can be competitive under nutrient limited environments. *In situ* microcosm experiments have shown an increase in some chlorophyte species under a warming environment (Moss et al. 2003) while other experiments report an increase in the early summer biomass of both chlorophytes and cyanobacteria at the expense of other groups (Weyhenmeyer 2001). Although cyanobacteria are reported to have a higher optimum temperature for growth than other phytoplankton groups, laboratory experiments have shown a similar mean optimum growth temperature of 29.2 °C for selected species of cyanobacteria and chlorophytes (Lürling et al. 2013). Modelled cyanobacterial group had a higher optimum growth temperature of 28 °C, compared to the optimum growth temperature of chlorophytes (25 °C). Additionally, chlorophytes were defined to be neutrally buoyant in our study as flagellated and mucilaginous colony-forming chlorophytes have reduced sinking velocities (Reynolds 1984, Demir et al. 2014). Simulated cyanobacterial group was assigned to be positively buoyant with a settling rate of $1.18\text{x}10^{-5}$ m/s to characterize the competitive advantage it may have by the possession of a gas vacuole (Reynolds et al. 1988). However, as neither increased temperature nor subsequent strengthening in stratification intensified cyanobacterial growth, it is likely that growth and nutrient related traits of chlorophyte had a superior influence on their productivity and led to their dominance under the nutrient rich scenarios.

Individual physiological traits and the trade-offs between traits determine phytoplankton growth and composition along environmental gradients (Litchman et al. 2010). Thus the model defined phytoplankton traits used in this study have a considerable impact on the observed phytoplankton responses to increasing temperatures and nutrients. In order to evaluate the influence of the selected traits on the modelled responses, a simple sensitivity analysis was performed. A key goal was to determine whether the chlorophyte dominance will be subdued under nutrient high, warm scenarios if different trait specific parameters are used. Hence the main parameters such as the growth rate and loss rates through respiration and sedimentation were modified to account for a higher loss of chlorophytes (Table 2.5). As chlorophytes were modelled as photoinhibted growth, parameters related to light were unchanged. Maximum internal nutrient concentration and uptake rates of nitrogen and phosphorus were also altered by -10% for chlorophytes and by +10% for cyanobacteria, relative to the originally calibrated values (Table 2.5). Resulting changes are analysed only for the base case scenario and for the scenario with the highest nutrient and highest temperature increase (SD4 for Tarawera and SC4 for MB).

Table 2.5 Chlorophyte (Chloro) and cyanpbacteria (Cyano) parameters as used in each simulation of the sensitivity analysis. Those that were changed from the base scenario are shaded in grey.

	Base		**Sim 1**	**Sim 2**	**Sim 3**	**Sim 4**	**Sim 5**	**Sim 6**	**Sim 7**	**Sim 8**	**Sim 9**	**Sim 10**	**Sim 11**	**Sim 12**	**Sim 13**	
	Chloro	**Cyano**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Chloro**	**Cyano**	**Cyano**	**Chloro**	**Cyano**
Maximum growth at 20 °C (Pmax) (/day)	1.20	0.70	1.00	1.20	1.20	1.20	1.20	1.20	1.20	1.00	1.00	1.00	0.80	0.80	1.00	0.80
Temperature scaling for growth (vT)	1.08	1.10	1.08	1.06	1.08	1.08	1.08	1.08	1.08	1.06	1.06	1.06	1.10	1.10	1.06	1.10
Fraction of metabolic loss through respiration (fres)	0.70	0.70	0.70	0.70	0.80	0.70	0.70	0.70	0.70	0.80	0.80	0.80	0.70	0.70	0.80	0.70
Maximum internal nitrogen concentration (INmax) (mg N/mg Chla)	9.47	7.00	9.47	9.47	9.47	8.53	9.47	9.47	9.47	8.53	8.53	8.53	7.00	7.70	8.53	7.70
Maximum nitrogen uptake rate (UNmax) (mg N/mg Chla/day)	4.81	2.33	4.81	4.81	4.81	4.81	4.33	4.81	4.81	4.33	4.33	4.33	2.33	2.57	4.33	2.57
Sedimentation rate (m/day)	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.10	-0.10	1.00	1.00	-0.10	1.00
Maximum internal phsophorus concentration (IPmax) (mg P/mg Chla)	0.98	1.99	0.98	0.98	0.98	0.98	0.98	0.88	0.98	0.98	0.98	0.88	1.99	2.19	0.88	2.19
Maximum phosphorus uptake rate (UPmax) (mg P/mg Chla/day)	0.50	0.35	0.50	0.50	0.50	0.50	0.50	0.50	0.45	0.50	0.50	0.45	0.35	0.39	0.45	0.39

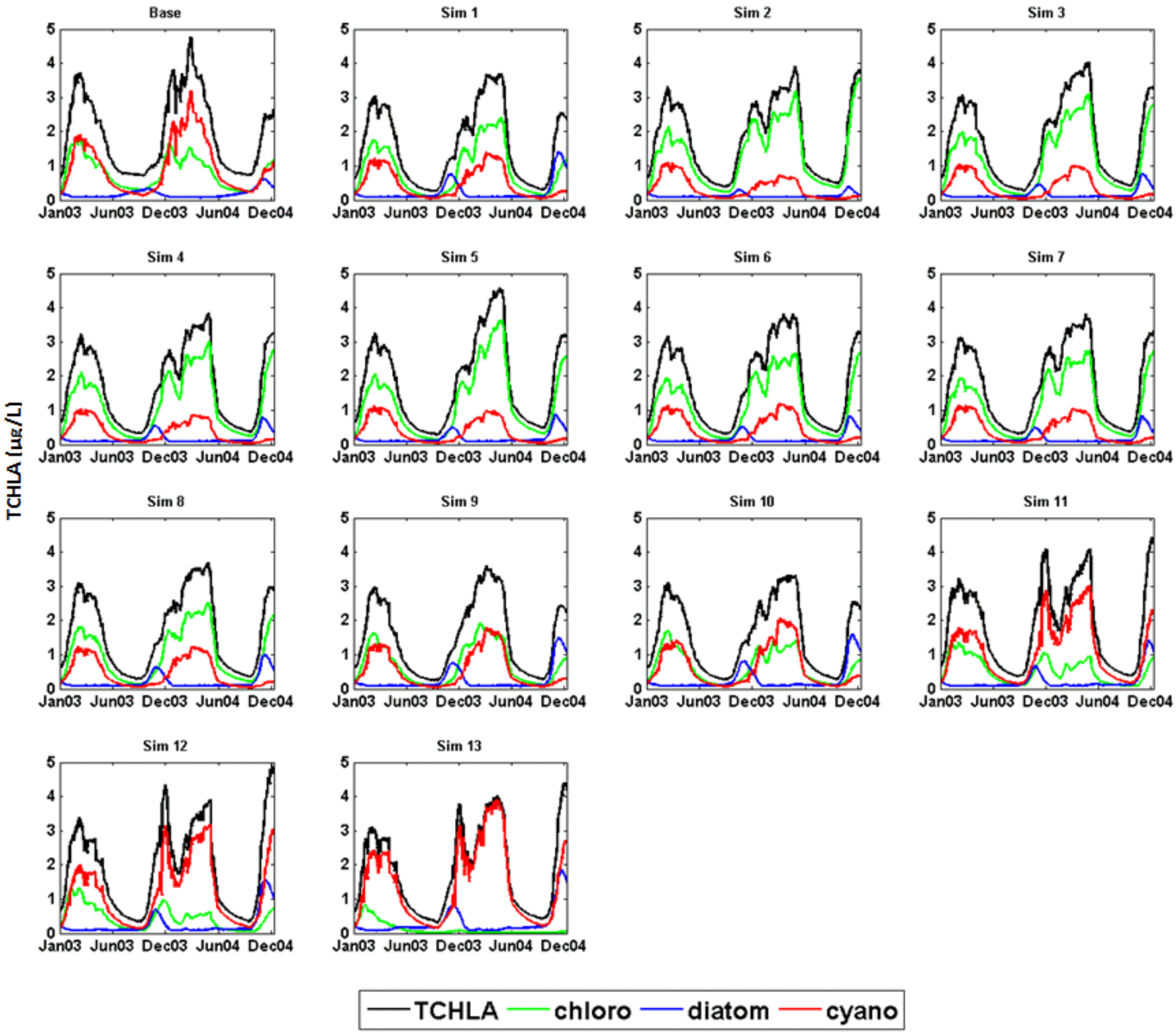


Figure 2.6 Phytoplankton abundance (TCHLA µg/L) in Tarawera for the base scenario with altered phytoplankton parameters

Modifying phytoplankton parameters changed the overall biomass but resulted in changes in the composition, as expected. The decrease in phytoplankton biomass in Tarawera was minor (0.6-1 µg/L) compared to the decrease in Mt Bold (4.3-10.8 µg/L) (Fig. 2.6 and 2.7). Delayed growth resulting from decreased chlorophyte growth rates (from 1.2 /day to 1.0 /day (Sim 1)) caused a shift in the chlorophyte peak in Tarawera (Fig. 2.6). This was accompanied by an increase in spring diatom concentrations by an amount of 0.4-0.8 µg/L and a decrease in cyanobacterial concentrations by a similar amount. Chlorophyte dominance was observed in simulations 1-7, where the individual chlorophyte parameters were changed. This provides confidence in the scenarios conducted using the calibrated parameters. Between simulation 8 and 9, including a settling rate of 0.1 m/day had a considerable decrease on the chlorophyte growth in Tarawera. However, the most notable change in the phytoplankton composition

(Sim 11-13) occurred in Tarawera when the growth rate of cyanobacteria is increased from 0.7 to 0.8 /day. Laboratory controlled studies have recorded a wide range of potential maximum growth rates for cyanobacteria, which are dependent upon the species and vary between 0.18-0.9 (Robarts and Zohary 1987, Lurling et al 2013). Most modelling studies that have computed phytoplankton dynamics based on the common functionality of cyanobacteria have used a general maximum growth rate <0.8 /day in most instances. The impact of increased cyanobacterial growth rate was less in Mt Bold where only a minor increase in the cyanobacterial concentration (0.4-1.0 µg/L) was observed (Sim 11). Instead, phytoplankton growth and composition was most sensitive to the chlorophyte growth rate parameter. Species specific maximum potential growth of chlorophytes could range widely, from 0.3 to 3.9 /day (Hamilton and Schladow 1997, Lurling 2013). These results suggest that the sensitivity of phytoplankton growth and composition to phytoplankton parameterisation may vary significantly between systems.

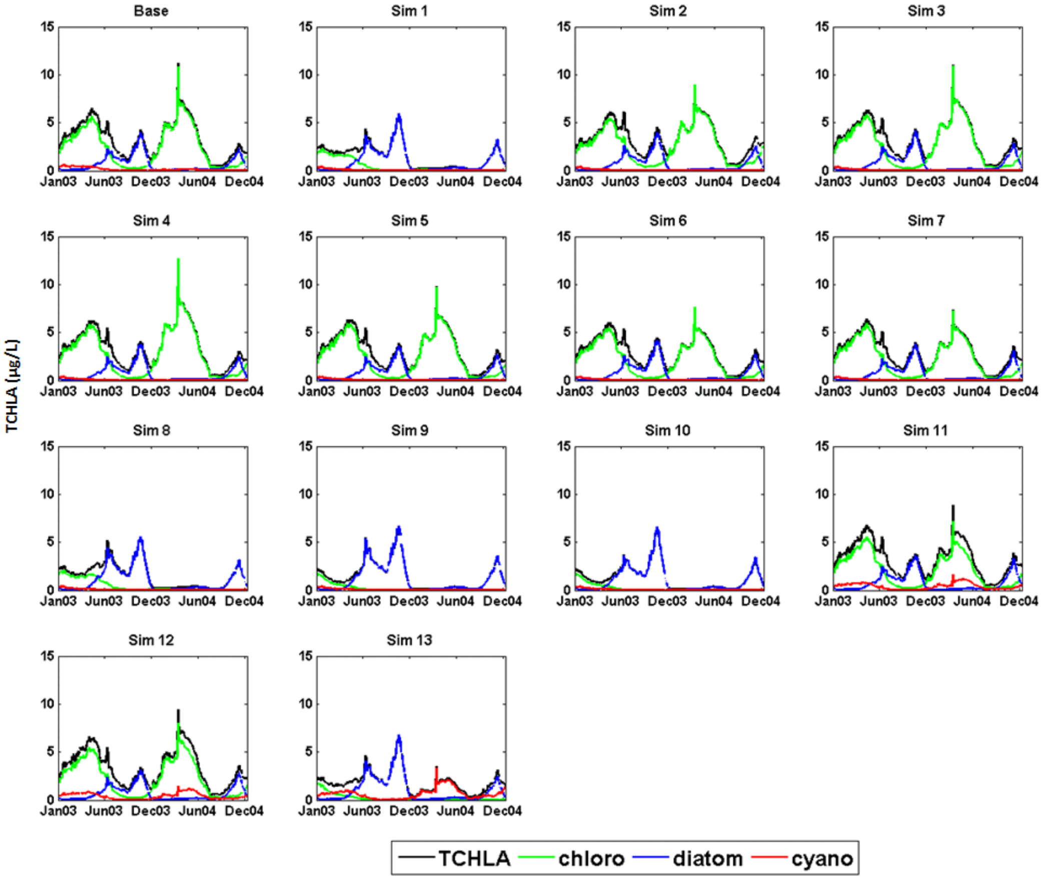


Figure 2.7 Phytoplankton abundance (TCHLA µg/L) in Mt Bold for the base scenario with altered phytoplankton parameters

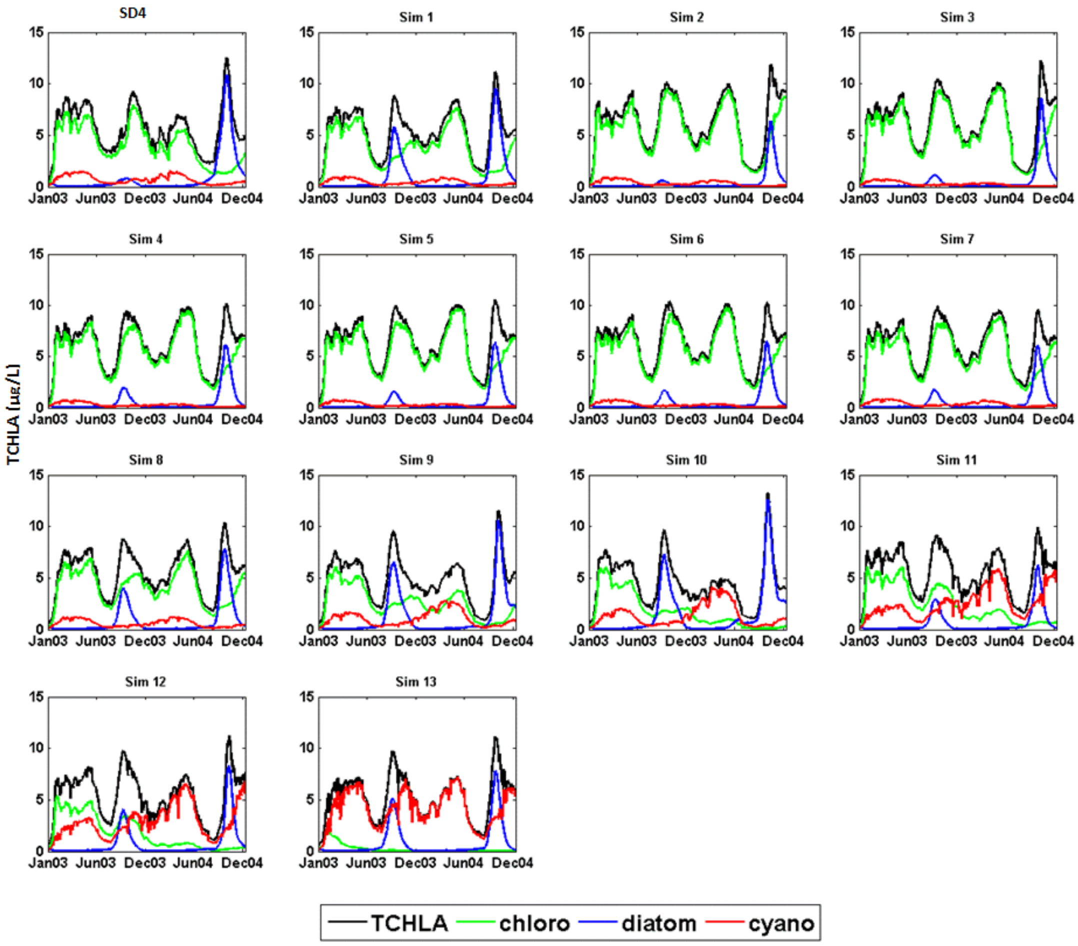


Figure 2.8 Phytoplankton abundance (TCHLA µg/L) in Tarawera for the nutrient enriched scenario with 4 °C temperature increase (SD4) with altered phytoplankton parameters

The interplay between the key resources, temperature and nutrients, control the rates of phytoplankton biomass production and yield and its impacts on competition influence the phytoplankton growth and community structure. The results from the sensitivity analysis carried out for the base case scenario translated to the scenario when the nutrients and temperature were increased (Fig. 2.8 and 2.9). Similar to base scenario, decreased chlorophyte growth led to an in increase in diatom and cyanobacterial growth in Tarawera (Sim 7 onwards). These simulations suggest that cyanobacteria would dominate under nutrient rich conditions if they had a higher growth rate. Their selective growth can be further facilitated if chlorophyte growth is subdued by altered functional traits (e.g. lower growth/nutrient uptake rate, lower internal nutrient concentrations, and negative settling rate). This was not the case for Mt Bold, where the decreased chlorophyte growth did not lead to cyanobacterial dominance even with high nutrient loading and increased temperatures. Although this further confirms that the oligotrophic lakes are more vulnerable to increases in nutrient loading and temperature, compared to eutrophic lakes, the response of any given lake to future climate change and landuse change will to depend upon the inherent traits of the phytoplankton species within that system.

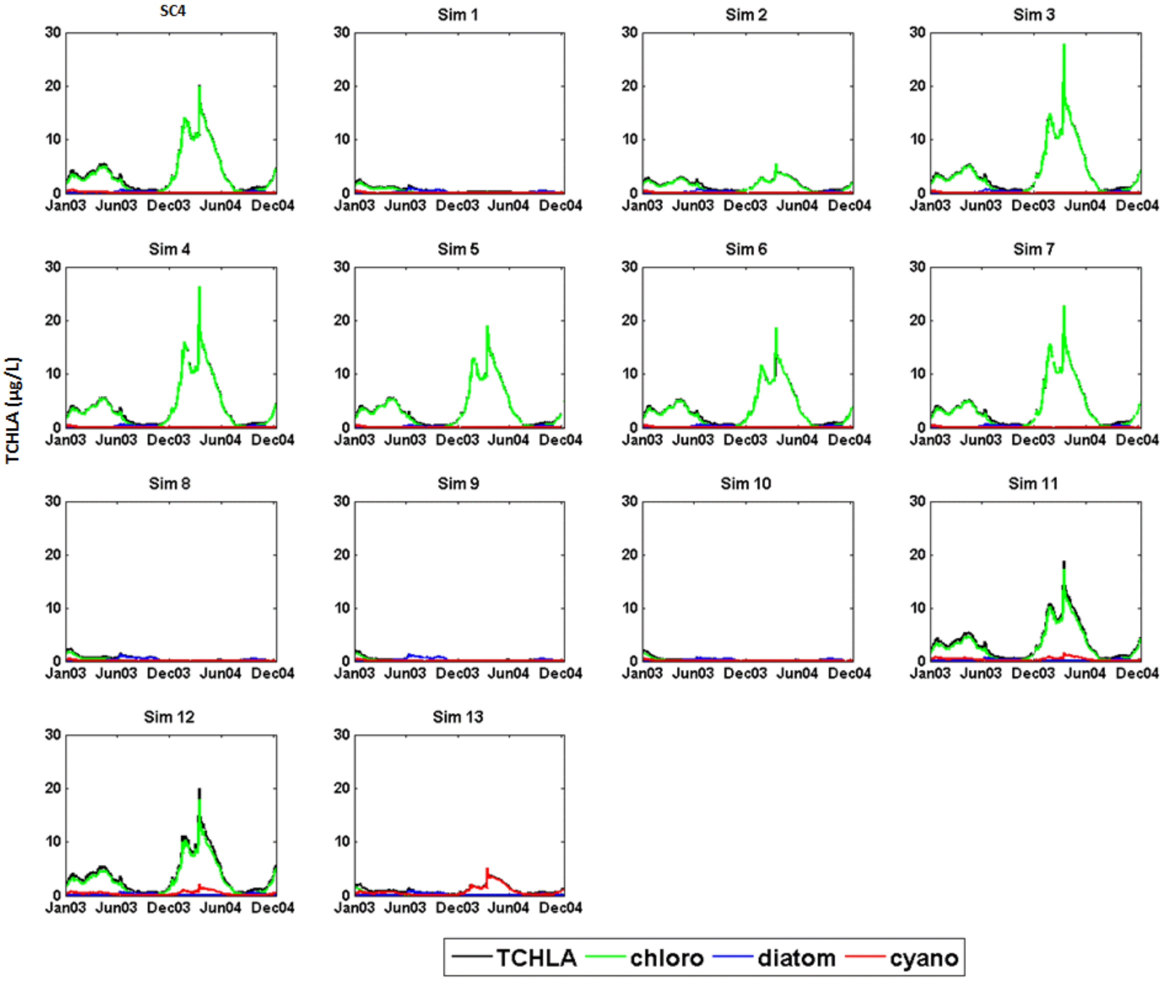


Figure 2.9 Phytoplankton abundance (TCHLA µg/L) in Tarawera for the most nutrient enriched scenario with 4 °C temperature increase (SC4) with altered phytoplankton parameters

Conclusion

Our study confirms that trophic status should be linked to considerations of effects of climate change on phytoplankton abundance and composition. The oligotrophic lake in our study experienced the highest relative increase in phytoplankton biomass under the scenario of a 10-fold increase in loading of dissolved nutrients. Contrary to our hypothesis, the hyper-eutrophic lake did not experience a cyanobacterial bloom under increased nutrients and temperature but experienced high chlorophyll levels contributed mostly by chlorophytes. The study results also indicate that, contrary to the popular notion that cyanobacterial blooms increase under nutrient enrichment and a warm climate (Paerl and Huisman 2008, Pearl and Paul 2012), it is likely that not all cyanobacterial species with average characteristics will benefit equally from such conditions. It is apparent from the modelling study presented here that the impact of nutrients and temperature on phytoplankton dynamics will not only, depend on the trophic status of the water body, but will be also dependent on the inherent physiological traits. While eutrophic lakes are affected by temperature rises, oligotrophic lakes are the most vulnerable to effects of nutrient loading and climate change and therefore, present implications for management.

Appendix

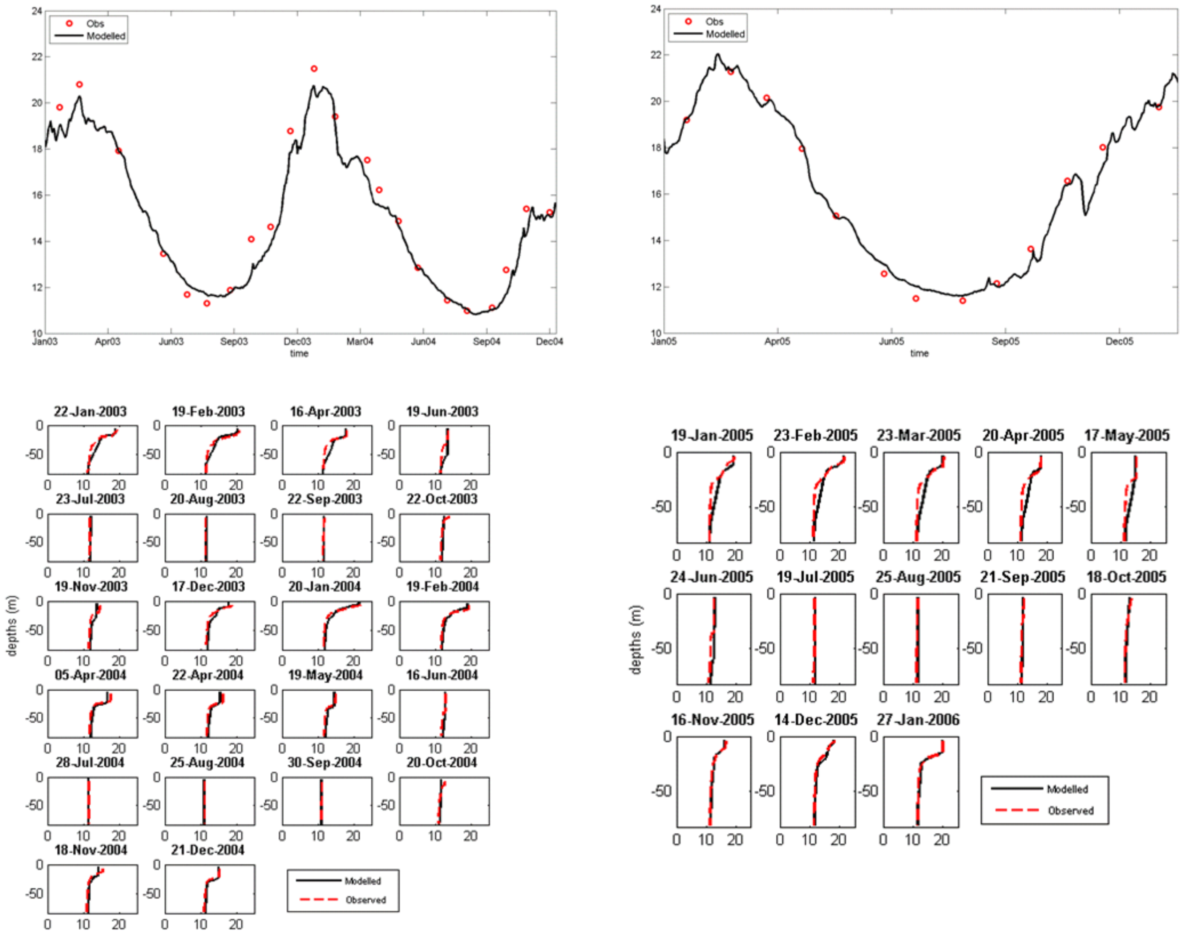


Figure A2.1 Surface 0-17 m integrated temperatures (upper) and temperature profiles (bottom) of Lake Tarawera for periods of calibration (left) and validation (right)

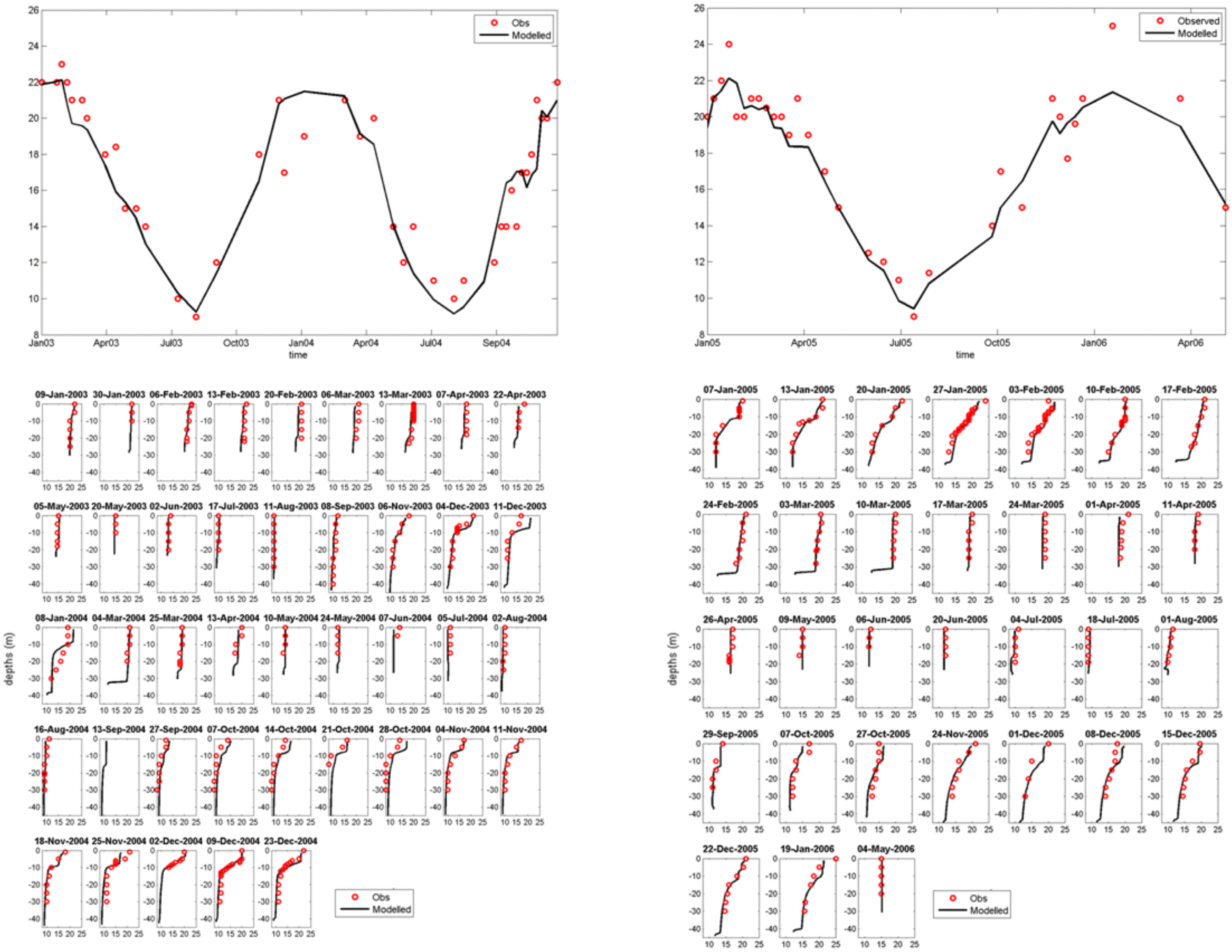


Figure A2.2 Surface 0-1.6 m integrated temperatures (upper) and temperature profiles (bottom) of Mt Bold for periods of calibration (left) and validation (right)

Results (contd.)

Validation and calibration of nutrient simulations

The base case simulations of surface nutrients captured the inter-annual variability of the observed data. The model tended to underestimate the DO in Lake Tarawera, with a mean difference of -0.28 ± 0.58 mg/L over the measured depths for simulation period (Appendix Fig 2.3). The model generally overestimated DO in Mt Bold with a mean difference of 1.5 ± 1.09 mg/L over the measured depths for the simulation period (Appendix Fig 2.4). The variability in TP and TN loadings to Lake Tarawera is generally low and this is captured well in the model simulations of nutrients in this lake (Appendix Fig 2.5). The mean difference between the simulated and observed TP and TN were 0.001 ± 0.007 and 0.0058 ± 0.016

mg/L, respectively. There was strong seasonality in nutrient loading in Mt Bold, driven by precipitation and run-off, with the highest nutrient concentrations in winter (Appendix Fig 2.6). The mean difference between the simulated and observed TP and TN were 0.035 ± 0.1 and -0.08 ± 0.29 mg/L, respectively.

