Spatial and temporal trends of phytoplankton and physiochemical variables in a hypertrophic, monomictic lake

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

Master of Science in Biological Sciences

at

The University of Waikato

by

BERNARD MICHAEL SIMMONDS

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

The University of Waikato

2011

Abstract

Spatial and temporal variations in the physical, chemical and biological composition of Lake Ōkaro were measured over 16 months. Lake Ōkaro is a small (0.32 km^2) hypertrophic, monomictic lake located in the Central Volcanic Zone of the North Island, New Zealand. Vertical profiles of temperature, chlorophyll fluorescence, dissolved oxygen concentration (DO), pH, specific conductance, photosynthetically active radiation (PAR) and nutrient species, including ammonium-nitrogen (NH_4-N), nitrite-nitrogen (NO_2-N), nitrate-nitrogen (NO_3-N) and phosphate-phosphorus (PO_4-P), were collected at up to nine stations at weekly to monthly frequencies. High-frequency variability was assessed during two separate 24-hour monitoring periods, coinciding with an *Anabaena spiroides*-dominated surface bloom, and a *Ceratium hirundinella*-dominated deep chlorophyll maximum. Additional data for wind direction and velocity, incident solar irradiance and rainfall was sourced from a meteorological weather station and a lake monitoring buoy at Rotorua, 20 km north of the lake.

Spatial variability was more pronounced during summer. Observed vertical gradients in chlorophyll fluorescence, DO, specific conductance and nutrient species were closely linked to thermal stability of the water column. There were large variations in chlorophyll fluorescence amongst stations in summer, which related to displacement of the metalimnion and associated changes in chlorophyll fluorescence. Winter mixing was characterised by relative homogeneity of the water column. Nutrient concentrations were elevated at all depths whereas high concentrations had previously been confined to lower depth strata (the hypolimnion).

Temperature profiles in summer displayed clear vertical gradients with a well-defined metalimnion that increased in depth until winter mixing generated isothermal conditions. Chlorophyll fluorescence profiles were characterised by the formation of a DCM that was recurrent over both summer periods, and was strongly statistically related to the depth of the thermocline for the duration of stratification. Dissolved oxygen, specific conductance and pH were relatively uniform horizontally, though pH was consistently lower at a well-sheltered near-shore station. All variables showed strong variations with depth during the stratified period. Dissolved oxygen was negligible or zero below the thermocline for much of the stratified period while specific conductance was lowest above or at the thermocline. There were also strong vertical gradients in nutrient concentrations in summer, with concentrations below the thermocline often an order of magnitude higher than those above.

The representativeness of fluorescence at a central station to a whole-lake scale was assessed using a vertical integrated value and the standard error derived from up to eight other stations. Values at the single station frequently deviated from the mean fluorescence of the wider lake, particularly at the DCM which suggests that extrapolating single-station measurements to a whole lake could provide highly exaggerated values of lake fluorescence.

High-frequency sampling during the *A. spiroides*-dominated surface bloom showed diel temperature variations attributed mostly to solar irradiance. There was high light attenuation from the high phytoplankton biomass and consistently elevated pH and DO. Fluorescence profiles suggested that the phytoplankton population was strongly buoyant and did not undergo diel vertical migration.

High-frequency sampling during a period when there was a dinoflagellate-dominated DCM showed two coinciding fluorescence peaks had formed at 6-7 and 7-8 m depth and contained morphologically and physiologically distinct taxa. The 6-7 m DCM was predominantly *Ceratium hirundinella*, while the 7-8 m DCM was composed of *C. hirundinella* and unidentified colonial picoplankton. Fluorescence profiles suggested diel vertical migration was not taking place, and strong gradients in light, nutrient availability and the relative biomass of the dominants suggested that the 6-7 and 7-8 m DCM populations potentially differed in their modes of nutrition, light history and susceptibility to grazing.

This research illustrates the degree of spatial variability that can exist in a small, monomictic hypertrophic lake at a given time, and highlights some of the potential limitations of using single-site monitoring stations to represent the physical, chemical and biological conditions of a whole lake. This information may be used to critically evaluate the reliability of phytoplankton biomass estimates that have been derived from spatially-limited sampling methods. This study further illustrates the role that thermal stratification plays in creating vertical gradients in a number of biological and chemical variables, and demonstrates that parallels exist with regard to DCM formation in oligotrophic and hypertrophic lakes, relating to the interplay between light, chlorophyll fluorescence and thermal stratification. Evidence is also provided showing that diel-scale variations in phytoplankton biomass can differ markedly between a cyanobacteria-dominated surface bloom and a dinoflagellate-dominated DCM, which further highlights the value of high-frequency sampling when seeking to estimate phytoplankton biomass using *in situ* methods.

Acknowledgements

First and foremost I would like to thank my supervisor Professor David Hamilton for taking me on as a M.Sc. student back when I had little more than some summer experience in phytoplankton counting. Your enthusiasm has been a great source of motivation and you have always found ways of making things challenging and interesting, ensuring I have learned an immense amount along the way. I thank you for fostering my interests in limnology, and for helping to build the platform that will launch me toward a great future in science.

I would like extend my gratitude to Dr Deniz Özkundakci for his support over the past year. Your seemingly endless knowledge of Lake Ōkaro has been a fantastic source of information, and you have always been ready to lend an ear, offer advice and drink a coffee. Thanks for everything.

Thank you to Dr Susie Wood (Cawthron) for being there from my very first day as David's M.Sc. student. You have always been so encouraging, and I truly appreciate all the advice and feedback you have provided along the way.

A very special thanks to my field buddy Marie Dennis for two years of boat trips (rain or shine), early starts and late finishes, the countless coffee stops and all the hard work you've put in collecting and processing my samples. I've been tremendously lucky to be able to count on you.

I would like to acknowledge Wendy Paul for helping to identify phytoplankton, teaching me lab methods, providing equipment, proof reading drafts and always being there to lend an ear and have a chat. Thank you for all your help over the past two years.

I would also like to express thanks to Kohji Muraoka. You have always been ready to drop everything and offer advice, or just get out of the office for Goura and coffee. Sharing a flat over the past year has been a blast, and I'm blessed to call you a friend.

All my love to my dad Mike, my mum Sue, and my brothers Tim, Andrew and Nick. Thanks for being there over the past few years; particularly when things have gotten tough and I've needed to escape for some awesome home cooked food and relaxation. You guys are the best.

Thanks to my partner Alyse Dombroski, for leaving your key out on cold winter nights when I've had to work late, for bringing me cooked meals and for all your support during those stressful times.

I would like to acknowledge the hard work of Louise Stewart for running my nutrient samples and for teaching me how to do chlorophyll *a* analysis. Thanks to Sean Taylor of Scion, for the calibration and occasional operation of the flow cytometer. Thanks to Andreas Rueckert and Sarah Kelly for helping me with ARISA and for allowing me to culture cyanobacteria. Thank you to Barry O'Brien for teaching me the ways of the IX-71 microscope, and for your perseverance in identifying the "mystery Lake Ōkaro chlorophyte".

A special thanks to my good friend Brennan Mahoney and to the M.Sc. students, doctoral candidates and staff of the biology department for all the coffees and hilarious conversations. I wish you all the best for the future.

Finally, I am grateful for the financial support provided by the University of Waikato in the form of a research scholarship that has kept me fed with a roof over my head for the past two years.

Table of contents

Abstract **iii**

Acknowledgements **vi**

Table of Contents **viii**

List of Figures **xii**

List of Tables **xvii**

1.0 Introduction **1**

1.1 Eutrophication **1**

1.2 Eutrophication in New Zealand **1**

1.3 Point source pollution **2**

1.4 Diffuse source pollution **3**

1.5 Consequences **3**

1.6 Management options **4**

1.7 Indicators of lake health **7**

1.8 The importance of representative sampling **10**

1.9 Scales of variability in lakes **11**

1.10 The Te Arawa Lakes **12**

1.11 Lake Ōkaro **15**

1.12 Previous studies **15**

1.13 Scales of temporal variability **17**

1.14 Spatial variability **18**

1.15 Overview and Objectives **20**

2.0 Methods **22**

2.1 Study stations **22**

2.2 Field methods **24**

2.3 Field measurements **25**

2.4 High-frequency sampling **27**

2.5 Laboratory methods **27**

2.6 Data analysis **31**

3.0 Results: Spatial variability

3.1 Relationships between thermocline depth, euphotic depth, and chlorophyll fluorescence **34**

3.2 Horizontal variation **40**

a. Temperature **40**

b. Fluorescence **44**

c. Dissolved oxygen **47**

d. pH **51**

e. Specific conductance **54**

f. Nutrients **57**

3.3 Representing whole lake chlorophyll fluorescence with a central lake station **62**

4. Results: Temporal variability study

4.1 Temporal variability during a cyanobacteria-dominated surface bloom **66**

a. Thermal structure **66**

b. Dissolved oxygen **68**

c. Light availability **68**

d. Specific conductance **69**

e. pH levels **70**

f. Cell concentrations **70**

g. Fluorescence **70**

h. Wind **71**

4.2. Temporal variability during a dinoflagellate-dominated dual-peak deep chlorophyll maximum **73**

a. Thermal structure **73**

b. Dissolved oxygen concentration **74**

c. Light availability **75**

d. Fluorescence **76**

e. Cell counts and biomass **77**

5 Discussion: Spatially comprehensive sampling

5.1 The relationship between thermocline depth, euphotic depth and chlorophyll fluorescence **81**

5.2 Spatial variability in physical, chemical and biological components **85**

5.3 Representing whole lake chlorophyll fluorescence with a central lake station **93**

5.4 Temporal variability during a cyanobacteria-dominated surface bloom **94**

5.5 Temporal variability during a dinoflagellate-dominated dual-peak deep chlorophyll maximum **97**

6 Summary and conclusions 107

7 Future work 111

8 References 113

9 Appendices 147

List of figures

Figure 2.1: Map of Lake Ōkaro showing sampling stations and location of the inflows and outflow (modified from Özkundakci et al. (2010)). **23**

Figure 3.1: Thermocline depth and peak fluorescence depth of a shallow station (S2) and a deep station (W1) from 01 December 2009 – 11 March 2011, and euphotic depth at station S1 from 17 December 2009 – 29 March 2011. **35**

Figure 3.2: Schmidt stability at deep stations (station names are given on the inset) from 01 December 2009 – 11 March 2011. **37**

Figure 3.3: Depth of peak fluorescence with mean thermocline depth at deep stations (station names are given on the inset) from 01 December 2009 – 11 March 2011. No thermocline was present from 01 June 2010 until 28 September 2010. **38**

Figure 3.4: Mean values of chlorophyll fluorescence at deep stations (W1, N1, O, S1 and E1) from 01 December 2009 to 11 March 2011. **39**

Figures 3.5a-f: Temperature profiles for all stations from 01 December 2009 – 05 January 2010. **41**

Figures 3.5g-o: Temperature profiles for all stations from 12 January 2010 – 01 June 2010. **42**

Figures 3.5p-x: Temperature profiles for all stations from 29 June 2010 – 11 March 2011. **43**

Figures 3.6a-i: Fluorescence profiles for all stations from 01 December 2009 – 26 January 2010. **45**

Figures 3.6j-r: Fluorescence profiles for all stations from 02 February 2010 – 28 September 2010. **46**

Figures 3.6s-v: Fluorescence profiles for all stations from 26 October 2010 – 10 February 2011. **47**

Figures 3.7a-c: Dissolved oxygen profiles for all stations from 12 December 2009 to 22 December 2009. **48**

Figures 3.7d-l: Dissolved oxygen profiles for all stations from 29 December 2009 to 31 March 2010. **49**

Figures 3.7m-u: Dissolved oxygen profiles for all stations from 27 April 2010 to 11 February 2011. **50**

Figures 3.7v-w: Dissolved oxygen profiles for all stations from 24 February 2011 to 11 March 2011. **51**

Figures 3.8a-i: pH at all stations from 01 December 2009 to 26 January 2010. **52**

Figures 3.8j-r: pH at all stations from 02 February 2010 to 28 September 2010. **53**

Figures 3.8s-u: pH at all stations from 26 October 2010 to 24 January 2011. **54**

Figures 3.9a-i: Specific conductance for all stations from 01 December 2009 to 26 January 2010. **55**

Figures 3.9j-r: Specific conductance for all stations from 02 February 2010 to 28 September 2010. **56**

Figures 3.9s-u: Specific conductance for all stations from 26 October 2010 to 24 January 2011 **57**

Figure 3.10a: Concentrations of NH4-N at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 01 December 2009 - 11 March 2011, and thermocline depth. Reference values are provided next to several sample points (mg L^{-1}). **59**

Figure 3.10b: Concentrations of NO3-N at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 08 December 2009 - 11 March 2011, and thermocline depth. Reference values are given next to several sample points (mg L^{-1}). **60**

Figure 3.10c: Concentrations of PO4-P at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 08 December 2009 - 11 March 2011, and thermocline depth. Reference values are given next to several sample points (mg L^{-1}). **61**

Figures 3.11a-i: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 01 December 2009 to 26 December 2009. **63**

Figures 3.11j-r: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 02 February 2010 to 28 September 2010. **64**

Figures 3.11s-u: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 26 October 2010 to 10 February 2011. **65**

Figure 4.1: Temperature profiles for the sampling period of 19-20 November 2010. **67**

Figure 4.2: Depth of the upper and lower metalimnion and of the thermocline on 18-19 November 2010. **67**

Figure 4.3: Dissolved oxygen concentrations on 18-19 November 2010. **68**

Figure 4.4: Specific conductance on 18-19 November 2010. **69**

Figure 4.5: pH profiles on 18-19 November 2010. **70**

Figure 4.6: Fluorescence on 18-19 November 2010. **71**

Figure 4.7: Temperature profiles on 24-25 March 2011. **74**

Figure 4.8: Depth of the upper and lower metalimnion, the thermocline and Schmidt stability on 24-25 March 2011. **74**

Figure 4.9: Dissolved oxygen concentrations on 24-25 March 2011. **75**

Figure 4.10: Chlorophyll fluorescence and mean temperature profile on 24-25 March 2011. **76**

Figure 4.11: Chlorophyll fluorescence in relative units, total cell concentrations and phytoplankton biovolumes at 19:00 h on 25 March 2011. **78**

Figure 9.1: Euphotic depth, Secchi depth and predicted euphotic depth (e.g., Tilzer, 1988) from 17 December 2009 to 29 March 2011. **147**

Figure 9.2: Image of *Anabaena spiroides* in Lake Ōkaro on 18-19 November 2010. Sample collected from 0 m depth at 11:00 h on 19 November 2010. Sample concentration was 137,777 cells mL^{-1}. **149**

Figure 9.3a: 400x magnification of an unconfirmed species of chlorophyte (picoplankton #2) collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien. **149**

Figure 9.3b: Picoplankton #2 at 1000x magnification, collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien. **150**

Figure 9.3c: Scanning electron microscope image of picoplankton #2 on tissue paper (background), collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien. **150**

List of tables

Table 1.1 Limnological and catchment data for the 12 Te Arawa Lakes. Adapted from Hamilton (2003) and Bay of Plenty Regional Council (2010). **14**

Table 2.1: Limnological characteristics of Lake Ōkaro (adapted from Cronin et al. (2006). **24**

Table 2.2: Geographical position and depth of sampling stations with associated sample methods. **25**

Table 3.1: Pearson correlation coefficient values for thermocline depth and depth of maximum fluorescence for different stations (see Figure 2.1 for location of stations). Significant correlations ($P < 0.05$) are shown in bold. **36**

Table 4.1: Mean wind speed and direction at 3 hour intervals ON 18-19 November 2010. **72**

Table 4.2: Light attenuation coefficients and euphotic depths for 25 March 2011. **75**

Table 4.3: Peak and mean relative units and depths of DCM fluorescence (24-25 March 2011). **77**

Table 4.4: Cell concentrations for sampled depths at 19:00, station W1, Lake Ōkaro on the 25 March, 2011. **79**

Table 4.5: Species biovolumes for sampled depths at 19:00, station W1, Lake Ōkaro on the 25 March, 2011. Data are cells/mL-1 x biovolume (µm3). Biovolumes from Dryden & Vincent (1986) and Olenina et al. (2004). **80**

Table 9.1: Light extinction coefficient (K_d, m^{-1}), surface irradiance (I (0)), euphotic depth (z_{eu}) and z_{eu} irradiance ($I(z_{eu})$) from 17 December 2009 to 29 March 2011. **147**

Table 9.2: Mean global irradiance between 06:00 h and 19:00 h from 16-19 November 2010. **148**

Table 9.3: Wind data from 18-19 November 2010. Closest sample times are in bold. **148**

1 Introduction

1.1 Eutrophication

Eutrophication is defined as the nutrient enrichment of aquatic ecosystems, which frequently results in an array of symptomatic changes that impair water use (Likens et al., 1971). Where this process is exacerbated by anthropogenic activities it commonly known as “cultural eutrophication” (Smith et al., 1999).

Many lakes are naturally eutrophic, particularly in warmer, temperate regions (Gannon and Stemberger, 1978). However, human population growth and changes in land use have accelerated rates of nutrient enrichment (Holling and Meffe, 1996, Hasler, 1969, Ehrlich and Holdren, 1971, Falkenmark, 1986), and cultural eutrophication has now been identified as the single most important form of detriment to global surface water quality (Smith and Schindler, 2009). The causal agents of cultural eutrophication are primarily activities that increase the bioavailability of naturally limiting elements for plant growth; nitrogen (N) and phosphorus (P) in water bodies. These include influxes of phosphorus containing detergents and cleaning products (Khan and Ansari, 2005), sewage and wastewater discharge (Smith, 2003), increased sedimentation from soil disturbances (Pimentel and Kounang, 1998) and agricultural land use practices with intensified stocking rates, and nitrogenous fertiliser applications (Glibert et al., 2006, Hamilton, 2005).

1.2 Eutrophication in New Zealand

Cultural eutrophication has become a major issue in New Zealand over the last century. Intensification of land use began in the 1920s with the development of

fertilisers and improvements in soil, animal and plant science (Molloy, 1980). By the 1970s, stocking rates had increased by 150% and the proportion of land converted for agriculture and exotic plantations had grown from 35% to 60% (Blaschke et al., 1992, MacLeod and Moller, 2006). Today, stocking rates and fertiliser usages have further increased (MacLeod and Moller, 2006), and high and low-producing grassland constitute 22% and 29% of the total land area, while exotic forestry covers a further 5% (MFE, 2010). Urbanisation, a known causal agent of eutrophication has increased rapidly. Urban centres currently comprise 0.6% of the total land area and contain 85% of the total population (Suren, 2000, Ministry for the Environment 2004). Declining water quality in NZ lakes is overwhelmingly consequential of cultural eutrophication, relating to total nitrogen (TN) and total phosphorus (TP) loading in areas of high intensity pastoral, exotic forestry, and urban land use (Abell et al., 2010).

1.3 Point source pollution

Waterways have long been used as convenient discharge sites for pollutants and organic wastes (Meybeck, 2003). Many of New Zealand's most significant lakes have a history of point source pollution. Direct inputs of phosphorus-treated sewage entered Lake Rotorua between 1973 and 1990 (Rutherford, 2003). In 1984-85, sewage-derived nutrients comprised 50% and 25% of the total load of TN and TP respectively, and in response to high TLI values and growing public concern for water quality, the regional council opted for land-based sewage disposal in the Whakarewarewa Forest from 1991 (Rutherford, 2003).

Lake Taupo is a 623 km^2 oligotrophic lake on the central plateau of the North Island (Hawes and Smith, 1993). The majority of sewage is disposed of in septic tanks, and is treated within the lake catchment. In 1986, a small sewage treatment

plant was built less than 300 m from the lake shore (Hawes and Smith, 1993). Within three years, significant increases in nitrate-N concentrations were recorded as groundwater seepage contaminated a nearby tributary (Hawes and Smith, 1993).

1.4 Diffuse source pollution

The Resource Management Act (1991) effectively restricts activities that directly degrade fresh water resources, including many point source pollutants. However, diffuse inputs associated with the harvesting of exotic forestry and high-intensity pasture are known to be the dominant causal agents of external nutrient loading in many New Zealand lakes (Abell et al., 2011). In a study of 101 catchments throughout New Zealand, Abell et al. (2011) found exotic forestry represented 15.1% of the mean proportion of catchment type, and proportionally accounted for 18.8% of the variability in in-lake TP. In the same study, high-producing grassland was found to represent 33.1% of the mean catchment land use, and accounted for 38.6% and 41.0% of the variation in in-lake TN and TP respectively.

1.5 Consequences

The process of eutrophication often occurs in sequential steps. Nutrient enrichment is followed by increased primary productivity and succession in phytoplankton communities and typically culminates with the dominance of cyanobacterial species (Carpenter et al., 1998, Khan and Ansari, 2005). Long periods of phytoplankton growth exhaust dissolved inorganic nutrient concentrations in the epilimnion, and senescence transports nutrients in organic form to the hypolimnion which stimulates enhanced microbial decomposition, leading to hypolimnetic anoxia, and the regeneration of ammonium (Borowiak et al., 2010, Meersche et al., 2004). Phosphorus in the water column becomes

aggregated into insoluble flocculent and particulate organic forms which settle out and continue to bind P at the sediment/water interface. Aggregates dissolve under anoxic conditions, allowing soluble reactive phosphorus (SRP) to diffuse into the hypolimnion further perpetuating eutrophic symptoms by creating a positive feedback loop (Johannessen and Dahl, 1996, Bennion et al., 1996, Kalff, 2002a). Other attributes of a eutrophic water body can include the loss of biodiversity by creating favourable conditions for competitive exotic species (Codd, 2000, Geurts et al., 2008), reductions in water transparency, and unsuitability of water for stock or human consumption (van den Brandt and Smit, 1998).

1.6 Management options

Efforts to mitigate the symptoms of eutrophication are frequently aimed at reducing the availability of specific macronutrients for primary production (e.g. nitrogen and phosphorus), as nutrient availability is a key variable regulating phytoplankton community composition and biomass (Tilman et al., 1982).

*External source reductions***:** Wetlands and riparian margins can intercept high proportions of catchment-derived P and N from reaching waterways (Woltemade, 2000, Osborne and Kovacic, 1993). Osborne & Kovacic (1993) tested the relative abilities of grass and forested buffer strips to assimilate nitrate-N, and dissolved and total phosphorus. Forested buffers removed up to 90% of nitrate-N in shallow groundwater, and grass systems removed a higher proportion of dissolved and total phosphorus (Osborne and Kovacic, 1993). In 2006, a 2.3 ha artificial wetland was constructed around Lake Ōkaro, predicted to remove 40% to 50% of the total nitrogen intercepted from the catchment (Sorrell, 2010). The extent of riparian vegetation around the lake margin has been increasing from 2006, as part of an ongoing lake restoration strategy (Cronin et al., 2006).

Bottom sediments are considered a source, as well as a sink of nutrients (Berg et al., 2004). Under anoxic conditions, concentrations of internally released nutrients can exceed those derived from external sources (Özkundakci et al., 2011). Sediment treatment options involve the application of chemical flocculants that bind to dissolved nutrients, predominantly phosphorus, reducing the proportion available for algal growth (Berg et al., 2004).

Attempts to reduce the in-lake concentrations of phosphate have been made using an aluminium sulphate solution (alum; 47% $Al_2(SO_4)_3 \cdot 14H_2O$). In 2003, alum was applied to the epilimnion (0–3 m) of Lake Ōkaro with a target concentration of 0.6 g Al m^3; considered to be low in comparison to other studies (Özkundakci et al., 2010). The application had limited long-term effects on internal loading (Paul et al., 2008), but other trials of alum at higher concentrations, while necessitating the use of a pH buffer in some cases, have been successful for periods up to 15 years (Cooke et al., 1993), with the best results typically recorded in the first 2-3 years (Søndergaard et al., 2007).

Another sediment capping agent; aluminium-modified zeolite (Z2G1) was evaluated in trials on Lake Ōkaro in 2007 and 2009, carried out by the Bay of Plenty Regional Council. The material has a high specific surface area and was engineered to have an enhanced nutrient uptake capacity for phosphorus over natural zeolite compounds (Özkundakci et al., 2010). The agent worked in a similar way to calcite described in Berg et al. (2004); forming a diffusion barrier by binding phosphate released at the sediment/water interface (Özkundakci et al., 2010).

Other management methods aim to disrupt the physical processes that support internal phosphorus loading and microbial regeneration of ammonium in lakes.

Hypolimnetic anoxia can be reduced by hypolimnetic oxygenation; the injection of oxygen in to the hypolimnion to concentrations where internal loading is minimised (Antenucci et al., 2005), or destratification, a mechanical process whereby bubbles are released from near the bottom sediment, simulating upwelling that erodes the base of the thermocline and reduces vertical gradients in oxygen, temperature and other dissolved and suspended particles (Schladow and Fisher, 1995).

Field & Prepas (1997) evaluated the effects of hypolimnetic oxygenation on zooplankton and phytoplankton communities in Amisk Lake, a large eutrophic lake in Alberta. The authors reported reduced phytoplankton biomass in surface waters after hypolimnetic oxygenation. Lackey (1973) used two aerators to destratify a mesotrophic reservoir with a surface area of 0.19 km^2. Results were circumstantial, with decreases in overall phytoplankton biomass, but no changes in the biomass of the cyanobacteria *Anabaena flos-aquae*. Antenucci et al. (2005) evaluated the success of a 'bubble plume' type of aerator in a storage reservoir with a surface area of 19.2 km^2. Post-installation, concentrations of chlorophyll *a* downstream from the aerator declined, and changes in the phytoplankton community; particularly relating to increases in low-light adapted species occurred. Dominance of the cyanobacteria *Cylindrospermopsis raciborskii* was not affected by aeration, however, an overall decline in chlorophyll *a* concentrations was evident. The results of both studies indicate destratification may not be suitable as a management option for all problematic genera, particularly those that are competitive under low-light and nutrient limited conditions.

Reducing planktivorous fish abundances can stimulate a positive population response in zooplankton, intensifying the effects of grazing on primary producers. A number of studies have reported success using biomanipulation to enhance top-down regulation on cyanobacteria. For example, in enclosure experiments by Sarnelle (2007), the zooplankton *Daphnia pulicaria* significantly reduced the biomass of *Microcystis aeruginosa*; a potentially toxic cyanobacteria. Hambright et al. (2007) excluded planktivorous fish from nitrogen-rich ponds, alleviating predation on zooplankton (daphniid), and contrasted the effects of N:P ratios and zooplankton grazing on the abundance of N-fixing cyanobacteria. The study found that grazing pressure had the potential to affect cyanobacterial biomass at similar magnitudes to P-limitation.

1.7 Indicators of lake health

There are a variety of monitoring tools that quantitatively assess a lakes water quality and health as a function of its biological and chemical components. Ecological indicators relate the overall health and functioning of an ecosystem to the presence, diversity and abundance of key biological components. These can be used as early warning signals or indicators of trends (Niemi and McDonald, 2004). In some cases, an organism is so closely dependent on a narrow subset of conditions, that its very presence will confirm the existence of those conditions (Caro and O'Doherty, 1999). Biological indicators can be derived using the Two-way Indicator Species Analysis (TWINSPAN), a hierarchical method proposed by Hill (1979) that characterises habitats based on the presence of species with known ecological preferences (Dufrene and Legendre, 1997).

The health of lake macrophytes can reflect water quality. Lake Submerged Plant Indicators (LakeSPI) was developed by the National Institute of Water and

Atmospheric Research (NIWA), and assesses the extent, diversity and condition of native macrophytes in relation to the impacts of exotic invasive plants (Neilson et al., 2007, Caffrey et al., 2006). LakeSPI has been used by the Waikato Regional Council to detect changes in lake water quality stemming from decreases in the depth extent of submerged plants, and signs of stress relating to numbers of unattached plants (Neilson et al., 2007).

Macroinvertebrates have a wide range of tolerances to changing environmental conditions, including nutrient concentrations and water clarity. Populations reflect lake water quality, with sediments in poorer quality lakes tending to be dominated by highly tolerant Chironomidae and Oligochaeta (Neilson et al., 2007, Gabriels et al., 2010). Macroinvertebrates are increasingly used as bioindicators outside of New Zealand, and have become incorporated into United States and European Union standards for water quality assessments (Neilson et al., 2007). Rotifer assemblages can reflect lake trophic state. The Rotifer Community Index (Duggan et al., 2001) is a quantitative bioindicator that uses rotifer community composition to express lake trophic state, and has been adopted by the Waikato and Auckland regional councils (Fowler and Duggan, 2008).

Increasing cyanobacterial biomass is a common symptom of eutrophication (Smith, 2003). Resolving trends in phytoplankton succession, primary productivity and changes in community composition and biomass can assist in the early detection of declining water quality (Goldman, 1988, Cottingham and Carpenter, 1998). Routine monitoring for cyanobacterial cell concentrations had originally been used to alert authorities to degrading water quality in the Te Arawa lakes of the Bay of Plenty region (Wilding, 2001). From 2008, biovolume

calculations have been opted for as a more representative assessment of public health risk (Wood et al., 2008).

A combination of mean values for chlorophyll *a* concentration (a surrogate for algal biomass), Secchi depth, and total phosphorus (TP) constitute the Trophic State Index (TSI) proposed by Carlson (1977); a numerical indicator of lake health used classify trophic status (e.g TSI 50 $\leq$ 70 eutrophic). Burns et al. (1999) modified the TSI for use in New Zealand lakes, which differ from northern hemisphere temperate lakes in that N more frequently limits productivity (Abell et al., 2010). The Trophic Level Index (TLI) predominantly differs from TSI in the inclusion of total nitrogen (TN) as a variable and a narrower numerical categorisation range. TLI is widely used by regional councils in New Zealand to identify long-term trends in water quality and set management goals (Rutherford, 2003).

Percent annual change (PAC) is used in conjunction with TLI, reducing the confounding influence of seasonal fluctuations in data by identifying significant changes in the four measured variables (chlorophyll *a*, Secchi depth, TP and TN) in relation to each other (Burns et al., 2009). PAC is based on the premise that key variables in a lake that has become more or less eutrophic should reflect the same degree of change toward trophic state by having similar PAC values (Burns et al., 2009).

Hypolimnetic anoxia is a symptom of increased primary productivity, and relates strongly to eutrophication (Borowiak et al., 2010). Volumetric Hypolimnetic Oxygen Demand (VHOD) describes the depletion rate of dissolved oxygen in the hypolimnion, and is regarded to be a reliable indicator of changes in organic matter generation and trophic state within lakes (Hamilton, 2006).

1.8 The importance of representative sampling

Natural ecosystems and their interacting components are complex, nonlinear, and often poorly understood (Holling and Meffe, 1996). Predictable outcomes that are expected are rarely obtained, partly because absolute representations of ecosystems are considered to be impossible in a statistical sense (Irvine et al., 2004). A major constraint of monitoring is that data derived from spatially-limited sampling programmes that do not encompass natural variability will not be representative of the wider lake environment. Results are further confounded when sampling is performed over temporal scales that exceed rates of natural change within the system.

A monitoring type that frequently falls into this category is phytoplankton monitoring (Heaney, 1976). The Rotorua Lakes' cyanobacterial monitoring programme procedure involves vertical tube samples from 0-1 m collected at weekly time scales from popular bathing sites. For the purposes of public health warnings for specific bathing locations, sampling at a weekly intensity may be sufficient to indicate general conditions. However, sampling at this spatial scale and frequency will typically miss around 30% of the spatial variability in chlorophyll across the lake (Kallio et al., 2003, Peters, 2002) and potentially omit major fluctuations in biomass that occur over relatively short time scales (Reynolds, 1984). Therefore, adequate sampling frequencies and spatially-representative sampling scales are paramount for studying lake-wide characteristics, such as changes in biomass or community composition. A major objective of any comprehensive sampling programme will be to first identify the spatial and temporal scales of variation that are relevant to the study.

1.9 Scales of variability in lakes

Spatiotemporal variability in the physical, chemical and biotic components of lacustrine ecosystems is a richly studied subject (Powell and Richerson, 1985, Pinel-Alloul and Ghadouani, 2007, Simon, 1976, Ganf and Oliver, 1982, George and Heaney, 1978). One of the most important physical characteristics of a lake is whether it becomes thermally stratified (Gorham and Boyce, 1989). The stability of thermal stratification is predominantly a function of lake depth, and ultimately determines the susceptibility of the water column to mixing (Kalff, 2002a).

In lakes with moderate stability, long periods of stratification are superimposed by short term mixing events relating to wind stress. These events can operate over a broad range of scales, influencing the distribution of phytoplankton, particulate matter and nutrients, reducing euphotic depth, and eroding temperature and oxygen gradients (Kalff, 2002a). Typical trends of succession in temperate lakes relate to the seasonal availability of light, nutrients and physical variables, including metalimnion development. Intermediate-sized temperate lakes frequently undergo a predictable sequence of succession (Reynolds, 1997b). During winter, the phytoplankton community is poorly diverse, consisting of centric diatoms and flagellates such as cryptophytes (Moss, 1973a, Grover and Chrzanowski, 2006). With increasing warmth and irradiance in spring, blooms of chrysophytes, diatoms, cryptophytes or chlorophytes occur, which are eventually suppressed by herbivorous grazers in late spring (Grover and Chrzanowski, 2006). The onset of stratification in summer results in the spatial segregation of nutrients and light, leading to the dominance of bloom-forming, buoyancy-regulating filamentous and colonial cyanobacterial genera (Reynolds, 1983). *Microcystis* is a colonial cyanobacteria genus that will typically outcompete *Anabaena*, a

filamentous cyanobacteria genus, by proliferating at a rapid rate over short time scales, before stabilising for long periods (Vincent and Dryden, 1989). However *Anabaena* and *Aphanizomenon* have the added ability to fix atmospheric nitrogen, giving these genera a competitive advantage under N-limiting conditions (Reynolds, 1997b). Mixing depth increases in late summer to autumn, and under these conditions pennate and centric (particularly chain-forming, e.g. *Aulacoseira* spp.) diatoms, dinoflagellates and filamentous cyanobacterial species predominate until populations crash with the onset of winter (Grover and Chrzanowski, 2006). The sequence follows a general pathway of decreasing growth rates and increasing investment in resource gathering, as nutrients and other variables become spatially segregated under stratified conditions (Reynolds, 1997b).

Phytoplankton primary productivity is a function of seasonally and spatially variable parameters, including temperature, light and nutrient availability, mixing depth and phytoplankton biomass and community composition (von Westernhagen et al., 2010). In a year-long study determining phytoplankton productivity rates (mg C m^{-3} h^{-1}) in a deep, warm monomictic lake, productivity was found to be seasonally variable, and range over horizontal and vertical spatial scales (von Westernhagen et al., 2010). At 0 m depth, productivity increased 10 to 11-fold at some sites between January and April, yet this was not reflected at 5 m depth, where increases were marginal between November to April (von Westernhagen et al., 2010).

1.10 The Te Arawa Lakes

The central Taupo Volcanic Zone (TVZ) in the North Island is a c. 300 km-long, and 60 km-wide region of intense Quaternary silicic volcanism that has produced over 30 caldera-forming ignimbrite eruptions from 1.6 Ma, and resulted in the

formation of a number of lakes (Houghton et al., 1995, Wilson et al., 1995). The region is home to 12 of the 15 Te Arawa lakes, categorised by trophic state and mixing regime as “eutrophic monomictic”, “mesotrophic monomictic”, “oligotrophic monomictic”, and “meso- and oligotrophic polymictic” (Hamilton, 2003). Trophic states of the Te Arawa Lakes correlate strongly with catchment land use, with higher proportions of exotic forest and pastoral land being associated with the poorest lake water quality (Table 1.1) (Bay of Plenty Regional Council 2010).

The lakes play a central role in attracting domestic and international tourism to the region (Bruesewitz et al., 2011). In the year ending December 1999, Rotorua was a destination for 30.2% of all international visitors to New Zealand (Horn and Simmons, 2002) and 18% of the total employment in the district was dependent on tourism (Fairweather and Simmons, 2000). The water quality of many of the Te Arawa Lakes has measurably declined and this is attributed to land use changes, predominantly the development and intensification of agricultural activities in the surrounding catchments (Özkundakci et al., 2009, Hamilton, 2005).

The Bay of Plenty Regional Council is responsible for managing 12 of the Te Arawa lakes. It uses a variety of monitoring strategies to assess lake water quality, including TLI (Burns et al., 1999), PAC, LakeSPI (Caffrey et al., 2006), and VHOD (Hamilton, 2006). Anchored high frequency monitoring buoys are also located on Lake Rotorua, Lake Rotoiti, Lake Tarawera, and Lake Rotoehu, and transmit data wirelessly to an online database, providing information on water column temperature at 2 m intervals, and dissolved oxygen concentration, phytoplankton pigment concentration (chlorophyll *a*), wind speed and other variables at 15-minute intervals (Zhang, 2010).

Table 1.1 Limnological and catchment data for the 12 Te Arawa Lakes. Adapted from Hamilton (2003) and Bay of Plenty Regional Council (2010).

Lake	2010 Trophic status (3 yearly average TLI)	Lake volume (km^3)	Catchment area (km^2)	Catchment to lake volume ratio (km^{-1})	Average depth (m)	Maximum depth (m)	Agricultural land use (%)
Rotorua	Eutrophic (4.7)	0.802	482.0	601	11	45	65
Tarawera	Oligotrophic (2.9)	2.274	150.0	66	50	87.5	32
Rotoiti	Mesotrophic (3.9)	1.042	578.0	555	31	93.5	62
Rotomā	Oligotrophic (2.6)	0.429	33.9	79	37	83	51
Rotoehu	Eutrophic (4.5)	0.061	42.3	693	8	13	64
Ōkataina	Oligotrophic (2.8)	0.466	63.6	136	39	79	16
Ōkareka	Mesotrophic (3.3)	0.064	17.5	275	20	34	45
Rotokakahi	Mesotrophic (4.0)	0.077	17.5	227	17.5	32	77
Rotomahana	Mesotrophic (4.0)	0.479	89.0	185	60	125	57
Rerewhakaaitu	Mesotrophic (3.7)	0.037	40.6	1107	7	15	86
Tikitapu	Mesotrophic (3.0)	0.026	6.0	227	18	27.5	16
Ōkaro	Hypertrophic (5.3)	0.003	3.6	1084	12.5	18	96

1.11 Lake Ōkaro

Lake Ōkaro (Figure 2.1) is a small hypertrophic, monomictic lake in the central North Island that has become increasingly eutrophic from the mid-1950s, with regular cyanobacterial blooms since the mid-60s (Forsyth et al., 1988). The decline in lake health has been attributed to agricultural intensification in the 3.89 km^2 catchment, and in recent years major restoration initiatives have focused on reducing internal and external nutrient loading in the lake (Paul et al., 2008, Scholes, 2010, Cronin et al., 2006, Özkundakci et al., 2010).

1.12 Previous studies

Lake Ōkaro's phytoplankton biota has been studied in varying detail over the past five decades (Wood et al., 2009). In 1987, Lake Ōkaro and Lake Rotongaio were the focus of an international cyanobacterial dominance forum (Vincent et al., 1987). Research addressed the aspects of the lake environment thought to fundamentally influence cyanobacterial abundance, including mixed layer processes (Imberger and Spigel, 1987), zooplankton grazing (Burns et al., 1987), and attributes of key cyanobacterial genera, including nutrient requirements (Lean et al., 1987), buoyancy properties (Walsby and McAllister, 1987) and photosynthetic productivity (Robarts and Howard-Williams, 1987).

Wood et al. (2009) resolved the historical cyanobacterial communities of Lake Ōkaro using germination experiments and automated rRNA intergenic spacer analysis (ARISA). The authors found evidence of cyanobacteria in sediment cores dated at 100 BP, which suggested there had been no major changes in the akinete-producing cyanobacteria community composition over the past 100 years, and

supported studies which describe trends of increasing cyanobacterial abundance in Lake Ōkaro since the 1950s (Dryden and Vincent, 1986, Flint, 1977).

A year-long analysis of dominant phytoplankton biovolumes and community succession was carried out by Dryden & Vincent (1986), who noted changes in the algal community had occurred since the early 1970s, relating this to increased eutrophication. In a later study, Vincent & Dryden (1989) further resolved phytoplankton succession in Lake Ōkaro, noting temperature was closely correlated to major shifts in community composition, and that large population sizes were typically reached after long periods of slow, persistent growth. The study also found that nitrogen-limited conditions did not necessarily influence the abundance of nitrogen-fixing species, as *Anabaena* were absent during periods of NO_3-N and NH_4-N depletion when PO_4-P concentrations were not considered limiting (Vincent and Dryden, 1989).

