Phytoplankton dynamics in North Island lakes, New Zealand

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Abstract

The dynamics of phytoplankton were investigated in 40 lakes of the North Island, New Zealand. A range of environmental variables was examined on different temporal and spatial scales in relation to the surface and DCM (deep chlorophyll maximum) phytoplankton communities in the lakes. The environmental variables that were considered relevant to these communities included turbulent mixing, limitation by light and nutrients, rates of sedimentation or ascent, and zooplankton grazing.

Cylindrospermopsis raciborskii is a potentially toxic species of cyanobacteria, that in summer 2002-3 formed dense water blooms (>100 000 cells/ml) in shallow (max. depth ≤ 5m) Waikato peat lakes and a hydro-electric dam on the Waikato River. Net rates of growth calculated within individual lakes demonstrated that *C. raciborskii* populations grew at rates close to maximum values observed under optimal conditions in laboratory cultures. Changes in species diversity in the lakes prior to and following the invasion of *C. raciborskii* were assessed. During occasions of *C. raciborskii* water blooms there was decreased diversity and the phytoplankton assemblage became nearly mono-specific. The shallow lakes in this study have high concentrations of nutrients and low water clarity, which are ideal conditions for growth of *C. raciborskii*, as it has a competitive advantage at low irradiance but limited capacity for buoyancy. The ability of *C. raciborskii* to fix nitrogen may also have enhanced its competitive ability amongst other phytoplankton species and, while nutrients were generally considered to be replete, nitrogen was more likely to limit growth of phytoplankton than phosphorus in the lakes studied.

Lake Tarawera, part of the Rotorua lakes region (area 41.6 km^2 and mean depth 50 m), was chosen to investigate variability of phytoplankton biomass with depth and between embayments and a mid-lake station. The variability of DCM depth was contributed by internal seiching, which was most prominent at the edge of the lake. A single mid-lake station was considered representative of lake-wide biomass at the DCM as the differences between stations were small. However, during a bloom of *Anabaena lemmermanni*, there was large inter-station variability in phytoplankton biomass in the surface mixed layer. Therefore, when quantifying surface populations,

particularly buoyant cyanobacterial species which tend to accumulate in bays, discrete samples at a single station and depth may not adequately represent lake-wide biomass. During periods when bloom-forming species are present, several sampling stations should be used to adequately quantify biomass and variability of phytoplankton in the surface mixed layer.

A population-dynamics theory of sinking phytoplankton, that utilizes interactions between growth limitation by light and nutrients, sinking rates and turbulent diffusion rates, was used to quantify factors contributing to DCM formation in Lake Tarawera. Five 'Modes' of vertical phytoplankton of biomass were categorised relating to four forcing functions. The first mode was a surface chlorophyll maximum (SCM); Mode 2 was a DCM; Mode 3 was a simultaneous double peak of buoyant cyanobacteria and a DCM assemblage; Mode 4 was a linear vertical distribution and Mode 5 was an exponential increase in biomass with depth. The incidence of these distributions and the existence of a DCM were examined in relation to different turbulent diffusion rates (< 0.1 to 10 $cm^2 s^{-1}$), sinking rates (+10 to -4 m day^{-1}), and light and nutrient limitation. A DCM was simulated when net growth of the population superceded losses from turbulent diffusion, sinking and zooplankton grazing. Light climate strongly influenced net rates of growth of the DCM assemblage and its position; surface blooms of cyanobacteria could obliterate the DCM by shading cells and suppressing light available for their growth. This finding has important implications for eutrophication of lakes with DCMs, as relatively small changes in surface phytoplankton communities, for example through additional nutrient inputs, could obliterate the DCM. The relevance of the diatom DCM phytoplankton is that it has important ecosystem-level effects through sedimentation of nutrients and organic matter, and transfer of biomass to higher trophic levels resulting from preferential grazing.

Further examination of DCM communities was carried out in Lake Tikitapu, a small lake (mean depth 18 m, area 1.5 km^2) in the Rotorua basin. The DCM assemblage in this lake comprised dinoflagellate species. The DCM persisted over the period of thermal stratification, in the metalimnion, and also at a depth where irradiance was approximately 2-3 % of the surface value. Statistical analysis found that the light level at the DCM was more important than the depth of thermocline in determining the depth of the DCM. There was no evidence of diurnal vertical migration of the DCM in Lake Tikitapu, but dispersion of the DCM varied seasonally, whereby the width was strongly positively correlated to the width of the metalimnion ($r^2 = 0.89$, $p < 0.01$). Light and nutrient incubation experiments provided further evidence for the dominant role of light in influencing the DCM position. There was a biomass decrease in DCM populations that were incubated at high irradiance (40 % of surface irradiance), suggesting that surface irradiances may be damaging or inhibitory to growth.

A wide range of North Island lakes was investigated in an attempt to delineate the roles of lake mixing, trophic state and light climate in the composition of lake phytoplankton assemblages. For 40 lakes mixing regimes were divided into three classes; stable seasonal stratification, intermittent stratification and mixed, and trophic states were separated in oligotrophic, mesotrophic and eutrophic. In addition, average photosynthetically available radiation experienced by phytoplankton was determined based on integrated levels over the surface mixed layer, and values were divided into three regimes where 5 % or less corresponded to low light, 5 – 20 % to medium light, and > 20 % to high light. Non-metric multi-dimensional scaling (MDS) and analysis of similarities (ANOSIM) were used to detect patterns in phytoplankton composition between lakes and to infer which environmental variables were associated with underlying trends in composition. MDS showed a clear separation of stratified from intermittently stratified and mixed lakes based on phytoplankton composition, and phytoplankton assemblages in stably stratified lakes were significantly different from those in intermittently stratified lakes ($p < 0.05$) and mixed lakes ($p < 0.05$). However, results of ANOSIM indicated that trophic state was not a statistically significant factor influencing phytoplankton assemblage composition. Mixing regime therefore provided a more accurate predictor of summer phytoplankton composition than trophic state or light climate, as lakes of different trophic state but similar mixing regime had similar phytoplankton assemblages

In this study, field work and modelling were used to contribute to the current understanding of spatial and temporal dynamics of phytoplankton in lakes, the roles and interactions of various environmental variables in governing populations, and implications of blooms on assemblage diversity. Phytoplankton assemblage

composition and biomass are highly variable, but much of this variation may be explained through detailed analysis. Investigations into the vertical distributions of phytoplankton communities to ascertain the presence of a SCM or DCM, along with quantification of vertical stratification/mixing regimes in lakes, and interactions of buoyancy with horizontal transport in the surface mixed layer, will greatly facilitate in explaining the variability.

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Preface

The main body of this thesis is comprised of five chapters (Chapters 2-6), which are papers written to be submitted for publication in peer reviewed scientific journals. I assumed the responsibility of the field work programme, laboratory and data analysis, and for writing this thesis. Except where referenced, the material in this thesis was produced from my own ideas and work undertaken under the supervision of David Hamilton, Julie Hall, Vivienne Cassie Cooper and John Green.

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Chapter 5 has been prepared to be submitted to *Journal of Plankton Research* with the title "Formation of a Deep Chlorophyll Maximum by *Peridinium* cf. *sydneyense* in an oligotrophic New Zealand lake" by E. F. Ryan, D. P. Hamilton and J. A. Hall.

Chapter 6, "Phytoplankton assemblage composition in North Island lakes of New Zealand: is trophic state, mixing, or light climate more important?", by E. F. Ryan, I. C. Duggan, D. P. Hamilton and D. F. Burger, was submitted to *New Zealand Journal of Marine and Freshwater Research* on 10 August 2005.

Chapter 1

Introduction

1.1 Motivation

Phytoplankton have been estimated to contribute approximately 70 % of dissolved oxygen in the atmosphere (Werner 1977), they represent a major global carbon sink as a result of photosynthesis and subsequent sedimentation (Harris 1978), and they are an integral component of food webs in aquatic systems (Reynolds 1996). In New Zealand over 2,000 species of phytoplankton have been described in freshwaters (Cassie-Cooper 1996), and the number of lake phytoplankton species is estimated to be greater than 5,000 globally (Padisak 2004). The numerous species differ in their evolutionary adaptations which influence their ability to grow, their rate of loss and their response to environmental factors (Reynolds 1990). There are many physiological properties of phytoplankton that govern their dynamics, such as adaptations to low nutrient concentrations or light levels, differential sinking, buoyancy regulation, interference with zooplankton grazing mechanisms and heterotrophic nutrition (Reynolds 1984, 1997; Harris 1986; Round 1988). The aim of the present study is to investigate the dynamics and distribution of phytoplankton species and biomass on different temporal and spatial scales. More specifically, it was to examine effects of blooms on diversity and vertical distributions of phytoplankton assemblages and the control of environmental factors such as limitation by light and nutrient and mixing regimes in controlling populations. These factors have important implications for the management of lakes.

1.2 Variability of phytoplankton

The dynamics and distribution of phytoplankton within lakes may be highly variable spatially, both vertically and horizontally, and temporally (Harris 1978; Reynolds 1984). Light and nutrients, which are critical for phytoplankton growth, vary along vertical gradients, whereby light is attenuated exponentially with depth, and nutrients are often strongly influenced by processes relating to density stratification. Turbulent mixing influences the vertical structure of phytoplankton as it has a large effect on the distribution and availability of nutrients, light harvesting capability of phytoplankton, and whether phytoplankton sink, float or maintain discrete depths (Ferris and Christian 1991; MacIntyre 1998; Reynolds 1994, 1998). The vertical distribution of phytoplankton has been a major focus of many limnological and oceanographic studies (Steele and Yentsch 1960; Fee 1976; Abbott *et al.* 1984; Barbiero and Tuchman 2001). One feature of phytoplankton vertical distributions is the accumulation of populations in deeper depth strata, referred to as a Deep Chlorophyll Maximum (DCM). DCMs can make an important contribution to primary productivity at a system scale (Pick et al. 1984). Reasons for the development of a DCM are diverse and include formation driven by physical factors (e.g., sinking of cells and interactions with lake mixing) or by biological factors (e.g., vertical migration). For a DCM to persist there must be sufficient light and nutrients available at depth for net growth, together with sufficiently low turbulence that populations do not become evenly dispersed or entrained into the surface mixed layer. The present study quantifies the relative effects of turbulent mixing, sedimentation and motility, and net growth and physiological adaptations of phytoplankton to understand the reasons for DCM development.

Surface phytoplankton populations, especially those of cyanobacteria, can also have high variability. Increased nutrient loads and the disappearance of macrophyte populations, together with increases in suspended sediment concentrations and reduced light availability in shallow New Zealand lakes (Hamilton and Mitchell 1997) have changed many of these lakes to an 'alternative stable state' of low water clarity and high phytoplankton biomass (cf. Scheffer 1998). This change of 'state' may increase the susceptibility of lakes to cyanobacterial blooms from species such as *Cylindrospermopsis raciborskii*, which has the ability to fix nitrogen and exist under a variety of stratification regimes and at low levels of irradiance (Padisák and Reynolds 1998). However, it is not only shallow lakes that are susceptible to cyanobacterial blooms. Bloom formation by many other species of cyanobacteria (e.g., *Microcystis* sp. and *Anabaena* sp.) is often linked to the occurrence of thermal stratification in deeper lakes (Reynolds 1998; Oliver and Ganf 2000), including diurnal stratification in the seasonally mixed surface layer.

Selection of sampling sites is very important when assessing the spatial variability of phytoplankton biomass. Phytoplankton biomass is often estimated from one mid-lake station, and intra-lake variation is over-looked (Fee 1976, Stauffer 1988), with consequential errors in lake-wide phytoplankton biomass estimates. The distribution of cyanobacterial populations can be highly variable horizontally, especially when there is wind that may produce accumulations of buoyant populations in bays. In this thesis the dynamics of cyanobacterial species are examined by mapping the rate of proliferation of bloom-forming species at different stations and by the use of *in situ* growth rates to show the rapid development of populations that may occur in individual lakes.

1.3 Overview

This thesis comprises six chapters, which form a coherent basis for examination of the structure and dynamics of phytoplankton communities in North Island lakes, New Zealand. Chapter 2 examines phytoplankton bloom dynamics in lakes of the Central Volcanic Plateau (CVP) of North Island, where potentially toxic species of cyanobacteria were prevalent in lakes and rivers of the CVP in summer periods of 2002-04. Dynamics of a previously un-recorded, potentially toxic cyanobacterium, *Cylindrospermopsis raciborskii*, were investigated and *in situ* growth rates were used to show the rapid development of populations that occurred in individual lakes, and the loss of phytoplankton species' diversity in the lakes in association with blooms of *C. raciborskii*. The study design in Chapter 2 did not allow for assessment of spatial variations of phytoplankton biomass, as surface samples were obtained only from one station. Therefore the objective of Chapter 3 was to examine spatial variations in phytoplankton biomass in a large, oligotrophic lake, Lake Tarawera. Embayments are often prone to phytoplankton blooms and Lake Tarawera was chosen because of the existence of several embayments adjoining the main lake basin. Spatial variations in phytoplankton biomass between embayments and the main lake were quantified and considerations were made of the applicability of sampling location in quantifying surface and deeper communities of phytoplankton. More specifically, the horizontal variability of a diatom DCM assemblage was examined in relation to phytoplankton assemblages in the surface chlorophyll maximum (SCM), particularly in relation to cyanobacteria.

Factors contributing to the formation of the diatom DCM in Lake Tarawera examined in Chapter 3 were quantified in Chapter 4 using a population-dynamics theory of sinking phytoplankton (Huisman et al. 2002). In Chapter 4 it was hypothesized that the DCM depth coincides with the depth of maximal net rate of phytoplankton growth, accounting for the influences of turbulent diffusion and sedimentation. Five 'Modes' of vertical phytoplankton biomass distribution were categorised in the water column. The occurrence of these distributions was examined using a modelling approach to investigate different turbulent diffusion rates and sinking rates, as well as light and nutrient limitation of phytoplankton. Selection pressures, such as zooplankton grazing, were also quantified.

An investigation was carried out in Chapter 5 to examine if similar processes to those that contribute to the formation of a DCM by flagellated phytoplankton (Chapter 4), are operative in a relatively large oligotrophic lake. The position of the DCM was quantified in relation to the depth of the thermocline, and the availability of light and nutrients at the depth of the DCM. The position and distribution of the DCM was examined in relation to the variability of environmental factors on a daily and seasonal basis.

In Chapters 2 to 5, factors controlling phytoplankton dynamics were investigated on relatively short temporal scales (hours to days) and were spatially restricted. Chapter 6 investigates whether similar processes such as availability of nutrients and light, and mixing regimes govern the composition of phytoplankton assemblages across different lakes. In Chapter 6 the hypothesis was tested that mixing regime, rather than trophic state or light climate, is the primary determinant of dissimilarity in phytoplankton assemblages among North Island lakes of New Zealand. Previous studies of New Zealand lakes (Pridmore and Etheredge 1987; Burns et al. 1997) have demonstrated that lakes of different trophic state support distinct assemblages of phytoplankton. Cyanobacterial species are generally thought to have a preference for eutrophic conditions (Rawson 1956; McColl 1972; Flint 1975), though other studies have shown the presence of cyanobacterial populations in oligotrophic conditions (Gibbs 2004). In Chapter 6 the hypothesis was tested that lake mixing regime, not trophic state or light climate, is the primary determinant of the composition of phytoplankton assemblages in 40 North Island lakes. Different patterns of summer stratification and mixing provided a basis for separating lakes and testing whether there were patterns of phytoplankton assemblage structure associated with the separation.

The overarching aim of this thesis is to provide a better understanding of how interactions between various environmental variables, at different temporal and spatial scales, govern phytoplankton dynamics and assemblage composition in lakes. Field work and modelling have been used to quantify effects of turbulent mixing, sedimentation, and growth, in order to understand the assemblages, biomass and distribution of lake phytoplankton communities.

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Chapter 2

Recent occurrence of *Cylindrospermopsis raciborskii* in Waikato lakes of New Zealand

2.1 Abstract

Cylindrospermopsis raciborskii is a toxin-producing species of cyanobacteria that in autumn 2003 was recorded for the first time in three shallow (max. depth $\leq$ 5m) Waikato lakes and a hydro-electric dam on the Waikato River, New Zealand. It formed water blooms at densities >100 000 cells/ml in lakes Waahi and Whangape. Net rates of population growth >0.2 day^{-1} were recorded for *C. raciborskii* in lakes Ngaroto, Waahi, and Karapiro, based on comparisons of low numbers (detection of <10 cells/ml) from initial samples and its presence at bloom densities (> 15 000 cells/ml) in the subsequent sample “x” – “y” days later. *C. raciborskii* may be well adapted to rapid proliferation in the Waikato lakes, which are eutrophic to hypertrophic, with high light attenuation, and where nitrogen (N) fixation may provide it with a competitive advantage over non-nitrogen fixing algae under N-limited conditions.

2.2 Introduction

Cylindrospermopsis raciborskii (Woloszyńska) Seenaya et Subba Raju is a highly adaptable freshwater cyanobacterium that is capable of N fixation and known to produce the cyanotoxin cylindrospermopsin (CYN) (Hawkins et al. 1997). It was first recorded in tropical and sub-tropical regions (Fabbro and Duivenvoorden 1996; Chapman and Schelske 1997) but has apparently spread rapidly over the past 10 years to invade temperate regions of Australia, Europe, and North and South America (Padisák 1997). The first confirmed identification of this species in New Zealand was by Wood and Stirling (2003) in Lake Waahi in March 2003. There is considerable morphological variation in *C. raciborskii* (McGregor and Fabbro 2000) and this is one of the reasons for the recent appearance in water bodies where it has been previously unrecorded. A morphologically similar species, *Cylindrospermum minutissimum* Collins, has previously been described in lakes in close proximity to our study lakes (Etheredge and Pridmore 1987). The identification was based upon earlier keys, and the emphasis on the position of the heterocyst being adjacent to the akinete led to material being identified as *C. minutissimum*, while the absence of heterocysts and tapering of trichomes led to identifications of the material as *Raphidiopsis*; both of these forms are described in the New Zealand literature. Correct identification of *Cylindrospermopsis raciborskii* is very difficult, due in part to the large range of morphological variants which have been documented in recent taxonomic investigations (McGregor and Fabbro 2000) and using genetic studies (Saker et al. 1999, Wilson et al. 2000).

Cylindrospermopsis raciborskii is highly tolerant of a range of salinity and nutrient concentrations and can grow in temperate climates under light and temperature regimes different from those of tropical environments (Briand et al. 2002). These factors make it difficult to predict the distribution and proliferation of this species. High water temperatures (> 19°C), however, appear to be a prerequisite for development of large populations (Saker and Griffiths 2001; Briand et al. 2002).

Cylindrospermopsis raciborskii has a high growth potential at low irradiance. This gives it an advantage over many other cyanobacteria, which tend to be well adapted to high irradiance (Padisák and Reynolds 1998). It also has a high affinity for phosphorus and can accumulate phosphorus at relatively low ambient concentrations (Isvanovics et al. 2000). Furthermore, heterocysts confer capacity for N fixation when this nutrient is directly limiting growth, and may provide it with a competitive advantage over non-N fixing phytoplankton when there are low ambient concentrations of inorganic nitrogen. These factors may act in isolation or synchronously to contribute to the capacity of *C. raciborskii* to form dense water blooms.

Cylindrospermopsis raciborskii produces the cytotoxic alkaloid cylindrospermopsin (CYN), which has been implicated in many human and animal poisonings (Bourke et al. 1983; Saker et al. 1999). It is also known to be capable of producing paralytic shellfish poisoning (PSP) (Lagos et al. 1999; Neilan et al. 2003). In a review of the cyanotoxin cylindrospermopsin, Griffiths and Saker (2003) describe recent developments in the application of molecular techniques for characterising strains of cyanobacteria that produce this toxin. They also summarise the chemistry and *in vitro* synthesis of the toxin.

Cylindrospermopsis raciborskii may have a detrimental effect on food-webs in lakes, by interfering with carbon transfers. It has been regarded as a poor food source for zooplankton because of the relative inedibility of the trichomes (Bouvy et al. 2000). Bouvy et al. (2001), however, found that rotifers and copepods were able to shorten trichomes to an edible size which enabled other zooplankton to graze on the shortened trichomes. They also noted that zooplankton species diversity was not affected by blooms of *C. raciborskii*.

In this paper I document the rapid proliferation of *C. raciborskii* in Waikato lakes following the first record of its presence in New Zealand in March 2003. *In situ* growth rates (Reynolds 1997) are used to show the rapid development of populations that occurred in individual lakes and I explore the possible impacts of this species on lake communities and water users.

2.3 Methods

Study sites

Water samples for phytoplankton enumeration were collected from four Waikato lakes (Fig. 2.1). Lakes Waahi and Whangape are lowland lakes which were once part of an extensive wetland system (Cromarty and Scott 1995). These lakes still support high diversity of waterfowl and have several threatened species of native birds and fish. The lakes are shallow, highly exposed as a result of vegetation clearance, and hypertrophic (Table 2.1) (Barnes 2002). Lake Ngaroto is a hypertrophic peat lake, with a largely pastoral catchment (Boswell et al. 1985). These three lakes receive surface and groundwater drainage from their surrounding wetland-catchment systems, but can be expected to have water residence times of several months (Vant, Environment Waikato, pers. comm.).

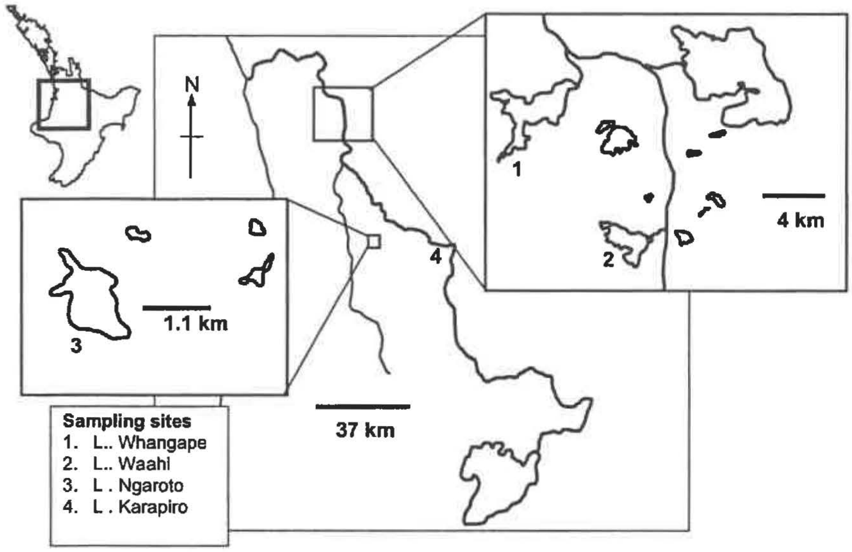

Figure 2.1. North Island expanded to show location of the four lakes sampled, with two areas further expanded. NZMS 265 Series.

Table 2.1. Physico-chemical features of the four study lakes. (TN, total nitrogen; TP, total phosphorus; Chl. *a*; Max. depth, maximum depth).

Lake	Secchi (m)	TN[+] (mg/m^3)	TP[+] (mg/m^3)	TN/TP	Chl. *a* (mg/m^3)	Trophic status[±]	Max. depth	Area (ha)[+]
Waahi	0.41*	915	49	18.9	34	Hypertrophic	5.0	522
Whangape	0.5	864	72	11.9	24	Hypertrophic[§]	3.5	450
Ngaroto	0.5	1900	118	16.1	37	Hypertrophic	4.0	108
Karapiro	2.6	360	34	10.6	12	Eutrophic	54.0	860

[*] Irwin (1981)
[+] Environment Waikato unpubl. data (1995 - 2003)
[±] Barnes (2002)
[§] Burns and Rutherford (1998)

Lake Karapiro, is one of eight hydro-electric dams along the Waikato River and is considered eutrophic (Livingston et al. 1986; Vant, Environment Waikato pers. comm) Based on storage volumes of Lake Karapiro and discharges in the Waikato River (Roper 2002), the mean water residence time is c. 4 days.

Collection of samples and algal enumeration

Water samples were taken from 30 January to 8 May 2003 as part of a regular monitoring programme of Waikato lakes. The lakes are generally monitored fortnightly to monthly during summer and autumn, depending on their level of recreational use, but sampling frequency was increased when high densities of *C. raciborskii* were recorded. The samples were collected from surface waters (depth = 0.2 m). The sample from Lake Karapiro was taken at the lake edge, and lakes Whangape, Waahi and Ngaroto were sampled by boat at a mid-lake station. Surface water temperatures were measured in Lakes Waahi and Whangape on each sampling occasion. Phytoplankton were preserved with Lugol's iodine and cell counts were conducted at 100x magnification using the sedimentation technique of Utermöhl (1958). Phytoplankton were identified to species level when possible and *C. raciborskii* was identified using the guide of Baker and Fabbro (2002). For *C. raciborskii* the average number of cells per trichome was calculated for each sample and cell densities were then approximated by multiplying this factor by the number of trichomes counted and adjusting for the sample volume. The maximum sample error with this technique was ±30%. The resolution of this technique was <10 cells/ml for individual species. Net rates of population growth of the phytoplankton between sample dates at individual lakes were calculated using the equation (Reynolds 1997):

$$r_n = \frac{\ln\left(\frac{N_t}{N_0}\right)}{t} \qquad (2.1)$$

where r_n is the net rate of growth (day^{-1}) and N_t and N_0 are cell densities at times t and 0, respectively. Phytoplankton counts were converted to relative abundances on the basis of organism density and then the index of diversity was calculated according to the method of Shannon and Weaver (Washington 1984):

$$H' = -\Sigma p_i \ln(p_i) \qquad (2.2)$$

where H' is the Shannon index of diversity and p_i is the relative abundance of species i:

$$p_i = \frac{N_i}{N_{tot}} \qquad (2.3)$$

where N_i is the cell density of species i and N_{tot} is the total cell density.

