Freshwater Biology

Freshwater Biology (2017) **62,** 161–177 doi:10.1111/fwb.12859

Effects of mixing on the pelagic food web in shallow lakes

LYDIE BLOTTIÈRE*, MOURAD JAFFAR-BANDJEE*, STÉPHAN JACQUET†, ALEXIS MILLOT‡ AND FLORENCE D. HULOT*

**Laboratoire Ecologie, Systématique et Evolution, UMR 8079, Univ Paris-Sud, Orsay, France*

†*INRA, UMR 42 CARRTEL, Thonon-les-Bains, France*

‡*Centre de Recherche en Ecologie Expérimentale et Prédictive - Ecotron Ile-de-France, UMS 3194 CNRS/ENS, Saint-Pierre-Lès-Nemours, France*

SUMMARY

1. We examined the effects of wind-induced mixing and particle resuspension on the pelagic food web in eutrophic shallow lakes. These processes are known to have a major impact on a variety of biological, physical or chemical parameters such as the underwater light climate, the nutrient availability in the water column and the abundance and composition of the phytoplankton community. However, little is known about the effects of these processes on other compartments of the freshwater food web.

2. We conducted a 9-week experiment comprising a manipulation of mixing intensity in 15 m^3 mesocosms equipped with wavemakers in order to explore the impact of two mixing regimes on water chemistry as well as viral, bacterial, phytoplankton and zooplankton communities.

3. The turbidity level in mixed mesocosms (compared to calm conditions) was higher on average, especially at the bottom, indicating a successful resuspension of the sediment bed. Mixing increased chlorophyll *a* concentration without any clear increase in algal abundance, measured as cell counts by flow cytometry, which pointed to a change in species composition or a physiological adaptation to mixing. pH increased strongly in mixed mesocosms, suggesting enhanced primary productivity in perturbed conditions. Zooplankton responses to mixing were neutral for cladocerans and negative for copepods, which potentially mediated top–down controls on the rotifer population.

4. Bacterial and viral abundances were not significantly changed by the mixing regimes; however, peaks of viral lysis of heterotrophic bacteria were seen in each mixed mesocosm, while none were observed in calm mesocosms. These results suggest that viral lysis is enhanced by the water column mixing.

5. 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.

Keywords: mixing, shallow lakes, mesocosms, food web

Introduction

Wind-induced mixing is a key process in shallow lakes (Reynolds *et al.*, 1983; Reynolds, Wiseman & Clarke, 1984; Carrick, Aldridge & Schelske, 1993; Schelske, Carrick & Aldridge, 1995; Søndergaard, Jensen & Jeppesen, 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,

Correspondence: Lydie Blottière, Laboratoire Ecologie, Systématique et Evolution UMR 8079, Bâtiment 362 Université Paris-Sud, 91405 Cedex, Orsay, France. E-mail: lydie.blottiere@upmc.fr

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 recognised 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, micro-stratification within the euphotic zone generally favours motile or buoyant species, while fast-sinking species like diatoms or desmids are quickly lost from suspension (Reynolds *et al*., 1983; Reynolds, 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). Furthermore, the different strategies exhibited by phytoplankton with regard to mixing intensity have been successfully studied through modelling (Huisman & Weissing, 1994; Huisman, van Oostveen & Weissing, 1999; Klausmeier & Litchman, 2001; Huisman *et al*., 2004; Aparicio Medrano *et al*., 2013; Blottière *et al*., 2013) and applied in water management to prevent bloom-forming cyanobacteria in stratified lakes and reservoirs using artificial mixing (Hawkins & Griffiths, 1993; Visser *et al*., 1996; Jungo *et al*., 2001; Burford & 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 & Hellström, 1990, 1992; Luettich, Harleman & Somlyody, 1990). Indeed, by resuspending matter from the sediment bed, mixing increases light attenuation, which can in turn reduce planktonic as well as macrophytes and meroplankton growth and productivity. For instance, Hellström (1991) calculated an 85% reduction in algal production following storm events in Lake Tämnaren (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 & 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, Jones & Bailey-Watts, 1999; Schallenberg & 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, Kristensen & Jeppesen, 1992; Søndergaard *et al*., 2003; Zhu, Qin & Guang, 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 & 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 at very high turbidity levels that coincide only 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, Lorke & Walz, 2000; Garstecki & Wickham, 2001). Eckert & Walz (1998) explored the link between the frequency of wind events and zooplankton succession in a shallow polymictic lake in Germany, while Levine, Zehrer & Burns (2005) studied how wind-induced resuspension decreased the feeding and clearance rates of *Daphnia* (Daphniidae) and *Boeckella hamate* (Centropagidae) in Lake Waihola (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 levels:bacteria, phytoplankton and rotifers, demonstrating a positive effect on bacteria and phytoplankton through enhanced nutrient availability, which could in turn favour rotifers. Nevertheless, more studies are needed on multiple trophic levels in order to better understand the global effects of mixing on the dynamics of the pelagic food web and the functioning of the whole ecosystem.

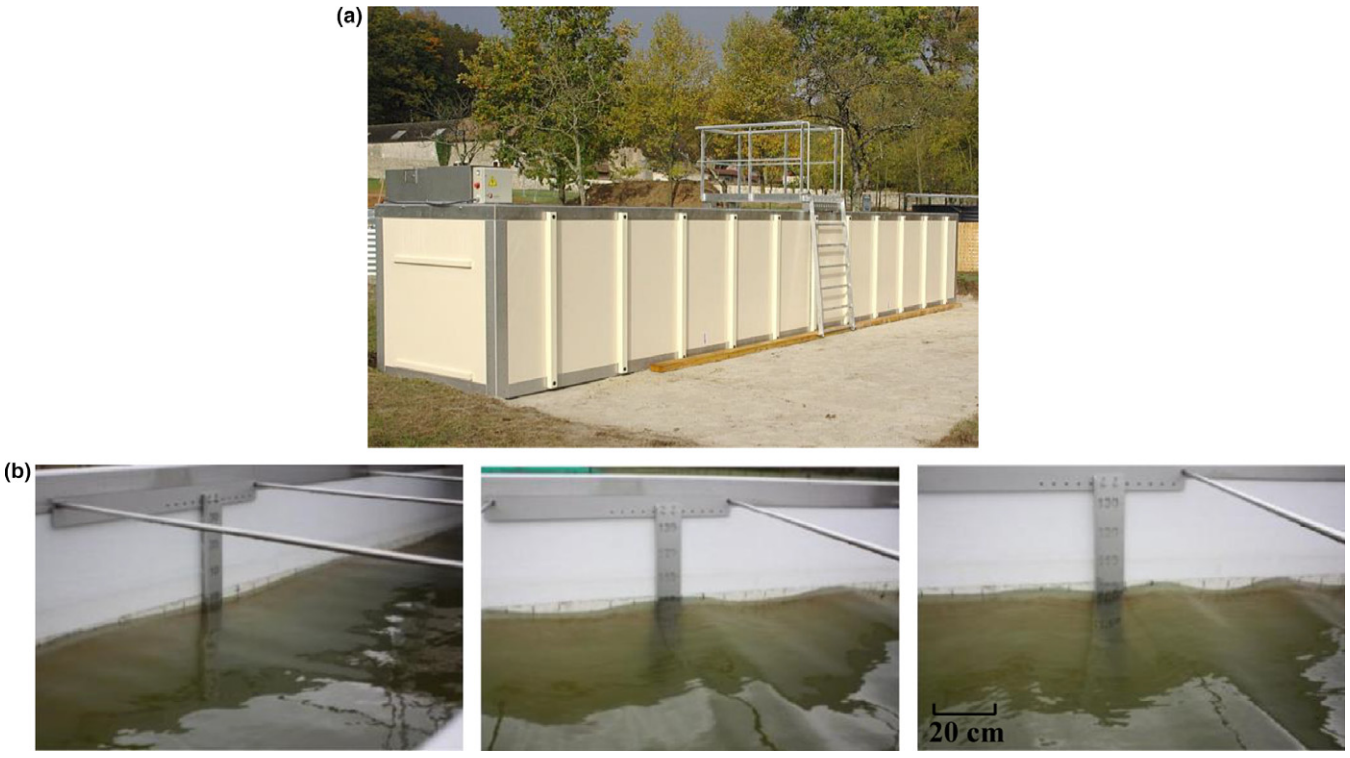
In this study, we attempted to show experimentally whether and how mixing and particle resuspension impact the trophic food web through direct physical effects or indirect pathways. To explore this phenomenon, we used a unique experimental set-up with mesocosms equipped with wavemakers. The goal was to mimic as closely as possible the natural water motion induced by continuous moderate winds in lakes. Previous attempts to study mixing have usually been conducted *in situ* using bubbling systems or manual mixing of the water column, both producing water motions that might not be representative of natural wind-induced mixing (Blottière, 2015). Furthermore, the use of large

mesocosms equipped with wavemakers provides a unique opportunity to isolate and study the effects of mixing under controlled conditions on a realistic pelagic community (Ledger *et al.*, 2009). We used these mesocosms over 9 weeks to follow the physical, chemical and biological responses of our systems to two mixing levels: (i) complete mixing of the water column plus resuspension, which mimics well-exposed shallow lakes; (ii) superficial mixing of the top water layer and no resuspension, which concerns sheltered shallow lakes.

