

Phytoplankton species turnover controlled by physical forcing at different time scales

Alexandrine Pannard, Myriam Bormans, and Yvan Lagadeuc

Abstract: Changes in the physical and chemical environment induced by forcing events such as wind and rain can control the short-term dynamics of the phytoplankton community of inland waters. In two temperate reservoirs, species composition, diversity index, and species dynamics were characterized over periods of 3 weeks during different seasons, in parallel with changes in the physical and chemical structure of the water column. Dominant species and diversity index were shown to be controlled by environmental factors fluctuating on a seasonal and weekly time scale, whereas some rarer species responded to wind events and were indicators of a very short-term environmental change. As a consequence of the response of indicator species, the rate of change in species composition increased following meteorological events. Shifts in species composition were observed during each sampling period, except during the strongest stratification period. The shifts were associated with a modification of resource availability or intensity of stratification. We found that the resistance of the phytoplankton community to short-term physical forcing by wind increased with intensity of stratification. After the forcing event, the community did not return to its original structure because of modifications of the physical and chemical conditions induced by meteorological forcing on a weekly time scale.

Résumé : Cette étude met en évidence la dynamique à court terme des communautés de phytoplancton lacustre en réponse aux modifications de l'environnement physico-chimique induites par des événements de forçage, comme le vent et la pluie. Dans deux réservoirs tempérés, l'indice de diversité, la dynamique des espèces et la composition en espèces ont été suivis sur des périodes de 3 semaines à différentes saisons, en parallèle avec les modifications de la structure physico-chimique de la colonne d'eau. Les espèces dominantes et l'indice de diversité étaient contrôlés à des échelles de temps saisonnière et hebdomadaire, alors que certaines espèces plus rares indicatrices de changements à très court terme ont répondu aux événements de vent. En conséquence de la réaction des espèces indicatrices le taux de changement des espèces a augmenté après les événements rapides de forçage. Des modifications brutales de la composition en espèces ont été observées pendant chaque campagne d'échantillonnage, excepté pendant la période de stratification maximale. Ces changements étaient associés à des modifications de la disponibilité des ressources ou de l'intensité de la stratification. Nous avons observé que la résistance de la communauté de phytoplancton au forçage physique à court terme par le vent augmentait avec l'intensité de la stratification. Après les événements de forçage, la communauté n'est pas retournée à sa structure initiale, à cause de modifications entre-temps des conditions physico-chimiques, induites par le forçage météorologique sur une échelle de temps hebdomadaire.

Introduction

The periodicity of phytoplankton community composition in lakes as a result of seasonal variations in physical forcing has often been investigated (Lewis 1978*b*; Noges et al. 1998; Anneville et al. 2002). Seasonal physical forcing is mainly due to factors such as changes in air temperature and solar radiation (Sommer et al. 1986), which control the vertical structure of the water column of a lake, water temperature, depth of the mixed layer, intensity of mixing, and consequently the nutrients available in the surface layer. The verti-

cal structure of the water column can also be modified on a shorter time scale by forcing events such as wind and rain (Imberger and Parker 1985; MacIntyre et al. 1999). These modifications take place on a time scale of a few days, similar to the time scale of the phytoplankton doubling, and can thus influence the phytoplankton community (Reynolds 1984*b*). Modification of the vertical structure of the water column on different time scales, from seasonal to daily, may thus affect the dynamics of the phytoplankton community. Three time scales are used here, short term (a few days), intermediate (the sampling period of 3 weeks), and seasonal,

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with a focus on the short term, as very few studies have examined the dynamics of phytoplankton at that time scale.

The vertical structure of the water column is a determining factor for the phytoplankton community, as it controls both losses by sedimentation rate and growth through nutrient and light availability. Meteorological forcing events can modify this vertical structure in several ways. For example, the mixed-layer depth can be increased, leading to lower light availability over the mixed layer (Diehl et al. 2002) and a decrease in sedimentation losses (Ptacnick et al. 2003), as well as an increase in the intensity of mixing and redistributing phytoplankton populations over depth. Species able to regulate their buoyancy, which therefore become concentrated during calm periods (Klausmeier and Litchman 2001), may be disadvantaged by this redistribution, as they temporarily lose their vertical position (Huisman et al. 2004). Species that tend to sink will be mixed through the water column and their sedimentation loss rate will thus be reduced (Huisman et al. 2002). Lastly, forcing events can modify nutrient availability by breaking down or weakening the nutricline or by modifying external inputs from the drainage basin. The resulting change in competition between species with different nutrient requirements and storage capacity may affect phytoplankton community structure (Sommer 1985); therefore meteorological forcing events may induce a short-term variability in the phytoplankton community.

In a previous study, we showed that short-term forcing events can modify both the size structure of phytoplankton and losses via sedimentation (Pannard et al. 2007). In this study, we address physical and chemical forcing at different time scales, with a focus on time scales of a few days. We use diversity index, rate of change of species composition and species community structure, to examine short-term dynamics of phytoplankton community during different seasons in two temperate reservoirs.

Materials and methods

Study sites

Two stratified temperate reservoirs located in Brittany, near Rennes (France), were studied (Fig. 1). La Cheze and Rophemel are both drowned river reservoirs. The volume of La Cheze is about $15 \times 10^6 \text{ m}^3$, with a mean depth of 14 m, whereas the smaller Rophemel reservoir has a volume of $5 \times 10^6 \text{ m}^3$ and a mean depth of about 6.5 m (Table 1). The reservoirs differ in their exposure to wind in terms of fetch (Table 1) and orientation to the dominant wind direction (Fig. 1), with La Cheze being more exposed to wind forcing than Rophemel. The reservoir of La Cheze has a smaller catchment area of about 30 km^2 , with a lake surface area of about 1 km^2 and a residence time between 3 months and 1 year, whereas Rophemel has a large catchment area (380 km^2) with a residence time between 1 and 4 weeks (Table 1).

Sampling

The reservoir of La Cheze was sampled during three seasons, summer (20 June 2003 – 14 July 2003), autumn (22 September 2003 – 14 October 2003), and early spring (24 March 2004 – 15 April 2004). Rophemel was sampled only in spring (5 May 2004 – 24 May 2004). For each pe-

riod, sampling was performed in the morning (0900 h), every 2 or 3 days, a few hundred metres from the outlet of the reservoir and in the vicinity of the old river bed, far away from tributaries. Water samples were collected using a 1 m 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) and analysed for nutrient and phytoplankton species community structure.

Physical and chemical structure

To characterize the physical forcing, meteorological data monitored in Rennes by Météo France were used (Fig. 1). Wind speed and direction (collected 10 m above the ground), solar radiation, and mean air temperature were averaged daily, whereas rainfall was measured daily.

To determine the water column stratification intensity, the potential energy (PE), which represents the quantity of energy needed to homogenize the entire water column (Lagadeuc et al. 1997), was calculated (in $\text{J}\cdot\text{m}^{-3}$) using the formula

$$(1) \quad \text{PE} = \frac{1}{h} \int_0^h (\bar{\rho} - \rho) g z dz$$

based on the mean density

$$(2) \quad \bar{\rho} = \frac{1}{h} \int_0^h \rho dz$$

where ρ is the water density at depth z , h is the total depth of the water column, and g is the gravitational constant. A greater amount of potential energy implies greater stability of the water column. Water temperature was profiled every metre with a YSI environmental 6920 probe (Anhydre, Vireux Molhain, France). Surface current velocities were measured once per second with a two-dimensional acoustic current meter probe (Falmouth Scientific Inc., Cataumet, Mass.) at a depth of about 0.5 m below the surface.