2.4 Results and Discussion

Figure 2.2 shows cell counts of the total phytoplankton assemblage and of *C. raciborskii* over the sampling period. *C. raciborskii* was first detected in Lake Waahi on 13 March 2003 by Wood and Stirling (2003) and subsequently in Lakes Whangape (10 April 2003), Karapiro (15 April 2003), and Ngaroto (24 April 2003). On 28 March 2003 the highest density of 205 500 cells/ml was recorded in Lake Waahi (Table 2). At this time *C. raciborskii* was not detected in samples from Lakes Ngaroto and Karapiro, and Lake Whangape was not sampled. The first confirmation of *C. raciborskii* in Lake Ngaroto was on 24 April 2003 (Table 2.2) following its absence from samples on 10 April 2003. Similarly, *C. raciborskii* was not detected in samples from Lake Karapiro on 25 March 2003 but attained 7 900 cells/ml on 15 April 2003 (Table 2.2).

Net rates of population growth (r_n) for *C. raciborskii* were calculated for the four lakes (Table 2.2) using Equation 1. Values of r_n represent a mean value between sampling intervals, which varied in frequency from daily to approximately monthly. I chose to use maximum values of r_n selected from successive sampling within individual lakes to support our assertion that *C. raciborskii* populations grew rapidly following its first detection. Maximum values of r_n were consistently high across all lakes, and varied from 0.17 to 0.26 day^{-1}. In Lake Karapiro r_n was 0.26 day^{-1}, but this value must be interpreted cautiously as the low water residence time (c. 4 days) suggests that populations may have been influenced by "seeding" from upstream impoundments of the Waikato River. Water residence times in several of these impoundments are substantially longer than those in Lake Karapiro (Roper 2002). By contrast, inflows to Lakes Waahi, Ngaroto, and Whangape are small, suggesting that population expansion could have been supported by recruitment, rapid germination events or growth. There may have been different population densities within the depth profile, however, the sampling regime did not allow assessment of any vertical variability of *C. raciborskii* populations. Further studies should obtain depth-integrated samples to assess the vertical distribution of biomass. The location of the lake-shore sampling site at Lake Karapiro could have potentially over-estimated the abundance of *C. raciborskii*, especially in the presence of a prevailing on-shore wind. Lakes Whangape, Waahi and Ngaroto were sampled by boat at a mid-lake station and sampling from one mid-lake station and it should be noted that central lake basins can often be distinctly different from shoreline sites, as shown in Chapter 3. Further investigations will need to take in account the mixing regime and variability of sampling position. This study had only limited lake physical measurements; and additional studies into the population dynamics of *C. raciborskii* should quantify the interactions of mixing regime, nutrient supply and light climate, to promote further understanding of the factors governing the distribution of this species.

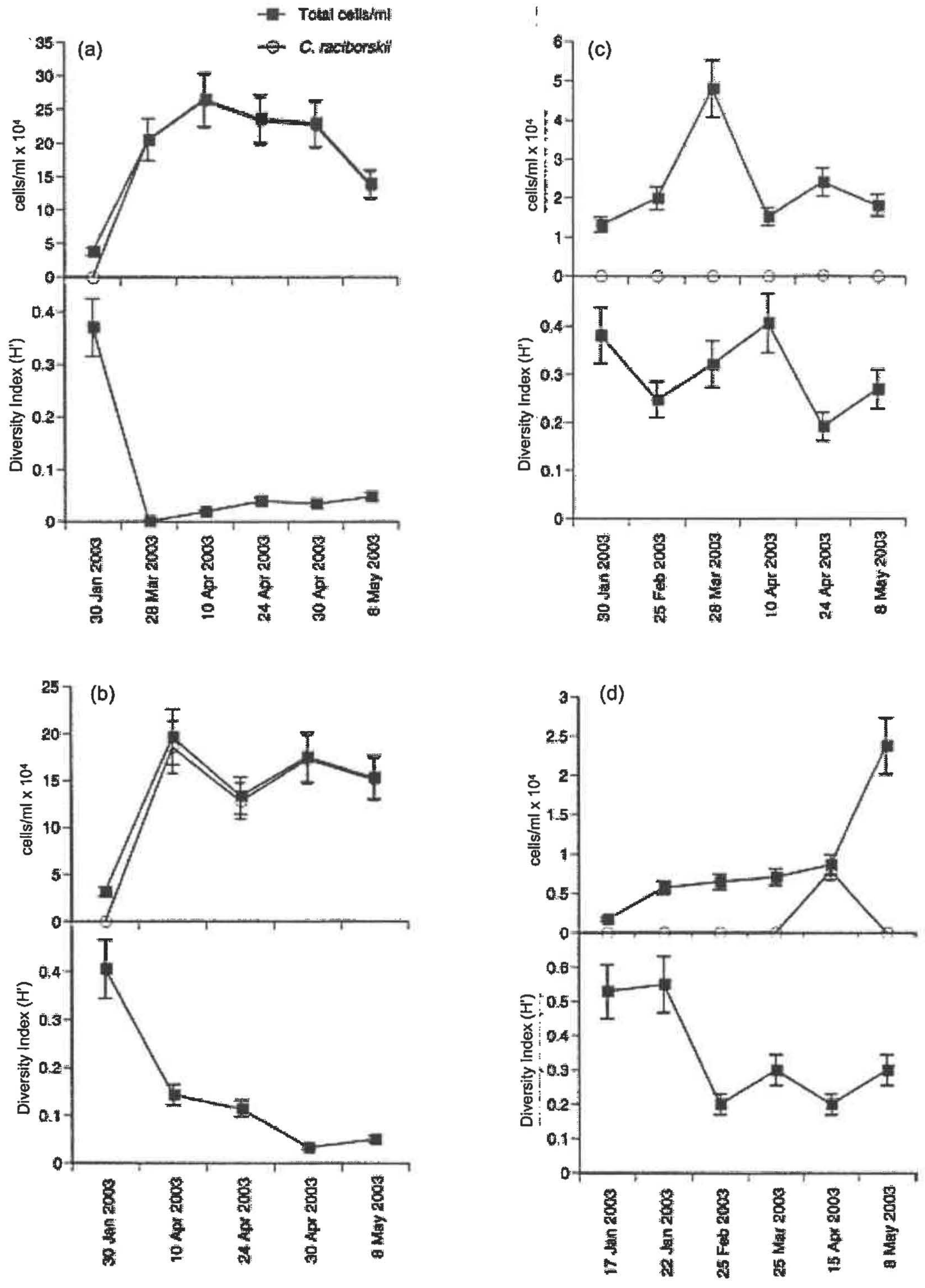

Figure 2.2. Temporal distribution of Shannon-Weiner diversity index and cell counts of the total phytoplankton assemblage, and *Cylindrospermopsis raciborskii* in the four study lakes. (a), Lake Waahi; (b), Lake Whangape; (c), Lake Ngaroto; (d), Lake Karapiro.

Table 2.2. Net rates of growth and cell counts of *Cylindrospermopsis raciborskii*.
* not sampled on this occasion.

Lake	Net rate of growth (day^{-1})	Time period	Counts cells/ml 28 Mar 03	24 Apr 03
Waahi	0.21	30 Jan – 28 Mar 03	*	128 000
Whangape	0.17	30 Jan – 10 Apr 03	205 000	233 000
Ngaroto	0.24	10 Apr – 24 Apr 03	< 10	372.0
Karapiro	0.26	25 Mar – 15 Apr 03	< 10	7 900

Saker and Griffiths (2000) found that *C. raciborskii* from isolates in culture at an incident light intensity of 50 μmol m^{-2} s^{-1} had a maximum growth rate (divisions/day) of 0.9-1.2 day^{-1} at its optimum temperature (>25°C), but a maximum growth rate of only 0.3-0.5 day^{-1} at 20°C. For our sampling days, measured surface water temperatures were 16.1 – 20.4°C in Lake Waahi and 16.0 – 20.8°C in Lake Whangape. Our *in situ* values of r_n suggest that *C. raciborskii* populations may have increased at rates close to maximum values observed under laboratory culture conditions for at least some of the period between sampling intervals.

Macrophyte populations in Lakes Waahi, Ngaroto and Whangape have decreased, and largely disappeared, over the past one to two decades (Boswell et al. 1985; Barnes 2002). This change can be expected to increase exposure of bottom sediments to the erosive effects of wind, leading to sediment resuspension and reduced light availability (Hamilton and Mitchell 1996; Scheffer 1998). These conditions may favour growth of *C. raciborskii*, with its capacity to grow well at low irradiance (Padisák and Reynolds 1998). These three lakes appear to provide ideal conditions for the proliferation of *C. raciborskii*, with high concentrations of nutrients and low water clarity (Table 2.1). Other shallow lakes in New Zealand which have changed to an "alternative stable state" (Scheffer 1998) signalled by nutrient enrichment, high turbidity, and loss of macrophytes (Hamilton and Mitchell 1997), could also be expected to be susceptible to blooms of *C. raciborskii*, depending on water temperature. *C. raciborskii* does not appear to be favoured by a specific thermal stratification regime (Antenucci et al. 2002) whereas bloom formation in many other species of cyanobacteria (e.g., *Microcystis* sp. and *Anabaena* sp.) may be closely linked to the presence of thermal stratification (Reynolds 1998; Oliver and Ganf 2000).

The ability of *C. raciborskii* to fix nitrogen may also be advantageous if its geographical range in New Zealand is extended, as phytoplankton in many lakes of the Central Volcanic Plateau of the North Island have previously been found to be nitrogen limited (White et al. 1985).

Cylindrospermopsis raciborskii can form water blooms which may be nearly monospecific, because of its ability to fix nitrogen and subsist under different stratification regimes and at low irradiance. On 10 April 2003, *C. raciborskii* formed an almost monospecific bloom in Lake Waahi comprising >262 700 cells/ml (Fig. 2.2a), with only one other species recorded, the diatom *Aulacoseira granulata*, observed at a density of 1900 cells/ml. As the bloom decreased, species diversity increased with the appearance of other species at densities <1000 cells/ml, including *Peridinium* sp., *Trachelmonas volvocina*, and *Scenedesmus* sp. The change in species diversity in lakes prior to and following the invasion of *C. raciborskii* was evaluated with the Shannon-Weiner index, H'. In Lakes Waahi and Whangape, H' decreased from 0.4 to 0.05 between 30 January and 8 May 2003 (Fig. 2.2a and b). This decrease demonstrates the trend of reduced species diversity and nearly monospecific blooms of *C. raciborskii* in these two lakes in early May. The change in species diversity was very small in Lakes Karapiro and Ngaroto with the introduction of *C. raciborskii*. Lake Ngaroto (Fig. 2.2c) had large blooms of *Microcystis aeruginosa* (>10 000 cells/ml) during the summer and *C. raciborskii* did not reach very high densities; species diversity was little affected by the introduction of *C. raciborskii*. In Lake Karapiro low water residence times may have prevented *C. raciborskii* from reaching densities c. 10 000 cells/mL that might have affected the diversity (Fig. 2.2d).

Cylindrospermopsis raciborskii may have comparable physiological characteristics to Reynolds' (1997) "Association S" group comprising solitary filamentous Oscillatoriales. This group may dominate the plankton of near-continuously mixed, exposed, turbid systems which are often nutrient-enriched; consistent with the shallow Waikato lakes in this study. "Association S" species are also highly adapted to low irradiance, as is *C. raciborskii*. *C. raciborskii* has been categorised as "Association H" by Reynolds (1997), corresponding to phytoplankton growth adapted to high light levels.

Cylindrospermopsis raciborskii appears to have high dispersal capabilities in view of its rapid establishment in temperate lakes worldwide. Padisák (1997) proposed likely mechanisms of dispersal of akinetes by migratory birds or vegetative forms with the importation of tropical fish. *C. raciborskii* has expanded its geographical range rapidly overseas and more recently in the Waikato region of New Zealand. The high rates of growth in the Waikato lakes, coupled with its apparent rapid dispersion, could have serious implications for lakes in New Zealand. Wood and Stirling (2003) detected the presence of the cyanotoxins cylindrospermopsin (CYN) and deoxy-cylindrospermopsin (do-CYN) in samples from Lake Waahi. These factors collectively suggest that the proliferation of *C. raciborskii* in individual lakes and its geographical dispersion in lakes with high recreational or user values should be closely monitored.

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Chapter 3

Lake phytoplankton composition and biomass along horizontal and vertical gradients

3.1 Introduction

Phytoplankton biomass and composition within a lake may be highly variable spatially, both vertically and horizontally (Bowers 1980, Schelske and Stoermer 1971, Hall et al. 2003). For example, phytoplankton communities in lake embayments are often markedly different from those in the main lake basin (Gray 1987). Embayments may be affected differently by inflows and outflows, and have different transport rates and nutrient levels, resulting in susceptibility to algal blooms (Tada et al. 2001).

Responses of phytoplankton in the middle of large lakes may not accurately reflect these embayments. Algal biomass is often estimated from one mid-lake station, and intra-lake variation is over-looked (Fee 1976, Stauffer 1988), with consequential errors in lake-wide phytoplankton biomass estimates. In this study spatial variations in phytoplankton biomass were examined in a large New Zealand lake in the central lake and in several embayments. Vertical gradients in phytoplankton biomass exist in the lake during summer with the development of a deep chlorophyll maximum (DCM). Our objectives were to quantify spatial and temporal variations in phytoplankton biomass between embayments and the main lake and demonstrate the effects on the underwater light climate. Also to resolve whether a mid-lake station is adequate for determining surface and DCM levels through-out the lake.

3.2 Methods and study site

Lake Tarawera is a large (41.6 km^2), deep (maximum depth 87.5 m) oligotrophic lake in North Island, New Zealand. Sampling stations were established in four major lake embayments (sites 1 – 4) and one mid-lake station (site 5) (Fig. 3.1). Depths of the embayment stations were 30-50m and the mid-lake station was 87m.

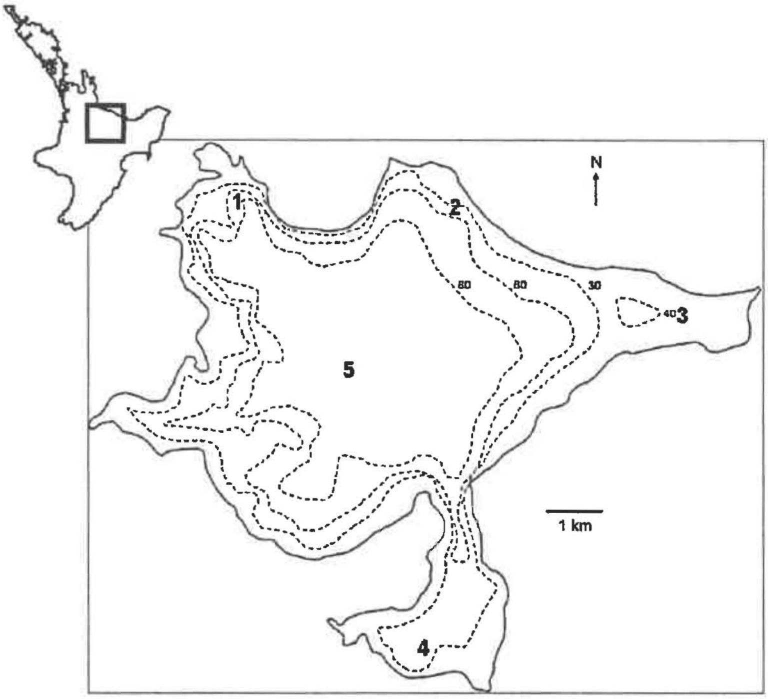

Figure 3.1. Sampling sites on Lake Tarawera. Numbers in bold indicate the five sampling sites. Dashed lines are depth contours (m).

Stations were sampled once a week over 3 weeks in November 2002 (late spring) and February 2003 (late summer), followed by twice daily sampling for one week during December 2002 and March 2003. A Seabird Electronics (SBE) 19plus Seacat Profiler was used to resolve the depth (z) of chlorophyll-fluorescence, temperature, density (ρ) and photosynthetically available radiation (PAR). Chlorophyll-fluorescence was calibrated against acetone-extracted chlorophyll *a* extracts and corrected for phaeophytin (Axler and Owen 1994) collected simultaneously with the fluorescence measurements. Chlorophyll-fluorescence casts were performed at 0600h and 1800h to reduce the effects of non-photochemical quenching of fluorescence in surface waters. Depth-integrated samples of the surface mixed layer were collected for determination of chlorophyll *a* and for phytoplankton enumeration. Discrete samples of the DCM and Surface Chlorophyll Maximum (SCM), resolved from the fluorometric profiles, were collected with a diaphragm pump. Odyssey (Dataflow Systems Ltd) loggers were used to record temperature at selected water depths (0, 10, 20, 25, 27, 40, and 50 m). Thermocline and metalimnion depths were defined according to Hoare and Spigel (1987) and averaging to 1m was used. The position of the thermocline depth is where $d\rho/dz$ = minimum and the limits of the metalimnion where $d^2\rho/dz^2 = 0$. The mid-point of the DCM was similarly defined from chlorophyll-fluorescence, where $d^2F/dz^2 = 0$. The SCM was defined as the depth of the peak chlorophyll fluorescence in surface waters.

Phytoplankton samples were preserved with 2% Lugol's iodine. Cell counts were conducted using the sedimentation technique of Utermöhl (1958), and algal biomass was approximated using the closest geometrical shape for each algal unit (Hillebrand et al. 1999). Phytoplankton biomass was estimated as cell carbon using the carbon-cell volume regressions of Menden-Deuer and Lessard (2000). Total biomass was calculated by multiplying cell carbon by cell abundance.

3.3 Results

A DCM was present in Lake Tarawera in early spring when the lake stratified. The species composition of the DCM was similar across the 5 sites and was dominated by diatoms, including *Stephanodiscus* spp., *Cyclotella* spp., *Aulacoseira granulata*, *Asterionella formosa* and *Fragilaria crotonensis.* On 16 – 18 December 2002 cell numbers at the five sites ranged from 200 to 310 cells ml^{-1} (Fig. 3.2a), however, during late summer (9 to 11 March 2003) cell numbers were < 120 cells ml^{-1} at the DCM. Phytoplankton densities in surface waters showed the opposite trend, with lowest cell numbers (< 500 cells ml^{-1}) on 16 – 18 December 2002 (Fig. 3.2b). A SCM of *Anabaena lemmermanni* developed in March 2003. Cell numbers in surface waters were 3,500 cells ml^{-1} between 9 to 11 March 2003, with maximum densities of > 6,000 cells ml^{-1} at site 1. Large horizontal variations were found in cell numbers in the embayments during the sampling period. For example, on 27 February 2003 the highest surface integrated algal biomass of 50,000 and 28,000 cells ml^{-1} was recorded at sites 3 and 5, respectively, compared with the other three sites which had < 3000 cells ml^{-1}. By contrast, on 22 March 2003 sites 1, 2 and 3 contained the highest algal biomass (> 30,000 cells ml^{-1}), sites 4 and 5 had low cell densities of < 100 cells ml^{-1}.

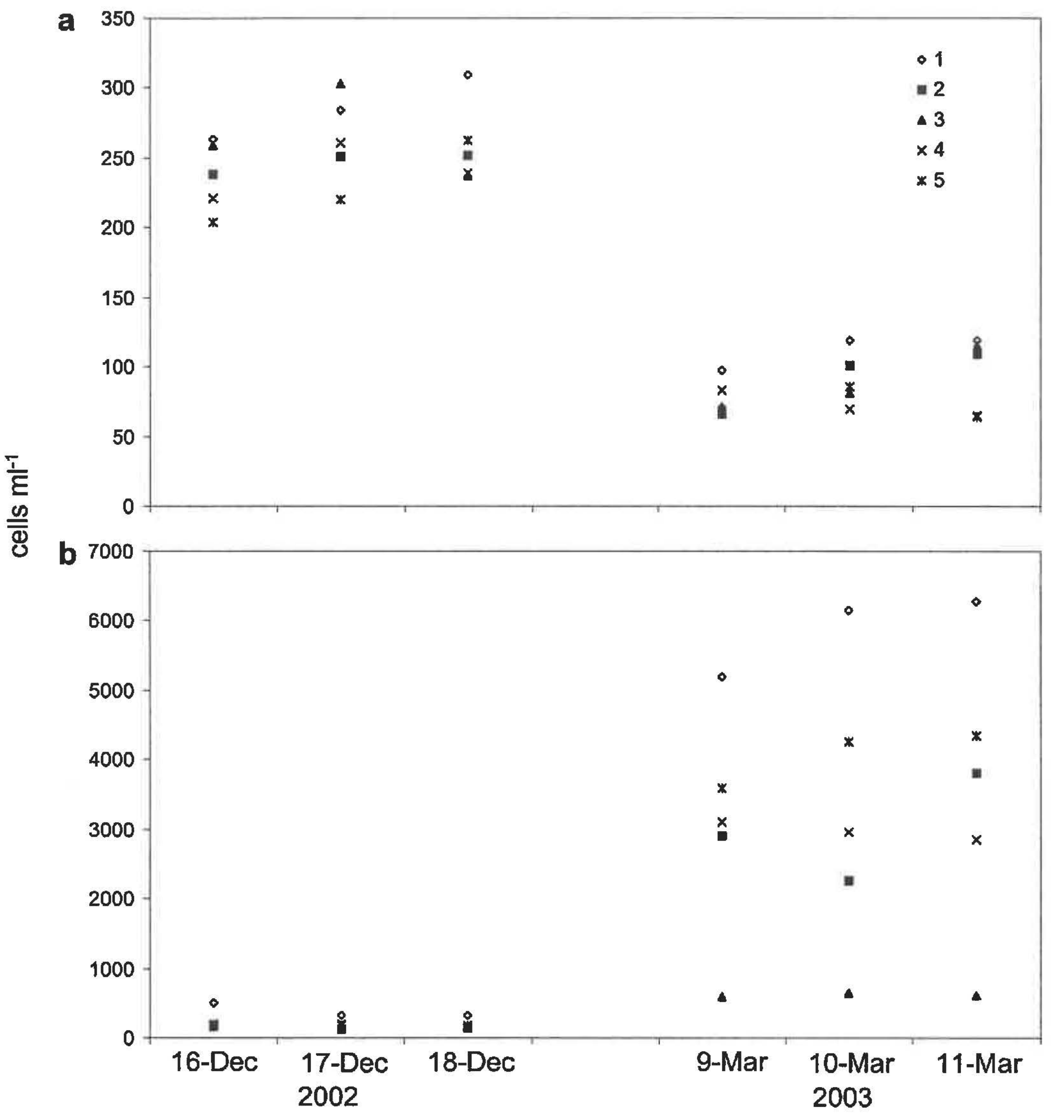

Figure 3.2. Phytoplankton biomass (cells ml^{-1}) in Lake Tarawera at (a) the DCM and (b) SCM at five sites from 16 – 18 December 2002 and 9 – 11 March 2003.

The depth of the DCM was 21 – 28m at the five sampling sites in Nov-Dec 2002 and was closely related to the depth of the thermocline ($r^2 = 0.78$) ($p < 0.01$) (Fig. 3.3), suggesting that basin-scale seiching contributed to most of the DCM displacement.

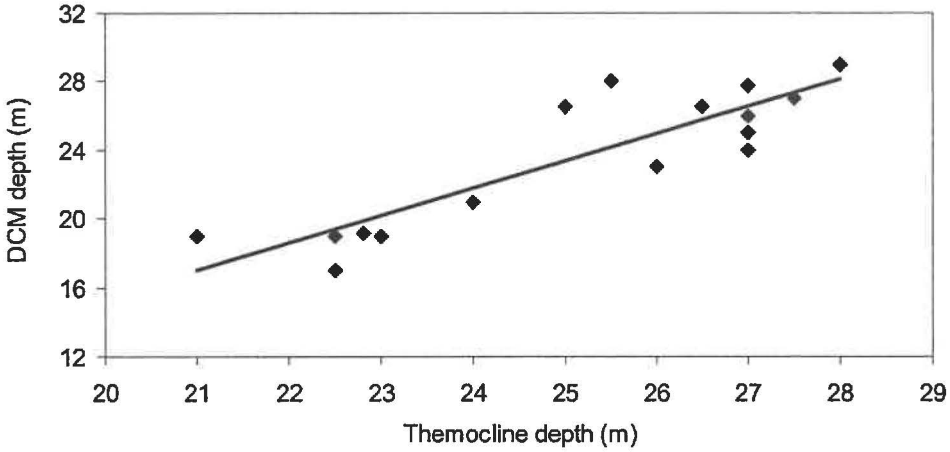

Figure 3.3. Depth of the DCM vs thermocline depth during November-December 2002. $z_{DCM} = 1.5863x - 16.322$ ($r^2 = 0.77$, $p<0.05$).

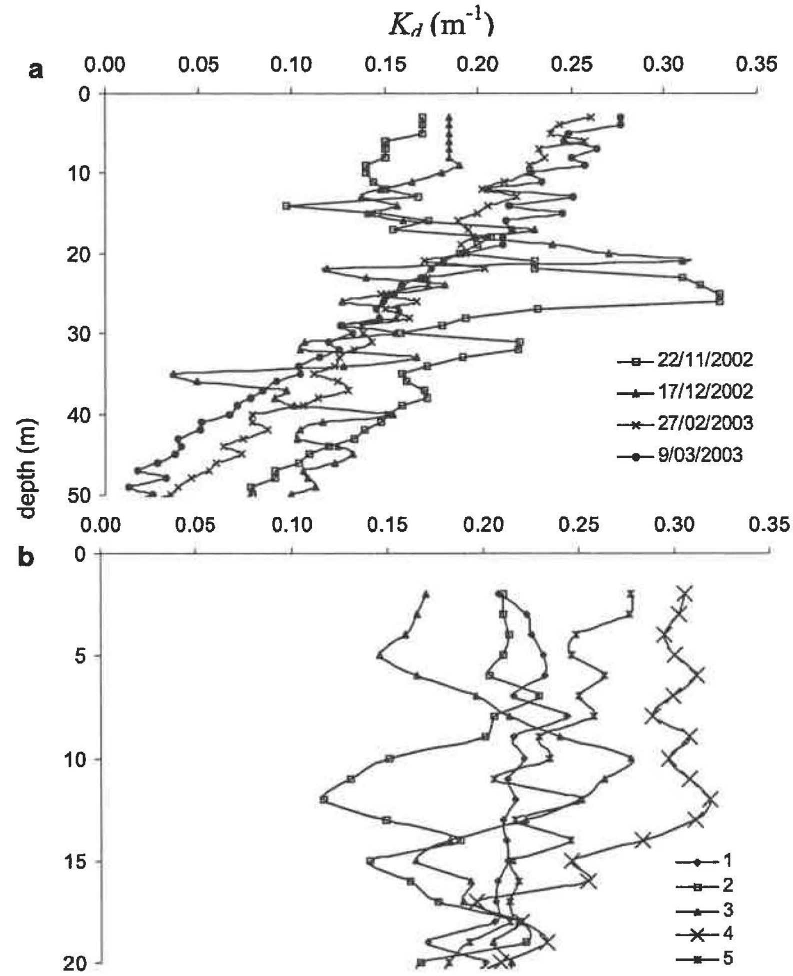

Figure 3.4. Variation of K_d at (a) site 5 on four sampling days and (b) at 5 sites on 9 March 2003.

