



The effects of wind-induced mixing on the structure and functioning of shallow freshwater lakes in a context of global change.

Lydie Blottiere

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THESE DE DOCTORAT
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Spécialité de doctorat (Biologie)

Par

Mme Lydie Blottière

The effects of wind-induced mixing on the structure and functioning of shallow
freshwater lakes in a context of global change.

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Introduction



Emerald Lake in the Candian Yukon. ©Matt Shetzer

1. Shallow lakes: context and definition

Shallow lakes have been a great source of scientific interest and questioning in the past century. The incredible biodiversity, daunting complexity and the tight historical link between these ecosystems and human societies, all represent a highway for scientific studies of all kinds. A simple analysis of the past century publications (using the “Publish or Perish” software, [Harzing 2007](#)) shows the high diversity of ecological inquiries focused on shallow lakes, from water chemistry and nutrient cycling, to modelling alternative equilibria, along with biomanipulation and trophic cascades analysis. However, because many considered inland water bodies to be insignificant component of the biosphere, they have often been ignored in global estimates of ecosystem processes in large scale studies ([Downing et al. 2006](#)).

Since the first estimations by [Schuiling in 1977](#), a great effort has been made to characterize the global abundance and distribution of freshwater bodies on Earth. Recently, [Downing and colleagues \(2006\)](#), using modern techniques, gave the staggering estimation of 304 million lakes covering approximately 4.2 million km² in area. In addition to the fact that water bodies smaller than 1 km² largely dominate lake abundance ([Schuiling 1977](#), [Wetzel 1990](#)), they showed that the two smallest size categories of lakes (0.001-0.01 and 0.01-0.1 km²) cover more area than the three largest size categories (1,000-10,000; 10,000-100,000 and >100,000 km²). Given the previous underestimation of small shallow lakes, it is likely that ecological processes handled by freshwater bodies, such as carbon and nitrogen cycling, might have also been underemphasized ([Downing et al. 2006](#)).

Shallow lakes and ponds form naturally in lowland areas with modest depressions in the landscape. The natural processes involved in the origin of shallow lakes are geological disturbances, glacial movements, or yet altered river courses or wind deflation. Humans are also

responsible for the creation of millions of small shallow lakes, either unintentionally, for instance after mining activities or willfully, for agricultural, industrial or aesthetic purposes (Wetzel 2001, Moss 2010). These lakes and ponds are extremely important for human activities and occupy a central place in the daily life of many people (for cleaning, drinking, bathing, fishing etc.). Lakes surroundings are usually densely populated either by necessity or for their aesthetic qualities (or both). This led to a strong anthropogenic pressure (pollution, eutrophication) on these ecosystems which are undergoing rapid changes in their functioning.

Lakes are also of primary importance to wildlife. As a source of drinking water and a haven for biodiversity, freshwater lakes are home to an amazing variety of species. One third of all vertebrates are estimated to live in freshwater habitats (Dudgeon et al. 2006). Among the 40 thousand fish species worldwide, 10 thousand occur in freshwater habitats (Lundberg et al., 2000, Moss 2010 p.64). A great diversity of macrophytes, algae, insects, crustaceans, gastropods, birds without forgetting the mighty hippopotamus, occupies these ecosystems. During a short work-related journey to the national park of Hwange in Zimbabwe, I witnessed how the wildlife articulates itself around shallow water ponds. More than hotspots of biodiversity, they can also be considered as hotspots of trophic interactions with a strong link with the terrestrial ecosystems.

Historically, limnologists have focused their attention on deep lakes, which differ profoundly from shallow lakes in terms of morphometry of course, but also in their functioning (Scheffer 2001). The principal difference lies in the stratification patterns and interactions with the sediments. In temperate regions, deep lakes go through an annual pattern of stratification and destratification directly linked to temperatures and wind regimes. In summer, when temperatures increase, the differential of temperature between the surface and the water beneath it leads to the formation of three layers following the water density gradient or thermocline: epilimnion (top of the lake with warm waters), metalimnion (zone of rapid change in temperatures, the size of which

depends on the steepness of temperature changes) and hypolimnion (layer with fairly homogeneous cold waters in contact with the sediment bed) (Dodds & Whiles 2010 p156-161; Reynolds 2006 p73-75). The differences in temperatures and water density between those three layers act as a barrier for heat diffusion, wind-generated turbulences, small organisms, nutrient exchanges or gas diffusion (Dodds & Whiles 2010 p160, Padisák and Reynolds 2003). By contrast, stratification in shallow lakes may occur for a few hours to a few days (*microstratifications*), but enhanced wind stress, reduced insolation or diel changes in temperature will eventually rapidly overcome any structure (Scheffer 1998 p32; Reynolds 2006 p73-75, Padisák and Reynolds 2003).

In addition to the structure of the water column, deep and shallow lakes also differ greatly in their interaction with the sediment bed. Because of the depth and stratification, the trophogenic zone of deep lakes is largely isolated from the sediment bed (especially in summer) while in shallow lakes, there is a quasi-constant interaction between the whole water column and the sediments because of the lack of long-lasting stratification. This lack of segregation is of great importance for geochemical processes (for instance, diffusion of oxygen and expulsion of carbon dioxide and phosphorus diffusion from the sediments), vertical distribution of organisms, and ability for macrophytes to colonize this habitat. In shallow lakes, recycling of organic matter is also distinct from deeper lakes. In the latter, biogenic materials sink through the water column, and while the decomposition process starts during the vertical descent, the rest of the decomposition will take place at the bottom beyond the range of entraining shear stress (Scheffer 1998 p49). In shallow lakes, the decomposition products will rapidly regain the trophogenic zone by diffusion or entrainment (Padisák and Reynolds 2003).

In all, shallow lakes can be defined as an aquatic ecosystem where at least two of the following compartments: the littoral, the sediment bed and the entire water column, are in constant interaction.

2. Structure of shallow lakes: the effect of wind-induced mixing

Because of their morphometry, shallow lakes are particularly vulnerable to the effects of wind. As previously mentioned, the wind action is one of the major sources of mixing and destratification of the water column, but it is also the main mechanism behind resuspension of the sediments. In this section, I will discuss in more details the mechanisms and consequences of wind-induced mixing.

2.1. Wind-induced mixing and resuspension events

As the wind blows over the surface of shallow lakes, surface waves are generated. The physics behind wave motion is extremely complex but there are three parameters that are highly important to understand wave action in shallow lakes: the depth (d), the fetch and the wind velocity.

The fetch is the length of the lake over which the wind blows without interruption (Figure 1). The longer the fetch, the higher the waves will be for a

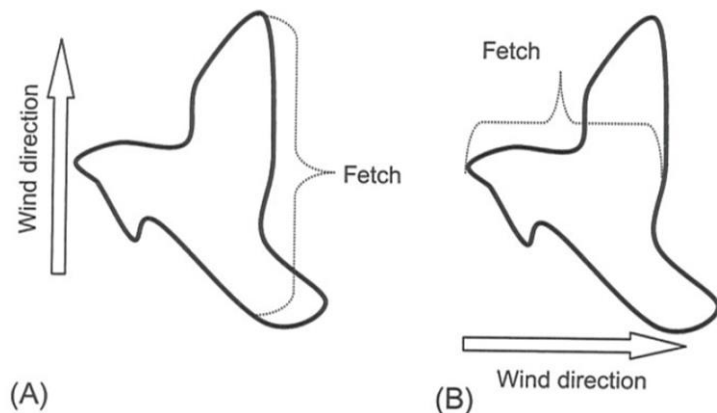


Figure 1. The fetch is the length of the lake (here irregularly shaped) on which the wind of a certain direction blows. (A) The maximal fetch of a wind blowing in the south-north direction, (B) The maximal fetch of a wind blowing in the east-west direction. From [Dodds & Whiles 2010](#).

given wind speed. This phenomenon can be easily observed in any lake on windy days. At the shoreline, often sheltered from the wind, the surface is quiet or slightly rippled. But further from the shore, waves build up and become higher as the fetch extends. The maximum height (h , in cm) of a wave on a lake appears to be proportional to the square root of the fetch (in cm) as follows:

$$h = 0.105\sqrt{\text{fetch}}$$

According to this equation, a lake with a fetch of 10 km will have a maximal wave height of 1.05 m (Wetzel 2001 p.103). When the wavelength (λ) of these waves is long enough and the lake shallow ($d < \lambda/2$), water particles underneath the surface move in an elliptical orbit. The radius of these orbits gets smaller as they move downward in the water column and flatten near the bottom. The horizontal oscillatory movements of the water at the bottom exert a shear stress on the sediment bed that can generate resuspension (Figure 2).

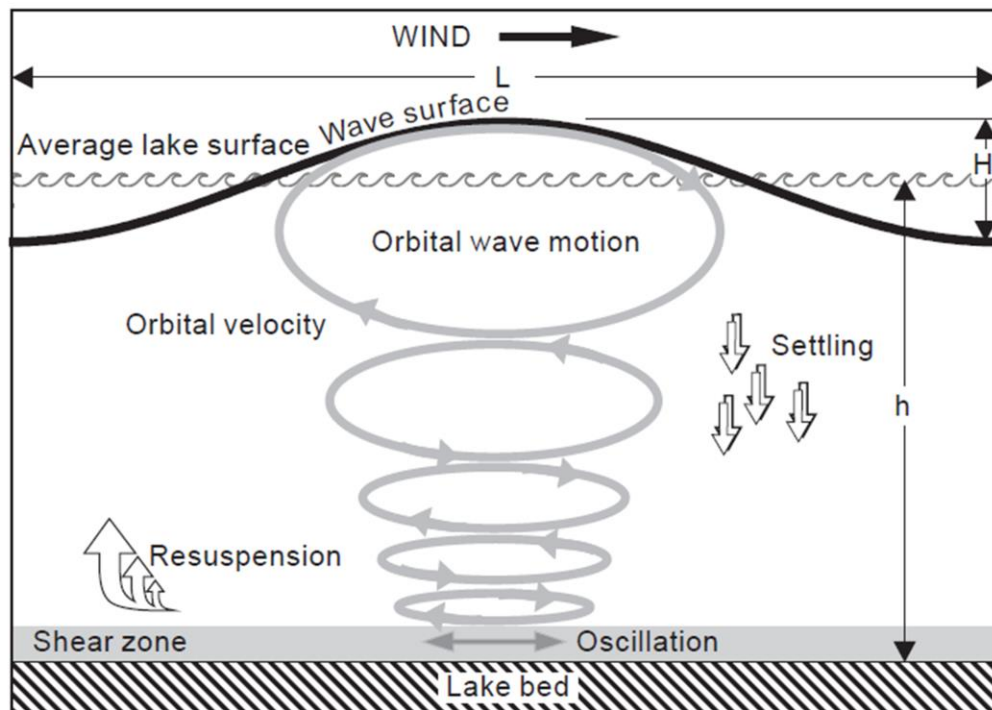


Figure 2. Schematic representation of wave action on the water column and sediment bed in a shallow lake. From Laenen and LeTourneau, U.S Geological survey, Portland Oregon, 1996.

As previously mentioned, whether resuspension occurs or not depends on the wind velocity, water depth and fetch, but also on the sediment characteristics. Typically, the fresh material at the top of the sediment bed requires a lower critical shear stress for resuspension than compacted material further down in the sediments (Bengtsson & Hellström 1992). The erodability of the sediments can be increased by bioturbation (Bakker 2012) or decreased by algae and bacteria biofilms (Lundkvist et al. 2007). Also, fine-grained particles, for instance silt and clay, are more easily transported than coarser particles (Luettich et al. 1990). Erosion of the sediment bed takes place until the depth is reached where the sediment strength/cohesiveness is equal to the erosive force (Mehta and Partheniades 1979). Therefore, the amount of resuspended material as a function of wind speed can be represented as in figure 3.

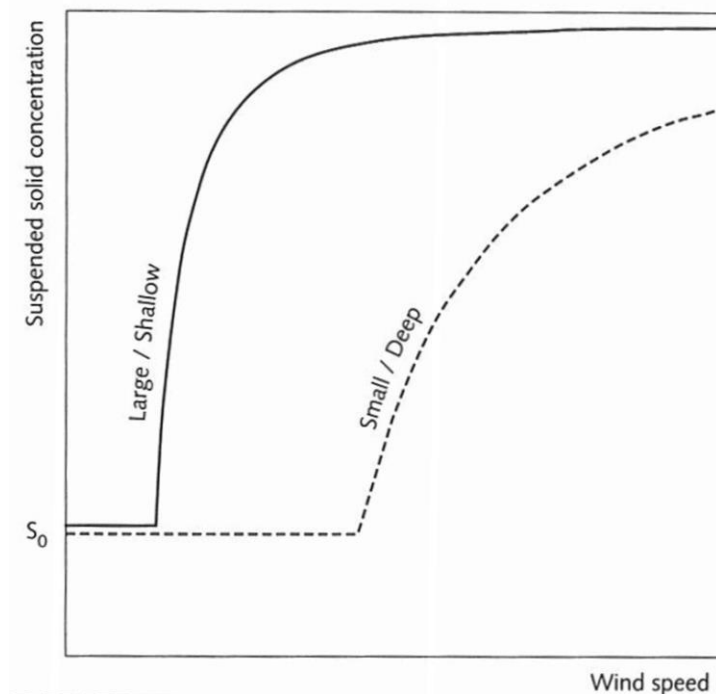


Figure 3. Theoretical link between suspended solid concentration and wind speed for a large/shallow lake and a smaller /deeper lake. No resuspension occurs for a certain range of wind velocity because either the wave energy dissipates in the water column and does not reach the sediment or the shear stress imposed at the bottom is weaker than the strength of the sediment. When the erosive force is superior to sediment strength, resuspension increases asymptotically until all suspendible material is in the water column. From Scheffer 1998.

As long as the wind blows over the lake and generates sufficient mixing, suspended particles are moved and distributed almost evenly in the lake water (Bengtsson & Hellström 1992). In some well-exposed shallow lakes, or in very large lakes, this phenomenon can be almost continuous. When the wind stops or at least is gentle enough, suspended particles settle at the bottom of the lake. The length of time that particles remain suspended in the water depends mainly on the particle settling velocity characterized by the particle size, shape and density (Hamilton & Mitchell 1996, Zhiyao et al. 2008). Fine-grained - low density particles sediment slowly while coarse - high density particles sediment quickly (Kristensen et al. 1992). The complex dynamic of sediment resuspension and deposition have been extensively studied and modelled in the 1990s' (Luettich et al. 1990, Van Duin et al. 1992, Bengtsson & Hellström 1992, Blom et al. 1992, Kristensen et al. 1992, Vlag 1992, Hamilton & Mitchell 1996).

The extent to which a lake will be influenced by the wind depends also on the topography of the lake and composition of the surroundings. Lakes surrounded by high trees blocking the wind will have smaller fetch. Human constructions as well as deforestation might alter the wind regimes experienced by a lake. An interesting example of this is from France 1997, who studied the impact of riparian deforestation on the thermocline depth in the Shield Lakes in Canada. He showed that deforestation deepened the thermocline thus compressing the hypolimnion and increased the water lake turbidity. In shallower lakes, such variations in the fetch length could greatly change the resuspension dynamics.

Macrophytes can also greatly influence the rate of resuspension in shallow lakes (Hamilton & Mitchell 1997, Jeppesen et al. 1998 chapter 25). In 1959, Jackson and Starret showed that the turbidity caused by wind-induced mixing was much higher in winter than in summer when the vegetation covered the lake bottom. In 2007, Huang et al. observed similar patterns in Lake Taihu in China where resuspension rates were significantly lower in zones covered by the floating-

leaved *Trapa quadrispinosa* than in zones without any macrophytes cover. Macrophytes, especially at high density, reduce strongly the movements of the water at the sediment surface, thus avoiding resuspension (Scheffer 1998 p48).

2.2. The effects of wind-induced mixing and resuspension on shallow lake ecosystems

2.2.1 Underwater light climate

Cycles of resuspension and sedimentation by wind-induced mixing affects the ecosystem in various ways. By increasing the concentration of suspended matter in the water column, resuspension affects greatly the underwater light climate. In water, the light intensity diminishes with depth in an approximately exponential manner:

$$I_z = I_0 e^{-Ez}$$

Where z represents the depth, I the light intensity and E the vertical attenuation coefficient for downward irradiance (Scheffer 1998 p21). When resuspension occurs, suspended particles either absorb the light or scatter it in all direction depending on their composition, size and shape (Davies-Colley & Smith 2001). For instance, clay

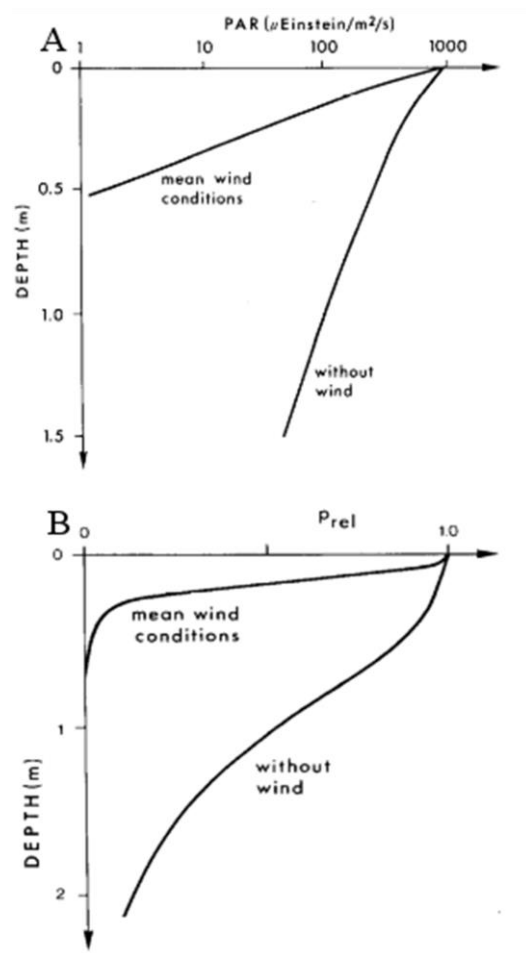


Figure 4. (A) Estimated PAR as a function of depth in condition of wind or without wind in Lake Tämnen (Sweden). (B) Corresponding predicted relative algal production (Prel). From Hellström 1991.

particles tend to cause scattering while dissolved organic substances absorb light (Davies-Colley & Smith 2001). In clear waters with little or no resuspension, light easily reach the bottom of shallow lakes, which allows for the growth of macrophytes and phytoplankton in the water column. Light attenuation due to resuspension has two major effects on the biota: increased light limitation for photosynthetic organisms and reduced visual range or kinetic perturbations of animals. In a successful attempt to quantify the effect of resuspension events on algal production in Lake Tåmnaren (Sweden) Hellström (1991) showed that algal production was reduced to 15% of its production in calm conditions (see figure 4).

In a more dramatic turn of events, the lake Apopka (128 km², mean depth 1.65m) in Florida was struck by a hurricane in 1947 that wiped out macrophytes. Since then, a thick layer of unstable sediment is frequently resuspended by windy episodes. This lake that was known for its clear water became highly turbid which completely prevented the recovery of the macrophytes bed due to the light limitation (Scheffer 1998 p5-6, Scheffer et al. 2001).

The frequency of resuspension events, which can be very high in wind-exposed large lakes, might be one of the main factors controlling phytoplankton and macrophytes growth and production in shallow lakes with important repercussions on the rest of the foodweb.

2.2.2 Nutrient release from the sediments

One of the most studied effect of wind-induced resuspension is the release of phosphorus from the sediment into the water column. Shallow lakes are very different from deep lakes in that particular matter. In deep lakes, particulate matter rich in nutrients sink through the water column and deposit at the bottom where they are mineralized. Nutrients will only return to the epilimnion with seasonal turnovers when the whole lake is mixed (autumn and spring). Following this logic, Guy et al. (1994) estimated that stratified lakes can lose up to 50% of its total phosphorus during

the summer. In shallow lakes, the short depth ensures rapid return of sedimented particles and mineralized nutrients into the water column. Therefore nutrients are unlikely to be lost from the system except when the lake is flushed, by sediment dredging or when restauration tools such as floating macrophytes bed are used to pump the nutrients.

Nevertheless, the concentration of phosphorus of the sediments in eutrophicated lakes can be considerable. S ndergaard et al. (2003) stated that the phosphorus pool in the sediment is often more than 100 times higher than the pool in the lake water. Consequently, the phosphorus content in the water will depend largely on the sediment-water interactions.

Three mechanisms are involved in phosphorus loading in shallow lakes : molecular diffusion, turbulent diffusion and resuspension (Thomas & Schallenberg 2008). The shear stress exerted at the top of the sediment by wind-induced mixing will determine which process will take place (see figure 5).

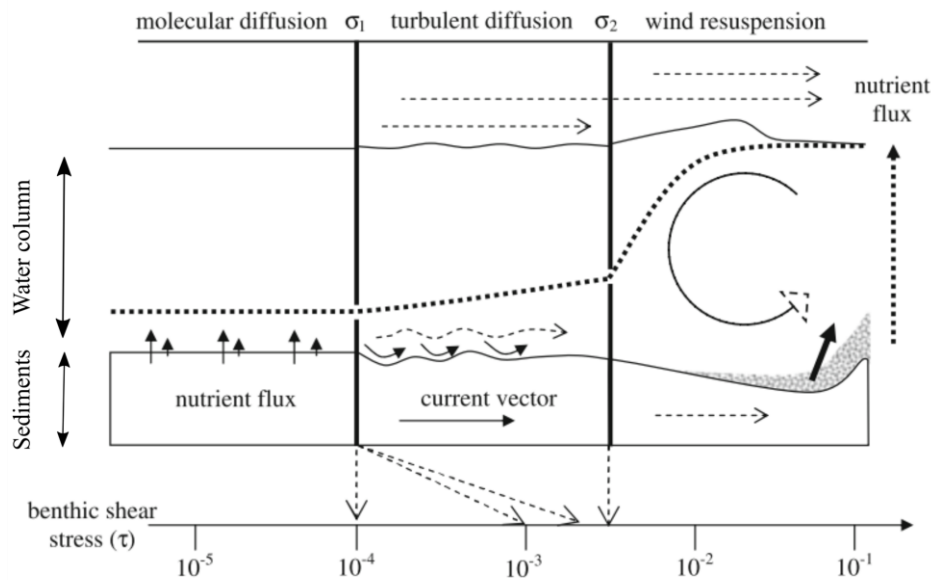


Figure 5. The three mechanisms of internal nutrient-loading in relation to wind-speed. In calm conditions, with benthic shear stress $\tau < \sigma_1$, molecular diffusion is the only loading process. When wind induces a shear stress at the bottom comprised between $\sigma_1 < \tau < \sigma_2$, pore-water nutrients are transported in eddies to the water column (turbulent diffusion). Finally, when the wind-induced mixing is high enough to erode the surface sediments ($\tau > \sigma_2$), the main mechanism of nutrient loading is through resuspension. From Thomas & Schallenberg 2008.

Molecular diffusion is a passive mechanism related to calm conditions that occur when there is a gradient of nutrient concentration between the sediments and the water column. The diffusion rate depends highly on physical and chemical properties of the water. The classic explanation of phosphorus diffusion is the Redox conditions in the surface sediment : [Einsele \(1936\)](#) and [Mortimer \(1941\)](#) described how iron (III) and phosphorus bind and precipitate under oxic conditions, whereas in anoxic conditions iron (III) is reduced to iron (II) and both phosphorus and iron are brought back in solution. In shallow lakes, we could stipulate that the water column is well oxygenated especially under mixing conditions. Soluble phosphorus coming from the anoxic sediment are therefore trapped in a narrow oxic layer at the bottom surface. When this layer becomes anoxic, for example when temperatures increase and oxygen is consumed by the organisms, this microlayer can break and release the retained phosphorus. In addition when this microlayer is saturated, phosphorus may simply pass through and reach the water column. High pH (which reduces iron-phosphorus binding, [Lijklema 1976](#)), increase in temperatures ([Jeppesen et al. 1997](#)) and benthic bioturbation, are, among other factors, also implicated in phosphorus diffusion (reviewed in [Søndergaard et al. \(2003\)](#)).

Turbulent diffusion happens when the shear stress due to wind action is enough to transport pore-water nutrients (nutrients contained in interstitial water of the surface sediments) in eddies. The fluxes of nutrient resulting from this mechanism are deemed several orders of magnitude greater than molecular diffusion ([Portielje & Lijklema 1999](#), [Haugan & Alendal 2005](#)).

Resuspension of the sediments can rapidly change the concentration of phosphorus in the water (example Figure 6; [Hamilton & Mitchell, 1997](#), [Ogilvie & Mitchell 1998](#), [Zhu et al. 2005](#)). By simulating resuspension events on sediments sampled in Lake Arresø, [Søndergaard et al. \(1992\)](#) deduced that a typical resuspension event in the lake would lead to the release of

150 mg of SRP m⁻² (SRP : soluble reactive phosphorus, used as the best estimate of the fraction directly available for algae). This number indicates that the internal loading induced by resuspension is 20-30 times more important than the release from undisturbed sediments in this lake. In other shallow lakes, inter-annual variation in internal phosphorus loading was shown to be controlled mostly by wind mixing (Jones and Welch, 1990). Thomas & Schallenberg (2008) also calculated that wind induced resuspension was the main mechanism involved in internal nutrient loading.



Figure 6. Example of a lake water changes in suspended solids concentrations (left) and the concomitant total phosphorus concentration (right) during 10 days of varying wind speed (0-2 to 5-7 to 2-3 m.s⁻¹). Lake Vest Stadil Fjord, 450 ha and mean depth 0.8 m, Denmark. Reproduced from Søndergaard et al. (1992).

However, it is important to note that while resuspension increases the concentration of suspended solids, concomitant increase in phosphorus concentration is not always observed. The release of phosphorus depends also on equilibrium conditions between the sediments and the water column. Søndergaard et al. (1992) showed that a second resuspension simulation conducted the day after the first one did not lead to any further release of soluble reactive phosphorus. In short, if there is an equilibrium between the phosphorus bound to suspended particles and the water content of phosphorus, then no release will be observed. As mentioned earlier, macrophytes can greatly reduce resuspension events, and consequently decrease the internal phosphorous loading in shallow lakes. For instance, dense macrophyte beds of submerged and

emergent plants have been shown to reduce internal loading on average by 12 and 26 mg m⁻² d⁻¹ respectively in the shallow Kirkkoja basin in Iceland (Horppila & Nurminen 2005).

2.2.3 Direct effects of mixing on phytoplankton: horizontal and vertical entrainment

Water movements generated by wind are essential to understand the horizontal and vertical distribution of phytoplankton in the water column. Far from being homogeneous, the phytoplankton distribution can be highly variable in both vertical and horizontal planes (Reynolds 2006 p.84). However, horizontal and vertical distributions do not depend on the same mechanisms and do not take place at the same time-scale.

In well-exposed lakes, wind forcing generates internal currents that transport phytoplankton cells. Using a complex model of hydrodynamic transport for a lake of medium depth (10km of fetch, 10m depth), Verhagen (1994) concluded that the horizontal distribution of phytoplankton in response to changes of wind speed can take weeks while the vertical response is usually within 24h. In the large shallow lake Taihu in China, the horizontal distribution of the buoyant, bloom-forming cyanobacteria *Microcystis aeruginosa* was shown to depend mainly on



Figure 7. Pictures taken at the Lake Viaud (Saint-Viaud, France). On the left picture, we can observe the high density of phytoplankton (*M. aeruginosa*) at the shoreline. A white dotted line is traced to show the color difference between the shore and the open lake area. On the right picture, close-up on the lake shore, where *M. aeruginosa* colonies accumulate due to wind-drift. Pictures from L. Blottière.

surface wind drift and to a lesser extent to internal currents (Wu et al. 2010). Wind drift is especially relevant for buoyant phytoplankton species that colonize the surface of the water (see figure 7).

The vertical distribution of the phytoplankton depends mainly on two parameters: their buoyancy and the degree of mixing. In calm conditions, most of non-motile phytoplankton species sink through the water column following Stokes equation:

$$v_s = \frac{2gr^2(\rho' - \rho)}{9\eta\phi}$$

Where v_s (m s^{-1}) is the sinking velocity, g (m s^{-2}) is the gravitational acceleration, r (m) is the radius of the sinking spherical particle, ρ' and ρ are the volumic mass (or density) of the particle and the volumic mass of the liquid medium (kg m^{-3}), respectively. η ($\text{kg m}^{-1} \text{s}^{-1}$) is the medium viscosity and ϕ is the form resistance factor (dimension-less) that captures the resistance to sinking due to the shape of the particle relatively to a sphere ($\phi_{\text{sphere}} = 1$) (Padisák et al. 2003). Sinking is a major constraint for phytoplankton cells. In order to maintain the population, at least a fraction of the cells must stay long enough in the photic zone to accumulate enough carbon via photosynthesis for the next cellular replication (Reynolds 2006 p38).

In the equation above, only three variables, the size r , the density ρ' and the form resistance ϕ , are properties of the organism and therefore open to adaptation and/or evolution. The smaller the particle, the slower it will sink through the water column. However, a trade-off seems to exist between being small and thus being easily predated by zooplankton grazers (Padisák et al. 2003, Litchman & Klausmeier 2008), and being large and sinking more rapidly. It is also hypothesized that by sinking through the water column, larger algae increase their chance of contact with nutrients by disrupting nutrient gradients around the cell (Wetzel 2010 p345).

The cytoplasm of living cells is composed mainly of water but also contains proteins, carbohydrates, nucleic acids, and in the case of diatoms : exoskeletal structures in silica which make the cells more dense than water. This excessive density can be overcome by multiple mechanisms: oil droplets or lipids accumulation in the cytoplasm (for instance, the green algae *Botryococcus sp.* can contain lipids up to 30-40% of dry weight which enables them to float (Fogg 1965), gas vacuols in cyanobacteria (such as *M. aeruginosa* seen earlier that can colonize the surface of calm, unexposed waters), or ion regulation (which occurs mainly in species living in salty or brackish waters and consists in replacing the heavy elements Na^+ and SO_4^{2-} by the lighter element K^+ and Cl^-).

Finally, the third variable that modulates cells sinking rate is the resistance form. In a truly original and pedagogic experiment, Padisák et al. (2003) reproduced phytoplankton cells of various shapes and sizes in PVC and measured the sinking velocity through a glycerine medium (the materials were specifically chosen to respect the density difference between algae and water). They demonstrated that a large variety of forms found in natural phytoplankton (rod-like, coiled filaments, flat coenobes, etc) have $\phi > 1$ and therefore contribute to the reduction of cell sinking velocity.

These differences in sinking velocities are crucial for understanding the competition between different species. Species that can regulate their position in the water column such as swimming or buoyant species have a clear advantage in calm conditions or in wind-sheltered part of lakes compared to heavy, sinking species that rely on mixing to reach the euphotic zone. A great example of that is the bloom-forming cyanobacterium *M. aeruginosa*. This ubiquitous colonial species is well-known for its massive surface scums (centimeters thick) in eutrophicated lakes in late summer (Figure 7) (Reynolds & Walsby 1975, Paerl et al. 2001, Chen et al. 2003, de Figueiredo et al. 2004, Jöhnk et al. 2008, Wu et al. 2010). Buoyancy regulation in this species is

achieved through changes in gas vacuole:cell-volume ratio and responds to various environmental variables such as light (Reynolds 1973, Thomas & Walsby 1985, Reynolds et al. 1987, Kromkamp & Mur 1984, Wallace & Hamilton 1999), temperatures (Thomas & Walsby 1986, Kromkamp et al. 1988) and nutrients availability (Brookes & Ganf 2001). Under weak mixing conditions, this cyanobacterium enhances its access to light while shading other non-buoyant species (diatoms and green algae). In 2004, Huisman and colleagues built a competition model to predict how turbulent mixing might affect the competition between a buoyant species (*M. aeruginosa*) and sinking species (green algae and diatoms). They showed that as long as the rate of vertical flotation is higher than the rate of turbulent mixing, *M. aeruginosa* will outcompete sinking species by forming surface bloom and therefore shading other species. Conversely, when the turbulence mixing exceeds the rate of flotation, then green algae and diatoms win the competition for light and exclude *M. aeruginosa* by increasing the overall turbidity. Their model reproduced well the phytoplankton community shifts they observed in the recreational Lake Nieuwe Meer (Netherlands) (Figure 8). This rather deep lake (1.3 km², mean

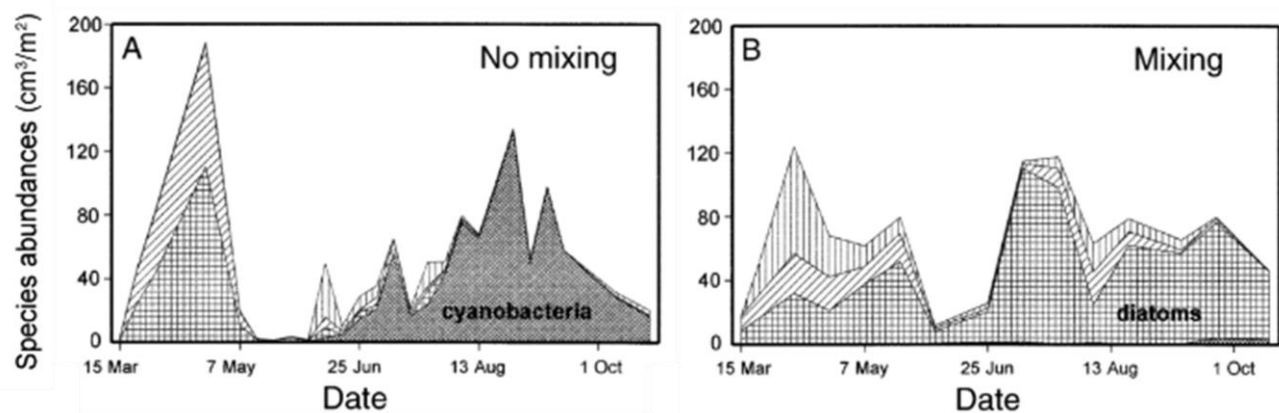


Figure 8. Seasonal pattern in phytoplankton composition in lake Nieuwe Meer. On the left, species abundance in 1990 where no mixing was applied. On the right, species abundance in 1993 with artificial mixing. Dark hatched area: cyanobacteria; boxes: diatoms, diagonal lines: green algae, vertical lines: flagellates. From Huisman et al. 2004.

depth: 18m) experiences dense blooms of *M. aeruginosa* during summer months. In order to solve this problem, bubbling systems have been installed above the sediment. This artificial mixing led to a dramatic change in community composition from almost monospecific population of *M. aeruginosa* to a mixture of green algae, diatoms and flagellates (Visser et al. 1996, Jungo et al. 2001).

This idea that the level of mixing (natural or artificial) led to shifts in community composition is not new. In the 1970s and 1980s, it became increasingly recognized that changes in mixing regimes, particularly changes in stratification-destratifications in deep lakes in autumn and spring, was responsible in part for the annual succession of phytoplankton groups (Round 1971, Reynolds 1980a, b, 1982, Reynolds et al. 1983, 1984, Sommer et al. 1986, 2012), diatoms being favored by intense mixing and buoyant species being favored by summer stratification. While artificial mixing was already used in many reservoirs in order to avoid anoxic hypolimnion and its consequences (Dunst et al. 1974); in 1984, Reynolds proposed to use intermittent artificial mixing to control phytoplankton biomass, especially in eutrophic storages suffering from cyanobacterial blooms.

Since then, artificial mixing using bubbling systems, has been widely used to control cyanobacterial blooms in eutrophic and hypereutrophic lakes. However, due to high energy consumption and cost, this method is not applicable in small lakes. Another drawback is that the influence of bubbling systems is limited to the plume of each air diffuser. Recently, another system called Solar Powered Circulation (SPC) has been tested on lakes of different sizes and depths (Hudnell et al. 2010). It proved very efficient except in very shallow lakes (less than 1m deep) where the system could not control the populations of cyanobacteria.

In shallow lakes, water mixing has a more complex outcome than in deep lakes. Whether the source of the mixing is artificial or wind-induced, the mixing extends usually to the whole water column. While it may increase water turbidity and therefore hinder algae growth and productivity, it may also resuspend nutrients, and bring back sedimented algae to the euphotic zone. In the absence of wind, sinking algae settle on top of the sediments. Many phytoplankton species are able to survive temporally in cellular resting stages that are induced by darkness. This benthic population of dormant algae (mainly composed of planktonic diatoms, vegetative colonies or asexual spores of cyanobacteria and cysts of dinoflagellates) is called the meroplankton and can be 5-10 cm thick with chlorophyll *a* concentrations up to 10-fold that of the surface waters (Reynolds 2006, Schelske et al. 1995). During wind-induced mixing, the meroplankton is brought back in the water column where it is exposed to light. Within a few hours of exposition, resting cells become physiologically active. Carrick et al. (1993) found that the resuspension of meroplankton could double the algal biomass in the surface water in Lake Apopka (Florida, surface area: 124.6 km², mean depth: 1.7m).

