Photosynthesis, carbon acquisition and primary productivity of phytoplankton: a review dedicated to *Colin Reynolds*

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Abstract The review intends to give an overview on developments, success, results of photosynthetic research and on primary productivity of algae both freshwater and marine with emphasis on more recent discoveries. Methods and techniques are briefly outlined focusing on latest improvements. Light harvesting and carbon acquisition are evaluated as a basis of regional and global primary productivity and algal growth. Thereafter, long-time series, remote sensing and river production are exemplified and linked to the potential effects of climate change. Lastly, the synthesis seeks to put the life achievements of Colin S. Reynolds into context of the subject review.

Keywords Production · Light harvesting · Growth · Regional · Global

All flesh is grass
(Isaiah 40:6).

Introduction

The assessment of photosynthetic rates and ecosystem production has a long tradition. Macfadyen (1948) recapitulated the early history and defined production, productivity and energy. Sakshaug et al. (1997) summarized theories, definitions and interpretations of photosynthetic parameters. A comprehensive recount of the history of plankton productivity measurements was compiled by Barber & Hiltling (2002).

Based on ecological energetics introduced by Lindemann (1942), the International Biological Program (IBP) analysed the transfer efficiency between trophic levels of ecosystems worldwide from 1964 to 1974 (Lith, 1975). Measurements of production at all major trophic levels in land, freshwater and marine ecosystems were an essential tool for the program (Cooper, 1975; Le Cren & Lowe-McConnell, 1980, Westlake et al., 1998) and the following 50 years (Williams et al., 2019). What is now called “Big data” and certainly is part of “Big Science” (Weinberg, 1961, 1967, Aronova et al., 2010) was perhaps

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founded during the IBP decade which formed the basis for the acceptance of long-term synoptic data collection often discriminated as “monitoring”. Consequently, the Long-Term Ecological Research Network (LTER) was initiated in 1977. Various aspects of production as well as standards for measuring primary production were assembled by Fahey and Knapp (2007) for a variety of ecosystems.

Ten years later in 1987, the Joint Global Ocean Flux Study (JGOFS) explored the exchange of carbon between the atmosphere, the ocean and the internal cycling. The program ran through to 2003 and became one of the early core projects of the International Geosphere-Biosphere Programme (IGBP, 1987–2015) dedicated to international research and climate change. In addition, two spin-off long-term projects were established in 1988 in the Atlantic and Pacific sea. Geider et al. (2001) offer a broad forum discussion on these developments and on biological factors and physical limitations of primary production of the planet.

The aim of the present review is to briefly summarize the historic development of primary productivity, highlight further progress and exemplify new insights into algal photosynthesis. A second aim is likewise to delineate the contributions Colin Reynolds has made to the field within his large oeuvre of publications. Since he amalgamated his expertise in two book chapters on ‘Pelagic and Benthic Ecology’ fusing marine and freshwater science (Reynolds, 2012a, b) and has worked on rivers as well (Reynolds & Descy, 1996) we decided to follow him at least partly in this respects.

A brief outline of methods and techniques

Numerous studies have compared methods for the estimation of primary production. To summarize the outcome, different techniques provide varying productivity rates, and no one produces “true” rates or estimates the “real” production. Methodology of production measurements, definition of major parameters and their common abbreviations are reviewed by Dokulil (2019). Concepts of phytoplankton productivity, a glossary of terms and common methods with an emphasis on fluorescence techniques are provided by Dokulil (2020). More information on fluorescence analysis can be gained from the reviews by Maxwell &

Johnson (2000), Murchie & Lawson (2013) and Kalaji et al. (2017). Estimation of production from growth or increase in biomass is outlined in Dokulil & Teubner (2020).

Most estimates of planktonic primary productivity originated in the past from in situ enclosures, mainly glass bottles, suspended at in situ depths for a certain period (e.g. Wetzel & Likens (1991)). A detailed history of the study of plankton productivity is provided by Barber & Hiltling (2002) and Berges & Reynolds (2003), extensively discussing various methods to measure primary productivity. Logistics of marine research vessels necessitated a change in methodology to ‘*simulated in situ*’ incubations on the deck of the ship. The procedure to simulate irradiances and temperature in deck incubations was also adopted for cruises on the River Danube by Dokulil & Holst (1990). The next logic step was to incubate samples under controlled conditions. Laboratory incubations in e.g. a photosynthetron were often used to evaluate photosynthetic characteristics of single taxa (e.g. Lengyel et al., 2015) or to develop algorithms to calculate in situ rates from these potential estimates (Kabas, 2004; Dokulil & Kabas, 2018). Simulated *in situ* conditions in the laboratory can be used to compare different biocoenoses, such as phytoplankton and phytobenthos (Riedler et al., 1999).

A multitude of techniques were developed using stable isotopes to routinely measure primary production. The most prominent isotopes for that are ^{13}C and ^{18}O . Relatively uncomplicated is the ^{13}C method in which H^{13}CO_3 is added as a tracer, like in the ^{14}C radiotracer procedure. Measuring productivity with ^{18}O is more laborious. Samples are usually enriched with H_2^{18}O over time. A brilliant overview has recently been published by Glibert et al. (2019). Details on isotope fractionation can be found in Fogel & Cifuentes (1993). Large-scale comparison of different methods was provided by Regaudie-de-Gioux et al. (2014).

The vast areas of the oceans necessitated a much higher spatial resolution of production estimates than conventional research operations by ship cruises could provide. Remote sensing from aircrafts and later from satellites paved the way (e.g. Sathyendranath & Platt 1993) and boosted a legion of algorithms, models and conversion factors (Behrenfeld & Falkowski, 1997b) still in progress as instrumentation and refinements evolve (Xu et al., 2016; Hampton et al., 2019). Remote

sensing and satellite observations were also adopted for inland waters (Bukata et al., 1995; Mishra et al., 2017) particularly for large lakes (e.g. Deng et al., 2017; Soomets et al., 2019).

Several different fluorescence techniques, briefly described in Dokulil (2020), tried to circumvent both the incubation and the associated timescale problem. Active in situ fluorescence allows quantification of productivity within seconds. A critical review with additional information on methodology is provided by Hughes et al. (2018a, b). The technique has been applied to freshwater by Kaiblinger et al. (2005), Kaiblinger & Dokulil (2006) and Kromkamp et al. (2008). A multiwavelength version of the instrument has been tested and applied in the Baltic Sea and Australian waters (Houliez et al., 2017; Hughes, 2018a). Recently, a new approach developed a bio-optical model of pelagic primary production based on variable fluorescence which was tested during two cruises in the Mediterranean Sea (Bonamano et al., 2020). When compared to concurrent estimates of ^{14}C -uptake, the new model came closer to radiocarbon measurements than other models predict. Performance in the open sea and inland lakes has yet to be tested.

An excellent overview and pairwise comparison of techniques for marine production was presented by Regaudie-de-Gioux et al. (2014) using oxygen evolution in light and dark (L/D) bottles, fast repetition rate fluorescence (FRRF) and approaches based on tracer additions (^{18}O , ^{14}C , and ^{13}C). The results of measurements by paired comparison of two different methods respectively are shown as ratios (Fig. 1). The authors conclude from many experiments that the ^{18}O method provides the most accurate measure of gross primary production (GPP).

Advanced sensor techniques allow now to return to the free water ΔO_2 estimates as in the early years of productivity measurements, particularly in streams and rivers (Odum, 1956). Data collected by high frequency measurements of diel O_2 or CO_2 changes and over depth profiles, if necessary, can be used to calculate primary production from free water gas exchange (Staehr et al., 2010; Obrador et al., 2014; Peeters et al., 2016). For further details consult Dokulil (2020) and the references therein. A detailed practical approach is included in Needoma et al. (2012).

For a comprehensive summary of respiration in aquatic ecosystems refer to del Giorgio & Williams

Fig. 1 Box whisker plot showing the variation of the primary production ratios measured by two different methods concurrently. The boxes show the 25% and 75% quartiles, the median as the central line, and the whiskers indicate maximum and minimum ratio. Modified from Regaudie-de-Gioux et al. (2014)

(2005). Carbon isotope fractionation in plant respiration is extensively discussed in Bathellier et al. (2017).

