

Effects of diurnal vertical mixing and stratification on phytoplankton productivity in geothermal Lake Rotowhero, New Zealand

Justin D. Brookes^{1*}, Katherine R. O'Brien², Michele A. Burford³, Denise A. Bruesewitz⁴, Ben R. Hodges⁵, Chris McBride⁴, David P. Hamilton⁴

¹ *Water Research Centre, The Environment Institute, School of Earth and Environmental Science, The University of Adelaide, Adelaide 5005, South Australia, Australia*

² *Environmental Engineering, University of Queensland, St Lucia, QLD 4067, Australia*

³ *Australian Rivers Institute, Griffith University, Nathan, QLD 4111, Australia*

⁴ *Environmental Research Institute, University of Waikato, Private Bag 3105, Hamilton 3240, New Zealand*

⁵ *Civil, Architectural and Environmental Engineering, University of Texas, Austin, USA*

* *Corresponding author email: justin.brookes@adelaide.edu.au*

Received 8 May 2013; accepted 17 June 2013; published 12 July 2013

Abstract

Mixing processes in lakes are key factors controlling light availability for phytoplankton growth, but understanding the contribution of mixing is often confounded by other factors such as nutrient availability and species dynamics. Our study examined this problem in a low pH, geothermally heated lake dominated by one phytoplankton genus and lacking the complexity of nutrient limitation, phytoplankton species interactions, or grazing pressure. We hypothesized that the continuous strong convectively driven circulation resulting from atmospheric instability and sediment heating would negate any tendency of thermal stratification, entraining phytoplankton and transporting them away from high surface irradiance that could induce photoinhibition. During our study, water temperatures were considerably warmer than air temperatures, with a diurnal maximum surface temperature of 37.5 °C and minimum of 35.5 °C. Surface heating induced stratification, with a temperature difference of 1–2 °C evident during the day, but there was sufficient heat loss and mixing during the night to erode the stratification and create isothermal conditions. The vertical entrainment velocity driven by convective circulation was on the order of 0.1 mm s⁻¹, but when there was strong solar heating, phytoplankton within the top 0.5 m of the water column still showed depressed photosynthetic quantum efficiencies, as determined with a Pulse Amplitude Modulated fluorometer (PHYTOPAM); however, this depression was less than for phytoplankton cells maintained throughout the day in surface waters with bottle incubations. At other times mixing generated by continuous heating and atmospheric instability meant that phytoplankton did not show photoinhibition; therefore, despite the geothermally driven mixing in Rotowhero, the intensity of solar radiation is still the key mechanism determining the stratification response and resultant photoinhibition of the phytoplankton.

Lake Rotowhero provides an excellent natural laboratory to examine the relative time scales of mixing and phytoplankton photoinhibition responses because small changes in solar radiation have such marked impacts on the diurnal stratification and radiation experienced by cells located above the diurnal thermocline.

Key words: entrainment, geothermal, photoinhibition, pulse amplitude modulated fluorometry

Introduction

Convection and wind shear create turbulence in the surface mixed layer of lakes, which affects the entrainment of phytoplankton and the light dose they experience (MacIntyre 1993, Oliver and Ganf 2000, Brookes et al. 2002). In geothermal lakes, 2 additional mechanisms may induce turbulence: gas bubbles that rise from thermal vents and entrain water from depth (e.g. Romero et al. 1996), and direct geothermal heating that creates convective cells (Pickrill 1993). In some lakes geothermal heating has been shown to be of sufficient magnitude to homogenize hypolimnetic waters (Priscu et al. 1986, Gibbs 1992). Theoretically, in the presence of high thermal loss rates through the water surface associated with an unstable atmosphere (heating from below), geothermal mixing could negate vertical stratification, with warm plumes rising to displace cooler surface waters to create continuous vertical circulation.

Rotowhero is a geothermal lake in the Rotorua district of New Zealand. Its bottom sediments are geothermally heated, and several small springs also discharge water of temperature ~ 70 °C into the lake (McCull and Forsyth 1973). We hypothesized that the geothermal activity associated with the bottom sediments would be the dominant mechanism for vertical mixing and may overcome solar heating of surface waters, making thermal stratification unlikely. Turbulent mixing can create conditions that deter phytoplankton from spending sufficient time at the water surface to sustain photo-damage. When mixing entrains cells and circulates them through a deeper mixed layer, the light dose experienced by the cells may be reduced, but they are also less likely to experience photoinhibition, and community productivity can be increased by as much as 16% (Oliver et al. 2003). The high temperature and low pH in Lake Rotowhero seems to have resulted in a major reduction in phytoplankton diversity, with one well-adapted genus (potentially one species) dominating in these conditions (Forsyth and McCull 1974). These characteristics make this system ideally suited to test the *in vivo* photosynthetic response to light of one dominant phytoplankton genus.