The mean vertical attenuation coefficient (K_d) was higher at the DCM (0.31 - 0.33 m^{-1}) than in the surface where K_d was c. 0.17 m^{-1} (Fig. 3.4a). In Feb-Mar 2003, K_d in surface waters was much higher than in December at >0.24 m^{-1}. There were large spatial variations in K_d at the five sites in Feb-Mar 2003. In surface waters of sites with high algal biomass there were correspondingly high K_d values, e.g., 9 March 2003 at sites 4 and 5 where there were > 3,000 cells ml^{-1} (Fig. 3.4b). By contrast, site 3 had < 600 cells ml^{-1} and a correspondingly low K_d value.

3.4 Discussion

The results indicate that a single mid-lake station may be appropriate for estimating biomass at the DCM and that thermocline seiching contributes most of the variability of DCM depth. When quantifying surface populations, however, discrete samples from one station depth may not represent lake-wide biomass. During the bloom of *Anabaena lemmermanni* phytoplankton biomass was highly variable between sites.

Vertical and horizontal differences in the light climate of Lake Tarawera were driven by spatial variations in phytoplankton biomass. Increase in K_d at the DCM may produce steep local light gradients, increasing potential for self shading (Presing et al. 1999).

In surface waters, algal blooms can greatly increase the rate of light extinction (Ferber et al. 2004) producing strong horizontal gradients of light attenuation. In Feb-Mar 2003 the high surface algal biomass reduced PAR at the DCM from 1.3 % to 0.1 % of the surface value. The decrease in algal biomass at the DCM between Dec 2002 and March 2003 may have been related to light limitation caused by substantially higher biomass at the surface in the latter period.

This study has shown that considerable horizontal variation in the distribution of phytoplankton can exist, especially when buoyant cyanobacteria are present. Therefore it is recommended that more than one sampling station be established in lakes with embayments, when quantifying surface phytoplankton biomass, while for quantifying a strong DCM biomass this may be potentially less important. Boundary mixing or interflows, however, may displace the vertical biomass of the DCM and produce horizontal discontinuities in DCM populations (MacIntyre et al. 1999). Boundary mixing enhances vertical mixing near lateral boundaries as internal wave fields interact with a sloping bottom. Depending on the bottom slope, the increased wave strain may lead to instabilities in the density profile that can collapse and create turbulent mixing. The increased mixing is likely to supply nutrients to the DCM (MacIntyre et al. 1999) and may therefore contribute to DCM variability among sites. The presence of boundary mixing or interflows merits sampling of a DCM at multiple stations. This study highlights the need to consider the variation in the spatial distribution of phytoplankton biomass over short time intervals. Quantifying this significance of the spatial variation of phytoplankton biomass is important when assessing phytoplankton production or water quality, variability may be especially important when there are large populations of cyanobacteria.

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Chapter 4

Dynamics of a diatom Deep Chlorophyll Maximum in an oligotrophic New Zealand lake

List of acronyms		units
DCM	deep chlorophyll maximum	
SCM	surface chlorophyll maximum	
SML	surface mixed layer	
EXP	exponential increase of phytoplankton biomass	
DP	double peak of phytoplankton biomass	
LIN	linear vertical distribution of phytoplankton	
K_z	turbulent diffusion rate	cm^2 s^{-1}
v	sinking rate	m day^{-1}
K_d	light extinction coefficient	m^{-1}
z	depth	m
F	chlorophyll-fluorescence	mV
T	temperature	°C
k_c	specific vertical light attenuation coefficient for chlorophyll *a*	m^2 mg chl a^{-1}
L_N	Lake number	
S_t	Schmidt stability	g cm/cm^2
N^2	Buoyancy frequency	s^{-2}
μ	growth rate of phytoplankton	day^{-1}
ω	phytoplankton population density	cells per unit vol
I	light intensity	μmol photons m^{2}s^{-1}
M	grazing mortality term for phytoplankton	mg chl *a* m^{-3} day^{-1}

4.1 Abstract

Vertical variations in the phytoplankton assemblage composition, C:Chl ratios and zooplankton grazing rates were examined in Lake Tarawera, a large (area = 42 km^2), deep (maximum depth = 87.5 m), oligotrophic lake in North Island, New Zealand. A deep chlorophyll maximum (DCM) composed of diatom species formed at the thermocline during Austral spring-summer of 2002-3. Factors contributing to DCM formation were examined using a population-dynamics theory of sinking phytoplankton that considered interactions between growth limitation by light and nutrients, sinking rates and turbulent diffusion rates. Five 'Modes' of vertical phytoplankton biomass distribution relating to four forcing functions were categorised. Mode 1 is a surface chlorophyll maximum (SCM); Mode 2 is a DCM; Mode 3 is a double peak consisting of buoyant cyanobacteria at the surface and a DCM; Mode 4 is a linear vertical distribution; and Mode 5 is an exponential increase with depth. The occurrence of these distributions was examined in relation to different turbulent diffusion rates (<0.1 – 10 cm^2 s^{-1}), sinking rates (+10 to -4 m day^{-1}) and light and nutrient limitation. At the DCM, vertical gradients of diatom populations were maintained when populations were able to 'outgrow' low rates of dispersion by turbulent diffusion ($K_Z = 0.1$ cm^2 s^{-1}) and losses due to sinking (1 m day^{-1}). With water column turnover and increased dispersion in winter, however, the DCM broke down but areal growth rates of phytoplankton remained high. The dominance of the DCM was simulated under a variety of regimes of light, nutrients and turbulence similar to those of Lake Tarawera, indicating that diatoms can overcome selection pressures imposed by sedimentation, to persist as a DCM.

4.2 Introduction

Diatom deep chlorophyll maxima (DCMs) have been well-documented in both freshwater and marine systems (e.g., Davey and Heaney 1989; Jackson et al. 1990). These communities are known to tolerate conditions of low temperature, moderate to low light availability and intermediate levels of available phosphorus that occur at the DCM (Dokulil and Teubner 2003; Kilham et al. 1996).

Several processes may lead to formation of DCMs in aquatic systems. Changes in vertical mixing affect diffusion and nutrient supply rates at the DCM (Barbosa et al. 1989; Howard-Williams et al. 1986; Pick et al. 1984; Wurtsbaugh et al. 2001). Phytoplankton settling velocities may also be reduced by an increase in water density (Yamamoto 1984) and variations in turbulent diffusion at the thermocline, where DCMs are most commonly observed (Gabric and Parslow 1989; Condie and Bormans 1997). The persistence of negatively buoyant phytoplankton species as a DCM is partly related to vertical distributions of turbulence in the water column. Huisman et al. (1999, 2002) demonstrated that there is a 'turbulent window' sustaining sinking phytoplankton species in deep water columns. At intermediate levels of turbulent diffusion, phytoplankton populations can 'outgrow' mixing and sinking, with suppression of turbulence in the thermocline allowing maintenance of vertical gradients in both water and particle densities (Condie and Bormans 1997; Fennel and Boss 2003; O'Brien et al. 2003). The vertical position of the DCM is generally close to the maximum vertical density gradient or thermocline (Bowers 1980; Barbosa et al. 1989), which provides protection from surface-driven turbulent mixing, but the DCM position is also constrained by the availability of light.

Biological explanations for DCMs usually focus on enhanced phytoplankton growth in response to strong vertical gradients of nutrients at the thermocline or reductions in zooplankton grazing pressure, as well as other physiological adaptations of phytoplankton, including suppression of sinking velocities as a physiological response to higher nutrient concentrations (Kiefer et al. 1972; Fee 1976; Shortreed and Stockner 1990).

To resolve the factors responsible for diatom DCM formation, I used the population-dynamics theory of sinking phytoplankton which has been used in previous studies of non-buoyant phytoplankton (Huisman et al. 2002; O'Brien et al. 2003). This theory describes the interactions between rates of phytoplankton growth, sinking, and turbulent diffusion. I used field data from Lake Tarawera to validate the theory. There is no historical information on reasons for the existence of a DCM in Lake Tarawera and I hypothesised that the DCM depth coincides with the depth of maximal rate of net phytoplankton growth, accounting for the influences of turbulent diffusion and sedimentation.

The largest biomass of diatoms in Lake Tarawera was recorded in winter; however the classical paradigm of phytoplankton seasonality in temperate monomictic lakes suggests that light, temperature and mixing regimes are mostly unsuitable for net phytoplankton growth in this season. Theoretically, integrated water column light levels in winter are too low to support net phytoplankton growth in deep lakes. However the diatom *Aulacoseira granulata* obtains maximum biomass during winter isothermy in deep (z_{max} = 160m) Lake Taupo (Vincent 1983), a lake similar in trophic status and in close proximity to Lake Tarawera. In addition, annual maxima of the diatoms *Synedra* sp. and *Cyclotella* sp. coincide with deep mixing in Lake Rotongaio (Viner and Kemp 1983). I hypothesise that the deepening of the thermocline during winter, with entrainment of nutrients from depth, may lead to the large winter biomass, in association with diatom species that are well adapted to light capture.

In this study I quantify the vertical and temporal differences in phytoplankton taxonomy, C:Chl ratios, zooplankton grazing and phytoplankton-specific light attenuation between waters in the surface mixed layer (SML) and the DCM of Lake Tarawera. Turbulent diffusion (K_Z) was calculated to predict times of nutrient-enhanced fluxes for re-supply of nutrients to the DCM. The primary objective of the study was to elucidate conditions leading to persistence of the DCM, using interactions between turbulent diffusion rates, light-dependent and nutrient-dependent growth rates, and phytoplankton sinking rates.

4.3 Methods

Study site

Lake Tarawera (176° 25' E, 38° 12' S) is a warm monomictic, oligotrophic lake on the Central Volcanic Plateau (CVP) of North Island, New Zealand (Fig. 4.1). The lake has an area of 41.6 km^2, and z_{max} of 87.5 m. Sampling stations were established in four major lake embayments of depths 30-50 m and one mid-lake station of depth 85 m (refer to Ryan et al. 2004).

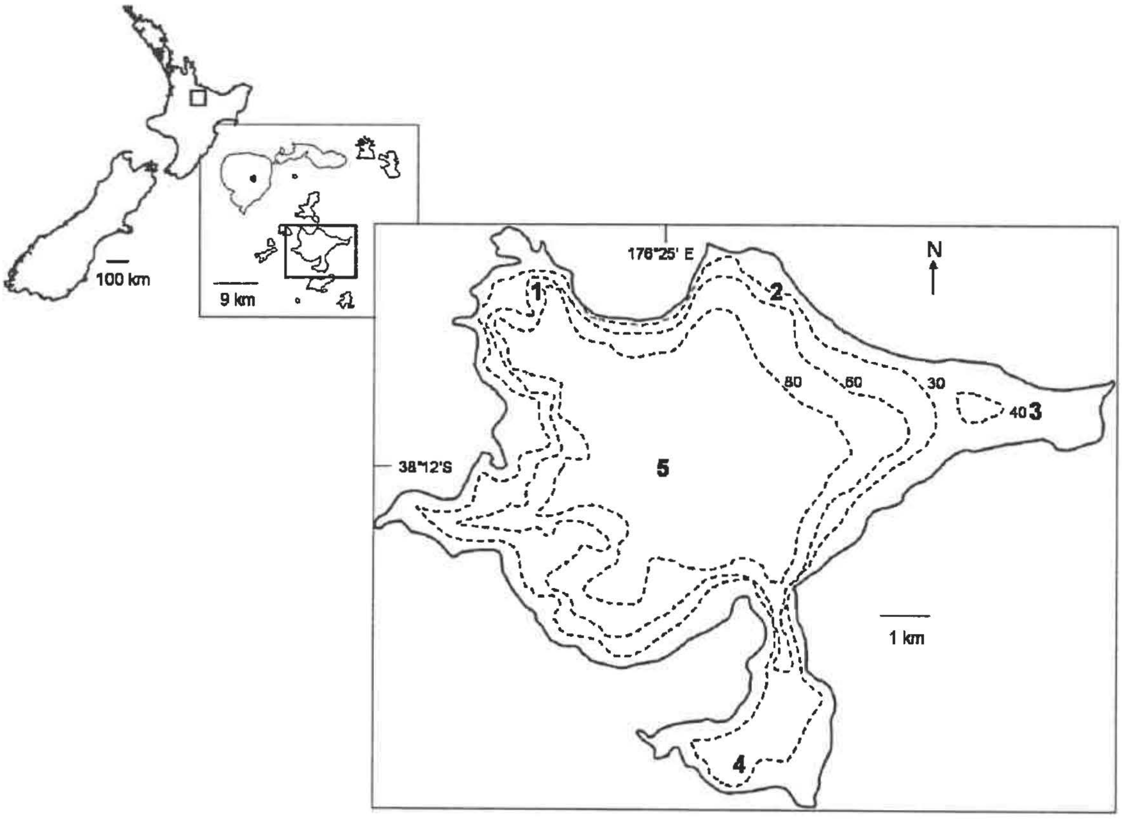

Figure 4.1. Location of Lake Tarawera in North Island, New Zealand, amongst lakes of the Rotorua district (first box) and showing sampling stations and bathymetry (m) (second box).

Water quality data

Lake Tarawera was sampled once a week over 3 weeks in November 2002 (late spring), February/March 2003 (late summer), July 2003 (winter) and October 2003 (early spring), followed by twice daily sampling for one week during December 2002, March 2003, August 2003 and November 2003. A Seabird Electronics (SBE) 19plus Seacat CTD Profiler was used to resolve the depth (z) variation of chlorophyll-fluorescence (F), temperature (T), density (ρ) and photosynthetically available radiation (PAR). To reduce the effect of quenching of fluorescence in well-lit surface waters, CTD casts were performed at 0600 h and 1800 h.

Chlorophyll fluorescence was calibrated against phaeophytin-corrected, acetone-extracted chlorophyll *a* extracts (Strickland and Parsons 1972) collected simultaneously with the fluorescence profiles. Chlorophyll fluorescence at the DCM was also calibrated against phytoplankton biomass derived from phytoplankton samples at the DCM.

Depth-integrated samples of the surface mixed layer were collected using a tube sampler for determination of filterable nutrients (0.45 μm GF/C-filtered) and chlorophyll *a*, and for phytoplankton and zooplankton enumeration at each station. The tube sampler was lowered to the depth of the thermocline, which was determined on-board from temperature profiles following a CTD cast. Filterable nutrient samples were stored on ice and then deep-frozen before analysis for ammonium (NH_4), oxidised nitrogen (NO_x) and reactive phosphorus (SRP) with a Lachat Instruments flow injection analyser using standard methods (Zellweger Analytics 2000).

Discrete samples of the DCM, located from the fluorescence profiles, were collected with a diaphragm pump with a specifically designed intake for minimising vertical dispersion. Attempts were made to lower the intake equipment as close as possible to the centre of the DCM, and assumed that the samples were considered to have been collected at the depth of the peak biomass of the DCM. During winter, relatively constant fluorescence profiles with depth indicated that phytoplankton were evenly dispersed through the water column; a 0 - 15 m depth-integrated tube sample was taken as representative of water column populations at this time. Climate data (wind and irradiance) were obtained from Rotorua Airport climate station situated 15 km from the lake. Daily averages of climate data were obtained from hourly averaged readings collected at the station.

Phytoplankton and zooplankton data

Phytoplankton samples were preserved immediately upon collection with 2 % Lugol's iodine. Cell counts were conducted using the sedimentation technique of Utermöhl (1958). A minimum of 400 algal units, cells, colonies or filaments were counted for each sample and dimensions of 20 - 40 individuals of each taxon were measured for determination of biomass, which was approximated using the closest geometrical shape for each algal unit (Hillebrand et al. 1999). Biomass was estimated as cell carbon using the carbon-cell volume regressions of Menden-Deuer and Lessard (2000). Separate conversions were used for diatom and non-diatom phytoplankton due to differences in biovolume:carbon ratios. Total biomass was calculated as the product of cell carbon and cell abundance.

Zooplankton samples were preserved with 10 % formalin after isolation by on-board filtration through a 75 μm mesh-net. In the laboratory, subsamples of 5 ml were placed in an open-topped perspex counting tray (50 x 80 mm) and enumerated using a Leica MZ12 microscope at 50 x magnification. Successive samples were counted until > 200 individuals were recorded. Zooplankton biomass was estimated from length-carbon regressions (Kankaala and Johansson 1986; Santer and van den Bosch 1994).

Nutrient-light limitation experiments

In-situ nutrient spiking incubations on SML and DCM phytoplankton were conducted to determine whether light or nutrients may potentially limit growth. Three litre PET® bottles were filled with unfiltered depth-integrated samples of the SML and discrete samples from the DCM. Replicate bottles were enriched with ammonium chloride (NH_4Cl), potassium dihydrogen phosphate (KH_2PO_4) or a ratio of both nutrients (10:1) to a final concentration of 1 mg L^{-1} for NH_4-N or 0.1 mg L^{-1} for PO_4-P. The bottles were spiked with N (1 mg L^{-1}) and P (0.1 mg L^{-1}) as high concentrations are needed, together with a substantial incubation period, before a biomass response becomes measurable (White and Payne 1977). A ratio of 10:1 was used to equate to the ratio in the ambient waters of Lake Tarawera. The bottles were incubated either near the lake surface (c. 3 m) or at the depth of the DCM (c. 25 m) for a 5-day period following the methodology recommended by White and Payne (1977). Control bottles containing no added nutrients were incubated at both depths. The DCM phytoplankton was also incubated in surface waters to determine the effect of exposure to higher irradiance (40 % of surface irradiance). All treatments were analysed for chlorophyll *a*, and cell counts were also made.

Mathematical framework

Thermocline and metalimnion depths were defined according to Hoare and Spigel (1987) and based on 0.5 m vertical intervals. The position of the thermocline depth is where $d\rho/dz$ = minimum, and the limits of the metalimnion where $d^2\rho/dz^2 = 0$. The mid-point of the DCM was similarly defined from chlorophyll-fluorescence, where $d^2F/dz^2 = 0$.

Lake number, L_N, which quantifies the amplitude of basin-scale internal waves in response to surface wind forcing (Imberger and Patterson 1990), was defined as:

$$L_N = \frac{gS_t(1 - z_T / z_m)}{\rho_0 u_*^2 A_0^{3/2}(1 - z_g / z_m)} \tag{1}$$

where z_T is the thermocline height, z_g the height of the centre of volume, u_* the surface shear velocity due to surface wind stresses, ρ_0 the surface density, A_0 the lake surface area and S_t the Schmidt stability parameter, given by:

$$S_t = \int_0^{z_m} (z - z_g)A(z)\rho(z)dz \quad . \tag{2}$$

The vertical eddy diffusion coefficient (K_Z) was estimated using a depth-dependent expression (Yeates and Imberger 2004):

$$Kz(z) = \frac{200N^2(z)}{L_N N^2} K_M \tag{3}$$

where K_M is the molecular diffusion coefficient for heat and N^2 is the Brunt-Väisälä buoyancy frequency calculated at 0.5 m vertical intervals defined by:

$$N^2 = \frac{-g}{\Delta\rho\left(\dfrac{\partial\rho}{\partial z}\right)} \tag{4}$$

where ρ is density and g is gravity.

Modelling DCM development

To resolve the factors that induce diatom DCM formation and persistence, the equation of Huisman et al. (2002) was used to describe the rate of change in phytoplankton population:

$$\frac{\partial \omega}{\partial t} = \mu(I)\omega - v\frac{\partial \omega}{\partial z} + K_z \frac{\partial^2 \omega}{\partial z^2} \tag{5}$$

where $\mu(I)$ is the specific growth rate of phytoplankton as a function of the local light intensity I, ω denotes the phytoplankton population density, t is time, v the sinking velocity and K_Z the vertical turbulent diffusion coefficient.

Photoinhibition is not expected at the DCM, therefore, to quantify the effects of light limitation of phytoplankton in the absence of photoinhibition, the model of Webb et al. (1974) was used:

$$f(I) = 1 - \exp\left(\frac{-I}{I_k}\right) \tag{6}$$

where $f(I)$ represents limitation of phytoplankton growth by light, I is irradiance and I_k is the half-saturation constant for irradiance.

The grazing mortality term for phytoplankton, M (mg chl *a* m^{-3} day^{-1}), is given by (Griffin et al. 2001):

$$M = \frac{k_i f(Z) f(T) Z}{Q_C} \tag{7}$$

where k_i is the grazing rate, Q_C is the ratio of phytoplankton carbon to chlorophyll *a*, $f(T)$ is a temperature multiplier, Z is zooplankton biomass and $f(Z)$ is a Michaelis-Menten grazing term given by:

$$f(Z) = \frac{Chla}{K_i + Chla} \tag{8}$$

where K_i is the half saturation constant for grazing by zooplankton.

4.4 Results

Phytoplankton assemblage composition

In Nov-Dec 2002 (spring – early summer) the DCM was dominated by the diatoms *Stephanodiscus* spp., *Aulacoseira granulata* var. *angustissima* (O. Müller) Simonsen, *Asterionella formosa* Hassall, and *Fragilaria crotonensis* Kitton. The highest biomass at the DCM (356 μm^3 ml^{-1}) was contributed by *Stephanodiscus* cf. *alpinus* (Fig 4.2a), followed by *A. granulata* (66 μm^3 ml^{-1}). By Feb-Mar 2003 (late summer), there was a large reduction in diatom biomass with depth, and *S. alpinus* was <100 μm^3 ml^{-1} (Fig. 4.2b). Areal values of biomass were calculated over the depth of the DCM; there was a decrease from 44 ± 7 mg C m^{-2} in Nov-Dec 2002 to 14 ± 5 mg C m^{-2} by Feb-Mar 2003.

With the cessation of stratification (July-Aug 2003), there was negligible vertical structure of phytoplankton biomass and composition, but areal biomass was substantially higher than Nov-Dec 2002 values. The maximum areal biomass of 158 mg C m^{-2} was recorded on 5 August 2003. *S. alpinus* and *A. granulata* increased during July-Aug 2003 (Fig. 4.3c); *S. alpinus* biomass was maximal at 1280 μm^3 ml^{-1} and *A. granulata* biomass increased from 25 μm^3 ml^{-1} in Feb 2003 to 110 μm^3 ml^{-1} in Aug 2003. By Oct and Nov 2003, the phytoplankton DCM assemblage had reformed, with similar biomass to the previous year, though *S. alpinus* was at higher density (770 μm^{3}ml^{-1}). From early stratification in spring (Nov 2002) through to mid-stratification (Dec 2002), there were large changes in biomass of the diatom assemblage. *S. alpinus* increased and dominated the DCM population during summer, whereas *A. granulata* decreased. *A. formosa* and *F. crotonensis* were recorded in low densities at the onset of stratification, however, from December (summer) there was an increase in biomass of *F. crotonensis*, but less so for *A. formosa*. During the following spring (Oct-Nov 2003) there was a similar pattern, with a large increase in *S. alpinus* biomass at the DCM from 15 Oct 2003 (440 μm^{3}ml^{-1}) to 5 Nov 2003 (770 μm^{3}ml^{-1}).

Surface waters contained a more diverse assemblage of phytoplankton, comprising desmids *Staurastrum* spp. and *Closterium* spp., the chrysophyte *Dinobryon cylindricum*, the dinoflagellates *Peridinium* spp. and *Ceratium hirundinella* and the cyanobacteria *Anabaena* spp. and *Aphanizomenon flos-aquae* (Fig. 4.3). These species were also present at the DCM but at low biomass. *Ceratium* and *Peridinium* dominated the biomass of surface waters (890 and 670 μm^3 ml^{-1} respectively) except during winter isothermy when *Stephanodiscus* spp. dominated. The areal biomass of the surface waters (43 ± 5 mg m^{-2}) was similar to that of the DCM in Nov-Dec 2002, despite the large vertical differences in species composition.

There was a bloom of *Anabaena circinalis* (10,000 μm^3 ml^{-1}) and elevated concentrations of *A. lemmermanni* (700 μm^3 ml^{-1}) in surface waters during Feb-Mar 2003 (Fig. 4.3b), coinciding with a reduction in biomass of other phytoplankton species. In Oct-Nov 2003 the surface waters were dominated again by dinoflagellates (Fig. 4.3c), but with lower biomass (270 μm^3 ml^{-1}) than in Nov 2002.

