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Influence of vertical mixing on light-dependency of phytoplankton growth

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Running head: phytoplankton growth at vertical mixing

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Abstract

Phytoplankton growth depends not only on mean intensity but also on the dynamics of the light supply. In surface mixed layers, phytoplankton may rapidly move between strong light and almost darkness. The non-linear light-dependency of growth may differ between constant and fluctuating light because of the different frequency distribution of light and/or acclimation processes. The present study compares for the first time light-dependency of photosynthesis and growth of phytoplankton communities *in situ* under defined mixing conditions and at fixed depths. Maximum growth rates per day were not significantly different, but the growth efficiency was much higher under constant light than under fluctuating light of sub-saturating daily irradiance. Phytoplankton incubated under fluctuating light needed about 3 times higher mean daily irradiances to balance photosynthesis and losses than under constant light. The difference in growth efficiency was mostly caused by the different frequency distribution of underwater light, as was estimated by a photosynthesis model of sufficient temporal resolution. The present study indicates a considerable overestimation of phytoplankton growth at sub-saturating light in well-mixed water layers by the common growth measurements under constant light. This implies an underestimation of the compensation light intensities and respective overestimations of the critical mixing depths.

Introduction

Planktonic algae contribute about 46% to global biogenic carbon fixation and thus play a crucial role for the global CO_2 budget (Field et al. 1998). They provide a major carbon source to aquatic food webs, strongly influence the functioning of aquatic ecosystems and may impair the usability of surface waters. The growth rate of a given algae species depends mainly on temperature and supply of nutrients and photosynthetically available radiation (PAR). The PAR supply influences both the temperature dependency (Edwards et al. 2016) and the nutrient dependency of growth (Litchman et al. 2004). Compared to nutrients, light is a more dynamic resource. Seasonal and diurnal changes as well as cloud cover influence the irradiance at the water surface. In the water column, irradiance exponentially declines with increasing optical depth, which is the product of depth and vertical light attenuation. Surface layers or even whole water bodies are frequently mixed by wind stress or heat loss. Even moderate wind intensities suffice to generate circular, counter-rotating eddies (Langmuir cells), which are the rule rather than the exception in larger water bodies (Harris & Piccinin 1977).

Suspended algae experience light of fluctuating intensity during transport in the mixing layer (Kirk 1994). Photosynthesis and growth are non-linearly related to light. Therefore, they depend not only on the mean intensity but also on the frequency distribution of received light intensities (Litchman 2000). Phytoplankton spend parts of the day in darkness if the mixing depth exceeds the depth of the euphotic zone. The shortened effective daylength causes respective declines in growth rates (Shatwell et al. 2012). Saturating light intensities near the water surface allow for less carbon fixation per available photon than under sub-saturating light. Therefore, growth should be less efficient when the light supply fluctuates between very low

and saturating or even inhibiting intensities than when the light supply is constant and sub-saturating at the same mean intensity. This effect of non-linearity can be estimated by photosynthesis models of sufficient temporal resolution (e.g., Cianelli et al. 2004, Ross et al. 2011) if the vertical movement of the algal cells is known. The second type of factor influencing growth efficiency under turbulent mixing is more difficult to assess: Phytoplankton in mixing water columns may be imperfectly adapted to the instantaneous light conditions if changes in PAR outpace their capacity to acclimate. Phytoplankton in a turbulent surface layer is potentially forced to avoid light inhibition of its photosystems near the water surface. However, mechanisms that protect against strong light diminish the efficiency of photosynthesis and growth at low light (Mac Intyre et al. 2002). Fluctuating light may increase physiological losses like respiration (Beardall et al. 1994) or exudation (Cosper 1982). Light flashes (Phillips & Myers 1954, Abu-Gosh et al. 2015) and periodical relaxing from otherwise inhibiting irradiance (Ibelings et al. 1994, Neale et al. 1998, Helbling et al. 2013) may also favour phytoplankton growth. Phytoplankton species adapted to moderate but dynamic irradiance ("mixers" *sensu* Cullen & MacIntyre 1998) may increase their photosynthesis when rapidly exposed to high irradiance (Kana & Glibert 1987). The ability to acclimate to fluctuating light is species-specific (e.g., Ibelings et al. 1994, Litchman 2000, Shatwell et al. 2012) and not always well-known. So far, we cannot adequately predict the effects of changed mixing conditions on phytoplankton development.

The light-dependency of growth has been measured for many phytoplankton species at constant irradiances (e.g., Jitts et al. 1964, Schwaderer et al. 2011). This relation is characterized by a small number of basic parameters: the compensation light intensity I_{comp}, where production

and losses are balanced, the growth efficiency at sub-saturation light α_μ, and the maximum growth rate under saturating light μ_{max}. An additional parameter may describe growth inhibition at strong light. Very few studies (Nicklisch et al. 2008, Shatwell et al. 2012) measured growth under fluctuating light at a sufficient number of mean light intensities to estimate the parameters of the growth-irradiance relationship. Therefore, the influence of light dynamics on μ_{max}, α_μ and I_{comp} is still largely unknown.

Each of the different response mechanisms matches only a limited range of light frequencies (e.g., Cullen & Lewis 1988). This study focuses on the common, relatively regular Langmuir cells which need, depending on wind speed and mixing depth, a few minutes to one hour per revolution (see Denman & Gargett 1983, Schubert & Forster 1997, Thorpe 2004).

We tested the following hypotheses for such mixing conditions:

H1: Differences in growth efficiency of phytoplankton between stagnant and turbulent conditions are mostly explainable by the different frequency distribution of the received light.

H2: At the same daily PAR, growth rates of phytoplankton are similar in mixed and in stratified water columns only at similar frequency distributions of light, i.e. at low optical depths. This would suggest similar maximum growth rates at mostly saturating irradiances.

H3: At deeper mixing, shortened effective daylength, the higher percentage of saturating or even inhibiting intensities and additional energy required to adapt to light fluctuations cause slower growth than under constant light of the same mean intensity. As a result, daily light requirements for zero growth (I_{comp}) and for light-saturated growth ($I_{k\,\mu}$) should be higher under fluctuating light than under constant light.

To test these hypotheses, we performed two series of experiments at the Xiangxi bay of the Three Gorges reservoir, China. We compared growth rates and photosynthesis of phytoplankton samples which were either vertically moved or incubated at fixed depths of similar daily irradiance. This “yo-yo technique” (Köhler 1997, Köhler et al. 2001, Mitrovic et al. 2003) combines the well-defined mixing conditions and avoided settling losses of laboratory experiments and the natural light field of mesocosms.

Methods

Site description: The experiments were performed in the Xiangxi Bay of the Three Gorges Reservoir, China, about 38 km upstream of the dam. A float anchored about 140 m offshore (31°06`50``N 110°46`52``E) was used for experimental installations, measurement of vertical profiles and a monitoring station (Wang et al. 2011a). The whole reservoir has a surface area of 1,080 km² and a length of about 600 km at normal water level (175 m a.s.l.). In Xiangxi Bay, high nutrient concentrations and sufficiently long residence time of water enable severe phytoplankton blooms in spring and summer (Wang et al. 2011b, Liu et al. 2012).