To characterize the influence of wind on the physical structure of the water column, and particularly on upwelling of hypolimnetic water, the dimensionless lake number L_N (Imberger and Patterson 1990) was calculated as follows:

$$(3) \quad L_N = \frac{\text{St}(H - h_T)}{u_*^2 A_S^{3/2} (H - h_V)}$$

where H is the total depth, h_T is the height from the bottom of the lake to the seasonal thermocline, h_V is the height from the bottom of the lake to the center of lake volume, and A_S is the surface area of the lake. The stability St was calculated as follows:

$$(4) \quad \text{St} = \frac{1}{\rho_0} \int_0^H g(h_V - z) \rho(z) A(z) dz$$

where ρ_0 is the density of water, g is the acceleration due to gravity, and $A(z)$ and $\rho(z)$ are the area and the water density, respectively, at the height z . The water shear velocity induced by the wind u_* was calculated as follows:

Fig. 1. Location of the study area and the sampling sites in Brittany, France. The wind rose summarizes local wind direction over four years (1999–2002) using Meteo France data.

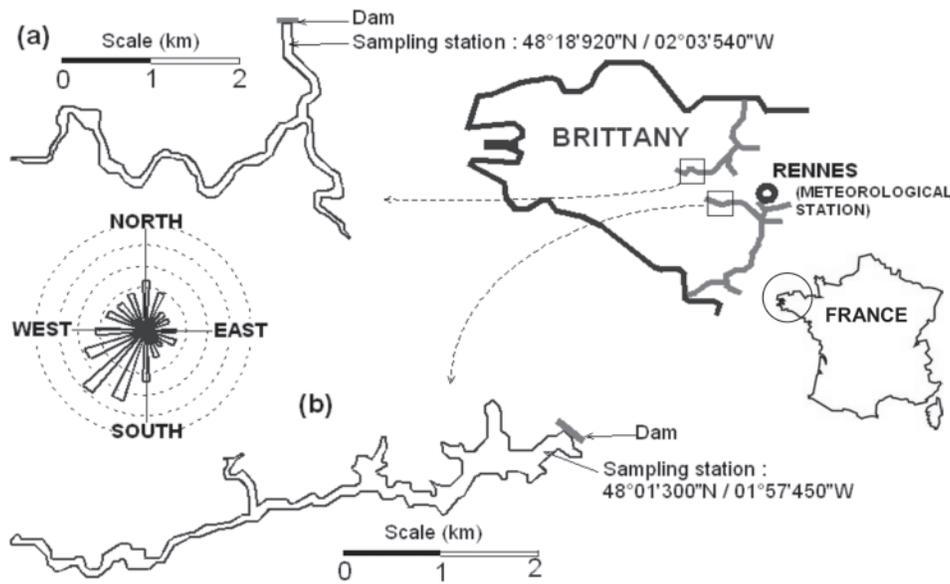


Table 1. Drainage basin and morphometric characteristics of the La Cheze and Rophemel reservoirs, France.

	La Cheze	Rophemel
Reservoir volume (10^6 m ³)	14.7	5
Surface area (km ²)	1.07	0.77
Mean depth (m)	13.7	6.5
Fetch (m) in predominant wind direction	900	120
Catchment area (km ²)	30	380
Water residence time	3 months to 1 year	1 week to 1 month

$$(5) \quad u_* = \left(\frac{C_D^S \rho_a}{\rho_0} \right)^{1/2} U$$

where ρ_a is the density of air, C_D^S is the surface drag coefficient, and U is the wind speed ($\text{m}\cdot\text{s}^{-1}$).

Maximal water discharge was estimated from rainfall, multiplied by the surface of the catchment area. These values are approximate as they do not take into account evapotranspiration or infiltration but they give a useful indication of the extent of the rain impact on the lake volume.

To characterize the availability of light, daily average solar radiation was converted to mean photosynthetically active radiation (PAR), I_0 , using a factor of 0.45 (Talling 1957). We then calculated the mean daily PAR, \bar{I}_{Z_M} , received by the phytoplankton over the mixed layer Z_M by integrating the light profile using the Beer–Lambert law:

$$(6) \quad \bar{I}_{Z_M} = \frac{1}{Z_M} \int_0^M I_0 e^{-K_d z} dz$$

where K_d is the measured light attenuation coefficient, calculated from an instantaneous irradiance profile measured every metre with a LiCor PAR sensor (Eurosep Instruments, Cergy Pontoise, France).

To characterize nutrient availability at the four sampled depths, dissolved nutrient concentrations were also analysed

through colorimetric methods: ammonium (Rossum and Villaruz 1963), nitrite and nitrate (Barnes and Folkard 1951), soluble reactive phosphorus (Murphy and Riley 1962), and silicon (Rodier 1978). Dissolved inorganic carbon was measured following filtration through a Whatman GF/F glass-fibre filter, using a total organic carbon analyser (Shimatzu TOC 5000; Shimatzu France, Champs-sur-Marne, France).

Species composition

To determine species composition of the phytoplankton community, subsamples (250 mL) containing cells from each of the four depths were concentrated on a $1 \mu\text{m}$ Poretics polycarbonate membrane filter, resuspended, and fixed with Lugol's iodine solution (final volume of 1 mL). Diatom chains and colonial chlorophytes were often observed, indicating that damage due to the concentration of cells was low. The alga taxa were identified according to standard references (Bourrelly 1966, 1968, 1970). All cells (both unicellular and cells grouped in filaments or colonies) were counted (magnification $100\times$ to $400\times$) using a Nageotte chamber, and concentrations in the water column were expressed as cells per millilitre. Rare species low in concentration were taken into account only if the number of cells counted was sufficient for statistical significance: a minimum of 50 cells or colonies were thus counted per species to give confidence

limits between 37 and 66 cells (Lund et al. 1958). The diversity index, rates of change, and statistical analyses were all based on data on cell concentrations, as outlined below.

Diversity index

To characterize the species diversity, the Shannon diversity index H' was calculated from the number of cells per millilitre, p_i , of each species following the widely used formula of Shannon (1948):

$$(7) \quad H' = -\sum_{i=1}^S (p_i \log_2 p_i)$$

Species rate of change

To characterize short-term modifications of the community structure, the succession rate of change σ (day^{-1}), also called the summed difference (SD) index, was calculated by adding together changes in proportions of the i th species between times t_1 and t_2 (Lewis 1978a; Cardoso and Marques 2003):

$$(8) \quad \sigma = \frac{\sum_i \left[\left[\frac{b_i(t_1)}{B(t_1)} \right] \left[\frac{b_i(t_2)}{B(t_2)} \right] \right]}{(t_2 - t_1)}$$

where b_i is the cell concentration of species i and B is the cell concentration per millilitre of the community.

Statistical analysis

To characterize the phytoplankton community according to seasons, in terms of dominant species and groups, a factorial correspondence analysis (CA) was undertaken. The analysis was performed on data from the four sampling periods using communities from the different dates and depths. The CA allowed us to highlight dominant species and gives an indication of the temporal and spatial variability of the community structure at the seasonal time scale.

Principal component analysis (PCA) was performed for each sampling period, separately on physical and chemical data and on species concentrations from each sampled depth and date. These two ordinations of species concentration and physical and chemical conditions were then compared with each other. From the results of the two PCA ordinations, a procrustean superimposition was performed (Dray et al. 2003b) to fit the two data sets in a euclidian multivariate space. The method minimizes a distance, which is the sum-of-squares of the differences between the two data sets in terms of variability (Peres-Neto and Jackson 2001). The residuals between configurations after optimal fit for each species are represented by the length of the arrows on the procrustean superimposition. The method thus draws a parallel between some environmental changes and some species concentration variations, so that it can associate a change in species concentration with an environmental change. The ordinations of the physical and chemical parameters and the species concentrations are shown, as well as the procrustean superimposition of both ordinations. To simplify figures, only species contributing to more than $1/S$, where S is species richness, are shown, even if all species with statistically significant concentrations were included in the analysis. The

fit between original data and the ordination of the common projection is measured by the sum of singular values of procrustean analysis (Dray et al. 2003a). A randomization test (the RV test; Heo and Gabriel 1997; Dray et al. 2003b) was used to evaluate the accuracy of the fit by the procrustean method, by randomly permuting rows and columns of one of the PCAs and calculating the new co-structure of the two PCAs matrices as explained above (1000 permutations). The better the fit, the stronger is the link between the two PCA matrices. Species that contribute most to the total variability of community structure also have the highest contributions to the axes and are not necessarily dominant species. All statistical analyses were performed using the ADE4 package of the R software (Kangas 2004).