The “fluorescence ratio” identified by Harris (1980), which is the DCMU-sensitive chlorophyll *a* fluorescence divided by the *in vivo* chlorophyll fluorescence, typically displays a vertical gradient during stratified conditions as the fluorescence ratio of surface phytoplankton populations becomes depressed. Because the time scales of mixing and photochemical processes of phytoplankton are similar (Denman and Gargett 1983), Harris (1986) concluded that the fluorescence ratio could be used as an indicator of

mixing in surface waters. With advances in fluorometry, the physiological basis for Harris’s observations is better understood (Oliver and Whittington 1998), and variable fluorescence has been used to determine rates of mixing, phytoplankton entrainment, and photoinhibition (Whittington et al. 2000, Brookes et al. 2002, Regel et al. 2004).

The aim of this study, therefore, was to characterise the mixing behaviour of Lake Rotowhero based on the vertical distribution of photoinhibition responses by phytoplankton and to compare this behaviour with those derived from considerations of the thermal structure of the lake. We used thermistors to investigate the mixing regime and PHYTOPAM-fluorometry to probe the phytoplankton community and assess its light history.

Methods

Lake Rotowhero is a geothermal lake in the Rotorua district in the North Island of New Zealand (38°19’S, 176°23’E). Also known as Green Lake, Rotowhero derives its names from the Maori “roto,” meaning lake and “whero” meaning red (with reference to heat). Water temperature has been shown to vary seasonally between 29.5 and 37.5°C, pH to be ~ 3.1 , and the lake has been considered highly eutrophic (Forsyth and McCull 1974). It has a single, dominant phytoplankton genus, *Chlorella* spp., and the insect invertebrate macrofauna is dominated by *Chironomus zealandicus* (McCull and Forsyth 1973).

The lake has a catchment area of 12 ha, surface area of 2.58 ha, and maximum depth of 14 m. The lake consists of 2 basins (Fig. 1) and receives water from 7 springs, which contribute an estimated combined discharge of 10 L s⁻¹ of hot water (~ 70 °C).

An intensive field campaign was undertaken on 14 December 2008. The water column thermal profile was measured using 10 thermistors (Onset stowaway tidbit) deployed at 1 m depth intervals on a string in the deepest point of the lake. Meteorological variables were measured 2 m above the water surface on the northern lake shore at 15 min intervals, including wind speed and direction, air temperature, relative humidity, and barometric pressure (Vaisala WXT510), as well as incoming shortwave radiation (Apogee Instruments SP-110; 380–1120 nm) and photosynthetically active radiation (PAR: Apogee Instruments SQ-110; 409–659 nm). Depth profiles of PAR were measured with a LICOR scalar underwater light sensor. PAR at depth was natural log transformed and regressed against depth to calculate the light attenuation coefficient, from which the percent surface light transmission with depth was calculated.

Measurement of fluorescence yield

Fluorescence yield was measured using a Pulse Amplitude Modulated Fluorometer (Phyto-PAM, Walz, Effeltrich, Germany; see Schreiber et al. 1994). Cells were dark-adapted in cuvettes for 15 min prior to analysis. The fluorescence of the dark-adapted cells, F_0 , was determined by stimulation with a weak probe light immediately following 15 min of darkness. The maximum fluorescence signal, F_m , was determined following the closure of all reaction centres by a 600 ms pulse of saturating irradiance. Variable fluorescence (F_v) was determined as the difference between F_m and F_0 ($F_v = F_m - F_0$) and the variable fluorescence ratio was calculated as F_v/F_m .