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). We used six outdoor rectangular mesocosms (10 × 1.5 × 1.5 m), located at the same place and made of 10 cm insulating polyester covered with a liner with a wavemaker fixed at one extremity (see Picture 1a). This experimental system is inspired by wave flumes or wave tanks used in fluid mechanics. In short, a paddle rotates around an axis assembled at its basis and, in a back and forth movement, pushes the water. The motions of the paddle generate surface travelling waves. The wavelength and amplitude of waves are determined by the frequency and amplitude of paddle oscillations respectively (see Picture 1b). The experimental system is able to generate waves from 0.1 to 6 m of wavelength and 1–5 cm of amplitude with a 1 m water column (Blottière, 2015). All enclosures were filled with tap water, reaching a final total volume of 15 m^3 and a water column of 1 m. The mesocosms were left untouched for a few days to let chlorine evaporate. To create a sediment bed, approximately 300 L of aged (several months) sieved sand from the Loire River (France; granulometry class: 0/4 with grain sizes ranging from 0.063 to 4 mm) were put into each mesocosm as homogeneously as possible. At the same time, we used four outdoor circular containers of *c.* 1.5 m^3 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. Two of these containers were specifically used to grow phytoplankton and the other two were used to grow zooplankton (the zooplankton density in the latter was



Picture 1 Photographies of (a) mesocosm prototype with the wavemaker motor on the left and the ramp in the middle from which all samplings were made (photography copyright: Bruno Verdier); (b) example of three different wavelengths that can be generated by the wavemakers (not representative of the ones we used in our experiment) (photography copyright to Florence Hulot). See online version for colour display. Colour figure can be viewed at wileyonlinelibrary.com.

artificially high as we captured large quantities of zooplankton on a net in the nearby ponds and lakes and inoculated them directly in the containers). All four containers were equally used as reservoirs for reseeding 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 favourable environmental conditions (Hulot, Lacroix & Loreau, 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 K_2HPO_4 solution to reach a final mesocosm concentration of 70 μg [PO_4^{3-}-P] L^{-1}. Four days after zooplankton introduction, eight or nine planktivorous cyprinid fish (*Carassius carassius*, purchased from SARL Vinal fishfarm, France; mean size: 10.56 ± 0.21 cm long) were added to each mesocosm with a mean density of 9.10 ± 1.02 g m^{-3}. Fish were used as a mean to control zooplankton populations during the experiment and to better mimic natural conditions by increasing the complexity of the pelagic food web. They were not studied further in the experiment, however, it should be noted that no fish died during this experiment. The machines were activated immediately after the fish addition on July 20.

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 (*c.* 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).

Sampling and measurements

All measurements and samples were taken weekly (July 23: date 0 to September 19: date 9) in all mesocosms at two discrete depths: below the surface and just above the sediment bed in order to detect gradients in the water column. 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 (Wildco, Yulee). This sampler allows for precise sampling at a chosen depth. Samples and measurements were taken at the centre of the enclosures from a small ramp fixed on top of each mesocosm. Mesocosms were sampled in random order on each occasion.

Physical measurements and water chemistry

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). Secchi disc transparency was measured whenever the bottom of the mesocosm was not visible.

Total suspended solids (in dry weight per litre) were obtained by filtering a known water volume (typically 1 L, more or less depending on the particulate density) through pre-weighed and dried 0.7 μm pore size Whatman GF/F filters and then weighing the filters again after at least 24 h 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, Düsseldorf). Orthophosphates (PO_4^{3-}-P) were determined using the vanadate–molybdate method (LCK349 Kit Hach Lange, Detection Range (DR): 0.05–1.50 mg L^{-1}). Total nitrogen was determined using the Koroleff digestion (peroxodisulphate) and photometric detection with 2.6-dimethylphenol (LCK138 Hach Lange Kit, DR: 1–16 mg L^{-1}). Nitrate (NO_3-N), ammonia (NH_3-N) and nitrite (NO_2-N) were, respectively, determined using the cadmium reduction, diazotation and salycilate methods (Hach Lange kits: Nitraver 5 DR: 0.1–10 mg L^{-1}, Nitriver 3 DR: 0.002–0.300 mg L^{-1} and Ammonia Nitrogen reagent set DR: 0.01–0.50 mg L^{-1}).

Phytoplankton, prokaryotes and viruses

Phytoplankton was studied by fluorometry and flow cytometry. The first technique provides information on chlorophyll *a* concentration of the different phytoplankton groups while the second technique provides precise algal counts informing on the phytoplankton dynamics. Phytoplankton samples were divided into three size classes directly on site using differential filtration, that is, a consecutive filtration through 100 and 30 μm mesh size nylon filters. Hence, we had three sub-samples: unfiltered water with algae of all sizes, a sub-sample with algae that passed through 100 μm filters, and a sub-sample with algae that passed through 100 and 30 μm filters. These sub-samples were kept in the dark for 15 min before taking fluorescence measurements using the BBE FluoroProbe™ spectrofluorometer (bbe Moldaenke GmbH, Schwentinental) 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

microorganisms (Beutler *et al.*, 2002; Leboulanger *et al.*, 2002; Rolland, Rimet & Jacquet, 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, we had two size classes: algae less than 30 μm and algae between 30 and 100 μm. The Chl-*a* concentration of the 30–100 μm fraction was obtained by subtracting the Chl-*a* concentration of the 30 μm fraction from the Chl-*a* concentration from the 100 μm-filtered fraction.

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 prokaryotes and virus-like particles (VLPs) were counted using a FACSCalibur flow cytometer (Becton Dickinson, Franklin Lakes) equipped with an air-cooled laser providing 15 mW at 488 nm. For the analysis of the VLPs and heterotrophic prokaryotes (mainly represented by 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; Thermo Fisher Scientific, Waltham) 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, Dorigo & Personnic, 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 (Polyscience) beads (i.e. calibrated microspheres in terms of size and fluorescence, used as a standard). The flow cytometer list mode files thus obtained were then transferred and analysed on a PC using the custom-designed software CYTOWIN (Vaulot, 1989).

Zooplankton

Three to five litres 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 taken separately at the surface and then at the bottom of each mesocosm. Samples were then exhaustively identified to the genus or species level and counted under a microscope. In order to assess whether top–down (predation), mechanical interference, or bottom–up control (food availability) was imposed on rotifer population, female egg ratios were established for two abundant species which carry their eggs: the brachionids *Keratella testudo* and *Anuraeopsis fissa* (Gonzales & Frost, 1992). Attached and detached eggs were counted under a compound microscope. Detached eggs were identified to species based on shape and size. The egg ratio was calculated as follows: ER = (attached eggs + detached eggs)/number of female.

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 analysed 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-effect 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. Temporal autocorrelation was tested for each variable using *acf* function in R and was never significant. Residuals were visually checked to assess the quality of the model. The effects of sampling 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 (2 weeks after P enrichment up to 0.70 mg L^{-1}), dissolved phosphorus and nitrogen concentrations were 0.02 ± 0.01 and 5.8 ± 0.1 mg L^{-1} respectively. Total chlorophyll *a* concentration was 24.6 ± 4.0 μg L^{-1} with a large dominance of green algae compared to cyanobacteria and diatoms (21.6 ± 3.8, 2.6 ± 1.8 and 0.3 ± 0.2 μg Chl-*a* L^{-1} respectively). Phytoplankton abundance assessed using FCM was $1.01 \times 10^5 \pm 4.12 \times 10^4$ and $1.08 \times 10^5 \pm 4.10 \times$

10^4 cells mL^{-1} in mixed and calm mesocosms respectively. Prokaryotes (essentially heterotrophic bacteria) as well as virus-like particles abundance were also very similar between mixed and calm treatments (prokaryotes: $4.6 \times 10^6 \pm 3.2 \times 10^6$ cells mL^{-1} versus $4.3 \times 10^6 \pm 5.8 \times 10^5$ cells mL^{-1}; virus: $6.5 \times 10^6 \pm 2.0 \times 10^5$ part mL^{-1} versus $6.1 \times 10^6 \pm 5.3 \times 10^5$ part mL^{-1}). Zooplankton was largely dominated by rotifers on the first date with 63 ± 13 individuals L^{-1}. Crustacean concentration was very low at the beginning with only a few *Bosmina longirostris* (Bosminidae), *Scapholebris mucronata* (Daphniidae) and calanoids. Between-treatments comparisons on the first date for all physical, chemical and biological variables showed no significant differences (Wilcoxon test, $P > 0.05$).