In a following paper on meroplankton resuspension, Schelske and colleagues (1995) demonstrated that chlorophyll concentrations above 100 µg L⁻¹ in Lake Apopka were highly correlated with wind speed, the latter explaining 53% of the temporal

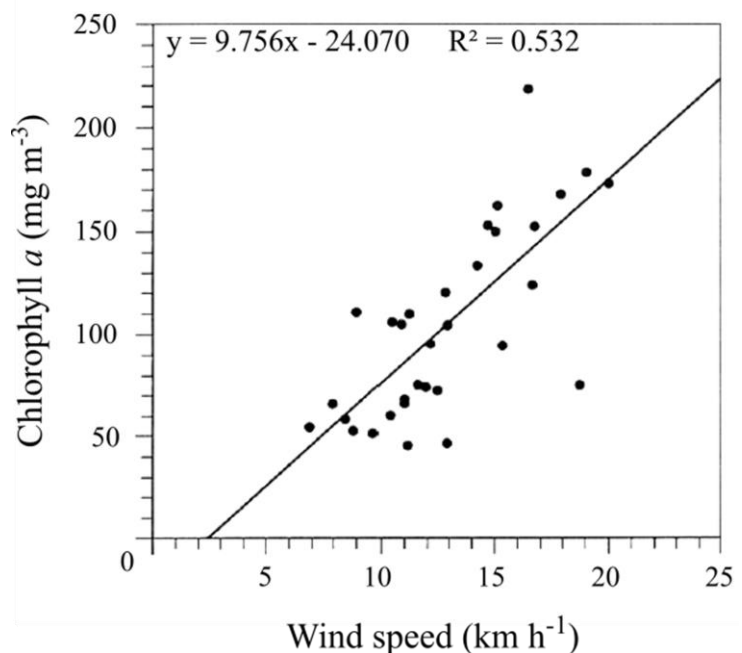


Figure 9. Regression of surface chlorophyll *a* in Lake Apopka (Florida) on average daily wind speed. Redrawn from Schelske et al. 1995.

variability in chlorophyll content (Figure 9).

Similarly, in 2004 and 2005 Verspagen and colleagues carried out field measurements in lake Volkerak (The Netherlands) in order to assess the importance of benthic recruitment of overwintering populations of *M. aeruginosa*. They discovered that without benthic recruitment, summer blooms would be reduced by 50%. In addition, it was shown that the most viable colonies were surviving in the shallow parts of the lake where resuspension events from wind action could easily inoculate *M. aeruginosa* propagules in the water column and lead to bloom formation.

2.2.3 Indirect effects of mixing on phytoplankton

In light of the foregoing, it is clear that wind-induced mixing affects the whole ecosystem of shallow lakes via different pathways: sediment resuspension, nutrient release and also via direct effect on phytoplankton recruitment and competition. Increased light-limitation due to sediment resuspension can hinder phytoplankton growth and can cause a drop in production as shown by Hellström (1991). At the same time, nutrient release, and especially phosphorus can act as a boost of phytoplanktonic growth when previous nutrient-limitation exists. And finally, the loss of phytoplankton due to high turbidity can be compensated or even overcome by benthic recruitment.

A few studies attempted to understand the relative importance of each process. In their study on meroplankton recruitment, Carrick et al. (1993), despite some uncertainties, considered that the release of nutrients following resuspension was not enough to explain the observed increase in chlorophyll *a*. In a controlled experiment, Schallenberg & Burns (2004) showed that entrainment of meroplankton was the most important effect following resuspension. The level of turbidity was not enough to induce light-limitation, and the nutrient release proved to be small

compared to the usual nutrient content of the water. Moreover, they showed that particulate total phosphorus and total nitrogen increased, but not dissolved nutrient concentration, which is the only form directly available for algae. Conversely, [Ogilvie and Mitchell \(1998\)](#) observed a positive effect of nutrient release on algal biomass and production and a positive effect of turbidity via a reduction of light-inhibition.

Clearly, the outcome of mixing is complex and depends on the duration and frequency of mixing events and on the previous state of the lake and the time scale considered. On the short term, resuspension induced by storms may deeply change the underwater light climate and the nutrient content. On larger time scale, regular wind-induced mixing plays a role on species selection and might be determinant for the trophic foodweb structure, nutrient cycles and overall productivity of the lake.

3. Shallow lakes under anthropogenic pressures – challenges ahead

3.1. Eutrophication

Shallow lakes, alongside all ecosystems, are facing multiple anthropogenic pressures, especially since the industrial revolution ([Strayer & Dudgeon 2010](#)). Among others, nutrient pollution, that is, man-made eutrophication can profoundly alter aquatic ecosystem structure and functioning. Compared to natural eutrophication, “cultural eutrophication” occurs rapidly, especially in densely populated area ([Dodds and Whiles, 2010](#)). Agricultural fertilizers, livestock practices, watershed disturbance and the release of nutrient-rich sewage into rivers and lakes are the main sources of phosphorus and nitrogen enrichment. Increased algal biomass and bloom frequency, loss of biodiversity and reduced water quality are typical consequences of nutrient loading (see Fig. 10).

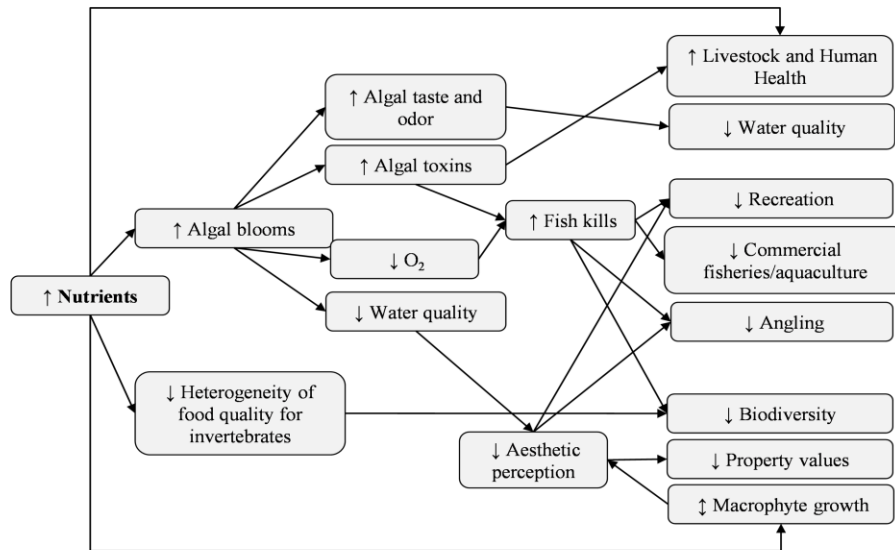


Figure 10. Some biological and economical effects of excessive nutrient loading on freshwater ecosystems. Up arrows : increase, down arrows : decrease, double arrows : increase or decrease depending on the amount of nutrient added to the system. . Reproduced from [Dodds et al. 2009](#).

Shallow lakes are particularly vulnerable to eutrophication because of their high surface/volume ratio and their intense water-sediment interactions. In order to limit the costly consequences of eutrophication, many restoration plans involving dramatic cuts in nutrient inputs have been put in place in the past 60 years such as the EU Water Framework Directive ([Søndergaard et al. 2001](#)). While some lakes respond rather rapidly to the reduced phosphorus loading, other lakes responses are very slow ([Marsden 1989](#), [Jeppesen et al. 1991](#), [van der Molen et al. 1994](#), [Phillips et al. 2005](#)). The reason behind this delay is the substantial quantities of phosphorus that accumulates in the sediments during periods of high external loading ([Søndergaard et al. 2001, 2003](#)). As seen in the previous sections (2.2.1), internal loading through

molecular diffusion, turbulent diffusion or resuspension maintain high phosphorus concentrations in the water column.

3.2. Climate change

In the last decades, climate change has been recognized as one of the major threat on biodiversity at global, regional and local scales (Heino et al. 2009). Since the 1950s, many changes due to climate warming have been observed and most of them are unprecedented over decades to millennia. Over the period 1880 to 2012, the combined land and ocean surface temperatures have increased by 0.85 [0.65 to 1.06]°C and are projected to keep on rising over the 21st century. In order to anticipate the effect of global change on temperatures, integrated assessment models have been used to produce four Representative Concentration Pathways (RCPs) based on greenhouse gases emission scenarios for the century (IPCC report, 2014). According to those scenarios, global average temperatures will increase by 1.0 [0.3 to 1.7]°C in the best case scenario and by 3.7 [2.6 to 4.8] in the worst case scenario by 2100 (Table 1).

Table 1. Projected change in global mean surface temperature for the mid- and late 21st century relative to the 1986-2005 period. From the IPCC climate change 2014 synthesis report p.60.

		2046-2065		2081-2100	
	Scenario	Mean	Likely range	Mean	Likely range
Global mean surface temperature change (°C)	RCP2.6	1.0	0.4 to 1.6	1.0	0.3 to 1.7
	RCP4.5	1.4	0.9 to 2.0	1.8	1.1 to 2.6
	RCP6.0	1.3	0.8 to 1.8	2.2	1.4 to 3.1
	RCP8.5	2.0	1.4 to 2.6	3.7	2.6 to 4.8

Changes in temperatures will not be homogeneous but rather patchy with steep increases in some regions (especially in high latitude regions with up to 10-12 °C increases) and more gradual increases in others (Figure 11). In addition to global increases in temperatures, wind regimes are expected to change and extreme events such as heat waves, droughts and floods are very likely to happen more frequently (IPCC report, 2014).

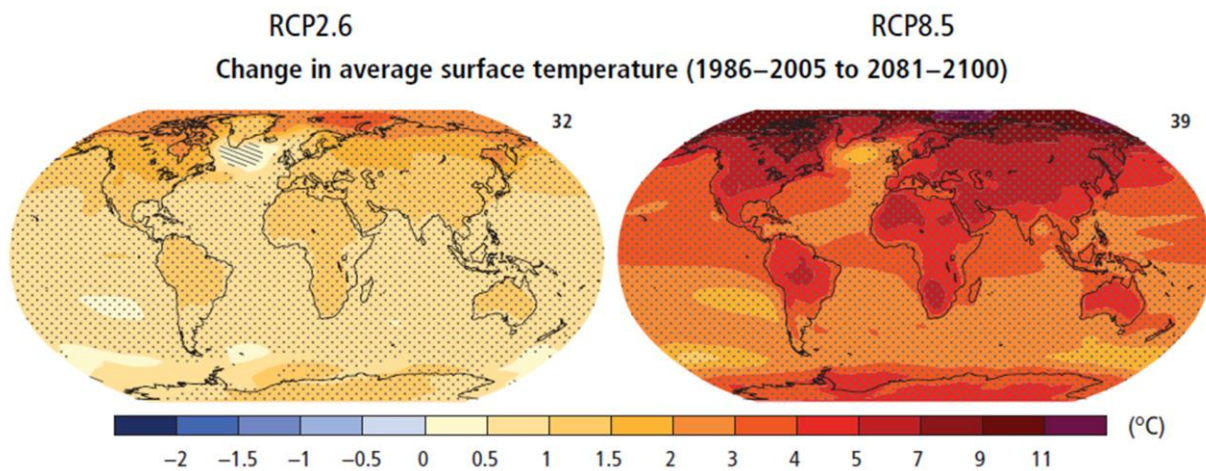


Figure 11. Illustration of two RCPs scenario on changes in average surface temperature for 2081-2100 relative to 1986-2005. The numbers 32 and 39 at the top right of each planisphere are the number of Coupled Model Intercomparison Project Phase 5 (CMIP5) models used to make these maps. In Europe for example, temperatures will increase by 1-1.5°C in the RCP2.6 scenario and by 4-5 °C in the RCP8.5 scenario. From the IPCC climate change 2014 synthesis report p.61.

Temperature is one of the most important abiotic drivers in biology. It influences enzymatic reactions speeds, growth rates, body sizes, communities organization, phenological events, distribution ranges etc. It also affects many global processes such as nutrient cycling, organic matter decomposition, and ecosystems respiration and production (Woodward et al. 2010). In freshwater ecosystems, warming also have direct physical consequences on water bodies as it affects water levels through evaporation, the structure of the water column with thermal stratification or even the duration of ice cover in boreal and temperate lakes.

Because of the urgency of the situation, many scientific studies have been published on the effect of changes in temperatures on freshwater ecosystems. One of the well-known consequences of rising temperatures and heat-waves is the increase in frequency and magnitude of cyanobacterial blooms (Paerl & Huisman 2008, Jöhnk et al. 2008, Kosten et al. 2011) which threatens water quality and ecosystem functioning. Losses in biodiversity are also predicted because of the insular nature of freshwater habitats (Strayer & Dudgeon 2010) which limits the ability of freshwater species to migrate across the landscape. Also, large-scale changes in ecosystem functioning have also been demonstrated in mesocosm experiments: for instance, increase in temperatures led to a faster rate of respiration relative to primary production causing a reduction of carbon sequestration by 13% (Yvon-Durocher et al. 2010).

Shallow lakes might be particularly vulnerable to climate change: because of the short depth, the thermal stress is expected to be greater than in deep lakes. Cold-water species will not be able to migrate in colder waters during heat-waves. Furthermore, these ecosystems are particularly at risk during droughts with longer periods of low water levels (Heino et al. 2009).

3.3. Interaction between anthropogenic stressors: warming and eutrophication

Another layer of complexity is emerging as it is becoming clear that warming and other anthropogenic pressures have synergistic effects on freshwater ecosystems (Moss et al. 2011). For instance, high temperatures have a positive effect on phosphorus release from the sediments through direct effect, anoxia-mediated effect and increased mineralization rates (Jensen & Andersen 1992, Søndergaard et al. 2003, McKee et al. 2003, Feuchtmayr et al. 2009). This phenomenon could exacerbate the effects of eutrophication that we have seen in section 3.1 (figure 10). Rising temperatures also favors floating vegetation and blooms of cyanobacteria,

which are a symptom of eutrophication, through higher growth rates and water stratifications (Paerl & Huisman 2008, Kosten et al. 2011).

Most of the water bodies in the world are suffering from cultural eutrophication and increases in temperatures seem more and more ineluctable (at least 2°C by the end of the 21st century). Therefore, in order to fully comprehend how freshwater shallow lakes function, it is necessary to take into account these anthropogenic pressures in experimental and modelling studies.

4. Objectives of the thesis

4.1 Questions and goals

The aim of this thesis is to gain a more comprehensive understanding of the influence of mixing on shallow lake ecosystems and how the processes involved articulate themselves in a context of anthropogenic pressures, here, eutrophication and global warming.

My work can be divided into three parts. First, I worked on a coupled hydrodynamic and competition model inspired from the work of Huisman and colleagues and adapted it to a shallow ecosystem. This model gave me the possibility to test multiple case-scenarios of wind-induced mixing, from short term storms (with resuspension and nutrient release) to long term effects of different wind-exposures on phytoplankton (a typical green algae versus *M. aeruginosa*) competitions (chapter I).

In a second part, I wanted to explore the effects of mixing on the whole pelagic ecosystem. As one can notice from the sections 2.2.1-2.2.2, the vast majority of studies on mixing focuses on phytoplankton. Only a few studies took into account the effects of mixing on other groups such as zooplankton (zooplankton succession: Eckert & Walz 1998, trophic-transfer: Weithoff et al. 2000, turbidity interference on zooplankton feeding rate: Levine et al. 2005), bacteria and

protists (Garstecki and Wickham 2001). To my knowledge, Weithoff's (2000) study on the effect of consecutive resuspension events is the only one to address the mixing effect on three trophic levels (bacteria, phytoplankton and rotifers). Considering the importance of wind-induced mixing on the local environment (turbidity, nutrient availability) and on phytoplankton growth and biomass, direct and indirect impacts on higher and lower trophic levels could be expected. To test this hypothesis, I carried out an experiment using mesocosms equipped with wave-makers. These new systems have been adapted from fluid mechanics to ecology by Florence Hulot (ESE, University Paris Sud, France) and Maurice Rossi (IJLRA, Paris, France). The amplitude, frequency and length of the waves are adjustable (details in chapter II). Using this, we successfully created two distinct environments: a water column fully mixed with resuspension of the top sediment bed, and a water column with only superficial mixing and no resuspension. In our experiments (2012 and 2013), we chose to work on pelagic communities without macrophytes. This restricts our conclusions to algae-dominated shallow lakes, which is typical of eutrophicated systems.

During the summer 2012, we followed the dynamic and composition of pelagic communities as well as standard chemical and physical variables during 9 weeks and compared the results between mixed and calm enclosures (chapter III). In 2013, I we applied the same mixing treatments but this time crossed with a warming experiment using polyethylen sheets causing a local-greenhouse effect. We followed the same variables as in 2012 and also analyzed the warming capacity of our heating system. This set-up allowed us to assess whether shallow ecosystems with different levels of mixing respond in a similar or different way to an increase in water temperatures (chapter IV).

4.2 Chapter 1: modelling the effect of wind on algal competition in shallow lakes

The goal of the study was to model the effect of wind speed on shallow lakes using a hydrodynamic model coupled to a phytoplankton species model. Here, the model was built to encompass three major effects of wind-induced mixing on shallow lakes: (i) sediment resuspension above a certain threshold of wind-induced mixing which changes the underwater light climate, (ii) nutrient release from those sediments, (iii) vertical distribution and competition between two phytoplankton species: a typical sinking green algae (*Chlorella* type) and a buoyant cyanobacteria *M. aeruginosa*. I studied different scenarios from short storm events to long-term effects of different level of regular mixing. In this work, I included a gradient of phosphorus concentration, from oligotrophic to hypereutrophic lakes, and also simulated a + 2°C warming to understand how lakes with differing mixing regimes will respond to anthropogenic pressures.

The key results are:

- Without warming, blooms of cyanobacteria are restricted to hypertrophic waters with low wind exposure. Wind speed above 2 m.s⁻¹ hinders bloom formation and favors the establishment of green algae, even in hypereutrophic conditions.
- With a 2°C warming, blooms of cyanobacteria are no longer confined to hypereutrophic waters, and start to form in mesotrophic waters. Green algae are excluded in low-wind and eutrophic conditions. They only win the competition in oligotrophic waters. Wind-induced mixing above 3m.s⁻¹ impairs dense bloom formation at the surface; however, there is still a coexistence of green and cyanobacteria in the water column. If the wind stops, dense surface scums will form immediately.
- Storm events lead to a decrease in phytoplankton density because of turbidity but this effect is rapidly compensated by the release of phosphorus.

The results of this modeling study were published in *Theoretical Ecology* in 2014.

4.3 Chapter 2 & 3: Testing the effects of mixing using wavemakers

Chapter 2 is a methodological paper describing the mesocosms used in the 2012 and 2013 experiments. A review of the effects of wind forcings and water motions is provided and other tools used in resuspension-mixing experiments are discussed. Theoretical description and in situ testing of the physical effect of wave makers on water motion are presented. This paper is in preparation for submission to *Limnology & Oceanography: Methods*.

Chapter 3 reports the study of the impact of mixing on freshwater pelagic communities. A 9-weeks long experiment was carried out in summer 2012 using 6 mesocosms equipped with wave-makers. Two mixing regimes were compared: “mixed” with a fully mixed water column and resuspension of the top sediment bed and “calm” with only superficial mixing and no resuspension. Standard chemical and physical variables were followed weekly alongside the dynamic of phytoplankton, zooplankton, bacteria and viruses.

The key results are:

- Mixing successfully induced resuspension on the sediment leading to a more turbid environment.
- Higher concentrations of chlorophyll *a* were found in mixed enclosures. However, we did not find any increase in phytoplankton abundance suggesting a physiological adaption to mixing.
- Photosynthetic activity was higher in mixed enclosures. This result could be explained by a positive response of phytoplankton to fluctuating light.
- Zooplankton responses varied among groups with neutral effect of rotifers and bosminas and a negative effect of mixing on copepods.

- Lysis of bacteria by viruses seemed enhanced in mixed enclosures probably because of an increased contact rate.
- Accumulation of nitrites, which was found in all mesocosms probably due to a dysfunction in the nitrogen cycle, was slightly alleviated by mixing.

This study is submitted to *Limnology & Oceanography*.

4.4 Chapter 4: impact of mixing and warming on freshwater foodwebs

In this chapter, I describe a study on the response of freshwater pelagic communities to the combined effects of mixing and warming. The experiment took place in the summer 2013. This year, 12 mesocosms were used. On half of them, polyethylen sheets were installed in order to generate a local greenhouse effect. Two mixing regimes (“Mixed” and “Calm”) were applied and crossed with the warming treatment. As in 2012, we followed for 9 weeks physical and chemical parameters as well as the dynamics of phytoplankton and zooplankton.

The key results:

- Using polyethylen sheets, we achieved in a few days a warming effect of $\sim 1^{\circ}\text{C}$ throughout the water column.
- No effect of warming was found on any of the variables followed during this experiment. However, due to technical difficulties, the warming took place only halfway through the experiment. This reduced greatly the statistical power of the analysis and calls for caution in the conclusions.
- The mixing effect was extremely similar to the one found in 2012 with similar effects on phytoplankton and zooplankton which suggest a robust and reproducible effect of mixing on pelagic communities.

- Further analyses are currently carried out in order to test the effects of mixing and warming on bacteria, virus and also size of phytoplankton and zooplankton.

Chapter I

Modeling the role of wind and warming on *Microcystis aeruginosa* blooms in shallow lakes with different trophic status

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Colonies of *M. aeruginosa* floating at the surface of the Lake Viaud in the summer 2013 (France).
Picture from: L. Blottière

Keywords: *Microcystis aeruginosa*; phosphorus resuspension; vertical mixing; wind; eutrophication; temperature

Abstract

This study focuses on the role of wind exposure, in interaction with trophic status and temperature, on the competition between two species: *M. aeruginosa* and a typical green alga. It is based on a water column model containing ecological and fluid mechanic features including mixing and shear stress at the bottom. This model addresses for the first time the impact of storm events (inducing sediment and nutrient resuspension) on algal dynamics. Simulations with realistic environmental forcings were performed with different sets of wind, temperatures and trophic conditions. With normal temperatures, conditions for dominance and bloom formation of *M. aeruginosa* in summer are restricted to hypertrophic waters with low wind exposure. Higher wind velocity (above 2m.s^{-1}) impairs the formation blooms even in phosphorus-rich waters and enhances the dominance of green algae. Warming increases the capacity of *M. aeruginosa* to develop at lower phosphorus concentrations and higher wind exposure. In hypereutrophic waters without wind, green algae are completely excluded. Nevertheless, high wind exposure (above 3m.s^{-1}) still prevents dense bloom formation and allows for the coexistence of both species. Storm events bring two counter-balancing features: sediment and nutrient resuspension. Higher turbidity leads to a decrease of phytoplankton density due to light-limitation, while the phosphorus release leads to an increase and better maintenance of *M. aeruginosa* blooms. This result depends on the timing of the event and on general wind exposure as phosphorus release only benefits to *M. aeruginosa* if exposure to wind is low.

Introduction

The past decades have seen an important increase of frequency and magnitude of cyanobacterial blooms in freshwater bodies throughout the world (Graham and Wilcox 2000; Hudnell et al. 2010a; Kosten et al. 2012). *Microcystis aeruginosa*, a cosmopolitan genus, often dominates the phytoplankton community in eutrophic lakes (Reynolds 2006; Baldia et al. 2007) and is known for its dense surface scums. Some strains produce toxins, such as microcystins, which are released into the water during the senescence of the bloom (Jacoby et al. 2000). These scums and toxins compromise drinking water production, recreational activities and above a certain threshold, may have negative effects on human health (Codd et al. 1999; Carmichael et al. 2001; Zegura et al. 2003; de Figueiredo et al. 2004; Falconer and Humpage 2005; Wiegand and Pflugmacher 2005; Hudnell et al. 2010a).

Understanding the seasonal dynamics and bloom magnitude of cyanobacteria in response to environmental conditions thus becomes a priority if prediction and eventual prevention of blooms are to be achieved. A variety of limnological, meteorological, chemical or biological processes are known to promote the growth of *M. aeruginosa* (Soranno 1997; Jacoby et al. 2000; Bonnet and Poulin 2002; Moss et al. 2003; Jöhnk et al. 2008; Kosten et al. 2012). First, increasing occurrences of cyanobacterial blooms are usually symptomatic of accelerating eutrophication, in particular of phosphorus enrichment (beyond $30 \mu\text{g.L}^{-1}$) in aquatic systems (Jacoby et al. 2000; Downing et al. 2001). Second, field observations and laboratory experiments also indicate a strong preference of *M. aeruginosa* for warm temperatures with blooms occurring predominantly during summer and beginning of autumn (Baldia et al. 2007; Havens 2008; Jöhnk et al. 2008). In addition to these two elements (lake trophic status, water temperature), a third factor seems particularly crucial: mixing due to wind or thermal effects. For instance, previous

field studies indicated that eutrophic waters, warm temperatures and little vertical mixing provide ideal conditions for surface blooms of *M. aeruginosa* (Jacoby et al. 2000; Chen et al. 2003; Jöhnk et al. 2008). This probably originates from the capacity of *M. aeruginosa* to regulate its buoyancy thanks to gas vesicles allowing it to gain better vertical positions in the light gradient and migrate to the water surface (Paerl 1988; Verspagen et al. 2004).

Several modelling studies have been performed to understand to what extent each factor might affect the phytoplankton dynamics. For instance, the roles of buoyancy regulation and mixing processes have been extensively studied by Huisman and collaborators (1994; 1999a, b; 2002a; 2004) in deep lake models. Klausmeier and Litchman (2001) studied the algal distribution in a water column under light and nutrient competition in poorly mixed conditions. Yoshiyama et al. (2009) examined the outcomes of phytoplankton competition for nutrients and light in a water column with a well-mixed surface layer and a poorly mixed deep layer. Other models reproduced the seasonal variations of phytoplankton densities in particular lakes by considering environmental forcings (Bonnet and Poulin 2002; Elliott et al. 2006; Jöhnk et al. 2008; Elliott and May 2008).

Field observations (Soranno 1997; Chen et al. 2003) and modelling by Jöhnk and collaborators (2008) indicate an important role of wind speed on phytoplankton dynamics and especially on bloom formation. In fact, there is a general consensus that buoyant species like *M. aeruginosa* profit from stable waters due to low-wind conditions as they benefit from a maximum light exposure and shade their sinking or neutral buoyant competitors (Huisman et al. 2004).

Despite a large amount of field data and observations, little attention has been paid to modelling the impact of wind on phytoplankton dynamics in shallow lakes. Yet, in addition to

increasing mixing efficiency, the wind plays another key role for shallow lakes: because of low water depth, moderate to high wind speed generates shear stress at the lake bottom which may be sufficient to resuspend sediments thus increasing turbidity and releasing nutrients in waters (Luettich et al. 1990; Bengtsson and Hellström 1992; Søndergaard et al., 2003; Zhu et al. 2005). By contrast, in deeper lakes, the sediments are protected from wave action and from most wind-generated shear. The amount of energy needed to resuspend sediments in those lakes increases steeply with depth. In shallow lakes, even moderate wind may induce mixing of the entire water column and the threshold for resuspension is lower (Reynolds, 2006 p250). Plus, the shallower the sediments are, the more intense the wind-generated shear will be. As a consequence, wind-induced resuspension may be a common event in shallow lakes and therefore an important characteristic to take into account. These features may have a strong impact on the phytoplankton bloom formation. Several models focused on sediment dynamics (settling and resuspension) (Bengtsson and Hellström 1992; Qin 2004; Chao et al. 2008), however, to our knowledge, our model is the first to capture both the effect of wind-induced mixing and sediment resuspension in shallow lakes and their consequences on algae dynamics.

In this paper, we address the significance of the wind exposure to explain the dynamics of phytoplankton species in shallow lakes with different trophic status. We developed a one-dimensional hydrodynamic model (*i.e.* a water column) coupled with phytoplankton dynamics with a buoyant cyanobacterium species (*M. aeruginosa*) and a sinking green alga. The model structure is based on the models built by Huisman et al. (2004) and Jöhnk et al. (2008). The model is driven by environmental forcings: wind, irradiance, water temperature and phosphorus input. Our aim is to gain a mechanistic understanding of the interactions between physical and ecological factors governing cyanobacterial blooms in freshwater systems. As stated by Sommer

et al. (2012), model formats vary in their degree of realism and complexity according to the questions addressed. In this gradient, our goal is to gain insights into general system behavior and to explore patterns observed in shallow lakes, especially phytoplankton dynamics, using realistic environmental parameters and forcings. Keeping this in mind, we address the following questions regarding the summer phytoplankton dynamics in shallow lakes: 1) what are the effects of different wind speed exposures, 2) what are the effects of storm events (which induce sediment resuspension and nutrient release) and their timing, and 3) how does the interaction between wind mixing and climate warming affect cyanobacterial blooms. All those questions are assessed in different trophic status scenarios.

Methods

A one-dimensional hydrodynamic water column model coupled with phytoplankton population dynamical model has been developed to simulate the phytoplankton dynamics. The model simulates the dynamics of different concentrations: nutrient (N) here phosphorus, suspended detritus (D), two phytoplankton species (P_1 , P_2) and sediment (S). The sinking green alga is P_1 and the buoyant cyanobacterium *M. aeruginosa* is P_2 .

Parameter forcings

The model is forced by three main factors: temperature (Fig. 1a), light (Fig. 1b) and wind. To cover the entire bloom dynamics (from growth period to complete crash of the population) of our species *M. aeruginosa* in a temperate environment, we specifically chose data of temperatures and light corresponding to the bloom period *i.e.*, July to November (5 months). In our model, the temperature is assumed uniform throughout the column and thus equal to the surface temperature. The underlying assumption that shallow lakes are mostly polymictic and

thermal stratification only occurs for short periods of time (from few hours to a few days) throughout summer (Reynolds 2006 p74; Scheffer 1998 p32). We used a dataset obtained through hourly measurements of water temperatures collected in a shallow lake located near Paris (France) in 2004 (unpublished data). This forcing plays only a role in determining the phytoplankton species growth rates (Fig. 1c).

The model is also forced by the incident light at the water surface (I_{in}) calculated as a function of date, latitude, longitude and cloud cover. In our model the values correspond to Paris (France) with a maximum of $1600 \mu\text{mol photon.m}^{-2}.\text{s}^{-1}$ in July slowly decreasing down to $660 \mu\text{mol photon.m}^{-2}.\text{s}^{-1}$ at the end of November (Fig. 1b) with a cloud cover set to 30%. This forcing also affects the growth rate of the phytoplankton species (see below the dynamical model, eq. 15).

Finally the wind forcing is introduced via the shear stress τ imposed at the lake free surface which is

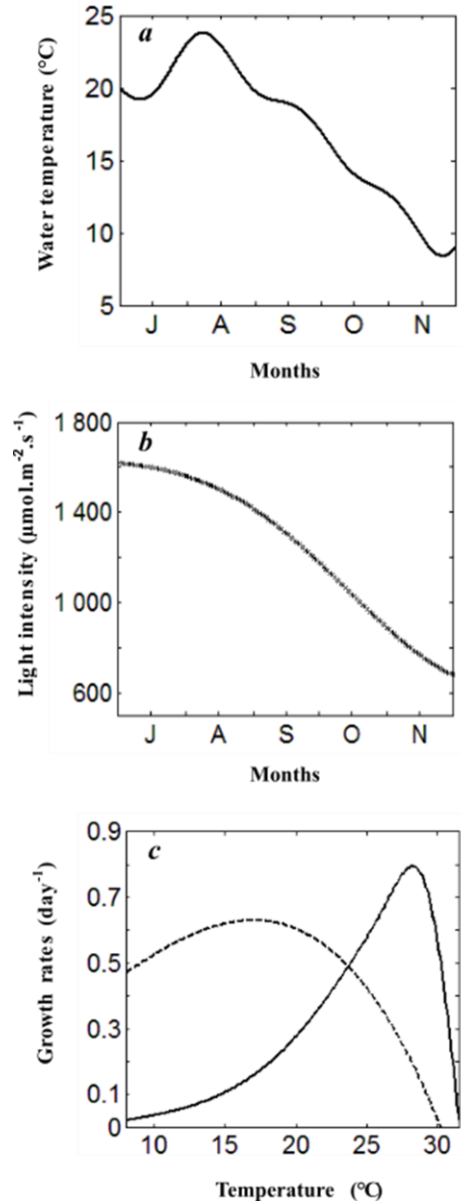


Figure 1. Model Forcings: (a) Water temperature in Celsius recorded in 2004 from July to beginning of December through hourly measurements. Data were obtained in a shallow lake south-east of Paris, France (unpublished data). (b) Daily maximum light intensity in $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ at the water surface calculated for the latitude and longitude of Paris (France) and for the same time period. (c) Growth rates of *M. aeruginosa* (plain line) and green algae (dashed line) as a function of temperature (extracted from Jöhnk et al. (2008) using the software ©g3data and fitted with ©Matlab. All rights reserved).

parameterized by the standard phenomenological law:

$$\tau_s = \rho_a C_D u_w^2 \quad (1)$$

where u_w denotes the wind velocity set at 10 m above water surface, ρ_a denotes air density and C_D is the wind drag coefficient (Chao et al. 2008). One defines the free surface shear velocity as:

$$u_{*s}^2 \equiv \tau_s / \rho \quad (2)$$

where ρ denotes water density. The wind directly produces two basic processes in a lake (a) turbulence intensity, i.e., mixing, and (b) currents. In turn, these two effects directly influence resuspension of bottom sediment, thus turbidity level and availability of resuspended nutrient. Below, it is explained how these processes are quantified in terms of u_{*s} .

The dynamical model

Each concentration X (i.e. N , D , P_1 , P_2 , S) is dependent on time and depth z (z runs from 0 at the bottom to d at the surface). Except for phosphorus $N(z, t)$ and detritus $D(z, t)$ expressed in mg of Phosphorus/m³, all concentrations are defined in mg.m⁻³.

Equation for light intensity

In the water column, the local light intensity $I(z, t)$ in the PAR range (400-700) needs to be computed since it affects phytoplankton growth rates (see below). Quantity $I(z, t)$ decreases with depth and is mathematically governed by a diagnostic equation:

$$\frac{\partial I}{\partial z} = \left(k_{bg} + k_D \frac{D}{m_D^N} + k_S S + \sum_{i=1}^2 k_{Pi} P_i \right) I \quad (3)$$

This Beer-Lambert law expresses several effects: pure lake water absorption (background coefficient k_{bg}), absorption by phytoplankton species (coefficients k_{P_1} , k_{P_2}), turbidity resulting from detritus (turbidity coefficient k_D), and turbidity due to other suspended particles (coefficient k_S). Note that the detritus being given in phosphorus biomass, one introduces $m_D^{N_1}$ the stoichiometric ratio of the phosphorus mass on the detritus biomass.

Equations for particle concentrations in the water column

Contrary to light intensity, each field $X(z, t)$ satisfies a prognostic equation i.e. a reaction-diffusion equation:

$$\frac{\partial X}{\partial t} = R_X - \frac{\partial J_X}{\partial z} \quad (4)$$

where the term R_X describes the reaction part (which will be explicitly described later) and the term $J_X(z, t)$ defines precisely the vertical fluxes by the following expression:

$$J_X(z, t) = v_X X(z, t) - d_X(z, t) \frac{\partial X(z, t)}{\partial z} \quad (5)$$

where v_X denotes the vertical sedimentation velocity of element X , and d_X its diffusivity.

Sedimentation velocities

Except for dissolved nutrients $N(z, t)$, all elements possess non-zero sedimentation velocities which are set to constant values (see Tables 1 and 2). Note that the cyanobacteria *M. aeruginosa* is assumed buoyant (lower density due to gas vesicles implying $v_{P_2} > 0$) while green algae, detritus and sediments are sinking particles ($v_{P_1}, v_D, v_S < 0$).

Diffusion coefficients

The diffusion coefficient d_X includes two terms:

$$d_X(z, t) = d_{min} + d_t(z, t) \quad (6)$$

The first term d_{min} (Table 1) is constant. It is the diffusivity due to minimum background turbulence. This implies that molecular diffusivity of constituents is neglected. The second term describes the wind action:

$$d_t(z, t) = (\lambda u_{*s} d)(z/d + z_b)(1 - z/d + z_s) \quad (7)$$

It represents a parabolic turbulent eddy diffusivity common to all constituents. The dimensionless parameter λ characterizes the intensity of turbulence. The dimensionless coefficients z_b , z_s respectively defines the location of the bottom and surface turbulent logarithmic boundary layer (Wu and Tsanis 1995, however our z_s and z_b correspond respectively to Wu and Tsanis' z_{sh} and z_{bh}).

Top boundary conditions

We impose no mass flux at the lake surface. For all elements, this is done through a zero-flux condition $J=0$.

Bottom boundary conditions

When wind blows, waves as well as currents are generated by the wind shear. For shallow lakes, this induces a bottom shear stress τ_b as a sum of a wave contribution τ_{bw} and a current contribution τ_{bTurb} :

$$\tau_b = |\tau_{bw}| + |\tau_{bTurb}| \quad (8)$$

In appendix A, the precise relation between τ_b and air velocity is indicated. When air velocity increases, bottom shear stress increases and can reach a critical value τ_{ce} capable to initiate bottom erosion or a critical value τ_{cd}^X above which the deposition is prevented. Both mechanisms are introduced via the value of the flux at the bottom:

$$J_X(z = 0, t)|_{z=0} = E_b^X + S_b^X \quad (9)$$

The term E_b expresses the erosion rate (Chao et al., 2008) as:

$$E_b^X = \beta_X E_b \quad (10)$$

With

$$E_b = \begin{cases} 0 & |\tau_b| < \tau_{ce} \\ M \left(\frac{|\tau_b|}{\tau_{ce}} - 1 \right) & |\tau_b| \geq \tau_{ce} \end{cases} \quad (11)$$

where M denotes the erodability coefficient. M and τ_{ce} are dependent on the cohesive nature of the bottom (which depends on the nature of the bottom or on the presence of rooted aquatic plants). The dimensionless variable β_X is the mass percentage of X in the eroded sediment: for S and N it is non-null, for all the other elements, it is set to 0. The percentage of phosphorus in the sediments is set to 0.0005% which means for example that for 1 kg of sediments released, 500 mg of phosphorus will be released in the water. The second term S_b^X mathematically expresses that the bottom shear stress can reach another critical value τ_{cd} above which particle redeposition is avoided.