Nutrient availability is one of the many variables regulating phytoplankton community composition and biomass (Tilman et al., 1982). A mesocosm survey measuring physiological and growth rate responses of phytoplankton to changing N and P ratios in Lake Ōkaro was conducted by Lean et al. (1987). The study recognised N as the primary nutrient limiting growth in the epilimnion, with chlorophyll *a* concentrations increasing by 250% in enclosures where N was added singly. Phosphorus appeared to have a complimentary effect on phytoplankton growth when N was not limiting, with an 800% increase in chlorophyll *a* in enclosures treated with both N and P. Even in extremely phosphate-deficient conditions (as indicated by physiological assays), P did not stimulate growth on its own, and chlorophyll *a* concentrations declined in enclosures where only P was added.

Imberger & Spigel (1987) studied microstructure stratification profiles for a single day in Lake Ōkaro on 26 February 1987. The study used eight sampling stations around the lake to resolve water column stability under prevailing wind conditions. During the study, a thermocline was located at c. 7 m, and "light and variable" wind of undisclosed velocity was found to be sufficient to cause internal wave activity (Imberger and Spigel, 1987). Water clarity was high enough to allow light to penetrate several metres, and stratification in the upper epilimnion was negligible, increasing the influence of wind mixing and boundary layer turbulence (Imberger and Spigel, 1987).

1.13 Scales of temporal variability

Temperatures in Lake Ōkaro are highly variable over the course of a year. During summer, surface waters reach up to 23 °C, decreasing to around 10 °C at the bottom of the water column. During isothermy temperatures decrease to a minimum of 8 °C (Dryden and Vincent, 1986, Vincent and Dryden, 1989). The stability of the metalimnion (resistance to mixing) varies over much shorter temporal scales, being regulated by surface heat flux, lake bathymetry, water clarity (biological activity and suspended solids), and wind (Imberger and Spigel, 1987, Vant and Davies-Colley, 1986, Davies-Colley, 1987).

The availability of nutrients for primary productivity is strongly influenced by the resistance of the water column to vertical mixing (Spigel and Imberger, 1987). As a warm monomictic lake, Lake Ōkaro undergoes a single extensive stable stratification period for c. 8 months of the year (Özkundakci et al., 2010). Schmidt stability; a measure of water column stability, is generally at its highest from December through January (Paul, 2006). The hypolimnion becomes anoxic for the

majority of the thermal stratification period (Özkundakci et al., 2011), and leads to internal loading of c. 2,410 kg N year, and 380 kg P year (Burns et al., 2009).

Lake Ōkaro is fully mixed for c. 4 months (Özkundakci et al., 2010). The depth of the metalimnion varies throughout the season, with an average depth of approximately 6 m (Dryden and Vincent, 1986, Paul, 2006). From May, atmospheric heat loss reduces the density gradient between the oxic surface and anoxic bottom waters, resulting in the erosion of the metalimnion and eventual overturn of the lake (Kalff, 2002a, Paul, 2006). With lake overturn, ammonium and sediment-derived P are resuspended into the epilimnion, becoming available for algal growth (Spears et al., 2006).

The phytoplankton community in Lake Ōkaro progresses through a sequence of successional steps through the year. The steps of the dominant taxa have been detailed by (Dryden and Vincent, 1986) as bloom-forming *Microcystis* and *Anabaena* cyanobacterial species from summer through to winter, overlapped by centric diatoms in autumn and winter, and followed by colonial chlorococcaleans in spring (Dryden and Vincent, 1986).

1.14 Spatial variability

Spatial heterogeneity, or "patchiness," generally describes variability at horizontal scales between about 10 m and 100 km, and at vertical scales between about 0.1 m and 50 m (Mackas et al., 1985). Phytoplankton patchiness is a known characteristic of phytoplankton in small thermally-stratified lakes (George and Heaney, 1978, Fasham, 1978), and can be caused by a number of factors. These include boundary-layer mixing associated with complex benthic topography (Imberger and Spigel, 1987), the physical characteristics of the resident

phytoplankton (e.g. buoyancy or depth-regulation) (George and Heaney, 1978), up- and downwelling at lake margins (George and Heaney, 1978), horizontal gradients in nutrient inputs (Fee, 1976), spatial variability in grazing effects (Therriault and Platt, 1978), wind forcing and water currents (e.g. Langmuir circulation cells) (Horne and Schneider, 1995), and internal waves (George and Heaney, 1978).

Phytoplankton surface blooms are generally formed by cyanobacterial and dinoflagellate species, and are a feature of productive lakes (Serizawa et al., 2010). It is understood that accumulation at the water surface is an adaptive strategy to maximise photosynthesis (Reynolds et al., 1981). Spatial variability during a surface bloom is pronounced on a vertical scale by high concentrations of phytoplankton at or near the surface during calm conditions (Reynolds and Walsby, 1975), and on a horizontal scale by uneven distribution of surface biomass, due to the influence of wind stress (Regel et al., 2004).

Deep chlorophyll maxima: In highly transparent lakes, phytoplankton biomass may become concentrated at intermediate depths, forming a deep chlorophyll maxima (DCM) (Hamilton et al., 2010). Gervais (1998) and Grigorszky et al. (2003) state the vertical positioning of cells can relate to the avoidance of damaging ultraviolet light levels (Modenutti et al., 2004), vertical gradients in mixotroph and zooplankton grazing intensity (Tittel et al., 2003, Longhurst, 1976), depth-differential sinking of phytoplankton (Padisák et al., 2003b), elevated nutrient concentrations at or below a thermocline (Gervais, 1998), *in situ* growth of autotrophic or mixotrophic algae (Padisák et al., 2003b) and behavioural aggregations of flagellates (Cullen, 1982, Grigorszky et al., 2003). DCMs are considered to be a feature of oligotrophic lakes (Serizawa et al., 2010), and are

able to be formed when the euphotic depth exceeds the maximum depth of the epilimnion (Hamilton et al., 2010). The occurrence of DCM in hypertrophic and hypertrophic lakes is not widely reported, however, some evidence exists for DCM formation in lakes with lower water quality. Klausmeier & Litchman (2001) hypothesised that a DCM formation could occur in eutrophic lakes at a depth where two components necessary for algal growth were equally limiting (e.g. a vertical separation of light and limiting nutrients). Gervais et al. (2003) state that a nutrient-deficient epilimnion, coupled with a metalimnetic oxygen gradient and nutrient-rich, anoxic hyplimnion will support sub-surface maxima of cyanobacteria or cryptophytes in mesotrophic lakes.

The physical, chemical and biological processes of a lake all combine to produce a complex system that is highly variable both in space and time; from broad-scale weather patterns down to micro-scale cellular processes. In order to be considered representative, monitoring must encompass spatial and temporal scales that are relevant to the natural variability of the subject and its setting. Spigel & Imberger (1987) discuss the importance of accounting for the rapid response of phytoplankton cells to changes in nutrients and light. They state that in order to explain short-term variations in algal properties, one must first resolve the small length and time scales relevant to phytoplankton (Spigel and Imberger, 1987).

1.15 Overview and Objectives

An analysis of spatial and temporal variability of phytoplankton community composition and biomass, and the physicochemical parameters governing these variables, forms the basis for this body of work. It is intended that the knowledge gained therein will assist in the interpretation of how key processes influence Lake Ōkaro's phytoplankton biota.

Objectives:

- To capture the extent of the vertical and horizontal spatial variability of phytoplankton biomass, nutrients, temperature and other parameters over a 15-month period in eutrophic, monomictic Lake Ōkaro, including two consecutive summers, and to determine the underlying processes.
- To ascertain the effectiveness of using a central lake station to estimate the vertical fluorescence characteristics of the whole lake.
- To capture two periods of contrasting phytoplankton distribution; an early-summer cyanobacterial, and late-summer dinoflagellate, and to contrast the vertical spatial and short-term temporal features of these periods.

2 Methods

2.1 Study stations

Lake Ōkaro (Figure 2.1) (38°17’55.77”S, 176°23’41.09”E) is a warm monomictic, caldera lake in the Waiotapu geothermal area of the central North Island, New Zealand (Hedenquist and Henley, 1985, Vincent et al., 1987). It is the most eutrophic of the 12 major Te Arawa Lakes. It has been the subject of a number of water quality studies and trials; several of which have focussed on restoration through reductions in internal or external nutrient loading (Özkundakci et al., 2010, Paul et al., 2008, Lean et al., 1987). The lake has a surface area of 0.32 km^2, and average and maximum depths of 12 m and 18 m, respectively (Vincent et al., 1987). Lake Ōkaro’s bathymetry has been described as “complex” (Imberger and Spigel, 1987) because the bottom topography is characterised by several centrally-located low-lying ridges, the tallest of which rises 5 m from the benthos (Hardy, 2005). There are two main inflows from small unnamed streams that enter the north-west margin of the lake through a constructed wetland (Figure 2.1) (Özkundakci et al., 2011). The Haumi Stream is the only outflow, draining the lake at its southern end (Forsyth et al., 1988) (Figure 2.1). Water in the lake has a theoretical mean residence time of 1.5 years (Özkundakci et al., 2011). Over 95% of the lake catchment area of 3.67 km^2 is exotic pasture and forest (Bay of Plenty Regional Council 2010) and agriculturally derived nutrients have supported recurrent blooms of cyanobacteria since the early 1960s (Hamilton, 2005, Forsyth et al., 1988, Özkundakci et al., 2010).

Lake Ōkaro is thermally stratified for around 8-9 months of the year. In the 2007-2008 period stratification persisted for 261 days, beginning intermittently as early as August and ending in mid-June (Özkundakci et al., 2011). From 1955 to 1964

Lake Ōkaro's hypolimnion became progressively anoxic as water quality declined (Forsyth et al., 1988). Bottom waters become deoxygenated within one month of thermal stratification (Gibbons-Davies, 2003), and remain anoxic (DO $\leq$ 1 mg L^{-1}) for the majority of stratification; typically persisting from late September to late May (Özkundakci et al., 2011). The extended periods of anoxia enhance internal nutrient loading, with estimates of 2410 kg N yr^{-1} and 380 kg P yr^{-1} from the bottom sediments (Burns et al., 2009). These high values mean major reductions in external loading are required in order to further improve the lake TLI. Lake water quality improved in the period 2007-2009 (Bay of Plenty Regional Council 2010), and the three-year average trophic level index (McFarland et al.) of 5.1 is consistent with a hypertrophic status (Scholes, 2010).

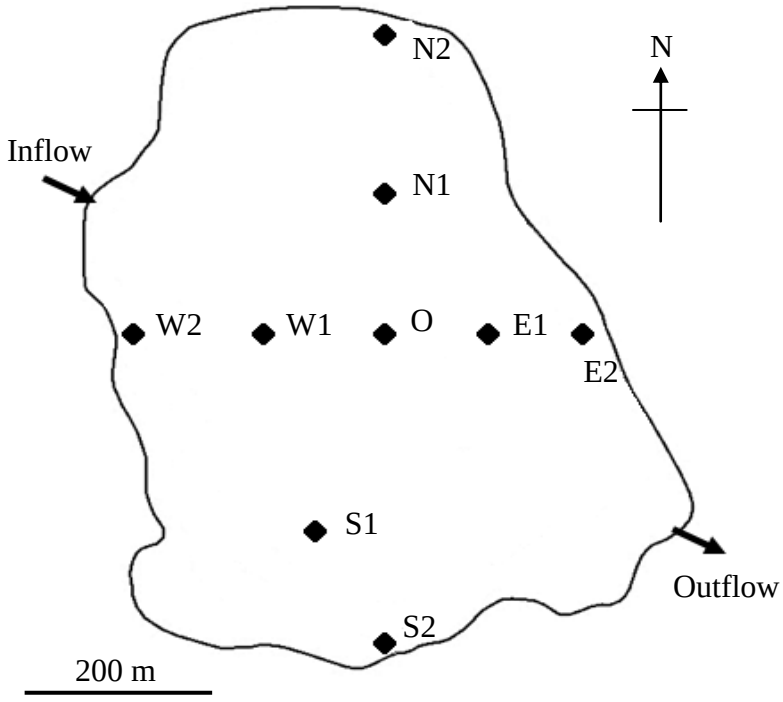


Figure 2.1: Map of Lake Ōkaro showing sampling stations and location of the inflows and outflow (modified from Özkundakci et al. (2010)).

Table 2.1: Limnological characteristics of Lake Ōkaro (adapted from Cronin et al. (2006)

Lake Surface area	0.32 km^2
Catchment area	367 ha (excluding lake)
Lake surface height	423 m above sea level
Average depth	12 m
Deepest point	18 m
Trophic state	Hypertrophic
Annual mean TP (surface)	46.5 mg m^{-3}
Annual mean TN (surface)	803.0 mg m^{-3}

2.2 Field methods

Weekly monitoring was conducted from 1 December 2009 to 2 February 2010, coinciding with thermally stratified conditions. Monthly monitoring began thereafter, concluding on 26 October 2010, and fortnightly monitoring resumed on 13 January 2011 and concluded on 11 March 2011. Routine monitoring included nine stations on Lake Ōkaro, including eight mid-lake and near-shore stations of north-south and east-west orientation, and one central lake station (Figure 2.1). Station S1 was at the deepest point in the lake (18 m), and is used by the Bay of Plenty Regional Council for routine monitoring as well as being used for earlier studies (Özkundakci et al., 2010, Vincent et al., 1987). Routine monitoring was performed between the hours of 08:00 h and 11:00 h, generally taking 1 h to complete. Station W1 was sampled over two separate 24-h periods (18 November, 2010 and 25 March, 2011) at intervals of 3-5 h.

Table 2.2: Geographical position and depth of sampling stations with associated sample methods

Station	Coordinates	Depth	Samples taken (depths in brackets)
N1	38°17’49.16”S, 176°23’41.09”E	13.7 m	Seabird electronics probe (CTD) for temperature, conductivity, fluorescence, pH, dissolved oxygen, photosynthetically active radiation (PAR)
N2	38°17’44.90”S, 176°23’41.09”E	10.2 m	CTD
E1	38°17’55.77”S, 176°23’45.87”E	13.9 m	CTD
E2	38°17’55.77”S, 176°23’51.77”E	5.8 m	CTD, dissolved nutrients (0, 3 m)
O	38°17’55.77”S, 176°23’41.09”E	15.9 m	CTD, dissolved nutrients (0, 3, 6, 9, 12, 14 m)
S1	38°18’02.32”S, 176°23’38.27”E	18.0 m	CTD, microscopy, chlorophyll *a* (0, 15 m)
S2	38°18’05.80”S, 176°23’41.09”E	7.5 m	CTD
W1	38°17’55.77”S, 176°23’36.29”E	15.0 m	CTD
W2	38°17’55.77”S, 176°23’30.41”E	8.2 m	CTD

2.3 Field measurements

A Seabird Electronics 19plus Seacat Profiler (Seabird Electronics, USA) hereby referred to as a CTD was used to resolve vertical profiles of temperature, pH, and conductivity, and was equipped with additional sensors for fluorescence (Turner Designs CYCLOPS-7), dissolved oxygen (SBE 43 Dissolved Oxygen Sensor), and photosynthetically active radiation (PAR) (LI-192SA Underwater Quantum Sensor). The CTD was deployed at all stations following a two-minute equilibration period. Profiles of fluorescence were checked for accuracy using biomass estimates derived from manual phytoplankton counts, with species biovolumes taken from taxonomic literature. On several occasions profiles were

also directly compared with chlorophyll *a* fluorescence from a second CTD (Chelsea Instruments Ltd) that was run at the same time.

A 10-L Schindler-Patellas trap was used to retrieve discrete depth samples. A breakdown of the subsample applications by station is given in Table 2. One sub-sample for microscopic enumeration was fixed immediately with 1% Lugols iodine solution, and stored in a 250 mL^{-1} specimen cup. Both preserved and unfixed samples were stored on ice in the dark. Additional phytoplankton samples were collected for microscopic enumeration from 0 m on 18 November, 2010, and from 0, 2, 4, 6, 7, 8, 9, and 10 m on 25 March, 2011 (station W1) and preserved with 1% Lugols solution.

Chlorophyll *a* samples were collected from depths of 0 m and 15 m (station S1). Samples were filtered immediately using a Swinnex 25 mm filter holder (Millipore), a Luer-Lok 60 mL^{-1} syringe (BD Biosciences) and a 0.45 µm glass fibre filter (GC50, Advantec). Filtered volume in each case was 60 mL^{-1}. Filters were folded in half, immediately wrapped in aluminium foil and stored on ice in the dark.

The dissolved nutrient species ammonium (NH_4-N), nitrite-nitrogen (NO_2-N), nitrate-nitrogen (NO_3-N), and dissolved reactive phosphorus (PO_4-P) were collected from depths of 0 and 3 m (station E2), and 0, 3, 6, 9, 12, and 14 m (station O). Samples were filtered immediately with a Swinnex 25 mm filter holder (Millipore), a Luer-Lok 60 mL^{-1} syringe (BD Biosciences) 0.45 µm glass fibre filter (GC50, Advantec) and stored in 50 mL^{-1} polypropylene conical centrifuge tubes (Falcon, BD Biosciences), and kept in the dark, on ice, until transfer to the laboratory freezer (-20 °C) approximately 8 hours after collection.

2.4 High-frequency sampling

On 18 November 2010 and 25 March, 2011, station W1 was monitored at three-hourly frequency. The purpose of the monitoring was to examine sub-daily variations in the vertical distribution of phytoplankton chlorophyll and composition. At both stations CTD profiles were taken, and a laptop running Sea-Bird Seasave-Win32 and Sea-Bird DataProcessing-Win32 software (Seabird Electronics, USA) were used to resolve profiles of fluorescence immediately after each cast in order to then target points of interest for subsequent discrete depth sampling. Samples were collected using a Schindler-Patellas trap at 0 m (18 November, 2010), and 0, 2, 4, 6, 7, 8, 9, and 10 m (25 March, 2011), and fixed in 1% Lugols iodine.

2.5 Laboratory methods

Concentrations of nutrients NH_4-N, NO*x*–N and PO_4-P were determined using an AQUAKEM 200 cD discrete photometric analyser (Thermo Scientific). Standard AQUAKEM operating procedures were followed at all times. NO_3-N was determined by subtracting NO_2-N from NO*x*-N. NO*x*-N was analysed using Standard Methods using (SMWW/APHA Standard Method 4500 - NOx^- E, and EPA Method 353.4 of Zhang et al. (1997) with a mean detection limit of 0.001 mg L^{-1}). NO_2-N concentrations were determined by SMWW/APHA Standard Method 4500 NO_2^- B with a mean detection limit of 0.001 mg L^{-1}. PO_4-P was analysed using Methods for the Examination of Water and Associated Materials: Phosphorus in Waters, Sewage and Effluents 1981. ISBN 011751582.5, and EPA Method 365.1 with a mean detection limit of 0.001 mg L^{-1}. NH_4-N was analysed for using Methods for the Examination of Water and Associated Materials:

Ammonia in Waters 1981, ISBN 0117516139 with a mean detection limit of 0.002 mg L^{-1}.

Microscopy

Phytoplankton enumeration was undertaken using an Olympus IX71 inverted light microscope, with UPlanFL N 20×/0.50 and UPlanFL N 40×/0.75 (Japan) objectives to achieve magnifications of 200× and 400×, respectively. Keys from Baker & Fabbro (1999), and Joosten (2006) were used to identify phytoplankton to species level where possible, and specific species' biovolumes were taken from studies by Dryden & Vincent (1986) and Olenina et al. (2004).

Phytoplankton enumeration was carried out following protocol established by Sandgren & Robinson (1984). Samples were stored out of light at all times and additional Lugols iodine was added when needed. Preliminary densities of the dominant species were estimated prior to settling in order to establish sub-sample volumes that would capture between 100 and 150 dominant planktonic units in a single central transect. Each sample was transferred with an autopipette (Eppendorf) to Ütermohl chambers, and reverse osmosis (RO) water was added up to a total volume of 10 mL^{-1}. Chambers were then covered and the contents settled for a minimum period of 6 h on a spirit-level glass plate.

A single central transect was counted on the Olympus IX71 inverted light microscope, and a running tally of all phytoplankton taxa was kept. A half plate count was subsequently carried out to enumerate all species with a concentration of less than 45 planktonic units per transect. The methodology of Paul et al. (2007) was used for filamentous and colonial aggregate species. When high concentrations of filamentous species were encountered, the number of cells comprising the first 30 filaments was averaged, and multiplied by the total

number of filaments when calculating the total cell count. For colonial aggregations, a 10 x 10 square whipple grid was used to count the average number of visible cells per grid square which was then multiplied by the total number of squares occupied by the colony. The depth of the colony was found by focusing through the depth of field to count the number of cells.

Cell concentrations were calculated as:

$N = C\ f\ (A/b\ a\ V)$

where:

N = number of planktonic units per mL^{-1} in original water sample

C = total number of planktonic units counted in all transects

A = total area of bottom of the settling chamber (mm^2)

a = total area of transect = (mm^2)

b = number of transects counted

f = dilution or concentration factor

V = volume of lake water that was settled (mL^{-1})

Chlorophyll a

Chlorophyll *a* extraction and analyses were carried out in accordance with standard protocol for fluorometric determination of chlorophyll *a* pigments (Paul,

2010) on a pre-calibrated Turner design 10 AU fluorometer. Frozen filters were thawed prior to processing. Each filter was combined with 5 mL^{-1} 90% $MgCO_3$-buffered acetone and ground with a mortar and pestle to fine slurry in a dimly-lit room. An additional 4-5 mL^{-1} of buffered acetone was added, and the slurry and remaining material were transferred to a 15 mL^{-1} centrifuge tube (BD Falcon) and topped up to 10 mL^{-1} with buffered acetone solution. Tubes were sealed with caps and shaken, then covered in aluminium foil and steeped for 2-24 hours at 4 °C in the dark. Samples were shaken once during this period. After steeping, the settled contents were re-suspended by vigorous shaking, and transferred to a Jouan B4i centrifuge for 10 minutes at 3300 rpm. Samples were then covered in aluminium foil and left to stand for 30 minutes.

The fluorometer was switched on 30 minutes prior to fluorometric analysis. Fluorometric analysis of 5 m L 90% buffered acetone solution in a clean glass cuvette was carried out as an analytical blank. Two replicates were taken of this step, and outputs were averaged. These values were subtracted from subsequent readings. Each sub-sample was processed individually, with 5 m L of sample supernatant added to a clean glass cuvette, then placed into the fluorometer for analysis. Samples were progressively diluted with buffered acetone by a factor of 2, 4 or 8 when chlorophyll levels were above the detection threshold. Acidification corrected for background levels of phaeopigments, with 150 µL of 0.1 N HCl thoroughly mixed into samples and left for 90 s before fluorescence was re-recorded.

Chlorophyll *a* concentrations were calculated as:

$$Chl\ a\ (\mu g\ L^{-1}) = F_s\ [(r/r\text{-}1)\ (R_1 - R_2)]\ [(V_e\ x\ df)/V_f\ ]$$

Where:

F_s = response factor for sensitivity setting (from most recent fluorometer calibration)

R_1 = reading before acidification minus blank reading

R_2 = reading after acidification minus blank reading

r = acidification coefficient (average of the unacidified and acidified readings of pure chlorophyll *a*)

df = dilution factor

V_e =extraction volume (mL^{-1})

V_f =volume of water filtered (mL^{-1})

2.6 Data analysis

Wind speed (m s^{-1}) and direction, and solar radiation (MJ m^{-2}) were taken from Rotorua Airport AWS Station B86133 (38.107 S, 176.316 E), 20 km north of Lake Ōkaro.

Metalimnion extent was determined using the program Lake Analyzer (Read et al., 2011). At a temperature of 9.5 °C (considered as the representative hypolimnion temperature in Lake Ōkaro) a temperature difference (ΔT) of 0.225 ^{o}C is

equivalent to a density difference ($\Delta\rho$), of 0.0455 kg m^{-3}. Therefore a vertical density gradient of 0.05 kg m^{-3} m^{-1} was used to define the metalimnion using the LakeAnalyzer programme. The value of ΔT of 0.225 ^{o}C is similar to that used to define significant density gradients in studies by Sherman et al. (1998) and Hamilton et al. (2010).

Pearsons correlation analyses was undertaken using STATISTICA 9 software to determine relationships within and between stations for fluorescence and temperature. Significant relationships were set at $P \leq 0.05$.

Thermocline depth (z_{mix}) was calculated as dT/dz = minimum, based on vertical temperature profiles from the CTD (Hoare and Spigel, 1987, Hamilton et al., 2010), excluding the uppermost 1 m of the water column where diurnal surface water heating sometimes created a strong but temporary (diurnal) density gradient. Solvent-extracted chlorophyll *a* samples collected from station S1 at 15 m depth were compared with CTD chlorophyll *a* fluorescence values. The CTD data were averaged between 15 m and 15.5 m to account for the existence of a potential gradient in the length of the Schindler-Patellas trap) (R^2 = 0.50, n = 12) (Hamilton et al., 2010).

The light attenuation coefficient (K_d) was resolved from vertical profiles of photosynthetically active radiation (PAR), collected at station S1 by the Bay of Plenty Regional Council during routine monitoring. The K_d value was found by expressing the natural log of the photosynthetically active (PAR) versus depth in a scatter plot, then truncating data in the upper and lower depths to achieve a linear regression of at least R^2 = 0.95. From this, K_d was derived from the natural log-transformed linear regression formula.

For example, a regression formula indicated by:

$y = -0.4656x + 2.6117$, gives

$z_{eu} = 2.6117$ m

$K_d = (2.6117/0.4656)/2.6117$ m^{-1}

$K_d = 2.1478$ m^{-1}

From 17 December 2009 to 20 April 2010, PAR calculations gave an extremely deep z_{eu} value (11.1 – 17.0 m) at station S1. This was not expected, given the high trophic status of Lake Ōkaro. To test for the possibility of error, an approximate relationship was derived from Secchi depth (z_s); a visual representation of water clarity. Tilzer (1988) showed $z_{eu} = \sim 5 \sqrt{z_s}$. Subsequent calculations showed that the PAR-calculated z_{eu} values from 17 December 2009 to 25 March 2010 differed from the Secchi-calculated z_{eu} by a mean of 4.0 m, but from 20 April 2010 to 29 March 2011 PAR and Secchi calculated z_{eu} differed by a mean of 0.1 m (Figure 9.1).Previous studies indicate December – March z_{eu} in Lake Ōkaro (1995-1996) is between 0.9 and 2.3 m (Paul, 2006). This suggested an error in the PAR-calculated z_{eu} values from 17 December 2009 to 25 March 2010, and thus a decision was made to omit these values from the study.

On the 29 June 2010 and 11 August 2010, high abundances of the submerged macrophyte *Lagarosiphon major* at station E2 were identified as a source of error in chlorophyll fluorescence measurements. These data have also been removed from the data set.

3 Results: Spatial variability

3.1 Relationships between thermocline depth, euphotic depth, and chlorophyll fluorescence

Solvent extracted chlorophyll *a* was not statistically correlated with chlorophyll fluorescence at 0 m depth, with Pearson's correlation of 0.37 (n = 11). However the relationship was statistically significant at 15 m depth 0.70 (n = 10).

Chlorophyll peak fluorescence and thermocline depth (dT/dz) data compiled from CTD casts for stations S2 (shallow, shoreward), and W1 (deep, mid-lake) were closely aligned between December 2009 to 11 March 2011; (Figure 3.1). At station W1 the depth of peak fluorescence increased with thermocline depth to 10.2 m (27 April 2010) after which Lake Ōkaro fully mixed. At station S2, the same relationship was observed until the boundary layer approached the maximum depth of the station (7.5 m; 02 February 2010), and the depths of peak fluorescence and the thermocline fluctuated synchronously until the lake destratified. Lake Ōkaro had restratified by 28 September 2010 at a depth $\leq$ 5 m. From 28 September 2010 to 11 March 2011 the thermocline depth and peak fluorescence at S2 and W1 became closely aligned until the end of the study period. Euphotic depth (z_{eu}) was calculated based on the profiles of photosynthetically active radiation (PAR) at station S1. It was calculated as the depth at which PAR was 1% of the maximum value recorded at the surface. Euphotic depth was greater than the depths of station W1 and S2 peak fluorescence and thermocline at all times (Figure 3.1). The euphotic depth was relatively stable over the mixed period (20 March 2010 to 29 September 2010) with a mean depth of 9.46 m. From 29 September 2010 to 18 November, z_{eu} decreased in depth reaching a minimum of 2.4 m coinciding with restratification,

becoming more closely aligned with the depths of the thermocline and peak fluorescence for the remainder of the study period (≤ 4 m vertical range).

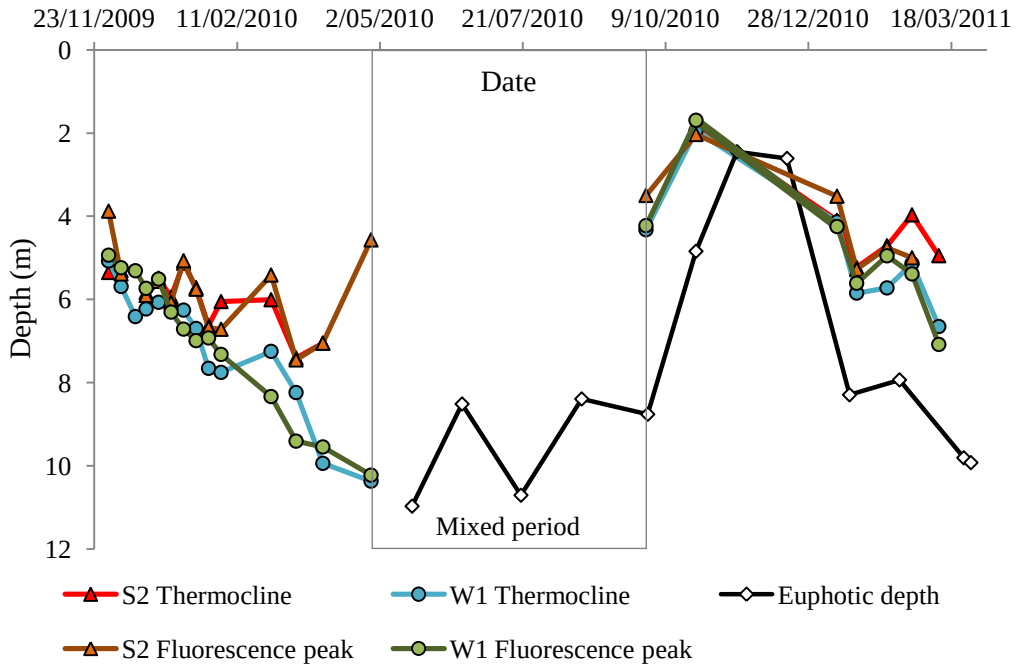


Figure 3.1: Thermocline depth and peak fluorescence depth of a shallow station (S2) and a deep station (W1) from 01 December 2009 – 11 March 2011, and euphotic depth at station S1 from 17 December 2009 – 29 March 2011.

The relationship between DCM depth and thermocline depth was not restricted to stations W1 and S2. Statistically significant ($P \leq 0.05$) correlations existed between all deep stations (Table 1), indicating thermocline depth and the depth of the fluorescence maxima was in general horizontally homogenous. Deep stations had the greatest number of statistically significant relationships, both for the depth of peak fluorescence and thermocline depth. The most representative station for peak fluorescence depth appeared to be S1, and the station with the fewest fluorescence correlations was E2. The most re Ō ative station for thermocline depth was W1, and the least representative station was E2. Overall, there was

greater inter-station variability associated with thermocline depth (21 significant correlations) than the depth of peak fluorescence (30 correlations).

Table 3.1: Pearson correlation coefficient values for thermocline depth and depth of maximum fluorescence for different stations (see Figure 2.1 for location of stations). Significant correlations ($P \leq 0.05$) are shown in bold.

		Depth of maximum fluorescence								
Thermocline depth	**Station**	W2	W1	O	S1	S2	E2	E1	N2	N1
	W2		**0.55**	0.47	**0.63**	**0.7**	0.4	**0.65**	0.27	**0.7**
	W1	0.36		**0.78**	**0.98**	**0.92**	**0.71**	**0.98**	**0.94**	**0.93**
	O	0.28	**0.98**		**0.76**	**0.55**	0.54	**0.79**	**0.92**	**0.73**
	S1	0.4	**0.9**	**0.88**		**0.93**	**0.79**	**0.97**	**0.93**	**0.9**
	S2	0.15	**0.54**	**0.5**	**0.53**		**0.7**	**0.92**	**0.69**	**0.92**
	E2	-0.1	0.31	0.25	0.31	0.31		**0.76**	0.52	0.47
	E1	0.39	**0.99**	**0.97**	**0.89**	**0.57**	0.31		**0.94**	**0.95**
	N2	0.29	**0.91**	**0.93**	**0.84**	0.42	0.37	**0.91**		**0.87**
	N1	**0.62**	**0.96**	**0.93**	**0.93**	**0.51**	0.24	**0.95**	**0.87**	

There was very little horizontal variation in Schmidt stability (J m^{-1}) amongst deep stations (Figure 3.2). From 01 December 2009, Schmidt stability gradually increased, reaching a maximum of 449 J m^{-1} on 02 February 2010 (W1). Schmidt stability began to decline significantly from 02 March 2010, and was $\leq$ 2 J m^{-1} on 29 June 2010 corresponding to the period when the lake was fully mixed. Schmidt stability increased thereafter, reaching a maximum of 422.4 J m^{-1} on 24 February 2011 (W1).

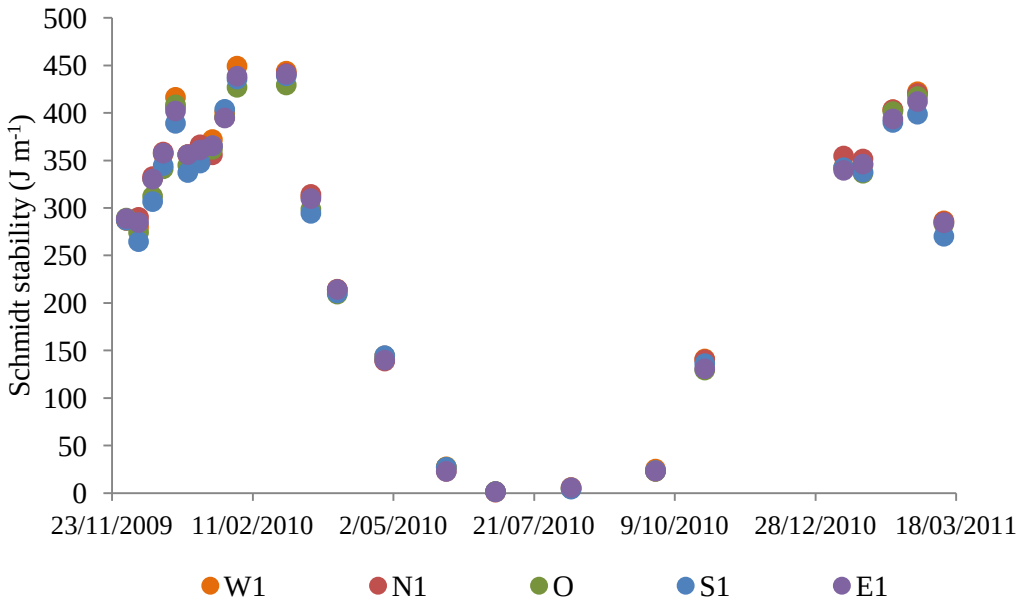


Figure 3.2: Schmidt stability at deep stations (station names are given on the inset) from 01 December 2009 – 11 March 2011.

During thermally stratified periods of the study, fluorescence profiles in Lake Ōkaro were characterised by a deep chlorophyll maximum (DCM). The DCM depth was horizontally homogenous when conditions were stratified, and was in close proximity to thermocline depth (Figure 3.3). From 01 December 2009 to 29 December 2009, thermocline depth was greater than DCM depth in all cases. From 05 January 2010 to 27 April 2010, DCM depth was generally greater (mean 0.37 m) than thermocline depth. Destratification and mixing were first evident on 01 June 2010, at which time peak fluorescence depths were highly variable between lake stations (Figure 3.3). On 28 September 2010 Lake Ōkaro had restratified and, like the summer period of the preceding year, the horizontal variability associated with the DCM began to decline and DCM depth increased in close proximity to the thermocline.

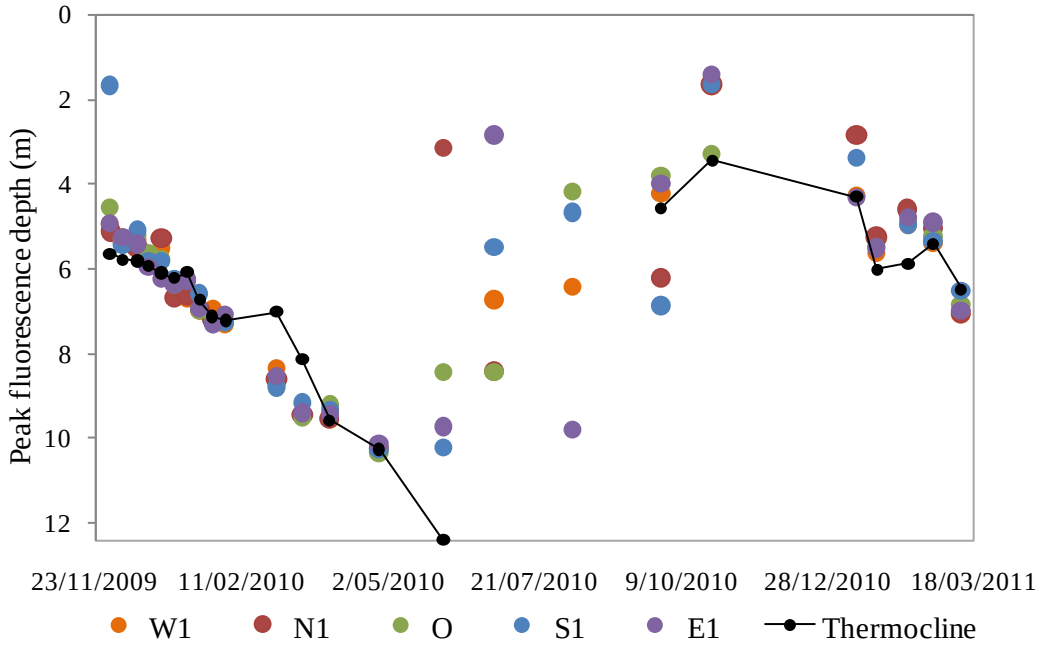


Figure 3.3: Depth of peak fluorescence with mean thermocline depth at deep stations (station names are given on the inset) from 01 December 2009 – 11 March 2011. No thermocline was present from 01 June 2010 until 28 September 2010.

During the period of stratification from 01 December 2009 to 31 March 2010, maximum peak fluorescence values were highly variable among stations. There was no discernible trend for any particular station to have higher or lower peak fluorescence (Figure 3.4). From 02 March 2010, variability in peak fluorescence values began to diminish, and from 27 April 2010 to 26 October 2010 fluorescence was almost homogenous across stations with a mean $\leq$ 20 relative fluorescence units (RFU). Mean chlorophyll fluorescence increased to $\geq$ 20 RFU from 13 January 2011 to 11 March 2011, and the degree of variability in DCM also increased. There were comparative levels of horizontal variability in DCM biomass between January and March in 2010 and 2011.