Terminology

Three time scales were used: short term, a time scale of 2 or 3 days; intermediate, the 3-week sampling period; and seasonal, a few months.

Dominant species are the most abundant in the phytoplankton community and are statistically defined by the results of a CA. Rare species are species low in density, but their density was statistically significant (more than 50 cells or colonies counted) at least at a moment in the sampling period. We consider indicator species to be those for which cell concentration varies with change in physical or chemical conditions and can thus be indicative of an environmental change or disturbance. Indicator species were identified by the procrustean analysis.

Results

Physical and chemical forcing

The four sampling periods differed in their physical and chemical conditions, e.g., stratification intensity, water temperature, availability of light, and concentrations of nutrients (Table 2). Critical concentrations were used to characterize resource conditions above which phytoplankton species are unlikely to be limited by the resource. Below these concentrations, some of the species, particularly large species, may be limited, following the size dependence of resource acquisition (Irwin et al. 2006). We hypothesized that some rare species requiring higher nutrient concentration may increase their density in response to sudden nutrient release. These critical values were $10 \mu\text{g P}\cdot\text{L}^{-1}$, $0.3 \text{ mg N}\cdot\text{L}^{-1}$ (Wetzel 2001), and $0.5 \text{ mg Si}\cdot\text{L}^{-1}$ (Reynolds 1984a). Similarly, light was considered as potentially limiting for the growth of some of the phytoplankton species, when the mean light received by cells over the mixed layer was lower than 4 to 6 $\mu\text{mol photons}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (Millard et al. 1996). A deep, well-mixed, nutrient-rich, and light-limited epilimnion was characteristic of the sampling period of early spring at La Cheze. In late spring, the phytoplankton community at Rophemel was limited neither by nutrient nor by light because of an increase of solar radiation. A shallow silicon-depleted epilimnion characterized the summer period at La Cheze, whereas the phytoplankton community in autumn at the same site was potentially limited by both nutrients (silicon, nitrate, and phosphorus) and light (data not shown). More details are reported in Pannard et al. (2007).

Table 2. Physical, chemical, and biological variables for each sampling period (data from Pannard et al. (2007); mean value \pm standard deviation).

	Rophemel	La Cheze		
	Spring	Spring	Summer	Autumn
Physical constraints				
Potential energy ($\text{J}\cdot\text{m}^{-3}$) (water column)	10.7 \pm 3.9	3.5 \pm 1.7	55.5 \pm 8.5	28.1 \pm 5.8
Mean temperature ($^{\circ}\text{C}$) (mixed layer)	15.2 \pm 1.8	9.1 \pm 0.9	22.5 \pm 0.9	16.8 \pm 0.9
Resources (mixed layer)				
Nitrate ($\text{mg N}\cdot\text{L}^{-1}$)	4.5 \pm 1.9	5.6 \pm 1.1	2.6 \pm 1.3	0.1 \pm 0.1
Ammonium ($\mu\text{g N}\cdot\text{L}^{-1}$)	3 \pm 4	65 \pm 14	93 \pm 13	28 \pm 13
Phosphate SRP ($\mu\text{g P}\cdot\text{L}^{-1}$)	43 \pm 19	42 \pm 5	16 \pm 3	6 \pm 9
Silica ($\text{mg Si}\cdot\text{L}^{-1}$)	3.5 \pm 0.6	1.1 \pm 0.2	0.3 \pm 0.1	0.4 \pm 0.2
Irradiance ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	11.6 \pm 4.8	2.5 \pm 0.9	15.2 \pm 7.6	1.3 \pm 1.0
Chlorophyll <i>a</i> ($\mu\text{g Chl } a\cdot\text{L}^{-1}$) (mixed layer)	13.1 \pm 3.7	4.7 \pm 1.2	3.9 \pm 1.0	6.6 \pm 0.5
Mean sedimentary fluxes ($\text{g}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$)	6.4 \pm 1.9	2.6 \pm 0.7	2.2 \pm 1.1	8.3 \pm 5.4

Temperature and solar radiation also underwent gradual variations over the 3 weeks of each sampling period because of seasonal transitions and meteorological forcing such as atmospheric depression. These variations were reflected in the evolution of the mean temperature of the mixed layer and the intensity of stratification during the 3-week sampling periods and had thus to be taken into account in the phytoplankton response.

Pannard et al. (2007) demonstrated in the same study that between two and three short-term forcing events occurred per 3-week sampling period, with physical and chemical modifications of different intensity. Three main physical and chemical modifications of the environment dominated within the sampling periods: an increase of dilution rate, a sudden increase of stratification intensity due to a spring warming-up (associated with a change in mixed-layer depth), and an input of potentially limiting nutrients (Pannard et al. 2007). Firstly, the phytoplankton community of Rophemel was exposed to heavy rain (Fig. 2a), which increased dilution rate of populations in the reservoir mainly on day 7. Secondly, the early spring community of La Cheze was exposed, particularly on day 10, to a strong wind event (with mean daily wind speed up to $7 \text{ m}\cdot\text{s}^{-1}$) associated with higher solar radiation, which induced a warming-up of the reservoir and increased the stratification intensity, resulting in an increase of the lake number above 1 (Fig. 2b). Thirdly, in autumn at La Cheze, a rainfall event on day 7 (Fig. 2d) induced a silicon input into the mixed layer, increasing it from 0.58 to $1.36 \text{ mg Si}\cdot\text{L}^{-1}$. A 5-day wind event just followed the rain event and was associated with a measurable increase in the availability of phosphorus on days 12 to 16, increasing it from below $1 \mu\text{g P}\cdot\text{L}^{-1}$ to $22 \mu\text{g P}\cdot\text{L}^{-1}$. However the lake number always greatly exceeded the critical value of 1 (Fig. 2d). No sudden physical and chemical modification of the environment was observed during the fourth sampling period, the summer period at La Cheze. The lake number remained greatly higher than 1 during the entire period, and only very little rainfall occurred (Fig. 2c).

Diversity index and rate of change of the phytoplankton community

Mean values of H' were calculated for sampling period and at the top three sampled depths, as we considered that

the vertical structure of diversity could provide information about the community response at the water column scale (Fig. 3a). The lowest values were observed at Rophemel, with an average over the 3-week period and the three sampled depths of 1.82 ± 0.75 (mean \pm standard deviation; $n = 7$), whereas H' at La Cheze was 2.95 ± 0.14 ($n = 8$) in April, 3.32 ± 0.24 ($n = 9$) in October, and 4.04 ± 0.20 ($n = 7$) in June. These diversity indices increased with the stratification intensity and the mean temperature of the mixed layer (Table 2). The diversity indices were also strongly correlated with the potential energy during the warming period in Rophemel in spring and the cooling period in La Cheze in autumn (Fig. 4). The other two sampling periods showed lower variations (and correlations) of temperature and potential energy (Fig. 4). A positive relation between the diversity index and the stratification intensity was thus observed on two time scales (seasonal and intermediate). However, on a daily time scale, the diversity index H' changed only gradually (Fig. 3a). The diversity index H' was thus not sensitive to physical forcing on a daily time scale but was sensitive to seasonal forcing such as that resulting from stratification and temperature.

Rates of community change were highly variable on a daily time scale compared with diversity indices, although mean values, averaged over dates and depths for each sampling period, were very close to one another, between 0.22 and 0.3 (Fig. 3b). This rate of change was not influenced by seasonal forcing, but on a daily time scale, it was controlled by the occurrence of forcing events, increasing after disturbances (Fig. 3b). This increase was sometimes observed only at the surface, e.g., sampling of Rophemel and La Cheze in June, sometimes at a depth of 7 m, as in October, and sometimes at the top three depths, as in April (Fig. 3b). This parameter was thus a good indicator of rapid change due to forcing on a daily time scale. We now examine the extent of change in the relative concentrations of species after forcing events.