Table 1. Physical parameters used in the model simulations

Parameters	Description	Value	Units	Source
Light				
k_{bg}	Background turbidity	0.7	m^{-1}	Jöhnk et al. (2008)
k_S	Sediment turbidity	0.03×10^{-3}	$m^{-1}.mg.m^{-3}$	Scheffer (1998)
k_D	Detritus turbidity	0.03×10^{-3}	$m^{-1}.mg.m^{-3}$	Same as sediments
Resuspension				
M	Soil erodability coefficient	50×10^4	$mg.m^{-2}.d^{-1}$	Modified from Chao et al. (2008)
u_w	Wind speed at 10m above the surface	0.5-8	$m.s^{-1}$	-
$beta_p$	Percentage of phosphorus in the sediments	0.0005	%	-
ρ_a	Air density	1225	$kg.m^{-3}$	Teeter et al. (2001)
ρ	Water density	1000	$kg.m^{-3}$	-
d_{min}	Minimum background turbulence diffusivity	0.864	$m^2.d^{-1}$	-
C_D	Drag coefficient	0.001	-	Chao et al. (2008)
g	Gravity constant	9.81	$m.s^{-1}$	-
λ	Constant to characterize the turbulence intensity	0.35	-	Wu and Tsanis (1995)
τ_{cd}	Critical shear stress for deposition	0.01	$N.m^{-2}$	Chao et al. (2008)
τ_{ce}	Critical shear stress for erosion	0.005	$N.m^{-2}$	Chao et al. (2008)
d	Water column height	3	M	-
$Fetch$	Fetch length of wind	100	M	-
z_s	Surface characteristic	2.2×10^{-4}	-	Wu and Tsanis (1995)
z_b	Bottom characteristic	0.6×10^{-4}	-	-
Detritus				
τ	Remineralization rate	30	d^{-1}	-
m_D^N	Stoichiometric ratio of Phosphorus/Biomass	1.8×10^{-3}	-	-
v_D	Sinking velocity	-1	$m.d^{-1}$	-
Sediment				
v_s	Sinking velocity	10	$m.d^{-1}$	Chao et al. (2008)

Table 2. Phytoplankton parameters used in the model simulations

Parameters	Description	<i>M. aeruginosa</i>	Green alga	Units	Source
$\mu_{max,i} (T_{opt})$	Maximal growth rate at T_{opt}	0.8	0.63	d ⁻¹	Jöhnk et al. (2008)
$T_{opt,i}$	Optimal temperatures	28	17	°C	Jöhnk et al. (2008)
l_{pi}	Loss rate	0.096	0.144	d ⁻¹	Huisman et al. (2004)
N_i	Half saturation constant for phosphorus	24	6	mg P.m ⁻³	Reynolds (1984), Baldia et al.(2007)
I_c^i	Half saturation constant for light	40	40	μmol photon.m ⁻² .s ⁻¹	Huisman et al. (2004)
m_c^i	Stoichiometric ratio Phosphorus/Biomass for 1 cell	1.8×10^{-3}	1.8×10^{-3}	-	Baldia et al. (2007)
v_i	Velocity	11.24	-0.11	m.d ⁻¹	Huisman et al. (2004), Reynolds (1984)
k_i	Light attenuation coefficient	3.4	70	μm ² .cell ⁻¹	Huisman et al. (2004)
$P(0)_i$	Initial population densities	50	100	mg.m ⁻³	-
Vol_i	Cellular volume	25×10^{-18}	33×10^{-18}	m ³	Reynolds (1984)
r_i	Cellular radius	1.8×10^{-6}	2×10^{-6}	μm	Reynolds (1984)
ρ_i	Cellular density	0.985×10^3	1.1×10^3	kg.m ⁻³	Reynolds (1984)
m_i	Cellular mass	36×10^{-9}	24×10^{-9}	Mg	Calculated

For all constituents with $v_X < 0$ (all except the buoyant *M. aeruginosa*), we define a deposition rate S_b^X (Chao et al., 2008):

$$S_b^X = \begin{cases} 0 & |\tau_b| > \tau_{cd}^X \\ v_X X(0, t) \left(1 - \frac{|\tau_b|}{\tau_{cd}^X}\right) & |\tau_b| \leq \tau_{cd}^X \end{cases} \quad (12)$$

Where τ_{cd}^X is the critical shear stress for deposition. τ_{cd}^X depends on the constituent X through

$$\tau_{cd}^X = Sh_c(\rho_X - \rho)gr_X \quad (13)$$

with Sh_c being a constant positive critical dimensionless shield parameter.

The reaction part

Let us now describe the reaction part R_X providing the biological interactions. All model parameters took standard values for lakes typical of temperate regions (See Tables 1 and 2). Sediment S is a passive scalar ($R_S = 0$). The two phytoplankton densities $P_i(z, t)$ ($i=1,2$) are driven by the local phosphorus concentration $N(z, t)$, light intensity $I(z, t)$, and water temperature $T(t)$ (in °C):

$$R_{P_i} = (F_{P_i}(N, I, T) - l_{P_i})P_i \quad (14)$$

with

$$F_{P_i} = \mu_i(T) \min \left\{ \frac{N}{N_c^i + N}, \frac{I}{I_c^i + I} \right\} \quad (15)$$

N_c^i and I_c^i is the half-saturation constant for phosphorus and for light for the species i (Baldia et al. 2007; Reynolds 2006; Huisman et al. 2004). The \min function indicates that phosphorus or light are the limiting elements for phytoplankton growth. The term l_{P_i} is the specific loss rate of the species i (Huisman et al. 2004) due to mortality or respiration. In our model this coefficient is assumed constant with temperature. Finally, the specific maximum growth rate

$\mu_i(T)$ of phytoplankton i ($i=1, 2$) is a function of the water temperature. This dependence has been fitted by analytical functions using the data from Figure 2 in Jöhnk et al. (2008) (Fig. 1c). As described in the literature (Reynolds 2006; Jöhnk et al. 2008, Pearl and Huisman 2008), *M. aeruginosa* growth rate increases very fast with temperature and reaches a maximum growth rates for temperature around 28°C.

When phytoplankton dies, it becomes detritus D which is then recycled into phosphorus thanks to the bacterial action during a decay time τ . The reaction part of $D(z, t)$ thus reads:

$$R_D = \sum_{i=1}^2 m_{P_i}^N l_{P_i} P_i - \frac{D}{\tau} \quad (16)$$

Where the ratio D/τ gives the quantity of detritus recycled into nutrients per day, $m_{P_i}^N$ represents the stoichiometric ratio of the phosphorus mass to the phytoplankton biomass.

Finally, the phosphorus is consumed by the phytoplankton species and recycled from detritus.

$$R_N = - \sum_{i=1}^2 m_{P_i}^N F_{P_i}(N, I) P_i + \frac{D}{\tau} + In_{Vol} - l_N N \quad (17)$$

Natural systems are seldom closed, so to maintain the level of phosphorus relatively stable in the environment, we added a volumic input In_{Vol} constant in space and time, and an output parameter l_N , these two parameters are set for each initial trophic status (detailed parameters in Table 3- Appendix B). The phosphorus is therefore homogeneously distributed in the water column. Note that the level of volumetric input and output of phosphorus were set in order to maintain the initial phosphorus concentration in the absence of phytoplankton species.

Numerical method

The numerical model which describes the constituent dynamics in space and time is discretized using finite differences methods with the equations written in a conservative form.

It is of second order in space. We use a semi-implicit method: the non-linear term (reaction term) is integrated explicitly using an Adams Bashforth method, while the advection diffusion terms (flux terms) are integrated by a fully implicit method. The water column of 3 m is discretized with 96 points.

Scenarios explored

We use the model to simulate the phytoplankton dynamics during 5 months, starting in summer in a shallow water column (for the numerical computations, the depth d is set to 3 m). To ease the description of figures and since our temperatures data and light were obtained during this period, we assume that computations start the first of July and end the first of December. Clearly such results should not depend very much on the precise date. As a consequence, when we mention in the following some precise dates, we refer to an interval of time between that date and the beginning of the simulations. In all the scenarios, we considered three water trophic status: mesotrophic (initial phosphorus concentration equal respectively to 20 mg.m^{-3}), eutrophic (65 mg.m^{-3}) and hypertrophic (150 mg.m^{-3}). The initial densities for both species were set to respect realistic values and allow *M. aeruginosa* to develop during the bloom period (Table 2, see Appendix C for the effect of initial densities on simulations results).

Wind less than 5 m.s⁻¹: mixing without resuspension

We present the results for two cases: a water column constantly exposed (a) to a very light breeze (ripples without crests) with a wind speed equal to 0.5 m.s^{-1} (Force 1 on the Beaufort scale) and (b) to a gentle breeze (large wavelets, crests begin to break; scattered whitecaps) with wind speed set to 4 m.s^{-1} (Force 3 on the Beaufort scale) ([Ogilvie and Mitchell 1998](#)).

Strong wind: mixing and resuspension

We study the impact of strong wind events on the phytoplankton density and dynamics. Here, we focus on simulations with a two days storm event with wind speed at 8 m.s^{-1} (Force 5 on the Beaufort scale). During the storm, the bottom shear stress is large enough to generate sediment and phosphorus resuspension. In the model, the minimum wind speed for erosion has been set to 5 m.s^{-1} (Luettich et al. 1990; Bengtsson and Hellstrom 1992; Zhu et al. 2005). The amount of sediment resuspended depends on its erodability and wind speed. The results are presented for two situations: (a) in mesotrophic water with a storm event happening mid-July to study how resuspended nutrient could impact the phytoplankton dynamic later in the season, (b) in eutrophic water with a storm event happening during the cyanobacterial peak to understand the impact of a storm on well-established species. Those storm events are simulated in calm waters (0.5 m.s^{-1}) and mixed waters (4 m.s^{-1}) to understand how general exposure affects the outcome of the storm.

Temperature increase

Finally in water columns exposed to 0.5 m.s^{-1} or 4 m.s^{-1} winds, we investigate the impact of a 2°C increase in water temperature on the algae populations.

Results

We present below the results of the three different scenarios. Note that at the end of all scenarios, both populations decrease with decreasing incident light intensity, light duration and water temperature.

Phytoplankton responses to pure mixing effect

For a constant exposure to wind velocities less than 5 m.s^{-1} , the wind affects phytoplankton density only via mixing. Let us first consider low wind conditions (0.5 m.s^{-1}) (Fig. 2 a,c, e). For mesotrophic environment (Fig. 2a), the green alga dominates throughout

the simulation with a maximum density of 484 mg.m^{-3} at the end of July and *M. aeruginosa* density stays under 50 mg.m^{-3} throughout the season. In eutrophic and hypertrophic environments (Fig. 2c, 2e), *M. aeruginosa* quickly builds up a dense population in August, *i.e.* a bloom. Note that, in the hypertrophic case (Fig. 2e), the density of *M. aeruginosa* becomes high enough ($\sim 2.6 \text{ g.m}^{-3}$) to affect noticeably the green algae growth, the density of which is globally lower throughout the simulations compared to eutrophic conditions (Fig. 2c).

For a constant exposure to medium wind conditions (4 m.s^{-1}), the results are quite different (Fig. 2b, 2d, 2f). For mesotrophic waters (Fig. 2b), the green alga reaches a higher maximum density of 732 mg.m^{-3} to be compared to 484 mg.m^{-3} in low wind conditions. Simulations with the green algae alone show that their maximum density is higher in case of mild wind (4 m.s^{-1}) compared to simulations with low wind (0.5 m.s^{-1}) (data not shown). Therefore, the wind affects positively the green algae via mixing. The increased diffusivity allows the green algae to stay longer in the water column and therefore to develop. The weak increase of *M. aeruginosa* density previously observed in low wind conditions is no longer visible (Fig. 2b). For eutrophic conditions (Fig. 2d), the green algae still dominate throughout the simulation with a density slightly higher than in mesotrophic waters though the phosphorus content is higher (Fig. 2d). More importantly, *M. aeruginosa* bloom no longer occurs since the maximum density is of 88.3 mg.m^{-3} (784 mg.m^{-3} for low wind). In hypertrophic conditions (Fig. 2f), despite the high phosphorus availability, *M. aeruginosa* density stays below 150 mg.m^{-3} while it reaches $2.6 \cdot 10^3 \text{ mg.m}^{-3}$ in the low wind conditions. The green alga is dominant. However, its density is almost identical in hypertrophic and eutrophic conditions under 4 m.s^{-1} winds. This indicates that, in this case, light availability is the limiting process for the green algae growth.

The shift in dominance observed between low (0.5 m.s^{-1}) and medium wind speed (4 m.s^{-1}) in eutrophic (going from Fig. 2 c to 2d) and hypertrophic environment (going from Fig.

2e to 2f) may be explained by the mixing process. In addition to light, mixing partially controls the vertical distribution of phytoplankton density, which in turn impacts the light availability. These distributions depend on mixing via the diffusion coefficient (d_x) and on the velocity (v_x) which is different for *M. aeruginosa* (buoyant species) and the green alga (sinking species). Let us focus on the vertical distribution of both species at different times during the simulations in the hypertrophic case.

Under low mixing (Fig. 3, top figures), the green alga is homogeneously distributed in the water column and its density is quite similar on July 11 and September 3. Consequently it cannot affect light intensity which varies between these two dates. On the contrary, *M. aeruginosa* population grows, colonizing the first 50 cm thanks to its buoyancy property: the cell concentration at the surface increases rapidly to reach $18 \cdot 10^3 \text{ mg.m}^{-3}$ at the end of the bloom period (Sept 3). Such densities impair the light penetration in the water column: 67% of the incident light is lost in the first 50 cm on September 3. By the end of the bloom, as both species density decrease, light availability increases. For higher mixing rates (Fig. 3, bottom figures), *M. aeruginosa* becomes almost as homogeneously distributed as the green alga. As in low wind case, one can observe a light intensity loss between July 11 (52% loss in the first 50cm) and September 3 (64% loss in the first 50cm). But this time, the light intensity is controlled more by the green alga than by the cyanobacterium as the latter's density stays constant between July 11 and September 3. Note that although the densities of the two algae are quite different between low and higher mixing, the light intensity loss is of the same order of magnitude. This is because the two algae species have different light attenuation coefficients (See Appendix D for details).

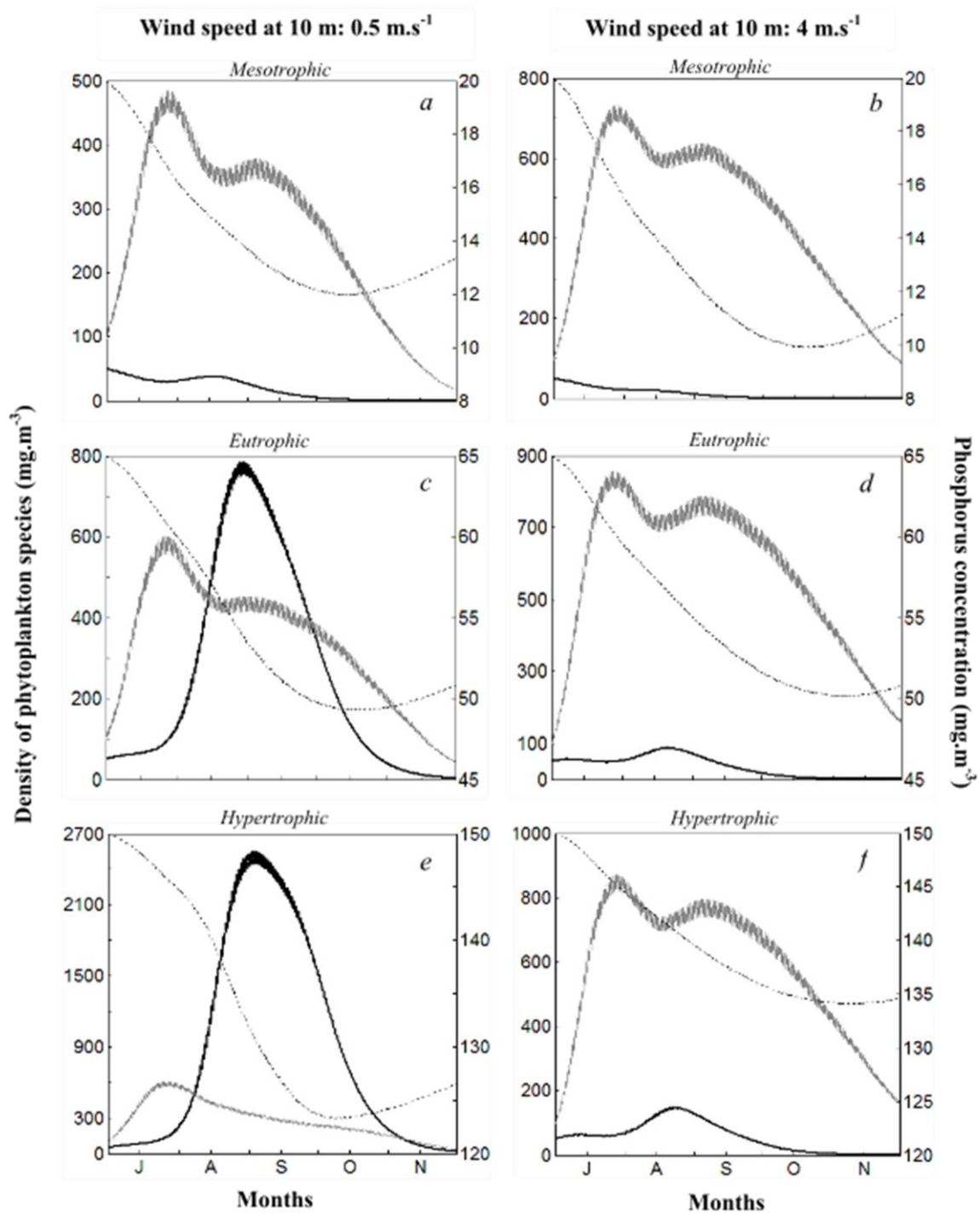


Figure 2. Effect of wind speed and trophic status on the mean value over the water column of phosphorus concentration (*dashed line*), *M. aeruginosa* density (*thick line*), and green algae density (*gray line*). Figures on the left and right correspond to constant wind speed of 0.5 and 4 m s⁻¹, respectively. The *first row* corresponds to mesotrophic conditions; the *second row* corresponds to eutrophic conditions; and the *third row* corresponds to hypertrophic conditions. Small oscillations are due to day/night variations of density. The vertical axes quantify on the left side the phytoplankton densities (in milligrams per cubic meter) and on the right side the phosphorus concentration (in milligrams of phosphorus per cubic meter)

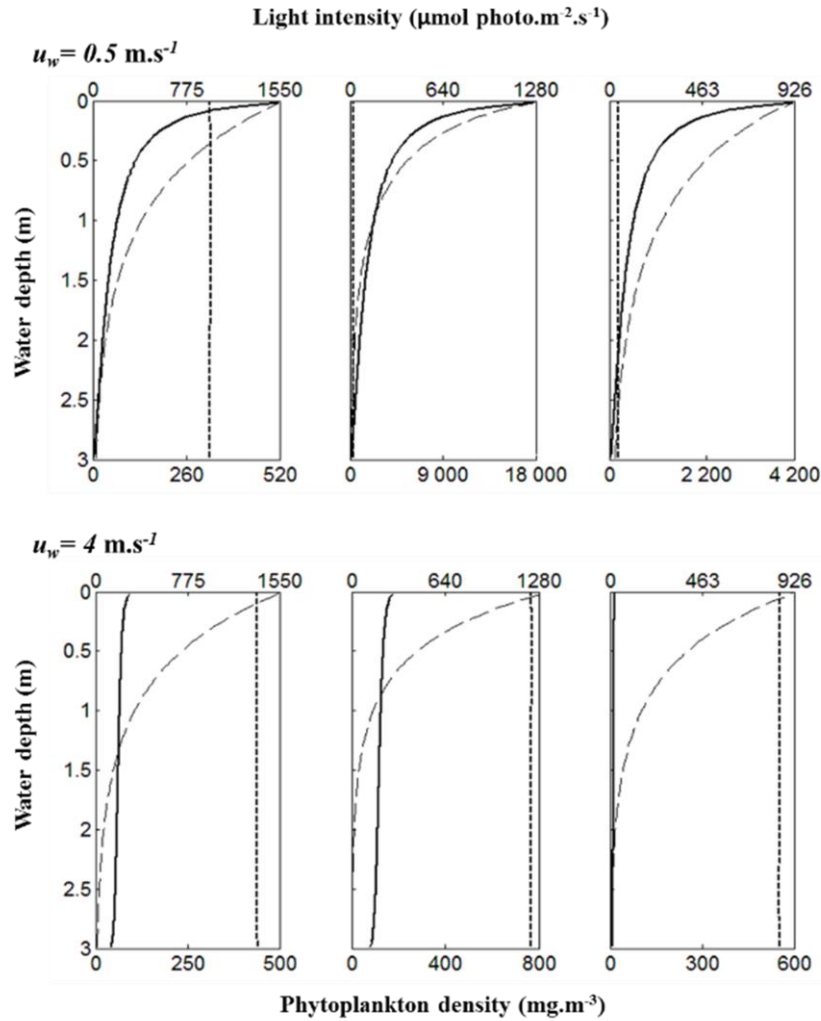


Figure 3. Vertical distribution, in hypertrophic waters, of phytoplankton densities (*M. aeruginosa*, thick line; green algae, bold dashed line) and light intensity (thin dashed line) as a function of water depth (here, 0 stands for the water surface). Top and bottom figures correspond to wind speed of 0.5 and 4 m s⁻¹, respectively. Profiles were taken on days corresponding to the beginning of the growth period (left), maximum density for cyanobacteria (middle), and end of the bloom (right).

Storm events: sediment and phosphorus resuspension

The 8 m.s⁻¹ storm event generates a bottom shear above the critical value for erosion leading to (a) the resuspension of an important quantity of sediments (around 650 g of sediments per.m⁻³ of water in the middle of the storm) and (b) a release of phosphorus previously stocked in sediments. The first effect strongly increases the turbidity level provoking a change in the underwater light climate (almost all the light is lost in the first 50 cm) and subsequently inducing a rapid decline of ~20% of both algal species during the storm

(Fig. 4). In the same time, the phosphorus concentration increases up to 400 mg.m^{-3} during the storm.

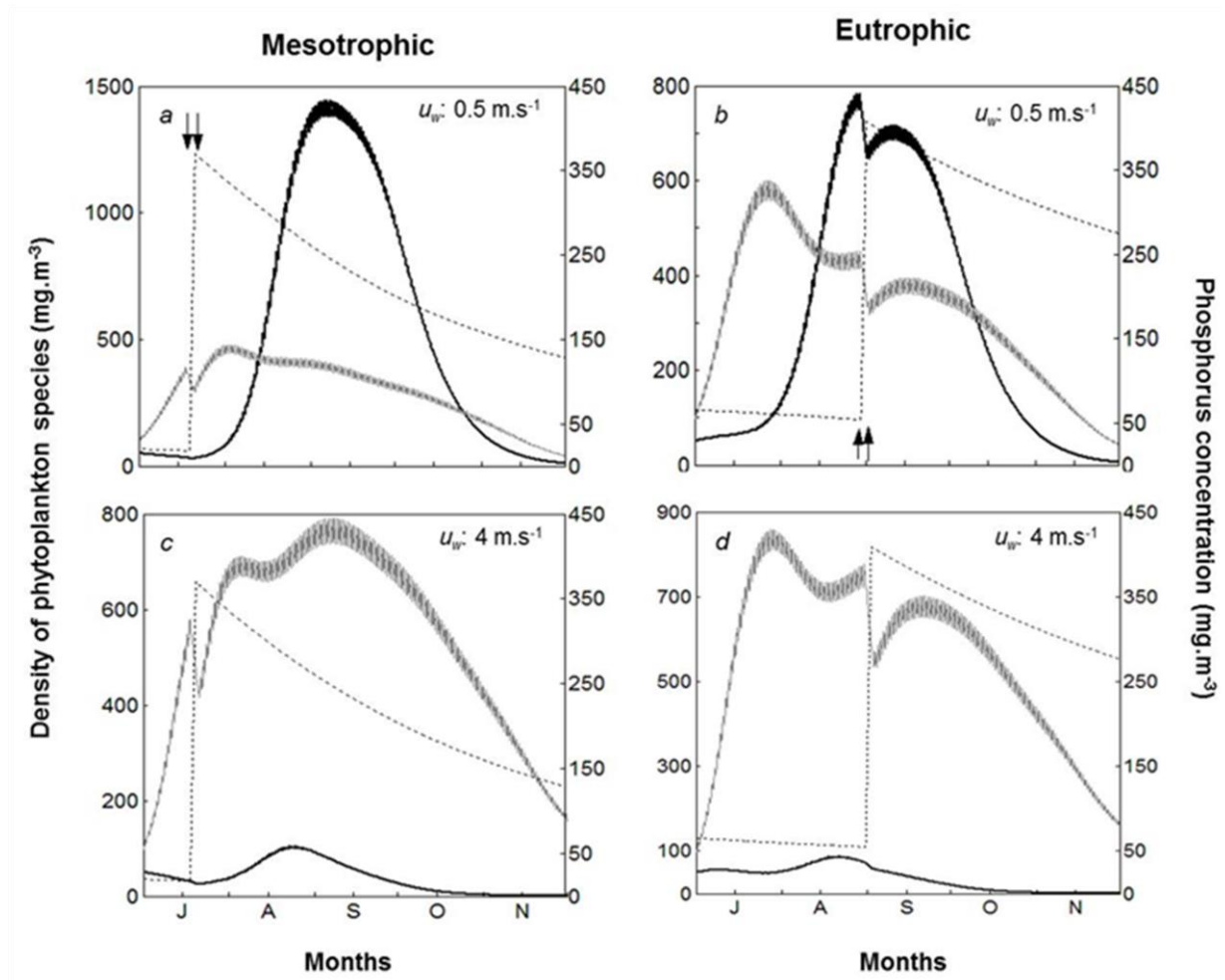


Figure 4. Effects of storm events (wind speed of 8 m s^{-1} during 2 days) on phosphorus concentration (dashed line), densities of *M. aeruginosa* (thick line), and green algae (gray line). Left and right figures display simulations for mesotrophic and eutrophic water, respectively, with storm happening at the end of August and mid-July, respectively. a, b Data for a storm event happening in a low wind exposure environment (0.5 m s^{-1} constant speed). c, d Data for a storm event happening in a medium wind exposure environment (4 m s^{-1} constant speed). Arrows indicate the beginning and the end of the storm.

In eutrophic waters with low regular wind exposure (Fig. 4b), the storm occurs during the cyanobacterium peak. The subsequent phosphorus release allows *M. aeruginosa* to maintain high densities longer in the season compared to simulations without any storm event. For instance, on mid-September (Fig. 4b), *M. aeruginosa* mean density is around 715 mg.m^{-3} after the storm event to be compared to 650 mg.m^{-3} without storm (Fig. 2c). However, the

overall dynamics is not much modified in terms of magnitude: the green algae dynamics is very similar, which suggests that it does not benefit from the resuspended phosphorus (Fig. 4b and 2c).

In eutrophic waters with medium regular wind exposure (Fig. 4d), the storm event does not change the dynamics of both species except for a slightly lower global density of the green algae after the storm compared to simulations without storm (Fig. 2d).

In mesotrophic waters with low regular wind exposure (Fig. 4a), the storm event happens just before the beginning of the cyanobacterial development. *M. aeruginosa* density reaches a maximum mean density of $1.4 \cdot 10^3 \text{ mg.m}^{-3}$ (Fig. 4a), which is much higher than in absence of a storm (Fig. 2a). As in eutrophic waters, the green alga does not benefit from the storm event. Therefore, the storm event creates a favorable environment for *M. aeruginosa* proliferation.

In mesotrophic waters with medium regular wind exposure (Fig. 4c), the phosphorus release due to the storm benefits slightly to *M. aeruginosa* with a density reaching 100 mg.m^{-3} compared to simulations without storm (density at the same time around 20 mg.m^{-3} Fig. 2b). It mostly benefits to the green algae that reach values comparable to simulations without storm in eutrophic environment (Fig. 2d).

The impact of warming on the phytoplankton growth

Let us now perform simulations with higher water temperature (previous temperature forcing increased by 2°C) in order to mimic a warmer climate (Fig. 5). The temperature increase is favorable to the cyanobacteria and unfavorable to the green alga. But these overall results can be strongly modulated by the wind-induced mixing.

For low wind speeds (0.5 m.s^{-1}) and mesotrophic conditions, the green algae growth is impaired by the temperature rise and reach smaller densities throughout the season (compare Fig. 5a and 2a). On the contrary, *M. aeruginosa* is favored by the temperature increase: density reaches a maximum of 200 mg.m^{-3} (Fig. 5a) to be compared with the value of 38.5 mg.m^{-3} with standard temperatures (Fig. 2a).

For low wind speeds and eutrophic conditions, the maximal cyanobacterial density is almost 10 times higher with warming than with standard temperatures ($8.1 \cdot 10^3 \text{ mg.m}^{-3}$ vs 784 mg.m^{-3}) (Fig. 5b and 2c). Moreover *M. aeruginosa* builds up a high density population in a shorter time and the bloom peak occurs a few days earlier than with standard temperatures (Fig. 5b). The phosphorus depletion by the cyanobacteria is very fast and the bloom can no longer maintain itself despite the favorable temperatures. The decline of the bloom is also faster than with standard temperatures. Besides, it is important to note that the green alga is strongly suppressed during the cyanobacterial bloom, decreasing below 50 mg.m^{-3} at the end of August (Fig. 5b).

For higher wind speeds (4 m.s^{-1}), in both mesotrophic and eutrophic situations (Fig. 5c, 5d), we observe the same trends caused by warming than those with weak winds, *i.e.* a lower density of the green alga and an enhancement of *M. aeruginosa* compared to simulations without warming (Fig 2b, 2d). Results show that the mixing process dampens the effects of warming (compare figures 5a and 5c or figures 5b and 5d). *M. aeruginosa* displays a decrease of its maximum density. For instance, in eutrophic and warm waters, maximum density is reduced by 83% in wind-exposed water-column by comparison to the non-exposed water column (Fig. 5b and 5d).

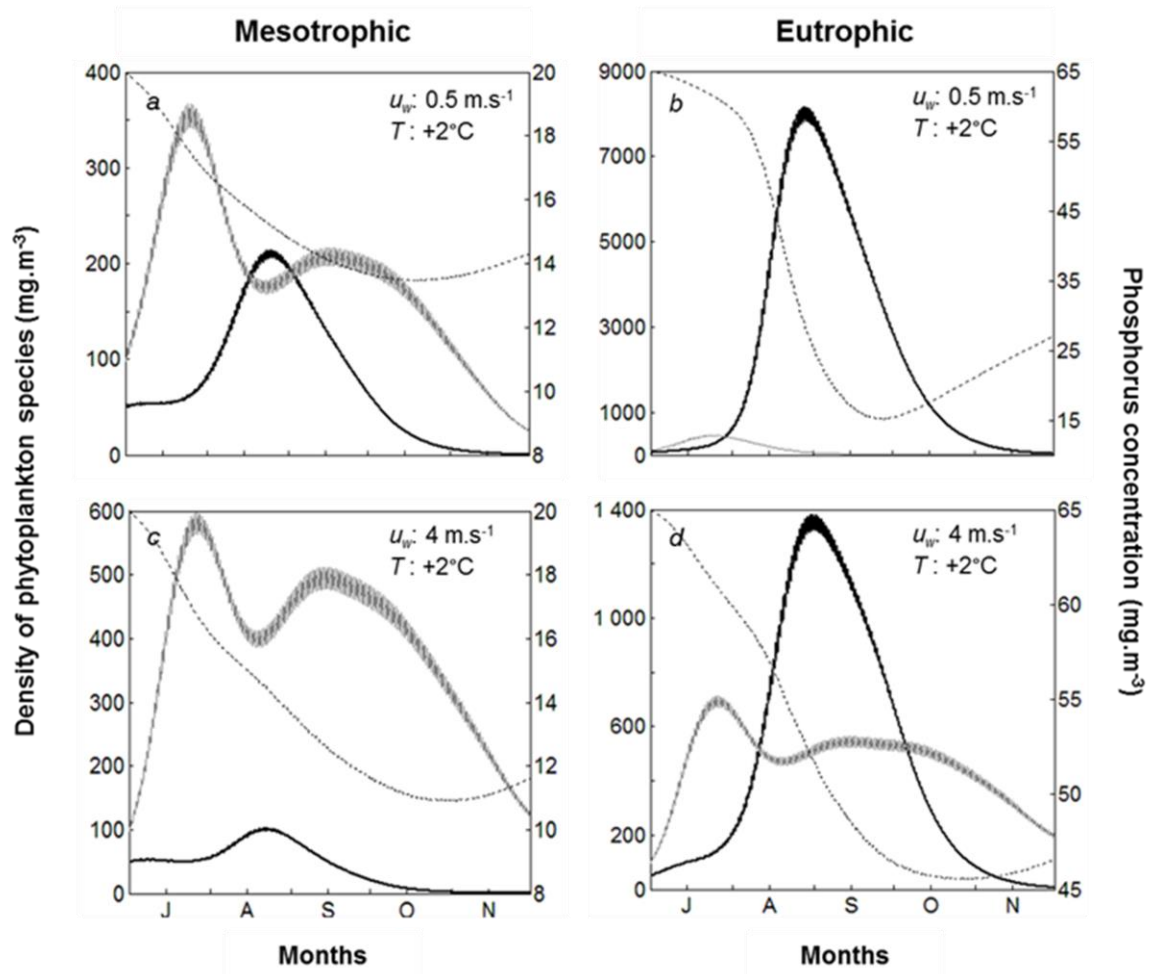


Figure 5. Effect of a 2 °C warming of the water column on phosphorus concentration (*dashed line*), densities of *M. aeruginosa* (*thick line*), and green algae (*gray line*). Left and right figures display simulations for mesotrophic and eutrophic water, respectively. a, b Data for 0.5 m s^{-1} wind speed; c, d data for 4 m s^{-1} wind speed.

The mixing slightly increases the green alga density in mesotrophic conditions (Fig. 5a and 5c), and it maintains a significant density throughout the season in eutrophic conditions despite the development of the cyanobacterium (Fig. 5d). The dynamics of both species in various environment conditions from July to December are detailed in figures 1-5.

The figure 6 displays, for standard temperatures (Fig. a) and 2°C increase in temperatures (Fig. b), the logarithm of the ratio of *M. aeruginosa* density over the green algae density when *M. aeruginosa* is at its peak (note that 0 corresponds to a ratio equal to 1). This is done on interval of wind speeds (from 0.5 to 5 m.s^{-1}) and initial phosphorus concentrations

(from 10 to 150 mg.m^{-3}). These figures show the conditions favorable for one species or the other and what conditions lead to net dominance of one species on the other or to coexistence.

The left panel (Fig. 6a) shows that most of the wind and trophic status conditions lead to green algae dominance or co-dominance. *M. aeruginosa* clear dominance is restricted to eutrophic/hypertrophic and low wind conditions. The preference of the green algae for medium wind exposure and low phosphorus concentrations is visible on the left of the panel with log values below -2. In comparison, the right panel (warming, Fig. 6b) displays a clear spread of the dominance domain of *M. aeruginosa* on the bottom right of the graph. This clear dominance extends to mesotrophic conditions ($\sim 30 \text{ mg.m}^{-3}$) and higher wind speeds ($\sim 3 \text{ m.s}^{-1}$). Regions of green algae dominance shrink to the left side, where the phosphorus concentration is very low (10-20 mg.m^{-3}). The top right area (log values between ~ 1 and ~ 2.5) corresponds to *M. aeruginosa* dominance but with the persistence of the green algae. The

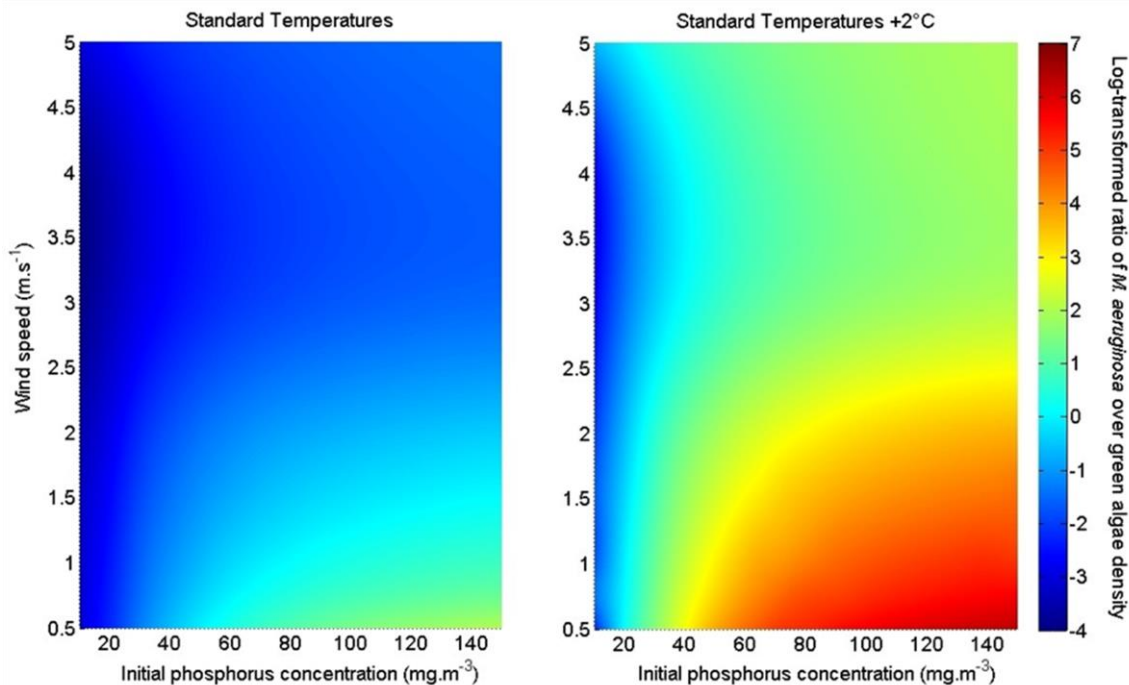


Figure 6. In the parameter plane (initial trophic status, wind), color chart of the log-transformed ratio of *M. aeruginosa* density over green algae density at the precise moment when *M. aeruginosa* density reaches its maximum (please note that the value of 0 on the color bar represents a ratio of 1). Left : simulations run with standard temperatures; right: the same simulations run with a 2 °C increase in temperatures. This figure is made from 256 simulation runs with cubic interpolation between points.

bottom right domain (log values above ~ 4) corresponds to a dense bloom with strong limitation of the green algae growth. On both figures, especially on the right one, the green algae dominance domain is reduced when the wind speed exceeds 4 m.s^{-1} . This is due to nutrient resuspension: at those wind speeds, the pool of available phosphorus increases, leading to favorable conditions for *M. aeruginosa*.