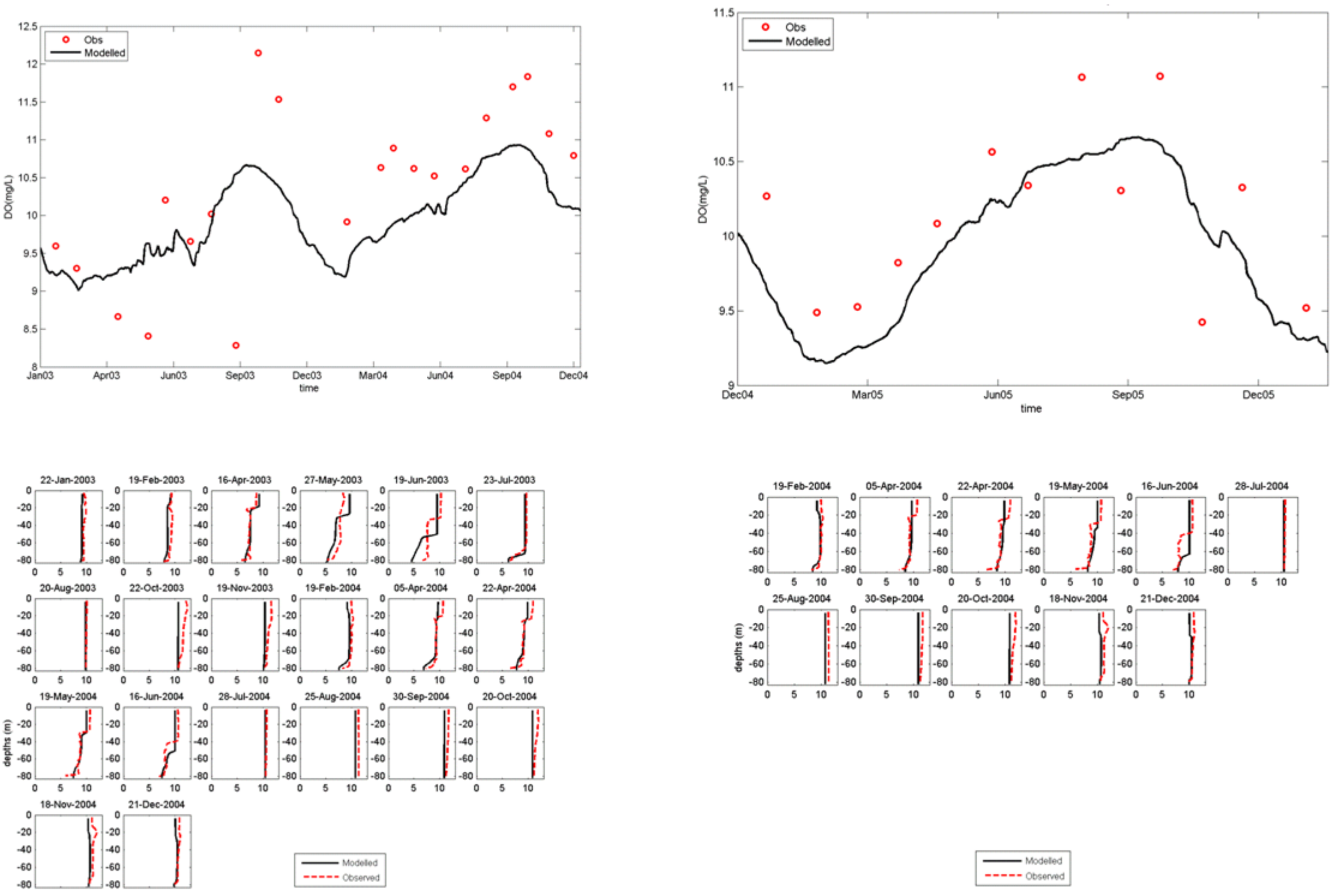


Figure A2.3 Surface 0-17 m integrated DO (upper) and DO profiles (bottom) of Lake Tarawera for periods of calibration (left) and validation (right)

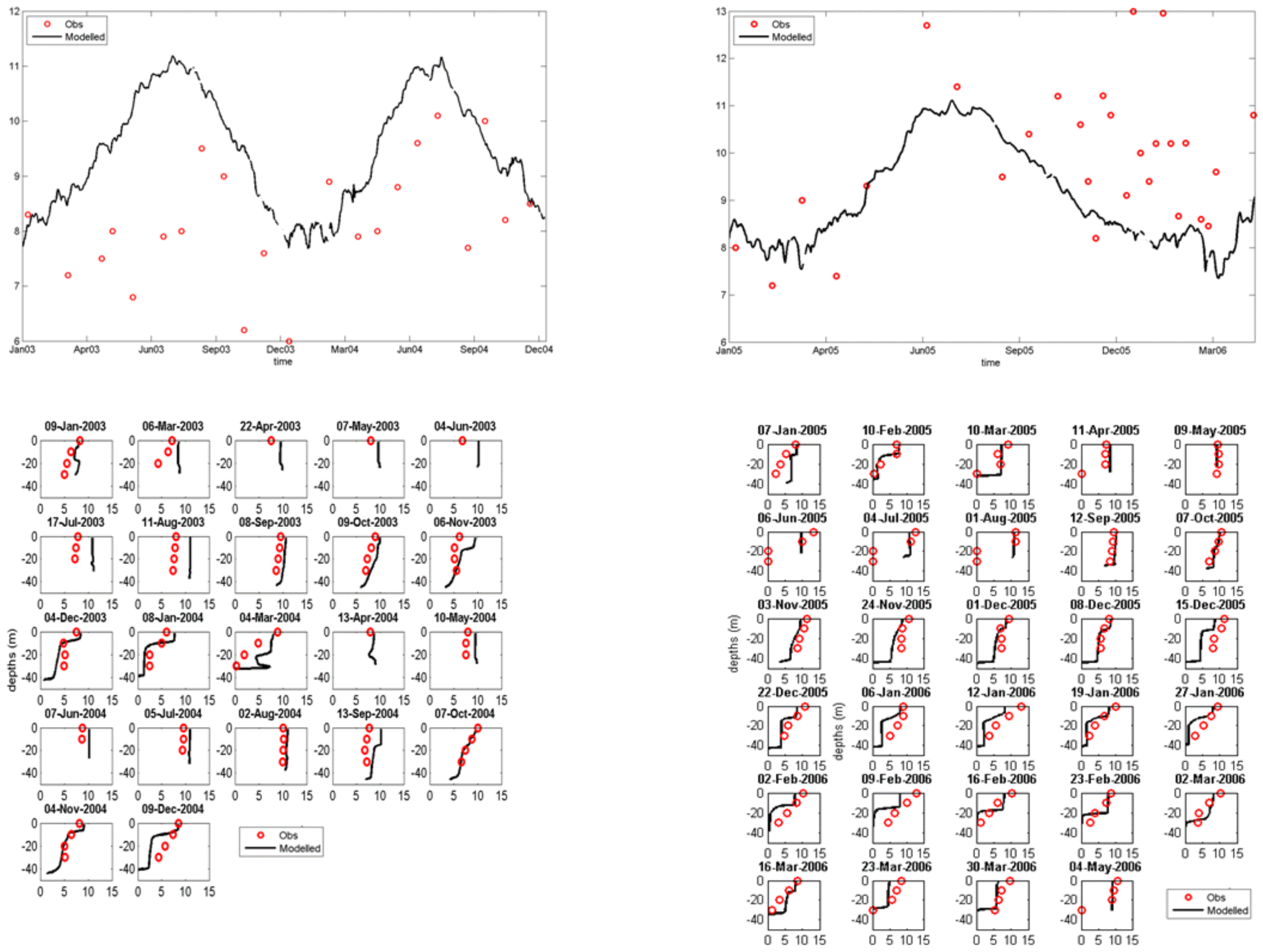


Figure A2.4 Surface 0-1.6 m integrated DO in Mt Bold - integrated DO (upper) and DO profiles (bottom) of Mt Bold for periods of calibration (left) and validation (right)

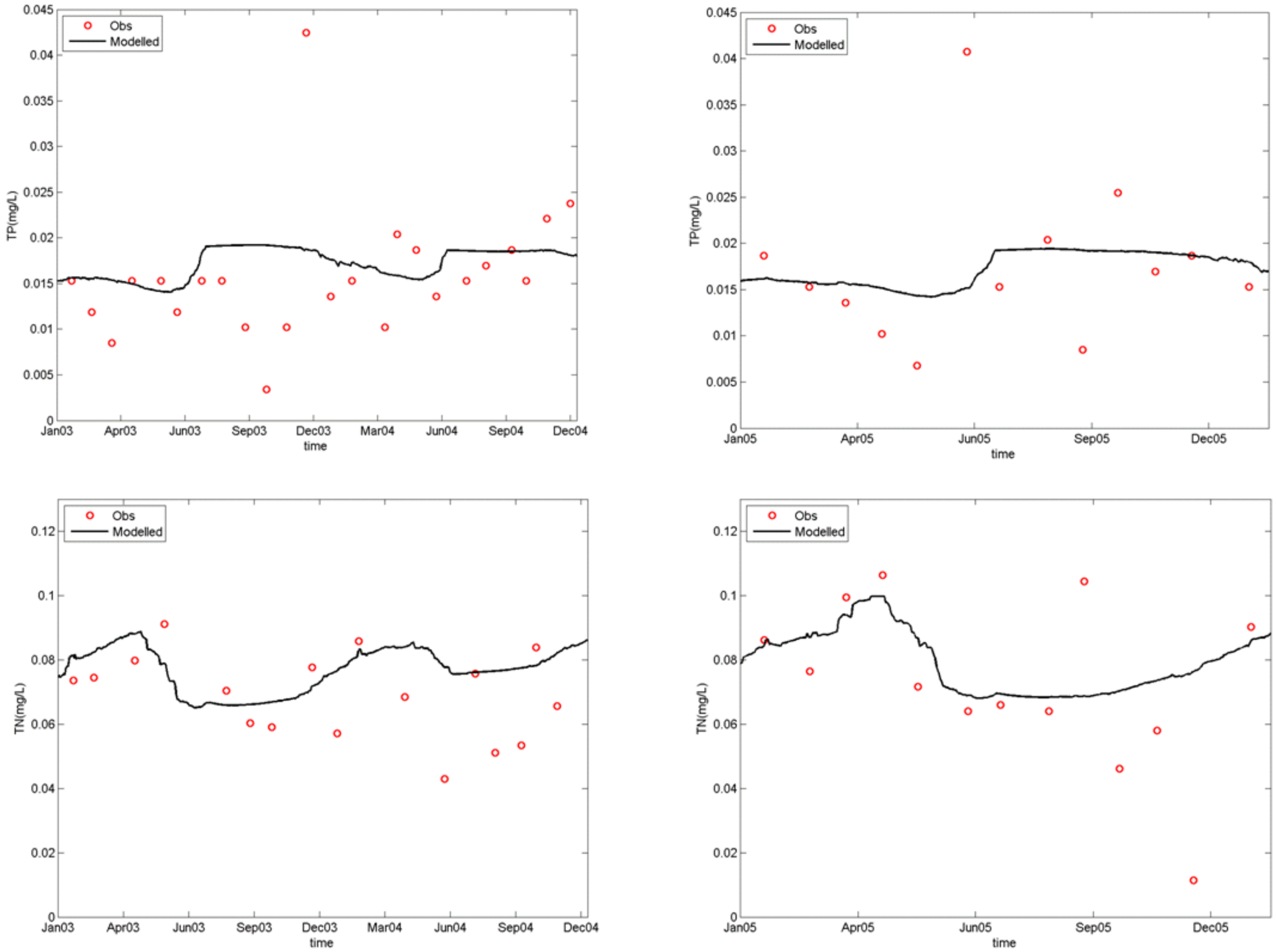


Figure A2.5 Surface integrated 0-17 m TP (top) and TN (bottom) in Lake Tarawera - calibration (left) and validation (right)

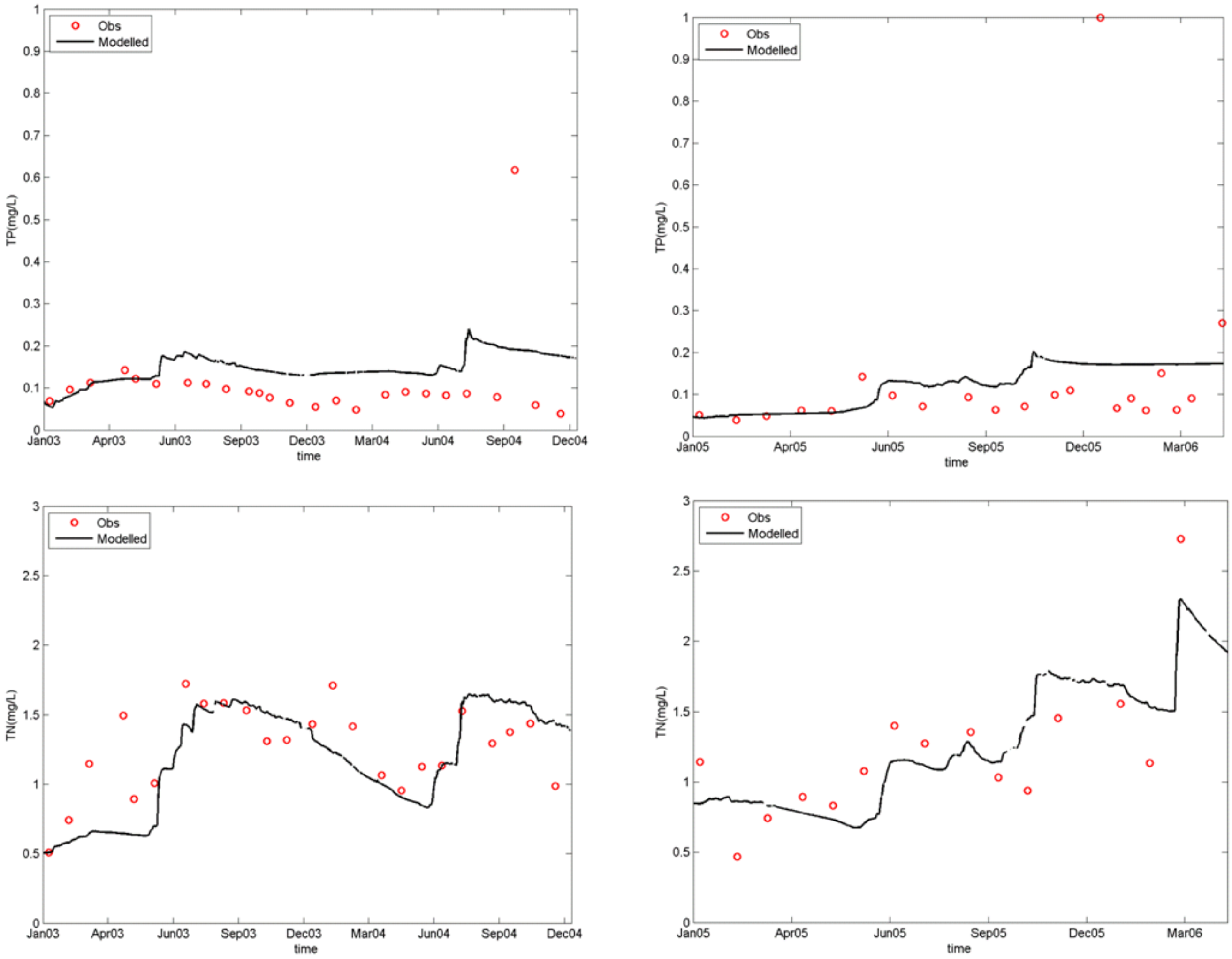


Figure A2.6 Surface integrated 0-1.6 m TP (top) and TN (bottom) in Mt Bold - calibration (left) and validation (right)

Validation and calibration of total chlorophyll

The model managed to capture average TCHLA values in both lakes; seasonal variability in TCHLA was also captured even though a slight lag was observed. The observed TCHLA of Tarawera was low, around 0.5-3.6 µg/L and this range was reproduced by the model at most times (Appendix Fig 2.7). The duration of the TCHLA peak in Tarawera was underestimated by the model and was slightly over predicted, with a mean difference of 0.34 ± 1.22 µg/L. The modelled growth of *cyano* and *chloro* functional groups in Lake Tarawera coincided with the onset of increasing temperatures. Most observed TCHLA values at Mt Bold were between 5-10 µg/L with the exception of one single outlier value of >40 µg/L (Appendix Fig 2.8). The simulated TCHLA concentrations were within the above range and but were under-predicted on average with a mean difference of 4.5± 6.9 µg/L. The chlorophyte functional group contributed most to the simulated TCHLA, with diatom and cyanobacterial functional groups accounting for less chlorophyll-a. The model-predicted spring diatom peak was earlier in the year than in the observations, however the magnitude of the peak was within the observed range in both calibration and validation periods (not shown).

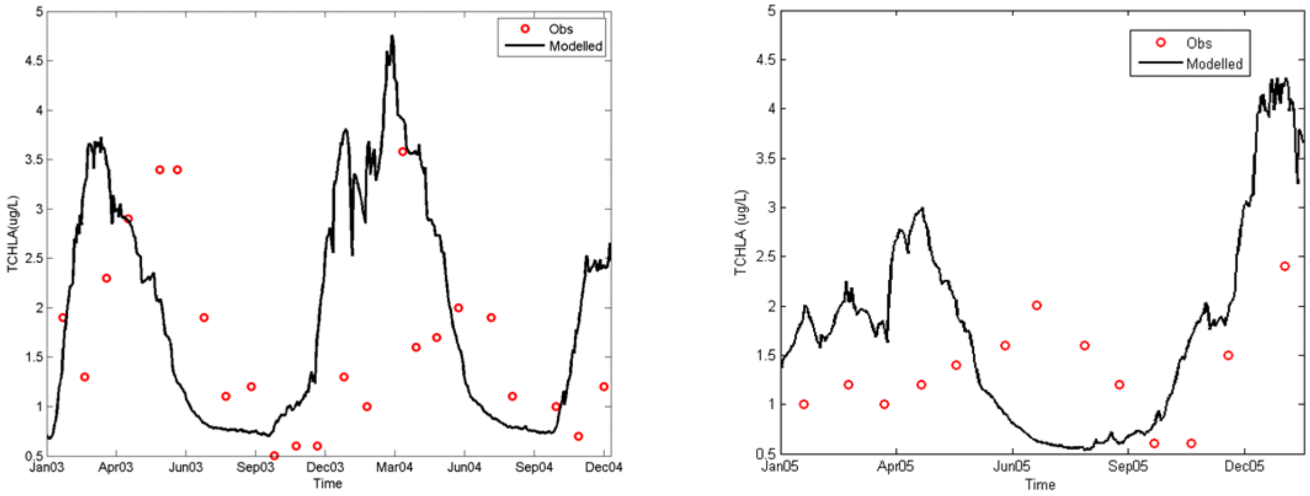


Figure A2.7 Phytoplankton conc. In Lake Tarawera - calibration (left) and validation (right)

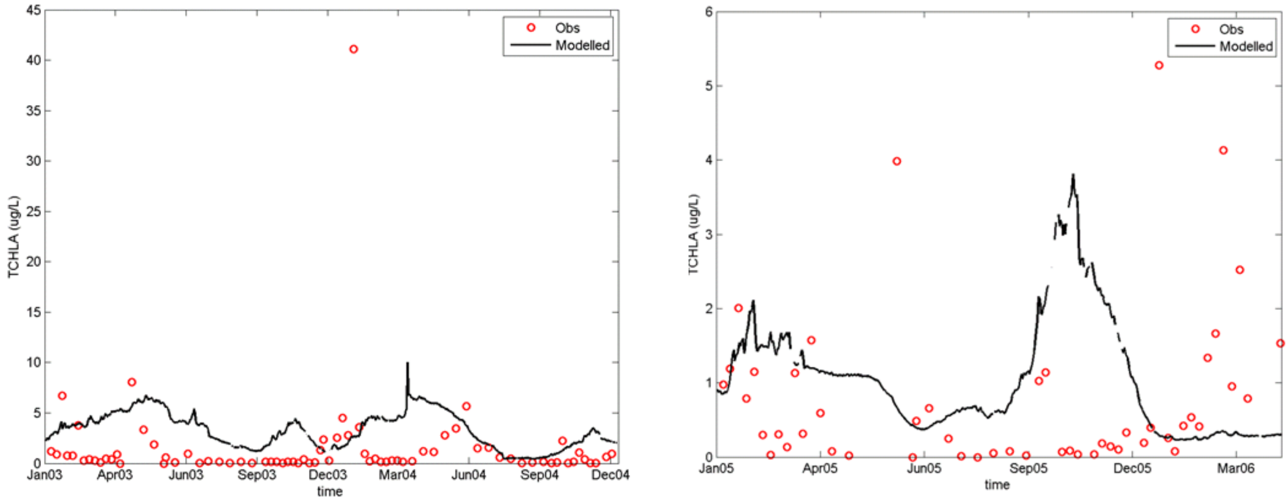


Figure A2.8 Phytoplankton conc. In Mt Bold - calibration (left) and validation (right)

Chapter 3 Effects of warming and nutrients on the thermal structure of a deep, oligotrophic lake

Introduction

The thermal structure of lakes controls the mixing and relative distribution of nutrient resources and gases resources over the water column which can strongly affect lake water chemistry and biota (De Stasio 1996, Adrian et al. 2009, Cantin et al. 2011). Deep and wind protected lakes show a characteristic thermal stratification resulting from surface heating and thermal expansion properties of water. Stratification is caused by the development of a stable vertical density gradient as a result of heating surface waters (Wetzel 2001, Fischer et al. 1979). As air temperature is rising with climate change, the average surface water temperatures are also observed to increase in a linear manner (Schneider and Hook 2010). Depending on lake characteristics and morphology, lakes are warming at a rate similar to the air temperature (small, shallow lakes) or at a rate twice as fast as the air temperatures (ice-covered lakes) (Sharma et al. 2015, O'Reilly et al. 2015). Worldwide air temperature has risen by 1.4–5.8 °C from the pre-industrial level as a result of anthropogenic climate change (Houghton et al. 2001, Lee et al. 2012) and is projected to rise by 0.3 – 4.8 °C by the end of 2100 (IPCC 2013). Accordingly, the water temperatures are expected to rise leading to warmer and more stable water columns.

Thermal stability of lakes can be influenced by the changes in the strength and duration of stratification and depth of the thermocline, which play key roles in determining lake productivity, phytoplankton composition, grazing activity and nutrient distribution within the water column (Coats et al. 2006, Sahoo and Schladow 2008). Strengthened stratification with increasing temperatures can lead to reduced vertical transport of dissolved oxygen resulting in hypolimnetic anoxia. Other important elements in lake ecosystems, such as phosphorus, nitrogen, and heavy metals are regulated by microbial activity, which is controlled primarily by temperature and dissolved oxygen concentration. Under low dissolved oxygen concentrations, reduced redox potential can trigger the release of nutrients from the sediment to the water column and increase internal nutrient loading in the system (Sahoo and Schladow 2008, Zhang et al. 2015). Restriction of nutrient movement under stratified conditions create nutrient depleted epilimnion and nutrient enriched hypolimnion, which can promote the development buoyancy regulating cyanobacteria that can degrade water quality and pose health risks (Paerl and Paul 2012, Reynolds 1984, Carey et al. 2011). Changes in the thermal structure also have important implications for the grazing community by influencing their vertical positioning and depth distribution (Thackeray et al. 2005, Hampton et al. 2014).

Eutrophication is another serious threat to water quality and aquatic ecosystem functioning (Kling et al. 2014, Jöhnk et al. 2008). Negative effects of rising temperatures on waters can be aggravated by increased nutrient loading related to catchment land use changes (Brookes and Carey 2011). Many studies that have focused on lake thermal stability in relation to anthropogenic changes have only considered the impacts of long term temperature variation while not integrating the influence of changing nutrient status. It is well known that trophic status, mostly determined by nutrients, affects lake productivity (Carlson 1975, Nurnberg 1984). High nutrients can change lake characteristics, such as its clarity, increasing phytoplankton biomass (Mazumder 1990, Jones et al. 2005). Water transparency can have a significant impact on the lake physics as it alters the light attenuation coefficient and subsequently, the distribution of heat within the water column (Kumagai et al. 2000, Rinke et al. 2010, Persson and Jones 2008). Due to the changes caused to the lake heat budget through absorption, increases in light attenuation coefficient are found to increase lake temperature gradients, strengthen stability and lower mixing depths (Schindler et al. 1996, Tanzentap et al. 2008). Many deep lakes that are oligotrophic and with high water clarity, can be sensitive to the combined effects of rising temperature and increasing nutrients as they affect the feedback mechanisms between physical and ecological processes.

Previous studies that have assessed the changes in thermal stability have focused on the long term variation in the temperature specifically (Winder and Schindler 2004, Coats et al. 2012, Zhang et al. 2014). Few studies have assessed the impacts of changing phytoplankton biomass and associated variations in light penetration on lake heat content and thermal structure (Schindler et al. 1996, Jones et al. 2005, Tanzentap et al. 2008, Persson and Jones et al. 2008, Rinke et al. 2010). The aim of this study is to determine the individual and combined effects of temperature and nutrient status on lake thermal structure mediated by the fluctuations in the heat fluxes as affected by the variation in light attenuation and phytoplankton abundance. Integrating the effects of effects of temperature-nutrient changes studies that quantify climate change impacts can provide valuable information on the effectiveness of nutrient remediation to offset some of the detrimental effects of climate change (Brookes and Carey 2011, Rigosi et al. 2014). This study focuses on the meso-oligotrophic Lake Tarawera from New Zealand, as a representative lake to predict the effects of future temperature increases and modified trophic status on thermal structure and evaluates the mechanisms that drive changes in thermal stability. It is also the intention to determine whether improvements to the trophic status can reduce the severity of the changes caused to stratification and mixing in the lake resulting from climate change and nutrient alteration.

Methods

Study Site

Lake Tarawera is located in the volcanic plateau of the North Island, New Zealand occupying part of the volcanic region of Haroharo Caldera (Fig 3.1). It is a deep monomictic lake with a maximum depth of 88 m, a volume of 2.3 km^3 and a surface area of 41.4 km^2. The catchment, of 150 km^2, is mainly covered by indigenous forest/scrub and exotic forest (75.5%) and only a small fraction is pasture and urban (Wells et al. 1997, Hamilton et al. 2006, Hamilton et al. 2010). Several small streams (e.g. Wairoa and Waitangi) drain the catchment and several hot springs inflow along the southern shore. Water is also contributed by six adjacent lakes close to Tarawera that play an important role in determining the water quality of the lake. Lake Tarawera is characterized by low summer mean chlorophyll-a values (~1.3 g L^{-1}) and the water quality is good compared to other Rotorua lakes due to low nutrients. However, recent changes in phytoplankton, nutrient concentrations and Secchi disk depth indicate a possible decline in water quality (Hamilton et al. 2006).

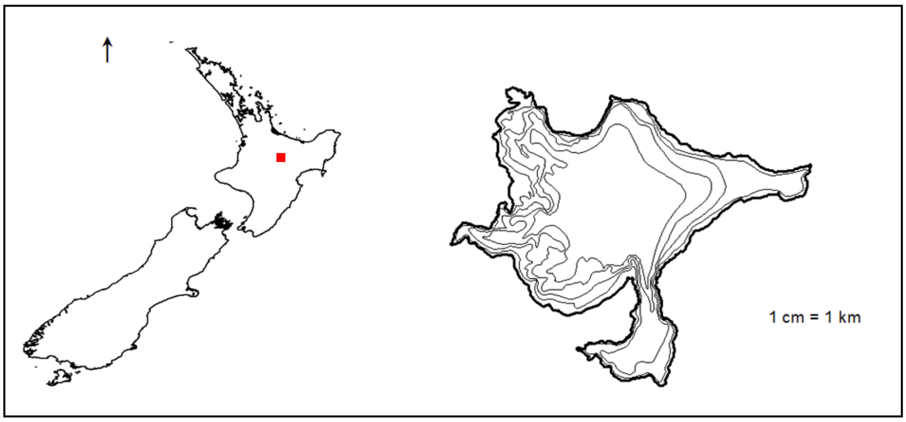


Figure 3.1 Study site and bathymetry of Lake Tarawera (contour lines every 20 m)

Hydrodynamic Model

A hydrodynamic-biogeochemical model was used in this study to conduct the scenario analysis with varying nutrients under climate change. General Lake Model (GLM) was used to model the lake hydrodynamics. GLM is an open-source, one dimensional, vertical stratification hydrodynamic model that can be used to resolve water balance considering the effects of inflows/outflows, mixing and surface heating/cooling to compute vertical profiles of temperature, salinity and density (Hipsey et al. 2014). GLM was coupled with the Framework for Aquatic Biogeochemical Model (FABM) which is used to simulate the nutrient and phytoplankton dynamics within the system to estimate variables that are commonly associated with water quality (e.g. TN, TP, total chlorophyll). The GLM-FABM model framework and parameters are comparable to the dynamic coupled ecological 1-D model DYRESM-CAEDYM (Hamilton and Schladow, 1997, Imberger and Patterson, 1990, Romero et al. 2004), that has been widely applied, to which readers are also referred (Gal et al. 2009, Kara et al. 2012, Rigosi et al. 2011).

Heat fluxes

Surface energy budgets indicate the heat lost or gained through latent heat exchange (Q_e), sensible heat exchange (Q_h) and long (Q_{lw}) and short-wave radiation (Qsw). Resulting net heat flux (Q_{net}) or the effective heat flux, estimated as the sum of the surface energy fluxes plus the net shortwave radiation into the mixing layer, determine lake stratification and mixing processes (MacIntyre and Melack 2010, Likens 2010).

Net heat flux

$$Q_{net} = Q_{sw} + Q_{lw} + Q_e + Q_h$$

Detailed description of the modelled processes can be found in Hipsey et al. (2014) but summarised heat flux calculations pertaining to the study that are computed in the model are shown below.

Shortwave radiation

$$Q_{sw} = (1 - \alpha_{sw})\, f_{sw} f_{par} Q_s e^{-K_w\, z}$$

where α_{sw} is the albedo, f_{sw} is a scaling factor that may be applied and adjusted as part of the calibration process, f_{par} is the photosynthetically active radiation (PAR) (45% of the incident light) and K_w is the light extinction coefficient (m^{-1}) (Kirk 1994). K_w is dynamically adjusted in the model depending on the variability in the phytoplankton concentrations and dissolved and particulate constituents. Individual contribution of various components to the overall Kw is not partitioned. For the initial hydrodynamic simulation an average K_w value was estimated with available PAR data, using $I_z = I_0^{-K_w z}$, where I_z is the irradiance at given depth z and I_0 is the irradiance at surface. The estimated average K_w value of 0.2 m^{-1} is comparable to values estimated for Lake Tarawera and other oligotrophic Rotorua lakes (Butterworth 2006, Hamilton et al. 2010).

Longwave radiation

$$Q_{lw} = Q_{lw_{in}} - Q_{lw_{out}}$$
$$Q_{lw_{in}} = (1 - \alpha_{lw})\, \varepsilon_a \sigma [T_a + 273.15]^4$$
$$Q_{lw_{out}} = \varepsilon_w \sigma [T_s + 273.15]^4$$

where α_{lw} is the longwave albedo (0.03) (Henderson-Sellers 1986), and the emissivity of the atmosphere is computed considering emissivity of cloud-free conditions (ε_a) based on air temperature and humidity, σ is the Stefan-Boltzmann constant (5.6697×10^{-8} W m^{-2} K^{-4}) and T_a is air temperature (°C). ε_w is the emissivity of the water surface (0.985) while T_s is the temperature of the water surface (°C).

Sensible heat flux

$$Q_h = -\rho_a c_p C_H U_x\,(T_s - T_a)$$

where ρ_a is density of air (kg m^{-3}), c_p is the specific heat capacity of air (1005 J kg^{-1} °C^{-1}), C_H is the bulk aerodynamic coefficient for sensible hear transfer (~1.3x10^{-3}) and U_x is the wind speed (m s^{-1}) from a reference height.

Latent heat flux

$$Q_e = -\rho_a C_E\, \lambda\, U_x \frac{k}{p} (e_s[T_s] - e_a[T_a])$$

where C_E is the bulk aerodynamic coefficient for latent heat transfer (0.0013), e_a is the air vapour pressure and e_s is the saturation vapour pressure (hPa) at the surface layer temperature and k is the ratio of molecular weight of water to molecular weight of air (0.622).

Model Simulations

Model simulations were carried out from 1 January 2003 to 12 February 2006 with two years being used for calibration and the rest used for validation. Daily meteorological input data for the model was obtained from the Rotorua Airport located approximately 9 km away from the study site. Daily averages of air temperature (T °C), wind speed (WS m s^{-1}), short wave radiation (SW W m^{-2}) and cloud cover (CC%) were used as the input data for the model (Fig

3.2). To avoid the discrepancies between the local weather data and remote weather data, in lake surface wind speed, air temperature and relative humidity data for Lake Tarawera that were recorded for a limited period between 2009 and 2012 were used to correct meteorological data prior to model simulations.

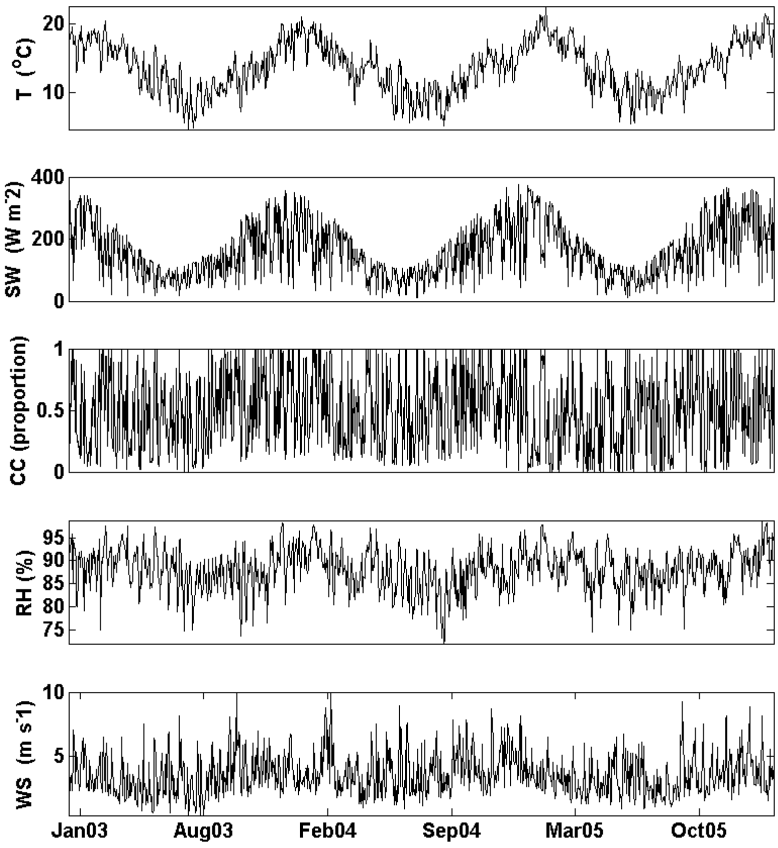


Figure 3.2 Meteorological data used in the model including air temperature (T °C), wind speed (WS m s^{-1}), short wave radiation (SW) (W m^{-2}) and cloud cover (CC%)

Four main inflows (grouped into rain, cold water, geothermal and ungauged) and a single outflow were defined based on the observations from the monitoring sites (Hamilton et al. 2006) (Fig 3.3). In addition to temperature records, other variables measured monthly and used for validation include: dissolved oxygen, measured from 0 to 83 m every 1-2 m; total and dissolved nutrients consisting of total phosphorus (TP), total nitrogen (TN), nitrate (NO_3) and filterable reactive phosphorus (PO_4) sampled at three depths (0, 30 and 65 m). Phytoplankton biomass was measured as total chlorophyll-a integrated over a surface layer (0 to 17 m).

