

Short-term variability in physical forcing in temperate reservoirs: effects on phytoplankton dynamics and sedimentary fluxes

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SUMMARY

1. The effects of wind events on phytoplankton dynamics were investigated in two temperate reservoirs.
2. Meteorological forcing, change in physical and chemical structure of the water column and biological responses of phytoplankton communities were followed for 3 weeks in three seasons.
3. Depending on the season, the phytoplankton response differed in response to nutrient and light conditions, and to the intensity of stratification and mixing.
4. We demonstrated that, on a time scale of a few days, wind events can modify phytoplankton dynamics, in terms of size structure and exported biomass. An increase of mixing favoured the largest size class and disadvantaged the smallest size class, while an increase in stratification had the opposite effects. The short-term change in size structure was reflected in the sedimentary fluxes but with a time lag.

Keywords: sedimentary fluxes, size-fractionated biomass, wind

Introduction

It is well known that seasonal phytoplankton dynamics are controlled by physical and chemical forcing and biotic interactions (Sommer *et al.*, 1986; Noges *et al.*, 1998; Anneville *et al.*, 2002), the dominant physical and chemical factors being temperature, solar radiation, nutrients, mixing and stratification (Richardson, Gibson & Heaney, 2000). On a shorter time scale, several studies have demonstrated that forcing variables such as wind also modify the physical structure of lakes (Podsetchine & Schernewski, 1999; Botte &

Kay, 2002). From a few hours to a few days, the vertical structure can thus be changed, in particular the depth of the mixed layer, the intensity of mixing, the thermal gradient and the stratification state (Imberger & Parker, 1985; Carmack *et al.*, 1986; MacIntyre & Jellison, 2001; Talling, 2004). These physical modifications take place on a similar time scale to the growth rate of phytoplankton and thus may affect the phytoplankton community over a few days (Nixdorf, Mischke & Rucker, 2003). These short-term changes in physical forcing because of wind we call 'events'.

To our knowledge, very few studies have been performed on the short-term response of freshwater phytoplankton to rapid variations in physical forcing. Short-term variability of physical forcing can, however, modify on a daily time scale several factors that directly influence the vertical distribution and consequently the dynamics of phytoplankton. For example, wind events can increase both the intensity of mixing and the depth of the mixed layer. Mixing can decrease the vertical flux of phytoplankton by redistributing

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the populations in the water (Huisman & Sommeijer, 2002b) and also by keeping cells within the euphotic layer. Sedimentation losses are also influenced by the depth of the mixed layer (Ptacnick, Diehl & Berger, 2003): the deeper the mixed layer, the lower the loss to sedimentation. Moreover, loss rate by sedimentation increases with cell size and a loss rate exceeding growth rate leads to the extinction of the population (Huisman, Van Oostveen & Weissing, 1999). The decrease of sedimentary loss because of both increases in mixing and mixed layer depth may thus favour populations of large and non-buoyant cells. Cells, which can regulate their buoyancy to remain at their optimal depth in terms of light availability, are likely to lose their vertically advantageous position and may be disadvantaged by such events. At the community level, increase of mixing may thus favour large sinking cells and be unfavourable for small or buoyant cells. A wind-forced event may also increase nutrient supply, in particular to the euphotic layer, by breaking down a nutricline or by lateral nutrient advection from shallower areas. Species, with high nutrient requirements, may increase in response to such nutrient influxes, depending on the background nutrient level. At the cellular scale, nutrient fluxes induced by an increase of small-scale mixing can also favour large cells, because of a decrease in the thickness of the boundary layer (Karp-Boss, Boss & Jumars, 1996; Metcalfe, Pedley & Thingstad, 2004). By keeping cells within the euphotic layer, reducing their sedimentary loss and increasing nutrient fluxes, we can expect events to increase the concentration of large

sinking cells, on a daily time scale, resulting in higher production and an increase of biomass. The standing stock biomass of large sinking cells being higher, sedimentary fluxes can also be expected to increase.

Our objective is to determine the influence of wind events on the short-term dynamics of phytoplankton, in terms of fluxes (production, stock and exported production to the sediments) and to discover whether such events favour large sinking cells. We thus compare the short-term dynamics of the phytoplankton communities divided into three size classes, coupled with exported biomass, from two temperate reservoirs which differ in their exposure to events. The effect of season is also determined by sampling one of the reservoirs during all phytoplankton growing seasons.

Methods

Study sites

Two temperate reservoirs located near Rennes in Brittany (France) were studied (Fig. 1): La Cheze and Rophemel are both channel-type reservoirs. La Cheze is larger and deeper than Rophemel (Table 1). At the sampling sites, La Cheze is about 25 m deep and Rophemel 16 m deep.

The reservoirs also differ in their exposure to wind. La Cheze is mostly exposed to wind forcing, its open-water mass being oriented in the main wind direction, South-East (Fig. 1). The drainage basin of La Cheze is also very flat, compared with the steep basin of Rophemel. Rophemel is characterised by a large

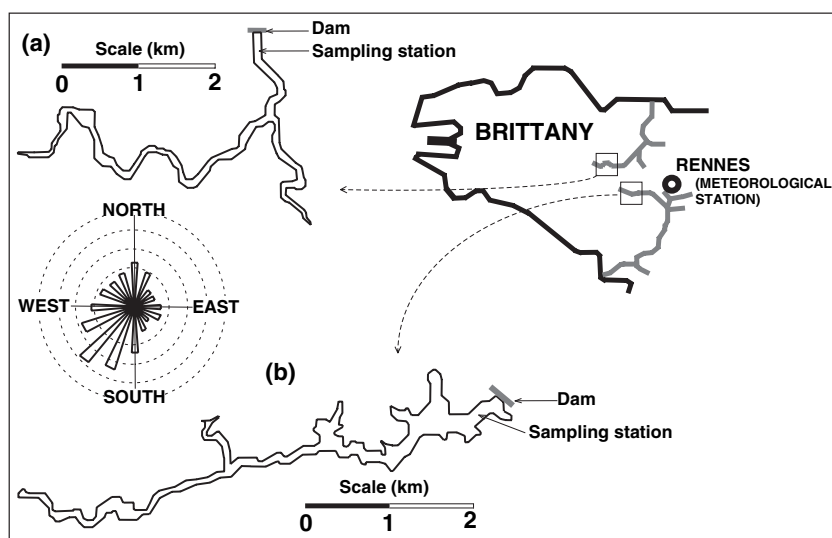


Fig. 1 Geographic location of the two reservoirs and the Meteo France station and maps of (a) Rophemel and (b) La Cheze reservoirs (dams and sampling stations are indicated). The wind rose summarises local wind direction over 4 years (1999–2002) using Meteo France data.

Table 1 Characteristics of the two reservoirs

Sites	La Cheze	Rophemel
Latitude Longitude	48°01'300"N 01°57'450"W	48°18'920"N 02°03'540"W
reservoir volume (m ³)	1.47 × 10 ⁷	5 × 10 ⁶
Surface area (km ²)	1.07	0.77
Mean depth (m)	13.7	6.5
Fetch (m)	900	120
Collecting area (km ²)	30	380
Residence time	3 month to 1 year	1 week to 1 month
Mean concentration of total P in spring	0.028 ± 0.004	0.048 ± 0.004

catchment area (380 km²) which is more than 400 times larger than the area of the lake, leading to a residence time of between 1 and 4 weeks (Table 1). The drainage basin of La Cheze is much smaller, only 30 km² (Table 1) or thirty times the area of the reservoir, leading to a longer residence time of between 3 months and 1 year (Table 1). The nutrient load at Rophemel is larger than at La Cheze because of high nutrient inputs (Table 1).

Data collection

La Cheze was sampled in summer (20 June 2003 to 14 July 2003), autumn (22 September 2003 to 14 October 2003) and spring (24 March 2004 to 15 April 2004). Rophemel was sampled only once, in spring (5 May 2004 to 24 May 2004). For each period, reservoir sampling was performed in the morning (09:00 hours) every 2 or 3 days for 14–19 days. One sampling site was chosen for each reservoir, a few hundred meters from the outlet of the reservoir and in the vicinity of the old river bed but remote from tributaries. Water samples were collected using a one-meter integrated vertical sampler (single valve bailer) at four depths (1, 7, 13 and 21 m for La Cheze and 1, 5, 9 and 14 m for Rophemel).

Physical parameters

Meteorological data were monitored by Meteo France in Rennes, about 30 km from both sites (Fig. 1). Wind speed and direction at 10 m above the ground, global solar radiation and mean air temperature were averaged daily from hourly data, while rainfall was measured daily in mm.