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 × 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.

Total suspended solids concentration increased in the mixed mesocosms from the fourth week until the end of the experiment, while it remained stable under calm conditions (Fig. 1b, Table 1). TSS concentrations at the end of the experimental period were 14.6 ± 5.4 and 8.0 ± 0.9 mg L^{-1} in mixed and calm mesocosms respectively. TSS concentration was strongly correlated with green algae biomass (spearman rank correlation, $\rho = 0.677$, $P \leq 0.0001$), suggesting that most of the suspended solids in our mesocosms were phytoplankton cells and cell debris. Secchi disc measurements were not useful in these experiments because the bottom was visible most of the time.

Mixing did not impact water temperatures, which were indistinguishable between treatments (Fig. 1c). When a small difference between depths appeared, the difference (*c.* 1 °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 168.6 ± 23.5 and 159 ± 26.1 %Sat. in mixed and calm mesocosms respectively (Fig. 1d). On average, oxygen concentration was greater at the bottom of the mesocosms (LME, Depth: $F_{1,99} = 26.295$, $P < 0.0001$). Oxygen concentrations were slightly more elevated in mixed mesocosms compared to

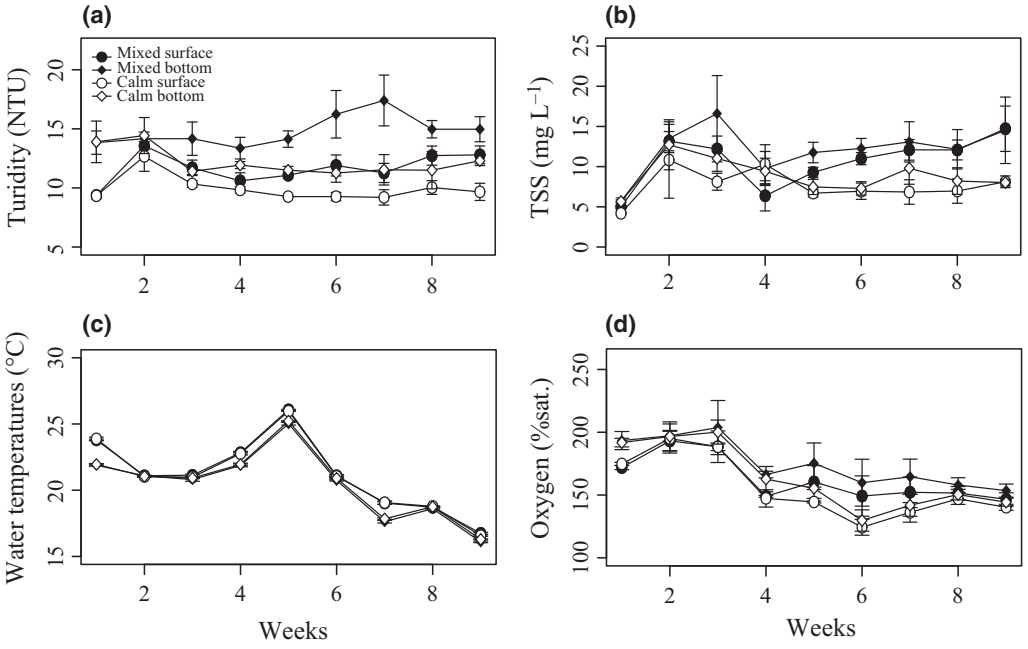


Fig. 1 Temporal dynamics of (a) nephelometric turbidity, (b) total suspended solids (TSS), (c) water temperature and (d) oxygen concentrations during the 9-week experiment. Black and white symbols represent mixed and calm mesocosms respectively. Spheres are measurements taken at the surface, while diamonds are those made above the sediments. Error bars show the standard error.

Table 1 Results of the mesocosm experiment carried out in summer 2012. n.s., not significant. Bold values indicate statistically significant results with significance limit set at P<0.05.

	P-values			
Response variable	Mixing (*M*)	Time (*T*)	*M* × *T*	Depth
Turbidity				
Nephelometric turbidity (NTU)	**0.0207**	n.s.	**0.0004**	**<0.0001**
TSS (mg L^{-1})	**0.0113**	0.0377	**0.0363**	**0.0478**
Chemistry				
Oxygen (%Sat.)	n.s.	<0.0001	n.s.	**<0.0001**
pH	**0.0129**	<0.0001	**0.0015**	n.s.
NO_3-N (mg L^{-1})	n.s.	<0.0001	n.s.	n.s.
NO_2-N (mg L^{-1})	0.0886*	<0.0001	**<0.0062**	n.s.
NH_3-N (mg L^{-1})	n.s.	0.0248	n.s.	n.s.
PO_4^{3-}-P (mg L^{-1})	n.s.	n.s.	n.s	n.s.
Phytoplankton				
Green algae (μg Chl-*a* L^{-1})	**0.0434**	0.0001	**0.0008**	n.s.
<30 μm (μg Chl-*a* L^{-1})	n.s.	0.0132	**0.0024**	n.s.
30 < green algae <100 μm (μg Chl-*a* L^{-1})	**0.0483**	<0.0001	**<0.0001**	n.s.
Abundance (cell mL^{-1})	n.s.	0.0093	n.s.	n.s.
Virus and heterotrophic bacteria				
Virus (VLP mL^{-1})	n.s.	0.0024	n.s.	n.s.
Heterotrophic bacteria (cell mL^{-1})	n.s.	n.s.	n.s.	n.s.
Zooplankton				
Zooplankton (ind. L^{-1})	n.s.	<0.0001	n.s.	n.s.
Rotifer (ind. L^{-1})	n.s.	<0.0001	n.s.	n.s.
Bosmina (ind. L^{-1})	n.s.	<0.0001	n.s.	n.s.
Nauplii (ind. L^{-1})	n.s.	<0.0001	n.s.	n.s.
Copepod (ind. L^{-1})	0.0644*	<0.0001	**0.0003**	n.s.
Egg ratios of *K. testudo*	n.s.	<0.0001	n.s.	n.s.
Egg ratios of *A. fissa*	n.s.	<0.0001	n.s.	n.s.

*Marginally significant.

calm mesocosms in weeks 4–7. Mixing had a positive effect on pH levels over the course of the experiment (LME, $M \times T$, $F_{1,46} = 11.38$, $P = 0.0015$), as it increased from an average of 8.3 ± 0.1 to 9.9 ± 0.3 in mixed mesocosms and 9.5 ± 0.1 in calm mesocosms (Fig. 2a).

The concentration of dissolved nitrates, ammonia and phosphates and their temporal dynamics were similar in mixed and calm mesocosms (Fig. 2b–d, Table 1). Nitrate concentration decreased over time from 3.5 ± 0.4 to 2.2 ± 0.2 mg L^{-1} in all mesocosms, suggesting assimilation by the phytoplankton. No significant variation was found in dissolved phosphorus as a function of time. Nitrite temporal dynamic differed significantly between treatments (Fig. 2e), with a greater accumulation of nitrites in calm mesocosms (LME, $M \times T$, $F_{1,46} = 8.23$, $P < 0.0001$).

Mixing effects on phytoplankton

During zooplankton counting, we could identify some abundant phytoplankton groups such as the three Chlorophyceae, *Coelastrum* sp., *Pediastrum* sp. and *Ankistrodesmus* sp. According to the BBE fluoroprobe profiles, more than 80% of chlorophyll *a* content was attributable to the 'green' algal group in all mesocosms (Fig. 3). Consequently, from now on, 'chlorophyll *a* concentration' only refers to green algae.

In both treatments, we observed an increase in chlorophyll *a* content for the first 3 weeks of the experiment (Fig. 4a). Chlorophyll *a* concentration subsequently decreased and stabilised in calm conditions, while it continued to increase in mixed mesocosms (LME, $M \times T$, $F_{1,46} = 12.872$, $P = 0.0008$). At the end of the experiment, 'green algae' chlorophyll *a* content reached 102.0 ± 31.1 μg Chl-*a* L^{-1} in mixed mesocosms compared to 41.5 ± 17.7 μg Chl-*a* L^{-1} in calm conditions. This positive response to mixing was found for both 'small' and 'large' green algae (Fig. 4b, c). Overall, 60% of the total chlorophyll *a* concentration was found in 'small' green algae (<30 μm) (Fig. 4b). Larger algae (between 30 and 100 μm, Fig. 4c) reached higher chlorophyll *a* content in mixed mesocosms compared to calm mesocosms (last week of the experiment: 34.1 ± 11.9 μg Chl-*a* L^{-1} versus 12.3 ± 2.5 μg Chl-*a* L^{-1}).

