

ORIGINAL ARTICLE

Impact of internal waves on the spatial distribution of *Planktothrix rubescens* (cyanobacteria) in an alpine lake

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The vertical and horizontal distribution of the cyanobacterium, *Planktothrix rubescens*, was studied in a deep alpine lake (Lac du Bourget) in a 2-year monitoring program with 11 sampling points, and a 24-h survey at one sampling station. This species is known to proliferate in the metalimnic layer of numerous deep mesotrophic lakes in temperate areas, and also to produce hepatotoxins. When looking at the distribution of *P. rubescens* at the scale of the entire lake, we found large variations (up to 10 m) in the depth of the biomass peak in the water column. These variations were closely correlated to isotherm displacements. We also found significant variations in the distribution of the cyanobacterial biomass in the northern and southern parts of the lake. We used a physical modeling approach to demonstrate that two internal wave modes can explain these variations. Internal waves are generated by wind events, but can still be detected several days after the end of these events. Finally, our 24-h survey at one sampling point demonstrated that the V1H1 sinusoidal motion could evolve into nonlinear fronts. All these findings show that internal waves have a major impact on the distribution of *P. rubescens* proliferating in the metalimnic layer of a deep lake, and that this process could influence the growth of this species by a direct impact on light availability.

The ISME Journal (2011) 5, 580–589; doi:10.1038/ismej.2010.154; published online 18 November 2010

Subject Category: microbial population and community ecology

Keywords: cyanobacteria; *Planktothrix rubescens*; seiches; spatial distribution; physical modeling

Introduction

The variability of the spatial distribution of cyanobacteria in freshwater ecosystems has stimulated little research despite its importance for both basic and applied purposes. Various physical processes can influence the spatial distribution of cyanobacteria, and most of them are linked to meteorological events. For example, Falconer *et al.* (1999) reported that the local cell density can increase by a factor of 1000 within few hours in response to the effect of wind. However, more complex physical processes, such as internal waves or seiches, can also generate large and persistent displacements of the water layers in stratified lakes (Mortimer, 1974; Lemmin and Mortimer, 1986).

Internal seiches, which have long been known to exist (Watson, 1904; Wedderburn, 1907), are standing waves on the interface between two fluid layers of differing density. They are generated by an initial displacement of the interface from the horizontal, caused by shear stress drag on the water surface. The surface water moves toward the lee shore and a corresponding rise of the isotherms occurs off the windward shore (Mortimer, 1952). After the wind stops, the water displacement relaxes resulting in oscillations of the isotherms, the amplitude of which is proportional to the inverse of the local density gradient. Once formed, the oscillations depend only on the geometry of the basin and will decay mainly as a result of the influence of friction on the shores. In large lakes, the Earth's rotation also affects the structure of internal seiches, as the Coriolis force imparts a transverse slope to the interface. This transverse motion added to the motion along the longitudinal axis results in an elliptic rotation of the water interface with the same period as the seiche itself, which is known as a Kelvin wave.

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Received 15 February 2010; revised 21 July 2010; accepted 23 July 2010; published online 18 November 2010

Seiches have been shown to have an impact on the structure of benthic algal communities (McCabe and Cyr, 2006), and on the spatial distribution of microalgae in the epilimnetic layer of the lake Constance (Gaedke and Schimmele, 1991) and of a reservoir (Marcé *et al.*, 2007). However, as far as we are aware, nothing has been published about their influence on the vertical and horizontal distribution of planktonic cyanobacteria. Among cyanobacteria proliferating in temperate areas, *Planktothrix rubescens* is characterized by its localization in the metalimnic layer of the water column of deep lakes. This species is particularly well adapted for growing at low light intensities and also at low temperatures (Oberhaus *et al.*, 2007) and has been found in many prealpine lakes (Walsby and Schanz, 2002; Ernst *et al.*, 2009). In addition, *P. rubescens* is able to produce microcystins (Briand *et al.*, 2005), which are dangerous hepatoxins that threaten both human and animal health (Kuiper-Goodman *et al.*, 1999; Briand *et al.*, 2003).

The goal of our study was to evaluate the impact of internal waves on the spatial distribution of *P. rubescens* in the Lac du Bourget. To do this, fortnightly monitoring of the cyanobacteria was performed for 2 years at 11 sampling stations. This spatial approach was completed by a 24-h monitoring cycle at a single sampling point. All these data were then used in a modeling approach, intended to elucidate the effects of internal waves on the vertical and horizontal distribution of the *P. rubescens* biomass in the lake.

