

Influence of water-column depth and mixing on phytoplankton biomass, community composition, and nutrients

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Abstract

We independently manipulated mixing intensity (strong artificial mixing vs. background turbulence) and water-column depth (2 m, 4 m, 8 m, and 12 m) in order to explore their separate and combined effects in a field enclosure experiment. To accentuate the vertical light gradient, enclosures had black walls, resulting in a euphotic depth of only 3.7 m. All enclosures were placed in a well-mixed water bath to equalize temperature across treatments. Phytoplankton responded to an initial phosphorus pulse with a transient increase in biomass, which was highest in the shallowest, least light-limited water columns where dissolved mineral phosphorus subsequently became strongly limiting. As a consequence, the depth-averaged mineral phosphorus concentration increased and the seston carbon (C):phosphorus (P) ratio decreased with increasing water-column depth. Low turbulence enclosures became quickly dominated by motile taxa (flagellates) in the upper water column, whereas mixed enclosures became gradually dominated by pennate diatoms, which resulted in higher average sedimentation rates in the mixed enclosures over the 35-d experimental period. Low turbulence enclosures showed pronounced vertical structure in water columns >4 m, where diversity was higher than in mixed enclosures, suggesting vertical niche partitioning. This interpretation is supported by a primary production assay, where phytoplankton originating from different water depths in low-turbulence treatments had the relatively highest primary productivity when incubated at their respective depths of origin.

Physical conditions, notably the depth of the water column and the intensity of mixing, influence population dynamics of pelagic primary producers by affecting the average light climate, sedimentation loss, and the availability of nutrients (Huisman et al. 1999; O'Brien et al. 2003; Huisman et al. 2006). For example, under well-mixed conditions phytoplankton are passively entrained in the entire water column and, over time, each algal cell experiences the depth-averaged light intensity, which is a decreasing function of water-column depth. Consequently, depth-averaged specific primary production decreases with increasing water-column depth (Huisman 1999; Diehl et al. 2002, 2005) and will become insufficient for the maintenance

of a viable population when the mixed water column exceeds a “critical depth” (Sverdrup 1953). In contrast, in a weakly mixed water column the velocity of entrainment will often be slower than the rate of algal reproduction. Consequently, algal cells can remain in the well-lit upper part of the water column for long enough to maintain a population even if the water column exceeds the critical depth (Huisman et al. 1999).

Water-column depth and mixing intensity also affect algal sedimentation losses. The probability that an individual algal cell or a colony will sink out of the water column increases with increasing sinking velocity and decreasing water-column depth, but decreases with increasing mixing intensity (Visser et al. 1996; Condie and Bormans 1997; Ptacnik et al. 2003). The latter occurs because turbulent mixing disperses phytoplankton in the water column and therefore partly counteracts sedimentation; overall, sinking losses should thus be most severe for fast-sinking algae in shallow and weakly mixed water columns (Diehl 2002; Huisman et al. 2002).

Algal sedimentation constantly removes particular nutrients from the water column, which are subsequently mineralized and recycled back into the water column from below. In sufficiently deep and weakly mixed water columns nutrients may therefore become strongly limiting

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close to the surface but be available in excess in deeper layers, creating a vertical gradient in mineral nutrient concentration (Klausmeier and Litchman 2001; Huisman et al. 2006). In well-mixed water columns vertical gradients are absent and nutrient availability is expected to depend exclusively on total water-column depth. Nutrient concentrations should be low in shallow water columns, from which algal sinking removes nutrients at high rates, and high in deep water columns, where algal production and nutrient use is strongly light limited (Huisman and Weissing 1995; Diehl 2002). Flexible algal stoichiometry may, however, weaken or even mask this relationship (Diehl et al. 2005). It is well known that the elemental composition (e.g., the carbon [C]-to-phosphorus [P] ratio [C:P]) of algal biomass varies in response to the relative supplies of light and nutrients (Sterner et al. 1997). "Excess" nutrients in deep water columns may therefore be taken up (and stored) by phytoplankton even if production is light limited, leading to pronounced differences in algal C:P—and less pronounced differences in mineral nutrient concentration—among well-mixed water columns of different depths (Diehl et al. 2005; Berger et al. 2006). Similarly, within weakly mixed water columns, gradients of vertically decreasing seston C:P ratios are to be expected (Rothhaupt 1991; Elser and George 1993; Park et al. 2004).

By mediating light and nutrient availability, water-column depth and mixing intensity may also profoundly affect the outcome of competition among planktonic algae. In well-mixed systems, nutrients and algae are homogeneously distributed in the water column. Strong mixing therefore minimizes the possibilities for spatial niche differentiation. Under constant environmental conditions, those taxa that reduce the light intensity at the bottom of the water column to the lowest level and the limiting nutrients to the lowest concentrations will then displace all other competitors, allowing at best a few species to persist in the long run (Sommer 1985; Huisman and Weissing 1995; Passarge et al. 2006). In contrast, coexistence by means of vertical niche separation is possible in weakly mixed systems (Reynolds 1992). For example, a superior competitor for light may coexist with a superior competitor for nutrients, with the former dominating at deeper water depths and the latter at shallower water depths (Huisman et al. 2006).

The outcome of algal competition in response to mixing intensity and water-column depth depends, however, not only on algal traits related to resource use but also on buoyancy. Several studies have reported that systems could be moved back and forth from dominance of buoyant taxa in weakly or shallowly mixed water columns to dominance of fast-sinking taxa in deeply mixed water columns by turning off and on artificial mixing (Reynolds et al. 1983; Visser et al. 1996; Huisman et al. 2004). Thus, buoyant taxa benefit from stratified conditions (Sherman et al. 1998). Buoyancy may also enable coexistence of a weaker competitor (for light) with a superior one (Litchman 2003). In particular, motile taxa may benefit from weak mixing intensity because low turbulence enables them to move to depths with optimal growth conditions (Klausme-

ier and Litchman 2001). Such habitat choice could accentuate vertical niche separation of different taxa (Elliott et al. 2002; Clegg et al. 2007). Thus, if weak mixing leads to the development of multiple gradients of growth-enhancing and growth-inhibiting environmental parameters, this could enable substantial vertical niche partitioning and enhance diversity compared to a well-mixed system of the same overall depth.

In conclusion, water-column depth and mixing intensity influence phytoplankton biomass, community composition, and vertical distribution through a multitude of interacting processes. Clearly, our understanding of the interplay among these processes would benefit from appropriately designed field experiments. So far, however, experiments on the role of mixing intensity have been limited to cases where periods of intermittent stratification and mixing were alternated (Reynolds et al. 1983, 1984; Flöder and Sommer 1999), and experiments on the role of water-column depth have been limited to well-mixed systems (Diehl et al. 2002; Ptacnik et al. 2003; Diehl et al. 2005). We therefore conducted a field experiment in which we manipulated mixing intensity and water-column depth independently from each other in a full factorial design. To our knowledge this is the first experiment of its kind.

Methods

Study site and experimental design—The experiment was carried out in Lake Brunnsee near the University of Munich's Limnological Research Station at Seon (90 km east of Munich, Germany). At the beginning of our experiment chlorophyll *a* (Chl *a*) concentration in this 5.8 ha, low-productivity, hard-water lake was $2.5 \mu\text{g L}^{-1}$, and total phosphorus concentration was $10 \mu\text{g L}^{-1}$. The concentrations of other potentially growth-limiting nutrients were far in excess of algal needs (nitrogen: 2.3 mg L^{-1} , silicate: 2.6 mg L^{-1}). The euphotic depth in the lake was $\sim 16 \text{ m}$ during the experiment.

We independently manipulated four enclosure depths (2 m, 4 m, 8 m, and 12 m) and two contrasting mixing intensities [no artificial mixing (subsequently called "non-mixing") and strong, artificial mixing (subsequently called "mixing")] in two replicates per treatment. The enclosures (cylindrical, transparent plastic bags of 0.95-m diameter, heat sealed at the bottom and open to the atmosphere) were suspended from a raft and filled with 30- μm -filtered epilimnetic lake water containing the ambient phytoplankton community on 27–28 July 2005. To stimulate algal production we fertilized the enclosures with $30 \mu\text{g P L}^{-1}$, added as KH_2PO_4 , on 02 August 2005 (day 0 of the experiment). We maintained the artificial mixing of the mixing enclosures for 56 d (until 27 September 2005). However, convective nightly mixing occurred frequently in the nonmixing treatments from day 35 onward, diminishing the differences between the two turbulence treatments. We therefore analyzed in detail only the samples covering the first 35 d of the experiment, and herein we have restricted the presentation of results to this period.