To determine the effect of light and vertical mixing on the photochemistry of the phytoplankton, the change in variable fluorescence was compared between samples taken periodically from the natural population during the day, and water samples collected early in the day and incubated at fixed depths throughout the day. Lake water was collected from the lake surface, mixed to ensure homogeneous distribution of phytoplankton, poured into 500 mL PET bottles, and suspended at 0.1, 0.25, 0.5, 0.9, 1.6, and 3.1 m depth, corresponding to 95, 70, 50, 30, 10, and 1% of surface irradiance. Commencing at dawn and at approximately 2 h intervals, a subsample was taken from each bottle and from the adjacent water column at corre-

sponding depths. F_v/F_m was measured using the PHYTO-PAM-fluorometer following 15 min of darkness (see above). The sampling was conducted adjacent to the thermistor chain so that the vertical stratification properties of the site were precisely known.

Water samples were collected from the surface and bottom water of each lake basin and analysed for nitrite and nitrate (NO_2^- and NO_3^- , respectively), ammonium (NH_4^+), and soluble reactive phosphorus (SRP). Casts with a Seabird CTD were made throughout the lake at each sampling interval and recorded temperature, dissolved oxygen, turbidity, chlorophyll fluorescence, pH, and conductivity.

Heat budget

A comparison of thermal balances during day heating and night cooling was used to estimate the vertical entrainment rate at the base of the thermocline driven by geothermal plumes. At night, the lake becomes fully mixed and isothermal, so a simple one-box, continuously stirred tank reactor (CSTR) model can be applied. During the day, geothermal energy becomes trapped by stratification and only leaks upward through entrainment. The daytime system can be approximated as a 2-box CSTR model with an upward entrainment flux between boxes. The combination of the 2 models provides estimates of the entrainment exchange.

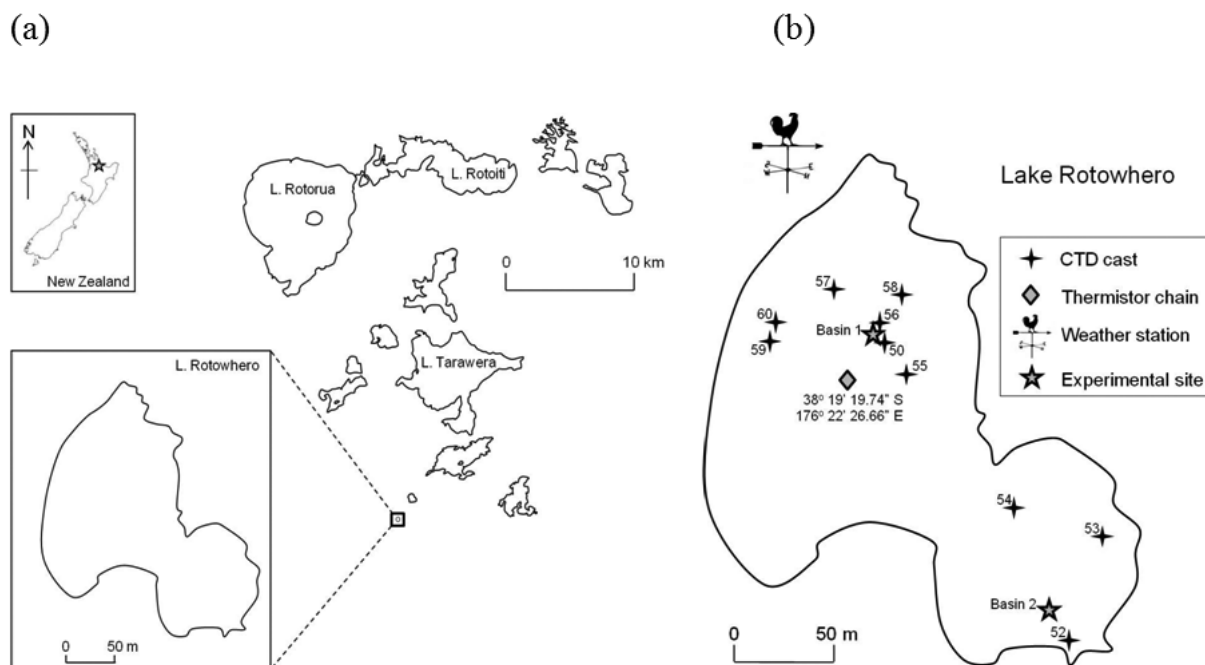


Fig. 1. (a) Location of Lake Rotowhero in New Zealand; (b) monitoring and sampling sites in the lake.