To characterise the physical structure of the reservoirs, temperature profiles were used to determine the

depth of the mixed layer, Z_M , which was approximated as the depth of maximum thermal gradient. Temperature, dissolved oxygen and fluorescence profiles were measured every meter for 30 s with an YSI probe environmental 6920 (15 readings per minute) (Anhydre, Vireux Molhain, France). Surface current velocities, measured about 0.5 m below the surface, were measured with a 2D-acoustic current meter probe (one data per second, with ±2% of accuracy) (Falmouth Scientific Inc., Acthyd SAS, Evry, France). An instantaneous irradiance profile was measured every meter with a LiCor PAR sensor (Eurosep Instruments, Cergy Pontoise, France). This profile of photosynthetically active radiation (PAR) was used to determine the light extinction coefficient K_d and the euphotic depth, defined as the depth with 1% of incident light, using Beer-Lambert's law. However we used the measured meteorological data to compute daily average solar radiation (being more representative than the instantaneous PAR profile) and converted it to mean PAR at the water surface I_0 using the correction factor of 0.45 (Nixdorf *et al.*, 2003). The daily PAR, \bar{I}_{ZM} , received on average by phytoplankton over the mixed layer, Z_m , was calculated by integrating the light profile as follow:

$$\bar{I}_{ZM} = \frac{1}{Z_m} \int_0^{Z_m} I_0 e^{-K_d z} dz$$

The stratification state of the water column is defined by measuring potential energy, which represents the quantity of energy needed to homogenise the entire water column (Lagadeuc, Brylinski & Aelbrecht, 1997). Potential energy PE (J m⁻³) is expressed as:

$$PE = \frac{1}{h} \int_0^h [(\bar{\rho} - \rho)gz] dz$$

with the mean density $\bar{\rho}$:

$$\bar{\rho} = \frac{1}{h} \int_0^h \rho dz$$

where ρ (kg m⁻³) is the density at the depth z , h the total depth of the water column (m) and g the gravity (m s⁻²) (Simpson *et al.*, 1979). Potential energy, which is a stabilising force, is opposed to the energy input by wind, which destabilizes the reservoir. To define how the energy input by wind is available to increase

mixing and the depth of the mixed layer, we used the vertical wind energy flux in $W\ m^{-2}$ (E_{10}) induced by wind. This index is calculated as (Kocsis *et al.*, 1998; Wuest, Piepke & Van-Senden, 2000):

$$E_{10} \approx \rho_a C_{10} U^3_{10}$$

where ρ_a is the air density ($1.25\ kg\ m^{-3}$), U_{10} the mean wind speed ($m\ s^{-1}$) measured 10 m above water and C_{10} the drag coefficient equal to 0.001 (Kocsis *et al.*, 1998).

Chemical parameters

Five dissolved nutrient parameters were measured using colorimetric methods: ammonium (Rossum & Villaruz, 1963), nitrite and nitrate (Barnes & Folkard, 1951), soluble reactive phosphorus (Murphy & Riley, 1975) and silicon (Rodier, 1978). Suspended matter in $mg\ DW\ L^{-1}$ was measured on Whatman GF/F glass-fibre filter after drying at $105\ ^\circ C$ (Noges *et al.*, 1999).

Biological parameters

Phytoplankton biomass and photosynthetic capacity were fractionated into three size classes (large, medium, small), by serial filtration on $20\ \mu m$ mesh, $5\ \mu m$ mesh and Whatman GF/F glass-fibre filter ($0.7\ \mu m$), following the methods in many marine studies (Rodriguez & Guerrero, 1994; Marañón *et al.*, 2001; Pesant *et al.*, 2002). Chlorophyll *a* was also measured with one filtration on Whatman GF/F and compared with the sum of the three components of the fractionated biomass: the sum of the three fractionated components and the total biomass were not significantly different, so the proportion of biomass lost by the fractionation is considered negligible. Concentrations of size-fractionated chlorophyll *a* were determined after extraction in 90% acetone overnight using the method of Lorenzen (1967). Size-fractionated primary production was measured by ^{14}C incorporation (Steemann-Nielsen, 1952) and postincubation filtrations. To avoid photo-acclimation and change of physiological parameters, incubations of 40 min were done during the hour following sampling in an incubator with a light gradient (Lizon & Lagadeuc, 1998). Primary production was divided by the chlorophyll concentration to give the photosynthetic capacity per unit of biomass for each size class. Platt's model of photosynthesis was then used to determine the physiological parameters to fit

these data, in particular the light saturated photosynthesis (Platt, Gallegos & Harrison, 1980).

Species composition and abundance of mesozooplankton were estimated and reported in number of individuals per litre. Sampling was done about once a week and zooplankton was fixed with a formaldehyde solution (5%). Samples were integrated from 2 m above the sediments to the surface using a $50\ \mu m$ mesh net.

Downward fluxes were estimated by sediment traps, with four replicates, placed below the mixed layer over a period of 3 weeks according to the method described by Weyhenmeyer & Bloesch (2001). Traps were made with polyvinyl chloride (PVC) pipes, $22.5\ cm^2$ surface area and a ratio of height to diameter equal to 6, to limit resuspension (Weyhenmeyer, 1996). The sediment was collected every 2 or 3 days, thus avoiding the use of preservative, and sediment was characterised in terms of chlorophyll *a* which represents fresh sinking phytoplankton, in terms of pheopigment which is more representative of flux induced by grazing and dying cells and in terms of dry weight mass which characterizes the global flux. The composition of the flux in carbon and nitrogen was also measured with a Perkin-Elmer 2400 Series II CHN Analyser (Perkin-Elmer Corporation, Norwalk, CT, U.S.A.), according to the method of Yoshida *et al.* (2003). Chlorophyll flux was converted to nitrogen flux, using the ratio of Stumm and Morgan (Reynolds, Irish & Elliott, 2001): 50 g carbon/8.3 g nitrogen/1.2 g phosphorus/1 g chlorophyll. The use of this ratio assumes that all species have the same stoichiometry in terms of carbon, nitrogen, phosphorus and chlorophyll. It also assumes that cells grow in well-resourced and constant conditions. We thus considered there was $8.3\ g\ N\ (g\ chl\ a)^{-1}$ in the traps, using the above ratio. To determine the proportion of the living proportion (biogenic flux) in total sedimentary flux, the result was divided by the total flux of nitrogen measured by the CHN analyser. Lastly sinking rates ($m\ day^{-1}$) were estimated by dividing the observed sedimentary fluxes in chlorophyll ($mg\ chl\ a\ m^{-2}\ day^{-1}$) by the biomass in the mixed layer ($mg\ chl\ a\ m^{-3}$).

Integration over the mixed layer and multivariate analysis

The results of the four depths analyses were used to calculate an integrated value over the mixed layer and

over the hypolimnion using a four layer model. Each layer was assumed to be homogeneous in terms of temperature, nutrient concentration, fractionated biomass and photosynthetic capacity. The thickness of each layer was determined by fitting the temperature profile based on four values corresponding to the four depths with the temperature profile measured every meter. This allowed the integration of chemical and biological parameters over the entire water column or over the mixed layer, without hypsographic correction, as we considered that the vertical variability of the water column predominated over the spatial one. To estimate the mean temperature, light and nutrient availability associated with seasonal variability, values were also averaged over time for each sampling period.

A principal component analysis (PCA) was undertaken to determine spatial and temporal changes of physical and chemical conditions. The analysis was performed on temperature, potential energy, mixed layer depth, irradiance and nutrients (silicon, nitrate and phosphorus) data.