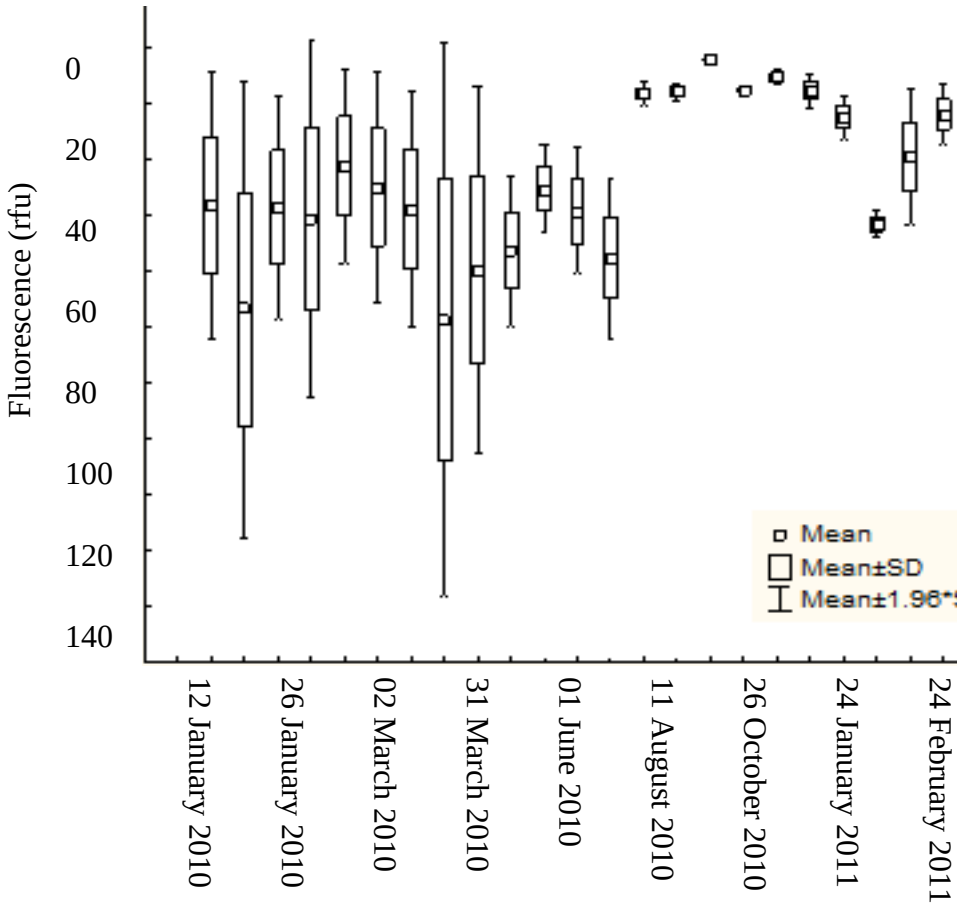
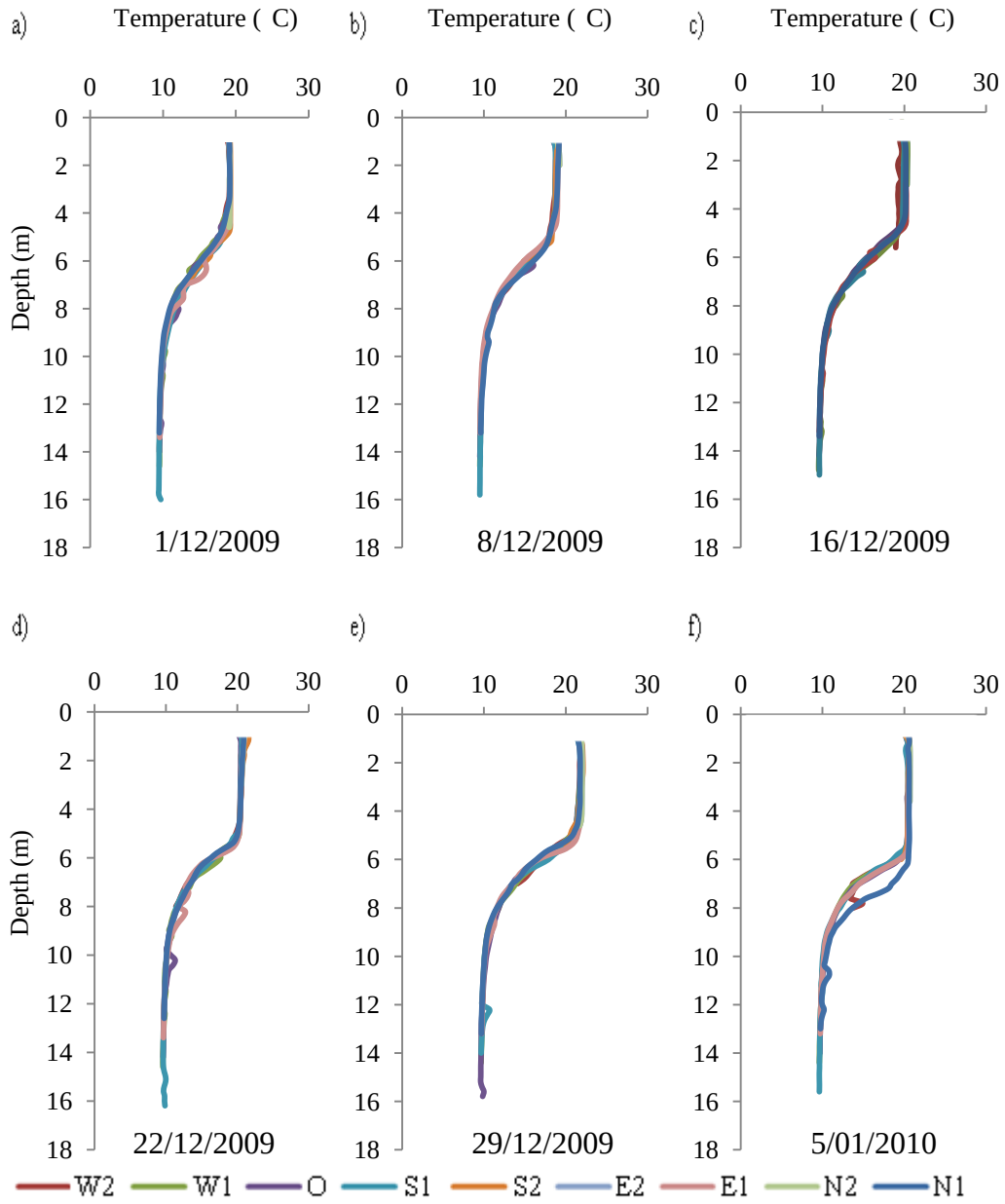


Figure 3.4: Mean values of chlorophyll fluorescence at deep stations (W1, N1, O, S1 and E1) from 01 December 2009 to 11 March 2011.

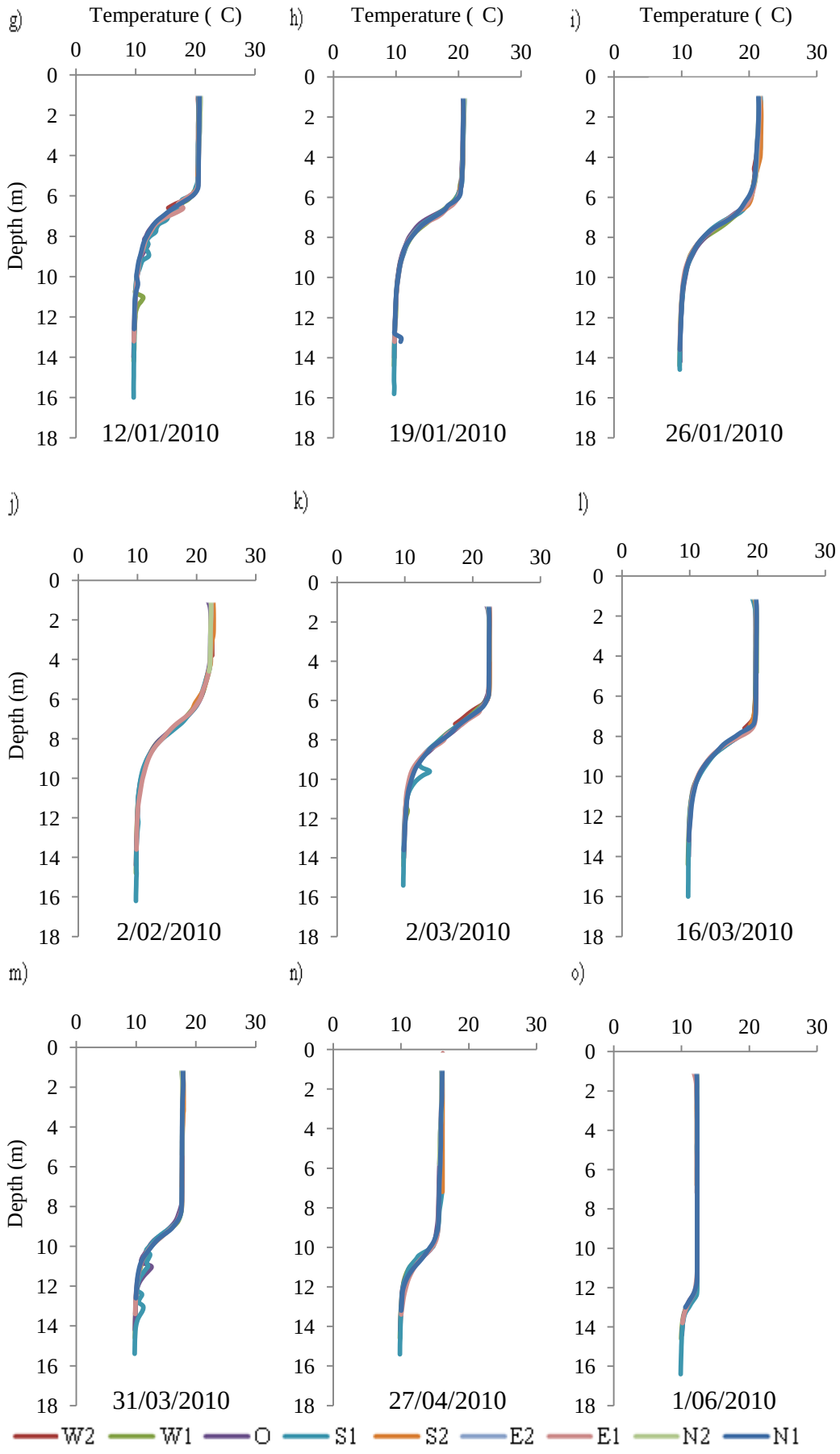
3.2 Horizontal variability

a. Temperature

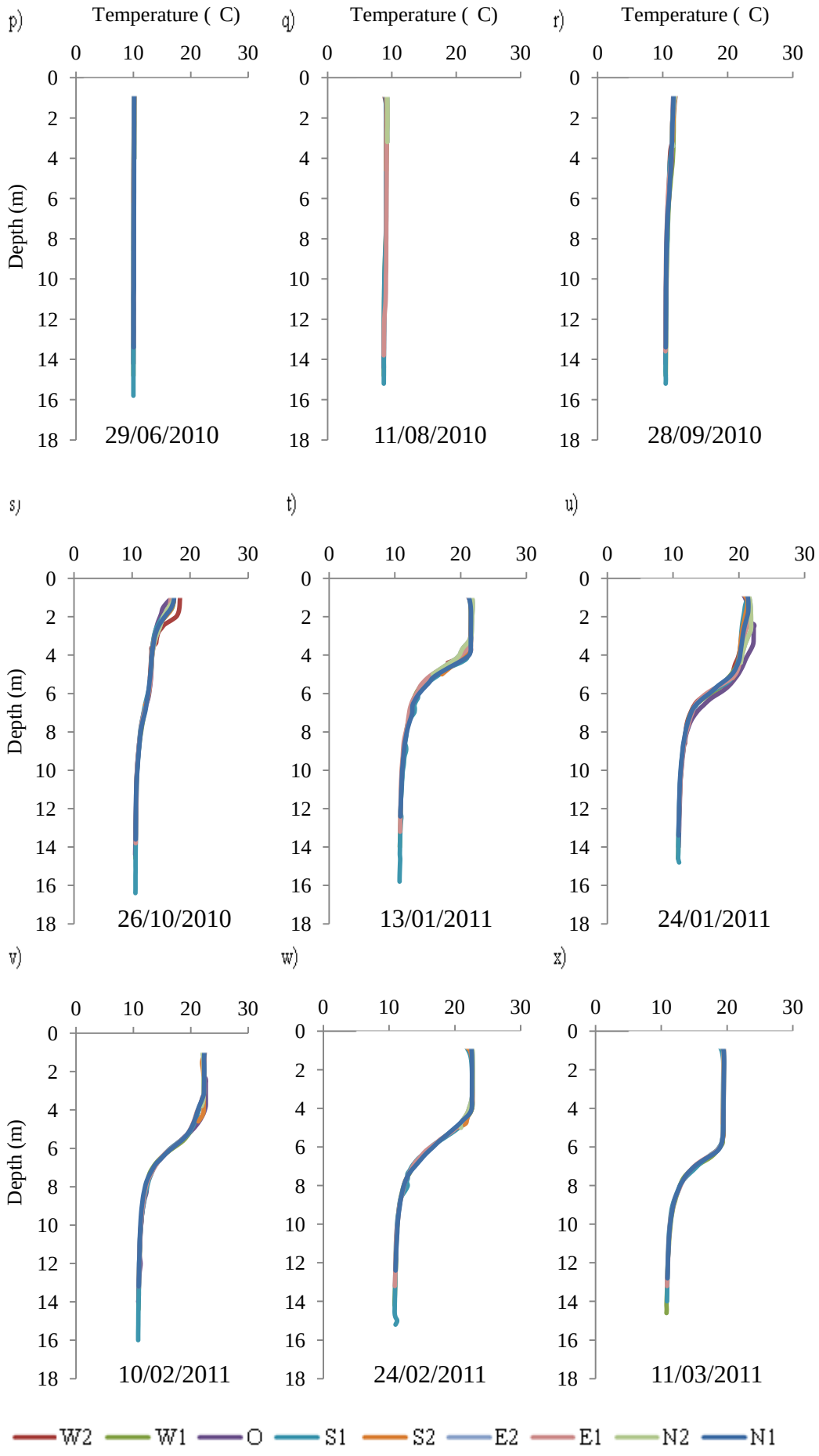
There was very little spatial variation in temperature profiles over the sampling period (Figures 6a-x). The mean surface mixed layer depth (z_{SML}) was 4.2 m on 01 December 2009 (Figure 3.5a) and the mean surface mixed layer (SML) temperature was 19.1 °C. Mean SML temperatures increased until 02 February 2010, reaching a maximum of 22.4 °C (Figure 3.5j). The z_{SML} progressively increased in depth over the following months to a maximum depth of 12.1 m on 01 June 2010 (Figure 3.5o) after which the lake became isothermal, with a mean temperature of 9.0 °C recorded on 11 August 2010. Horizontal temperature variation was evident on 26 October 2010 as Lake Ōkaro began to restratify, ranging by up to 1.0 °C from 2-3 m depth (Figure 3.5s). On 13 January 2011 SML temperatures were fairly uniform at 21.5 °C, and z_{SML} was 3.2 m (Figure 3.5t). The surface mixed layer increased in depth over the remainder of the study, reaching 6 m on 11 March 2011 when SML temperatures were uniform at 19.4 °C (Figure 3.5x). Temperatures at $\geq$ 12 m depth were nearly constant at around 9 °C for the duration of the sampling period.



Figures 3.5a-f: Temperature profiles for all stations from 01 December 2009 – 05 January 2010.



Figures 3.5g-o: Temperature profiles for all stations from 12 January 2010 – 01 June 2010.

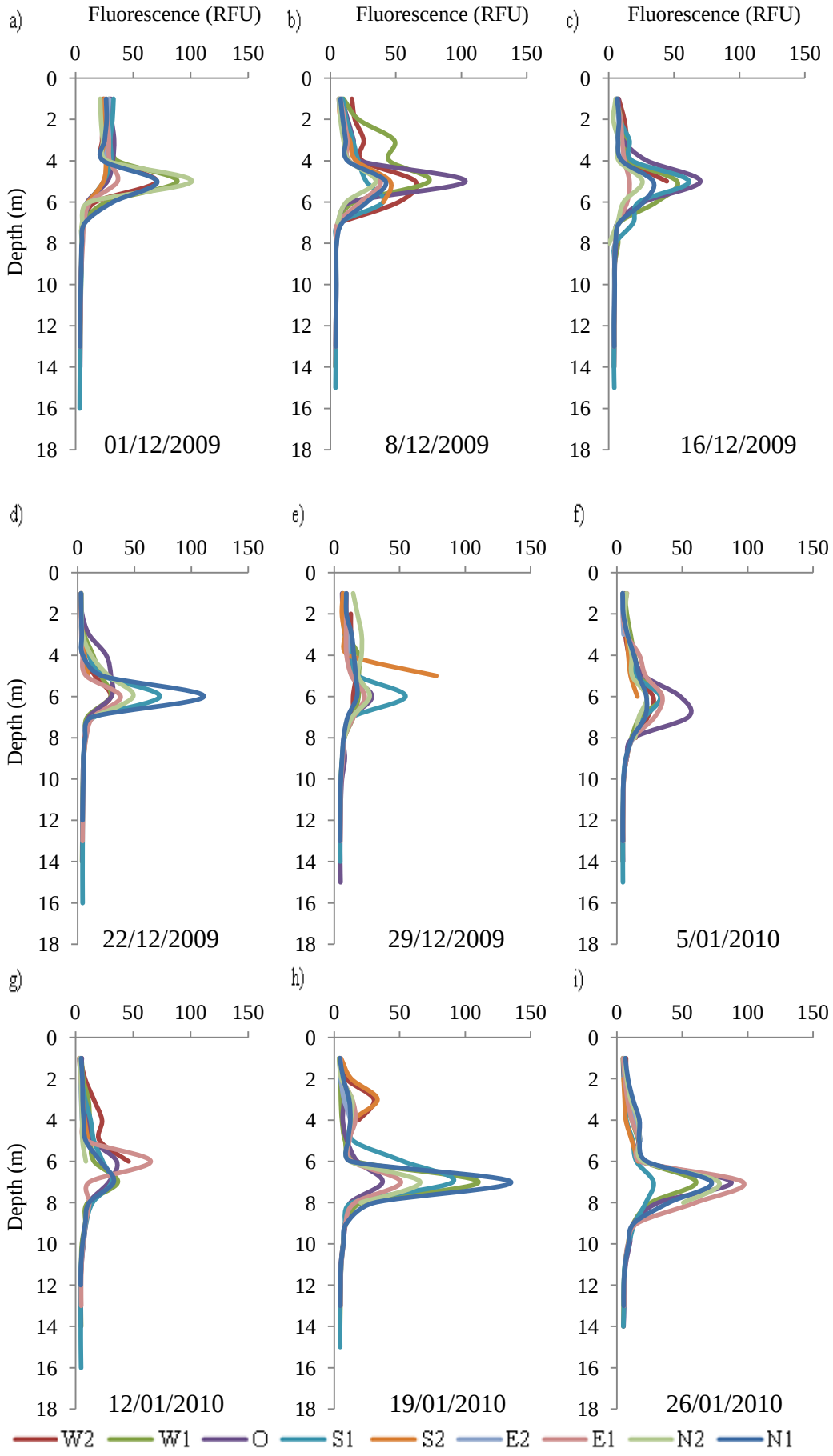


Figures 3.5p-x: Temperature profiles for all stations from 29 June 2010 – 11 March 2011.

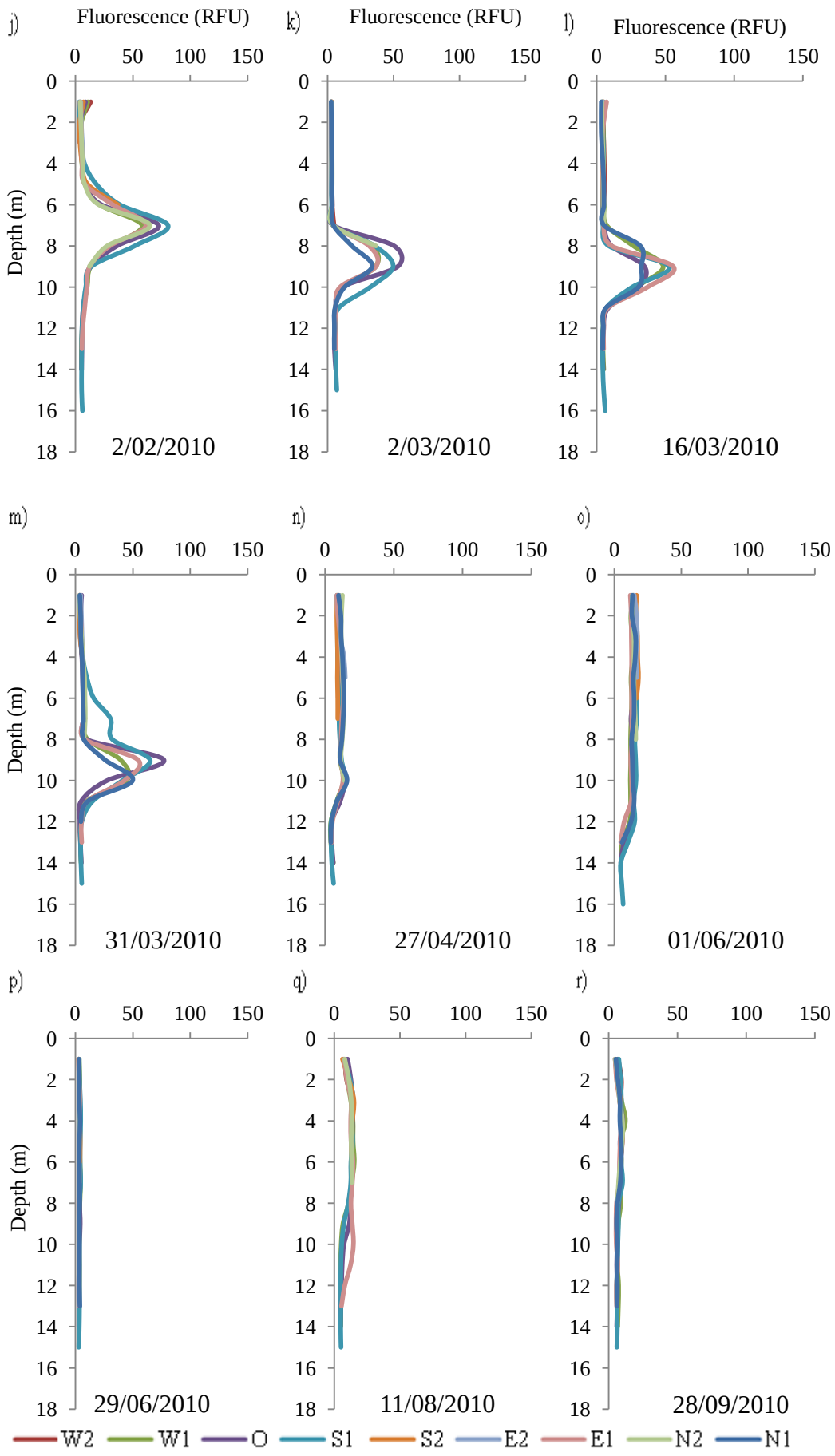
b. Fluorescence

Lake Ōkaro was characterised by a fluorescence DCM from 01 December 2009 to 01 June 2010, and 13 January 2011 to 11 March 2011, corresponding to periods of thermal stratification (Figures 3.6a-v). Throughout the sampling period, there was a trend of increasing DCM depth in line with increasing thermocline depth. On each sampling date, the depth of the DCM was nearly homogenous on a horizontal scale, with statistically significant correlations between all deep stations and most shallow stations (Table 3.1). However, chlorophyll fluorescence was extremely variable horizontally.

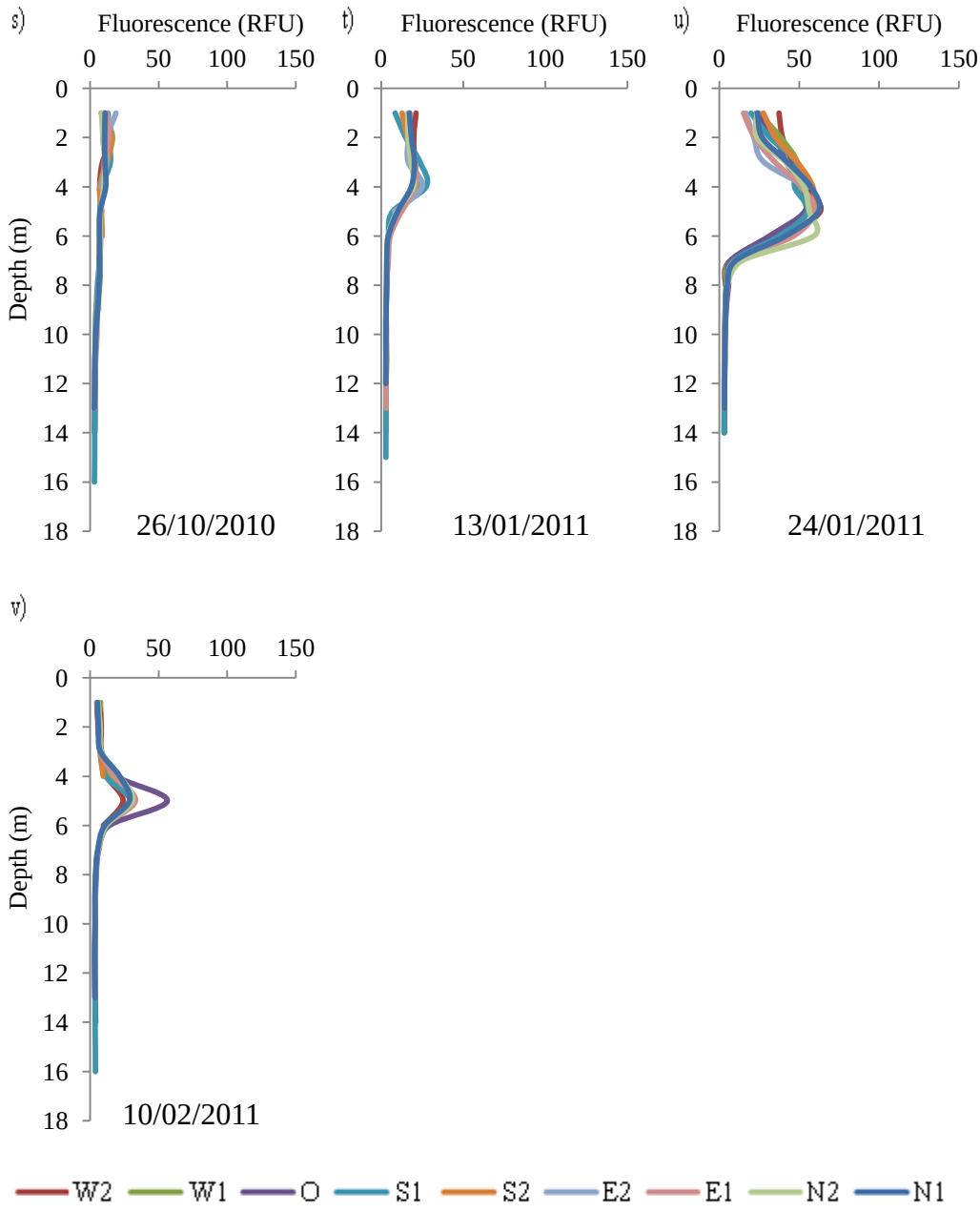
Peaks in DCM fluorescence of $\geq$ 100 RFU occurred between 01 December 2009 and 19 January 2010 (with the exception of 11 August 2010, E2). On 01 December 2009, the DCM at stations N2 and W1 was $\geq$ 70 RFU, while all other stations had $\leq$ 40 RFU (Figures 3.6a). On 08 December 2009, two distinct DCMs had developed at stations W1 and W2, at depths of 3.5 m and 5.2 m, respectively (Figures 3.6b). This occurred again on 29 December 2009 at station S1 (Figures 3.6e), and on 12 January 2010, when horizontal variation was evident in a dual DCM at station W2, and in DCM depth with E1 and O fluorescence peaks at 6.2 m; 0.5 m shallower than all other stations (Figures 3.6g). On 02 February 2010, DCM biomass and depth was homogenous across stations (Figures 3.6j). On 27 April 2010 the DCM was only evident as a slight increase at 10 m depth (Figures 3.6n), and from 01 June 2010 to 26 October 2010 (Figures 3.6o-s) fluorescence profiles were vertically and horizontally homogenous as the lake became mixed. A subsequent DCM had developed at 4 m depth by 13 January 2011 (Figure 3.6t), and increased to 5 m depth by 10 February 2011 (Figures 3.6v).



Figures 3.6a-i: Fluorescence profiles for all stations from 01 December 2009 – 26 January 2010.



Figures 3.6j-r: Fluorescence profiles for all stations from 02 February 2010 – 28 September 2010.

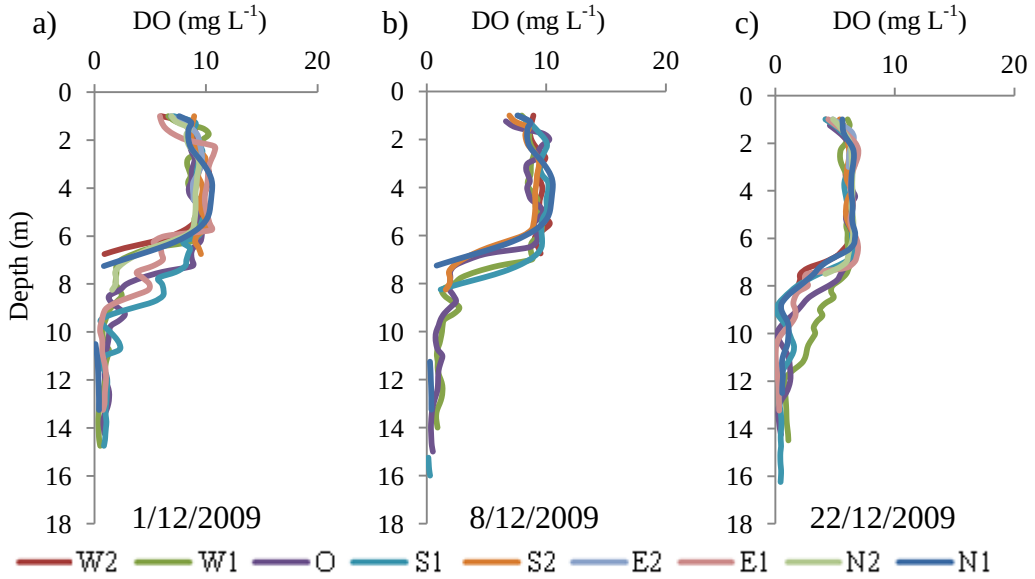


Figures 3.6s-v: Fluorescence profiles for all stations from 26 October 2010 – 10 February 2011.

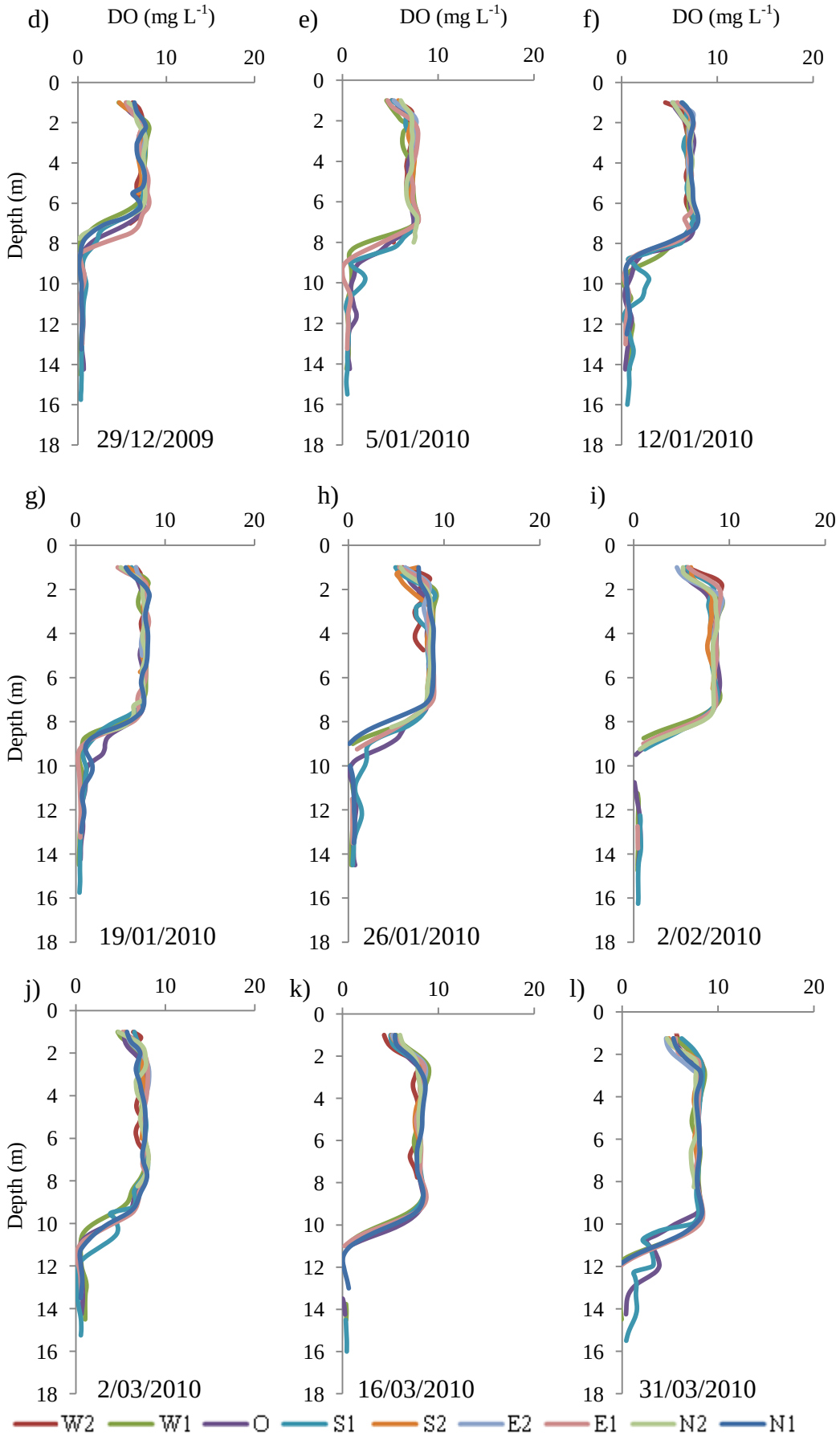
c. Dissolved oxygen (mg L^{-1})

The degree of spatial heterogeneity in dissolved oxygen (DO) profiles changed over the sampling period. A large amount of horizontal variation ($\geq$ 3 mg L^{-1}) was evident from 01 - 08 December 2009 (Figure 3.7a-b). DO profiles became more horizontally homogenous thereafter, with a few outlying stations on occasion (e.g., station W1 on 22 December 2009). Figure 3.7a-l indicate that water at depths $\leq$ 2 m had the lowest oxygen concentration in the epilimnion, and the water column

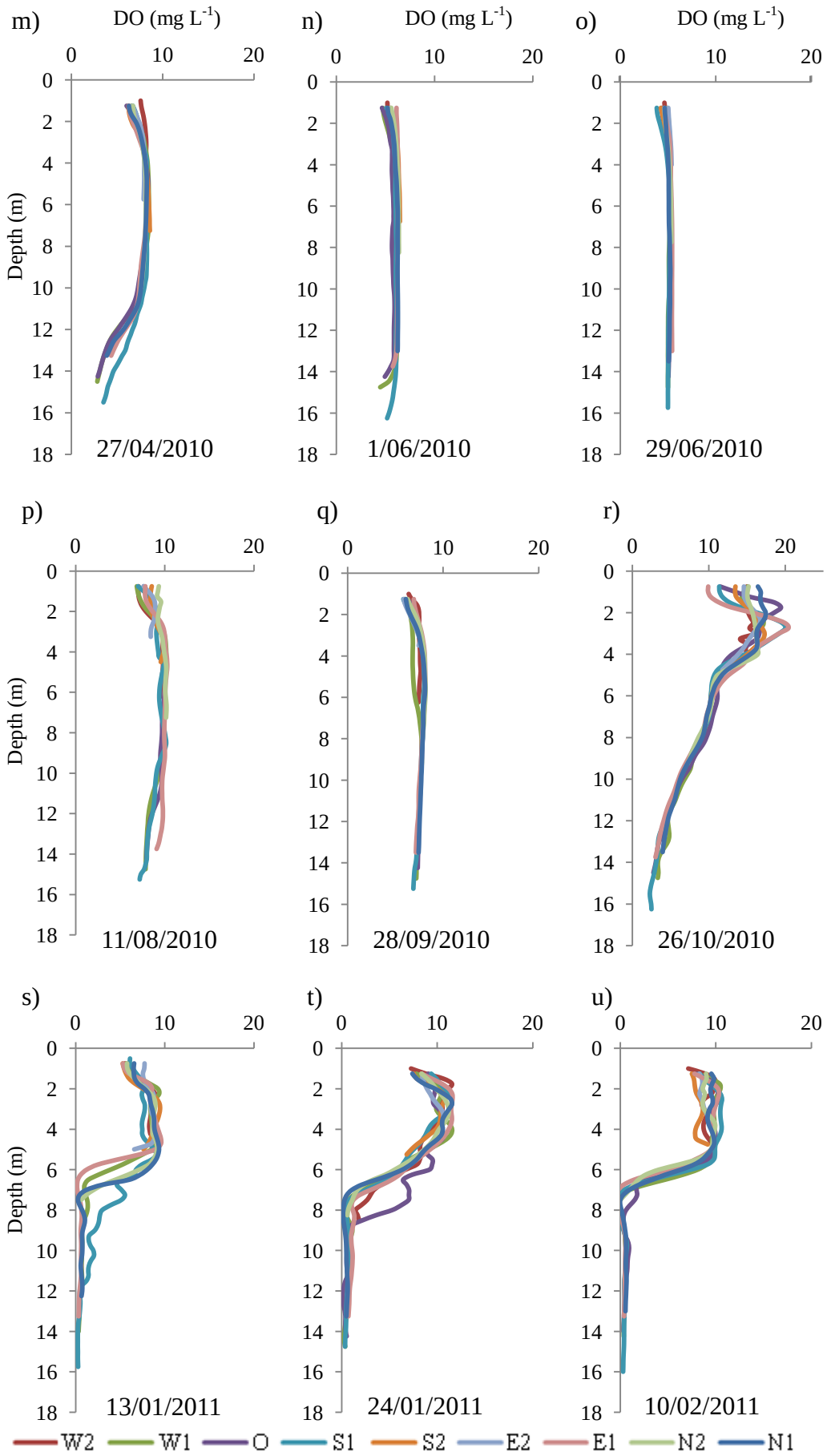
between 2 m depth and the thermocline had the highest oxygen concentration, generally ranging between 6 – 8 mg L^{-1}, with peak DO concentrations corresponding to the thermocline and DCM depth (e.g., 9.5 m on 16 March 2010 (Figures 3.5l, 3.6l, 3.7k)). From the 01 December 2009, bottom waters were oxygen depleted ($\leq$ 1 mg L^{-1}) at depths $\geq$ 10 m. The depth of anoxia increased over the summer to a maximum of 11.5 m on 31 March 2011. DO concentrations became relatively spatially uniform from 27 April 2011 coinciding with winter mixing (Figure 3.7m-q). DO concentrations at depths $\leq$ 6 m became elevated to $\geq$ 8 mg L^{-1} and reached up to 19.5 mg L^{-1} on 26 October 2010 during a cyanobacterial bloom. From 26 October 2010 to 11 March 2011 DO concentrations at depths $\leq$ 2 m were lower than those at 2 – 6 m depth with a mean concentration of 5 mg L^{-1} (Figure 3.7s-w) and were horizontally variable by up to 3 mg L^{-1} on 13 and 24 January 2011. DO was $\geq$ 7 mg L^{-1} between 2 – 5 m depth from 13 January 2011 to 24 January 2011 (Figure 3.7s-t), increasing to 2 – 6 m depth by 11 March 2011 (Figure 3.7w) corresponding to the upper limit of the thermocline (Figure 3.5x).



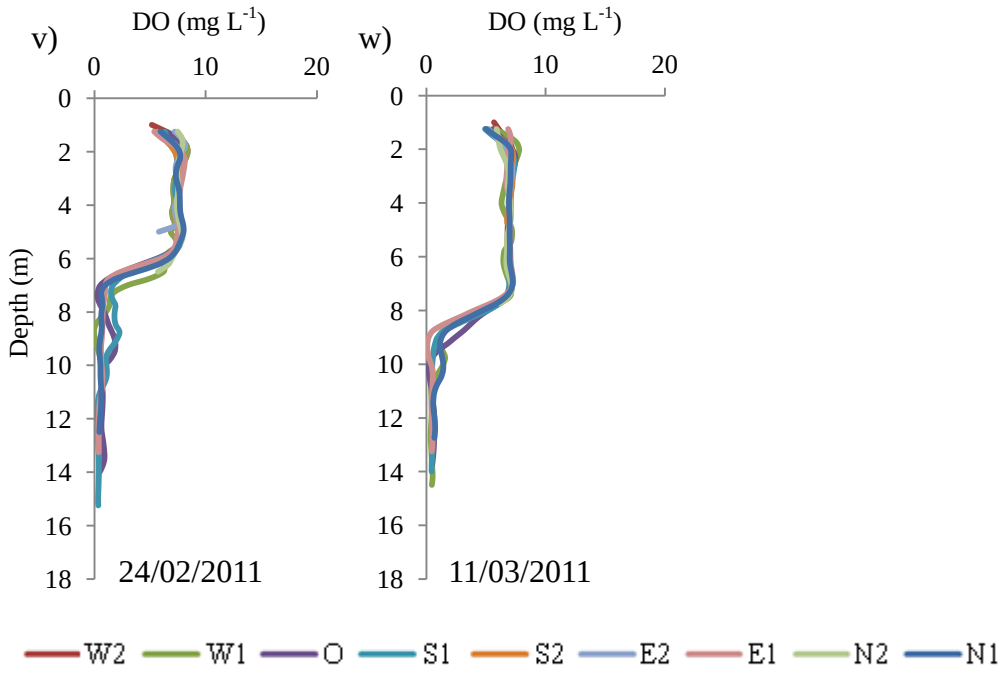
Figures 3.7a-c: Dissolved oxygen profiles for all stations from 12 December 2009 to 22 December 2009.