Light harvesting

The reviews by Larkum (2016) and Duanmu et al. (2017) provide superb summaries on algal light sensing, light harvesting and photo-acclimation as well as a short outline on the evolution of photosynthesis. Although evolution of eukaryote photosystems occurred independently from cyanobacteria for very long time, PSII and PSI reaction centres remain similar. Accessory light-harvesting complexes (LHCs) increase the absorption cross section of the core antennae of PSII and PSI of eukaryotic phototrophs. These LHCs exhibit a high degree of variability. In addition to the LHCs, 'algae have evolved a plethora of photoprotective mechanisms to

prevent damage by excess light’ as stated by Larkum (2016).

Photosynthetic species use light sensors to optimize light capture and light energy conversion in response to changing light conditions in the environment. Light sensors are rather diverse among photosynthetic eukaryotes with Flavin-based receptors as the most diversified class. For a detailed description and discussion on signalling, photoreceptors and their distribution consult Duanmu et al. (2017). See also subchapter on light harvesting in Dokulil (2020).

Effects of light acclimation and pigment adaptation on photosynthetic rates and efficiencies of phytoplankton indicate size related strategies as more important than the taxonomic composition of the assemblage. Adaptation to low light intensities occurs as result of a high chlorophyll-a to β -carotene ratio in small size fractions ($< 10 \mu\text{m}$) that have a high maximum light utilization coefficient (Teubner et al., 2001).

Experimental characterization of *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault (Cyanobacteria) from a bloom under ice indicated that photoadaptation to low light at temperatures of 2–5°C enabled effective photosynthesis of the overwintering population (Üveges et al., 2012).

Picocystis salinarum R.A. Lewin, a widespread planktonic green alga in saline lakes of the world, has been tested for its photosynthetic characteristic in chemostat culture by Pálmai et al. (2020). Photosynthetic activity remained low ($0.097\text{--}1.233 \text{ mg C mg}^{-1} \text{ Chl a h}^{-1}$) within the experimental temperature gradient (optimum at 31.9°C). This and all other photosynthetic characteristics indicate a preference for low light intensities by the taxon. Highest growth rates were obtained when grown in high concentrations of chloride and carbonate. The slow growth observed, and the low photosynthetic activity cannot explain the success of the species and must perhaps be seen in the high conductivity tolerance.

In the common “static” incubations of light and dark bottles, phytoplankton primary production may be incorrectly estimated because exposure time may be significantly longer than the response-time of phytoplankton to changing light. Ferris & Christian (1991) provide a critical review of experimental and modelling results. The inconclusive findings from both ‘reflect weaknesses in the simple formulations used to describe photosynthesis in relation to

irradiance and the dynamic responses to changing light’ as stated by Ferris & Christian (1991).

Carbon acquisition

An essential pre-requisite for photosynthesis is the availability and acquisition of inorganic carbon. The complex speciation and pH dependency of the inorganic carbon system triggered a debate already early in the 20th century whether only CO_2 or also bicarbonate can be used. The controversy was experimentally resolved by Ruttner (1921, 1948, 1949) who concluded that submersed macrophytes can use HCO_3^- in addition to CO_2 . Ruttner established two types of carbon uptake, the *Elodea*-type which can use HCO_3^- and the *Fontinalis*-type which cannot. Further development with indirect and direct methods is documented in Allen & Spence (1981) who analysed several species of microalgae and macrophytes. A major contribution to the photosynthesis and usage of carbon dioxide by *Fontinalis antipyretica* L. ex Hedw., a species also used by Rutter (1948, 1949), was provided by Maberly (1985a, b).

Carbon acquisition and associated algal evolution has been reviewed by Raven et al. (2012), Beardall & Raven (2016) and the ecological constraints have been elegantly summarized by Maberly (2014), Maberly & Gontero (2017), and Maberly & Madsen (2002) for angiosperms.

For net assimilation of dissolved inorganic carbon (DIC) to organic substance, all cyanobacteria and eukaryotic microalgae rely on the enzyme ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) and the Photosynthetic Carbon Reduction Cycle (known as the Calvin Cycle). Rubisco is thus the core carboxylation enzyme and is involved in over 99% of primary production on the planet. All cyanobacteria and dinoflagellates, and most other eukaryotic microalgae, have biophysical CO_2 concentrating mechanisms (CCMs) with active transport across membranes.

Aquatic autotrophs primarily need to maximize CO_2 uptake, exploit carbon reserves and avoid carbon limitation. Both carbon dioxide limitation and stimulation of productivity has been recently reconsidered (Kragh & Sand-Jensen, 2018, Hamdan et al., 2018). The speciation of DIC in inland waters contains carbon dioxide, bicarbonate and carbonate linked by

equilibria related to pH-increase. It must be noted here that the rate of gas diffusion in water is exceedingly different from the one in air. For CO₂, for instance, the rate is about 10,000 × lower in water than in air. Rates of O₂ diffusion in water are similarly lower.

Influx and efflux of DIC is difficult to differentiate in plant cells. Raven & Beardall (2016) present schematic models of inorganic carbon transport in cyanobacteria (see also Price et al., 2002) and eukaryotic algae. The relative role of permeation and movement is still controversial. There is some evidence of active CO₂ transport at the plasmalemma of algae. All cyanobacterial and some algal CCMs also have an active influx of HCO₃[−] at the plasmalemma and can enter chloroplasts of some algae. Half or less of the gross inorganic C entering in the CCM can leak from the intracellular pool, sometimes as HCO₃[−], but usually as CO₂. Significant leakage in many photoautotrophs with CCMs increases the energetic cost of net inorganic carbon fixation.

In this context, the question arises how freshwater biota will cope with rising atmospheric concentrations (reviewed by Low-Décarie et al., 2014) and its partial pressure (Hasler et al., 2016). The partial pressure of CO₂ (pCO₂) varies across systems controlled by a variety of factors. Rising CO₂ levels due to climate change will have direct and indirect effects on pCO₂. The pCO₂ might increase photosynthesis of plankton and macrophytes and alter community structure (Hasler et al., 2016). A meta-analysis of 22 microalgal studies by Brown et al. (2019) indicates substantial alterations of water chemistry, nutrient acquisition, photosynthesis, carbon uptake and growth (see Fig. 1 in Brown et al., 2019). Since these results are all based on controlled experiments, long-term field measurements in various types of freshwater ecosystems are needed to increase predictability.

Finally, some cyanobacteria and eukaryotic microalgae can take up dissolved organic matter by osmochemoorganotrophy or combined with photosynthesis in osmomixotrophy. Some eukaryotic microalgae obtain energy by phagochemoorganotrophy or, combined with photosynthesis, in phagomixotrophy. Regardless of whether the organic carbon needed for growth is obtained by photolithotrophy or (mixo)chemoorganotrophy, anaplerotic DIC assimilation is needed to supply C skeletons for synthesis of a range of cell components. Known as

‘dark fixation’ this is the only DICC assimilation occurring in the dark (Beardall & Raven, 2016).

Moreover, aerobic anoxygenic phototrophic bacteria (AAP) have been detected in several inland waters (Mašín et al., 2008; Ferrera et al., 2017; Tian et al., 2018). These organisms represent a functional group belonging to Alpha- Beta- and Gammaproteobacteria, are obligate aerobic and photoheterotrophic. AAP bacteria harvest light by anoxygenic photosynthesis as energy source using Bacteriochlorophyll but lack carbon fixation and do not produce oxygen (Koblížek, 2015). Global impact of anoxygenic photosynthesis is usually considered as negligible but might still be an indispensable component of ecosystems (Hanada, 2016).

Primary productivity and growth

Primary production and growth are intimately connected depending on each other or are two sides of the same medal as discussed by Reynolds (1983a) in his publication ‘production and dynamics of *Fragilaria*’. Consequently, growth rates formed a focal point in Colin’s research (Reynolds, 1972, 1983b, 1985). He developed the concept of population increase subsequently further linking growth to physical variability of the environment (Reynolds, 1989, 1996a). For model building Reynolds & Irish (1997) recommended to use maximum specific growth rates from cultures as base. In the introduction to his essay on ‘interannual variability in phytoplankton production’ (Reynolds, 2002), he questioned the immanent controversy between production and growth e.g. doubted by Berman-Frank & Dubinsky (1999) and Dubinsky & Berman-Frank (2001).

