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

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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 (Pickrell 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 (McColl 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 McColl 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 it 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 McColl 1974). It has a single, dominant phytoplankton genus, Chlorella spp., and the insect invertebrate macrofauna is dominated by Chironomus zealandicus (McColl 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, Fo, was determined by stimulation with a weak probe light immediately following 15 min of darkness. The maximum fluorescence signal, Fm, was determined following the closure of all reaction centres by a 600 ms pulse of saturating irradiance. Variable fluorescence (Fv) was determined as the difference between Fm and Fo (Fv = Fm − Fo) and the variable fluorescence ratio was calculated as Fv/Fm.

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 corresponding depths. Fv/Fm 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

$$\frac{\Delta E}{\Delta t} = Q_g - Q_{ec} - Q_{hc} - Q_{nc},$$

(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

$$\frac{\Delta E_{H}}{\Delta t} = Q_m + Q_{sh} - Q_{eh} - Q_{sh} - Q_{ah},$$

(2)

The thermal balance below the thermocline during the day is

$$\frac{\Delta E_{HL}}{\Delta t} = Q_g - Q_m,$$

(3)

where $Q_g$ is the geothermal heat flux into the lower layer, $\Delta E_{HL}$ 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

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

(4)

where $\Delta T$ is the temperature difference between layers, $\rho$ is the water density, and $c_p$ is the heat capacity at constant pressure.

The surface fluxes $Q_s$, $Q_{eh}$, $Q_{sh}$, 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, $\Delta E$, 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.](image-url) (a) Air temperature (°C), relative humidity (%), and wind speed (m s⁻¹); and (b) Solar radiation (W m⁻²) and PAR (mmol m⁻² s⁻¹) measured with a meteorological station deployed on the north shore of Lake Rotowhero. WS = wind speed, RH = relative humidity, AT = air temperature, SR = solar radiation.
Results

Dissolved nutrients concentrations did not vary between basins or with depth. Mean NH\textsubscript{4}\textsuperscript{+} concentration was 1900 µg N L\textsuperscript{-1}, NO\textsubscript{3} was 2.0 µg N L\textsuperscript{-1}, and SRP was 45.5 µg L\textsuperscript{-1}, and the chlorophyll concentration was 45 µg L\textsuperscript{-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 relatively humidity was highest early in the day (Fig. 2a). Wind speed was <2 m s\textsuperscript{-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 1–2 °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);
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 ~1 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 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 (~70 °C) and the main basin (35.5–37.5 °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

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**Table 1. Components of the thermal budget; see equations 1–4. \(Q_{ec}\) = evaporative heat flux, \(Q_{sc}\) = sensible heat flux, \(Q_{ac}\) = net longwave radiation, \(Q_e\) = solar radiation, \(\Delta E\) = change in internal energy, \(t\) = time, \(Q_g\) = geothermal flux, \(w_e\) = rate of thermal transfer between layers, \(w_e\) = net entrainment velocity. See text for further details of variables.**

<table>
<thead>
<tr>
<th></th>
<th>cooling</th>
<th>heating upper layer</th>
<th>heating lower layer</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Q_{ec}) (W m(^{-2}))</td>
<td>−19</td>
<td>−52</td>
<td>n/a</td>
</tr>
<tr>
<td>(Q_{sc}) (W m(^{-2}))</td>
<td>−94</td>
<td>−70</td>
<td>n/a</td>
</tr>
<tr>
<td>(Q_{ac}) (W m(^{-2}))</td>
<td>−284</td>
<td>−258</td>
<td>n/a</td>
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<tr>
<td>(Q_{ot}) (W m(^{-2}))</td>
<td>0</td>
<td>691</td>
<td>n/a</td>
</tr>
<tr>
<td>(\Delta E/\Delta t) (W m(^{-2}))</td>
<td>−325</td>
<td>143</td>
<td>361</td>
</tr>
<tr>
<td>(Q_g) (W m(^{-2}))</td>
<td>72</td>
<td>n/a</td>
<td>72*</td>
</tr>
<tr>
<td>(Q_m) (W m(^{-2}))</td>
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<td>289</td>
</tr>
<tr>
<td>(w_e) (mm s(^{-1}))</td>
<td>n/a</td>
<td>0.08</td>
<td>0.13</td>
</tr>
</tbody>
</table>

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

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