Flow cytometry data on phytoplankton indicated an increase in abundance (in cells mL^{-1}) during the first 3 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 with no significant differences between treatments.

Mixing effects on zooplankton

The zooplankton communities in this experiment were found to be typical of a high predation rate by planktivorous fishes, that is, the dominant species were small, mainly comprising herbivorous rotifers and the cladoceran *Bosmina longirostris* (Fig. 5a–d). Rotifers formed more than 90% of zooplankton abundance at all times. Rotifer community composition changed over time, but it was dominated by planktonic brachionids such as *Keratella testudo*, *Anuraeopsis fissa*, and *Brachionus* sp., as well as *Polyartha* sp. (Synchaetidae). Small cladocerans such as *Scapholebris* sp., *Ceriodaphnia* sp.

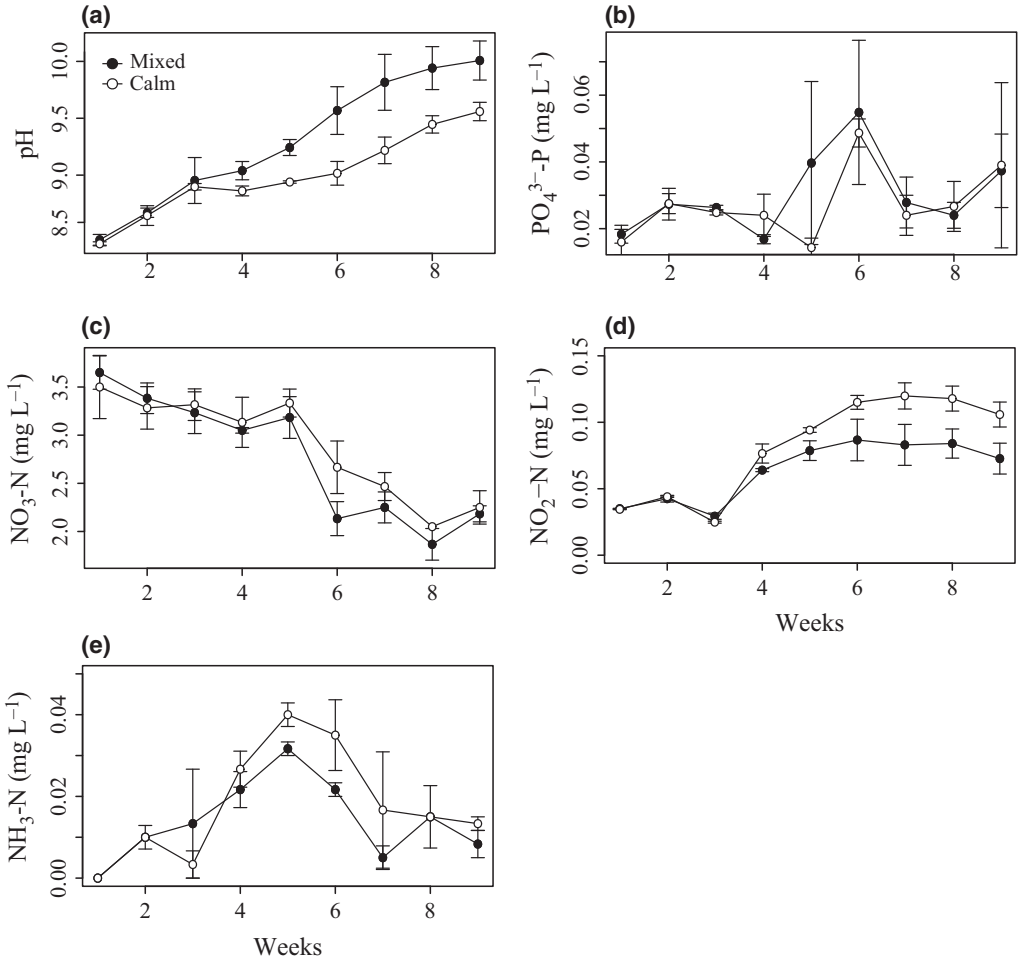


Fig. 2 Temporal dynamics of (a) pH, (b) PO_4^{3-}-P, (c) NO_3-N, (d) NO_2-N and (e) NH_3-N, during the 9-week experiment. Black and white symbols denote mixed and calm mesocosms respectively. Each dot represents the mean between surface and bottom measurements. Error bars show the standard error.

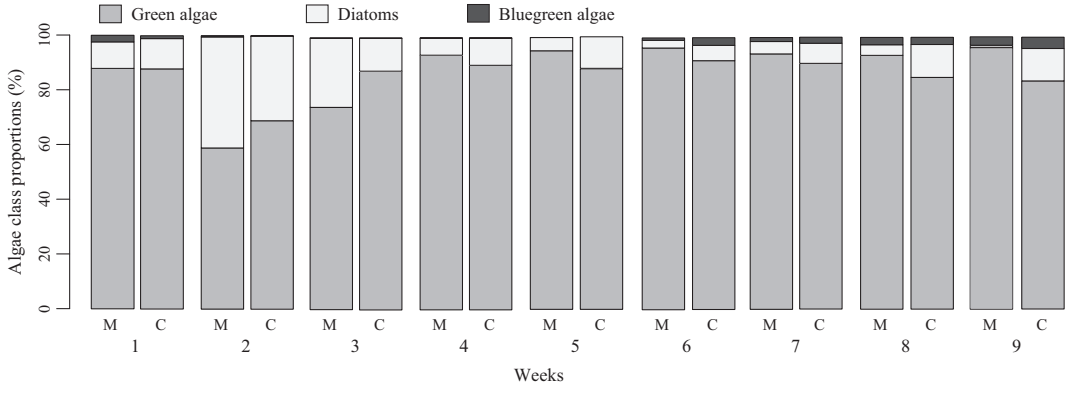


Fig. 3 Proportion of phytoplankton classes during the 9-week experiment. 'M' and 'C' denote mixed and calm mesocosms respectively. Green algae are shown in grey, diatoms in light grey and blue-green algae in black.

(Daphniidae) and *Diaphanosoma brachyurum* (Sididae) also appeared occasionally during the experiment. Nauplii and copepods (calanids and cyclopids) were mainly found from the second half of the experiment onwards. The copepod community was largely dominated by calanids.

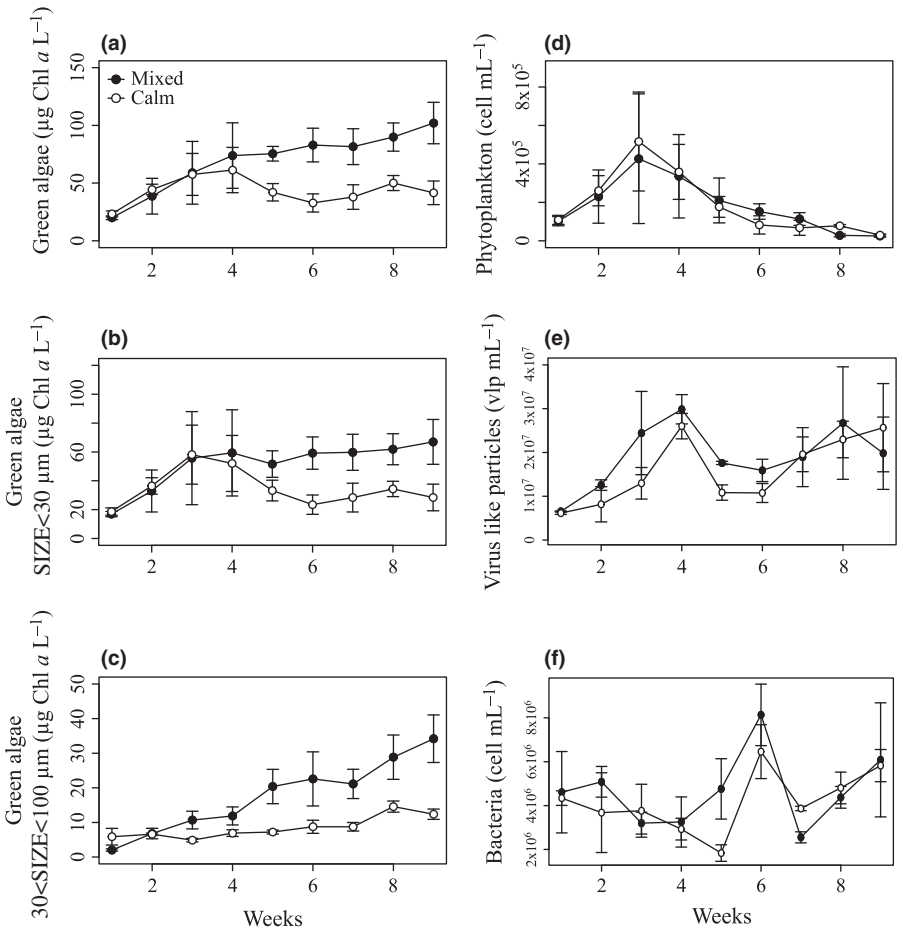


Fig. 4 Temporal dynamics of (a) total green algae biomass (in eq. µg Chl-*a* L^{-1}), (b) green algae biomass with diameter under 30 µm, (c) green algae biomass with diameter between 30 and 100 µm measured using the BBE fluoroprobe, as well as (d) phytoplankton, (e) virus and (f) bacteria abundance measured using flow cytometry during the 9-week experiment. Legends as in Fig. 2.