Discussion

This study proposes a model on shallow lakes which addresses the transient effects of the interaction of physical and ecological processes, in particular storm events, on phytoplankton dynamics. To our knowledge, it is the first to include sediment and nutrient resuspension. Our model results stress the importance of wind effects in interactions with trophic status and water temperature for understanding the magnitude and dynamics of *M. aeruginosa* blooms.

Eutrophication and wind exposure

In accordance with field observations, our results confirm the importance of the trophic status of a lake to understand the dominance of one algal group on another. These results might be mechanistically supported by a difference in physiological characteristics between phytoplankton groups. The half saturation constant of the green alga (6 mg P.m^{-3}) is lower than *M. aeruginosa* (24 mg P.m^{-3}). This means that (a) in mesotrophic environment (in the model $[\text{P}]_{\text{initial}}=20 \text{ mg.m}^{-3}$), the green alga is very much favored compared to *M. aeruginosa* and therefore dominates in this environment (for this sets of temperatures); (b) in eutrophic and hypertrophic conditions ($[\text{P}]_{\text{initial}}>65 \text{ mg.m}^{-3}$), the green alga is at its saturating level for phosphorus while *M. aeruginosa* still benefits from the concentration increase, giving it a clear advantage when temperatures become favorable. To sum up, phosphorus concentration will condition the “carrying capacity” of the water column. Phosphorus is an

important driver of the competition when its level is low. At higher trophic status, other constraints, like light availability and temperatures drive the competition. Everything being equal, the only effect of phosphorus at higher trophic level is to accentuate the formation of *M. aeruginosa* scums, which in turns reinforce its impact on underwater climate.

The buoyancy of *M. aeruginosa* explains its high surface density, forming dense scums at the water surface as observed in the field (See for instance: Soranno 1997; Ahmed et al. 2008; Homma et al. 2008). For instance our results in hypertrophic waters show a surface density around $18 \cdot 10^3 \text{ mg.m}^{-3}$ which is of the same order of magnitude as densities found at the surface of water ponds by Homma et al. (2008) and Ahmed et al. (2008) (respectively $15 \cdot 10^3 \text{ mg.m}^{-3}$ and $14.9 \cdot 10^3 \text{ mg.m}^{-3}$ using a *M. aeruginosa* cell mass equal to $24 \cdot 10^{-9} \text{ mg}$). Despite the small size of one *M. aeruginosa* cell compared to the green alga, their high surface density in calm waters allows them to dramatically change the underwater climate and therefore strengthen their dominance in eutrophic and hypertrophic waters. In the simulations with low wind, the light availability under 50 cm is dramatically reduced (58% reduction in eutrophic waters and 67% in hypertrophic waters during the blooms) impairing the development of competitors with neutral or sinking properties. As most of *M. aeruginosa* population is at the surface, it does not suffer from light limitation and therefore benefits highly from high phosphorus availability which in turn worsens the shading due to their high density scums.

The dominance of *M. aeruginosa* can be altered by the wind regimes. Our results show that a water column regularly mixed by the wind ($u_w=4 \text{ m.s}^{-1}$) does not suffer from *M. aeruginosa* blooms of the same magnitude as non-exposed ($u_w=0.5 \text{ m.s}^{-1}$), stagnant waters. Because of the strong water mixing, *M. aeruginosa* loses its capacity to colonize the surface and the green algae take over the dominance thus creating a turbid environment impairing the development of their competitor (Huisman et al, 2004). Therefore, the competition for light depends strongly on the stability of the water column. These results are in accordance to those

of Soranno (1997) who pointed out that scums can only appear in low wind conditions. Also, the deep-lake model developed by Huisman et al. (2004) explicitly shows that turbulence and currents on one hand prevent *M. aeruginosa* from gaining the water surface and, on the other hand, allow the sinking species to stay longer in the euphotic zone.

The wind-induced mixing allows a greater development of the green algae in all the simulations, which is consistent with field experiments with artificial mixing (Visser et al. 1996; Ptacnik et al. 2003; Jöhnk et al. 2008; Hudnell et al. 2010b) and early modelling work (Huisman et al. 2002b). This leads to the interesting result that, even in eutrophic and hypertrophic conditions, a water column regularly mixed will not experience high density *M. aeruginosa* blooms, as has been shown in eutrophic or hypertrophic lakes with artificial mixing (Visser et al. 1996, Hudnell et al 2010b). These results may explain in part the variability observed between water ponds experiencing different wind regimes according to their location, surrounding vegetation and urbanization. Our results stress that the presence/absence of cyanobacterial blooms do not only depend on lake trophic status. Even if natural mixing intensity is enough to prevent blooms of buoyant species, it does not mean that the trophic status of the lake is not high and its water quality poor.

Impacts of storm events

In this study, we distinguished two kinds of wind effects: low to medium wind speeds that only mix the water column without disrupting the sediment surface, and high wind speeds, *i.e.* storm events, that induce enough bottom shear stress to induce sediment resuspension. In our simulations, we show two distinct effects of short storm events. First, the sediment resuspension, depending on the erodability of the soil and wind speed, strongly decreases the light availability in the water column. As a consequence, the density of phytoplankton species decreases rapidly. For a two days long storm, the overall phytoplankton density is reduced by ~20%. Hellström (1991) estimated that algal production

was reduced by 85% when resuspension occurred in the lake Tåmnaren in Sweden. Second, we observe an important increase of phosphorus concentration in the water which reaches values around 400 mg.m^{-3} ; this value is comparable to those obtained in resuspension experiments (Ogilvie and Mitchell 1998). This newly available phosphorus is in part consumed by the phytoplankton species. But the phosphorus concentration does not decrease as fast as measured by Ogilvie and Mitchell (1998). This discrepancy may be explained by the absence in the model of 1) phosphorus sedimentation velocity and 2) phosphorus sedimentation due to binding to the settling sediments.

The results show that, when the storm occurs during the *M. aeruginosa* bloom peak, the cyanobacterial density slightly decreases but recovers readily (Fig. 4b). As explained above, this decrease is due to increased turbidity but the cyanobacteria benefits from the release of phosphorus from the resuspended sediments. Therefore storm events allow *M. aeruginosa* to reach higher overall densities than without any storm event. In the eutrophic shallow lake Taihu in China, Zhu et al (2005) showed that the strong and regular wind events might be the main mode for internal release of phosphorus in the lake waters. As this lake regularly suffers from *M. aeruginosa* blooms, the authors conclude that the storm events must have important effects on the nutrient supply during blooms.

In mesotrophic waters with enriched sediments, our results show that storm events can sufficiently change the phosphorus availability to allow the development of the cyanobacteria (Fig. 4a). According to our simulations, those results depend on the meteorological conditions. For instance, if regular wind exposure is rather high, and therefore not really favorable to *M. aeruginosa*, it will only slightly or not at all benefit from the phosphorus release. Conversely, it might benefit to its competitors that are doing better at higher wind speeds. So the outcome of storm events can be strongly modulated by the general wind exposure before and after the event.

Indeed, phosphorus concentration in sediments is usually high. The phosphorus pool in the sediments can be more than 100 times higher than the pool present in the lake water (Søndergaard et al. 2003). Besides, the quantity of phosphorus in one compartment is highly dependent on the density in the other. This is particularly clear in lakes under restoration plans. Even if the phosphorus input is steeply reduced, some lakes do not show any improvement of the water quality for a considerable period after the loading reduction (Søndergaard et al. 2003; Spears et al. 2007). Søndergaard et al. (2003) also stated that wind-induced resuspension is a mechanism frequently causing increased sediment and phosphorus concentrations in shallow lakes. Medium to strong mixing also allows the oxygen to be homogeneously distributed throughout the water column, which can lead to less phosphorus release from the sediment through complex iron-oxygen interactions (Gächter and Müller, 2003).

The model does not take into account the recruitment and flocculation of *Microcystis* cells in relation to sediment. Verspagen et al. (2006) showed that aggregation to clay particles may cause sedimentation of buoyant *Microcystis*. The aggregation efficiency depends on many variables such as clay concentration and type, concentration and physiological status of the cells. Therefore, storm events, which resuspends large amount of sediment might cause massive sedimentation of *Microcystis* cells. However, storm events also affect the recruitment of *Microcystis* cells living in the sediment. Verspagen et al. (2004) stated that a non-negligible amount of *Microcystis* cells overwinter in sediments and stay photochemically active, especially in shallow waters. These cells might inoculate the water column and promote the development of blooms in summer if they can leave the sediments. Their study showed that physiological changes (buoyancy and ballast content in cells) were unlikely to be the recruitment cause; therefore, resuspension of sediment via mixing seems to be the most possible recruitment mechanism.

Effects of warming on *M. aeruginosa* dominance and bloom-formation

High temperatures are usually associated with cyanobacterial blooms. Indeed, *Microcystis sp.* is known to proliferate under warm climate, but also in temperate regions during summer (Havens 2008; Jöhnk et al. 2008; Paerl & Huisman 2008; Kosten et al. 2012). With a maximum growth rate around 28°C, *M. aeruginosa* is particularly adapted to summer heatwaves and warm temperatures (Jöhnk et al. 2008). Conversely, low temperatures are also one of the most limiting factor of *M. aeruginosa* development (Oberholster et al. 2004), as its growth is critically impaired below 15°C (Jöhnk et al. 2008). The GIEC scenarios indicate that global temperatures are rising rapidly and Rogelj et al. (2011) recently stated that if plans to reduce global emissions are not put in place, the actual target of a 2°C increase limit will not be achieved. Our results on the effects of a 2°C increase in water temperatures confirms the hypothesis that rising temperatures will have a strong impact on freshwater bodies. In fact, in eutrophic and hypertrophic conditions (results for hypertrophic conditions not shown), we observe a strong increase in the densities reached by *M. aeruginosa*, an earlier bloom formation, and also a quicker bloom die-off. In our warming simulations (with low wind), the maximum density of *Microcystis* is about 10 times higher than with normal temperatures. This trend is in accordance with other studies and observations (Jöhnk et al. 2008, Kosten et al. 2012, Mooij et al. 2005). This is in part due to the relationship between *Microcystis* growth rate vs temperature. In our simulations, with only 2°C increase in mean water temperatures, we approach the maximum growth rate of *Microcystis* (about 0.8 day⁻¹), which allows a quick growth of *Microcystis* population. However, it is important to keep in mind that our model does not take into account natural meteorological variability, which could dampen the importance of warming although the trend is correct.

In addition, the green alga is totally excluded in some conditions. As a consequence, the warming worsens the effects of nutrient enrichment especially in stagnant waters. In

particular, we observe a cyanobacterial development even in mesotrophic conditions. The disadvantage of *M. aeruginosa* in low phosphorus environment is compensated by the increased growth rate due to high temperatures. In the field, this conclusion strongly depends on the adaptation of the competitors to high temperatures, but [Kosten et al. \(2012\)](#) stated that cyanobacteria may have higher optimum temperatures for growth than eukaryotes. Therefore, among other well-studied negative impact of warming, such as fish kills or increased anoxic conditions, the risk for freshwater bodies is to suffer from the loss of numerous algal species during summer with particularly hot temperatures ([Jöhnk et al. 2008](#)). Warming also allows the development of dense blooms at higher wind speed, but a clear limit is set around 3 m.s^{-1} where mixing starts to limit the maximum density reachable by *M. aeruginosa*. Moreover, when the wind speed is above 3 m.s^{-1} the green alga maintains itself thanks to the wind induced mixing. The wind exposure is therefore an important feature to take into account to understand the impacts of warming on phytoplankton dynamics and diversity in shallow lakes.

In the last decades, we saw changes in distribution and increased density of *M. aeruginosa* blooms. Our predictions and recent literature ([Kosten et al 2011](#), [Jöhnk et al. 2008](#)) indicate that the problem is worsening with rising temperatures. This is a costly problem, from ecological and economical points of view. A lot of research has been carried to find ways to prevent and eliminate blooms (for a review see for example [Hudnell 2010a and Gumbo et al. 2008](#)). Chemical solutions based on algaecide are one of the mostly used methods to suppress and terminate blooms. However, those methods are potentially dangerous for the whole ecosystem and even favor the release of high amount of toxins from lysed cyanobacterial cells ([Touchette et al., 2008](#)). Studies on the effect of mixing have opened new perspectives for bloom prevention: bubbling systems have been tested in deeper lakes suffering from *Microcystis* sp. blooms during the warm season ([Visser et al. 1996](#), [Jungo et al.](#)

2001; Huisman et al. 2004; Jöhnk et al. 2008). The results are an efficient suppression of blooms and algal diversity enhancement. However, those systems are costly to put in place, need to be constantly powered and have a very limited range of action. Moreover, intermittent use enables *M. aeruginosa* to develop again as soon as the system is turned off (Jöhnk et al. 2008). Another concern is that bubbling creates a transport of nutrient from the rich hypolimnion to the epilimnion which might favor blooms (Singleton and Little 2006). Some of those disadvantages are covered by another system called SPC (Solar Powered Circulation), which creates a current only in the epilimnion and is powered by solar panels. Results have been efficient bloom suppression in most of the lake tested, with the reestablishment of a balanced algal community years after the deployment (Hudnell et al. 2010b). So the question is: are those systems adaptable to shallow lakes? In Hudnell et al. (2010b) experiments, the SPC system failed in very shallow lakes where fish densities, affluents carrying cyanobacteria and other factors might have overcome or counteract the effect of mixing (Hudnell et al. 2010b). Our study points out another difficulty: mixing in shallow lakes may disrupt the sediment surface and enhance phosphorus release as shown in our simulations with storm events. Adapting this technic to shallow lakes (< 1m depth) might prove to be risky and uncertain.

Conclusion

In shallow lakes, wind has a key role in the structure and dynamic of phytoplankton populations. By mixing the water column and inducing sediment and nutrient resuspension, it affects strongly the competition for light and nutrients. Regular mixing by medium wind prevents the development of the buoyant *M. aeruginosa*. Punctual storm events have two successive effects: 1) a global decrease in phytoplankton density due to increased turbidity, 2) species can benefit from the phosphorus release by sediments depending on the timing of the event and the general wind exposure. The consequences of a 2°C warming are an earlier and a

denser *M. aeruginosa* bloom in summer and blooms in mesotrophic waters. However, the symptoms of warming can be masked by the wind-regime experienced by the lake. The interactions between eutrophication, warming and wind regimes may produce unexpected effects on cyanobacterial dynamics in shallow lakes.

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Appendix A: Computation of the bottom shear stress

Wave contribution

The wave contribution τ_{bw} is effective mainly for shallow lakes. It expresses the action of the oscillating boundary layer associated with waves as

$$\tau_{bw} = \frac{1}{2} \rho f_w U_b^2 \quad (1)$$

with the friction factor f_w .

$$f_w = 2 \left(\frac{U_b A_b}{\nu} \right)^{-0.5} \quad (2)$$

Where A_b stands for the maximum wave orbital amplitude and U_b the maximum wave orbital velocity. Using standard wave theory, these quantities A_b and U_b are given by

$$A_b = \frac{H}{2 \sinh(2\pi d/L)} \quad (3)$$

$$U_b = \rho \frac{H}{T \sinh(2\pi d/L)} \quad (4)$$

where the wave height H , wave period T and wave length L are estimated using the following formula (CERC 1984)

$$H = \frac{u_w^2}{g} 0.283 \tanh \left[0.53 \left(\frac{gd}{u_w^2} \right)^{3/4} \right] \tanh \left[\frac{0.00565 \left(\frac{gFetch}{u_w^2} \right)^{1/2}}{\tanh \left[0.53 \left(\frac{gd}{u_w^2} \right)^{3/8} \right]} \right] \quad (5)$$

$$T = \frac{u_w}{g} 7.54 \tanh \left[0.833 \left(\frac{gd}{u_w^2} \right)^{3/8} \right] \tanh \left[\frac{0.0379 \left(\frac{gFetch}{u_w^2} \right)^{1/2}}{\tanh \left[0.833 \left(\frac{gd}{u_w^2} \right)^{3/8} \right]} \right] \quad (6)$$

$$L = \frac{gT^2}{2\pi} \tanh \frac{2\pi d}{L} \quad (7)$$

where *Fetch* denotes the fetch length (m) of wind.

Current contribution

The contribution for the shear stress due to currents follows from the choice of eddy diffusivity. In a parallel flow approximation with constant pressure gradient, the velocity profile satisfies

$$\frac{\partial u}{\partial t} = d_t(z, t) \frac{\partial^2 u}{\partial z^2} - \frac{1}{\rho} \frac{dp}{dx} \quad (8)$$

For a steady velocity, this imposes a linear variation of shear with z . The parabolic form of d_t coupled with the constancy of shear and mass conservation for a steady velocity, imposes the following profile:

$$u(z) = Au_{*s} \ln(1 + z/(dz_b)) + Bu_{*s} \ln(1 - z/(dz_s + d)) + C \quad (9)$$

where the coefficients A , B and C are functions of z_b and z_s . This profile leads to the bottom shear stress exerted for the turbulent countercurrent:

$$\tau_{bTurb} = A_1 \rho u_{*s}^2 \quad (10)$$

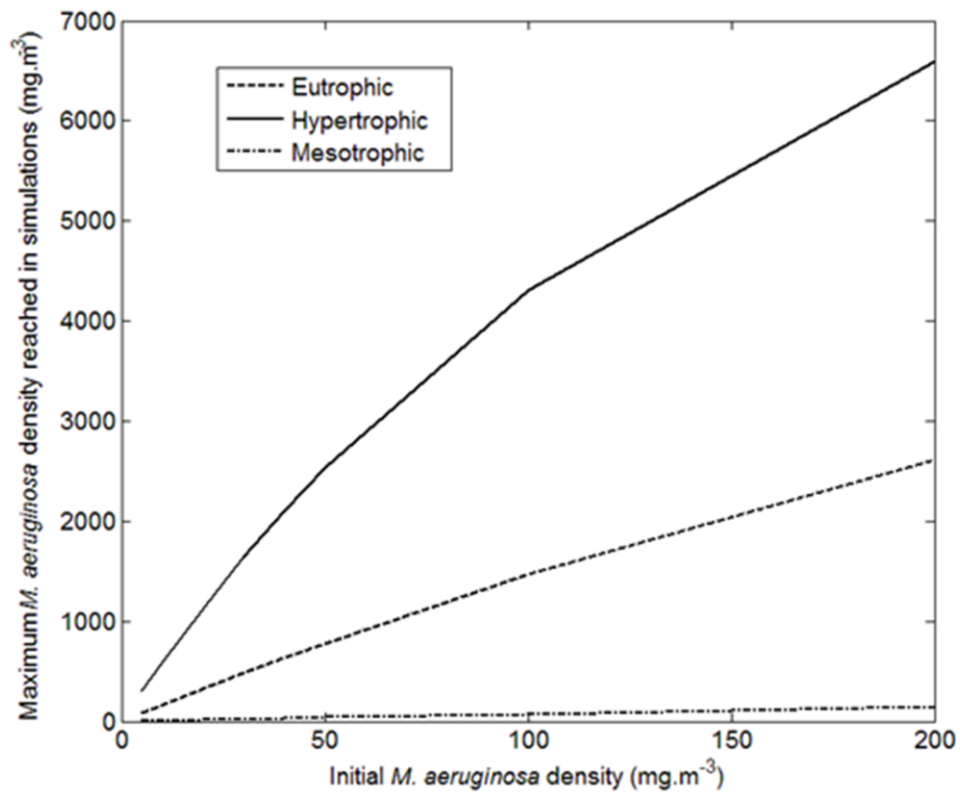
in which A_1 is an involved function of the two dimensionless quantities z_s and z_b .

Appendix B: Phosphorus parameters

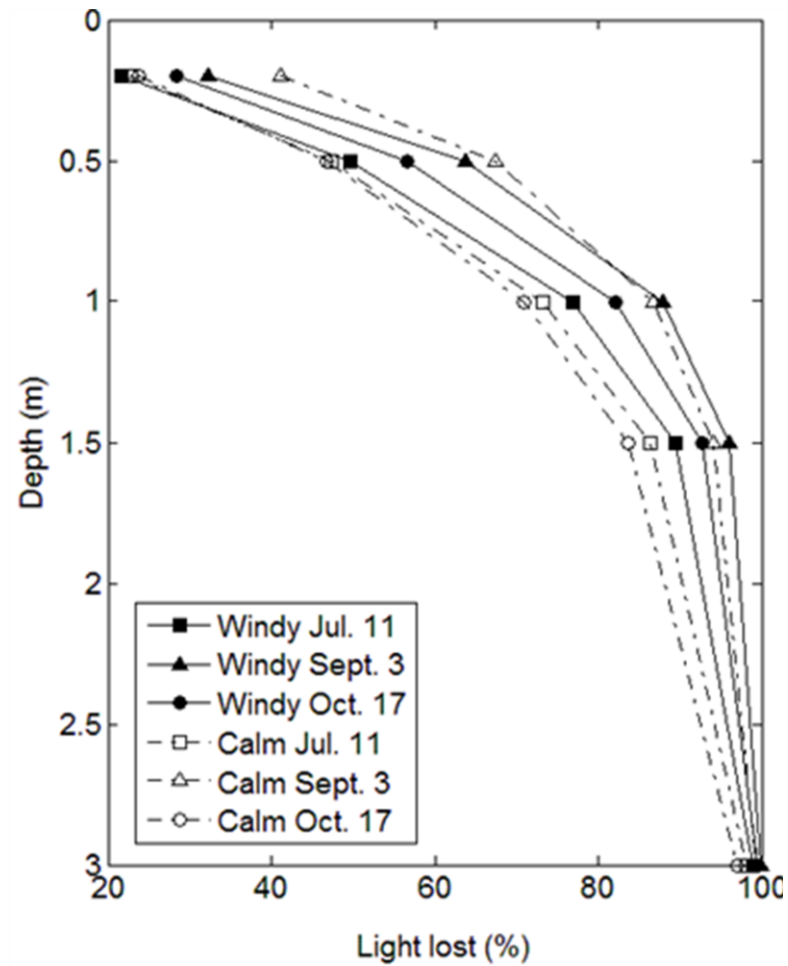
Table 3. Phosphorus parameters

Initial phosphorus concentration (mg/m ³)	Volumic input (mg/m ³ /day)	In_{vol}	Nutrient loss rate I_N
10	0.01		0.0008
20	0.15		0.008
30	0.18		0.006
40	0.20		0.005
50	0.22		0.005
60	0.30		0.005
70	0.35		0.005
80	0.39		0.005
90	0.45		0.005
100	0.50		0.005
110	0.55		0.005
120	0.59		0.005
130	0.6		0.0045
140	0.6		0.0043
150	0.6		0.004

Appendix C: Figure of the effect of initial *M. aeruginosa* density on simulations results



Appendix D: Figure of the percentage of light lost for all depths and dates of the figure 3.

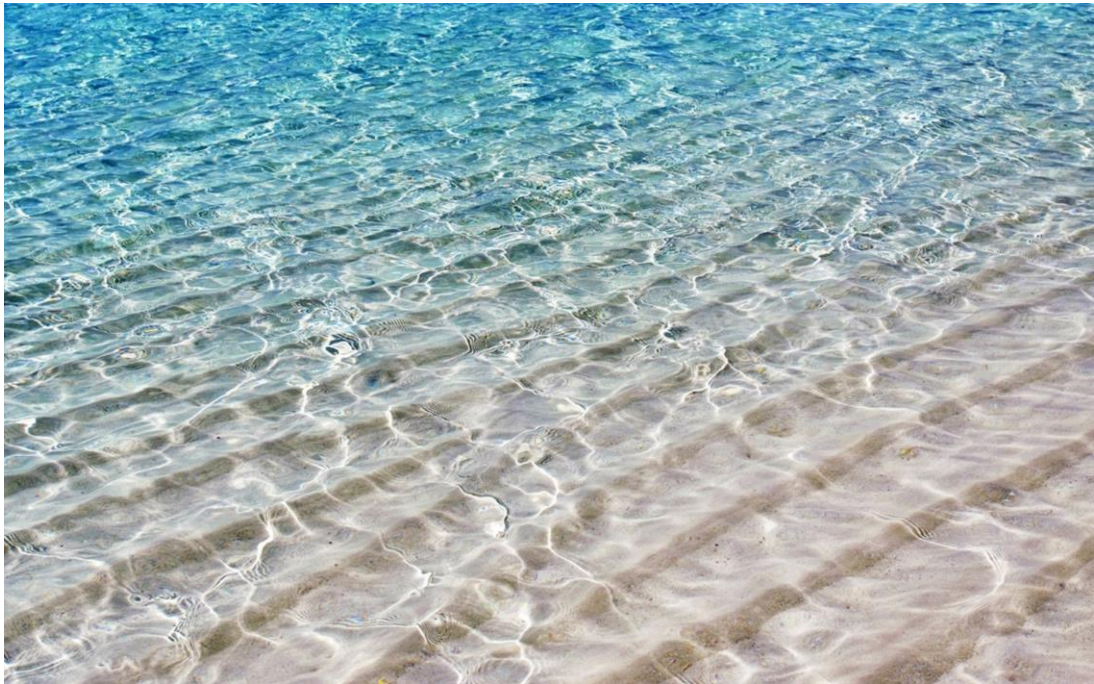


Chapter II

Mesocosms with wavemakers: a new device to study the effects of water-mixing on lake ecology

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Abstract

Water structuration, either by wind or by solar radiation, is a physical characteristic of aquatic ecosystems. Wind forcing is a transfer of energy to the water, which responds with currents, surface and internal waves that greatly influence chemical parameters and food web dynamics (Wetzel 2001). In order to manage freshwater ecosystems, different devices have been developed to modify lake's physical structure. Other studies seek to emulate some physical processes in experimental systems. Here we review succinctly these experimental works. Most devices generate turbulence flows that are a particular flow regime characterized by chaotic changes in properties. They do not reproduce precisely natural physical processes occurring in lakes but seek to emulate them. By contrast, surface and internal waves, generated by wind, affect the surface of the water and induce circular motions of water particles with a slow horizontal displacement of water and orbital motions of water particles in the water column. In fluid mechanics, the study of fluid motions under different forces stimulated the development of different experimental designs. Tanks with wave or tidal generators are common devices installed to reproduce natural processes and are used for research or applied purposes. To better understand the interaction between the physical and biological properties of aquatic ecosystems, one may want to reproduce predictable water motions. Indeed the importance of surface waves on the lake functioning justifies the development of a device designed to reproduce the effects of wind forcing. In this paper, we present new original 15 m³ mesocoms with wavemakers designed to reproduce the effects surface and internal waves. We detail the theoretical effects of waves on the water column and the choices that have been made to design our device.

Introduction

Water motions are of primary importance for aquatic ecosystems functioning. Common thought sees the water column as spatially homogeneous system except for the summer and winter stratifications (Wetzel 2001). Water masses however are submitted to inhomogeneous turbulence and surface and internal waves that greatly influence chemical parameters and food web dynamics (Reynolds 2006; Scheffer 1998; Wetzel 2001). Studying the interactions between the physical and the ecological structures of aquatic ecosystems needs specific experimental systems. The aim of this paper is to present a new experimental system for freshwater ecology that generates surface waves whose effects propagate in the water column. First we introduce the importance of physical characteristics for ecosystems and the effects of wind forcing on lake physical structure. Second we review succinctly experimental systems that have been developed to modify the physical structure of freshwater ecosystems in real lakes or in mesocosms, either to study them or for management purposes. We then focus on surface and internal waves and their effects on deep and shallow lakes. We finally give the underlying theory and describe the original experimental system.

Physical characteristics, wind forcing and water motions in lakes

Following the definition of Tansley (1935) that is still widely accepted (Gignoux et al. 2011), an ecosystem is the union of two components, a physical system and a biological system. The study and management of ecosystems may either focus on one of these two systems or consider them as indivisible parts of one system (For a discussion on the definition of ecosystem, see Gignoux et al. 2011). For instance, the experimental studies of nutrient enrichment on food web dynamics explore how the change of a chemical factor affects the biological system with a focus on energy and matter flows. In these studies, the physical system may be either the habitat, i.e. the physical container characterized by a set of fixed

variables, or else the arena, i.e. the place with unsteady characteristics in which organisms interact. In this context, the physical system is not the focus of the study and it has the underlying hypothesis that the biological system is driven by a physical factor. By contrast, in other studies, the ecosystem is defined as a dual object by nature and physics and biology are aspects, rather than components, and they can affect each other (Gignoux et al. 2011). This approach has been fruitful for the study of *Microcystis aeruginosa*, a cyanobacteria that forms dense blooms in freshwater (Blottière et al. 2014). Thanks to gas vesicles that increase cell buoyancy, these cyanobacteria flows up to the surface and may outcompete other photosynthetic organisms by changing a physical parameter, the light climate in the water column. The buoyancy is a physical competitive advantage as surface cells shade the water column. However this competitive advantage depends on a major physical factor, water mixing by wind forcing. Either water is not well-mixed by wind forcing and still water allows the expression of the buoyant characteristics of *M. aeruginosa* cells; or water is well-mixed by wind forcing and the cells lose their competitive advantage for light as they are dispersed in the water column. The study of the dual nature of the ecosystem implies the development of adapted systems when studying or managing them.

The physical state of a lake, temperature and chemical stratifications for instance, is modified by external forces that derive from energy or matter exchanges at its boundaries. The main exchange arises from the wind stress and the thermal energy input by solar radiation or evaporation. Other main processes that affect the lake physical states are inputs and outputs of water and matter from rivers and groundwater tables. Wind forcing is a transfer of energy to the water, which responds with currents, surface and internal waves that generate large scale flows as well as turbulent motions. This transfer depends on (1) the fetch, the lake distance to leeward, (2) the morphometry, that is the lake surface:volume ratio and shape, and (3) the stratification, the thermic structure defined by solar radiation.

Coherent water motions induced by wind forcing in lakes appear at different spatial scales: large scale surface or internal seiches, internal waves, surface (or progressive) waves and Langmuir circulations. Seiches appear after long-standing winds in a constant direction. As a consequence water piles up at one end of the lake and, when the wind stops, the water flows back to equilibrium with a rocking motion of the entire water mass. Seiches affect the motion of the entire water mass. Internal waves are smaller scale structures but are long enough to affect the metalimnion and the lake bottom. Surface waves affect only the surface of the water. Finally Langmuir circulation is a vortex, which arises through the interaction of a drift induced by surface wave and the presence of a vertical shear in turbulent fluid (Thorpe 2004). These different flows are characterised by large scale current structures and not simply small scale turbulence.

Small scale turbulence in lakes results from different processes: mainly natural convection at the surface, breaking of internal waves and shear. Vertical shear may take place at the surface, at the pycnocline and at the bottom and generates turbulences through various instability processes (Kelvin-Helmholtz instability, boundary layer instability, for instance).

Experimental devices manipulating the water-column structuration

In order to study or manage freshwater ecosystems, different devices have been developed to modify lake's spatial structure. The Table 1 summarizes the operating principles of these devices and the physical processes involved. The objectives in management are to improve water quality, that is in most of the cases to obtain the lake destratification to alleviate problems linked to bloom-forming cyanobacteria (Burford and O'donohue 2006; Hawkins and Griffiths 1993; Hudnell et al. 2010; Oberholster et al. 2006; Steinberg 1983; Upadhyay et al. 2013; Visser et al. 1996). The objectives in research encompass the study of mixing depth and background turbidity on phytoplankton species (Diehl et al. 2002), the

effects of destratification and water column-mixing on bacteria and plankton (Becker et al. 2006; Read et al. 2011; Reynolds et al. 1983; Weithoff et al. 2000) and the effects of sediment resuspension on phytoplankton biomass and plant nutrient concentration (Ogilvie and Mitchell 1998). The operating principles of the devices can be split in five categories (Table 1): (1) bubble plume or air bubble curtain that generates a mixed water layer; (2) long-distance circulation of the epilimnion that disrupts the quiescent surface water or deepens the epilimnion; (3) up and down water motions that increase high-frequency internal waves and generate turbulences; (4) air-providing tubs that generate turbulence; and (5) manual mixing that also generates turbulences in water-column. All these devices aim to modify the water-column structuration, i.e. destratification, but do not seek to reproduce natural physical processes occurring in lakes. Most of the devices generate turbulent flows that have a particular flow regime characterized by chaotic properties changes. However, in order to better understand the interaction between the physical and biological properties of aquatic ecosystems, it is necessary to reproduce predictable water motions.

Effects of waves in deep and shallow lakes

The shear stress produced by wind at the water surface generates traveling (progressive) surface waves as well as internal waves. These waves induce orbital motions of water particles (Figure 1A). Surface waves have an effect on mixing only at the water surface. Internal waves whose amplitude is maximum near the pycnocline possess much larger wavelength and are much slower. According to the ratio between the lake depth d and the wave wavelength λ of internal waves, the effects on the water column are very different. When the lake is deep that is to say the wave wavelength is small relative to the lake depth, the shear at the bottom boundary is negligible. When the lake is shallow that is the internal wave wavelength is long compared to the depth, the orbital motions of water particles reach

Table 1. Review of the systems developed to modify lake's spatial structure

Operating principles	Processes involved	References
Bubble plume or air bubble curtains. Long diffuser-pipe with nozzles connected to an off-shore compressor with an air-providing pipe.	Generation of turbulence in the water column creating a mixed water layer, possibly below a thin warm surface layer not affected by the turbulence	Becker et al (2006); Burford and O'Donohue (2006); Hawkins and Griffiths (1993); Oberholster et al (2006); Visser et al (1996)
Long-distances circulation of the epilimnion. Flexible intake hose attached to the base of a (solar-powered) impeller with an intake depth usually above the thermocline for epilimnion circulation or air lift apparatus that discharges water through airlift.	Turbulent mixing with deep epilimnion water pumping and disruption of quiescent surface water or deepening of the epilimnion by drawing hypolimnetic water and discharging it into the epilimnion.	Hudnell et al (2010); Reynolds et al (1983) ; Upadhyay et al (2013)
Up and down water motions. 8.25 m diameter rubber membrane surrounded by a buoyancy-controlled ring that can be raised and lowered repeatedly through the water column using compressed air (Gradual Entrainment Lake Inverter [GELI])	Up and down motions (1) increase high-frequency internal waves, (2) generate shear stress in the water column and turbulence and (3) generates turbulence with cold water lifted by the GELI spreading at the surface.	Read et al (2011)
Air providing tub. Air-providing tub connected at one end to a compressor, which pumps regularly air, and to a diffuser to the other end situated at the deepest part of a lake basin or at the bottom end of an enclosure.	Generation of turbulence in the water column	Diehl et al (2002) ; Steinberg (1983)
Manual mixing (small scale). Water mixing with a wooden oar or mixing by vertically hauling a 60-cm diameter metal plate in 1.5 m diameter enclosures	Generation of turbulence in the water column and vertical flows generated by the vertical motions of the metal plate	Ogilvie and Mitchell (1998); Weithoff et al (2000)

the benthic zones and are able to generate a stress at the bottom boundary. If the resistance of the bottom substrate is low in relation to the flow speed, sediments may be resuspended in the water column (Niemisto et al. 2008; Kleeberg and Herzog, 2014). The effects of waves are hence of particular importance in lakes. Interactions between the benthic, pelagic and littoral zones form the core of the functioning of these ecosystems (Scheffer 1998). The effects of waves on freshwater column mixing have been widely studied in deep lakes in order to understand the relationship between sinking and non-sinking phytoplankton (Diehl et al. 2002; Huisman et al. 1999a; Huisman et al. 1999b).

Mesocosms with wavemakers: a new ecological device

The importance of internal waves on the lake functioning justifies the development of a device designed to reproduce the effects of this wind forcing. Tanks with wave makers are common devices installed to reproduce natural processes and are used for research or applied purposes. For instance, different wave and swell makers have been designed worldwide by national navies for testing model warships and measuring their wave drag. (Fascinating pictures and movies can be found on the worldwide web.) The functioning of a tank with a wavemaker is well known (see for a short history [Hyun 1976](#)) and the originality of our system relies in the adaptation for research in freshwater ecology. The principle of our device is to emulate in a mesocosm internal waves with surface waves generated by the wavemaker. Next paragraph, we describe the effect of surface waves on the water column and explain the choices that have been made to design our device.

Theoretical background

Progressive surface wave are characterized by the displacement in time and space of a point at the water surface. This displacement induces a distortion ζ of the surface described as follows:

$$\zeta(x, t) = a \cos(kx - \omega t) \quad (1)$$

Where x and t are the space and time dimensions, a is the wave amplitude ($2a$ is the distance between the wave's trough and crest), $k = 2\pi/\lambda$, is the wave number with λ the wave wavelength (the distance between two crests), and ω the wave temporal frequency.