Experimental approach: Experiments started at sunrise of April 4 and 10, 2011 and lasted for 96 h each. Water was sampled from 0.3 m depth and pre-filtered (64 µm) to remove large zooplankton. In each experiment, 18 bottles (Duran glass, 280 mL) were filled from the same bucket. They were incubated in triplicate either at a fixed depth or vertically moved by a computer-controlled lift. The stationary samples were fixed at depths of about the same daily irradiances as received by their moved counterparts. The lift simulated a circular path from the water surface to 3, 7 or 14 m depth (10 m during the second experiment) with a 20 minute

period. The applied sinusoidal variation of vertical velocity is an approximation to more complex turbulent processes which may cause accumulation of buoyant algae in near-surface windrows (Denman & Gargett 1983), stronger downward than upward velocities (Gargett & Wells 2007) or extended residence time in the middle of the Langmuir cell (Thorpe 2004). The revolution period was chosen according to Denman & Gargett (1983), Schubert & Forster (1997) and Riddle & Lewis (2000), who found periods of about 20 minutes for full overturn in typical Langmuir cells. Subsamples of 50 mL were taken from each bottle after thorough homogenisation at sunrise of days 2-4. Bottles were topped up with filtered reservoir water (Whatman GF/C) to avoid nutrient limitation and self-shading and were re-incubated within 20 minutes.

Phytoplankton biomass and species composition: Samples were transferred in a dark cooler to the nearby laboratory. After at least 20 minutes dark adaptation, three subsamples were taken from each bottle to measure chlorophyll fluorescence yields at very low light intensity (F_0) in a Phyto-PAM fluorometer (Walz, Germany). F_0 values were converted into chlorophyll *a* (chl*a*) concentrations using HPLC-based calibration factors. Additionally, subsamples were fixed with Lugol´s solution. The abundance of dominant phytoplankton taxa was calculated after counting 300-800 cells per sample under an inverted microscope (Utermöhl 1958). Relevant dimensions of at least 20 cells per species were measured to calculate biovolumes. Total phytoplankton biovolume was closely correlated to PAM-derived chl*a* (r^2=0.93, n=14, p<0.001). The specific chl*a* content (chl*a* / biovolume) was not significantly different between vertically moved and stationary samples (p=0.30). The phytoplankton in the first experiment was initially dominated by dinoflagellates (*Peridinopsis niei*) and, to a much lesser extent, by green algae (*Pandorina morum*, *Eudorina elegans*), whereas each diatom taxon (*Asterionella formosa*, *Synedra* spec.,

Fragilaria spec., centric diatoms) contributed less than 1% to the total biovolume. Phytoplankton in the second experiment mainly consisted of *Fragilaria* spec. and *Synedra* spec. (74%), *Peridinopsis niei* and centric diatoms.

Photosynthesis: Rapid photosynthesis-light curves were measured in the Phyto-PAM immediately after F_0. Relative electron transport rates (ETR) were quantified at 11 PAR intensities (1-600 µE m^{-2} s^{-1}) after 30 seconds adaptation at each intensity. Efficiency of light-limited ETR (α_P), maximum relative electron transport rates (ETR_{max}) and the transition parameter from limiting to saturating light ($I_{KP} = ETR_{max}/\alpha_P$) were fitted using the model of Webb et al. (1974). This model, α_P, ETR_{max} and the diurnal courses of PAR received by the vertically moved or the stationary algae were used to calculate relative electron transport rates of each sample every 75 s which were afterwards integrated per day. The time step of 75 seconds corresponds to the velocity segments of the circular path simulated by the lifts.

Abiotic conditions: Vertical profiles of temperature, chlorophyll fluorescence, oxygen concentration and photosynthetically active radiation were measured at 0.5 m intervals from the water surface to 20 m depth at 10 am and 4 pm each day using a YSI 6600 EDS multiprobe (Yellowsprings) and a Li-192 SA (LiCor) quantum sensor, respectively. The mean coefficient of vertical light attenuation (ε) was calculated by applying the Lambert-Beer law. A moored monitoring station recorded downwelling PAR above the water surface with a cosine-corrected quantum sensor (Li-190), as well as air temperature, wind speed and humidity (meteoMS, ecotech, Germany).

Calculations and statistics: Growth rates (d^{-1}) were calculated from changes in chl*a* taking into account dilution after sampling of the previous day:

$\mu = \ln(\text{chl}a_{i+1} / (\text{chl}a_i \cdot (V - 50)/V))$ eq. 1,

where $\text{chl}a_i$ is the chlorophyll *a* concentration at day i and V the volume of the bottle in mL. The light-dependency of growth was modelled according to Webb et al. (1974) as

$$\mu = \mu_{max}\left(1 - exp\left(\frac{-\alpha_\mu(Iz - I_{comp})}{\mu_{max}}\right)\right) \quad \text{eq. 2,}$$

where μ_{max} is the growth rate under saturating light (d^{-1}), α_μ the growth-efficiency under sub-saturating light ($m^2\ E^{-1}$), I_z is the intensity of PAR at depth z and I_{comp} the compensation light intensity at zero growth ($E\ m^{-2}\ d^{-1}$). The model can also be formulated in terms of $I_{k\mu} = \mu_{max} / \alpha_\mu + I_{comp}$. Model parameters were estimated using non-linear least-square fits.

The critical depth z_{crit} is the thickness of the thoroughly mixed water column in which the mean light intensity equals I_{comp}. It can be approximated using measured intensities of the photosynthetically active radiation at the water surface (I_0), the mean vertical light attenuation coefficient (ε) and I_{comp} using the Lambert-Beer law as

$z_{crit} = I_0 / (\varepsilon \cdot I_{comp})$ eq. 3.

Differences in the light-growth parameters between experimental treatments were assessed using the non-linear model given in equation 2. To compare the effects of fluctuating and constant light, we tested the null hypothesis that the model parameters did not vary between the two treatments (fixed depth or vertically moved) against the alternative hypothesis that one or more of the parameters did vary between treatments. Conclusions on treatment effects were based on model comparisons with F-tests according to Bates and Watts (1988, p. 105ff.). Parameters of the photosynthesis curves (α_P, ETR_{max}, I_{kP}) were compared using t-tests. Statistical tests were performed with R version 3.1.3 (R core team, 2015) and SPSS V22.

Results

Mixing conditions and light supply

The near-surface (0-3 m) water temperature increased from 13.3±0.1 °C to 14.6±0.06 °C during our experiments (from the mornings of April 4 to 14, supplemental material, Fig. S1). At the same time, mean temperatures at 10-14 m depth increased from 12.4±0.3 °C to 13.7±0.5 °C. Temperature gradients above 0.5 °C m^{-1} were measured at depths between 11.5 and 15 m in the first experiment and between 10.5 and 13 m in the second one. Weak secondary thermoclines were observed in the afternoons of warmer days: at depths of about 1.5 m on April 4, 8-10 and 13, and at 3.5 m on April 10 and 11. The thermal stratification was always weak, and the squared stability frequency N^2 never exceeded 0.002 s^{-2}. Increased phytoplankton concentrations (measured as chlorophyll fluorescence *in situ*) near the water surface were found in the afternoons of all days except for April 5 and 13, as well as in the mornings of April 4, 6 and 11 (Fig. S1).