Information on phytoplankton growth and photosynthesis was comprehensively reviewed for clonal cultures by Geider (1993) and Sakshaug (1993). The maximum quantum efficiency of photosynthesis appeared to be largely independent of irradiance. Respiration and excretion rates and the variability in the chlorophyll-a:carbon ratio cause uncoupling of growth from gross photosynthesis.

Based on growth rates, Moigis & Gocke (2003) developed a dilution method to estimate phytoplankton primary production. A grazer impact study on marine phytoplankton showed that estimates of production from dilution experiments are reasonable

proxies for ^{14}C determined production (Calbet & Landry, 2004). Simultaneous experiments with both methods in three ocean regions correlated with an r^2 of 0.76 (Fig. 2), for details see Laws et al. (2000). Dilution experiments have also been carried out to assess the dynamics of marine picophytoplankton (Worden et al., 2004). It seems that the dilution technique has not been tested in inland waters so far as turned out from an extensive literature survey.

Long-time series of primary production

Very long-time series of primary production measurements are not quite common. Such long-term observations can be used ‘inter alia’ to detect structural changes, trends, shifts and as calibration sets for remote sensing and model building.

Perhaps the longest continuous time series anywhere in the world is a 55-year sequence in the Adriatic Sea (Kovač et al., 2018). Monthly measurements in the photic zone began in 1962 and continue to date. Most of the chlorophyll-specific C-uptake rates

(PB, $\text{mg C mg Chl}^{-1} \text{ h}^{-1}$) from the 185 cruises fell in the range of 2–4 (median 3.7, mean 5.2 ± 4 , see Fig. 2 in Kovač et al., 2018). During the 55-year period, five distinct regimes were distinguished by the regime shift detection method of Rodionov (2004). Regimes are differentiated by either lower or higher average production associated with changes in chlorophyll-a concentration. Variation of average PB rates, however, were marginal. Results of the 55 observational years were used to calibrate remotely sensed chlorophyll, to model depth profiles of production and to improve production model calculations.

In freshwaters, long-term records of primary production estimation derive from several lakes. Records of annual primary production start in Lake Peipsi, Estonia in 1970 and continue to 2005. Long-term average production is $200 \text{ g C m}^{-2} \text{ y}^{-1}$ (Laugaste et al., 2008). For Lake Võrtsjärv, Estonia carbon uptake per year is reported since 1982 (Nöges et al., 2004, 2011). The long-term annual primary production of $208 \pm 27 \text{ g C m}^{-2} \text{ y}^{-1}$ is close to the nutrient-saturated production boundary for the latitude where light limitation dominates. In Lake Kinneret, Israel measurements persist for now 40 years starting in 1972 (Berman et al., 1995; Yacobi, 2006; Ostrovsky et al., 2013). The most interesting fact in these examples is that annual production does not show any trend. Chlorophyll-a concentrations increased, and chlorophyll-specific productivity declined since 1990 in all three lakes. These changes were related to adaptation to reduced light availability.

Lakes Võrtsjärv and Peipsi also served to estimate whole lake production Nöges et al. (2010). Epiphyte production in both lakes was very low in comparison with that of phytoplankton and macrophytes 0.01 , 5.04 , and $6.97 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively, in Lake Võrtsjärv, and 0.02 , 1.93 , and $10.5 \text{ g C m}^{-2} \text{ day}^{-1}$, respectively, in Lake Peipsi. Production of the littoral area contributed 10% of the total summer primary production of Lake Peipsi and 35.5% of the total summer production of Lake Võrtsjärv (see also Table 7 in Dokulil & Teubner, 2020).

Average annual production in the water column was $97 \text{ g C m}^{-2} \text{ year}^{-1}$ for the period 1970 to 1982 indicating oligotrophic conditions in a time series in Stechlinsee 1970 to present (Koschel et al., 2002). After a nine-year break from 1983 to 1991, column production of $123 \text{ g C m}^{-2} \text{ year}^{-1}$ for the 1990s signal a slightly eutrophic status if $120 \text{ g C m}^{-2} \text{ year}^{-1}$ are

Fig. 2 Relation of calculated (CP) to ^{14}C -based estimates of daily primary production (PP) from dilution experiments conducted in three ocean regions (not differentiated here). Calculated primary production was obtained by multiplying phytoplankton growth rates times mean phytoplankton concentration expressed in terms of carbon. Carbon conversion was obtained from volumetric estimates of the phytoplanktonic community and established carbon to biovolume conversions Modified and re-plotted as log–log after Calbet & Landry (2004)

accepted as boundary for dimictic temperate lowland lakes (Dokulil, 2014a). The 1990s were a period characterized by year-to-year changes in phytoplankton composition, primary production, and specific photosynthetic activity (Padisak et al., 1997), perhaps representing an ecosystem in a primitive stage of persistent re-establishment' sensu Reynolds (1997).

In an urban lake in Vienna, average annual column chlorophyll-specific production declined from 13 mg C mg Chl-a⁻¹ during the eutrophic years 1993–1995 to about 6 mg C mg Chl-a⁻¹ almost 20 years later due to rehabilitation of the system following restoration (Dokulil & Kabas, 2018). The system switched from phytoplankton to macrophyte dominated in 2004. Consequently, the quotient of phytoplankton to macrophyte carbon calculated in tons for the whole lake declined from 2489 to 0.8 (see Table 10.4 in Dokulil & Kabas, 2018).

Miller (2013) compared changes in productivity of Arctic tundra ponds over 40 years estimated via historic and modern methods. Average chlorophyll-a concentrations exceeded the 1970–1973 values (0.2–1.5 µg Chl-a L⁻¹) in July and August ranging from 1.3 to 2.2 µg Chl-a L⁻¹. Carbon uptake rates by phytoplankton were marginally greater in June 2011/2012 when compared to the 1970/1973 data. Rates in both periods varied considerably over the growing season from 0.8 to 6.3 mg C L⁻¹ h⁻¹ peaking in June. Rising temperatures, increased nutrient concentrations and permafrost thaw are driving factors for the observed changes. Moreover, free water metabolism of oxygen indicated ponds to be net autotrophic.

Remote sensing

The spatio-temporal primary production of Lake Taihu, China, was mapped using the Moderate Resolution Imaging Spectroradiometer (MODIS) and a vertically generalized production model (Deng et al., 2017). Model result correlated significantly with in situ measurements ($R^2 = 0.753$, $P < 0.001$, $n = 63$). The average annual mean daily primary production of Lake Taihu was 1094 ± 720 mg C m⁻² d⁻¹ for the 11-year period 2003 to 2013. Long-term primary production maps estimated from the MODIS data demonstrated marked temporal and spatial variations. Production in bays was consistently higher than in the open water of Taihu caused by higher

chlorophyll-a levels as a result of higher nutrient concentrations in-shore. Spatial variations were also affected by wind in this large, eutrophic, and shallow lake.

Combining a model with remote sensing data, Rousseaux & Gregg (2014) evaluated the contribution of four phytoplankton groups to the annual total primary production in the ocean for the period 1998–2011. Diatoms contributed the most with about 50% (equivalent of 20 PgC·y⁻¹). Coccolithophores and chlorophytes contributed ~ 20% each (~ 7 PgC·y⁻¹) while cyanobacterial added around 10% (~ 4 PgC·y⁻¹). Greatest interannual variability occurred in the Equatorial Pacific associated with climate variability as indicated by significant correlation ($p < 0.05$) between the Multivariate El Niño Index and the group-specific primary production of all groups except coccolithophores. In the Atlantic, climate variability was significantly correlated to the primary production of two groups out of four, namely diatoms and cyanobacteria in the North Central Atlantic, and chlorophytes plus coccolithophores in the North Atlantic, as indicated by the NAO Index.