Community structure

On seasonal and intermediate time scales, dominant species differed between the four sampling periods (Fig. 5). Large diatoms such as *Aulacoseira* sp. dominated the cold, well-mixed, light-limited waters in early spring at La Cheze

Fig. 2. Temporal pattern of lake number L_N (open squares) and maximal water discharge (solid diamonds) in (a) Rophemel reservoir and (b–c) La Cheze reservoir in (b) early spring, (c) summer, and (d) autumn. Horizontal broken lines indicate the critical value of L_N below which we consider there is upwelling of hypolimnetic water during the wind episode.

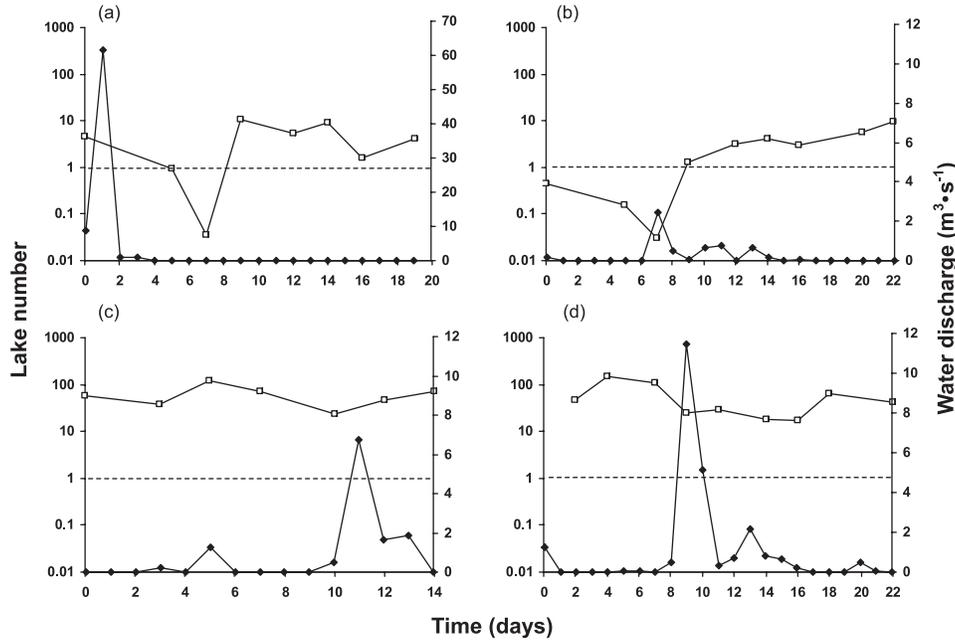
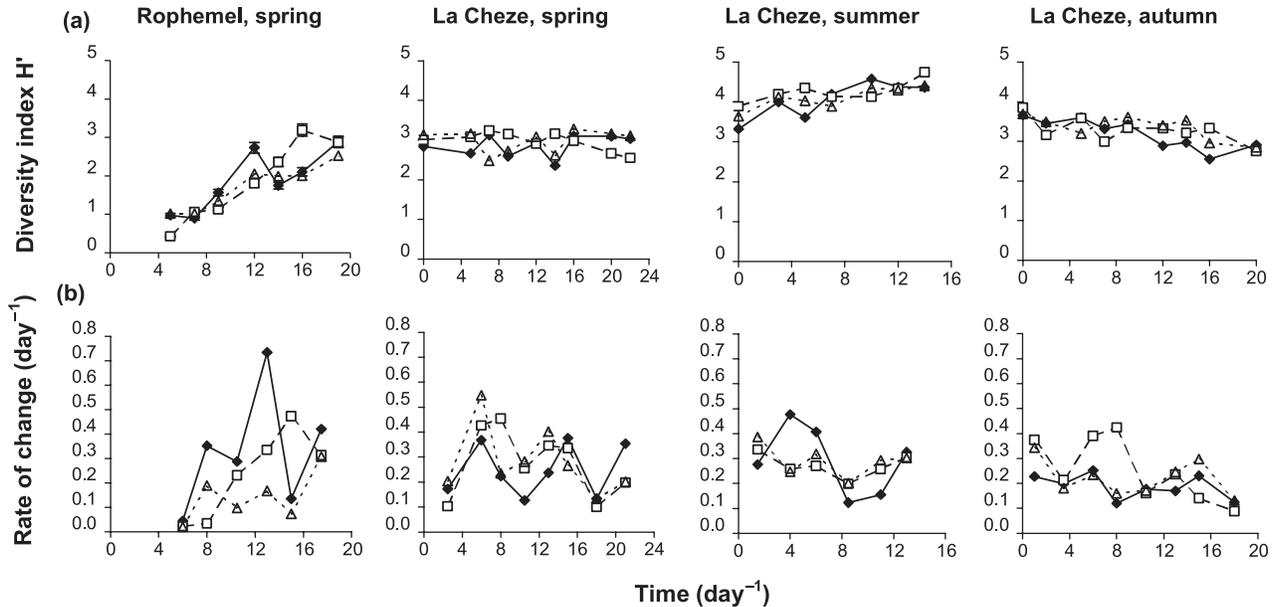


Fig. 3. Temporal patterns of (a) diversity index H' and (b) the rate of change for each sampling period and each sampled depth: 1 m (solid diamonds and solid lines), 5 m (Rophemel) or 7 m (La Cheze) (open squares and broken lines), and 9 m (Rophemel) or 13 m (La Cheze) (open triangles and dotted lines).

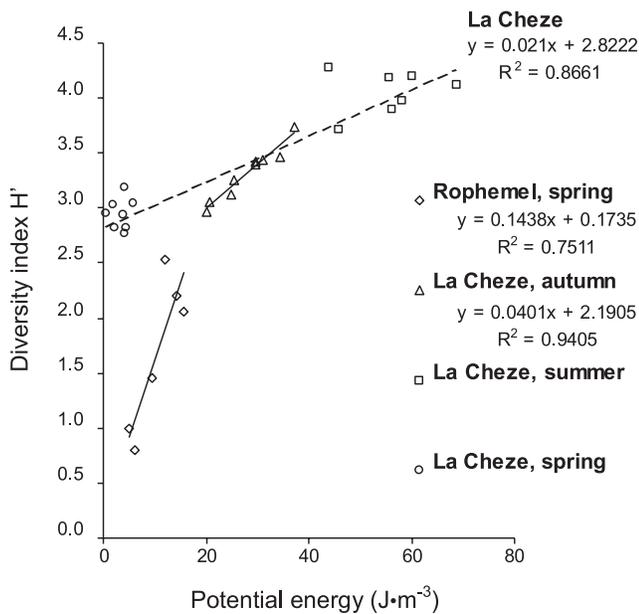


and at the beginning of the sampling period of Rophemel, whereas chlorophytes and cyanobacteria dominated the stratified, nutrient-depleted surface in summer and early autumn at La Cheze (Fig. 5; Table 2). In the short term, the concentration of some species that did not necessarily dominate the community could also be modified, as shown by the procrustean analysis (Figs. 6–9).

The procrustean analysis of Rophemel in spring ($RV = 0.514$, $p < 0.001$) highlighted a temporal variability in the

physical and chemical environment and in the phytoplankton community structure, with forcing factors and biological response on day 5 as one side of the first axis and forcing factors and biological response on days 14, 16, and 19 on the other side (Fig. 6c). The physical and chemical parameters that contributed to the first axis of the first PCA were nitrate (37.8%), silica (24.4%), and temperature (15.9%) (Fig. 6a). The contributing species to the second PCA were diatoms such as *Navicula* sp. (11.7%), *Aulacoseira* sp. (8.6%),

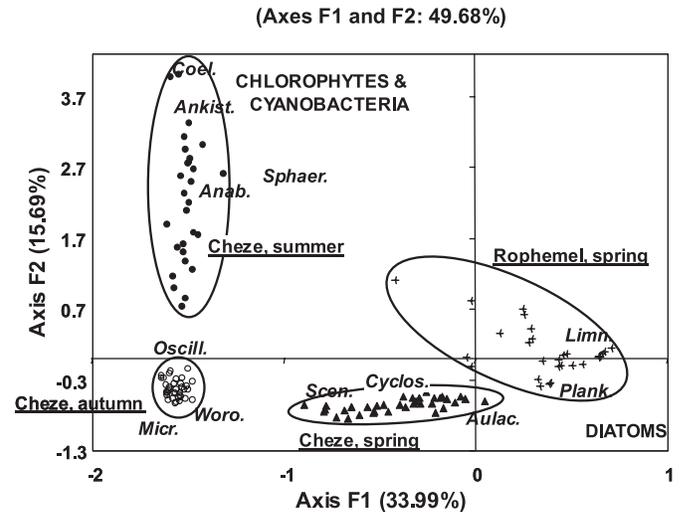
Fig. 4. Diversity index H' as a function of potential energy for each sampling period; correlations between both parameters are shown when highly significant.