Results

Seasonal variability of the environmental conditions

The PCA, performed on physical and chemical data summarizes the seasonal context, in terms of stratification and resource availability for each period, with more than 80% of the data variability explained by the first two axes (Fig. 2). The first axis separates stratified nutrient-depleted conditions in summer (Cheze in summer) and early autumn (Cheze in autumn) and well-mixed nutrient-replete conditions in spring (Rophemel and Cheze in spring); the second axis separates high light availability because of strong solar radiation in late spring (Rophemel) and summer (Cheze in summer) and low light availability because of low solar radiation and a deep mixed layer in early spring (Cheze in spring) and autumn (Cheze in autumn). To characterise resource availability in the mixed layer, observed values were compared with reported 'critical' values of $10 \mu\text{g P L}^{-1}$, 0.3 mg N L^{-1} (Wetzel, 2001) and 0.5 mg Si L^{-1} (Reynolds, 1984) for nutrient concentrations and $5 \mu\text{mol photons s}^{-1} \text{ m}^{-2}$ for light received by cells over the mixed layer (Millard *et al.*, 1996), as potentially limiting for growth. Below these critical values, some species potentially limited by

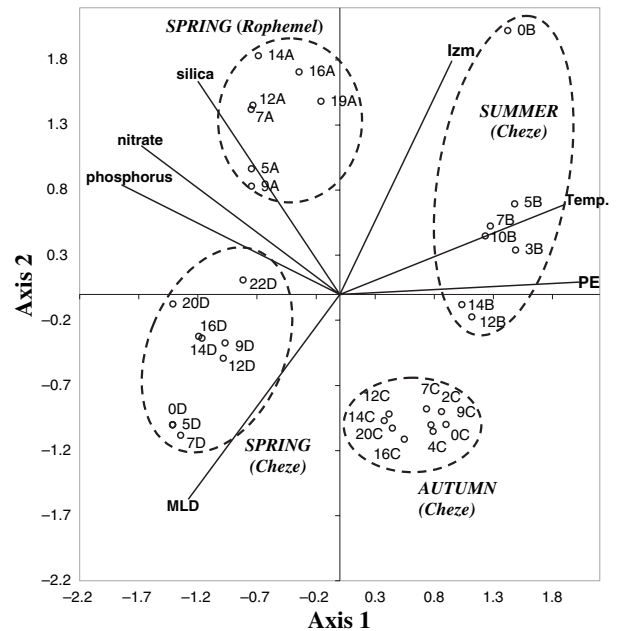


Fig. 2 Principal Components Analysis of physical and chemical parameters: Temperature (Temp.), potential energy (PE), depth of the mixed layer (MLD), nutrients (silicon, phosphorus and nitrate) and mean irradiance in the mixed layer (Izm) for the four periods (notation: time in days since the beginning of the study followed by A, Rophemel; B, La Cheze in summer; C, La Cheze in autumn; D, La Cheze in spring).

a resource may respond to a sudden increase of this resource by an increase in growth rate which may, in turn, be reflected in the size structure or the sedimentary fluxes. The four sampling periods were thus distinguished in terms of resource conditions, with two periods potentially limited by one resource: La Cheze in summer was limited by nutrient and La Cheze in spring was limited by light. One period was potentially limited by both light and nutrient (La Cheze in autumn) and one period was not limited at all (Rophemel in spring).

The predatory community was also seasonally variable. Zooplankton community structure is represented for Rophemel and La Cheze and for each period on Fig. 3. Cladocerans were more abundant than copepods in spring, both at Rophemel and La Cheze (Fig. 3). Copepods, dominated by *Eucyclops* sp., were present all year-round and at both sites, with a density always lower than $20 \text{ individuals L}^{-1}$ (Fig. 3). During the four sampling periods, *Bosmina longirostris* (O.F. Mueller) was the dominant cladoceran, except at La Cheze in early spring where *Daphnia* sp. had a similar

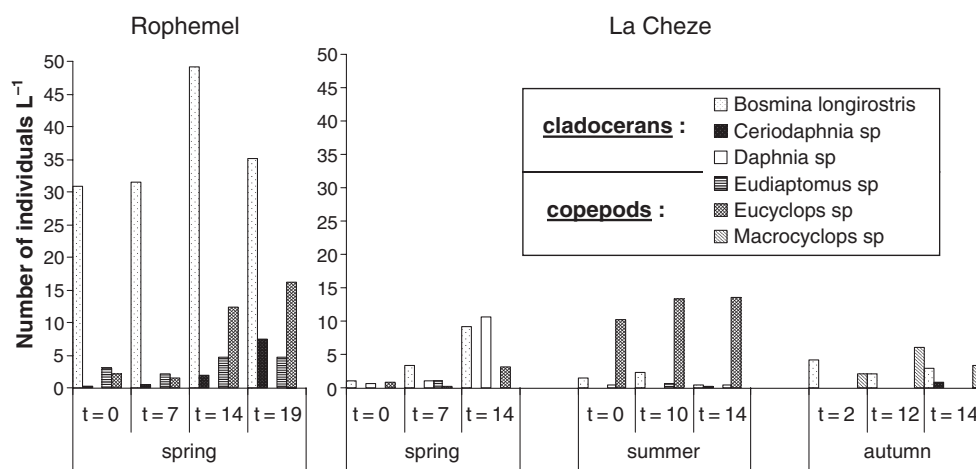


Fig. 3 Abundance of the dominant zooplankton species for the four sampling periods in terms of time t in days from the beginning of the period.

density, with on average 10 individuals L^{-1} (Fig. 3). At Rophemel, the density of *B. longirostris* in late spring reached at least 30 individuals L^{-1} (Fig. 3).

Seasonal variability of the phytoplankton community

Total phytoplankton biomass at Rophemel was higher than at La Cheze, with on average 13.1 μg chl a L^{-1} (Table 2), because of a higher trophic status. The contribution of size classes to biomass varied with season, but the medium size class always remained low, with a mean chlorophyll a concentration of $<0.7 \pm 0.6$ μg chl a L^{-1} (Fig. 4). Therefore only the largest and the smallest size classes will be discussed further, the former representing buoyant colonies or

sinking cells depending on the season. The large size class represented on average from 13.2% to 61.3% of total biomass, whereas the small size class represented from 25.6% to 76.9% (Fig. 4). Dominance by the large size class was observed only in autumn (Fig. 4), representing 4–5 μg chl a L^{-1} , while in summer at La Cheze the concentration of large cells remained lower than 1 μg chl a L^{-1} (Fig. 5a). Concentrations of small cells were maximal at Rophemel, with values between 4 and 16 μg chl a L^{-1} , whereas at La Cheze, concentration of small cells was always lower than 4 μg chl a L^{-1} (Fig. 5b).

The maximal photosynthetic capacity of large cells was on average (\pm SD) 1.2 ± 0.6 mg C mg chl a^{-1} h^{-1} when all data from both reservoirs are combined

Table 2 Characteristic values of physical, chemical and biological parameters for each sampling period (mean value \pm standard deviation)

	Rophemel, spring 2004	La Cheze, spring 2004	La Cheze, summer 2003	La Cheze, autumn 2003
Physical constraints				
Potential energy (J m^{-3}) (entire water column)	171 \pm 62	94 \pm 46	1500 \pm 230	675 \pm 139
Mean temperature ($^{\circ}C$) (over mixed layer)	15.2 \pm 1.8	9.1 \pm 0.9	22.5 \pm 0.9	16.8 \pm 0.9
Resources (integrated value over mixed layer)				
Nitrate NO_3^- -N (mg L^{-1})	4.5 \pm 1.9	5.6 \pm 1.1	2.6 \pm 1.3	0.1 \pm 0.1
Phosphorus PO_4^{3-} -P (μg L^{-1})	43 \pm 19	42 \pm 5	16 \pm 3	6 \pm 9
Silicon SiO_3^4 -Si (mg L^{-1})	3.5 \pm 0.6	1.1 \pm 0.2	0.3 \pm 0.1	0.4 \pm 0.2
Mean irradiance in the mixed layer (μmol photon m^{-2} s^{-1})	11.6 \pm 4.8	2.5 \pm 0.9	15.2 \pm 7.6	1.3 \pm 1.0
Chlorophyll a integrated value over mixed layer (μg chl a L^{-1})	13.1 \pm 3.7	4.7 \pm 1.2	3.9 \pm 1.0	6.6 \pm 0.5
Mean sedimentary fluxes (g m^{-2} d^{-1})	6.4 \pm 1.9	2.6 \pm 0.7	2.2 \pm 1.1	8.3 \pm 5.4

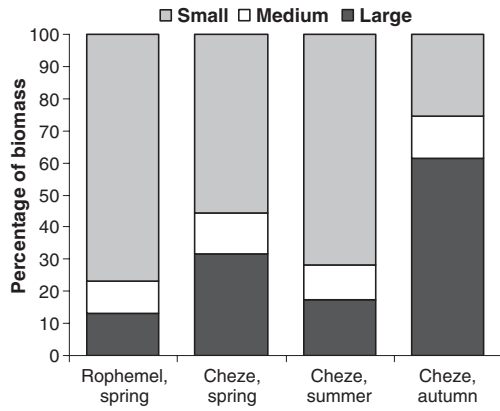


Fig. 4 Mean percentage of phytoplankton biomass in the three size classes: large (20–200 μm), medium (5–20 μm) and small (0.7–5 μm), for the four sampling periods.