Materials and methods

Study area and sampling strategy

Lac du Bourget is a monomictic lake located in France and the direction of the winds blowing over

its surface is essentially north-south. These winds can get quite strong (15 m s^{-1}), and are characterized by a 24 h period from June to October. During the stratification period (April–December), considerable internal wave activity is recorded in response to wind forcing (Bournet, 2000; Cuypers *et al.*, 2006). The most common internal response to wind stress is a tilt of the thermocline along the north–south axis of the lake. Spectral analysis of the isotherms has identified a combination of several internal seiche modes and the most energetic modes in Lac du Bourget (V1H1 and V2H1) have been characterized on the basis of long-term temperature records (1995–1996 and 2004–2005) (Bournet *et al.*, 1996; Bournet, 2000; Cuypers *et al.*, submitted). The V1H1 mode, associated with a vertical node at the thermocline depth and a horizontal node in the middle of the lake, is dominant. The V2H1 mode displays two vertical nodes at depths corresponding to the upper and lower limits of the metalimnion. During a large part of the stratification period, the V2H1 structure is altered significantly by the Earth's rotation, which creates a transverse motion of the interface. Indeed, the average Rossby radius reaches a typical maximum value of 1.5–2 km in summer and is therefore always smaller than the average lake width of 2.5 km (Cuypers *et al.*, submitted). In this case, the internal waves, known as Kelvin waves (K2), rotate counterclockwise around the lake basin. The V1H1 period is about 50–80 h in early spring, and decreases to approximately 24 h in July–August, whereas the V2H1 and K2 periods are longer (Supplementary Table 1).

A total of 11 stations (Figure 1) were sampled fortnightly during surveys conducted along one north–south transect and three east–west transects in 2002 and 2003. The duration of each field survey session was about 3 h, which is equivalent to one-eighth of the shortest seiche period observed in Lake

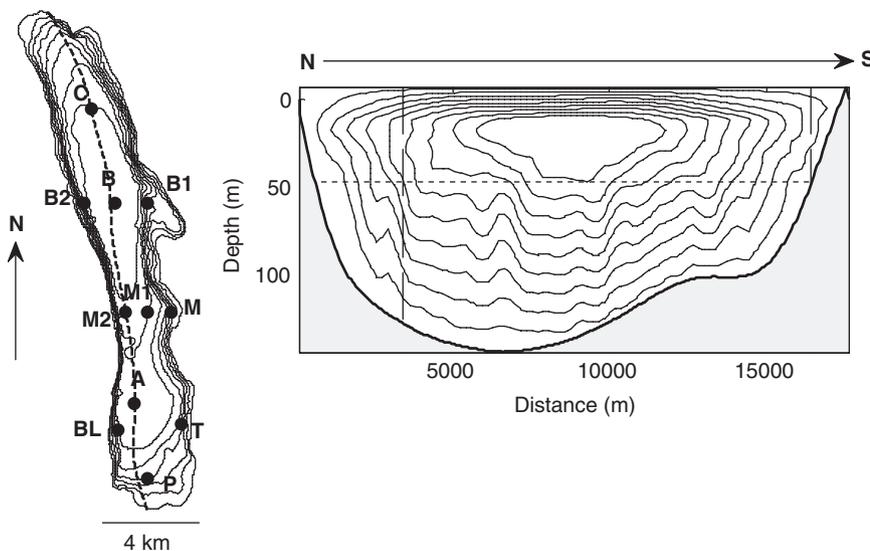


Figure 1 Mapping of the sampling points in Lake Bourget (left) during the 2002–2003 monitoring program and smoothed bathymetry profiles (right) along the thalweg (dashed gray line in the map).

Bourget (Supplementary Table 1), and so the survey provided a virtually synoptic view of seiche dynamics. At each sampling station, the BBE spectrofluoroprobe was used to estimate the vertical distribution of the biomasses of *P. rubescens*, other cyanobacteria, green algae and diatoms (Leboulanger *et al.*, 2002). All spectrofluoroprobe data profiles were first interpolated on a regular vertical grid with a slight smoothing using a 'loess' method (local-weighted regression). The new set of regularly spaced profiles was then linearly interpolated on a three-dimensional regular grid using Matlab Delaunay triangulation.

A 24-h cycle was also monitored in August 2003 at station T (Figure 1). Eight fluoroprobe profiles were measured at variable time intervals, on 19 August (1520, 1723, 1924 and 2117 h.) (day 231) and 20 August (0345, 0656, 0944 and 1235 h GMT) (day 232). Moreover, CTD profiles (SBE16, Sea-Bird Electronics, Inc., Bellevue, WA, USA.) were performed simultaneously. At the same station, temperature time series were provided from June to December 2003, by temperature sensors (resolution of 0.05 °C) located at five depths (three Starmon sensors, Star-Oddi (Reykjavik, Iceland) at 7, 9.5 and 11.5 m; two optodes, AADI (Bergen, Norway), at 8 and 13 m). The acquisition time step was 30 min.

Finally, water samples for cyanobacterial counts were taken at reference station 'B' (Figure 1) from seven depths (2, 6, 10, 15, 20, 30 and 50 m) and *P. rubescens* cellular abundance was estimated as described in Jacquet *et al.* (2005).

Water column stability

Dimensionless numbers have been developed for characterizing the hydrodynamics of lakes (Imberger and Patterson, 1990). The Wedderburn number (We), based on the two-layer representation of thermal stratification in the water column, provides a simple assessment of the response of the surface mixed layer to wind stress. We is defined as $We = (g'h^2)/u^{*2}L$, where g' , reduced gravity, is equal to $g\Delta\rho/\rho_o$, $\Delta\rho$ is the density difference across the pycnocline, ρ_o is mean density, g is gravity, h is the depth from the surface to the maximal density gradient, u^* is the friction velocity in water computed as $u^* = (\rho_a/\rho_w C_d U^2)^{1/2}$, where C_d is the drag coefficient, U the wind speed, ρ_a the air density, ρ_w the surface water density and L the length of the lake in the direction of the wind.