Figures 3.7d-l: Dissolved oxygen profiles for all stations from 29 December 2009 to 31 March 2010.



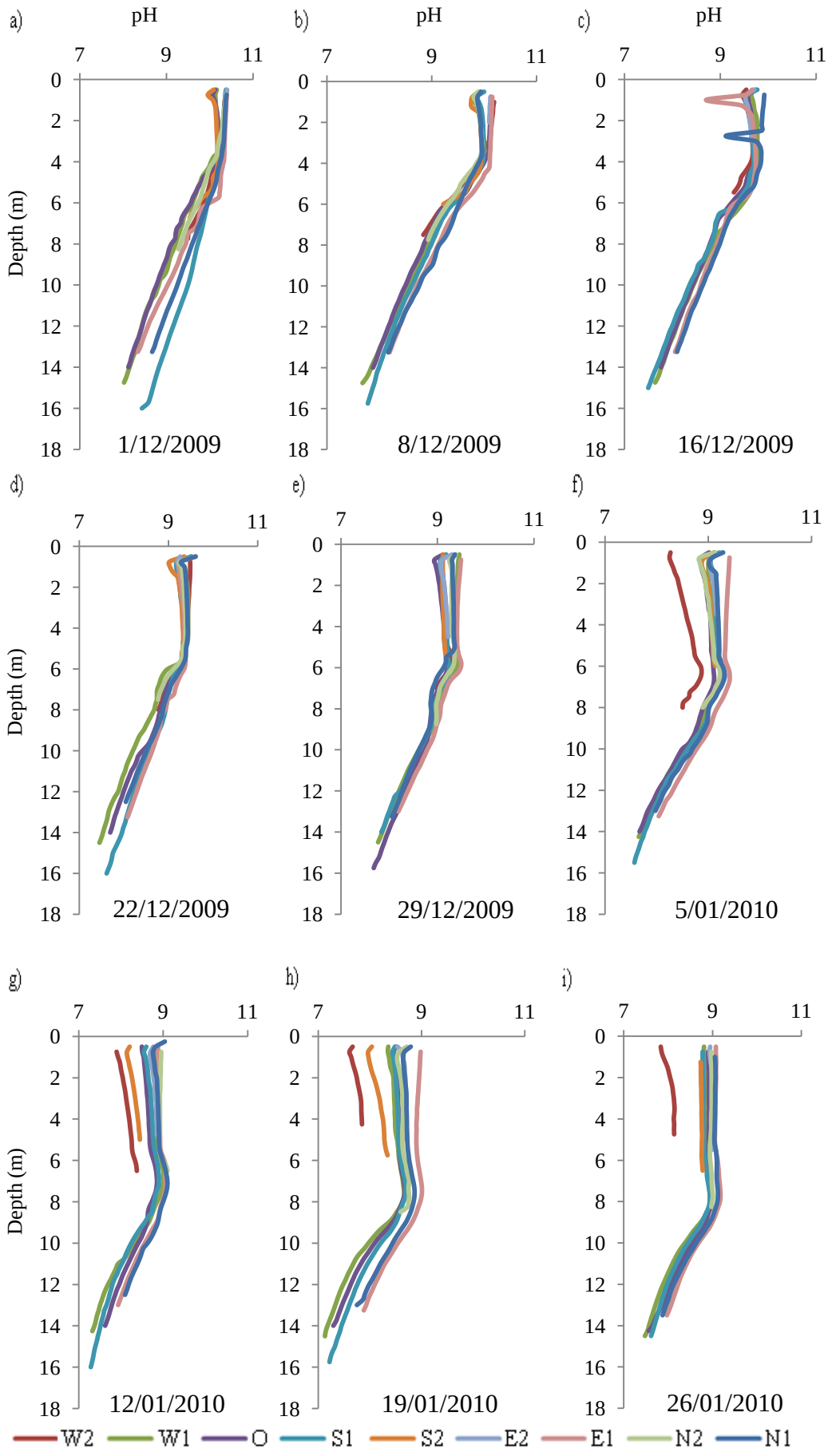
Figures 3.7m-u: Dissolved oxygen profiles for all stations from 27 April 2010 to 11 February 2011.



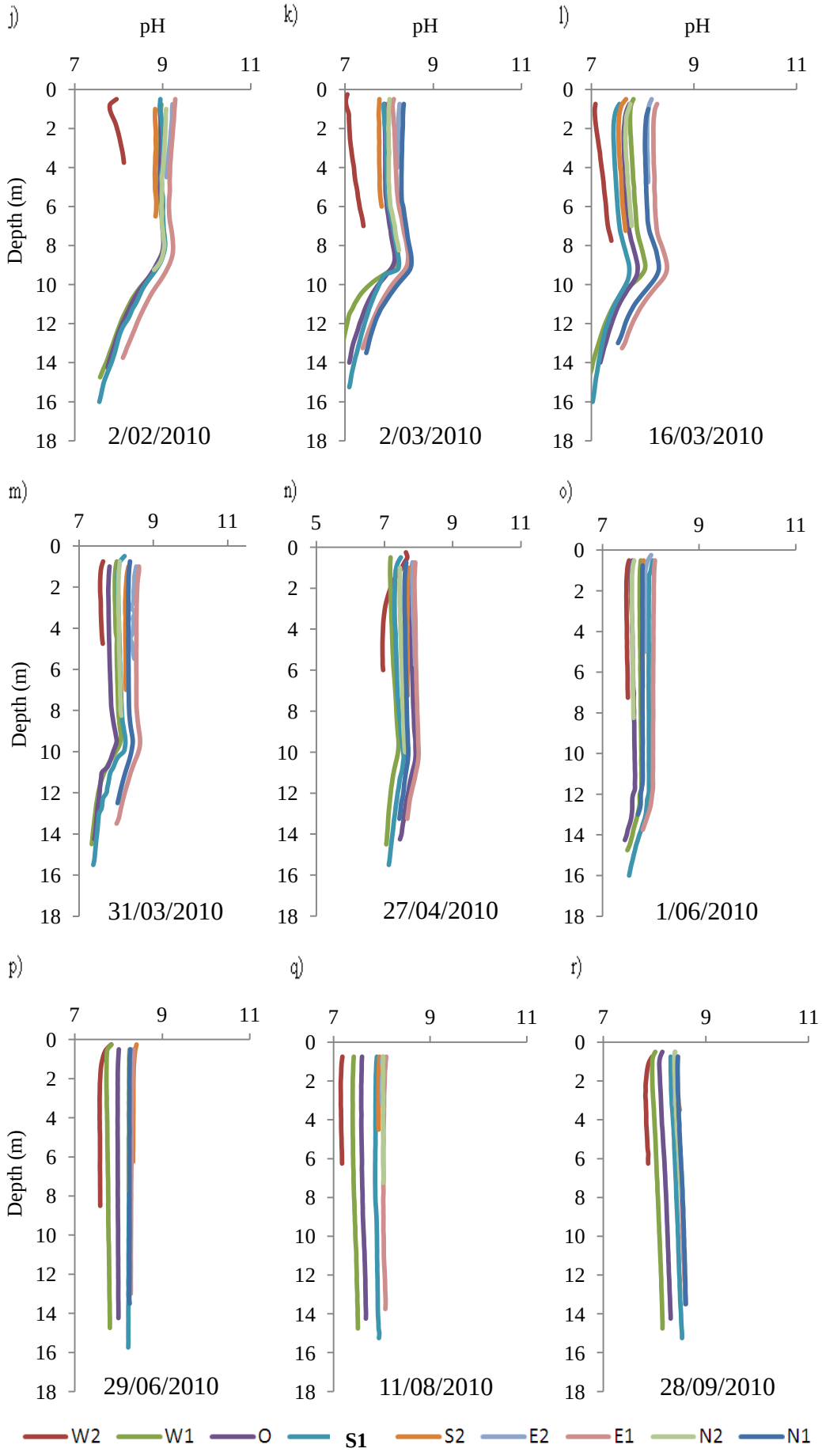
Figures 3.7v-w: Dissolved oxygen profiles for all stations from 24 February 2011 to 11 March 2011.

d. pH

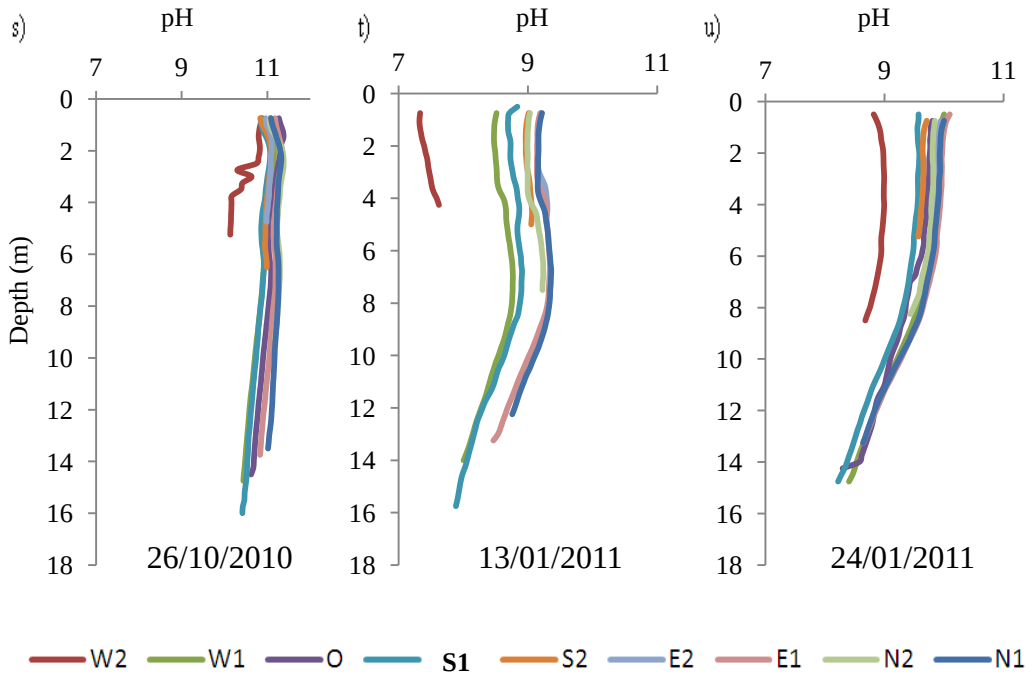
Throughout the stratified period of sampling, pH was highest at depths above the thermocline (Figures 3.8a-d) or at the thermocline (Figures 3.8e-n). Below the thermocline, pH decreased with increasing depth to a minimum of 6.9 (Figure 3.8m). With the exception of station W2, pH profiles were relatively horizontally uniform from 01 December 2009 (Figure 3.8a) to 12 January 2010 (Figure 3.8g). From 19 January 2010 (Figure 3.8h) to 24 January 2011 (Figure 3.8u) pH was quite horizontally variable with a maximum range of 1.2 (Figure 3.8j-l).



Figures 3.8a-i: pH for all stations from 01 December 2009 to 26 January 2010.



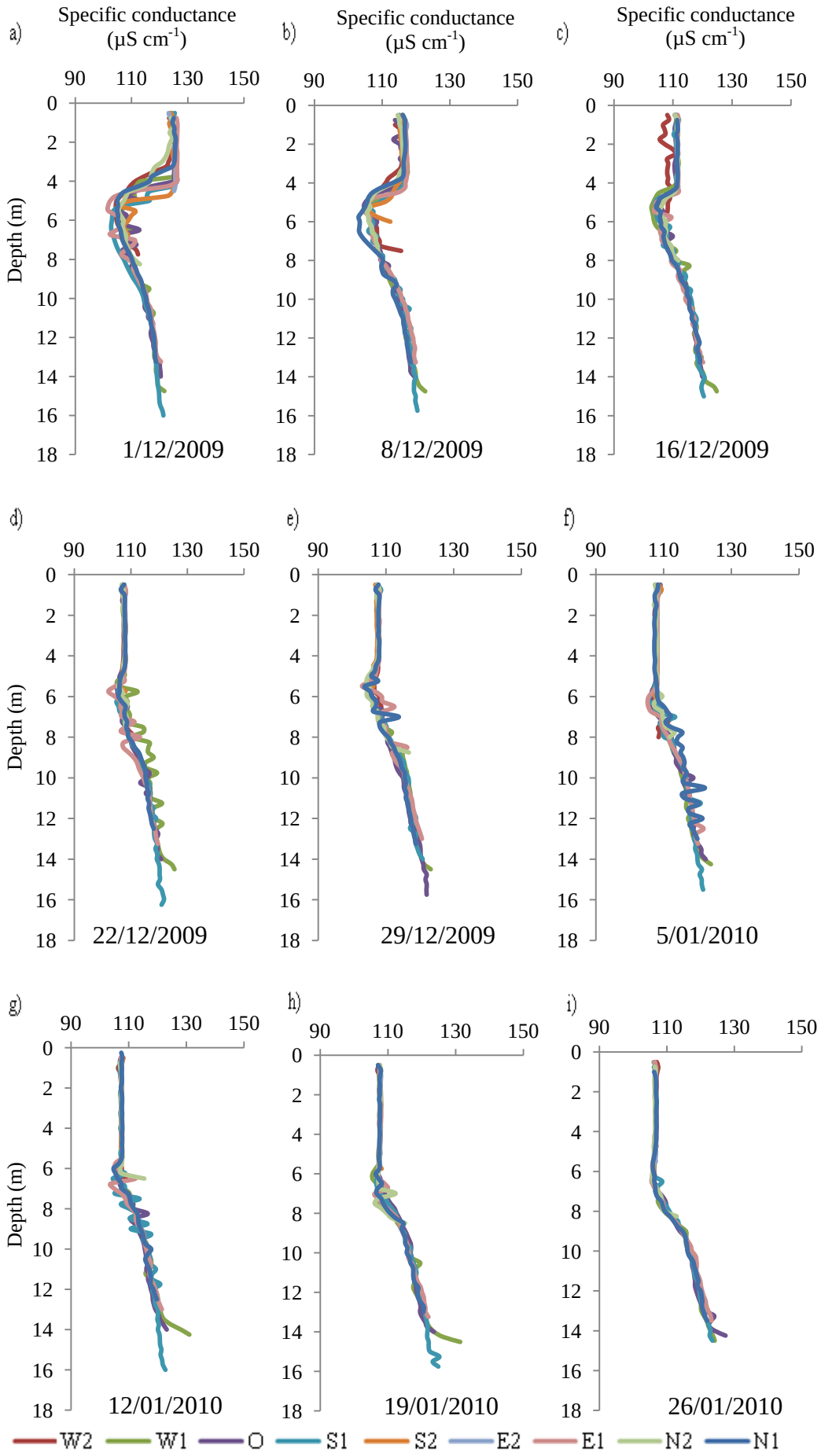
Figures 3.8j-r: pH for all stations from 02 February 2010 to 28 September 2010.



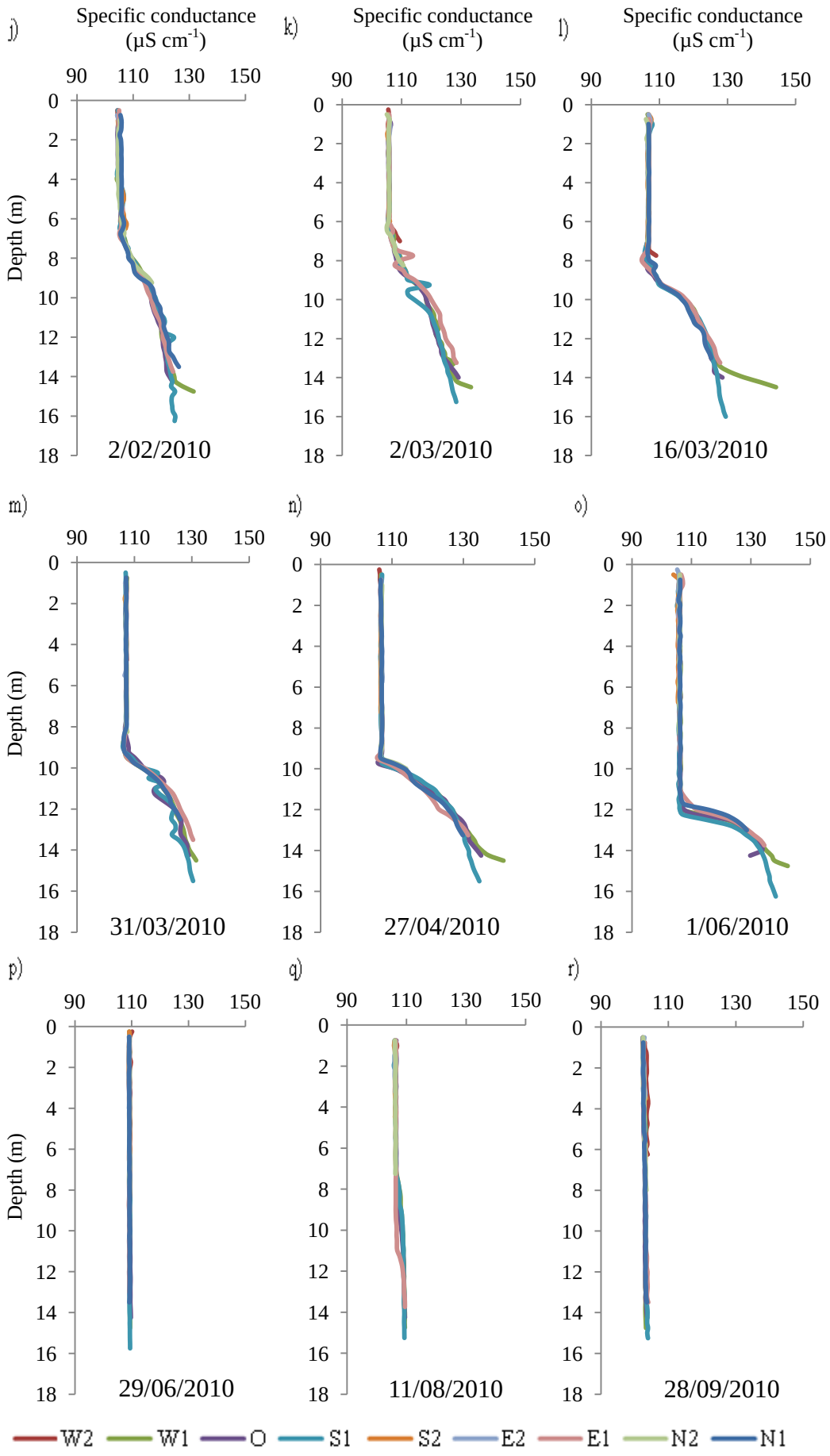
Figures 3.8s-u: pH for all stations from 26 October 2010 to 24 January 2011.

e. Specific conductance

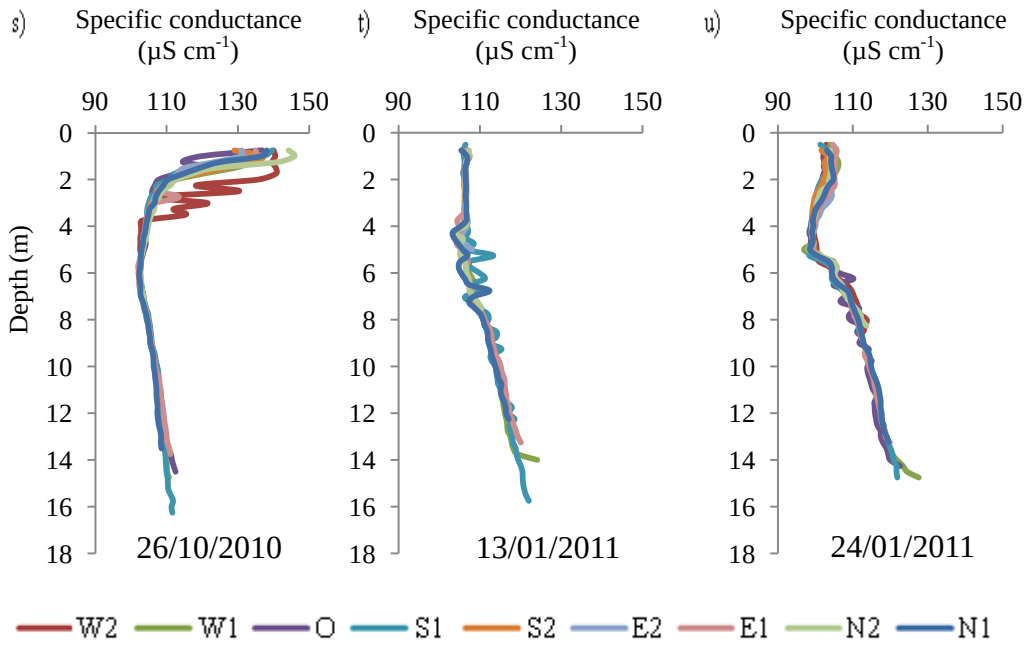
From 01 December 2009 to 01 June 2010 (Figures 3.9a-o) the most horizontal variation in specific conductance was measured in the hypolimnion. Above the thermocline depth, specific conductance was relatively horizontally uniform, decreasing from a mean of 125 µS cm^{-1} (Figure 3.9a), to 107 µS cm^{-1} (Figure 3.9d), where it remained stable between 103-107 µS cm^{-1} until 28 September 2010 (Figure 3.9r). On 26 October 2010 (Figure 3.9s) specific conductance was $\geq$ 110 µS cm^{-1} at all stations at depths $\leq$ 2 m and elevated to a maximum of 144 µS cm^{-1} at 1 m depth (W2). At depths $\geq$ 6 m, there was almost no spatial variation in conductance. From 13 January 2011 to 24 January 2011 (Figures 10t-u), conductance at depths $\leq$ 2 m was nearly uniform at 107 µS cm^{-1}, and became more variable at depths below this. On 24 January 2011 specific conductance decreased to 99 µS cm^{-1} at 5 m, corresponding to a depth of $\leq$ 1 m from the thermocline depth (Figure 3.5u).



Figures 3.9a-i: Specific conductance for all stations from 01 December 2009 to 26 January 2010



Figures 3.9j-r: Specific conductance for all stations from 02 February 2010 to 28 September 2010.



Figures 3.9s-u: Specific conductance for all stations from 26 October 2010 to 24 January 2011.

f. Nutrients

Detectable levels of nitrite (NO_2-N) (not illustrated) were only recorded from 11 August 2010 to 26 September 2010, coinciding with the winter mixed period (mean 0.002 mg L^{-1}).

There was a strong vertical gradient in ammonium (NH_4-N) concentrations during thermal stratification (Figure 3.10a). The highest concentrations of NH_4-N were located at 12 - 14 m depth over the sampling period with a maximum of 1.457 mg L^{-1} (14 m, 10 February 2011). The mean concentration of NH_4-N above the thermocline from 01 December 2009 to 27 April 2010 was 0.027 mg L^{-1}, reaching a maximum of 0.076 mg L^{-1} at 0 m on 12 January 2010. NH_4-N concentrations below the thermocline at this time ranged from 0.005 mg L^{-1} (6m, 16 December 2009) to 1.347 mg L^{-1} (26 January 2010), with a mean concentration of 0.498 mg L^{-1}. The water column was mixed from 29 June 2010 to 28 September 2010 and NH_4-N concentrations were relatively homogenous (mean = 0.347 mg L^{-1}). Lake Ōkaro had restratified on 13 January 2011 at which time mean NH_4-N

concentrations above and below the thermocline were 0.209 mg L^{-1} and 0.90 mg L^{-1}, respectively. From 24 January 2011 to 11 March 2011, the mean NH_4-N concentration above the thermocline decreased to 0.031 mg L^{-1}, and the mean concentration below the thermocline had increased to 0.818 mg L^{-1}, reaching a maximum of 1.457 mg L^{-1} at 14 m on 10 February 2011.

Nitrate (NO_3-N) concentrations were vertically homogenous for the majority of the sampling period (Figure 3.10b) with exceptions from 19 January 2010 to 27 April 2010. From 08 December 2009 to 12 January 2010, NO_3-N concentrations were relatively homogenous (mean = 0.051 mg L^{-1}). From 19 January 2010 to 27 April 2010, NO_3-N concentrations above the thermocline ranged from 0.012 mg L^{-1} (6 m, 16 February 2010) to 0.064 mg L^{-1} (6 m, 19 January 2010), with a mean concentration of 0.028 mg L^{-1}. Concentrations below the thermocline ranged from 0.035 mg L^{-1} (14 m, 30 March 2010) to 0.082 mg L^{-1} (14 m, 02 February 2010). From 01 June 2010 to 11 March 2011 vertical concentrations of NO_3-N were relatively homogenous and high, with a mean concentration of 0.133 mg L^{-1} on 28 September 2010. Mean concentrations decreased from 13 January 2011 (0.103 mg L^{-1}) to 11 March 2011 (0.071 mg L^{-1}).

There was a well defined vertical gradient in phosphate (PO_4-P) over the sampling period (Figure 3.10c). During stratification, PO_4-P concentrations above the thermocline were $\leq$ 10 % of the maximum values observed at depths below the thermocline at all times with a mean of 0.004 mg L^{-1}. From 29 June 2010 to 28 September 2010 PO_4-P concentrations were homogenous, with a mean of 0.033 mg L^{-1}. From 13 January 2011 to 11 March 2011 PO_4-P concentrations were highest between 9 – 14 m depth, with a mean of 0.165 mg L^{-1} and a maximum concentration of 0.256 mg L^{-1} at 12 m 10 February 2011.

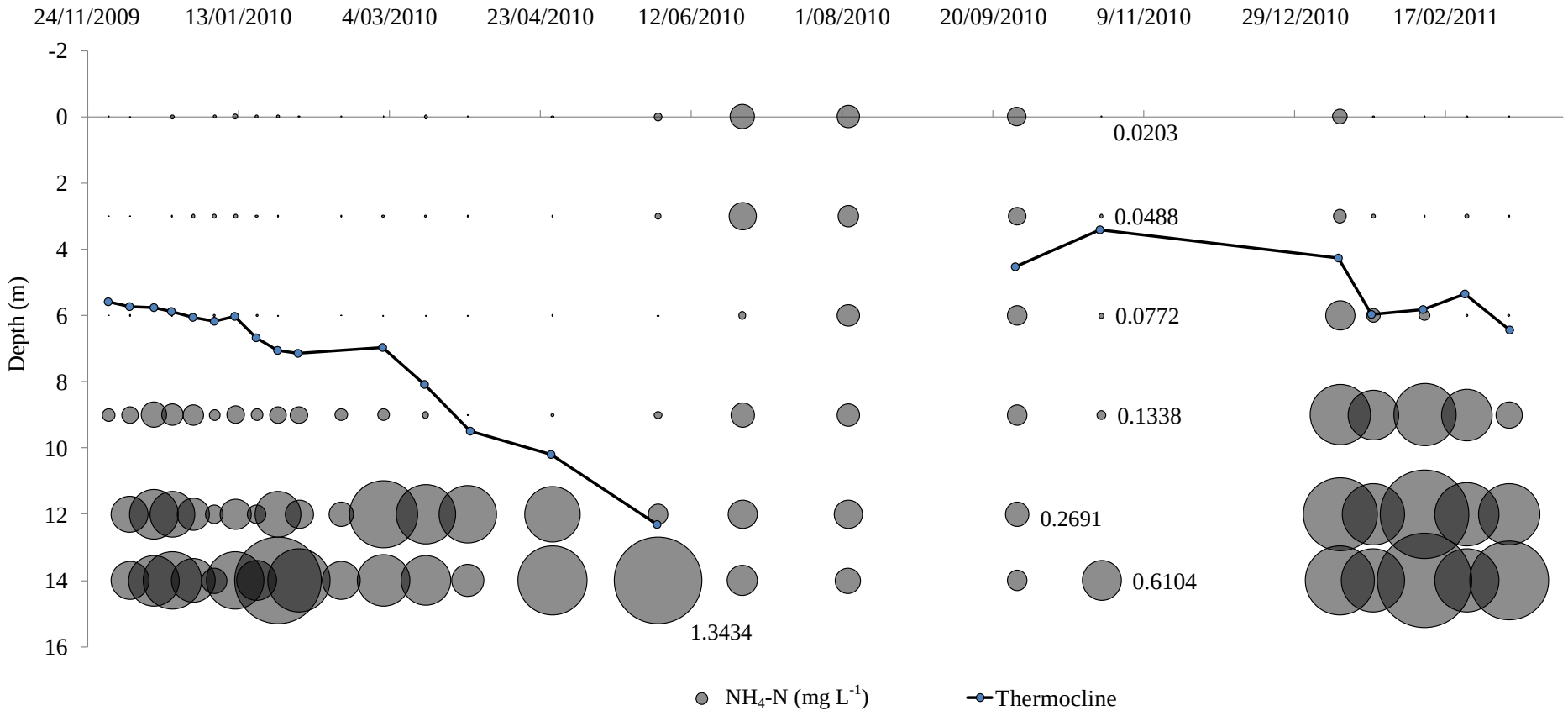


Figure 3.10a: Concentrations of NH_4-N at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 01 December 2009 - 11 March 2011, and thermocline depth. Reference values are provided next to several sample points (mg L^{-1}).

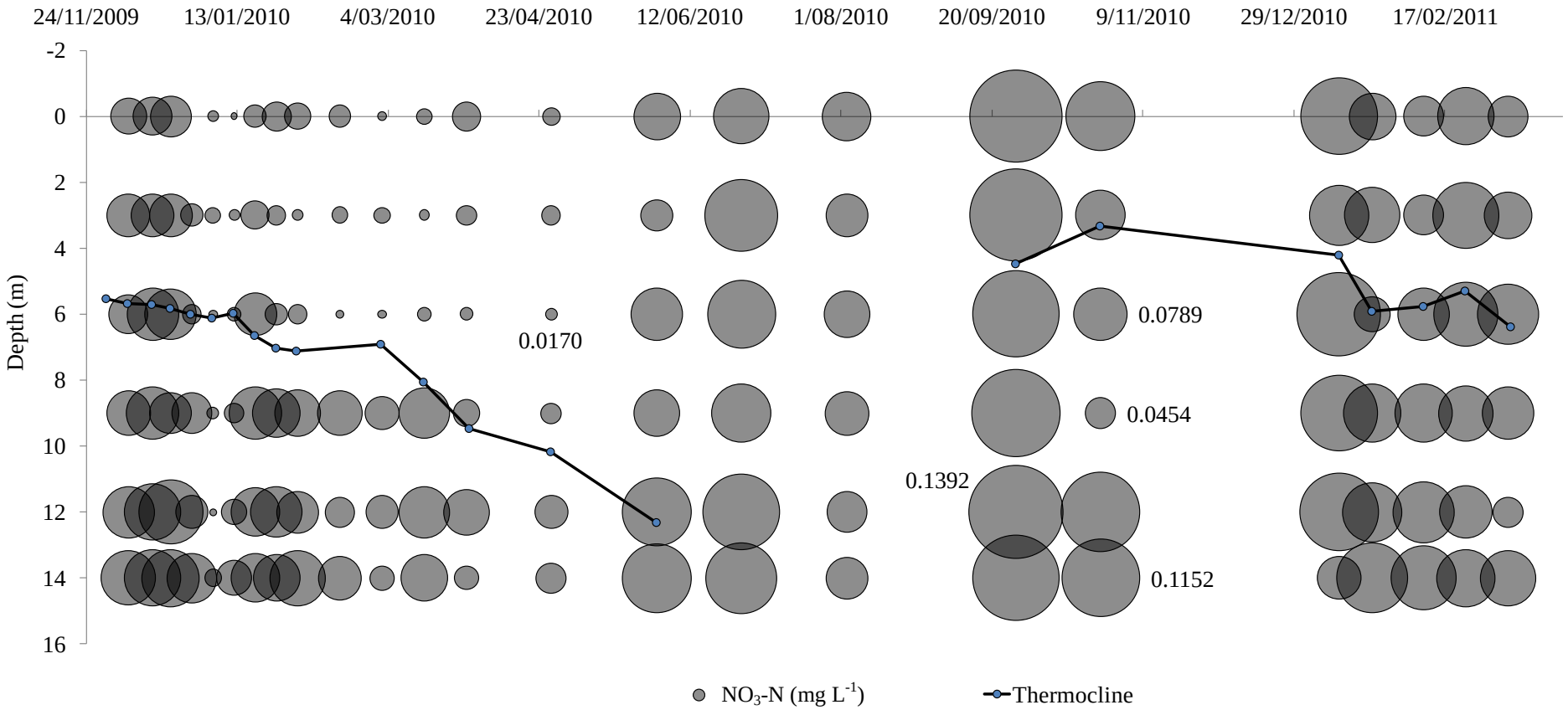


Figure 3.10b: Concentrations of NO_3-N at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 08 December 2009 - 11 March 2011, and thermocline depth. Reference values are given next to several sample points (mg L^{-1}).

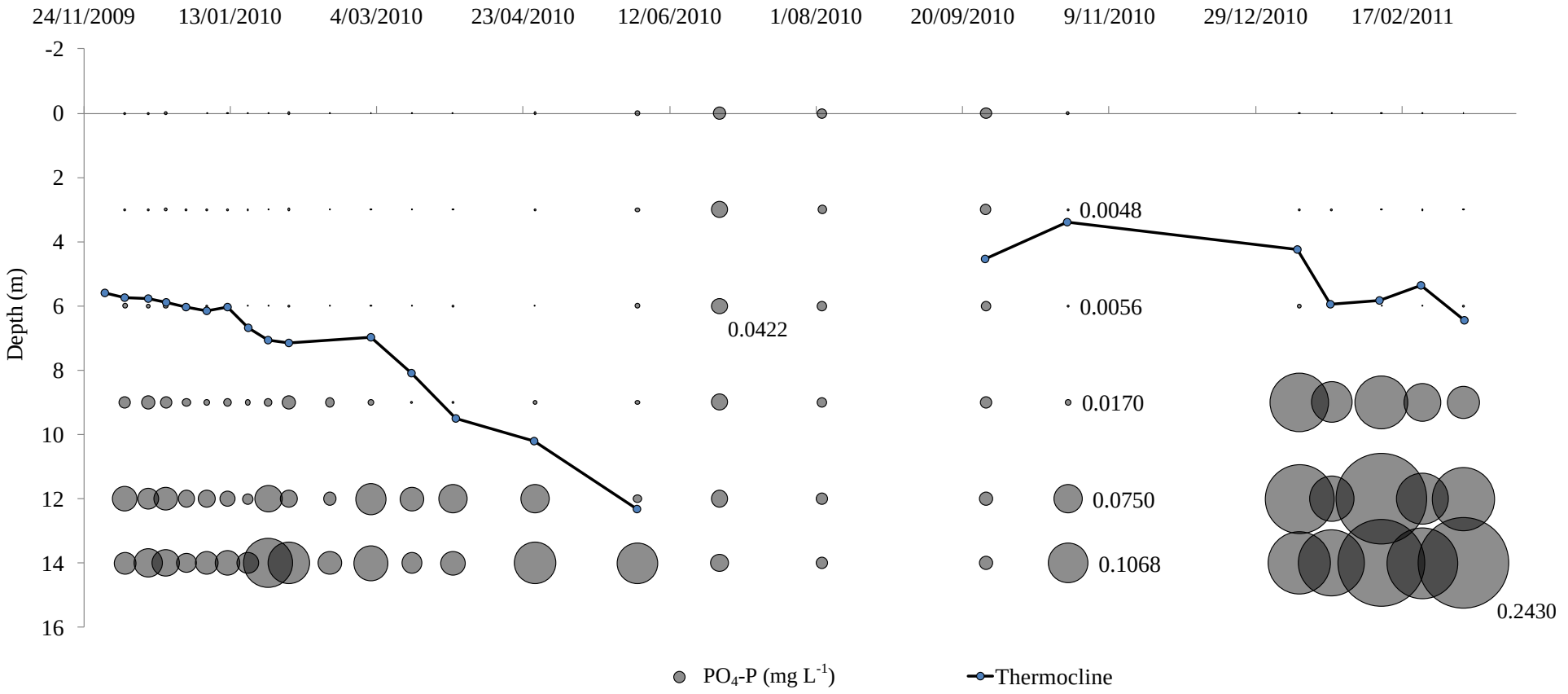


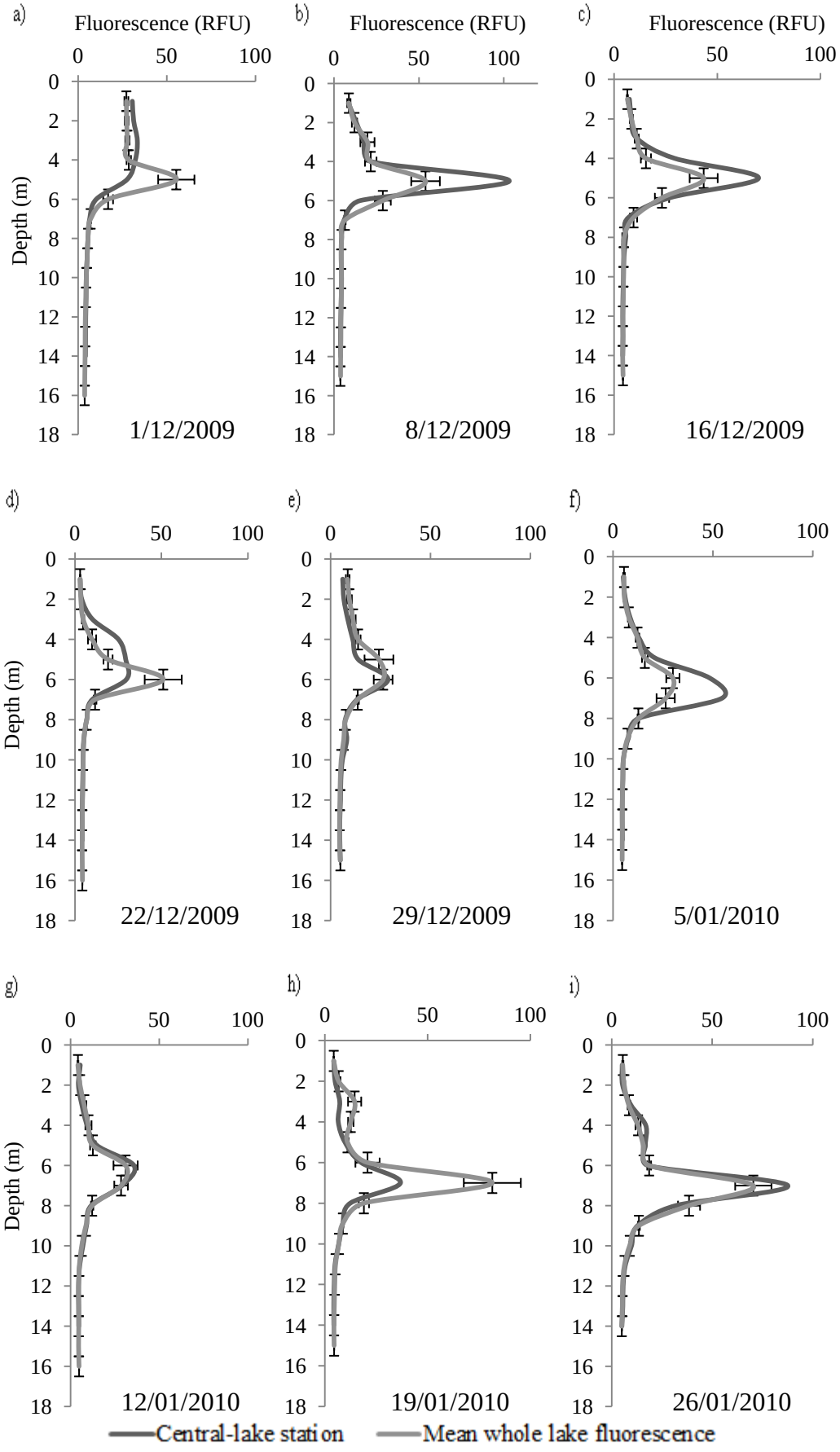
Figure 3.10c: Concentrations of PO_4-P at 0, 3, 6, 9, 12 and 14 m depth in samples taken from 08 December 2009 - 11 March 2011, and thermocline depth. Reference values are given next to several sample points (mg L^{-1}).