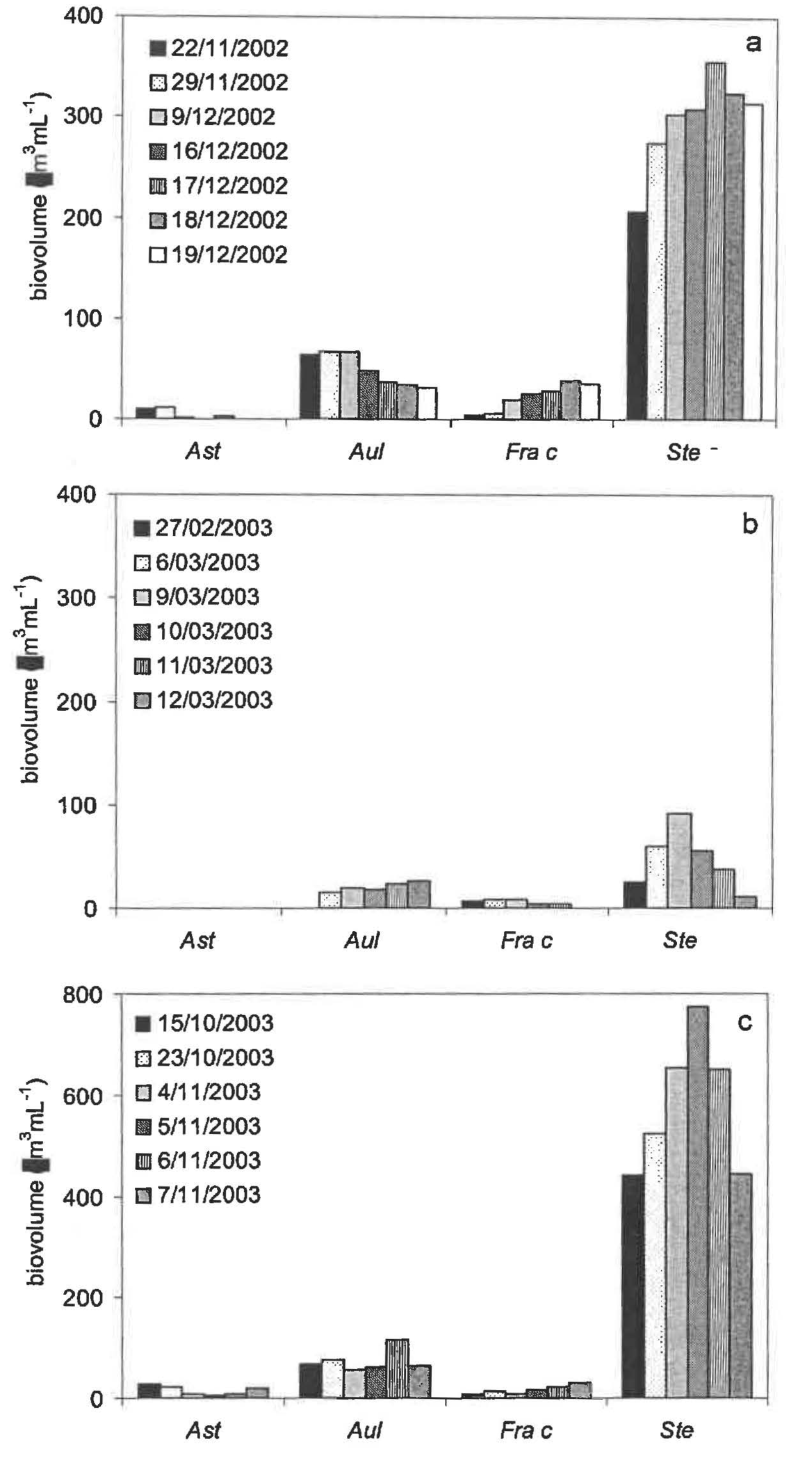

Figure 4.2. Phytoplankton species composition by biomass for the DCM at station 5 (a) Nov-Dec 2002 (early summer), (b) Feb-Mar 2003 (summer) and (c) Oct-Nov 2003 (spring). Ast - *Asterionella formosa*; Aul – *Aulacoseira granulata* var. *angustissima*; Fra c - *Fragilaria crotonensis*; Ste - *Stephanodiscus* spp.

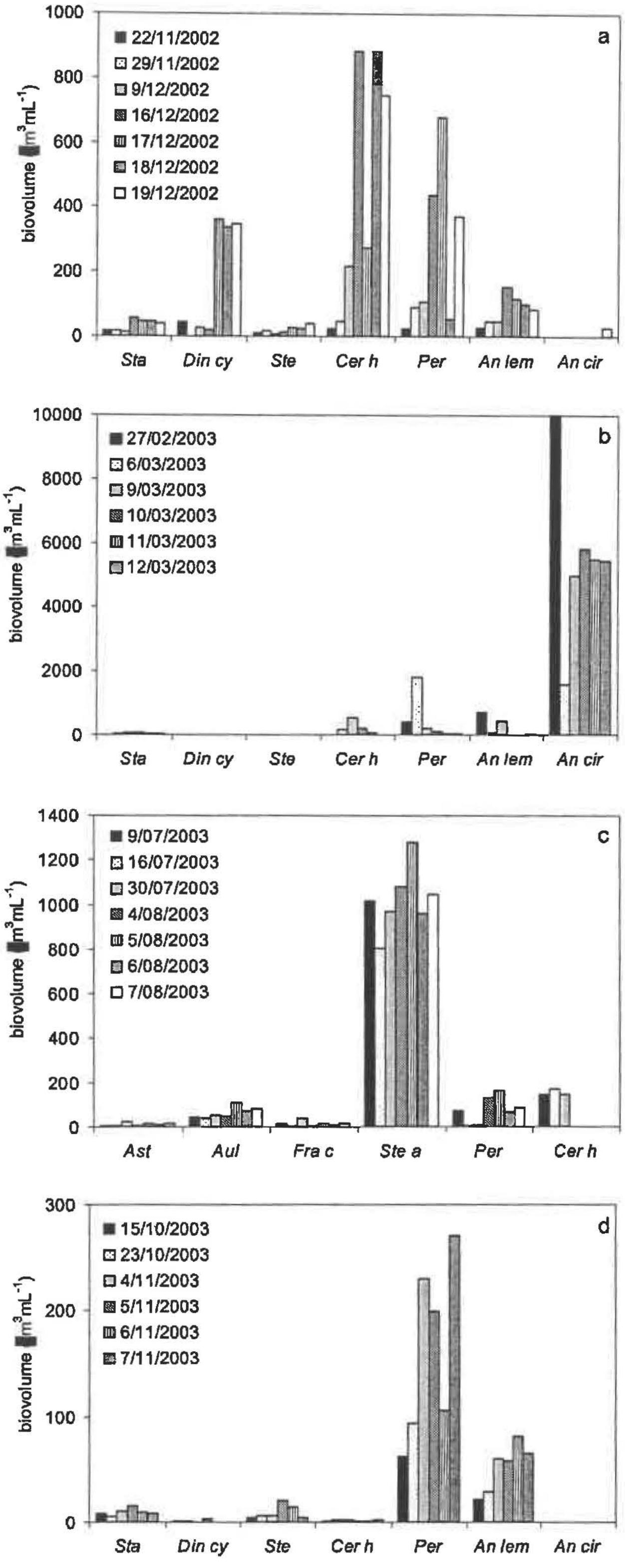

Figure 4.3. SML phytoplankton assemblage composition at station 5 for (a) Nov-Dec 2002, (b) Feb-Mar 2003 (c) July-August 2003 (winter) and (d) Oct-Nov 2003. Sta – *Staurastrum* spp.; Din cy – *Dinobryon cylindricum*; Ste - *Stephanodiscus* spp.; Ast - *Asterionella formosa*; Aul – *Aulacoseira granulata* var. *angustissima*; Ste -

Stephanodiscus spp.; Fra c - *Fragilaria crotonensis*; Cer h – *Ceratium hirundinella*; Per - *Peridinium* spp.; An lem – *Anabaena lemmermanni*; An cir – *Anabaena circinalis.*

C:Chl ratios

Surface concentrations of chlorophyll *a* were 0.3 – 1.2 mg m^{-3} as the DCM formed in Nov-Dec 2002, whereas concentrations in the DCM were 2 – 2.8 mg m^{-3}. The C:Chl ratios were significantly higher ($p < 0.01$) in the SML (mean = 93) than at the DCM (mean = 40) (Table 4.1), suggesting that there were differences between the respective communities or that physiological adaptation to the low light intensities occurred at the DCM.

Table 4.1. C:Chl ratios (± SD) in the SML and DCM during the four sampling periods. Samples in Aug 2003 were depth integrated to 15m as the lake was isothermal.

	SML	n	DCM	n
Dec 2002	94 ± 6	7	45 ± 3	7
Mar 2003	95 ± 5	7	34 ± 8	7
Aug 2003	66 ± 1	6		
Nov 2003	89 ± 7	7	42 ± 5	7

Fluorescence profiles

Fluorescence profiles taken at 0600h on 22 and 29 Nov 2002, demonstrate the presence of a DCM between 20 and 30m, corresponding closely with the metalimnion depth (Fig. 4.4a). Basin-scale seiching of the thermocline was responsible for most of the variation in DCM depth (Ryan et al. 2004). By Feb-Mar 2003 there was a shift from a chlorophyll peak at the DCM to one in surface waters where concentrations were 5-6 mg m^{-3} (Fig. 4.4b), coinciding with a surface 'bloom' of *Anabaena circinalis.* With the onset of winter mixing in Jul-Aug 2003, the vertical structure of fluorescence diminished (Fig. 4.4c) and chlorophyll *a* concentrations were 3 – 3.3 mg m^{-3} throughout the water column. The DCM began to reform in spring (Oct 2003) (Fig. 4.4d), and was well established by Nov 2003 at depths similar to the previous year (Fig. 4.4a).

Thermal structure

In Dec (early summer) 2002, Lake Tarawera was strongly thermally stratified (Fig. 4.5a), and the thermocline (i.e. $\partial\rho / \partial z$ = minimum) was between 19.5 and 21.5 m. By Mar 2003 (late summer) stratification was more pronounced (Fig. 4.5b), $\partial\rho / \partial z$ was at a minimum of depth 19.5 m and the SML was homogeneous. In Aug 2003 (winter) the lake was isothermal (Fig. 4.5c). Although the thermal stratification pattern of Lake Tarawera follows the characteristic pattern for temperate warm monomictic lakes, the highest areal phytoplankton biomass (126 mg C m^{-2}) was recorded in surface waters (0 – 15 m depth-integrated sample) during winter mixing, concurrent with the annual minimum of water temperature (Fig. 4.5c). By Nov 2003 a thermocline had re-established ($\partial\rho / \partial z$ minimum = 21 m) (Fig. 4.5d).

Metalimnetic dynamics

Lake Number, L_N, and eddy diffusivity, K_Z, were calculated from CTD casts, to predict times of nutrient-enhanced fluxes for the re-supply of nutrients to the DCM (Fig. 4.6a). Only L_N and K_Z values at the thermocline are reported here. From 16-19 Dec 2002 and 4-7 Nov 2003, L_N was 2 - 8. Low values of L_N (< 5) signify when enhanced metalimnetic mixing is likely to increase nutrient fluxes to the DCM. High L_N (Fig. 4.6a) and low K_Z values occurred from 9-12 Mar 2003, even though wind speeds were occasionally relatively high (6 m s^{-1}). Estimates of eddy diffusivity (K_Z) calculated at the depth of the thermocline during thermal stratification were in the order of 10^{-6}-10^{-5} m^2 s^{-1} (Fig. 4.6b). Calculations of K_Z were not made for winter (August 2003), when $\partial\rho / \partial z$ was negligible.

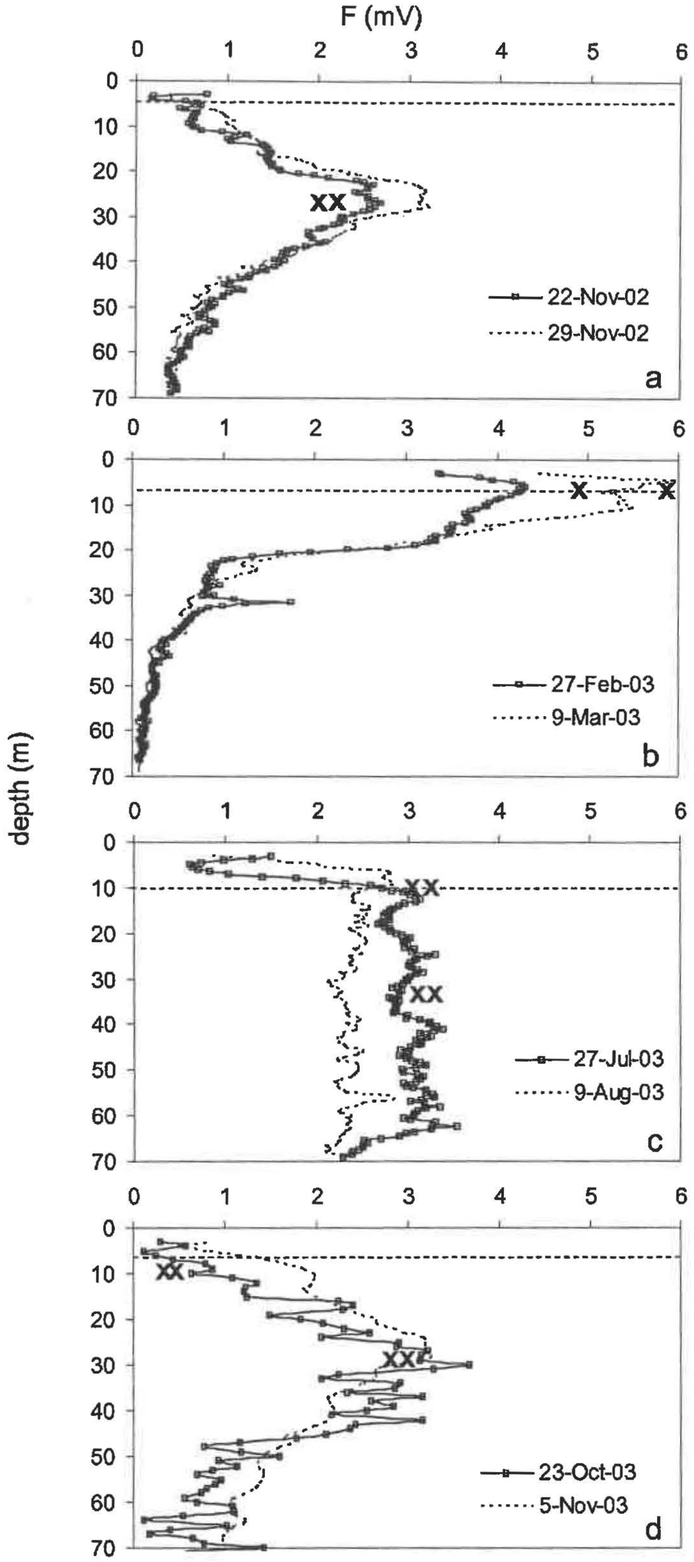

Figure 4.4. Vertical profiles of chlorophyll fluorescence, F, and acetone extracted chlorophyll *a* (**x x** mg m^{-3}) on (a) 22 and 29 Nov 2002 (b) 27 Feb and 9 Mar 2003 (c) 27 July and 9 Aug 2003 and (d) 23 Oct and 5 Nov 2003. The dashed line represents the depth above which fluorescence casts are considered to be affected by quenching from high near-surface irradiance.

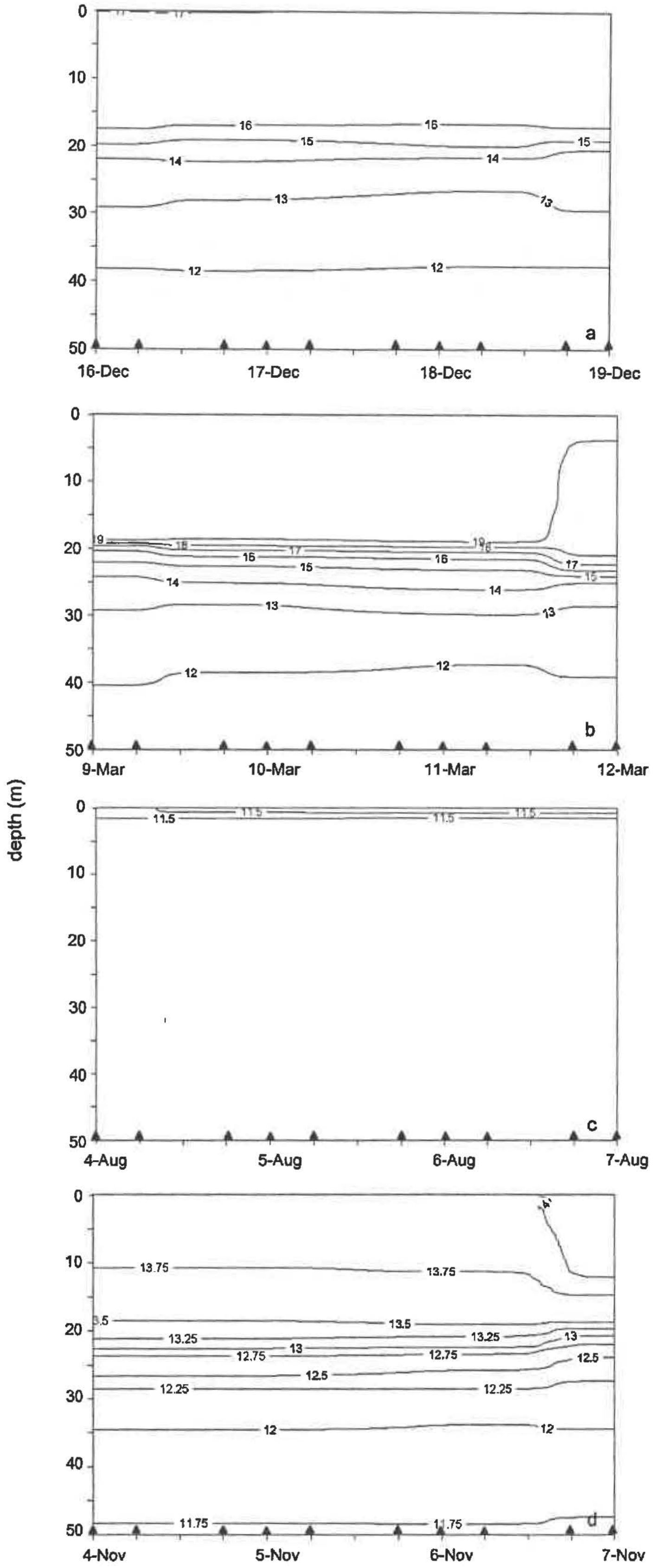

Figure 4.5. Thermal structure of Lake Tarawera at station 5 during (a) 16-19 Dec 2002, (b) 9-12 Mar 2003, (c) 4-7 Aug 2003 and (d) 4-7 Nov 2003.

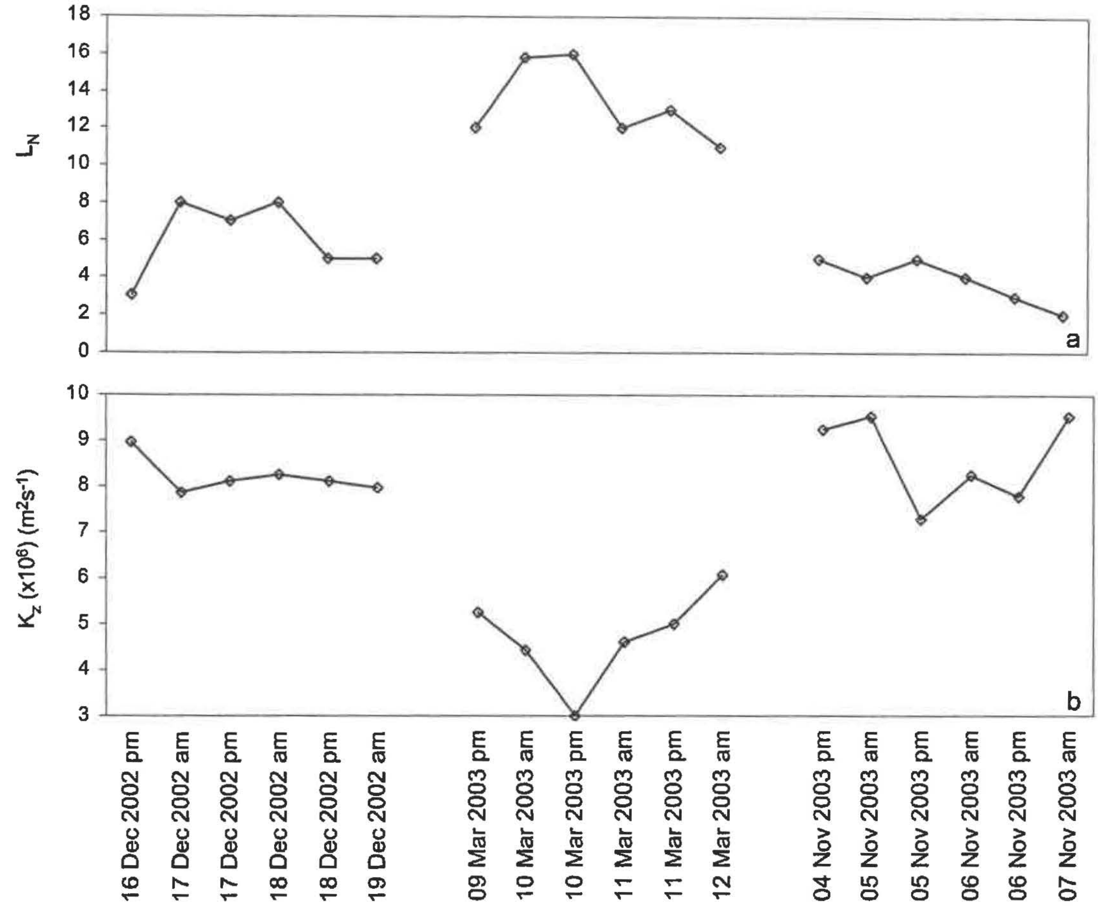

Figure 4.6. Lake Number (L_N) and turbulent diffusion rate (K_Z) calculated at the depth of the thermocline from CTD casts for 16-19 Dec 2002, 9-12 Mar 2003 and 4-7 Nov 2003. Note: K_Z calculations were not performed for August 2003 when $\partial \rho / \partial z$ was negligible.

Light climate

The vertical light attenuation coefficient (K_d) was determined from the slope of the regression of $ln(I(z))$ versus depth, where $I(z)$ is the light intensity at depth z. K_d was significantly higher ($p < 0.05$) at the DCM (mean 0.27 ± standard error 0.03 m^{-1}) than in surface waters (0.15 ± 0.02 m^{-1}) during Nov-Dec 2003 (Fig. 4.7a). In Feb-Mar 2003, during the bloom of *Anabaena circinalis*, K_d increased to 0.24 ± 0.02 m^{-1} in surface waters. The DCM was situated at 1-2 % of surface irradiance in Nov-Dec 2002. In Feb-Mar 2003, when there was high surface phytoplankton biomass, irradiance at the DCM was reduced to ~ 0.1 % of that at the surface. During winter isothermy, the vertical structure of K_d diminished (Fig. 4.7b).

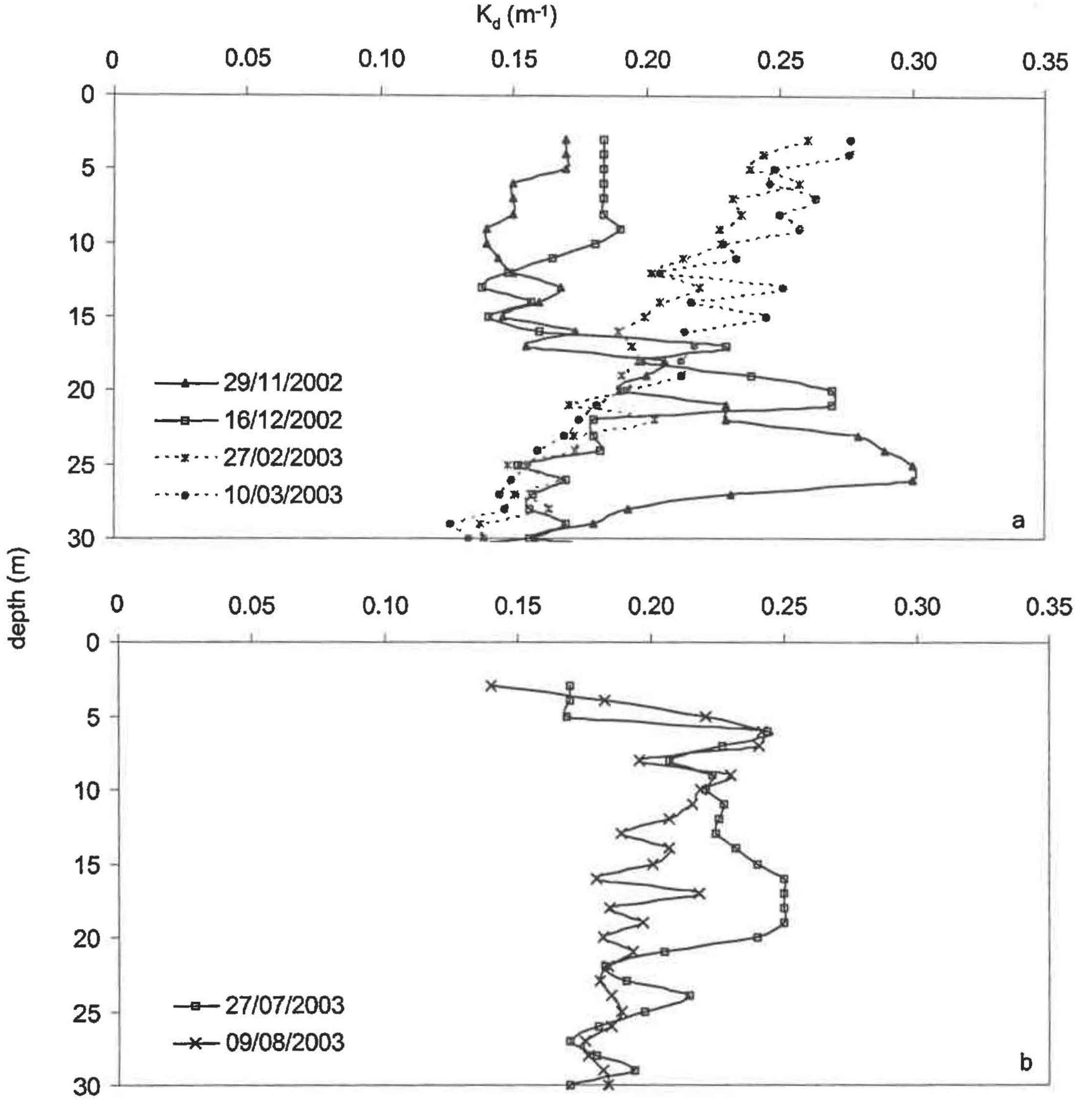

Figure 4.7. Values of the light extinction coefficient, K_d, for (a) Nov 2002-Mar 2003 and (b) Jul-Aug 2003.