Daily PAR at the water surface varied between 2.4 and 31.2 E m^{-2} d^{-1} (Table 1). During the first experiment, one sunny day was followed by one dull and two hazy days. The second experiment was performed in a rather sunny period, with thin cloud cover on the second day and a rainy third day. Vertical light attenuation ranged from 0.91-1.19 m^{-1} (average 0-6 m). The calculated daily PAR intensities in the water column and at the depths of the stationary samples are given in Table 1. Instantaneous PAR in the vertically moved bottles fluctuated by 2-3 orders of magnitude within 20 minutes but remained nearly constant in samples at fixed depths (see Fig. 1 as an example). Fig. 2 depicts the cumulative frequency of PAR received by algae moved in the

upper 7 m and by the respective stationary samples from sunrise to sunset. Even on sunny days, the vertically moved algae spent 60% of the day at PAR below 10 $\mu E m^{-2} s^{-1}$. At constant depth, this percentage ranged between 14% on sunny days and 28% on overcast days. On the other hand, the vertically moved algae were also exposed to PAR stronger than 200 $\mu E\ m^{-2} s^{-1}$ during 7% of the overcast days and 18% of the sunny days. The corresponding sample at constant depth never received such strong light. On average, mixing shortened the available daylengths (with PAR > 10 $\mu E\ m^{-2} s^{-1}$) by 33±14% (0-3 m), 64±5% (0-7 m), 69±4% (0-10 m) and 72±6% (0-14 m), respectively. On very hazy days (< 1 E $m^{-2}d^{-1}$), phytoplankton at fixed depths spent 39-100% of the period between sunrise and sunset at PAR intensities below 10 $\mu E\ m^{-2} s^{-1}$. At all higher daily light exposures, this percentage (25.5±8.3%) was significantly lower for stationary samples than for vertically moved samples ($p<0.001$).

Light dependency of growth

Growth rates increased with increasing global radiation and with declining mixing depth. Growth was saturated in the stationary samples at a daily light supply of 1.18 E m^{-2} ($I_{k\mu}$). The vertically moved algae needed 3.77 E $m^{-2}\ d^{-1}$ to obtain maximum growth rates (fig. 3, table 2). Assuming 12.5 hours daylength, growth was light-saturated at a mean PAR of 26 and 84 $\mu E\ m^{-2} s^{-1}$, respectively. The maximum growth rates μ_{max} did not significantly differ between light regimes ($p=0.27$). Maximum growth rates averaged at 0.44 ± 0.11 (moved) and 0.38 ± 0.05 per day (fixed depth). At sub-saturating daily PAR, phytoplankton used fluctuating light less efficiently than relatively constant light ($p<0.001$). The slope of the relation between growth and daily PAR at limiting intensities (α_μ) was calculated as 0.12 ± 0.02 $m^2 E^{-1}$ under fluctuating light and 0.32 ± 0.08 $m^2 E^{-1}$ in fixed depth samples. Accordingly, the compensation light intensity

(I_{comp} = daily PAR at zero net growth) was higher for vertically moved than for stationary samples. Photosynthesis and losses were balanced at 0.76 E m^{-2} d^{-1} under relatively constant light (fixed depths) but only at 2.50 E m^{-2} d^{-1} under fluctuating light (moved bottles). These minimum daily light requirements would be equivalent to a mean PAR of about 17 and 55 µE m^{-2} s^{-1}, assuming a 12.5 hours daylength. The difference between I_{comp} and $I_{k\mu}$ was surprisingly small because of unavoidable grazing losses, which affect I_{comp} but not $I_{k\mu}$.

The high I_{comp} of vertically moved phytoplankton resulted in critical depths between near-zero on a dull day and 13.9 m on a sunny day (Fig. 4). I_{comp} of samples at fixed depths was about 69% lower, and accordingly the critical depths were higher (3.1 m - 45 m, depending on daily global radiation and underwater light attenuation). On dull days (April 5-7), all approaches resulted in critical depths above the thermocline.

Photosynthesis

The maximum relative electron transport rates were on average higher after mixing than after stagnant conditions (Table 2). ETR_{max} increased with increasing mixing depth, from 47 (0-3m) to 55 (0-7m) to 61 rel. units (0-10/14m) but did not significantly change with depth under stagnant conditions. There was no significant difference between moved and fixed samples near the surface (0-3 m) but ETR_{max} was higher in bottles moved between the surface and 7m or deeper than in the respective bottles at fixed depth. Photosynthesis was usually saturated at higher PAR intensities I_{kP} (= ETR_{max} / α_P) in moved samples than in stationary samples (Table 2). The only exception was the near-surface (0-3 m) sample during the first run. Photosynthesis was

saturated at much higher light intensities than growth ($I_{kp} > I_{k\mu}$). The photosynthetic efficiency at sub-saturating light (α_p) did not significantly differ between depths or treatments.

These photosynthesis-light parameters and the diurnal courses of underwater light intensities were used for modeling of the diurnal ETR. Near the water surface, instantaneous PAR exceeded I_{kp} for most of the time on sunny days. Accordingly, photosynthesis of vertically moved algae approached ETR_{max}, which implies a lowered photosynthetic efficiency (ETR / PAR) during their stay in upper water layers (see Fig.5 as an example). The ETR of the respective stationary samples never reached this upper limit; their photosynthesis mostly operated at maximum efficiency. The mean ETR per revolution in moved samples was lower than that of the respective stationary sample during most of the day (from about 9:30 to 16:30). The relations between modeled daily production and daily light supply are given in Fig. 6. Here, the same set of parameters (from stationary samples) was applied to both modes of light dynamics to quantify the effect of the different light distribution. The fitted daily maximum ETR was similar ($p=0.94$) but α_p per day was 47% lower for vertically moved (0.129 rel. units) than for stationary algae (0.243 rel. units; $p<0.0001$).

Discussion

Maximum growth rates

The effects of fluctuating light on algal growth most probably depend on the range of light intensities received. At high surface irradiance and low optical mixing depth ($\varepsilon \cdot z_{mix}$), planktonic

algae may receive growth-saturating light intensities in the largest part of the mixed water column. Under such conditions, algae transported over moderate vertical distances should grow at the same maximum rates as algae residing at an optimum depth. Such low optical mixing depths are typically found in clear waters (ocean, oligotrophic lakes) with shallow mixing layers, e.g. at the beginning of thermal stratification or on calm days, and in shallow waters of low to moderate turbidity (e.g., slightly eutrophic shallow lakes or rivers). In our experiment, such conditions occurred on the two days with the highest global radiation (April 4 and 13) in the near-surface layer (0-3m) with z_{eu}:z_{mix} ratios of 1.32 and 1.67, respectively. There, both stationary and vertically moved algae received saturating PAR for more than 70% of the day (Fig. 7a), spent about 20% of the day in effective darkness (Fig. 7b) and attained similar maximum growth rates. Litchman (2000) and Dimier et al. (2009) also found no significant influence of light dynamics on growth rates if light intensities always exceeded $I_{k\mu}$. Nicklisch & Fietz (2001) and Shatwell et al. (2012) simulated deeper mixing under lab conditions and found lower μ_{max} at fluctuating than at constant light. The difference increased with declining z_{eu}:z_{mix} ratios (or shorter effective daylength). In the latter experiment, phytoplankton spent 25% of the day with PAR <10 µE m^{-2} s^{-1} at z_{eu}:z_{mix} = 1 and 58% of the day at z_{eu}:z_{mix} = 0.5 whereas the respective percentages ranged between 2.6% and 3.1% under constant light of the same daily intensity (8.3 E m^{-2} d^{-1}).