3.2 Central lake fluorescence as a surrogate for whole lake values

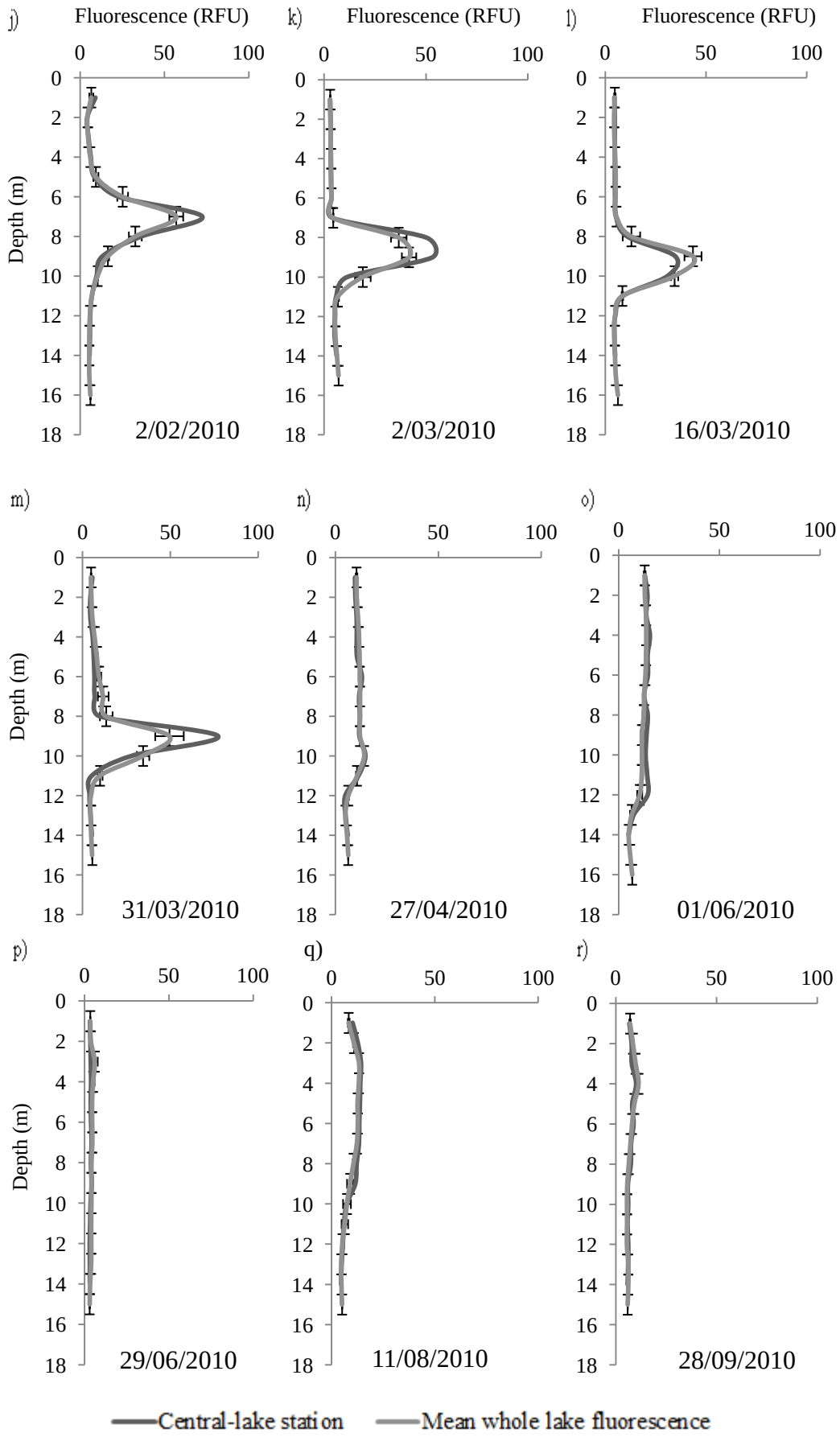
In order to evaluate how representative fluorescence measurements taken at the central lake station are in comparison with the whole lake environment, vertical profiles of chlorophyll fluorescence from nine stations were interpolated at 1 m intervals and averaged to find the mean "whole lake" fluorescence profile for each date. Standard error (SE) ranges were then calculated at each 1 m depth intervals, and the mean "whole lake" fluorescence profiles were compared to the actual measured fluorescence profiles of the centre-lake station for each date.

For the majority of thermal stratification, variation between the central station and the whole lake was predominantly only statistically significant along the *x*-axis not the *y*-axis, indicating that differences amongst stations, and between the whole lake and the central station were related to variations in fluorescence intensity, not variations in fluorescence depth. The centre-lake station over and underrepresented the mean DCM intensity of the whole lake during thermal stratification. On 08 December 2009 (Figure 3.11b) DCM fluorescence for station O was 103.2 RFU at 5 m depth, over-representing the mean lake DCM fluorescence, which was 53.9 RFU with a SE of 10.2 RFU. On 19 January 2010 the central-lake station DCM was 36.8 RFU at 7 m, under-representing mean lake DCM fluorescence which was 81.5 RFU with a SE of 15.0 RFU.

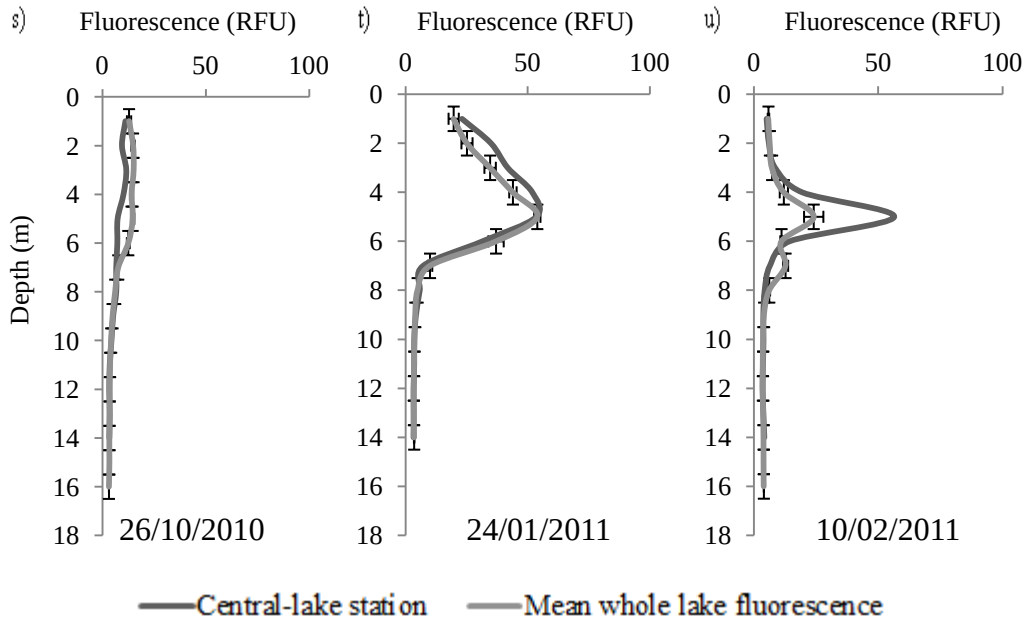
Differences between the DCM depth at the central station and the mean whole lake did occasionally occur. On 01 December 2009 (Figure 3.11a), the DCM depth at the central station was 33.4 RFU at 3 m depth, and mean lake DCM depth at 5 m was 55.4 RFU with a standard error of 10.2 RFU. During the winter mixed period, there were no statistically significant differences in fluorescence (Figure 3.11o-r).



Figures 3.11a-i: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 01 December 2009 to 26 December 2009.



Figures 3.11j-r: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 02 February 2010 to 28 September 2010.



Figures 3.11s-u: Fluorescence (RFU) at central station and whole lake mean fluorescence with standard error from 26 October 2010 to 10 February 2011.

4 Results: Temporal variability study

4.1 Variability during a cyanobacteria-dominated surface bloom

a. Thermal structure

Temperature profiles were very similar over the sampling period (Figure 4.1). Temperatures at a depth of 0.6 m (the minimum depth registered by the CTD) varied by 1.7 °C during the sampling period, with a mean of 20.8 °C. At 14:00 h on 18 November, temperature at the surface was lowest, and there was a slightly deeper thermocline. The warmest temperatures were recorded at depths $\leq$ 2 m on 18:30 and 23:30 (18 November 2010). The mean Pearson's correlation coefficient for temperature profiles was $R^2 = 0.99$, the minimum was $R^2 = 0.95$. Relationships were significant ($P \leq 0.05$) in all cases.

A metalimnion was evident during the 18/19 November 2010 sampling period (Figure 4.2). Mean Schmidt stability was 255.5 J m^{-2}. Metalimnion thickness varied from 6.2 m at 11:00 h on 19 November to only 0.72 m at 23:30 h on 18 November. The depth of the upper layer of the metalimnion was highly variable. Shallowest values occurred on 18 November 2010 at 14:00 h (2.36 m) and 18:30 h (0.73 m), and 19 November 2010 at 11:00 h (0.87 m). The lower layer of the metalimnion was deepest on 18 November 2010 at 23:30 h (6.95 m) and at 09:00 h (5.76 m) on 19 November 2010. The mean depth of the upper metalimnion was 3.25 m. Thermocline depth followed the same pattern of temporal variation as the upper metalimnion. It ranged from 3.62 m (18 November 2010, 18:30 h) to 7.18 m (18 November 2010, 23:30 h) with a mean depth of 5.93 m. The base of the metalimnion was relatively stable in depth during the sampling period, varying

between 6.68 m (18:30 h) on 18 November 2010 and 7.90 m (09:00 h) on 19 November 2010 with a mean depth of 7.28 m.

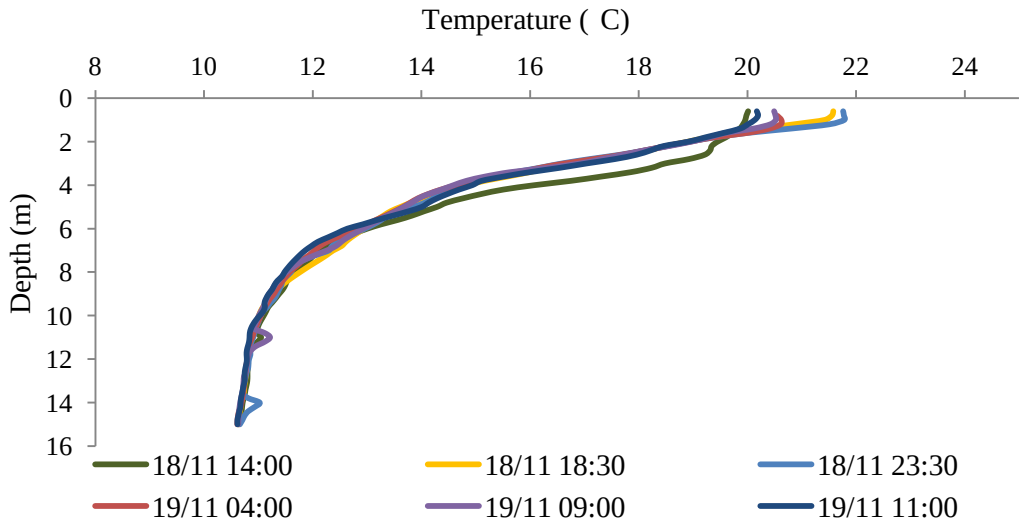


Figure 4.1: Temperature profiles for the sampling period of 19-20 November 2010. Date and time (h) of each profile are given in inset.

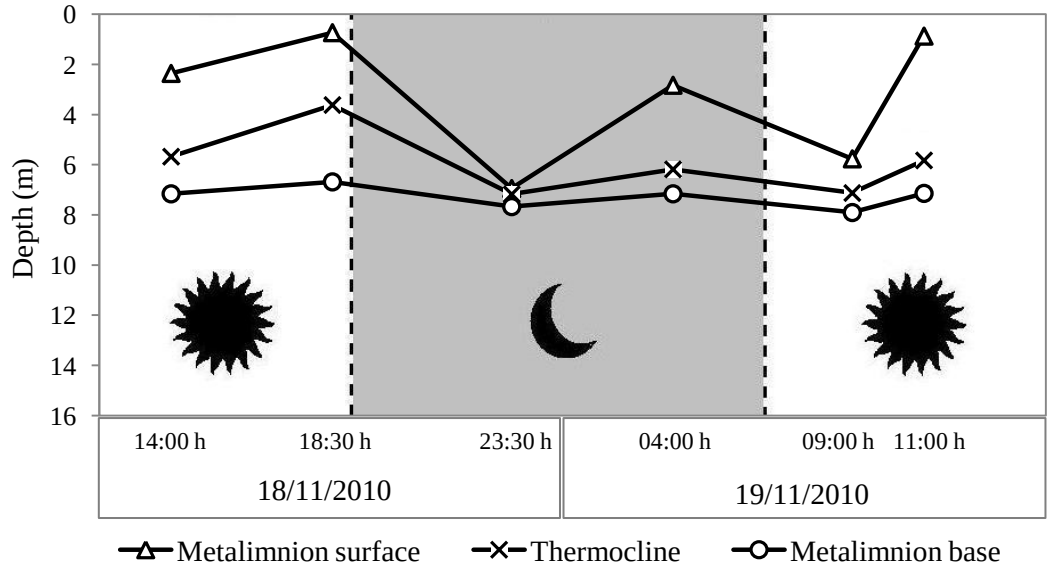


Figure 4.2: Depth of the upper and lower metalimnion and of the thermocline on 18-19 November 2010. Date and time (h) of each profile are given in inset.

b. Dissolved oxygen

Dissolved oxygen (DO) concentrations were generally highest in the upper 3 m of the water column (Figure 4.3). The exception was 14:00 h on 18 November 2010, at which time the peak concentration (12.4 mg L^{-1}) was at 4.9 m, corresponding to a depth at which concentrations were substantially lower in all other profiles (mean 6.6 mg L^{-1}). There was a slight increase in DO concentrations at depths of 6 – 10 m for all profiles with the exception of 14:00 h on 18 November 2010. DO concentrations steadily decreased thereafter from a mean of 4.1 mg L^{-1} at 10 m, to $\leq$ 1 mg L^{-1} at depths $\geq$ 14.5 m.

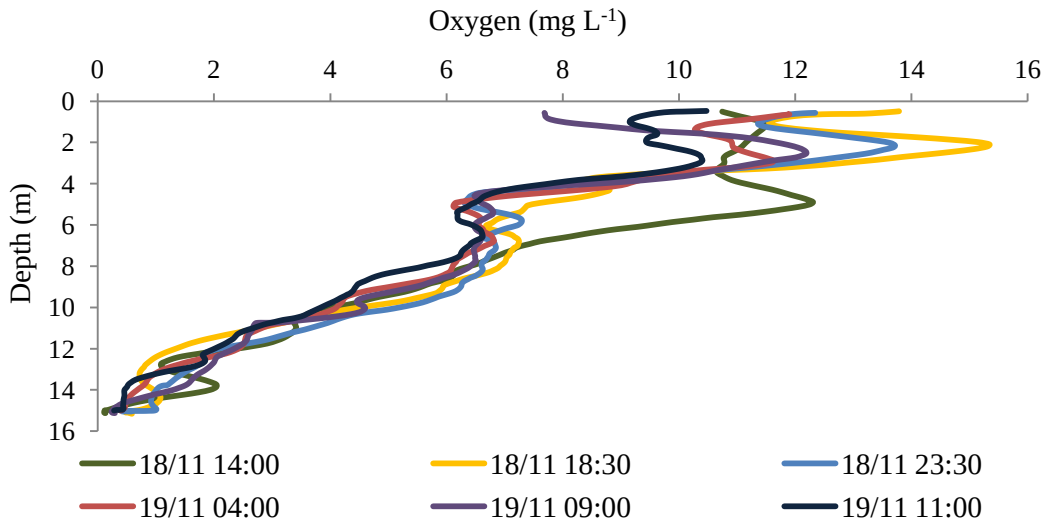


Figure 4.3: Dissolved oxygen concentrations on 18-19 November 2010. Date and time (h) of each profile are given in inset.

c. Light availability

Euphotic depth (z_{eu}) was 2.09 m (18 November 2010, 14:00 h) calculated as the depth where PAR was 1% of the maximum value recorded at the surface. The light extinction coefficient (K_d) was 2.98 m^{-1} (19 November 2010, 11:00 h). No other casts taken over the sampling period captured photosynthetically active

radiation (PAR). Mean irradiance from 06:00 h to 19:00 h was 1.57 MJ m^{-2} h^{-1} on 18 November 2010, and 1.53 MJ m^{-2} h^{-1} on 19 November 2010 (Table 9.2).

d. Specific conductance

At depths ≤ 5 m there was the strongest gradient in specific conductance, particularly in the upper 2 m of the water column (Figure 4.4). At 18:30 h and 23:30 h (18 November 2010) specific conductance levels for depths ≤ 1.0 m were the highest recorded over the sampling period, reaching 158 µS cm^{-1} and 153 µS cm^{-1} respectively. At 14:00 h (18 November 2010), specific conductance was stable in the upper 2.2 m of the water column at c. 135 µS cm^{-1}

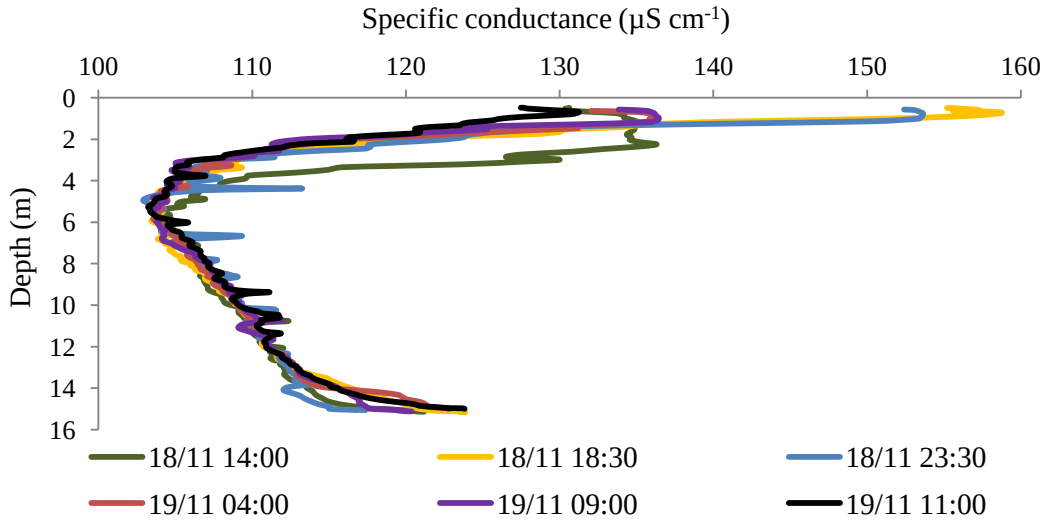


Figure 4.4: Specific conductance on 18-19 November 2010. Date and time (h) of each profile are given in inset.

e. pH levels

The pH was ≥ 10 in the upper 13 m of the water column in all profiles (Figure 4.5). The depth of the peak of pH was aligned closely amongst all profiles, at c. 5 m. For depths ≤ 13 m pH was substantially elevated (≥ 0.5 units) at 14:00 h (18 November 2010) compared with the other profiles.

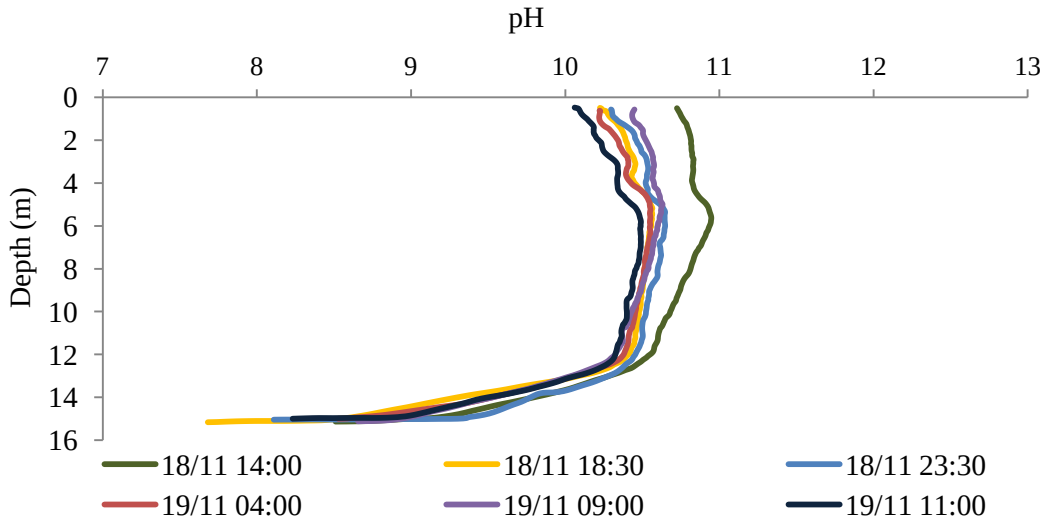


Figure 4.5: pH profiles on 18-19 November 2010. Date and time (h) of each profile are given in inset.

f. Cell concentrations

Microscopic analysis of the phytoplankton revealed the bloom to be nearly monospecific, predominantly composed of *Anabaena spiroides* (Figure 9.2). Cell concentrations at the surface (0 m) were ≥ 137,777 cells mL^{-1}.

g. Fluorescence

Between 43.8% (23:30 h, 18 November 2010), and 51.8% (04:00 h, 19 November 2010) of the total fluorescence was concentrated at 1 m to 7 m depth in the water column (Figure 4.6), corresponding to the maximum depth of the metalimnion

(Figure 4.2). While fluorescence profiles were relatively homogenous over the sampling period, at depths ≤ 4 m 14:00 h (18 November 2010) was the lowest overall (mean = 5.45 RFU), and 04:00 h (19 November 2010) was the highest (mean = 6.07 RFU), 10.2% higher than 14:00 h.

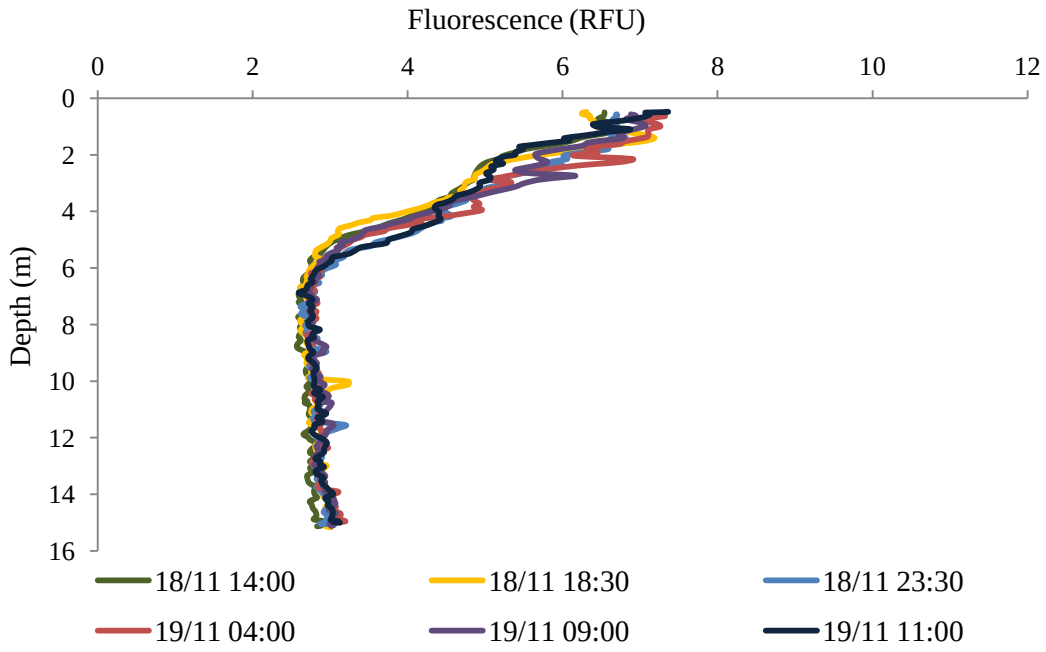


Figure 4.6: Fluorescence on 18-19 November 2010. Date and time (h) of each profile are given in inset.

h. Wind

Mean wind speeds and direction were variable at the Rotorua International Airport over the sampling period (Table 4.1). Between 11:00 h, 18 November 2010 and 11:00 h, 19 November 2010 mean wind speed was 3.16 ms^{-1}, with a mean direction of 87.9º (westerly) (Table 9.3). In the 24 h prior to the first sample, the mean wind speed was 2.24 ms^{-1}, and the maximum wind speed was 6.20 ms^{-1} (18:00 h, 17 November 2010). Mean wind speed and direction changed from a 2.87 ms^{-1} north-easterly between 11:00 h to 14:00 h (18 November 2010) to a 4.90

ms^{-1} south-westerly between 17:00 and 20:00 (18 November 2010). Mean wind speed dropped off thereafter to a mean of 1.60 ms^{-1} between 05:00 h and 08:00 h, and 2.77 ms^{-1} between 08:00 and 11:00 (19 November 2010), expressed as a north-westerly.

Table 4.1: Mean wind speed and direction at 3 hour intervals from 18-19 November 2010:

Date	Time range (24 h)	Mean wind speed ($m\ s^{-1}$)	Mean direction (deg ^{o})
18/11/2010	11:00 - 14:00	2.87	210.3
	14:00 - 17:00	4.23	9.7
	17:00 - 20:00	4.90	24.0
	20:00 - 23:00	3.87	24. 7
19/11/2010	23:00 - 02:00	2.70	143.0
	02:00 - 05:00	2.40	39.67
	05:00 - 08:00	1.60	139.0
	08:00 - 11:00	2.77	113.0

4.2. Temporal variability during a dinoflagellate-dominated deep chlorophyll maximum

a. Thermal structure:

The temperature profile at W1 was relatively stable over the sampling period (Figure 4.7). The mean temperature at 1 m depth was 19.4 °C, and varied by up to 0.6 °C. On 25 March 2011 at 01:00 h, 05:00 h and 08:00 h, temperatures appeared to increase sharply between 0.4 m to 1.5 m depth. Between depths of 1.5 m to 6 m, temperatures were relatively stable. For depths $\leq$ 6 m, the temperatures varied by a mean of 0.43 °C over time. The mean Pearson's correlation coefficient for temperature profiles was R^2 = 0.99, the minimum was R^2 = 0.99. Relationships were significant ($P \leq 0.05$) in all cases.

Schmidt stability decreased from 296.0 J m^{-2} at 21:00 h (24 March) to 262.8 J m^{-2} at 08:00 h (25 March), increasing thereafter to 287.3 at 16:00 h before declining to 279.0 J m^{-2} at 19:00 h (25 March; Figure 4.8). Mean Schmidt stability was 279.8 J m^{-2}. A metalimnion was evident from 24-25 March 2011 (Figure 4.8). Temporal variation in the depth and thickness of the metalimnion was apparent. Metalimnion thickness varied from 2.75 m at 08:00 h (25 March 2011) to 3.99 m at 16:00 h (25 March 2011). The mean depth of the surface of the metalimnion was 6.12 m, with a maximum depth range of 1.39 m, and the mean depth of the metalimnion base was 9.34 m, with a maximum range of 0.79 m. The mean thermocline depth was 7.96 m, and had a maximum range of 2.39 m from 01:00 h to 05:00 h (25 March 2011; Figure 4.8).

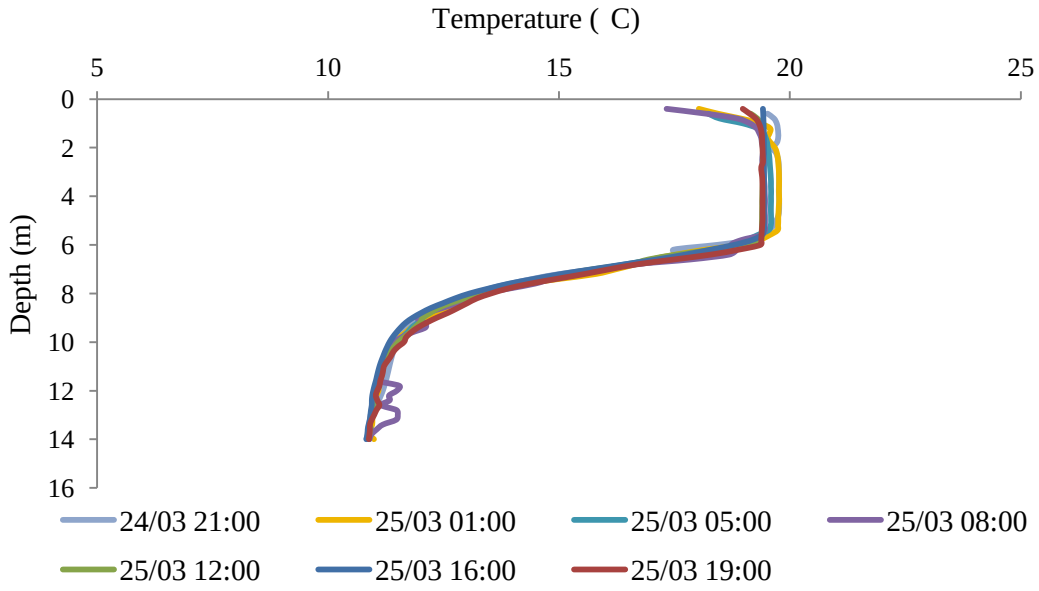


Figure 4.7: Temperature profiles on 24-25 March 2011. Date and time (h) of each profile are given in inset.

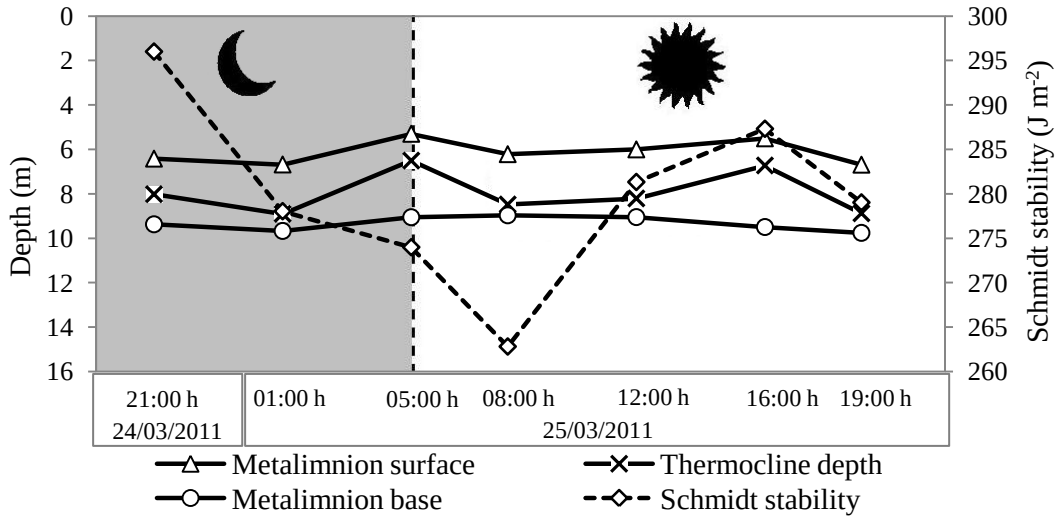


Figure 4.8: Depth of the upper and lower metalimnion, the thermocline and Schmidt stability on 24-25 March 2011. Date and time (h) of each profile are given in inset.

b. Dissolved oxygen concentration

Variation in DO concentration was evident over the sampling period, but there was no distinct diurnal pattern to the changes (Figure 4.9). At depths $\leq$ 2 m, DO varied between a minimum of 3.9 mg L^{-1} at 21:00 (24 March 2011), to a

maximum of 6.5 mg L^{-1} at 16:00 (25 March 2011). From depths 2 m – 10 m, DO was stable above 6.5 mg L^{-1}. The highest concentrations occurred on 25 March 2011 between the depths of 7.1 m at 16:00 h (7.7 mg L^{-1}), and 8.2 m at 19:00 h (7.7 mg L^{-1}). At 10 m, DO ranged from 3.3 mg L^{-1} (16:00 h) to 6.2 mg L^{-1} (19:00 h), and profiles tapered off with increased depth.

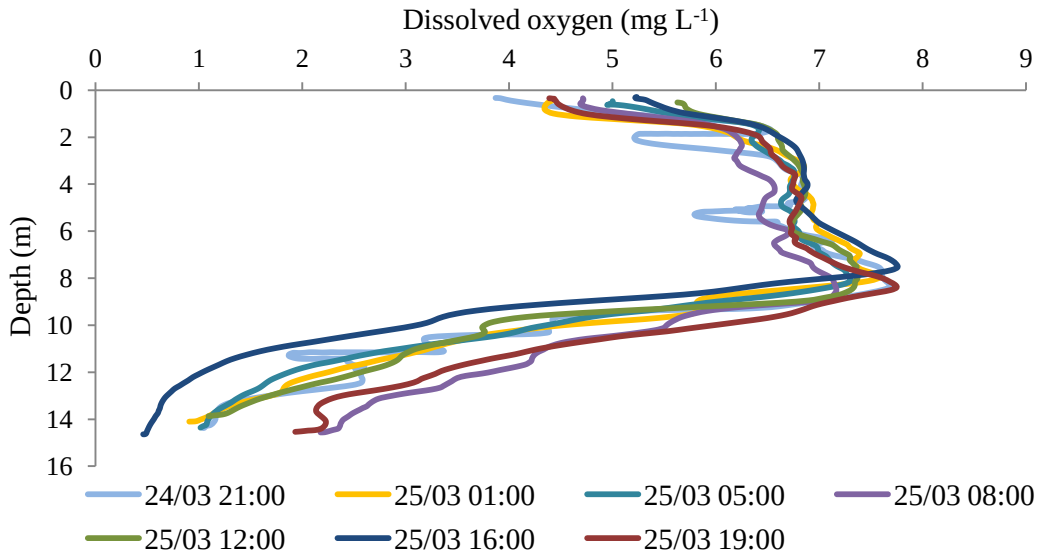


Figure 4.9: Dissolved oxygen concentrations on 24-25 March 2011. Date and time (h) of each profile are given in inset.

c. Light availability

z_{eu}, calculated as the depth where PAR was 1% of the maximum value recorded at the surface varied by 0.6 m from 12:00-16:00 (25 March 2011) (Table 4.2). Mean z_{eu} was 9.98 m. K_d varied by 0.02 m^{-1} from 12:00-16:00 (25 March 2011). Mean K_d was 0.51 m^{-1}.

Table 4.2: Light attenuation coefficients and euphotic depths for 25 March 2011.

Date	Time (h)	K_d (m^{-1})	Z_{eu} (m)
25 March 2011	12:00	0.51	10.15
	16:00	0.50	9.80

d. Fluorescence

Chlorophyll fluorescence at depths ≤ 5.5 m and ≥ 11.0 m was stable from 21:00 h (24 March 2011) to 19:00 h (25 March 2011) (Figure 4.10). A deep chlorophyll maximum (DCM) was evident throughout the sampling period; with singular peaks forming on the 25 March 2011 at 12:00 h and 16:00 h. Dual DCM formation was evident at all other times. Peak fluorescence values ranged from 35.4 RFU (12:00 h, 25 March 2011) to 99.5 RFU (01:00 h, 25 March 2011) (Table 4.3). Mean fluorescence from 6 to 7 m depth was 43.7 RFU. Mean fluorescence from 7 to 8 m depth was 43.0 RFU.

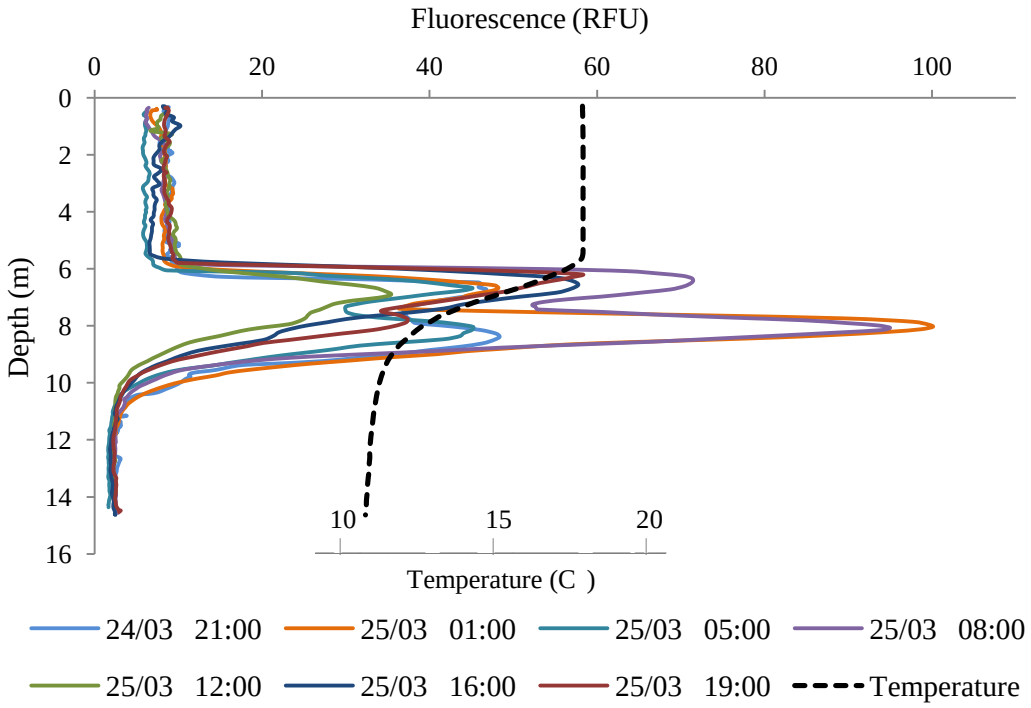


Figure 4.10: Chlorophyll fluorescence and mean temperature profile on 24-25 March 2011. Date and time (h) of each profile are given in inset.

Table 4.3: Peak and mean relative units and depths of DCM fluorescence (24-25 March 2011)

Date	Time (h)	Peak RFU depth (m)	Fluorescence (RFU)	Depth range (m)	Mean fluorescence over depth range (RFU)
24 March 2011	21:00	7.0	47.4	6 - 7	33.0
		8.2	47.9	7 - 8	38.7
25 March 2011	01:00	6.6	47.7	6 - 7	39.0
		7.9	99.5	7 - 8	60.0
	05:00	6.7	45.0	6 - 7	34.4
		8.0	45.0	7 - 8	33.8
	08:00	6.4	71.5	6 - 7	66.4
		8.0	95.0	7 - 8	67.2
	12:00	6.9	35.4	6 - 7	27.6
		-	-	7 - 8	27.2
	16:00	6.6	57.7	6 - 7	52.9
		-	-	7 - 8	35.8
	19:00	6.2	58.2	6 - 7	52.5
		8.1	38.7	7 - 8	38.3

e. Cell counts and biomass

Phytoplankton biovolumes at depth intervals of 0, 2, 4, 6, 7, 8, 9, 10 m corresponded to relative concentrations of chlorophyll fluorescence (RFU) at 19:00 h (25 March 2011) (Figure 4.11). The highest biovolume (3.5×10^7 µm mL^{-1}) corresponded to the depth of the upper fluorescence peak at 6 m (50.8 RFU), while the lowest biovolume (2.5×10^6 µm mL^{-1}) corresponded to 9 m depth, where fluorescence was 11.8 RFU. The relationship between fluorescence and biomass was statistically significant, with a Pearson correlation coefficient of R^2 = 0.78 ($P \leq 0.05$) when the biovolume at 0 m was compared with fluorescence at 0.34 m (the minimum depth of CTD). The statistical relationship improved to R^2 = 0.83 ($P \leq 0.05$) with the omission of 0 m biovolume data point.

Total cell concentrations were not representative of the fluorescence profile (Table 4.4). The lowest total cell count (1.3×10^4 cells mL^{-1}) corresponded to the

upper fluorescence peak at 6 m, while the highest total cell count (5.8 x 10^4 cells mL^{-1}) corresponded to the lower fluorescence peak at 8 m (35.7 RFU).