Cyclotellus sp. (6.0%), and *Synedra* sp. (6.0%), chlorophytes such as *Scenedesmus* sp. (9.9%), or cyanobacteria such as *Planktothrix* sp. (7.4%) (Fig. 6b). All of these species decreased following the environmental change, a sudden increase in the water column stratification intensity. The contributing species favoured by the environmental change were colonial chlorophytes *Coelastrum* sp. (9.3%) and *Pediastrum* sp. (5.6%) (Fig. 6b). In the procrustean analysis, surface communities (1 and 5 m deep represented by the letters A and B, respectively) were on one side of the second axis of both PCAs and bottom communities (9 and 14 m deep represented by the letters C and D, respectively) were on the opposite side (Fig. 6c). The physical and chemical parameters that contributed to this second axis of the first PCA were ammonium (25.6%), light availability (mean PAR) over the mixed layer (23.9%), and temperature (13.5%) (Fig. 6a). Contributing species were the colonial chlorophytes *Sphaerocystis* sp. (18.4%), *Coelastrum* sp. (12.5%), and *Pediastrum* sp. (12.3%) (Fig. 6b). The shift, occurring on day 7 and associated with a dilution induced by a large rain event, led to the disappearance of many species, particularly diatoms, which were replaced by new ones, mainly colonial chlorophytes.

The procrustean analysis for the period of early spring at La Cheze ($RV = 0.313$, $p = 0.007$) also highlighted a temporal variability, observed both in the physical and chemical environment and in the community structure (Fig. 7c). Sampling dates before the strongest wind event (day 10) can be distinguished from sampling dates after the disturbance (Fig. 7c). Silicon (37.8%), temperature (27.4%), inorganic carbon (21.6%), and nitrate (10.4%) were the main variables contributing to the first axis of the PCA of the physical and chemical parameters (Fig. 7a). Temperature and nitrate were increased following the disturbance. Large diatoms such as *Aulacoseira* sp. (14.4%) and *Synedra* sp. (9.0%) were re-

Fig. 5. Principal component analysis of the species composition used to highlight dominant species (contributing species to the axis). The dominant species belong to chlorophytes (*Ankist.*, *Ankistrodesmus*; *Coel.*, *Coelosphaerium*; *Scen.*, *Scenedesmus*; *Sphaer.*, *Sphaerocystis*), cyanobacteria (*Anab.*, *Anabaena*; *Limn.*, *Limnothrix*; *Micr.*, *Microcystis*; *Oscill.*, *Oscillatoria*; *Plank.*, *Planktothrix*; *Woro.*, *Woronichinia*), and diatoms (*Aulac.*, *Aulacoseira*; *Cyclos.*, *Cyclotellus*).

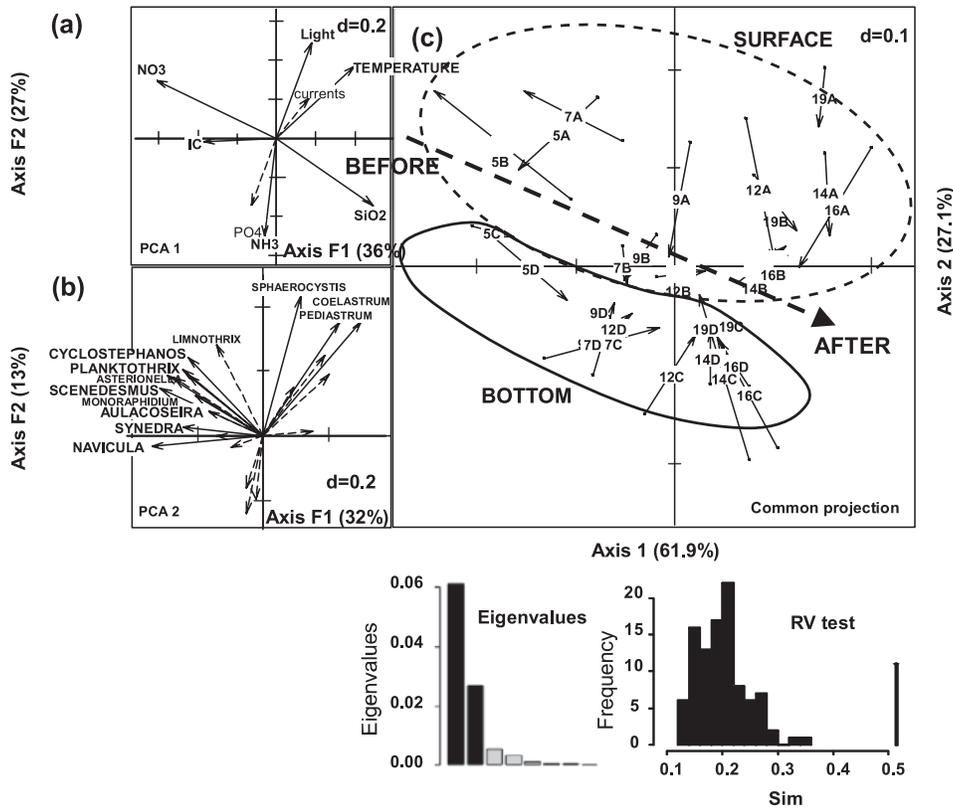


placed by smaller diatoms such as *Cyclotella* sp. (22.9%) (Fig. 7b). Some cyanobacteria and chlorophytes were also favoured by the increase in temperature and water column stratification intensity, e.g., *Aphanizomenon* sp. (8.4%) and *Sphaerocystis* sp. (7.6%) (Fig. 7b). Surface community could not be distinguished from bottom community in the procrustean analysis, indicating no depth-related variations in spring.

A spatial variability related to depth was observed in the procrustean analysis for the summer period at La Cheze ($RV = 0.547$, $p < 0.001$), with surface samples on the right side of the graph (depths of 1 and 7 m represented by letters A and B, respectively) and bottom samples on the left side (depths of 13 and 21 m represented by letters C and D, respectively) (Fig. 8c). The vertical structure of phytoplankton communities thus dominated over temporal changes. Physical and chemical parameters that were dependent on depth were temperature (34.7%), silicon (22.4%), current velocity (17.7%), and light availability over the mixed layer (14%) (Fig. 8a). Contributing species were *Anabaena* sp. (14.7%), *Monoraphidium* sp. (14.3%), *Botryococcus* sp. (12.6%), and *Coelosphaerium* sp. (9.8%), with higher concentrations in the surface layer (Fig. 8b). The second axis of the procrustean analysis was not linked to time or to the occurrence of forcing events and the inertia of the axis remained low compared with the first axis, as shown by its eigenvalue, which was five times lower (Fig. 8).