Near the water surface, phytoplankton may be exposed to inhibiting light intensities, mostly due to ultraviolet radiation (e.g. Cullen et al. 1992). The effects of strong light exposure on algal growth are dosage-dependent (e.g. Marra 1978). Algae can repair effects of short term exposures but suffer permanent damage if inhibiting light intensities last too long. Repair

mechanisms are most efficient at low light (Anderson et al. 1997). Therefore, turbulent mixing may mitigate inhibition of photosynthesis (Ibelings et al. 1994) but this effect depends, among other factors, on the z_{eu}:z_{mix} ratio (Neale et al. 1998, Köhler et al. 2001, Barbieri et al. 2002). The Duran glass bottles used for our incubations absorbed more than 90% of UV-B and about 50% of the radiation at 340 nm (Köhler et al. 2001). Therefore, photoinhibition was unlikely in our experiment but it may favour vertically moved algae over algae residing near the water surface on bright days. Without this incubation effect, the maximum growth rate under fluctuating light may exceed that under constant light of the same mean intensity.

Growth efficiency

In our experiment, vertically moved algae grew more slowly than algae at constant depth of equivalent sub-saturating daily PAR. Again, the different distribution of light intensities probably caused these differences in growth rates: Already at 7m mixing depth, the vertically moved algae spent two to four times longer at an instantaneous PAR below 10 µE m^{-2} s^{-1} than their stationary counterparts (Fig. 2). The shorter effective daylength available to vertically moved algae results in decreased growth rates (Boelen et al. 2011, Shatwell et al. 2012, Hoppe et al. 2015). Vertically moved algae also received saturating light during longer parts of the day than the stationary algae (Fig. 2). Light intensities above $I_{k\mu}$ increased the mean daily light supply but not the growth rate. Accordingly, the higher percentage of saturating light may explain lower growth rates under fluctuating than under constant light of the same intensity found by van de Poll et al. (2007). Nicklisch & Fietz (2001) and Shatwell et al. (2012) compared growth rates at several mean intensities of constant and fluctuating light. Light fluctuations reduced growth efficiency α_μ of *Planktothrix agardhii*, *Stephanodiscus neoastraea* (Nicklisch & Fietz (2001) and

Limnothrix redekei, but not of *Stephanodiscus minutulus* or *Nitzschia acicularis* (Shatwell et al. 2012).

The lower growth efficiency implies a higher daily light demand $I_{K\mu}$ to saturate growth under fluctuating light. Interestingly, growth saturated at much lower light intensities than photosynthesis. In our study, electron transport rates of stationary and of vertically moved phytoplankton saturated at 183 and 199 µE m^{-2} s^{-1} whereas growth saturated at a mean PAR of 26 and 84 µE m^{-2} s^{-1}, respectively (at 12.5 hours daylength). Shatwell et al. (2012) found electron transport rates of diatom and cyanobacteria cultures saturated at a PAR between 182 and 289 µE m^{-2} s^{-1} whereas growth saturated at 24-44 µE m^{-2} s^{-1}(daily average). Similar differences were found for the cyanobacterium *Limnothrix redekei* by Gibson & Foy (1983). Stagnant growth but still increasing photosynthesis at light intensities between $I_{K\mu}$ and I_{KP} is explainable only by an increase of physiological losses with increasing light. Indeed, the few available studies indicate higher rates of respiration (Grande et al. 1989, Luz et al. 2002) and exudation (Zlotnik & Dubinsky 1989, Maranon et al. 2004) in the light compared to the dark.

Compensation light intensity and critical mixing depth

Almost all estimates of I_{comp} are based on measurements of growth (Hobson & Guest 1983, Falkowski et al. 1985) or photosynthesis and losses (Langdon 1988) under constant light. In stratified water columns, phytoplankton may adapt to relatively constant low light to form distinct deep chlorophyll maxima. Adaptive strategies involve the reduction of metabolic maintenance costs (e.g., lower dark respiration) and increased photosynthetic efficiency (e.g., higher absorption cross section, higher ratio of photosynthetic to protective pigments, see

review of Dubinsky & Stambler 2009). Some species adapted to permanently low light may grow at a mean PAR of 1-2 µE m^{-2} s^{-1} or 0.05-0.1 E m^{-2} d^{-1} (e.g., Geider et al. 1985, Bright & Walsby 2000). Marra et al. (2014) estimated zero daily net carbon assimilation of phytoplankton samples kept at water depths with a daily PAR of about 0.1-0.2 E m^{-2}. Laboratory experiments under constant low light found zero growth at light intensities in the range of 0.1 to 0.8 E m^{-2} d^{-1}, with the exceptions of higher I_{comp} for dinoflagellates (Langdon 1988) or chlorophytes (Richardson et al. 1983). Our phytoplankton samples incubated at constant depths needed about 0.77 E m^{-2} d^{-1} to balance production and losses. This I_{comp} value ranges at the upper end of the published data, probably because of additional losses in our samples (e.g., grazing by microzooplankton) compared to experiments with algal cultures (see Nelson & Smith 1991).

Only very few compensation light intensities were experimentally determined under fluctuating light. The laboratory study of Nicklisch & Fietz (2001) indicated I_{comp} close to zero regardless of the light regime. Gibson (1985) measured I_{comp} of 0.1-0.2 E m^{-2} d^{-1} in short on-off cycles of saturating light but this is hardly comparable to natural light fluctuations. On an ecosystem level, a mean radiation of about 0.03 cal cm^{-2} min^{-1} (or about 1.9 E m^{-2} d^{-1}) in the water column was critical for initiation of spring development of phytoplankton in coastal waters (Riley 1957). Siegel et al. (2002) estimated I_{comp} as mean light intensity in the mixed surface layer at the start of the spring development of phytoplankton in the North Atlantic. This approach gave a mean I_{comp} of 1.0-1.7 E m^{-2} d^{-1} in large parts of the ocean. In our “yo-yo” experiment, phytoplankton communities needed about 2.5 E m^{-2} d^{-1} to compensate losses. In accordance with our findings, the few published relevant field studies indicate much higher minimum daily light requirements of phytoplankton under mixing conditions than for algae adapted to constant low light. Again,

this difference is probably caused by the much longer part of the day spent at very low light intensities under mixing than under stagnant conditions. For instance, at z_{mix}=7m, vertically moved algae spent about 50% of the day at light intensities below 2 µE m^{-2} s^{-1} whereas this percentage ranged between 6 and 12% for stationary algae (Fig. 2).