Dörnhöfer & Oppelt (2016) summarized recent advances in remote sensing indicators to study various aspects of inland waters. Primary production is only circumstantially mentioned via related parameters such as transparency. Nevertheless, the review is worth reading since it provides a review of available sensors, methods and algorithms, as well as lists of studies in the field.

Productivity of rivers

Primary production in flowing waters is commonly evaluated as community production in streams from diurnal open water oxygen curves (Cox, 2003; Webster et al., 2005; Uehlinger, 2006). Estimates of plankton production in large rivers are not as common as assessments in lakes. Several ecologists have argued that the characteristics of many large rivers, deep and turbid, prevent phytoplankton to be of any significant importance. In contrast, Reynolds (1994a, b) investigated river plankton intensively both theoretical (1988, 1996b) and practical (Reynolds & Glaister, 1989, 1993). A few investigations shall illustrate the present status. Production in tropical

stream and rivers is summarized by Davies et al. (2008).

Daily integrated production measured in the main-stem along a 1700-km stretch of the Congo River, DR Kongo, Africa varied between 64.3 and 434.1 mg C m⁻² day⁻¹ in falling water conditions and between 51.5 and 247.6 mg C m⁻² day⁻¹ when water was high (Descy et al., 2017). Phytoplankton biomass in the Congo River was likely restricted by hydrological factors. Results from this study indicate that phytoplankton growth in the main channel of the Congo River can occur due to hydrological processes maintaining phytoplankton biomass even during high water. This contrasts with other tropical river systems where connectivity with the floodplain, the presence of natural lakes and man-made reservoirs play a prominent role in the recruitment of phytoplankton to the main river.

During a longitudinal survey of the River Danube from km 2510 downstream to the delta (Dokulil, 2014b) instantaneous FRRF signals were obtained and converted to daily integral oxygen production (Fig. 3). Column production remained below 1 g O₂ m⁻² day⁻¹ in the upper reach until river km 1500 and increased thereafter rapidly up to 12.6 g O₂ m⁻² day⁻¹

at river km 1262 (Fig. 3B). Similarly, the low chlorophyll-a concentration of the upper reach increased between river km 1481 and 1132 reaching its maximum of 18.3 mg Chl-a m⁻³ at km 1200 downstream of the River Tisa confluent (Fig. 3A). The following rapid decline of both chlorophyll and production, previously ascribed to zooplankton grazing, has now be assigned by more detailed analysis to sedimentation and loss rates by dilution due to discharge from large tributaries (Dokulil, 2015, Fig. 4 and associated text). Chlorophyll concentrations increased again for the lower 800 river km towards the delta but are not reflected in production or PB rates because of strongly increasing turbidity intercepting photosynthetic light (Dokulil, 2015). Chlorophyll-specific production (PB) varied considerably between stations (Fig. 3C). Rates were in the range of 2–25 g O₂ g Chl-a⁻¹ h⁻¹. Highest rates occurred in the impounded section Gabčíkovo (River km 1842) and Iron Gate II (river km 865). Potamoplankton and primary production proliferate in the middle section of the River Danube where environmental conditions are optimal for planktonic growth.

Dynamics of phytoplankton primary production were followed in the Rybinsk reservoir, Upper Volga,

Fig. 3 Longitudinal transect of the Danube from stream km 2500 to the delta obtained from FRRF-measurements during JDS2 in August/September 2007. **A** Concentration of chlorophyll-a (Chl-a) from delayed fluorescence (DF). **B** Daily integrated column production ($\Sigma\Sigma$ PP) as g O₂ m⁻² d⁻¹ calculated from fast repetition rate fluorescence (FRRF). **C** Hourly maximum chlorophyll-specific productivity (PB) calculated from A and B. Samples were taken in the middle of the river at all stations. Data were redrawn from Dokulil & Kaiblinger (2008) and modified from Dokulil (2014b)

Fig. 4 Average depth-integrated daily primary production (ΣP g C m⁻² d⁻¹) for six stations in the Rybinsk Reservoir, River Wolga, Russia in the years 2009 and 2010 Modified from Kopylov et al. (2019)

Russia during the years 2005 to 2014 (Kopylov et al., 2019). Production increased significantly during these years (Table 1) particularly in 2010 when water temperatures rose to 27.9°C (Fig. 4). Besides various environmental factors, the authors claim that production was related to the index of the North Atlantic Oscillation.

River systems play an important role in the carbon transport between terrestrial ecosystems, the atmosphere and the ocean affecting the global carbon cycle. When rivers are regulated, carbon processing is altered

Table 1 Annual gross primary production per m³ (GPP) and column production per m² (ΣP) both per day in Rybinsk Reservoir, Volga for 2005 to 2014

Year	GPP mg C m ⁻³ d ⁻¹		ΣP mg C m ⁻² d ⁻¹	
	Min–max	Mean ± SD	Min–max	Mean ± SD
2005	13–955	225 ± 38	59–2005	588 ± 100
2006	1–832	192 ± 28	4–2095	564 ± 52
2007	2–736	256 ± 46	5–2205	808 ± 160
2008	2–559	122 ± 10	11–1762	408 ± 122
2009	1–763	207 ± 51	4–1911	554 ± 118
2010	9–1667	360 ± 97	10–5249	859 ± 242
2011	49–2056	495 ± 95	93–3058	936 ± 170
2012	14–1475	419 ± 84	45–2789	883 ± 84
2013	14–2208	485 ± 61	24–3246	834 ± 88
2014	14–1093	397 ± 44	24–2834	803 ± 102

Indicated is the range minimum to maximum and mean plus standard deviation (SD). From Kopylov et al. (2019)

along the river continuum. Engel et al. (2019) examined the phytoplankton along a 74 km river stretch of the River Saar, Germany to analyse the effect of cascading impoundments (six navigation dams) on riverine metabolism. GPP was calculated from continuous measurements of dissolved oxygen. For the first 26.5 km of the river, production rose 3.5-fold (difference 0.45 g C m⁻³ d⁻¹) while chlorophyll-a increased over the entire stretch by 2.9 (8.7 µg L⁻¹). Cascading impoundments potentially promote river-GPP and hence C-uptake can become important in dammed rivers.

Sellers & Bukaveckas (2003) based their analysis of a regulated section of the Ohio River on mass balance assessment. Development of phytoplankton biomass was constraint by light availability and transit time. NPP per day was negative during high discharge, varied between 100 mg C m⁻³ d⁻¹ and near zero at moderate discharge, and between 300 mg C m⁻³ d⁻¹ and negative NPP at low discharge. Observations were generally in good agreement with model predictions.

Regional productivity of lakes

The huge number of studies on lake production worldwide makes it virtually impossible to summarize results exhaustively. The intention here is to present a few regional-specific examples of primary productivity estimates using advanced techniques or obtaining results for certain assemblages. The wide range of regional production estimates from lakes worldwide is then summarized on a geographical basis.

Fluorescence techniques enable the estimation of photosynthetic efficiency of specific phytoplankton assemblages in situ. Using a Phyto-PAM analyser, Li et al. (2014, 2016) and Sheng et al. (2014) measured variable to maximum fluorescence (Fv/Fm), a proxy of potential photosynthesis in Lake Taihu and Lake Qiandao, China (Table 2). Low Fv/Fm ratio of diatom-dinoflagellate assemblage in spring suggest high efficiency at low light intensity. Highest quantum yield occurred in Chlorophytes in spring and autumn while significant photosynthetic activity of diatoms was observed in winter. These results highlight the need for more algal group-specific in situ studies as well as the importance of observations during winter.

Floodplain lakes are controlled by their hydrological connectivity determining through flooding and

Table 2 Ranges of variable to maximal fluorescence (Fv/Fm) for Cyanobacteria, *Microcystis*, Chlorophytes and a diatom-dinoflagellate assemblage in Tai Hu for spring and autumn (Li et al., 2014, 2016) and for diatoms in Qiandao Hu, a dendritic reservoir in winter (Sheng et al. 2014)

Taihu	Spring	Autumn	Winter
Cyanobacteria	0.35–0.49	0.34–0.53	n.m.
<i>Microcystis</i>	0.28–0.55	0.28–0.45	n.m.
Chlorophytes	0.34–0.68	0.55–0.68	n.m.
Diatoms/Dinos	0.09–0.56	0.28–0.61	n.m.
<i>Qiandao Lake</i>			
Diatoms	n.m.	n.m.	0.48–0.63

n.m. not measured

water level changes macrophyte or plankton dominance (Dokulil et al., 2006). Singh et al. (2018) provide an example from two floodplain lakes of north Bihar, India. Estimates of photosynthetic productivity by phytoplankton were based on conventional oxygen L/D -bottle technique. Production was rather similar in both lakes, but community respiration was remarkably high due to eutrophication by sewage input (Table 3). Flood water and level changes determined phytoplankton biomass versus macrophyte development.