Dinoflagellates were the dominant taxa by volume in the metalimnion, with *Ceratium* sp. biomass ranging between 1.0 x 10^7 µm mL^{-1} and 2.5 x 10^7 µm mL^{-1} over 6-8 m depth, and were below the detection limit at depths outside that range (Table 4.5). *Aulacoseira italica* var. *tenuissima*; a filamentous diatom was dominant from 0-4 m, and represented a large proportion of the biomass at 7 m depth, with 7.0 x 10^6 µm mL^{-1} (39 %). The dominant taxa overall by cell concentration was an unidentified chlorophyte (picoplankton #2) which was too small to visually enumerate to the cells mL^{-1} level and was thus classified by the total number of colonies (6 µm, spherical) counted. Picoplankton #2 reached concentrations of 1.7 x 10^4 colonies mL^{-1} at 9 m and 10 m. The second most abundant species in terms of cells mL^{-1} was a small (6 µm, spherical) unidentified colonial chlorophyte (#1), common to almost all depths and reaching a maximum concentration of 3.8 x 10^4 cells mL^{-1} at 8 m depth.

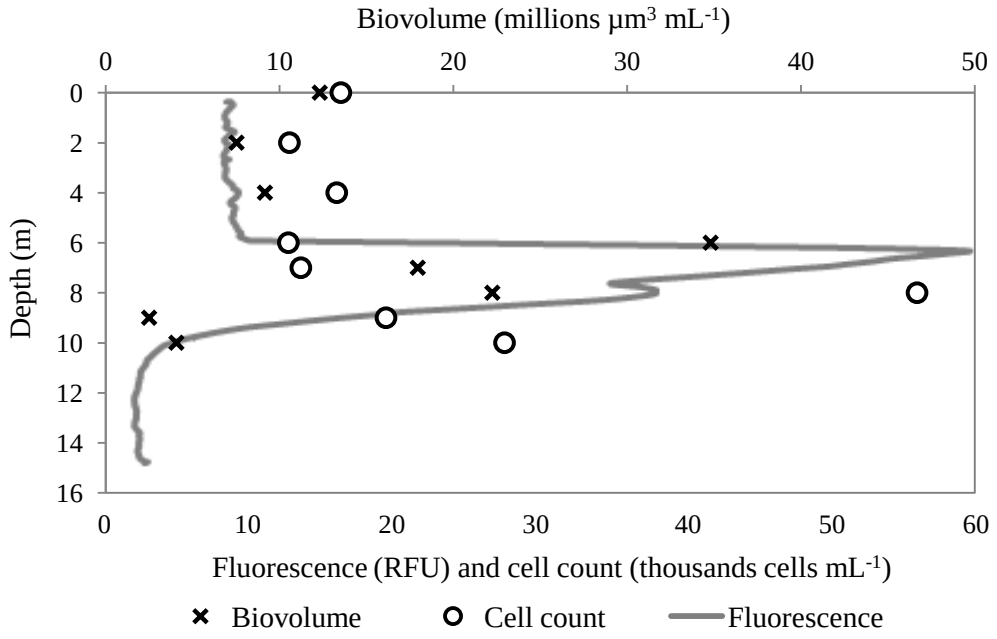


Figure 4.11: Chlorophyll fluorescence in relative units, total cell concentrations and phytoplankton biovolumes at 19:00 h on 25 March 2011

Table 4.4: Cell concentrations for sampled depths at 19:00, station W1, Lake Ōkaro on the 25 March, 2011

W1 25 March 2011	Om	2 m	4 m	6 m	7 m	8 m	9 m	10 m	Spp. total cells mL^{-1}
Aulocosiera italica var. tenuissima	4,297.4	9,875.8	15,161.6	5,628.0	12,348.6	4,942.7	145.8	729.1	53,129.1
Planktothrix isothrix	1,293.0								1,293.0
Fragileria sp.	189.3		429.5	244.7					863.5
Ceratium				232.7	97.0	116.7			446.4
Dinobryon				267.8					267.8
Large cryptophyte			32.3	9.2				145.8	187.4
Trachelomonas		18.5	18.5	9.2	46.2	58.3			150.7
Anabaena lemmermanii	55.4								55.4
Peridinium				9.2					9.2
Unid. colonial chlorophyte	1,754.8	568.0		277.1	138.5	38,063.3	2,070.8	10,305.1	53,177.6
Unid. colonial picoplankton #2 (colonies mL^{-1})						9,887.1	17,178.5	17,295.2	44,360.7
Phacus	7,942.7	1,385.4		5,910.9					15,239.0
Chlamydomonas	1,269.9	1,339.2	955.9	544.9	1,348.4	4,579.0	554.1		10,591.5
Merismopedia						700.0			700.0
Pseudobaena limnetica							204.2	116.7	320.8
Nitzschia spp.	23.1	13.9	13.9					58.3	109.1
Staurastrum sp.	13.9	9.2			18.5			29.2	70.7
Oocystis	69.3								69.3
Actinastrum					32.3				32.3
Sample total (cells mL^{-1})	16,908.8	13,210	16,611.7	13,133.7	14,029.5	58,347.1	20,153.4	28,679.4	

Table 4.5: Species biovolumes for sampled depths at 19:00, station W1, Lake Ōkaro on the 25 March, 2011. Data are cells/mL^{-1} x biovolume (µm^3). Biovolumes from Dryden & Vincent (1986) and Olenina et al. (2004).

W1 25 March 2011	**Biovol. (µm^3)**	**Om**	**2 m**	**4 m**	**6 m**	**7 m**	**8 m**	**9 m**	**10 m**	**Spp. total (µm^3)**
Aulocosiera italica var. tenuissima	571	2,453,815	5,639,081	8,657,273	3,213,588	7,051,050	2,822,281	83,251	416,316	30,336,659
Planktothrix isothrix	962	1,243,866								1,243,866
Fragileria sp.	210	39,753		90,195	51,387					181,335
Ceratium	107452				25,004,080	10,422,844	12,539,648			47,966,573
Dinobryon	42				11,247					11,247
Large cryptophyte	2657			85,821	24,444				387,390	497,656
Trachelomonas	523		9,675	9,675	4,811	24,162	30,490			78,816
Anabaena lemmermanii	1308	72,463								72,463
Peridinium	48605				447,166					447,166
Unid. colonial chlorophyte	113	198,292	64,184		31,312	15,650	4,301,152	234,000	1,164,476	6,009,068
Unid. colonial picoplankton #2 (colony µm^3)	113						1,117,242	1,941,171	1,954,358	5,012,770
Phacus	989	7,855,330	1,370,160		5,845,880					15,071,371
Chlamydomonas	310	393,669	415,152	296,329	168,919	418,004	1,419,490	171,771		3,283,334
Merismopedia	14						9,800			9,800
Pseudobaena limnetica	314							64,118	36,643	100,763
Nitzschia spp.	1280	29,568	17,792	17,792					74,624	139,776
Staurastrum sp.	1019	14,164	9,374			18,851			29,754	72,145
Oocystis	138	9,563								9,563
Actinastrum	28					904				904
Total µm^3 with depth		12,310,485	7,525,421	9,157,086	34,802,836	17,951,468	22,240,106	2,494,313	4,063,563	

5 Discussion: Spatially comprehensive sampling

5.1 Relationships between thermocline depth, euphotic depth and chlorophyll fluorescence:

During thermally stratified periods in the study, a deep chlorophyll maximum (DCM) formed at all stations. Its depth was closely statistically related to the thermocline depth (Table 3.1). A thermocline is considered to be a prerequisite for the development of a DCM as it offers protection from surface-driven mixing that could entrain and expose populations to harmful levels of irradiance (Abbott et al., 1984, Whittington et al., 2000, Kamykowski and Yamazaki, 1997). Additionally, a number of studies have highlighted a close relationship between DCM depth and euphotic depth (Modenutti et al., 2004, Hamilton et al., 2010, e.g., Heaney and Talling, 1980, Whittington et al., 2000), while other studies have correlated DCM depth with inverse gradients in two or more equally growth-limiting variables, e.g., inorganic nutrients and irradiance (Ryabov et al., 2010, Klausmeier and Litchman, 2001).

For the duration of the study the euphotic depth was greater than the depths of both the DCM and the thermocline (Figure 3.1). This is a prerequisite for DCM formation in clear-water lakes, in that the euphotic depth will exceed the depth of the lower metalimnion ($z_{eu} \geq z_{SML}$) (Hamilton et al., 2010). However, it is worth noting that z_{eu} represents 1% of the irradiance at the surface, and the actual radiation level at that depth will vary seasonally. Additionally, the strength of the relationship between z_{eu} and the DCM will depend to some extent on the preferences of the constituent species. To illustrate this, under nutrient-limited conditions, the dinoflagellate *Ceratium hirundinella* has been shown to form subsurface populations located where irradiance is c. 250 µmol m^{-2} s^{-1}, around 10%

of the *in vitro* surface irradiance (Cullen and Horrigan, 1981). Conversely, under similar conditions the dinoflagellate *Peridinium cinctum* form subsurface populations at c. 714 µmol m^{-2} s^{-1} or about 30% of *in vitro* surface irradiance (Regel et al., 2004). These studies and others (e.g., Walsby et al., 2001) have recognised that the relationship between photon irradiance and DCM depth corresponded to the photosynthetic compensation (saturation) point specific to the constituent population. The compensation point may even vary within populations, with variations in the age of cells, their individual tolerances to irradiance (e.g. higher carotenoid concentrations at high irradiance levels (Kellar and Paerl, 1980)), their internal structure (e.g., chloroplast shape and thylakoid content (Sicko-Goad et al., 1977)) and previous light history (Regel et al., 2004).

The relationship between z_{eu}, DCM and thermocline depth improved significantly from 20 January 2011 when the depths of each parameter became very closely aligned. This period corresponded to when the DCM population was positioned around 1% of surface irradiance, at the thermocline (Figure 3.1). The depth of the DCM was horizontally homogenous between stations during thermal stratification, but was highly variable in terms of the relative fluorescence (RFU) value (Figure 3.4). Conversely, during the winter mixed period, the DCM was non-existent and peak RFU values were homogenous and low. This demonstrates that although chlorophyll fluorescence (a proxy for phytoplankton biomass (e.g., Gregor et al., 2005, Hamilton et al., 2010)) can vary markedly across horizontal scales, thermal stratification plays an important role in influencing the vertical distribution of phytoplankton.

Thermal stratification also limits the exchange of inorganic nutrients between the epilimnion and the hypolimnion (Kufel and Kalinowska, 1997). Biological uptake

depletes nutrients in the epilimnion and facilitates the dominance of highly competitive species with an ability to regulate their position in the water column (e.g., Talling et al., 2005). Phytoplankton biomass can then become concentrated at discrete depths where there may be contrasting gradients in light and nutrients that limit growth (Klausmeier and Litchman, 2001). Ostrovsky & Yacobi (1999) demonstrated that when nutrient concentrations in epilimnetic waters are extremely limiting, the addition of small amounts of nutrients can enhance productivity at the location where they are introduced. During most of summer, the allochthonous supply of nutrients was likely to be minimal due to low rainfall, and discrete depth measurements showed that NH_4-N and PO_4-P were strongly depleted in the epilimnion during thermal stratification (Figures 3.10a, b). Thus, it follows that any entrainment of the nutrient-rich hypolimnetic waters into surface waters was likely to have been the dominant source of nutrients for short-term phytoplankton growth responses.

Data in the 2010-2011 period of thermal stratification show that z_{eu} followed a similar trend of increasing depth to the thermocline and DCM, even at depths $\geq$ 8 m (Figure 3.1). An increase in z_{eu} could occur when higher irradiance levels typical of summer coincide with a reduced phytoplankton biomass in the nutrient-poor epilimnion (Fee, 1976) and low levels of rainfall (i.e., reduced particulate suspension), facilitating clear-water conditions in the epilimnion; analogous to lakes of a lower trophic status. The reverse occurrence would be in lakes where reductions in water clarity cause the thermocline depth to migrate upwards, but z_{eu} still becomes shallower than z_{SML}, leading to insufficient light to support the DCM, and therefore the occurrence of a surface chlorophyll maxima (Hamilton et al., 2010).

High-frequency monitoring from 24-25 March 2011 provided evidence of a non-migrating DCM population. However, it is not known whether the DCM remained static near the thermocline for the entire period of thermal stratification, or if it was comprised of organisms that frequently undertook vertical migration to optimise growth conditions (e.g., Whittington et al., 2000). The taxa comprising DCMs can vary markedly in their behavioural and physiological adaptations to vertical gradients in resources; ranging from diatoms with reduced sinking velocities (Coon et al., 1987), to buoyancy-regulating cyanobacteria (Padisák et al., 2004) and motile ciliates and dinoflagellates (Modenutti et al., 2004). Succession between species occurs as environmental conditions change over time (Reynolds, 1997b) and the dominant DCM species may also change within the sampling period (e.g., Felip and Catalan, 2000, Abbott et al., 1984). The dinoflagellates *Peridinium palustre* and *Ceratium hirundinella* appear to be the most probable candidates for a DCM population in Lake Ōkaro, as *P. palustre* have previously been observed to form subsurface summer peaks in the lake (Dryden and Vincent, 1986), and *C. hirundinella* dominated the DCM biomass during the high-frequency 24-hour sampling period from 24-25 March 2011. *C. hirundinella* can migrate vertically at rates of up to 0.97 m h^{-1} (Whittington et al., 2000) and *Peridinium cinctum*; a species morphologically similar to *P. palustre* can migrate at rates of up to 1.93 m h^{-1} (Regel et al., 2004). At these speeds, it would have theoretically been possible for either species to travel between the epilimnion and hypolimnion over the course of a day, before settling to a uniform depth by morning. As all CTD casts were undertaken between 08:00 and 11:00 h, and were completed within each day over $\leq$ 1 h total, the window for any observable changes to occur between stations was very small and diel vertical migration cannot be discounted entirely.

5.2 Spatial variability in physical, chemical and biological components

There was very little horizontal variability in temperature profiles observed during the study, with the exception of occasion single outlying stations. For example, on 5 January 2010, the metalimnion depth at station N1 was approximately 1 m lower than all other stations. This occurrence may have been due to an internal seiche, where strong winds had tilted the metalimnion and subsequently relaxed, causing an oscillation and depression of the thermocline (Kalff, 2002c), however it seems unlikely that these basin-scale processes would not be reflected at other stations, given the short sampling time frame (1 h) and distance between stations ($\leq$ 200 m).

On 26 October the upper 3 m of the water column had a high degree of horizontal temperature variability. Potentially, this was caused by a patchily-distributed surface aggregation of cyanobacteria cells. Rinke et al. (2010) described a similar phenomenon where during a cyanobacterial bloom, epilimnion temperatures were observed to increase increased as cells intercepted and absorbed incoming shortwave radiation. This assertion is supported by the high specific conductance measurements and associated high DO concentrations in surface waters at the time.

For the duration of thermal stratification, chlorophyll fluorescence profiles were characterised by DCMs at all deep stations, and most shallow stations (Figures 3.6a-v), positioned at depths corresponding to the metalimnion (Figures 3.5a-x). However, in contrast to temperature profiles, there was a high degree of horizontal heterogeneity between stations, relating to differences in the peak relative fluorescence. The horizontal variability at the DCM could be the result of advective processes near the metalimnion causing patchiness in phytoplankton

productivity or distribution. The advection of nutrients derived from near-shore upwelling into the metalimnion by seiching is described by Kalff (2002c) as having a major effect on primary productivity in DCMs. This was also recognised by Ostrovsky & Yacobi (1999), who determined seiche-induced metalimnetic jets (intrusions) as the causal agent for horizontally transported particulate matter resuspended at the benthic boundary layer, and found small enhancements of nutrients resulted in measureable and localised increases in primary productivity. MacIntyre et al. (1999) reported that turbulence and benthic heat flux at the metalimnion-benthic interface resulted in lateral advection of particulate matter within the metalimnion, and also hypothesised that mixing near topographical features would have a critical influence in introducing hypolimnetic nutrients to the euphotic zone. The benthos of Lake Ōkaro is characterised by several ridges that locally reduce the depth of the lake to between 5 and 10 m (Hardy, 2005). It could be speculated that in combination with internal seiches and waves, these ridges could have stimulated the introduction of hypolimnetic waters into the metalimnion and epilimnion, resulting in the horizontal variability observed in DCM fluorescence. Imberger and Spigel (1987) resolved microstructure isotherm profiles at eight stations in Lake Ōkaro to demonstrate internal mixing and circulation processes. The authors found that isotherms indicated the presence of internal wave activity during thermal stratification, even under light wind. The authors also described boundary mixing associated with internal ridges, and found evidence of benthic turbulence induced by internal wave activity at the c. 7 m deep metalimnion (Imberger and Spigel, 1987). This suggests that the processes responsible for the horizontal patchiness of fluorescence at the DCM are related to the lateral advection of nutrients and particulate matter in the metalimnion, and are further influenced by horizontally variable introductions of hypolimnetic

water into the metalimnion caused by internal waves or seiching, and possible boundary mixing near benthic ridges.

On several occasions the depth of the DCM differed between shallow and deep stations without a corresponding change to the thermocline depth. This could be the result of powerful wind shear entraining cells from the DCM up into the epilimnion, causing them to become continually cycled in the surface mixed layer and transported down-wind into the shallow margins of the lake (Kalff, 2002c). Similar effects have been seen during surface blooms of buoyant cyanobacteria (Ibelings et al., 2003). On other occasions, horizontal heterogeneity was marked by an additional fluorescence peak at a shallower depth to the primary (maximum) DCM; i.e., the occurrence of a dual DCM (e.g., station S1, Figure 3.6m). These observations show that DCM formation is not necessarily horizontally homogenous, and may occur in patches in a lake. The 'dual' DCMs were not associated with horizontal heterogeneity of other measured variables, e.g., temperature change, which indicates that the phenomenon was likely the result of biological processes (e.g., vertical migration) rather than mixing and advection.

The elucidation of a dual DCM based on high-frequency measurements from 24-25 March 2011 supports the assertion that the phenomenon was a function of behavioural and physiological differences in the species comprising the DCM, because the upper DCM was dominated by the large motile dinoflagellate *C. hirundinella*, while the lower DCM was co-dominated by *C. hirundinella* and an unidentified colonial picoplankton that was unique to the lower depth stratum. *Ceratium hirundinella* have a recognised propensity to undertake diel vertical (Cullen, 1985) with well-defined subsurface aggregations rising toward the surface during daylight hours to maximise photosynthetic yield and store

carbohydrates, then moving downward at night to assimilate inorganic nutrients in the hypolimnion (Regel et al., 2004, Ault, 2000). It appears that the upper DCM could have separated from the metalimnion due to the *C. hirundinella* DCM population undergoing diel vertical migration. However, the apparent rarity of dual DCMs (with respect to the spatial data) and the lack of migration observed over the high-frequency sampling period suggest that is not a common occurrence in Lake Ōkaro. This could be related to the shallow depth of Lake Ōkaro, as dual chlorophyll peaks have previously been noted in deeper, oligotrophic lakes. Abbott et al. (1984) described the occurrence of a dual DCM in Lake Tahoe; an ultraoligotrophic subalpine lake with a mean depth of c. 313 m and z_{eu} of c. 120 m. In Lake Tahoe, an upper chlorophyll peak was evident at c. 10 m, while a lower, consistently larger peak was evident from 30-50 m. The phytoplankton community at the time was dominated by a small diatom, with a chrysophyte as a subdominant. The authors hypothesised that a subsequent transition to nutrient limited conditions in the epilimnion had facilitated the disappearance of the upper chlorophyll peak.

If diel vertical migration were more common than the data set illustrates, the dual DCM could potentially be explained by differences in the vertical migration rates of the DCM population. For example, DCM populations have been shown to migrate relatively asynchronously, as opposed to migrating simultaneously (e.g., Regel et al., 2004). Therefore there may be differences between the constituent species in the DCM population. For example, Regel et al. (2004) demonstrate that individual swimming speeds vary within and between species. Kamykowski and Yamazaki (1997) have also demonstrated that migrating dinoflagellates vary in their behavioural responses to environmental cues, e.g., photosynthetically active

radiation. These effects could result in differences in the distribution of a DCM or multiple DCMs through the water column.

Fluorescence was generally horizontally homogenous in the epilimnion, particularly at depths shallower than the thermocline, and during the winter mixed period. This is likely to be due to the homogenising effect of wind-induced mixing in the surface mixed layer. Kalff (2002b) states that as epilimnion temperatures cool with decreasing atmospheric temperatures, the metalimnion is progressively incorporated into the epilimnion and the surface mixed layer increases in depth. The greater depth of thermal stratification allows kinetic energy imparted by wind at the surface of the lake to penetrate to greater depths, mixing and homogenising the water column (Kalff, 2002b). This effect was observed early in the study period (Figures 3.5a-p) and was supported by Schmidt stability (Figure 3.4).

For the majority of the sampling period, dissolved oxygen (DO) profiles were relatively horizontally homogenous; particularly at depths shallower than the thermocline depth. During stratification, peak DO values generally corresponded to the depth of the DCM. High DO concentrations are typical of DCMs (George and Heaney, 1978, Heaney and Talling, 1980). For example, photosynthetically-induced subsurface peaks in DO have been described by Holm-Hansen & Hewes (2004), who studied the physiochemical and optical conditions relating to DCMs in Antarctica. The authors reported that elevated DO concentrations corresponded to the depth (50-100 m) of DCMs in all cases, stating that the phenomenon was evidence of metabolic (photosynthetic) activity.

On 26 October 2010 (Figure 3.7r), there was a high degree of patchiness in DO at depths $\leq$ 3 m. This may be related to the occurrence of a surface bloom of cyanobacteria at that time. Surface blooms can be highly horizontally variable, as

demonstrated by Galat and Verdin (1989) who used satellite remote sensing and quantitative physical measures to resolve horizontal variability in a surface bloom of the cyanobacterium *Nodularia spumigena* in a saline Nevada lake. The authors found that surface chlorophyll *a* concentrations varied between 3.6 and 9790 mg m^3. High concentrations of surface bloom-forming *Anabaena* species have previously been recorded in Lake Ōkaro in October (Paul, 2006), so it seems possible that patchiness in primary productivity could have resulted in the observed horizontal variability in DO concentrations produced by the bloom.

pH tended to be more horizontally heterogeneous than many other variables through the sampling period, and pH at stations W2 and S2 could be up to 2 units higher than at other stations on the same day. These stations are located at the most sheltered end of Lake Ōkaro, surrounded by 20 m-high, tree-covered cliffs (Hardy, 2005). The stations were also in close proximity ($\leq$ 4 m) to overhanging and partially-submerged riparian vegetation, particularly willow trees (*Salix* spp.). This suggests that the lower pH may be related to some aspect of the riparian vegetation or to the shelter from westerly winds provided by the surrounding cliffs. *Salix* spp. decrease soil pH by releasing H^+ in order to compensate for an unbalanced cation-anion uptake at the root-soil interface (Wang et al., 2005, Hinsinger et al., 2003). It is possible that localised leaching from the soil in addition to the direct release of H^+ from submerged roots could have reduced the pH.

Vertical profiles of specific conductance indicated the surface mixed layer was almost homogenous over the lake, due to wind-driven circulation and mixing, whilst the specific conductivity increased with depth to higher values in the hypolimnion. Increasing specific conductance in the hypolimnion is considered to

be an attribute of lakes with infrequent mixing, with accumulated suspended material near the benthos and vertical gradients in nutrients (Wierenga, 2004).

Seasonal trends in rainfall and evaporation can influence specific conductivity values in the surface mixed layer by diluting (i.e., rainfall) or increasing (i.e., evaporation) the ionic concentration of the water (e.g., Pilgrim et al., 1979). This was evident as surface mixed layer specific conductivity values were highest in the summer, particularly in December 2009 (110 - 125 µS cm^{-1}) when evaporation rates were highest. During winter, surface layer conductivity decreased (mean 107 µS cm^{-1}), which was most likely due to rainfall.

On 26 October 2010, specific conductivity near the surface increased to 144 µS cm^{-1}, coinciding with increases in DO. This is potentially due to the occurrence of a cyanobacterial surface bloom. Specific conductance levels are known to increase during cyanobacterial blooms because extended periods of increased primary productivity cause dissolved inorganic carbon (e.g., CO_2) concentrations to become depleted (Paerl and Ustach, 1982). Carbonic acid (H_2CO_3) is then formed as dissolved atmospheric CO_2 reacts with water and subsequently dissociates into bicarbonate ions (HCO_3^-), raising the pH of the water column (Wurts and Durborow, 1992, Kalff, 2002a). The associated changes to the carbonate-bicarbonate equilibrium of the water can be registered as increases in specific conductivity.

During thermal stratification, concentrations of nutrient species below the thermocline were frequently an order of magnitude greater than those above the thermocline (Figures 3.10a-c). The relatively low concentrations in the epilimnion suggest that biological uptake had been occurring, and this had potentially exceeded rates of replenishment from allochthonous and autochthonous sources

(Bormans et al., 1999, Coon et al., 1987). Mean epilimnetic NH_4-N and PO_4-P concentrations over the December 2009 – April 2010 period were 0.027 mg L^{-1} and 0.004 mg L^{-1}, respectively, and are comparable to the 0.014 mg L^{-1} NH_4-N and 0.002 mg L^{-1} PO_4-P concentrations that White et al. (1991) determined to be limiting to phytoplankton biomass. The highest concentrations of nutrients at the deepest sampling station were frequently recorded at the deepest sampling depth of 14 m. At these depths biological uptake would be minimal because of insufficient light. Additionally, dissolved oxygen levels suggest the presence of anoxic conditions below the thermocline (Figure 3.7a-l). The hypolimnion of Lake Ōkaro is known to contain H_2S soon after anoxic conditions occur, and it has been shown that many species of phytoplankton will avoid H_2S, as it substantially inhibits photosynthesis (Gervais et al., 2003). Hydrogen sulphide (H_2S) concentrations were not determined in this thesis, but field observations lend support to this theory because discrete depth samples collected in the Schindler-Patalas trap smelt strongly of 'rotten eggs' indicative of the presence of H_2S.

The high summer concentrations of NH_4-N and PO_4-P in deep waters of Lake Ōkaro have been noted in previous studies (Özkundakci et al., 2011), and in other Rotorua lakes, e.g., Lake Rotorua (Burger et al., 2007). These studies attributed the flux of NH_4-N to high supply rates of organic matter to the benthos, where subsequent decomposition by bacterial mineralisation would occur (ammonification). Enhanced P concentrations were attributed to processes involving anoxic P release from inorganic molecular complexes (e.g., iron), diffusion into the water column from sediment porewaters, and bacterial mineralisation of organic matter (Burger et al., 2007).

In comparison to NH_4-N, NO_3-N concentrations were relatively high. This has been noted in previous studies (e.g., White et al., 1991, Présing et al., 2001) and occurs because NH_4-N is the preferred N source for phytoplankton, as it is readily assimilated into cells, whereas NO_3-N must be transformed by nitrate reductase before it can be metabolised (Reynolds, 1997a). When NH_4-N is limiting, PO_4-P is an important source of the energy required to metabolise NO_3-N. Thus, P deficiency will further inhibit the biological assimilation of NO_3-N (Spalinger and Bouwens, 2003). The fact that NO_3-N only began to decline in the epilimnion from early January potentially suggests that NH_4-N had become depleted and phytoplankton opted for a less efficient form of nitrogen. This is in line with Présing et al. (2001), who found NO_3-N uptake would only exceed NH_4-N on occasions when the ambient concentration of NO_3-N was four and nine times higher than NH_4-N. Additionally, this period of N and P depletion could have been marked by succession to phytoplankton with an enhanced capacity to scavenge for nutrients from the water column. For example, dinoflagellates will migrate vertically to gain access to resources (Raven and Richardson, 1984), and subsurface populations of *Peridinium palustre* (Lindemann) have previously formed in Lake Ōkaro from January to May, coinciding with epilimnetic nutrient depletion (Dryden and Vincent, 1986).

5.3 Central lake site as a surrogate for whole-lake fluorescence

On most sampling days there were large differences between the chlorophyll fluorescence profile of the central station and the mean of the whole lake. Differences in the relative peak fluorescence intensity were most pronounced at the depth of the thermocline where the DCM was located. In some cases, the central lake station underrepresented the mean fluorescence of the stations at that

depth by up to 45% (e.g., Figure 3.11h), or vice-versa on other occasions (e.g., Figure 3.11b, 52%). Differences in the relative fluorescence values at the metalimnion may relate to seiche-induced mixing and transport of nutrients and phytoplankton, both across the metalimnion, and laterally through the metalimnion (e.g., Ostrovsky and Yacobi, 1999, MacIntyre et al., 1999).

Many studies use a single-station to derive estimates of phytoplankton community attributes (e.g. species composition, biomass and primary productivity) (Berman et al., 1995, Carrick et al., 1993, 1988). With respect to the present data, it could be speculated that the information provided on phytoplankton in the cited studies potentially has a high degree of variability associated, and may not represent the mean conditions that existed in the lakes at the time the studies were conducted.

5.4 Temporal variability during a cyanobacteria-dominated surface bloom

During the high-frequency study from 18-19 November 2010, there was a high degree of temporal variability in the thickness of the metalimnion. Most of this variability was associated with fluctuations in the depth of the upper metalimnion (Figure 2). In a study by (Bormans et al., 1999), the depth of the upper metalimnion increased when mean wind speeds were $\geq$ 2.5 m s^{-1} and were sustained at $\geq$ 4.5 m s^{-1}. These wind speed values are comparable to those measured from 18-19 November 2010; however the increasing depth of the upper metalimnion occurred at a time when mean wind speed declined compared with previous sampling times. It is possible that this phenomenon was caused by a combination of wind speed and solar radiation causing a density gradient or a more accentuated diurnal thermocline to form during the day which became reduced during night time convective cooling, resulting in an increase in upper

metalimnion depth. There was a large amount of temperature variation between 2.4 m to 4.4 m on 18-19 November 2010. This may have been caused by an internal wave. Imberger and Spigel (1987) have described the occurrence of internal waves in Lake Ōkaro under light to moderate wind conditions, and Kalff (2002c) states that internal wave formation and breaking can heavily influence the vertical position of the thermocline.

The high K_d and low z_{eu} values indicate light was rapidly attenuated in the epilimnion on 18-19 November 2010. An *Anabaena spiroides*-dominated surface bloom was present at Lake Ōkaro on 18-19 November 2010, so it is likely that the rapid attenuation of light was caused by the high concentrations of cells. This assertion is supported by Rinke et al. (2010), who reported high light extinction coefficients in association with cyanobacterial surface blooms.

The high concentrations of dissolved oxygen measured near the surface of Lake Ōkaro are typical of lakes with high levels of productivity (Rodger et al., 1994). For example, Mitrovic et al. (2001) found that the daily-integrated oxygen production in a buoyant *Anabaena circinalis* population was five times greater than that of an evenly distributed population in the Darling River (Mitrovic et al., 2001). High concentrations of DO have been associated with increased rates of photosynthesis during cyanobacterial blooms (e.g., Bowling and Baker, 1996, Paerl and Ustach, 1982). Elevated pH levels are also typical of cyanobacterial surface blooms. Dissolved inorganic carbon (DIC) is of major importance for buffering against changes in pH (Kalff, 2002a). Phytoplankton obtain DIC directly from their immediate environment, either as CO_2, HCO_3^-, or CO_3^{2-} depending on the preference of the species (Moss, 1973b). DIC concentrations can become depleted in the epilimnion under thermally stratified, calm conditions

(Paerl and Ustach, 1982), particularly when algal productivity levels are high (Hein, 1997) and rates of free CO_2 uptake into cell tissues exceed the rates of diffusion of atmospheric CO_2 across the lake surface (Reynolds, 1997a). Under these conditions, buoyancy-regulating cyanobacteria can accumulate in the surface near the air-water interface where rates of DIC replenishment are highest (Paerl and Ustach, 1982). Free CO_2 supplies become exhausted from photosynthesis and carbonic acid (H_2CO_3) that is formed as dissolved atmospheric CO_2 reacts with water and subsequently dissociates into bicarbonate (HCO_3^-). HCO_3^- sources are drawn upon to bring the carbon balance into equilibrium, producing residual OH^- ions that increase the pH (Kalff, 2002a, Hendy, 2011 Pers. comm.).

The *A. spiroides* fluorescence maxima remained at depths $\leq$ 1.4 m on 18-19 November 2010. The propensity for some cyanobacteria genera to undertake diel vertical migration has been well documented (e.g., Ganf and Oliver, 1982, Reynolds, 1984, Kromkamp and Walsby, 1990) and it has been proposed that this is an adaptive strategy used to overcome the vertical separation of light and nutrients under stratified conditions (Fogg and Walsby, 1971).

Extended exposure to high irradiance reduces photosynthetic CO_2 fixation, and results in exposure to elevated O_2 levels that decrease CO_2 and N_2 fixation rates, leading to cell senescence and loss of buoyancy in many cyanobacteria species (Paerl and Ustach, 1982). However, Kellar and Paerl (1980) reported a surface population of *A. spiroides* in a small, stratified eutrophic lake that persisted for two months, in spite of repeated exposure to high light irradiance. The population produced carotenoids that protected chlorophyll from direct photo-oxidation. The populations also temporally separated CO_2 uptake and N_2 fixation when levels of

dissolved oxygen had built up in the surface layer, fixing CO_2 in the morning prior to build up of O_2, and fixing N_2 during nightfall when surface O_2 levels were highest. On 19 November 2010, morning (09:00 h, 11:00 h) concentrations of dissolved oxygen ranged between 7.7–10.5 mg L^{-1} in the upper 2 m of the epilimnion, and increased to 13.7 mg L^{-1} in the afternoon (16:30 h). Euphotic depth during the bloom was low (z_{eu} = 2.092 m, 11:00 h), so the optimal conditions for photosynthesis in this environment would likely be limited to the uppermost 2 m of the water column. As the upper 2 m also corresponded to the depth of highest fluorescence on 18–19 November 2010, it seems possible that the *A. spiroides* populations had adopted the same physiological responses described in Kellar & Paerl (1980), enabling cells to persist in the epilimnion without migrating to avoid damaging irradiance that would ordinarily result in senescence.

5.5 Temporal variability during a dual-peak deep chlorophyll maximum

There was relatively little variation between temperature profiles during the high-frequency sampling period, 24-25 March, 2011 (Figure 4.7). The majority of variability was confined to the upper 2 m of the water column and appeared to be related to diel heating and cooling. This is supported by Schmidt stability, which declined at night, reaching a minimum at 08:00 h (Figure 4.8). The thickness of the metalimnion varied from 24-25 March, 2011 (Figure 4.8). The majority of the variation in the thickness of the metalimnion was associated with changes in the depth of the metalimnion surface. This could be caused by the formation and breakage of an internal wave, as demonstrated by Kalff (2002c).

At 12:00 h on 25 March 2011, the mean light extinction coefficient ($K_d \leq 0.51$ m^{-1}) was low, and the deep euphotic depth indicates that solar radiation could penetrate to depths $\geq$ 10 m at times (Table 4.2). It is likely that low amounts of organic

matter in the nutrient-poor epilimnion would facilitate this. The fluorescence profiles and phytoplankton biomass support this assertion, as the mean phytoplankton biomass at depths $\leq$ 4 m was $\leq$ 8.8% of the total.

On 24-25 March 2011, the highest dissolved oxygen (DO) concentrations corresponded to the depth of the deep chlorophyll maximum (DCM) (Figure 4.9). This is likely to be related to photosynthetic activity yet this occurrence does not appear to be typical of all DCMs in small lakes. For example, Gervais et al. (2003) investigated the vertical distribution and relative abundance of phytoplankton in a small (0.12 km^2), mesotrophic lake with a *Ceratium* sp. and cyanobacteria-dominated summer DCM, reporting that the lowest DO occurred near the depth of the DCM. However, George & Heaney (1978) and Heaney & Talling (1980) also described the occurrences of *Ceratium hirundinella* dominated DCMs in Esthwaite Water. Both studies reported considerable diel variation in the DO concentration of the water column, and related this to the position and photosynthetic activity of the vertically migrating *C. hirundinella* populations.

Microscopic identification and enumeration of Lake Ōkaro phytoplankton collected at 19:00 h on 25 March 2011 revealed that the upper fluorescence peak was predominantly comprised of *C. hirundinella* (as described by Dryden & Vincent (1986)) and *Phacus* sp., while the lower fluorescence peak was comprised of *C. hirundinella* and an unidentified colonial chlorophyte (picoplankton #2) (Table 4.4). Due to the vertical stability of the fluorescence profiles over the sampling period (Figure 4.10), it is assumed that the dominant species comprising each peak remained relatively unchanged from 24-25 March 2011; however the relative abundances of each may have changed over time. Temporal variations in the fluorescence peak of each profile (Table 4.3) could

potentially be attributed to up-wind lateral transport at the metalimnion created by opposing wind currents at the lake surface (e.g., George and Heaney, 1978), or by differential heating and cooling at lake margins, internal waves and other physical processes that can redistribute particulate matter through a lake (Spigel and Imberger, 1987, Marti and Imberger, 2004). For example, MacIntyre et al. (1999) found that in a stable stratified system, heat flux caused by boundary layer mixing at depths where the lake bottom and metalimnion intersect (nearshore) generated lateral advection within the metalimnion. In much the same way, Ostrovsky & Yacobi (1999) determined seiche-induced metalimnetic jets (intrusions) to be the causal agent for horizontally transported particulate matter resuspended at the benthic boundary layer. It is likely that any number of these factors could have resulted in the temporal variability that was observed in peak fluorescence on 24-25 March, 2011.

The use of biovolume (which takes into account the size differences between species) instead of cell concentrations substantially improved the correlation with chlorophyll fluorescence. The chlorophyll content of a cell (the property measured by the fluorometer) increases with size, and thus higher cell biovolumes will tend to be reflected in higher chlorophyll fluorescence (Rigosi et al., 2011). This is supported by Friedrich et al. (1998), who compared methods for estimating phytoplankton composition, productivity and chlorophyll concentrations. They found that biovolumes and extracted chlorophyll *a* concentrations were well correlated with photosynthetic activity (R^2= 0.92), while cell counts were not.

Cell concentration and biovolume are high relative to fluorescence at the surface, compared with 2 and 4 m depth. It is possible that colonies near the surface had become adapted to higher light irradiance and had a reduced number of stacked

thylakoids in their chloroplasts resulting in a relatively low fluorescence reading from the CTD. This is in line with a study conducted by Post et al. (1985), who found diatoms grown in a high light (593 µmol m^{-2} s^{-1}) environment were characterised by low pigment content when compared to cells grown in low light (72 µmol m^{-2} s^{-1}) conditions.

Alternatively, the low fluorescence reading could have been caused by non-photochemical quenching (NPQ) of phytoplankton near the surface. This occurs as high irradiance levels trigger a response in light-harvesting proteins within the cell that causes excess energy to be harmlessly dissipated as heat, lowering fluorescence (Horton and Ruban, 2005). A survey by Hamilton et al. (2010) resolved the effects of NPQ in a biofish transect survey, where *in vivo* chlorophyll fluorescence values obtained near the surface indicated little to no phytoplankton were present.

The phytoplankton community at depths ≤ 6 m on 25 March 2011 was predominantly comprised of *Aulacoseira italica* var. *tenuissima* and *Phacus* sp. (Table 4.5). The vertical homogeneity over this depth range is likely to be due to wind mixing entraining cells, although this process would be severely limited by thermal stratification (e.g., Regel et al., 2004). *Aulacoseira* spp. are recognised as a competitive species in well mixed lakes and are well adapted to low light levels (McCausland et al., 2001). Most of *A. italica* var. *tenuissima* biomass at 19:00 h (25 March) was recorded at depths ≤ 8 m (Table 4.5). This was 0.8 m above the depth of the thermocline at that time (Figure 4.8). The high relative abundance and biomass of *A. italica* var. *tenuissima* at these depths is surprising, given the stability of thermal stratification in Lake Ōkaro at the time of sampling, and the fact that *A. italica* var. *tenuissima* is a large, non-buoyant chain diatom with

colonial fragments frequently ≥ 1000 µm in length. Walsby & Reynolds (1980) state that the sinking velocity of a cylinder of constant diameter (e.g., an *Aulacoseira* sp. cell) increases in proportion to its length, to a maximum length of five times the cylinder diameter. Additionally, Stokes Law indicates a higher settling velocity for cells with a low surface to volume ratio due to a reduced frictional coefficient (Reynolds, 1972). Thus, it can be inferred that the cellular density of the *A. italica* var. *tenuissima* population must have been in close approximation to the water density at 8 m (999.4 kg m^3) or concentrations would have been higher at 9 and 10 m depth, below the thermocline. Settling speeds of non-motile diatoms reduce when higher water densities are encountered (Condie and Bormans, 1997), so it seems likely that sinking velocities had decreased near the thermocline to such an extent that mixing forces were sufficient to overcome the density of the cells, allowing populations to become entrained in the euphotic zone during the sampling period (e.g., McCausland et al., 2001).