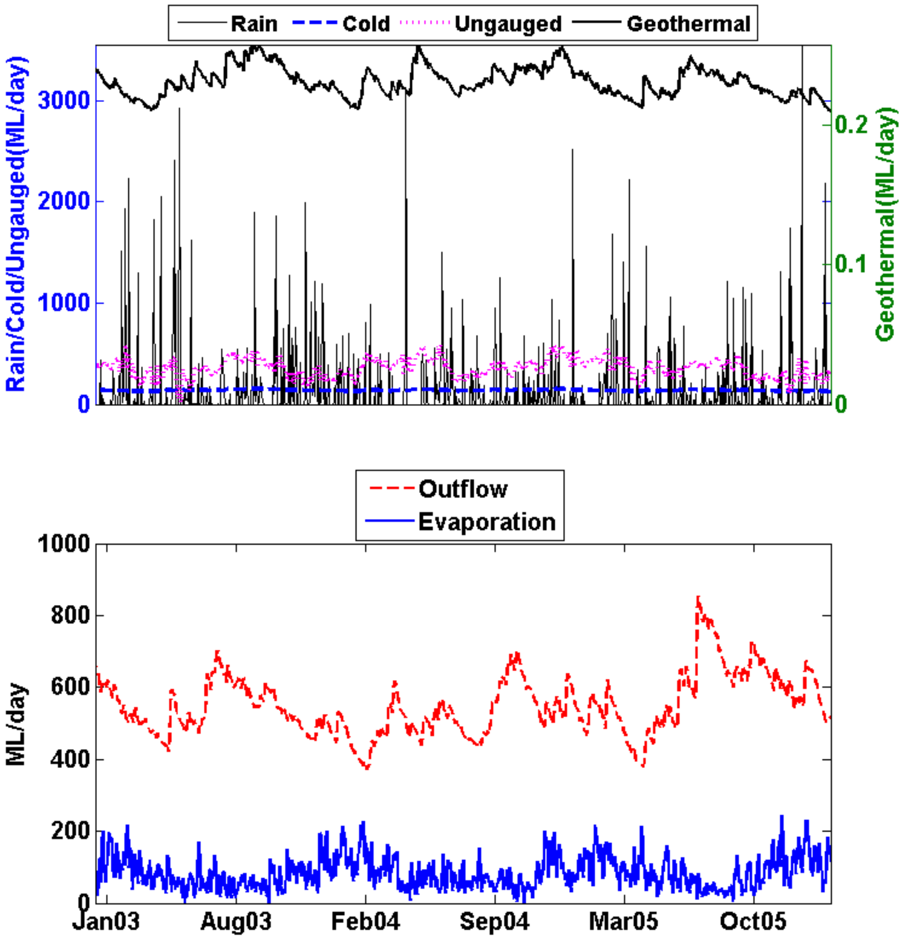


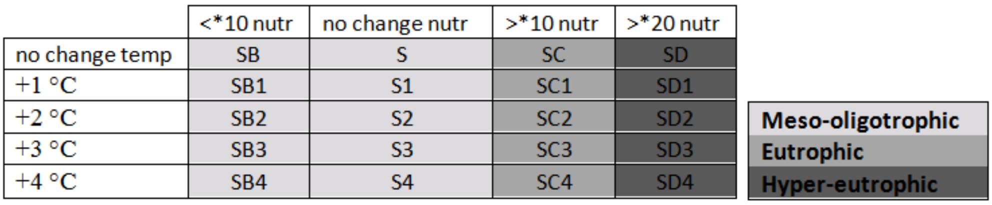
Figure 3.3 Top diagram presents the average daily inflows consisting of main gauged inflow (cold), geothermal input (geothermal), ungauged inflows (ungauged) and rainfall. Bottom diagram presents the withdrawals from the site consisting of the main outflow and evaporation

Model calibration was carried out for a period of two years extending from 1 Jan 2003 to 31 Dec 2004 and validation was conducted from 1 Jan 2005 to 12 Feb 2006. Parameters were manually adjusted, within a set range determined using literature, until satisfactory results were obtained from model simulations, following the comparison with observed data. The used parameters were within the ranges defined in other studies done using a similar 1D hydrodynamic model (Gal et al. 2009, Trolle et al. 2011, Burger et al. 2008). Model performance was estimated using graphical visualisation, and qualitatively by evaluating coefficient of determination (r^2) and calculating the Root Mean Square Error (RMSE) values between the simulated and the observed. The parameters were adjusted in order to obtain the minimal RMSE while maintaining the consistency with the observed data.

Scenarios

To determine the impacts of nutrients and temperature on the thermal structure of the lake, a combination of scenarios with increasing temperatures and varying nutrients were carried out. The temperature increases were guided by the IPCC projections and the nutrients were increased and decreased by 10 and 20 fold in order to cause a change in the trophic status of the system (Table 3.1). Trophic status classification was based on TP concentrations (Nürnberg, 1996): oligotrophic (<10 µg L^{-1}); mesotrophic (10≤TP ≤30 µg L^{-1}); eutrophic (30<TP ≥100 µg L^{-1}), and hyper-eutrophic (TP>100 µg L^{-1}). The temperatures were increased by 1-4 °C and TP was increased and decreased by 10 and 20 fold and TN was increased accordingly as guided by the Redfield ratio (Redfield 1958).

Table 3.1 Matrix of the temperature (temp) and nutrients (nutr) scenarios simulated. <*20 nutr and <*10 nutr refer to a decrease in nutrients by 20 and 10-fold, while >*10 nutr and >*20 nutr refer to an increase in nutrients by 10 and 20 fold, respectively. Scenario S (no change in nutrients and temperature) represents the base case



	<*10 nutr	no change nutr	>*10 nutr	>*20 nutr
no change temp	SB	S	SC	SD
+1 °C	SB1	S1	SC1	SD1
+2 °C	SB2	S2	SC2	SD2
+3 °C	SB3	S3	SC3	SD3
+4 °C	SB4	S4	SC4	SD4

Meso-oligotrophic
Eutrophic
Hyper-eutrophic

Analysing lake thermal structure

Following scenario modelling, characteristics related to thermal structure of lakes were assessed using the Schmidt stability index and thermocline depth. The changes in the magnitude of thermal stability, mixing and onset and duration of stratification were determined to gain an understanding of how thermal regime of oligotrophic lakes would respond to a changing environment.

The Lake Analyzer program was used to calculate indices related to mixing and stratification (Read et al. 2012). The program uses information on bathymetry and time series of wind and water temperature measurements to calculate user defined output such as thermocline depth and Schmidt stability. Wind records for the period between 01/01/2003-31/12/2004 were obtained from Rotorua Airport. In the absence of high frequency data, temperature measured monthly at discrete depths (0 to 83 m at 1 m intervals) were used. Lake Analyzer has been used to study mixing dynamics of a number of lakes of various sizes located in numerous geographical locations.

Strength of thermal stratification is estimated using the Schmidt stability (St) index which calculates the energy or mechanical work required to completely mix the water column (Read et al. 2012, Winder and Schindler 2004). A value of 0 indicates isothermal conditions while higher values indicate stratified water columns. Thermocline depth is a characteristic feature of stratifying lakes and is commonly used to assess the influence of prevailing conditions on thermal structure (Hambright et al. 1994, Zhang et al. 2014). There are various definitions and terminology used to explain lake characteristics such as the depth of the mixed layer or the depth of the thermocline (Read et al. 2011). Density or temperature gradient threshold used for the identification of thermocline depth or surface mixed layer depth is arbitrary (Fee et al. 1996, Coloso et al. 2011, Zhang et al. 2014). Following Lamont et al. (2004), who noted the density variation below the surface layer to be less than 0.1 kg/m^3, the density gradient criterion was defined as 0.1 kg/m^3 in the current study. Water density is calculated in Lake Analyzer using discrete temperature-depth measurements and a discrete maximum change in density with respect to changes in depth is identified by using weighting from adjacent locations. For the purpose of this study, the maximum density gradient relative to depth as computed by Lake Analyzer program is used as the thermocline depth.

Derived measures of lake properties were calculated as below:

1) Schmidt Stability (St):

$$\mathrm{St} = \frac{g}{A_S} \int_{0}^{z_D} (z - z_v)\rho_z A_z \partial z$$

where g is the acceleration due to gravity, A_s is the surface area of the lake, A_z is the area of the lake at depth z, z_D is the maximum depth of the lake, and z_v is the depth to the centre of volume of the lake.

2) Thermocline depth (thermD):

For k number of thermistor measurements, $i = 1 \xrightarrow{to} i = k - 1$, water density ($\rho$) based on temperature and salinity is calculated as follows,

$$\frac{\partial \rho}{\partial z_{i\Delta}} = \frac{\rho_{i+1} - \rho_i}{z_{i+1} - z_i}$$

which applies to the depth characterized by $z_{i\Delta} = (z_{i+1} + z_i)/2$, where $z_{i\Delta}$ represents a midpoint depth between thermistors i and i+1. If the maximum $\partial\rho/\partial z_{i\Delta}$ is found when $i = \zeta$ for discrete thermistor measurements, then the true depth of the maximum change in density (thermD) is presumed to occur within the bounds defined by the two thermistors at which the discrete measurements were taken ($z_\zeta < z_T < z_{\zeta+1}$). This presumption is further improved by weighing the magnitudes of the difference between the maximum calculated density change and the adjacent calculation

$$\text{thermD} \approx z_{\zeta+1}\left(\frac{\Delta\rho_{+1}}{\Delta\rho_{-1} + \Delta\rho_{+1}}\right) + z_\zeta\left(\frac{\Delta\rho_{-1}}{\Delta\rho_{-1} + \Delta\rho_{+1}}\right)$$

where $(z_{\zeta\Delta+1} - z_{\zeta\Delta})/(\partial\rho/\partial z_{\zeta\Delta} - \partial\rho/\partial z_{\zeta\Delta+1})$ has been simplified to $\Delta\rho_{+1}$ and $(z_{\zeta\Delta} - z_{\zeta\Delta-1})/(\partial\rho/\partial z_{\zeta\Delta} - \partial\rho/\partial z_{\zeta\Delta-1})$ to $\Delta\rho_{-1}$.

Effects of increasing temperatures and altered nutrient regimes were determined by assessing the changes in the onset and the duration of stratification by defining threshold values for St and thermD. Thresholds of St and thermD used to determine stratification and mixing are mostly arbitrary, varying depending on the lake characteristics (Winder and Schindler 2004, Coloso et al. 2011, Wang et al. 2012, Zhang et al. 2014). In this study, we have used the accessibility of phytoplankton to light as a guideline when determining the approximate thresholds for St and thermD to identify a stratification event. The Euphotic zone is defined as the depth beyond which light levels fall below 1% of the surface irradiance and is an important regulator of the light available for phytoplankton growth (Scheffer 2004). The lake was considered to be first stratified when the thermocline depth drops below 2.5*Z_{eu} and the corresponding thermD and St values when bottom of Z_{eu}*2.5≥thermD were estimated to be 55 m and 600 J m^{-2} respectively. We considered the onset of stratification as the first day of spring-summer period (Sept 2003-Feb 2004) when the St exceeded 600 J m^{-2} and thermD was less than 55 m. The duration of stratification was determined by the number of days when the St and thermD were above and below thresholds respectively during the period of spring-autumn (Sept 2003-May 2004).

Results

Performance of the model - calibration and validation

Mixing and stratification events were well captured by GLM, and aligned with the temperature profiles of the interpolated field data from Lake Tarawera (monthly at 1 m intervals) (Fig 3.4). thermD and St calculated using Lake Analyzer generally coincided with the visually observed temperature gradients (Fig 3.4). Details on the calibration and validation of the model related to temperature, DO, TP, TN, NO_3 and PO_4 are discussed in Chapter 2.

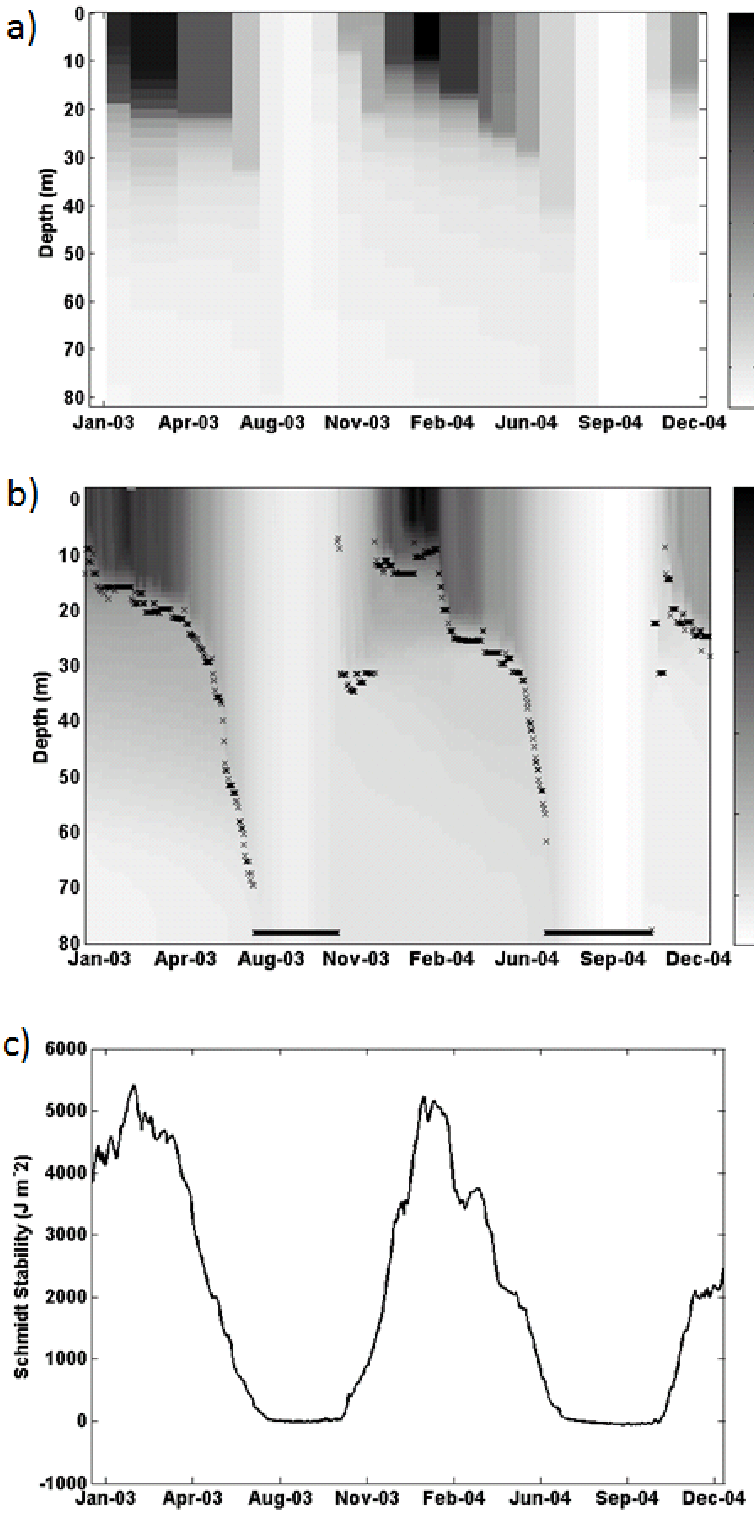


Figure 3.4 Interpolated temperature profiles using the observed temperature-depth data (a), temperature-depth profile simulated using GLM and black crosses (x) presenting thermD computed using Lake Analyzer (b), Schmidt stability computed using Lake Analyzer (c)

Changes in chlorophyll a, light attenuation and euphotic depth

Annual average total chlorophyll a (TCHLA) concentrations as the temperatures and nutrients increased, with values increasing from 7.6 μg L^{-1} in the reference scenario to 22.3 μg L^{-1} under the warmest and nutrient enriched scenario (SD4) (Fig. 3.5). Steady increase in mean winter TCHLA can be noted under nutrient enriched conditions, while mean winter TCHLA under low nutrient conditions varied by less than 1 μg L^{-1}. In the base scenario, the highest mean TCHLA in the studied oligotrophic system is observed in the summer-autumn between December-May (5.6 μg L^{-1}), which decreased as the temperatures increased (Fig. 3.5). In scenarios with a temperature increase <3 °C, summer-autumn phytoplankton biomass was higher than spring phytoplankton biomass, but this reversed as the temperatures increased beyond 2 °C, indicating an advancement in the growth season under a warming climate.

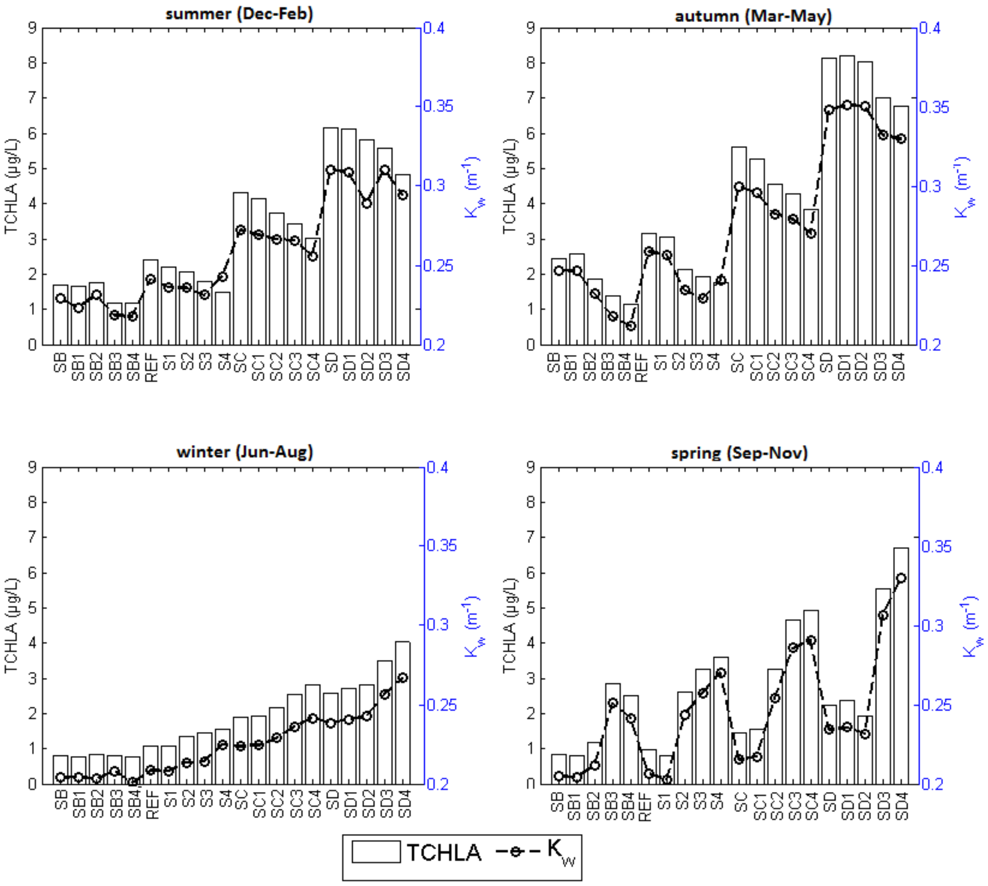


Figure 3.5 Seasonal variation in TCHLA and K_w under different scenarios

The extinction coefficient of light (K_w) varied between 0.19 and 0.47 m^{-1} and followed a similar trend to TCHLA, showing a strong relationship between the two variables under different scenarios (mean $R^2 = 0.9$, $p<0.001$) (Fig. 3.6). Annual mean K_w in the reference scenario is 0.23 m^{-1} and show minor seasonal differences, with K_w being the lowest in winter and spring seasons (<0.21 m^{-1}) and the highest during the summer and autumn overturn (>0.24 m^{-1}). In accordance with the increasing phytoplankton growth, K_w values exceeded 0.3 m^{-1} as the trophic state changed to hyper-eutrophic.

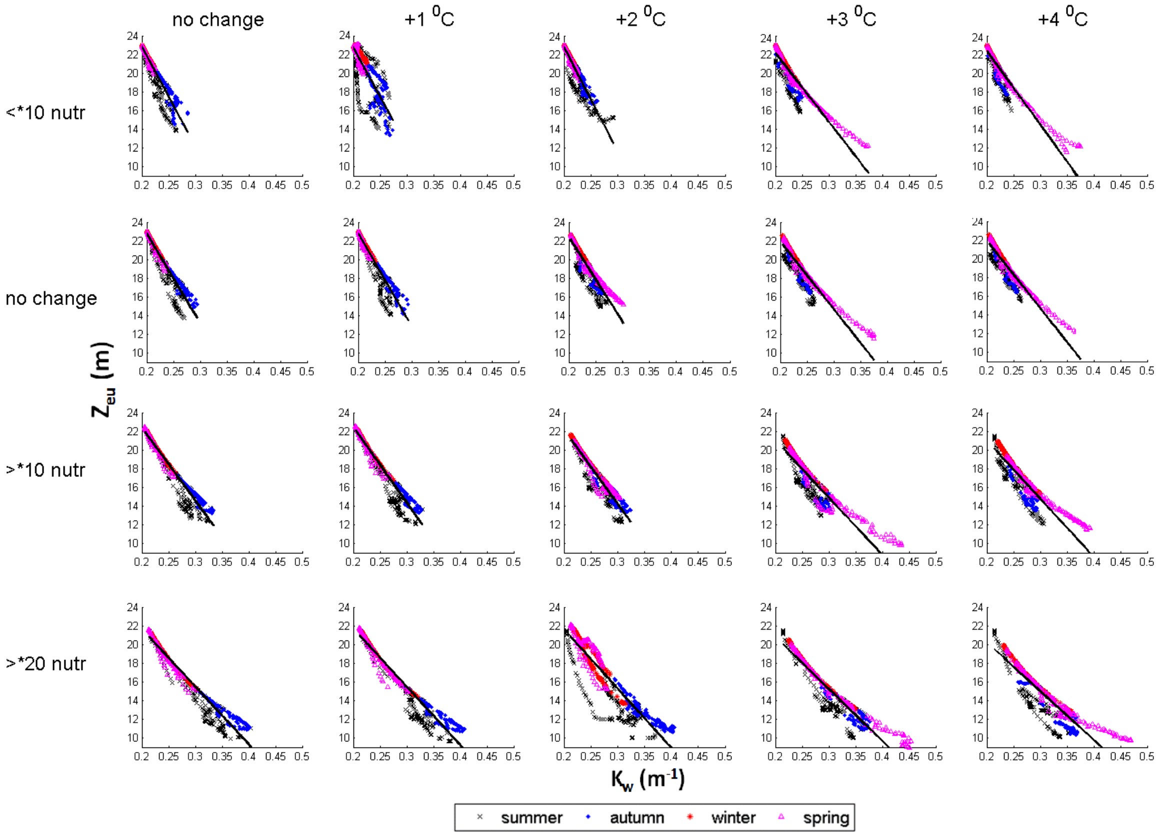


Figure 3.6 Relationship between K_w and Z_{eu}

Oligotrophic Lake Tarawera has a Z_{eu} of ~21.5 m under stratified conditions which decreases to ~16 m during mixed events. Decreasing water transparency as a result of increasing K_w lowered the Z_{eu} and the correlation between the two variables was high ($R^2 > 0.8$, $p < 0.001$) (Fig.3.6). Decreases in the gradients (slope) are most notable in the autumn and spring seasons as the K_w values increase and Z_{eu} decreases in concomitant with the increase in TCHLA, especially as the temperatures increase above 2 °C under nutrient rich conditions.

Water temperature

Seasonal variation in maximum temperatures observed in the surface (surface integrated 17 m) and bottom waters (bottom integrated 65-80 m) in Tarawera under different scenarios is presented in Fig. 3.7. Surface water temperatures in the base case scenario displayed seasonal variation with summer temperatures ranging from 18 to 20 °C and winter temperatures ranging from 10 to 12 °C. The surface water temperatures increased in a linear manner as temperatures increased and the maximum surface water temperature increased in all scenarios by 2.5 °C on average. Most prominent increase in surface temperatures is noted in spring for all scenarios. Spring surface temperature in the hyper-eutrophic lake under the highest temperature rise was 0.4 °C higher than that of the oligotrophic lake. The nutrient reduced lake also recorded lower surface summer-autumn temperatures (mean <0.1 °C) compared to the base scenario.

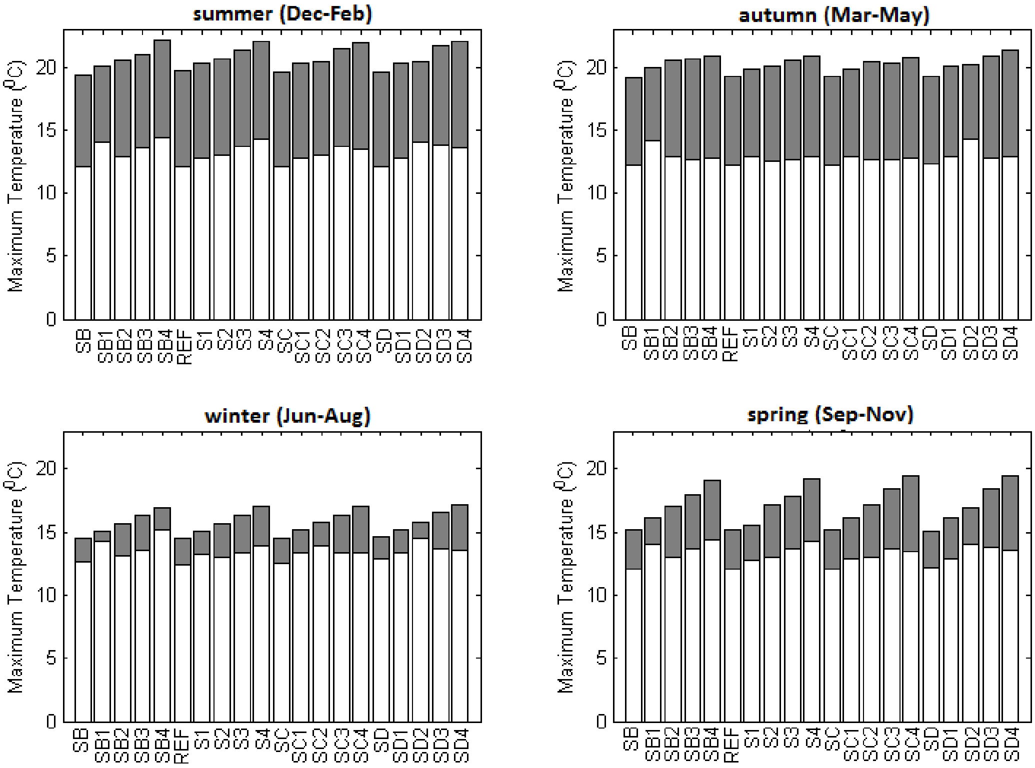


Figure 3.7 Seasonal maximum surface (filled) and bottom (hollow) water temperatures (°C)

The trend in bottom water temperature variation under different scenarios is not clear, but an average increase in maximum temperatures by 1.5 °C in summer is observed. Under a temperature rise of 4 °C, the highest bottom water temperature of 15.3 °C in winter was observed under reduced nutrients conditions. The highest temperature difference between the maximum surface and bottom waters of 8.5 °C, observed in summer-autumn seasons in the SD4 scenario (Fig. 3.7), is an increase in the temperature difference by 1.1 °C relative to the base scenario.

Thermal structure

Figure 3.8 presents the changes observed in the thermal stability when the temperatures and nutrients were varied. In the base case scenario, an average maximum of 5300 J m^{-2} was observed during summer, when the lake is stratified. As the temperatures increased, the overall St also increased with the maximum Schmidt stability values ranging between 5700-7000 J m^{-2}, observed during summer stratification. The St showed an average increase of 1430 J m^{-2} in the SD4 scenario relative to the base case. Changes in St observed under varied nutrient loads were minute compared to the changes in St that were observed when the temperatures were increased. Considering the changes in the nutrient loading, the highest overall increase in St relative to the reference scenario (30 J m^{-2}) was observed under hyper-eutrophic conditions. Under hyper-eutrophic conditions, increase in temperature had a minor influence in the St. Under a 4 °C increase, the scenarios with the highest nutrient loading experienced only a mere increase of 180 J m^{-2} relative to the scenario with no change in nutrients.

Under rising temperatures, a distinct drop in St was observed during the peak of stratification, with the above descent being more pronounced in the second year of simulation. The magnitude of the average decrease in St ranged from 1200-1750 J m^{-2} while the duration ranged from 5-41 days between the scenarios with 1 °C in temperature and scenarios with a 4 °C increase in temperature. This occurrence was observed even in the scenarios when the nutrients were lowered by 10 folds, except under 1 °C increase in temperature, indicating that this is potentially an effect of temperature rise than of nutrient alterations. However, the decrease was only 10-15% of the maximum St observed under all nutrient states.

The onset of stratification is indicated by the first day of the year when the St exceeded the threshold value of 600 J m^{-2}. In the base scenario was observed to be on the 3/11/2003 (day 306) and the stratification persisted for 212 days. In general, the onset of stratification advanced and the duration of stratification increased compared to the base but this variation was less intense under a low temperature rise of 1 °C in all trophic states. The onset of stratification advanced to as early as the beginning of September (02/09/2003) in all scenarios and the duration of stratification (> 600 J m^{-2}) increased from 212 days to 274 days, in the 4 °C increase scenario.

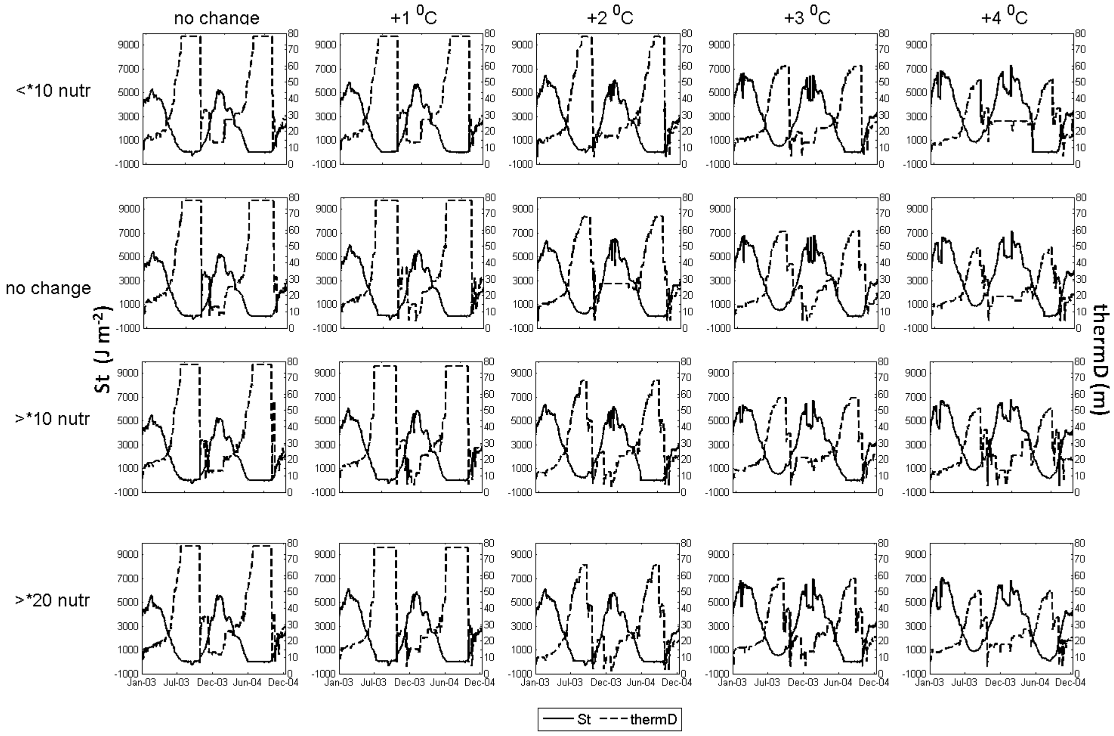


Figure 3.8 Change in Schmidt Stability (St) (J m^{-2}) and thermocline depth (thermD) (m) under different scenarios

In the base case, the deepest thermocline depth of 69.5 m is observed in mid-July 2003, just before the lake became isothermal. Mixed conditions lasted for around 3 months till the end of October 2003 (Fig 3.8). The shallowest, stable thermocline of 7.4 m was observed during the stratified period at the end of January. Daily fluctuations in the thermocline depth were observed during the study period, and these were more notable during the transition period from spring to summer. In general, thermD decreased as the temperatures rose during summer, with the lowest average thermD of 16-17 m during the spring-summer period observed in nutrient enriched scenarios (SC4-SD4). Under rising temperatures, mixing strongly reduced during winter with the thermocline depth dropping by 28 m compared to the base case. The highest summer thermocline depth of 25 m under a 4 °C temperature increase was observed when the nutrients were reduced (SB4). Furthermore, except in the oligiotrophic state scenarios, a thermocline was detected even in winter period in all scenarios with a temperature increase above 1 °C. Under a temperature rise by 2 °C, the nutrient poor lake (<*10 nutr) experienced completely mixed conditions, though the duration was shorter compared to the less warmer scenarios. But as the temperatures rose beyond 2 °C, complete overturning was absent in the oligotrophic lake and a persistent shallow thermocline was detected as similar to the other nutrient scenarios.