For $We \gg 1$, the tilting of the isopycnals will be slight, and the horizontal heterogeneity is negligible. For $We \ll 1$, a broad upwelling at the upwind end of the lake occurs. Intermediate We values ($We \sim 1$) correspond to near upwelling situations in which horizontal gradients are considerable. Furthermore, the maximum displacement of the isopycnal separating the upper and the lower layers, η_o , can be derived from the We (Heaps and Ramsbottom, 1966; Monismith, 1987; Bournet *et al.*, 1996) according

to the following equation: $We^{-1} = \eta_o/h$. For each field data set presented in the Results section, the damping with time and the amplitude of the thermocline tilting have been assessed according to Spigel and Imberger (1980).

Physical modeling

A simple physical model of the transportation of phytoplankton by internal seiche motion is proposed. In the first step, we assumed the internal seiche motion along the lake main axis to be that given by a two-dimensional linear, hydrostatic seiche model using the Boussinesq approximation (Münnich, 1996). Using this model, we obtain the pulsation ω and the stream function $\Phi_n(x, z)$ for each internal seiche mode, then we reconstruct the velocity as

$$\begin{aligned} V_{x,n} &= -\frac{\partial\phi_n}{\partial x} A \cos(\omega t + \varphi), \\ V_{z,n} &= \frac{\partial\phi_n}{\partial z} A \cos(\omega t + \varphi) \end{aligned} \quad (1)$$

where $V_{x,n}$ and $V_{z,n}$ are the horizontal and vertical velocities, t the time and, x and z the horizontal and vertical coordinates. The amplitude A and phase φ of the seiches have to be estimated from an analysis of field data.

The second step was to assume that phytoplankton are transported as a passive scalar, which was supported by field measurements and by data of Walsby (2005) on *P. rubescens* vertical migrations. We also ignored the vertical transportation of the cyanobacterium by turbulent diffusion, because *P. rubescens* is located near the thermocline, and because turbulent diffusion is usually very low in this area (Denman and Gargett, 1983).

Therefore, the equation for the transportation of a concentration $c(x, z)$ of passively advected phytoplankton in response to the motion induced by the velocity field associated with the n th mode is given by:

$$\frac{\partial c}{\partial t} = -V_{x,n} \frac{\partial c}{\partial x} - V_{z,n} \frac{\partial c}{\partial z} \quad (2)$$

This equation was solved numerically, using a very accurate pseudospectral method.

Results

Changes in the cell concentrations and in the distribution of *P. rubescens* in the lake

The evolution of *P. rubescens* cell concentrations at point B during this study is shown in Supplementary Figure 1. During the thermal stratification of the lake (from late spring to the end of September), *P. rubescens* was located in the metalimnetic layer and cellular concentrations remained below 2000 cells per l in 2002 and below 9000 cells per l in 2003. In October 2002, the *P. rubescens* cells were homogeneously distributed throughout the epilimnetic and the metalimnetic layers, and the

concentrations reached progressively 8000 cells per l. When destratification occurred from December 2002 to March 2003, the cells were mixed progressively down to the bottom of the lake and the maximal cell concentrations were observed in January (>10 000 cells per l). Very surprisingly, the cyanobacteria disappeared from the lake in late August 2003 and a green alga located just above the cyanobacteria, *Mougeotia gracillima*, dominated the phytoplanktonic community (data not shown).

Marked variations were found during the thermal stratification period, in the vertical distribution of the biomass of *P. rubescens*, depending on the geographic location of the sampling points in the lake. Figure 2 provides an illustration of the variations observed on 19 August 2003. The epilimnetic layer ('a' in Figure 2) was significantly thinner (Mann–Whitney *U*-test, $P < 0.05$) in the northern part of the lake than in the southern part. Moreover, the *P. rubescens* biomass peak ('b' in Figure 2) was significantly shallower (Mann–Whitney *U*-test, $P < 0.05$) at the points located in the northern part of the lake than at those in the southern part.

The peak of *P. rubescens* biomass was associated with the same isotherm throughout the lake at most of the sampling dates. For example, on 29 August 2002, there was a highly significant correlation ($P < 0.01$) between the depth of the 19.8 °C isotherm and the depth of the biomass peak at the 11 sampling stations (Figure 3). There was also a significant correlation ($P < 0.05$) between the depth of the 19.8 °C isotherm and the total integrated biomass of the cyanobacterial peak (Figure 3). These

two positive correlations suggested that *P. rubescens* was passively transported by the internal waves and that there was a link between the depth of the cyanobacterial peak and the biomass.