The net change in the internal energy of the lake must exactly balance the thermal energy fluxes through the lake surface (evaporation, sensible heat transfer, longwave radiation) and the geothermal flux through the lake bottom. In terms of flux rates, the thermal energy balance during the night cooling period (subscript C) is

$$\frac{\Delta E_C}{\Delta t} = Q_g - Q_{eC} - Q_{hC} - Q_{nC}, \quad (1)$$

where Q_g is the geothermal flux rate, Q_{eC} is the evaporative heat flux, Q_{hC} is the sensible heat flux and Q_{nC} is the net longwave radiation. Note that for convenience in exposition, signs are assigned in equation 1 so that fluxes into the lake are positive and fluxes out are negative.

During daytime heating (subscript H), the upper layer is similar to equation 1 with the addition of shortwave radiation (Q_s) and an entrainment (mixing) flux from the lower layer (Q_m), so the thermal energy balance is

$$\frac{\Delta E_{HU}}{\Delta t} = Q_m + Q_{sH} - Q_{eH} - Q_{hH} - Q_{nH}. \quad (2)$$

The thermal balance below the thermocline during the day is

$$\frac{\Delta E_{HL}}{\Delta t} = Q_g - Q_m, \quad (3)$$

where Q_g is the geothermal heat flux into the lower layer, ΔE_{HL} is the change in internal energy in the lower layer during heating, and Q_m is the upward rate of thermal entrainment. The net entrainment velocity (w_e) associated with a thermal flux of Q_m is

$$w_e = Q_m(\rho c_p \Delta T)^{-1}, \quad (4)$$

where ΔT is the temperature difference between layers, ρ is the water density, and c_p is the heat capacity at constant pressure.

The surface fluxes Q_s , Q_e , Q_h , and Q_n can be modeled using the approach of Verburg and Antenucci (2010) for unstable atmospheres over lakes with standard coefficients. The net change in internal energy, ΔE , is computed from the measured lake temperatures (Fig. 3). Equation 1 can be solved for Q_g because all other terms are known; equation 2 can be solved for Q_m because all other terms are known; and equation 3 can be solved for Q_m assuming that Q_g at night is the same as Q_g during the day. This approach provides 2 estimates for the entrainment between upper and lower layers during the day, which is used with equation 4 to obtain 2 estimates of w_e . The 2 estimates are not expected to be identical because the CSTR box model neglects horizontal gradients across the lake.

