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PRIMARY RESEARCH PAPER

Productivity related to ambient photon flux for phytoplankton communities under different turbid conditions

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Abstract Phytoplankton productivity standardized to chlorophyll *a* and photon flux (mg C mg chl. a^{-1} mol photons^{-1}) of natural communities from northern Bothnian Sea under dynamic (vertically rotating) incubations and different optical conditions was studied during four mesocosm experiments between April 2013 and April 2016. The standardized productivity showed a positive exponential relationship with calculated optical depth ($P < 0.001$ in all four cases) although a considerably weaker one for one of the series where the community was pre-adapted to the same optical condition as used in the measurements. This series also showed a lower regression slope than the three non-adapted series, which in turn showed identical regression slopes, thus indicating a similar response on the standardized productivity to short-term changes in average ambient photon flux and mixing depth. These results indicate that phytoplankton communities in environments with episodic inflow and mixing of humus-rich water can partly compensate for the reduced photon flux by increased production efficiency.

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Introduction

Dissolved organic matter (DOM) is of profound importance for the productivity of aquatic ecosystems through its content of brown humus that effects the light attenuation (e.g., Karlsson et al., 2009; Hessen et al., 2017), and for its function as a bacterial carbon source (e.g., Jansson et al., 2000; Sandberg et al., 2004; Ask et al., 2009b; Båmstedt & Wikner, 2016). The range in light attenuation of natural systems is high, as shown for 15 small lakes in northern Sweden by Ask et al. (2009a), and tends to increase, due to global warming that causes increased precipitation (Zhang et al., 2007) with increased leaching of DOM from the surrounding terrestrial environment. Increasing brownification of surface waters in northern latitudes is therefore common (e.g., Forsberg, 1992; Evans et al., 2005, 2006; Vuorenmaa et al., 2006; Johansson et al., 2010; Kritzberg & Ekström, 2012) and might radically chance the trophic balance in aquatic ecosystems. Although long-term trends in the optical environment are well documented, short-term variability in the optical environment, caused e.g., by increased river runoff into an estuary due to heavy rainfall, will be of significance for the phytoplankton

production on a short time scale. Several studies on monocultured phytoplankton species have shown that the production can increase if the photon flux is not continuous (e.g., Sforza et al., 2012; Chen et al., 2013; Veirazka et al., 2013) and both laboratory and field studies have shown that dynamic incubations, i.e., incubations with variable light intensities, have given different phytoplankton production compared to static incubations (e.g., Marra, 1978a, b; Gallegos & Platt, 1982; Yoder & Bishop, 1985; Kromkamp & Limbeek, 1993; Helbling et al., 2003, 2013; Bertoni & Balseiro, 2005; Bertoni et al., 2011; Gali et al., 2013; Lawrenz & Richardson, 2017). In a situation where light is the single limiting factor for primary production, we would expect that a measure of the average photon flux in the mixed water column together with a biomass estimate (e.g., chlorophyll *a*) and a previously determined photosynthetic efficiency (i.e., production per unit of photons) would be sufficient to estimate primary production. This requires that the photosynthetic efficiency is constant over different optical environments. By using mesocosm experiments I here evaluated if this is true in the coastal Bothnian Sea, northern Sweden, where intrusion of humus-rich river water are common episodic events.

Materials and methods

Experimental facility

Phytoplankton primary production was measured during four experimental periods, in April 2013, 2014 and 2016 and in October 2014. The experiments were conducted in the indoor mesocosm facility at Umeå Marine Sciences Centre, University of Umeå, Sweden, situated at the northern Bothnian Sea (N63°34′; E19°50′) in the Baltic Sea. The facility is described by Båmstedt & Larsson (2018). For my experiments I used two of the 12 mesocosm tanks, 5 m high and 0.73 m in diameter, filled with pre-filtered (300 µm porosity) brackish water with salinity ranging between 4.03 and 5.10, and taken from 2 m depth through the seawater supply system of the laboratory. One tank was used for maintaining the natural plankton community and to supply water samples for the experiments, the other one was used for incubations of the water samples. In April 2013 the same treatment of humus was given to both tanks, whereas humus additions were only given to the incubation tank in the three other experimental series. The temperature was held at 15 ± 0.2°C, and the whole water column was mixed by using a higher temperature setting in the lowest section, 3.6–5 m depth. This method of thermal convection is very efficient, without influencing the temperature in the water column (see Båmstedt & Larsson, 2018). To prevent surface heating from the light source, the upper 0.6 m was slowly bubbled with air (see Båmstedt & Larsson, 2018). The methods used in the experiments have been recently described by Båmstedt (2019), and parts of the results from April 2013 and 2014 have been used for a comparison of primary production estimates from static and dynamic incubations (Båmstedt, 2019). In the present study I have used results of 462 dynamic (vertically rotating) incubations from the four mentioned periods. Nutrients (nitrate, ammonium, and phosphate) were added to the tank where the plankton community was maintained, in amounts for saturated conditions throughout each experiment, and measurements were started around 1 week after nutrient additions.