The classical theory gives the general propagation velocity of surface waves:

$$V = \frac{g}{\omega} \tanh\left(\frac{2\pi h}{\lambda}\right) \quad (2)$$

where h is water depth and g is the gravity,

and the velocity of a water particles at a depth z :

- Horizontal component: $u = a\omega \frac{\cosh[k(z+h)]}{\sinh(kh)} \cos(kx - \omega t)$ (3)

- Vertical component: $w = a\omega \frac{\sinh[k(z+h)]}{\sinh(kh)} \sin(kx - \omega t)$ (4)

The equations (3-4) show that 1) the velocity of a water particle decreases with depth, and 2) the decrease with depth is a function of the wave's wavelength.

When two waves of identical frequency but traveling opposite directions in the same medium encounter each other, they interfere with one another and the result of the interference is a new wave described as standing or stationary wave. This superposition of two individual waves occurs in tank with vertical edges where progressive waves bounce, travel back and encounter newly generated progressive waves. Standing waves are described as follow by the classical theory:

- the distortion ζ of the surface is $\zeta(x, t) = 2a \cos(kx) \cos(\omega t)$ (5)

and the velocity of a water particles at a depth z :

- Horizontal component: $u = a\omega \frac{\cosh[k(z+h)]}{\sinh(kh)} \sin(kx) \sin(\omega t)$ (6)

- Vertical component: $w = -a\omega \frac{\sinh[k(z+h)]}{\sinh(kh)} \cos(kx) \sin(\omega t)$ (7)

The classical theory allows us to describe water particle motions according to water depth in shallow and deep waters where the ratio water depth:wavelength is small or large respectively (Figure 1, Table 2). With progressive waves, In deep lakes, the motions are orbital and the velocity decrease with depth and, below a depth of around $\lambda/2$, their effects become negligible. In shallow lakes, water particle motions become ellipsoidal, their amplitude decreases slowly and are constant for very shallow water ($h/\lambda \ll 0.05$), and they may provoke a shear stress at the bottom boundary. With standing waves, water particle motions have the same pattern in deep lake than with progressive waves. In shallow lakes, motions are ellipsoidal but not flat as with progressive waves.

The aim of developing mesocosms with wavemakers is to reproduce the effects of internal waves with different wave amplitude, number and frequency and see their effects on the water column. The theory for wavemakers has been developed by Hyun (1976). We report here the characteristics of our system. Most tanks use one of the two types of wavemakers called after the motion of the oscillating paddle: either flap or piston. In the flap wavemaker, the paddle rotates around an axis assembled at its basis (Figure 2). Paddle oscillations generate at the surface orbital motions of water particles that decay with depth. With piston wavemaker, the paddle slides and generates elliptical motions of water particle at all depth. Flap wavemakers are better adapted to reproduce waves in a deep water column while piston wavemakers reproduce water motions in shallow water column. However, the effects of flap wavemakers on the water column depend on the ratio water depth:wavelength as detailed above and they may generate ellipsoidal water particle motions at the bottom if the parameters (see below) are set to get a small ratio. We choose to develop a flap wavemaker because it is more flexible for the type of effects it may generate.

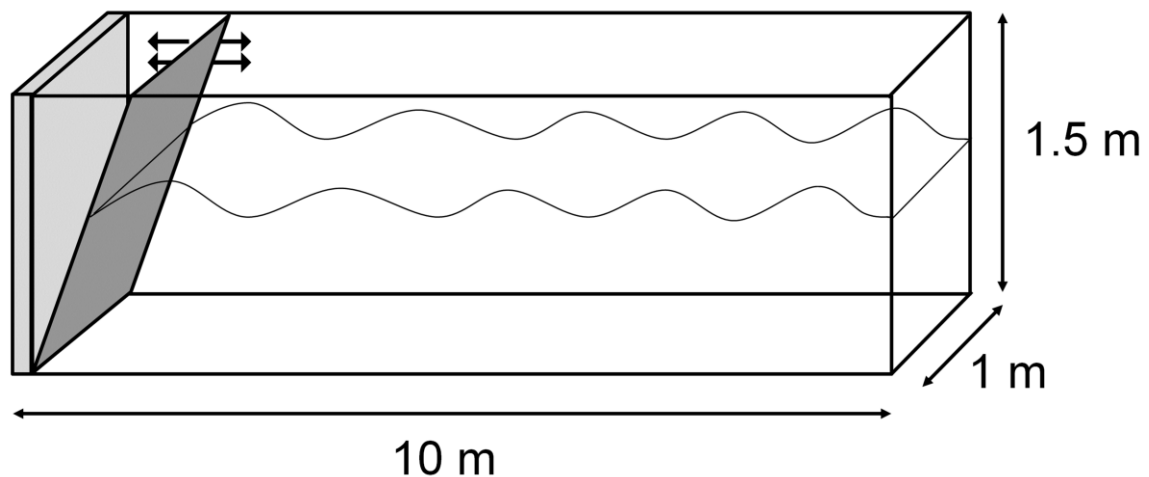


Figure 2. Schematic representation of a mesocosm with a wave-generator. The tank is rectangular with a wave-generator at one end. The engine is the light-grey box and the paddle is the dark-grey plane. Dimensions are indicated on the diagram but water depth cannot exceed 1 m.

Table 2. Horizontal (u) and vertical (w) components of a water particle velocity at a depth z in deep and shallow waters for progressive and standing waves. See text for explanations.

Deep water $h/\lambda > 0.5$	Shallow water $h/\lambda < 0.05$
Progressive wave	
$u = a\omega e^{kz} \cos(kx - \omega t)$ $w = a\omega e^{kz} \sin(kx - \omega t)$	$u = a \sqrt{\frac{g}{h}} \cos(kx - \omega t)$ $w = 0$
Standing wave	
$u = a\omega e^{kz} \sin(kx) \sin(\omega t)$ $w = -a\omega e^{kz} \cos(kx) \sin(\omega t)$	$u = \frac{a\omega}{kh} \sin(kx) \sin(\omega t)$ $w = -a\omega \left(1 + \frac{z}{h}\right) \cos(kx) \sin(\omega t)$

Specifications of the mesocosm with a wavemaker

While mesocosms are generally circular tanks in order to decrease the surface:volume ratio, producing waves implies a rectangular mesocosm with the wavemaker at one end. The characteristic parameters of a mesocosm with a wavemaker are the dimensions of the tanks (water column depth h , width w and length L), the height H of the paddle, and the frequency F and draft D of the paddle strokes. The specifications are to produce waves that affect either the water surface only or the water column and the sediment with shear stress. All the calculations are done for progressive waves. The constraints are (1) the ratio between the wavelength and the water column depth $\lambda:h$, (2) the ratio between the flap height and the water column depth $H:h$, (3) the ratio between the tank length and the water depth, $L:h$, and (4) the relationship between the wave number and amplitude, $k.a$. (1) The first constraint governs the effects of water mixing on the water column as detailed above. Given a water column depth h , shear stress at the bottom appears for $\lambda > 2h$ with progressive waves (Hyun 1976; Wetzel 2001). For $h = 1$ m, the minimum wavelength we want to produce is at least $\lambda =$

2 m. (2) The second constraint governs the paddle size relative to the water depth. Generating waves induces hydrodynamically induced torque and hydrodynamic force on the flap that we want to minimize. These physical effects decrease with an increase of the $\lambda:h$ ratio, and increase with the $H:h$ ratio (Hyun 1976). The maximum value of the ratio is 1 when the paddle height equals the water depth. Reducing the ratio implies reducing the height of the paddle and fixing it at the corresponding height of the tank. For instance, a ratio of 0.5 or 0.25 implies fixing the paddle at mid-height or quarter-height of the tank respectively. However, attaching a small paddle on the top of the tank precludes experiments with a small water depth. Therefore, we set the $H:h$ ratio to 1. (3) The third constraint governs the water column distortion by spatially transitory perturbations near the wavemaker. These perturbations decay rapidly and virtually disappear after traveling a distance of $3h$ (Hyun 1976). (4) The fourth constraint governs the crest formation and wave breaking. To observe the effects of surface waves, we want to avoid wave breaking that generates turbulences. This is insured when $ka < 0.1$, that is $2\pi a/\lambda < 0.1$. Taking into account all these constraints lead to a tank of a length $L = 10$ m, a width $w = 1.5$ m, and a height of 1.5 m for a water column $0.6 \text{ m} \leq h \leq 1$ m. The maximum water volume is 15 m^3 . The paddle height, draft and frequency are respectively $H = 1.2$ m, $0 \text{ mm} \leq D \leq 60 \text{ mm}$ at 1 m height and $0.21 \text{ Hz} \leq F \leq 1.5 \text{ Hz}$. Hence in normal use, the wavemaker may produce waves with a wavelength between 0.06 and 3.6 m and a maximum amplitude of 60 mm at a maximum water column of 1 m.

Technical study of a prototype

A prototype was developed with a collaboration of the Aissor firm and tested at the CEREEP Ecotron IleDeFrance (Saint-Pierre-lès-Nemours, France) during Spring 2011 (Figure 3). We show here results about the effect of waves' wavelength and amplitude on water circulation in the water column with standing waves. We explored the wave generator

parameters that is the frequency of paddle stroke and its draft angle, and the produced waves that do not break. The water velocity was measured with an Acoustic Doppler Velocimeter (MicroADV 16 MHz, Aqualyse) at different depth in a mesocosm where the water height was 1 m. Because surface waves induce a circular motion of water particles, their mean velocity is close to null and their standard deviation changes with waves' wavelength and amplitude. As detailed above, waves with a large amplitude and wave number form crests and break. Wave number is inversely related to wave wavelength. So the smaller the wave wavelength and the larger the amplitude, the higher the probability of producing crests. This constrained the number of parameters' combinations that we could explore so that for large wave amplitudes we were limited to long wavelength. This is illustrated in Figure 4 by the number of parameters' combinations tested.

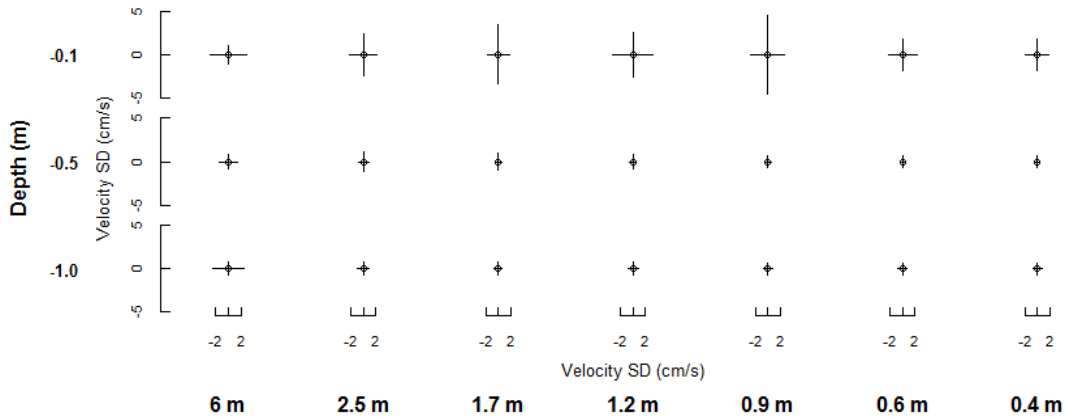
As shown in figure 4, when the wave amplitude increases (panels A to D), the standard deviation of water velocity increases for a given wave wavelength. The standard deviation decreases with water depth but this decrease is less pronounced for large wavelength and depends on the wave amplitude. When the amplitude increases, the decrease in velocity standard deviation with depth is less pronounced. For a very large wavelength of 6 m, one can see that the x component of the water velocity standard deviation does not decrease with depth, suggesting an elliptical motion of water at the bottom able to produce a shear stress.

A.

B.

C.

A.



B.

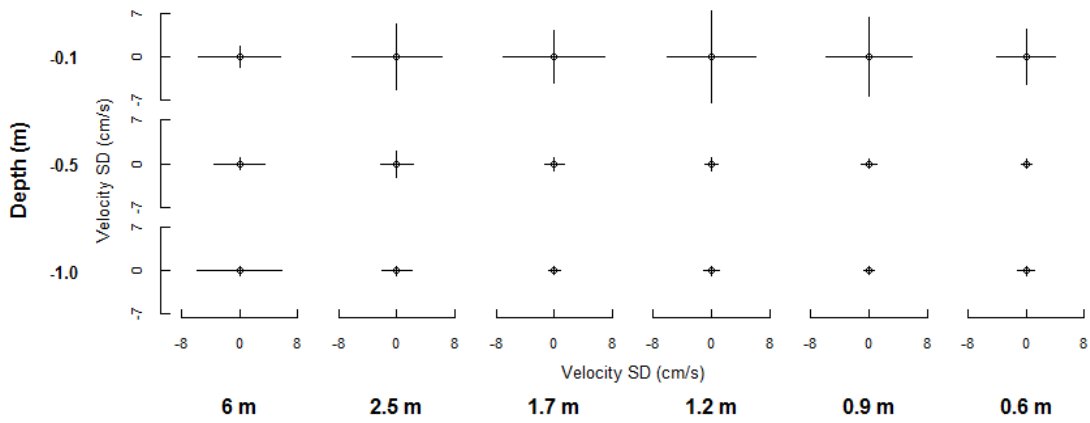


Figure 4.a Standard deviation of water velocity at different depth in a mesocosm according to wave wavelength and amplitude. The figure shows for four amplitude (A. 3 cm; B. 5,5 cm) the standard deviation of the x and y components of water velocity for different wavelengths. Wavelength values are given below each column of measures. Note the change of scale for the x and y between each panel.

Comments and recommendations

The results of the tests of the prototype allowed us to conclude that the wave generator and tank technical specifications could reproduce the water mixing in the wave column generated by the surface waves. By comparison to theoretical specifications, the system is more flexible and, for instance, it is possible to produce waves of 6.0 m wavelength with a small amplitude is possible. Five additional mesocosms were installed in Spring 2012 and six more in Spring 2013. Besides classical tanks of different volumes, the aquatic platform of the CEREEP Ecotron IleDeFrance (Saint-Pierre-lès-Nemours, France) is equipped with 12 mesocosms with wave generators.

A first experiment was conducted in Summer 2012 by [Blottière et al \(in prep\)](#) to test the effects of mixing on water chemistry and the food-web dynamics of a freshwater community. Two mixing regimes were compared and the experiment lasted nine weeks. The results show effects of the treatment on water turbidity, phytoplankton and some zooplankton functional groups and chemical parameters (Blottière et al. submitted). The results of this experiment suggest that mixing affects the foodweb and chemical properties via a complex combination of direct interaction through vertical displacement and indirect interaction through turbidity and sediment resuspension.

Beyond the classical tank experiments focusing on the study of aquatic ecosystems, though this experimental setup it is possible to also explores the different physical factors structuring them. We give here four examples: 1) The nature and quantity of the sediments may be manipulated as well as the timing of the surface waves. Our experimental setup allows one to study the effects of shear stress at the sediment surface after different consolidation times. ([Kleeberg and Herzog 2014](#); [Niemisto et al. 2008](#)). 2) Light is the fuel of photosynthesis and light

absorption (see for instance [Gallegos et al. 2008](#)) determines light reflectance. Our experimental setup can be used to the effects of surface water roughness due to waves, in interactions with the concentration and quality of suspended matter and colored dissolved organic matter, on light reflectance, a measure used for remote-sensing monitoring of lakes ([Kutser et al. 2005](#); [Yacobi et al. 1995](#)). 3) Contact surfaces of water with air and sediments are habitats for different species. Benthic species, leaving in the sediments or at their surface, are better known than species using water superficial tensions to stay afloat. ([Suter 2013](#)). 4) In addition, an artificial beach, with different lengths and inclinations, can be put into the tank at the opposite side of the wave generator. This set up could, for instance, reproduce in controlled experiments the beach or bank erosion by waves ([Liedermann et al. 2014](#); [Lorang and Stanford 1993](#)).

In conclusion, the mesocosm with a wave generator is a multipurpose tool to explore surface and internal waves and the water motions they generate in the water column and at the interfaces of water with air and sediments, respectively. This original experimental device opens new opportunities for studying multiple interactions between ecological and physical processes in ecosystems.

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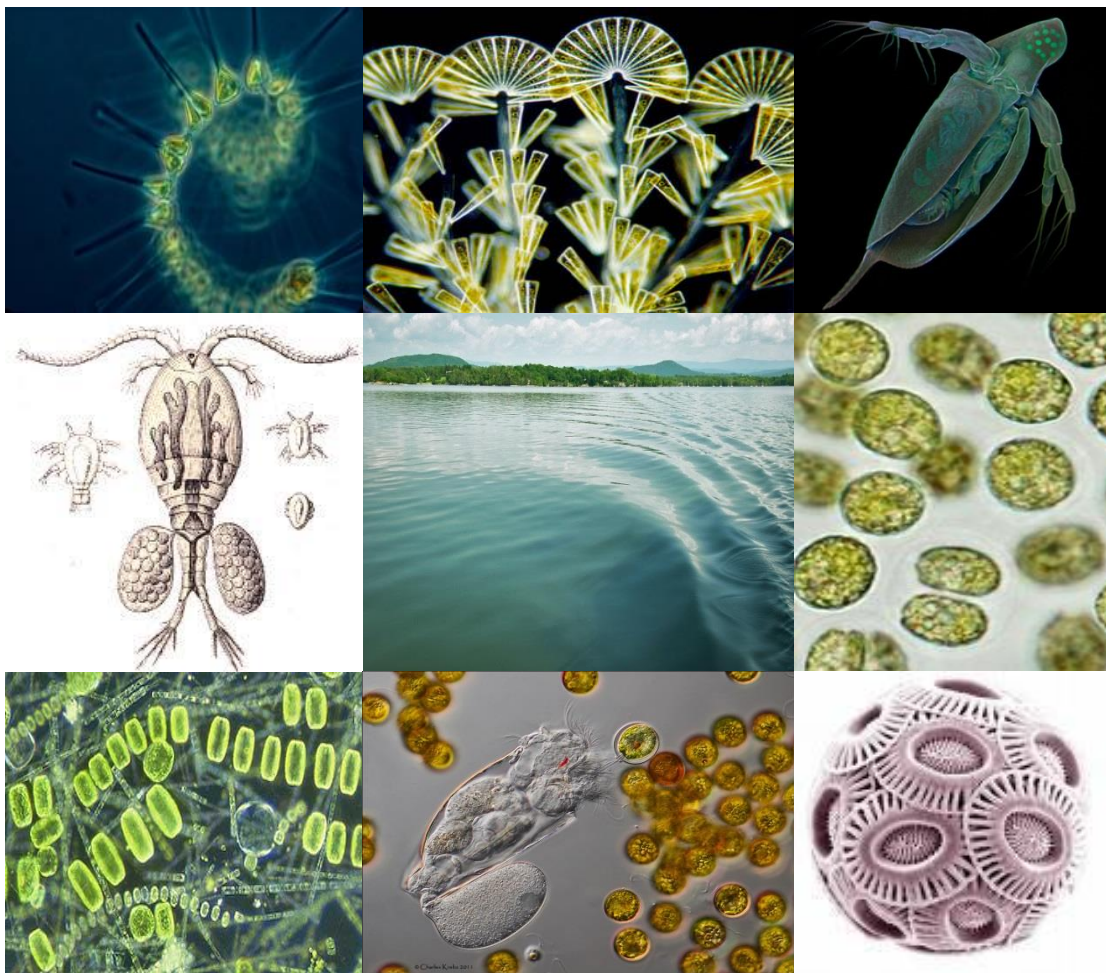
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Chapter III

How does water mixing affect the pelagic food-web in shallow lakes?

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Keywords: Shallow lake, mixing, phytoplankton, zooplankton, foodweb, mesocosms, wave-makers, water chemistry, wind

Abstract

We examined the effects of wind-induced mixing and sediment resuspension on typical food webs of temperate shallow lakes. These processes are known to have a major impact on the phytoplankton community, light penetration, and nutrient availability in the water column. However, little is known about the global effects of these processes on freshwater food webs. We thus conducted a 9-week experiment comprising a manipulation of mixing intensity in 15 m³ mesocosms with wave-makers in order to explore the impact of two mixing intensities on water chemistry as well as viral, bacterial, phytoplankton, and zooplankton communities. The turbidity level in mixed mesocosms (compared to calm conditions) was higher on average, especially at the bottom, indicating resuspension of the sediment bed. Mixing increased chlorophyll *a* concentration without any clear increase in algal abundance, which pointed to a physiological adaptation to mixing. A strong positive effect was also found on pH, suggesting an increased primary productivity in well-mixed systems. Zooplankton responses to mixing were neutral for cladocerans and rotifers, but negative for copepods. Finally, bacterial and viral abundances were unchanged by the mixing regimes, but viral lysis of heterotrophic bacteria could be enhanced by the water column mixing. Our experiment demonstrates that mixing is likely to influence shallow lake functioning through a complex combination of direct and indirect effects on the underwater light climate and water chemistry, phytoplankton physiology and productivity, zooplankton growth, and possibly virus-host interactions. These complex effects could play a major role in structuring pelagic and benthic communities in shallow lakes.

Introduction

Wind-induced mixing is a key process in shallow lakes ([Reynolds et al. 1983, 1984; Carrick et al. 1993; Schelske et al. 1995; Søndergaard et al. 2003; Reynolds 2006](#)). In addition to mixing the water column, wind forcing usually generates sufficient shear stress to cause the erosion and resuspension of bottom material. As a result, vertical mixing can significantly affect the underwater light climate, nutrient availability, and distribution of organisms ([Wetzel 2001](#)). In nature, freshwater lakes experience different mixing regimes depending on the local climate, their morphometry, thermal stratification, and exposure to wind. Indeed, this natural heterogeneity in mixing regimes might have important consequences on the functioning and structure of such ecosystems.

Wind-induced mixing has long been recognized as a major factor impacting phytoplankton biomass, growth, and community composition. Phytoplankton species, whether motile, non-motile, or buoyant, respond differently to water stability. Typically, microstratification within the euphotic zone generally favors motile or buoyant species, while fast-sinking species like diatoms or desmids are quickly lost from suspension ([Reynolds et al. 1983; 2006](#)). Sinking species rely heavily on mixing processes to maintain or be resuspended in the photic zone. The seasonal succession of phytoplankton groups in temperate lakes has been shown to be regulated in part by shifts in mixing patterns and intensities (typically in autumn and spring) ([Reynolds et al. 1983, 1984; Sommer et al. 2012](#)). Further, the different strategies exhibited by phytoplankton with regard to mixing intensity have been successfully studied through modelling ([Huisman and Weissing 1994; Huisman et al. 1999, 2004; Klausmeier and Litchman 2001; Blottière et al. 2013; Aparicio Medrano et al. 2013](#)) and used in water management to prevent bloom-forming cyanobacteria in stratified lakes and reservoirs using artificial mixing ([Hawkins and Griffiths](#)

1993; Visser et al. 1996; Jungo et al. 2001; Burford and O'Donohue 2006; Jöhnk et al. 2008; Hudnell et al. 2010).

In shallow lakes, mixing has a direct influence on water quality as it affects turbidity levels (Bengtsson and Hellström 1990; Luetlich et al. 1990; Bengtsson and Hellstrom 1992). Indeed, by resuspending matter from the sediment bed, mixing increases light attenuation, which can in turn reduce algal growth and productivity. For instance, Hellström (1991) calculated a 85% reduction in algal production following storm events in Lake Tämnaaren (Sweden). However, most studies with a simulation of resuspension events showed a short- and long-term increase (from a few hours to a week) in chlorophyll concentrations, algal productivity, and growth, with no visible adverse effect of turbidity (Ogilvie and Mitchell 1998). This positive outcome of mixing and resuspension is mainly explained by the inoculation of meroplanktonic algae in resting stages into the water column, thus changing community compositions and increasing phytoplankton biomass and chlorophyll *a* concentration (Carrick et al. 1993; Schelske et al. 1995; Head et al. 1999; Schallenberg and Burns 2004; Verspagen et al. 2004, 2005). Through the resuspension of sediments, mixing also increases the possibility of releasing high quantities of nutrients and, especially, phosphorus into the water (Søndergaard et al. 1992; Søndergaard et al. 2003; Zhu et al. 2005; Reynolds 2006). Nutrient input from the sediment might alleviate nutrient limitation and thus positively affect phytoplankton growth and biomass. In an attempt to disentangle the influences of light, nutrients, and algal entrainment, Schallenberg and Burns (2004) reported that meroplankton resuspension and, to a lesser extent, nutrient release were the main mechanisms through which phytoplankton was impacted by mixing. Light limitation due to increased turbidity was shown to be unlikely, except in very high turbidity levels that only coincide with extreme weather events.

Despite the large number of studies on mixing in shallow lakes, little is known about the overall impact of mixing on trophic levels other than phytoplankton. A few studies have investigated the effects of mixing and resuspension on bacteria and the benthic microbial food web, observing a global positive effect of resuspension on bacterial and protist growth (Weithoff et al. 2000; Garstecki and Wickham 2001). Eckert and Walz (1998) explored the link between the frequency of wind events and zooplankton succession in a shallow polymictic lake in Germany, while Levine et al. (2005) studied how wind-induced resuspension decreased the feeding and clearance rates of *Daphnia* and *Boeckella hamate* in Lake Waihole (New Zealand). Weithoff et al. (2000) studied more than one trophic level by simultaneously testing the effect of two consecutive resuspension events on three trophic bacteria, phytoplankton, and rotifers, demonstrating a positive effect on bacteria and phytoplankton through enhanced nutrient availability, which could in turn favor rotifers. Nevertheless, more studies are needed on multiple trophic levels in order to better understand the global effects of mixing on the whole ecosystem.

In this study, we aim to present a general pattern to show whether and how water mixing impacts the trophic food web through direct physical effects or indirect pathways. To explore this phenomenon, we used a unique experimental set-up with mesocosms equipped with wave-makers (Hulot et al. *in prep.*). The goal was to mimic as closely as possible the natural water motion induced by continuous moderate winds in lakes. Previous attempts to study mixing were usually conducted *in situ* using bubbling systems or manual mixing of the water column, which might not be representative of natural wind-induced mixing (reviewed in Hulot et al. *in prep.*). We used these mesocosms over 9 weeks to follow the physical, chemical, and biological responses of our systems to two mixing levels: 1) complete mixing of the water column plus resuspension, which

mimics well-exposed shallow lakes; 2) superficial mixing of the top water layer and no resuspension, which concerns unexposed shallow lakes.

Materials and methods

Study site and experimental design

The experiment was run from July to September 2012 at the CEREEP-Ecotron Ile-de-France (Equipex Planaqua, St-Pierre-lès-Nemours, France). We used six rectangular mesocosms (10 x 1.5 x 1.5 m) made of 10 cm insulating polyester covered with a liner. Each mesocosm has a wave generator fixed at one extremity, with the mechanism described in detail in Hulot et al. (submitted). In short, a paddle rotates around an axis assembled at its basis, while the paddle oscillations generate surface stationary waves. The wavelength and amplitude of waves are determined by the frequency and amplitude of paddle oscillations, respectively. All enclosures were filled with tap water, reaching a final total volume of 15 m³ and a water column of 1 m. To create a sediment bed, approximately 300 L of sieved sand from the Loire River (France) were put into each mesocosm as homogeneously as possible. At the same time, we used four circular containers of ~1.5 m³ to cultivate algae and zooplankton collected from natural communal lakes and ponds nearby the experimental site. The diversity in these containers was maintained by regularly adding water from the same lakes and ponds. They were used as reservoirs for reseeded the mesocosms on a weekly basis throughout the experiments in order to limit the loss of diversity due to species selection (Mette et al. 2011) and ensure the development of potential populations in favorable environmental conditions (Hulot et al. 2014). On July 10, each mesocosm was seeded with phytoplankton and then the following week with zooplankton. Phosphorus was added along with phytoplankton using a K₂HPO₄ solution to reach a final mesocosm concentration of 70 µg P. L⁻¹. Four days after zooplankton introduction, eight or nine

planktivorous cyprinid fish (*Carassius carassius*, purchased from SARL Vinal fishfarm, France) were added to each mesocosm with a mean density of $9.10 \pm 1.02 \text{ g m}^{-3}$.

To test the impact of mixing on shallow lakes, the experimental design had two treatment levels (“mixed” and “calm”) run in triplicates. In three of the mesocosms, we generated long wavelength waves (about 3.5 m) to mix the entire water column and create friction forces at the sediment surface so as to ensure the regular resuspension of the bottom-top layer and sedimented particles (“mixed” treatment). In the other three mesocosms, short wavelength waves were generated to create a very superficial mixing (“calm” treatment). The machines were activated immediately after the fish addition on July 20.

Physical measurements and water chemistry

All mesocosms were sampled weekly (July 23: date 0 to September 19: date 9), and all measurements were taken at two different depths: below the surface and just above the sediment bed. Samples and measurements were taken at the center of the enclosures from a small ramp fixed on top of each mesocosm. Mesocosms were sampled in random order on each occasion. Physical parameters such as temperature, pH, oxygen concentration, conductivity, and nephelometric turbidity (expressed in NTU) were measured directly in the mesocosms using a multiparameter probe (YSI 6600 V2-4-M).

Water samples for total suspended solids (TSS), dissolved nutrient concentrations, phytoplankton, zooplankton, and flow cytometry analyses were taken with a 2.2-l Alpha model Van Dorn horizontal water sampler (Anhydre). TSS (in dry weight per liter) were obtained by filtering a known water volume (typically 1 L, more or less depending on the particulate density) through pre-weighted and dried $0.7 \text{ }\mu\text{m}$ pore size Whatman GF/F filters and then weighting the

filters again after at least 24 hours of drying in an oven at 105 °C. The filtered water was then used in the laboratory to measure dissolved nutrient concentrations with a spectrophotometer (DR3900 Hach Lange). Orthophosphates were determined using the vanadate-molybdate method (LCK349 Kit Hach Lange). Total nitrogen was determined using the Koroleff digestion (Peroxodisulphate) and photometric detection with 2,6-Dimethylphenol (LCK138 Hach Lange Kit). Nitrate, ammonium, and nitrite were respectively determined using the cadmium reduction, diazotation, and salicylate methods (Hach Lange kits: Nitraver 5, Nitriver 3, and Ammonia Nitrogen reagent set).

Phytoplankton and zooplankton

Phytoplankton samples were divided into three size classes directly on site using differential filtration, i.e., a consecutive filtration through 100 µm and 30 µm mesh-size nylon filters. Hence, we had three subsamples: unfiltered water with algae of all sizes, a subsample with algae below 100 µm in the greatest axial linear dimension (GALD), and a subsample with algae below 30 µm in GALD. These subsamples were kept in the dark for 15 min before taking fluorescence measurements using the BBE FluoroProbeTM spectrofluorometer (Moldaenke) in laboratory. This fluoroprobe provides an estimate of chlorophyll *a* content (expressed in equivalent µg L⁻¹ of Chl-*a*) by measuring *in vivo* autofluorescence of pigment-containing micro-organisms (Beutler et al. 2002, Leboulanger et al. 2002, Rolland et al. 2010). The probe allows us to differentiate four phytoplankton groups referred to as “green” (chlorophyta and Euglenophyta), “brown” (Bacillariophyta, Chrysophyta, and Euglenophyta), “blue” (Cyanophyta), and “red” algae (Cryptophyta). Preliminary results showed that there were no algae larger than 100 µm, therefore the biomass of algae between 30 and 100 µm in GALD was obtained by subtracting the biomass values of algae under 30 µm from the 100 µm filtered sample value.

Three to five liters were filtered through 30 µm mesh-size nylon filters to collect zooplankton, which were immediately fixed in a solution of 96% ethanol and 4% glycerol (72% and 1% final concentration, respectively) to avoid body deformation. Samples were then exhaustively identified to the genus or species level and counted under a microscope.

For flow cytometry (FCM) analysis of small phytoplankton, prokaryote, and virus abundance, 4 mL of water was filtered through 30 µm mesh-size nylon filters and immediately fixed with paraformaldehyde (1% final concentration). The samples were then plunged into liquid nitrogen for 1 min before storage at -80 °C. Just before FCM analysis, samples were thawed at room temperature for a few minutes. Autotrophic small eukaryotes, picocyanobacteria, heterotrophic bacteria, and virus-like particles (VLPs) were counted using a FACSCalibur flow cytometer (Becton Dickinson) equipped with an air cooled laser providing 15 mW at 488 nm. For the analysis of VLPs and bacteria, samples were diluted in 0.02 µm filtered TE buffer (0.1 mM Tris-HCL and 1 mM EDTA, pH 8), and incubated with SYBR Green I (at a final 10^{-4} dilution of the commercial stock solution; Molecular Probes) for 5 min at ambient temperature, followed by 10 min heating at 75°C and then another 5 min at room temperature, prior to FCM analysis (based on [Brussaard 2004](#) and modified by [Jacquet et al. 2013](#)). For photosynthetic cells (i.e., picocyanobacteria and small eukaryotes), no fluorochrome was used; analysis was thus made on fixed samples to which we added a suspension of 1-µm beads (molecular probes). The flow cytometer list mode files thus obtained were then transferred and analyzed on a PC using the custom-designed software CYTOWIN ([Vaulot 1989](#)).

Statistical analysis

Statistical analyses were performed using the R software version 3.0.3 (www.r-project.org). The data set from the first date was analyzed using the Wilcoxon test in order to test

the homogeneity between mesocosms. To test the effects of mixing on the biological and chemical variables measured, we constructed linear mixed-effects models (LME, fit by REML - nlme packages -, [Pinheiro et al. 2013](#), [R Core Team. 2014](#)) with time, treatment, and their interaction as fixed effects. Individual mesocosms were treated as a random effect. Furthermore, heteroscedasticity correction and auto-correlation structures using AR(1) function ([Pinheiro and Bates 2000](#)) were added to the models when the homogeneity and independence hypothesis were violated. Residuals were visually checked to assess the quality of the model. The effects of depth were tested on every variable, and when non-significant, further statistical analyses were conducted on the mean values between depths (every variable except for turbidity and TSS). Prior to these analyses, the normality and homoscedasticity of each variable were assessed visually, and log or sqrt corrections were applied when necessary.

Results

Initial conditions

At the start of the experiment (date 0), dissolved phosphorus and nitrogen concentrations were $0.017 \pm 0.005 \text{ mg L}^{-1}$ and $5.855 \pm 0.097 \text{ mg L}^{-1}$, respectively. Total chlorophyll *a* concentration was $24.60 \pm 4.00 \text{ } \mu\text{g L}^{-1}$ with a large dominance of green algae compared to cyanobacteria and diatoms (21.61 ± 3.80 , 2.63 ± 1.84 , and $0.35 \pm 0.24 \text{ } \mu\text{g Chl } a \text{ L}^{-1}$, respectively). Phytoplankton abundance assessed using FCM was $1.01 \times 10^6 \pm 4.12 \times 10^4$ and $1.08 \times 10^6 \pm 4.10 \times 10^4 \text{ cells mL}^{-1}$ in mixed and calm mesocosms, respectively. Prokaryote (essentially heterotrophic bacteria) as well as virus-like particle abundance were also very similar between mixed and calm treatments (prokaryotes: $4.6 \times 10^6 \pm 3.2 \times 10^6$ vs. $4.3 \times 10^6 \pm 5.8 \times 10^5 \text{ cells mL}^{-1}$; virus: $6.5 \times 10^6 \pm 2.0 \times 10^5$ vs. $6.1 \times 10^6 \pm 5.3 \times 10^5 \text{ part mL}^{-1}$). Zooplankton was largely dominated by rotifers on the first date with $63 \pm 13 \text{ individuals L}^{-1}$. Crustacean concentration was very low at the beginning with

only a few *Bosmina longirostris*, *Scapholebris mucronata*, and calanoids. Between-treatment comparison on the first date for all physical, chemical, and biological variables showed no significant differences (Wilcoxon test, $P>0.05$).

Water mixing effects on turbidity and water chemistry

Mixing increased the nephelometric turbidity in the more turbulent mesocosms, while it decreased slightly in calm conditions (Fig.1a, Table 1, LME, Mixing x Time: $F_{1,99}=13.556$, $p=0.0004$). Surface turbidity of mixed mesocosms was similar to the turbidity level at the bottom of the calm mesocosms (Fig.1a). Overall, the nephelometric turbidity was always greater at the bottom compared to the surface, except during the first week of the experiment (LME, Depth: $F_{1,99}=77.863$, $p<0.0001$). On average, the turbidity was maximal at the bottom of mixed mesocosms with a mean value of 14.8 ± 2.2 NTU, suggesting the continuous resuspension of the sediment top layer.

TSS had similar dynamics. TSS concentration increased in the mixed mesocosms from the 4th week until the end of the experiment, while it remained stable under calm conditions (Fig.1b, Table 1). TSS concentrations at the end were 14.6 ± 5.4 mg L⁻¹ and 8.0 ± 0.9 mg L⁻¹ in mixed and calm mesocosms, respectively. TSS concentration was strongly correlated to green algae biomass (spearman rank correlation, $\rho=0.677$, $p<0.0001$), suggesting that most of the suspended solids in our mesocosms were phytoplankton cells and cell debris.