The specific vertical attenuation coefficient for phytoplankton, k_c, was determined from the slope of the regression of K_d (m^{-1}) against chlorophyll *a* (mg m^{-3}) for both surface waters and at the DCM (Fig. 4.8). Mean values of K_d within the SML were used to determine surface k_c, and discrete values corresponding to the mid-point of the DCM were used for DCM k_c values. For the SML, k_c during Nov-Dec 2002 was 0.028 m^2 mg chl a^{-1} (Fig. 4.8), whereas the DCM had a higher value of 0.032 m^2 mg chl a^{-1} (Fig. 4.8). The highest value of k_c, 0.039 m^2 mg chl a^{-1} (Fig. 4.8) was recorded in the SML during Feb-Mar 2003, concurrent with the relatively high biomass of *Anabaena* *circinalis*. Testing for homogeneity of the regression slopes showed that the DCM vs SCM slope was not significantly different ($p = 0.06$), indicating that light-capturing efficiency of phytoplankton at the DCM is no different to the SCM. However, there was a significant difference between the regression slopes for the SML and DCM ($p < 0.05$). Over the entire data set, the background attenuation coefficient ($K_{bg,}$), corresponding to the intercept on the attenuation coefficient axis, was 0.13 m^{-1} (Fig. 4.8).

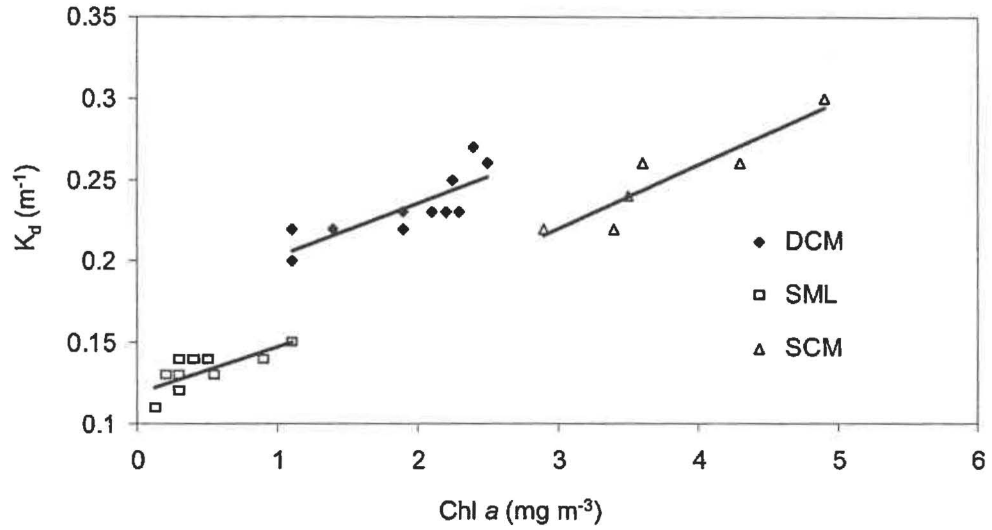

Figure 4.8. K_d (vertical light extinction coefficient) versus chlorophyll *a* at the DCM and in the SML during 16-19 Dec 2002, 4-7 Aug 2003 and 4-7 Nov 2003, and in the SCM during an *Anabaena* 'bloom' in Feb-Mar 2003. The slope of the regressions (all significant at $p < 0.05$) is the value of k_c, the specific vertical light attenuation coefficient for phytoplankton chlorophyll. DCM: $k_c = 0.032$ chl $a + 0.17$, $R^2 = 0.646$; SML: $k_c = 0.028$ chl $a + 0.12$, $R^2 = 0.532$; SCM: $k_c = 0.039$ chl $a + 0.10$, $R^2 = 0.851$.

Nutrient analysis and spiking

Levels of filterable nutrients in Lake Tarawera were relatively low (Table 4.2). In nutrient spiking incubations, phytoplankton biomass and chlorophyll *a* concentrations increased most with addition of PO_4-P, compared with addition of NH_4-N or a combination of both nutrients. Phytoplankton biomass and chlorophyll *a* were 660 ± 175 cells ml^{-1} and 2.1 mg m^{-3} chl *a*, respectively, in the SML samples, and increased significantly ($p < 0.05$) with PO_4-P addition, to 2960 ± 712 cells ml^{-1} and 5.3 mg m^{-3}

chl *a*), suggesting phosphorus limitation of surface phytoplankton. DCM incubations, however, indicated light-limitation rather than nutrient-limitation. The largest increase in biomass compared with control samples was when DCM phytoplankton were incubated in surface waters (z = 3 m) where they were exposed on average to 40 % of surface irradiance. The biomass and chlorophyll *a* increased significantly ($p < 0.05$), from 112 ± 13 cells ml^{-1} and 0.7 mg m^{-3} chl *a* in the control samples to 280 ± 36 cells ml^{-1} and the chl *a* at the higher irradiance level. There was little increase in DCM biomass with additions of PO_4-P, NH_4-N or a combination of these nutrients (10N:1P).

Table 4.2. Nutrient concentrations (mg L^{-1}) (mean) from the SML and DCM for sampling periods Nov-Dec 2002, Mar-Apr 2003, July-Aug 2003 and Oct-Nov 2003.

Date	Depth	n	NO_3-N	NH_4-N	PO_4-P
Nov-Dec 2002	SML	13	0.014	0.033	0.006
	DCM	13	0.012	0.025	0.004
Mar-Apr 2003	SML	16	0.007	0.024	0.014
	DCM	16	0.015	0.031	0.004
Jul-Aug 2003	0 – 15 m	13	0.007	0.035	0.018
Oct-Nov 2003	SML	10	0.017	0.015	0.005
	DCM	10	0.011	0.017	0.004

Modelling vertical distributions of phytoplankton

The first term on the right-hand side of Eq. 5 indicates that specific growth rate at a given depth depends on light intensity. Further additions to account for effects of water temperature and available nutrients can be incorporated as follows:

$$\mu_g = \mu_{\max} \cdot f(T) \cdot \min[f(I), f(P), f(N)] \tag{9}$$

where μ_{max} (day^{-1}) is the maximum growth rate at 20°C in the absence of significant limitation by light or nutrients, and $f(T)$, $f(I)$, $f(P)$ and $f(N)$ represent effect of temperature and limitation by light, phosphorus and nitrogen, respectively (Robson and Hamilton 2004). Equation 6 can now be written as:

$$\frac{\partial \omega}{\partial t} = \mu_g(z)\omega - v\frac{\partial \omega}{\partial z} + K_z\frac{\partial^2 \omega}{\partial z^2} \tag{10}$$

To solve Eq. 10, consider that there are no phytoplankton at any depth, $\omega(z) = 0$. Equation 10 is then reduced to a second-order ordinary differential equation (ODE):

$$\mu_g(z)\omega - v\frac{\partial\omega}{\partial z} + K_z\frac{\partial^2\omega}{\partial z^2} = 0 \tag{11}$$

Equation 11 can be rewritten as two coupled first-order ODEs:

$$\frac{\partial\omega}{\partial z} = \psi \tag{12}$$

and

$$\frac{\partial\psi}{\partial z} = -\frac{1}{K_z}\mu_g(z)\omega + \frac{v}{K_z}\psi \tag{13}$$

Assuming that there is no influx or efflux of phytoplankton at the top or bottom of the water column, and phytoplankton biomass is negligible at the bottom of the water column, the boundary conditions are:

$$v\omega(0) - K_z\frac{\partial\omega}{dz}(0) = 0 \text{ and } v\omega(z_m) - K_z\psi(z_m) = 0, \text{ at } z = 0 \text{ and } z = z_m \tag{14}$$

Starting with an initial condition of $\omega(0) = 1$ and the first boundary condition in Eq. 14, the initial conditions for the simulation for the two ODEs in Eqs 12 and 13 can be defined as:

$$\omega(0) = 1 \qquad \psi(0) = \frac{v}{K_z} \tag{15}$$

Simulations were performed using Matlab® starting from the initial conditions given in Eq. 15, substituting values of K_z and v and μ_g into Eq. 13 and integrating forward in z. The parameter values used in the simulations were chosen to be as realistic as possible and provided the basis of a sensitivity analysis (Table 4.3).

The phytoplankton distribution profiles were divided into five 'Modes' relating to four forcing functions (Table 4.3). The first mode is a surface chlorophyll maximum, SCM; Mode 2, a DCM; Mode 3, a double peak, DP, where the first peak represents a buoyant cyanobacterial assemblage, and the second peak a DCM; Mode 4, a linear vertical distribution of phytoplankton; and Mode 5, an exponential increase with depth. The first forcing function examines the effect of different turbulent diffusion rates on the vertical distribution of phytoplankton. K_Z was varied from 10 to <0.1 cm^2 s^{-1} with a constant sinking rate of 1 m day^{-1} and phytoplankton growth calculated as a function of light. The second function examines changes in sinking rates with a constant turbulent diffusion profile of 0.25 cm^2 s^{-1}. The sinking rates range from positive, 10 m day^{-1}, representing highly buoyant cyanobacterial populations, to -4 m day^{-1}, for fast sinking species. In the third forcing function, the light extinction coefficient in Eq. 9 is increased from 0.1 – 2 m^{-1}, again with a constant turbulent diffusion profile of 0.25 cm^2 s^{-1} and with a phytoplankton sinking rate of 1 m day^{-1}. The fourth forcing function examines phytoplankton distributions relating to different nutrient concentrations, with the same turbulent diffusion and sinking rates as for the third forcing function (0.25 cm^2 s^{-1} and 1 m day^{-1}).

Figure 4.9 demonstrates a range of phytoplankton distribution profiles obtained by numerical simulation. Figure 4.9a shows a uniform vertical profile of phytoplankton biomass (Mode 4) when K_Z is increased to 10 cm^2 s^{-1}. A vertically varying K_Z was used to create a diffusion profile similar to what might occur in a stratified lake, with high K_Z (10 cm^2 s^{-1}) in the SML (0 – 20 m) and benthic boundary layer (30 – 60 m) and an intermediate K_Z (0.25 cm^2 s^{-1}) (21 – 29 m) at the DCM. At intermediate K_Z, phytoplankton growth rates exceed losses from turbulent diffusion and sinking, allowing formation of a DCM (Mode 2). Reducing the turbulent diffusion to < 0.1 cm^2 s^{-1} leads to a profile of exponentially increasing phytoplankton biomass with depth (Mode 5).

Table 4.3. Parameters used in the simulations of Fig. 4.9. K_Z, turbulent diffusion rate ($cm^2\ s^{-1}$); v, sinking rate ($m\ day^{-1}$); K_d, light extinction coefficient (m^{-1}); PO_4-P, soluble reactive phosphorus ($mg\ L^{-1}$). The mode codes are: SCM, surface chlorophyll maximum; DCM, deep chlorophyll maximum; EXP, exponential increase; LIN, linear distribution; DP, double peak.

	Simulation	Forcing function				Mode
		K_z	v	K_d	PO_4-P	
a	1	0.5	-1	0.1	0.001[G]	1 - SCM
	2	10, 0.25[A]	-1	0.1	0.001	2 - DCM
	3	10	-1	0.1	0.001	4 - LIN
	4	<0.1	-1	0.1	0.001	5 - EXP
b	1	0.1	+10, -1[B]	0.1	0.001	3 - DP
	2	0.1	-4[C]	0.1	0.001	4 - LIN
c	1	0.1	-1	0.1[D]	0.001	2 - DCM
	2	0.1	-1	0.2	0.001	2 - DCM
	3	0.1	-1	0.5	0.001	1 - SCM
	4	0.1	-1	1[E]	0.001[F]	1 - SCM
d	1	0.1	-1	0.1	0.1[G]	1 - SCM
	2	0.1	-1	0.1	0.01	2 - DCM
	3	0.1	-1	0.1	0.001 - 0.1[H]	5 - EXP

[A] A value of 10 $cm^2\ s^{-1}$ was assumed in surface mixed layer (0-20 m) and bottom boundary layer (30-60 m) (MacIntyre 1999), 0.25 $cm^2\ s^{-1}$ calculated at thermocline of Lake Tarawera and applied to depths 21-29 m.

[B] Buoyancy of 10 $m\ day^{-1}$ for *Anabaena circinalis* (Brookes et al. 1999) in surface waters (depth 0-4 m). Simulations with a sinking rate of 1 $m\ day^{-1}$ to approximate those observed in this species (Sherman et al. 1998) for depths > 4 m.

[C] Sinking rate of 4 $m\ day^{-1}$ for filaments of *Aulacoseira* spp. (Reynolds 1984).

[D] 0.1 m^{-1} approximates the value of K_d in the SML in the absence of phytoplankton blooms in Lake Tarawera.

[E] K_d of 1 m^{-1} used to approximate nutrient-enriched lake of reduced clarity.

[F] Lower limit of PO_4-P concentrations measured in Lake Tarawera.

[G] Surface waters (0-4 m) enriched with 0.1 $mg\ L^{-1}$ PO_4-P, the concentration used in nutrient-spiking experiments for Lake Tarawera.

[H] Exponential increase in PO_4-P of 0.001 - 0.1 $mg\ L^{-1}$ over the water column depth.

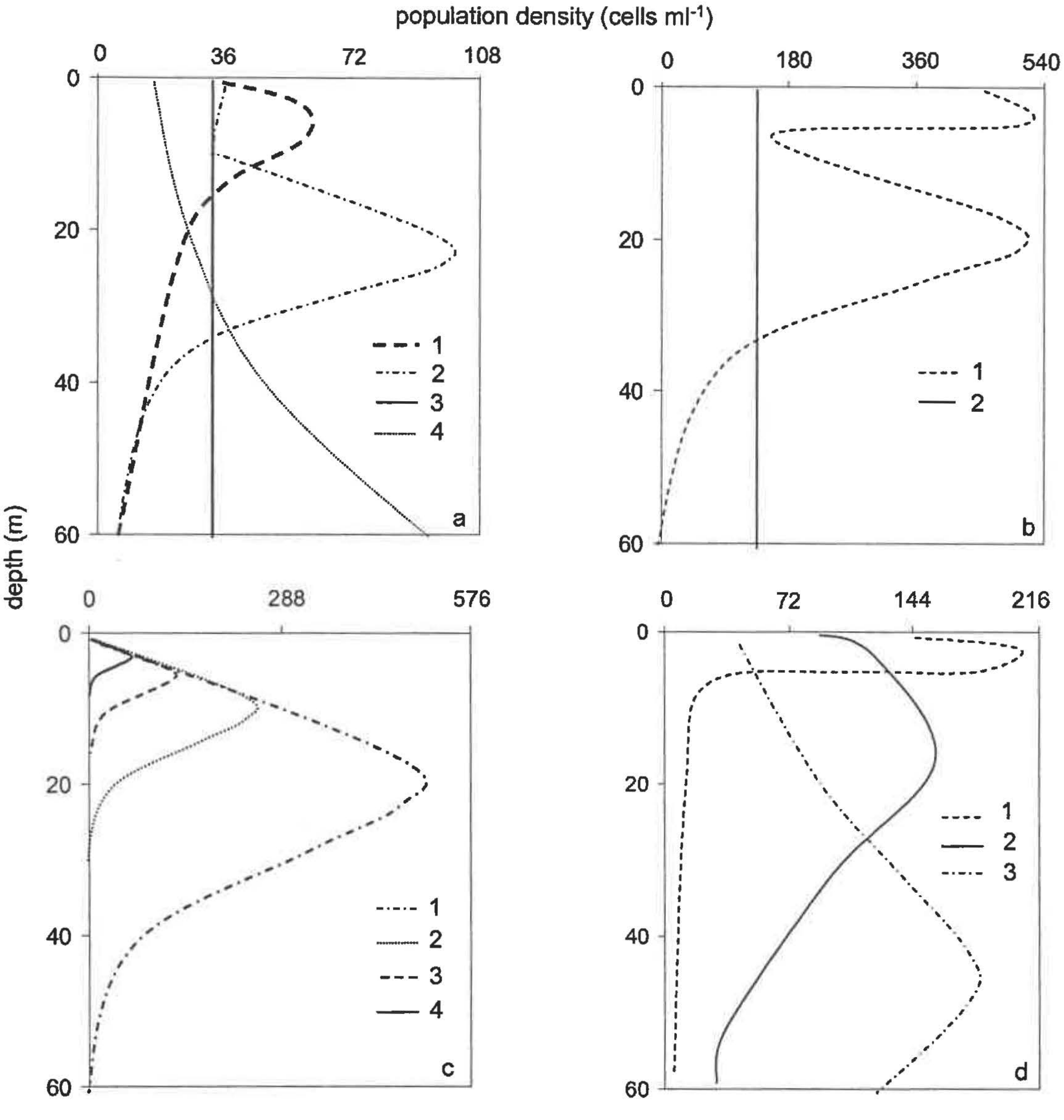

Figure 4.9. Vertical profiles of phytoplankton illustrating five modes of distribution. Parameter values are given in Table 4.3. Distributions were reproduced with variations in (a) K_Z of <0.1 – 10 cm^2 s^{-1} (b) v of +10 to -4 m day^{-1} (c) K_d of 0.1 to 1 m^{-1} (d) PO$_4$-P of 0.001 to 0.1 mg L^{-1}, while other variables were held constant (refer Table 4.3).

In Figure 9b, a SCM (Mode 1) is present when phytoplankton are positively buoyant ($v = +2$ m day^{-1}). A vertically varying v was used in one of the simulations, with $v = +2$ m day^{-1} applied to surface waters (0 – 7 m), to represent buoyant cyanobacterial communities, and $v = -1$m day^{-1} (sinking) applied to deeper waters (> 7 m). The vertically varying regime produces a double peak (Mode 3), with the first peak representing a buoyant cyanobacterial population and the second peak, a DCM. When sinking rate is increased to 4 m day^{-1}, there is no vertical structure in phytoplankton distribution (Mode 4).

Figure 9c demonstrates the effect on phytoplankton profiles of increasing the light extinction coefficient. When K_d was low, 0.1 - 0.5 m^{-1}, a DCM is present (Mode 2), but for $K_d > 0.5$ m^{-1}, the DCM dissipates and peak concentrations are confined to surface waters (Mode 1).

Assuming a half-saturation constant of 0.011 mg L^{-1} for phytoplankton phosphorus uptake (Zohary 2004), if the surface waters are enriched with PO_4-P (from a background concentration of 0.001 mg L^{-1} to 0.1 mg L^{-1}) under vertically constant K_Z of 0.25 cm^2 s^{-1} and phytoplankton sinking at 1 m day^{-1}, the majority of phytoplankton biomass occurs in surface waters (Mode 1) (Fig. 4.9d). A concentration of 0.1 mg L^{-1} was chosen for this simulation as the phytoplankton in the SML in the nutrient-spiking incubation experiment responded strongly to addition of phosphate at this concentration (Table 4.2). With a constant water column nutrient concentration (0.001 mg L^{-1} phosphate) and other parameters identical, there is formation of a DCM (Mode 2). If nutrient concentrations are increased with depth (0.001 – 0.1 mg L^{-1} phosphate), the phytoplankton biomass initially increases exponentially (Mode 5) until light strongly limits growth and biomass decreases with depth.

Zooplankton grazing

The zooplankton assemblages at both the SCM and DCM were dominated by the calanoid copepod *Boeckella* sp., but also included cladocerans *Ceriodaphnia* sp. and *Bosmina* sp., as well as the rotifers *Asplanchna* sp., *Keratella* sp., *Polyarthra* sp. and *Trichocerca* sp. Vertical differences in zooplankton density occurred between the SML and the DCM samples during thermal stratification (Nov 2002 and Mar 2003). Zooplankton biomass was significantly lower ($p < 0.01$) at the DCM (0.03 ±0.02 mg

C L^{-1}) compared with surface waters (0.13 ± 0.07 mg C L^{-1}). At the onset of thermal stratification in Oct 2002, zooplankton biomass was similar in SML and DCM samples (0.14 ± 0.08 mg C L^{-1}). When the lake was fully mixed in Aug 2003, zooplankton biomass from 0-15m depth was similar to that of Oct 2002 (0.14 ± 0.02 mg C L^{-1}). By Nov 2003, there was again a clear distinction in zooplankton biomass between the surface (0.13 ± 0.02 mg C l^{-1}) and the DCM (0.03 ± 0.004 mg C l^{-1}) samples.

The potential impact of zooplankton grazing on phytoplankton was assessed at the DCM using Eq. 7 and a grazing rate of 0.72 g phytoplankton C (g zoop C)$^{-1}$ day^{-1} was applied to equate to zooplankton in the size class > 300 μm, of similar size to those observed in this study and a half saturation constant of 1.4 g phyto C m^{-3} for zooplankton grazing (Griffin et al. 2001). At the DCM the grazing pressure was low, with potential for removal of 0.04 μg chl*a* m^{-3} day^{-1} of the phytoplankton population, i.e., approximately 1 % of the phytoplankton population at the DCM. As the zooplankton assemblages were dominated by large zooplankton (> 300 μm), and microzooplankton comprised only a small percentage of the biomass, the grazing rate and half saturation constant for grazing were obtained from the literature, to equate to zooplankton of similar size. The zooplankton assemblage was dominated by large grazers, i.e., macrozooplankton, some of which may be omnivorous or carnivorous, and the use of a large grazing rate was considered to be an upper limit of the rate of loss of DCM phytoplankton to grazing.

4.5 Discussion

Vertical distribution of phytoplankton

At intermediate rates of vertical turbulent diffusion, phytoplankton growth rates may exceed losses from turbulent diffusion and sinking, resulting in formation of a DCM (Mode 2) (Fig. 4.9a). The formation of the DCM in Lake Tarawera during Nov-Dec 2002 may be attributed to these mechanisms acting so that phytoplankton adapted to low light are able to 'outgrow' losses due to turbulence, settling and grazing. The light levels at the DCM in Lake Tarawera are within the range (c. 1 % of surface light) reported in association with DCMs in other lakes and in the ocean.

Phytoplankton growth rates sufficiently high to sustain a DCM may be associated with elevated nutrient concentrations in the metalimnion and deeper in the water column, with the elevated chlorophyll levels trapping almost all available downwelling light in the DCM (Fahnenstiel and Scavia 1987).

If the sinking rate of phytoplankton is too high, then a DCM cannot exist and phytoplankton will sink to the bottom of the water column. For example, in simulations with v of 4 m day^{-1} and an intermediate K_Z of 0.25 cm^2 s^{-1}, a DCM cannot be supported and there is a Mode 4 distribution. However, a DCM may persist at a moderate sinking rate of 1 m day^{-1} and a K_Z of 0.25 cm^2 s^{-1}. Reductions in phytoplankton sedimentation are believed to be an important mechanism in DCM formation and some diatoms decrease their sinking velocity and achieve near neutral buoyancy under low light at the DCM (Davey and Heaney 1989). The mechanism behind regulation of sinking rate, however, has still to be fully elucidated (Tilman and Kilham 1976; Richardson and Cullen 1995; Reynolds 1997).

Light climate plays an important role in the position and size of the DCM. A shift from a Mode 2 (DCM) to a Mode 1 (SCM) distribution occurred in Lake Tarawera during Feb-Mar 2003 when there were surface blooms of *Anabaena circinalis* which strongly reduced available light and suppressed phytoplankton growth in the metalimnion. Figure 9c clearly illustrates the theoretical effect on the DCM position of increasing the light extinction coefficient due to such an increase in surface biomass. As K_d was increased from 0.1 to 1 m^{-1}, the DCM moved progressively towards the surface, to the point where the simulated DCM was well within the surface mixed layer and would almost certainly have disappeared under natural conditions associated with the high rates of turbulent diffusion in this layer. The simulations demonstrate that the biomass of phytoplankton in the SCM strongly influences availability of light in the DCM, to the point where relatively small changes in SCM biomass have a critical influence on the existence of the DCM.

The change from a Mode 2 to a Mode 1 distribution associated with surface blooms of *Anabaena circinalis* in Feb-Mar 2003 was also reflected in changes in the specific light attenuation coefficient, which varies with composition of the phytoplankton assemblage due to changes in cell size, geometry and physiological state. The diatoms at the DCM in this study have comparable physiological characteristics to Reynolds' (1997) "Association C and D" which comprises diatoms from the genera *Stephanodiscus*, *Asterionella* and *Aulacoseira*, which are often prevalent in low light conditions. Their physiological adaptations, such as increased cellular chlorophyll *a* (Anderson 1969; Shortreed and Stockner 1990; Venrick 1988) enhance the steepness of the cell-specific photosynthetic efficiency, which improves the ability to grow in low light conditions.

With the breakdown of stratification in Lake Tarawera in winter, a linear vertical distribution of phytoplankton was present (Mode 4). Yoshiyama and Nakajima (2002) demonstrated how a continuous increase in the depth of the thermocline, generally associated with a period preceding overturn, causes a 'catastrophic transition' from a subsurface maximum of biomass (i.e., a DCM) to greater biomass in surface waters than deep waters. Thermal stratification in Lake Tarawera follows the classic pattern for temperate warm-monomictic lakes, however, it differs biologically as the maximum phytoplankton biomass occurs during winter isothermy in association with the annual minimum water temperature. Winter mixing may increase the supply of growth limiting nutrients to phytoplankton, which can offset the effects of low light availability and low water temperature; as demonstrated in other lakes of the CVP of North Island, New Zealand (McColl 1972; Vincent 1983).

Some studies of DCMs have indicated that there may be nitrogen or phosphorus limitation of the population (LeBrasseur et al. 1978; Schindler et al. 1980). *In situ* incubation experiments indicated that the DCM in Lake Tarawera is strongly light-limited rather than nutrient-limited. The largest increase in biomass was when DCM phytoplankton were incubated in the surface waters (c. 3 m depth) and thus exposed to higher irradiances (~ 40 % of surface irradiance), producing a Mode 1 distribution (SCM). Similarly, Shortreed and Stockner (1990) found in Sproat Lake, British Columbia, that water transparency and euphotic depth were reduced due to increased phytoplankton biomass in the epilimnion after artificial fertilization; there was a coincident reduction of DCM biomass. A similar simulation case is evident in Fig. 4.9c, where the light extinction coefficient is increased to 1 m^{-1}. A DCM forms at intermediate levels of turbulence but with adequate light a DCM may still be supported in the presence of low nutrient concentrations.