The transparent enclosure walls were snugly and completely surrounded by black silage film to mimic higher

background turbidity and to isolate them optically from the surrounding water. This resulted in a depth-averaged light attenuation coefficient of 1.2 m^{-1} and a euphotic depth [where photosynthetic active radiation (PAR) was reduced to 1% of incident PAR] of 3.7 m during the experiment. The depth-averaged light availabilities in the 2-m, 4-m, 8-m, and 12-m mixing enclosures corresponded to the ambient light levels at water depths of 0.8 m, 1.3 m, 1.9 m, and 2.2 m, respectively, in a nonmixed enclosure. The mixing enclosures were intermittently mixed (for 5 min every 30 min) by pumping air to the bottom of each enclosure in order to maintain homogeneous conditions.

To accomplish true independence of the turbulence and water-column depth treatments, vertical gradients in turbulence had to be avoided inside the enclosures, which required the absence of vertical temperature gradients. To this end we surrounded the entire raft with a giant, 14-m deep "bag" of clear plastic. The water inside this bag was intermittently mixed (for 5 min every 30 min), creating a water bath of homogeneous temperature. The mixing of the outer water bath was highly effective. Water temperatures in any two enclosures differed by $<0.5^\circ\text{C}$ at a 1-m depth, and vertical temperature differences between the surface and 11 m in the outside bag were, averaged over the experimental duration, $<1^\circ\text{C}$. A further average decline of 1.3°C occurred at the bottom of the 12-m nonmixing enclosures. Despite the heat exchange with the well-mixed outside bag, slight warming (mean 0.6°C , maximum 1.6°C) could not be entirely prevented near the surface of the nonmixing enclosures during daytime. To prevent nonmixing enclosures from being convectively mixed by nightly cooling, we covered all enclosures with isolating styrofoam boards (specific heat conductivity: $0.040 \text{ W m}^{-1} \text{ K}^{-1}$) ~ 10 cm above the water surface during nighttime. We monitored the isolating effect of this procedure by recording the water temperature at the surface and the air temperature between the water surface and the isolating boards (K204 Datalogger; Voltcraft Plus, Conrad Elektronik) in one deep nonmixing enclosure and one shallow nonmixing enclosure once every 30 min. Simultaneously, the air temperature on the raft and the water temperature at the surface of the outside bag were recorded. During the reported experimental period (days 0–35) surface temperatures in the outside bag ranged from 13.3°C to 16.4°C .

We roughly estimated the intensity of turbulence in the two mixing treatments by measuring the vertical spread of a fluorescein–sodium tracer released in the middle of the water columns (Peeters et al. 1996). The coefficient of vertical turbulent diffusion was $\sim 330 \text{ m}^2 \text{ d}^{-1}$ ($= 3.8 \times 10^{-3} \text{ m}^2 \text{ s}^{-1}$) in the mixing enclosures, measured once at the end of the experiment. In the nonmixing enclosures we expected mixing intensity to vary over time (depending on water and air temperatures) and therefore performed several tracer measurements during the course of the experiment. To avoid interference with the experiment we performed these measurements in separate, nonmixed enclosures (one per enclosure depth). Mixing intensities in these additional nonmixing enclosures ranged from $0.02 \text{ m}^2 \text{ d}^{-1}$ ($= 2.3 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$, during daytime on a sunny day) to $3.2 \text{ m}^2 \text{ d}^{-1}$ ($= 3.7 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$, in the

morning hours of a cold night) during the first 35 d. Because measurements of mixing intensities were only taken sporadically, we used the continuous temperature recordings to estimate the occurrence of nightly convective mixing events. When early morning water temperatures at the surface of the nonmixing enclosures were lower than the water temperature in the surrounding, well-mixed outside bag, we took this as evidence of nightly convective mixing events. Two such (very short) events were recorded in the mornings of days 25 and day 34, but became increasingly common after day 35. This was corroborated by our turbulence measurements, which showed a complete convective mixing up to a 4-m water depth with a corresponding diffusivity constant higher than $17.5 \text{ m}^2 \text{ d}^{-1}$ ($= 2.0 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$) on day 56. The measured constants of diffusivity cover the full range observed in natural systems from about $0.01 \text{ m}^2 \text{ d}^{-1}$ ($\sim 10^{-7} \text{ m}^2 \text{ s}^{-1}$) in stratified systems up to $1000 \text{ m}^2 \text{ d}^{-1}$ ($\sim 10^{-2} \text{ m}^2 \text{ s}^{-1}$) in highly mixed systems (MacIntyre et al. 1999; Peeters et al. 2007).

Sampling program and laboratory analyses—Three times during the experiment we measured vertical profiles of photosynthetic active radiation (PAR) in 1-m steps with a spherical quantum sensor (LI-193SA, Licor). Once per week all enclosures were sampled for physical, chemical, and biological parameters. In vertical steps of 1 m, we measured water temperature and electrical conductivity (Lf 191 with probe LT1/T, Wissenschaftlich-Technische Werkstätten GmbH). In the mixing enclosures we sampled water at a depth of 0.5 m just after a mixing event. In the nonmixing enclosures we sampled water from the depths of 0.5 m, 2.0 m, 3.5 m, 5.0 m, 7.5 m, and 11.5 m (where available) with a hand pump that did not disrupt the vertical structure of the water column. Water samples were analyzed within a few hours after sampling. The concentration of dissolved inorganic phosphorus (SRP) was measured using standard methods (Wetzel and Likens 1991). Seston was filtered on pre-combusted acid-washed glass fiber filters (Whatman GF/F) to determine particulate organic carbon (POC) with an elemental analyzer (EA 1110 CHNS, CE Instruments) and particulate phosphorus (PP) by sulphuric acid digestion followed by molybdate reaction. Chlorophyll a (Chl a) concentrations were determined *in vivo* with a fluorometer (TD 700, Turner Design).

Phytoplankton samples were immediately preserved with acidic Lugol's iodine and later counted in an inverted microscope. In each sample we counted at least 100 individual cells from every abundant taxon, and we measured 20–50 individual cells using a digital image analysis system. Length measurements were converted to biovolume using appropriate geometrical forms.

To estimate sedimentation loss rates of phytoplankton, we suspended sedimentation traps just above the bottom of each enclosure. Each trap was a screw-lock glass jar (depth, 90 mm; opening diameter, 34 mm) with its locks removed. We replaced the traps weekly and filtered the contents on pre-combusted glass fiber filters (GF6, Schleicher & Schüll). Sedimented POC was determined by infrared-spectrophotometry (C-Mat 500, Stöhlein).

Depth-specific primary production assay—To examine possible adaptations of the phytoplankton communities to the vertical light gradient, we performed a primary production assay in the two 12-m nonmixing enclosures on 01 September 2005 (day 30). To this end we took water from 0.5-m, 2.0-m, and 5.0-m water depths (depths of origin) and incubated them in a reciprocal transplant design in culture flasks at 0.5-m, 2.0-m, and 5.0-m water depths (depths of incubation) with ^{14}C -marked sodium bicarbonate ($\text{NaH}^{14}\text{CO}_3$). Soluble reactive phosphorus (SRP) concentrations were similar at all depths ($\sim 2.5 \mu\text{g P L}^{-1}$), but Chl *a* concentrations differed slightly ($4.5 \mu\text{g Chl } a \text{ L}^{-1}$, $5.7 \mu\text{g Chl } a \text{ L}^{-1}$, and $3.4 \mu\text{g Chl } a \text{ L}^{-1}$ in the water originating from 0.5 m, 2.0 m, and 5.0 m, respectively). The incubation took place on a sunny day around noon and lasted for 2.5 h, with PAR intensities of $\sim 1600 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$, $40 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$, and $3.5 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ at incubation depths of 0.5 m, 2.0 m, and 5.0 m, respectively. Since we were only interested in relative differences in specific production, we incubated light bottles from each depth of origin in duplicate at each depth of incubation and used no dark bottles. We present data as decays per minute (DPM) per Chl *a* as a relative measure of the specific production of the algal community during the incubation.