Rotifer abundance increased up to *c.* 2200 individuals per litre 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. To distinguish between predation, mechanical interference and bottom–up control on rotifer populations, egg ratios of the two dominant species *K. testudo* and *A. fissa* (both combined make up for more than 40% of the rotifer population from week 3 onwards, data not shown) were compared. No differences were found for *K. testudo* and *A. fissa* egg ratios between mixed and calm enclosures (Fig. 6a, b). For both species, no correlation was found between egg ratios and phytoplankton abundance (<30 µm) which may suggest that there was no food limitation. Even though the egg ratios tended to decrease, especially for *A. fissa*, egg ratios remained above 0.2 for most of the experiments.

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, $M \times T$: $F_{1,46} = 15.415$, $P = 0.0003$), reaching higher densities in calm mesocosms (Fig. 5d). This result was not found for copepod larvae, that is, nauplii, even though the graphical patterns are similar (Fig. 5e).

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. 7: weeks 3, 4 and 7 for mesocosms 3, 5 and 1 respectively).

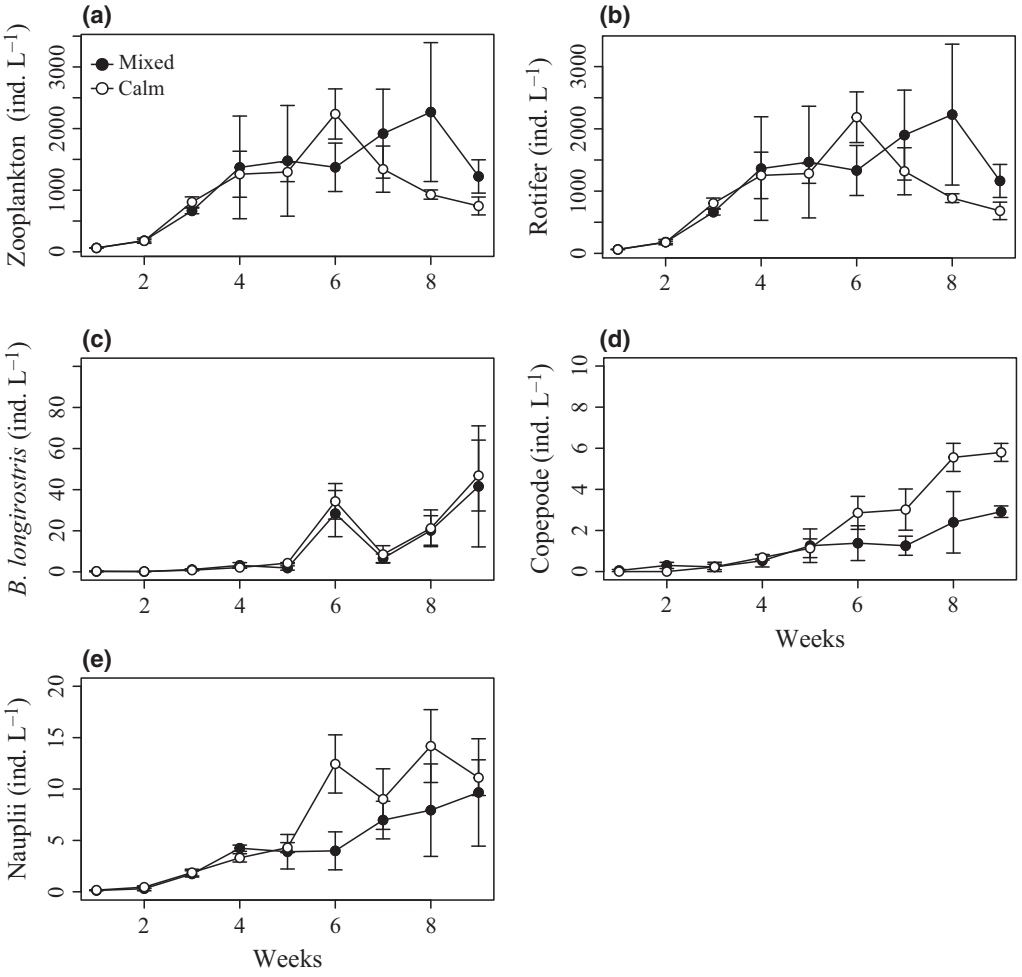


Fig. 5 Temporal dynamics of (a) total zooplankton, (b) rotifers, (c) bosminas, (d) copepods and (e) nauplii abundance during the 9-week experiment. Legends as in Fig. 2.

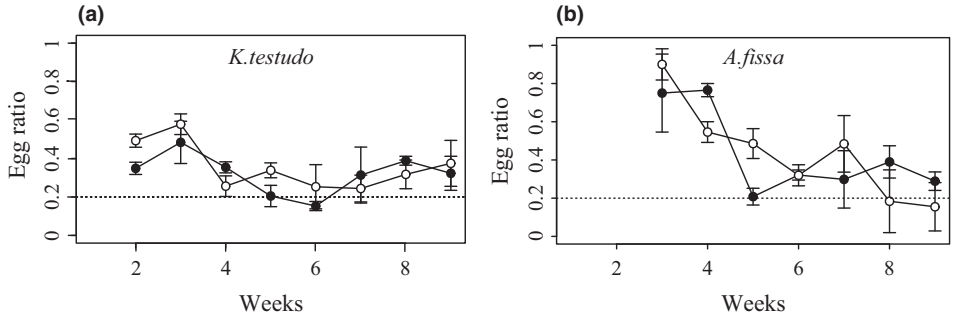


Fig. 6 Temporal dynamics of the egg ratios of two major rotifer species: (a) *K. testudo* and (b) *A. fissa*. No values are given prior to week 2 or 3 when both species are not sufficiently abundant. The dotted line represents the egg ratio limit below which rotifers risk food limitation (limit established for *Keratella* by Gonzales & Frost, 1992 and extrapolated here for *A. fissa*). Legend as in Fig. 2.

Discussion

To the best of our knowledge, this is the first experiment investigating the effects of mixing and resuspension of inorganic matter on eutrophic shallow freshwater using mesocosms especially built to reproduce natural water movements. In our experiment, we successfully created two distinct environments: (i) a well-mixed and

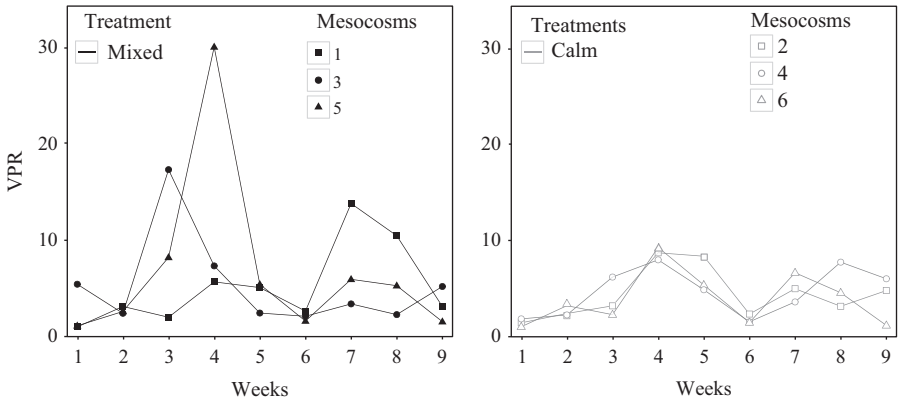


Fig. 7 Temporal dynamics of the virus-to-prokaryote ratio 'VPR' ratio in each mesocosm. Black line: mixed mesocosms, grey line: calm mesocosms. Each mesocosm (from 1 to 6) is identified by a specific dot shape.

turbulent water column with the resuspension of bottom materials leading to higher turbidity; (ii) a stable water column with only superficial mixing (comparable to calm conditions) and no resuspension. *In fine*, we found multiple differences between those systems that we 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. The difference of turbidity between the surface and bottom of mixed mesocosms comes from the equilibrium between sedimentation and resuspension in the upper part of the water column; while the coarser particles sink rapidly, fine inorganic and organic particles, small cells and cell debris are kept in suspension thanks to water movements. 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 planktonic, benthic and attached algae 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 & Burns (2004) showed that the threshold for light limitation of phytoplankton is rather high, for example, >200 NTU in Lake Waihola (New Zealand). Keeping in mind that NTU values and corresponding thresholds for light limitation can vary from lakes to lakes depending on depth and nutrient concentration, 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, but following the turbidity gradient, algae at the bottom of the mesocosms could still be light limited.