As measured by the thermocline depth, thermD, the onset of stratification in the base case was observed on the 23/10/2003, which is 11 days before the stratification in relation to St was observed. However, similar to St, the onset of stratification advanced to early September with the increase in temperatures in all scenarios. However, the progression of stratification under 1, 2 or 3 °C increase in the oligotrophic lake was less (by 10 days) while in the nutrient enriched conditions, stratification occurs one month in advance relative to the scenarios with no temperature rise. As it starts to warm, the number of days when the thermD was less than 55 m during the spring-autumn period also increased with the duration of 223 days in the base case scenario rising to 274 days under 4 °C increase in temperature, as observed with St. A delay in the onset and lowered duration of the thermocline depth <55 m were observed under low nutrients and a temperature rise of 2 and 3 °C. Small to no change in the onset and duration was observed as a result of nutrient variation under temperature increases by 4 °C.

Heat fluxes

A monthly running mean was applied to all the relative heat fluxes to minimize the scatter and identify the seasonal patterns visibly (Fig. 3.9). In the base scenario, highest net heat (Q_{net}) loss of about 75 W m^{-2} is observed in June and the highest gain of about 150 W m^{-2} is observed in December. Under increasing temperature and nutrients, the highest change in the net flux is observed through winter, between autumn and spring. It is to be noted that the net gain observed during colder seasons under changed trophic status and warming condition is due to reduced loss in heat content in comparison to the base scenario. In the most nutrient enriched lake under +4 °C, the maximum gain in net heat storage was 32 W m^{-2}. In the same scenario, from mid spring (October) towards the end of summer (January), there is a maximum loss in net heat content in the lake by a similar amount of 37 W m^{-2}. Latent heat flux contributed to more than half of the total heat loss during spring-summer period, while the net heat gain in autumn-winter period was due to an increase in sensible and latent heat, followed by an increase in net longwave radiation. Though much of the flux changes appear to be mostly resulting from increasing temperatures, some variation in fluxes could be found between lakes of different trophic status. For instance, the most nutrient enriched lake had a net heat gain of about 7 W m^{-2} in autumn and experienced a loss of net heat of about 12 W m^{-2} in summer relative to the nutrient poor lake (<*10 nutr) under a 4 °C temperature rise. Thus, the overall increase in heat content in the oligotrophic lake was higher (8.5 W m^{-2}) compared to the increase in net heat in the hyper-eutrophic lake (1.47 W m^{-2}). Changes in the shortwave radiation were largely minor in comparison to the changes in other fluxes, indicating that other fluxes mainly drive the changes in the lake heat budget as the trophic status changed under warming. Increased gain in net heat during cooling periods had a strong positive effect on the thermal stability observed in the spring-summer period ($R^2 = 0.84$, $p<0.005$).

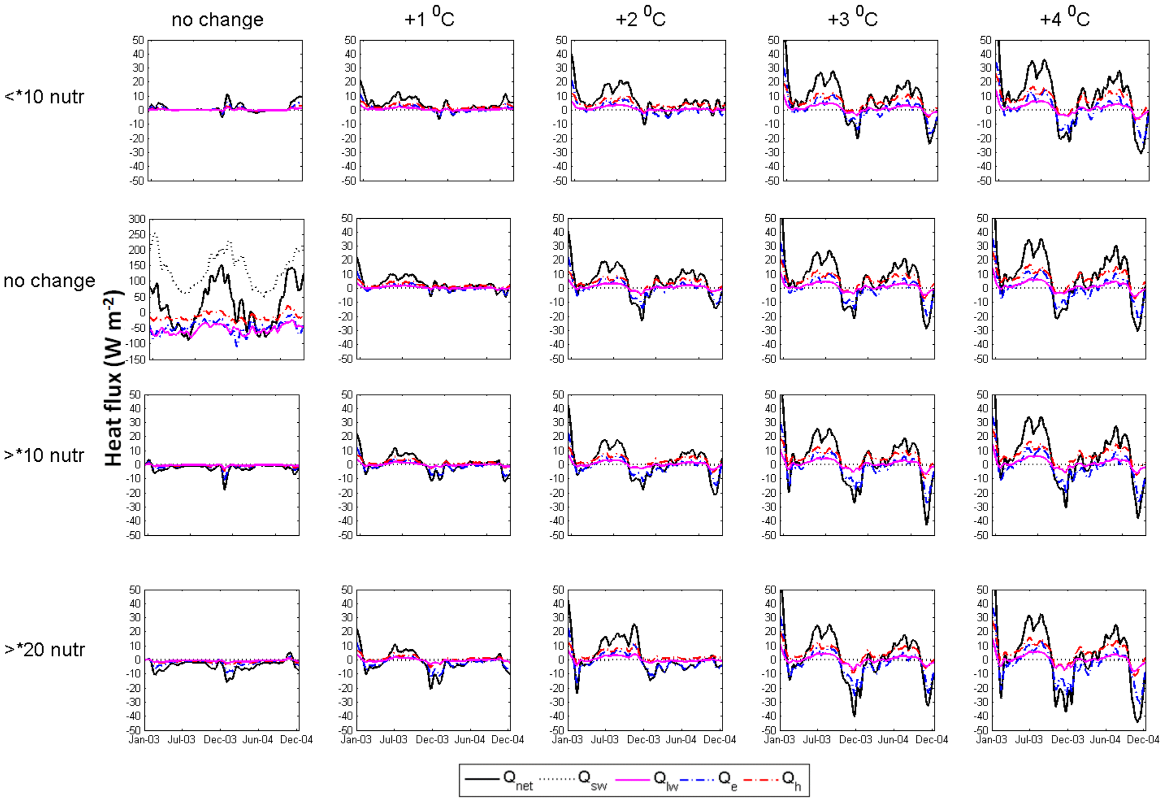


Figure 3.9 Time series of heat fluxes presented as monthly running means for the simulated years 2003 and 2004. Variation in heat fluxes are given as a change relative to the base scenario (1st column, 2nd row) estimated as $Q = Q_{scen} - Q_{base}$. Base scenario contains absolute values.

Discussion

Increased water temperatures, heightened by increased nutrient loading, resulted in intensified thermal stability accompanied by advanced onset and increased duration of thermal stratification in the oligotrophic Lake Tarawera. Average year round surface water temperature of Lake Tarawera increased as a result of increasing air temperatures and is in consistent with the other studies where large, deep lakes were found to be warming with climate change, (Sahoo and Schladow 2008, Winslow et al. 2015, Sharma et al. 2015). Hypolimnion temperatures in Lake Tarawera showed inconsistent variation, but showed a gradual increase over time. De Stasio et al. 1996 and Honzo and Stefan 1996 also observed that bottom-water temperatures were more variable, irrespective of the atmospheric changes and the variability was mostly associated with the mixing events in spring and lake morphometries. The highest temperature difference between the surface and bottom temperatures in Tarawera was observed under the nutrient enriched scenario. This creates a feedback mechanism, where strong temperature disparity further intensifies the barrier between the epilimnion and hypolimnion, leading to intense thermoclines and highly stable water columns that persist for longer. Such characteristic were observed in Lake Zurich from the 1950s to the 1990s where increased warming rates in the epilimnion (upper 20 m) and lower warming rates in bottom waters (below 20 m) led to a 20% increase in thermal stability and caused stratification to extend in duration by 2-3 weeks (Livingstone 2003).

Advancing vernal establishment of thermal stratification and continuous increase in water temperatures lead to an earlier growing season and accelerated growth of phytoplankton as indicated by higher chlorophyll levels in the winter-spring period. Light attenuation followed a similar pattern to that of primary production and varied between 0.2-0.4 m^{-1}. Light attenuation and associated solar absorption are important components that contribute to the heat content of water and thermal stratification characteristics (Mazumder et al. 1990). Regardless of the temperature increase, highest surface temperatures were found in the nutrient rich scenarios while the lowest were recorded under nutrient poor conditions. The thermal structures of a lake is found to be sensitive to changes in K_w of less than 0.5 m^{-1} (Heiskanen et al. 2015, Rinke et al. 2010, Persson and Jones 2008) as conductive fluxes influence the overall lake heat budgets. The increase in daily shortwave fluxes observed in Lake Tarawera was very minor (<0.05 W m^{-2}) and may appear to be unaffected by water transparency, given that solar radiation was kept constant in all scenarios. It has been suggested that extinction coefficient has no significant effect on the thermal structure of large lakes with a surface area of >500 ha (Fee et al. 1996). However high surface water temperatures observed under increased nutrients and high bottom water temperatures observed under reduced nutrients in Lake Tarawera indicate heat penetration into the water layers is affected by transparency. High temperatures and high light attenuation increase radiative absorption which accumulates heat in the epilimnion during day time, which is then readily lost to the atmosphere (Hocking and Straškraba 1999, Jones et al. 2005). But in clear lakes, heat absorbed by the hypolimnion is lost slowly due to the lack of contact with the atmosphere and the energy loss via conduction is slow (Hocking and Straškraba 1999). Thus there is a gradual increase in heat content stored in deep layers, as noted by the increase in bottom water temperatures, which subsequently leads to an overall increase in lake net heat content.

Lake Tarawera experienced high evaporative losses during spring-summer period as the atmospheric temperatures increased. The lake experienced only a minor change in the annual mean lake heat content (gain of <1.5 W m^{-2}) as a result of increasing temperatures and nutrients, but showed atypical changes in the seasonal heat fluxes. In the spring-summer period, when the highest surface temperatures and highest K_w are experienced, rapid warming of the lake surface occurs. Warming lake surfaces lose more heat through sensible, latent and longwave fluxes and subsequently lead to a loss of heat content. Associated increase in stratification and shallow thermocline mean greater surface area per given surface layer volume, which further facilitates the loss of heat (Bowling 1990, Mazumder 1990, Houser 2006). Stronger stratification also restricts the transfer of heat to deeper layers and lower the atmospheric energy input to the lake as the energy exchange between lake and atmosphere rapidly reach a stable state (Rinke et al. 2010).

Evaporative losses were the major contributor to the net heat loss during spring-summer period in Lake Tarawera, as temperatures and nutrients increased. Previous studies that have assessed the sensitivity of lake thermal structure to changing light attenuation found a similar loss of heat during warming through both back radiation and evaporation. Using a modelling study, Persson and Jones (2008) showed an increased loss in latent heat flux at the beginning of summer under high K_w values. A similar study by Rinke et al. (2010) found high K_w associated with increasing eutrophication leading to higher surface temperatures, stronger stratification, low thermocline depths and reduced heat content in Lake Constance during its heating phase. Change in the type of heat flux and the magnitude of change are dependent upon the meteorological conditions and the morphometry (Bowling 1990, Jones et al. 2005).

In contrast to the losses in heat content through summer, the highest gain in the net heat storage occurred during autumn and winter due to reduced quantity of outgoing heat. Lower thermal stability and deeper thermocline during these seasons mean less resistance to vertical mixing and consequent integration of climate signal into the deep water layers. This increase in heat storage combined with a decrease in latent heat flux, sensible heat and longwave emission due to cool water surface can result in a net increase in overall thermal content. This was followed by a loss in heat during spring-summer seasons as described above. When considering the overall longterm variation, the hyper-eutrophic lake showed a relatively minor increase in the net heat content under increased temperatures whereas the nutrient poor lake, which showed higher gains and fewer losses in the seasonal fluxes, showed a greater increase in the overall heat flux. Although this partially supports some studies that have observed greater resistance of eutrophic, coloured lakes to increasing temperatures (Tanzentap et al. 2008), Lake Tarawera does not show a cooling effect under increased temperatures and light attenuation. Furthermore the opposing trends in seasonal heat fluxes is an indication that surface water temperature does not directly reflect the patterns in heat fluxes due to heat storage. Fink et al. (2014), who analysed the climate change induced heat flux alterations in Lake Constance over the period of 1984-2011, found the change in total heat budget to be relatively minor due to the counteracting incoming and outgoing heat fluxes under slowly increasing water temperatures.

The net heat flux gain earlier in the season (winter-autumn) under climate change causes an earlier onset of stratification, which subsequently has a significant impact on the chemical and biotic component of the system. The overall thermal stability in summer increased from 5300 J m^{-2} in the base case scenario to 7000 J m^{-2} in the SD4 scenario in Lake Tarawera. Under warm, nutrient rich conditions, the thermocline depth decreased, severely reducing winter mixing and resulting in a persistent thermocline that extended into the spring-summer period. Such strengthened stratification and reduced thermocline depth have been observed in other lakes as a result of increasing air temperatures (Zhang et al. 2014, Stainsby et al. 2012, O’Reilly et al. 2003). As the temperatures increased by 2 °C and beyond, Lake Tarawera did not mix completely during winter resulting in a deep thermocline. McCormick (1990) applied a one-dimensional temperature model to show that climate warming decreases summer thermocline depth, increases resistance to mixing, and could even lead to the evolution of a permanent deep-water thermocline, as observed in this study. Density stratification prevents the flux of nutrients between the nutrient rich, low light hypolimnion and the warm, nutrient depleted, light enriched epilimnion. Isolation of hypolimentic waters reduce the exchange with the atmosphere and oxygenated epilimnion leading to reduced oxygen concentrations at the lake bottom (Mackenthun and Stefan 1998, Sahoo and Schladow 2008). Anoxic conditions (<2 mg/L of DO) near the sediment water interface even for a short period of time can influence the redox potential resulting in higher mineralization rates and subsequent release of P and heavy metals (Nürnberg 2004).

The onset of stratification in Lake Tarawera advanced by nearly two months and its breakdown was delayed by two months in excess when the temperature rose by 4 °C, under nutrient enriched conditions. The persistence of stratification for an additional four months under future warming and eutrophication would have profound effects on the lake processes and biota, especially plankton composition and timing of successional events (Gerten and Adrian 2000, Adrian et al. 2009, Thackeray et al. 2008). The nutrient and light gradients created as a result of stratification can enable phytoplankton with specifically adapted physiological traits to dominate and thrive in such environments. While increase in N and P concentrations could be the main cause of dominance of phytoplankton genera in oligotrophic lakes, rising temperatures could further increase the metabolic rates of the species resulting in increased growth and reproduction (Carey et al. 2012, Robarts and Zohary 1987). This was observed in the study conducted to determine the effects of rising temperatures and varying nutrients in two lakes with different trophic status (Chapter 2) where the increase in phytoplankton concentration relative to the base case scenario was the highest in the oligo-mesotrophic lake Tarawera. In addition to intensifying stratification, the effects of thermocline depth can also lead to changes in the phytoplankton composition by varying light:nutrient ratio (Diehl et al. 2002, Cantin et al. 2011). Except under reduced nutrients, overall thermocline depth decreased and deep winter mixing was absent beyond a temperature rise of 1 °C. As the thermocline depth reduces, certain phytoplankton taxa, such as diatoms, will not be able to thrive due to high sinking losses arising from a shallow mixed layer (Cantin et al. 2011). Instead, buoyancy regulating cyanobacteria or chlorophytes that can withhold fluctuating light conditions will be favoured under weak mixing.

Using a combination of scenarios where only air temperatures and trophic status are changed, while keeping solar radiation and wind speed constant, the study enabled the understanding of how temperature and nutrients individually and interactively affect lake thermal structure. Light attenuation mediated by water transparency increased with the primary productivity and contributed to high surface water temperatures. K_w also had a considerable influence on the nutrient poor lake where the overall increase in heat storage is the greatest under rising temperatures. Hence, heat budgets of oligotrophic lakes are likely to be more sensitive to variations in climate than eutrophic lakes. In all nutrient scenarios under increased temperatures, the net gain in the heat content during autumn-winter period is outweighed by the net loss of heat during spring-summer seasons. These changes in the outgoing and incoming heat fluxes followed an opposing pattern to that of the surface temperatures as a result of cumulative heat effects. In accordance with increasing water temperatures, Lake Tarawera experienced the stratification to advance by nearly two months and last two months in excess when the trophic status was hyper-eutrophic and temperatures have increased by 4 °C. Additionally, the shallower thermocline prevented the overturning of the lake during winter, leading to the occurrence of a persistent thermocline. Such alterations may have detrimental effects on water quality and ecosystem health. Global climate change is likely to be associated with regional changes in solar radiation and wind speed, which have a significant influence on lake heat fluxes and therefore, should be taken into consideration in future studies that aim to assess the impacts of climate change on thermal characteristics.

Chapter 4 Effect of disturbances on taxonomic and functional diversity during spring to summer in an eutrophic reservoir

Introduction

Impact of environmental gradients on phytoplankton diversity can occur due to various factors, including competition for resources and periodic disturbances. Disturbances in aquatic ecosystems occur at much more rapid timescales than in terrestrial ecosystems. There are annual transitions that occur as the lake moves from stratified to mixed conditions and back to stratified conditions. Superimposed on this seasonal change in hydrodynamics are other disturbance events which interact with the seasonal change to shape the phytoplankton communities (Salmaso 2003). Phytoplankton have high growth rates and are sensitive to disturbances which makes them good bio-indicators that can trace small scale changes in the environment (McCormick and Cairns Jr 1994). Oscillations in the environment can occur at various frequencies and intensities and will regulate phytoplankton succession and its diversity. While disturbances of low frequency can drive a phytoplankton assemblage in to a state of equilibrium or towards a steady state assemblage and reduced diversity, some lakes have experienced reduced diversity with frequent mixing (Hutchinson 1961, Naselli-Flores et al. 2003, Reynolds 2006, Chorus and Schlag 1993). Steady state in a system can arise if losses and growth processes occurring through time result in an invariance in the assemblage (Rojo and Álvarez-Cobelaz 2003). Definition of disturbance is ambiguous (Borics et al. 2013, Hambright and Zohary 2000), but can be considered to be any event that affects the community structure and alters resources, substrate availability, or the physical environment (White and Pickett 1985, Miller et al. 2011, Tanentzap et al. 2013).

The main controls on lake phytoplankton dynamics fluctuate depending on the trophic status, lake morphometry, local climate and in-lake processes (Fee 1979, Winder and Sommer 2012). The widely referenced phytoplankton ecological model (PEG) describes the role of biotic and abiotic factors in driving seasonal phytoplankton succession in 24 sequential steps (Sommer et al. 1986, Sommer et al. 2012). The model determines how trophic status can influence seasonal biomass patterns and demonstrates that eutrophic waters tend to experience a spring clear-water phase and a summer bloom of grazing-resistant algae. Several allogenic (abiotic) and autogenic (biotic) factors have been identified to have a primary control over phytoplankton succession (Sommer et al. 1986, Reynolds 1984). Physical stability or instability can be the main factor that regulates the change in phytoplankton composition (Caljuri et al. 2002, Verburg et al. 2003, Winder and Hunter 2008) while other studies have highlighted the importance of zooplankton predation as the driver of changes in the phytoplankton community (Sterner 1989, Sarnelle 2005, Ward et al. 2014). Abiotic factors related to the thermal structure and mixing depth of a water column control the light climate and the nutrient distribution and availability which can induce competition between different phytoplankton species. Mixing in freshwaters can be determined by external climatic factors such as heat exchange and wind action (Huisman et al. 2004) which too are considered as important allogenic or abiotic factors that cause changes to the phytoplankton succession (Reynolds 1984, Sommer et al. 1986, Chorus and Schlag 1993). Biotic factors under biological control refer to the variables that are partially controlled by the phytoplankton community, such as selective nutrient depletion inducing interspecific competition and changes in water quality that alter light attenuation (Holm and Armstrong 1981, Wetzel 2001, Huszar and Reynolds 1997). The grazing community also plays an important role in the food web dynamics, having a top down or bottom up control over the phytoplankton. As grazers, zooplankton can affect the phytoplankton primary production, directly, through predation (top down), and indirectly, through nutrient recycling (bottom-up) (Lehman 1980, Lehman and Sandgren 1985, Flynn 1989).

Temporal heterogeneity in disturbances can ensure that phytoplankton communities include a combination of different stages of succession (Torsvik and Øvreås 2002). Temporal scale is an important factor that determines the difference between an unstable state and an equilibrium state. Frequency and intensity of periodic disturbances can have differential effects on organisms, allowing dominance, coexistence or competitive exclusion of species (Gaedeke and Sommer 1986, Padisák 1993, Naselli-Flores et al. 2003). Temporal scale of disturbances can be of short to medium scale events mostly consisting of meteorological factors, hydrological changes and grazing that last hours-days-weeks and long term or seasonal changes in stratification and insolation (Salmaso 2003). Given that phytoplankton have short generation times of 0.3-3 days (Reynolds 2006, Rojo and Álvarez-Cobelaz 2003), some studies have demonstrated that weekly intervals between observations are insufficient for capturing most of the major events in phytoplankton succession (Zohary 2004). Consequently a short interval sampling (twice a week) was carried out in this study to obtain insight into fine scale changes in phytoplankton dynamics.

During the transition from spring to summer there are a number of changes in the physical environment that occur. It is expected that distribution, abundance and succession patterns of phytoplankton are influenced by the temporal scale and magnitude of disturbances. In addition to the taxonomic features, functional properties of phytoplankton cells could provide insight into their growth rates, efficiency in utilising resources and susceptibility to grazing which determine their ability to thrive and dominate under varying environmental constraints (Reynolds et al. 2002, Weithoff 2003, Salmaso and Padisák 2007, Kruk et al. 2010). Functional associations are expected to be more responsive to environmental factors than taxonomic-based classification (Kruk et al. 2010, Longhi and Beisner 2009). Trait based approaches can therefore assist in studying factors that affect community structure and functioning which ultimately lead to selection (Pomati et al. 2013).

The trade-off between competitive abilities for different resources, either different nutrients or nutrients and light can explain species shifts across supply ratio gradients under disturbance and the coexistence of many species (Tilman et al. 1982). Clustering of taxonomic entities into functional groups can be used to assess community assembly and patterns of species co-occurrence and persistence over time (Weithoff et al. 2015). Therefore changes in the functional trait diversity of the phytoplankton community based on their ecological, morphological and physiological features were also assessed in the study. Understanding the temporal variability in the structure and functional diversity of phytoplankton under changing ecological disturbances can not only provide insight into the ecosystem functioning in a particular aquatic system but also provide insight into how a system would respond under future environmental changes (Calijuri et al. 2002, Litchman and Klausemeier 2008, Ward et al. 2014). This study was carried out with the aim of determining and understanding the impacts of abiotic and biotic disturbances with fluctuating magnitude and frequency on the phytoplankton taxonomic and functional diversity during the period extending from spring to summer in an eutrophic reservoir.

Methods

Study Site

Mount Bold Reservoir is the largest potable water storage reservoir in South Australia (35° 07'S, 138° 43'E) with a surface area of approximately 3.1 km^2 and a maximum depth of 47 m (Fig. 4.1). The catchment area of 388 km^2 consists predominantly of agricultural land, which drains into the reservoir primarily by the Onkaparinga River. The reservoir is also supplemented with water piped from the River Murray to increase the natural supply and maintain the water levels, especially during summer when the consumption is high (Merrick 1990). Mt Bold reservoir is a warm monomictic system has a high external nutrient load and frequently experiences cyanobacterial blooms during summer (Brookes et al. 1994, Oliver 1981, Oliver and Ganf 1988).

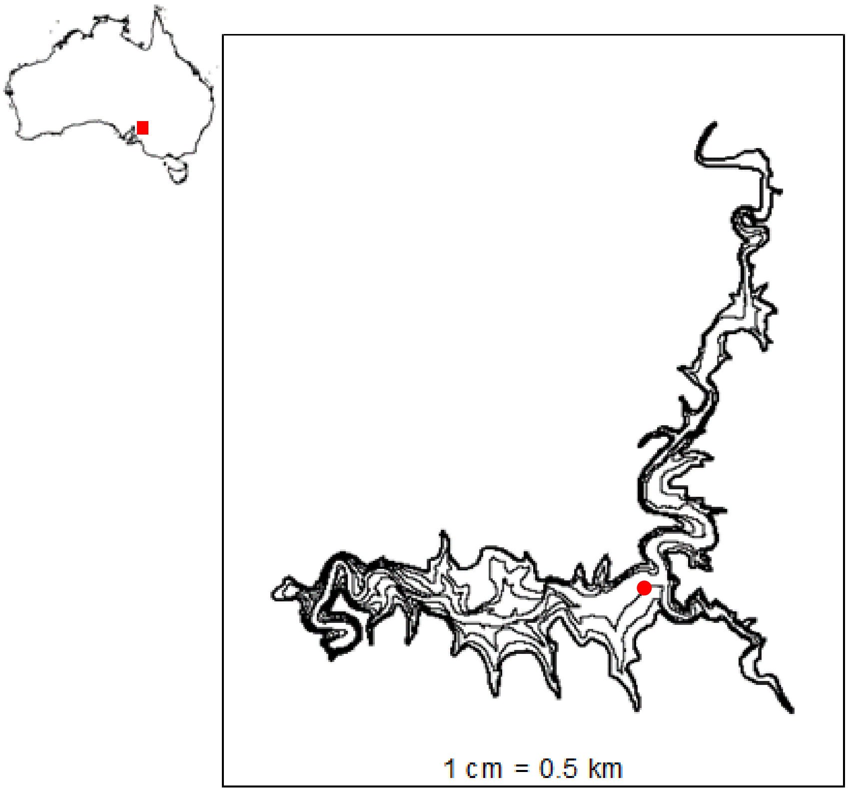


Figure 4.1 Location of the Mt Bold reservoir with the sampling site (solid circle)

Field and laboratory methods

Field sampling was carried out at Mt Bold Reservoir twice a week for approximately three months extending from spring to summer at the point where the water column depth was the greatest. *In-situ* measurements of water temperature (WT), dissolved oxygen (DO), electrical conductivity (EC) and chlorophyll fluorescence were measured using multi-parameter sondes YSI 6600 and YSI EXO2. Photosynthetically Active Radiation (PAR) was recorded using a handheld light meter (LICOR LI-193) at 20 cm increments. Euphotic depth was calculated as the depth at which 1% of surface PAR was intercepted. The samples for laboratory analysis were taken at two discrete depths using a Van Dorn sampler; surface and euphotic depth. Vertically integrated samples over the depth of the euphotic zone were taken using nets of mesh sizes of 20 µm and 53 µm for phytoplankton and zooplankton, respectively. Phytoplankton samples were preserved in Lugol's iodine solution while zooplankton samples were preserved in 90% ethanol.

Nutrient samples were filtered through a 0.45 µm pore diameter membrane in the laboratory within 1-2 hours of sampling. Samples for microbial analysis were collected in sterile bottles which were then used for microbial abundance analyses. Samples were analysed for Chlorophyll a spectrophotometrically after a known volume of reservoir water was filtered onto GF/C filters and the pigment extracted in methanol in the dark (HMSO, UK 1983). Nutrients including filterable reactive phosphorus (FRP), nitrate/nitrite (NO_3/NO_2), ammonium (NH), total phosphorus (TP) and total nitrogen (TN) were analysed using standard methods (APHA 2005). Phytoplankton samples were concentrated and cells were enumerated under inverted microscope at x400 magnification and were identified to the genus level. Biovolumes in μm^3/mL of the different phytoplankton genera were estimated using mean cell bio-volumes. The above biovolumes have been pre-determined for common genera found in the South Australian water bodies using cell dimensions and relative geometric equations according to Hillebrand (1999). Zooplankton cells were counted in 5 mL sub-samples using a binocular dissection microscope at 200x to 400x magnification and were identified to the lowest practical taxonomic level.

Thermal profiles for Mt Bold were obtained using the thermistors deployed at the beginning of the sampling period (at 1 m, 3 m, 5 m, 10 m and 20 m) and the thermistor chains (at every 0.1m in the first metre, at every 0.5 m til 5 m, at every 1 m from 5 m-40 m depth) deployed and maintained by South Australian Water Corporation (SA Water).

Daily air temperature, wind speed and rainfall data were obtained from the weather station based in the Kuitpo Nature Reserve located approximately 20 km south of the Mt Bold reservoir. A good agreement has been found between the limited wind speed data measured using a floating weather station at Mt Bold and the corresponding wind data from Kuitpo (Fig. 4.2) (van der Linden and Burch 2016). Rainfall and solar radiation data were obtained from the automatic weather station located in the reservoir. Information on the main inflow to the reservoir, Onkaparinga River, was acquired from the WaterConnect data base. The details of the inflow of a minor tributary, Echunga Creek, were absent for the period beyond 08/2013 due to the termination of the gauge at the respective site. Consequently, the inflow from the Echunga Creek was estimated using the rainfall-runoff model GR4J (Perrin et al. 2003). However, inflows and outflows were not considered in the statistical analysis as the average daily dilution rate calculated was minor (0.004 /day) in relation to the rates of phytoplankton growth (Reynolds 2006).

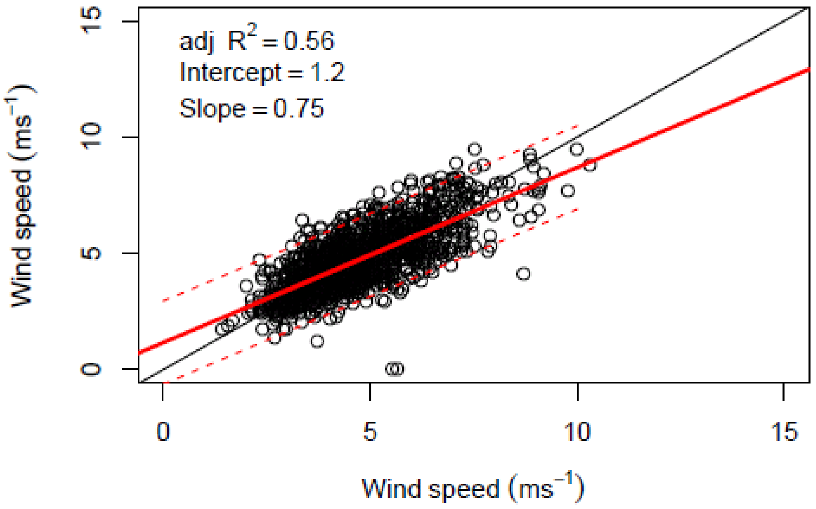


Figure 4.2 Daily average wind speed at Mount Bold predicted by observed daily average wind speed data from Kuitpo Nature Reserve. The black line is the 1:1 line while the red line is the fitted line. (van der Linden and Burch 2016)

Quantification of mixing and stratification

The Lake Analyzer program was used to calculate several indices to estimate the magnitude of stratification and mixing as a method of quantifying effect of physical forcing on phytoplankton communities. Lake Analyzer is a numerical program developed by Read et al. 2011 as a method of evaluating high-frequency lake data recorded from buoys and can be used to derive selected indices from a range of output options. The primary input files consist of temperature-depth information, bathymetry and wind speed. Schmidt stability (St) is a commonly used index to estimate the stability of the water column (Hutchinson 1957) and is an estimation of the energy required to mix the entire lake to an isothermal condition (Winder and Schindler 2004). Lake number (LN) was calculated to be used as an indicator of relative turbulence and stability conditions in the water column (Lindenshmidt and Chorus 1998). LN is a non-dimensional ratio of the buoyancy forces in the lake due to stratification to the external forces applied to the water column, such as wind, that act counter to the buoyancy forces and thereby counteract the effects (Imberger and Patterson, 1990). Surface mixed layer (Zsml) refers to the depth of the surface layer of the lake which will be directly affected by wind and convective cooling. Although several definitions exist for the Zsml for the purpose of this study Zsml is defined as the area above the water column where the density gradient is less than 0.5 kg/m^3 per metre (Lamont et al. 2004, Read et al. 2011). Thermocline depth in Lake Analyzer is calculated as the depth at which the maximum density gradient occurs.

Derived measures of lake properties were calculated as:

1) Schmidt Stability (St):

$$\mathrm{St} = \frac{g}{A_S}\int_0^{z_D} (z - z_v)\rho_z A_z \partial z$$

2) Lake Number (LN):

$$\mathrm{LN} = \frac{\mathrm{St}\,(z_e - z_h)}{2\rho_h u_*^2 A_s^{1/2} z_v}$$

where g is the acceleration due to gravity, A_s is the surface area of the lake, A_z is the area of the lake at depth z, z_D is the maximum depth of the lake, and z_v is the depth to the centre of volume of the lake. z_e and z_h are the depths to the top and bottom of the metalimnion, respectively, while ρ_z is the water density at depth z, ρ_h is the average density of the hypolimnion and u_* is the surface friction velocity.

Estimating phytoplankton diversity

Structural and functional traits of phytoplankton species determine their ability to thrive, cope, exist and exploit resources in different environments under various stresses. To assess the diversity in the functionality, observed algae were categorised using the morphology based functional groups (MBFG) (Kruk et al. 2010). Morphological characteristics determine main phytoplankton traits that are related to growth and mortality and therefore, are generally good predictors of the functional properties (Litchaman et al., 2010, Kruk et al., 2010).

MBFG classification categorises phytoplankton species on the basis of their morphology and seven main phytoplankton groups are determined based on the cell size (volume, surface area, volume: surface area ratio (S/V), maximum linear dimension) and based on the presence of mucilage, flagella, gas vesicles, heterocysts and/or siliceous exoskeletal structures (Kruk et al., 2010). These types of phytoplankton classification systems that use morphological and functional characteristics to explain the distribution of communities across an environmental gradient, was initiated by Margalef (1978), Reynolds (1984) and Sommer (1984) and have continuously extended into further development in the recent years (Reynolds et al., 2002, Salmaso and Padisák 2007, Litchman et al., 2010).