Data processing and statistics—For all comparisons of nonmixing with mixing treatments, we calculated depth-averaged values for the nonmixing enclosures by linearly interpolating between samples at different water depths.

As a measurement of algal diversity we calculated a biomass-based version of the Shannon-Wiener index (H) as

$$H = - \sum_i^n \frac{B_i}{B_{\text{sum}}} \log_2 \left(\frac{B_i}{B_{\text{sum}}} \right) \quad (1)$$

where B_i is the biovolume of algal taxon i , B_{sum} is the biovolume of the entire algal community, and n is the number of algal taxa. For nonmixing enclosures we calculated H based on the depth-integrated total algal biovolume per enclosure.

From our weekly measurements of sedimented POC and the concurrent changes in water-column POC, we calculated the specific sedimentation loss rate, l_s , of seston POC in each enclosure over weekly intervals as described in (Visser et al. 1996). These calculations assume that specific primary production and l_s were constant over the weekly intervals and that sedimentation was the only significant loss process besides respiration. We calculated mean l_s during the first 35 d as the average of the weekly sedimentation rates of week 1 to week 5.

We analyzed effects of enclosure depth (z_{max}) and mixing intensity (mixis) on depth-averaged values on day 7, day 14, day 21, day 28, and day 35 with repeated-measures ANOVA, where sampling dates are the repeated measures. To detect vertical gradients within the nonmixing enclosures of a given water-column depth, we performed repeated-measures ANOVA on the two replicates, using sampling depth within each enclosure as the repeated measure. Percentages were arcsine transformed (Sokal and

Rohlf 1981) and we log-transformed all biovolume data to improve homogeneity of variances. The effects of enclosure depth and mixing intensity on the heights of transient algal biomass peaks and on seston sedimentation rates were examined by two-way ANOVA. Two-way ANOVA was also used to analyze effects of incubation depth and depth of origin in the primary production assay.

Mesozooplankton—To monitor the occurrence of (unwanted) crustacean zooplankton, we sampled the mixing enclosures by means of vertical hauls with a 250- μm mesh net on day 36, day 49, and day 56. To minimize disturbance of the vertical water-column structure, we sampled the nonmixing enclosures only at the end of the experiment (day 56). On day 36 and day 49, crustacean zooplankton densities were below 0.1 individuals (ind.) L^{-1} in all mixing enclosures. At the end of the experiment crustacean zooplankton densities were still far below 0.1 ind. L^{-1} in all enclosures, except for one 12-m nonmixing enclosure (0.37 ind. L^{-1}) and one 4-m mixing enclosure (0.12 ind. L^{-1}). Hence grazing pressure of crustacean zooplankton on phytoplankton was negligible during the experiment.

Results

Effects of water-column depth and mixing on phytoplankton and nutrients—In spite of the initial fertilization, depth-averaged algal biovolume (Fig. 1, Table 1a) showed only minor changes during the first 14 d. Subsequently algal biovolume increased to a peak followed by a decrease in all enclosures except for one 12-m mixing enclosure where algal biomass increased until day 35 (Fig. 1; Table 1a: Time). In the mixing enclosures the time needed to reach the peak increased with increasing enclosure depth, whereas in the nonmixing enclosures the timing of the peak seemed to be less dependent on enclosure depth (Fig. 1; Table 1a: Time $\times z_{\text{max}} \times \text{mixis}$). Averaged over the entire 35-d period, algal biovolume decreased with increasing enclosure depth, but showed no clear difference between the mixing treatments (Fig. 1; Table 1a: z_{max}). The latter was also true for peak biovolume, which was negatively affected by water-column depth but unaffected by the mixing treatment (ANOVA, z_{max} : $p = 0.006$; ANOVA, mixis: $p = 0.14$; ANOVA, $z_{\text{max}} \times \text{mixis}$: $p = 0.54$).

Mixing intensity in the nonmixing enclosures was sufficiently low to allow the establishment of vertical gradients in phytoplankton biomass (Figs. 1, 2). Not surprisingly, these gradients were most distinct in the 8-m and 12-m enclosures, weakly expressed in the 4 m enclosures, and almost absent from the 2-m enclosures. This pattern was probably related to the steep, vertical light gradient yielding an estimated compensation depth of only 3.7 m. Algal production should thus have been very low at depths >4 m, promoting the establishment of vertical biomass gradients in the 8-m and 12-m enclosures.

A statistically significant vertical heterogeneity of algal biovolume had already developed on day 7 in several of the deeper nonmixing enclosures (Fig. 1). Vertical profiles were, however, only weakly expressed on days 7–14, when

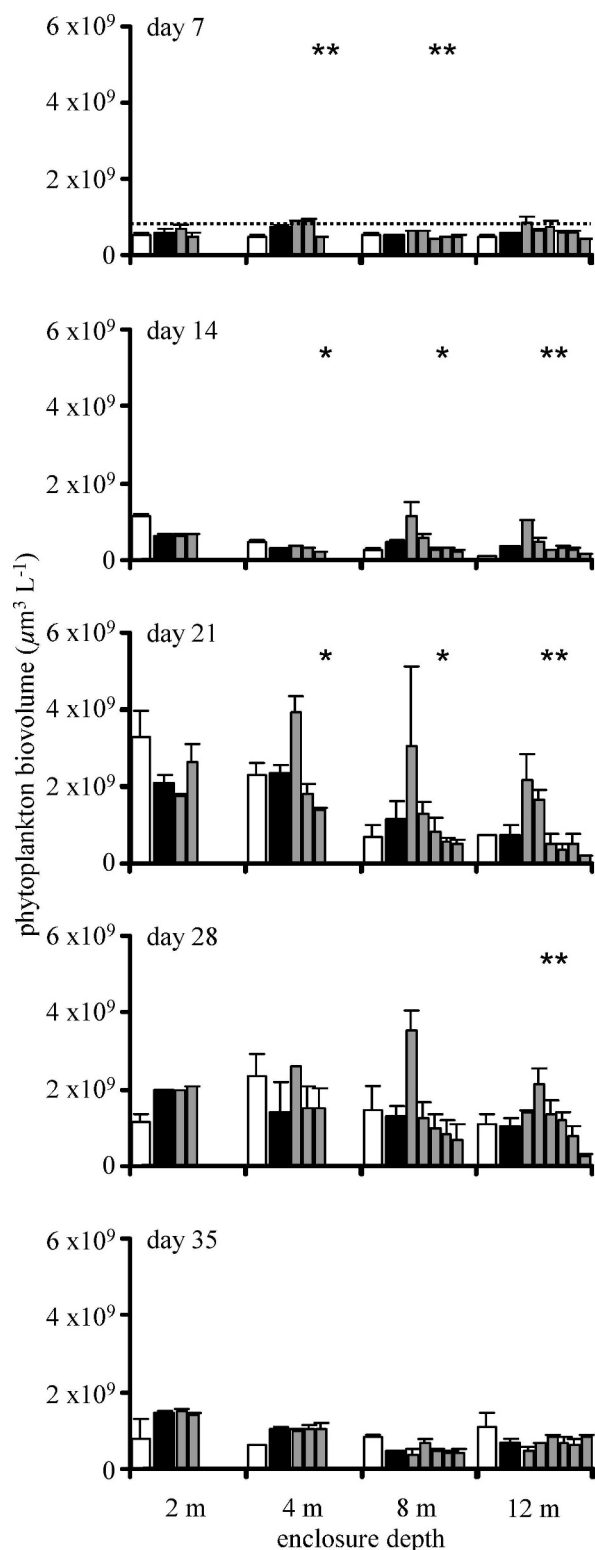


Fig. 1. Effects of enclosure depth and mixing intensity on algal biovolume on days 7–35. White and black bars show depth-averaged values (white = mixing; black = nonmixing). The vertical profiles in nonmixing enclosures are shown as thin gray bars at 0.5 m, 2.0 m, 3.5 m, 5.0 m, 7.5 m, and 11.5 m where present. Shown are means +1 SE. Asterisks indicate that vertical profiles were nonuniform as determined by repeated-measures ANOVAs of the homogeneity of the vertical profile: *** $p < 0.001$; ** $p <$

algal biomass had not yet increased. Vertical profiles of algal biomass were much steeper in the 4–12-m enclosures on days 21–28, when most enclosures had reached their depth-averaged algal biovolume peaks. When vertical profiles were present the concentration of algal biovolume was, in most cases, highest near the surface and, in a few cases, at the 2-m water depth (Fig. 1). On day 35 no clear vertical profile could no longer be seen, which may be related to the nightly convective mixing event on day 34.