These variations in the horizontal distribution of *P. rubescens* were also clearly highlighted by a correspondence analysis performed on all the integrated *P. rubescens* biomass data obtained during the thermal stratification period. This analysis revealed a global opposition between the biomass values of samples from the northern part of the lake (C, B, B1 and B2 in Figure 1) and those of samples from the southern part of the lake (BL, P, T and A) (data not shown).

To confirm that daily variations occur in the depth and in the biomass of the *P. rubescens* peak, we performed a 24-h survey of the cyanobacteria in the water column at one sampling point in the lake in August 2003. We showed that the shape of the peak of *P. rubescens* biomass displayed major changes at the daily scale, both in the depth and in the maximum value of the chlorophyll concentration (Supplementary Figure 2). The depth of the biomass peak ranged from 12.4 m to 16.4 m, and the maximum concentration from 6 to 9 $\mu\text{g l}^{-1}$.

Effects of internal waves on the distribution of *P. rubescens* in the lake

The impact of internal seiches on the distribution of cyanobacteria and of green algae, as well as on the water temperatures was evident at several sampling dates. The Wedderburn number (*We*) and the corresponding maximum expected interface displa-

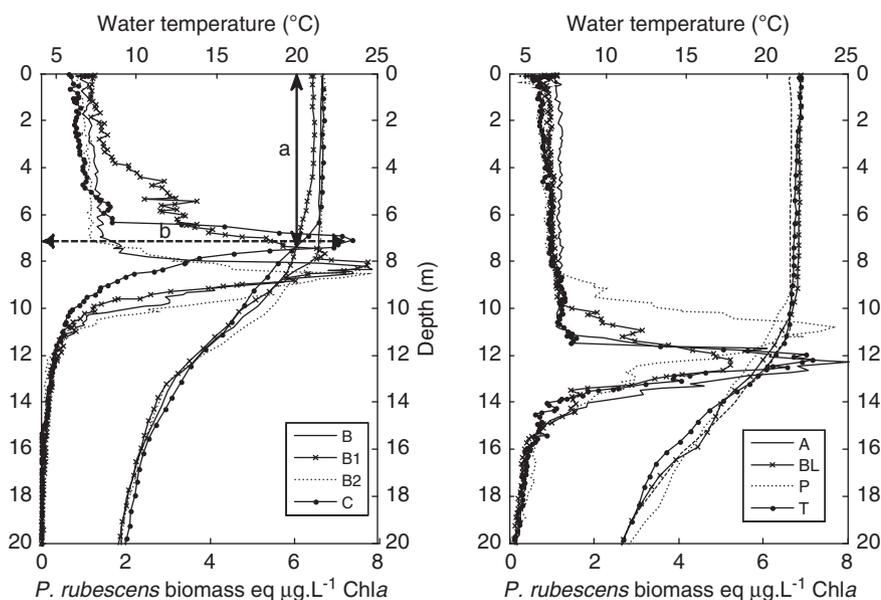


Figure 2 Vertical distribution of the *Plankthotrix rubescens* biomass and partial water thermal profiles in the north (left) and the south (right) of the Lac du Bourget measured using the BBE fluoroprobe on 19 August 2003.

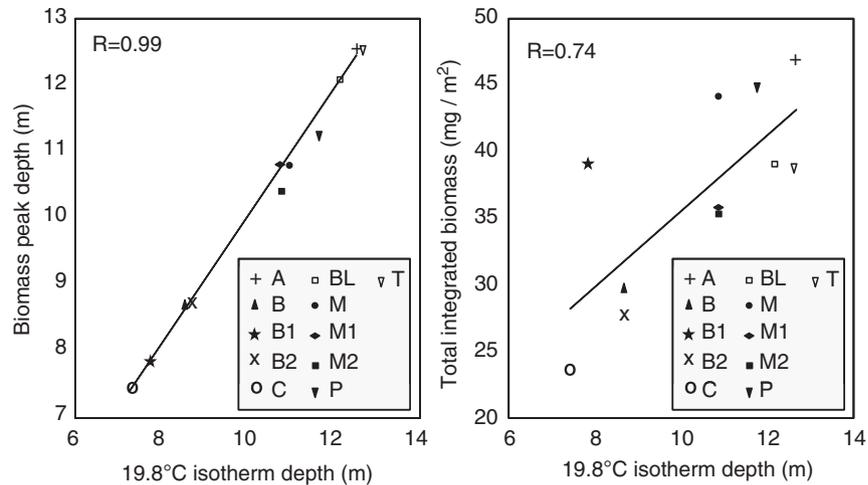


Figure 3 Correlations for one sampling date (29 August 2002) (1) between the depths of the peak of *P. rubescens* biomass and the depths of the 19.8 °C isotherm (left) and (2) between the 19.8 °C isotherm depths and the total integrated biomasses of the *P. rubescens* peak (right).

cement (η_0) have been plotted for the period around each sampling date (Supplementary Figure 3). From the high We values and low η_0 values found, it can be inferred that the observed tilting of the thermocline was generated by a wind event that had occurred some days before, and not by the piling up of the water at the upwind end of the lake generated by a strong wind event during the sampling day.