In MBFG classification, seven main types of phytoplankton groups are determined using the most relevant morphological characteristics that govern the ecological performance. Group I contains small organisms with high S/V. Cell size is proven to be a “master trait” that determine the efficiency of resource (nutrients and light) acquisition and therefore, organisms with high S/V have increased efficiency in acquiring resources and low sinking losses (Litchman et al., 2010, Reynolds 1984). Group II contains small flagellated organisms that contain exoskeletal structures and contain exclusively Chrysophyceae species. In these species, flagella assisted motility enable them to access nutrients and reduce sedimentation (Reynolds 1997). Group III contains mainly large filamentous organisms with aerotopes that enable buoyancy regulation. The species are generally slow growing due to the large body size but are tolerant to light limiting conditions and also some may be able to fix N under low nutrient conditions (Naselli-Flores and Barone 2007, Kruk et al., 2010). Group IV has species that are of medium size that lack specialized traits. Hence, these organisms have moderate tolerances to limiting resources and have modest sinking losses, but due to being a good source of food to the grazers, can experience high grazing pressure (Sterner and Elser 2002). Group V contains unicellular flagellates of medium to large size that can effectively forage nutrients and light and avoid rapid sinking due to motility (Reynolds 1997). Group VI contains non-flagellated organisms with siliceous exoskeletons and contains diatoms exclusively. These species experience high rapid rates of sinking due to high cell density and lack of motility but can avoid predation by certain grazers due to the presence of siliceous walls (Hamm et al., 2003, Kruk et al, 2010). Group VII contains large mucilaginous colonies that have beneficial buoyancy properties due to the presence of low density lipids and aerotopes. While low S/V can limit the efficiency in resource uptake, these characteristics can also promote the survival of these species by decreasing predation (Reynolds 1984).

Taxonomic diversity and functional diversity were estimated using the commonly used Shannon-Weaver index (Shannon and Weaver 1949), where B is the total biomass and b_i is the biomass of the *i*th genus or the functional group present.

$$H' = -\sum\left(\frac{b_i}{B}\right)\log_2\left(\frac{b_i}{B}\right)$$

In addition to the phytoplankton diversity, the species richness, measured by the total number of species within a given sample was also recorded.

Variance, lag effects and moving average

Time series consist of different components which often include a combination of long term trends, regular oscillations about the trend, fixed seasonal factors and residual irregular movements which too may act as disturbances (Jassby and Powell 1990). Variance of a time series can be used to explain the abrupt shifts in the time series (Carpenter and Brock 2006) and can sometimes be used to explain the phytoplankton abundance at a given point in time.

Time lagging of the limnetic reactions to the driving energy inputs can delay the attainment of true state (Reynolds 1990). Time lagged effects are often overlooked and therefore time lagged effects of the physical variables (St, LN, Zsml), water temperature and important meteorological variables (air temperature, wind speed) were considered in this study to determine whether they assert any control over the development and succession of phytoplankton. A 1-day lag and a 3-day lag were considered as phytoplankton have generation times that can range from in the order of 0.1-1.0 doublings per day (Reynolds 2006).

Trend and other components can be separated by a variety of techniques, including through the application of the moving average filters (Jassby and Powell 1990). Moving average replaces an observation by the mean of the adjacent observations and thereby “smoothing” the data which reveals low-frequency cycles (Livingstone 1979). Three-day and 6-day moving average were used to characterise the variability within the time series of meteorological factors (air temperature, wind speed), water temperature and lake physics (St, LN, Zsml).

Standard deviations of the moving averages were used to characterise the variability within the time series. The differences between the standard deviation and the moving averages were used to represent the variance around and between the explanatory variables used above.

Data Analysis

Exploration of the trends in phytoplankton diversity over the sampling period indicated that different linear relationships tend to be occurring at varying periods of times. Model fitting of diversity data using linear and polynomial regression was informed by the Akaike's information criterion (AIC), where lower AIC values indicate stronger support for the model, balancing model fit and parsimony (Burnham and Anderson 1998, Fierer and Jackson 2006). As relationships between the response variable and the predictor variable were shown to be piecewise linear, segmented regression models were used to identify the discrete breakpoints. First a linear model was constructed between time and diversity and then a segmented regression relationship is added by re-fitting the overall model (Muggeo 2008) to find breakpoints where the slope of the linear function changes.

Univariate regression trees and multivariate regression trees were used to determine the influence of environmental variables (Table 4.1) on species and their diversity, following De'ath (2002). Regression trees are predictive trees resulting from recursive partitioning of the response data, with the effect of the explanatory variable indicated at each split. The explanatory variables given in Table 4.1 are only being considered as tree structuring variables (tree splits) based on the variables that are selected to have the best predictive power. For instance, to structure the first split, the analysis will search for the best partition of the response variable in two groups, constrained by each explanatory variable. Values of the first explanatory variable are then arranged in an increasing order and then grouped according to all possible cut-off points, following which sum of within-group sums-of squares (squared error) is calculated for all the groups. This is carried out consecutively for all the variables, and the variable that has the lowest total sum of squares or the lowest total squared error is used to draw the first split (Legendre and Legendre 2012). Regression trees are a robust and powerful method that can be used under numerous situations, with complex ecological data that show multicollinearity, non-linear relationships and high-order interactions (De'ath and Fabricius 2000, Borcard et al. 2011, O'Reilly et al. 2015).

Euclidean distance was used to calculate the splits in the trees where leaves are composed of samples chosen to minimize the within-groups sums of squares (Borcard et al. 2011). Pruning of the tree is based on the one standard error (SE) rule (Breimen et al. 1984, De’ath 2002, Oksanen et al. 2013), where the optimum tree size is chosen based on the cross validation relative error (CVRE) plus one SE of the CVRE values. Exploratory analysis was initially carried calculating large trees to identify a hierarchical sequence of environmental factors that explain the biological variables. As there were a large number of explanatory variables, initial models were calculated for each of the time series component (i.e. 1-day lag, 3-day lag, 3-day moving average, 6-day moving average, standard deviation and variance) of the meteorological and physical variables and subsequently, only the ones that showed the highest predictive power (1-day lag and 3-day moving average) were included in the final model (Table 4.1). The final multivariate regression tree was pruned (to 5 nodes) based on 100 cross-validations to a complexity parameter of 0.085, corresponding to the highest tree size where CVRE is still within the one SE above the minimum CVRE. The final univariate regression trees that are used to examine the influence of environmental variables on the taxonomic and functional diversities were pruned based on the tree size with the minimum CVRE.

Table 4.1 Phytoplankton genera and explanatory variables used in the analysis

Phytoplankton Genera			**Main Explanatory variables**			**Explanatory variables associated time components**		
1	Botry	*Botryococcus*	1	WS	Wind Speed	19	St_lag1	1-day lag of Schmidt Stability
2	Chlam	*Chlamydomonas*	2	St	Schmidt Stability	20	LN_lag1	1-day lag of Lake Number
3	Sphe	*Sphaerocystis*	3	LN	Lake Number	21	Zsml_lag1	1-day lag of surface mixed layer depth
4	Ooc	*Oocystis*	4	Zsml	Surface Mixed Layer depth	22	WS_lag1	1-day lag of wind speed
5	Ank	*Ankyra*	5	Zeu	Euphotic Depth	23	WT_lag1	1-day lag of surface water temperature
6	Clost	*Closterium*	6	WTSurf	Surface water temperature	24	St.ma3	3-day moving average of Schmidt Stability
7	Crypt	*Cryptomonas*	7	ZsmltoZeu	ZSML/Zeu ratio	25	LN.ma3	3-day moving average of Lake Number
8	Chro	*Chroomonas*	8	TP	Total Phosphorus	26	Zsml.ma3	3-day moving average of surface mixed layer depth
9	PenDia	*Pennate Diatoms*	9	TN	Total Nitrogen	27	WS.ma3	3-day moving average of wind speed
10	Tab	*Tabellaria*	10	FRP	Filterable Reactive Phosphorus	28	WT.ma3	3-day moving average of surface water temperature
11	Aul	*Aulacoseira*	11	NO3	Nitrate			
12	Cyc	*Cyclotella*	12	NO2	Nitrite			
13	Cer	*Ceratium*	13	NH4	Ammonia			
14	Tra	*Trachelomonas*	14	Tbacto	Total bacterial counts			
15	Eug	*Euglena*	15	ROTI	Rotifers			
16	Mal	*Mallomonas*	16	CLADO	Cladocerans			
17	Mic	*Microcystis*	17	COPE	Copepods			
			18	ciliates	Ciliates			

All data analysis was carried out using R software (R Core Team 2014). Prior to analysis, phytoplankton genera present in very low abundances (<3 observations) were removed and the phytoplankton concentration data were transformed using $\log_{10}$ to down-weigh the abundance data that would present the variation in absolute values over time (Oksanen et al. 2013).

Results

Abiotic features

Meteorological data - On average, the maximum air temperature increased over the sampling period which spanned the transition in seasons from winter to spring. However with the seasonal trend there was large daily variation of minimum and maximum air temperatures (Fig. 4.3), often differing by approximately 10 °C and at times by even 22 °C (on the 18/11/2013). The wind speeds at Mt Bold ranged between 1.5 m/s and 9.2 m/s and showed no marked trend over the studied period (Fig. 4.4). Standard deviation (sd) values provide details on the variation in wind speed with closer to 0 values demonstrating less variation in the wind speed. The fluctuating standard deviation (sd) and variance (var) values suggest constant oscillations in the wind speed that occurred throughout the transition from spring to summer that can be considered as the disturbances in the environment.

Thermal structure- At the start of the sampling period the lake was fully mixed, with the minimum temperature water temperatures close to 10.5 °C. Strong stratification along with a persistent thermocline occurred in September and October, and by the beginning of November, an intense thermocline was formed (Fig. 4.5 and Fig. 4.6). Towards the end of spring, with the increasing temperatures, the stratification strengthened with the temperature difference between the top and bottom waters reached approximately 7 °C. In the presence of the persistent thermocline, oxygen concentrations in the bottom waters declined from 8.73 mg/L at the end of August to 2.4 mg/L at the end of November, indicating close to anoxic conditions.

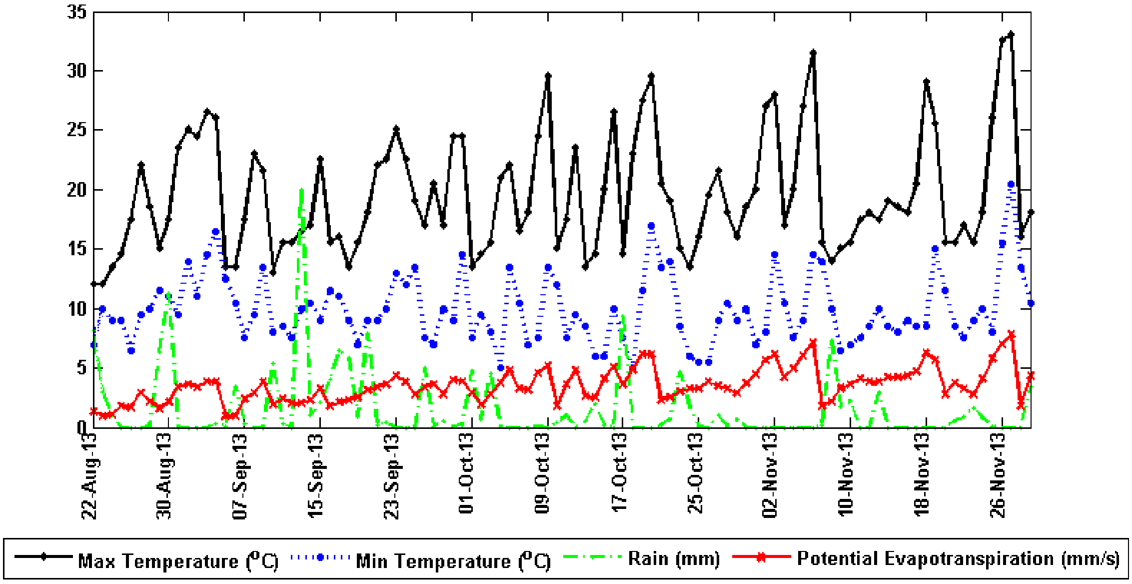


Figure 4.3 Maximum (Max) temperature, minimum (Min) temperature, rain, and potential evaporation during the study period

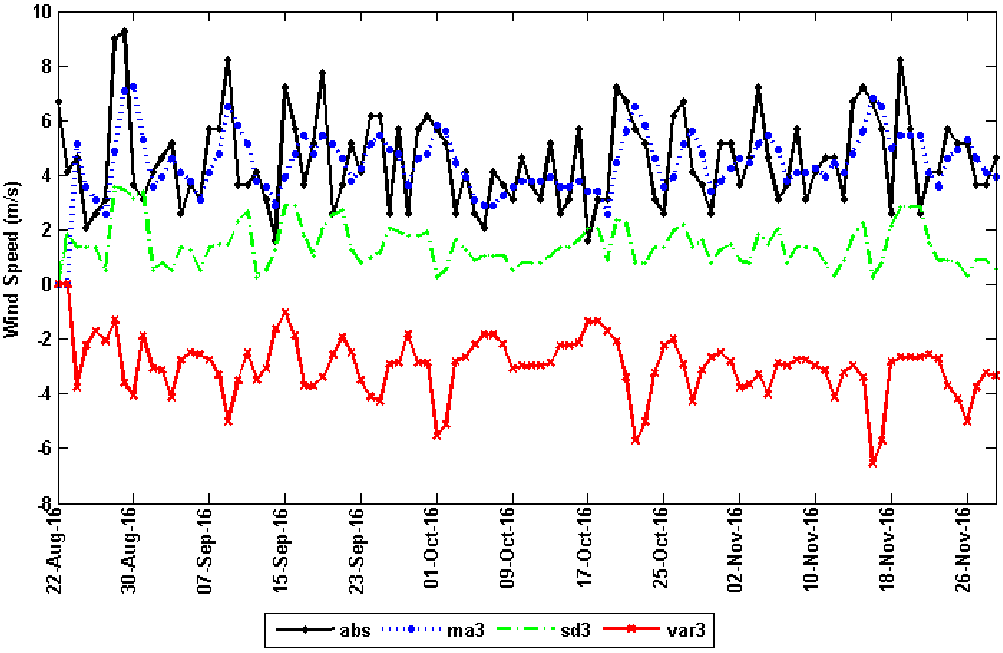


Figure 4.4 Daily changes in wind speed (m/s) for the period 24/08/2013-29/11/2013. Absolute values (abs), 3-day moving average (ma3), standard deviation around the moving average (sd3) and the variability (var3) around the wind speed data are presented

Light climate - Mt Bold reservoir had a shallow euphotic depth of 1.97 m on average, most likely due to high content of coloured matter (Oliver 1980) (Fig. 4.7). From the period of end of winter to end of spring/beginning of summer, the euphotic depth increased linearly by 0.5 m (R^2 = 0.47) with the increase in thermal stability and the decrease in turbidity associated with the low inflow volumes. Accordingly, Zsml:Zeu ratio decreased linearly with the increasing photic depth but the trend was weak (R^2 = 0.1). However, Zeu remained lower than the depth of the surface mixed layer (Zsml:Zeu>1) at most times (Fig. 4.7), suggesting possible light limitation in the system. Furthermore the samples from the euphotic depth can be considered similar to the surface samples as water was always mixed over this depth. Consequently only the phytoplankton and zooplankton samples from the surface and the samples integrated over the euphotic depth samples were used in this study.

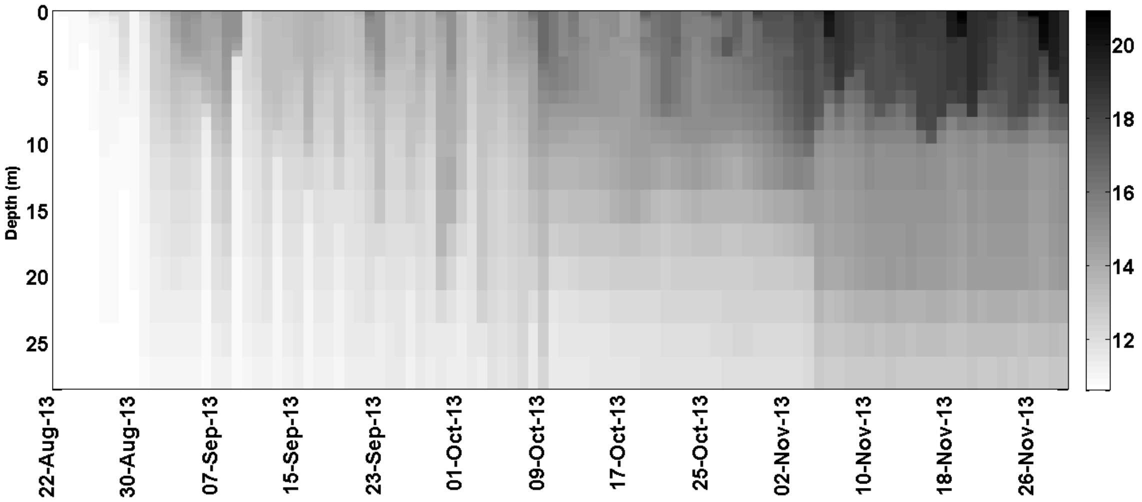


Figure 4.5 Temperature (°C)-depth (m) profile observed at Mt Bold during the sampling period

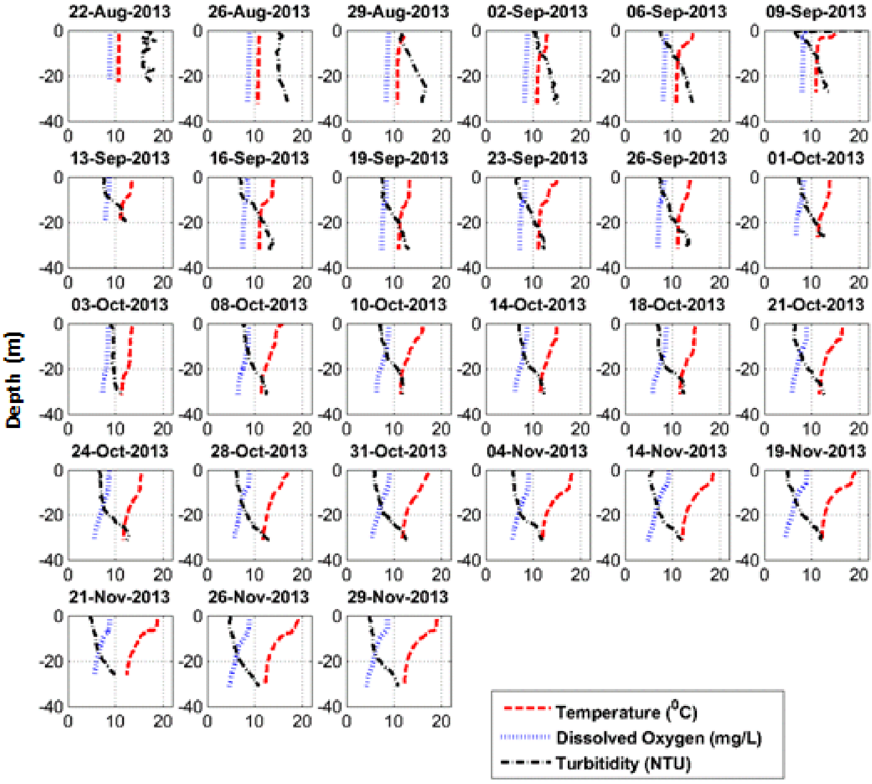


Figure 4.6 Temperature, Dissolved Oxygen and Turbidity profiles for Mt Bold on the sampling dates extending from 22-08-2013 to 29-11-2013

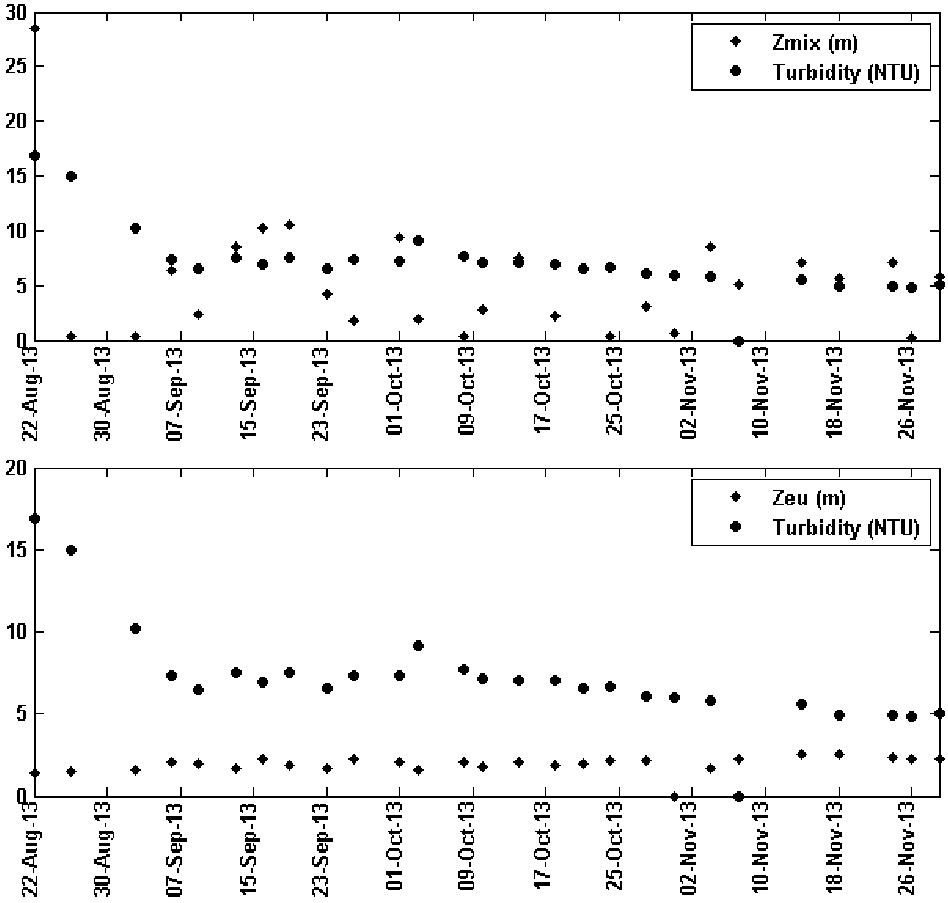


Figure 4.7 Variation in Zmix (top) and Zeu (bottom) from spring to summer in Mt Bold for the year 2013

Lake Physics – Seasonal transition from the end of winter to beginning of summer captured regular variations in the physical structure of the lake as expected. In accordance with the alternations in meteorological conditions (minimum and maximum temperature, wind speed), LN and Zsml (Fig. 4.8) showed short-term fluctuations during the sampling period with the highest Zsml being observed at the beginning of the sampling period, when the water column was completely isothermal. Changes in mixing indicated by LN were mostly driven by the variation in wind speed, which at times increased by 5.6 m/s (on the 19/11/2013), leading to highly turbulent conditions (LN<<1). Schmidt stability increased over the study period as warming conditions resulted in temperature stratification and greater resistance to mixing (Fig. 4.8). Standard deviation (sd) values expressed the highest variation at the commencement of sampling period under fully mixed conditions. Closer to 0 values towards summer indicated less variation in stability with absolute values being close to the mean.

LN values for Mt Bold were usually ≥0 with values increasing towards the end of September as the water column stratified (Fig. 4.8b). High LN values indicate poor wind induced mixing resulting from low wind speeds at Mt Bold having only minor effects on the water column stability. Low LN values close to 0 during the initial period is related to the completely mixed conditions prevailing in the system at the time of sampling. Although a general increasing trend in LN was noted (R^2=0.28) with a warming epilimnion, strong intermittent mixing events occurred during the studied period resulting in low LN values. These events were more pronounced and occurred with high intensity and increased frequency during the period between 29/10/2013-29/11/2013. At most times LN values ≤150 increased up to values between 500-1000 within a span of 1-4 days. Moderate variation in LN values (var) between 08/09/2013-28/10/2013 could be resulting from the mixing events that are occurring at a medium scale intensity and frequency compared to the period before the 08/09/2013 and after the 28/10/2013.

Depth of the surface mixed layer, Zsml, also showed intermittent fluctuations over time but showed an overall weak trend of decreasing ($R^2 = 0.006$) (Fig. 4.8c). Rapidly oscillating Zsml of high intensity can be observed initially but beyond the first week of September, the var values show regular variance in Zsml till the end of October. With establishment of strong stratification in early November, the var and sd values are close to 0 indicating low variance and fluctuations in Zsml that occur in low frequency.

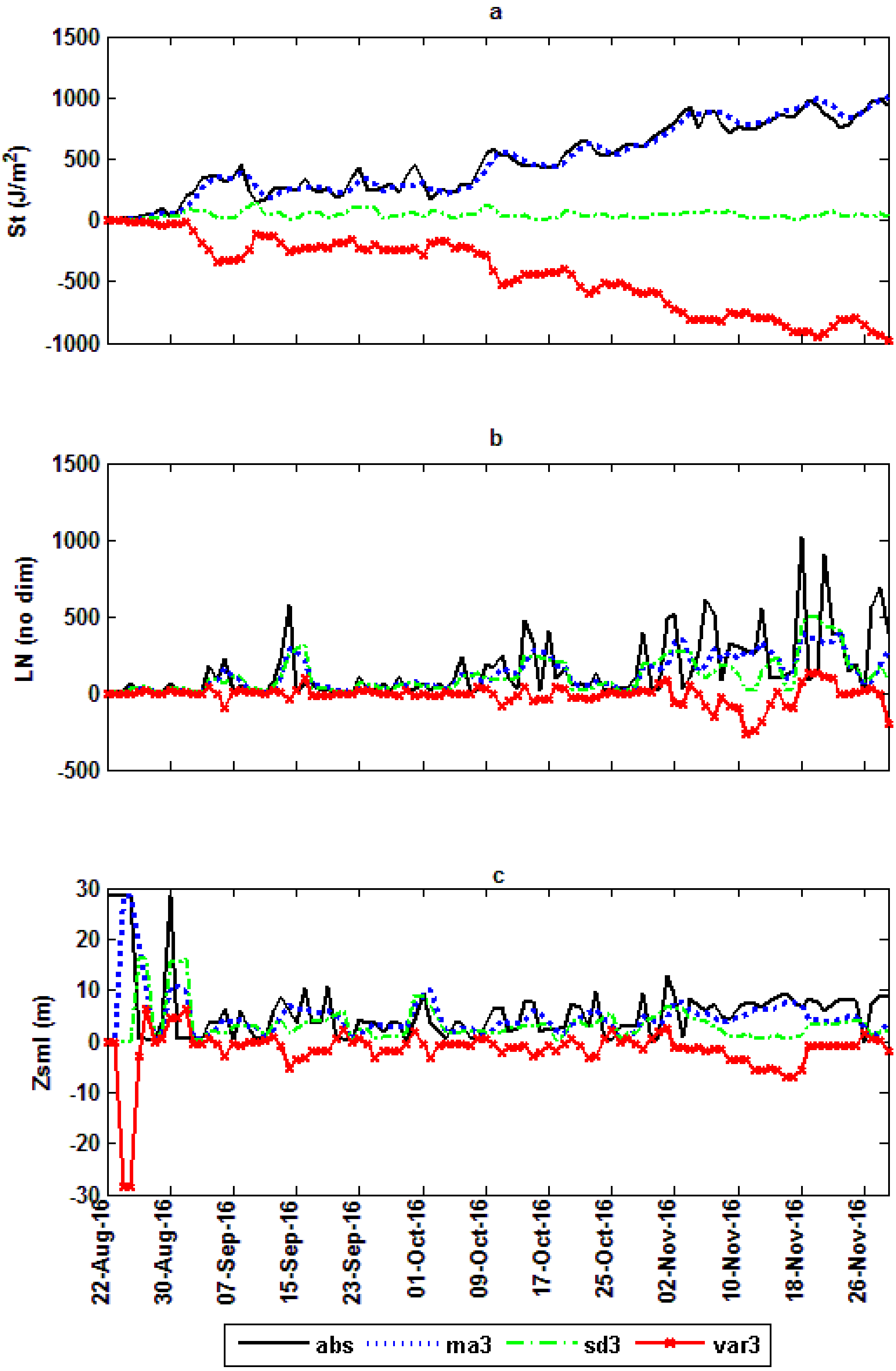


Figure 4.8 Daily changes in the Schmidt stability (a), Lake Number (b) and surface mixed layer depth (c) for the studied period 24/08/2013-29/11/2013. Absolute values (abs), 3-day moving average (ma3), standard deviation around the moving average (sd3) and the variability (var3) around the data are presented

Nutrients –Total and dissolved nutrient concentrations recorded during the sampling period are shown in Appendix Fig. 4.1 and Fig. 4.2. The average surface TP and PO_4 concentrations were high (>0.05 mg/L) with concentrations decreasing towards summer and is in accordance with the Chla maximum which occurred in mid-November. TN concentration was high at the beginning, reaching 1.8 mg/L, but decreased in early spring and remained relatively constant, with an average of 1.02 mg/L till early-November. Following the phytoplankton overgrowth, TN and TP decreased by nearly 50%, reflecting the increased algal uptake causing nutrient depletion in the surface waters.

Concentrations of NO_3 and PO_4 increased up to 0.8 mg/L and 0.038 mg/L, respectively at the end of September with the increase in water contribution from the surrounding catchment (Appendix Fig. 4.3) but decreased to a constant of 0.02 mg/L towards the end of spring. In between beginning and end of spring, PO_4 concentrations fluctuated by 0.03 mg/L. TP concentrations were within eutrophic levels (>0.03 mg/L) even under low flows which indicated sufficient nutrient cycling that can restrict nutrient limitation within the system. NO_2 and NH_4 both showed decreasing concentrations as the inflow volumes reduced to less than 500 ML/day (Appendix Fig. 4.3).

Biotic features

Phytoplankton abundance – The phytoplankton biomass observed at the beginning of spring was low with TCHLA concentrations <10 µg/L (Fig. 4.9). The average concentration for the period between the end of winter and mid-spring was 1.6 µg/L. With increasing stability conditions and the development of the strong thermocline, the surface phytoplankton biomass increased, with the highest recorded TCHLA of 22.7 µg/L being observed in mid-November. Following the above peak, the TCHLA dropped again to average value of 10.9 µg/L.

Species richness, given by the total number of genera observed in the sample, varied between 1 and 13 (mean = 9.8), with the highest being observed during the beginning of spring (Fig. 4.9). Variation in the species richness showed a wave like pattern with a minor decreasing trend (R^2 =0.03), but the values not decreasing below 7, except during the instance when only Microcystis was observed.

A total of 27 phytoplankton genera were observed (Appendix Table 1) and mostly genera of chlorophytes (average 47%) and cryptophytes (average 27%) contributed to the recorded phytoplankton composition till the beginning of November (Fig. 4.10). As the thermal stability started to strengthen, chlorophytes managed to thrive contributing to more than 50% of the phytoplankton composition and cyanobacterial concentrations increased relative to other phytoplankton groups.

Zooplankton abundance - The changes in the zooplankton composition indicated competitive selection between the different groups with copepods mostly dominating in Mt Bold, especially in the middle of spring when they accounted for 50% of the zooplankton community (Fig. 4.11). Rotifers were generally low in numbers but increased in concentrations during the high frequency and high intensity fluctuations in LN that occurred at the end of Oct-Nov. Cladocera dominated the beginning of spring but showed a steep decrease during the period of relatively moderate disturbances resulting in an overall decreasing trend.