Michelutti et al. (2005) used a novel technique, reflectance spectroscopy, to infer historical trends in lacustrine primary production from lake sediment chlorophyll-a concentration from six arctic lakes on Baffin Island, Canada. Concentrations of sediment chlorophyll and derivatives dramatically increased within the upper-most 4 cm of the cores deposited during the 20th century parallel to other proxies of aquatic production. Increasing aquatic production

seems to be triggered by climate warming as these lakes enter into new biological regimes.

The oxygen flux method was applied by Attard et al. (2014) to measure rates of benthic primary production habitats in a Greenland fjord. The shallow sites produced up to $43.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ during spring and summer which were therefore on average autotrophic. During winter and spring these sites were heterotrophic or near to metabolic equilibrium. Gross primary production occurred all year-round responding seasonally to changing light levels by keeping photosynthetic efficiency high. The annual average rate was $11.5 \text{ mol O}_2 \text{ m}^{-2} \text{ y}^{-1}$ which is approximately 1.4 times greater than the column integrated GPP of the fjord. These results point to the significance benthic photosynthesis can have in ecosystems.

Since lakes are not uniformly distributed around the globe, regional freshwater primary production largely depends on climatic zone, latitude and altitude (Lewis, 1996). Further components are the availability of dissolved organic carbon (DOC) summarized by Sobek et al. (2007) and the trophic level of the waterbody (Dokulil, 2014a), among others. Gradients of ecosystem components across latitude represent a high degree of complexity described with information theory by Fernández et al. (2017). The simulation analysis considered a wide variety of variables including GPP in four lake regions: arctic, northern highland, northern lowland, and the tropics. Results indicate that temporal variables significantly influence seasonality within the gradient. These latitudinal gradients can be similar or may deviate from gradients in elevation.

To visualize and evaluate potential gradients of lake GPP versus latitude and elevation, data from 140

Table 3 Range and mean with standard deviation (SD) of gross primary production (GPP), net primary production (NPP) and community respiration (CR) as $\text{gC m}^{-2} \text{ day}^{-1}$; ratio

Parameters	Tarawe <i>chaur</i>		Gamharia <i>chaur</i>	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
GPP	1.85–4.99	2.87 ± 1.11	1.32–3.96	2.40 ± 0.78
NPP	1.04–3.38	1.85 ± 0.84	0.73–2.62	1.38 ± 0.54
CR	0.49–1.82	1.07 ± 0.33	0.59–1.48	1.01 ± 0.28
NPP:GPP	0.51–0.76	0.64 ± 0.08	0.50–0.66	0.57 ± 0.04
CR as % of GPP	24.18–49.23	34.46 ± 8.05	33.9–49.53	42.79 ± 4.40

NPP:GPP and *R* as % of GPP for two floodplain lakes (Chaur) in North Bihar (from Singh et al., 2018)

lakes from the southern and northern hemisphere have been assembled in Fig. 5 in three-dimensional form (Fig. 5A) and as projection into the latitude-altitude space (Fig. 5B) to facilitate interpretation. The basic data and their references are attached as Table A in the Annex. Data are classified into trophic categories according to annual average column production using tables summarized in Dokulil (2014a). Productivity north and south of 60° latitude is in general low and hence lakes are oligotrophic. The same is true for altitudes above 2000 m and latitudes between 20° and 60°. At elevations lower than 1000 m lake production is highly variable and can therefore attain any trophic level. Closer to the equator (< 25° N or S) production rates generally increase and, consequently, the number of eutrophic and particularly hypertrophic lakes dramatically rises at all altitudes. Lakes with production rates qualifying them into meso- to hypertrophic status occur even around 3000 meters altitude. However, some lakes remain low in productivity even near the equator. This largely reflects lake characteristics not included here, such as surface area, depth, mixing regime or nutrient status (e.g. Staehr et al., 2012). The pattern emerging in Fig. 5A, B however, agrees with Lewis (2011) that incident irradiance has a pronounced effect on potential primary production in lakes at different latitudes and that both light and nutrients are important as Staehr et al. (2016) concluded. This view was extended to predict how pelagic production in lakes will respond to global changes in the environment (Häder et al., 2014; Kelly et al., 2018).

Production at the global scale

World-wide many vertical profiles of daily integrated photosynthetic rates have been acquired from many freshwater ecosystems and regions of the sea. These profiles vary by 4–5 orders of magnitude between stations, but their variability can be accounted for by chlorophyll concentration, photoperiod and optical depth as Behrenfeld & Falkowski (1997a) demonstrated with 1000 randomly selected profiles from the ocean (reproduced in Falkowski & Raven, 2007 as Fig. 9.6). Normalized to chlorophyll-specific hourly production versus optical depth, daily production ranging from 0.1 to over 1000 mg C m⁻³ d⁻¹ was thus reduced to 0.1 to 30 mg C m⁻³ h⁻¹. Similarly,

one hundred profiles from inland lakes covering about the same range as the ocean profiles normalize to (0.1)1–20 mg C m⁻³ h⁻¹ (Dokulil et al., 2005 Abb.8, reproduced in Dokulil, 2020).

The global distribution of net production seems somewhat paradoxical because the seemingly high tropical productivity on land has no counterpart in tropical marine productivity, at least not for the open sea. Instead, greatest ocean production occurs at high latitude, particularly in the northern hemisphere declining towards the equator. Huston & Wolverton (2009) resolved this paradox by the unexpected conclusion from their meta-analysis that ecological relevant terrestrial productivity is highest at temperate latitudes.

Global net primary productivity per unit area was currently estimated by Lewis (2011) for lakes as 260 g C m⁻² y⁻¹ (GPP 360 g C m⁻² y⁻¹, respiration 100 g C m⁻² y⁻¹). The global totals add up to 1.3 Pg C y⁻¹ GPP and 0.3 Pg C y⁻¹ algal respiration, leaving about 1 Pg y⁻¹ net production derived from lakes. An estimated 1% of all global net photosynthesis is due to lake production. NPP per unit area is depicted for several global components in Fig. 6. With some 1200 g C m⁻² y⁻¹, wetlands are 3 × more productive than terrestrial vegetation per unit area and almost 10x greater than NPP in marine environments which in turn is substantial smaller than Lake net production per area.

The above estimate for annual net production for lakes of 1 Pg y⁻¹ nicely fits to the perhaps more detailed analysis of the carbon cycle by Cole et al. (2007). Cole and his co-authors conservatively estimated that inland waters receive about 1.9 Pg y⁻¹ from terrestrial sources. Approximately 0.2 Pg are buried in aquatic sediments while at least 0.8 Pg are returned to the atmosphere by gas exchange and the remaining 0.9 Pg y⁻¹ are exported to the sea. That means that roughly half of the carbon entering inland waters is finally transported from land to the oceans. Freshwater systems although small in area can have profound effects on regional carbon balance.

Global net primary production integrated over terrestrial and oceanic components yielded 104.9 petagrams carbon per year according to Field et al. (1998). Total NPP is unevenly distributed from north to south with a maximum near the equator, essentially due to terrestrial production and a second high between 30° and 60° N. Two seasonal maxima appear

Fig. 5 Annual average column gross primary production ($\Sigma\Sigma P$ g C m⁻² y⁻¹) versus latitude and altitude for 140 lakes from the northern and southern hemisphere (not differentiated on the x axis). Annual average daily GPP was multiplied by 365 when necessary. The trophic status is indicated in four production categories for each case (see Dokulil, 2014a). A. as 3D graph, B as 2D using latitude and altitude. The complete data are listed in Table A in the Annex

Fig. 6 Net primary production per unit area for global components Modified from Lewis (2011, Fig. 38)

in ocean NPP at 60° to 40° N and at about 40° S (see Fig. 2 in Field et al., 1998, or Fig. 11 in Dokulil, 2020).