(Fig. 5a). Small cells had a higher photosynthetic capacity, with an average of 3.1 pmol $\text{mg C mg chl } a^{-1} \text{ h}^{-1}$ (Fig. 5b).

The exported biomass also changed depending on the season: mean sedimentary flux varied between 2 and 8 $\text{g m}^{-2} \text{ day}^{-1}$, with smallest values in summer and early spring and highest values in autumn (Table 2). The origin of the material collected in the traps was mainly autochthonous production as indicated by the low C/N ratio of the sediments, which was on average 8.6 ± 1.7 and never exceeded 12 (not shown). The highest C/N ratio values can be attributed to diagenesis of the phytoplankton cells (Kaushal & Binford, 1999), because the C/N ratio would have been higher than 20 for terrestrial inputs (Meyers & Takemura, 1997; Kaushal & Binford, 1999). For the combined database, chlorophyll *a* biomass of the large

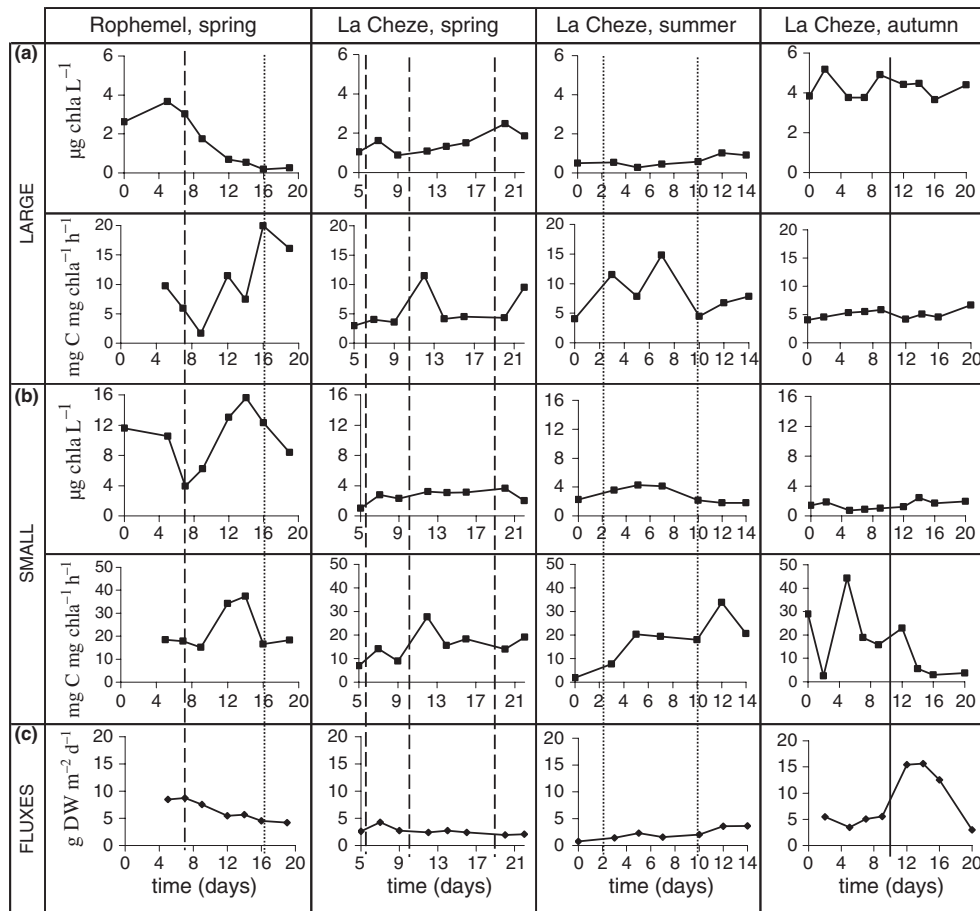


Fig. 5 Temporal patterns in biological parameters during the four sampling periods: integrated biomass over the mixed layer of (a) the largest and (b) the smallest size classes and (c) sedimentary flux. Vertical lines show main disturbances by wind: nutrient inputs (solid line), increase of stratification (dotted line) and mixing (thin dotted line).

size class was positively correlated with sedimentary fluxes, in terms of dry mass ($P = 0.001$), chlorophyll *a* (Fig. 6; $P < 0.001$) and pheopigment ($P = 0.001$), whereas the biomass of small cells was never correlated with these fluxes. Large cells contributed mainly to the downward fluxes and thus explained a large part of the variability of these sedimentary fluxes. If we consider the available biomass of large cells in the mixed layer, which can potentially sink into the sedimentary traps, the sinking rate varied between 0.07 m day^{-1} at La Cheze in summer and 2.65 m day^{-1} at Rophemel, with a mean of 0.74 m day^{-1} , which is similar to values found in the literature (Titman & Kilham, 1976; Huisman & Sommeijer, 2002a; Fennel & Boss, 2003). The contribution of pheopigment to downward fluxes was always higher than the contribution of chlorophyll, representing 63–72% of the sum of chlorophyll and pheopigments, despite the fact that pheopigment represented

on average only 17% of the total pigment in the water column. A negative correlation was also found with temperature of the mixed layer and/or stratification expressed as potential energy and sedimentary fluxes for chlorophyll *a* (Pearson correlation coefficients -0.401 , -0.486 , respectively; $P < 0.05$ in both cases), pheopigment ($r = -0.419$; $P < 0.05$ for potential energy only) and percentage of biological fluxes ($r = -0.719$ and -0.598 ; $P \leq 0.001$ in both cases). Thus stratification of the reservoir significantly decreased biological downward fluxes, while global fluxes measured by dry mass were influenced neither by temperature nor stratification.

Characterisation of wind events and disturbances

We first defined a critical value for the energy input by wind, corresponding to a wind event. In both reservoirs, an increase of the mixed layer depth was generally observed when daily mean wind speed exceeded 4 m s^{-1} , in accordance with what has been observed in other studies (Boehrer, Imberger & Munnich, 2000). This value was thus used as a critical daily mean wind speed, corresponding to an energy input of 64 mW m^{-2} using the formula defined earlier.

The energy input by wind generally resulted in an increase in surface current velocity (Fig. 7), suggesting active mixing in the surface layer. If the energy input by wind was large enough, the depth of the mixed layer also increased, leading to a decrease of the average light received by cells over the mixed layer (Fig. 8). Examples of such events occurred at La Cheze in summer, on days 2 and 10 (Fig. 7). In both cases, a slight increase in mixed layer depth because of wind accentuated the decrease of light availability observed on a larger time scale, which was due to a decrease of solar radiation (Fig. 8). An increase of mixing intensity also occurred at Rophemel in spring (Fig. 7), following a wind event (from day 16).

In most cases, the potential energy of the entire water column decreased, but if the event was associated over the next few days with a warming because of solar radiation, the potential energy increased (Fig. 7). The increase of stratification intensity over a few days dominated in spring as expected. During the spring sampling period at La Cheze, three wind disturbances (on days 5, 8–14 and 19) occurred (Fig. 7), which were all associated with at least a slight increase in potential energy (Fig. 7). The strong-

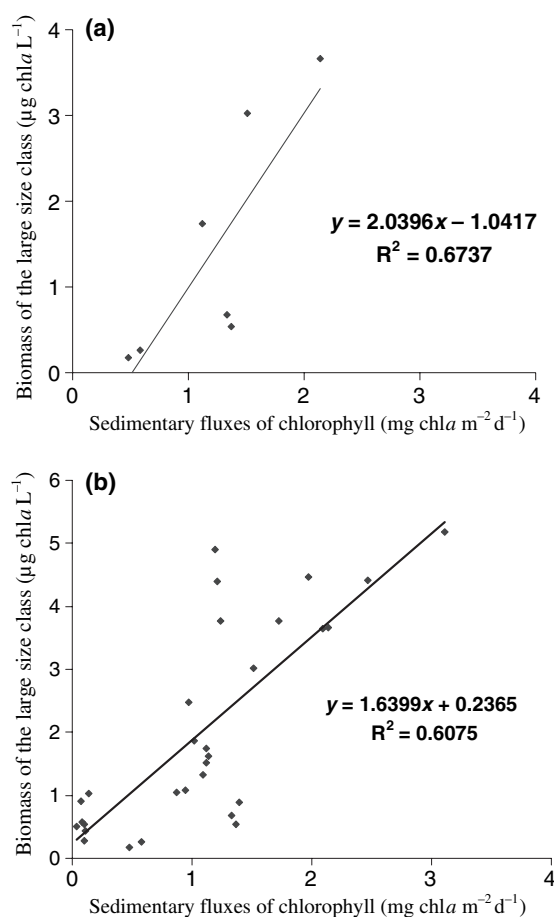


Fig. 6 Biomass of the large size class, measured as chlorophyll *a*, in relation to sedimentary flux (a) for Rophemel and (b) for both sites combined.