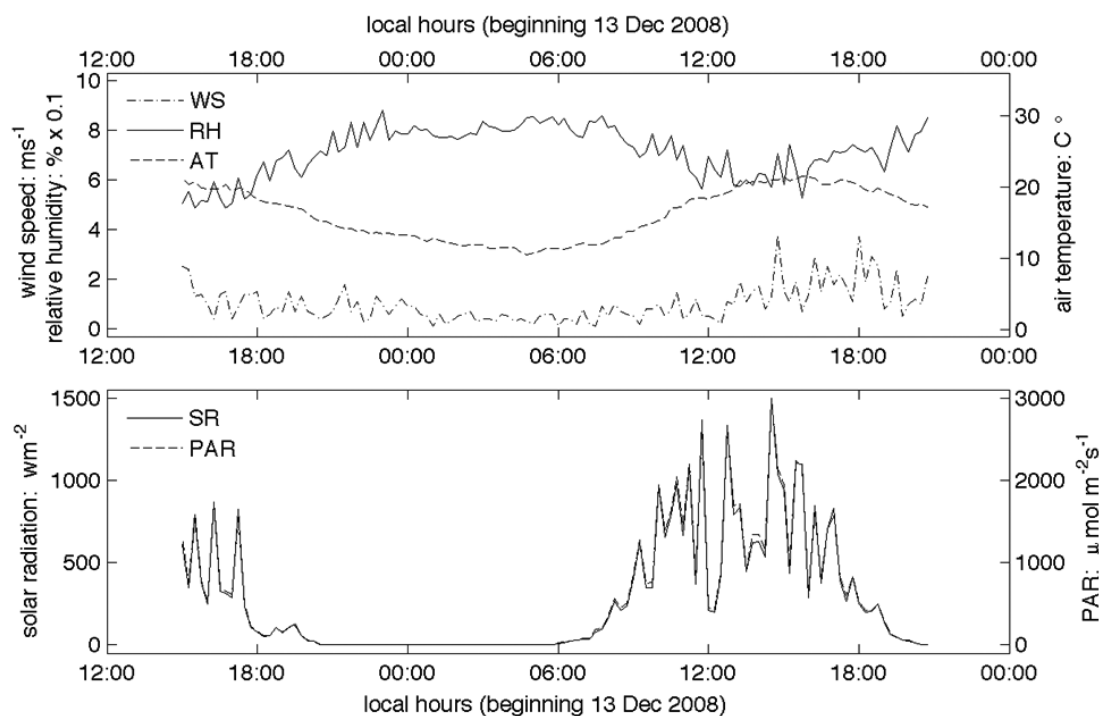


Fig. 2. (a) Air temperature ($^{\circ}\text{C}$), relative humidity (%), and wind speed (m s^{-1}); and (b) Solar radiation (W m^{-2}) and PAR ($\text{mmol m}^{-2} \text{s}^{-1}$) measured with a meteorological station deployed on the north shore of Lake Rotowhero. WS = wind speed, RS = relative humidity, AR = air temperature, SR = solar radiation.

Results

Dissolved nutrients concentrations did not vary between basins or with depth. Mean NH_4^+ concentration was $1900 \mu\text{g N L}^{-1}$, NO_3^- was $2.0 \mu\text{g N L}^{-1}$, and SRP was $45.5 \mu\text{g L}^{-1}$, and the chlorophyll concentration was $45 \mu\text{g L}^{-1}$. The phytoplankton community was dominated by the chlorophyte, *Chlorella* spp., with one species tentatively identified as *Chlorella protothecoides*; however, no genetic analysis was conducted to confirm the identification.

Air temperature ranged between 12°C at dawn to 22°C in mid-afternoon, and relative humidity was highest early in the day (Fig. 2a). Wind speed was $<2 \text{ m s}^{-1}$ during daylight hours, increasing at night. Photosynthetically active radiation increased from approximately 07:00 h and was highly variable throughout the day, decreasing to zero by 19:00 h (Fig. 2b). Water temperature was considerably

warmer than air temperature with a diurnal maximum surface temperature of 37.5°C and minimum of 35.5°C (Fig. 3). Surface heating leading to stratification with a temperature difference $1\text{--}2^\circ\text{C}$ evident during the day, but heat loss and mixing during the night was sufficient to erode the stratification and create isothermal conditions.

Results for equations 1–4 (Table 1) are for a period of sustained cooling (00:00–03:00 h on 14 Dec) and for a period of heating when stratification was reasonably continuous (11:00–14:00 h on 14 Dec). Equation 4 provides 2 different estimates for w_e ; the difference between them provides some indication of uncertainty in the estimate.

The photophysiology of phytoplankton was compared between bottle samples suspended at discrete depths and water samples collected periodically through the water column. Phytoplankton sampled throughout the water column had similar Fv/Fm values at dawn (Fig. 4a);

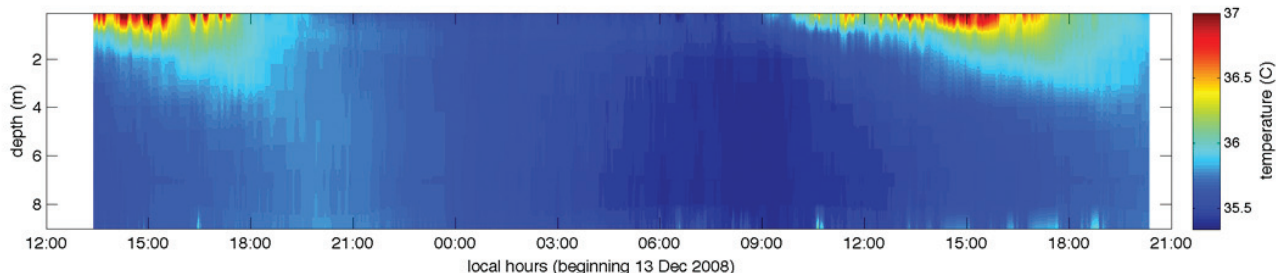


Fig. 3. Water temperature measured with a thermistor chain at various depth increments through the water column in Lake Rotowhero.