We categorized phytoplankton into motile taxa (flagellates) and nonmotile taxa (all other taxa). Motile taxa consisted mostly of *Carteria* sp., *Chlamydomonas* sp., *Cryptomonas* spp., *Rhodomonas* sp., *Dinobryon* spp., *Mallomonas* sp., and *Gymnodinium* sp. Averaged over the entire 35-d period there was a clear, positive effect of reduced mixing intensity on the proportion of motile taxa (Fig. 2; Table 1b: mixis). In contrast, the effect of enclosure depth on the proportion of motile taxa was time dependent and mixis dependent. Seven days after the start of the experiment, the proportional contribution of motile taxa to total (depth-integrated) algal biovolume had already increased in the nonmixing enclosures, while no such increase was observed in the mixing enclosures throughout the entire experiment (Fig. 2; Table 1b: Time × mixis). In the 2-m nonmixing enclosures the proportion of motile taxa peaked on day 7 and was higher than in the mixing treatment until day 14; in contrast, in most of the deeper, nonmixing enclosures the proportion of motile taxa peaked on day 14 and remained higher than in the mixing treatments until day 28 (Fig. 2; Table 1b: Time × z_{\max} × mixis). On day 35, after the first convective mixing events, only one 8-m nonmixing enclosure still showed an elevated proportion of motile algae. Within the water column the proportion of motile taxa tended to decrease with increasing water depth in all nonmixing enclosures throughout the entire experiment; this pattern was statistically significant in the 8-m and 12-m enclosures, where the proportion of motile taxa in the upper strata was usually at least two times as high as in the deepest ones. Also, motile taxa dominated algal biomass in the uppermost layer (0.5 m) of all nonmixing treatments that had a water-column depth ≥ 4 m throughout the entire experiment (Figs. 1, 2).

We classified nonmotile taxa further into centric diatoms (mostly *Cyclotella* spp.), pennate diatoms (mostly single-celled *Fragillaria* sp. and *Synedra* sp.), non-flagellated chlorophytes (mostly *Ankistrodesmus* sp., *Coenochloris* sp., *Elakatothrix* sp., *Oocystis* sp., and *Scenedesmus* sp.), and cyanobacteria (mostly *Anabaena* sp., *Chroococcus* sp., and *Stigonema* sp.). At the beginning of the experiment, nonmotile chlorophytes, centric diatoms and motile taxa contributed with approximately 30%, 40%, and 30%, respectively, to total phytoplankton biovolume, whereas pennate diatoms were almost absent. In addition to the

←

0.01; * $p < 0.05$. The dashed line in the upper panel indicates the starting concentration. One replicate of the 4-m nonmixing enclosures at 0.5 m is missing on day 28.

Table 1. p values of repeated-measures ANOVA of the effects of water-column depth (z_{\max}) and mixing intensity (mixis) on the depth-averaged response variables phytoplankton biovolume, proportion by biovolume of motile taxa, Shannon-Wiener index (H), soluble reactive phosphorus (SRP) concentration and seston C:P.

Factor	df	(a) biovolume	(b) prop. motile	(c) H	(d) SRP	(e) C:P ratio
z_{\max}	3,8	0.002	0.060	0.279	0.000	0.000
Mixis	1,8	0.339	0.001	0.001	0.001	0.121
$z_{\max} \times \text{mixis}$	3,8	0.769	0.135	0.040	0.044	0.024
Time	4,5	0.000	0.004	0.000	0.000	0.000
Time $\times z_{\max}$	12,21	0.014	0.024	0.137	0.160	0.197
Time $\times \text{mixis}$	4,5	0.896	0.015	0.181	0.002	0.173
Time $\times z_{\max} \times \text{mixis}$	12,21	0.030	0.008	0.129	0.095	0.160

increase of motile taxa in the nonmixing enclosures, the main successional pattern was an almost complete disappearance of centric diatoms and an increasing dominance of pennate diatoms in all enclosures (Fig. 3). In all mixing enclosures and in the 2-m nonmixing enclosures pennate diatoms became the dominant group from day 21 onward; in the deeper, nonmixing enclosures, pennate diatoms replaced flagellates as the dominant group on day 35. Cyanobacteria contributed <1% to total biomass throughout the experiment (Fig. 3).

Algal diversity as measured by the Shannon-Wiener index was positively related to the occurrence of motile taxa. With the exception of the 2-m enclosures (where motile taxa had already declined on day 21), diversity was therefore higher in the nonmixing than in the mixing enclosures on days 7–28 (Fig. 4; Table 1c: Mixis, $z_{\max} \times \text{mixis}$). On day 35, when the proportion of motile taxa had declined in almost all nonmixing enclosures, there were no longer any clear differences in diversity between the nonmixing and mixing treatments.

Although algal biomass did not immediately respond to the initial fertilization, much of the added P was taken up by the algal community already in the first week, especially in shallow enclosures. Consequently, the depth-averaged SRP concentration was positively related to enclosure depth on day 7 (Fig. 5). This pattern was subsequently weakened in the mixing enclosures but accentuated in the nonmixing enclosures (Fig. 5; Table 1d: z_{\max} , $z_{\max} \times \text{mixis}$). In the deeper, nonmixing enclosures increasing concentrations of SRP remained unused at water depths >5 m (where light was presumably insufficient to support net algal growth), resulting in a distinct, vertically increasing SRP gradient in the 8-m enclosures (days 14–21) and in the 12-m enclosures (days 21–35; Fig. 5). (The reversed vertical gradient in the 12-m enclosures on days 7–14 was an artifact of insufficient vertical mixing after the initial addition of the fertilizer.) In the 12-m enclosures, deep water SRP concentrations eventually exceeded initial concentrations, suggesting that remineralized P (originating from sedimented algae) was accumulating. In contrast, in the mixing enclosures remineralized P was constantly mixed to the surface where it could be utilized by the phytoplankton community. Consequently, SRP concentrations were generally lower in mixing than in nonmixing

enclosures throughout the latter half of the experiment (Fig. 5; Table 1d: Time $\times \text{mixis}$).

Corresponding to the high phosphorus uptake following fertilization, depth-averaged seston C:P ratios were low on day 7 and subsequently increased over time, particularly in the shallowest enclosures (Fig. 6; Table 1e: Time). In parallel with the light gradient, the seston C:P ratio decreased with increasing enclosure depth on days 7–35, indicating a higher algal production at shallower enclosure depth (Fig. 6; Table 1e: z_{\max}). Compared to the mixing enclosures, depth-averaged C:P ratios in the nonmixing enclosures were lower at shallower enclosure depths and slightly higher at deeper enclosure depths (Fig. 6; Table 1e: $z_{\max} \times \text{mixis}$). The seston C:P ratio did not show any strong or consistent vertical gradients in the nonmixing enclosures on any of the sampling dates.

Sedimentation losses—As expected, the specific sedimentation loss rate of seston POC (averaged over days 0–35) decreased with increasing enclosure depth in both mixing and nonmixing enclosures (Fig. 7; ANOVA, effects of z_{\max} : $p < 0.001$). Congruent with the higher proportion of motile, nonsinking taxa in the nonmixing enclosures, sedimentation rates were lower in nonmixing than in mixing enclosures, except for the deepest enclosures (ANOVA, effects of mixis: $p < 0.001$, ANOVA, $z_{\max} \times \text{mixis}$: $p < 0.001$). Fitting the mechanistic equation for specific sedimentation rate in well-mixed systems, $l_s = v/z_{\max}$ (where v is sinking velocity and z_{\max} is enclosure depth; Reynolds et al. 1984), to the data of the mixing enclosures yielded estimated average seston sinking velocities of 0.32 m d^{-1} ($R^2 = 0.99$, $p = 0.000$).