The compensation light intensity is crucial for calculations of the critical mixing depth z_{crit}, the depth of the surface mixing layer with a mean light intensity approaching I_{comp}. Under nutrient-replete steady-state conditions, phytoplankton grows until self-shading reduces the mean light intensity in the mixing layer to I_{comp}. Therefore, estimates of z_{crit} are as precise as I_{comp}. As was demonstrated in our experiment, the estimation of I_{comp} under invariable light seriously underestimates minimum light requirements of phytoplankton in mixed water layers. Accordingly, it overestimates the critical mixing depth. In our experiment, z_{crit} was often smaller than z_{mix} (Fig. 4), suggesting a dominance of loss processes in such periods. However, z_{mix} was, as usual, estimated from vertical temperature gradients. Potentially, the upper mixed layer was not turbulent enough to homogeneously distribute the phytoplankton (see Franks 2015). Below a critical turbulence, growth rates may exceed rates of vertical transport, enabling phytoplankton growth irrespective of z_{mix} (Huisman et al. 1999).

Effects of non-linearity vs. effects of acclimation

The frequency distribution of underwater light can be generalized mathematically in terms of the mean daily light to which algae are exposed (I_{mean}). At fixed depth, the proportion of the day f that algae spend below instantaneous light intensity I, assuming that incoming radiation follows a sine curve during the day, is

$$f(I) = \frac{2}{\pi}\sin^{-1}\left(\frac{2ID}{\pi I_{mean}}\right)$$

where *D* is the solar daylength as a fraction of a 24-hour day. Accordingly, algae at fixed depth spend $f(I_{comp})$ at subcompensation intensities and $1\text{-}f(I_{k\mu})$ at supersaturating intensities (see lines for fixed samples in Fig. 7). Under well-mixed conditions, the proportion of the water column with intensity greater than *I* is z_I/z_{mix}. (assuming $0 < z_I < z_{mix}$), where z_I is the depth of intensity *I:*

$$\frac{z_I}{z_{mix}} = \frac{\ln\left(\frac{I_0}{I}\right)}{\varepsilon z_{mix}}$$

Considering that I_0 varies over time (t in days), the proportion of the day algae spend above *I* is given by integrating over t as $\int_0^D z_I z_{mix}^{-1} dt$ (see lines for moved samples in Fig. 7). Therefore as shown in Fig. 7, stationary samples spend a greater part of the day above compensation intensities than moved samples. Moreover, stationary samples are exposed longer to intensities between I_{comp} and $I_{k\mu}$, which can be used most efficiently, and this amount of exposure increases relative to moved samples as mean daily light supply decreases. This helps to explain why, when averaged over a day, vertically moved samples grew more slowly at low light, but no difference was observed at high daily light.

In order to estimate the effect of different frequency distributions of light intensity, production rates were calculated at a temporal resolution of 75 secs using the photosynthesis-light parameters of stationary algae for both modes and the instantaneous light intensities experienced by vertically moved or by static samples (Fig. 5). The daily integrals of production indicated a 47% lower efficiency of vertically moved than of stationary algae (Fig. 6). According

to the measured daily growth rates, α_μ was 64% lower under fluctuating than under constant light (table 2). In other words, roughly three quarter of the found gap in growth efficiency between vertically moved and stationary algae can be attributed to the different frequency distribution of light intensities, e.g. the higher percentage of less efficiently used saturating light under mixing. This comparison confirms our first hypothesis, even though it provides rough estimates rather than exact numbers. The approach could be further improved by taking the diurnal course of photosynthesis-light parameters into account. If the photosynthetic electron transport saturates at higher PAR than carbon assimilation (e.g., Hancke et al. 2015) the fluorometric method used would overestimate I_{kp} and thus slightly underestimate the effect of non-linearity in the photosynthetic response to fluctuating light.

The remaining quarter of the efficiency gap should be caused by light-dependent losses or by imperfect acclimation to fluctuating light. At the time scale of Langmuir cells, phytoplankton can acclimate to light fluctuations by state-transitions (Falkowski et al. 1994) and changes in the activation state of Rubisco (MacIntyre et al. 2000). The xanthophyll cycle is another important short-term light acclimation mechanism in diatoms and chlorophytes, but is not possessed by cyanobacteria or cryptophytes (e.g. Demming-Adams & Adams 1996). The interplay of an orange carotenoid protein and the phycobilisome can regulate photosynthesis vs. energy quenching in cyanobacteria (Kirilovsky & Kerfeld 2016). Under natural conditions, movement of phytoplankton is certainly less constant. Turbulent mixing may cause more irregular light fluctuations which require even faster acclimation.

These mechanisms are based on assembly of enzymes or pigments or on dissipation of absorbed energy. They inevitably reduce the efficiency of conversion of irradiance into biomass

compared to constant light of the same mean intensity (e.g., Su et al. 2012). Energy requirements of acclimations should be more relevant under limiting than under saturating light supply. Accordingly, dynamic irradiance should affect growth efficiency at sub-saturating light α_μ more than maximum growth at saturating light μ_{max}, as was observed in this study.

On the other hand, fluctuating light may force acclimation to stronger light intensities in order to avoid damage to the photosystems and to better exploit bright light near the surface. The acclimation to light intensities higher than what is on average available is advantageous only under mixing conditions (Cullen & MacIntyre 1998). Such acclimation explains the higher maximum rates of photosynthesis under mixing than under stagnant conditions, as were found in our study (Table 2). This difference was probably even underestimated in our measurements after dark adaptation.

Conclusions

The present study provides some evidence for substantial effects of vertical mixing on compensation light intensity and on growth efficiency of phytoplankton at sub-saturating light. The decline in growth-efficiency under vertical mixing was largely caused by the non-linear light-dependency of photosynthesis and growth. This part of the mixing effects can be calculated if the frequency distribution of the light received by the mixed algae is known. The remaining gap in growth efficiencies can be attributed to (species-specific) acclimation mechanisms and to light-dependency of physiological losses. The dynamics of these processes requires more simultaneous studies of physiology and turbulence-driven vertical movement of planktonic

algae. This would allow a better understanding and prediction of the effects of mixing on phytoplankton development.

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Table 1: Photosynthetically active radiation per day at the water surface and received by algal samples which were either vertically moved between the water surface and 3, 7, 10 or 14 m depth, or incubated at respective fixed depths (in E m^{-2} d^{-1}).

Day	surface	0 – 3m		0 – 7m		0 – 10/14m	
		fixed	moved	fixed	moved	fixed	moved
April 4	29.58	6.56	10.59	3.28	6.63	1.71	4.29
April 5	2.44	0.68	0.96	0.38	0.59	0.23	0.39
April 6	10.75	1.87	3.37	0.47	2.33	0.14	1.50
April 7	8.19	2.71	3.10	1.07	1.89	0.51	1.23
April 10	31.23	10.31	12.58	4.49	7.96	2.96	6.47
April 11	18.02	5.17	6.75	2.03	4.30	1.27	3.47
April 12	9.94	3.48	3.89	1.48	2.43	0.92	1.98
April 13	25.66	8.92	10.32	4.31	6.49	3.10	5.28

Table 2: Parameters of light-dependency of growth and photosynthesis. Averages, standard deviations and significance of differences between stationary and vertically moved samples.