Our simulations showed that 'fertilisation' of surface waters (i.e., SRP increase from 0.001 to 0.1 mg L^{-1}) increased phytoplankton growth rates in the surface mixed layer, resulting in a development of a SCM (Mode 1). This is reflected in Lake Tarawera, where nutrient-spiked incubations of phytoplankton from the SML showed that both biomass and chlorophyll *a* concentrations increased with addition of phosphate. This incubation shows similarities to the Mode 1 distribution, whereby with the addition of nutrients in the surface waters, there is a SCM.

Zooplankton can play an important influence in structuring the DCM The zooplankton assemblage composition in Lake Tarawera generally had low species diversity and was dominated by the calanoid copepod, *Boeckella* sp., in both surface waters and at the DCM. Zooplankton densities were reasonably low and grazing may have had a relatively modest effect on phytoplankton biomass. Howard-Williams et al. (1986) suggested that the cooler water temperatures with depth may influence zooplankton distribution, also likely reducing zooplankton grazing rates with depth.

I used Lake Number and calculations of turbulent diffusion to predict times of increased metalimnetic mixing and thus supply of nutrients to the DCM from deeper waters (MacIntyre et al. 1999). MacIntyre and Romero (2000) showed when $L_N < 5$ there is enhanced metalimnetic mixing. During sampling periods when the DCM was forming (16-19 Dec 2002 and 4-7 Nov 2003), daily values of L_N were often < 5. The higher turbulent diffusion rate at the metalimnion during these periods of low L_N is likely to be important in the re-supply of nutrients to the DCM. New Zealand's maritime climate leads to a depression in seasonal lake temperature ranges relative to the latitude, with relatively cool summer and warm winter temperatures, and deep mixed layers (Green et al. 1987). The relatively deep water column mixing in New Zealand lakes such as Tarawera tends to increase transfer of nutrients from the hypolimnion, but increases the potential for light limitation of both SML and DCM phytoplankton; the DCM in these lakes may be especially vulnerable to any effects of nutrient enrichment that would enhance phytoplankton populations in the surface mixed layer.

Turbulent diffusion in this study was estimated at the depth of the thermocline using Lake number. More direct measurements of turbulence (e.g., using 3-D profilers or temperature microstructure profilers) would provide greater insights into the rates of circulation and vertical and horizontal transports that could affect the variability of the DCM, i.e., effects of boundary mixing and internal waves (MacIntyre et al. 1999). Boundary mixing or interflows could have an effect on DCM variability among sites as enhanced mixing often occurs near lateral boundaries, as internal wave fields interact with sloping edges of a lake. Depending on the bottom slope, internal waves may contribute to instabilities in the temperature profile that can collapse and lead to turbulent mixing. The increased mixing could supply nutrients to a DCM (MacIntyre et al. 1999) and consequently contribute to DCM variability among sites. Interflows may also act to disperse the DCM, although interflows may benefit DCM growth by enhancing nutrient supply. These processes need to be quantified to allow a better understanding of the structure and function of the DCM in Lake Tarawera.

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Chapter 5

Formation of a Deep Chlorophyll Maximum by *Peridinium* cf. *sydneyense* in an oligotrophic New Zealand lake

5.1 Abstract

Vertical and seasonal distributions of phytoplankton biomass were observed for one year in Lake Tikitapu, an oligotrophic lake with maximum depth 27.5 m and area 1.5 km^2. During thermal stratification a deep chlorophyll maximum (DCM) formed at approximately 2-3 % of surface irradiance. The DCM comprised of dinoflagellate species and was dominated by *Peridinium* cf. *sydneyense*. During some periods (April 2003) the depth of the DCM corresponded closely with the thermocline depth but not during others (November 2003). The light level at the DCM was found statistically to be more important than the depth of the thermocline in determining the DCM depth. The width of the DCM was significantly positively correlated ($p < 0.01$) with the metalimnion width. Weaker turbulence in the metalimnion may have assisted *Peridinium* in maintaining its position around its optimal irradiance level. *In situ* incubation experiments provided further evidence for the dominant role of light in regulating the DCM position. Biomass decreased in DCM populations that were incubated at high irradiance (40 % of surface irradiance), suggesting that high irradiance is damaging or inhibitory to non-light adapted populations of *Peridinium* cf. *sydneyense*.

5.2 Introduction

In stratified lakes, light and nutrients are often separated vertically, and flagellated or buoyancy-regulating species capable of exploiting these vertical gradients may have a competitive advantage (Ganf and Oliver 1982; Reynolds 1997). Dinoflagellates are able to develop a discrete horizontal layer, i.e., a deep chlorophyll maximum, in these environments (e.g., Berman and Rodhe 1971; Burns and Mitchell 1974; Kononen et al. 2003). Various attributes of dinoflagellates may contribute to their ability to form

DCM populations at low light levels, including vertical migration (Pick et al. 1984), *in situ* net growth (Fee 1976) and physiological adaptations such as increases in cellular chlorophyll concentration in low light environments (Abbott et al. 1984).

Vertical migration by dinoflagellates may be used to exploit increased nutrient concentrations below the surface mixed layer (Moll and Stoermer 1982; Raven and Richardson 1984) and to utilize light intensities optimal for photosynthesis in the water column (Regel et al. 2004). Diel vertical migration by dinoflagellates has been confirmed by experimental studies which have established a tendency for daytime ascent well into the photic zone to optimise photosynthesis, and nighttime descent to nutrient rich waters (Kamykowski 1995; Levandowski and Kaneta 1987). Migration downwards by dinoflagellates has also been shown to occur in response to high surface irradiances that may be damaging or inhibitory (Passow 1991; Whittington et al. 2000), though occasionally migration does not occur at all (Smayda 1997). Water column turbulence also plays a key role in redistributing water column nutrients and in regulating DCM formation and migration directly by negating the swimming capabilities of dinoflagellates (e.g. Margalef 1978; Smayda 1997).

In Lake Tikitapu the formation of a DCM dominated by *Peridinium* cf. *sydneyense* (Playf.) Thom. during spring/summer of 2002 and 2003 provided an opportunity to study the formation and dynamics of this DCM population. The primary hypothesis of this study was that the DCM position is closely linked with the depth of the thermocline, and the corresponding availability of light and nutrients at the depth of the DCM. A further objective was to quantify how the DCM varied diurnally and between seasons in relation to thermal stratification.

5.3 Methods

Lake Tikitapu (176°21' E, 38°12' S) is a warm monomictic, oligotrophic lake on the Central Volcanic Plateau (CVP) of North Island, New Zealand (Fig. 5.1). The lake has an area of 1.5 km^2, maximum depth of 27.5 m and mean depth of 18 m. Sampling was conducted at one sampling station near the centre of the lake at a depth of 25 m (Fig. 5.1).

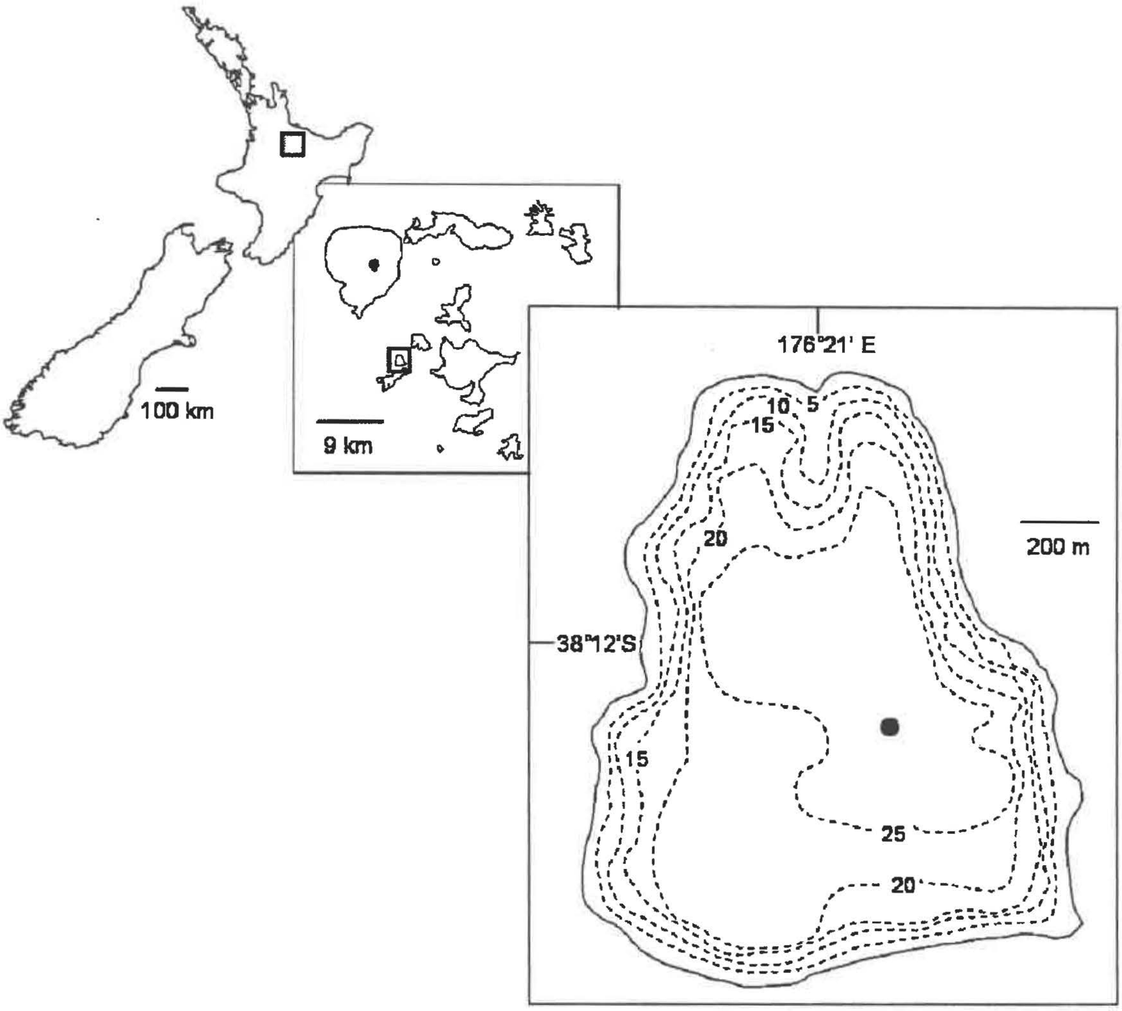

Figure 5.1. Location of Lake Tikitapu in North Island, New Zealand, amongst lakes of the Rotorua district (first inset) and showing the sampling site, bathymetry (m) and sampling station (●) (second inset).

Lake Tikitapu was sampled once a week over three weeks in November 2002 (late spring), March 2003 (late summer), July 2003 (winter) and October 2003 (early spring), and four times daily for one week during December 2002, April 2003, August 2003 and November 2003. A Seabird Electronics 19plus Seacat CTD Profiler was used to resolve the depth (z) variation of chlorophyll-fluorescence (F), temperature (T), density (ρ) and photosynthetically available radiation (PAR). To reduce the effect of high irradiance leading to quenching of fluorescence in surface waters, CTD casts were performed at 0600 h, 1800 h and 2400 h, as well as at 1200 h.

Chlorophyll fluorescence was calibrated against acetone extracted chlorophyll *a* (Strickland and Parsons 1972) from GF/C-filtered samples collected simultaneously with fluorescence profiles. Calibrations were performed for samples collected at both the DCM and SML.

Odyssey temperature loggers (Dataflow Systems Ltd) were set at fixed water depths of 0, 6, 12, 15, 17, 20 and 22 m, to record temperature at 10-minute intervals. Depth-integrated samples (0-12 m), corresponding approximately to the vertical extent of the surface mixed layer (SML), were collected with a hose pipe for determination of filterable nutrients (0.45 µm GF/C-filtered) and chlorophyll *a*, and for phytoplankton enumeration. Filterable nutrient samples were stored on ice and deep frozen upon return to the laboratory, before analysis for ammonium (NH_4), oxidised nitrogen (NO_x), and reactive phosphorus (SRP) with a Lachat Instruments flow injection analyser using standard methods (Zellweger Analytics 2000).

Discrete samples of the DCM, located at the sub-surface peak of chlorophyll-fluorescence, were collected with a diaphragm pump with a specifically designed intake for minimising vertical dispersion. During July and August 2003, when fluorescence profiles were relatively uniform, discrete measurements of the DCM were not made. Climate data (wind speed and irradiance) were obtained from Rotorua Airport climate station, 9 km north of the lake.

Phytoplankton samples were preserved with 2 % Lugol's solution and cell counts were conducted using the sedimentation technique of Utermöhl (1958). A minimum of 400 phytoplankton units, cells, colonies or filaments was counted for each sample, and 20-40 individuals of each taxa were measured. Phytoplankton biomass was approximated using the closest geometrical shape for each algal unit (Hillebrand et al. 1999), and was expressed as carbon concentration (mg C m^{-3}) using cell counts together with carbon-cell volume regressions of Menden-Deuer and Lessard (2000).

Thermocline and metalimnion depths were defined according to Hoare and Spigel (1987), using temperature measurements averaged to 0.5 m vertical intervals. The position of the thermocline depth is where $d\rho/dz$ = minimum, and the limits of the metalimnion where $d^2\rho/dz^2 = 0$. The limits of the DCM were similarly defined from chlorophyll-fluorescence as $d^2F/dz^2 = 0$ and the mid-point of the DCM as dF/dz = minimum.

Nutrient and light limitation experiments

In situ nutrient spiking incubations were performed on SML and DCM phytoplankton to provide information on growth limitation by nutrients and light. Unfiltered depth-integrated samples (0-12 m) of the SML and samples taken discretely at the DCM were placed into 3L PET® bottles. Duplicate bottles were enriched with ammonium chloride (NH_4Cl), potassium dihydrogen phosphate (KH_2PO_4) or a combination of both nutrients to a final concentration of 1 mg L^{-1} NH_4-N and/or 0.1 mg L^{-1} PO_4-P. The bottles were incubated either near the lake surface (c. 2 m) or at the depth of the DCM (c. 15 m) for a 5 day period. Control bottles containing no added nutrients were incubated at both depths. Samples from the DCM were also incubated in surface waters to determine the effect of exposure to higher irradiances (40 % surface irradiance). After 5 days phytoplankton biomass was enumerated in the treatments using the methods described above.

5.4 Results

Phytoplankton distributions

Peridinium cf. *sydneyense* was the dominant species of the DCM assemblage in Lake Tikitapu. The SML contained a more diverse assemblage comprised of desmids *Mougeotia* sp., *Staurastrum* spp. and *Staurodesmus* spp., a chrysophyte, *Dinobryon cylindricum*, as well as *Peridinium* cf. *sydneyense*. Phytoplankton biomass at the DCM ranged between 201 mg C m^{-3} (October 2003) and 407 mg C m^{-3} (March 2003) over the sampling period from November 2002 to November 2003 (Fig. 5.2). Biomass was considerably lower in the SML, ranging from 63 mg C m^{-3} in November 2002 to 90 mg C m^{-3} in November 2003. Under vertically mixed conditions in July-August 2003, phytoplankton distributions were relatively uniform throughout the water column and biomass in the 0 - 12 m sample was c. 300 mg C m^{-3}.

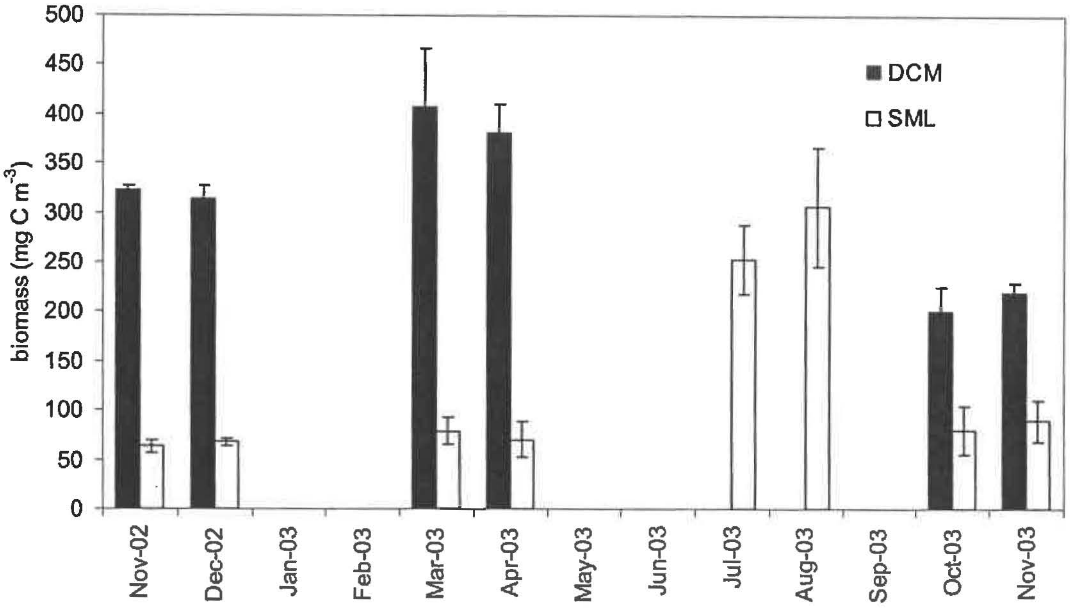

Figure 5.2. Phytoplankton biomass (mg C m^{-3}) (± SD) at the DCM and in the SML (0-12 m). Values are means for weekly interval samples taken three times in November 2002, March, July and October 2003, and for the intensive one-week sampling in December 2002, April 2003 and August 2003.

Phytoplankton biomass was significantly higher ($p < 0.01$) at the DCM than in the SML in all sampling periods except during winter isothermy. Carbon:chlorophyll (C:Chl) ratios were significantly higher ($p < 0.05$) in the SML (mean = 89) than at the DCM (mean = 64) for sampling periods when the DCM was present (December 2002, April and November 2003) (Table 5.1).

Table 5.1. Seasonal mean ratios of C:Chl (± SD) for the surface mixed layer (SML) and deep chlorophyll maximum (DCM), and % PAR at the DCM (± SD). There was no DCM is August 2003.

Variable	Dec. 2002	Apr. 2003	Aug. 2003	Nov. 2003
C:Chl (SML)	88 ±6	87 ±2	87 ±4	89 ±3
C:Chl (DCM)	61 ±3	64 ±4		59 ±2
% PAR (DCM)	3.0 ±0.29	2.7 ±0.20		2.4 ±0.15

Thermal structure and fluorescence profiles

Lake Tikitapu was thermally stratified in December (summer) 2002, and the thermocline (i.e. $d\rho / dz =$ minimum) was between 14 and 15 m (Fig. 5.3a), with a metalimnion width of approximately 9 m. By April (autumn) 2003 stratification was more pronounced, with a metalimnion width of 5 m and the thermocline situated at 15 m (Fig. 5.3b). The lake was isothermal in August 2003 (winter) (Fig. 5.3c). By November 2003 the DCM had re-established and the thermocline was between 11 and 12 m (Fig. 5.3d).

Chlorophyll fluorescence profiles for the sampling periods 9 to 12 Dec 2002 (Fig. 5.3e) and 3 to 5 April 2003 (Fig. 5.3f), indicate a DCM between 15 and 16m. The depth of the DCM coincided closely with that of the metalimnion (Figs. 5.3a and 5.3b) during December and April 2003. Between July and August 2003, there was negligible vertical structure of fluorescence (Fig. 5.3g). The DCM had reformed by 12 to 14 November 2003, at a depth of approximately 16 m (Fig. 5.3h) which was below the thermocline depth (Fig. 5.3d).

The DCM was consistently at a depth equating to 2-3 % of surface irradiance (Table 5.1) and during some periods coincided closely with the thermocline depth (April 2003) but not in others (November 2003). Regression analysis was used resolve which variable; the depth of the thermocline or the light level at the DCM, was most closely related to the position of the DCM. The depth of the midpoint DCM was significantly related to the 2 % light level ($r^2 = 0.65$, $p < 0.01$) and also to the depth of the thermocline ($r^2 = 0.54$ $p < 0.01$). The depth of the 2 % light level was, however, related to the depth of the thermocline ($r^2 = 24.1$, $p < 0.001$). A stepwise multiple regression indicated that thermocline depth explained only an additional 2 % of the variation in DCM depth above that explained by the 2 % light level, and that thermocline depth was significant only at $p < 0.1$. A time series plot of DCM depth, 2 % light depth and thermocline depth provided further insights into the role of stratification and light in the DCM position (Fig. 5.4). In November-December 2002, the depth ranges of the DCM and 2 % light level were similar (15 – 17 m), whereas the thermocline depth range was shallower (10.5 – 13.5 m).

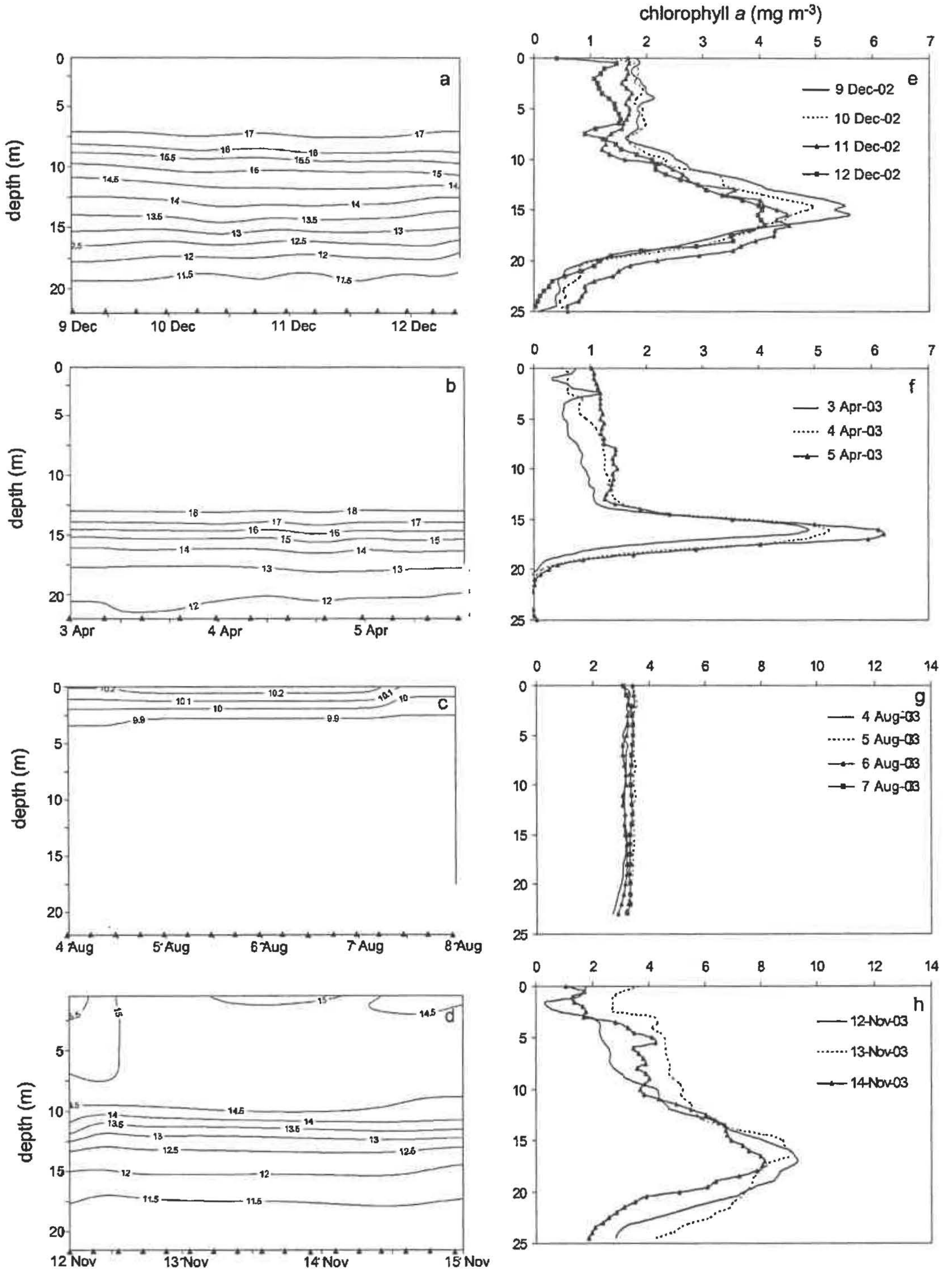

Figure 5.3. Thermal structure (a – d) and vertical profiles of fluorescence (calibrated to chlorophyll *a*) (e – h) in Lake Tikitapu during the sampling periods 9 -12 December 2002, 3 - 5 April 2003, 4-8 August 2003 and 12-15 November 2003.

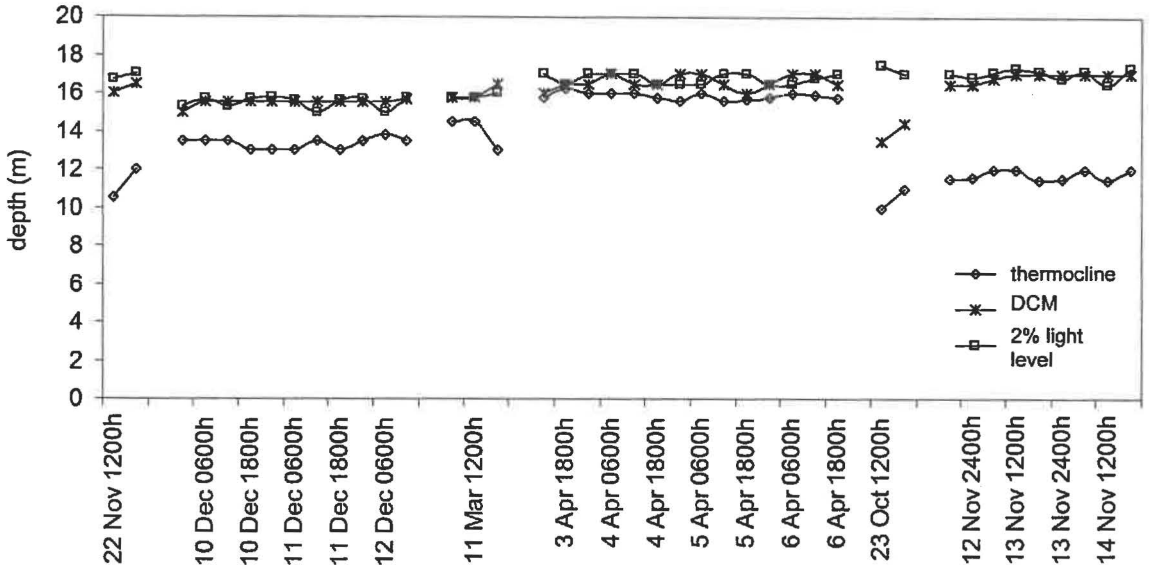

Figure 5.4. Time series plot of thermocline depth, DCM depth and depth of the 2 % light level during all sampling periods in Lake Tikitapu.