Measurements of primary production

All incubations were done in 23 ml screw-cap glass vials. The incubations consisted of two groups of five or six incubation vials each, one group was fixed to a 3-m rubber loop, rotating down to 1.5 m depth, the other one to a 9-m rubber loop, rotating down to 4.5 m depth, with the bottles fixed to the rubber loops with roughly equal distance between them (around 0.5 m for 3-m loop and around 1.5 m for 9-m loop). Three rotation speeds were used in each optical environment. A previous evaluation showed that there were usually no sustainable differences between the different speeds I used (cf. ANOVA results in Båmstedt, 2019), and in this study I used them together, thereby increasing sample size, but thereby also increasing total variability from each optical environment. I used three different optical environments for the incubations by adding either laboratory grade humic acid (Aldrich pnr: 536080) or earth extract dissolved in distilled water. Details of the experimental design as well as analytical procedures can be found in Båmstedt (2019). The PAR (Photosynthetic Available Radiation, 400–700 nm) attenuation coefficient ranged from 0.806 to 2.515 m^{-1}. Results of measured primary

production as mg C m^{-3} h^{-1} were multiplied with the mixing depth to get production m^{-2}, and this was standardized to average chlorophyll *a* and photon flux in the mixed layer, the standardized productivity was thereby expressed as mg C mg chl. a^{-1} mol photons^{-1}. Using Lambert-Beers law, Huisman et al. (2002) showed that the average photon flux in a well-mixed water parcel (E_{mix}) can be mathematically described as $[E_0 - E_d]/[\ln(E_0) - \ln(E_d)]$, where E_0 and E_d is the photon flux at the top and bottom of the mixed water parcel. I here use optical depth (OD) in the expression, which then becomes:

$$E_{mix} = E_0/OD * [1 - \exp(-OD)]$$

OD is the product of the PAR attenuation coefficient (k) in the water column and the mixing depth (m), i.e., k*m (se e.g., Reynolds, 2006). In the present experiments m was either 1.5 or 4.5 m. Optical depth is a dimensionless measure of opacity for the whole mixed layer and is commonly used in studies of algal photobioreactor efficiency (e.g., Flynn et al., 2010; Kenny & Flynn, 2015, Martinez et al., 2018), but also in studies of effects of vertical mixing on algal production (e.g., Ross et al., 2011; Diehl et al., 2015). These standardized results, hereafter named production efficiencies, were plotted against the calculated optical depth (OD). A summary of the relevant characteristics of the water column in the different experiments is given in Table 1.

A statistical evaluation of the results of production efficiency was made by regression analysis of the ln-transformed data versus optical depth for each of the four experimental series, using the statistical package SPSS Statistics 25 (https://www.ibm.com/analytics/spss-statistics-software).

Results

The production efficiency during the four periods were all significantly related to optical depth (Fig. 1) with the probability of no relationship being < 0.001 for all four series (Table 2). The coefficient of determination for the series from April 2013 differed from the three other series by showing considerably lower value ($R^2 = 0.219$), with the latter in turn showed almost identical values (R^2 between 0.734 and 0.748). The intercept value ($\ln(a)$ in Table 2) differed between the four series, as shown by non-overlapping standard errors. The slope of the regression lines (b) were almost identical for the three later series, ranging from 0.374 to 0.376, whereas the series from April 2013 diverged through a value of 0.144 (Table 2). The probability of zero slope was < 0.001 for all four series (Table 2).