During the autumn period, vertical structuring also dominated, as shown by the procrustean analysis ($RV = 0.462$, $p < 0.001$), with surface samples (depths of 1 and 7 m represented by letters A and B, respectively) on the right side of the graph and bottom ones (depths of 13 and 21 m represented by letters C and D, respectively) on the left side

Figs. 6–9. Procrustean analysis with (a) PCA of the physical and chemical conditions (temperature, inorganic carbon (IC), silicon (SiO₂), phosphorus (PO₄), ammonium (NH₄), nitrate (NO₃), current velocity (currents), and mean irradiance in the mixed layer (Light)), (b) PCA of the species composition, with indicator species written in larger characters than other species, and (c) common projection. Solid arrows on the PCA indicate physical and chemical parameters or species, which significantly contribute to one of the two axis (compared with dotted arrows). In (a, b, and c), the *d* value indicates the size of the square for each ordination. In (c), the letters A, B, C, and D represent the four sampled depths (see each figure legend) and are preceded by the time in days from the beginning of the period. The small solid arrows in (c) show the change in the location of each date and depth between the structure of physical and chemical parameters and the community structure. The large broken arrow in (c) represents the mean modification of the community structure. Circles are used when possible to group together communities from the surface (broken circles), from the bottom (solid circles), or from the same period (double-line circles), with indication of the group nearby. Histograms of eigenvalues are shown in the bottom of the figure, with the first two solid bars representing the first two axes. The results of the randomization test are shown in the bottom right histogram, with the observed RV coefficient value represented by the vertical line. **Fig. 6.** Procrustean analysis of Rophemel in spring. In (c), the letters A, B, C, and D represent the four sampled depths 1, 5, 9, and 14 m, respectively.



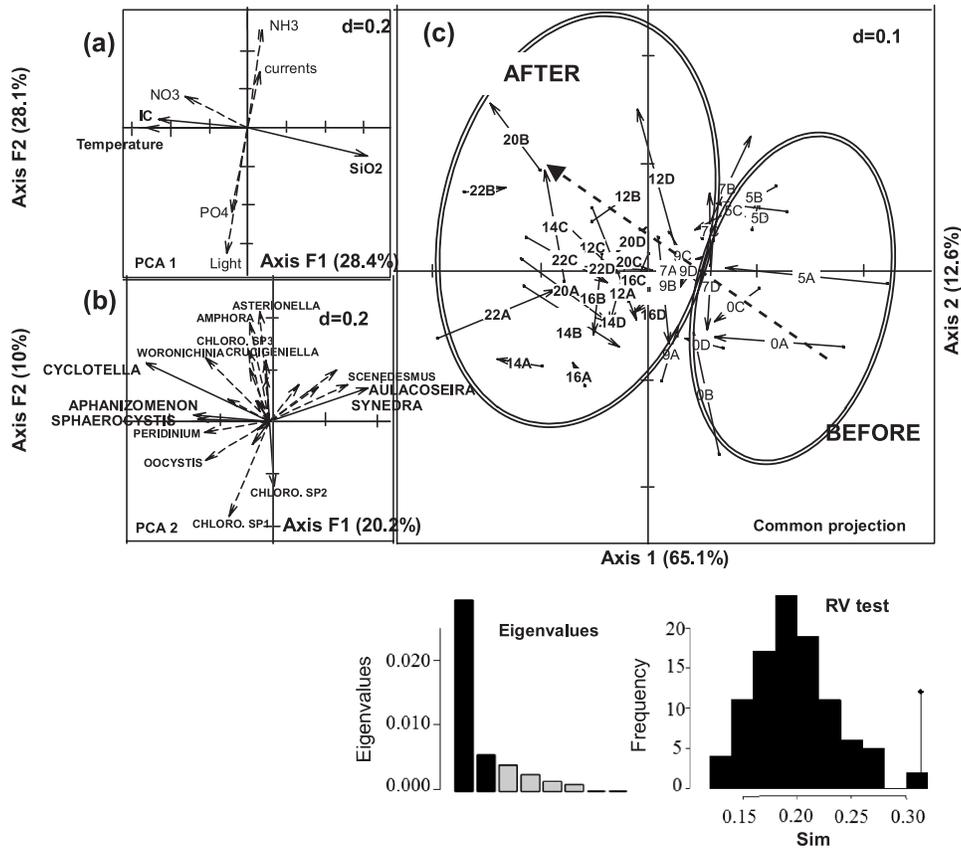
(Fig. 9c). The first axis of the PCA of the physical and chemical variables thus coincides with depth, temperature (35.2%), light availability over the mixed layer (25.1%), and inorganic carbon (20.0%), the main contributing physical and chemical variables (Fig. 9a). *Botryococcus* sp. (9.4%), *Tetraedron* sp. (8.7%), *Nephrocycium* sp. (6.3%), *Aulacoseira* sp. (5.9%), and *Asterionella* sp. (5.7%) were the main species contributing to the first axis of the PCA of community structure (Fig. 9b). The procrustean analysis also distinguished sampling dates before the 5-day wind event (highest wind speed on day 12) on the upper side of the second axis and sampling dates after on the bottom side (Fig. 9c). The second axis thus coincides with time and wind disturbance, with phosphorus (32.9%) and silicon (26.3%) as the main contributors to the short-term environmental change (Fig. 9a). The contributing species, which decreased following the disturbance, were *Pseudanabaena* sp. (8.3%), *Selemastrum* sp. (7.3%), and *Cosmarium* sp. (6.9%). Large

diatoms such as *Aulacoseira* sp. (6.3%) and chlorophytes such as *Coelastrum* sp. (5.7%) were favoured by nutrient inputs (Fig. 9b). A shift in the community structure was thus observed in parallel with a change in nutrient availability.

Discussion

Depending on forcing events, modifications of the community structure were variable and induced by a change in the availability of resources or in the intensity of stratification. Shifts in the community occurred over a few days, during and following disturbances, and no return to the original community structure was observed. In several of the sampling periods, a gradual change of physical and chemical conditions occurred on a weekly time scale, as shown by Pannard et al. (2007), leading to significant modifications of the phytoplankton community between the beginning and the end of the sampling period. Forcing affected light and nutrient avail-

Fig. 7. Procrustean analysis of La Cheze in early spring. In (c), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



ability and stratification intensity at different time scales, which were in turn reflected in phytoplankton dynamics (Fig. 10). Seasonal modification of the phytoplankton community structure (represented by the large solid arrow in Fig. 10) shows change in the concentration of dominant groups (cyanobacteria, diatoms, and chlorophytes) and in the diversity index. Modifications on a time scale of a few weeks, represented by the small solid arrow (Fig. 10), show similar changes to seasonal modifications, but to a lesser extent, observed over the time scale of the sampling period, whereas shifts in the phytoplankton community on a time scale of a few days, represented by the small dotted arrow (Fig. 10), characterize changes in concentration of indicator species and in species turnover.

Initial community structure: a response to seasonal forcing

The community in place (i.e., the dominant species) changed with season, being mainly diatoms during the nutrient-repleted and well-mixed conditions and mainly cyanobacteria and chlorophytes during the stratified period. The community structure, in terms of dominant species, may be regarded as a response to the seasonal forcing. The initial community structure may influence the response to short-term physical forcing, as the initial conditions and competing species that make up the community represent key factors affecting the outcome of competition (Huisman and Weissing 1999). The response to disturbance will thus change with season.