In April 2003 the three variables were located at similar depths (15.6 – 17 m). By November 2003 the positions were similar to those of November-December 2003; the depths of the DCM and 2 % light levels were similar, but the thermocline depth was higher in the water column.

The average DCM width ($d^2F/dz^2 = 0$) was 5 m in December 2002 but by April 2003 it had contracted to only 2 m (Fig. 5.5). In November 2003, after winter isothermy, the DCM extended over 10 m. Linear regression analysis indicated that the DCM width was closely related to the metalimnion width ($r^2 = 0.89$, $p < 0.01$).

To determine if there was diurnal vertical migration of phytoplankton in the DCM, chlorophyll-fluorescence casts were performed four times over a 24-hour period during the weekly sampling periods of December 2002, April and November 2003) and over a 48 hour period on 11-12 December 2002. There was no evidence of vertical migration on 11-12 December 2002 (Fig. 5.6), nor for any of the other intensive sampling periods.

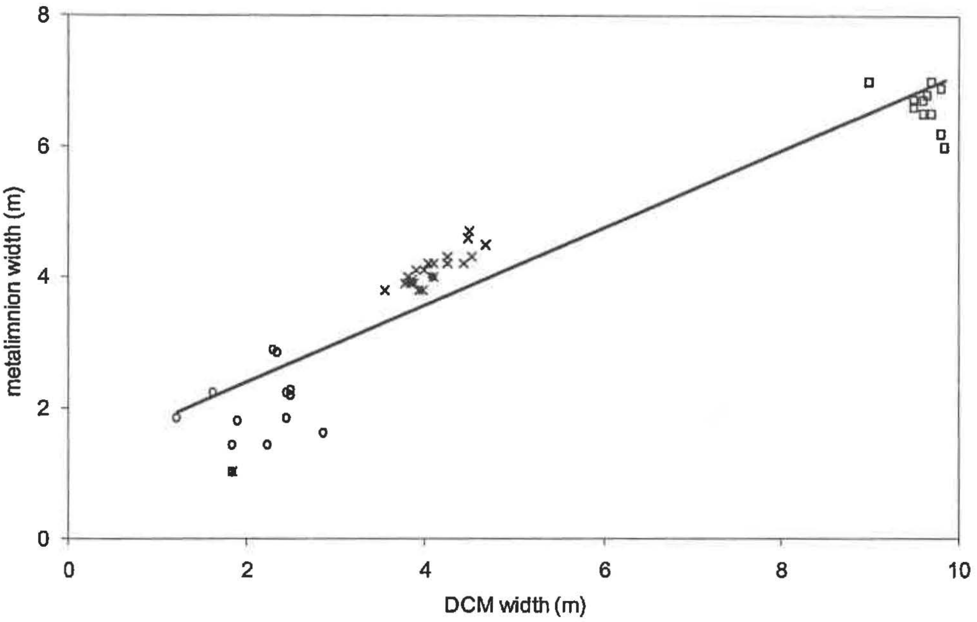

Figure 5.5. Metalimnion width vs DCM width during the sampling periods where a DCM was present through November and December 2002 (○), March and April 2003 (×), and October and November 2003 (□). ($r^2 = 0.89$, $p < 0.01$).

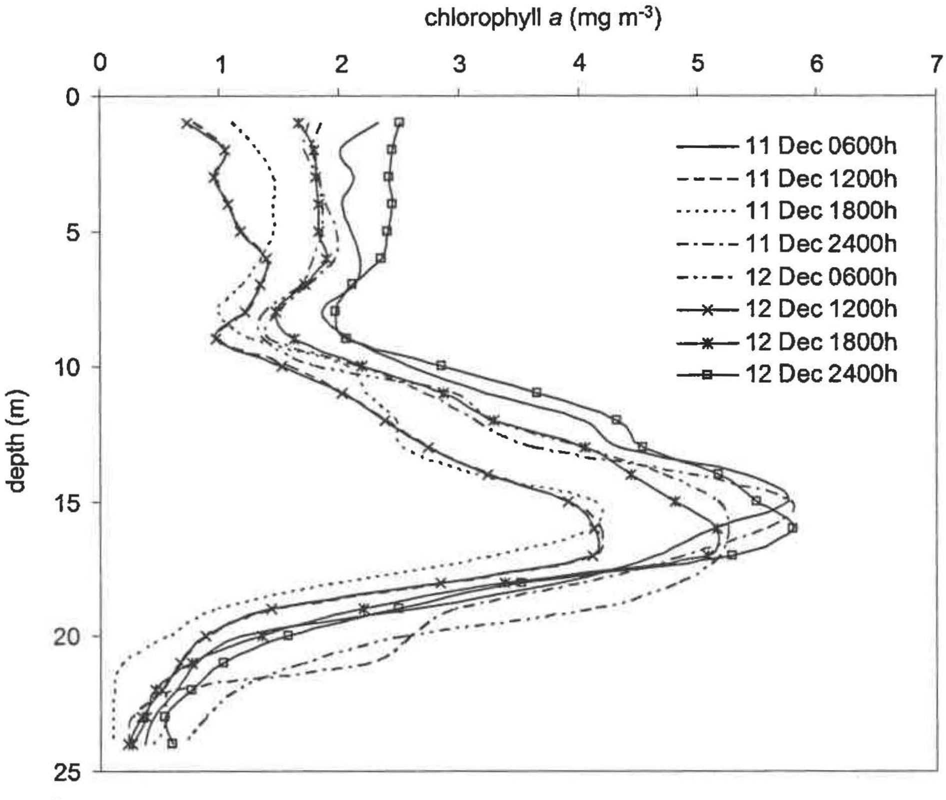

Figure 5.6. Chlorophyll *a* profiles on 11-12 December 2002 performed four times a day over a 48 hour period.

Light climate

The vertical light attenuation coefficient (K_d) was determined from the slope of the regression of $ln(I(z))$ versus depth, where $I(z)$ is the light intensity at depth z. During sampling periods when a DCM was present (November 2002 to April 2003, and October to November 2003), K_d was higher at the DCM than in the SML (Fig. 5.7). The increase in K_d at the DCM is illustrated in Fig. 5.7 for periods in December 2002, April 2003 and November 2003. In winter (July – August 2003), when the lake was well mixed, there was negligible vertical structure of K_d.

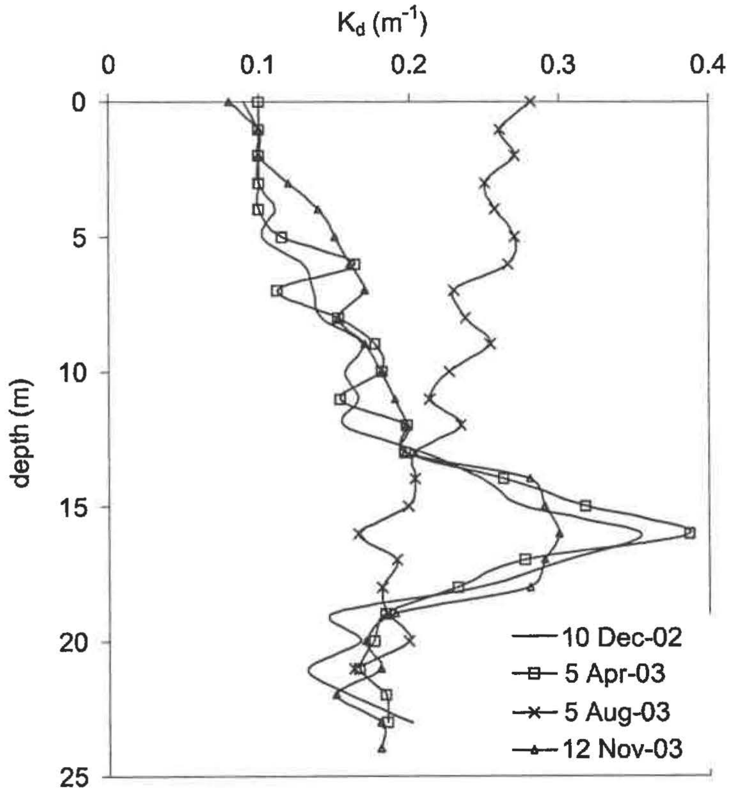

Figure 5.7. Vertical variation in the light extinction coefficient, K_d, on 10 December 2002, 5 April 2003, 5 August 2003 and 12 November 2003.

Nutrients

Levels of filterable nutrients in Lake Tikitapu were relatively low, with little difference in concentration between the SML and DCM. For stratified periods (December 2002 to April 2003, and October to November 2003), mean concentrations (n = 32) in the SML were 1.6 ± 1.2 $\mu g\ L^{-1}$ for filterable reactive phosphorus (SRP), 14

± 3 µg L^{-1} for ammonium (NH_4) and 17 ± 2 µg L^{-1} for oxidised nitrogen species. At the DCM during the same time periods (n = 32), SRP was 1.5± 0.9 µg L^{-1}, NH_4 was 15 ± 2 µg L^{-1} and NO_x was 17 ± 2 µg L^{-1}.

Five-day incubations were performed to examine potential for light or nutrient limitation of phytoplankton in the SML and at the DCM. Phytoplankton biomass was significantly higher ($p < 0.05$) at 323 ± 20 mg C m^{-3} in DCM samples with the addition of 10N:1P compared with control samples at 176 ± 5 mg C m^{-3} (Table 5.2). There was a reduced response of DCM biomass in incubations with individual additions of NH_4-N (215 ± 30 mg C m^{-3}) and PO_4-P (194 ± 15 mg C m^{-3}) and these increases were not statistically significant ($p > 0.05$). When DCM samples were incubated at a depth of 2 m, corresponding to c. 40 % of surface irradiance, biomass declined significantly ($p < 0.05$) to 98 ± 7 mg C m^{-3} compared with the control (176 ± 5 mg C m^{-3} as above). The response of SML phytoplankton biomass to additions of NH_4-N, PO_4-P, a combination of these nutrients (10N:1P) or incubation at the depth of the DCM was not significantly different from the control.

Table 5.2. Cell densities (cells ml^{-1}, ± standard deviation) for five-day *in situ* incubations of SML and DCM phytoplankton. Control had no nutrient addition, +NH_4-N had addition of 1 mg L^{-1} of NH_4-N, +PO_4-P had addition of 0.1 mg L^{-1} of PO_4-P, +10N:1P had additions of both NH_4-N at 1 mg L^{-1} and PO_4-P at 0.1 mg L^{-1}. $z_{Surface}$ was a DCM sample incubated at the lake surface (c. 2 m) and z_{DCM} was incubated in the region of the DCM (c. 15 m). Significant differences ($p < 0.05$) of cell counts in test samples from those of controls are denoted by *.

Treatment	DCM	SML
Control	176 ± 5	60 ± 5
+NH_4-N	215 ± 30	55 ± 10
+PO_4-P	194 ± 15	58 ± 8
+10N:1P	323 ± 20^*	62 ± 5
$z_{Surface}$	98 ± 7^*	-
z_{DCM}	-	30 ± 11

5.5 Discussion

Deep chlorophyll maxima are commonly located in the metalimnion, often near the thermocline or nutricline (Steele and Yentsch 1960), and frequently around a depth where irradiance is 1 % of that at the water surface. The DCM in Lake Tikitapu was present at high irradiance levels (2 to 3 % of surface irradiance) relative to other studies in which the DCM was present at depths of 1 % of surface irradiance (e.g., Pick et al. 1984; Perez et al. 2002). There was little evidence to indicate that DCM phytoplankton took advantage of nutrients diffusing upwards from below the thermocline (cf. Steele and Yentsch 1960; Kiefer and Kremer 1981) as nutrient concentrations were not significantly different between the SML and DCM. Nevertheless there was a significant growth response to combined additions of N and P for *in situ* bioassays of DCM phytoplankton.

The depth of the DCM was most strongly correlated with the depth where light was 2 % of the surface, and less so with the depth of the thermocline, though the 2 % light depth and thermocline depth were significantly inter-related. Figure 5.4 provides arguably the most telling evidence, however, that light was the primary driver of vertical position of the DCM, as during December 2002 and November 2003 there was a noticeable departure of thermocline depth from both the 2 % light depth and the DCM depth. While light strongly regulates the position of DCM phytoplankton in Lake Tikitapu, presence of a metalimnion is also a prerequisite in allowing cells to utilise their locomotory capacity to overcome turbulence that would otherwise randomly redistribute them through a turbulent mixed layer. Studies on the physiology of *Peridinium* cf. *sydneyense* are needed to provide further insight into the migratory capabilities of this species.

Several studies (Passow 1991; Whittington et al. 2000) have shown that some dinoflagellate species migrate downwards to escape inhibiting irradiances in near–surface waters. Migration to the low light environment at the DCM may not hinder growth of phytoplankton in the DCM substantially, however, and several studies have shown that many dinoflagellate genera have low light requirements to achieve their maximum photosynthetic rate (Reynolds 1997) and that compensation depth is greater than that of many other taxa (Langdon 1993). Further evidence for light inhibition influencing DCM position was provided in this study by displacement bioassays in which DCM phytoplankton biomass decreased significantly in incubations at higher irradiances typical of the surface mixed layer.

There was no evidence of vertical migration by dinoflagellates at the DCM in Lake Tikitapu. Migration demands an expenditure of energy, and it is plausible that investiture in greater light capture (i.e., higher chlorophyll *a* per unit biomass) may yield greater energy efficiency than motility for *Peridinium.* Increases in chlorophyll *a* per unit biomass are common in DCM phytoplankton (Fee 1976; Kiefer et al. 1976) though water column biomass is not necessarily maximal, as is the case in Lake Tikitapu.

The vertical spread of the DCM was positively correlated with the intensity of stratification denoted by the vertical width of the metalimnion. This observation suggests that modest levels of turbulence are sufficient to overcome the migratory capabilities of *Peridinium* cf. *sydneyense* or that in Lake Tikitapu this phytoplankter is prepared to trade variability in vertical position against the energy expenditure to maintain a highly discrete depth range under more weakly stratified conditions. It is also possible that *Peridinium* cf. *sydneyense* has only limited swimming capacity and that the metalimnion provides a low turbulence environment which aids this species in maintaining its vertical position close to optimal light levels.

It is not known whether mixotrophy is important in the nutrition of dinoflagellates in Lake Tikitapu though it is increasingly recognised as important to different species of dinoflagellates (Hansen 1998). Analyses by Broekhuizen (1999) suggest that less motile species may indulge in mixotrophy to supplement their energy resources in low light environments, and that vertical migration is only beneficial to fast swimming species that are not so prone to disruption by turbulence (Crawford and Purdie 1992). While these observations suggest that neither the environment nor the species of phytoplankton in Lake Tikitapu should promote heterotrophy, it should still be considered in fully evaluating the nutrition of phytoplankton in the DCM, as mixotrophy could offset inadequacy of light or nutrients for would shift the nutritional status of the DCM from autotrophy to mixotrophic production.

Other species of *Peridinium*, and dinoflagellate genera in general, may have large amplitudes of vertical migration (Talling 1971; Regel et al. 2004), particularly compared with the species in Lake Tikitapu. The maximum swimming velocity of *Peridinium cinctum* in Torrens Lake ($z_{max} = 6$ m) was equivalent to 46 m day^{-1} (Regel et al. 2004), and swimming velocities of 14 to 23 m day^{-1} have been reported for dinoflagellates of similar size (Whittington et al. 2000). The large vertical migrations reported by Regel et al. (2004) and Whittington et al. (2000) were observed in smaller systems with low wind speeds and quiescent water columns, i.e., lower turbulence. Unlike diatoms, strong vertical mixing can be detrimental to dinoflagellate growth as it can overcome their swimming efforts, cause physical damage and impair physiological function (Pollingher and Zemal 1981; Thomas and Gibson 1990). Though some large species of dinoflagellates, such as *Peridinium gatunense*, form blooms and perform vertical migrations in large lakes such as Lake Kinneret (Viner-Mozzini 2003), the widespread appearance of smaller *Peridinium* species in environments with low turbulence, commonly smaller lakes, suggests a close interaction of light and turbulence regulation of DCM development.

5.6 References

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Chapter 6

Phytoplankton assemblage composition in North Island lakes of New Zealand: is trophic state, mixing, or light climate more important?

6.1 Abstract

Relationships between phytoplankton assemblage composition and lake trophic state, mixing regime and light climate were investigated in 40 North Island, New Zealand, lakes. The hypothesis was tested that mixing regime is more important than trophic state or light climate in determining the composition of phytoplankton assemblages, which were represented as presence/absence of cyanobacteria and diatom genera. Mixing regime, characterised as a function of lake size (Davies-Colley 1998), more accurately predicted summer phytoplankton composition than indices related to trophic state or light regime. Analysis of similarities indicated distinct differences in phytoplankton assemblage composition between mixed lakes and those that intermittently or periodically stratify. In mixed lakes a greater variety of cyanobacteria genera than diatom genera were recorded compared with lakes that stratify stably in summer. Conversely, relatively high numbers of diatom to cyanobacteria genera were found in lakes that stratify compared with mixed lakes. Lakes with different trophic states but similar mixing regimes shared very similar summer phytoplankton assemblages. None of the three variables tested was a good predictor of winter phytoplankton composition. While phytoplankton biomass may be regulated to a large extent by nutrient status, this study has shown that mixing regime plays a more important role in regulating phytoplankton composition than either nutrient status or light climate.

6.2 Introduction

Phytoplankton ecologists have long noted that composition of taxa changes along trophic gradients. For example, it is generally accepted that cyanobacteria taxa dominate the assemblage in eutrophic conditions (e.g., Pridmore and Etheredge 1987; Reynolds 1998). Physical processes also influence phytoplankton composition, with buoyant cyanobacteria often dominating biomass when lakes stratify or if turbulence is weak, while negatively buoyant diatoms dominate at times of high turbulence often associated with winter mixing in dimictic or warm monomictic lakes (e.g., Chorus and Schlag 1993; Huisman et al. 2004). It follows that during summer, when some lakes stratify and others are regularly or intermittently mixed, phytoplankton assemblage composition may be strongly influenced by factors related to mixing, and not trophic state. Indeed, the supposition that phytoplankton assemblage composition is related to trophic state may be partly an artefact related to the frequent or continuous mixing of shallow lakes that tend to have higher trophic status compared with deeper lakes that stratify and tend to be oligotrophic (Tilzer 1990).

I tested the hypothesis that mixing regime, rather than trophic state or light climate, is the primary determinant of dissimilarity in phytoplankton composition among North Island lakes of New Zealand. Phytoplankton composition was assessed using presence/absence data of diatom and cyanobacteria identified to genus level; I examined only assemblage 'composition' of phytoplankton, not abundance or biomass. Only cyanobacteria and diatom genera were used in the analysis as they are considered to be good indicators of trophic state (Rawson 1956; McColl 1972; Flint 1975). Presence of other groups, e.g., chrysophytes, may be indicative of oligotrophic lakes (Willen 2000), but these groups tended to be less well represented amongst our phytoplankton assemblages and were not assessed.

6.3 Methods

Samples were collected from North Island lakes (Table 6.1) once during summer (January - February) and once during winter (July - August), in 2002.

Table 6.1. List of lakes sampled, with key to numbers (Lake) for MDS plots.

n	Lake	*n*	Lake	*n*	Lake	*n*	Lake
1	Kai-iwi	11	Rotoehu	21	Okataina	31	Karapiro
2	Taharoa	12	Rotoiti	22	Taupo	32	Waipapa
3	Waikere (Nthland)	13	Rotorua	23	Waahi	33	Ohakuri
4	Ototoa	14	Okareka	24	Rotokauri	34	Rotorangi
5	Kereta	15	Tikitapu	25	Rotoroa	35	Waikaremoana
6	Kuwakatai	16	Tarawera	26	Rotomanuka	36	Tutira
7	Wainamu	17	Rotoma	27	Rotopiko	37	Horowhenua
8	Spectacle	18	Rotomahana	28	Ngaroto	38	Wairarapa
9	Tomarata	19	Rerewhakaaitu	29	Waikare	39	Pukepuke
10	Pupuke	20	Okaro	30	Maratoto	40	Waitawa

I was restricted to only two samples per year, mostly near the deepest point of the lake, as existing sampling programs governed the collection frequency for many lakes. Phytoplankton samples were collected either from surface waters (depth ≈ 0.2 m) or from depth-integrated samples of the surface mixed layer. Samples were preserved with 2 % Lugol's iodine immediately upon collection, and diatoms and cyanobacteria were identified to genus level using standard taxonomic texts, e.g., Pridmore and Hewitt (1982). A minimum of 400 algal units, cells, colonies or filaments was counted for each sample. One algal cell was required in a sample to constitute a positive identification of 'presence'. Lakes were divided into three trophic states (oligotrophic, mesotrophic, eutrophic) based on total phosphorus (TP), total nitrogen (TN), Secchi depth and chlorophyll *a* measurements using the guidelines of Burns et al. (2000), or trophic state was estimated based on historical data using the method of Burns et al. (2000). Secchi depth and concentrations of chlorophyll *a* and nutrients were determined using standard protocols. Although Secchi depth is one of the variables used to define lake trophic state (Burns et al. 2000), its influence is small and therefore does not overlap greatly with the index used in this study to quantify light regime.

As profiles of water column temperature were not taken for many of the lakes, mixing depth was estimated using morphometric data (Davies-Colley 1998). The mixing regime in each lake was characterised by the ratio of estimated epilimnion depth, $\hat{E}$, to maximum water depth, z_m ($\hat{E}/z_m$). Values of $\hat{E}/z_m$ were taken directly from Davies-Colley (1988) or were estimated indirectly from tabulated values of z_m (Livingston et al. 1986; Viner 1987; Davies-Colley 1988) and with $\hat{E}$ calculated as follows (Davies-Colley 1988):

$$\hat{E} = 7.69 f^{0.463} \quad (r^2 = 0.940) \tag{1}$$

where f is the mean fetch length (m), which is in turn related to lake area (m^2), A:

$$f = A^{0.5} \tag{2}$$

Lakes with $\hat{E}/z_m < 0.5$ have been classified as having an annual period of "stable stratification", lakes with $0.5 < \hat{E}/z_m < 2$ as having "intermittent stratification", and those with $\hat{E}/z_m > 2$ as "mixed" (Davies-Colley 1988).

The vertically integrated percentage of surface photosynthetically available radiation (PAR) that phytoplankton are exposed to in the mixed layer of each lake, $E_{average}$, was quantified as:

$$E_{average} = 100\frac{1-e^{-K_d z}}{K_d z} \tag{3}$$

where z is either the depth of the surface mixed layer in stratified lakes or the lake depth in mixed lakes, and K_d is the light extinction coefficient. K_d was determined from the slope of the regression of $ln(E(z))$ versus depth, where $E(z)$ is the light intensity at depth z, or was approximated from Secchi depth (z_{SD}) readings as:

$$K_d \approx \frac{2.2}{z_{SD}} \tag{4}$$

It should be noted that the numerator of 2.2 is a mid-range approximation of values that have been found to range from 1.2 to 3.5 in different systems (Holmes 1970; Kirk 1994). The lakes were divided into three classes based on values of $E_{average}$: < 5 % corresponding to low light; 5 – 20 %, medium light; and > 20 %, high light.

Statistical Analysis

Non-metric multi-dimensional scaling (MDS) and analysis of similarities (ANOSIM) were used to detect patterns in phytoplankton composition between lakes and to infer which environmental variables were associated with underlying trends in composition. MDS was performed on the ranked Bray-Curtis similarity matrix calculated on the presence-absence (equivalent to Jaccard's index) of phytoplankton genera. Results of MDS are displayed as two-dimensional ordination plots, where distances between points (lakes) in the plot indicate their degree of similarity based on phytoplankton composition. Only cyanobacterial and diatom genera common to three or more of the study lakes, and only lakes with greater than three phytoplankton genera, were included in our analyses.

ANOSIM was applied to the similarity matrix underlying the ordination to test whether differences between sample groups (lakes) and environmental data (mixing regime, trophic state, light climate) were statistically significant. ANOSIM is a non-parametric permutation analysis used to test *a priori* hypotheses. This analysis provides a measure of the dissimilarity of groups of samples in terms of an R-statistic, which generally ranges between 0 and 1; values near zero indicate that groups are very similar and values near 1 indicate increasing dissimilarity. A p-value is computed to indicate statistical significance of the R-value. For all tests, 999 permutations were executed.

A matrix diagram was constructed for the summer data by re-ordering the original data matrix to indicate which taxa were primarily responsible for the observed patterns. Lakes were ordered on the *y*-axis based on the dominant underlying environmental variable, and their approximate distribution in the MDS ordination. On the *x*-axis, phytoplankton genera were ordered based on their distribution in a MDS analysis plot of taxa based on lake. MDS and ANOSIM analyses were repeated on a subset of 26 lakes from winter (July - August 2002) samples to evaluate if factors determining phytoplankton assemblage composition during summer were also apparent during winter isothermy. Analyses were conducted using the Plymouth Routines in Multivariate Research statistical package (Clarke and Warwick 1994; PRIMER 2001). The acceptable *p*-values ($\alpha = 0.05$) for summer and winter analyses were adjusted using a Dunn-Šidák correction to allow for non-independence of tests. For each recorded diatom and cyanobacterial genus, the number of lakes each occurred in was compared for two mixing categories: stratified and mixed (which includes intermittently stratified lakes).