Evidence for V1H1 mode. Three examples that provide evidence for the impact of V1H1 mode on the location of the phytoplankton in the lake are provided in Figure 4 (a, b and c). On 25 April 2002, a tilting of the thermocline was detected in a north–south transect (Figure 4a) and most of the phytoplankton biomass was concentrated in the southern part of the lake. The north–south transect performed on 29 August 2002 (Figure 4b) also illustrates this V1H1 mode. The thermal stratification was more marked, and the tilting of the thermocline along the longitudinal axes was clearly defined. At this time, *P. rubescens* biomass remained fairly uniformly distributed from north to south in the metalimnic layer, but there was a difference of about 7 m in the depths of the cyanobacteria peak. During the sampling day, and also during the few days preceding it, wind speed was very low ($<1 \text{ m s}^{-1}$), and we estimated that any potential thermocline displacement directly induced by wind forcing would not exceed 1 m (Supplementary Figure 3c). This implies that the observed peak displacement of *P. rubescens* resulted from a seiche motion generated probably in the afternoon of 23 August. At this date, a strong wind burst reached 10 m s^{-1} , and generated a computed thermocline displacement (η_0) of 5.5 m, corresponding to a height difference of $2\eta_0 = 11 \text{ m}$ between north and south. A very similar situation

was encountered on 19 August 2003 (Figure 4c). *M. gracillima* was located in the epilimnetic layer just above *P. rubescens*. Owing to the lack of wind during the sampling day, we estimated that the seiche motion had very probably been induced by a 15-m s^{-1} wind on 13 August. The thermocline displacement was estimated to be equal to 10 m ($\eta_0 = 10 \text{ m}$ and $We^1 = 1$), which corresponds to a near-upwelling situation in which the thermocline reaches the surface of the lake at its upwind end. The seiche motion had been neatly damped between 14 and 19 August, leading to an estimate seiche amplitude of 3 m at the sampling date.

During the nychthemeral survey (2003), the variations in the depth of the *P. rubescens* peak of biomass closely paralleled those of the depth of the isotherms, and thus the wave motions. The observed maximum displacement of the thermocline and *P. rubescens* biomass was equal to 5.5 m, in agreement with the estimated seiche amplitude of 3 m found above. These variations were characterized by a rapid drop in the isotherm depth in the front of the wave (Supplementary Figure 4) and also in the depth of the peak of biomass (Figure 5). Moreover, large variations in the *P. rubescens* biomass were associated with wave motions. For example, 150% variation in the integrated biomass of *P. rubescens* was found to occur over an interval of just 6 h between day 232.2 and day 232.4 (Figure 5).

Evidence for K2 modes. On 30 July 2002, we found that the upper and lower isotherms defining the metalimnion in the north–south transect were tilting in opposite directions (Figure 4d), meaning that the metalimnic layer was thinner in the northern part of the lake than in the south. Similarly, the biomasses of *P. rubescens* and green algae located in the

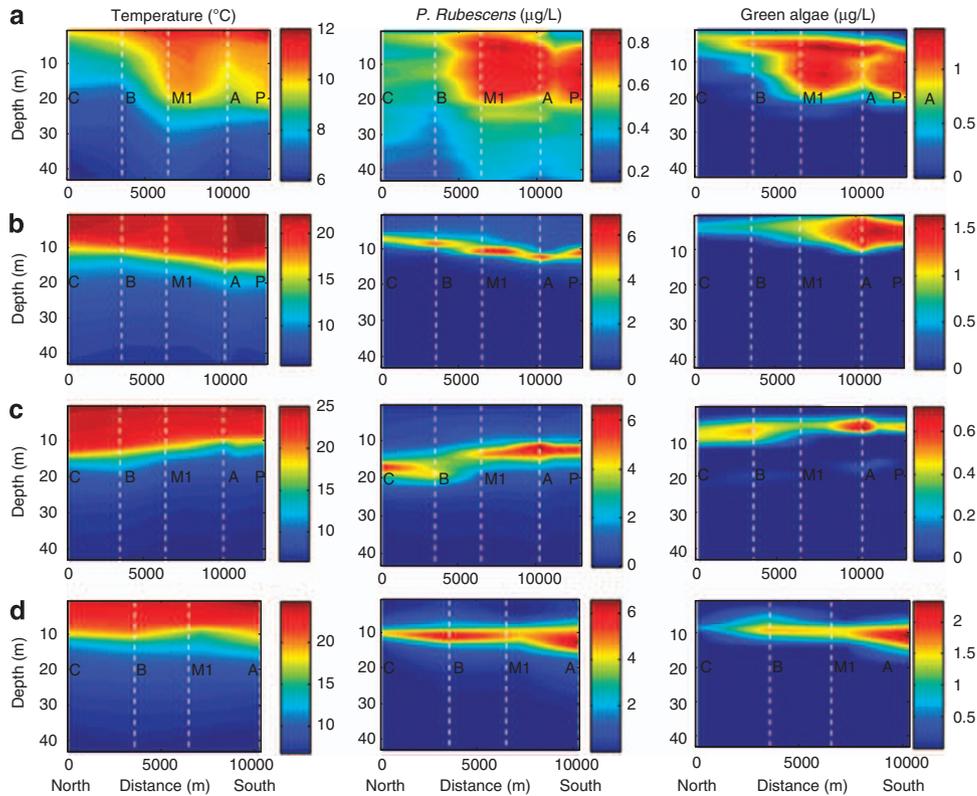


Figure 4 Two-dimensional transects of the temperature ($^{\circ}\text{C}$), and the distributions of cyanobacteria ($\mu\text{g Chl1}^{-1}$) and green algae ($\mu\text{g Chl1}^{-1}$) in the Lac du Bourget. (a): 25 April, 2002, north–south transect; (b): 29 August 2002, north–south transect; (c): 19 August 2003; north–south transect; (d): 30 July 2002, north–south transect.