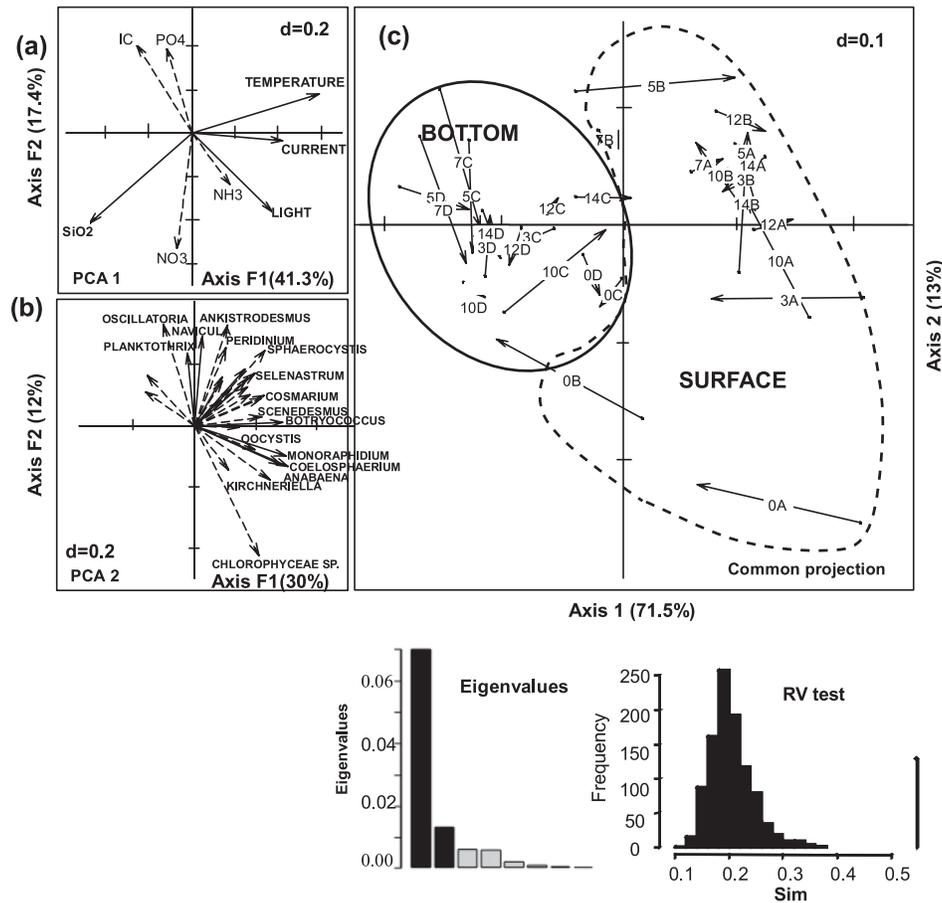
Short-term physical forcing and community responses

During and following the sudden environmental changes, indicator species responses occurred over time scales of a few days. Following a rainfall event in Rophemel reservoir in late spring, a transition between large diatoms and colonial chlorophytes was observed on a time scale of a few days. This transition was in accordance with expectations from phytoplankton succession (Garnier et al. 1995). The higher growth rate of chlorophytes, about twice that of diatoms, may have been an advantage that counteracted the higher dilution rate associated with heavy rainfall.

The absence of return to the original community structure at the end of the sampling period is probably due to forcing on the intermediate time scale from changes in air temperature and solar radiation, which increased the intensity of stratification, water temperature, and light availability. Diatoms underwent higher loss by sedimentation following the disturbance, so that the populations could not be sustained, as discussed in Huisman et al. (2002). Conditions thus became more favourable for chlorophytes.

During the period of high nutrient availability in spring at La Cheze, a shift in terms of indicator species was induced by a sudden increase in the intensity of stratification and of temperature in the mixed layer. During the nutrient-replete, well-mixed, low-light conditions, large diatoms dominated the phytoplankton community in accordance with previous studies (Anneville et al. 2002), but they were replaced by a smaller diatom species following the short-term environmen-

Fig. 8. Procrustean analysis of La Cheze in early summer. In (c), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



tal change. The increase of the intensity of stratification was thus disadvantageous to large diatoms, which undergo higher loss rates by sedimentation than small diatoms in accordance with Stokes law and which require a higher mixing rate to stay in suspension.

In early autumn at La Cheze, the shift in terms of indicator species was associated with a double pulse of silicon and phosphorus at a 2-day interval in a community initially limited both by these nutrients and by light. The modification of the phytoplankton community was probably due not to external input of populations, but rather to an internal redistribution of nutrients, as species that increased, e.g., *Synedra* sp. and *Aulacoseira* sp., were already present in the water column before the disturbance, through in low concentrations. Moreover, some species were not influenced by the occurrence of the forcing events, e.g., *Oscillatoria* sp. Responses thus varied with species. Lastly, we estimated the mean growth rate from differences in species concentrations between two dates and for each depth. Mean growth rate remained plausible with values always smaller than 1-day^{-1} . We therefore favour the internal redistribution of nutrients and the shift in the community structure hypothesis.

In a community dominated by chlorophytes and cyanobacteria, the forcing events promoted the increased concentration of large colonial diatoms, with a peak of concentration on day 14. The absence of return to the original community structure, in terms of indicator species, was also due to forcing on

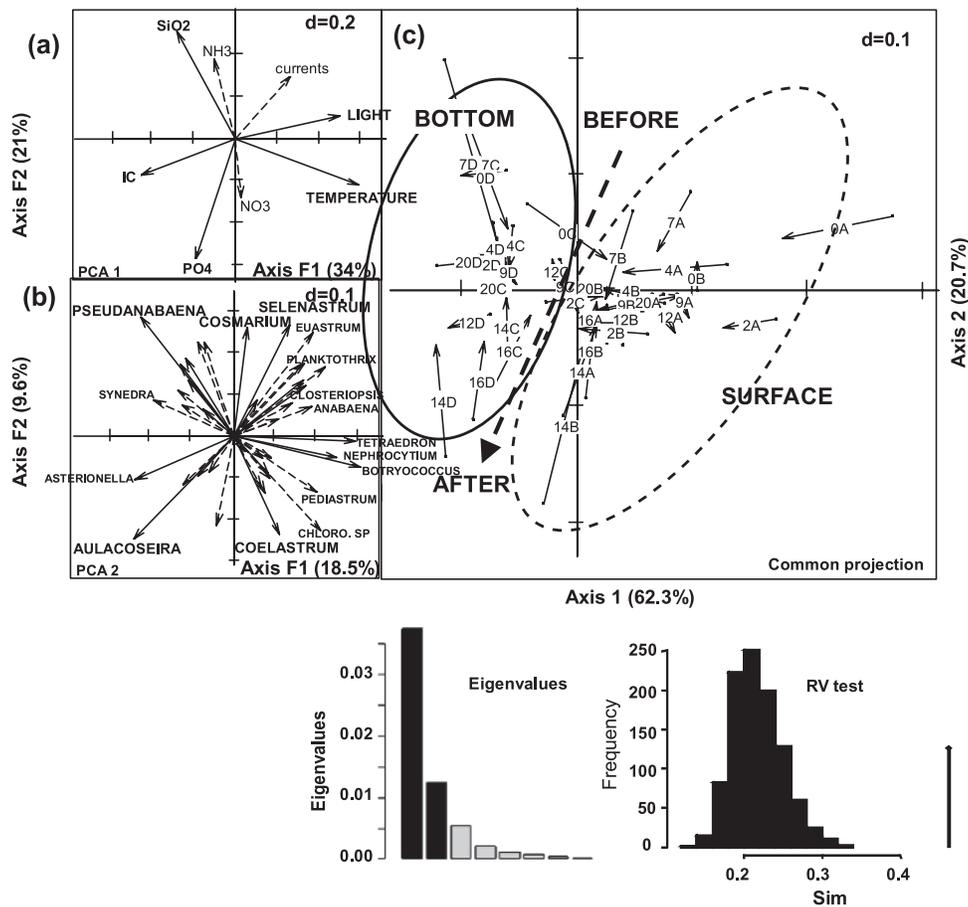
the intermediate time scale with the autumnal decrease of water temperature and light availability, which was disadvantageous to several species of cyanobacteria and chlorophytes.

Regardless of the induced environmental changes, the same response of the community was observed: over a few days, some species were replaced by indicator species, always in the direction of the seasonal succession, leading to an increase in the rate of turnover of species without a shift back to the original community. One could argue that forcing events should induce a short successional episode followed by a reversion of the seasonal succession after the events, as observed in tropical Lake Lanao, where Lewis (1978b) observed a series of successional episodes initiated by abrupt environmental changes, generally nutrient inputs, that induced a return to the early stage of the succession. The higher irregularity of resource supply in tropical lakes compared with temperate ones (Lewis 1978b) may lead to the return to an early stage of succession. In our case, the modifications of the communities after a short-term environmental change remained in the direction of the seasonal succession, which proceeded as a series of short-term physical forcings.