Depth-specific primary production assay—Specific carbon incorporation of “high light” and “intermediate light” phytoplankton communities (originating from 0.5-m and 2.0-m water depth, respectively) decreased strongly with incubation depth, almost in parallel with the decreasing light intensity; in contrast, carbon incorporation of the “low light” community (originating from 5.0-m water depth) was much less dependent on incubation depth (Fig. 8; ANOVA, incubation depth: $p = 0.001$, ANOVA, depth of origin: $p = 0.021$, ANOVA, interaction: $p = 0.063$). The high light community

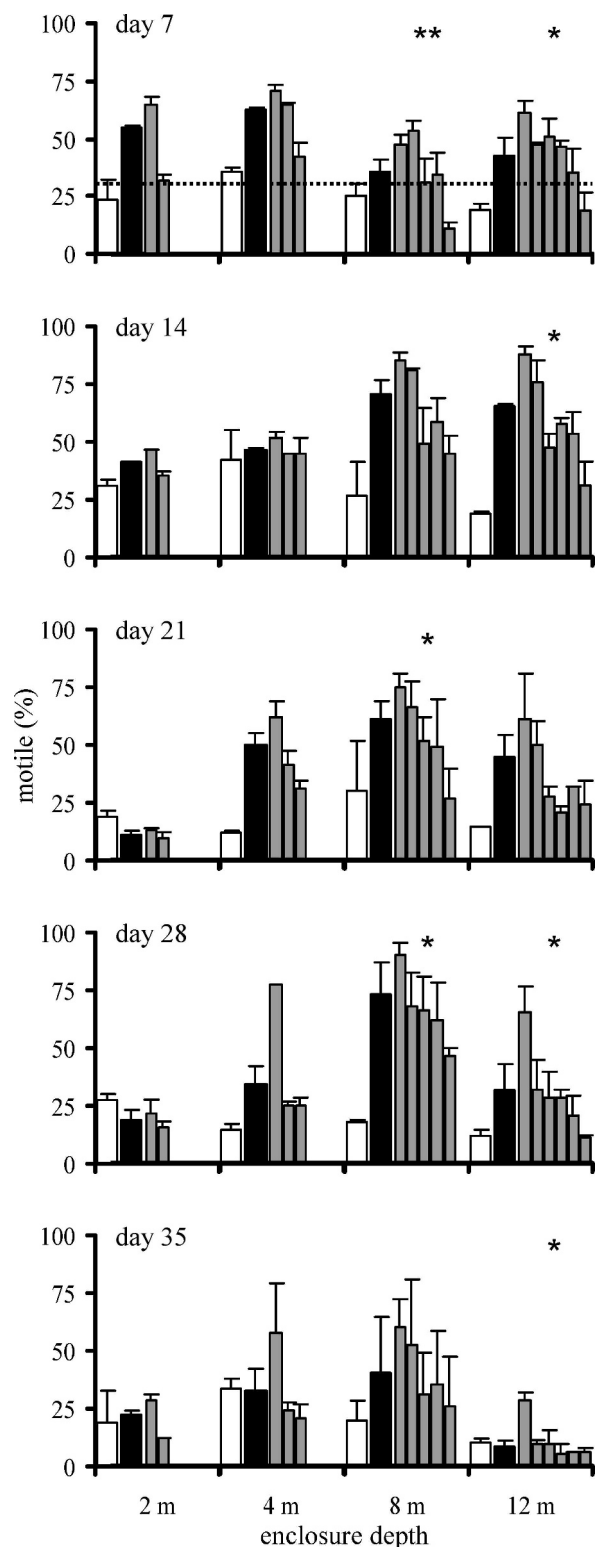


Fig. 2. Effects of enclosure depth and mixing intensity on the proportional contribution of motile taxa (flagellates) to total algal biovolume on days 7–35. White and black bars show depth-averaged values (white = mixing; black = nonmixing). The vertical profiles in nonmixing enclosures are shown as thin gray bars at 0.5 m, 2.0 m, 3.5 m, 5.0 m, 7.5 m, and 11.5 m where present. Shown are means +1 SE. Asterisks indicate that vertical profiles were nonuniform as determined by repeated-measures

(from 0.5-m depth of origin) showed the highest carbon incorporation at a 0.5-m incubation depth, whereas the low light community (from 5.0-m depth of origin) showed the highest carbon incorporation at a 5.0-m incubation depth, suggesting that the communities were adapted to the respective light climate at their depth of origin. The observed differences in light-dependent performance of high light and low light communities may have been related to differences in taxonomic composition: The phytoplankton biomass of high light communities was dominated by 65% motile taxa, whereas the biomass of low light communities was dominated by 70% pennate diatoms.

Discussion

Algal biomass responses in mixing vs. nonmixing enclosures—After an initial lag phase of 7–14 d, which coincided with a major change in taxonomic composition, phytoplankton in both mixing and nonmixing treatments responded to the initial nutrient pulse with a transient increase in (depth-averaged) biomass, the initial increase being highest in either the 2-m or 4-m enclosures. In the mixing enclosures the resulting transient phytoplankton peak was reached the earlier the shallower the water column. Both results conform to theoretical expectations: First, the time until a transient biomass peak is reached is expected to follow the inverse of algal growth rate and, consequently, should increase with increasing light limitation and, thus, with increasing water-column depth (Jäger et al. 2008); second, the height of a transient biomass peak should be limited by high sinking losses in very shallow (<2 m) water columns and by low light availability in deeper water columns, and therefore be highest at intermediate water-column depths, which, under the prevailing conditions of high background turbidity and high initial nutrient availability, should span the approximate range of 2–5 m (Diehl et al. 2005; Jäger et al. 2008). While the transient nature of the phytoplankton peak in this experiment was likely a consequence of nutrient depletion caused by sedimentation losses (Huppert et al. 2002), similar observations have been made in well-mixed water columns in the presence of grazers, where the phytoplankton decline was a consequence of grazing from an increasing herbivore population (Berger et al. 2007; Jäger et al. 2008).

In contrast to the mixing enclosures, the timing of the transient phytoplankton peak was only weakly related to water-column depth in the nonmixing enclosures. The latter developed steep vertical biomass gradients early on. Most algae contributing to the biomass peak in the nonmixing treatments had therefore been growing in the

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ANOVAs of the homogeneity of the vertical profile: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. The dashed line in the upper panel indicates the starting proportional contribution. One replicate of the 4-m nonmixing enclosures at 0.5 m is missing on day 28.