A report on the world's coastal phytoplankton primary production synthesizing 1148 values, largely based on ¹⁴C measurements, from estuaries, bays, lagoons, fjords and inland seas covering latitudes from 80°N to 40°S was compiled by Cloern et al. (2014). The median value for annual phytoplankton primary production was 185 g C m⁻² y⁻¹ and the mean 252 g C m⁻² y⁻¹ in 131 ecosystems widely ranging from 105 to 1890 g C m⁻² y⁻¹. Production varied 10-fold within ecosystems and fivefold interannually.

Resumé

When we embarked on this endeavour, our expectation was that the hype of primary productivity studies in marine and freshwaters lays in the past. A quick survey crystalized that even after about 100 years of theoretical and practical efforts to estimate aquatic primary production, many challenges and open questions remain which are reflected in an almost overwhelming number of publications in the field. In addition, new problems and their interactions such as climate warming (Williamson et al., 2019), toxic algal blooms (Wurtsbaugh et al., 2019) or microplastic (Yokota et al., 2017) among many others need further concepts, experiments and methodological improvements linking research with practice.

The combination of fundamental research and practical application has always been imperative for Colin Reynolds. Perhaps his most undervalued

publication, 'Vegetation processes in the pelagic: A model for ecosystem theory' (Reynolds, 1997), evidently synthesizes the logic structure of his theories, achievements, and conclusions. In this book chapters III and IV review all details of photosynthesis, primary production and growth known at that time while chapter IX summarizes lessons and applications.

To quote from Colin's tailpiece: 'If we understood our own ecology better, we might become more responsible citizens of the Earth and become the architects of a planetary rehabilitation.'

You cannot add anything to that statement.

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References

- Allen, E. D. & D. H. N. Spence, 1981. The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytology* 87: 269–283.
- Aranova, E., K. S. Baker & N. Orekes, 2010. Big Science and Big Data in Biology: from the International Geophysical Year through the International Biological Program to the Long Term Ecological Research (LTER) Network, 1957–Present. *Historical Studies in the Natural Sciences* 40: 183–224.
- Attard, K. M., R. N. Glud, D. F. McGinnis & S. Rysgaard, 2014. Seasonal rates of benthic primary production in a Greenland fjord measured by aquatic eddy correlation. *Limnology Oceanography* 59: 1555–1569.
- Barber, R. T. & A. K. Hilting, 2002. History of the study of plankton productivity. In Williams, P. J., D. N. Thomas & C. S. Reynolds (eds), *Phytoplankton Productivity*. Carbon

- Assimilation in Marine and Freshwater Ecosystems. Blackwell Science, Oxford: 16–43.
- Bathellier, C., F. W. Badeck & J. Ghashghaie, 2017. Carbon isotope fractionation in plant respiration. In Tcherkez, G. & J. Ghashghaie (eds), *Plant Respiration: Metabolic Fluxes and Carbon Balance Advances in Photosynthesis and Respiration (Including Bioenergy and Related Processes)*. Springer, Cham.
- Beardall, J. & J. A. Raven, 2016. Carbon acquisition by microalgae. In Borowitzka, M., J. Beardall & J. Raven (eds), *The Physiology of Microalgae. Developments in Applied Phycology*. Springer, Cham: 89–100.
- Behrenfeld, M. J. & P. G. Falkowski, 1997a. Photosynthetic rates derived from satellite-based chloro-phyll concentration. *Limnology* 42: 1–20.
- Behrenfeld, M. J. & P. G. Falkowski, 1997b. A consumer's guide to phytoplankton primary productivity models. *Limnology Oceanography* 42: 1479–1491.
- Berges, J.A. & C.S. Reynolds, 2003. Microalgal ecology. In: Norton T.A. (ed), *Out of the Past. Collected reviews to celebrate the Jubilee of the British Phycological Society*. Publ. by BPS, print. in Belfast, pp. 131–150.
- Berman, T., L. Stone, Y. Z. Yacobi, B. Kaplan, M. Schlichter, A. Nishri & U. Pollinger, 1995. Primary production and phytoplankton in Lake Kinneret: a long-term record (1972–1993). *Limnology Oceanography* 40: 1064–1076.
- Berman-Frank, I. & Z. Dubinsky, 1999. Balanced growth in aquatic plants: myth or reality? *Bioscience* 49: 29–37.
- Bonamano, S., A. Madonia, V. Piermattei, C. Stefani, L. Lazara, I. Nardello, F. Decembrini & M. Marcelli, 2020. Phyto-VFP: a new bio-optical model of pelagic primary production based on variable fluorescence measures. *Journal of Marine System* 204: 103304.
- Brown, T.-R., M. J. Lajeunesse & K. M. Scott, 2019. Strong effects of elevated CO₂ on freshwater microalgae and ecosystem chemistry. *Limnology Oceanography* 65: 304–313.
- Bukata, R. P., J. H. Jerome, A. S. Kondratyev & D. V. Pozdnyakov, 1995. *Optical Properties and Remote Sensing of Inland and Coastal Waters*. CRC Press, Boca Raton.
- Calbet, A. & M. R. Landry, 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology Oceanography* 49: 51–57.
- Cloern, J. E., S. Q. Foster & A. E. Kleckner, 2014. Phytoplankton primary production in the world's estuarine-coastal ecosystems. *Biogeosciences* 11: 2477–2501.
- Cole, J. J., Y. T. Prairie, N. F. Caraco, W. H. McDowell, L. J. Tranvik, R. G. Striegl, C. M. Duarte, P. Kortelainen, J. A. Downing, J. J. Middelburg & J. Melack, 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10: 171–184.
- Cooper, J. P. (ed.), 1975. *Photosynthesis and productivity in different environments*. University Press, Cambridge.
- Cox, B. A., 2003. A review of dissolved oxygen modelling techniques for lowland rivers. *Scientific Total Environment* 314–316: 303–334.
- Davies, P. M., S. E. Bunn & K. St. Hamilton, 2008. Primary production in tropical streams and rivers. In Dudgeon, D. (ed.), *Tropical Stream Ecology*. Elsevier, Amsterdam: 23–42.
- Del Giorgio, P. & P. Williams, 2005. *Respiration in Aquatic Ecosystems*. Oxford University Press, Oxford.
- Deng, Y., Y. Zhang, D. Li, K. Shi & Y. Zhang, 2017. Temporal and spatial dynamics of phytoplankton primary production in Lake Taihu derived from MODIS data. *Remote Sensing* 9: 195.
- Descy, J.-P., F. Darchambeau, T. Lambert, M. P. Stoyneva-Gaertner, S. Bouillon & A. V. Borges, 2017. Phytoplankton dynamics in the Congo River. *Freshwater Biology* 62: 87–101.
- Dokulil, M. T., 2014a. Photoautotrophic productivity in eutrophic ecosystems. In Ansari, A. A. & S. S. Gill (eds), *Eutrophication: Causes, Consequences and Control*. Springer, Dordrecht: 99–110.
- Dokulil, M. T., 2014b. Potamoplankton and primary productivity in the River Danube. *Hydrobiologia* 729: 209–227.
- Dokulil, M. T., 2015. Phytoplankton of the River Danube: composition, seasonality and long-term dynamics. In Liska, I. (ed.), *The Danube River Basin Handbook Environmental Chemistry*. Springer, Berlin: 411–428.
- Dokulil, M. T., 2019. Gross and net production in different environments. In Fath, B. D. (ed.), *Encyclopedia of Ecology*, 2nd ed. Elsevier, Oxford.
- Dokulil, M. T., 2020. Phytoplankton productivity. In Mehner, T. & K. Tockner (eds), *Encyclopedia of Inland Waters*, 2nd ed. Elsevier, Oxford.
- Dokulil, M.T. & I. Holst, 1990. Methods of biological sampling. Phytoplankton–photosynthesis. In: Humpesch, U.H. & J.M. Elliott (eds), *Methods of Biological Sampling in a Large Deep River: the Danube in Austria*. Wasser und Abwasser 2/90: 17–23.
- Dokulil, M. T. & W. Kabas, 2018. Phytoplankton photosynthesis and production. In Dokulil, M. T., K. Donabaum & K. Teubner (eds), *The Alte Donau: Successful restoration and sustainable management*. Aquatic Ecology Series, Vol. 10. Springer, Berlin: 149–162.
- Dokulil, M. T. & C. Kaiblinger, 2008. Phytoplankton. In: Liška, I., F. Wagner & J. Slobodník (eds), *Joint Danube Survey 2, Final Scientific Report*. ICPDR—International Commission for the Protection of the Danube River, 68–71. http://www.danubesurvey.org/jds2/files/ICPDR_Technical_Report_for_web_low_corrected.pdf.
- Dokulil, M. T. & K. Teubner, 2020. Comparative primary production. In Mehner, T. & K. Tockner (eds), *Encyclopedia of Inland Waters*, 2nd ed. Elsevier, Oxford.
- Dokulil, M.T., K. Teubner, K. & C. Kaiblinger, 2005. Produktivität aquatischer Systeme. Primär-produktion (autotrophe Produktion). In: Steinberg, C., W. Calmano, H. Klapper & R.-D. Wilken. (Hg.), *Handbuch angewandte Limnologie*, IV-9.2, 1-30, 21. Erg. Lfg, 4/05, ecomed, Landsberg.
- Dokulil, M. T., K. Donabaum & K. Pall, 2006. Alternative stable states in floodplain ecosystems. *Ecohydrology Hydrobiology* 6: 37–42.
- Dörnhöfer, K. & N. Oppelt, 2016. Remote sensing for lake research and monitoring: recent advances. *Ecological Indicators* 64: 105–122.
- Duanmu, D., N. C. Rockwell & J. C. Lagarias, 2017. Algal light sensing and photoacclimation in aquatic environments. *Plant Cell Environment* 40: 2558–2570.
- Dubinsky, Z. & I. Berman-Frank, 2001. Uncoupling primary production from population growth in photosynthesizing