Resistance to short-term physical forcing induced by stratification

No shift of phytoplankton communities was observed during the strong stratification period of summer when the

Fig. 9. Procrustean analysis of La Cheze in autumn. In (c), the letters A, B, C, and D represent the four sampled depths 1, 7, 13, and 21 m, respectively.



water column was strongly stratified. During the summer period, two wind events occurred that led to a small increase of the mixed-layer depth (Pannard et al. 2007), but the wind events were not sufficient to affect L_N . The high stratification intensity of the water column and the lack of a nutrient pulse may explain the absence of response of the community structure in terms of indicator species.

The vertical segregation of phytoplankton community associated with the stratification can thus influence the response of phytoplankton community. In spring, particularly in early spring, as opposed to summer and autumn, the water column was mixed, as shown by the low potential energy, so that no vertical structuring of the phytoplankton community occurred. Consequently, only the surface community responded to forcing events when the water column was stratified, whereas both surface and bottom communities were affected when the stratification was weak, as indicated by the increase of the rate of change following disturbance events at all depths in spring and only in the surface mixed layer in summer.

Diversity index and rate of community change

The evolution of the community structure, demonstrated through multivariate analysis, indicated sensitivity to all species, whereas the two indices diversity and rate of change were, by definition, sensitive to the evolution of dominant species. Values of the diversity index between the different sampling periods and lakes are close to values given in the

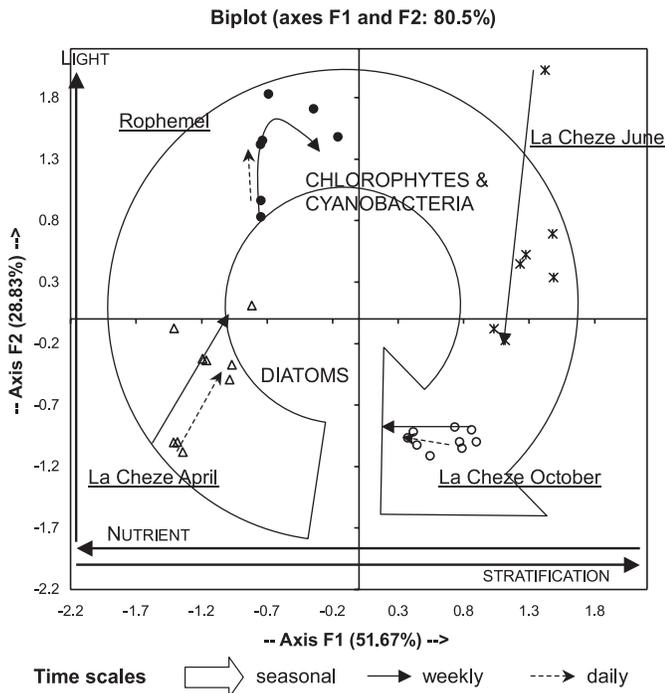
literature, often 3 or 4 (Huszar and Reynolds 1997; Padišák et al. 1998). However, the values of the rate of change between the different sampling periods and lakes were high, exceeding $0.1 \cdot \text{day}^{-1}$ (Lewis 1978a). Values higher than $0.1 \cdot \text{h}^{-1}$ have been observed in a shallow lake (Cardoso and Marques 2003) where resuspension associated with wind induced these rapid changes.

The two indices diversity and rate of change were complementary as they were controlled by different time scales of physical and chemical forcing. The diversity index is found to be a good indicator of a biological response to forcing on a seasonal and intermediate time scale, as it is mainly controlled by stratification, whereas the rate of change is a good indicator of short-term forcing events on a daily time scale.

The link observed between the stratification intensity and the diversity index may be indirect, as the intensity of the stratification represents a good proxy of temperature and seasonal cycle. The diversity increased during the year, as the temperature increased. However, one would need further investigation (in particular sampling throughout the year and later in the autumn) to be more confident of the observed relation between diversity index, temperature, and seasonal succession.

Shifts in the community structure were not reflected in the diversity index; it was the rate of change that highlighted shorter-term community responses. We had expected that forcing events would also modify the diversity index, in par-

Fig. 10. Summary of changes in phytoplankton communities over seasonal, weekly, and daily time scales (the arrows represent phytoplankton response to each forcing).



ticular when a shift in community structure was observed. However, species that decreased in concentration were replaced by other species in such a way that all niches were always occupied and, thus, diversity remained about the same. Moreover, we expected the diversity index H' to show greater fluctuations, being calculated using cell abundances. Indeed, changes in the concentration of colonial species were responsible for high variations of the index and may have affected it too strongly (Figueredo and Giani 2001). Despite using cells as the ecological unit, the diversity indices did not show fluctuations, whereas most of the forcing events induced, at least in the surface layer, an increase of the successional rate of change. In several cases, in particular in summer, the rate of change thus increased in the surface layer without a change in the species composition in terms of indicator species. This discrepancy may be explained by an oversensitivity of the parameter: the rate of change is the sum of the differences in the proportion of each species between two sampling dates, so that a modification in the concentration of a dominant species, such as large colonial ones, can affect the proportions of all other species. Large colonial species are mainly represented by cyanobacteria, which are disfavoured by mixing (Reynolds 1984a). Forcing events may affect populations of colonial species, with repercussions on the index rate of change, even if the community species structure did not really change significantly.

We demonstrated that wind disturbances can induce modifications of phytoplankton community on a daily time scale, both in terms of size structure (Pannard et al. 2007) and species composition. Through temporal variability of the envi-

ronmental conditions, short-term physical forcing may decrease competitive exclusion and thus increase species diversity (Grover 1988), even if in our study, the diversity index was not increased by the occurrence of disturbances. For example, it was demonstrated that disturbances such as an artificial deepening of the mixed layer in enclosures leading to a higher nutrient availability increased the diversity of phytoplankton in a lake with a very stable stratification, in particular with a disturbance frequency of 6 days (Flöder and Sommer 1999). In that study, undisturbed communities were compared with disturbed ones at different frequencies, where the highest value of H' was between 2.5 and 3. In our study, the phytoplankton communities changed in response to a natural pattern of disturbances, with about one forcing event per week and one large forcing event per sampling period. Changes in the diversity index may have been masked by modifications of the community by species replacement.

Forcing events may thus be seen as intermediate disturbances for the phytoplankton community (Reynolds 1988), sensu Connell's intermediate disturbance hypothesis (1978). This hypothesis postulates that disturbance opens space for colonization. On an intermediate frequency of disturbances, the community is composed of a mosaic of patches at different stages of succession so that species richness at the community level is the highest (Ricklefs and Miller 1999). With more frequent disturbances, many populations do not persist, whereas with less frequent disturbances, the mosaic of patches disappears, leading to competitive exclusion. However, the phytoplankton communities in our study change over three time scales in response to physical forcing, from a time scale of a few days to weekly and seasonal time scales. Consequently, successive disturbances affected different communities, and the species that are considered as indicators for the following disturbance may be different ones. This is also observable on the seasonal time scale, in which the initial composition of the communities is quite different, in particular with respect to the dominant group (diatoms, cyanobacteria). As the phytoplankton community changes following seasonal succession, disturbances by wind or rain events will accelerate the transitions between dominant groups, but they will not favor their codominance or increase the diversity of the community. Therefore such events were not considered here as intermediate disturbances. In sum, the phytoplankton community is seen to be embedded in a hierarchical pattern of forcing events, with short-term events accelerating community changes towards seasonal succession, which in turn responds to forces evolving over a longer time scale.

This study has shown that three time scales of physical and chemical forcing induced different responses in the phytoplankton community in terms of diversity, successional rate of community change, dominant species, and indicator species. The successional rate of change was the most sensitive response parameter to the occurrence of short-term forcing events, whereas the diversity index was most sensitive to seasonal and intermediate forcing, in particular to the stratification intensity. Most of the forcing events, while increasing the rate of change, did not induce a change in the phytoplankton community structure or in the concentration of indicator species. Only multivariate analysis of the community structure revealed that a shift in community had oc-

curred. Moreover, the community did not revert to the initial community after the disturbance because of intermediate time scale forcing having modified the background physical and chemical conditions. Short-term forcing accelerated species turnover with shifts in the phytoplankton community over a few days, always in the direction of the seasonal succession because of the intermediate time scale of forcing.

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