parameter	unit	stationary	moved	p
μ_{max}	d^{-1}	0.383 ± 0.053	0.443 ± 0.106	0.27
α_{μ}	$m^2\ E^{-1}$	0.324 ± 0.080	0.117 ± 0.021	<0.001
I_{comp}	$E\ m^{-2}\ d^{-1}$	0.764 ± 0.126	2.496 ± 0.304	<0.001
$I_{k\mu}$	$E\ m^{-2}\ d^{-1}$	1.18 ± 0.39	3.77 ± 1.35	<0.001
ETR_{max}	Rel. units	46.9 ± 5.1	54.5 ± 8.5	<0.001
α_P	Rel. units $(\mu E\ m^{-2}\ s^{-1})^{-1}$	0.267 ± 0.045	0.278 ± 0.029	0.065
I_{kP}	$\mu E\ m^{-2}\ s^{-1}$	183 ± 51	199 ± 46	0.047

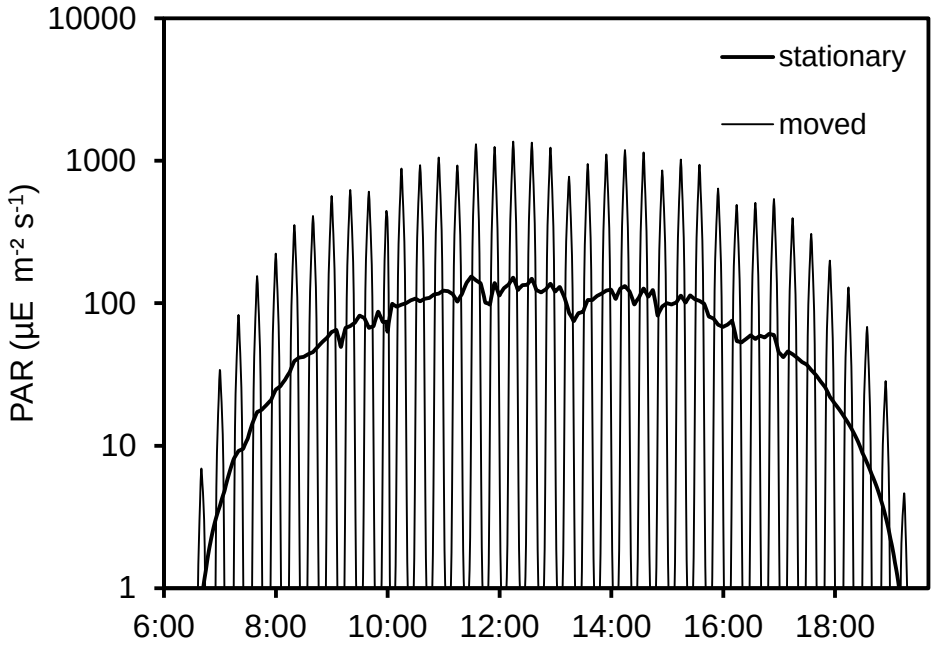


Fig. 1: Typical diurnal courses of photosynthetically active radiation experienced by phytoplankton samples moved between the water surface and 7 m depth (fine line), and kept at a fixed depth (1.9 m, thick line), April 4, 2011.

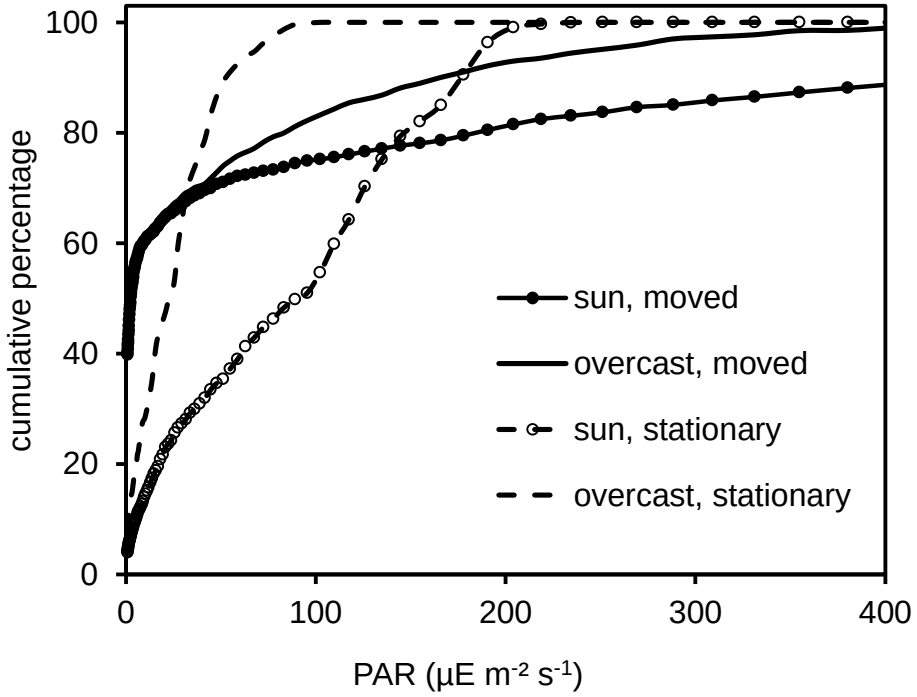


Fig. 2: Cumulative percentage of light intensities received by vertically moved (0-7m; solid lines, filled circles) and by the respective stationary samples (broken lines, open circles). Averages of the sunny (April 4, 10 and 13; circles) and of the overcast days (April 6, 7 and 12).

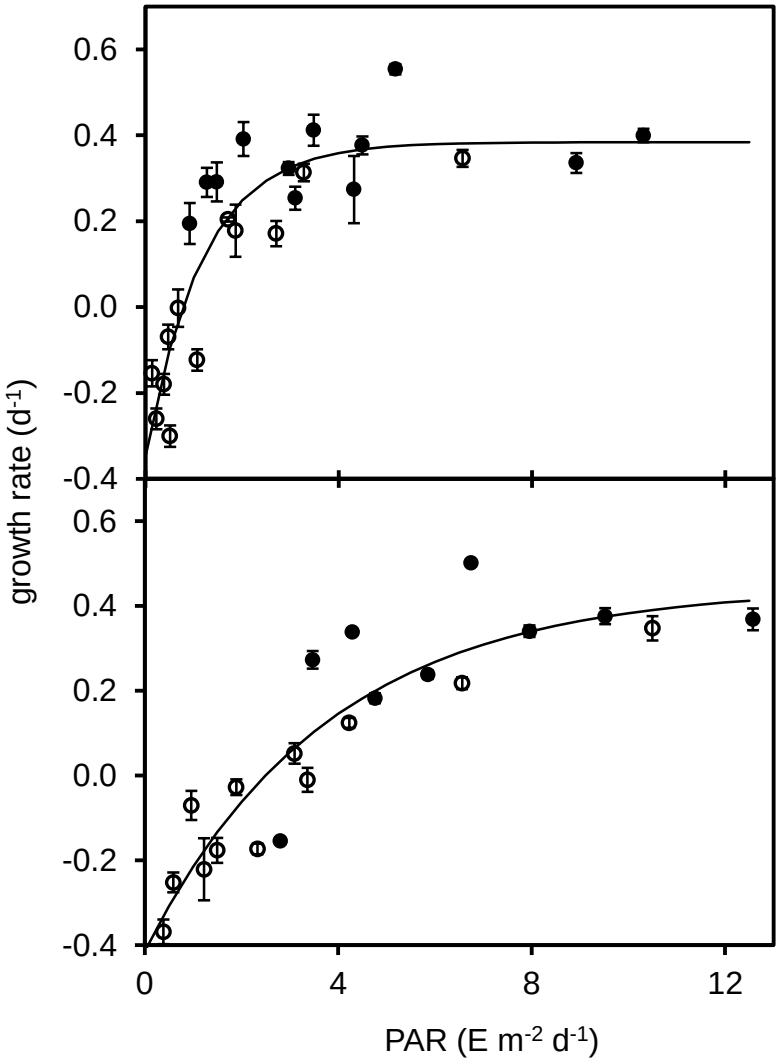


Fig. 3: Light-dependency of growth of phytoplankton incubated at constant depth (top) and vertically moved (bottom), mean growth rates and standard deviations. Open symbols: April 4-8, filled symbols: April 10-14.