- organisms in aquatic ecosystems. *Aquatic Science* 63: 4–17.
- Engel, F., K. Attermeyer, A. I. Ayala, H. Fischer, V. Kirchesch, D. C. Pierson & G. Weyhenmeyer, 2019. Phytoplankton gross primary production increases along cascading impoundments in a temperate, low-discharge river: insights from high frequency water quality monitoring. *Scientific Reports* 9: 6701.
- Häder, V.-P., V. E. Villafañe & E. W. Helbling, 2014. Productivity of aquatic primary producers under global climate change. *Photochemical Photobiological Sciences* 13: 1370.
- Hamdan, M., P. Byström, E. R. Hotchkiss, M. J. Al-Haidarey, J. Ask & J. Karlsson, 2018. Carbon dioxide stimulates lake primary production. *Scientific Reports* 6: 10878.
- Hampton, S. E., M. D. Scheuerell, M. J. Church & J. M. Melack, 2019. Long-term perspectives in aquatic research. *Limnology Oceanography* 64: S2–S10.
- Fahey, T. J. & A. K. Knapp, 2007. *Principles and Standards for Measuring Primary Production*. Oxford University Press, Oxford.
- Falkowski, P. G. & J. A. Raven, 2007. *Aquatic Photosynthesis*, 2nd ed. Princeton University Press, Princeton.
- Fernández, N., J. Aguilar & C.-A.- Piña-García, 2017. Complexity of lakes in a latitudinal gradient. *Ecological Complexity* 31: 1–20.
- Ferrera, I., H. Sarmiento, J. P. Priscu, A. Chiuchiolo, J. M. González & H.-P. Grossart, 2017. Diversity and distribution of freshwater aerobic anoxygenic phototrophic bacteria across a wide latitudinal gradient. *Frontiers Microbiology* 8: 175.
- Ferris, J. M. & R. Christian, 1991. Aquatic primary production in relation to microalgal responses to changing light: a review. *Aquatic Science* 53: 187–217.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson & P. Falkowski, 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281: 237–240.
- Fogel, M. L. & L. A. Cifuentes, 1993. Isotope fractionation during primary production. In Engel, M. H. & S. A. Macko (eds), *Organic Geochemistry Topics in Geobiology* 11. Springer, Boston.
- Geider, R. J., 1993. Quantitative phytoplankton physiology: implications for primary production and phytoplankton growth. *ICES Marine Science Symposia* 197: 52–62.
- Geider, R. J., E. H. DeLucia, P. G. Falkowski, A. C. Finzi, J. P. Grime, J. Grace, T. M. Kana, J. La Roche, S. P. Long, B. A. Osborne, T. Platt, I. C. Prentice, J. A. Raven, W. H. Schlesinger, V. Smetacek, V. Stuart, S. Sathyendranath, R. B. Thomas, T. C. Vogelmann, P. Williams & F. I. Woodward, 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology* 7: 849–882.
- Glibert, P. M., J. J. Middelburg, J. W. McClelland & M. J. Vander Zanden, 2019. Stable isotope tracers: enriching our perspectives and questions on sources, fates, rates, and pathways of major elements in aquatic systems. *Limnology Oceanography* 64: 950–981.
- Hanada, S., 2016. Anoxygenic photosynthesis: a photochemical reaction that does not contribute to oxygen reproduction. *Microbes Environment* 31: 1–3.
- Hasler, C. T., D. Butman, J. D. Jeffrey & C. D. Suski, 2016. Freshwater biota and rising pCO₂? *Ecological Letters* 19: 98–108.
- Houliet, E., S. Simis, S. Nenonen, P. Ylöstalo & J. Seppälä, 2017. Basin-scale spatio-temporal variability and control of phytoplankton photosynthesis in the Baltic Sea: the first multiwavelength fast repetition rate fluorescence study operated on a ship-of-opportunity. *Journal Marine Science* 169: 40–51.
- Hughes, D.J., 2018a. Using next-generation multi-spectral FRRF to improve current estimates of marine primary production (MPP) within Australian waters. Ph.D. Thesis, University of Technology, Sydney.
- Hughes, D. J., D. A. Campbell, M. A. Doblin, J. C. Kromkamp, E. Lawrenz, C. M. Moore, K. Oxborough, O. Prášil, P. J. Ralph, M. F. Alvarez & D. J. Suggett, 2018b. Roadmaps and detours: active chlorophyll-a assessments of primary productivity across marine and freshwater systems. *Environmental Science Technology* 52: 12039–12054.
- Huston, M. A. & S. Wolverton, 2009. The global distribution of net primary production: resolving the paradox. *Ecological Monography* 79: 343–377.
- Kabas, W., 2004. Die Veränderungen der Primärproduktion in der Alten Donau in den Jahren 1995–2002. Mit einem Methodenvergleich. Ph.D. Thesis. University, Vienna.
- Kaiblinger, C., K. Teubner & M. T. Dokulil, 2005. Comparative assessment of phytoplankton photosynthesis using conventional ¹⁴C-determination and Fast Repetition Rate Fluorometry in freshwaters. *Verhandlungen Internationale Vereinigung Limnologie* 29: 254–256.
- Kaiblinger, C. & M. T. Dokulil, 2006. Application of fast repetition rate fluorometry to phytoplankton photosynthetic parameters in freshwaters. *Photosynthetic Research* 88: 19–30.
- Laws, E. A., M. R. Landry, R. T. Barber, C. Campbell, M.-L. Dickson & J. Marra, 2000. Carbon cycling in primary production bottle incubations: inferences from grazing experiments and photosynthetic studies using ¹⁴C and ¹⁸O in the Arabian Sea. *Deep-Sea Research. II* 47: 1339–1352.
- Lewis, W. M., 1996. Tropical lakes: how latitude makes a difference. In Schiemer, F. & K. T. Boland (eds), *Perspectives in Tropical Limnology*. SPB Academic Publishing, Amsterdam: 43–64.
- Lindemann, R., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399–417.
- Kalaji, H. M., G. Schansker, M. Brestic, F. Bussotti, A. Calatayud, L. Ferroni, V. Goltsev, L. Guidi, A. Ajao, P. Li, P. Losciale, V. K. Mishra, A. N. Misra, S. G. Nebauer, S. Pancaldi, C. Penella, M. Pollastrini, K. Suresh, E. Tambussi, M. Yannicari, M. Zivcak, M. D. Cetner, I. A. Samborska, A. Stirbet, K. Olsovska, K. Kunderlikova, H. Shelonzek, S. Rusinowski & W. Baba, 2017. Frequently asked questions about chlorophyll fluorescence, the sequel. *Photosynthetic Research* 132: 13–66.
- Kelly, P. T., C. T. Solomon, J. A. Zwart & S. E. Jones, 2018. A framework for understanding variation in pelagic gross primary production of lake ecosystems. *Ecosystems* 21: 1364–13760.
- Koschel, R. H., T. Gonsiorczyk, L. Krienitz, J. Padisák & W. Scheffler, 2002. Primary production of phytoplankton and nutrient metabolism during and after thermal pollution in a