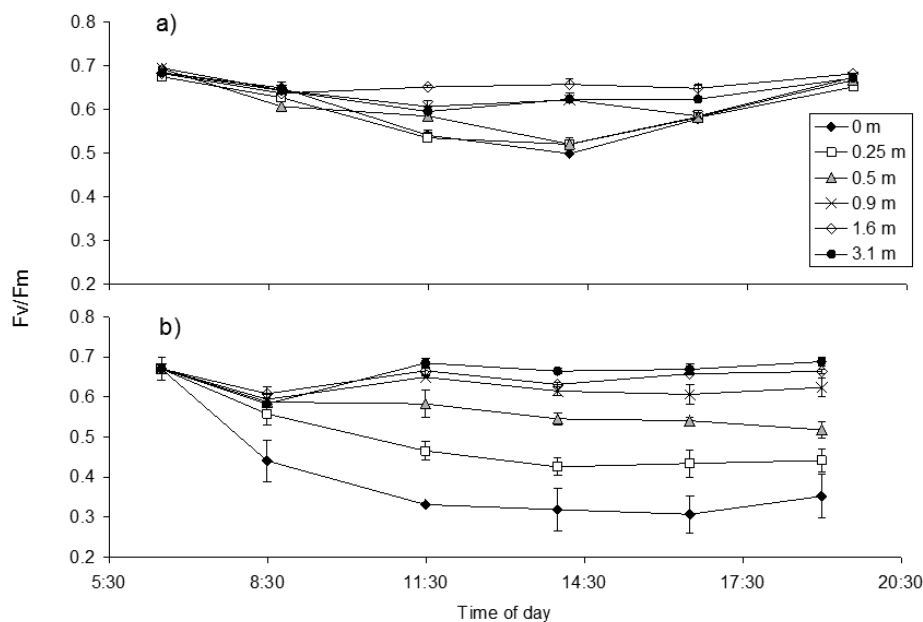


Fig. 4. Photosynthetic yield in (a) water samples collected from a range of depths through the water column, and (b) incubated water samples at fixed depths over 1 day in Lake Rotowhero.

however, as ambient irradiance increased through the morning, Fv/Fm decreased in samples from the top 0.5 m. The Fv/Fm in surface waters increased in the afternoon as irradiance decreased, and by 19:00 h Fv/Fm was again maximal as the surface waters had cooled and mixed to a depth of 3 m. In contrast, water samples suspended in bottles at discrete depths within the top 0.9 m of the water column had a greater light-dependent decrease in Fv/Fm throughout the day, and there was little increase in Fv/Fm in surface samples by early evening (Fig. 4b).

Discussion

In Lake Rotowhero, the difference between water surface and air temperatures led to a continuously unstable atmosphere, which accentuated latent and sensible heat losses from the water. During the day, the low wind speeds and heat losses did not compensate for heating due to incoming solar radiation, leading to diurnal thermal stratification. Later in the day, as solar radiation decreased, the vertical thermal structure became homogeneous. The vertical entrainment velocity of 0.1 mm s^{-1} was capable of eroding the thermal gradient in $\sim 1 \text{ m}$ water in 3 h, so the entrainment computed during the stratification period seems consistent with the homogenization processes in the early evening.

The thermistors at 0.1 and 0.5 m had identical temperatures throughout the night and for at least part of the time during the day, supporting the hypothesis that water was mixed downward from the surface. Stratification did not develop monotonically, but was interspersed with apparent mixing events that weakened the stratification and amplified exchange between surface and lower layers. Our computations of w_e and Q_m do not imply a one-way physical transport from deep waters into the surface mixed layer, however, but rather a net exchange with transport in both directions. The geothermal plumes eroded the stratification from below at the same time as wind-driven mixing acted from above to entrain near-surface waters to greater depth, with solar radiation acting to counter the two, but typically only being effective for a few hours centred about the middle of the day.

In our study, the phytoplankton collected at discrete depths within the lake during the day had depressed Fv/Fm within the top 0.5 m of the water column; however, this value was not as low as that of the bottled phytoplankton maintained at discrete depths. This suggests that in contrast to bottled phytoplankton, phytoplankton in surface waters were mixed to depths greater than 0.5 m on occasions. Additionally cells from deeper in the water column, with higher Fv/Fm values, could have been entrained into the top 0.5 m, increasing the mean observed Fv/Fm. The constant mixing generated by continuous

Table 1. Components of the thermal budget; see equations 1–4. Q_{ec} = evaporative heat flux, Q_{hc} = sensible heat flux, Q_{nc} = net longwave radiation, Q_s = solar radiation, ΔE = change in internal energy, t = time, Q_g = geothermal flux, Q_m = rate of thermal transfer between layers, w_e = net entrainment velocity. See text for further details of variables.