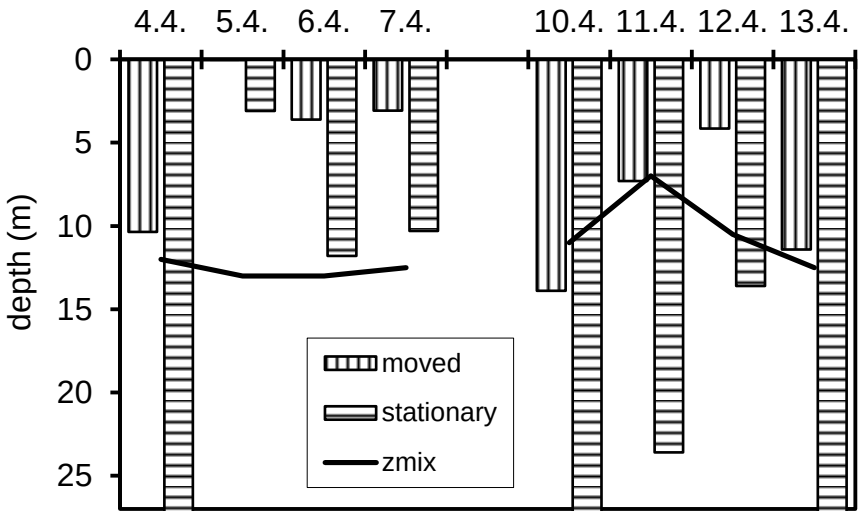


Fig. 4: Critical depths and mixing depths during the experiments (April 4-13). Critical depths were calculated using I_{comp} obtained from growth experiments with vertically moved (vertical lines) or stationary samples (horizontal lines).

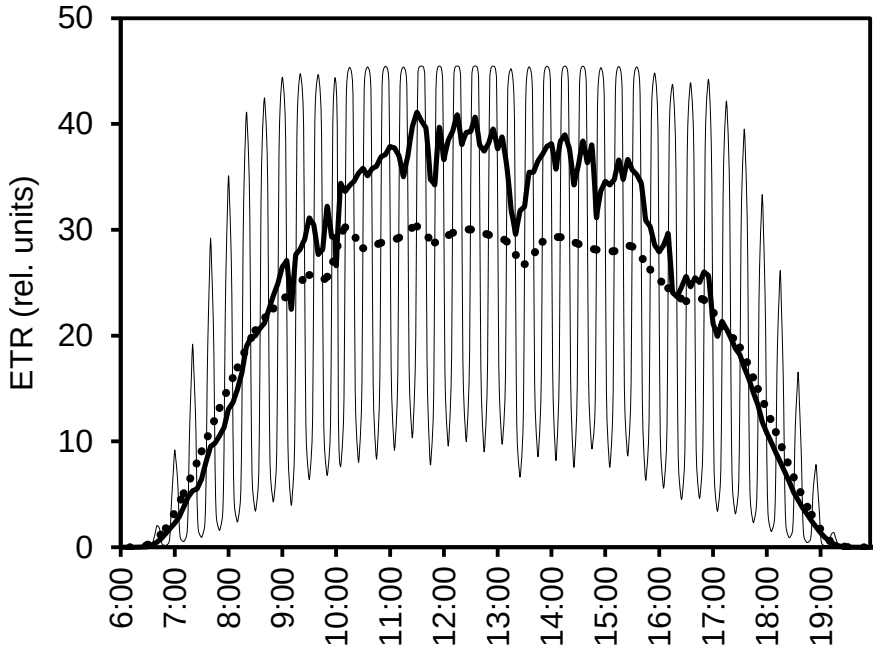


Fig. 5: Diurnal courses of photosynthesis (in relative electron transport rates) of phytoplankton at 1.3 m depth (thick solid line) and moved between water surface and 3 m depth (thin solid line; the dots illustrate the averages per revolution). April 4, 2011.

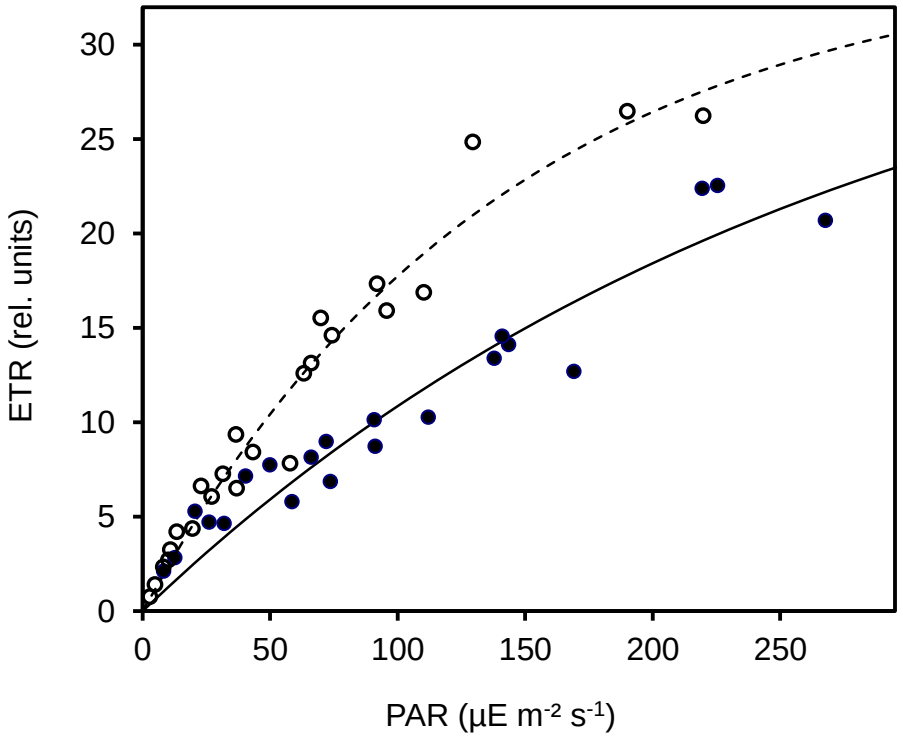


Fig. 6: Light-dependency of daily production (in relative electron transport rates). Daily production was integrated from photosynthesis calculated every 75 secs using the parameters of the photosynthesis-light relation of stationary samples and the PhAR available to either vertically moved (filled circles) or stationary samples (open circles).