Mixing did not impact water temperatures, which were indistinguishable between treatments (Fig. 1c). When a small difference between depths appeared, the difference ($\sim 1^{\circ}\text{C}$) was similar in both treatments (see weeks 1, 4, 5, and 7). Oxygen concentrations decreased from week 3 until the end, but remained elevated throughout the experiment with an average of 168.56 ± 23.50 %Sat. and 159 ± 26.06 %Sat. in mixed and calm mesocosms, respectively (Fig. 1d). On average, oxygen concentration was greater at the bottom of the mesocosms (LME, Depth: $F_{1,99}=26.295$, $p<0.0001$). Mixing had a positive effect on pH levels over the course of the experiment (LME, MxT, $F_{1,46}=11.38$, $p=0.0015$), as it increased from an average of 8.32 ± 0.05 to 9.92 ± 0.29 in mixed mesocosms and 9.47 ± 0.14 in calm mesocosms (Fig. 2a).

Table 1. Results of the mesocosm experiment carried out in summer 2012.

Response variables	<i>P</i> -values			
	Mixing (M)	Time (T)	M x T	Depth
<i>Turbidity</i>				
Nephelometric turbidity (NTU)	0.0207	n.s.	0.0004	<0.0001
TSS (mg L ⁻¹)	0.0113	0.0377	0.0363	0.0478
<i>Chemistry</i>				
Oxygen (% Sat.)	n.s.	<0.0001	n.s.	<0.0001
pH	0.0129	<0.0001	0.0015	
NO ₃ -N (mg L ⁻¹)	n.s.	<0.0001	n.s.	
NO ₂ -N (mg L ⁻¹)	0.0886*	<0.0001	<0.0062	
NH ₃ -N (mg L ⁻¹)	n.s.	0.0248	n.s.	
PO ₄ ³⁻ (mg L ⁻¹)	n.s.	n.s.	n.s.	
<i>Phytoplankton</i>				
Green algae (µg Chl <i>a</i> L ⁻¹)	0.0434	0.0001	0.0008	
GALD<30 µm (µg Chl <i>a</i> L ⁻¹)	n.s.	0.0132	0.0024	
30<GALD<100 µm (µg Chl <i>a</i> L ⁻¹)	0.0483	<0.0001	<0.0001	
Abundance (cell mL ⁻¹)	n.s.	0.0093	n.s.	
<i>Virus and bacteria</i>				
Virus (VLP mL ⁻¹)	n.s.	0.0024	n.s.	
Bacteria (cell mL ⁻¹)	n.s.	n.s.	n.s.	
<i>Zooplankton</i>				
Zooplankton (ind. L ⁻¹)	n.s.	<0.0001	n.s.	
Rotifer (ind. L ⁻¹)	n.s.	<0.0001	n.s.	
Bosmina (ind. L ⁻¹)	n.s.	<0.0001	n.s.	
Nauplii (ind. L ⁻¹)	n.s.	<0.0001	n.s.	
Copepode (ind. L ⁻¹)	0.0644*	<0.0001	0.0003	

n.s. = not significant, * marginally significant.

The concentration of dissolved nitrates, ammonium, and phosphates and their temporal dynamics were similar in mixed and calm mesocosms (Fig. 2b, c, d, Table 1). Nitrate concentration decreased over time from $3.57 \pm 0.41 \text{ mg L}^{-1}$ to $2.21 \pm 0.21 \text{ mg L}^{-1}$ in all mesocosms, suggesting assimilation by the phytoplankton. Nitrite temporal dynamic differed significantly between treatments (Fig. 2e), with a greater accumulation of nitrites in calm mesocosms (LME, MxT, $F_{1,46}=8.23$, $p<0.0001$).

Water mixing effects on phytoplankton

The most abundant phytoplankton species found in the mesocosms throughout the experiment were the three chlorophyceae, *Coelastrum sp.*, *Pediastrum sp.*, and *Ankistrodesmus sp.* According to the BBE fluoroprobe, more than 80% of chlorophyll *a* content was attributable to the “green” algal group in all mesocosms (Fig. 3). As a result, we will mainly focus on green algae.

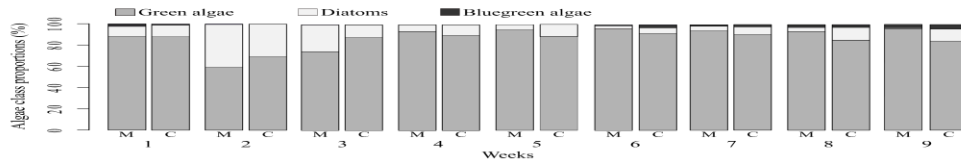


Figure 3. Proportion of phytoplankton classes during the 9 weeks experiment. “M” and “C” are respectively mixed and calm mesocosms. Green algae are in light grey, diatoms in light grey and bluegreen algae in black.

In both treatments, we observed an increase in chlorophyll *a* content for the first three weeks of the experiment (Fig. 4a). Chlorophyll *a* concentration subsequently decreased and stabilized in calm conditions, while it continued to increase in mixed mesocosms (LME, MxT, $F_{1,46}=12.872$, $p=0.0008$). At the end of the experiment, “green algae” chlorophyll *a* content reached $102.01 \pm 31.11 \mu\text{g Chl } a \text{ L}^{-1}$ in mixed mesocosms compared to $41.54 \pm 17.71 \mu\text{g Chl } a \text{ L}^{-1}$ in calm conditions. This positive response to mixing was found for both “small” and “large” green algae (Fig. 4b, 4c). Overall, 60% of the total chlorophyll *a* concentration was found in “small” green

algae (less than 30 μm in GALD) (Fig. 4b). Larger algae (between 30 μm and 100 μm , Fig. 4c) reached higher chlorophyll *a* content in mixed mesocosms (last week of the experiment: 34.18 ± 11.90 vs 12.37 ± 2.58 $\mu\text{g Chl } a \text{ L}^{-1}$).

FCM data on phytoplankton indicated an increase in abundance (in cells mL⁻¹) during the first three weeks of the experiment in accordance with chlorophyll *a* measurements (Fig. 4d). However, while we observed a between-treatment divergence in chlorophyll *a* concentration using the BBE probe, here we found a steady decline in cell abundance until the end of the experiment in both treatments.

Water mixing effects on zooplankton

The zooplankton communities in this experiment were found to be typical of a high predation rate by planktivorous fishes, i.e., the dominant species were small, mainly comprising herbivorous rotifers and the cladoceran *Bosmina longirostris* (Fig. 5a, b, c, and d). Rotifers formed more than 90% of zooplankton abundance at all times. Rotifer community composition changed over time, but it was dominated by planktonic genera such as *Keratella cochlearis*, *Anueropsis fissa*, *Polyarthra* sp., and *Brachionus* sp. Other small cladocerans like *Scapholebris* sp., *Ceriodaphnia* sp., and *Diaphanosoma brachyurum* also appeared during the experiment, albeit rarely. Nauplii and copepods (calanids and cyclopids) were mainly found from the second half of the experiment onwards.

Rotifer abundance increased up to ~2200 individuals per liter in both treatments. The abundance peak was reached at week 6 in calm mesocosms and week 8 in mixed mesocosms (Fig. 5b). In calm conditions, we then observed a steady decline until the end of the experiment. Despite this difference in dynamic, no statistical effect of mixing was found for rotifer abundance. *Bosmina longirostris* abundance and dynamic was very similar in both treatments over time, with increasing abundance in the second half of the experiment (Fig. 5c). Mixing intensity only had a significant effect on copepods over time (LME, MxT: $F_{1,46}=15.415$,

$p=0.0003$), reaching higher densities in clam mesocosms (Fig. 5d). This result was not found for copepod larvae, i.e., nauplii, even though the graphical patterns are similar (Fig. 5e).

Water mixing effects on prokaryotes and virus-like particles

Temporal dynamics of virus-like particles and prokaryotes were globally indistinguishable between the mixing treatments (Fig. 4e, f). Virus abundance increased during the first 4 weeks, while prokaryote abundance decreased. Inversely, the prokaryote abundance suddenly increased in weeks 5 and 6, while virus abundance dropped. In calm conditions, the virus-to-prokaryote ratio (VPR) remained relatively low and homogenous between mesocosm replicates. Conversely, in mixed conditions, each replicate displayed a relatively high VPR value at different moments of the experiment (Fig. 6: weeks 3, 4, and 7 for mesocosms 3, 5, and 1, respectively).

Figure 6. Temporal dynamics of the VPR ratio in each mesocosms. Black line: mixed mesocosms, grey line: calm mesocosms. Each mesocosm (from 1 to 6) is identified by a specific dot shape.

Discussion

To the best of our knowledge, this is the first experiment to investigate the effects of water mixing and resuspension on shallow ecosystems using a new, efficient, and more appropriate artificial wave-maker tool than previously proposed in the literature. In our experiment, we successfully created two distinct environments: 1) a well-mixed and turbulent water column with the resuspension of bottom materials leading to higher turbidity; 2) a stable water column with only superficial mixing (comparable to calm conditions) and no resuspension. *In fine*, we found two different types of food web functioning that we will discuss below.

Mixing effects on turbidity and sediments

As expected, turbidity and TSS concentration were greater in mixed mesocosms, with maximum values at the bottom indicating the resuspension of the top layer of the sediment bed. However, the impact on overall turbidity was moderate, with values never exceeding 20 NTU in mixed mesocosms. Turbidity levels in lakes are of great importance for primary production, as it reduces light availability for phytoplankton and macrophytes. The effect of resuspension on phytoplankton production depends on the amount of matter that is resuspended for a given mixing intensity (which depends on the sediment composition and cohesion) and on the threshold of phytoplankton species for light limitation. [Schallenberg and Burns \(2004\)](#) showed that the threshold for light limitation of phytoplankton was rather high, e.g., >200 NTU. These levels of turbidity are most likely to be seen after strong weather events like storms. It is therefore unlikely that algae would suffer from strong light limitation with the moderate level of continuous mixing as seen in our experiment.

Mixing effects on nutrient concentration

In eutrophic shallow lakes, wind-induced resuspension is usually associated with the release of total phosphorus from the sediments (Sondergaard et al. 1992; Hamilton and Mitchell 1997; Zhu et al. 2005; Thomas and Schallenberg 2008). Visible effects on dissolved phosphorus are less common, as dissolved nutrients are subject to rapid biological assimilation and depend on the difference in concentration between sediment-bound and dissolved phosphorus in the water (Gunatilaka 1982; Hamilton and Mitchell 1997; Schallenberg and Burns 2004). In this experiment, we did not observe any significant differences in dissolved phosphorus concentrations between the mixed and unmixed enclosures. This can partly be explained by the nature of the sediments chosen in our experiment, that is, sieved sand from the Loire River (France). Even though we did not measure nutrient concentrations in the sand prior to the experiment, it is rather safe to suggest that phosphorus concentration was very low compared to a fresh sediment layer from a eutrophic shallow lake. Phosphorus release following mixing events has been shown to have a positive impact on phytoplankton (Schallenberg and Burns 2004; Zhu et al. 2005) and bacterial biomass (Weithoff et al. 2000). Indeed, this positive effect will only be found when phytoplankton and procaryotes are in a state of nutrient limitation (Schallenberg and Burns 2004).

No difference was observed in nitrogen concentration and dynamics except for nitrite nitrogen. NO_2 increased in both mixed and calm mesocosms, which usually indicates a dysfunctioning of the nitrogen cycle. Nitrite accumulation often occurs in anoxic waters, which was not the case in this experiment where oxygen levels in the water column were elevated throughout the experiment. However, it is known that *Nitrobacter*, the primary bacterial genus involved in the oxidation of nitrites to nitrates, is less tolerant of high pH values (Wetzel 2001).

In both treatments, pH levels were rather high, which could explain this trend. Further, NO₂ accumulation was greater in calm as opposed to more turbulent conditions. The lack of oxygenation of the sediment in unmixed mesocosms could reduce the nitrification activity in this compartment (Chen et al. 1972). Similar results were found in the resuspension experiment of Kang et al. (2013), where nitrites accumulated in mesocosms without resuspension, an effect that was less pronounced when mixing was applied.

Mixing effects on phytoplankton and chlorophyll *a* concentrations

Higher concentrations of chlorophyll *a* were found in the mixed mesocosms. A positive relationship between mixing and chlorophyll *a* has been found in numerous studies (Carrick et al. 1993; Schelske et al. 1995; Hamilton and Mitchell 1997; Ogilvie and Mitchell 1998; Schallenberg and Burns 2004). For example, Schelske et al. (1995) showed that chlorophyll *a* concentrations exceeding 100 µg/L were highly correlated with wind speed in Lake Apopka (Florida, USA). In all cases, however, an increase in algae abundance through the recruitment of meroplanktonic algae was the leading cause of change in chlorophyll *a* concentration. In contrast, we found no increase in the abundance of small algae (<30 µm in diameter) in our mesocosms. This discrepancy between chlorophyll *a* measurements and abundance data suggests that the increase in chlorophyll *a* was not due to the entrainment of sedimented or meroplanktonic algae. This was more likely a physiological response of algae cells to mixing, leading to higher chlorophyll *a* content (a hypothesis that was indeed corroborated by FCM fluorescence data, not shown). Photosynthetic organisms have the capacity to regulate the amount of pigments in response to the light climate and nutrient concentration (Falkowski 1984; Shin et al. 1987; Longhurst and Glen Harrison 1989; Ibelings et al. 1994; Felip and Catalan 2000). An increase in chlorophyll *a* content is usually a response to a more turbid environment, known as shade

adaptation. Therefore, the higher global turbidity level observed in our mixed mesocosms could have induced an increase in chlorophyll *a* cell content. Another hypothesis to explain the discrepancy between abundance data and chlorophyll *a* might be a shift in community toward species with higher chlorophyll *a* cell content (Visser et al. 1996; Felip and Catalan 2000). Large algae ($30\text{ }\mu\text{m} < \text{GALD} < 100\text{ }\mu\text{m}$) also respond positively to mixing in terms of chlorophyll content. In addition to the physiological adaptation described for smaller algae, large algae abundance could also be enhanced through a reduction of loss rate by sedimentation.

Mixing effects on pH and primary productivity

Although not measured directly, we observed a greater photosynthetic activity in mixed as opposed to calm mesocosms, as shown by the higher pH values. In summer, pH usually increases in natural environments as a consequence of the uptake of inorganic carbon by the primary producers for their photosynthetic activity (Schelske et al. 1974; Scheffer 1998; Reynolds 2006; Moss 2010; Kosten et al. 2011). Previous studies on the effects of fluctuating light due to mixing showed diverse physiological responses, often leading to an increase in photosynthetic rates (see references in Litchman 2000). Early experiments evaluating the phytoplankton photosynthetic response to vertical movement in oceans showed an enhancement of photosynthesis for phytoplankton grown at fluctuating depths compared to the same phytoplankton species maintained at a fixed depth (Marra 1978). The reduction in photoinhibition experienced in clear waters and/or the reduction in light limitation in turbid environments are two mechanisms proposed to explain this positive effect of mixing on primary production (Mallin and Paerl 1992). On the one hand, regular mixing allows phytoplankton cells to be exposed to sufficient light by increasing their probability of passing through the well-exposed surface layer. On the other hand,

it also decreases the risk of photoinhibition by moving phytoplankton cells rapidly through the water column to less exposed depth.

Mixing effects on zooplankton dynamics

Zooplankton responses to mixing varied from one group to another. Small cladoceran, mainly *Bosmina longirostris*, and rotifer abundances were consistent in calm and mixed mesocosms. Nonetheless, rotifers dynamics slightly differed with an abundance peak in week 6 in calm mesocosms followed by a steady decline, while rotifer abundance increased until week 8 in mixed mesocosms. This difference in timing might be explained by copepod density, which was higher in calm mesocosms during the second half of the experiment. Most copepod species in their adult stages are very efficient predators, with rotifers often being their preferred prey. It has been demonstrated that their feeding rate on rotifers is high enough to produce top-down control (Brandl 2005). As to why copepod densities are significantly higher in calm mesocosms, we propose three non-exclusive hypotheses that might explain these results. First, the turbulent flows caused by mixing could hinder the kinematics of copepods. It might therefore be more difficult and energy-consuming for individuals to maintain their position in the water (Yen et al. 2008), leading to reduced feeding and growth rates. Second, copepods in mixed enclosures could proportionally absorb more resuspended material that is lower in nutrient content as compared to in low turbidity environments, thus reducing the efficiency of food assimilation (Gasparini et al. 1999). Copepods could also expend more energy sorting food from sediment, although according to Levine et al. (2005), NTU levels around 15 NTU as in our mixed mesocosms only reduce clearance rates by 3-8%. Kang (2012) also showed non-statistical differences in the ingestion rates of food particles by a marine copepod at suspended sediment concentration of 10 mg L⁻¹. Third, it is possible that suspended sediments could interfere with the mechanical or chemical

signals from both copepod preys ([Levine et al. 2005](#)) and their predators. This could in turn lower their feeding success, growth rates, and reproduction rates ([Paffenhöfer 1972](#); [Oviatt 1981](#); [Turner and Tester 1989](#); [Gasparini et al. 1999](#); [Kang 2012](#)).

Mixing effects on prokaryotes and viruses

Bacteria are a crucial component in limnetic food webs, yet very little is known about the impacts of mixing on this specific group in lakes. [Weithoff et al. \(2000\)](#) showed that bacterial abundance increases strongly after mixing events due to the nutrient input in the water column. In our experiment, we did not observe any differences in abundance between mixed and calm enclosures, which is not surprising considering that we did not observe any changes in nutrient content.

In the last decades, viruses have been recognized as an important component in the microbial food web. They have an especially strong impact on bacterial mortality and diversity ([Wommack and Colwell 2000](#); [Weinbauer 2004](#)). Our results on the VRP ratio (generally considered as a proxy of the interactions between viruses and hosts, e.g., [Parikka et al. in revision](#)) could suggest that the lysis activity was stronger in mixed compared to calm conditions. We hypothesize that this result could reflect enhanced contact rates in mixed conditions. A similar effect of water motion was proposed by [Hudnell et al. \(2010\)](#) regarding the control of cyanobacteria by cyanophages. Further studies would be necessary to confirm our finding, which could have important consequences on ecosystem microbial functioning.

Ecosystem level

This medium-term experiment reveals that water mixing may have multiple impacts on shallow water bodies, either directly through mechanic action or turbidity levels or indirectly

through the food web. In Figure 7, inspired by the framework proposed by Olf et al. (2009), we have illustrated the effects of mixing based on our experimental results and the hypothetical mechanisms behind them. Our results show how mixing changes the conditions of the water column through either direct physical effects (e.g., sediment resuspension, copepod kinetics, virus and prokaryote interactions, green algae chlorophyll *a* content and productivity) or indirect effects (e.g., increasing green algae productivity, which in turn causes the pH to rise, or resuspension of sediments, leading to a more turbid environment for algae and possibly impairing copepod feeding activity).

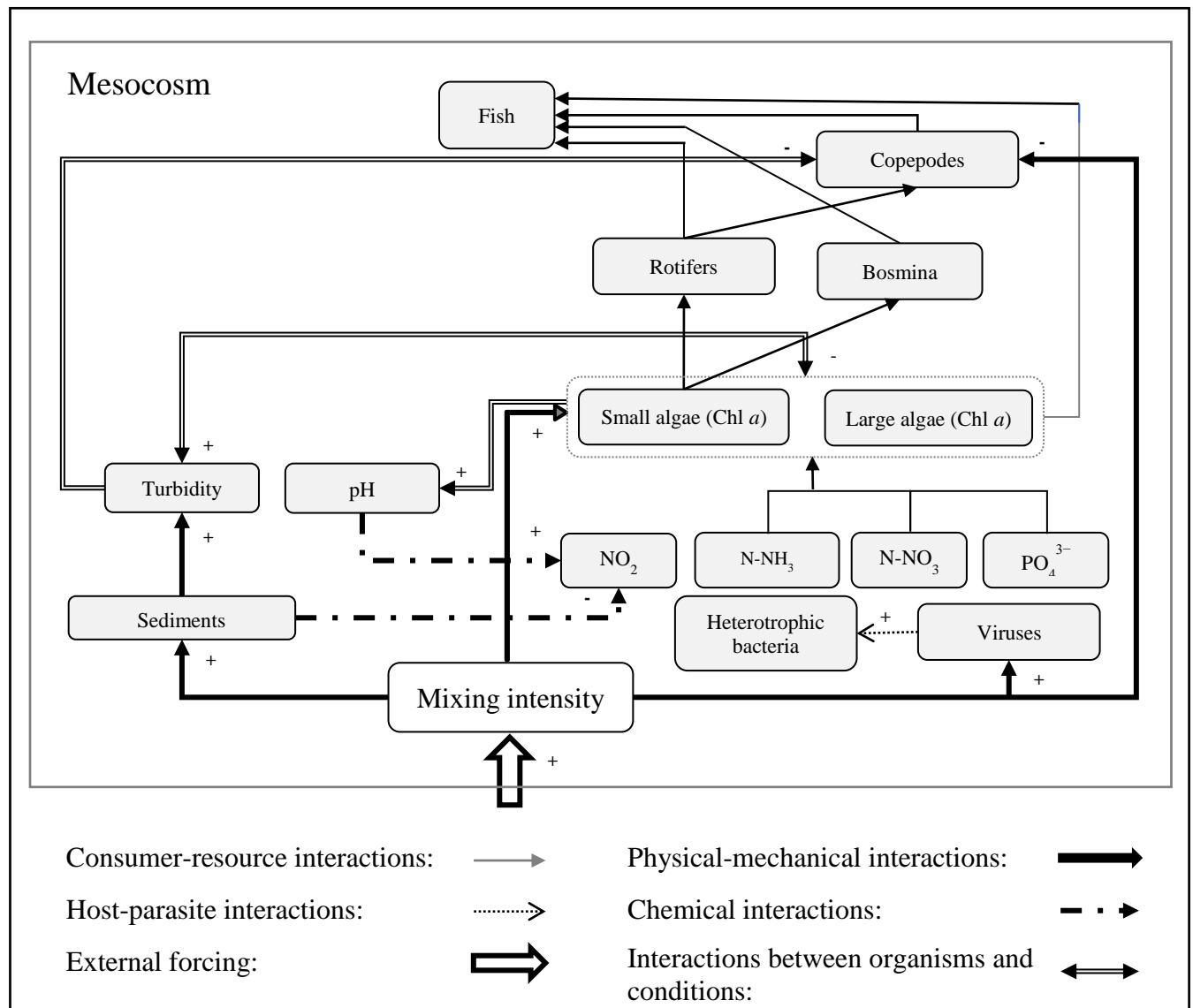


Figure 7. Synthetic schema of the effects of mixing based on our experimental results. The different types of arrow represent 6 interactions that structure the environment.

In our experiment, mixing changed ecosystem functioning by enhancing the primary productivity. Yet it also changed the structure of the community by differently affecting the zooplankton community and possibly strengthening the viral impact on the prokaryotes. This could have an important impact on energy pathways from lower to upper trophic levels. Mixing and resuspension events are common features in shallow lakes that demand a broader analysis on multiple trophic levels to fully comprehend their action on the ecosystem functioning. The inclusion of abiotic factors and different types of interactions, albeit challenging, gives a better understanding of how the food web behaves and adjusts to different environmental conditions.

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Chapter IV

Response of shallow lakes with different mixing regimes to 1°C warming

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Abstract

Freshwater ecosystems will experience an increase of average temperatures in the next decades (from 1° to 3.7°C increase on average for the end of the 21th century depending on the IPCC scenarios). In addition to other anthropogenic pressures, such as land-use changes, pollution and eutrophication, climate warming is likely to affect phenological events, communities' assemblages, metabolic balance, water chemistry and trophic cascades. Shallow lakes are extremely complex ecosystems that can greatly differ in terms of functioning and composition from one lake to another. Among the sources of variability, the degree to which a shallow lake is exposed to wind-induced mixing seems highly important. Mixing has been shown to impact phytoplankton communities, biomass and photosynthetic activity. It can also have a strong impact on nutrient and sediment resuspension through the erosion of the sediment bed. In this two-month experiment, we followed the response to 1°C warming of typical pelagic communities in mesocosms with two distinct mixing regimes. Due to technical problems, the warming experiment started only at the end of the first month. In this experiment, results show that an increase of 1°C does not affect the functioning or composition of freshwater communities. By contrast, mixing had a visible effect on phytoplankton biomass, primary productivity and copepods abundance. This experience calls for replication as technical difficulties shortened the length of the warming experiment which might have not been enough to observe subtle changes due to 1°C warming.

Introduction

In the past decades, climate warming has sparked a great interest in the scientific community. The IPCC report ([IPCC climate change-synthesis Report 2014](#)) gives four estimates of mean global temperature increase for the end of the 21th century (2081-2100 relative to the 1986–2005 period) based on four green-house gases emission scenario (RCP) : RCP2.6 : 1°C (likely range 0.3 to 1.7°C), RCP4.5 : 1.8°C (likely range : 1.1 to 2.6°C), RCP6.0 : 2.2°C (likely range: 1.4 to 3.1°C) and last RCP8.5 : 3.7°C (likely range : 2.6 to 4.8°C). In addition to an average increase of global temperature, IPCC climate experts also predict an increase in the frequency and duration of summer heat-waves. Temperature is a major abiotic forcing on freshwater ecosystems. It impacts every unit of biomes, from the physiology of single cells to phenological events and distribution ranges of entire populations. It is also very likely to affect biogeochemical cycles, lake stratification and water levels. Taking into account all possible drivers of global change (land use, climate, biotic exchanges, nitrogen deposition and CO_{2atm} increases), freshwater biodiversity might be declining at a faster rate than any other ecosystem ([Sala et al. 2000](#)). It is therefore crucial to understand and anticipate the responses of freshwater ecosystems to the current accelerating global change.

In response to these challenging tasks, an abundant literature is already available on the effects of warming and heat waves on freshwater ecosystems. One of the well-known and already observable consequences of warming is the increasing frequency and magnitude of cyanobacterial blooms in eutrophic lakes ([Paerl and Huisman 2008](#); [Kosten et al. 2011](#)). Cyanobacteria, like the potentially toxic *Microcystis aeruginosa*, grow better at high temperature than other groups such as diatoms, and supposedly green algae but the latter point is controversial ([Lürling et al. 2013](#)). Buoyant cyanobacteria also benefit from the still water due to increased

stratification (Jöhnk et al. 2008). These blooms can seriously damage the functioning of these lakes and prevent fishery and recreational activities (Dodds et al. 2009). Other observations on shallow lakes across latitudinal gradients suggest longer growing seasons, increased dominance of phytoplankton over macrophytes, development of floating plant communities, greater diversity and fecundity of fish, and reduced zooplankton grazing (McKee et al. 2003; Moss et al. 2004; Gyllström et al. 2005; Jeppesen et al. 2005; Mooij et al. 2005; Meerhoff et al. 2007). All these changes could have potentially great impacts on trophic interactions, energy pathways and global functioning of lakes.

Mesocosm experiments have also been carried out in order to experimentally test the effects of increased temperatures in freshwater lakes. These experiments usually use computer-controlled heating systems with hot water injections or heating elements at the bottom of mesocosms (McKee et al.; McKee et al. 2003; Liboriussen et al. 2005; Feuchtmayr et al. 2009; Yvon-Durocher et al. 2010; Kratina et al. 2012; Stewart et al. 2013); others simulate local greenhouse effects using transparent plastic covers (Strecker et al. 2004; Netten et al. 2010). The temperature target in warming experiment is usually high with 3°C to 5°C above ambient temperatures. Month and year-long experiments manipulating warming in shallow enclosures gave interesting results, for instance : ecosystem respiration increases at a faster rate than primary production leading to a reduction of carbon sequestration by 13% (Yvon-Durocher et al. 2010), increases in phosphorus concentration and frequency of severe deoxygenation (McKee et al. 2003), earlier onset of phytoplankton and zooplankton growth with earlier biomass peaks and strong positive responses of zooplankton abundance (cladoceran, copepodes and rotifers) (Nicolle et al. 2012), decreased phytoplankton biomass through light competition with developing floating

plants (Feuchtmayr et al. 2009), and increased top-down control in winter and reduced algal blooms in summer (Kratina et al. 2012).

While the majority of warming experiments manipulate two or three elements (nutrient charge, predation through fish abundance and temperature), in our study, we considered another angle which is the structure of the water column with different mixing regimes. Wind-induced mixing is a key element in shallow lakes structure (Reynolds et al. 1983, 1984; Carrick et al. 1993; Schelske et al. 1995; Søndergaard et al. 2003; Reynolds 2006). When strong enough, mixing causes resuspension of sediments changing the under-water light climate and can also release nutrients (especially phosphorus) into the water column. Water motion is also an important factor in the competition between different groups of algae and favors sinking species such as diatoms or green algae while calm condition favors buoyant cyanobacteria (Reynolds et al. 1983, 1984; Huisman et al. 1999, 2004; Sommer et al. 2012; Blottière et al. 2013). In a large mesocosm experiment with wave-makers, we showed that mixing had a clear and positive effect on chlorophyll *a* concentration, on pH (due to increased photosynthetic activity and pumping of CO₂) and negative impact on copepods growth (Blottière et al. in prep.). Mixing is also an important process in the oxygenation of the water column, especially during warm periods.

In this paper, we studied the response of typical freshwater pelagic communities to warming (+1°C) under two mixing regimes: well-mixed conditions and calm conditions. We hypothesize that warming will affect phytoplankton communities differently between mixing regimes by favoring cyanobacterial groups in calm enclosures. It is also expected that photosynthetic activity will be further promoted in mixed and heated enclosures. Considering water chemistry, mixing should have an antagonistic effect with warming on oxygen

concentration. Zooplankton are expected to respond positively in terms of abundance to warming, especially rotifers as [Nicolle et al. \(2012\)](#) showed.

Materials and Methods

Study site and experimental design

The experiment was run during the summer 2013 at the CEREEP-Ecotron Ile-de-France (Equipex Planaqua, St-Pierre-lès-Nemours, France). We used 12 rectangular mesocosms (10 x 1.5 x 1.5 m) made of 10 cm insulating polyester covered with a liner. A wave generator is fixed at one extremity which mechanism is described in detail in [Hulot et al. \(in prep.\)](#). A paddle rotates around an axis assembled at its basis and the paddle oscillations generate surface stationary wave. The wavelength and amplitude of waves are determined by respectively the frequency and amplitude of paddle oscillations. All enclosures were filled at 50% from tap water and 50% from a rain reservoir of the station, reaching a final total volume of 15m³ and water column of 1 m. 200L of sieved sand from Loire River (France) were put in each mesocosm as homogeneously as possible to serve as a sediment bed. 20 L of fresh sediments from a lake (Base de loisir, Champ-sur-Marne, France) were added on top on the sand in each mesocosms. This particular lake was chosen because it is hypereutrophic and experiences heavy cyanobacterial blooms every summer. Consequently, sediments were very likely to contain dormant cyanobacterial cells and high phosphorus concentration. In the same time, we used 4 circular containers ~1.5m³ to cultivate algae and zooplankton collected in lakes and ponds around the station. They were used as reservoirs for reseeding the mesocosms weekly throughout the experiments in order to limit the loss of diversity due to species selection ([Mette et al. 2011](#)) and ensuring the development of potential populations when environmental conditions are met ([Hulot et al. 2014](#)). Also, water charged with *M. aeruginosa* cells from the lake of Champ-sur-Marne

was regularly added to each mesocosms. On June 27th, phosphorus was added in all mesocosms using a K_2HPO_4 solution to reach a final mesocosm concentration of $100 \mu\text{g P. L}^{-1}$. On the same day, each mesocosm was seeded with phytoplankton and zooplankton from the containers. On July 1st, 14 planktivorous cyprinid fish (*Carassius carassius*) were added in each mesocosm with a mean density of $9.82 \pm 0.22 \text{ g m}^{-3}$.

Mixing

To test the impacts of mixing and warming on shallow lakes, the experimental design had 4 treatment levels: “Mixed” (M), “Mixed and Warmed” (MW), “Calm”(C), “Calm and Warmed” (CW). Each treatment was run in triplicates. In M and MW enclosures, we generated long wave-length waves (about 3.5 m) in order to mix the entire water column and create friction forces at the sediment surface. This ensures regular resuspension of the bottom top layer and sedimented particles. In C and CW enclosures, short wave-length waves were generated to create a very superficial mixing. The machines were activated right after fish addition on July 1st.

Warming

In order to increase the water temperature in warmed mesocosms (MW and CW), we used 200 μm thick polyethylene films fixed on metal rods on top of the enclosures as shown on figure 1. Ten polyethylen films were necessary to cover each mesocosms. Each piece of film was mobile and could be opened or closed at will. A space between the edges and the films and between two films was left to ensure the air circulation above the water. This set up ensures a “green-house” effect from the top of the water column and does not mechanically interfere with the water column structure. We verified that the plastic films did not alter the quality of the light by realizing absorption spectra of natural light under the films and compared them to natural light

spectra taken at the same time. As expected, the light spectrum under the polyethylen films is highly similar to natural light spectrum (Annex 1).

The plastic films were installed on all mesocosms but only opened on 6 of them on July 31th (the 5th week of the experiment). The delay between the beginning of the experiment and the beginning of the warming was due to technical problems.

Air and water temperatures were followed using iButton® (Maxim Integrated, U.S.). To make a complete depth profile of temperature in each mesocosms, we hooked 5 iButtons on a rope fixed on a metal rod and weighed with a bottle of sand. The iButtons took temperatures measurements every 10 minutes above the surface, at the subsurface, at depth of -30cm, -60cm and at the bottom ~-80cm. The measurements started on July 12th and ended on August 19th. In addition, meteorological data (air temperature, wind speed, rain and atmospheric pressures) were taken every 10 minutes by a multi-sensors acquisition unit (CR23X, Campbell scientific, U.S.) directly on site.

Physical measurements and water chemistry

All mesocosms were sampled weekly (July 1st: date 0 to August 26th: date 9) and all measurements were made at two depths: below the surface and just above the sediment bed. Samples and measurements were made at the center of the enclosures from a ramp fixed on top of



Figure 1. Photography of one mesocosm with polyethynel films fully deployed.

each mesocosm. Physical parameters such as temperature, pH, oxygen concentration, conductivity and nephelometric turbidity (expressed in FNU) were measured directly in the mesocosms using a multiparameter probe (YSI 6600 V2-4-M).

Water samples for total suspended solids (TSS), total and dissolved nutrient concentrations, phytoplankton, zooplankton and flow cytometry analyses were taken with a 2.2-l Alpha model Van Dorn horizontal water sampler (Anhydre). TSS (in dry weight per liter) were obtained by filtering a known water volume (typically 1 L, more or less depending on the particulate density) through pre- weighted and dried 0.7 μm pore size Whatman GF/F filters and then weighting the filters again after at least 24 hours of drying in an oven at 105° C. The filtered water was then used in laboratory to measure dissolved nutrient concentrations with a spectrophotometer (DR3900 Hach Lange). Orthophosphates were determined using the ascorbic acid method (PhosVer3 powder Kit Hach Lange). Nitrate, ammonium, nitrite were determined using cadmium reduction method, the diazotation method and the salicylate method (Hach Lange kits: Nitriver 5, Nitriver 3 and Ammonia Nitrogen reagent set), respectively. Total phosphorus (TP) and Total Nitrogen (TN) were determined on unfiltered water samples using the vanadate-molybdate method (LCK349 Kit Hach Lange) and the Koroleff Digestion (Peroxodisulphate) with photometric Detection with 2,6-Dimethylphenol (LCK138 Hach Lange Kit). Total organic carbon (TOC) determination was carried out with the purging method and persulphate digestion (LCK385 Hach Lange Kit)

Phytoplankton and zooplankton

Phytoplankton samples were divided in three size classes directly on site using differential filtration, *i.e.* a consecutive filtration through 100 μm and 30 μm mesh sizes nylon filters. Hence, we had three subsamples: unfiltered water with algae of all sizes, a subsample with algae below

100 µm in GALD (greatest axial linear dimension) and a subsample with algae below 30 µm in GALD. These subsamples were kept in the dark for 15 minutes before fluorescence measurements using the BBE FluoroProbeTM spectrofluorometer (Moldaenke) in laboratory. This fluoroprobe provides an estimate of chlorophyll *a* content (expressed in equivalent µg L⁻¹ of Chl-*a*) by measuring *in vivo* autofluorescence of pigment-containing micro-organisms (Beutler et al 2002, Leboulanger et al. 2002, Rolland et al. 2010). The probe allows for discrimination among four phytoplankton groups referred to as ‘green’ algae (chlorophyta and Euglenophyta), ‘brown’ algae (Bacillariophyta, Chrysophyta and Euglenophyta), ‘blue’ algae (Cyanophyta) and ‘red’ algae (Cryptophyta). Preliminary results showed that there were no algae larger than 30 µm in GALD.

Three to five liters were filtered on 30 µm mesh size nylon filters to collect zooplankton. They were immediately fixed in a solution of 96% ethanol and 4% glycerol (respectively 72% and 1% final concentration) to avoid body deformation. Samples were then exhaustively counted and identified to the genus or species under a microscope.

Statistical analysis

Quantifying the warming effect of polyethylen films.

In order to quantify the warming effect of polyethylen films, we fitted robust linear regressions between warmed (W) and non-warmed (NW) systems on iButtons temperature data before and after the set-up date as follow;

$$W_{before} \sim a_1 NW_{before} + b_1$$

$$W_{after} \sim a_2 NW_{after} + b_2$$

Slope (a_1 , a_2) and intercepts (b_1 , b_2) were extracted. When slopes were not significantly different (as expected), then the difference between the intercepts was used as an estimation of the warming effect. All combinations of mesocosms were tested (MW vs M, CW vs C, MW vs C, CW vs M, CW vs MW and C vs M) at all depths (subsurface, -30cm, -60cm and at the bottom).