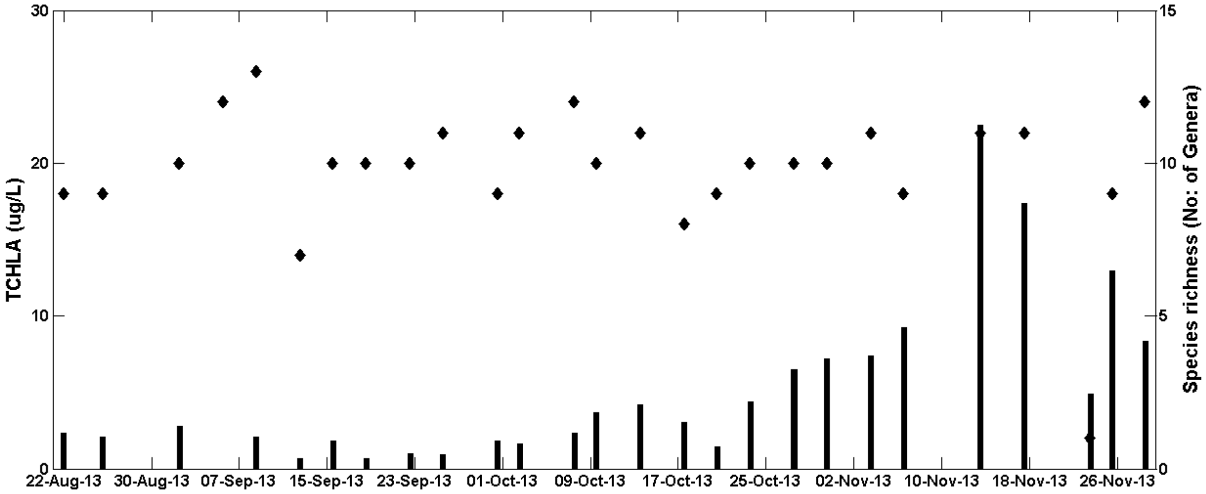


Figure 4.9 Total Chlorophyll a (TCHLA) shown in bars and species richness shown in ♦

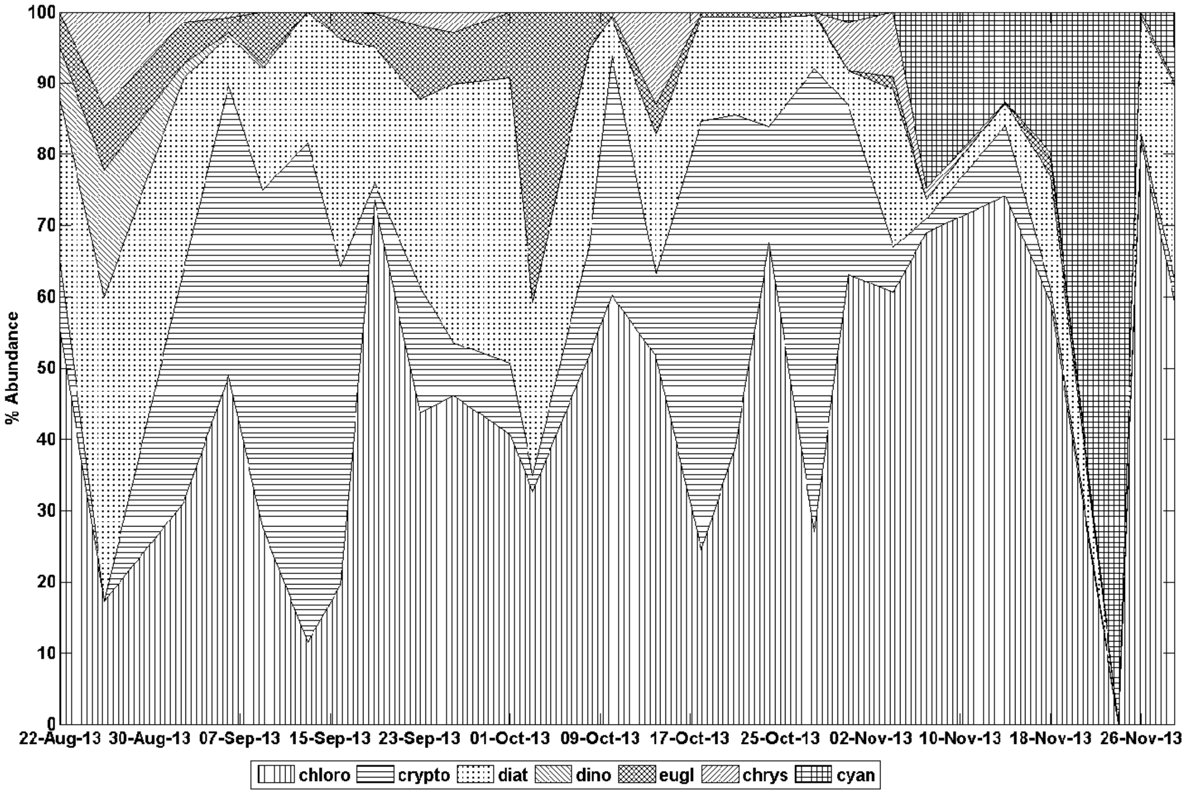


Figure 4.10 Biovolume percentage of major phytoplankton groups observed consisting of Chlorophytes (chloro), Cryptophytes (crypto), Diatoms (diat), Euglenoids (eugl), Chrysophytes (chrys) and Cyanobacteria (cyano).

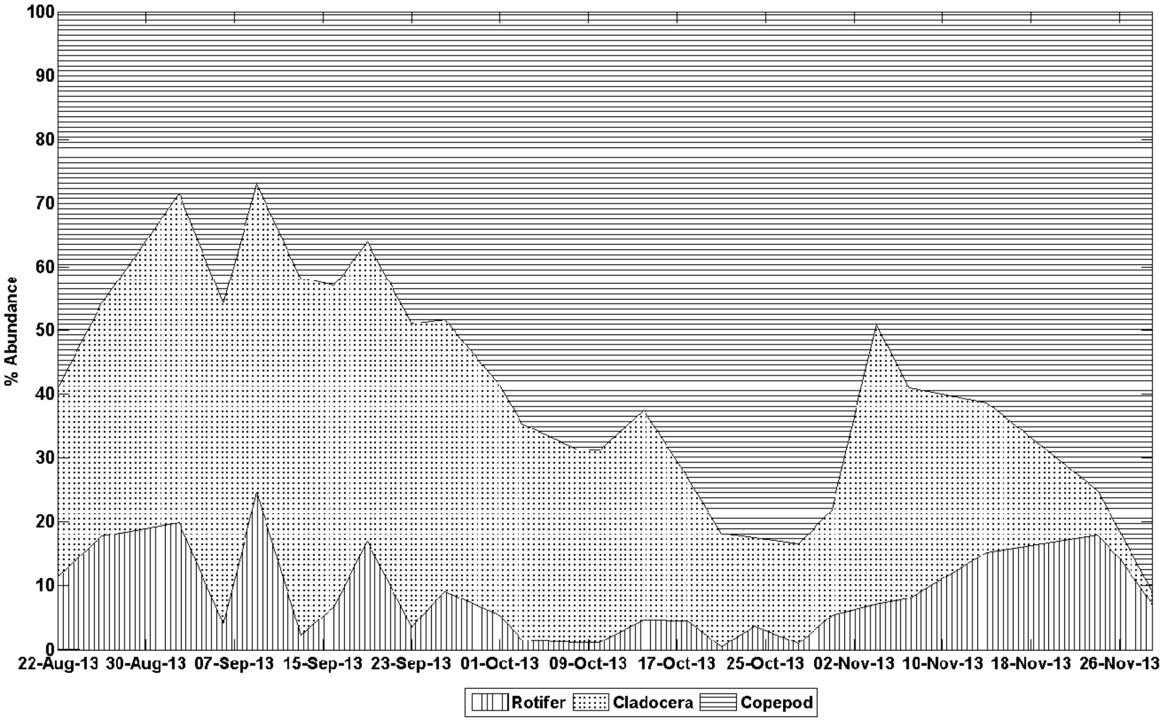


Figure 4.11 Cell count percentage of zooplankton groups observed consisting of Rotifer, Cladocera and Copepod

Phytoplankton diversity

Shannon-weaver diversity of genera showed a linear decreasing trend (R^2 = 0.24, p<0.03) while the functional trait diversity (MBFG) based exclusively on the organismic morphology showed a concave-downward (R^2 = 0.26, p<0.03) (Fig. 4.12). Decreasing trend in genera diversity is higher in the first period till 10/10/2013 (DOY 283) but then reached an almost plateau level afterwards 10/10/2013. Changes in MBFG expressed a different trend to that pf genera diversity. MBFG diversity exhibited a decreasing trend till 09/09/2013 (DOY 252) and started increasing till mid-October (DOY 287), after which it declined again (Fig. 12).

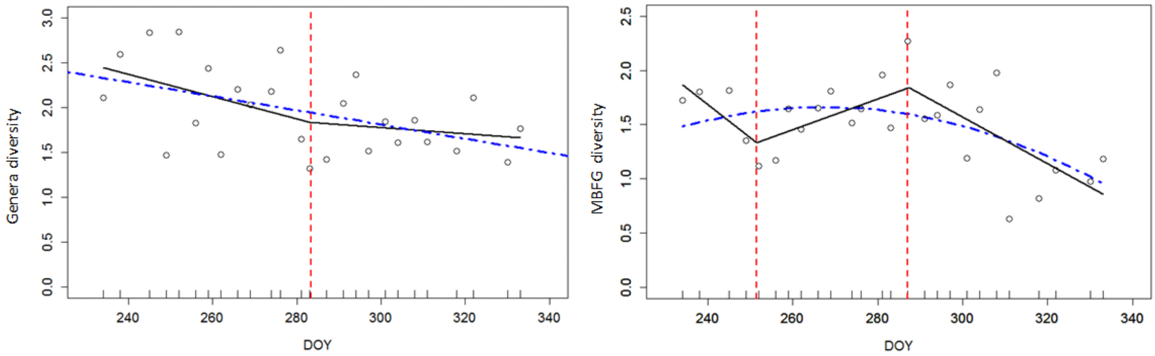


Figure 4.12 Variation in phytoplankton genera diversity (left) and morphology based functional group diversity (right) over the time period starting from day of the year (DOY) 234 in 2013 (22/08/2013). Dot-sash-dot lines show the model fit while the vertical dashed lines show the break points

Phytoplankton abundance explained by the environmental variables

A multivariate regression tree (MRT) with 5 terminal nodes was used to explain the occurrence of different phytoplankton genera on the basis of environmental drivers (Fig. 4.13). The hierarchical regression tree delimited by all allogenic factors explained 70% of the total species variance (Appendix Table 4.2). Surface water temperature (WTSurf) delimited the first two splits and was selected as the most important variable that influences the phytoplankton abundance. The bar plots at the nodes represent the transformed mean absolute abundance of each of the phytoplankton genera. The genera that contribute to more than 10% of the explained variance at each clustering event are defined as the indicator species and are presented at the split and at each terminal node.

The first split delimited by WTSurf separated the samples into the 19 and 7 groups and is characterised by the threshold/critical value of 17.35 °C which is the mean of the values delimiting the split. WTSurf explains 24% of the total genera variance with *Botryococcus* and *Microcystis* contributing highest to the above variance (4.15% and 7.7% of the 24% respectively) (Appendix Table 4.2). Mucilaginous *Botryococcus*, which belongs to the highly diverse Chlorophyte division, was the indicator genus in the cluster determined by WTSurf ≤ 17.35 °C with a log transformed mean abundance of 2.53 (Appendix Table 4.3) indicating their strong preference to waters with lower temperatures. *Microcystis* was the discriminant genus in the cluster WTSurf ≥ 17.35 °C with a mean abundance of 3.46 suggesting their dominance in warm waters.

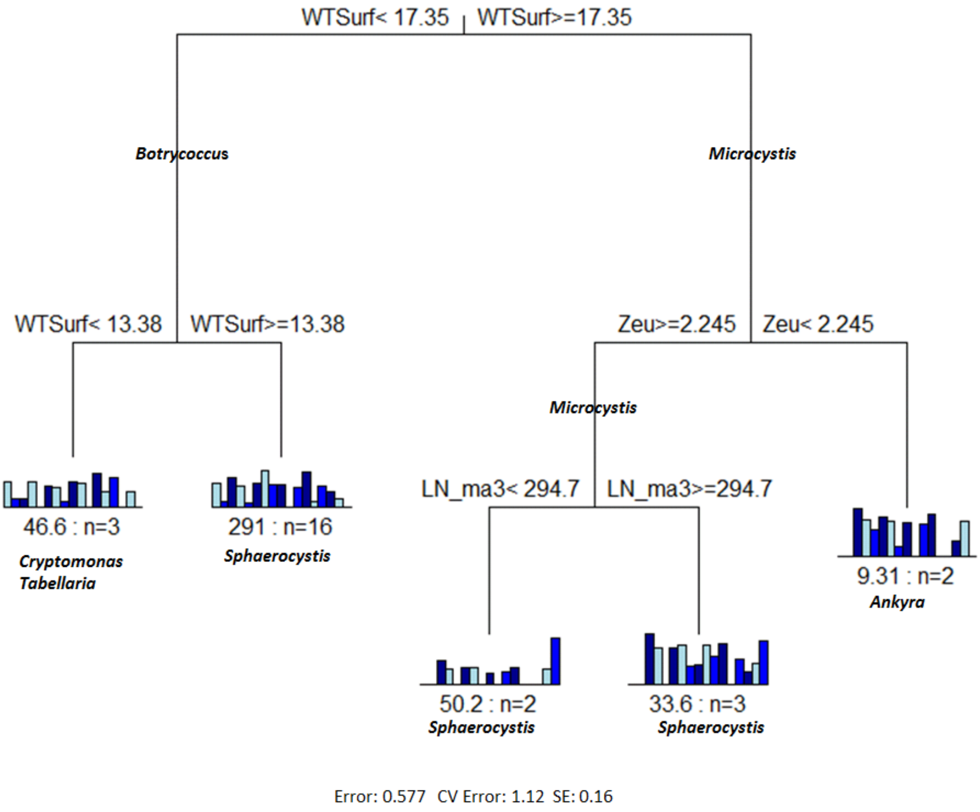


Figure 4.13 Multivariate regression tree analysis of the absolute abundance of phytoplankton genera explained by the environmental variables. Phytoplankton abundance data were log transformed. Error, CV and SE refer to the residual error, cross-validated error and standard error respectively

The third split was delimited by Zeu with a threshold of 2.245 m and explained 8% of the total genera variance (Appendix Table 4.2). *Ankyra* was the discriminant species in the cluster when light was limited ($Zeu \leq 2.245$) while *Microcystis* dominated in the cluster $Zeu \geq 2.245$ m with log transformed mean abundances of 2.98 and 4.84, respectively (Appendix Table 4.3). The final split in the regression tree was determined by the 3-day moving average of the Lake Number (LN_rm) which describes the mixing conditions over a period of 3 days. *Sphaerocystis* dominated when LN_rm was above and below the critical value of 294.7, suggesting their adaptability to both relatively mixed and stable conditions. However, they showed greater dominance under a steady environment with the highest mean abundance of 5.39 being recorded when the LN_rm was ≥ 294.7.

Phytoplankton diversity explained by the environmental variables

Univariate regressions trees used to explain the relationship between diversities and environmental variables are presented in Fig. 4.14. Schmidt stability (St), with a threshold value of 253.5 J/m^2, was the primary factor that explained the variation in genera diversity

(Fig 4.14a). The first split explained 36% of the variance and the highest number of samples (n=21) was observed when the St ≥ 253.5 J/m^2. The second was defined by one day lag in the wind speed (WS_lag1), which explained 24.7% of the variance. Direct impacts of warming temperatures (WTSurf) was the dominant factor that affected the trait based (MBFG) diversity (Fig 4.14b), which explained 56.7% of the variance.

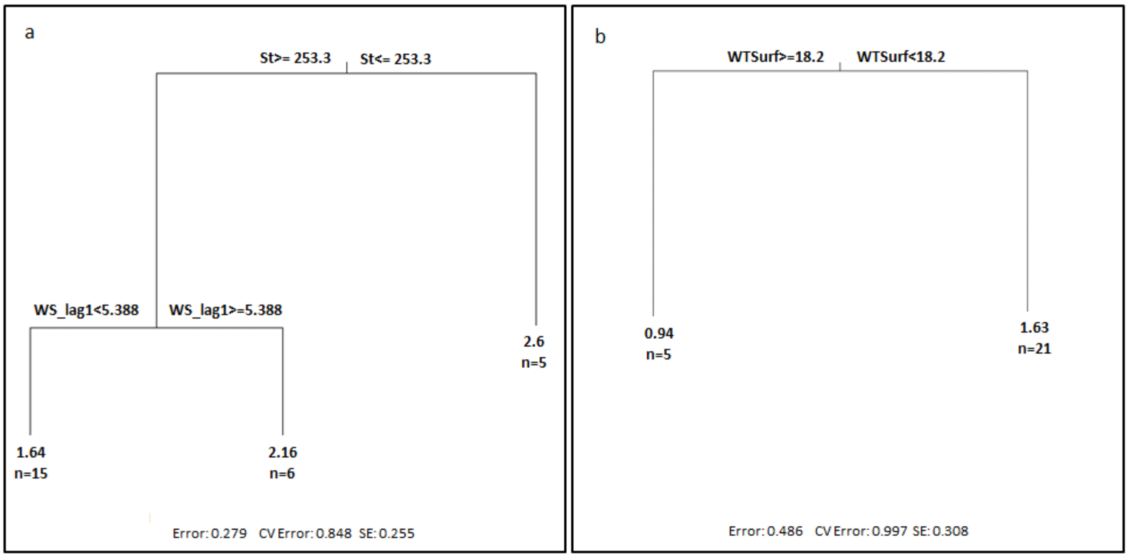


Figure 4.14 Univariate regression tree analysis of genera diversity (a) and MBFG (b) explained by the environmental variables

Discussion

Complex interactions between abiotic disturbances contributed to the heterogeneous patterns of phytoplankton community observed during the period from spring to summer in Mt Bold. Both abiotic features (meteorological conditions and lake hydrodynamics) and biotic features (zooplankton abundance and composition) showed long and short term trends, as expected. Water temperature and stability emerged as the main drivers of phytoplankton abundance and diversity, respectively. Water temperature and stability indicated the strongest increasing trend over a long term period while wind speed, lake number and the surface mixed layer depth fluctuated with varying intensities and frequencies. Similar to many eutrophic lakes, the species richness was low and presented minor changes throughout the period (Figueredo and Giani 2001). Phytoplankton taxonomic (genera) diversity showed a decreasing trend with the long term increase in the epilimnion temperature and water column stability. These results are in accordance with the findings of other studies where prolonged stable conditions showed a declination in phytoplankton species diversity (Lindenschmidt and Chorus 1998, Weithoff et al. 2001).

The variation in the diversity of functional and ecological traits was different to that of taxonomic diversity. Functional diversity showed a slight increase, which remained nearly constant during the middle of spring, followed by a gradual declination as summer advanced. Weithoff et al. 2015 also noticed a divergence in the taxonomic diversity and functional diversity in Upper Lake Constance during the spring-summer period. In the previous study, the taxonomic diversity decreased until early spring whilst the highest functional diversity was observed during early spring. The declination of functional diversity, following mid-spring, in Mt Bold is directly resulting from the increasing dominance by phytoplankton belonging to Group VII (Appendix Fig 4.4) containing all phytoplankton divisions that contain large mucilaginous colonies, including *Sphaerocystis, Oocystis* and *Microcystis.*

Understanding the driving forces behind the patterns observed in diversity requires the study of disturbances in relation to its frequency, intensity and duration (Rojo and Alvarez-Cobelas 1993, Padisák 1994, Reynolds 2006). Frequency of disturbances is generally classified based on phytoplankton generation times (Reynolds 1988, Padisák 1994) and the sampling frequency. Given that sampling in the study was carried out every 3-4 days on average, the perturbations observed during the period investigated can be classified into two; low frequency (>10 days) and intermediate frequency (3-8 days or 20-200 hours) (Reynolds 1988, Padisák 1993). High frequency disturbances are rare in temperate climates as the average frequency of climatic variations generally fit the time scale specified for intermediate frequency (Padisák 1993). Time period between oscillations during the study did not exceed 10 days and therefore all fluctuations in environmental variables were of intermediate frequency.

The intensity of the disturbance determines whether it is adequate to disrupt the existing structure by reducing the phytoplankton growth or by substituting with efficient species (Reynolds 2006). Unlike the frequency, the intensity of a disturbance that is required to result in changes in community composition cannot be quantified by way of low, intermediate or high, as their impacts vary from one system to another (Reynolds et al. 1993). Hence, the disturbance intensity or the strength of the stimulus impacting upon the phytoplankton biomass and composition can only be quantified in relative terms. Variation in LN and relative mixing indicated relatively low, medium and high intensities over different periods of time. Beyond late October, LN fluctuated with increasing intensities while Zsml remained almost constant or varied with very low intensities. The opposite was true for Zsml for the period prior to mid-September. Relating this trend to the changes in MBFG diversity indicated that the highest diversity is maintained in the period during which the disturbances related to mixing was occurring at a relatively medium intensity (Fig. 4.15). Intermediate Disturbance Hypothesis (IDH) (Connell 1978, Grime 1979) states that disturbances of intermediate frequency and intensity result in the highest phytoplankton diversity. This hypothesis has been widely supported by observational evidence from various communities occupying a range of habitats (Grime and Pierce 2012). Although testing the validity of IDH was not the main aim of the study, the resulting variation in phytoplankton diversity based exclusively on morphological traits indicated that it fits the theory of IDH. It is possible that the high magnitude of the physical disturbances occurring during the end period can not only disrupt community development but are also not of adequate duration for new community establishment. Weithoff et al. 2001 also found the diversity in functional traits from field data to provide improved explanation into the organization of phytoplankton communities within the framework of IDH. However, given that some field studies and controlled mesocosm and microcosm experiments have failed to find the predicted increase in diversity under intermediate disturbances, validity of the IDH and applicability of it to motile organisms remain questionable (Fox 2013, Sheil and Burslem 2013). The hypothesis is negated on the basis that disturbances that are considered to promote species coexistence might also reduce the strength of competition that is required for competitive exclusion by dominant species. The increase in diversity could be associated with the relative fitness of different species that regulate the rate of exclusion, regardless of the frequency of the environmental change (Fox 2013). Hence, species specific traits and trade-offs strongly determine the conditions under which they can thrive on its own and their impacts on other species.

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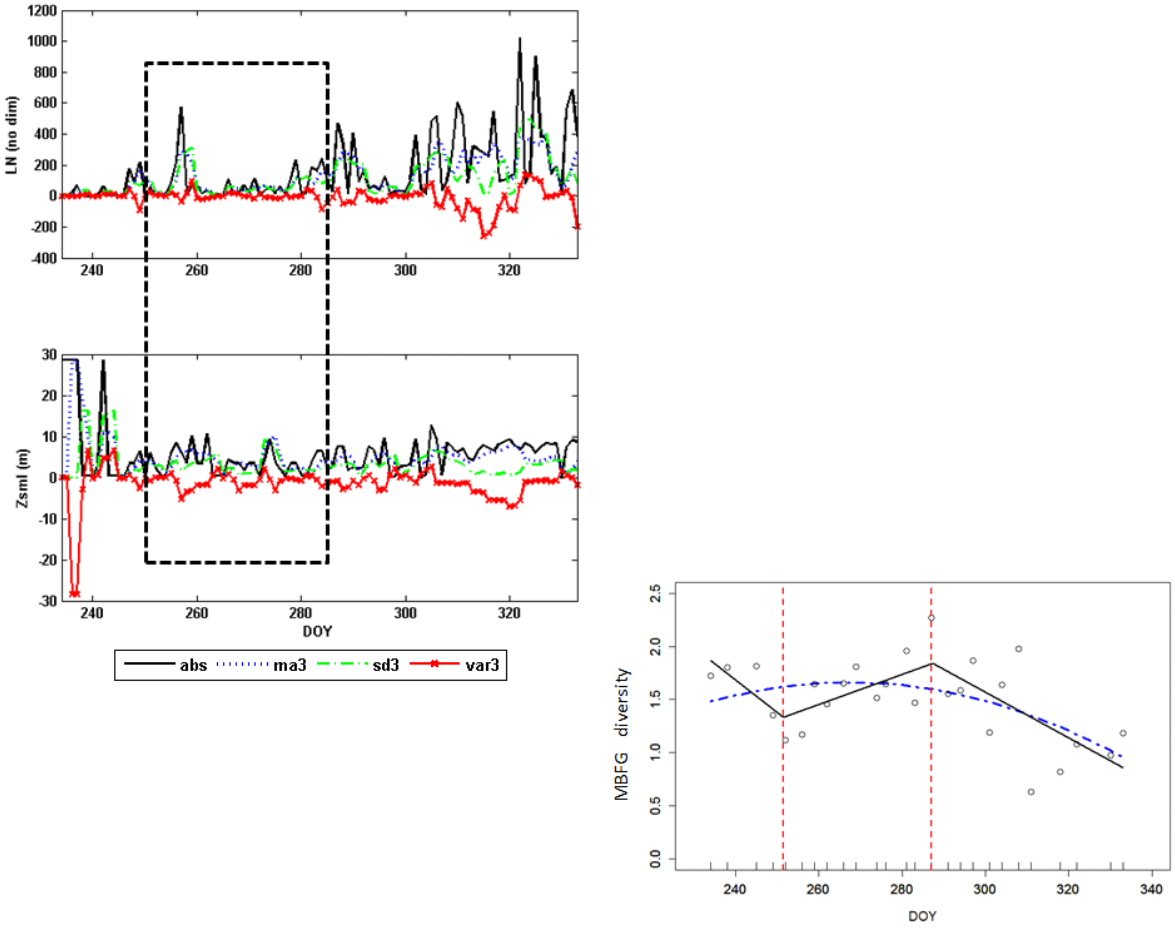

Figure 4.15 Oscillations in mixing of moderate intensity promote the highest trait based diversity in Mt Bold

As opposed to the wind driven fluctuations in LN and Zsml, stability showed oscillations of less intensity, increased duration and indicated a strong increasing trend. Development of stable conditions over a long course of time can create resource depletion that may lead to specific species selection under equilibrium conditions. Sommer et al. 1993 describes equilibrium conditions as the phase when one, two or three species at most contribute to more than 80% of the phytoplankton biomass and that this coexistence persists for more than 1-2 weeks during which time no significant changes in the total biomass occurs. Considering the changes in the phytoplankton in Mt Bold over the last two weeks of November when the water column is stratified (>678 J/m^2/day), more than three genera were recorded and the total biomass increased by 50% at the end of the second week. The non-equilibrium conditions are potentially arising from the short term oscillations in the physical factors, such as the changes in surface mixed layer depth and LN that were embedded within the long term trend of increasing stability. Sufficiently long periods of fluctuations in lake hydrodynamics (LN, Zsml) and selective grazing pressure could prevent competition from reaching the stages of equilibrium and support the growth and persistence of species to result in coexistence (Litchman and Klausmeier 2008). Lindenschmidt and Chorus 1998 observed diversity to remain high for extended periods during summer where frequent occurrences of low lake numbers supported a mixture of species to enhance vertical niche separation and promote diversity.

Diversity amongst species and coexistence are known to arise to from the ecological differences and the trade-offs that determine the resource exploitation abilities and resistance to predators (Reynolds et al. 2002, Weithoff et al. 2015). A combination of phytoplankton genera belonging to MBFG Groups II, IV, V, VI and VII were observed in Mt Bold (Appendix Fig. 4.4). Stable coexistence is identified when species biomass do not show long term trends and manage to recover when the densities got low (Chesson 2000). Such increasing and decreasing pattern in phytoplankton abundance, especially of Group V, showed stable coexistence with other groups, even while genera belonging to Group VII were increasing in dominance. Specific morphological characteristics of Group V species (e.g. *Cryptomonas*) such as the possession flagella to facilitate motility, reduce sinking losses and can benefit under high grazing pressures (Kruk et al. 2010). The composition of phytoplankton in Mt Bold under stratified conditions consisted mostly of Group VII genera that showed a variety of survival adaptations. For instance, the observed colonial cells such as *Sphaerocystis*, *Oocystis* and *Microcystis* (Group VII) have similar morphological adaptations made up of large mucilaginous sheath that lower sinking losses and decrease the susceptibility to grazing. Size and shape of phytoplankton cells and colonies regulate the growth and vulnerability to predators and can express species-interaction traits (Pomati et al. 2013). Even the appearance of diatoms belonging to Group VI (i.e. *Cyclotella*, *Tabellaria*) contributing to >20% of the biomass on average during the last two weeks of spring, indicated that short term, mixed environments created by the lowered LN favoured these low light tolerant organisms with high sinking losses (Reynolds et al. 2002). The coexistence between a mixture of competitors, stress-tolerant and ruderals (sensu Reynolds 1984) suggests that the influence of regular disturbances on the functional group selection was higher than the continuous increase in stability. This study further demonstrates that diversity of natural communities is influenced by traits that define species strategies for tolerance, exploitation of resources and resistance to predation (Pomati et al. 2013, Weithoff 2003). Hence functional diversity appears to be an invaluable predictor of environmental conditions that can be applicable to test ecological theories.

Conclusion

The transition period between spring to summer signified a range of environmental disturbances that varied in intensity and duration, underlying the long term increase in thermal stability. Under short term changes in the wind induced mixing conditions and steadying stratification, there was selection of a set of specialised phytoplankton morphological traits that occupied the non-equilibrium state. High functional diversity was observed when the oscillations in the mixing were of relatively intermediate intensity and the lowest was found when the intensity and frequency of the disturbances were both relatively low and high, as stated by IDH. Coexistence amongst species was promoted as a result of the frequent disturbances that created changes in the resource gradients enabling the survival of phytoplankton groups with specialised traits for resource acquisition under modified environments.

Appendix

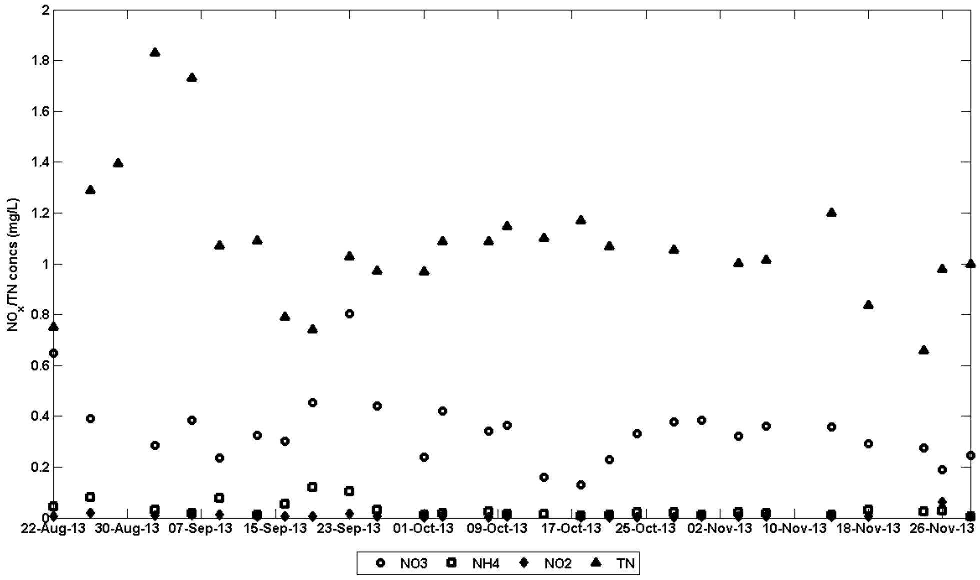

Figure A4.1 Concentrations of nitrate (NO3), ammonia (NH4), nitrite (NO2) and total nitrogen (TN)

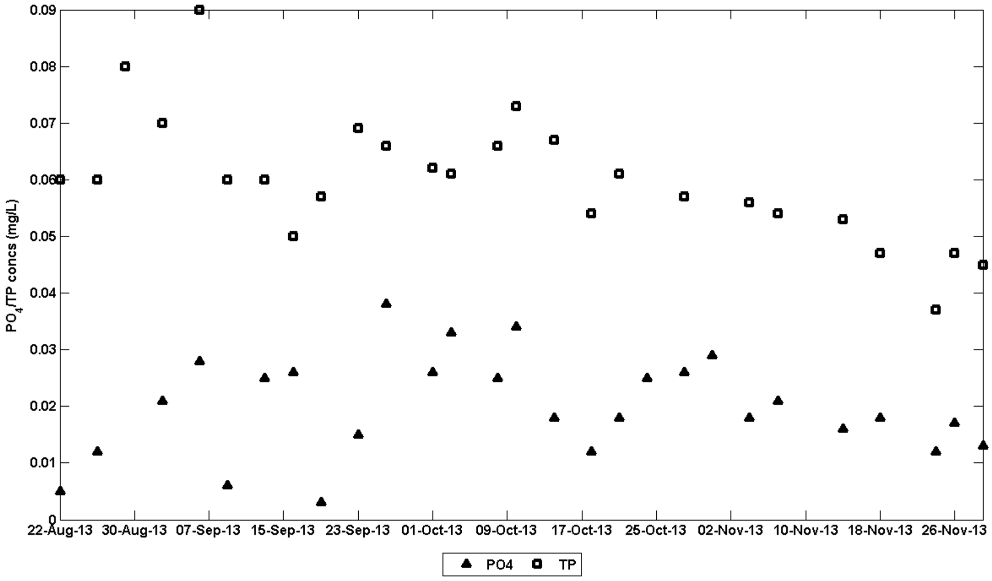

Figure A4.2 Concentrations of filterable reactive phosphorus (PO4) and total phosphorus (TP)

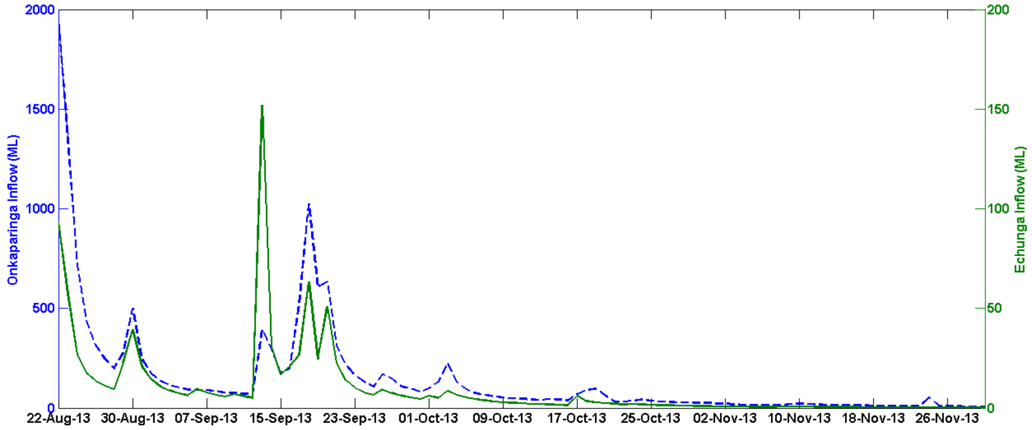

Figure A4.3 Daily inflow volumes of Onkaparinga (dashed line) and Echunga (thick line) to the Mt Bold reservoir during the sampling period