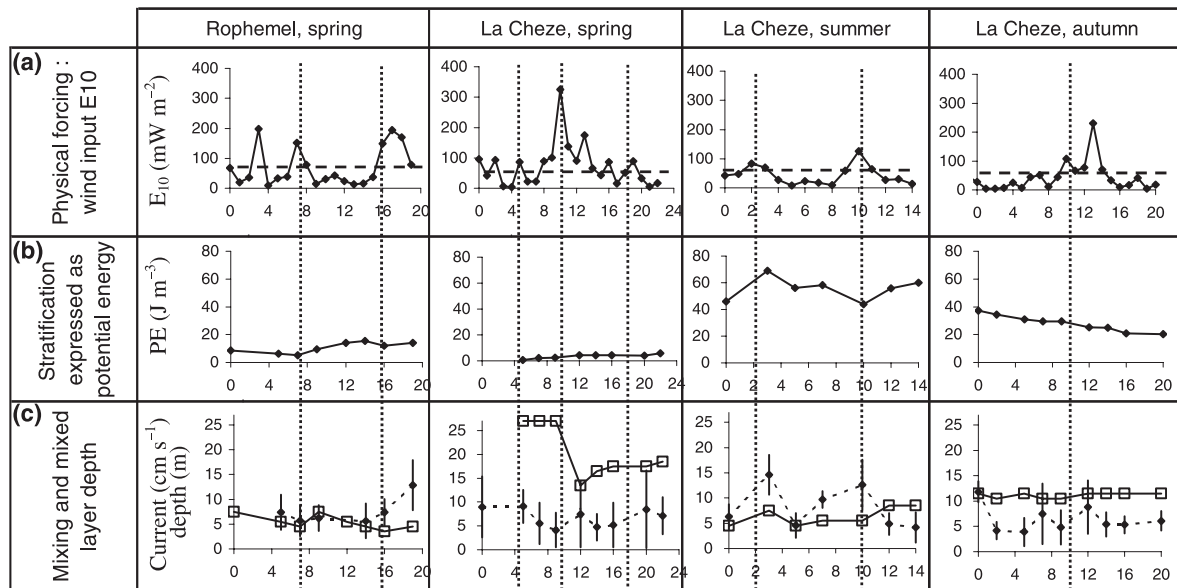


Fig. 7 Temporal patterns in physical and chemical parameters during the four sampling periods – horizontal dotted lines represent critical value of wind energy input and vertical ones show disturbances by wind: (a) wind energy input E_{10} , (b) stratification of the water column expressed as the mean potential energy, (c) mixing expressed as mean current velocity \pm SD (diamonds and vertical bars) and depth of the mixed layer (squares).

est wind event lasted 7 days (from day 8; Fig. 7), with a maximal value on day 10, and was associated with the strongest warming of the reservoir and a deepening of the mixed layer (Fig. 7). This led to a temporary decrease over the mixed layer in available light, which was already potentially limiting for growth (Fig. 8). An increase in stratification intensity over a few days also occurred in Rophemel following a windy event (on day 7), associated with an increase of the mixed layer depth (Fig. 7).

The last type of modification associated with an event was an increase of nutrient input induced by a wind event associated with rain, during a period of potential limitation by nutrients (Fig. 8). At La Cheze in autumn, a rain event (on day 7) followed by a 5 day wind event (from day 10 to 14; Fig. 7) induced an increase in silicon (by rain) followed by an increase in phosphorus availability, while nitrate availability remained the same (Fig. 8). Increases in both nutrients occurred both in the epilimnion and the hypolimnion (Fig. 8), while the mixed layer depth only moved down slightly. Nutrient inputs were most probably external. Moreover, resuspension of bottom sediment would have been associated with an increase of suspended matter within the water column, which was not observed here. Following this disturbance,

nutrient became temporarily non-limiting for growth, while light conditions remained potentially limiting during the entire period.

Only one heavy rainfall occurred over the four periods (day 1 of the spring period at Rophemel; Fig. 7), which led to a strong dilution of water, as the rainfall volume in 1 day was equivalent to the volume of the lake. The other wind events not described did not significantly affect the physical and chemical structure of the reservoirs. Finally, on average two wind events were observed per period (Fig. 7), associated with at least one of the following physical and chemical modifications: change in stratification and light intensities, mixing or nutrient inputs. These modifications are represented by the different vertical lines on the graphs of biomass, photosynthetic activity and sedimentary fluxes (Fig. 5).

Responses of the size-fractionated phytoplankton community

Photosynthetic activity. Both small and large cells responded to disturbances. An increase of photosynthetic activity of large cells was observed three times (Fig. 5a), associated with different types of disturbance. The increased mixing associated with the

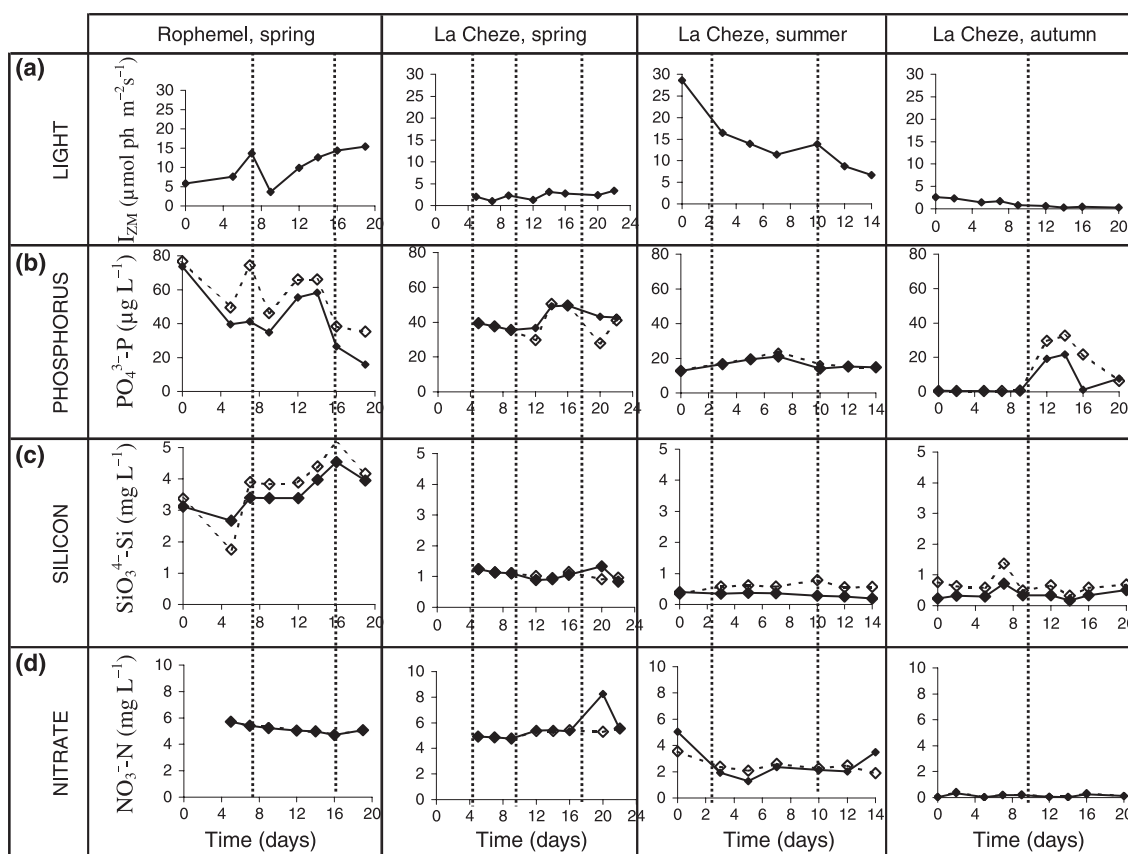


Fig. 8 Temporal patterns in physical and chemical parameters during the four sampling periods – horizontal dotted lines represent critical value of wind energy input and vertical ones show disturbances by wind. (a) light ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$), (b) phosphorus, (c) silicon, (d) nitrate. Nutrient availability is averaged over the mixed layer (solid diamonds and solid lines) and over the hypolimnion (open diamonds and dotted lines).

second event at Rophemel led to higher photosynthetic activity during the disturbance and over the next few days (Fig. 5a). Similarly, wind disturbances at La Cheze in spring, which enhanced mixing and warming, increased the biological activity of large cells during the disturbance (Fig. 5a). Nutrient input in autumn did not increase photosynthetic activity of large cells integrated over the mixed layer (Fig. 5a). However, their activity increased near the surface from 7.8 to 11.2 mg C mg chl $a^{-1} \text{h}^{-1}$. An increase in photosynthetic activity of small cells following a disturbance was observed only once, after the strongest wind recorded at La Cheze in spring when mixing was enhanced and the water warmed (Fig. 5b). Biological activity remained slightly higher after the disturbance, associated with higher temperatures (Fig. 5b). A decrease in photosynthetic activity of small cells was also observed in response to higher

mixing at Rophemel in spring (Fig. 5b). Daily physical forcing can thus induce a modification in photosynthetic activity of both large and small cells, as early as the day of the disturbance, with an increase particularly for large cells. This change in biological activity should be reflected in the fractionated biomass.