There was no diel vertical migration of the DCM observed on 24-25 March 2011 (Figure 4.10). This appears to contradict a number of other studies which have highlighted a clear tendency for sub-surface populations of flagellates (e.g., *Ceratium* spp.) to actively control their position in the water column in response to vertical gradients in temperature, light, nutrients or other resources (e.g., CO_2 concentration) (Ault, 2000, Tilzer, 1973, Cullen, 1982, Heaney and Eppley, 1981, Grigorszky et al., 2003, Clegg et al., 2004). As the energy expenditure associated with the use of flagella for movement is considered to be small, with running costs roughly approximating to the minimum maintenance costs for a non-flagellated cell (Raven and Richardson, 1984), the vertical position of flagellates could be expected to reflect their immediate requirements in terms of access to

resources or the avoidance of harmful conditions (e.g. super-saturating light intensities).

Ryan (2005) examined a *Peridinium* cf. *sydneyense*-dominated DCM in an oligotrophic lake, and found that the depth of the DCM was statistically correlated to the light level. Incubation experiments determined the depth of the non-migrating DCM was most likely to be related to the avoidance of high irradiance at the surface, as levels of 40% surface irradiance caused a loss of biomass in the DCM population (Ryan, 2005).

Klausmeier and Litchman (2001) emphasised the role of light and nutrient limitation in proposing a model of vertical phytoplankton distribution for poorly mixed water columns. The authors inferred that phytoplankton maxima would occur at depths corresponding to equal limitation by light and nutrients. This observation was supported by Clegg et al. (2004) who exposed five species of phytoplankton to a combination of physical and chemical gradients representative of field conditions, in laboratory chambers. The authors found that peak concentrations of the dinoflagellate *Ceratium furcoides* (also known as *C. hirundinella*) formed at intermediate zones between opposing gradients of light and O_2 concentration, light and CO_2 concentration, and CO_2 and O_2 concentrations. The authors attributed this 'compromise strategy' to the prevention of photoinhibition, photooxidative damage and photorespiration near the surface which would also have minimised detrimental exposure to very low levels of O_2 and light, and high O_2 and low CO_2 (leading to photorespiration) at greater depths. In much the same way, a compromise strategy has also been reported by Modenutti et al. (2004) who studied a non-migrating dinoflagellate-populated DCM in an oligotrophic lake. The authors hypothesised that the depth

and stability of the DCM at a depth of 30 m represented a trade off between lower cell-specific net primary production, and the avoidance of strong wind-driven vertical mixing processes that would potentially transport cells to where solar radiation levels would be harmful (Modenutti et al., 2004).

On 24-25 March 2011, the upper region of the DCM occurred within close proximity to the thermocline, and the lower region of the DCM occurred at the base of the metalimnion, characterised by much lower light climate and cooler water temperatures. Nutrient concentrations were not assessed on 24-25 March 2011, however the most proximal nutrient data (11 March 2011) indicated that NH_4-N concentrations at depths $\leq$ 6 m were $\leq$ 0.03 mg L^{-1} and PO_4-P was near the detection limit (0.001 mg L^{-1}), while concentrations at depths $\geq$ 9 m were significantly higher ($\geq$ 0.09 mg L^{-1} PO_4-P and $\geq$ 0.41 mg L^{-1} NH_4-N). This suggests that light availability and the introduction of nutrient-rich hypolimnetic water to the metalimnion may be important to maintain a stable population. Regel et al. (2004) presented *in vitro* growth rates of the dinoflagellate *Peridinium cinctum*, which often co-dominates with *Ceratium* sp. (Baykal et al., 2004, Padisák et al., 2003a). The authors found that rates of *P. cinctum* growth were maximal at 0.7 m depth corresponding to 30% surface irradiance, and irradiances outside that value induced negative growth rates (Regel et al., 2004). While the values were not specified, it seems likely that growth conditions at z_{eu} would not be sufficient to maximise *C. hirundinella* growth, given the irradiance levels at the depth of the population peak (6-7 m). Ostrovsky et al. (1996) investigated the biological response of phytoplankton *in vitro* after the introduction of hypolimnetic water to nutrient-depleted epilimnetic water. The authors found that significantly enhanced productivity ($P \leq 0.05$) was stimulated by concentrations of 5 and 10% hypolimnion water. However, at concentrations considered realistic

of seiche mixing processes (1% hypolimnion water) responses were not statistically significant (Ostrovsky et al., 1996). Therefore, on 24-25 March 2011, it seems likely that the level of irradiance available at depth $\geq$ 6 m would have been sub-optimal for *C. hirundinella*, and that nutrients supplied to the DCM by shear-generated turbulence at the thermocline would have been insufficient to support the large biomass of phytoplankton measured there. This suggests a "compromise strategy" as described by Clegg et al. (2004), undertaken in response to nutrient and light availability, although it does not explain the lack of diel vertical migration.

Populations of *C. hirundinella* could, however, alternatively adopted for an alternative mode of nutrition. The dominant population of *C. hirundinella* at the DCM in Lake Ōkaro is also known to be a facultative mixotroph (Clegg et al., 2004, Pérez-Martínez and Sánchez-Castillo, 2002). Mixotrophy is defined as the ability to live as an autotrophic primary producer and as a secondary or tertiary consumer by phagocytic ingestion and digestion of organic particles (Sanders, 1991). Heterotrophic bacteria are frequently recorded at high densities in the lower metalimnion forming a "bacterial maximum" (Bloem and Bar-Gilissen, 1989, Cappenberg, 1972, McDonough et al., 1986). Nutrient-limited conditions like those measured in March 2011 have been known to trigger a feeding response in dinoflagellate species, with N and P subsequently sourced from ingested bacteria and other particulate organic forms (Caron et al., 1990, Li et al., 2000, Nygaard and Tobiesen, 1993). Pålsson & Granéli (2004) assessed the relative importance of light, N and P in limiting the abundance of mixotrophic and autotrophic phytoplankton. They found that in temperate lakes, the relative abundances of mixotrophic phytoplankton increased regardless of nutrient concentration, or light availability. Therefore, it is plausible that the *C.*

hirundinella population could have met its resource requirements through heterotrophy, without any need for vertical migration. This also indicates that the depth of the DCM was a function of some other external factor, for example zooplankton grazing (Tijdens et al., 2008).

Gervais et al. (2003) hypothesised top-down regulation by zooplankton grazing as a factor influencing the depth of the DCM. Zooplankton descend into the poorly-lit hypolimnion during daylight hours to avoid predation by visually-oriented predators (Reichwaldt et al., 2004). The diel migration process is primarily undertaken by large zooplankton as they are the most prone to predation, while smaller zooplankton tend to persist in the epilimnion at all times. Because larger size-classes of phytoplankton have less susceptibility to grazing from small zooplankton, grazing in the epilimnion becomes biased toward smaller phytoplankton with continuous grazing on smaller cells, and nocturnal grazing on larger cells (Reichwaldt et al., 2004). It has been found that zooplankton grazing tends to be size-selective and skewed toward smaller phytoplankton cells, with even large zooplankton that are capable of ingesting large algae opting for small to medium-sized prey (Cyr and Curtis, 1999). The relationship between zooplankton size and ingested particle (prey) size was investigated by Burns (1968). According to calculations provided in Burns (1968), grazing of a 400 µm-long *Ceratium* cell (the dominant size class measured on 25 March 2011) would require a zooplankton with a minimum carapace length of 19 mm. The largest algae grazed upon by *Daphnia* have a maximum length of 78 µm (Cyr and Curtis, 1999), and the zooplankton community of Lake Ōkaro is comprised mostly of $\leq$ 1 mm animals (Dryden and Vincent, 1986). This implies that the grazing pressure on *C. hirundinella* and other large, dominant phytoplankton would be low in comparison to smaller phytoplankton. The significance of this is that while the

upper limit of the *C. hirundinella* and *Phacus* sp.-dominated DCM is not likely to have been regulated by grazing, the upper limit of the smaller phytoplankton comprising the lower DCM peak may have been. This appears to be supported by data from 19:00 h (25 March) when the abundances of colonial chlorophyte and picoplankton #2 colonies were $\leq$ 3.5% of their total concentrations at depths $\leq$ 8 m, and reached maximum abundances at 9 m depth corresponding to where DO concentrations were $\leq$ 1 mg L^{-1}, which is below the DO threshold for survival of some zooplankton grazers (e.g., a threshold of 3.5 mg L^{-1} DO for *Daphnia pulex* (Weider and Lampert, 1985)).

The abundance of picoplankton #2 at deeper stratum may be able to be explained by a mixotrophic life strategy, as this would provide a competitive advantage to light-limited populations in a nutrient-rich hypolimnion (Cantin et al., 2011). A number of marine and freshwater colonial picoplankton are mixotrophic (Kobayashi et al., 1992, Ukeles and Rose, 1976, Lee et al., 1996, Jones, 1997). Arenovski (1994) reported DCM formation by mixotrophic nanoplankton in four meso-oligotrophic seepage ponds. The author reported that the DCMs were generally comprised of colonial and solitary forms and occurred at the base of the metalimnion. These conditions appear to reflect those during 24-25 March 2011, and therefore it seems likely that the populations comprising the lower peak of the dual DCM could have been mixotrophic and garnered energy through the phagocytosis of the bacteria that are abundant at the base of the metalimnion.

6 Summary and conclusions

The development of a thermocline is one of the most influential factors determining the spatial distribution of phytoplankton in Lake Ōkaro. The thermocline represents a barrier to the vertical exchange of nutrients from the light-poor hypolimnion to the epilimnion, leading to conditions that are potentially growth-limiting to phytoplankton species. The thermocline itself represents a focal point for deep phytoplankton growth and from the available data it appears that in Lake Ōkaro, the strength of the relationships between the DCM, z_{eu} and thermocline depth relates to a strategy employed by the constituent DCM species which compromises between low light levels, the demand for nutrients sourced predominantly from the hypolimnion and the avoidance of entrainment toward potentially damaging irradiance levels near the surface.

Horizontal variability in chlorophyll fluorescence is a major feature of Lake Ōkaro and is particularly pronounced during periods of thermal stratification. Much of the variability in fluorescence correlates to the depth of the thermocline, and relates to interplay the between physiological and behavioural characteristics of the resident DCM populations and physical transport processes operating within the metalimnion. Near the surface, circulation in the surface mixed layer (SML) homogenises gradients in chemical and physical and biological variables. The SML increases in depth as atmospheric temperatures and solar radiation levels decrease, eroding the thermocline and eventually leading to full lake mixing when wind energy is able to overcome the physical stability of the lake; a homogenising process that essentially resets the system every year. Seasonal processes have an influence on nutrient availability, increasing allochthonous supply in the form of runoff from the surrounding catchment, while

autochthonous supply is predominantly from internal phosphate loading and benthic nitrogen flux, and ammonification.

This study has shown that because of horizontal variability, a central lake station is not an adequate surrogate for chlorophyll fluorescence over the whole lake. The values taken at the central lake station frequently over or underrepresented the mean and standard error of the whole lake. This information can be used to critically evaluate phytoplankton community estimates derived from spatially-limited sampling methodologies.

The high-frequency data have highlighted the important interplay amongst physical, chemical and biological parameters that occur on diel time frames within lakes. Temporal variations in surface temperature are very pronounced, and relate to diurnal heating and cooling, while high light attenuation relates to high cyanobacterial biomass in the epilimnion. Elevated levels of pH and DO near the surface are the result of enhanced primary productivity in the epilimnion. Minimal changes to the vertical distribution of fluorescence at the surface throughout the 2-day period of high-frequency sampling suggest diel vertical migration was not occurring, in spite of extended exposure to potentially damaging levels of solar radiation during the day. The *A. spiroides* population in Lake Ōkaro is likely to have been able to survive extended exposure to high irradiance using production of protective pigments such as carotenoids.

In contrast to the large amount of temporal variability during the 18-19 November 2010 cyanobacterial bloom, there was minimal temporal variability in the measured physical and chemical parameters during the 24-h study period on 24-25 March 2011. Temperature profiles showed some variability at the surface related to diurnal heating and cooling, while the thickness and depth of the

metalimnion also showed weak evidence of diel temperature change. Dissolved oxygen profiles were relatively homogenous and peaks corresponded to the depths of highest fluorescence (i.e., DCM), relating to increased photosynthetic activity. The chain-forming diatom *A. italica* var. *tenuissima* was the dominant species in terms of cellular abundance and biomass above the thermocline depth; however it was not abundant at depths $\geq$ 8 m. This observation was surprising given its large size and lack of buoyancy. It is likely that members of the population were able to be maintained in the epilimnion through a combination of wind driven mixing and possessing a density close to that of the surrounding water column.

A lack of vertical migration by the population dominants was a shared attribute of the two high-frequency studies. In the March 2011 study, the majority of the phytoplankton biomass was evident in the form of two DCM peaks that had stabilised at depths corresponding to sub-optimal levels of irradiance. While the depth of the peaks were relatively stable over the sampling period, the fluorescence values associated with the maxima were highly variable, which could be related to wind-induced horizontal transport at the metalimnion, internal wave formation and breaking and near-shore heat-fluxes inducing lateral advective transport. The formation of the upper peak is likely to have been a function of a "compromise strategy" between light penetration, nutrient supply from the hypolimnion and the avoidance of damaging irradiance levels at the surface. It was also speculated that higher bacterial concentrations at the metalimnion would have supported facultative mixotrophy. The upper range of the picoplankton comprising the lower peak is likely to have been a function of zooplankton grazing in the epilimnion and high abundances of bacteria at the corresponding depth, supporting a mixotrophic mode of nutrition.

The two high-frequency temporal studies have shown that physiochemical variables such as DO and temperature can vary markedly on a diel scale during an early summer surface bloom as well as during a well constrained DCM. The findings also describe limited variability in the depths of the peak chlorophyll fluorescence associated with both phytoplankton aggregate types, and there was no clear indication of daily migrations. These similarities contrast with large fluctuations in peak chlorophyll fluorescence in spring at the stage of DCM formation, but little temporal variation in the peak chlorophyll fluorescence recorded during the surface bloom. These observations are predominantly related to the physiological and behavioural characteristics of the constituent species, particularly in their responses to irradiance, which have resulted in the unique expressions of peak fluorescence values and depths that were observed during this study.

7 Future work

Use of isolumes to interpret the position of DCM populations

There was a close relationship measured between euphotic depth (z_{eu}) and the depth of the DCM in this study. However, there is also evidence to suggest that z_{eu} is not a suitable determinant of the light conditions preferred by a population, because incident solar radiation levels vary seasonally, and the preferences of the constituent species, and even individuals of a population can vary considerably. The use of isolumes would help to understand if DCM populations were adjusting to actual irradiance levels rather than a simple fraction of the surface value given by z_{eu}. It could be expected that the DCM population would stay in close proximity to a given photon level (indicating the depth of the DCM is dictated by light), or alternatively, the increasing depth of the DCM with thermocline erosion could highlight a departure from previous photon levels (indicating the DCM is a function of some other variable, e.g., nutrient availability).

Interpret life strategy of phytoplankton in a dual DCM peak

The life strategy of picoplankton #2 was not clear during this study, as the cells appeared to contain chlorophyll but were potentially light-limited. Further study could involve identification of the presence of mixotrophy in a similar way to Arenovski (1994), by fluorescently labelling bacteria prepared from cultures, and adding these to fresh hypolimnetic water samples to a density representative of natural prey levels. Arenovski (1994) incubated their samples for five hours and fixed cells with 0.05% nickel chloride ($NiCl_2$) (to prevent egestion of tracers) and 1% gluteraldehyde. Using epifluoresence microscopy in this way would make it

possible for ingested florescent bacteria to be recognised, as mixotrophic colonies would visibly show signs of the tracer.

Identify and/or classify the genus and species of picoplankton #2.

Attempts were made to identify picoplankton #2 to a genus or species level. Measures included identification keys of taxonomic literature, posting descriptions of the colonies including epifluorescence images and scanning electron micrograph images (e.g., Figure 9.3) and environmental conditions on 'Austalgae' and 'algae-l' mailing list servers, as well as sending emails to leading phytoplankton, zooplankton, pollen and fungal taxonomy consultants around the world. This did not result in a clear classification to either a genus or species level. Further attempts at classification would necessitate the use of a molecular technique such as DNA sequencing. A simple method for this would involve manually extracting at least around 100 clean colonies, and analysing the 28S rRNA using PCR with general eukaryote primers, in a similar way to that of Jerome & Lynn (1996)

8 References

ABBOTT, M. R., DENMAN, K. L., POWELL, T. M., RICHERSON, P. J., RICHARDS, R. C. & GOLDMAN, C. R. 1984. Mixing and the dynamics of the deep chlorophyll maximum in Lake Tahoe. *Limnology and Oceanography*, 29, 862-878.

ABELL, J., ÖZKUNDAKCI, D. & HAMILTON, D. 2010. Nitrogen and phosphorus limitation of phytoplankton growth in New Zealand lakes: implications for eutrophication control. *Ecosystems,* 13, 966-977.

ABELL, J. M., D, Ö., HAMILTON, D. P. & MILLER, S. D. 2011. Relationships between land use and nitrogen and phosphorus in New Zealand lakes. *Marine and Freshwater Research,* 62, 162-175.

ANTENUCCI, J. P., A., G., BURFORD, M. A. & ROMERO, J. R. 2005. The long-term effect of artificial destratification on phytoplankton species composition in a subtropical reservoir. *Freshwater Biology*, 50, 1081-1093.

ARENOVSKI, A. L. (1994) Distribution, abundance and ecology of mixotrophic algae in marine and freshwater plankton communities. *Woods Hole Oceanographic Institution.* Massachusetts, Massachusetts Institute of Technology.

AULT, T. R. 2000. Vertical migration by the marine dinoflagellate *Prorocentrum triestinum* maximises photosynthetic yield. *Oecologia*, 125, 466-475.

BAKER, P. D. & FABBRO, L. D. 1999. A guide to the identification of common blue-green algae (Cyanoprokaryotes) in Australian freshwaters. *Cooperative Research Centre for Freshwater Biology, N.S.W., Australia*.

BAY OF PLENTY REGIONAL COUNCIL 2010. State of the Rotorua/Te Arawa Lakes 2009/2010. *The Rotorua Lakes Protection and Restoration Action Programme.* Bay of Plenty Regional Council, Rotorua District Council and Te Arawa Lakes Trust

BAYKAL, T., AÇIKOZ, I., YILDIZ, K. & BEKLEYEN, A. 2004. A Study on Algae in Devegeçidi Dam Lake. *Turkish Journal of Botany,* 28, 457-472.

BENNION, H., JUGGINS, S. & ANDERSON, N. J. 1996. Predicting epilimnetic phosphorus concentrations using an improved diatom-based transfer function and its application to lake eutrophication management. *Environmental Science & Technology,* 30, 2004-2007.

BERG, U., NEUMANN, T., DONNERT, D., NÜESCH, R. & STÜBEN, D. 2004. Sediment capping in eutrophic lakes - efficiency of undisturbed calcite barriers to immobilize phosphorus. *Applied Geochemistry,* 19, 1759-1771.

BERMAN, T., STONE, L., YACOBI, Y. Z., KAPLAN, B., SCHLICHTER, M., NISHRI, A. & POLLINGHER, U. 1995. Primary production and phytoplankton in Lake Kinneret: a long-term record (1972-1993). *Limnology and Oceanography,* 40, 1064-1076.

BLASCHKE, P. M., TRUSTRUM, N. A. & DEROSE, R. C. 1992. Ecosystem processes and sustainable land use in New Zealand steeplands. *Agriculture, Ecosystems & Environment,* 41, 153-178.

BLOEM, J. & BAR-GILISSEN, M. J. B. 1989. Bacterial activity and protozoan grazing potential in a stratified lake. *Limnology and Oceanography,* 34, 297-309.

BOPRC 2010. State of the Rotorua/Te Arawa Lakes 2009/2010. *The Rotorua Lakes Protection and Restoration Action Programme.* Bay of Plenty Regional Council, Rotorua District Council and Te Arawa Lakes Trust

BORMANS, M., SHERMAN, B. S. & WEBSTER, I. T. 1999. Is buoyancy regulation in cyanobacteria an adaptation to exploit separation of light and nutrients? *Marine and Freshwater Research,* 50, 897-906.

BOROWIAK, D., NOWIŃSKI, K., BARAŃCZUK, J., SKOWRON, R., SOLARCZYK, A. & MARSZELEWSKI, W. 2010. Interactions between Areal Hypolimnetic Oxygen Depletion rate and trophic state of lakes in northern Poland. *BALWOIS.* Ohrid, Macedonia.

BOWLING, L. C. & BAKER, P. D. 1996. Major cyanobacterial bloom in the Barwon-Darling River, Australia, in 1991, and underlying limnological conditions. *Marine and Freshwater Research,* 47, 643-657.

BRUESEWITZ, D., HAMILTON, D. & SCHIPPER, L. 2011. Denitrification potential in lake sediment increases across a gradient of catchment agriculture. *Ecosystems,* 14, 341-352.

BURGER, D. F., HAMILTON, D. P., PILDITCH, C. A., GIBBS, M. M., GULATI, R. D., LAMMENS, E., PAUW, N. & DONK, E. 2007. Benthic nutrient fluxes in a eutrophic, polymictic lake *In:* DUMONT, H. J. (ed.) *Shallow lakes in a changing world.* Springer Netherlands.

BURNS, C. W. 1968. The relationship between body size of filterfeeding Cladocera and the maximum size of particle ingested. *Limnology and Oceanography*, 13, 675-678.

BURNS, C. W., FORSYTH, D. J., HANEY, J. F., JAMES, M. R., LAMPERT, W. & PRIDMORE, R. D. 1987. Mechanisms of co-existence and exclusion of zooplankton by cyanobacteria in Lake Rotongaio. *New Zealand Journal of Marine and Freshwater Research,* 21, 537-538.

BURNS, N., MCINTOSH, J. & SCHOLES, P. 2009. Managing the lakes of the Rotorua District, New Zealand. *Lake and Reservoir Management,* 25, 284-296.

BURNS, N. M., RUTHERFORD, J. C. & CLAYTON, J. S. 1999. A monitoring and classification system for new zealand lakes and reservoirs. *Lake and Reservoir Management*, 15, 255-271.

CAFFREY, J. M., DUTARTRE, A., HAURY, J., MURPHY, K. J., WADE, P. M., CLAYTON, J. & EDWARDS, T. 2006. Aquatic plants as environmental indicators of ecological condition in New Zealand lakes. *In:* DUMONT, H. J. (ed.) *Macrophytes in Aquatic Ecosystems: From Biology to Management.* Springer Netherlands.

CANTIN, A., BEISNER, B. E., GUNN, J. M., PRAIRIE, Y. T. & WINTER, J. G. 2011. Effects of thermocline deepening on lake plankton communities. *Canadian Journal of Fisheries and Aquatic Sciences,* 68, 260-276.

CAPPENBERG, T. E. 1972. Ecological observations on Heterotrophic, methane oxidizing and sulfate reducing bacteria in Pond. *Hydrobiologia*, 40, 471-485.

CARLSON, R. E. 1977. A Trophic State Index for Lakes. *Limnology and Oceanography*, 22, 361-369.

CARO, T. M. & O'DOHERTY, G. 1999. On the use of surrogate species in conservation biology. *Conservation Biology*, 13, 805-814.

CARON, D. A., PORTER, K. G. & SANDERS, R. W. 1990. Carbon, nitrogen, and phosphorus budgets for the mixotrophic phytoflagellate *Poterioochromonas malhamensis* (Chrysophyceae) during bacterial ingestion. *Limnology and Oceanography*, 35, 433-443.

CARPENTER, S. R., CARACO, N. F., CORRELL, D. L., HOWARTH, R. W., SHARPLEY, A. N. & SMITH, V. H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications,* 8, 559-568.

CARRICK, H. J., ALDRIDGE, F. J. & SCHELSKE, C. L. 1993. Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnology and Oceanography,* 38, 1179-1192.

CLEGG, M. R., MABERLY, S. C. & JONES, R. I. 2004. Dominance and compromise in freshwater phytoplanktonic flagellates: the interaction of behavioural preferences for conflicting environmental gradients. *Functional Ecology,* 18, 371-380.

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

CONDIE, S. A. & BORMANS, M. 1997. The influence of density stratification on particle settling, dispersion and population growth. *Journal of Theoretical Biology*, 187, 65-75.

COOKE, G. D., WELCH, E. B., PETERSON, S. A. & NEWOTH, P. R. (eds.) 1993. *Restoration and management of lakes and reservoirs. 2nd ed.,* Ann Arbor, Michigan, USA: Lewis Publishers.

COON, T. G., LOPEZ, M. M., RICHERSON, P. J., POWELL, T. M. & GOLDMAN, C. R. 1987. Summer dynamics of the deep chlorophyll maximum in Lake Tahoe. *Journal of Plankton Research*, 9, 327-344.

COTTINGHAM, K. L. & CARPENTER, S. R. 1998. Population, community, and ecosystem variates as ecological indicators: phytoplankton responses to whole-lake enrichment. *Ecological Applications,* 8, 508-530.

CRONIN, J. C., WINTERS, K. & RANGIHEUEA, A. 2006. Lake Ōkaro action plan. *Environment Bay of Plenty Publication 2006/03.*

CULLEN, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Canadian Journal of Fisheries and Aquatic Sciences,* 39, 791-803.

CULLEN, J. J. 1985. Diel vertical migration by dinoflagellates: roles of carbohydrate metabolism and behavioral flexibility. *Contributions to Marine Science*, 27, 135-152.

CULLEN, J. J. & HORRIGAN, S. G. 1981. Effects of nitrate on the diurnal vertical migration, carbon to nitrogen ratio, and the photosynthetic capacity of the dinoflagellate *Gymnodinium splendens*. *Marine Biology,* 62, 81-89.

CYR, H. & CURTIS, J. M. 1999. Zooplankton community size structure and taxonomic composition affects size-selective grazing in natural communities. *Oecologia,* 118, 306-315.

DAVIES-COLLEY, R. J. 1987. Water appearance: survey and interpretation. *In:* VANT, W. N. (ed.) *Lake manager's handbook: a guide to undertaking and understanding investigations into lake ecosystems, so as to assess management options for lakes. Water and Soil Miscellaneous Publication No.103.* Water and Soil Division. Wellington, New Zealand.

DRYDEN, S. & VINCENT, W. 1986. Phytoplankton species of Lake Ōkaro, central North Island. *New Zealand Journal of Marine and Freshwater Research,* 20, 191-198.

DUFRENE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs,* 67, 345-366.

DUGGAN, I. C., GREEN, J. D. & SHIEL, R. J. 2001. Distribution of rotifers in North Island, New Zealand, and their potential use as bioindicators of lake trophic state. *Hydrobiologia,* 446-447, 155-164.

EHRLICH, P. R. & HOLDREN, J. P. 1971. Impact of population growth. *Science,* 171, 1212-1217.

FAIRWEATHER, J. R. & SIMMONS, D. G. 2000. The economic impact of tourism on Rotorua *Tourism Research and Education Centre,* Report No. 18.

FALKENMARK, M. 1986. Fresh water: time for a modified approach. *Ambio,* 15, 192-200.

FASHAM, M. J. R. (1978) The application of some stochastic processes to the study of plankton patchiness. IN STEELE, J. H. (Ed.). Plenum, New York.

FEE, E. J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, Northwestern Ontario: implications for primary production estimates. *Limnology and Oceanography,* 21, 767-783.

FELIP, M. & CATALAN, J. 2000. The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima. *Journal of Plankton Research,* 22, 91-106.

FIELD, K. M. & PREPAS, E. E. 1997. Increased abundance and depth distribution of pelagic crustacean zooplankton during hypolimnetic oxygenation in a deep, eutrophic Alberta lake. *Canadian Journal of Fisheries and Aquatic Sciences,* 54, 2146-2156.

FLINT, E. A. 1977. Phytoplankton in seven monomictic lakes near Rotorua, New Zealand. *New Zealand Journal of Botany,* 15, 197-208.

FOGG, G. E. & WALSBY, A. E. 1971. Buoyancy regulation and the growth of planktonic blue-green algae. *Mitteilungen der Internationalen Vereinigung für Limnologie,* 19, 182-188.

FORSYTH, D. J., DRYDEN, S. J., JAMES, M. R. & VINCENT, W. F. 1988. The Lake Ōkaro ecosystem.1. Background limnology. *New Zealand Journal of Marine and Freshwater Research,* 22, 17-27.

FOWLER, E. C. & DUGGAN, I. C. 2008. Assessment of trophic state change in selected lakes of the Auckland Region based on rotifer assemblages: 2005-2008. *Prepared by the Centre for Biodiversity and Ecology Research, University of Waikato, for Auckland Regional Council.,* Auckland Regional Council Document TR 2009/001.

FRIEDRICH, G., GERHARDT, V., BODEMER, U. & POHLMANN, M. 1998. Phytoplankton composition and chlorophyll concentration in freshwaters: comparison of delayed fluorescence excitation spectroscopy, extractive spectrophotometric method, and UTERMOEHL-method. *Limnologica,* 28, 323-328.

GABRIELS, W., LOCK, K., DE PAUW, N. & GOETHALS, P. L. M. 2010. Multimetric Macroinvertebrate Index Flanders (MMIF) for biological assessment of rivers and lakes in Flanders (Belgium). *Limnologica - Ecology and Management of Inland Waters,* 40, 199-207.

GALAT, D. L. & VERDIN, J. P. 1989. Patchiness, collapse and succession of a cyanobacterial bloom evaluated by synoptic sampling and remote sensing. *Journal of Plankton Research,* 11, 925-948.

GANF, G. & OLIVER, R. 1982. Vertical separation of light and available nutrients as a factor causing replacement of green algae by blue-green algae in the plankton of a stratified lake. *Journal of Ecology,* 70, 829-844.

GANNON, J. E. & STEMBERGER, R. S. 1978. Zooplankton (especially Crustaceans and Rotifers) as indicators of water quality. *Transactions of the American Microscopical Society,* 97, 16-35.

GEORGE, D. G. & HEANEY, S. I. 1978. Factors influencing the spatial distribution of phytoplankton in a small productive lake. *Journal of Ecology,* 66, 133-155.

GERVAIS, F. 1998. Ecology of cryptophytes coexisting near a freshwater chemocline. *Freshwater Biology,* 39, 61-78.

GERVAIS, F., SIEDEL, U., HEILMANN, B., WEITHOFF, G., HEISIG-GUNKEL, G. & NICKLISCH, A. 2003. Small-scale vertical distribution of phytoplankton, nutrients and sulphide below the oxycline of a mesotrophic lake. *Journal of Plankton Research,* 25, 273-278.

GEURTS, J. J. M., SMOLDERS, A. J. P., VERHOEVEN, J. T. A., ROELOFS, J. G. M. & LAMERS, L. P. M. 2008. Sediment Fe:PO_4 ratio as a diagnostic and prognostic tool for the restoration of macrophyte biodiversity in fen waters. *Freshwater Biology,* 53, 2101-2116.

GIBBONS-DAVIES, J. 2003. Rotorua Lakes water quality 2002. *Environmental Publication 2003/02*.

GLIBERT, P. M., HARRISON, J., HEIL, C. & SEITZINGER, S. 2006. Escalating worldwide use of urea: a global change contributing to coastal eutrophication. *Biogeochemistry,* 77, 441-463.

GOLDMAN, C. R. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. *Limnology and Oceanography,* 33, 1321-1333.

GORHAM, E. & BOYCE, F. M. 1989. Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. *Journal of Great Lakes Research,* 15, 233-245.

GREGOR, J., GERIŠ, R., MARŠÁLEK, B., HETEŠA, J. & MARVAN, P. 2005. *In situ* quantification of phytoplankton in reservoirs using a submersible spectrofluorometer. *Hydrobiologia,* 548, 141-151.

GRIGORSZKY, I., PADISÁK, J., BORICS, G., SCHITCHEN, C. & BORBÉLY, G. 2003. Deep chlorophyll maximum by *Ceratium hirundinella* (O. F. Müller) Bergh in a shallow oxbow in Hungary. *Hydrobiologia,* 506-509, 209-212.

GROVER, J. P. & CHRZANOWSKI, T. H. 2006. Seasonal dynamics of phytoplankton in two warm temperate reservoirs: association of taxonomic composition with temperature. *Journal of Plankton Research,* 28, 1-17.

HAMBRIGHT, K. D., HAIRSTON JR, N. G., SCHAFFNER, W. R. & HOWARTH, R. W. 2007. Grazer control of nitrogen fixation: phytoplankton taxonomic composition and ecosystem functioning. *Hydrobiologia,* 170, 103-124.

HAMILTON, D. P. Year. An historical and contemporary review of water quality in the Rotorua Lakes *In:* MILLER, N., ed. Proceedings of the Rotorua

Lakes 2003 symposium: Practical management for good lake water quality, October, 2003 2003 Rotorua. 3-15.

HAMILTON, D. P. 2005. Land use impacts on nutrient export in the Central Volcanic Plateau, North Island. *New Zealand Journal of Forestry,* 49, 27–31.

HAMILTON, D. P. Year. The environmental status and problems facing the Rotorua Lakes. *In:* GREEN, A., ed. Rotorua Lakes 2006 - Wonderful Lakes - What Value? - Who pays?, 2006 Rotorua.

HAMILTON, D. P., O'BRIEN, K. R., BURFORD, M. A. & BROOKES, J. D. 2010. Vertical distributions of chlorophyll in deep, warm monomictic lakes. *Aquatic Sciences-Research Across Boundaries,* 72, 295-307.

HARDY, L. 2005. *Lake Ōkaro: Explosions and erosion.* BSc (Hons) Thesis, The University of Otago.

HASLER, A. D. 1969. Cultural eutrophication is reversible. *BioScience,* 19, 425-431.

HAWES, I. & SMITH, R. 1993. Effect of localised nutrient enrichment on the shallow epilithic periphyton of oligotrophic Lake Taupo, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* 27, 365-372.

HEANEY, S. I. 1976. Temporal and spatial distribution of the dinoflagellate *Ceratium hirundinella* O.F. Müller within a small productive lake. *Freshwater Biology,* 6, 531-542.

HEANEY, S. I. & EPPLEY, R. W. 1981. Light, temperature and nitrogen as interacting factors affecting diel vertical migrations of dinoflagellates in culture. *Journal of Plankton Research,* 3, 331-344.

HEANEY, S. I. & TALLING, J. F. 1980. Dynamic aspects of dinoflagellate distribution patterns in a small productive lake. *Journal of Ecology,* 68, 75-94.

HEDENQUIST, J. W. & HENLEY, R. W. 1985. Hydrothermal eruptions in the Waiotapu geothermal system, New Zealand: Their origin, associated breccias, and relation to precious metal mineralization. *Economic Geology,* 80, 1640-1668.

HEIN, M. 1997. Inorganic carbon limitation of photosynthesis in lake phytoplankton. *Freshwater Biology,* 37, 545-552.

HENDY, C. 12/08/2011 Personal communications with Bernard Simmonds. *RE: Discussion on bicarbonate equilibrium changes in freshwater ecosystems.*

HILL, M. O. 1979. *TWINSPAN: a fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes,* Cornell University, New York, USA.

HINSINGER, P., PLASSARD, C., TANG, C. & JAILLARD, B. T. 2003. Origins of root-mediated pH changes in the rhizosphere and their responses to environmental constraints: A review. *Plant and Soil,* 248, 43-59.

HOARE, R. A. & SPIGEL, R. H. 1987. Water balances, mechanics and thermal properties. . *In:* VANT, W. N. (ed.) *Lake managers handbook. Water and*

soil miscellaneous publication 103:41-58. Wellington: Ministry of Works and Development.

HOLLING, C. S. & MEFFE, G. K. 1996. command and control and the pathology of natural resource management. *Conservation Biology,* 10, 328-337.

HOLM-HANSEN, O. & HEWES, C. D. 2004. Deep chlorophyll-*a* maxima (DCMs) in Antarctic waters. *Polar Biology,* 27, 699-710.

HORN, C. & SIMMONS, D. 2002. Community adaptation to tourism: comparisons between Rotorua and Kaikoura, New Zealand. *Tourism Management,* 23, 133-143.

HORNE, J. K. & SCHNEIDER, D. C. 1995. Spatial variance in ecology. *Oikos,* 74, 18-26.

HORTON, P. & RUBAN, A. 2005. Molecular design of the photosystem II light-harvesting antenna: photosynthesis and photoprotection. *Journal of Experimental Botany*, 56, 365-373.

HOUGHTON, B. F., WILSON, C. J. N., MCWILLIAMS, M. O., LANPHERE, M. A., WEAVER, S. D., BRIGGS, R. M. & PRINGLE, M. S. 1995. Chronology and dynamics of a large silicic magmatic system: Central Taupo Volcanic Zone, New Zealand. *Geology,* 23, 13-16.

IBELINGS, B. W., VONK, M., LOS, H. F. J., MOLEN, D. T. V. D. & MOOD, W. M. 2003. Fuzzy modeling of cyanobacterial surface waterblooms: validation with NOAA-AVHRR satellite images. *Ecological Applications,* 13, 1456-1472.

IMBERGER, J. & SPIGEL, R. H. 1987. Circulation and mixing in Lake Rotongaio and Lake Ōkaro under conditions of light to moderate winds - preliminary results. *New Zealand Journal of Marine and Freshwater Research*, 21, 515-519.

IRVINE, R. L., CRONE, E. E., JACKSON, L. J. & MACISAAC, E. A. 2004. Does scale affect ecological model predictions? A test with lake responses to fertilization. *Ecological Applications,* 14, 1178-1188.

JEROME, C. A. & LYNN, D. H. 1996. Identifying and distinguishing sibling species in the *Tetrahymena pyriformis* complex (Ciliophora, Oligohymenophorea) using PCR/RFLP analysis of nuclear ribosomal DNA. *Journal of Eukaryotic Microbiology*, 43, 492-497.

JOHANNESSEN, T. & DAHL, E. 1996. Declines in oxygen concentrations along the Norwegian Skagerrak Coast, 1927-1993: A signal of ecosystem changes due to eutrophication? *Limnology and Oceanography*, 41, 766-778.

JONES, H. 1997. A classification of mixotrophic protists based on their behaviour. *Freshwater Biology*, 37, 35-43.

JOOSTEN, A. M. T. 2006. *Flora of the blue-green algae of the Netherlands: The non-filamentous species of inland waters*, KNNV Publishing, Utrecht.

KALFF, J. 2002a. Inorganic carbon and pH. *In:* RYU, T. (ed.) *Limnology.* New Jersey: Prentice-Hall, Inc.

KALFF, J. 2002b. Temperature cycles, lake stratification, and heat budgets. *In:* RYU, T. (ed.) *Limnology.* New Jersey: Prentice-Hall, Inc.

KALFF, J. 2002c. Water movements. *In:* RYU, T. (ed.) *Limnology*. New Jersey: Prentice-Hall, Inc.

KALLIO, K., KOPONEN, S. & PULLIAINEN, J. 2003. Feasibility of airborne imaging spectrometry for lake monitoring: A case study of spatial chlorophyll *a* distribution in two meso-eutrophic lakes. *International Journal of Remote Sensing,* 24, 3771 - 3790.

KAMYKOWSKI, D. & YAMAZAKI, H. 1997. A study of metabolism-influenced orientation in the diel vertical migration of marine dinoflagellates. *Limnology and Oceanography,* 42, 1189-1202.

KELLAR, P. E. & PAERL, H. W. 1980. Physiological adaptations in response to environmental stress during an N_2-fixing *Anabaena* bloom. *Applied Environmental Microbiology,* 40, 587-595.

KHAN, F. A. & ANSARI, A. A. 2005. Eutrophication - An ecological vision. *The Botanical Review,* 71, 449-482.

KLAUSMEIER, C. A. & LITCHMAN, E. 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. *Limnology and Oceanography,* 46, 1998-2007.

KOBAYASHI, M., KAKIZONO, T., YAMAGUCHI, K., NISHIO, N. & NAGAI, S. 1992. Growth and astaxanthin formation of *Haematococcus pluvialis* in heterotrophic and mixotrophic conditions. *Journal of Fermentation and Bioengineering,* 74, 17-20.

KROMKAMP, J. & WALSBY, A. E. 1990. A computer model of buoyancy and vertical migration in cyanobacteria. *Journal of Plankton Research,* 12, 161-183.

KUFEL, L. & KALINOWSKA, K. 1997. Metalimnetic gradients and the vertical distribution of phosphorus in a eutrophic lake. *Archiv fur Hydrobiologie,* 140, 309-320.