Mixing effects on nutrient concentration

In eutrophic shallow lakes, wind-induced resuspension is usually associated with the release of total phosphorus from the sediments (Søndergaard *et al.*, 1992; Hamilton & Mitchell, 1997; Zhu *et al.*, 2005; Thomas & Schallenberg, 2008). Detectable 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 & Mitchell, 1997; Schallenberg & 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). With usually poor organic matter content, it is rather safe to suggest that the sand 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 & Burns, 2004; Zhu *et al.*, 2005) and bacterial biomass (Weithoff *et al.*, 2000). This positive effect will only be found when phytoplankton and prokaryotes are in a state of nutrient limitation (Schallenberg & Burns, 2004). In our experiment, there was no indication of nutrient release from the sand nor nutrient limitation, given the concentration of dissolved phosphorus throughout the experiment which was never completely

depleted and remained relatively stable. This set-up is quite unlikely in nature as sediment beds of eutrophic lakes often behave as reservoirs of phosphorus and nutrients that can be released during mixing events (Søndergaard *et al.*, 2003). However, this helps us to determine the effect of resuspension of matter alone, without possible confounding effects of phosphorus release.

No difference was observed in nitrogen concentration and dynamics except for nitrite nitrogen. NO_2-N increased in both mixed and calm mesocosms. Nitrite accumulation usually results from differential inhibition or disruption of the different steps in nitrification and/or denitrification processes (Philips, Laanbroek & Verstraete, 2002). High pH, as found in our experiment, values are often cited as a major cause for nitrite accumulation through the inhibition of nitrite-oxidising bacteria (NOB) in case of nitrification or through decreasing denitrification (Merkel, Böhler & Frimmerl, 1993; Wetzel, 2001; Kim, Lee & Keller, 2006). Furthermore, NO_2 accumulation was greater in calm as opposed to more turbulent conditions. The lack of oxygenation of the sediment in unmixed mesocosms could impair the nitrification activity in this compartment and lead to greater accumulation in calm mesocosms at lower pH values than mixed mesocosms (Chen, Keeney & Konrad, 1972). Similar results were found in the resuspension experiment of Kang, Song & Liu (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

After 3 weeks of the experiment, we observed a clear divergence in green algae Chl-*a* concentrations between mixed and calm mesocosms. Detailed observations of algae class-sizes show that (i) both size classes of algae respond positively to mixing and (ii) the general increase in Chl-*a* concentration observed after the fourth week in mixed mesocosms is mainly attributable to algae greater than 30 μm. In contrast, algae counting by flow cytometry, which accounts only for algae smaller than 30 μm, revealed a different pattern. First, cell numbers were similar between mixed and calm mesocosms. Second, we observed a decrease in phytoplankton cell number in both mixed and calm mesocosms from week 3 up to the end of the experiment. This decrease in small phytoplankton abundance could be easily explained by the development and top–down control of a rather dense population of rotifers in all mesocosms. However, these results raise the following questions (i) why do we observe a difference in chlorophyll *a* concentration between mixed and calm mesocosms? (ii) why do we observe an increase in Chl-*a* in mixed mesocosms while the cell number is decreasing?

Field studies that found a positive relationship between mixing and chlorophyll *a* (Carrick *et al.*, 1993; Schelske *et al.*, 1995; Hamilton & Mitchell, 1997; Ogilvie & Mitchell, 1998; Schallenberg & Burns, 2004) explained this result by an increase in algae abundance through the recruitment of meroplanktonic algae. In our case, the increase in chlorophyll *a* concentration in mixed enclosures is not linked to any increase in algae abundance for small algae (<30 μm). Moreover, it is fairly unlikely that any meroplanktonic population would have the time to settle in the mesocosms before the onset of the experiment. We therefore propose two non-exclusive hypotheses to explain this discrepancy: (i) a shift in species composition towards larger species with higher chlorophyll content; (ii) a physiological response of algae cells to mixing.

The duration of this experiment is enough to observe shifts in algae community composition (Harris 1986). Mixing is known to alter phytoplankton community composition (Fraisse, Bormans & Lagadeuc, 2015) and usually enables larger and heavier species to stay in suspension, therefore it is likely that, within 'small' algae (<30 μm), the increase in chlorophyll *a* is due to a higher proportion of large species (Visser *et al.*, 1996; Felip & Catalan, 2000). The continuous increase in chlorophyll *a* observed for 'large' species (between 30 and 100 μm) also supports this first hypothesis. This could be easily verified in further experiments by studying the evolution of the phytoplankton composition, either through sequencing or microscopic identification and measurement of algae sizes.

The other hypothesis to explain the discrepancy between abundance data and chlorophyll *a* might be a physiological response of cells to mixing. Photosynthetic organisms have the capacity to regulate the amount of pigments in response to the light climate and nutrient concentration (Falkowski, 1984; Shin, Rhee & Chen, 1987; Longhurst & Glen Harrison, 1989; Ibelings, Kroon & Mur, 1994; Felip & 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. However, this hypothesis does not satisfactorily explain our results as these processes

usually occur within one or two generations of algae cells (Harris 1986) and effects on the chlorophyll *a* measurements should have appeared earlier in the experiment.

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. This is also supported by higher oxygen concentrations in weeks 4–7 in mixed mesocosms. 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 & 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 could also theoretically affect gas exchanges at the water/air interface with an enhancement of CO_2 dissolution, thus allowing greater uptake by primary producers or alleviating any carbon limitation. However, if this was the case here, a difference in pH should have been observed at the beginning of the experiment (with lower pH values in mixed mesocosms due to continuous supply of CO_2). Here, the pH is the same between calm and mixed mesocosms up until the third to fourth week, which coincides temporally with the divergence in Chl-*a* concentration between treatments. Important impacts on gas exchanges can be expected when mixing provokes breaking waves, vortexes and bubbles, which is not the presently the case.

Mixing effects on zooplankton dynamics

Zooplankton responses to mixing varied from one group to another. Small cladocerans, mainly *Bosmina longirostris*, and rotifer abundances were consistent in calm and mixed mesocosms. Nonetheless, rotifers dynamics slightly differed with an abundance peak on 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. This hypothesis is in agreement with egg ratios analysis. Egg ratios rarely dropped below 0.2 which is considered as a limit for food limitation for *Keratella* (Gonzales & Frost, 1992; Weithoff *et al.*, 2000). Moreover, in the case of *K. testudo*, the egg ratio was stable, especially in calm enclosures; while rotifer population dropped suggesting that predation and/or mechanical interference were the main form of control. We can exclude mechanical interference because most cladocerans were smaller than 1.2 mm which is the critical value for mechanical interference (Burns & Gilbert, 1986; MacIsaac & Gilbert, 1989). 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, Rasberry & Webster, 2008), leading to reduced feeding and growth rates. Second, copepods in mixed enclosures could proportionally ingest more resuspended material that is lower in nutrient content as compared to low turbidity environments, thus reducing the efficiency of food assimilation (Gasparini, Castel & Irigoien, 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 reduce clearance rates by only 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 which could in turn lower their feeding success, growth rates and reproduction rates (Paffenhöfer, 1972; Oviatt, 1981; Turner & Tester, 1989; Gasparini *et al.*, 1999; Kang, 2012). For instance, predation by the planktivorous fish in our mesocosms could be responsible for the difference in copepods density between calm and mixed conditions. Härkönen *et al.* (2014) showed that under turbulent condition with low visibility, planktivorous fish increase their predation on copepods. They explain this result to a lower escape ability of copepods, thus making them more vulnerable to fish predation. This could have major consequences on top–down regulations in lakes with different turbulence and visibility levels.

Mixing effects on prokaryotes and viruses

Bacteria are a crucial component in limnetic food webs, yet, very little is known about the impact of mixing on this community 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. However, bacteria are also dependent on other factors such as biological interactions.