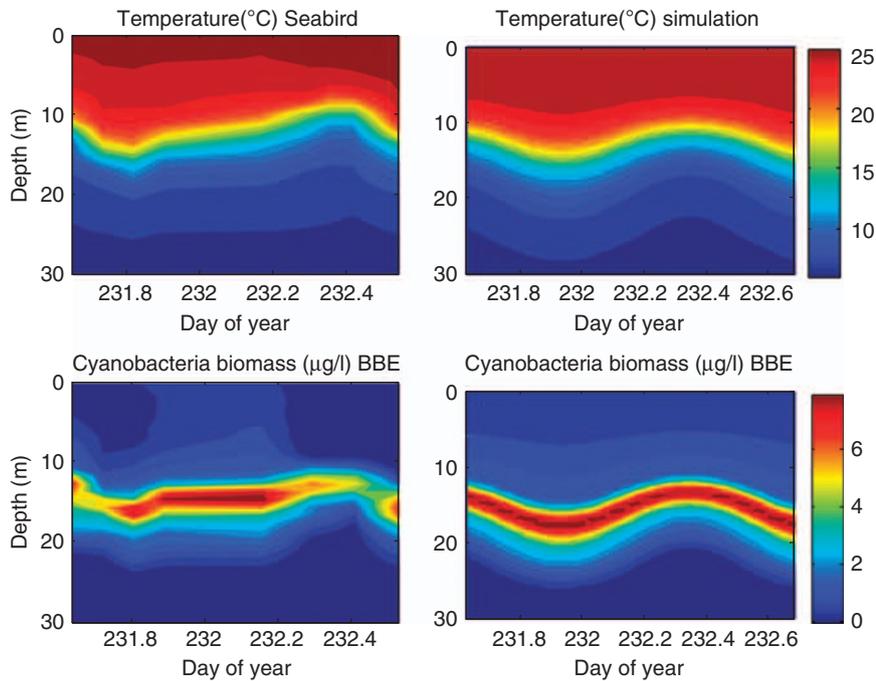


Figure 5 Nychthemeral measurements of temperature and cyanobacteria biomass at point T (left) and simulations of the temperature and of the cyanobacteria biomass (right) (day 231 = 19 August).

metalimnic layer appeared to be more abundant in the south. This pattern was characteristic of a vertical mode 2 with a single node on the horizontal

(V2H1) (Wiegand and Chamberlain, 1987). However, because of the long period of this mode (~ 70 h, Supplementary Table 1), the effect of rotation cannot