	cooling	heating upper layer	heating lower layer
Q_{ec} (W m^{-2})	–19	–52	n/a
Q_{hc} (W m^{-2})	–94	–70	n/a
Q_{nc} (W m^{-2})	–284	–258	n/a
Q_{sh} (W m^{-2})	0	691	n/a
$\Delta E/\Delta t$ (W m^{-2})	–325	143	361
Q_g (W m^{-2})	72	n/a	72*
Q_m (W m^{-2})	n/a	167	289
w_e (mm s^{-1})	n/a	0.08	0.13

* Q_g value from cooling period used as estimate for lower layer during heating period.

geothermal heating from the bottom sediments and from atmospheric instability means that phytoplankton are mostly continuously circulated through the light field during daylight hours, and hence are not subject either to light deprivation or severe photoinhibition associated with constant position in the water column. The only exception to this pattern is in the middle of the day when solar radiation is sufficient to induce a shallow, thermally stratified surface layer in which Fv/Fm is depressed in phytoplankton within this layer. Surprisingly, therefore, the intensity of solar radiation is still the key mechanism determining the stratification response and subsequent photoinhibition of the phytoplankton.

There was a temperature difference between the hot spring input ($\sim 70 \text{ }^\circ\text{C}$) and the main basin ($35.5\text{--}37.5 \text{ }^\circ\text{C}$), which would have driven convective currents (Monismith et al. 1990) and potentially transported cells laterally and to different depths, despite the intact stratification at the central basin site. Evidence of such currents was not measured directly in this study; however, in the period from 0:300 to 12:00 h on 14 December, the deeper water was slightly cooler than the surface water. This behaviour is likely caused by convective differential cooling (Verburg et al. 2011) where water from shallower regions was cooled more rapidly and flowed downslope into the basin centre.

The variable fluorescence ratio (Fv/Fm) of the chlorophyte *Chlorella* spp., (nominally *C. protothecoides* but possibly other *Chlorella* species), in Rotowhero in the early morning was approximately 0.7 (Fig. 4a and b), which is within the range expected for optimally growing chlorophytes (Oliver and Whittington 1998). There was

no evidence of thermal stress in these *Chlorella*, which contrasts sharply with that of phytoplankton (Li 1985, Morris and Kromkamp 2003), seagrasses (Campbell et al. 2006), and coral symbiotic zooxanthellae (Jones et al. 1998) from cooler habitats exposed to higher temperatures. The high temperatures and low pH of Lake Rotowhero select strongly for the single thermophilic genus, and so competition for resources in the lake is low. Coupled with the continuous mixing, this makes Lake Rotowhero a unique habitat for these organisms to exploit.

Lake Rotowhero provided a natural laboratory in which to explore short-term photosynthetic responses of a single indigenous phytoplankton population to the interplay of mixing and solar radiation. Typically in lakes with strong diurnal stratification the phytoplankton cells are maintained at discrete depths for sufficiently long periods for them to experience intense photoinhibition. This process is over-ridden by mixing, the mean light dose that cells experience is reduced and the resultant photoinhibition is less. While mixing in most lakes is driven by convection and wind, Lake Rotowhero also has geothermally driven mixing and disruption of stratification. Although solar radiation remained an important factor affecting photoinhibition in Lake Rotowhero, the effect was dampened due to geothermally driven mixing.

Acknowledgements

This work was assisted with funding from the New Zealand Ministry of

Business, Innovation and Employment (UOWX0505). Hodges was partially supported by the US National Science Foundation under Grant No. 0710901. The team thanks GLEON for supporting this project through the development of collaborative networks.