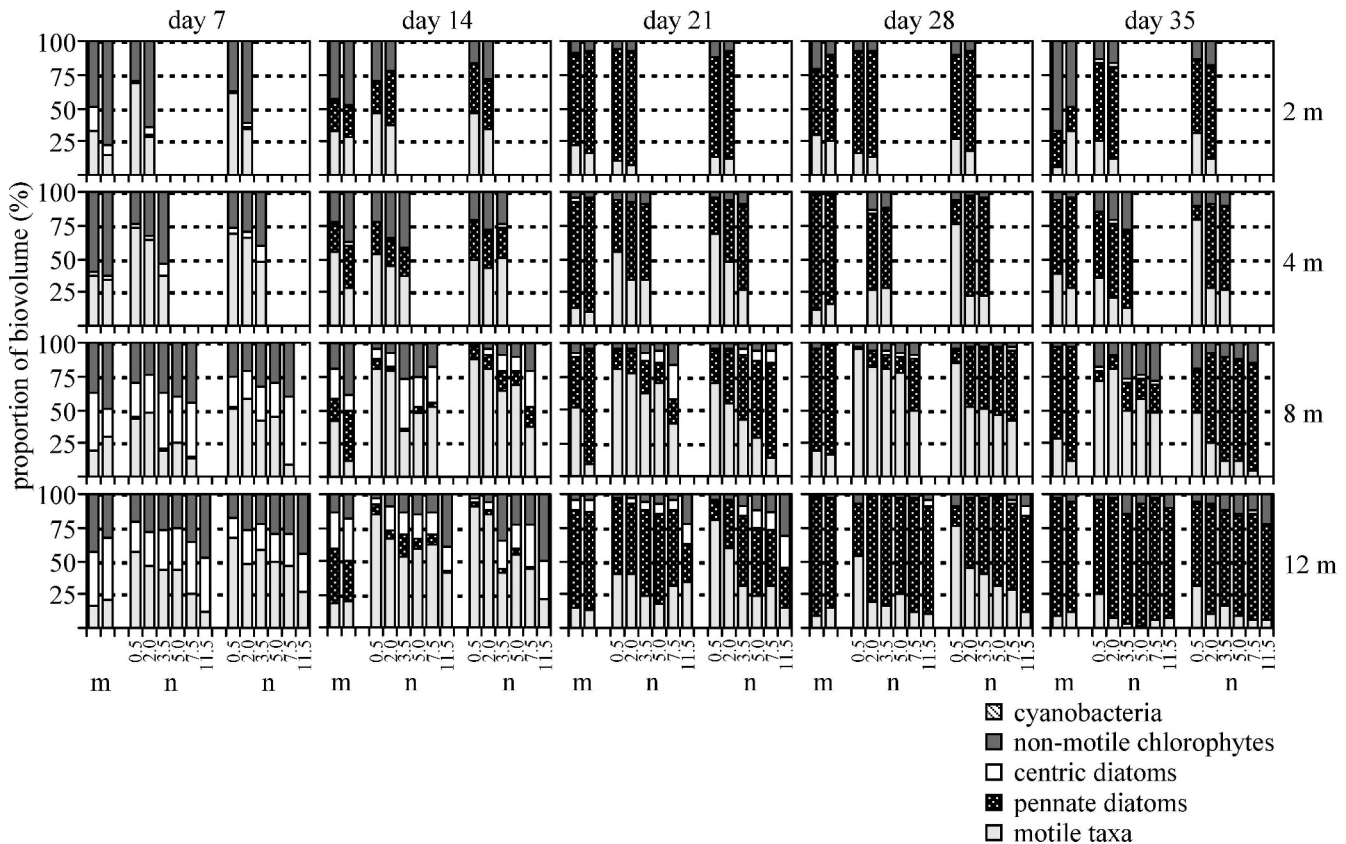


Fig. 3. Proportional contributions of different phytoplankton taxa (*see* legend) to total phytoplankton biovolume on days 7–35. The panels are organized in rows according to total water-column depth (indicated to the right) and in columns according to the date. Within each panel, the two bars to the left (marked by “m” at the bottom) are the two mixing enclosures. The remaining bars indicate the different depth strata (0.5 m, 2.0 m, 3.5 m, 5.0 m, 7.5 m, and 11.5 m, as indicated at the bottom) of the two nonmixing enclosures (marked by “n” at the bottom). One replicate of the 4-m nonmixing enclosures at 0.5-m is missing on day 28.

well-lit surface layer where initial growth rates were probably largely independent of total water-column depth.

Patterns of succession and vertical segregation of functional algal groups—High initial phytoplankton production in shallow water columns was accompanied by a subsequent reduction in SRP and a concomitant increase in algal P limitation, as indicated by a decrease in depth-averaged SRP concentration and an increase in seston C:P with decreasing water-column depth in both mixing and nonmixing treatments. These trends were more strongly expressed in mixing than in nonmixing treatments, probably because phytoplankton in mixing enclosures experienced higher sinking losses, removing limiting nutrients from the water column at a faster rate. The latter was likely a consequence of contrasting successional patterns in mixing vs. nonmixing enclosures. While mixing treatments became quickly dominated by fast-sinking, pennate diatoms, algal biomass in nonmixing enclosures with a total depth ≥ 4 m was dominated by $\geq 50\%$ motile, nonsinking algae throughout most of the experiment.

The early dominance of pennate diatoms in the mixing enclosures was likely related to their competitive abilities. Strong vertical mixing prevents spatial niche differentia-

tion, and, under constant environmental conditions, those taxa that reduce light in the water column to the lowest level and the limiting nutrient to the lowest concentration will displace all other competitors (Sommer 1985; Huisman and Weissing 1995; Passarge et al. 2006). Pennate diatoms are superior competitors for phosphorus if silicon is available in excess (Smith and Kalff 1983; Sommer 1985; Grover 1997), and they can become a dominant group under low light intensities (Litchman 1998; Flöder et al. 2002). Both environmental conditions were met in our experiment, at least until day 28 (*see* below). Thus the dominance of pennate diatoms in the mixing enclosures from day 21 onward (when P had become limiting) was not unexpected and was in good accordance with previous enclosure experiments in Lake Brunnsee (Ptacnik et al. 2003).

In spite of their high sinking velocities, pennate diatoms became dominant even in the shallowest (the 2-m) mixing treatments. This contrasts with the experimental results of Reynolds et al. (1983, 1984), who found that fast-sinking diatoms were replaced by buoyant and motile taxa when the depth of (artificial) mixing fell below 2 m. Reynolds et al. (1983, 1984) used stratified enclosures with a deep water layer, where sinking removed algae permanently from the mixed surface layer. In contrast, sedimented algae in our 2-

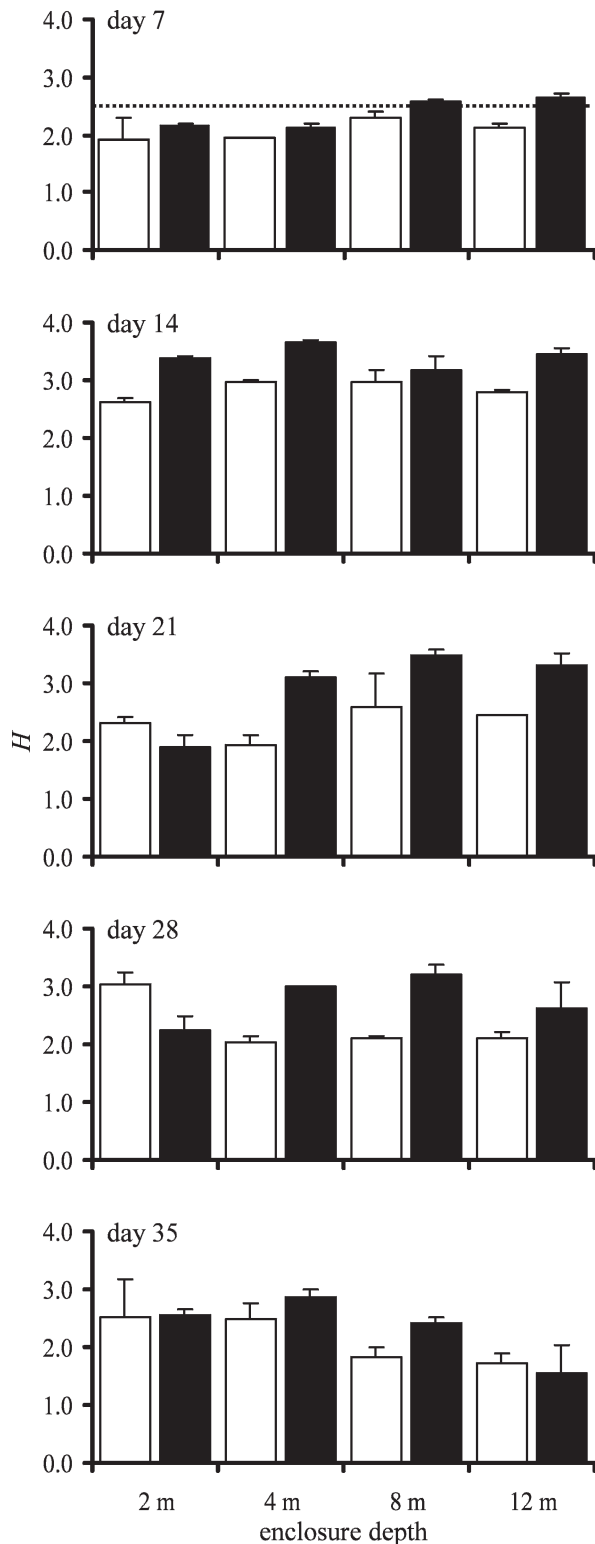


Fig. 4. Effects of enclosure depth and mixing intensity on taxonomic diversity of depth-averaged algal communities as calculated by the Shannon-Wiener index (H) on days 7–35 (white = mixing; black = nonmixing). Shown are means +1 SE. The dashed line in the upper panel indicates the starting taxonomic diversity.

m mixing enclosures accumulated at the enclosure bottom, where light levels were still sufficient to support algal growth and where artificial mixing may have produced some resuspension. Still, on the final day of the experiment (day 35), the proportional contribution of pennate diatoms to total algal biovolume increased with increasing water-column depth in the mixing enclosures (linear regression of the arcsine square-root-transformed proportion of pennate diatoms vs. enclosure depth: $p = 0.005$, $R^2 = 0.77$, $n = 8$), suggesting a measurable competitive disadvantage for these fast-sinking algae at the most shallow depths (see Ptacnik et al. 2003 for a similar result). This competitive disadvantage of diatoms was probably not only a consequence of high sinking losses. Silicon was available in excess (2.6 mg L^{-1}) at the beginning of the experiment, but decreased with increasing dominance of diatoms. With the exception of one 2-m mixing enclosure on day 21, molar dissolved mineral Si:P ratios were always >50 before day 28. Consequently, relative to phosphorus, silicon supply was sufficient to not limit diatom growth (Sommer 1985). On day 28, the mineral Si:P ratio dropped below 30 in the 2-m and 4-m mixing enclosures and in the 2-m nonmixing enclosures. Thus pennate diatoms were likely to have suffered from increasing silicon limitation in the shallow enclosures toward the end of the experiment.