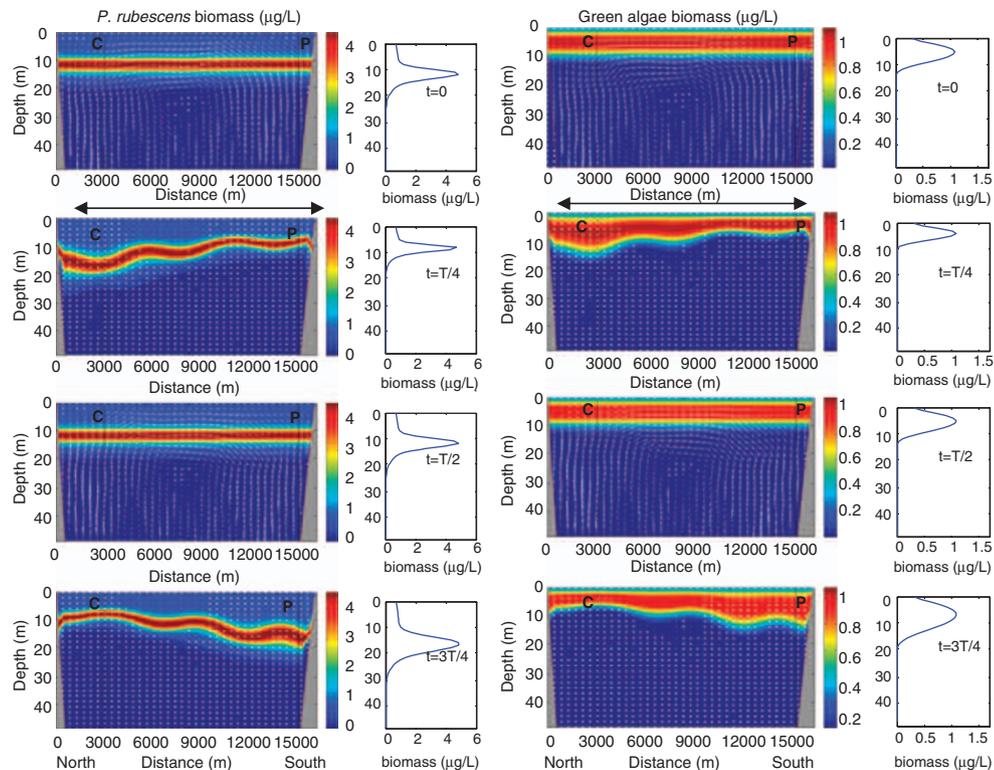


Figure 6 Model results simulating the spatial variations, along a north–south transect, of *P. rubescens* biomass and green algae biomass on 29 August 2002. C and P indicate the location of the farthest sampling stations in the north–south transect. The white arrows indicate the water velocities and directions. The right panels show the modeled depth distribution of cyanobacteria and green algae biomass (eq. $\mu\text{g Chl-}a\text{ l}^{-1}$) at sampling point T at time = 0, $T/4$, $T/2$ and $3T/4$.

be ignored, and the internal seiche would be expected to evolve as a progressive wave rotating counter clockwise around the lake (Cuypers *et al.*, submitted).

Numerical modeling of the movement of phytoplankton by the V1H1 mode

We applied our numerical model to simulate the spatial variations in the *P. rubescens* biomasses recorded on 29 August 2002 (Figure 4b). At this date, the variations of the spatial biomass distribution along a north–south transect seemed to be mainly driven by V1H1 motion, the linear tilting of the interface and cyanobacteria layer observed on transect data, suggests notably low deformation of the wave by nonlinear effect (as opposed to the case of 19 August 2003 discussed below). We therefore used the V1H1 mode for the simulation. The structure of the mode was fixed by the bathymetry profile (Figure 1) and by a density profile obtained by averaging the 11 density profiles measured on 29 August. The equations used to resolve the seiche motion were discretized on a 25×50 -point grid. The seiche amplitude was set to 3 m, based on field observations. Figure 6 shows the results of modeling the distributions of cyanobacteria and green algae at $T=0$, $T/4$, $T/2$, $3T/4$, with a 17.25 h period for the V1H1 mode. The model provided a good simulation of the vertical displacement of the cyanobacterial peak along the north–south transect between sampling points C and P (Figure 4b). Moreover,

vertical displacements induced horizontal water transportation as the epilimnion thickened or narrowed, leading to vertically integrated biomass variations of $\pm 50\%$ of the initial ($t=0$) integrated biomass concentration. For the green algae, the model reproduced an accumulation in the northern part of the basin at $t=T/4$ and in the southern part at $t=3T/4$, simultaneously with thickening of the epilimnion. However, according to the field data, the increase in biomass was in fact much higher (Figure 4b). This discrepancy may have resulted from existing of horizontal heterogeneity, with higher concentrations being found at the southern end independently of the seiche effect.

A similar simulation of the V1H1 mode was tested against nychthemeral cycle data, and provided clear evidence that such a mode was indeed present. Determination of the amplitude and phase of the V1H1 motion was obtained by fitting a sinusoidal motion to the 20.5°C isotherm time series at point T. The model was initialized with the temperature and cyanobacterial biomass measured at point T on 20 August (0345 h) 2003. The general form of the reconstructed V1H1 phase and amplitude displacement matched the 20.5°C isotherm displacement shown in Figure 5. However, this displacement differs from a sinusoidal motion, and looks more like an asymmetric saw-tooth signal, with a slow rise and abrupt fall of the isotherm, suggesting the effect of nonlinear processes. In the same way,

the simulated variations in the peak position of *P. rubescens* generally fit well with the measured values, although the simulation did not reproduce the rapid drop found in the two-wave fronts (33% for day 231.7 and 60% for day 232.3). Moreover, the simulation displayed smaller and much smoother biomass variations ($\pm 15\%$). Low biomasses were associated with slight compression of the isotherms corresponding to the maximum wave elevation, whereas maximum biomass values were associated with the minimum wave elevation and a slight dilatation of the isotherms.

Discussion

This paper clearly demonstrates for the first time that *P. rubescens*, which lives in the metalimnetic layer of deep alpine lakes, displays marked heterogeneity in its vertical and horizontal distribution, and that this heterogeneity is attributable to the impact of internal waves generated by winds blowing over surface of the lake. It has long been known that the spatial distribution of phytoplankton species is driven by interactions between physical and biological processes (Fietz *et al.*, 2005; Hillmer *et al.*, 2008) and that wind has an important role in these physical processes (George and Heaney, 1978; Schernewski *et al.*, 2005; Moreno-Ostos *et al.*, 2008; Alexander and Imberger, 2009; Pobel *et al.*, in press). However, all existing knowledge was mainly based on the study of phytoplankton communities living in the well-mixed epilimnetic layer, the spatial distribution of which is affected by direct forcing by the wind. Very little was known about species occupying deeper layers, and in particular the metalimnetic layer of deep stratified lakes.