Discussion

The scientific reports on effects of intermittent illumination for the productivity of microalgae are important for an explanation of my results. Many studies have shown that a cyclic change between light and dark environments improve algal productivity. Thus, Chen et al. (2013) drastically improved algal biomass productivity by circulation between a fully illuminated shallow pond and a fully darkened tank. Other studies show similar positive effects of intermittent periods of light and dark, although algal production has been measured in different ways, e.g., oxygen production (Vejrazka et al., 2013), biomass change (e.g., Vejrazka et al., 2011; Xue et al., 2011; Chen et al., 2013), cell numbers (e.g., Sforza et al., 2012) and specific growth rate (doublings hour^{-1}, Janssen et al., 2001). Most studies are based on monocultured phytoplankton and the optimal frequency therefore differs between different studies (e.g., Janssen et al., 2001; Vejrazka et al. 2011, 2013; Xue et al., 2011). Although my results are based on measurements of CO_2 assimilation, they should be comparable to measurements of changes in biomass and cell numbers as well as oxygen production, since they all are based on the photosynthetic harvesting of photons. My results showed that the standardized production efficiency was strongly related to the optical depth as best described by an exponential function (Fig. 1). Since the calculated efficiency is expressed per units of chlorophyll *a*, changed efficiency due to change in chlorophyll content is compensated for in the formula. One potential explanation for increased efficiency with increased OD could be that an increase in optical depth will gradually make the optical environment like that of a light/dark cycle, which, according to many studies (see above), have shown positive effects on algal productivity. Sforza et al. (2012) measured microalgal productivity normalized to light intensity in photobioreactors, both with continuous and intermittent

Table 1 Optical characteristics of the water column in the different experiments

Experiment	E_0	$E_{1.5}$	$E_{4.5}$	k (m^{-1})	Euphotic depth (m)	Chlorophyll a (mg m^{-3})
April-13						
No humus	184	100.8	44.5	0.903	5.1	6.1
Medium humus	80	28.1	10.1	1.761	2.6	7.8
High humus	50	13.5	4.6	2.397	1.9	7.8
April-14						
No humus	241	107.3	41.8	1.277	3.6	4.1
Medium humus	177	61.6	22.0	1.785	2.6	2.7
High humus	251	65.0	22.2	2.515	1.8	2.8
October-14						
No humus	145	84.1	38.9	0.806	5.7	5.8
Medium humus	181	73.1	27.4	1.467	3.1	4.6
High humus	187	56.5	19.6	2.116	2.2	4.0
April-16						
No humus	188	88.3	35.3	1.176	2.8	10.8
Medium humus	110	43.8	16.3	1.496	3.1	11.8
High humus	117	44.3	16.2	1.602	2.9	11.8

E_0 (in µmol photons m^{-2} s^{-1}) is the intercept of the exponential regression equation describing the vertical profile of photon flux versus depth, $E_{1.5}$ and $E_{4.5}$ is the average photon flux (µmol photons m^{-2} s^{-1}) during dynamic incubations rotating between the surface and 1.5 respectively 4.5 m depth, and k is the slope of the regression line. The euphotic depth is given as the depth where 1% of the surface photon flux remains. The chl. a value is the average for the whole water column

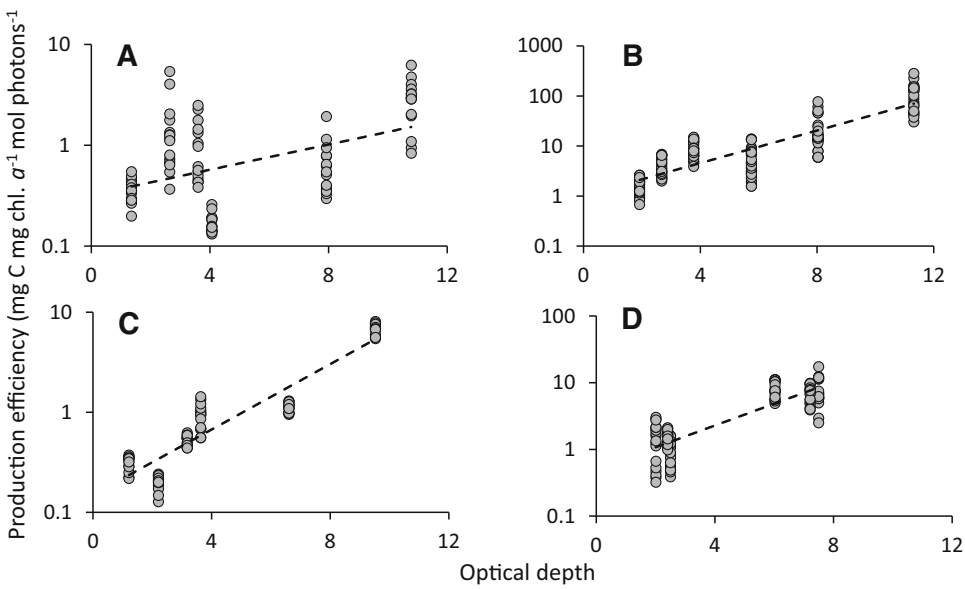

Fig. 1 Standardized production efficiency (mg C mg chl. a^{-1} mol $photons^{-1}$) from dynamic (rotating) incubations, measured in four different experimental series, April 2013 (**A**), April 2014 (**B**), October 2014 (**C**) and April 2016 (**D**). Results plotted versus the actual optical depth, $k \times$ m, where k is the attenuation coefficient and m is the mixing (rotation) depth, being 1.5 or 4.5 m. The best fit exponential regression line is shown in each graph. Corresponding regression parameters and results of statistical regression analyses are given in Table 2. Note the different scales on the Y-axis