LACKEY, R. T. 1973. Artificial reservoir destratification effects on phytoplankton. *Journal (Water Pollution Control Federation),* 45, 668-673.

LEAN, D. R. S., MITCHELL, S. F., PICK, F. R., RUETER, J. G., DOWNES, M. T., PAYNE, G. W., PICKMERE, S. E., WHITE, E. & WOODS, P. H. 1987. The effects of changes in both the abundance of nitrogen and phosphorus and their ratio on Lake Ōkaro phytoplankton, with comment on 6 other central volcanic plateau lakes. *New Zealand Journal of Marine and Freshwater Research,* 21, 539-542.

LEE, Y.-K., DING, S.-Y., HOE, C.-H. & LOW, C.-S. 1996. Mixotrophic growth of *Chlorella sorokiniana* in outdoor enclosed photobioreactor. *Journal of Applied Phycology,* 8, 163-169.

LI, A., STOECKER, D. K. & COATS, D. W. 2000. Mixotrophy in *Gyrodinium galatheanum* (DINOPHYCEAE): grazing responses to light intensity and inorganic nutrients. *Journal of Phycology,* 36, 33-45.

LIKENS, G. E., BARTSCH, A. F., LAUFF, G. H. & HOBBIE, J. E. 1971. Nutrients and eutrophication. *Science,* 172, 873-874.

LONGHURST, A. R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep Sea Research and Oceanographic Abstracts*, 23, 729-754.

MACINTYRE, S., FLYNN, K. M., JELLISON, R. & ROMERO, J. R. 1999. Boundary mixing and nutrient fluxes in Mono Lake, California. *Limnology and Oceanography*, 44, 512-529.

MACKAS, D. L., DENMAN, K. L. & ABBOTT, M. R. 1985. Plankton patchiness: biology in the physical vernacular. *Bulletin of Marine Science,* 37, 652-674.

MACLEOD, C. J. & MOLLER, H. 2006. Intensification and diversification of New Zealand agriculture since 1960: An evaluation of current indicators of land use change. *Agriculture, Ecosystems & Environment*, 115, 201-218.

MARTI, C. L. & IMBERGER, J. 2004. Exchange processes between littoral and pelagic waters in a stratified lake. *In:* BUSCAGLIA, G., DARI, E. & ZAMONSKY, O. (eds.) *Mecanica Computacional Vol. XXIII.* Bariloche, Argentina.

MCCAUSLAND, M. A., THOMPSON, P. A. & S.I, B. 2001. The effect of changes in light availability caused by mixing on the growth of *Anabaena circinalis* (Nostocales, Cyanobacteria) and *Aulacoseira* sp. (Centrales, Bacillariophyceae). *Phycologia,* 40, 530-541.

MCDONOUGH, R. J., SANDERS, R. W., PORTER, K. G. & KIRCHMAN, D. L. 1986. Depth distribution of bacterial production in a stratified lake with an anoxic hypolimnion. *Applied Environmental Microbiology,* 52, 992-1000.

MCFARLAND, D. C., ZHANG, C., THOMAS, H. C. & T.L., R. 2005. Confounding effects of plateletson flow cytometric analysis and cell-sorting experiments using blood-derived cells. *International Society for Analytical Cytology,* 69, 86-94.

MEERSCHE, K. V. D., MIDDELBURG, J. J., SOETAERT, K., RIJSWIJK, P. V., BOSCHKER, H. T. S. & HEIP, C. H. R. 2004. Carbon-nitrogen coupling and algal-bacterial interactions during an experimental bloom: modeling a 13c tracer experiment. *Limnology and Oceanography,* 49, 862-878.

MEYBECK, M. 2003. Global analysis of river systems: from Earth system controls to Anthropocene syndromes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,* 358, 1935-1955.

MINISTRY FOR THE ENVIRONMENT 2004. New Zealand Land Cover Database 2 User Guide. *Ministry for the Environment Report*. Wellington, New Zealand.

MINISTRY FOR THE ENVIRONMENT 2010. Land: Land use. *Ministry for the Environment Report: Environmental Snapshot - January 2010.* Wellington, New Zealand.

MITROVIC, S. M., BOWLING, L. C. & BUCKNEY, R. T. 2001. Vertical disentrainment of *Anabaena circinalis* in the turbid, freshwater Darling River, Australia: quantifying potential benefits from buoyancy. *Journal of Plankton Research,* 23, 47-55.

MODENUTTI, B., BALSEIRO, E., CALLIERI, C., QUEIMALIÑOS, C. & BERTONI, R. 2004. Increase in photosynthetic efficiency as a strategy of

planktonic organisms exploiting deep lake layers. *Freshwater Biology,* 49, 160-169.

MOLLOY, L. F. 1980. Land alone endures. Land use and the role of research. *New Zealand Department of Scientific and Industrial Research. Discussion Paper,* 3, 1-286.

MORRIS, D. P. & LEWIS, W. M. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. *Freshwater Biology*, 20, 315-327.

MOSS, B. 1973a. Diversity in fresh-water phytoplankton. *American Midland Naturalist,* 90, 341-355.

MOSS, B. 1973b. The influence of environmental factors on the distribution of freshwater algae: an experimental study: II. The role of pH and the carbon dioxide-bicarbonate system. *Journal of Ecology,* 61, 157-177.

NEILSON, K., COLLIER, K. & HAMER, M. 2007. Assessment of biological indicators of lake health in Waikato shallow lakes - a pilot study 2006/07. *In:* VANT, B. (ed.) *Environment Waikato Technical Report 2008/18.* Hamilton: Environment Waikato.

NIEMI, G. J. & MCDONALD, M. E. 2004. Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics,* 35, 89-111.

NYGAARD, K. & TOBIESEN, A. 1993. Bacterivory in algae: a survival strategy during nutrient limitation. *Limnology and Oceanography,* 38, 273-279.

OLENINA, I., HAJDU, S., EDLER, L., ANDERSSON, A., WASMUND, N., BUSCH, S., GÖBEL, J., GROMISZ, S., HUSEBY, S., HUTTUNEN, M.,

JAANUS, A., PIRKKO KOKKONEN, P., LEDAINE, I. & NIEMKIEWICZ, E. 2004. Biovolumes and size-classes of phytoplankton in the Baltic Sea. *Baltic Marine Environment Protection Commission.* Helsinki Commission.

OSBORNE, L. L. & KOVACIC, D. A. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. *Freshwater Biology,* 29, 243-258.

OSTROVSKY, I. & YACOBI, Y. Z. 1999. Organic matter and pigments in surface sediments: possible mechanisms of their horizontal distributions in a stratified lake. *Canadian Journal of Fisheries and Aquatic Sciences,* 56, 1001.

OSTROVSKY, I., YACOBI, Y. Z., WALLINE, P. & KALIKHMAN, I. 1996. Seiche-induced mixing: its impact on lake productivity. *Limnology and Oceanography,* 41, 323-332.

ÖZKUNDAKCI, D., DUGGAN, I. & HAMILTON, D. 2009. Does sediment capping have post-application effects on zooplankton and phytoplankton? *Hydrobiologia*, 661, 55-64.

ÖZKUNDAKCI, D., HAMILTON, D. P. & GIBBS, M. M. 2011. Hypolimnetic phosphorus and nitrogen dynamics in a small, eutrophic lake with a seasonally anoxic hypolimnion. *Hydrobiologia,* 661, 5-20.

ÖZKUNDAKCI, D., HAMILTON, D. P. & SCHOLES, P. 2010. Effect of intensive catchment and in-lake restoration procedures on phosphorus concentrations in a eutrophic lake. *Ecological Engineering,* 36, 396-405.

PADISÁK, J., BORICS, G., FEHÉR, G., GRIGORSZKY, I., OLDAL, I., SCHMIDT, A. & ZÁMBÓNÉ-DOMA, Z. 2003a. Dominant species, functional assemblages and frequency of equilibrium phases in late summer phytoplankton assemblages in Hungarian small shallow lakes. *Hydrobiologia,* 502, 157-168.

PADISÁK, J., SCHEFFLER, W., KOSCHEL, R. & KRIENITZ, L. 2004. Seasonal patterns and interannual variability of phytoplankton in Lake Stechlin (1994-2003). *Leibniz-Institute of Freshwater Ecology and Inland Fisheries: Annual report 2003.* Berlin.

PADISÁK, J. F., BARBOSA, A. R., KOSCHEL, R. & KRIENITZ, L. 2003b. Deep layer cyanoprokaryota maxima are constitutional features of lakes: examples from temperate and tropical regions. *Archive for Hydrobiology - Advances in Limnology,* 58, 175-199.

PAERL, H. W. & USTACH, J. F. 1982. Blue-green algal scums: an explanation for their occurrence during freshwater blooms. *Limnology and Oceanography,* 27, 212-217.

PÅLSSON, C. & GRANÉLI, W. 2004. Nutrient limitation of autotrophic and mixotrophic phytoplankton in a temperate and tropical humic lake gradient. *Journal of Plankton Research,* 26, 1005-1014.

PAUL, W. J. 2006. Carbon and nitrogen transfers between phytoplankton and bacteria, and management of internal nutrient loads with alum in Lake Ōkaro, New Zealand. *The University of Waikato.,* Chapter 2, 10-60.

PAUL, W. J. 2010. Standard protocol for fluorometric determination of chlorophyll a pigments. Hamilton: The University of Waikato.

PAUL, W. J., HAMILTON, D. P. & GIBBS, M. M. 2008. Low-dose alum application trialled as a management tool for internal nutrient loads in Lake Ōkaro, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* 42, 207-217.

PAUL, W. J., WOOD, S. & DEICHMAN, B. 2007. University of Waikato protocol for the analyses of freshwater phytoplankton samples. *CBER Report 57.* The University of Waikato.

PÉREZ-MARTÍNEZ, C. & SÁNCHEZ-CASTILLO, P. 2002. Winter dominance of *Ceratium hirundinella* in a southern north-temperate reservoir. *Journal of Plankton Research,* 24, 89-96.

PETERS, S. W. M. 2002. Analytical algorithms for lake water TSM estimation for retrospective analyses of TM and SPOT sensor data. *International Journal of Remote Sensing,* 23, 15.

PILGRIM, D. H., HUFF, D. D. & STEELE, T. D. 1979. Use of specific conductance and contact time relations for separating flow components in storm runoff. *Water Resources Research,* 15, 1-11.

PIMENTEL, D. & KOUNANG, N. 1998. Ecology of Soil Erosion in Ecosystems. *Ecosystems,* 1, 416-426.

PINEL-ALLOUL, B. & GHADOUANI, A. 2007. Spatial heterogeneity of planktonic microorganisms in aquatic systems - Multiscale patterns and

processes. *In:* FRANKLIN, R. B. & MILLS, A. L. (eds.) *The Spatial Distribution of Microbes in the Environment.* Dordrecht: Springer.

POST, A. F., DUBINSKY, Z., WYMAN, K. & FALKOWSKI, P. G. 1985. Physiological responses of a marine planktonic diatom to transitions in growth irradiance. *Marine Ecology - Progress Series*, 25, 141-149.

POWELL, T. & RICHERSON, P. J. 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model. *The American Naturalist,* 125, 431-464.

PRÉSING, M., HERODEK, S., PRESTON, T. & VÖRÖS, L. 2001. Nitrogen uptake and the importance of internal nitrogen loading in Lake Balaton. *Freshwater Biology*, 46, 125-139.

RAVEN, J. A. & RICHARDSON, K. 1984. Dinophyte flagella: a cost-benefit analysis. *New Phytologist*, 98, 259-276.

READ, J. S., HAMILTON, D. P., JONES, I. D., MURAOKA, K., WINSLOW, L. A., KROISS, R., WU, C. H. & GAISER, E. 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software*, 26, 1325-1336.

REGEL, R. H., BROOKES, J. D. & GANF, G. G. 2004. Vertical migration, entrainment and photosynthesis of the freshwater dinoflagellate *Peridinium cinctum* in a shallow urban lake. *Journal of Plankton Research,* 26, 143-157.

REICHWALDT, E. S., WOLF, I. D. & STIBOR, H. 2004. The effect of different zooplankton grazing patterns resulting from diel vertical migration on

phytoplankton growth and composition: a laboratory experiment. *Oecologia,* 141, 411-419.

REYNOLDS, C. S. 1972. Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green alga. *Freshwater Biology,* 2, 87-106.

REYNOLDS, C. S. 1983. Growth-rate responses of *Volvox aureus* Ehrenb. (Chlorophyta, Volvocales) to variability in the physical environment. *British Phycological Journal,* 18, 433-442.

REYNOLDS, C. S. 1984. The ecology of freshwater phytoplankton. *Cambridge University Press, Cambridge, Great Britain.*

REYNOLDS, C. S. 1997a. Resource gathering in pelagic plants. *In:* KINNE, O. (ed.) *Excellence in ecology.* Oldendorf/Luhe, Germany: Ecology Institute.

REYNOLDS, C. S. 1997b. Succession in pelagic communities. *In:* KINNE, O. (ed.) *Excellence in ecology.* Oldendorf/Luhe, Germany: Ecology Institute.

REYNOLDS, C. S., JAWORSKI, G. H. M., CMIECH, H. A. & LEEDALE, G. F. 1981. On the annual cycle of the blue-green alga *Microcystis Aeruginosa* Kutz. emend. Elenkin. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,* 293, 419-477.

REYNOLDS, C. S. & WALSBY, A. E. (1975) WATER-BLOOMS. *Biological Reviews.* Blackwell Publishing Ltd.

RIGOSI, A., MARCÉ, R., ESCOT, C. & RUEDA, F. J. 2011. A calibration strategy for dynamic succession models including several phytoplankton groups. *Environmental Modelling & Software,* 26, 697-710.

RINKE, K., YEATES, P. & ROTHHAUPT, K.-O. 2010. A simulation study of the feedback of phytoplankton on thermal structure via light extinction. *Freshwater Biology*, 55, 1674-1693.

ROBARTS, R. D. & HOWARD-WILLIAMS, C. 1987. Photosynthesis of Anabaena in Lake Rotongaio: short-term responses to a changing light environment. *New Zealand Journal of Marine and Freshwater Research*, 21, 531.

RODGER, H. D., TURNBULL, T., EDWARDS, C. & CODD, G. A. 1994. Cyanobacterial (blue-green algal) bloom associated pathology in brown trout, *Salmo trutta*, in Loch Leven, Scotland. *Journal of Fish Diseases*, 17, 177-181.

RUTHERFORD, K. 2003. Lake Rotorua nutrient load targets. *NIWA Client Report: HAM2003-155*. Hamilton: National Institute of Water & Atmospheric Research Ltd.

RYABOV, A., RUDOLF, L. & BLASIUS, B. 2010. Vertical distribution and composition of phytoplankton under the influence of an upper mixed layer. *Journal of Theoretical Biology*, 263, 120-133.

RYAN, E. 2005. *Chapter 5: Formation of a deep chlorophyll maximum by Peridinium cf. sydneyense in an oligotrophic New Zealand lake.* Phytoplankton dynamics in North Island lakes, New Zealand. Doctor of Philosophy, The University of Waikato.

SANDERS, R. W. 1991. Trophic strategies among heterotrophic flagellates. *In:* PATTERSON, D. J. & LARSEN, J. (eds.) *The biology of freeliving heterotrophic flagellates.* Oxford: Clarendon Press.

SANDGREN, C. D. & ROBINSON, J. V. 1984. A stratified sampling approach to compensating for non-random sedimentation of phytoplankton cells in inverted microscope settling chambers. *British Phycological Journal,* 19, 67-72.

SARNELLE, O. 2007. Initial conditions mediate the interaction between *Daphnia* and bloom-forming cyanobacteria. *Limnology and Oceanography,* 52, 2120-2127.

SCHLADOW, S. G. & FISHER, I. H. 1995. The physical response of temperate lakes to artificial destratification. *Limnology and Oceanography,* 40, 359-373.

SCHOLES, P. 2010. 2009/2010 Rotorua Lakes TLI Update. *In:* SCHOLES, P. (ed.) *Environmental Publication 2010/18.* Whakatane: Bay of Plenty Regional Council.

SERIZAWA, H., AMEMIYA, T. & ITOH, K. 2010. Effects of buoyancy, transparency and zooplankton feeding on surface maxima and deep maxima: Comprehensive mathematical model for vertical distribution in cyanobacterial biomass. *Ecological Modelling,* 221, 2028-2037.

SHERMAN, B. S., WEBSTER, I. T., JONES, G. T. & OLIVER, R. L. 1998. Transitions between *Aulacoseira* and *Anabaena* dominance in a turbid river weir pool. *Limnological Oceanography,* 43, 1902-1915.

SICKO-GOAD, L., STOERMER, E. F. & LADEWSKI, B. G. 1977. A morphometric method for correcting phytoplankton cell volume estimates. *Protoplasma,* 93, 147-163.

SIMON, A. L. 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics,* 7, 287-310.

SMITH, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. *Environmental Science & Pollution Research,* 10, 126-139.

SMITH, V. H. & SCHINDLER, D. W. 2009. Eutrophication science: where do we go from here? *Trends in Ecology & Evolution,* 24, 201-207.

SMITH, V. H., TILMAN, G. D. & NEKOLA, J. C. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution,* 100, 179-196.

SØNDERGAARD, M., JEPPESEN, E., LAURIDSEN, T. L., SKOV, C., VAN NES, E. H., ROIJACKERS, R., LAMMENS, E. & PORTIELJE, R. O. B. 2007. Lake restoration: successes, failures and long-term effects. *Journal of Applied Ecology,* 44, 1095-1105.

SORRELL, B. 2010. Nutrients. *In:* PETERS, M. & CLARKSON, B. (eds.) *Wetland restoration: A handbook for New Zealand freshwater systems.* Manaaki Whenua Press.

SPALINGER, K. & BOUWENS, K. 2003. The roles of phosphorus and nitrogen in lake ecosystems. *Regional Information Report No. 4K03-42. Alaska Department of Fish and Game. Kodiak, Alaska.*

SPEARS, B. M., CARVALHO, L., PERKINS, R., KIRIKA, A. & PATERSON, D. M. 2006. Spatial and historical variation in sediment phosphorus fractions and mobility in a large shallow lake. *Water Research,* 40, 383-391.

SPIGEL, R. H. & IMBERGER, J. 1987. Mixing processes relevant to phytoplankton dynamics in lakes. *New Zealand Journal of Marine and Freshwater Research,* 21, 361-377.

STANDING COMMITTEE OF ANALYSTS 1982. *Ammonia in Waters. Methods for the examination of waters and associated materials.* ISBN: 0117516139, Great Britain, HMSO.

STANDING COMMITTEE OF ANALYSTS 1982. *Phosphorus in Waters, Sewage and Effluents. Methods for the examination of waters and associated materials.* ISBN: 011751582.5. Great Britain, HMSO.

SUREN, A. M. 2000. Effects of urbanisation. *In:* COLLIER, K. J. & WINTERBOURN, M. J. (eds.) *New Zealand Stream Invertebrates: Ecology and Implications for Management.* Christchurch, New Zealand.: New Zealand Limnological Society.

TALLING, J. F., SPENCER, H. J. & MORISON, H. R. 2005. The 'shock period': dynamics of phytoplankton during the spring–summer transition of a stratifying English lake. *Hydrobiologia,* 533, 15-28.

THERRIAULT, J.-C. & PLATT, T. 1978. Spatial heterogeneity of phytoplankton biomass and related factors in the near-surface waters of an exposed coastal embayment. *Limnology and Oceanography,* 23, 888-899.

TIJDENS, M., VAN DE WAAL, D., SLOVACKOVA, H., HOOGVELD, H. & GONS, H. 2008. Estimates of bacterial and phytoplankton mortality caused by viral lysis and microzooplankton grazing in a shallow eutrophic lake. *Freshwater Biology,* 53, 1126-1141.

TILMAN, D., KILHAM, S. S. & KILHAM, P. 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics,* 13, 349-372.

TILZER, M. M. 1973. Diurnal periodicity in the phytoplankton assemblage of a high mountain lake. *Limnology and Oceanography,* 18, 15-30.

TILZER, M. M. 1988. Secchi disk — chlorophyll relationships in a lake with highly variable phytoplankton biomass. *Hydrobiologia,* 162, 163-171.

TITTEL, J. R., BISSINGER, V., ZIPPEL, B., GAEDKE, U., BELL, E., LORKE, A. & KAMJUNKE, N. 2003. Mixotrophs combine resource use to outcompete specialists: implications for aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America,* 100, 12776-12781.

UKELES, R. & ROSE, W. E. 1976. Observations on organic carbon utilization by photosynthetic marine microalgae. *Marine Biology,* 37, 11-28.

U. S. ENVIRONMENTAL PROTECTION AGENCY. 1983. Phosphorus, All Forms. Method 365.1 (Colorimetric, Automated, Ascorbic Acid). *Methods for Chemical Analysis of Water and Wastes, EPA-600/ 4-79-020,* 365 (1.1) -365 (1.7), Cincinnati, Ohio, USA.

VAN DEN BRANDT, H. M. P. & SMIT, H. P. 1998. Mineral accounting: the way to combat eutrophication and to achieve the drinking water objective. *Environmental Pollution,* 102, 705-709.

VANT, W. N. & DAVIES-COLLEY, R. J. 1986. Relative importance of clarity determinants in Lake Ōkaro and Lake Rotorua. *New Zealand Journal of Marine and Freshwater Research,* 20, 355-363.

VINCENT, W. F. & DRYDEN, S. J. 1989. Phytoplankton succession and cyanobacterial dominance in a eutrophic lake of the mid-temperate zone (Lake Ōkaro, New Zealand). *Hydrobiologia,* 32, 137-163.

VINCENT, W. F., HOWARD-WILLIAMS, C., FORSYTH, D. J. & WHITE, E. 1987. Cyanobacterial dominance forum: Introduction to the short communications. *New Zealand Journal of Marine and Freshwater Research,* 21, 509-513.

VIVES-REGO, J., LEBARON, P. & NEBE-VON CARON, G. 2000. Current and future applications of flow cytometry in aquatic microbiology. *FEMS Microbiology Reviews,* 24, 429-448.

VON WESTERNHAGEN, N., HAMILTON, D. P. & PILDITCH, C. 2010. Temporal and spatial variations in phytoplankton productivity in surface waters of a warm-temperate, monomictic lake in New Zealand. *Hydrobiologia,* 652, 57.

WALSBY, A. E., DUBINSKY, Z., KROMKAMP, J., LEHMANN, C. & SCHANZ, F. 2001. The effects of diel changes in photosynthetic

coefficients and depth of *Planktothrix rubescens* on the daily integral of photosynthesis in Lake Zürich. *Aquatic Sciences,* 63, 326-349.

WALSBY, A. E. & MCALLISTER, G. K. 1987. Buoyancy regulation by *Microcystis* in Lake Ōkaro. *New Zealand Journal of Marine and Freshwater Research,* 21, 521-524.

WALSBY, A. E. & REYNOLDS, C. S. (1980) Sinking and floating. IN MORRIS, I. (Ed.) *The physiological ecology of phytoplankton.* Blackwell Scientific Publications, Oxford.

WANG, Y., STAUFFER, C., KELLER, C. & GREGER, M. 2005. Changes in Hg fractionation in soil induced by willow. *Plant and Soil,* 275, 67-75.

WEIDER, L. J. & LAMPERT, W. 1985. Differential response of *Daphnia* genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. *Oecologia,* 65, 487-491.

WHITE, E., PAYNE, G., PICKMERE, S. & WOODS, P. 1991. Seasonal variation in nutrient limitation of the algal community in Lake Horowhenua, New Zealand. *New Zealand Journal of Marine and Freshwater Research,* 25, 311-316.

WHITTINGTON, J., SHERMAN, B., GREEN, D. & OLIVER, R. L. 2000. Growth of *Ceratium hirundinella* in a subtropical Australian reservoir: the role of vertical migration. *Journal of Plankton Research,* 22, 1025-1045.

WIERENGA, R. 2004. Battle Ground lake assessment - Technical report. Washington State: Clark County Public Works Water Resources Section.

WILDING, T. Year. Rotorua Lakes blue-green algae monitoring. *In:* MCLEAN, I., ed. Rotorua Lakes 2001 - A symposium on research needs in the Rotorua Lakes, 2001 Rotorua.

WILSON, C. J. N., HOUGHTON, B. F., MCWILLIAMS, M. O., LANPHERE, M. A., WEAVER, S. D. & BRIGGS, R. M. 1995. Volcanic and structural evolution of Taupo Volcanic Zone, New Zealand: a review. *Journal of Volcanology and Geothermal Research,* 68, 1-28.

WOLTEMADE, C. J. 2000. Ability of restored wetlands to reduce nitrogen and phosphorous concentrations in agricultural drainage water. *Journal of Soil and Water Conservation,* 55, 303-310.

WOOD, S., JENTZSCH, K., RUECKERT, A., HAMILTON, D. & CARY, C. 2009. Hindcasting cyanobacterial communities in Lake Ōkaro with germination experiments and genetic analyses. *FEMS Microbiological Ecology* 67, 252-260.

WOOD, S. A., PAUL, W. J. & HAMILTON, D. P. 2008. Cyanobacterial biovolumes for the Rotorua Lakes. *Prepared for Environment Bay of Plenty,* Cawthron Report No 1504, 19 p.

WURTS, W. A. & DURBOROW, R. M. 1992. Interactions of pH, carbon dioxide, alkalinity and hardness in fish ponds. *Southern Regional Aquaculture Center,* Publication No. 464.

ZHANG, C. 2010. *High frequency monitoring and three-dimensional modelling of temporal variations in water quality of Lake Rotorua, New Zealand.* Master of Science in Biological Sciences, The University of Waikato.

ZHANG, J. Z., ORTNER, P. B. & FISCHER, C. J. 1997. Method 353.4: Determination of nitrate and nitrite in estuarine and coastal waters by gas segmented continuous flow colorimetric analysis. *In:* ARAR, E. J. (ed.) *National Exposure Research Laboratory. Office of Research and Development - U.S. Environmental Protection Agency.* Cincinnati, Ohio.

9 Appendices

Appendix 1: Spatial variability

Table 9.1: Light extinction coefficient (K_d, m^{-1}), surface irradiance (I (0)), euphotic depth (z_{eu}) and z_{eu} irradiance ($I(z_{eu})$) from 17 December 2009 to 29 March 2011.

17/12/2009	K_d	0.71	19/01/2010	K_d	0.50	16/02/2010	K_d	0.34
	I(0)	3255.22		I(0)	663.24		I(0)	350.77
	z_{eu}	11.41		z_{eu}	13.03		z_{eu}	17.01
	$I(z_{eu})$	32.55		$I(z_{eu})$	6.63		$I(z_{eu})$	3.51
25/03/2010	K_d	0.53	20/04/2010	K_d	0.53	20/05/2010	K_d	0.57
	I(0)	1163.72		I(0)	333.72		I(0)	526.51
	z_{eu}	13.43		z_{eu}	11.06		z_{eu}	10.97
	$I(z_{eu})$	11.64		$I(z_{eu})$	3.34		$I(z_{eu})$	5.27
17/06/2010	K_d	0.61	20/07/2010	K_d	0.53	23/08/2010	K_d	0.67
	I(0)	179.25		I(0)	286.35		I(0)	277.85
	z_{eu}	8.51		z_{eu}	10.71		z_{eu}	8.39
	$I(z_{eu})$	1.79		$I(z_{eu})$	2.86		$I(z_{eu})$	2.78
29/09/2010	K_d	0.79	26/10/2010	K_d	1.14	18/11/2010	K_d	2.75
	I(0)	979.51		I(0)	248.65		I(0)	843.09
	z_{eu}	8.76		z_{eu}	4.84		z_{eu}	2.45
	$I(z_{eu})$	9.80		$I(z_{eu})$	2.49		$I(z_{eu})$	8.43
16/12/2010	K_d	2.15	20/01/2011	K_d	0.94	17/02/2011	K_d	0.94
	I(0)	272.96		I(0)	2385.12		I(0)	1680.59
	z_{eu}	2.61		z_{eu}	8.29		z_{eu}	7.93
	$I(z_{eu})$	2.73		$I(z_{eu})$	23.85		$I(z_{eu})$	16.81
29/03/2011	K_d	0.79						
	I(0)	2432.52						
	z_{eu}	9.92						
	$I(z_{eu})$	24.33						

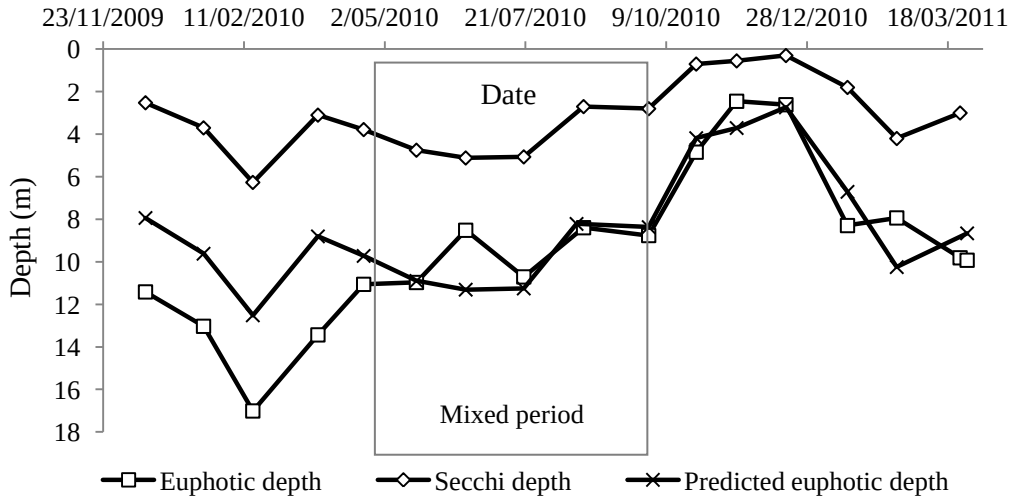


Figure 9.1: Euphotic depth, Secchi depth and predicted euphotic depth (e.g., Tilzer, 1988) from 17 December 2009 to 29 March 2011

Appendix 2: Temporal variation during a cyanobacterial surface bloom

Table 9.2: Mean global irradiance between 06:00 h and 19:00 h from 16-19 November 2010

Date	Mean irradiance (MJ m^{-2} h^{-1}) from 06:00 h – 19:00 h
16/11/2010	1.523
17/11/2010	2.187
18/11/2010	1.567
19/11/2010	1.529

Table 9.3: Wind data from 18-19 November 2010. Closest sample times are in bold.

Date	Time (h)	Direction (DegT)	Speed (m s^{-1})
18/11/2010	6:00:00	85	0.9
18/11/2010	7:00:00	31	0.9
18/11/2010	8:00:00	321	1
18/11/2010	9:00:00	189	1
18/11/2010	10:00:00	17	1.7
18/11/2010	11:00:00	318	2.7
18/11/2010	12:00:00	298	2.9
18/11/2010	13:00:00	15	3
18/11/2010	**14:00:00**	**12**	**3.6**
18/11/2010	15:00:00	3	4.3
18/11/2010	16:00:00	14	4.8
18/11/2010	17:00:00	23	5
18/11/2010	**18:00:00**	**23**	**5.1**
18/11/2010	19:00:00	26	4.6
18/11/2010	20:00:00	37	3.9
18/11/2010	21:00:00	17	3.5
18/11/2010	22:00:00	20	4.2
18/11/2010	**23:00:00**	**37**	**3.3**
19/11/2010	24:00:00	34	2.5
19/11/2010	1:00:00	358	2.3
19/11/2010	2:00:00	40	2
19/11/2010	3:00:00	51	2.4
19/11/2010	**4:00:00**	**28**	**2.7**
19/11/2010	5:00:00	26	2.1
19/11/2010	6:00:00	343	1.1
19/11/2010	7:00:00	48	1.6
19/11/2010	8:00:00	1	2.5
19/11/2010	**9:00:00**	**6**	**3.2**
19/11/2010	10:00:00	332	2.6
19/11/2010	**11:00:00**	**346**	**3.2**

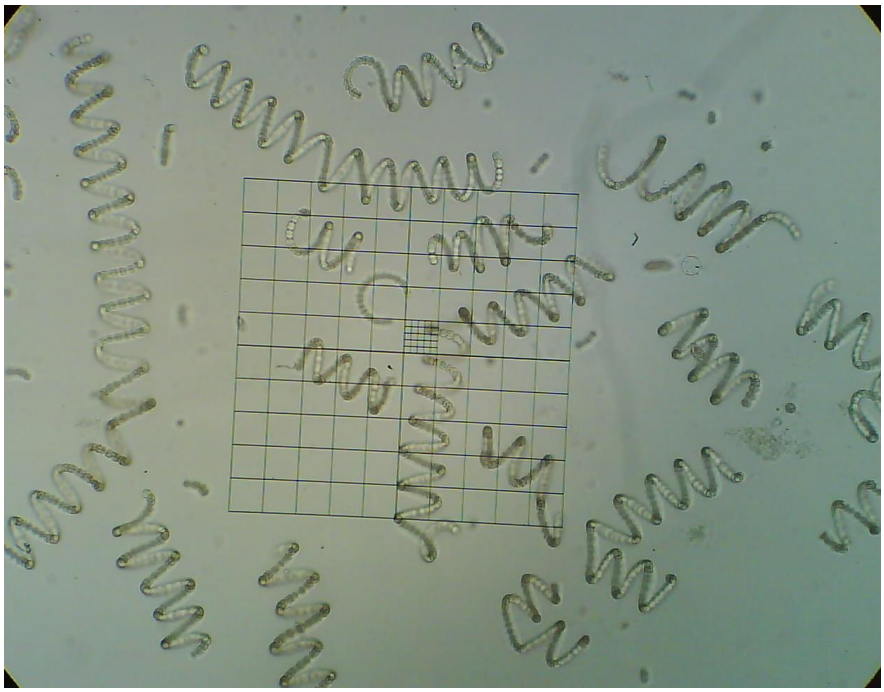


Figure 9.2: Image of *Anabaena spiroides* in Lake Ōkaro on 18-19 November 2010. Sample collected from 0 m depth at 11:00 h on 19 November 2010. Sample concentration was 137,777 cells mL^{-1}.

Appendix 4: Temporal variability during a dual-peak deep chlorophyll maximum (DCM)

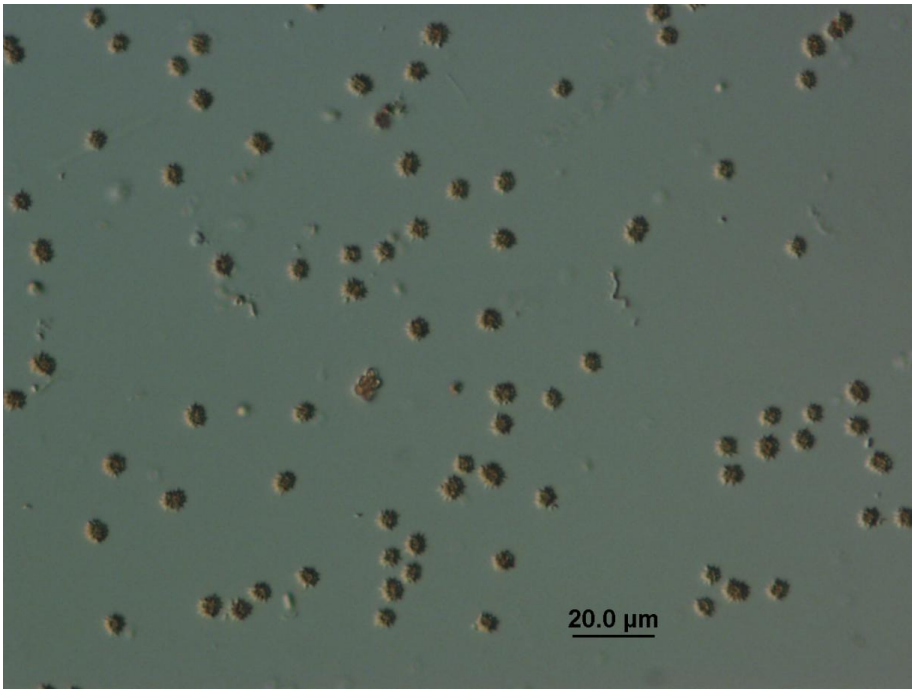


Figure 9.3a: 400x magnification of an unconfirmed species of chlorophyte (picoplankton #2) collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien.

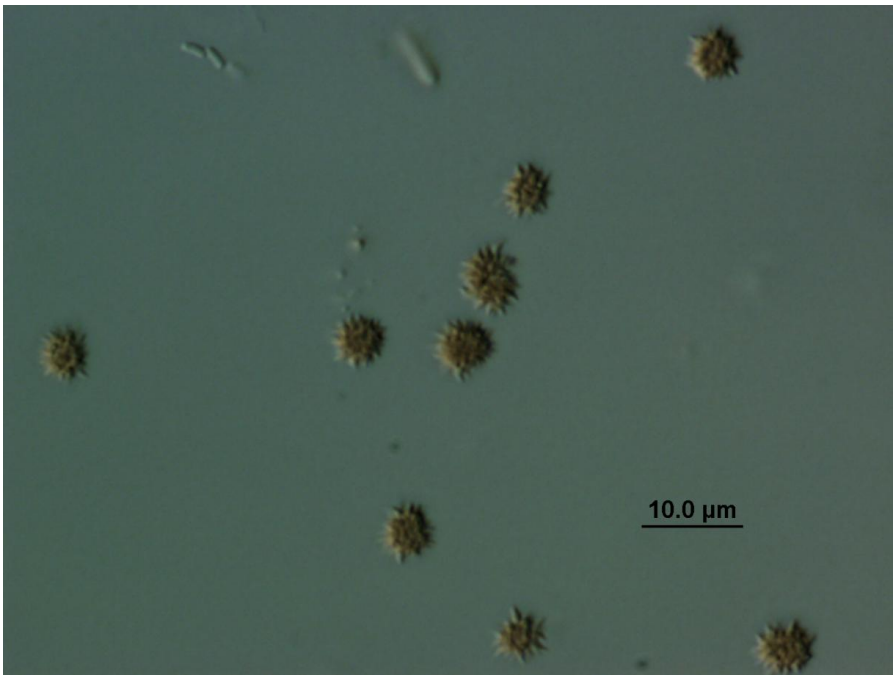


Figure 9.3b: Picoplankton #2 at 1000x magnification, collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien.

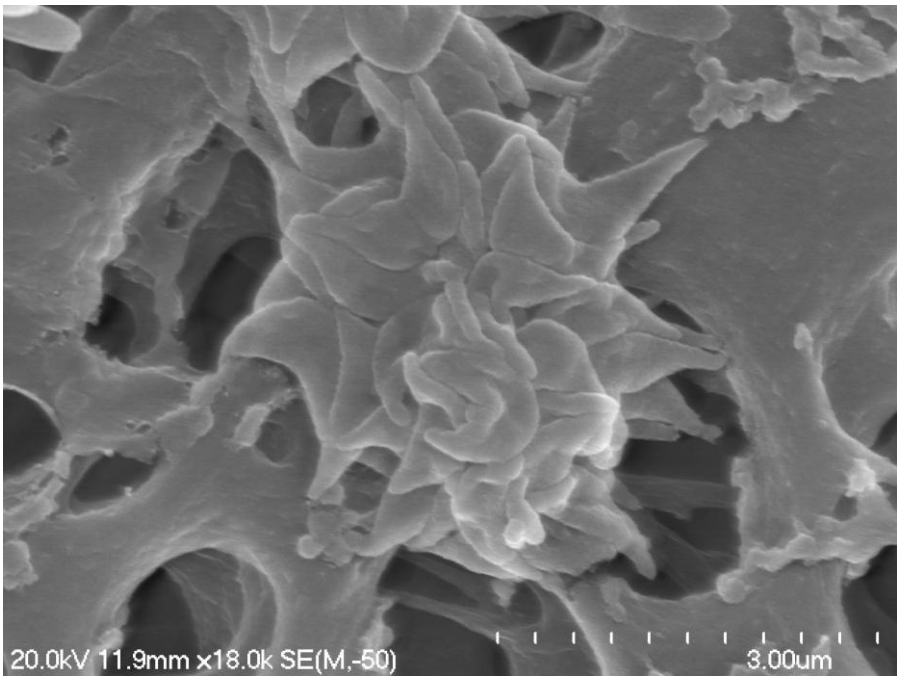


Figure 9.3c: Scanning electron microscope image of picoplankton #2 on tissue paper (background), collected from Lake Ōkaro on 23 March 2011 at 10 m depth. Image courtesy of Barry O'Brien.