Biomass. Modifications of the fractionated biomass were also observed in response to disturbances by wind. Five disturbances induced a change in the concentration of large cells. Disturbances associated with mixing, such as the two wind events at La Cheze in June, induced a slight increase in biomass of large cells (Fig. 5a). Two of the three events of La Cheze in spring, which were associated with warming, also induced an increase in biomass (Fig. 5a). However the warming which occurred at Rophemel induced the opposite response, with the disappearance of large

cells (Fig. 5a). This warming occurred later in spring and was associated with a shallower mixed layer. Lastly, the nutrient input of La Cheze in autumn led to an increase in biomass of large cells at 7 m depth, which was confirmed by an increase of fluorescence at that depth, but was not significant when biomass was integrated over the mixed layer (Fig. 5a). The biomass of small cells was increased by a disturbance, if associated with nutrient input, such as La Cheze in autumn, or with increased stratification intensity, such as at Rophemel following the first wind events (Fig. 5b). However mixing decreased small cell biomass, such as at Rophemel with the second wind event (Fig. 5b). Wind disturbances can therefore modify the biomass of both large and small cells, generally 2 days after the beginning of the disturbance. These modifications were not always related to a previous change in photosynthetic activity, but sedimentary fluxes should reflect both modifications.

Sedimentary fluxes. The increase of stratification intensity in spring led to decreased sedimentary fluxes, associated with the disappearance of large cells, such as followed the first wind event at Rophemel (Fig. 5c). In that case, biomass of large cells in the mixed layer and sedimentary fluxes were strongly correlated ($r^2 = 0.90$; Fig. 6a). The slight increase in biomass of large cells following the increase of mixing at La Cheze in summer was also associated with a small increase in sedimentary fluxes (Fig. 5c). Nutrient inputs associated with the wind event at La Cheze in autumn increased sedimentary fluxes by a factor of 3, during and after the disturbance (Fig. 5c).

Discussion

Seasonal variability in phytoplankton size structure and sedimentary fluxes

The size structure of the phytoplankton community and the associated sedimentary fluxes were influenced by physical and chemical conditions on a seasonal time scale. Photosynthetic capacity was always dominated by small cells, in accordance with allometric rules and other experimental data showing that photosynthetic rate is negatively correlated with cell size (Finkel & Irwin, 2000; Kagami & Urabe, 2001; Ray *et al.*, 2001). The size structure of biomass depen-

ded on both resource availability and loss by sedimentation. High stratification was associated with a high loss rate by sedimentation of large cells and therefore induced a small-size community structure, in summer. On the contrary, mixing favoured a large size structure, such as in autumn. Grazing pressure also influences size structure of the phytoplankton community (Cottingham, 1999; Jiang, Schofield & Falkowski, 2005) and one might expect that size structure would be influenced by zooplankton in our study. However, our data cannot be used to detect a zooplankton effect, which is likely to occur over a seasonal time scale and not on a time scale of a few days.

According to the well-known Stokes equation, the settling velocity of non-motile cells will depend on their density, their shape and their size. Given a general trend between size (of cells and colonies) and settling velocity, seasonal variability in the fractionated biomass may thus be partly reflected in sedimentary fluxes. Sedimentary fluxes varied between 2 and 8 g m⁻² day⁻¹, with maximal values in autumn and minimal ones during summer, in accordance with values found in the literature (Weyhenmeyer & Bloesch, 2001). In our study, sedimentary fluxes depended on both the size structure of phytoplankton and the degree of stratification of the water column. Downward flux was positively correlated with biomass of large cells, data from both reservoirs combined, in accordance with the initial hypothesis that large cells contribute more to sedimentation in reservoirs than other size classes. Pakhomov *et al.* (2002) also found that microphytoplankton (20–200 µm) represents 15–75% of the total fluxes of particulate organic carbon, with highest values in periods of bloom. Moreover, in our study, the downward fluxes were negatively correlated with temperature and potential energy, which is in accordance with the small size structure associated with strong stratification. Organic matter may also be recycled faster because of a higher temperature (Naiman & Bilby, 1998) and therefore reduce the downward flux. Bloesch, Stadelmann & Bührer (1977) demonstrated a high remineralisation rate in the deepest part of the epilimnion of two Swiss lakes with 77–79% of the total phytoplankton being decomposed in the epilimnion in both cases. Moreover the contribution of pheopigment to sedimentary fluxes was also high, in our study, compared with its

contribution to the suspended biomass. Grazing of phytoplankton cells could partly explain the downward flux of pheopigment, through the formation of faecal pellets. Degradation of chlorophyll during sedimentation can also contribute to increased pheopigment with depth, in particular in the case of diatoms (Poister, Armstrong & Hurley, 1999). Lastly, dying cells sink faster and may accumulate more quickly in traps compared with viable cells (Smayda, 1974).

Control of phytoplankton size structure and sedimentary fluxes by seasonal forcing was in accordance with previous freshwater and marine studies (Tamigneaux *et al.*, 1999; Vezina *et al.*, 2000; Arin *et al.*, 2005). However, short-term variability in both phytoplankton size structure and sedimentary fluxes is expected to be controlled by daily fluctuations of forcing.

Seasonal variability of the wind induced disturbances

Wind events influenced both sites, despite Rophemel having a smaller fetch and being more protected by the steepness of its basin. Wind may in fact have been funnelled in the channel created by the steep-sided basin. Local winds should be recorded on a daily time scale to confirm any short-term wind effect on a reservoir. Rainfall also occurred (two events, one with heavy rain, over the four sampling periods), but disturbances induced by rainfall occurred with a time lag, corresponding to the time for the water to reach the reservoir. The effects of rainfall were only taken into account through the change in nutrient availability that they induced.

Similar wind events induced different disturbances of the physical and chemical structure of the reservoirs depending on the season. During seasonal transitions of temperature such as in spring and autumn, events were associated with a modification of temperature in the mixed layer and of the intensity of stratification, because of a warming up or a cooling down of the reservoir over a few days. During summer, high stratification counteracted more strongly the mixing effect of wind events. Resource limitation fluctuated during the year and the occurrence of nutrient inputs associated with events, through river inputs or release from the hypolimnion, influenced the phytoplankton community only in periods of nutrient limitation.

Disturbances and phytoplankton responses

When wind events increased the intensity of mixing of the water column, the response of small cells was a decrease in both biomass and photosynthetic capacity, because of a redistribution of populations of small cells in the mixed layer and to a decrease of the mean light they received. Large cells increased in terms of both biomass and photosynthetic capacity, sedimentary loss rate of large cells being temporarily decreased because of the redistribution of cells in the mixed layer (Huisman & Sommeijer, 2002a). This led to higher sedimentary fluxes. Higher production induced by increased mixing had been previously observed (Gervais, Opitz & Behrendt, 1997), but resuspension and external inputs because of water mass movements could also partially explain the observed biomass increase. In this study the increase in biomass was always observed at intermediate depth (5–7 m) and was therefore not influenced by either external inputs or resuspension, which would have increased biomass at the surface because of wind induced currents or near the bottom because of resuspension (Malmaeus & Hakanson, 2003; Hakanson & Eckhell, 2005). Moreover, because the studied reservoirs are stratified, the hypolimnion should not have been affected by surface mixing.