Reduced turbulence has been suggested to give buoyant plankton taxa a competitive advantage over sinking taxa (Visser et al. 1996; Huisman et al. 2004), and several authors have proposed that reduced turbulence may favor vertical niche separation (Elliott et al. 2002; Clegg et al. 2007). Our data support both hypotheses. Motile taxa became quickly dominant in all nonmixing treatments and remained so in water columns with a total depth ≥ 4 m until day 28. The dominance of motile taxa in the nonmixing treatments was accompanied by a pronounced vertical structure in water columns ≥ 4 m, with higher phytoplankton biomass and higher proportions of motile taxa in the well-lit, uppermost strata, and higher proportions of pennate diatoms and higher concentrations of SRP in the deeper, darker strata. As a result of this vertical separation of taxa phytoplankton diversity was higher in nonmixing enclosures than in mixing enclosures with a total depth ≥ 4 m, suggesting that reduced turbulence provided opportunities for vertical niche separation. The “primary production assay” did indeed suggest local depth adaptation of the algal community in nonmixing enclosures. Water samples originating from 0.5 m and 5 m, respectively, performed best when incubated at their depths of origin.

The dominance of pennate diatoms in the deeper layers of nonmixing enclosures was probably related to their high sinking velocities (Ptacnik et al. 2003) and their tolerance for low-light conditions (Litchman 1998; Flöder et al. 2002). In contrast, under the prevailing conditions of low turbulence, motile species should have been able to actively move along opposing vertical gradients of light and nutrient availability to a depth where their growth was maximized (Klausmeier and Litchman 2001). Given the high background turbidity and the relatively weak vertical SRP gradients in the euphotic zone (0–4 m), the depth of

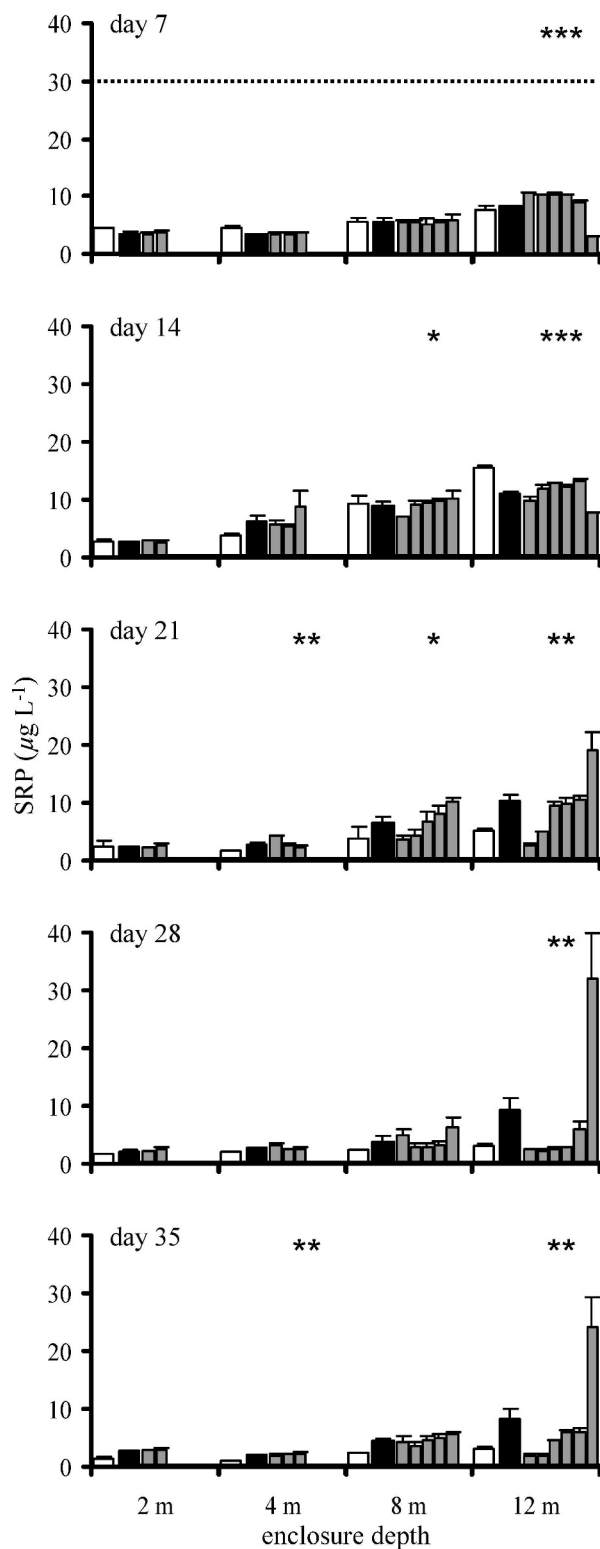


Fig. 5. Effects of enclosure depth and mixing intensity on soluble reactive phosphorus (SRP) concentrations on days 7–35. White and black bars show depth-averaged values (white = mixing; black = nonmixing). The vertical profiles in nonmixing enclosures are shown as thin gray bars at 0.5 m, 2.0 m, 3.5 m, 5.0 m, 7.5 m, and 11.5 m where present. Shown are means ± 1 SE. Asterisks indicate that vertical profiles were nonuniform as

maximal production should have been close to the surface throughout the experiment, which conforms with the observation that the biomass of motile taxa was always highest in the uppermost layer of the nonmixing enclosures (Figs. 1, 2).

In spite of their long-lasting dominance, motile taxa were eventually also replaced by pennate diatoms in nonmixing enclosures. There are at least two nonexclusive explanations for this shift. First, pennate diatoms already dominant in deeper layers may have intercepted the upward transport of recycled nutrients from the sediment to shallow strata. As nutrients from the initial fertilization pulse became increasingly depleted near the surface, motile species may therefore have been outcompeted by pennate diatoms. Second, turbulence gradually increased in the nonmixing enclosures, and weak nightly mixing events such as the ones recorded on days 25 and day 34 may have eroded the competitive advantage of motile species.

Both of the above mechanisms may also explain the relatively early shift towards pennate diatoms in the 2-m nonmixing enclosures, which experienced phosphorus depletion fairly early and should have been most strongly affected by nightly mixing events. The latter can be estimated from the Peclet number $Pe = v z_{\text{max}} D^{-1}$, which describes the relative importance of the transports by sedimentation vs. turbulent mixing based on algal sinking velocity v , water-column depth z_{max} , and the coefficient of vertical diffusion D . Specifically, $Pe \ll 1$ implies that transport by turbulent mixing dominates over sedimentation losses (Peeters et al. 2007). In a similar experiment we observed sinking velocities of pennate diatoms ranging from 0.5 m d^{-1} to 0.9 m d^{-1} (Ptacnik et al. 2003) and our sporadic turbulence measurements indicated that nighttime mixing intensities were $>3 \text{ m}^2 \text{ d}^{-1}$ during cold nights. Based on these numbers, Pe should have been at least occasionally <1 in the 2-m nonmixing enclosures but always >1 in all other nonmixing enclosures during the 35 d of our experiment, suggesting that nightly convective mixing events should have been sufficiently strong to favor pennate diatoms only in the shallowest nonmixing treatments.