Statistical analysis on biotic and abiotic variables

We verified the homogeneity between mixed and unmixed mesocosms at the beginning of the experiment using a Wilcox test on the first date. Due to the delay between the start of the experiment and the set-up of polyethylen films, we took the decision to split the data set in half. The warming effect was tested on the second part of the data set, using the last sampling date before the installation (29-30/07/2013) as the initial point as the date 0. The effect of mixing was then tested on the whole dataset.

In order to test the effects of mixing and warming on the biological and chemical variables measured, we constructed linear mixed-effects models (LME, fit by REML - nlme packages -, Pinheiro et al. 2013, R Core Team. 2014) with time, warming (for the analysis on the second part of the dataset) and mixing, plus their interactions as fixed effects. Individual mesocosms were treated as a random effect. The majority of variables had non-linear dynamic across time, so we used quadratic, log or exponential model to fit the observation as closely as possible. Residuals were visually checked to assess the quality of the model. The effects of the depth were tested on every variable, and when non-significant, further statistical analyses were made on the mean values between depths. Prior to these analyses, normality and homoscedasticity of each variable were assessed visually and log or sqrt corrections were applied when necessary. Statistical analyses were performed using the R software version 3.0.3 (www.r-project.org).

Results

Temperatures evolution and quantification of the warming effect

The figure 2 shows the evolution of subsurface temperatures by treatments (iButton data) and air temperatures (from the acquisition unit) from July 12th to August 19th. The month of July was particularly hot for the region with peaks of temperature reaching 35°C. This month was officially declared as the 3rd hottest month of July since 1900 with temperature 1.9°C higher than average. At the end of July, a thunderstorm broke out with heavy rains and we observed a drop in temperatures. Polyethylen films were installed after the storm on July 31th and remained deployed until the end of the experiment. The month of August was closer to summer averages with only temperatures 0.2°C higher than average. On figure 2, we clearly see that temperatures were homogeneous between enclosures during July and diverged rapidly after polyethylen film installation. The temperature difference between warmed and normal enclosures remained more or less the same until the end of the experiment. Figure 3 shows water temperature evolution of the different groups of mesocosms at different depths. We can observe a decrease of average temperatures with depth but more importantly a clear diminution of daily temperature fluctuations. The temperature increase due to polyethylen films is similar throughout the water column. Regression analyses confirm these visual observations and allows for a valid estimation of the warming effects. When regression slopes a_1 and a_2 were not statistically different, the differences of b_2 and b_1 were around 0.8-1°C. However, in most regressions, slopes were statistically different and therefore intercepts were not comparable. Another visual approach is given in figure 4, where the difference of temperatures between warmed and non-warmed mesocosm is shown. Temperature depth profiles taken 1 month apart illustrates the difference of ~1°C between warmed and normal enclosures (figure 5). This difference is also kept at night

(data not shown). We observe that water temperature structure is affected neither by warming nor by mixing. This indicates that the warming effect due to the polyethylen sheets warms the water column rapidly as a whole and does not increase microstratification in warmed mesocosms, at least on this range of air temperature.

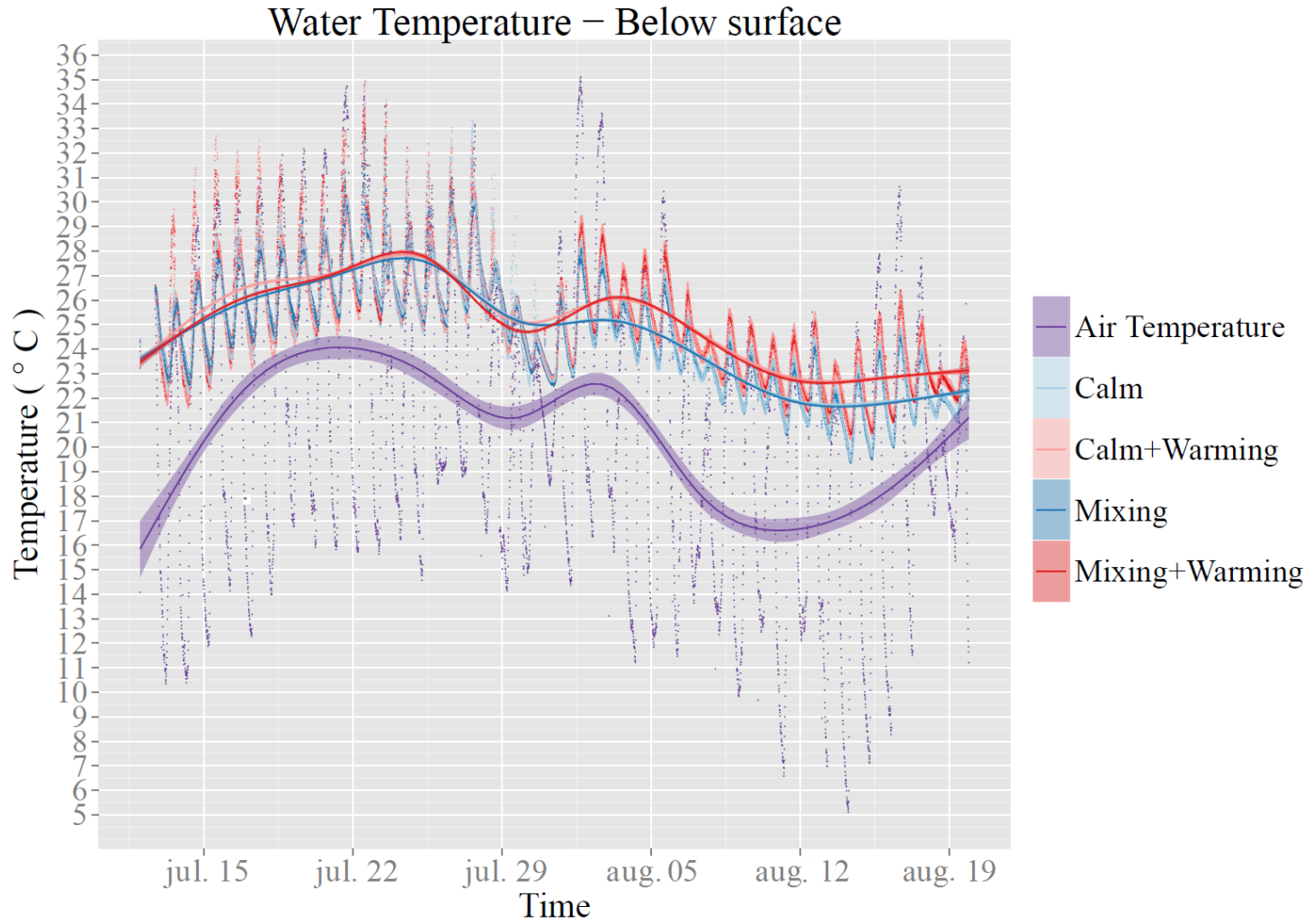


Figure 2. Evolution of air and subsurface water temperatures during the experiment. A GAM model was fitted on each data set with a 99% confidence interval on parameters and with a span of 0.5 (50% of the points were used for the fit) to show the global temperature trends without the noise of daily fluctuations.

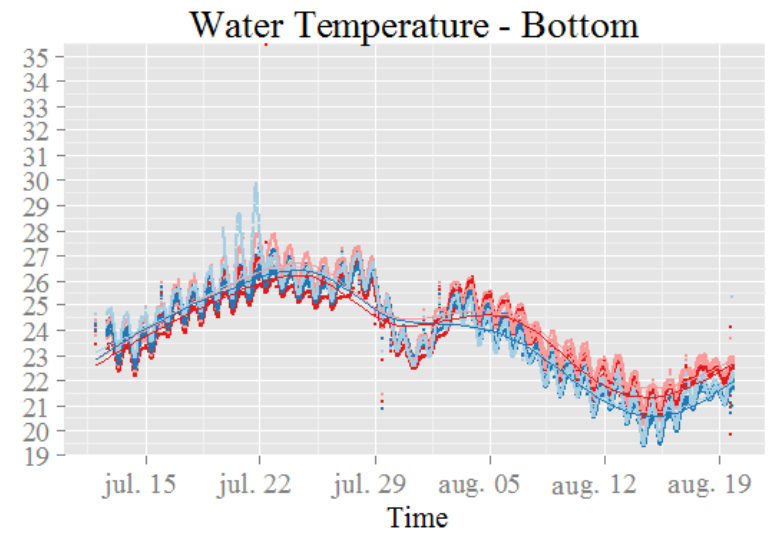
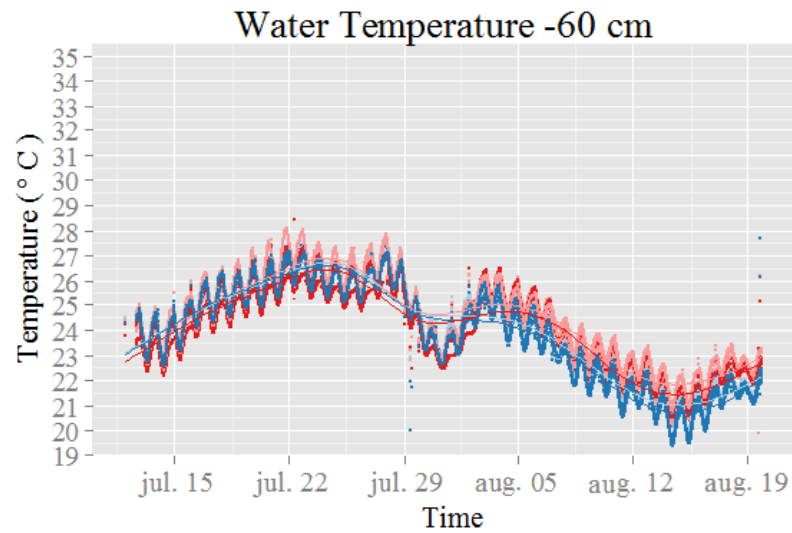
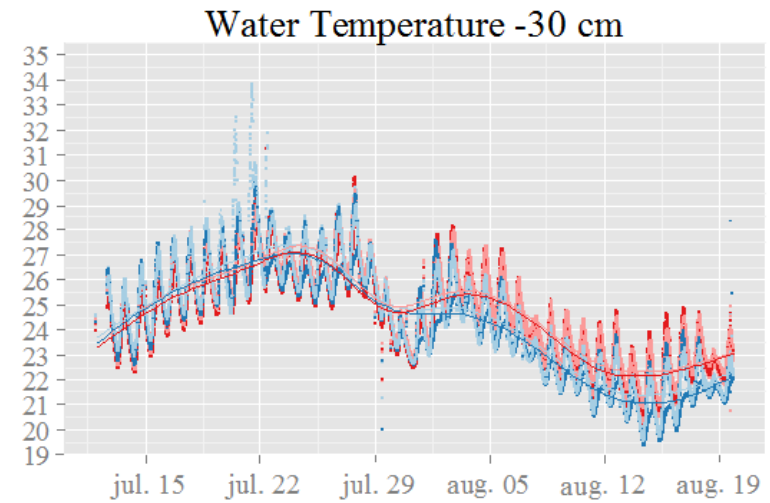
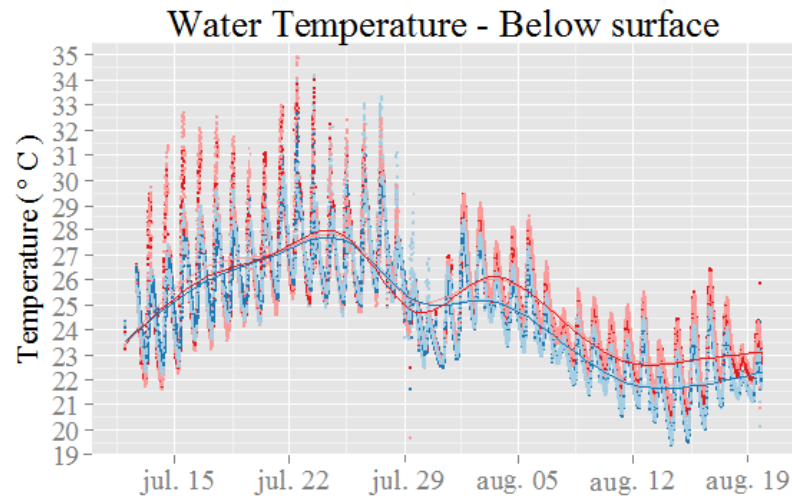


Figure 3. Temperatures at different depth (subsurface, -30cm, -60cm and at the bottom) during the experiment. Legend same as figure 2. GAM models are fitted on each treatment.

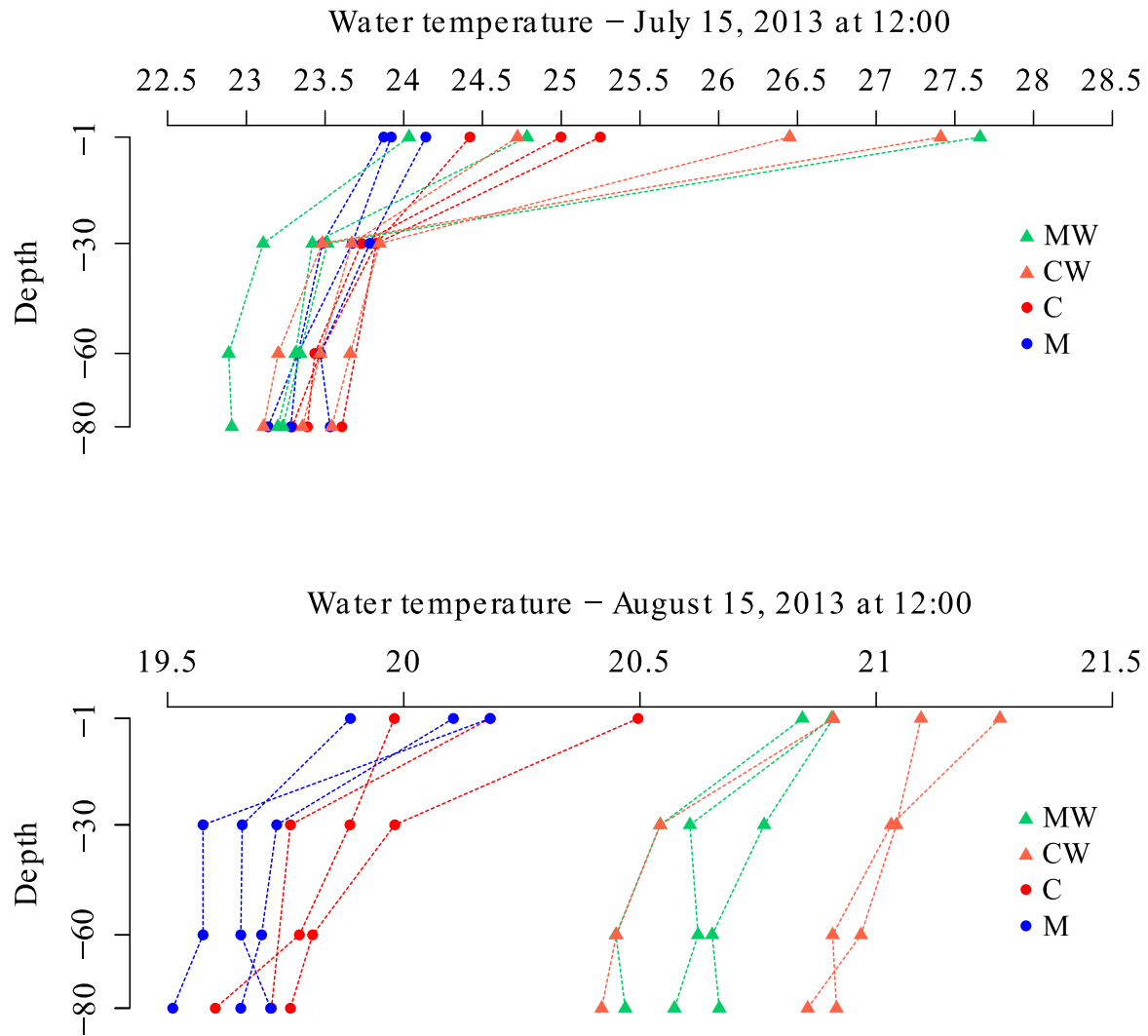


Figure 5. Depth profiles of water temperatures in all mesocosms at two distinct dates at noon. The top panel corresponds to temperatures taken on the 15th of July (without polyethylene films) and the bottom panel corresponds to temperatures taken on August 15 (with polyethylene films). Mesocosms of the same treatment group (3 mesocosms per treatment) share the same color.

Effect of warming on biotic and abiotic variables

Statistical analysis on the second period showed no significant effect of warming on any of the 18 variables followed (See table 1 and figures 7, 8, 10). Considering the latter results, the effect of mixing was tested on the whole data set and the warming effect was not taken into account in the statistical models.

Effects of mixing on abiotic and biotic variables

Turbidity

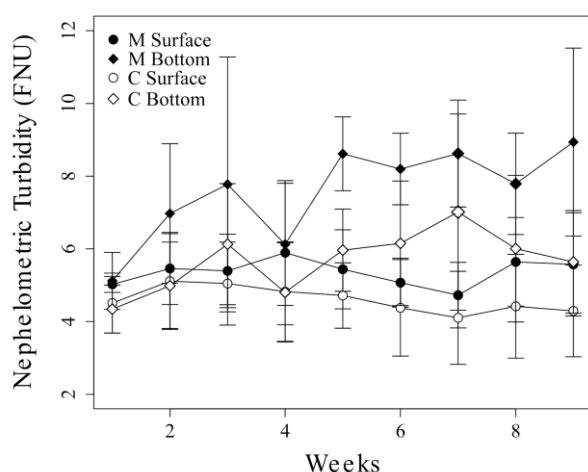


Figure 6. Temporal dynamic of the nephelometric turbidity (FNU). Black symbols : mixed mesocosms, white symbols : calm mesocosms. Round dots : surface measurements, diamond shapes : bottom measurements. Error bars are standard deviation. The decrease of turbidity seen on the 4th week was due to an power outage on the site that stopped the wave machines for one or two days.

Mixing increased the nephelometric turbidity significantly (M, $F_{1,10}=10.30$, $p=0.0015$, table 2). The highest turbidity values were found at the bottom of mixed mesocosms and the lowest values at the surface of calm mesocosms (Fig. 6). There was a clear difference between depths with higher turbidity values at the bottom in calm and mixed mesocosms (Depth, $F_{1,198}=75.64$, $p<0.0001$). The difference between surface and bottom turbidity was more important in mixed mesocosms compared to calm ones (DxM, $F_{1,198}=9.176$, $p=0.0028$).

Chemistry

No effect of mixing was detected on any of the chemical variables except for TOC (Fig. 7f). Nitrate-nitrogen concentration decreased rapidly from 2.13 ± 0.25 mg L⁻¹ to 0.67 ± 0.15 mg L⁻¹ during the first half (week 1- week 5, all mesocosms pooled) of the experiment and stabilized

around 0.65 mg L^{-1} in the second half of the experiment (Fig. 7b). Nitrite-nitrogen followed the same pattern with a rapid decrease from $0.029 \pm 0.006 \text{ mg L}^{-1}$ to $0.009 \pm 0.007 \text{ mg L}^{-1}$ in 5 weeks and then stabilized (Fig. 7c). Ammonium remained at very low concentrations during the experiment suggesting that the nitrogen cycle was functioning well (Fig. 7e). Total nitrogen displayed an interesting temporal dynamic (Fig. 7a) with a decrease from $3.88 \pm 1.42 \text{ mg L}^{-1}$ to $1.56 \pm 0.33 \text{ mg L}^{-1}$ in the first half of the experiment in accordance with the decrease of nitrate-nitrogen but then we observed a net increase from date 6 to 8 reaching concentrations of $3.79 \pm 0.79 \text{ mg L}^{-1}$ while nitrate-nitrogen were still low suggesting a strong increase in organically-bounded nitrogen. Total phosphorus showed a complex dynamic that we could not successfully analyze with usual statistical method. Very high values were found in some mesocosms, high above the original enrichment level of 0.1 mg L^{-1} suggesting that the sediment and the water from Champ-Sur-Marne Lake were highly enriched in phosphorus. Total Organic Carbon concentration almost doubled (from $14.42 \pm 1.43 \text{ mg L}^{-1}$ to $26.42 \pm 1.94 \text{ mg L}^{-1}$, all mesocosm pooled) in the first week of the experiment (Fig. 7f). Then, we observed a separation between mixed and calm mesocosms with higher TOC concentrations in mixed mesocosms compared to calm ones ($M \times T$, $F_{1,93}=13.11$, $p=0.0005$, table 2).

Table 1. Results of the warming experiment carried out in summer 2013.

Response variable	<i>P</i> -values					
	<i>Data set : 29/07-26/08</i>					
	Mixing (M)	Warming (W)	Time (T)	M x T	WxT	MxWxT
<i>Turbidity</i>						
Nephelometric turbidity (FNU)	0.0476	n.s	n.s.	n.s	n.s	n.s.
<i>Chemistry</i>						
Oxygen (mg L ⁻¹)	n.s	n.s	n.s.	n.s.	n.s.	n.s.
pH	n.s	n.s	n.s.	n.s.	n.s.	n.s.
Ntot (mg L ⁻¹)	n.s	n.s	<0.0001	n.s	n.s	n.s.
NO ₃ -N (mg L ⁻¹)	n.s	n.s	n.s.	n.s.	n.s.	n.s.
NO ₂ -N (mg L ⁻¹)	n.s	n.s	<0.0001	n.s	n.s	n.s.
NH ₃ -N (mg L ⁻¹)	n.s	n.s	n.s.	n.s.	n.s.	n.s.
COT (mg L ⁻¹)	0.0592*	n.s	<0.0001	0.0565*	n.s.	n.s.
PO ₄ ³⁻ (mg L ⁻¹) not applicable						
<i>Phytoplankton</i>						
Chlorophyll YSI (µg Chl <i>a</i> L ⁻¹)	0.0512*	n.s	0.0035	n.s.	n.s.	n.s.
Green algae (µg Chl <i>a</i> L ⁻¹)	0.0449	n.s	0.0053	n.s.	n.s.	n.s.
Blue green algae (µg Chl <i>a</i> L ⁻¹)	0.0804	n.s.	0.0053	n.s.	n.s.	n.s.
<i>Zooplankton</i>						
Zooplankton (ind. L ⁻¹)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rotifer (ind. L ⁻¹)	n.s.	n.s.	0.0067	n.s.	n.s.	n.s.
Bosmina (ind. L ⁻¹)	n.s.	n.s.	<0.0001	n.s.	n.s.	n.s.
Nauplii (ind. L ⁻¹)	n.s.	n.s.	0.0065	n.s.	n.s.	n.s.
Diaphanosoma Brachyurum	n.s	n.s	0.0217	n.s	n.s	n.s.
Copepode (ind. L ⁻¹)	n.s.	n.s.	<0.0001	<0.0001	n.s.	n.s.

n.s = not significant, * marginally significant.

Table 2.Results of mixing experiment carried out in summer 2013.

<i>P</i> -values							
Response variable	<i>Data set : 01/07 - 26/08</i>						
	Mixing (M)	Time (T)	Depth (D)	M x T	M x D	D x T	M x D x T
<i>Turbidity</i>							
Nephelometric turbidity (FNU)	0.0079	0.0015	<0.0001	0.0004	0.0028	0.0001	n.s
<i>Chemistry</i>							
Oxygen (mg L ⁻¹)	n.s.	<0.0001	n.s.	0.0665*	n.s.	n.s.	n.s.
pH	0.0477	<0.0001	n.s.	0.0204	n.s.	n.s.	n.s.
Ntot	n.s	<0.0001	n.s.	0.0621	n.s.	n.s.	n.s.
NO ₃ -N (mg L ⁻¹)	n.s	<0.0001	n.s.	n.s.	n.s.	n.s.	n.s.
NO ₂ -N (mg L ⁻¹)	n.s	<0.0001	n.s.	n.s	n.s.	n.s.	n.s.
NH ₃ -N (mg L ⁻¹)	n.s	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
COT (mg L-1)	0.0336	<0.0001	n.s.	0.0005	n.s.	n.s.	n.s.
PO ₄ ³⁻ (mg L ⁻¹) not applicable							
<i>Phytoplankton</i>							
Chlorophyll a in situ (µg L ⁻¹)	0.0648	<0.0001	<0.0001	0.0051	0.0101	0.0017	0.0562*
Green algae (µg Chl a L ⁻¹)	0.0449	0.0001	n.s.	0.0083	n.s.	n.s.	n.s.
Blue-green in situ (µg Chl a L ⁻¹)	0.0556*	0.0001	0.0001	0.0021	0.0259	0.0160	n.s.
<i>Zooplankton</i>							
Zooplankton (ind. L ⁻¹)	n.s.	<0.0001	n.s.	n.s.	n.s.	n.s.	n.s.
Rotifer (ind. L ⁻¹)	n.s.	<0.0001	n.s.	n.s.	n.s.	n.s.	n.s.
Bosmina (ind. L ⁻¹)	0.0188	<0.0001	0.0002	0.086	n.s	0.0329	n.s.
Diaphanosoma brachyurum	n.s	<0.0001	0.0099	0.053*	n.s.	n.s.	n.s.
Nauplii (ind. L ⁻¹)	0.0624*	<0.0001	n.s.	0.0120	n.s.	n.s.	n.s.
Copepod (ind. L ⁻¹)	n.s	<0.0001	n.s.	0.0001	n.s.	n.s.	n.s.

n.s = not significant, * marginally significant.

*Effects of mixing on chlorophyll *a*, pH of dissolved oxygen*

According to the BBE data, green algae chlorophyll *a* content accounted for more than 98% of total chlorophyll *a* during the experiment. Diatoms and cyanobacteria signals were very low, most of the time below detection limit. In contrast, the ISY probe gave a clear, positive dynamics for blue-green algae, even though they still represented less than 6% of the total chlorophyll *a* measured.

Green algae density increased rapidly during the first 5 weeks followed by a decline until the end of the experiment (Fig. 8). Green algae reached higher density and decreased less rapidly in mixed mesocosms compared to calm ones (MxT, $F_{1,93}=7.28$, $p=0.0083$, table 2).

BBE and YSI measurements yielded comparable results in terms of global dynamic and range of chlorophyll *a* concentration (linear regression : $R^2=0.62$, $p<0.0001$) (Fig. 8a, b). However, *in situ* data from the YSI probe showed a difference of chlorophyll *a* between the surface and the bottom measurements (D: $F_{1,197}=36.67$, $p<0.0001$). Detailed observations of the dynamics of chlorophyll *a* in each mesocosms show that concentrations are homogeneous in calm mesocosms while chlorophyll *a* concentrations were always higher at the bottom than at the surface in mixed mesocosms (data not shown, MxD: $F_{1,197}=6.75$, $p=0.0151$ and MxDxT: $F_{1,197}=3.68$, $p=0.0562$, table 2).

Blue-green algae measured with the YSI probe were positively affected by mixing and grew better in mixed enclosures (Fig. 8c; MxT, $F_{1,197}=9.72$, $p=0.0021$). They were more abundant at the bottom of the enclosures (D: $F_{1,197}=36.67$, $p<0.0001$), especially in mixed mesocosms while they remained homogeneously distributed in calm enclosures.

The pH reached very high values during this experiment with an increase from 9.13 ± 0.13 to 10.28 ± 0.33 (all mesocosms pooled) in the first 4 weeks (Fig. 8d). Then, pH decreased in calm mesocosm while it remained elevated in mixed mesocosms (MxT: $F_{1,93}=5.56$, $p=0.0204$, table 2).

Day-concentrations of dissolved oxygen were relatively high throughout the experiment. Oxygen concentration in the water decreased steadily from the third to the sixth week and then plateaued in both mixed and calm mesocosms (Fig. 8e). Dissolved oxygen (DO) concentrations seemed to decrease to a lesser extent in mixed mesocosms but this effect was only marginally significant (M x T: $F_{1,92}=3.44$, $p=0.0665$, table 2). Night measurements (between 4 and 5 am) were also done in August the night after day-measurements (6/08, 13/08 and 20/08) to evaluate the effect of respiration on dissolved oxygen content at night (Fig. 9). The differential of concentration between day and night measurements was significantly higher in mixed mesocosms (Wilcox-test were performed on each date separately and yielded the following results date 6: $n=12$ $p=0.0076$; date 7: $n=12$ $p=0.0193$; date 8: $n=12$ $p=0.0166$, see figure 8).

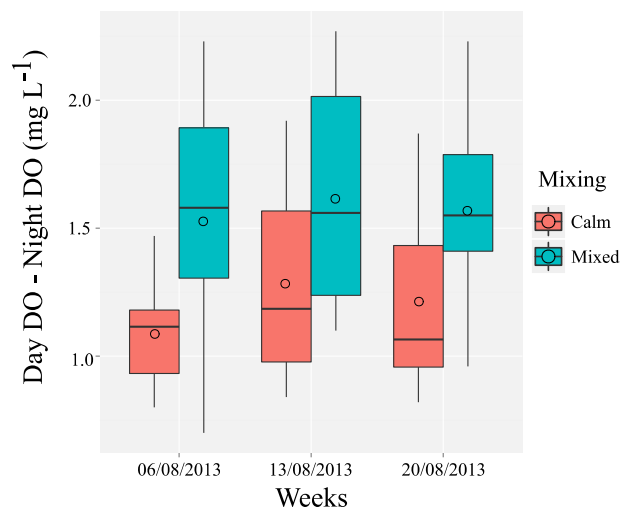


Figure 9. Difference between day and night concentration of dissolved oxygen (DO) in the water. Measurements were done on three dates in August. The night-measurements were done the night after the day-measurements between 4 and 5 am. Round dots in boxplots represents the mean.

Effects of mixing on zooplankton

The zooplankton community was composed of 3 major groups : rotifers with large dominance of the polyarthra, lecanidae and trichocera families, cladocerans with two prevalent species *Bosmina longirostris* and *Diaphanosoma brachyurum*, and last, copepodes (large dominance of cyclopides) and their nauplii larvae.

Rotifers were the only abundant zooplankton group for the first 4 weeks of experiment (Fig. 10a). Their population dropped in mixed and calm mesocosms from 642 ± 236 to 114 ± 58 ind. L^{-1} in the first 3 weeks. Rotifers reached a peak of abundance on the fifth week (867 ± 498 and 419 ± 262 ind. L^{-1} in calm and mixed mesocosms, respectively) and then declined and stabilized. Mixing had no noticeable effects on rotifer dynamics or abundance except that the peak of abundance was slightly more important in calm mesocosms (wilcox-test on week 5, $n=6$ $p=0.0465$).

Cladocerans (*B. longirostris* and *D. brachyurum*) became relatively abundant in the second part of the experiment (Fig. 10b, e). *B. longirostris* abundance was always higher at the bottom of the water column than at the surface (D: $F_{1, 102}=14.55$ $p=0.0002$, table 2). No significant effect of mixing was found for either species dynamics.

Nauplii and cyclopide copepods also became noticeable in the second part of the experiment (Fig. 10c, d). Mixing had a significant negative effect on both age classes (Nauplii: M x T: $F_{1, 70}=6.65$, $p=0.0120$; Copepodes: M x T: $F_{1, 70}=18.29$ $p=0.0001$, table 2).

Discussion

Use of polyethylene films as a warming tool

To our knowledge, only two other warming experiments used a similar heating system based on local green-house effect in aquatic mesocosm experiments ([Strecker et al., 2004](#), [Netten et al., 2010](#)). This system presents multiple advantages: 1/ this is a simple and cheap method, 2/ polyethylen films do not modify the sun spectrum, 3/ the warming of the water column comes from the top as in natural systems 4/ the plastic films do not interfere with the structure of the water column as immersed resistances or hot water injection would. This last point deserves some emphasis as spatial heterogeneity is often overlooked in shallow ecosystems. In warmer climate, the heat will come from the top of the water column and diffuse. Even if shallow lakes do not experience strong and long-term stratifications, it is virtually certain that temperatures at the surface will be higher than the temperatures at the bottom of the lakes. This difference of a few degrees might be absolutely crucial to the species survival. Migration and patchiness are common in freshwater and marine ecosystems. In this experiment, we noticed a clear pattern in the spatial distribution of *B. longirostris* and *D. brachyurum* which were always more abundant at the bottom than at the surface of our enclosures. Whatever the reason for this behavior, it indicates that vertical distributions are not homogenous even in shallow environments. Homogeneously warming mesocosms from the bottom might impair migration mechanisms to take place. It might also unrealistically disturb the benthic fauna and chemical reactions at the water-sediment interface like the release of phosphorus or deoxygenation.

On the (non)-effects of experimental warming

No significant effect of warming was found on any of the 18 variables followed during this experiment. The statistical power of our analysis was greatly reduced by the fact that we had to split the data set in half. Four weeks of warming did not seem enough to observe any sensible effect of 1°C warming, especially on species such as copepods which take a rather long time to develop. Other warming experiment usually last for months or even years. Another important point is that the month of July was especially hot this year for this region, with maximum water temperatures around 35°C. Five fish died in calm enclosures during this period (1 on July 8th, 3 on July 16 and 17th, 1 on July 23rd which was the hottest day); with no indication of disease which suggests that they died from the heat or severe deoxygenation during the night. These extreme temperatures in July might have selected very rapidly well-adapted species to warm waters. Thus, the following 1°C warming might not have had any impact on neither selection nor physiology of the species already in place. Very high temperatures might also have put pressure on cladocerans and copepods which started to develop only after the atmospheric temperature dropped at the end of July. Rotifers abundance also decreased rapidly during the first 3 weeks while their food source (i.e phytoplankton) was increasing and their natural predators (mainly copepods here) were still absent which might indicate a negative effect of the July heatwave.

One degree Celsius warming is far below the usual temperature targets of warming experiment in freshwater studies. However, before reaching 3 to 5°C warming, ecosystems will go through a more or less continuous warming that should be addressed. 1°C warming corresponds to predictions of the IPCC experts for the mid-century (3 out 4 climatic scenarios for 2046-2065). Will the response of freshwater ecosystems be gradual or will it be sudden? Is there a temperature threshold that will trigger the changes observed today in warming experiments?

Will communities be able to evolve or at least adapt? New approaches with gradual temperature increase seem necessary in order to understand how present-day communities will respond to gradual warming. Implementing a sudden 3°C to 5°C temperature increase on present-day community assemblages might relate more to heatwaves than long-term changes in average temperatures.

Effects of mixing – comparison with 2012 experiment

Mixing had a noticeable impact on our mesocosms by increasing global turbidity and mixing the whole water column. Higher concentrations of chlorophyll *a*, TOC, pH values and oxygen concentrations suggests that the standing crop of autotrophic organisms was greater in mixed enclosures. The difference between day and night oxygen concentrations was significantly greater in mixed enclosures supporting the idea that mixing allows the system to have higher global biomass.

Higher concentrations of chlorophyll *a* can be due to 1/ increased abundance of phytoplankton 2/ at similar abundance: bigger cells with higher chlorophyll *a* content or 3/ for the same size and abundance: higher concentration of chlorophyll per cells. Our data set does not yet allow us to differentiate between those 3 possibilities. However, in a previous mixing experiment (Blottière et al. submitted), we showed that higher chlorophyll *a* concentrations were not attributable to increased abundance of phytoplankton. It seems rather that cells had higher content of chlorophyll *a* suggesting physiological adaptation to mixing. As in 2012, we also observe increased pH values in our mixed enclosure, again suggesting increased withdrawal of CO₂ due to higher photosynthetic activity. The hypothesis developed in the previous experiment was that by circulating regularly in the whole water column, phytoplankton had regular access to high light intensity but was less likely to suffer from photoinhibition due to surface high irradiance.

Nutrient availability was not affected by mixing. We did not observe higher release of phosphorus in mixed mesocosms despite the addition of enriched sediments. It is possible that with the important temperature experienced in July, most of the phosphorus held in the sediment was rapidly released in the water in all mesocosms, and the effect of mixing was therefore negligible compared to diffusion from the sediments (Jensen and Andersen 1992; Søndergaard et al. 2003; Jensen et al. 2006).

Copepodes and nauplii were the only zooplankton group to significantly respond to mixing. Adult and nauplii grew better in calm enclosures. Whether the mixing negatively impacted nauplii, adults or both remains uncertain. Many nonexclusive hypotheses may be proposed to explain this result: 1/ a negative effect of turbidity on nauplii and copepodes hunting skills, 2/ physical interference of mixing which could increase energy expenditures, 3/ higher turbidity could impair copepodes detection of their predators.

Altogether, the results of this experiment are remarkably similar to results obtained with the mixing experiment carried out in 2012 (Blottière et al. in prep.). The only major difference with 2012 is the effect of mixing on nitrites. In 2012, nitrites accumulated in calm and mixed mesocosms, but significantly less in mixed mesocosms. In 2013, nitrites were at very low concentration throughout the experiment. This comparison suggests that in 2012, there was a general dysfunction of the nitrogen cycle which led to nitrite accumulation, and in that case, mixing tended to reduce this accumulation. This dysfunction was likely due to the fact that tanks were filled with tap water, which lacked nitrogen cycling bacterial communities. This was not the case in 2013 as the water came at 50% from a local reservoir with a well-established nitrogen cycle.

Despite differences in enrichment (being more important in 2013 than in 2012), timing (2012: August-September 2013: July-August) and overall biomass (higher in 2013 than in 2012) the effect of mixing seems robust and repeatable.

Conclusion

Our experiment was not long enough to observe any subtle change in communities responses due to 1°C increase. More experiments with gradual increases of temperatures are necessary to comprehend how freshwater communities will respond to the future changes in average temperatures. On the other hand, this experiment strongly support the idea that mixing is an important element in shallow lake functioning. Lake to lake variability or even intra-lake variability might come in part from different wind-exposure and mixing intensity. Further studies are needed to fully comprehend how different structural parameters will interact with an increase in global temperatures.