Seiches have an impact on both the vertical and the horizontal distribution of *P. rubescens* in the lake. The depth of the peak of biomass can vary up to 10 m at a given sampling point within a single day, or between different sampling stations in the lake at the same time. At the horizontal scale, there was contrast between *P. rubescens* biomasses in the northern and southern parts of the lake, that is, when high biomasses were found in the northern part, low biomasses were present in the southern part, and *vice versa*. We also found that the effect of internal waves persisted for several days after the end of a high-wind event, and this has been confirmed by recent data obtained by a buoy equipped with various different sensors (Le Vu *et al.*, 2010) showing that internal waves can be detected throughout the stratified period of the water column. This finding suggests that *P. rubescens* is subjected to the impact of seiches throughout its development in the metalimnetic layer from the lake from April to late September.

Similar findings have been already reported for cyanobacteria living in the top few meters of the water column (Olsen *et al.*, 2000; Welker *et al.*, 2003) and more generally, several papers have highlighted

horizontal mass transfers occurring in phytoplankton and zooplankton communities living in the epilimnetic layer (Verhagen, 1994; Rinke *et al.*, 2007; Serra *et al.*, 2007). However, the main difference between this direct impact of the wind on phytoplankton and its indirect impact through internal waves is that the impact of internal waves persists for several days after the end of the wind event.

Our modeling approach has provided a better understanding of the factors that determine the variations in the distribution of *P. rubescens* cells. The VIH1 mode was clearly associated with the vertical displacements of the peak of biomass in the water column. However, as the nychthemeral monitoring data show, the presence of nonlinear internal processes seems to entrain an abrupt fall of the biomass peak, and the linear standing V1H1 seiches seem to evolve into internal fronts as previously observed in Lac du Bourget (Cuypers *et al.*, 2006; Cuypers *et al.*, submitted). The abrupt wave front is associated with a marked depletion of biomass and shows the strong impact of nonlinear effect on the biomass distribution by strong mixing (Macintyre *et al.*, 2009). As shown by Horn *et al.* (2001), the conditions required to generate nonlinear fronts may frequently occur in lakes as soon as the seiche amplitude becomes comparable to the epilimnion width. This was the case in the Lac du Bourget in August 2003. This process was not taken into account by the model described here, and this probably accounts for most of the differences observed between our simulated results and field data.

With regard to the heterogeneity in the horizontal distribution of biomass, vertical mode-2 seiches, such as the K2 mode, are characterized by periodic compression and dilatation of the metalimnion, and a corresponding velocity maximum near the thermocline. This mode is therefore, the one that could induce the largest biomass transfer of a metalimnetic species such as *P. rubescens*. In the Lac du Bourget, vertical mode-2 seiches take the form of rotating Kelvin waves, and they occur frequently (Cuypers *et al.*, submitted). The 30 July 2002 sampling provides a good illustration of the impact of this mode on the *P. rubescens* biomass, with compression of the isotherms at the northern end of the lake and dilatation at the southern end, and corresponding marked biomass depletion at the northern end and accumulation at the southern end. Our numerical model provides an approximate assessment of the longitudinal north–south variations in temperature and biomass. However, this model does not take the Earth's rotation into account, and so it cannot reliably simulate the three-dimensional temperature and biomass fields.

Vertical displacements of the peak *P. rubescens* biomass generated by seiches might have a potential impact on the growth of this species in the metalimnetic layer. Indeed, depending on the depth of the peak biomass in the water column, the

amount of light available differs considerably, which could potentially influence the growth rate of the cyanobacteria. Recently, the enhancement of photosynthesis induced by internal waves has been thoroughly investigated by Evans *et al.* (2008), who used both experimentation and modeling to demonstrate that internal waves, combined with surface irradiance can cause marked increases or decreases in photosynthesis. In addition to their impact on the availability of light, internal waves could also influence that of nutrients, as evidenced for example in Lake Kinneret (Nishri *et al.*, 2000). In the benthic boundary layer, the higher nutrient concentrations associated with a greater turbulence could be sufficiently great to generate biogeochemical fluxes, which would then be transported horizontally to the pelagic area.

To conclude, we have shown here that in the Lac du Bourget, hydrodynamic processes generated by wind have a major impact on the two-dimensional distribution of the *P. rubescens* biomass, and probably on the population dynamics of this species. From a practical point of view, our findings suggest that because of horizontal variations in the *P. rubescens* biomasses, monitoring programs for the survey of this toxic species should be based on, at least, two sampling points, located in the northern and southern parts of the lake. Moreover, the impact of internal waves on the depth of the peak of cyanobacteria in the water column must be taken in account to evaluate the risk of contamination of drinking water, which is pumped at 30 m depth.

Acknowledgements

We would like to thank B Le Berre, S Jacquet and G Paolini for their contribution to the *P. rubescens* sampling programs in Lac du Bourget and Monika Gosh for improving the English text. This work was part of the Sacytox project, funded by the RITEAU program (French Ministry of Ecology and Sustainable Development) IGP 3014.

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