Table A4.1 Biovolumes (µm^3/cell) of the observed phytoplankton genera

	Botry	Chlam	Sphe	Ooc	Ank	Clost	Crypt	Chro	PenDia	Tab	Aul	Cyc	Cer	Tra	Eug	Mal	Mic
22/08/2013	1689.42	0.00	0.00	249.23	0.00	321.56	394.68	0.00	85.95	41.00	0.00	784.91	62.77	192.49	0.00	0.00	0.00
26/08/2013	0.00	83.81	81.30	325.22	0.00	0.00	0.00	0.00	122.24	38.87	0.00	1013.49	79.36	252.02	0.00	379.82	0.00
2/09/2013	0.00	0.00	322.10	195.14	0.00	188.08	738.09	388.46	94.26	0.00	0.00	839.47	73.43	201.04	0.00	50.21	0.00
6/09/2013	4784.57	36.74	38.11	54.45	0.00	0.00	3720.99	362.95	43.66	0.00	0.00	663.20	42.51	173.81	39.88	77.52	0.00
9/09/2013	113.47	1362.64	93.05	61.38	0.00	316.76	3169.14	436.94	15.88	0.00	2.89	1281.29	54.11	325.05	217.50	0.00	0.00
13/09/2013	0.00	0.00	0.00	0.00	121.63	712.71	4514.87	528.96	80.37	0.00	39.08	1199.14	0.00	0.00	0.00	0.00	0.00
16/09/2013	0.00	0.00	217.70	72.01	144.03	803.78	2609.17	215.86	100.71	0.00	71.01	1849.86	0.00	234.84	0.00	0.00	0.00
19/09/2013	4373.25	0.00	0.00	8.25	0.00	577.43	159.86	8.06	66.15	157.77	0.00	1064.29	0.00	324.49	0.00	11.01	0.00
23/09/2013	1148.86	0.00	233.87	173.73	0.00	0.00	561.12	67.86	26.79	0.00	9.77	894.69	0.00	365.68	0.00	71.35	0.00
26/09/2013	291.27	0.00	277.83	76.23	0.00	67.76	111.62	3.31	20.38	0.00	12.38	529.27	0.00	110.09	0.00	45.22	0.00
1/10/2013	1616.92	0.00	178.68	0.00	0.00	0.00	437.39	2.20	15.08	0.00	41.25	1705.16	0.00	160.83	247.95	0.00	0.00
3/10/2013	1506.48	0.00	71.69	97.98	0.00	95.58	101.88	20.53	67.06	0.00	164.22	1106.53	0.00	81.73	2152.64	0.00	0.00
8/10/2013	420.25	0.00	933.11	128.33	0.00	806.56	611.03	68.74	80.85	0.00	24.12	1109.67	7.16	106.59	120.83	0.00	0.00
10/10/2013	14153.44	0.00	695.39	77.99	0.00	1559.65	8186.14	1000.16	0.00	0.00	19.00	1468.42	0.00	44.46	142.79	0.00	0.00
14/10/2013	0.00	0.00	1539.70	158.96	0.00	1404.68	644.74	46.21	133.39	0.00	56.75	989.95	0.00	50.58	203.06	789.48	0.00
18/10/2013	0.00	0.00	2137.06	0.00	0.00	919.11	7205.84	308.44	376.89	0.00	216.87	1241.20	0.00	85.74	0.00	0.00	0.00
21/10/2013	663.85	0.00	2934.43	108.11	0.00	308.87	4818.57	0.00	294.12	0.00	175.01	958.56	0.00	66.03	0.00	0.00	0.00
24/10/2013	408.49	0.00	3531.70	377.76	0.00	2423.21	1629.84	9.74	142.88	0.00	88.58	1292.34	0.00	0.00	78.30	0.00	0.00
28/10/2013	704.92	14.49	3384.25	321.56	0.00	0.00	10657.95	40.49	324.06	0.00	146.44	779.34	0.00	0.00	77.21	0.00	0.00
31/10/2013	0.00	0.00	20814.56	377.59	64.43	1887.82	8231.79	467.53	0.00	0.00	690.11	1053.27	0.00	0.00	0.00	2519.93	517.68
4/11/2013	0.00	0.00	15313.11	890.94	190.04	4454.43	2158.16	32.19	1116.25	0.00	1260.35	3727.89	0.00	0.00	587.25	3127.57	0.00
7/11/2013	0.00	0.00	23301.94	606.28	0.00	1126.34	693.37	0.00	53.13	0.00	79.93	845.60	0.00	0.00	0.00	592.55	8961.27
14/11/2013	0.00	0.00	47899.30	340.66	0.00	1513.93	6525.17	60.32	224.59	579.13	221.37	1161.42	0.00	62.14	0.00	0.00	8462.63
18/11/2013	0.00	0.00	38384.85	2301.61	0.00	1484.81	1294.90	0.00	0.00	4589.33	223.63	6523.81	0.00	126.97	1631.26	594.59	14003.27
24/11/2013	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	48702.66
26/11/2013	0.00	0.00	83368.26	4702.82	233.46	3420.01	994.19	0.00	1028.44	0.00	375.07	16934.63	0.00	0.00	0.00	913.03	0.00
29/11/2013	0.00	0.00	87769.58	5840.18	0.00	3136.81	4526.99	488.82	374.63	30636.45	243.98	13032.80	0.00	256.83	0.00	445.44	16295.39

Table A4.2 Numerical summary of the MRT (Chapter 4 Fig 4.13 - absolute abundance vs environmental variables). Explained variance at each split for each genera represents the contributions of individual genera at each split and how well each genera is explained by the tree.

	WTSurf 17.35	Zeu 2.245	LN_rm 294.7	WTSurf 13.38	col_total_tree	col_total_species
Botry	4.16	0.02	0.00	0.00	4.17	11.07
Chlam	0.19	0.04	0.00	0.00	0.23	2.91
Sphe	2.13	1.50	0.15	1.15	4.94	8.80
Ooc	0.64	0.04	0.15	0.64	1.47	4.67
Ank	0.64	0.04	1.46	0.00	2.13	3.69
Clost	0.71	0.03	0.21	0.60	1.55	7.39
Crypt	0.14	0.93	0.06	0.82	1.96	4.12
Chro	0.79	1.02	0.00	0.51	2.33	5.27
PenDia	0.64	0.01	0.63	0.11	1.40	3.51
Tab	1.31	1.76	1.09	2.55	6.70	6.90
Aul	0.81	1.17	0.23	0.42	2.63	4.54
Cyc	0.00	0.00	0.26	0.88	1.14	2.01
Cer	0.34	0.37	0.00	0.00	0.71	2.90
Tra	1.29	0.19	0.45	1.05	2.99	5.27
Eug	0.24	0.76	0.15	0.23	1.38	7.18
Mal	2.30	0.19	0.56	0.04	3.10	8.18
Mic	7.71	0.00	3.86	0.01	11.57	11.60
total_col	24.05	8.08	9.27	9.01	50.40	100.00

Table A4.3 Discriminant genera that contribute to >10% of the explained variance and the mean (transformed) abundances for the branches of the node

	WTSurf<17.35WTSurf>=17.35				
	Botry	Mic			
% of expl. deviance	17.28	32.04			
Mean on the left	2.53	0.00			
Mean on the right	0.00	3.46			
	WTSurf<13.38WTSurf>=13.38				
	Sphe	Crypt	Chro	Tab	Aul
% of expl. deviance	18.59	11.54	12.62	21.74	14.51
Mean on the left	0.86	2.04	0.52	2.46	0.00
Mean on the right	3.13	3.83	2.39	0.00	2.01
	Zeu>=2.245Zeu<2.245				
	Ank	Tab	Mic		
% of expl. deviance	15.77	11.78	41.62		
Mean on the left	0.00	2.58	4.84		
Mean on the right	2.98	0.00	0.00		
	LN_ma3<294.7LN_ma3>=294.7				
	Sphe	Tab	Tra		
% of expl. deviance	12.73	28.28	11.68		
Mean on the left	2.51	0.00	0.00		
Mean on the right	5.39	4.29	2.76		

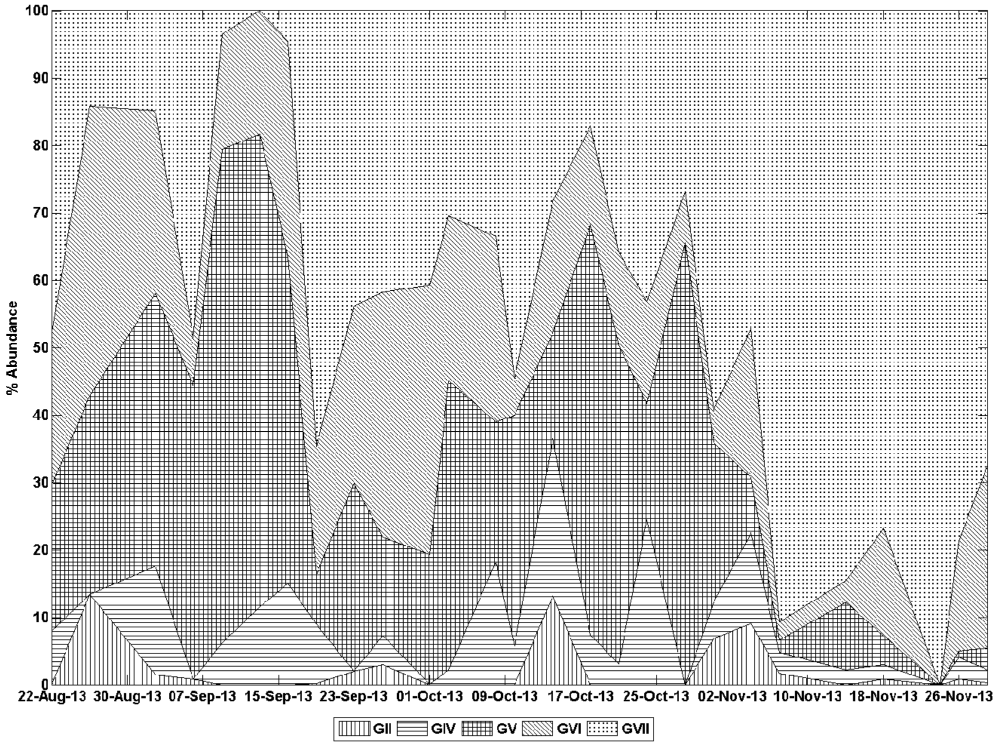

Figure A4.4 Percentage biovolume of morphology based functional groups

Chapter 5 General Discussion and Conclusion

Climate change and land use modification are major challenges that have, individually and together, implicated water resources in the recent history (Brookes and Carey 2011, Paerl et al. 2011). The growing consensus about the inevitability of global warming and climate change is forcing both decision makers and researchers to determine the possible consequences for lakes and reservoir ecosystems (Sahoo and Schladow 2008). Climate change will directly affect the physical, chemical and biological attributes of lakes due to the changes in the thermodynamic balance between the air-water interface that results in high thermal stability under a warming atmosphere. Thermal stratification is accepted as a prime environmental variable affecting plankton population dynamics (Reynolds 1984, Sommer 1986).

Catchment alteration and eutrophication directly influence the nutrient availability and regulate the rate of production of phytoplankton biomass or primary productivity. A warming climate together with altered nutrient loads increase particulate matter, creating variations in light attenuation and heat entrapment and thereby, further affecting thermal stability (Mazumder et al. 1990, Kumagai etal., 2000). While temperature and nutrients may exert significant control of phytoplankton growth and composition, relative importance of each factor is expected to differ depending on the lake nutrient status and the type of phytoplankton species (Rigosi et al. 2014). This study was initiated with the purpose of gaining a better understanding on how warming and nutrient loading will affect multiple aspects of the lake dynamics. Specifically, the objectives were to interpret how: a) nutrients and temperature would individually and synergistically exert control over the development of phytoplankton in lakes with varying nutrient status; b) how mixing and stratification would be altered under a changing environment; and c) how these changes in return govern the phytoplankton abundance and diversity.

The trophic status and the relative nutrient availability of a lake affect the rates of resource supply that allow growth populations of cells and ultimately lead to phytoplankton species selection (Reynolds 1998). The meso-oligotrophic, Lake Tarawera in New Zealand and the eutrophic lake, Mt Bold Reservoir in South Australia, were used as examples to study and compare the responses of three different phytoplankton functional groups, chlorophytes, cyanobacteria and diatoms, to varying nutrient status and temperature (Chapter 2). There was a marked three-fold increase in the phytoplankton biomass relative to the base conditions in the oligotrophic lake as a result of nutrient enrichment. Nutrient addition is observed to result in exponential growth of phytoplankton and has been commonly associated with increased productivity in lakes (Fogg 1968, Reynolds 1984, Carpenter et al. 1998, Moss et al. 2003). The eutrophic lake showed a rise in phytoplankton biomass as a result of increased nutrients, but this increase was more pronounced when the temperatures were high. Similar results were observed during lab controlled experiments, where higher temperature increased phytoplankton growth rate under all conditions but the temperature influence was significantly enhanced by nutrient addition (Staehr and Sand-Jensen 2006). Rhee & Gotham (1981) suggested that elevated temperatures also increase the biological demand for nutrients, which explains the beneficial nature of nutrient enrichment under warm conditions as observed in this study. This was further demonstrated by the limitation functions, which showed a marked increase in P limitation under high temperatures, indicating an enhanced uptake of nutrients and augmented phytoplankton growth as the metabolic rates increased. However, Toseland et al. (2013) found that at higher temperatures, phytoplankton requires a lower density of ribosomes to produce the required amounts of cellular protein and thereby, have low N requirements. Ambient temperature under which the nutrient uptake is maximised vary from one phytoplankton species to another and this strong temperature dependence of most physiological traits affect seasonal productivity, abundance and species selection in lakes (Raven and Geider 1988, Ibelings et al. 2011).

In scenarios where the original meso-oligotrophic status in Lake Tarawera was unchanged, increasing temperatures shifted the summer biomass peak but did not increase phytoplankton growth, indicating that nutrient enrichment was required for algal growth development. On the other hand, under similar conditions, the eutrophic Mt Bold experienced increased phytoplankton productivity as a result of temperature increases under its base nutrient status. A decrease in nutrient inputs had a little effect on the total algal biomass in Lake Tarawera, but in Mt Bold, it prevented the increase in phytoplankton biomass which would have otherwise occurred under high temperatures. This highlights the sensitivity of oligotrophic lakes to nutrients and high sensitivity of eutrophic lakes to both temperatures and nutrients. The impacts of rising temperatures, especially in the oligotrophic lake, were masked by the profound effects of increasing nutrients. The eutrophic lake, on the contrary, could experience large increases in phytoplankton growth and degrading water quality as a result of both nutrient enrichment and warming. Hence, it was evident that trophic status plays a complimentary role in determining the detrimental effects of climate change and nutrient poor, oligotrophic lakes are more resilient to the impacts of warming.

In addition to the phytoplankton abundance, changes in the trophic status under warming conditions altered community composition and dynamics as observed in previous studies (Anneville et al. 2015, De Senerpont Domis et al. 2013, Gallina et al. 2011, Paerl and Huisman 2008). Some modelling studies have observed cyanobacteria to dominate under nutrient enriched and warm conditions (Markensten et al. 2010, Elliott et al. 2006), while other experimental and observational studies have recorded no change in cyanobacterial biomass (Moss et al. 2003, Anneville et al. 2005). A threshold of cyanobacterial concentrations above 10 µg/L is generally used as the reference for posing a health risk by the World Health Organization (Chorus and Bartram 1999). A harmful cyanobacterial bloom (>10 µg/L) was not promoted by increasing temperature and nutrients in the studied lakes, where the phytoplankton assemblage predominantly consisted of a combination of chlorophytes and cyanobacteria. Chlorophytes with higher growth rates (Gal et al. 2009, Reynolds 1984) showed an advantage over cyanobacteria under eutrophic/hyper-eutrophic conditions. Chlorophytes are commonly found in water bodies and show a widespread distribution, both in terms of the latitude and with the characteristics of the lake, as they are found in a wide range of environments (i.e. even in extreme desert, snow and hypersaline conditions) (Happey-Wood 1988). Their excessive growth and dominance have been observed in some lakes as the nutrient status changed to hyper-eutrophy (Jensen et al. 1994).

Changes in phytoplankton communities are associated with variations in the physical (light climate) and the chemical (nutrient availability) constraints for algal growth (Reynolds, 1984). Recent experimental studies have also supported the observations of this modelling study where chlorophytes were recorded to dominate over cyanobacteria when N and P concentrations are high (Wang et al. 2010, Deng et al. 2014, Ma et al. 2015). This is not surprising due to the physiological adaptations of different phytoplankton groups as discussed in detail in Chapter 2. Average characteristics were used to represent the three phytoplankton groups modelled in the study. Chlorophytes were defined to have the highest growth rate and were parameterized to have higher nutrient uptake rates (compared to cyanobacteria) due to the high surface area:volume ratio of some smaller genera (e.g. Sphaerocystis, Chlorella) that enable efficiency. Some chlorophyte species also possess flagella (e.g. Chlamydomonas) and some have mucilaginous sheaths around colonies (e.g. Sphaerocystis, Oocystis) that assist them with motility under stagnant conditions (Reynolds 1984, Sandgren 1988, Demir et al. 2014). Hence, the modelled chlorophyte group was specified to have neutral buoyancy. Wang et al. (2010) observed the growth of edible algae, such as species of chlorophyta, to be promoted in the absence of zooplankton predation, while blooms of cyanobacteria (Microcystis) were formed in the presence of heavy grazing. Selective predation by zooplankton is an important biotic factor that affects phytoplankton dynamics and studies have observed cyanobacterial blooms to occur only when there is decreased abundance of large-sized cladocerans (Wang et al. 2010, Lürling et al. 2013). Due to the absence of zooplankton information in both Lake Tarawera and Mt Bold, grazing was integrated into the model through the mortality function. Shifts in zooplankton community structure towards a dominance by specialist grazers under warming conditions could have an impact on the interactions between the phytoplankton groups and therefore, should be exclusively modelled in future studies.

Nevertheless, increasing overall phytoplankton biomass poses considerable threats to water quality. Although chlorophytes are generally not considered as a toxic group, there are instances when some form distinctive nuisance blooms that on rare occasions proliferate and persist to cause changes in taste and odour, affect water treatment by clogging filters and interfere with gills of fish (Reynolds 1984, Paerl et al. 2001). Additionally, large blooms of chlorophytes can simplify food webs, decrease biodiversity and alter biogeochemical cycling (Turner et al. 1995). Therefore, increased overall phytoplankton biomass under a warming climate and intense eutrophication will alter food webs and affect water quality. Formation of large scale phytoplankton scums will lower provision of amenities by water bodies and may incur high economic costs in relation to water treatment (Atech 2000, Dodds et al. 2009).

Mechanistic biogeochemical models have been widely used as a management tool for predicting future responses of aquatic systems to changing environmental conditions (Hamilton and Schladow 1997, Elliott et al. 2006, Gal et al. 2009, Trolle et al. 2011). These models typically contain a large number of parameters, with values that are site-specific but the selection of the model complexity is generally driven by the system being studied, the objectives of the study and the availability of data (Arhonditsis and Brett 2004). The conceptual biota model in this study used for Lake Tarawera and Mt Bold included chlorophytes, cyanobacteria and diatoms as the dominant phytoplankton groups, and the overall model included a low number of model parameters (<20). While automated calibration approaches are an effective method when there are many parameters, the capacity to carry out these computational costly techniques is not readily available. Hence manual trial and error calibration strategies that are guided by expert knowledge and scientific literature describing previous laboratory, field and modelling work were adopted in this instance. In the few studies where auto-calibration techniques have been applied to the outcome of the auto-calibration was only slightly better than that achieved by manual calibration by experts and in some cases even worse (Dean et al. 2009). Some studies, however, suggest a combination of both manual and auto calibration techniques to improve the model efficiency (Rigosi et al. 2011).

The calibration and validation of the model for Lake Tarawera and Mt Bold surface waters generally showed good agreement with observed data for temperature, DO and total nutrients. The model did not reproduce accurately the timing of the peak of total phytoplankton biomass, but it captured correctly the magnitude of these peaks. Additionally, the model simulated the chlorophyll a levels were within observed range in both calibration and validation periods that contained very different chlorophyll levels in Mt Bold. Thus the model's ability to predict new conditions with scenarios analysis was unequivocally tested (Arhonditsis and Brett 2004). Phytoplankton traits play a significant role in determining what species occur under given environmental conditions and thereby, affect how phytoplankton communities might reorganize in the future (Litchman et al. 2010). Hence the phytoplankton traits defined in the model will evidently have a considerable impact on the observed phytoplankton responses under the various scenarios tested.

To evaluate how these responses may have varied if different traits were defined in the model, a simple sensitivity analysis was carried out by varying growth rates, nutrient uptake rate and settling rates of chlorophytes and cyanobacteria. The main objective of this sensitivity analysis was to identify which selected specific traits influence the competition between chlorophytes and cyanobacteria and does not aim to provide a comprehensive analysis thorough quantification of model sensitivity to all phytoplankton parameters. Light parameters were unchanged as the chlorophytes were nonetheless simulated to be photoinhibited when irradiance exceeds 40 µmol/m2/s. The responses of the two lakes to the modified parameter values were different. Delayed growth resulting from decreased chlorophyte growth rates caused a shift in the chlorophyte peak in Tarawera and increased spring diatom chlorophyll concentrations and decreased cyanobacterial concentrations by a similar amount. Including a higher settling rate of 0.1 m/day had a considerable decrease on the chlorophyte growth in Tarawera. However, the most notable change in the phytoplankton composition occurred in Tarawera when the growth rate of cyanobacteria is increased, leading to cyanobacterial dominance. The impact of increased cyanobacterial growth rate was less in Mt Bold, where increased growth rate resulted in a minor increase in the cyanobacterial concentration. Instead, chlorophyte growth rate was the most sensitive parameter that affected the phytoplankton growth and composition, indicating that parameter sensitivity of phytoplankton groups in different systems could vary greatly.

Another important aspect of nutrients and temperature changes is the individual and interactive influences on the lake's thermal structure, which is a central feature that regulates fluxes of nutrients and distribution of light, and therefore affects phytoplankton development (Reynolds 1998, Cantin et al. 2011, Becker et al. 2011). Variations in heat budget and subsequent changes in thermal structure are valuable for quantifying the energetics involved in the heating and cooling of lakes and their resistance to mixing under altered environmental conditions (Bowling 1990). Hence, the lake heat content and associated changes in Schmidt stability and thermocline depth in the oligotrophic Lake Tarawera as a result of varying nutrients and temperature were explored in detail in Chapter 3. An important intrinsic factor that impacts the distribution of radiation within the water column is water clarity and in most lakes, water clarity is largely determined by the plankton content (Mazumder et al. 1990). Subsequently, light extinction coefficient (K_w) in lake models influence thermal dynamics, surface temperature, and heat storage in a lake and therefore directly influences the lake atmosphere interaction (Rinke et al. 2010, Heiskanen et al. 2015). Under high nutrient and warm conditions, increased phytoplankton abundance in Lake Tarawera led to high light attenuation coefficients (from 0.2 to 0.4).

Only minor changes in the annual mean lake heat content occurred as a result of increasing temperatures and nutrients. However, the lake experienced atypical changes in the seasonal heat fluxes. Highest evaporative losses occurred in spring-summer period, when the highest surface temperatures and highest Kw are experienced. High surface water temperatures and high light attenuation increase radiative absorption and accumulates heat in the epilimnion during day time, but this is then readily lost to the atmosphere (Hocking and Straškraba 1999, Jones et al. 2005). In contrast, the highest gain in the net heat storage occurred during autumn and winter seasons in the nutrient rich, high temperature scenarios. This is due to the heat content that is accumulated during spring-summer period that is lost slowly to the atmosphere as a result of diminished outgoing heat fluxes. Thus, the increase in net heat during winter-autumn period cause advancement in the onset of stratification as the trophic status changed from oligotrophic to hyper-eutrophic under rising temperatures.

If the temperatures were to increase by 1 to 4 °C by year 2100 as projected by the IPCC (IPCC 2013), the overall thermal stability of the deep, oligotrophic lake was found to increase in a linear manner. Under the most extreme warming scenario (4 °C), the onset of stratification commenced two months earlier and extended for two months extra compared to present conditions. A warming climate also reduced the thermocline depth as a result of incomplete mixing during winter and resulted in a persistent shallow thermocline that extended onto spring-summer period. This supports the increasing evidence that a warmer climate cause alterations in the thermal structure of deep lakes, including high resistance to water column homogenization (Straile et al. 2003, Coats et al. 2006, Sahoo and Schladow 2008) and reduced thermocline depth (Stainsby et al. 2011, Zhang et al. 2014).

Increasing epilimnetic temperatures and stratified water columns have significant implications for water chemistry and aquatic species. High water temperatures directly affect the oxygen content in the water bodies by reducing the gas holding capacity (Sahoo and Schladow 2008). Increased thermal stability resulting from high water temperatures can hinder the vertical movement of gases, such as DO, which can lead to anoxic conditions as respiration of heterotrophs in the sediment tend to utilize the available oxygen (Livingstone 2003, Fang and Stefan 2009, Foley et al. 2012). Hypolimnion anoxia can cause internal nutrient loading (Paerl et al. 2011), with some studies finding that even a short extreme anoxic period (<2 mg/L of DO) (Nürnberg 2004) can induce P entrainment from the sediment to the water column (Hupfer and Lewandowski 2008). Prolonged periods of warm waters, stratification and subsequent extension of the growing season have been observed to result in larger phytoplankton biomass with a few dominating phytoplankton taxa consisting of cyanobacteria and large dinoflagellates (De Senerpont Domis et al. 2013, Paerl and Huisman 2008, Blencker 2007).

Changes in the thermal structure caused by warming in Lake Tarawera were further intensified by excessive nutrient loading, especially under intermediate temperature rises of 1-2 °C. Surface water temperature, density dependent thermocline depth and nutrient driven total chlorophyll emerged as the main regulators of thermal stability in Lake Tarawera. Under extreme temperature rises and increased nutrients and/or phytoplankton overgrowth, the stable conditions and increased turbidity can prevent the penetration of heat to deep layers and enhance the disparity between the surface and bottom waters (De Stasio et al. 1996, Hondzo and Stefan 1996). Lake Tarawera also experienced inconsistent variation in the hypolimnion temperatures in comparison to the surface waters. Large differences between the warming rates in the epilimnion and hypolimnion can lead to steep thermoclines and highly stable conditions that extend over weeks, as observed in other large temperate lakes (Livingstone 2003). Different rates of warming surface and bottom waters in Lake Tarawera may have contributed to the establishment of shallower thermoclines with no deep winter mixing and stable conditions which persisted for two months in excess under high air temperatures.

As the temperatures started to rise, the relative contribution of surface water temperature, thermocline depth and total chlorophyll driving thermal stability differed, depending on the nutrient status of the lake. Increased phytoplankton biomass resulting from high nutrients and subsequent increase in total chlorophyll had the highest influence under intermediate temperature rises of 1-2 °C. Under extreme temperature rises of 3-4 °C, temperature had the highest control over stability of the water column. Under a temperature increase of 2 °C, nutrient reduction was found to improve winter mixing by increasing thermocline depth, as opposed to the poor winter mixing that was observed under eutrophic conditions. The improved transparency resulting from reduced nutrients can increase heat penetration to the deep waters and will allow the hypolimnion to warm at a rate similar to the surface waters. Lowered nutrients and increased clarity, therefore, can ultimately allow similar rates of heat distribution through the water column and enable deep mixing in lakes to create isothermal conditions in winter and thereby prevent the evolution of a persistent thermocline under intermediate temperature rises. This highlights the role of nutrients in driving mixing and stability in lakes under a warming climate. Nutrient load reduction can assist in lessening the severity of warming effects on thermal structure by improving winter mixing and increasing thermocline depths, under intermediate temperature rises of 1-2 °C.

Distribution of phytoplankton is largely governed by physical mixing processes (Reynolds and Irish 1997, Diehl et al. 2002). Mixing in lakes determines the vertical distribution of light and nutrients and thereby, regulating the ratios at which limiting resources are supplied. Changes in resource distribution can shift the competition between phytoplankton species that have the adaptive capabilities and favourable functional traits to dominate and thrive under resource limiting conditions (Huisman et al. 2004). Under stratified conditions and shallow mixed layers, phytoplankton productivity will be limited by sedimentation losses where as in deep mixed layers, light shortage will be the limiting factor (Reynolds 1989). Chapter 4 explored in detail the changes that occur in taxonomic abundance and diversity and the associated changes in the functional groups when transitioning from a state of mixed to stratified. Intensive sampling was carried out from the period of spring to summer with the aim of capturing short scale changes in the ecological processes that may affect phytoplankton dynamics. Changes in the physical, chemical and biological environment were considered to be disturbances to the system and were expected to drive the changes in the phytoplankton community and functionality during the transition period.

The seasonal transition period from spring to summer was characterised by the expected increase in thermal stability in conjunction with other biotic and abiotic disturbances that occurred in varying frequency and intensity. Changes in surface water temperatures, water column stability and euphotic depth, which showed strong seasonal upward trends, emerged as the main variables that drive phytoplankton growth and diversity. Functional diversity related to ecosystem functioning was assessed by grouping the phytoplankton genera based on the characteristic morphological and physiological traits that determine their rates of growth, rates of resource uptake and resistance to predation. Changes mixing often lead to the formation of resource gradients and when competition for multiple resources is considered, species are considered to have trade-offs in their competitive ability for one resource vs a different resource (e.g. N, P, silica and light) (Tilman 1982). Morphology based functional group (MBFG) classification presented by Kruk et al. (2010) was used to categorise the phytoplankton genera based on their cell size, motility (presence or absence of flagella) and presence of mucilaginous sheath. Functional group classification, through reduced complexity, provides an efficient tool to explore the effects of environmental changes on phytoplankton independently from geographical location and specific composition (Kruk and Segura 2012).

Increasing water temperatures and Schmidt stability, which accompanied the warming air temperatures towards summer, led to a decrease in the phytoplankton taxonomic diversity. Stabilising conditions can lead to equilibrium conditions, defined as the state when only three or less phytoplankton genera contribute to more than 80% of the total phytoplankton biomass and this coexistence persists for more than 1-2 weeks during which time no significant changes in the total biomass occur (Sommer et al. 1993). Equilibrium conditions were not observed during the seasonal transition period in this study where more than three phytoplankton genera contributed to the total biomass and this composition changed weekly. Additionally, the diversity in morphological traits expressed a different pattern to the taxonomic diversity, where the functional diversity increased towards mid-spring and then decreased following towards beginning of summer. Relating this sequence to the frequency and intensity at which the disturbances in mixing were occurring showed that Mt Bold experienced the highest functional diversity when the fluctuations in the lake number and surface mixed layer depth were occurring at a relatively intermediate or moderate intensity. This observation supports the Intermediate Disturbance Hypothesis (IDH) (Grime 1973, Connell 1978, Padisák 1993) which states that under the influence of disturbances of intermediate frequency and intensity, there will be more opportunities of high duration for community development where a greater number of species will be able to establish in the wake of each disturbance but the duration is short enough to prevent the maturity to reach a competitively excluded state of equilibrium (Reynolds 2006). As observed by Weithoff et al. 2001, the occurrence of high functional diversity indicates the coexistence of species with varying ecological demands and reflects the ecological diversity in the sense of IDH in a practical manner.

Although competitive exclusion didn’t occur to the point of equilibrium state, increased competition between species under stabilising conditions led to the dominance of several functional groups which caused a decline of diversity. However, trade-offs between the grazing resistance and environmental tolerance traits enabled coexistence amongst motile genera such as *Cryptomonas* (Group V*)* and large siliceous, non-motile diatoms (Group VI) co-occurring with large mucilaginous colony forming genera such as *Sphaerocystis* and *Microcystis* (Group VII). Existence of diatoms such as *Cyclotella* and *Tabellaria*, that have high density cells and experience rapid sinking, indicates that the intermittent turbulent conditions shown by low lake numbers provided a favourable environment for the diatoms to remain suspended within the water column. *Cryptomonas* with flagella, on the other hand, possibly thrived under the steadying conditions due to their ability to move and conduct effective nutrient foraging (Kruk et al. 2010). Similarly, genera in Group VII have the added benefit of not being susceptible to grazing and having controllable buoyant properties which promote their fitness if the nutrients are of low supply or if predation is great. In hyper-eutrophic lakes such as Mt Bold where nutrients are in abundance, the role played by cell size in exploiting nutrients would be secondary to the roles played by mucilaginous sheath which assists in buoyancy regulation under stratified conditions and cell/colony size that assists in avoiding herbivory. Each functional group or a group of genera with complimentary traits seems to occur in a characteristic, yet limited range of the multi-dimensional habitat space, known to be its ecological niche. Within this niche, each group tends to be the most abundant around a specific environmental optimum. The coexistence amongst certain taxonomic genera was observed to be due to the functional trait based selection driven by the varying ecological disturbances and the occurrence of a particular functional group could be largely explained by the mixing regime and zooplankton grazing, as observed in other studies (Weithoff et al. 2001, Weithoff 2003, Pomati et al. 2013).