6.4 Results

The stress value (0.2) of MDS based on phytoplankton genera from the summer sampling period indicates that the ordination accurately reflects the underlying similarity matrix (Fig. 6.1a). A clear separation of stratified from intermittently stratified and mixed lakes is apparent based on phytoplankton composition (Fig. 6.1c), with stratified lakes generally at the top of the ordination and mixed lakes grouped at the bottom. Results of ANOSIM for mixing-related differences in phytoplankton assemblages show that groupings based on mixing regime are significantly different (Global $R = 0.249$; $p = 0.006$). Phytoplankton assemblages in stably stratified lakes were significantly different from those in intermittently stratified lakes ($p = 0.01$) and mixed lakes ($p = 0.03$), but there was no significant difference between intermittently stratified and mixed lakes ($p > 0.05$).

The MDS plot based on summer phytoplankton taxa and trophic state produces less distinct lake groupings (Fig. 6.1e), and there is no clear gradient of phytoplankton composition specific to the three trophic levels. Oligotrophic lakes are generally near the top of the ordination (all of which stratified; Fig. 6.1c), and eutrophic lakes are lower on the ordination (and commonly mixed). However, mesotrophic lakes have phytoplankton assemblages that vary greatly on the ordination. For example, lakes Okareka, Rerewhakaaitu and Tutira are near the top of the ordination, with phytoplankton communities mostly comprised of diatom genera (e.g., *Cyclotella*, *Navicula* and *Aulacoseira*), while lakes Ototoa (intermittently stratified) and Kereta (mixed) are at the bottom of the ordination and the phytoplankton assemblage comprises mostly cyanobacterial genera (e.g., *Anabaena*, *Coelosphaerium*; Fig. 6.2). The composition of phytoplankton communities in mesotrophic lakes therefore appears to be better explained by mixing pattern than trophic state. Results of ANOSIM indicate that trophic state is not a statistically significant factor influencing phytoplankton assemblage composition (Global $R = 0.249$; $p = 0.09$).

For light climate, lakes with high mean light intensities through the water column or surface mixed layer are commonly at the top of the ordination, with the low- and mid-light lakes mostly lower on the ordination. However, results of ANOSIM indicate differences between groups are not statistically significant (Global $R = 0.156$, $p = 0.14$) (Fig. 6.1g).

Comparing mixing regimes, trophic states, and light climates of the lakes, it is apparent that lakes that stratify permanently during summer (i.e., warm monomictic) are commonly oligotrophic and have a high mixed layer irradiance, while the intermittently stratified and mixed lakes commonly have higher trophic status and an intermediate to low irradiance level. Pearson correlations were performed to test for cross-correlations of $\hat{E}/z_m$, $E_{average}$ and trophic state. The variables are all significantly correlated ($p < 0.05$). Trophic state is negatively correlated with $E_{average}$ ($r = -0.821$), signifying that as trophic state increases, the average light intensity generally decreases. Trophic state is positively correlated with $\hat{E}/z_m$ ($r = 0.586$), whereas $\hat{E}/z_m$ and $E_{average}$ are negatively correlated ($r = -0.456$). The relationships between $\hat{E}/z_m$, $E_{average}$ and trophic state indicate in general terms that oligotrophic lakes commonly stratify permanently during summer and have a higher mixed layer irradiance, while the lakes with higher trophic status are generally intermittently stratified or mixed, with a lower irradiance level. However, eutrophic stratified lakes (e.g., lakes Rotomanuka, Pupuke and Okaro) have phytoplankton composition similar to that of oligotrophic stratified lakes. For example, amongst stratified lakes, eutrophic Lake Okaro had summer diatom and cyanobacteria composition most similar to oligotrophic Lake Taupo.

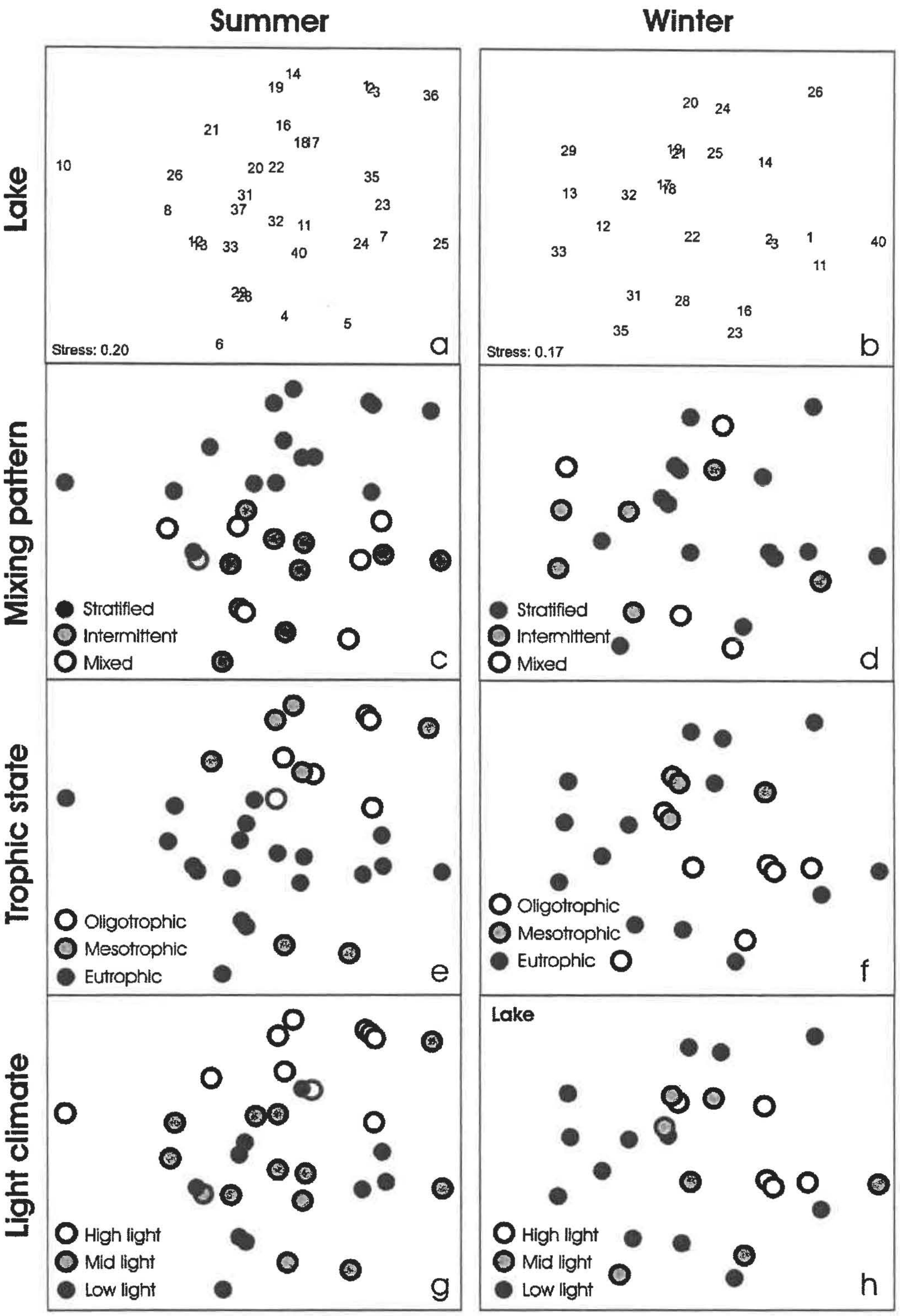

Figure 6.1. Multidimensional scaling (MDS) plot of lakes based on phytoplankton genera during (a) summer and (b) winter. Overlaid on the MDS are (c, d) mixing patterns, (e, f) trophic state and (g, h) light climate for summer and winter, respectively. Numbers on (a) and (b) correspond to assigned lake numbers (Table 6.1).

Diatom genera generally occur at higher frequency in stratified lakes than in mixed lakes except for *Synedra* and *Aulacoseira* (Fig. 6.2). *Synedra* was found more commonly in polymictic lakes while *Aulacoseira* was relatively evenly distributed between stratified and mixed lakes. Cyanobacteria followed the opposite pattern, with all genera occurring at greater frequency in mixed lakes than in stratified lakes. Lakes of different trophic state but similar mixing regime thus share similar phytoplankton assemblages based on cyanobacteria and diatom genera present, e.g., eutrophic lakes Okaro and Pupuke have phytoplankton composition similar to that of other stratified lakes that are oligotrophic (e.g., Taupo) or mesotrophic (e.g., Rotomahana). Conversely, lakes of similar trophic state but different mixing regime commonly have dissimilar phytoplankton assemblages, e.g., eutrophic lakes Okaro (stratified) and Ngaroto (mixed).

The MDS plots for the winter period illustrate a wide spread of lake mixing types (Fig. 6.1d), trophic states (Fig. 6.1f) and light climates (Fig. 6.1h). Phytoplankton composition therefore appears to be largely unrelated to any of these environmental factors at this time of year. ANOSIM indicates no significant differences between the assemblages of phytoplankton with mixing type (Global $R = 0.135$; $p = 0.20$), trophic state (Global $R = -0.150$; $p = 1.00$) or light climate (Global $R = 0.026$; $p = 0.66$). Phytoplankton assemblage composition at this time may therefore be related to factors other than those assessed here.

6.5 Discussion

The presence of different phytoplankton genera or species is often used to infer lake trophic state (Rawson 1956, Reynolds 1998). Conversely, however, Reynolds et al. (1998) found an increase in phytoplankton biomass but no detectable change in assemblage composition when examining the effects of artificial phosphorus additions to a small, oligotrophic mountain lake in the English Lake District. Similarly, Pick (1989) showed that enrichment with P and decreased N:P ratios did not alter the assemblage composition or effect a shift to nitrogen-fixing cyanobacteria in enclosures. In the present study of 40 North Island lakes, our mixing regime indicator provides a better tool for prediction of summer phytoplankton composition than indicators of trophic state or light climate, and lakes of different trophic state but similar mixing regime tend to have similar phytoplankton composition based on presence of cyanobacteria and diatom genera.

Other indicators of the importance of mixing regime on phytoplankton composition are provided by studies of responses to artificial mixing in lakes that would otherwise stratify. Direct effects on phytoplankton composition of artificial mixing appear to be more profound than secondary effects related to changes in trophic state or light climate (e.g., Visser et al. 1996; Huisman et al. 2004). Increased mixing can result in a change in the phytoplankton assemblage from a high abundance of cyanobacteria (Westwood and Ganf 2004) to diatom species that normally have high sedimentation losses (Visser et al. 1996; Jungo et al. 2001) or selection of apparently low light-adapted species, e.g., *Oscillatoria* (Burgi and Stadelmann 2002).

Relatively high numbers of cyanobacteria genera and low numbers of diatom genera were generally observed in mixed lakes. This result may be from high light attenuation in shallow lakes that are generally mixed and eutrophic, conditions that may favour a high richness of cyanobacteria. In eutrophic lakes cyanobacteria are often in higher abundance than other phytoplankton. During mixing, adaptations such as effective light harvesting for photosynthesis and low energy requirements can contribute to high cyanobacterial abundance despite low irradiances (Tilzer 1987). Although cyanobacteria tend to have lower maximum growth rates than most other phytoplankton taxa, reductions in growth rates at low light intensities may be less marked for cyanobacteria than for other taxa (e.g., diatoms), as a result of high photoadaptation capacity associated with increases in cellular chlorophyll *a* and accessory pigments (Reynolds 1998). Therefore, some cyanobacteria genera, e.g., species of *Anabaena* that constitute functional group S_N and tolerate light deficient conditions (refer to Reynolds 2002), may be at a competitive advantage in low PAR environments often associated with shallow lakes.

	Genera	*Navicula*	*Asterionella*	*Cocconeis*	*Fragilaria*	*Cyclotella*	*Aulacoseira*	*Anabaena*	*Aphanizomenon*	*Oscillatoria*	*Microcystis*	*Coelosphaerium*	*Synedra*
	Lake	Diatoms						Blue-Greens					Di.
MIXED	Kuwakatai							*			*		*
	Ototoa					*		*			*	*	*
	Kereta						*	*	*			*	
	Ngaroto						*	*			*		
	Waikare (Waikato)						*	*			*		
	Waitawa					*	*	*			*		
	Rotokauri					*	*	*					*
	Wainamu					*	*	*		*			
	Waahi	*					*	*		*			*
	Rotoroa		*			*		*					
	Ohakuri		*		*		*	*	*		*		*
	Waipapa		*		*		*	*	*		*		*
	Rotoehu	*		*	*	*	*	*	*		*	*	*
	Rotorua				*		*	*			*	*	
	Horowhenua	*			*		*	*			*		*
	Karapiro	*	*		*		*	*	*		*		*
STRATIFIED	Rotoiti				*		*	*	*		*		*
	Waikaremoana	*	*				*	*					
	Okaro	*			*	*	*	*	*		*	*	
	Taupo		*		*	*	*	*			*		
	Pupuke	*			*	*	*	*					
	Rotomanuka			*	*						*		
	Okataina				*	*		*		*	*		
	Tarawera				*	*	*				*		
	Rotomahana	*	*	*	*	*	*	*	*			*	
	Rotoma	*			*	*	*					*	
	Rerewhakaaitu	*	*	*	*	*	*						
	Okareka	*				*							*
	Tutira	*				*	*						
	Kai-iwi	*				*	*						
	Taharoa	*				*	*						
	Waikere (Nthland)	*	*		*	*	*	*					
Polymictic richness		4	4	1	6	6	13	16	5	2	11	4	9
Monomictic richness		11	5	3	11	13	13	8	3	1	6	3	2

Figure 6.2. Shade matrix for the phytoplankton genera and lake groupings for the summer sampling period. The intermittently stratified and mixed lakes are grouped under the 'mixed' group. Rows and columns of the array are ordered on the basis of MDS distributions of taxa and samples.

Mixing resulted in a decreased diversity of diatom genera in this study, however even with a decrease in diversity, diatoms generally respond to increased mixing by increasing biomass (Vincent 1983; Ryan et al. 2005) as mixing may increase the supply of growth limiting nutrients. Diatom genera may be largely excluded from these assemblages as several diatoms are known to have low survival in low light conditions (Kilham et al. 1996). Levels of suspended sediment can also be high as a result of sediment resuspension in shallow mixed waters (Hamilton and Mitchell 1996), which will have similar effects on composition as high phytoplankton biomass. The ability for several cyanobacteria genera to coexist in our mixed lakes is likely a result of constant levels of disturbance, a factor commonly associated with high community richness (e.g., Rosenweig 1995).

Conversely in stratified lakes, fewer cyanobacteria genera were found relative to numbers of diatom genera. Some species of cyanobacteria may be abundant in surface waters of stratified lakes as a result of permanent or intermittent buoyancy, which optimises light capture (Huisman et al. 1999). For example species, such as *Microcystis*, categorised by Reynolds et al. (2002) as functional group M which is tolerant of high insolation, may be in high abundance in the upper illuminated layer and shade other species (Wallace and Hamilton 1999). Under such undisturbed conditions, a limited variety of cyanobacteria may thus survive relative to the mixed, disturbed, conditions. For example, Viner (1989) showed that in Lake Okaro, a large biomass of buoyant *Anabaena* precluded potentially competing species via light limitation.

These findings suggest that changes in mixing patterns associated with global climate change may impact on phytoplankton assemblage composition in New Zealand lakes to a greater extent than eutrophication (*sensu* Huisman et al. 2004). An increase in the duration of summer stratification in dimictic (Weyhenmeyer et al. 1999; Winder and Schindler 2005) and monomictic lakes can be expected with increases in temperature associated with global warming. The increase in stratification with higher temperatures would likely result in a lower diversity of cyanobacteria genera due to competition between taxa (i.e., Viner 1989).

Eutrophic lakes are subject to rapid physical, chemical and biological changes (Scheffer 1997), and the distribution of phytoplankton within lakes may be highly variable with depth (Vincent and Dryden 1989) and temporally (Ryan et al. 2005). Confirmation of the relationships between phytoplankton assemblage composition and mixing regime observed in this study will be assisted by sampling that focuses on stratified lakes of higher trophic status and also on mixed lakes of lower trophic status, both of which are not well represented in the current data set. Additionally, the effect of mixing regime on phytoplankton assemblage composition could be confirmed through artificial de-stratification of oligotrophic and eutrophic lakes that stably stratify in summer. I was unable to address temporal variability of phytoplankton assemblage composition within lakes as only one sample was collected in each of two seasons. Thus short-term variability (e.g., due to seiching and wind; Ryan et al., 2005) and inter-annual variability (e.g., due to El Niño-Southern Oscillation (ENSO) cycles) were not explicitly included in our analyses. For example, in Lake Rotongaio there have been strong inter-annual variations of cyanobacteria and diatom species, whereby a summer of strong mixing was associated with a shift from cyanobacterial species to diatom species (Viner and Kemp 1983). Understanding the nature of these shifts requires finer temporal and spatial scales of sampling as well as commitment to long-term monitoring.

The indices used in this study to classify trophic state, light climate and mixing regime are not intended to be definitive, and I do not aim to simplify prediction of phytoplankton composition to a single variable. Morphometric data were used in this study to characterise the mixing regime of the lakes as temperature profiles were not available and in many cases only grab samples from one lake location were available. It is possible that there may be complex inter-relationships amongst a variety of morphometric indicators. For example, various lake area and depth indices can also be related to lake trophic state (e.g., Nürnberg 1999). Further quantification of mixing regimes, e.g., using Schmidt stability or other stratification criteria (e.g., Hamilton et al. 2004), may also aid in confirming relationships between mixing and phytoplankton assemblage composition established in the present study. The impact of zooplankton grazing on phytoplankton assemblage composition should also be assessed, as some species of cyanobacteria are inedible to zooplankton (Burns et al. 1987). Our study attempted to isolate the relative importance of each predictor, and mixing regime was found to be a more important predictor of phytoplankton assemblage composition than lake trophic status or light climate.

6.6 References

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Chapter 7

General Conclusions

7.1 Summary

Quantifying the phenomena that influence the geographical and temporal distribution of phytoplankton is important in studies of aquatic ecosystems, global carbon budgets and understanding implications for quality and management of lakes. This study has provided insights into the interactions of various environmental variables in governing both surface and DCM phytoplankton dynamics and assemblage composition, at different spatial and temporal scales. In each chapter the horizontal or vertical variability of phytoplankton dynamics was examined in relation to variables that included turbulent mixing, sedimentation/buoyancy, net rates of growth, and light and nutrient limitation.

In Chapter 2, net rates of phytoplankton growth were calculated within individual Waikato peat lakes. It was demonstrated that *C. raciborskii* populations grew at rates close to maxima observed under laboratory culture conditions; the result for these lakes was large blooms. The change in species diversity in lakes prior to and following the invasion of *C. raciborskii* was evaluated with the Shannon index, with low values indicating instances of *C. raciborskii* water blooms; the phytoplankton assemblage became nearly mono-specific and there was very little diversity. Conditions in the shallow lakes described in Chapter 2 were almost ideal for the proliferation of *C. raciborskii*, with high concentrations of nutrients and low water clarity, as *C. raciborskii* has the capacity to be highly competitive at low irradiance in the presence of abundant nutrients (Padisák and Reynolds 1998). *Cylindrospermopsis raciborskii* also has the ability to fix nitrogen, which may aid its competitive ability amongst phytoplankton communities and its range extension in other North Island lakes, as phytoplankton in many lakes of the Central Volcanic Plateau of North Island have previously been found to be nitrogen-limited (White et al. 1985).

Horizontal and vertical spatial variations in phytoplankton biomass between embayments and a mid-lake station were quantified in Lake Tarawera in Chapter 3. A single mid-lake station was considered to be an appropriate site for estimating lake-wide biomass at the DCM. It was found that during a surface bloom of *Anabaena lemmermanni*, however, phytoplankton biomass in the surface mixed layer was highly variable between sites. Therefore, when quantifying surface populations, particularly buoyant bloom-forming species, discrete samples from one station depth may not adequately represent lake-wide biomass. Under these circumstances, where bloom-forming species proliferate, multiple sampling stations are recommended to quantify lake-wide biomass.

Factors contributing to DCM formation were examined in Chapter 4 using a population-dynamics theory of sinking phytoplankton that considered interactions between growth limitation by light and nutrients, sinking rates and turbulent diffusion rates. Five 'Modes' of vertical phytoplankton biomass distribution were categorised relating to four forcing functions. The first mode was defined as a surface chlorophyll maximum (SCM); Mode 2 as a DCM; Mode 3 as a simultaneous double peak of buoyant surface cyanobacteria as well as a DCM assemblage; Mode 4 as a linear vertical distribution and Mode 5 as an exponential increase with depth. The occurrence of these distributions and the presence of a DCM were examined in relation to different turbulent diffusion rates ($<0.1 - 10$ cm^2s^{-1}), sinking rates (+10 to -4 m day^{-1}) and light and nutrient limitation. A DCM was maintained when populations were able to 'outgrow' losses from dispersion by turbulent diffusion and losses due to sinking. Light climate plays an important role in the position of the DCM, and large surface blooms of cyanobacteria can destroy the DCM by shading and suppressing light available for these populations.

The formation of the dinoflagellate DCM examined in Chapter 5 was from 'midwater regulation' by the dinoflagellate *Perdinium* cf. *sydneyense*. This dinoflagellate population maintained its vertical position relative to irradiance levels and using water column density stratification that prevented dispersion of populations. The DCM persisted for several months at depths where there was approximately 2-3 % of surface irradiance. Further evidence for light governing the position was provided by the nutrient incubation experiments that showed a decrease in DCM biomass with incubations at high irradiance (40 % of surface irradiance).

In Chapter 6, the relationship between the composition of phytoplankton assemblages, lake mixing, trophic state and light climate was investigated in 40 North Island, New Zealand, lakes. Mixing regime was categorised into three classes; stable seasonal stratification, intermittent stratification and mixed. Lakes were divided into three trophic states (oligotrophic, mesotrophic, eutrophic) using the guidelines of Burns et al. (2000), or trophic state was estimated via literature sources. The average PAR that phytoplankton are exposed to was also divided into three classes, where 5 % or less corresponded to low light, 5 – 20 % to medium light, and > 20 % to high light. Mixing regime provided a more accurate prediction of phytoplankton assemblage composition than trophic state, as there were differences in the composition of phytoplankton assemblages between mixed and stratified lakes. High abundance of cyanobacteria genera and low abundance of diatom genera was recorded in mixed lakes compared to those that stably stratify in summer. Conversely, lakes with different trophic states but similar mixing regimes shared very similar phytoplankton assemblages.

7.2 Future work

Sampling of surface waters by use of a tube sampler to sample the SML may not necessarily accurately represent phytoplankton biomass. There are large vertical variations in phytoplankton biomass within the depth profile, and sampling of surface waters will not capture the DCM biomass, which may be very important to the overall productivity of oligotrophic lakes. In lakes where a DCM is present, it is important to resolve phytoplankton biomass and assemblage composition through the whole water column in order to quantify biomass accurately at the whole lake scale and to elucidate the ecology of the different species assemblages. Where there are surface populations of potentially bloom-forming species, horizontally dispersed sampling is recommended in order to quantify variations in biomass accurately over the surface mixed layer.

The study of *Cylindrospermopsis* dynamics in Chapter 2 had access to only limited data pertaining to lake physics. *Cylindrospermopsis* populations may have been distributed unevenly in the water column but the sampling regime was not designed to assess any of this vertical variability. Further insight into the population dynamics of *C. raciborskii* should focus on the interactions of mixing regime, nutrient supply and light climate, to develop a better understanding of the structure and function of this potentially toxic species, which could have widespread implications for lake health at high concentrations.

In Chapter 4, factors contributing to DCM formation were examined using a population-dynamics theory of sinking phytoplankton that considered interactions between growth limitation by light and nutrients, sinking rates and turbulent diffusion rates. Sinking rates were estimated indirectly in this study. Experimental or *in* situ studies of sinking rates under different nutrient and light regimes could have improved the reliability of predictions of DCM populations in the present study. For example, some diatoms are known to decrease their sinking velocity and achieve near neutral buoyancy under low light and high nutrient conditions (Davey and Heaney 1989). In Chapters 5 and 6 turbulent diffusion was estimated at the thermocline using Lake Number. Direct measures of turbulence (e.g., using a temperature microstructure profiler) could be used to obtain a full water column turbulence profile which would allow a more complete assessment of rates of circulation within the surface mixed layer and vertical and horizontal transports (e.g., MacIntyre et al. 1999; 2002).

In Chapter 5 studies on the physiology of *Peridinium* cf. *sydneyense* would provide further insight into the migratory capabilities of this species. Measurements of photosynthesis in the *in situ* incubation experiments would verify if the position of the DCM is at the depth that is optimal for photosynthesis (e.g., Regel et al. 2004) or whether other factors play a role in the very discrete depth profile of *Peridinium.* There is a need to assess whether mixotrophy is an important supplement for the nutritional status of *Peridinium* cf. *sydneyense* in Lake Tikitapu and in other lakes where it forms a DCM.

To validate the relationships between phytoplankton assemblage composition and mixing regime that were found in Chapter 6, further quantification of mixing regimes, e.g., using Schmidt stability, with sampling on a finer temporal scale, could be used to confirm or reject some of relationships established in this study. Additionally, the effect of mixing regime on phytoplankton assemblage composition could also be tested through artificial de-stratification of oligotrophic and eutrophic lakes which stably stratify in summer.

This study has contributed to a greater understanding of the factors governing the spatial and temporal variability of phytoplankton dynamics in lakes. Field work and modelling were used to quantify effects of turbulent mixing, sedimentation, and growth, in order to understand the role of these variables in governing assemblages, biomass and distribution of phytoplankton communities. The results of this research illustrate the importance of hydrodynamic controls on phytoplankton dynamics in both space and time, and the need to pay close attention to species composition for water quality and ecological analyses.

7.3 References

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