Table 2 Regression analysis of the relationship between standardized primary production efficiency (Y) and optical depth (X), given by the equation ln(Y) = ln(a) + b*X, where the Y is given as mg C mg chl. a^{-1} mol photons^{-1}

Time	N	ln(a)	b	$P_{(b)}$	R^2	F-ratio	$P_{(regr)}$
April-13	90	− 1.135 ± 0.174	0.144 ± 0.029	< 0.001	0.219	24.716	< 0.001
April-14	176	0.023 ± 0.110	0.374 ± 0.017	< 0.001	0.748	463.998	< 0.001
October-14	89	− 1.901 ± 0.081	0.376 ± 0.016	< 0.001	0.734	569.983	< 0.001
April-16	107	− 0.680 ± 0.114	0.376 ± 0.022	< 0.001	0.734	289.587	< 0.001

N is the number of measurements, ln(a) is the intercept ± standard error, b is the slope ± standard error, R^2 is the coefficient of determination for the regression line and ($P_{(b)}$) and ($P_{(regr)}$) are the probability of zero regression slope respectively no relationship between standardized production efficiency and optical depth

light, and found a critical level of 150 µmol photons m^{-2} s^{-1} above which the productivity was drastically decreased. A photon flux of 120 µmol photons m^{-2} s^{-1} supported optimal productivity, both with continuous light, with 1200 µmol photons m^{-2} s^{-1} and a frequency of 10 Hz or with 350 µmol photons m^{-2} s^{-1} and a frequency of 35 Hz. Lower frequencies with these high intensities and the same photon flux supported lower productivity. Thus, the same average photon flux in an optically variable environment might support different productivity, due to differences in variability of the photon flux. My experimental design caused a gradual and cyclic change in photon flux between maximum (surface) and minimum (mixing depth), and by humus additions a range in optical depth of 1.3 to 11.5, was generated. Phytoplankton in my experiments experienced average photon fluxes ranging from 16.2 to 107.3 µmol photons m^{-2} s^{-1} (see $E_{1.5}$ and $E_{4.5}$ in Table 1), i.e., much lower than the critical level of Sforza et al. (2012), as referred above, although the vertical rotation would cause a short and repeated exposure to sub-surface levels of up to 251 µmol photons m^{-2} s^{-1} (see E_0 in Table 1). In contrast to the findings by Sforza et al. (2012) of a high and constant productivity per unit of photon flux, my results indicate a positive relationship between standardized production efficiency and optical depth, i.e., a strong increase in the efficiency of harvesting photon-flux energy with decreased available light. However, the considerably weaker relationship for the series from April 2013, where the phytoplankton community was adapted to the different humus additions before the actual measurements of primary production (see methods) points on the importance of response time of phytoplankton for changes in photon flux. Ferris & Christian (1991) compiled data from the literature showing that adaptations to high photon flux are usually immediate or occur within minutes whereas adaptations to low photon flux appear to be slower, although the literature data do not give a straightforward picture of these effects. Resistance to adapt might also be important for the results during variable photon flux. In my experiments with dynamic incubations a complete vertical revolution took between 1.1 and 25.0 min for deep mixing (4.5 m), and between 0.4 and 8.3 min for shallow mixing (1.5 m), and the continuous and gradual changes in optical environment in my experiments, defined both by quantity (photon flux) and quality (spectral composition) differed from a sudden change in photon flux alone. However, since my results cover only relatively high optical depths, corresponding to waters with considerable content of humus substances and the PAR attenuation coefficient also spans a rather wide range with high values (k = 0.8–2.5), we cannot yet generalize these results to environments with attenuation coefficients far below 1.0 and a narrow span of attenuation coefficients, characteristic of clearwater lakes and offshore marine environments. In the coastal Bothnian Sea, from where the present experimental plankton community was collected, the recorded range in attenuation coefficients between June and December 2013 was 0.300–1.425 (Båmstedt & Wikner, 2016). Unpublished own data from a moored Aanderaa Sea Guard instrument at 2 m depth also showed large hourly variations in turbidity and CDOM (Chromatic Dissolved Organic Matter), indicating mixing between water parcels with different optical characteristics. For estuaries, lakes, and rivers where episodic intrusion of brownified water are common, the present results should thus be of high relevance by showing that the phytoplankton community might

compensate for decreased photon flux by increased production efficiency.

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