Seston C:P ratios—In agreement with theoretical expectations and with earlier experiments (Diehl et al. 2002; Diehl et al. 2005) we observed a strong negative influence of water-column depth on the depth-averaged seston C:P ratio. In accordance with field observations (Sterner et al. 1997) this result paralleled a similar trend in the supply ratio of depth-averaged light intensity vs. depth-averaged SRP concentration. Interestingly, the negative effect of water-column depth on depth-averaged seston C:P was much more strongly expressed in mixing enclosures than in nonmixing enclosures. Moreover, and in spite of the strong and opposing vertical light and nutrient gradients, there were no consistent indications of a

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determined by repeated-measures ANOVAs of the homogeneity of the vertical profile: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. The dashed line in the upper panel indicates the starting concentration.

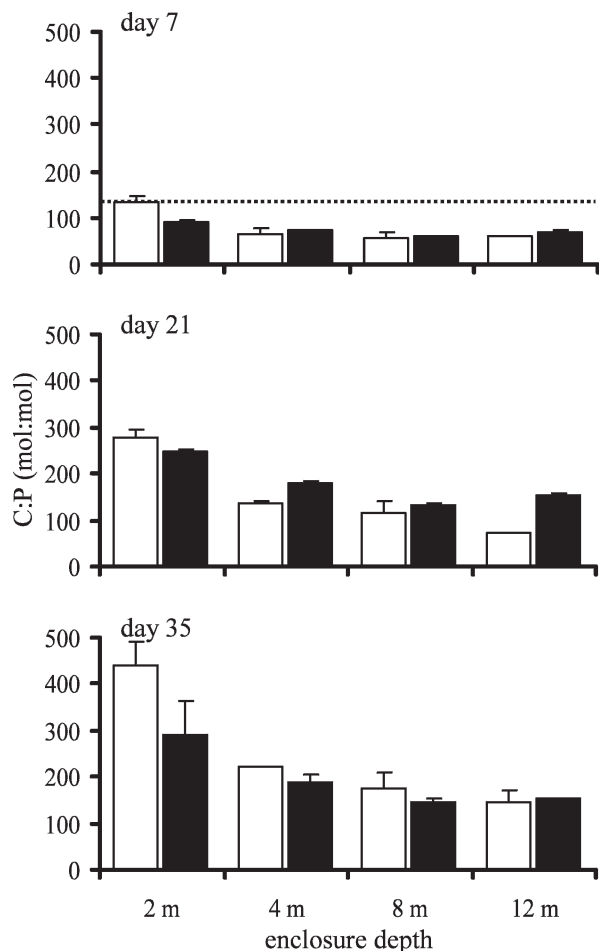


Fig. 6. Effects of enclosure depth and mixing intensity on depth averaged seston C:P ratios on day 7, day 21, and day 35 (white = mixing; black = nonmixing). Shown are means \pm 1 SE. The dashed line in the upper panel indicates the starting seston C:P ratio. Vertical profiles in the nonmixing enclosures were very weak and not statistically significant. Because the effects of z_{\max} and mixing were similar on all days the data from day 14 and day 28 are not shown.

vertical gradient in seston C:P ratio within the nonmixing enclosures.

The latter two results are largely a consequence of the relatively low seston C:P ratios in nonmixing high light environments (i.e., in 2-m enclosures and in the upper layers of deeper enclosures), and we propose that they may have been related to the high proportion of motile taxa in the nonmixing enclosures. Occasional sampling of the diurnal vertical distribution of phytoplankton in several of the nonmixing enclosures indicated that motile taxa stayed close to the well-lit surface during daytime but moved towards deeper strata with higher SRP concentrations at nighttime (Schmidt 2006). The latter suggests that motile taxa residing in shallow strata during the day could have balanced increased C fixation by increased P uptake at night. Most of the flagellates included in our category of motile taxa are furthermore known to be mixotrophic. A recent study (Katechakis et al. 2005) has shown that mixotrophic flagellates maintained relatively low and

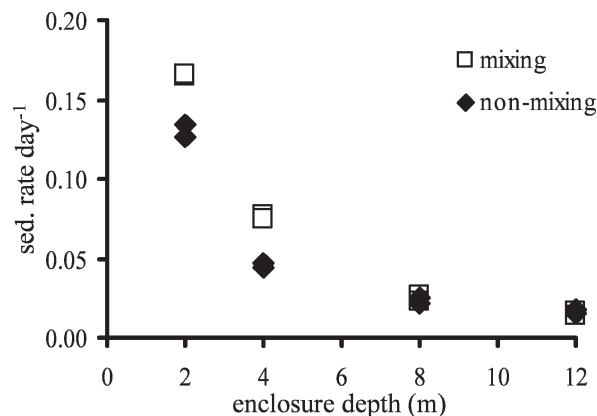


Fig. 7. Effects of enclosure depth and mixing intensity on the specific sedimentation rate averaged over days 0–35.

almost invariant cellular C:P ratios when exposed to a large gradient of light:P supply regimes, possibly because they could balance increased C fixation at high light levels by uptake of particulate P in the form of bacteria, which are known to be rich in P (Vadstein 2000). Our hypothesis that limited variability in seston C:P in the nonmixing enclosures was related to high proportions of flagellates is supported by the fact that only the 2-m enclosures showed elevated C:P ratios and only after the proportion motile taxa there had dropped to similar levels as in the mixing enclosures.

General effects of turbulence—In our experiment, water-column depth had strong effects on phytoplankton biomass, seston C:P ratio, and dissolved nutrients. In contrast, mixing intensity had no clear effects on any of these (depth-integrated) variables, but strongly affected functional community composition (motile vs. sinking taxa) and taxonomic diversity. The latter suggests that different algal communities in different mixing treatments were equally well adapted to their respective mixing environments and were therefore

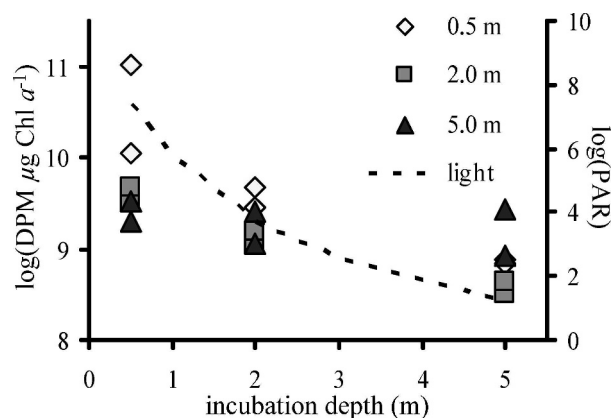


Fig. 8. Effects of incubation depth and depth of origin (shown in legend) on specific carbon incorporation in the primary production assay. Left axis shows the natural logarithm of decays per minute per $\mu\text{g Chl } a$. Right axis shows the natural logarithm of photosynthetic active radiation ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) during the incubation.

equally successful in transforming the available resources into biomass. Although the initial phosphorus fertilization created mesotrophic to eutrophic conditions, algal community development was constrained by the taxonomic composition of the starting community, which is typical for an oligotrophic lake. In naturally eutrophic or nitrogen-limited systems buoyant cyanobacteria rather than flagellates would be expected to become dominant in stratified water columns (Visser et al. 1996; Scheffer et al. 1997; Huisman et al. 2004). Under such conditions cyanobacteria are expected to form surface blooms, which strongly shade lower strata and therefore greatly diminish the possibility of coexistence for negatively buoyant species (Visser et al. 1996; Scheffer et al. 1997; Huisman et al. 2004). Similar to our experiment, increased vertical mixing can affect phytoplankton taxonomic composition also in eutrophic systems and move them from a dominance of surface-dwelling cyanobacteria to a dominance of green algae, with relatively minor effects on depth-integrated phytoplankton biomass (Huisman et al. 2004). The available empirical evidence thus suggests that mixing intensity primarily affects functional composition of the phytoplankton but not its biomass. This pattern is consistent with theoretical expectations for water columns of shallow to intermediate depth (Huisman et al. 2002). In very deep water columns phytoplankton biomass is, however, always expected to decrease at high mixing intensities, because algal motility and buoyancy regulation then cannot counteract downmixing to aphotic depths.

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