References

- Brookes JD, Regel R, Ganf GG. 2002. Changes in the photochemistry of *Microcystis aeruginosa* in response to light and mixing. *New Phytol.* 158:151–164.
- Campbell D, Hurry V, Clarke AK, Gustafsson P, Oquist G. 1998. Chlorophyll fluorescence analysis of cyanobacterial photosynthesis and acclimation. *Microbiol Mol Biol R.* 62:667–683.
- Campbell SJ, McKenzie LJ, Kerville SP. 2006. Photosynthetic responses of seven tropical seagrasses to elevated seawater temperature. *J Exp Mar Biol Ecol.* 330:455–468.
- Denman KL, Gargett AE. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol Oceanogr.* 28:801–815.
- Forsyth DJ, McColl RHS. 1974. The limnology of a thermal lake: Lake Rotowhero, New Zealand: II. Biology with emphasis on the benthic fauna of Chironomids. *Hydrobiologia.* 44:91–104.
- Gibbs MM. 1992. Influence of hypolimnetic stirring and underflow on the limnology of Lake Rotoiti, New Zealand. *New Zeal J Mar Fresh Res.* 26:453–463.
- Harris GP. 1980. The relationship between chlorophyll a fluorescence, diffuse attenuation changes and photosynthesis in natural phytoplankton populations. *J Plankton Res.* 2:109–127.
- Harris GP. 1986. *Phytoplankton Ecology*. London (UK): Chapman and Hall.
- Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schrieber U. 1998. Temperature-induced bleaching of corals begins with impairment of the CO₂ fixation mechanism in zooxanthellae. *Plant Cell Env.* 21:1219–1230.
- Li WKW. 1985. Photosynthetic response to temperature of marine phytoplankton along a latitudinal gradient (16°N to 74°N). *Deep Sea Res.* 32:1381–1391.
- MacIntyre S. 1993. Vertical mixing in a shallow, eutrophic lake: Possible consequences for the light climate of phytoplankton. *Limnol Oceanogr.* 38:798–817.
- McColl RHS, Forsyth DJ. 1973. The limnology of a thermal lake: Lake Rotowhero, New Zealand: I. description and water chemistry. *Hydrobiologia.* 43:313–332.
- Monismith SG, Imberger J, Morison ML. 1990. Convective motions in the sidearm of a small reservoir. *Limnol Oceanogr.* 35:1676–1702.
- Morris EP, Kromkamp JC. 2003. Influence of temperature on the relationship between oxygen- and fluorescence-based estimates of photosynthetic parameters in a marine benthic diatom (*Cylindrotheca closterium*). *Euro J Phycol.* 38:133–142.
- Oliver RL, Ganf GG. 2000. Freshwater Blooms. In: Whitton BA, Potts M, editors. *The Ecology of Cyanobacteria*. p. 149–194.
- Oliver RL, Whittington J. 1998. Using measurements of variable chlorophyll-a fluorescence to investigate the influence of water movement on the photochemistry of phytoplankton. In: Imberger J, editor. *Physical processes in lakes and oceans*. American Geophysical Union Coastal and Estuarine Studies; Vol. 54. p. 517–534.
- Oliver RL, Whittington J, Lorenz Z, Webster T. 2003. The influence of vertical mixing on the photoinhibition of variable chlorophyll a fluorescence and its inclusion in a model of phytoplankton photosynthesis. *J Plankton Res.* 25:1107–1129.
- Pickrill RA. 1993. Shallow seismic stratigraphy and pockmarks of a hydrothermally influenced lake, Lake Rotoiti, New Zealand. *Sedimentology.* 40:813–828.
- Priscu JC, Spigel RH, Gibbs MM, Downes MT. 1986. A numerical analysis of hypolimnetic nitrogen and phosphorus transformations in Lake Rotoiti, New Zealand: A geothermally influenced lake. *Limnol Oceanogr.* 31:812–831.
- Regel RH, Brookes JD, Ganf GG. 2004. Vertical migration, entrainment and photosynthesis of the freshwater dinoflagellate *Peridinium cinctum* in a shallow urban lake. *J Plankton Res.* 26(2):1–15.
- Romero JR, Patterson JC, Melack JM. 1996. Simulation of the effect of methane bubble plumes on vertical mixing in Mono Lake. *Aquat Sci.* 58:210–223.
- Schrieber U, Neubauer C, Schliwa U. 1994. PAM fluorometer based on medium-frequency pulsed Xe-flash measuring light: A highly

- sensitive new tool in basic and applied research. *Photosynth Res.* 36:65–72.
- Verburg P, Antenucci JP. 2010. Persistent unstable atmospheric boundary layer enhances sensible and latent heat loss in a tropical great lake: Lake Tanganyika. *J Geophys Res.* 115, D11109. Doi:10.1029/2009JD012839
- Verburg P, Antenucci JP, Hecky RE. 2011. Differential cooling drives large-scale convective circulation in Lake Tanganyika. *Limnol Oceanogr.* 56:910–926.
- Whittington J, Sherman B, Green D, Oliver RL. 2000. Growth of *Ceratium hirundinella* in a subtropical Australian reservoir: the role of vertical migration. *J Plankton Res.* 22:1025–1045.