Wind events were also associated with an increase in stratification intensity when followed by warming of the reservoir, particularly in spring. Modifications induced by wind on phytoplankton dynamics were thus because of a change in sedimentary loss. Small cells were favoured, as shown by their increase in biomass, in accordance with their low sedimentary loss. Their photosynthetic capacity may have also increased, but this increase could be related to the increase in temperature. Response of large cells was more variable. In late spring, following the intensification of the stratification, large cells disappeared quickly, leading to high sedimentary fluxes initially. Consequently, sedimentary fluxes followed the biomass of large cells and declined progressively. Large cells underwent higher sinking rates after the intensification of stratification and their populations became extinct. In early spring, the mixed layer was much deeper and remained deep enough to sustain the growth of large-size populations in accordance with Ptacnick *et al.* (2003). The biomass of large cells also increased slightly because of low temperature,

growth being correlated with temperature (Montagnes & Franklin, 2001), but the increase was insufficient to be reflected in sedimentary fluxes. In summary, the fact that large cells can be favoured by mixing, which has already been observed on a large time scale (Legendre & Le-Fèvre, 1989; Chen *et al.*, 2002), was also observed on a time scale of a few days and this was reflected in higher sedimentary fluxes.

Wind events can also increase the depth of the mixed layer, leading to a decrease of the mean availability of light received by cells in the mixed layer (Huisman & Sommeijer, 2002b). Sedimentary loss rate also decreases with increasing mixed layer, the probability of leaving the mixed layer decreasing (Diehl *et al.*, 2002; Ptacnick *et al.*, 2003). Cells thus remained longer within the mixed layer and the euphotic layer, leading to higher production. But nutrient availability also depends on the depth of the mixed layer and a deepening of the mixed layer may be associated with nutrient inputs (MacIntyre & Jellison, 2001). These nutrient inputs affect the phytoplankton community according to initial nutrient availability. Critical values were thus used to characterise resource conditions. We considered that above these critical values, the probability that resources were limiting growth of phytoplankton was low, so that increased availability of these resources may not change the competition outcome between species. Below these critical values, change in resource availability was taken into account. In periods of potential nutrient limitation, the deepening of the mixed layer was observed but each time the hypolimnion was also relatively depleted, particularly in phosphorus, indicating external nutrient origins. External input of nutrient was observed twice, with increased uniform concentrations at all depths, with silicon input by rainfall and phosphorus input associated with a wind event. Large cells responded to nutrient inputs by an increase, only at the surface, of their photosynthetic capacity, associated with a doubling of sedimentary fluxes. In autumn, light availability was low, while the depth of the mixed layer was deep, so that the integrated value of photosynthetic capacity, as well as the integrated value of biomass, remained about the same. The higher photosynthetic capacity of large cells at the surface led to a larger size structure of the phytoplankton community there. Consequently, the mean value of phytoplankton sedimentary loss rate increased, leading to a rapid export of biomass with

suspended biomass remaining approximately the same. The photosynthetic capacity of small cells remained the same whatever the depth, indicating that large cells took more advantage of the sudden increase in nutrients, possibly through nutrient storage, compared with the small cells (Spijkerman & Coesel, 1998).

Responses of phytoplankton to a deeper mixed layer may thus be difficult to isolate using field data, as it is difficult to determine whether light, sedimentary loss or nutrient concentration, has the greatest effect on phytoplankton dynamics. Many field studies have demonstrated the positive effect of deepening of the mixed layer, but this was always associated with an increase in mixing and nutrient release (Iverson *et al.*, 1974; MacIntyre & Jellison, 2001). Recent studies using models and mesocosms have highlighted the role of the decrease in sedimentary loss rate associated with a deeper mixed layer (Diehl *et al.*, 2002; Kunz & Diehl, 2003). But only laboratory experiments and models can distinguish the roles of the different factors.

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References

- Anneville O., Ginot V., Druart J.-C. & Angeli N. (2002) Long-term study (1974–1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach. *Journal of Plankton Research*, **24**, 993–1008.
- Arin L., Estrada M., Salat J. & Cruzado A. (2005) Spatio-temporal variability of size fractionated phytoplankton on the shelf adjacent to the Ebro river (NW Mediterranean). *Continental Shelf Research*, **25**, 1081.

- Barnes H. & Folkard A.R. (1951) The determination of nitrite. *The Analyst (London)*, **76**, 599–603.
- Bloesch J., Stadelmann P. & Bührer H. (1977) Primary production, mineralization and sedimentation in the euphotic zone of two Swiss lakes. *Limnology and Oceanography*, **22**, 511–525.
- Boehrer B., Imberger J. & Munnich K. (2000) Vertical structure of currents in western Lake Constance. *Journal of Geophysical Research Oceans*, **105**, 28823–28835.
- Botte V. & Kay A. (2002) A model of the wind-driven circulation in Lake Baikal. *Dynamics of Atmospheres and Oceans*, **35**, 131–152.
- Carmack E.C., Wiegand R.C., Daley R.J., Gray C.B.J., Jasper S. & Pharo C.H. (1986) Mechanisms influencing the circulation and distribution of water mass in a medium residence-time lake. *Limnology Oceanography*, **31**, 249–265.
- Chen C., Ji R., Schwab D.J., Beletsky D., Fahnenstiel G.L., Jiang M., Johengen T.H., Vanderploeg H., Eadie B. & Budd J.W. (2002) A model study of the coupled biological and physical dynamics in Lake Michigan. *Ecological Modelling*, **152**, 145–168.
- Cottingham K. (1999) Nutrients and zooplankton as multiple stressors of phytoplankton communities: evidence from size structure. *Limnology and Oceanography*, **44**, 810–827.
- Diehl S., Berger S., Ptacnik R. & Wild A. (2002) Phytoplankton, light and nutrients in a gradient of mixing depths: theory. *Ecology*, **83**, 386–398.
- Fennel K. & Boss E. (2003) Subsurface maxima of phytoplankton and chlorophyll: steady state solutions from a simple model. *Limnology and Oceanography*, **48**, 1521–1534.
- Finkel Z.V. & Irwin A.J. (2000) modeling size-dependent photosynthesis: light absorption and the allometric rule. *Journal of Theoretical Biology*, **204**, 361–369.
- Gervais F., Opitz D. & Behrendt H. (1997) Influence of small-scale turbulence and large-scale mixing on phytoplankton primary production. *Hydrobiologia*, **342–343**, 95–105.
- Hakanson L. & Eckhell J. (2005) Suspended particulate matter (SPM) in the Baltic Sea – new empirical data and models. *Ecological Modelling*, **189**, 130–150.
- Huisman J. & Sommeijer B. (2002a) maximal sustainable sinking velocity of phytoplankton. *Marine Ecology Progress Series*, **244**, 39–48.
- Huisman J. & Sommeijer B. (2002b) Population dynamics of sinking phytoplankton in light-limited environments: simulation techniques and critical parameters. *Journal of Sea Research*, **48**, 83–96.
- Huisman J., Van Oostveen P. & Weissing F.J. (1999) Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. *American Naturalist*, **154**, 46–68.
- Imberger J. & Parker G. (1985) Mixed layer dynamics in a lake exposed to a spatially variable wind field. *Limnology and Oceanography*, **30**, 473–488.
- Iverson R., Curl H., O'Connors J.H., Kirk J.D. & Zakar K. (1974) Summer phytoplankton blooms in Auke Bay, Alaska, driven by wind mixing of the water column. *Limnology and Oceanography*, **19**, 271–278.
- Jiang L., Schofield O.M.E. & Falkowski P.G. (2005) Adaptive Evolution of Phytoplankton Cell Size. *The American Naturalist*, **166**, 496–505.
- Kagami M. & Urabe J. (2001) Phytoplankton growth rate as a function of cell size: an experimental test in Lake Biwa. *Oecologia: Limnology*, **2**, 111–117.
- Karp-Boss L., Boss E. & Jumars P. (1996) Nutrient fluxes to planktonic osmotrophs in the presence of fluid motion. *Oceanography and Marine Biology, an Annual Review*, **34**, 71–107.
- Kaushal S. & Binford M.W. (1999) Relationship between C:N ratios of lake sediments, organic matter sources, and historical deforestation in Lake Pleasant, Massachusetts, USA. *Journal of Paleolimnology*, **22**, 439–442.
- Kocsis O., Mathis B., Gloor M., Schurter M. & Wüest A. (1998) Enhanced mixing in narrows: A case study at the Mainau sill (Lake Constance). *Aquatic Sciences*, **60**, 236–252.
- Kunz T.J. & Diehl S. (2003) Phytoplankton, light and nutrients along a gradient of mixing depth: a field test of producer-resource theory. *Freshwater Biology*, **48**, 1050–1063.
- Lagadeuc Y., Brylinski J. & Aelbrecht D. (1997) Temporal variability of the vertical stratification of a front in a tidal Region Of Freshwater Influence (ROFI) system. *Journal of Marine Systems*, **12**, 147–155.
- Legendre L., and Le-Fèvre J. (1989) Hydrodynamical singularities as controls of recycled versus export production in oceans. In: *Productivity of the Ocean: Present and Past* (Eds W.H. Berger, V.S. Smetacek & G. Wefer), pp. 49–63. John Wiley & Sons, Chichester.
- Lizon F. & Lagadeuc Y. (1998) Comparisons of primary production values estimated from different incubation times in a coastal sea. *Journal of Plankton Research*, **20**, 371–381.
- Lorenzen C. (1967) Determination of chlorophyll and pheo-pigments: spectrophotometric equations. *Limnology and Oceanography*, **12**, 343–346.
- MacIntyre S. & Jellison R. (2001) Nutrient fluxes from upwelling and enhanced turbulence at the top of the pycnocline in Mono Lake, California. *Hydrobiologia*, **466**, 13–29.