In the last decades, viruses have been recognised as an important component in the microbial food web and can have a strong impact on bacterial mortality and diversity (Wommack & Colwell, 2000; Weinbauer & Stanier, 2004; Meunier & Jacquet, 2015). Our results on the VRP ratio (generally considered as a proxy of the interactions between viruses and hosts, e.g. Parikka *et al.*, 2016) could suggest that the lysis activity was stronger in mixed compared to calm conditions. We hypothesise that this result could reflect enhanced contact rates in mixed conditions, which is a key process to explain virus–host interactions. A similar effect of water motion was proposed by Hudnell *et al.* (2010) regarding the control of cyanobacteria by cyanophages. Further studies using precise genomic tools would be necessary to confirm our finding, which could have important consequences on ecosystem microbial functioning.

Ecosystem level

This medium-term experiment reveals that mixing may have multiple impacts on shallow waterbodies, either directly through mechanical action or turbidity levels or indirectly through the food web. 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).

The first important result is that mixing impacted the phytoplankton and possibly its primary productivity as indicated by pH and oxygen variations. Yet, it also changed the structure of the community by differently affecting the zooplankton functional groups 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.

Acknowledgments

We thank François Rocher and Jean-Jacques Lamandé of the CEREEP Ecotron station for their technical help regarding the repairs, maintenance and setting up of the ramps on the enclosures. We also thank the CNRS station for their help and technical support. L.B. and this work are financially supported by the ANR Pulse 2010 CEPL 01004 and ANR Equipex PLANAQUA (ANR-10-EQPX-13-01) coordinated by the CEREEP-Ecotron IleDe-France (UMS 3194).

References

Aparicio Medrano E., Uittenbogaard R.E., Dionisio Pires L.M., van de Wiel B.J.H. & Clercx H.J.H. (2013) Coupling hydrodynamics and buoyancy regulation in *Microcystis aeruginosa* for its vertical distribution in lakes. *Ecological Modelling*, **248**, 41–56.

Bengtsson L. & Hellström T. (1990) Redistribution of sediments in three Swedish lakes. *Hydrobiologia*, **192**, 167–181.

Bengtsson L. & Hellström T. (1992) Wind-induced resuspension in a small shallow lake. *Hydrobiologia*, **241**, 163–172.

Beutler M., Wilshire K.H., Meyer B., Moldaenke C., Lüring C., Meyerhöfer M. *et al.* (2002) A fluorometric method for

the differentiation of algal populations *in vivo* and *in situ*. *Photosynthesis Research*, **72**, 39–53.

Blottière L. (2015) *The Effects of Wind-Induced Mixing on the Structure and Functioning of Shallow Freshwater Lakes in a Context of Global Change*. PhD Dissertation, Paris Sud University, Paris.

Blottière L., Rossi M., Madricardo F. & Hulot F.D. (2013) Modeling the role of wind and warming on *Microcystis aeruginosa* blooms in shallow lakes with different trophic status. *Theoretical Ecology*, **7**, 35–52.

Brandl Z. (2005) Freshwater copepods and rotifers: predators and their prey. *Hydrobiologia*, **546**, 457–489.

Brussaard C.P.D. (2004) Optimization of procedures for counting viruses by flow cytometry. *Applied and Environmental Microbiology*, **70**, 1506–1513.

Burford M.A. & O'Donohue M.J. (2006) A comparison of phytoplankton community assemblages in artificially and naturally mixed subtropical water reservoirs. *Freshwater Biology*, **51**, 973–982.

Burns C.W. & Gilbert J.J. (1986) Effects of daphnid size and density on interference between *Daphnia* and *Keratella cochlearis*. *Limnology and Oceanography*, **31**, 848–858.

Carrick H.J., Aldridge F.J. & Schelske C.L. (1993) Wind influences phytoplankton biomass and composition in a shallow, productive lake. *Limnology and Oceanography*, **38**, 1179–1192.

Chen R.L., Keeney D.R. & Konrad J.G. (1972) Nitrification in lake sediments. *Journal of Environmental Quality*, **1**, 151–154.

Eckert B. & Walz N. (1998) Zooplankton succession and thermal stratification in the polymictic shallow Müggelsee (Berlin, Germany): a case for the intermediate disturbance hypothesis? *Hydrobiologia*, **387–388**, 199–206.

Falkowski P.G. (1984) Physiological responses of phytoplankton to natural light regimes. *Journal of Plankton Research*, **6**, 295–307.

Felip M. & Catalan C. (2000) The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima. *Journal of Plankton Research*, **22**, 91–105.

Fraisse S., Bormans M. & Lagadeuc Y. (2015) Turbulence effects on phytoplankton morphofunctional traits selection. *Limnology and Oceanography*, **00**, 1–24.

Garstecki T. & Wickham S. (2001) Effects of resuspension and mixing on population dynamics and trophic interactions in a model benthic microbial food web. *Aquatic Microbial Ecology*, **25**, 281–292.

Gasparini S., Castel J. & Irigoien X. (1999) Impact of suspended particulate matter on egg production of the estuarine copepod, *Eurytemora affinis*. *Journal of Marine Systems*, **22**, 195–205.

Gonzales M.J. & Frost T.M. (1992) Food limitation and seasonal population declines of rotifers. *Oecologia*, **89**, 560–566.

Gunatilaka A. (1982) Phosphate adsorption kinetics of resuspended sediments in a shallow lake, Neusiedlersee, Austria. *Hydrobiologia*, **91–92**, 293–298.

Hamilton D.P. & Mitchell S.F. (1997) Wave-induced shear stresses, plant nutrients and chlorophyll in seven shallow lakes. *Freshwater Biology*, **38**, 159–168.

Härkönen L., Peckan-Hekim Z., Hellén N., Ojala A. & Horppila J. (2014) Combined effects of turbulence and different predation regimes on zooplankton in highly colored water – implications for environmental change in lakes. *PLoS ONE*, **9**, e111942.

Harris G.P. (1986) Phytoplankton Ecology. Structure, Function and Fluctuation. Chapman and Hall, London

Hawkins P.R. & Griffiths D.J. (1993) Artificial destratification of a small tropical reservoir: effects upon the phytoplankton. *Hydrobiologia*, **254**, 169–181.

Head R.M., Jones R.I. & Bailey-Watts A.E. (1999) An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. *Freshwater Biology*, **41**, 759–769.

Hellström T. (1991) The effect of resuspension on algal production in a shallow lake. *Hydrobiologia*, **213**, 183–190.

Hudnell H.K., Jones C., Labisi B., Lucero V., Hill D.R. & Eilers J. (2010) Freshwater harmful algal bloom (FHAB) suppression with solar powered circulation (SPC). *Harmful Algae*, **9**, 208–217.

Huisman J., Sharples J., Stroom J.M., Visser P.M., Kardinaal W.E.A., Verspagen J.M.H. *et al.* (2004) Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, **85**, 2960–2970.

Huisman J., van Oostveen P. & Weissing F.J. (1999) Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. *The American Naturalist*, **154**, 46–68.

Huisman J. & Weissing F.J. (1994) Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology*, **75**, 507–520.

Hulot F.D., Lacroix G. & Loreau M. (2014) Differential responses of size-based functional groups to bottom-up and top-down perturbations in pelagic food webs: a meta-analysis. *Oikos*, **123**, 1291–1300.

Ibelings B.W., Kroon B.M.A. & Mur L.R. (1994) Mixing in lakes acclimation to high of photosystem a in a green cyanobacterium and flux eukaryotic simulating alga fluctuating densities, photosynthetic light in photon regimes induced mixing lakes. *New Phytologist*, **128**, 407–424.

Jacquet S., Dorigo U. & Personnic S. (2013) A few tests prior to flow cytometry and epifluorescence analysis of freshwater samples. In: *Flow Cytometry: Principles, Methodology and Applications* (Ed. S. Papandreou), Chapter 1, pp. 1–30. Related Nova publication, Nova Publishers Inc., New York.

Jöhnk K.D., Huisman J., Sharples J., Sommeijer B., Visser P.M. & Stroom J.M. (2008) Summer heatwaves promote blooms of harmful cyanobacteria. *Global Change Biology*, **14**, 495–512.

Jungo E., Visser P.M., Stroom J. & Mur L.R. (2001) Artificial mixing to reduce growth of the blue-green alga Microcystis in Lake Nieuwe Meer, Amsterdam : an evaluation of 7 years of experience. *Water Science and Technology: Water Supply*, **1**, 17–23.

Kang H.K. (2012) Effects of suspended sediments on reproductive responses of *Paracalanus sp.* (Copepoda: Calanoida) in the laboratory. *Journal of Plankton Research*, **34**, 626–635.

Kang Y., Song X. & Liu Z. (2013) Sediment resuspension dampens the effect of nutrient inputs on the phytoplankton community: a mesocosm experiment study. *Hydrobiologia*, **710**, 117–127.

Kim D.J., Lee D.I. & Keller J. (2006) Effect of temperature and free ammonia on nitrification and nitrite accumulation in landfill leachate and analysis of its nitrifying bacterial community by FISH. *Bioresource Technology*, **97**, 459–468.