Results from the field study further signified the impact of changing environments on the chemical and biological composition, as predicted with the modelling work. On one hand the intermittent hydrographic disruptions of the water column through wind-induced mixing managed to allow the coexistence between phytoplankton groups. On the other, the overall increasing thermal stability was progressive (low frequency) and occurred at high intensity leading to the trait based selection of colonial forms of chlorophytes and toxic producing cyanobacterial that possess functional adaptations to thrive under warm, stratified environments. If the transition from mixed to stratified conditions commences earlier and is of higher intensity and of longer duration under climate change, this will have significant implications for the phytoplankton community and will result in dominance of species with complimentary traits.

Conclusion

This study facilitated the understanding of interactions between climate change and nutrients in lakes with different trophic status using deterministic models to simulate multiple phytoplankton functional groups. It provided insight into the mechanisms that govern phytoplankton growth and competition under a changing environment by evaluating the direct effects on the metabolic rates, the indirect effects on hydrological conditions and the potential feedback processes (Fig. 5.1). The modelled study contributed partly to an international collaborative project that aimed to test and run the open-source model on lakes from different geographical regions and with varying morphometry in order to facilitate global water quality management. The field study contributed to a global lake study (named 'Spring Blitz'), where 11 lakes covering wide geographical locations carried out similar sampling from spring to summer to understand the finer scale changes in physical, chemical and biological components during spring-summer transition.

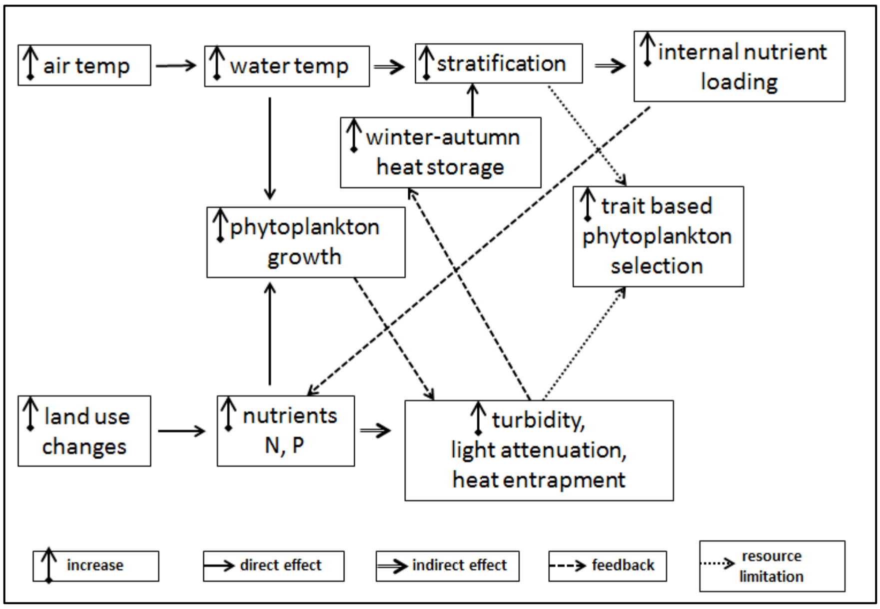

Figure 5.1 Schematic representation of the direct and indirect impacts of climate change and nutrients on phytoplankton dynamics as evaluated in this study

Global warming will continue through the 21st century, despite efforts to reduce greenhouse gas emissions (Wigley 2005). It is clear that in most cases climate change will cause degradation of water quality in lakes. Mitigation of climate change impacts will require regulation of other drivers of environmental change, such as effective land use management. The results from the current study predominantly observed the negative impacts on water quality through production of large scale algal blooms and decreased water clarity, if climate change is to continue and eutrophication is to increase. Model simulations and field study showed increasing temperatures and nutrients and subsequent reduction in mixing leading to excessive growth of trait specific phytoplankton groups. The results from the scenario analysis further indicated that improved water quality (e.g., reduced nuisance algal growth and cyanobacterial dominance, increased water clarity) in a future climate with increased air temperatures can only be achieved if external nutrient loadings to lakes are reduced considerably. While it is true that climate change demands a global response, local managers have the opportunity to offset some of the impacts through catchment management and reducing nutrients at the local and catchment scale as argued by Brookes and Carey 2011. Nutrient concentrations may have to be reduced substantially from present day values in many lakes if lake resilience to the detrimental impacts of climate change is to be promoted.

Way forward

Only a simple air temperature offset was used in representing future meteorological conditions in this model, as this variable is the most influential. The severity of climate changes impacts is bound to increase if additional potential changes in other meteorological variables and hydrologic processes are accounted for. Changes in cloud cover can affect both long-wave and shortwave radiation while changes in relative humidity and wind influence the exchange of latent heat (Trolle et al. 2011). Additionally, changes in the rainfall-runoff patterns determine the timing and volume of stream delivery into a lake (Chiew and Macmahon 2002, Sahoo and Schladow 2008). Considering all above, climate change poses a great challenge for lake managers, and failure to reduce nutrient loadings may compromise the success of traditional lake restoration techniques (e.g., artificial destratification). Climate change impacts and load reduction targets required to gain lake resilience would be different from one lake to another and a customized approach, used with the assistance of ecological models, should be integrated into lake management strategies developed under a changing environment.

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Main Model Equations

Main processes modelled in General Lake Model (GLM)

Energy fluxes
$Q_{sw} = (1-\alpha_{sw})\, f_{sw} f_{par} Q_s e^{-K_w z}$
$Q_{lw_{in}} = (1-\alpha_{lw})\, \varepsilon_a \sigma [T_a + 273.15]^4$ $Q_{lw_{out}} = \varepsilon_w \sigma [T_s + 273.15]^4$
$Q_h = -\rho_a c_p C_H U_x (T_s - T_a)$
$Q_e = -\rho_a C_E \lambda U_x \frac{k}{p} (e_s[T_s] - e_a[T_a])$
Surface mixing
$E_{TKE} = 0.5 C_K (w_*^3)\, \Delta t + 0.5 C_K (C_W u_*^3)\, \Delta t + 0.5\, C_S \left[u_b^2 + \frac{u_b^2}{6} \frac{d\xi}{dz_{sml}} + \frac{u_b \xi}{3} \frac{du_b}{dz_{sml}} \right] \Delta z_{k-1}$ =convective overturn + wind stirring + (shear production + K-H production)
$\xi = C_{KH} u_b^2 / g'_{EH}$
$u_b = \frac{u_*^2 t}{z_{sml}} + u_o$
$E_{PE} = \left[0.5 C_T (w_*^3 + C_W u_*^3)^{2/3} + \frac{\Delta\rho}{\rho_o} g\, z_{SML} + \frac{g \xi^2}{24 \rho_o} \frac{d(\Delta\rho)}{dz_{sml}} + \frac{g \xi \Delta\rho}{12 \rho_o} \frac{d\xi}{dz_{sml}} \right] \Delta z_{k-1}$ =acceleration + lifting + K-H consumption
Deep mixing
$K_z = \frac{\alpha_{TKE} \varepsilon_{TKE}}{N^2 + 0.6\, k_{TKE}^2 u_*^2}$
$\varepsilon_{TKE} = \frac{1}{(V \bar{\rho}) 10^3} \frac{m\, C_D \rho_a\, f_S\, U_x^3\, A_l}{10^6} + \frac{1}{(V_{mix} \bar{\rho}) 10^3} \sum_i^{N_{INF}} g\, \Delta\rho_i\, Q_i (h_{top} - h_i)$ = rate of working by wind + rate of working by inflows
$K_{z_l} = \begin{cases} 0 & h_l \geq (h_{top} - z_{mix}) \\ K_z\ exp\left[\frac{-(h_{top} - z_{mix} - h_l)^2}{\sigma} \right] & h_l < (h_{top} - z_{mix}) \end{cases}$

Symbol	**Description**
$\mathrm{Q_{sw}}$	Surface flux of sensible heat
$\mathrm{\alpha_{sw}}$	Albedo
$\mathrm{f_{sw}}$	Scaling factor
$\mathrm{f_{par}}$	Photosynthetically active radiation
$\mathrm{Q_s}$	Total down-welling solar radiation
$\mathrm{K_w}$	Light extinction coefficient
$\mathrm{Q_{lw_{in}}}$	Longwave radiation input to surface layer
$\mathrm{Q_{lw_{out}}}$	Longwave radiation output from the surface layer
$\mathrm{\alpha_{lw}}$	Long-wave albedo
$\mathrm{\varepsilon_a}$	Emissivity of the atmosphere
σ	Stefan-Boltzmann constant
$\mathrm{T_a}$	Air temperature
$\mathrm{Q_h}$	Surface flux of sensible heat
$\mathrm{\rho_a}$	Density of air
$\mathrm{c_p}$	Specific heat capacity of air
$\mathrm{C_H}$	Bulk aerodynamic coefficient for sensible hear transfer
$\mathrm{U_x}$	Wind speed from a reference height
$\mathrm{Q_e}$	Surface flux of latent heat
$\mathrm{C_E}$	Bulk aerodynamic coefficient for latent heat transfer
$\mathrm{e_a}$	Air vapour pressure
$\mathrm{e_s}$	Saturation vapour pressure at the surface layer temperature
k	Ratio of molecular weight of water to molecular weight of air
E_{TKE}	Balance between turbulent kinetic energy due to convective mixing, wind stirring and shear mixing
C_K	coef_mix_conv
C_S	coef_wind_stir
C_W	coef_mix_shear
w_*	Turbulent velocity scale associated with convection
u_*	Velocity scale associated with wind stress
u_b	Velocity of the lower layer
C_{KH}	Mixing efficiency - Kelvin- Helmholtz turbulent billows
z	Depth from the surface
t	Model time step
ξ	Length scale of the K-H billows
g'_{EH}	Difference in gravity between the epilimnion and hypolimnion
z_{SML}	Surface mixed layer depth
ρ_0	Density of lake surface
E_{PE}	Potential energy to undergo mixing
g	Acceleration due to gravity
C_T	Coef_mix_turb

α_{TKE}	Mixing efficiency of hypolimnetic TKE
k_{TKE}	Turbulence wavenumber
N^2	Brunt–Väisälä (buoyancy) frequency
ρ_a	Air density (
C_D	Drag coefficient
ρ_i	Water density at layer i
A_i	Surface area of layer i below the surface mixed layer
h_{top}	Thickness of top layer
h_i	Inflow thickness
Q_i	Increasing flow
σ	Variance in the N^2 distribution below Z_{mix}
K_z	Vertical diffusivity

Main components and processes modelled in Framework for Aquatic Biogeochemical Model (FABM)

Processes	
atm	Atmospheric exchange
sed	Sediment demand
miner	Mineralisation
nitrif	Nitrification
uptake	Uptake of nutrients
resp	Respiration
decomp	Decomposition
excr	Excretion
sett	Settling
mort	Mortality
assim	Assimilation
General notation	
N	Number of groups
a, om, z	Indices of various sub-groups pf algae/phytoplankton, organic matter and zooplankton (integer)
$\chi_{\mathrm{C:Y}}^{\mathrm{group}}$	The stoichiometric ratio of “group” between carbon (C) and element “Y” (mmol C/mmol Y)
$\mathrm{f}_{\mathrm{processes}}^{\mathrm{var}}$	Function that returns the mass flux of “process” on variable “var” (mmol var/time)
$\mathrm{R}_{\mathrm{processes}}^{\mathrm{var}}$	The rate of “process” influencing the variable “var” (/time)
$\mathrm{F}_{\mathrm{max}}^{\mathrm{var}}$	The maximum benthic areal flux of variable “var” (mmol var/area/time)
$\mathrm{p}_{\mathrm{source}}^{\mathrm{group}}$	The preference of “group” for “source” (0-1)
$\phi_{\mathrm{lim}}^{\mathrm{group}}$	Dimensionless limitation or scaling function account for the effect of “lim” on “group” (-)
$\mathrm{k}^{\mathrm{var}}$	Generic fraction related to “var” (0-1)
$\theta_{\mathrm{config}}^{\mathrm{group}}$	Switch to configure selectable model component “config” for “group” (0,1,2,…)
c, $\boldsymbol{\theta}$, $\boldsymbol{\gamma}$	Coefficient (various units)
PHY	Phytoplankton
ZOO	Zooplankton

ads	Adsorption

Light

$$K_w = K_b + K_e\,SS + K_e\,DOC + K_e\,POC + \sum_{a}^{N_{PHY}} K_{e_a}\,PHY_{C_a}$$

= background extinction coefficient + Light extinction due to suspended solids + Light extinction due to dissolved organic carbon + Light extinction due to particulate organic carbon + Light extinction due to algal carbon

Oxygen cycling

$$\frac{dO_2}{dt} = \pm f_{atm}^{O_2} - f_{sed}^{O_2} - \frac{f_{miner}^{DOC}}{\chi_{C:O_2}^{miner}} - \frac{f_{nitrif}}{\chi_{N:O_2}^{nitrif}} + \sum_{a}^{N_{PHY}}\left(\frac{f_{uptake}^{PHY\_C_a}}{\chi_{C:O_2}^{PHY}}\right) - \sum_{a}^{N_{PHY}}\left(\frac{f_{resp}^{PHY\_C_a}}{\chi_{C:O_2}^{PHY}}\right) - \sum_{z}^{N_{ZOO}}\left(\frac{f_{resp}^{ZOO_z}}{\chi_{C:O_2}^{ZOO}}\right)$$

= ± atmospheric O2 exchange ± sediment O2 demand – O2 consumption by mineralisation of DOC (bacterial respiration) – O2 consumption by nitrification + O2 production by photosynthesis – O2 consumption by phytoplankton respiration – O2 consumption by zooplankton respiration

$$f_{atm}^{O_2} = \begin{cases} \dfrac{c_{atm}^{O_2}([O_2]_{atm} - [O_2]_z)}{dz_s} & if\ z = z_s \\ 0 & if\ z \neq z_s \end{cases}$$

Atmospheric oxygen exchange

$$f_{sed}^{O_2} = F_{max}^{O_2}\frac{O_2}{K_{sed}^{O_2} + O_2}\left(\theta_{sed}^{O_2}\right)^{T-20}\left(\frac{\widehat{A_z}}{dz_z}\right)$$

Sediment oxygen demand

where $\widehat{A} = A_z^{ben} / A_z$ and dz_z is the thickness of the z^{th} layer/cell.

Carbon cycling

$$\frac{dDOC}{dt} = f_{decom}^{POC} - f_{miner}^{DOC} + f_{sed}^{DOC} + \sum_{a}^{N_{PHY}} f_{excr}^{PHY\_C_a} + \sum_{z}^{N_{ZOOP}} f_{excr}^{z}$$

= POC decomposition – DOC mineralisation + sediment flux + phytoplankton excretion/exudation + zooplankton excretion

$$\frac{dPOC}{dt} = -f_{decom}^{POC} - f_{sett}^{POC} + \sum_{a}^{N_{PHY}} f_{mort}^{PHY\_C_i} + \sum_{z}^{N_{ZOOP}}\left[(1 - k_{assim}^{z})f_{assim}^{z} + (1 - k_{fsed}^{z})f_{fecal}^{z} + f_{mort}^{z}\right]$$

= – POC hydrolysis and decomposition – POC settling + phytoplankton mortality + zooplankton messy feeding + zooplankton fecal pellet + zooplankton mortality

$$\frac{d(PHY\_C_a)}{dt} = +f_{uptake}^{PHY\_C_a} - f_{excr}^{PHY\_C_a} - f_{mort}^{PHY\_C_a} - f_{resp}^{PHY\_C_a} - f_{sett}^{PHY\_C_a} - \sum_{z}^{N_{ZOO}} f_{assim}^{z} \times p_a^{z}$$

= + carbon fixation through photosynthesis + excretion/exudation of DOC – mortality – respiration – sedimentation – zooplankton grazing

$$\frac{d(ZOO_z)}{dt} = k_{assim}^{z} \times f_{assim}^{z} - f_{loss}^{z} - f_{mort}^{z}$$

= + carbon assimilation via grazing – carbon loss via respiration, excretion of DOC, fecal pellets production – mortality

$$TOC = DOC + POC + \sum_{a}^{N_{PHY}} PHY\_C_a + \sum_{z}^{N_{ZOO}} ZOO_z$$

$$f_{sett}^{POC} = \frac{\omega_{POC}}{dz_z}[POC]$$

Sedimentation of POC

$$f_{decom}^{POC} = R_{decom}^{POC}\frac{[O_2]}{K_{miner}+[O_2]}\left(\theta_{decom}\right)^{T-20}[POC]$$

Hydrolysis/decomposition of POC

$$f_{miner}^{DOC} = R_{miner}^{DOC}\frac{[O_2]}{K_{miner}+[O_2]}\left(\theta_{miner}\right)^{T-20}[DOC]$$

Mineralisation of DOC

$$f_{sed}^{DOC} = F_{max}^{DOC}\frac{K_{sed}^{DOC}}{K_{sed}^{DOC}+[DOC]}\left(\theta_{sed}^{DOC}\right)^{T-20}\left(\frac{\widehat{A_z}}{dz_z}\right)$$

DOC sediment flux

where $\widehat{A} = A_z^{ben} / A_z$ and dz_z is the thickness of the zth layer/cell.

Nitrogen cycling

$$\frac{dNH_4}{dt} = +f_{sed}^{NH_4} + f_{miner}^{DON} - f_{nitrif}^{NH_4} - \sum_{i}^{N_{PHY}}\left[p_{NH_4}^{a}\times f_{uptake}^{PHY\_N_a}\right]$$

= + sediment flux + mineralisation of DON – nitrification – phytoplankton NH_4 uptake

$$\frac{dNO_3}{dt} = -f_{sed}^{NO_3} + f_{nitrif}^{NH_4} - f_{denit}^{NO_3} - \sum_{a}^{N_{PHY}}\left[p_{NO_3}^{a}\times f_{uptake}^{PHY\_N_a}\right]$$

= + sediment flux + nitrification – denitrification – phytoplankton NO_3 uptake

$$\frac{dDON}{dt} = +f_{decom}^{PON} + f_{sed}^{DON} - f_{miner}^{DON} + \sum_{a}^{N_{PHY}} f_{excr}^{PHY\_N_a} + \sum_{z}^{N_{ZOO}}\frac{f_{excr}^{z}}{\chi_{C:N}^{z}}$$

= + PON decomposition/hydrolysis + sediment flux – DON mineralisation + phytoplankton excretion
+ zooplankton excretion

$$\frac{dPON}{dt} = -f_{decom}^{PON} - f_{sett}^{PON} + \sum_{i}^{N_{PHY}} f_{mort}^{PHY\_N_a} + \sum_{z}^{N_{ZOO}}\left[(1-k_{assim}^{z})f_{assim}^{z} + \left(1-k_{fsed}^{z}\right)f_{fecal}^{z} + f_{mort}^{z}\right]\frac{1}{\chi_{C:N}^{z}}$$

= – PON decomposition/hydrolysis – PON settling + phytoplankton mortality + zooplankton messy feeding
+ zooplankton fecal pellet + zooplankton mortality

$$\frac{d(PHY\_N_a)}{dt} = +f_{uptake}^{PHY\_N_a} - f_{excr}^{PHY\_N_a} - f_{mort}^{PHY\_N_a} - f_{sett}^{PHY\_N_a} - \sum_{z}^{N_{ZOO}}\left(f_{assim}^{z}\times p_a^{z}\times\frac{PHY\_P_a}{PHY\_C_a}\right)$$

= + N uptake + excretion of DON – mortality– sedimentation – zooplankton grazing

$$TN = NO_3 + NH_4 + DON + PON + \sum_{a}^{N_{PHY}} PHY\_N_a \sum_{z}^{N_{ZOO}}\frac{ZOO_z}{\chi_{C:N}^{z}}$$

$$f_{sed}^{NH_4} = F_{max}^{NH_4} \frac{K_{sed}^{NH_4}}{K_{sed}^{NH_4}+[O_2]} \left(\theta_{sed}^{NH_4}\right)^{T-20} \left(\frac{\widehat{A_z}}{dz_z}\right)$$

Ammonium sediment flux

$$f_{sed}^{NO_3} = F_{max}^{NO_3} \frac{[O_2]}{K_{sed}^{NO_3}+[O_2]} \left(\theta_{sed}^{NO_3}\right)^{T-20} \left(\frac{\widehat{A_z}}{dz_z}\right)$$

Nitrate sediment flux

$$f_{sed}^{DON} = F_{max}^{DON} \frac{K_{sed}^{DON}}{K_{sed}^{DON}+[DON]} \left(\theta_{sed}^{DON}\right)^{T-20} \left(\frac{\widehat{A_z}}{dz_z}\right)$$

DON sediment flux

$$f_{sett}^{PON} = \frac{\omega_{PON}}{dz_z} [PON]$$

Sedimentation of PON

$$f_{sett}^{PHY-N_i} = \frac{\omega_{PHY_i}}{dz_z} [PHY\_N_a]$$

Sedimentation of phytoplankton

$$f_{decom}^{PON} = R_{decom}^{PON} \frac{[O_2]}{K_{miner}+[O_2]} \left(\theta_{decom}\right)^{T-20} [PON]$$

Hydrolysis/decomposition of PON

where $\widehat{A} = A_z^{ben} / A_z$ and dz_z is the thickness of the z^th^ layer/cell.

Phosphorus Cycling

$$\frac{dPO_4}{dt} = +f_{sed}^{PO_4} + f_{miner}^{DOP} \pm f_{ads}^{PO_4} - \sum_{a}^{N_{PHY}} \left[f_{uptake}^{PHY\_P_a}\right]$$

= + sediment flux + mineralisation of DOP ± adsorption/desorption – phytoplankton PO$_4$ uptake

$$\frac{dPO_4^{ads}}{dt} = \pm f_{ads}^{PO_4} - f_{sett}^{PO_4^{ads}}$$

= ± adsorption/desorption – sedimentation

$$\frac{dPOP}{dt} = -f_{decom}^{POP} - f_{sett}^{POP} + \sum_{a}^{N_{PHY}} f_{mort}^{PHY\_P_a} + \sum_{z}^{N_{ZOO}} \left[\left(1-k_{assim}^{z}\right) f_{assim}^{z} + \left(1-k_{fsed}^{z}\right) f_{fecal}^{z} + f_{mort}^{z}\right] \frac{1}{\chi_{C:P}^{z}}$$

= – POP decomposition/hydrolysis – POP settling + phytoplankton mortality + zooplankton messy feeding + zooplankton fecal pellet + zooplankton mortality

$$\frac{dDOP}{dt} = f_{decom}^{POP} - f_{miner}^{DOP} + f_{sed}^{DOP} + \sum_{a}^{N_{PHY}} f_{excr}^{PHY\_P_a} + \sum_{z}^{N_{ZOO}} {}^{1}\!/_{\chi_{C:P}^{z}}\, f_{excr}^{z}$$

= + POP mineralisation – DOP mineralisation ± sediment flux + phytoplankton excretion + zooplankton excretion

$$\frac{d(PHY\_P_i)}{dt} = +f_{uptake}^{PHY\_P_i} - f_{excr}^{PHY\_P_i} - f_{mort}^{PHY\_P_i} - f_{sett}^{PHY\_P_i} - \sum_{z}^{N_{ZOO}} \left(f_{assim}^{z} \times p_a^z \times \frac{PHY\_P_a}{PHY\_C_a}\right)$$

=+ P uptake - excretion of DOP – mortality – sedimentation – zooplankton grazing

$$TP = PO_4 + DOP + POP + \sum_{a}^{N_{PHY}} PHY\_P_a + \sum_{z}^{N_{ZOO}} \frac{ZOO_z}{\chi_{C:P}^{z}}$$

$$f_{sed}^{PO_4} = F_{max}^{PO_4}\frac{K_{sed}^{PO_4}}{K_{sed}^{PO_4}+[O_2]}\left(\theta_{sed}^{PO_4}\right)^{T-20}\left(\frac{\widehat{A_z}}{dz_z}\right)$$

Phosphate sediment flux

$$f_{sed}^{DOP} = F_{max}^{DOP}\frac{K_{sed}^{DOP}}{K_{sed}^{DOP}+[DOP]}\left(\theta_{sed}^{DOP}\right)^{T-20}\left(\frac{\widehat{A_z}}{dz_z}\right)$$

DOP sediment flux

$$f_{sett}^{POP} = \frac{\omega_{POP}}{dz_z}[POP]$$

POP sediment flux

$$f_{sett}^{PHY\_P_a} = \frac{\omega_{PHY_a}}{dz_z}[PHY\_P_a]$$

Sedimentation of phytoplankton

$$f_{sett}^{PO_4^{ads}} = \frac{\omega_{SS}}{dz_z}\left[PO_4^{ads}\right]$$

Sedimentation of adsorbed phosphorus

$$f_{ads}^{PO_4} = \left[\Phi_{ads}^{PO_4}\left([TPO_4]^{t+1}, SS, pH\right)\times[TPO_4]^{t+1} - PO_4^{ads^*}\right]\frac{1}{\Delta t}$$

Adsorption/desorption ‘rate’ of phosphorus

where $\widehat{A} = A_z^{ben} / A_z$ and dz_z is the thickness of the z^th layer/cell.

Silica Cycling

$$\frac{dRSi}{dt} = +f_{sed}^{RSi} - \sum_{a}^{N_{PHY}} f_{uptake}^{PHY-Si_a} + \sum_{a}^{N_{PHY}} f_{excr}^{PHY-Si_a}$$

= + sediment flux – uptake by phytoplankton – excretion by phytoplankton

$$\frac{dPHY\_Si_a}{dt} = +f_{sett}^{PHY\_Si_a} + \sum_{a}^{N_{PHY}} f_{uptake}^{PHY-Si_a} - \sum_{a}^{N_{PHY}} f_{excr}^{PHY-Si_a} - \sum_{z}^{N_{ZOO}}\left(\frac{f_{assim}^{z}}{\chi_{C:Si}^{PHY_a}}p_a^z\right)$$

= + sedimentation of PHY_Si! + uptake by phytoplankton – excretion by phytoplankton – grazing by zooplankton

$$f_{sed}^{O_2} = F_{max}^{O_2}\frac{O_2}{K_{sed}^{O_2}+O_2}\left(\theta_{sed}^{O_2}\right)^{T-20}\left(\frac{\widehat{A_z}}{dz_z}\right)$$

Sediment reactive Si flux

where $\widehat{A} = A_z^{ben} / A_z$ and dz_z is the thickness of the z^th layer/cell.

Nutrient uptake functions in the phytoplankton model

$$f_{uptake}^{PHY_{C_a}} = R_{growth}^{PHY_a}\left(1-k_{pr}^{PHY_a}\right)\ \Phi_{tem}^{PHY_a}(T)\ \Phi_{str}^{PHY_a}(T)\ \ldots$$

$$\ldots\ \min\left\{\Phi_{light}^{PHY_a}(I),\ \Phi_{N}^{PHY_a}\left(NO_3, NH_4, PHY_{N_a}\right),\ \Phi_{P}^{PHY_a}\left(PO_4, PHY_{P_a}\right),\ \Phi_{Si}^{PHY_a}(RSi)\right\}\left[PHY_{C_a}\right]$$

=max growth rate at 20 °C, photorespiratory loss, temperature scaling, metabolic stress, light limitation, N limitation, P limitation, Si limitation

$$\Phi_{tem}^{PHY_a}(T) = \vartheta_a^{T-20} - \vartheta_a^{k[T-c1_a]} + c0_a$$

where $c1_a$ and $c0_a$ are solved numerically given input values of standard temperature (T_{std}), optimum temperature (T_{opt}) and maximum temperature (T_{max})

$$\Phi_{light}^{PHY_a}(I) = 1 - e^{\left(-\frac{I}{I_{K_a}}\right)}$$

Non-photoinhibited

$\Phi_{light}^{PHY_a}(I) = \frac{I}{I_{S_a}} e^{\left(1-\frac{I}{I_{S_a}}\right)}$	Photoinhibited
$f_{uptake}^{PHY_{N_a}} = R_{NUptake}^{PHY_a} \; \Phi_{tem}^{PHY_a}(T) \left\{ \Phi_N^{PHY_a} \frac{\left(\frac{[PHY_{N_a}]}{[PHY_{C_a}]} - \chi_{NMIN}^{PHY_a}\right)}{\left(\chi_{NMAX}^{PHY_a} - \chi_{NMIN}^{PHY_a}\right)} \right\} [PHY_{N_a}]$	Dynamic N uptake
$f_{uptake}^{PHY_{P_a}} = R_{PUptake}^{PHY_a} \; \Phi_{tem}^{PHY_a}(T) \left\{ \Phi_P^{PHY_a} \frac{\left(\frac{[PHY_{P_a}]}{[PHY_{C_a}]} - \chi_{PMIN}^{PHY_a}\right)}{\left(\chi_{PMAX}^{PHY_a} - \chi_{PMIN}^{PHY_a}\right)} \right\} [PHY_{P_a}]$	Dynamic P uptake
$f_{uptake}^{PHY_{Si_a}} = f_{uptake}^{PHY\_C_a} \Big/ \chi_{C:Si}^{PHY_a}$	Static Si uptake, linked to photosynthetic rate
Respiration, mortality and excretion	
$\hat{R} = R_{resp}^{PHY_a} \; \Phi_{sal}^{PHY_a}(S) \; \left(\vartheta_{resp}^{PHY_a}\right)^{T-20}$ $\Phi_{sal}^{PHY_a}(S) = 1$	No salinity effect on respiration multiplier $\hat{R}$
$f_{resp}^{PHY_{C_a}} = k_{fres}^{PHY_a} \; \hat{R} \; [PHY_{C_a}]$	
$f_{excr}^{PHY_{C_a}} = \left(1 - k_{fres}^{PHY_a}\right) \; k_{fdom}^{PHY_a} \; \hat{R} \; [PHY_{C_a}]$	
$f_{mort}^{PHY_{C_a}} = \left(1 - k_{fres}^{PHY_a}\right) \left(1 - k_{fdom}^{PHY_a}\right) \hat{R} \; [PHY_{C_a}]$	
$f_{excr}^{PHY_{N_a}} = k_{fdom}^{PHY_a} \; \hat{R} \; [PHY_{N_a}]$	
$f_{mort}^{PHY_{N_a}} = \left(1 - k_{fdom}^{PHY_a}\right) \hat{R} \; [PHY_{N_a}]$	
$f_{excr}^{PHY_{P_a}} = k_{fdom}^{PHY_a} \; \hat{R} \; [PHY_{P_a}]$	
$f_{mort}^{PHY_{P_a}} = \left(1 - k_{fdom}^{PHY_a}\right) \hat{R} \; [PHY_{P_a}]$	
$f_{excr}^{PHY_{Si_a}} = \hat{R} \; [PHY_{Si_a}]$	

Parameter Descriptions

Symbol	Description	Units
$k_{atm}^{O_2}$	Oxygen transfer coefficient	m/s
$[O_2]_{atm}$	Atmospheric oxygen concentration	mmol O_2/m^3

$\chi_{C:O_2}^{miner}, \chi_{C:O_2}^{PHY}$	Stoichiometric conversion of C to O_2	mmol C/mmol O_2
$\chi_{N:O_2}^{nitrif}$	Stoichiometric conversion of N to O_2	mmol N/mmol O_2
R_{nitrif}	Maximum rate of nitrification	/d
K_{nitrif}	Half saturation constant for oxygen dependence of nitrification rate	mmol O_2/m^3
θ_{nitrif}	Temperature multiplier for temperature dependence of nitrification rate	
R_{denit}	Maximum rate of denitrification	/day
K_{denit}	Half saturation constant for oxygen dependence of denitrification rate	mmol O_2/m^3
θ_{denit}	Temperature multiplier for temperature dependence of denitrification rate	
R_{decom}^{PON}	Maximum rate of decomposition of particulate organic nitrogen	/day
K_{decom}^{PON}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{miner}^{PON}	Temperature multiplier for temperature dependence of mineralization rate	
R_{miner}^{DON}	Maximum rate of decomposition of dissolved organic nitrogen	/day
K_{miner}^{DON}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{miner}^{DON}	Temperature multiplier for temperature dependence of mineralization rate	
ω_{PON}	Settling rate of particulate organic matter	m/day
R_{decom}^{POC}	Maximum rate of decomposition of particulate organic carbon	/day
K_{decom}^{POC}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{decom}^{POC}	Temperature multiplier for temperature dependence of mineralization rate	
R_{miner}^{DOC}	Maximum rate of decomposition of dissolved organic carbon	/day
K_{decom}^{DOC}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{miner}^{DOC}	Temperature multiplier for temperature dependence of mineralization rate	
ω_{POC}	Settling rate of particulate organic matter	m/day
R_{decom}^{POP}	Maximum rate of decomposition of particulate organic phosphorus	/day
k_{decom}^{POP}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{decom}^{DOP}	Temperature multiplier for temperature dependence of mineralization rate	
R_{miner}^{DOP}	Maximum rate of decomposition of dissolved organic phosphorus	/day
K_{decom}^{DOP}	Half saturation constant for oxygen dependence of mineralisation rate	mmol O_2/m^3
θ_{miner}^{DOP}	Temperature multiplier for temperature dependence of mineralization rate	
ω_{POP}	Settling rate of particulate organic matter	m/day
Φ_{ads}^{pH}	Function characterising pH effect on	
C_{ads}^{r}	Ratio of adsorption and desorption rate coefficients	l/mg
C_{ads}^{max}	Maximum adsorption capacity of suspended sediment (SS)	mmol P/mg SS