- Malmaeus J.M. & Hakanson L. (2003) A dynamic model to predict suspended particulate matter in lakes. *Ecological Modelling*, **167**, 247–262.
- Marañón E., Holligan P.M., Barciela R., González N., Mouriño B., Pazó M.J. & Varela M. (2001) Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments. *Marine Ecology Progress Series*, **216**, 43–56.
- Metcalfe A.M., Pedley T.J. & Thingstad T.F. (2004) Incorporating turbulence into a plankton foodweb model. *Journal of Marine Systems*, **49**, 105–122.
- Meyers P.A. & Takemura K. (1997) Quaternary changes in delivery and accumulation of organic matter in sediments of Lake Biwa, Japan. *Journal of Paleolimnology*, **18**, 211–218.
- Millard E., Myles D., Johannsson O. & Ralph K. (1996) seasonal phosphorus deficiency of lake Ontario phytoplankton at two index stations: light versus phosphorus limitation of growth. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1112–1124.
- Montagnes D.J.S. & Franklin D.J. (2001) Effect of temperature on diatom volume, growth rate, and carbon and nitrogen content: Reconsidering some paradigms. *Limnology and Oceanography*, **46**, 2008–2018.
- Murphy J. & Riley J.P. (1962) A modified single-solution for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31–36.
- Naiman R. & Bilby R. (1998) *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*. Springer, New York.
- Nixdorf B., Mischke U. & Rucker J. (2003) Phytoplankton assemblages and steady state in deep and shallow eutrophic lakes – an approach to differentiate the habitat properties of Oscillatoriales. *Hydrobiologia*, **502**, 111–121.
- Noges P., Tuvikene L., Noges T. & Kisand A. (1999) Primary production, sedimentation and resuspension in large shallow Lake Võrtsjarv. *Aquatic Sciences*, **61**, 168–182.
- Noges T., Kisand V., Noges P., Pollumae A., Tuvikene L. & Zingel P. (1998) Plankton seasonal dynamics and its controlling factors in shallow polymictic eutrophic Lake Võrtsjarv, Estonia. *International Review of Hydrobiology*, **83**, 279–296.
- Pakhomov E.A., Froneman P.W., Wassmann P., Ratkova T. & Arashkevich E. (2002) Contribution of algal sinking and zooplankton grazing to downward flux in the Lazarev Sea (Southern Ocean) during the onset of phytoplankton bloom: A lagrangian study. *Marine Ecology Progress Series*, **233**, 73–88.
- Pesant S., Legendre L., Gosselin M., Bauerfeind E. & Budeus G. (2002) Wind-triggered events of phytoplankton downward flux in the Northeast Water Polynya. *Journal of Marine Systems*, **31**, 261–278.
- Platt T., Gallegos C.L. & Harrison W.G. (1980) Photo-inhibition of photosynthesis in natural assemblages of marine phytoplankton. *Journal of Marine Research*, **38**, 687–701.
- Podsetchine V. & Schernewski G. (1999) The influence of spatial wind inhomogeneity on flow patterns in a small lake. *Water Research*, **33**, 3348–3356.
- Poister D., Armstrong D.E. & Hurley J.P. (1999) Influences of grazing on temporal patterns of algal pigments in suspended and sedimenting algae in a north temperate lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 60–69.
- Ptacnick R., Diehl S. & Berger S. (2003) Performance of sinking and non-sinking phytoplankton taxa in a gradient of mixing depths. *Limnology and Oceanography*, **48**, 1903–1912.
- Ray S., Berc L., Straskraba M. & Jorgensen S.E. (2001) Optimization of energy and implications of body sizes of phytoplankton and zooplankton in an aquatic ecosystem model. *Ecological Modelling*, **140**, 219–234.
- Reynolds C.S. (1984) *The Ecology of Freshwater Phytoplankton*. University Press, Cambridge, UK.
- Reynolds C.S., Irish A.E. & Elliott J.A. (2001) The ecological basis for simulating phytoplankton responses to environmental change (PROTECH). *Ecological Modelling*, **140**, 271–291.
- Richardson T.L., Gibson C.E. & Heaney S.I. (2000) Temperature, growth and seasonal succession of phytoplankton in Lake Baikal, Siberia. *Freshwater Biology*, **44**, 431–440.
- Rodier J. (1978) *L'analyse de l'eau*. Dunod, Paris.
- Rodriguez V. & Guerrero F.J. (1994) Chlorophyll a of size-fractionated summer phytoplankton blooms at a coastal station in Malaga Bay, Alboran Sea. *Estuarine, Coastal and Shelf Science*, **39**, 413–419.
- Rossum J.R. & Villaruz P.A. (1963) Determination of ammonia by the indophenol method. *Journal of American Water Works Association*, **55**, 657–658.
- Simpson J., Edelman D., Edwards A. & Morris N. (1979) The Islay Front: physical structure and phytoplankton distribution. *Estuarine and Coastal Marine Science*, **9**, 713–726.
- Smayda T.J. (1974) Some experiments on the sinking characteristics of two freshwater diatoms. *Limnology and Oceanography*, **19**, 628–635.
- Sommer U., Gliwicz Z.M., Lampert W. & Duncan A. (1986) The PEG-model of seasonal succession of planktonic events in fresh waters. *Archiv für Hydrobiologie*, **106**, 433–471.
- Spijkerman E. & Coesel P.F.M. (1998) Different response mechanisms of two planktonic desmid species (Chlorophyceae) to a single, saturating addition of phosphate. *Journal of Phycology*, **34**, 438–445.

- Steemann-Nielsen. (1952) The use of radioactive carbon (C14) for measuring organic production in the sea. *International Council for the Exploration of the Sea*, **18**, 117–140.
- Talling J.F. (2004) Interrelation of diel and seasonal change, involving summer thermal stratification, weather variables and a mobile dinoflagellate in a productive English Lake. *Hydrobiologia*, **524**, 215–227.
- Tamigneaux E., Legendre L., Klein B. & Mingelbier M. (1999) Seasonal dynamics and potential fate of size-fractionated phytoplankton in a temperate nearshore environment (Western Gulf of St Lawrence, Canada). *Estuarine, Coastal and Shelf Science*, **48**, 253–269.
- Titman D. & Kilham P. (1976) Sinking in freshwater phytoplankton: some ecological implications of cell nutrient status and physical mixing processes. *Limnology and Oceanography*, **21**, 409–417.
- Vezina A.F., Savenkoff C., Roy S., Klein B., Rivkin R., Therriault J.-C. & Legendre L. (2000) Export of biogenic carbon and structure and dynamics of the pelagic food web in the Gulf of St. Lawrence Part 2. Inverse analysis. *Deep Sea Research Part II: Topical Studies in Oceanography*, **47**, 609–635.
- Wetzel R.G. (2001) *Limnology Lake and River Ecosystems*, 3rd edn. Academic press, San Diego.
- Weyhenmeyer G.A. (1996) The influence of stratification on the amount and distribution of different settling particles in Lake Erken. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1254–1262.
- Weyhenmeyer G.A. & Bloesch J. (2001) The pattern of particle flux variability in Swedish and Swiss lakes. *The Science of The Total Environment*, **266**, 69–78.
- Wuest A., Piepke G. & Van-Senden D. (2000) Turbulent kinetic energy balance as a tool for estimating vertical diffusivity in wind-forced stratified waters. *Limnology and Oceanography*, **45**, 1388–1400.
- Yoshida T., Sekino T., Genkai-Kato M. *et al.* (2003) Seasonal dynamics of primary production in the pelagic zone of southern Lake Baikal. *Limnology*, **4**, 53–62.

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