Klausmeier C.A. & Litchman E. (2001) Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. *Limnology and Oceanography*, **46**, 1998–2007.

Kosten S., Huszar V.L.M., Bécares E., Costa L.S., Donk E., Hansson L.-A. *et al.* (2011) Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, **18**, 118–126.

Leboulanger C., Dorigo U., Jacquet S., Le Berre B., Paolini G. & Humbert J.F. (2002) Application of a submersible spectrofluorometer for rapid monitoring of freshwater cyanobacterial blooms: a case study. *Aquatic Microbial Ecology*, **30**, 83–89.

Ledger M.E., Harris R.M.L., Armitage P.D. & Milner A.M. (2009) Realism of model ecosystems: an evaluation of physicochemistry and macroinvertebrate assemblages in artificial streams. *Hydrobiologia*, **617**, 91–99.

Levine S.N., Zehrer R.F. & Burns C.W. (2005) Impact of resuspended sediment on zooplankton feeding in Lake Waihola, New Zealand. *Freshwater Biology*, **50**, 1515–1536.

Litchman E. (2000) Growth rates of phytoplankton under fluctuating light. *Freshwater Biology*, **44**, 223–235.

Longhurst A.R. & Glen Harrison W. (1989) The biological pump: profiles of plankton production and consumption in the upper ocean. *Progress in Oceanography*, **22**, 47–123.

Luettich R.A., Harleman D.R. & Somlyody L. (1990) Dynamic behavior of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. *Limnology and Oceanography*, **35**, 1050–1067.

MacIsaac H.J. & Gilbert J.J. (1989) Competition between rotifers and cladocerans of different body sizes. *Oecologia*, **81**, 295–301.

Mallin M.A. & Paerl H.W. (1992) Effects of variable irradiance on phytoplankton productivity in shallow estuaries. *Limnology and Oceanography*, **37**, 54–62.

Marra J. (1978) Phytoplankton photosynthetic response to vertical movement in a mixed layer. *Marine Biology*, **46**, 203–208.

Merkel W., Böhler E. & Frimmerl F.H. (1993) Zum Einfluß von Sauerstoffkonzentration und pH-Wert bei der heterotrophen Denitrifikation Heterotrophic Denitrification: the influence of oxygen and pH value. *Acta Hydrochimica et Hydrobiologica*, **21**, 249–257.

Mette E.M., Vanni M.J., Newell J.M. & González M.J. (2011) Phytoplankton communities and stoichiometry are interactively affected by light, nutrients, and fish. *Limnology and Oceanography*, **56**, 1959–1975.

Meunier A. & Jacquet S. (2015) Do phages impact microbial dynamics, prokaryotic community structure and nutrient dynamics in Lake Bourget? *Biology Open*, **4**, 1528–1537.

Moss B. (2010) *Ecology of Fresh Waters: A View for the Twenty-First Century*, 4th edn. Wiley-Blackwell, Oxford.

Ogilvie B.G. & Mitchell S.F. (1998) Does sediment resuspension have persistent effects on phytoplankton? Experimental studies in three shallow lakes. *Freshwater Biology*, **40**, 51–63.

Oviatt C. (1981) Effects of different mixing schedules on phytoplankton, zooplankton and nutrients in marine microcosms. *Marine Ecology Progress Series*, **4**, 57–67.

Paffenhöfer G.A. (1972) The effects of suspended 'red mud' on mortality, body weight, and growth of the marine planktonic copepod, *Calanus helgolandicus*. *Water, Air, & Soil Pollution*, **1**, 314–321.

Parikka K.J., LeRomancer M., Wauters N. & Jacquet S. (2016) Deciphering the virus-to-prokaryote ratio: insights into the virus-host relationships in a variety of ecosystems. *Biological Reviews*, in press.

Philips S., Laanbroek H.J. & Verstraete W. (2002) Origin, causes and effects of increased nitrite concentrations in aquatic environments. *Re/Views in Environmental Sciences & Bio/Technology*, **1**, 115–141.

Pinheiro J.C., Bates D., DebRoy S. & Sarkar D. & R Core Team (2013) *Nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-107. Available at: http://CRAN.R-project.org/package=nlme

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org/.

Reynolds C.S. (2006) The Ecology of Phytoplankton. Cambridge University Press, Cambridge.

Reynolds C.S., Wiseman S.W. & Clarke M.J.O. (1984) Growth- and loss-rate responses of phytoplankton to intermittent artificial mixing and their potential application to the control of planktonic algal biomass. *Journal of Applied Ecology*, **21**, 11–39.

Reynolds C.S., Wiseman S.W., Godfrey B.M. & Butterwick C. (1983) Some effects of artificial mixing on the dynamics of phytoplankton populations in large limnetic enclosures. *Journal of Plankton Research*, **5**, 203–234.

Rolland A., Rimet F. & Jacquet S. (2010) A 2-year phytoplanktonic survey in the Reservoir Marne (France): a case study validating the use of a spectrofluorometer by comparison to algal taxonomy and chlorophyll a measurements. *Knowledge and Management of Aquatic Ecosystems*, **398**, 1–19.

Schallenberg M. & Burns C.W. (2004) Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. *Freshwater Biology*, **49**, 143–159.

Scheffer M. (1998) *Ecology of Shallow Lakes*. Springer, New York.

Schelske C.L., Carrick H.J. & Aldridge F.J. (1995) Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *Journal of the North American Benthological Society*, **14**, 616–630.

Schelske C.L., Rothman E.D., Stoermer E.F. & Santiago M.A. (1974) Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. *Limnology and Oceanography*, **19**, 409–419.

Shin C.N., Rhee G.-Y. & Chen J. (1987) Phosphate requirement, photosynthesis, and diel cell cycle of *Scenedesmus obliquus* under fluctuating light. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 1753–1758.

Sommer U., Adrian R., De Senerpont Domis L., Elser J.J., Gaedke U., Ibelings B. *et al.* (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 429–448.

Søndergaard M., Jensen J.P. & Jeppesen E. (2003) Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia*, **506–509**, 135–145.

Søndergaard M., Kristensen P. & Jeppesen E. (1992) Phosphorus release from resuspended sediment in the shallow and wind-exposed Lake Arreso, Denmark. *Hydrobiologia*, **228**, 91–99.

Thomas D.B. & Schallenberg M. (2008) Benthic shear stress gradient defines three mutually exclusive modes of non-biological internal nutrient loading in shallow lakes. *Hydrobiologia*, **610**, 1–11.

Turner J.T. & Tester P.A. (1989) Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* Giesbrecht in the plume of the Mississippi River. *Journal of Experimental Marine Biology and Ecology*, **126**, 21–23.

Vaulot D. (1989) CYTOPC: processing software for flow cytometric data. *Signal and Noise*, **2**, 8.

Verspagen J.M.H., Snelder E.O.F.M., Visser P.M., Huisman J., Mur L.R. & Ibelings B.W. (2004) Recruitment of benthic *Microcystis* (Cyanophyceae) to the water column: internal buoyancy changes or resuspension? *Journal of Phycology*, **40**, 260–270.

Verspagen J.M.H., Snelder E.O.F.M., Visser P.M., Jöhnk K.D., Ibelings B.W., Mur L.R. *et al.* (2005) Benthic-pelagic coupling in the population dynamics of the harmful cyanobacterium *Microcystis*. *Freshwater Biology*, **50**, 854–867.

Visser P., Ibelings B., van der Veer B., Koedood J. & Mur R. (1996) Artificial mixing prevents nuisance blooms of the cyanobacterium *Microcystis* in Lake Nieuwe Meer, the Netherlands. *Freshwater Biology*, **36**, 435–450.

Weinbauer J. & Stanier R. (2004) Ecology of prokaryotic viruses. *FEMS Microbiology Reviews*, **28**, 127–181.

Weithoff G., Lorke A. & Walz N. (2000) Effects of water-column mixing on bacteria, phytoplankton, and rotifers under different levels of herbivory in a shallow eutrophic lake. *Oecologia*, **125**, 91–100.

Wetzel R.G. (2001) Limnology, 3rd edn. Academic Press, New York.

Wommack K.E. & Colwell R.R. (2000) Virioplankton: viruses in aquatic ecosystems. *Microbiology and Molecular Biology Reviews*, **64**, 69–114.

Yen J., Rasberry K.D. & Webster D.R. (2008) Quantifying copepod kinematics in a laboratory turbulence apparatus. *Journal of Marine Systems*, **69**, 283–294.

Zhu G., Qin B. & Guang G. (2005) Direct evidence of phosphorus outbreak release from sediment to overlying water in a large shallow lake caused by strong wind wave disturbance. *Chinese Science Bulletin*, **50**, 577–582.

(Manuscript accepted 26 September 2016)