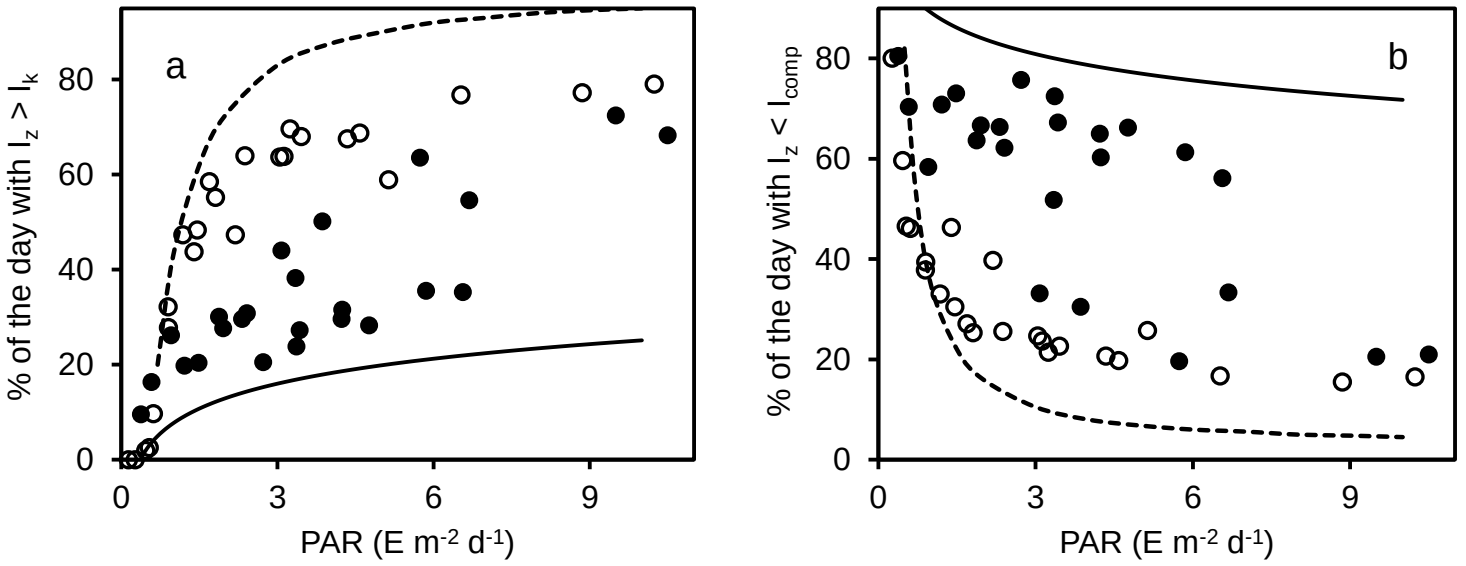
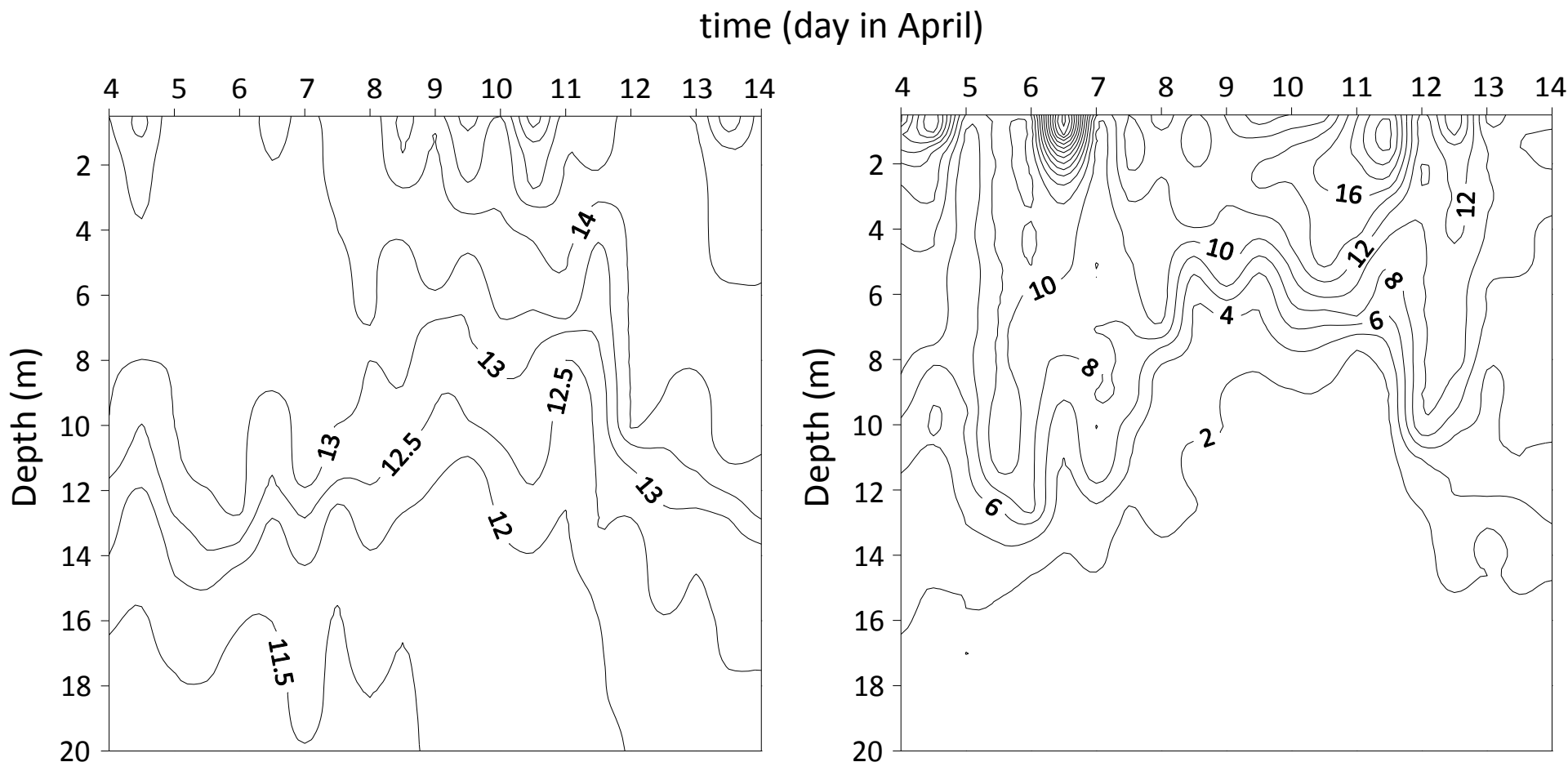


Fig. 7: Percentage of the day with a) saturating light intensities (> 26 µE m^{-2} s^{-1}) and b) in the aphotic zone (< 10 µE m^{-2} s^{-1}) versus daily light supply. Here, the same thresholds were set for both modes to facilitate comparability. Circles indicate measured data and lines the model results (see text for explanation). Open circles and broken lines: stationary samples, filled circles and solid lines: vertically moved samples. The model assumes that the diurnal course of global radiation follows a sine curve whereas the real light intensities often fell below this optimum.



Supplement

Fig. S1: Vertical distribution of water temperature (in °C, left) and of phytoplankton biomass (measured as fluorescence in µg L^{-1} chl*a*, right) during the experiments.