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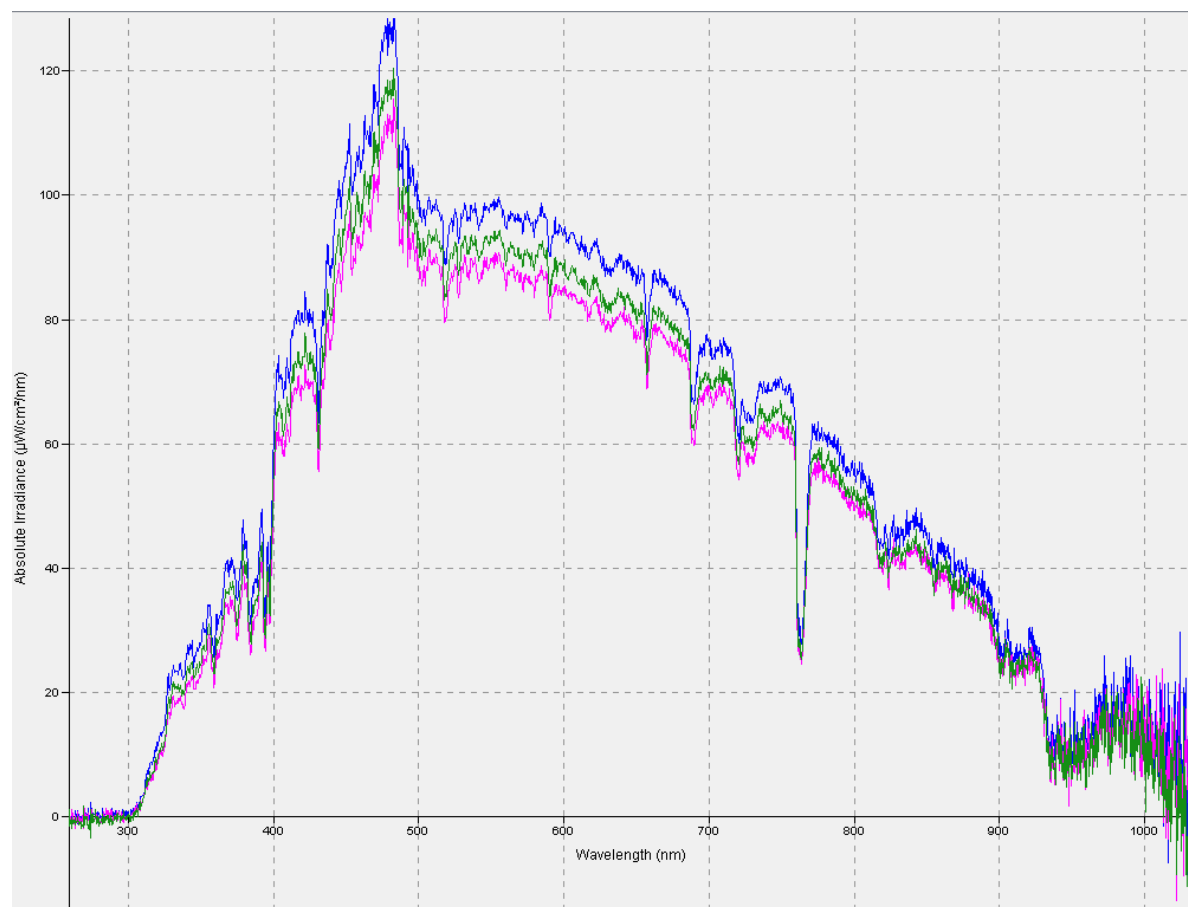
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Annexe 1



Natural light spectra. Blue : direct sunlight. Green : 100µm polyethylen film. Pink : 200µm polyethylen film.

Conclusion and perspectives

During the last four years, we have documented the effects of wind-induced mixing on pelagic communities in shallow lakes with modeling and experimental approaches. Throughout this work, we included two anthropogenic stressors: nutrient enrichment and increased temperatures in order to integrate ongoing changes in freshwater ecosystems.

One of the challenges of ecological studies is to understand the intricate relationships between abiotic and biotic drivers in the organization of communities, foodwebs and on a larger scale, the functioning of ecosystems. In this regard, freshwater lakes are particularly interesting models since a great deal of knowledge has been accumulated on their physical structure as well as on the composition and organization of their foodwebs ([Strong 1992](#), [Chase 2000](#), [Hulot et al. 2000](#), [Shurin et al. 2006](#)). In freshwater environments, foodwebs and communities are shaped by biotic interactions such as predator-prey or allelopathic interactions but also by abiotic variables such as light, temperature and of course mixing. However, for a long time, the representation of these different drivers and interactions lacked a general framework.

Recently, [Olf and his colleagues \(2009\)](#) proposed new frameworks in which multiple kinds of interactions could be represented in addition to predator-prey interactions. Typically, the first framework they proposed (Figure 12), allows for the inclusion of an abiotic factor and its effects on the rest of the foodweb. This kind of representation could prove to be particularly useful when an abiotic factor is a strong driver of population dynamics with different responses for each trophic level. In the light of previous studies and the results of this thesis, it seems clear that wind-induced mixing is a key abiotic process driving shallow freshwater ecosystems through direct and indirect pathways (Figure 7 in chapter III). In the following section, I will discuss the results obtained during the last four years and the perspectives they offer for further studies. To do so, I will first comment on my major experimental results and how they add to current

knowledge, then I will address the concept of temporality of wind-induced events, and finally, I will discuss some questions raised by our warming experiment.

Figure 12. Framework proposed by Olff et al. 2009 allowing the inclusion of abiotic factors and various types of interactions in foodweb representation.

Reproducibility and major experimental results

A key aspect of science is the reproducibility of experimental results. Often confused with the notion of replicates, which is performed within an experiment, reproducibility is an independent repetition of an experiment which gives similar results every time. The latter is a necessary condition for establishing facts in any field of science. In 2012 and 2013 we carried out two experiments with similar treatments regarding the mixing intensity. Both gave the same results, and when divergence occurred, it was explained by the specificity of each year initial conditions. For instance, in 2012 and 2013, mixing increased the chlorophyll *a* content in mixed enclosures and had a negative impact on copepodes but we did not observe the same effect in the consecutive years on nitrite-nitrogen. However, in 2012, there was a general dysfunction of the nitrogen cycle leading to nitrite-nitrogen accumulation in calm and mixed enclosures. This accumulation was alleviated by mixing, probably through a better oxygenation of the sediments where most of the nitrification activity takes place. In 2013, there was no accumulation of nitrite-nitrogen, therefore in this particular case, no effect of mixing was observed.

*Effects of mixing on chlorophyll *a* content*

Although two independent experiments are not enough, and this experiment should be reproduced by other scientists, the fact that we observed similar patterns gives us confidence in the experimental results. In 2012 and 2013, mixing had a positive effect on chlorophyll *a* concentration in the water column. According to the literature on the subject, two mechanisms could be behind this effect: (i) increased availability of nutrients in the water column, (ii) phytoplankton cells are more abundant in the water column of mixed enclosures due to the absence of loss rate via sedimentation. However, both hypotheses were rapidly ruled out as nutrient content and phytoplankton cell counts were similar between treatments (phytoplankton

count-analyses for 2013 still underway). There was a clear discrepancy between cell counts and chlorophyll *a* content suggesting a physiological adaptation of primary producers to either turbidity or mixing or both. Changes in intracellular pigment content are characteristic of light-shade adaptation in plants and phytoplankton (Beale & Appleman 1971, Falkowski & Owens 1980, Reynolds 2006 p. 113-114). Typically, phytoplankton cells respond to decreased light by increasing their photosynthetic pigment content. Variations of cell pigment content between individuals grown under different light intensity may vary from two up to -nine folds (Falkowski 1980, Reynolds 1997). Reynolds (2006 p. 113) states that most phytoplankton are able to adjust their chlorophyll *a* content within a range of $\pm 50\%$ of average and so within one or two cell generations. This capacity allows for the cell to adapt its harvesting capacity to light availability. In turbid environment such as well-mixed shallow lakes, it is thus very likely to find higher chlorophyll *a* content per cell compared to phytoplankton in wind-protected area.

The chlorophyll *a* content can also vary gapingly between different species. Using a large data set of unpublished field measurements, Reynolds found in 1984 that biomass-specific estimates of chlorophyll *a* content ranged from 0.0015 to 0.0197 $\text{pg } \mu\text{m}^{-3}$ of live cell volume. Felip & Catalan (2000) reported in a field study that differences in the taxonomic composition of phytoplankton accounted for most of the variability in the chlorophyll-biovolume relationship. In conclusion, in our experiment, the increase in chlorophyll *a* observed in mixed enclosures could be due to (i) increased pigment synthesis as a mean of photoadaptation to higher turbidity caused by resuspended materials, (ii) change in species composition toward species with higher chlorophyll content. Further analysis of DNA sampled during our experiment might help determine if one of these hypothesis or both is responsible for the discrepancy between algae count and chlorophyll *a* concentration. In all, our results add to the debate on the utilization of

chlorophyll concentration as a proxy of phytoplankton biomass and productivity (Felip & Catalan 2000, Kruskopf & Flynn 2006).

Effect of fluctuating light on phytoplankton productivity

In our mesocosm experiments, pH was higher in mixed enclosures compared to calm ones. In natural system, high pH is indicative of high photosynthesis activity depleting the water of its dissolved inorganic carbon (Schelske & Callender 1970, Schelske et al. 1974, Heaney et al. 1986, observed in Litchman 1998 and Feuchtmayr et al. 2009). Therefore we concluded that mixing enhances photosynthetic activity. First, we thought that it was a direct consequence of higher chlorophyll *a* content in phytoplankton cells; however, this is not likely the case as cells with higher chlorophyll content only compensate for the reduced light availability caused by turbidity. In theory, these cells are capable of fixing the same amount of carbon as cells growing at higher irradiance (Reynolds 2006 p. 144). The observed increase in photosynthetic activity is rather linked to the regime of fluctuating light experience in mixed mesocosms.

An abundant literature exists on the physiology of phytoplankton in response to fluctuating light experienced by cells in the mixing layer (Marra, 1978, Walsh & Legendre 1983, Falkowski 1984, Cullen & Lewis 1988, Kroon et al. 1992, Mallin & Paerl 1992, MacIntyre 1993, Litchman 1998, 2000). This was studied first on marine phytoplankton. In 1978, John Marra made an experiment measuring the production of phytoplankton (via carbon-14 uptake rates) suspended in bottles that were either fixed at a certain depth or moved through the water column. He found that estimates of integral photosynthesis were 19 to 87% higher under variable light condition that was probably explained by higher light-saturated photosynthetic rates. Traveling through the water column may be an advantage as cells are regularly brought up to surface-light intensities which allow phytoplankton to photosynthesize at light-saturated rates. In turn, they are unlikely

to suffer from photoinhibition as they are moved downward to lower irradiance layers (Ibelings et al. 1994). Similarly, algae are very unlikely to be light-limited as might be the case for sedimented algae in calm waters (Mallin & Paerl 1992). In all, rapid light fluctuations due to continuous mixing might generate optimal conditions for photosynthetic activity. Nevertheless, precise monitoring and physiological measurements would be necessary in further studies to validate these hypotheses.

Interestingly, some studies suggest that phytoplankton species are unequally adapted to fluctuating light. In an impressive study, Ibelings et al. (1994) compared the responses of cyanobacterium *M. aeruginosa* and the green algae *Scenedesmus protuberans* to simulated fluctuating light corresponding to wind-induced mixing. They concluded that *S. protuberans* was more flexible in its acclimation to fluctuating lights compared to the cyanobacterium which relates well to their specific strategies regarding buoyancy and vertical placement. In 1998, Elena Litchman studied the impact of fluctuating light on the diversity, composition and structure of 2 and 18-species communities of freshwater phytoplankton. She showed that diatoms were favored under fluctuating light where they became the dominant group. This positive effect of fluctuating light on growth of diatoms add to the already known positive effect of mixing which keeps these heavy cells suspended in the water column. This was not observed in our mixed enclosures where densities of diatoms remained very low throughout the experiment. However, other elements such as initial input and climatic conditions were probably unfavorable to diatoms. Litchman (1998, 2000) also added that the very species-specific growth rates responses to fluctuating light could be of major importance for differences in community composition in natural systems. As mentioned previously, analysis of DNA samples could give us further information on whether mixing impacted species composition and diversity in our mesocosm experiments.

Effects of mixing on zooplankton communities

In our studies, we monitored not only the response of phytoplankton to mixing but also the responses of other functional groups, especially zooplankton. In 2012 as well as in 2013, copepods were the only group affected (negatively) by mixing. With our data set, it was not possible to give a specific mechanism behind this negative effect, however, we could speculate direct physical disturbance on copepods kinematics, which could be energy-consuming and lead to lower growth rates (Yen et al. 2008). Indirect effect through turbidity and suspended material could also be responsible for lower food quality, with a proportionally higher consumption of resuspended materials with low nutritional value (Paffenhöfer 1972, Gasparini et al. 1999), and/or lower feeding rates due to interference of resuspended material on copepods hunting capacity (Levine et al. 2005).

In 2012, I suspected the difference in copepod density in the second half of the experiment to be responsible for the shift in population maxima of rotifers. In calm enclosures where copepods were more abundant, rotifer population decreased earlier than in mixed enclosures. Copepods are known to exert a strong top-down control on rotifers as they are usually considered as their favorite preys (Brandl 2005). This could be an interesting outcome of mixing on the organization and force of feeding links in the foodweb. However, this result is uncertain as this pattern was not clearly observed in 2013.

Effects of mixing on bacteria and viruses

Our analysis also showed a difference in the lysis activity of virus on prokaryotes depending on the mixing regime. In contrast to calm enclosures where lysis activity remained low and rather homogenous, we observed a high peak of lysis activity in the three mixed mesocosms. This could be the result of a higher contact rate between the viruses and their hosts. In the last

decades, the impacts of viruses on foodwebs and community organization have sparked the interests of the scientific community. For instance, viruses have been shown to be a major control agent of phytoplankton blooms (Jacquet et al. 2002, Frada et al. 2008, review in Paerl & Otten, 2013). Hudnell et al. (2010) proposed that one of the mechanisms through which artificial mixing controlled harmful algal blooms was the promotion of cyanophage distribution in the water column. Our results support the idea that communities in well-mixed water bodies could be subjected to stronger regulation by pathogens such as viruses.

In conclusion, our experiment brought additional informations on the impact of wind-induced mixing on pelagic communities. Usual effects, such as benthic recruitment or important releases of nutrients from the sediment bed were not observed due to the time-scale and set-up of mesocosms. However, this allowed us to uncover important effects of mixing on phytoplankton physiology and photosynthetic activity. Furthermore, we showed that other compartment of the foodweb were also sensitive to mixing with differential responses among groups. Here only copepods responded with a possible top-down consequence on rotifers while cladocerans remained undisturbed. In addition, virus-prokaryote interaction seemed enhanced by mixing and deserves more emphasis in further studies. Furthermore, there is still a huge gap of knowledge on the microbial community and activity which needs further analysis.

Temporality of wind-induced mixing episodes

In our modeling and field studies, mixing was applied continuously on our systems, except for simulations of storm events with net changes in wind regimes. In natural environments, the frequency and length of wind-induced mixing episodes may be highly different depending on the lakes morphometry, exposure and location. On coastal region and/or in very large lakes with

important fetch and low depth, mixing might be almost continuous whereas in less exposed regions, wind-induced mixing may be less frequent with long pauses between windy episodes.

The frequency of resuspension events is of great importance to the sediment structure. Long-lasting calm periods will allow sediment deposition and consolidation. The stability of the sediment cohesion depends to a large extent on chemical factors such as electrostatic attraction caused by ion pairing, which modulates sediment flocculation processes (Lundkvist et al. 2007). In addition, given enough time between windy episodes, bacteria, microalgae and fungi may form biofilms at the surface of the sediments that increase the erosion threshold, decrease erosion rates and enhance deposition (Grant et al. 1986, Madsen et al. 1993, Lundkvist et al. 2007, Righetti & Lucarelli 2010, Fang et al. 2014, Ubertini et al. 2015). Also, bacteria within the sediment matrix can also promote the binding of the sediment via the excretion of extracellular polymers. For instance, in an experiment analyzing the contribution of physical-chemical factors and microbiobial factors on marine sediment cohesion, Lundkvist et al. 2007 found that the presence of benthic diatoms increased the erosion threshold by 120% and bacteria by 20%. When both were present, this threshold was increased by 150% suggesting synergistic effects. After a mechanical disturbance of the sediment, 10 days were necessary to reach a plateau of sediment stability. As we have seen previously, the sediment is also a reservoir of nutrients, especially phosphorus in shallow ecosystems. In the case of intermittent resuspension, wind events will have a stronger impact on phosphorus release as concentration gradients between the sediments and the water column will have time to establish between resuspension events (Søndergaard et al. 1992).

In some cases, wind has a specific pattern. In a very well documented and interesting paper, Arfi & Bouvy (1995) described the clear diel wind cycle experienced by the tropical shallow

Ebrié lagoon in Côte d'Ivoire. From midnight to midday, the wind blows at low speed ($\sim 1.2 \text{ m s}^{-1}$), the water is flat and sedimentation occurs whereas from midday to midnight, the wind blows at higher speeds ($>3 \text{ m s}^{-1}$, range: $4\text{-}6 \text{ m s}^{-1}$), waves form and resuspension of sedimented particles takes over. The authors showed that this pattern was the main physical factor controlling the pelagic ecosystem. For instance, daily changes in nutrient content (specifically $\text{NH}_4\text{-N}$ and $\text{PO}_4\text{-P}$) were due to resuspension of algae cells, which led to increased uptake during windy episodes. When the wind speed decreased, nutrient standing stock reconstituted rapidly. They also demonstrated that the size distribution of bacterial cells changed with windy episodes as large benthic bacteria were brought into the water column. Similarly, the composition of phytoplankton communities temporarily changed with higher proportion of diatoms, chlorophytes such as *Chlorella sp.* and some species of cyanobacteria. Particle size was greatly influenced by the wind, and small particles stayed longer than heavy and large particles during the relaxation period. The authors hypothesized that all these changes were likely to modify the food-web organization on a short time-scale with regular formation or suppression of feeding links. Micrograzers (like ciliates) seemed permanently favored as small size-particles (small bacteria and picoalgae) were regularly resuspended and stayed longer in the water column, while the food resource of predators feeding on larger particles were dependent on resuspension event and length.

Rapid shifts in community structure have also been observed in Lake Balaton in Hungary due to storm events. Padisák (1988, 1990) showed that storm events occurring after 5-15 days of calm weather cause “jump-like” changes in phytoplankton community composition with a rapid growth of small algae that last for a few days, which are then replaced by larger algae until the next storm. Furthermore, the dominant filamentous cyanobacteria significantly decreased because

of the storm. The explanation given by the authors was physiological death of cells of unknown cause. However, one may think of direct physical effect of strong small-scale turbulence on the structure of filaments or mechanical damage due to collision with other particles (Moisander et al. 2002). Resuspension events can also induce loss of pelagic phytoplankton biomass through aggregation (also called flocculation) between cells and sediment particles such as clay (Avnimelech et al. 1982). This process is driven in part by mass action, i. e. the flocculation rate is proportional to concentration of suspended particles, in part by the type of clay (size and surface charges), and also by the “stickiness” of the phytoplankton species. The latter is often linked to the amount of extracellular polymers excreted by algae, such as mucilage (Walsby 1968, Kiørboe & Hansen 1993). This mechanism may even cause buoyant species to sediment. For instance, Verspagen et al. (2004, 2006) showed that aggregation with clay particles was the main mechanism behind *Microcystis spp.* sedimentation in Lake Volkerak (The Netherlands).

As knowledge of freshwater ecosystem accumulates, it becomes clear that physical factors such as wind events are a key process driving those ecosystems. Continuous mixing in well-exposed lakes generates specific conditions of turbidity and fluctuating light that will affect the phytoplankton as well as zooplankton. Periodic wind events act as “pulses” that can change the underwater light climate and nutrient availability as well as the organization and composition of planktonic communities. With our mesocosm experiment, we studied only one kind of mixing pattern, but storm events, intermittent wind episodes with varying time-lags and diel patterns are also among the possible scenarios that could be explored. In addition, different kinds of sediments could also be used to determine the importance of sediment composition in resuspension events.

Warming – results and questions

In 2013, we crossed a mixing treatment with a warming treatment using polyethylen films to produce local greenhouse effects. Originally, the warming was supposed to start at the beginning of the mixing treatment; however, due to delays in the delivery of polyethylen sheets, it only began halfway through the experiment. This led to a short-term warming effect of 4 weeks which, compared to other warming experiments, is quite short. In addition, the polyethylen sheets were specifically made to fit on our mesocosms and we had no previous knowledge on the intensity of warming we would get. Post-experiment quantification of warming indicated that the greenhouse effect led to a temperature rise of $\sim 1^{\circ}\text{C}$ throughout the water column. This increase was surprisingly well-maintained until the end of the experiment, suggesting that equilibrium between the greenhouse effect and temperature exchanges with the atmosphere was reached.

Does the fact that we did not observe any effect of 1°C warming mean that there is none? This is quite unlikely. Most of freshwater species, from bacteria to phytoplankton, to zooplankton and fish, have temperatures optimum for growth, reproduction and steps in life-cycles. These optimums correspond to hardwired metabolic activities and rates. In nature, there are increasing evidences that relatively small increases in temperature (0.6°C in the past 100 years) can affect phenological events (Walther et al. 2002). For example, flowering and bud-breaking in plants tend to happen earlier in spring (1.4-3.1 days earlier per decade in Europe), butterflies appear earlier (2.8-3.2 days per decade) and amphibians and birds also breed earlier. In freshwater ecosystems, the timing and magnitude of seasonal phytoplankton blooms are also shifting in response to recent climate changes (Thackeray et al. 2010, Winder et al. 2012). In our modelling work, we also found that blooms of *M. aeruginosa* happen sooner in summer with 2°C warming due to a physiological advantage at higher temperatures. Herbivores, such as the key-stone

species of the genus *Daphnia* are also known to be strongly regulated by water temperatures and respond to higher temperatures by reaching their maximum density sooner (Thackeray et al. 2012, Straile et al. 2012). In our experiment, time was a limiting factor and phenological changes could not be observed due to the experimental time scale. However, changes in community assemblages (for example an increase in abundance of cyanobacteria relative to green algae) and changes in abundance of fast-growing organisms such as phytoplankton, rotifers and bosmines were expected (Strecker et al. 2004, Walters et al. 2013). We did not observe any changes on community assemblages with the present data set however, phytoplankton and bacteria counting is still ongoing at the moment. Those groups with high turn-overs are the most likely to respond to warming in short periods of time. Any effects on other groups with longer growth such as copepods are unlikely to be detectable in short-term experiments.

In order to better anticipate the effects of global warming on shallow freshwater ecosystems, many experiments have been carried out in mesocosms (McKee et al. 2003, Moss et al. 2003, Strecker et al. 2004, Feuchtmayr et al. 2009, 2010, Kratina et al. 2012, Nicolle et al. 2012). Most of these experiments use complex heating systems, often fixed just above the sediment, injecting hot (up to 60°C) water into the enclosures. The water temperature increase targeted is often between 3 and 5°C above non-heated adjacent mesocosms, which is considerable. These set-ups raise some questions on the effects produced. First, as we have seen, the physical structure of shallow lake is key to many processes, and especially the interface between the water column and the sediments. Injecting hot water or heating the systems from the bottom just above the sediments is likely to disrupt important processes such as nutrient cycles, phosphorus release, nitrification etc. Moreover, in nature, the warming comes from a greenhouse effect from the atmosphere. The temperature dissipates throughout the water column and

gradients of temperature, even small, appear. For example, with our heating systems, we observed a structure in temperatures in the water column even though the enclosures are only 1m deep. This heterogeneity seems crucial, as it gives the possibility of vertical migration for some species where they can find a relief from hot temperatures or, on the contrary, migrate to hotter waters. In our experiment, we found that some species, especially cladocerans were not distributed homogeneously with depth and were more abundant at the bottom of enclosures. However, many hypotheses could explain this phenomenon: predation avoidance, hot temperature avoidance, better access to food resources at the bottom etc.

Another question that should be raised concerning experimental warming in mesocosm is what are we testing when we apply 3 to 5°C of warming to present-day communities? According to the 2014 IPCC reports, these temperature increases will be reached at the end of the 21st century. Before then, global average temperatures will increase in an almost linear fashion as in figure 13.



Many changes in processes, communities' organization and phenology will probably occur during the next 85 years in response to small, gradual increases in temperatures. Acclimation, adaptation and evolution will also take place (Parmesan 2006). It would be interesting to make controlled experiments with smaller increases in temperature and also investigate what are the responses of communities to slow, gradual increases rather than abrupt and considerable temperatures increases.

General conclusion

Wind-induced mixing plays a major role on freshwater ecosystems. From physiological adaptations of phytoplankton cells to fluctuating light to changes in diversity, community successions and foodweb organization, water column mixing affects water bodies through multiple pathways. Intra-lake variability of wind-exposure could generate patchiness in the community composition and foodweb organization. For instance, we could speculate that biological control is the main driver in wind-protected area where the medium is stable, whereas in continuously wind-exposed regions, physical constraints will become the major driver of community organization. Similarly, inter-lake variability in wind exposure could explain in part the differences between lakes with similar morphometry and localization. These hypotheses could be tested in shallow lakes by searching for a correlation between wind action and foodweb composition and structure. With our work, we started to uncover the effect of mixing on other trophic levels than phytoplankton. However, longer experiments are necessary in order to fully understand the impacts of mixing on zooplankton communities, especially on species with long life-cycles, and the potential feedbacks within the trophic network. Experiments with storm events, diel pattern or intermittent mixing with long calm periods and with different sorts of

sediments could also provide interesting information on the interaction between mixing, sediment resuspension, phosphorus release and the food web dynamics.

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Synthèse

Les écosystèmes aquatiques d'eau douce sont d'une importance cruciale du point de vue écologique, social et économique. Or ces écosystèmes sont soumis à de nombreuses pressions anthropiques, tels que l'eutrophisation et le réchauffement climatique qui tendent à modifier leur fonctionnement, à engendrer des pertes de biodiversité et à favoriser la dominance de cyanobactéries formant des efflorescences néfastes pour la qualité de l'eau. En raison de leur importance dans la biosphère, il est nécessaire de comprendre les éléments qui structurent ces écosystèmes afin d'améliorer les méthodes de restauration ainsi que la qualité des modèles de prédiction. Historiquement, l'intérêt des limnologues s'est concentré sur les grands lacs profonds or, la grande majorité des étendues d'eau douce sur terre sont des lacs de petite taille et de faible profondeur. Parmi les éléments structurants les lacs peu profonds, le vent tient une place prépondérante. En effet, lorsque le vent souffle sur une surface d'eau, le frottement de l'air va induire des mouvements de brassage de la colonne d'eau et éventuellement des phénomènes de resuspension des sédiments. La structure de la colonne d'eau est un élément crucial pour de nombreuses espèces planctoniques dont la distribution verticale et horizontale dépend de leur motilité d'une part, mais également des courants et mouvements d'eau dans lesquels ils sont pris. Le brassage de la colonne d'eau est notamment impliqué dans la compétition entre les différentes espèces de phytoplancton dont les stratégies de positionnement vertical varient largement entre groupes. Par exemple, les cyanobactéries sont globalement favorisées par des conditions de brassage faible grâce à des mécanismes physiologiques de flottaison leur permettant de se maintenir à une profondeur désirée, alors que les diatomées et les algues vertes qui n'ont pas de système de flottaison dépendent d'un brassage important et régulier pour être suspendues dans la zone euphotique. Le vent est donc d'une importance fondamentale pour la structure et la composition des communautés phytoplanctoniques. Parallèlement, dans les lacs peu profonds, le brassage généré par le vent est généralement suffisant pour entraîner la resuspension des sédiments. Ceci a pour conséquence directe une augmentation de la turbidité qui peut directement impacter la croissance et la productivité algale. La conséquence indirecte est la libération de phosphore précédemment stocké dans les sédiments. Le relargage massif de nutriments pendant les épisodes de resuspension peut avoir un impact important sur les communautés en place, notamment lorsque les ressources sont limitantes dans la colonne d'eau, et contribuer aux difficultés de restauration des lacs eutrophisés.

Le but de cette thèse est l'étude des effets du brassage induit par le vent sur les écosystèmes aquatiques d'eau douce dans le contexte actuel de changements globaux. Pour réaliser cette étude, deux axes ont été développés :

Axe 1 : le premier objectif est de modéliser de façon mécaniste l'effet du brassage dû au vent sur la compétition entre une cyanobactérie et une algue verte dans une colonne d'eau de lac peu profond prenant en compte la possibilité de resuspension des sédiments et de phosphore. Par ailleurs, afin de prendre en considération les différentes pressions anthropiques, les niveaux

d'eutrophisation et la température ont été inclus dans le modèle. Différents niveaux de brassage ont été testés: de quasi-stagnant à tempête. Les simulations indiquent qu'au-delà de 3 m.s^{-1} , le brassage induit par le vent est suffisant pour limiter la prolifération de cyanobactéries en surface et permet à l'algue verte de dominer la colonne d'eau. En deçà de cette limite, la cyanobactérie domine lorsque les ressources en phosphore sont abondantes. Lorsque le vent est suffisamment puissant pour générer de la resuspension, la turbidité augmente rapidement et provoque une réduction de la biomasse algale globale. Par contre, le relargage de phosphore peut éventuellement eutrophiser la colonne d'eau et permettent la formation d'efflorescences denses de la cyanobactérie si la tempête est suivie d'une période de calme. En parallèle, des centaines de simulations ont été réalisées dans différentes conditions de brassage, d'eutrophisation (de oligo- à hypereutrophe) et de réchauffement climatique (actuel et $+2^{\circ}\text{C}$) permettant d'établir des domaines de conditions de dominance d'une espèce ou de l'autre. Les résultats démontrent qu'avec le réchauffement climatique, les conditions favorables aux efflorescences de cyanobactéries s'étendent à des conditions de brassage plus important en raison d'une augmentation de leur vitesse de croissance leur permettant de pallier les effets négatifs du brassage.

Axe 2 : le second objectif est d'explorer les impacts potentiels du brassage sur l'ensemble du réseau trophique pélagique. En effet, la grande majorité des études portant sur le brassage sont des études in situ focalisées sur le phytoplancton. Dans le cas présent, nous avons utilisé des mésocosmes de 15m^3 équipés de batteurs à vagues dont les amplitudes, fréquences et longueurs d'ondes sont modifiables. Une première expérience en 2012 a eu pour objet de suivre durant 9 semaines la dynamique des variables physico-chimiques standards et des communautés de phytoplancton, zooplancton, bactéries et virus dans deux modalités de brassage : brassage superficiel et brassage de l'ensemble de la colonne d'eau avec resuspension des sédiments. L'année suivante, la même expérience a été conduite mais cette fois-ci couplée à un traitement de réchauffement appliqué grâce à des bâches de polyéthylène transparentes posées sur les mésocosmes. Les résultats combinés de ces deux expériences montrent un effet important du brassage dans différents compartiments : chimie de l'eau, phytoplancton, zooplancton et au niveau microbien. Par exemple, on observe une augmentation du contenu en chlorophyll *a* et une augmentation de la productivité phytoplanctonique via une forte augmentation du pH en mésocosmes brassés. A l'inverse des prédictions, l'augmentation de la chlorophyll *a* n'est pas dû à une augmentation de l'abondance algale, mais plutôt à un changement de composition ou une adaptation physiologique au brassage. Au niveau du zooplancton, la réponse dépend du sous-groupe. Dans nos expériences, uniquement les copépodes ont répondu négativement au régime de brassage avec un potentiel effet cascade sur la population de rotifers. En parallèle, les cladocères n'ont pas répondu au traitement ce qui suggère que les effets du brassage sont très dépendants du mode de déplacement des espèces. L'expérience de 2012 suggère également un renforcement de l'activité de lyse bactérienne par les virus dans des conditions de brassage important, probablement dû à une augmentation de la probabilité de contact. Par contre, aucun effet du réchauffement de 1°C n'a été détecté en 2013.

Titre : Rôles du brassage dans le fonctionnement des écosystèmes aquatiques peu profonds dans un contexte de réchauffement climatique.

Mots clés : brassage, vent, lacs peu profonds, réseau trophique, resuspension, eutrophisation, changements globaux

Résumé : Le vent joue un rôle clé dans la structure et le fonctionnement des lacs. Le brassage de la colonne d'eau est notamment impliqué dans la compétition entre les différentes espèces de phytoplancton dont les stratégies de positionnement vertical varient largement entre groupes. Par exemple, les cyanobactéries sont globalement favorisées par des conditions de brassage faible grâce à des mécanismes physiologiques de flottaison leur permettant de se maintenir à une profondeur désirée, alors que les diatomées et les algues vertes qui n'ont pas de système de flottaison dépendent d'un brassage important pour être suspendues dans la zone euphotique. Dans les lacs peu profonds, le brassage généré par le vent est généralement suffisant pour entraîner la resuspension des sédiments. Ceci a pour conséquence directe une augmentation de la turbidité qui peut directement impacter la croissance et la productivité algale. La seconde conséquence est la libération de phosphore précédemment stocké dans les sédiments. La pollution et l'usage d'engrais ont provoqué un important import de phosphore dans les lacs qui sont pour la plupart dans un état d'eutrophisation. Dans un premier temps, cette thèse a eu pour objectif de modéliser la compétition entre une cyanobactérie et une algue verte dans une colonne d'eau de lac peu profond prenant en compte la possibilité de resuspension des sédiments et de phosphore. Différents niveaux de brassage ont été testés: de quasi-stagnant à tempête. Des centaines de simulation ont été réalisées dans différentes conditions de brassage, d'eutrophisation (de oligo-à hypereutrophe) et de réchauffement climatique (actuel et +2°C) permettant d'établir des domaines de conditions de dominance d'une espèce ou de

l'autre. Dans une seconde partie, la thèse a eu pour objectif d'explorer les impacts potentiels du brassage sur l'ensemble du réseau trophique pélagique. En effet, la grande majorité des études portant sur le brassage sont des études *in situ* focalisées sur le phytoplancton. Dans le cas présent, nous avons utilisé des mésocosmes de 15m³ équipés de batteurs à vagues dont les amplitudes, fréquences et longueurs d'ondes sont modifiables. Une première expérience en 2012 a eu pour objet de suivre durant 9 semaines la dynamique des variables physico-chimiques standards et des communautés de phytoplancton, zooplancton, bactéries et virus dans deux modalités de brassage : brassage superficiel et brassage de l'ensemble de la colonne d'eau avec resuspension des sédiments. L'année suivante, la même expérience a été conduite mais cette fois-ci couplée à un traitement de réchauffement appliqué grâce à des bâches de polyéthylène transparentes posées sur les mésocosmes. Ces deux expériences montrent un effet important du brassage sur le phytoplancton avec une augmentation du contenu en chlorophyll *a* et une augmentation de la productivité. Au niveau du zooplancton, la réponse dépend du sous-groupe. Dans nos expériences, uniquement les copépodes ont répondu négativement au régime de brassage avec un potentiel effet cascade sur la population de rotifers. L'expérience de 2012 suggère également un renforcement de l'activité de lyse bactérienne par les virus dans des conditions de brassage important. En 2013, aucun effet du réchauffement de l'eau de 1°C n'a été observé sur les variables mesurées. Des analyses supplémentaires en cours devraient permettre de compléter les informations obtenues et de vérifier l'absence d'effet du réchauffement.

Title: Rôles du brassage dans le fonctionnement des écosystèmes aquatiques peu profonds dans un contexte de réchauffement climatique.

Key words: brassage, vent, lacs peu profonds, réseau trophique, resuspension, eutrophisation, changements globaux

Summary: The wind plays a key role in the structure and functioning of lakes. Water column mixing is involved in the competition between different species of phytoplankton with different vertical positioning strategies. For example, buoyant cyanobacteria are generally favored by low mixing conditions, while sinking diatoms and green algae depend on mixing to be suspended in the photic zone. In addition, in shallow lakes, wind-induced mixing is usually sufficient to cause sediment resuspension. This leads to an increase in turbidity which can directly impact the algal growth and productivity. Resuspension can also induce the release of phosphorus previously stored in sediments. This internal loading via resuspension can boost algal production and growth. The first goal of this thesis was to model the competition between the buoyant cyanobacterium *Microcystis aeruginosa* and a sinking green algae under different mixing conditions: from quasi-stagnant to storm-like events. Hundreds of simulations were carried out in different conditions of mixing, phosphorus concentration and water temperatures in order to establish the conditions necessary for the dominance of one species on the other. In the second part of this thesis, we explored the potential impacts of mixing on the pelagic food

web. The vast majority of previous studies on mixing in shallow lakes are in situ studies focused on phytoplankton. In the summer 2012, we used 15m³ mesocosms equipped with wave-makers and followed during nine weeks the dynamics of physical and chemical variables and the dynamic of phytoplankton, zooplankton, bacteria and viruses under two mixing conditions: whole column mixing with sediment resuspension and superficial mixing without resuspension. The following year, the same experiment was conducted but this time crossed with a warming treatment. Both experiments gave similar results in regards to mixing. We observed a significant effect of mixing on phytoplankton with an increase in chlorophyll content and an increase in productivity. The response of zooplankton to mixing depended on the subgroup. In our experiments, only copepods responded negatively to mixing with a potential cascade effect on the rotifer population while bosminas remained unaffected throughout the experiments. The 2012 experience also suggests an increase in bacterial lysis activity by virus in mixed enclosures. In 2013, no effect of water warming (+1°C) was observed on the measured variables, however, additional analysis are still underway to confirm or infirm these results.