- deep, oligotrophic lowland lake (Lake Stechlin, Germany). *Verhandlungen Internationale Vereinigung Limnologie* 28: 569–575.
- Kopylov, A. I., T. S. Maslennikova & D. B. Kosolapov, 2019. Seasonal and interannual fluctuations of phytoplankton primary production in the Rybinsk water reservoir: effect of the weather and climatic changes. *Water Resources* 46: 270–277. **(in Russian with English summary)**.
- Kovač, Ž., T. Platt, Ž. N. Gladan, M. Morović, S. Sathyanathan, D. E. Raitsos, B. Grbec, F. Matić & J. Veža, 2018. A 55-year time series station for primary production in the adriatic sea: data correction, extraction of photosynthesis parameters and regime shifts. *Remote Sensing* 10: 1460.
- Kragh, T. & K. Sand-Jensen, 2018. Carbon limitation of lake productivity. *Proceedings Royal Society B* 285: 20181415.
- Kobližek, M., 2015. Ecology of aerobic anoxygenic phototrophs in aquatic environments. *FEMS Microbiology Reviews* 32: 854–870.
- Kromkamp, J. C., N. A. Dijkman, J. Peene, S. G. H. Simis & H. J. Gons, 2008. Estimating phytoplankton primary production in Lake IJsselmeer (The Netherlands) using variable fluorescence (PAM-FRRF) and C-uptake techniques. *European Journal Phycology* 43: 327–344.
- Larkum, A. W., 2016. Photosynthesis and light harvesting in algae. In Borowitzka, M., J. Beardall & J. Raven (eds), *The Physiology of Microalgae Developments in Applied Phycology*, Vol. 6. Springer, Cham.
- Laugaste, R., T. Nõges & I. Tõnno, 2008. Vetikad. In Haberman, J., T. Timm & A. Raukas (eds), *Peipsi. Eesti Maaülikooli Põllumajandus- ja Keskkonnainstituut, Tartu: 251–270. in Estonian*. ISBN 978-9985-830-83-3.
- Le Cren, E. D. & R. H. Lowe-McConnell (eds), 1980. *The Functioning of Freshwater Ecosystems*. International Biological Programme. Cambridge University Press, Cambridge.
- Lengyel, E., A. W. Kovács, J. Padisák & C. S. Kovács, 2015. Photosynthetic characteristics of the benthic diatom species *Nitzschia frustulum* (Kützinger) Grunow isolated from a soda pan along temperature, sulfate- and chloride gradients. *Aquatic Ecology* 49: 401–416.
- Lewis Jr., W. M., 2011. Global primary production of lakes: 19th Baldi Memorial Lecture. *Inland Waters* 1: 1–28.
- Li, D., Y. Yu, T. Zhang, D.-K. Tang, et al., 2014. Photochemical activity of phyto-plankton in Taihu Lake in spring and autumn. *Research of Environmental Sciences* 27: 848–856. **(in Chinese with English summary)**.
- Li, D. M., T. Q. Zhang, S. K. Tang, C. Duan, J. Lu & X. Liu, 2016. The dynamics of photosynthetic activity of *Microcystis* in Lake Taihu. *Acta Scientiae Circumstantiae* 36: 3066–3072.
- Lith, H., 1975. Historical survey of primary productivity research. In Lieth, H. & R. H. Whittaker (eds), *Primary Productivity of the Biosphere*. Springer, New York: 7–16.
- Low-Décarie, E., G.-F. Fussmann & G. Bell, 2014. Aquatic primary production in a high-CO₂ world. *Trends in Ecology & Evolution* 29: 223–232.
- Maberly, S. C., 1985a. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytologist* 100: 127–140.
- Maberly, S. C., 1985b. Photosynthesis by *Fontinalis antipyretica* II. Assessment of environmental factors limiting photosynthesis and production. *New Phytologist* 100: 141–155.
- Maberly, S. C., 2014. The fitness of the environments of air and water for photosynthesis, growth, reproduction and dispersal of photoautotrophs: an evolutionary and biogeochemical perspective. *Aquatic Botany* 118: 4–13.
- Maberly, S. C. & T. V. Madsen, 2002. Freshwater angiosperm carbon concentrating mechanisms: processes and patterns. *Functional Plant Biology* 29: 393–405.
- Maberly, S. C. & B. Gontero, 2017. Ecological imperatives for aquatic CO₂-concentrating mechanisms. *Journal of Experimental Botany* 68: 3797–3814.
- Macfadyen, A., 1948. The meaning of productivity in biological systems. *Journal Animal Ecology* 17: 75–80.
- Mašin, M., J. Nedoma, L. Pechar & M. Kobližek, 2008. Distribution of aerobic anoxygenic phototrophs in temperate freshwater systems. *Environmental Microbiology* 10: 1988–1996.
- Maxwell, K. & G. N. Johnson, 2000. Chlorophyll fluorescence—a practical guide. *Journal Experimental Botany* 51: 659–668.
- Michelutti, N., A. P. Wolfe, R. D. Vinebrooke, B. Rivard & J. P. Briner, 2005. Recent primary production increases in arctic lakes. *Geophysical Research Letters* 32: L19715.
- Miller, N.A., 2013. Changes in Net Ecosystem Production over the past 40 years in Arctic tundra ponds near Barrow, Alaska: Application of historic and modern techniques. *Open Access Theses & Dissertations*. 1885. https://digitalcommons.utep.edu/open_etd/1885.
- Mishra, D., I. Ogashawara & A. Gitelson (eds), 2017. *Bio-optical Modeling and Remote Sensing of Inland Waters*. Elsevier, Amsterdam.
- Moigis, A. G. & K. Gocke, 2003. Primary production of phytoplankton estimated by means of the dilution method in coastal waters. *Journal Plankton Research* 25: 1291–1300.
- Murchie, E. H. & I. Lawson, 2013. Chlorophyll fluorescence analysis: a guide to good practice and understanding some new applications. *Journal of Experimental Botany* 64: 3983–3998.
- Needoba, J. A., T. D. Peterson & K. S. Johnson, 2012. Method for the quantification of aquatic primary production and net ecosystem metabolism using in situ dissolved oxygen sensors. In Tiquia-Arashiro, S. M. (ed.), *Molecular Biological Technologies for Ocean Sensing*. Springer, New York.
- Nõges, P., R. Laugaste & T. Nõges, 2004. Phytoplankton. In Haberman, J., E. Pihu & A. Raukas (eds), *Lake Võrtsjärv*. Estonia Encyclopedia Publications Ltd., Tallinn: 217–232.
- Nõges, T., H. Luup & T. Feldmann, 2010. Primary production of aquatic macrophytes and their epiphytes in two shallow lakes (Peipsi and Võrtsjärv) in Estonia. *Aquatic Ecology* 44: 83–92.
- Nõges, T., H. Arst, A. Laas, T. Kauer, P. Nõges & K. Toiming, 2011. Reconstructed long-term time series of phytoplankton primary production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity. *Hydrobiologia* 667: 205–222.
- Obrador, B., P. A. Staehr & P. C. Christiansen, 2014. Vertical patterns of metabolism in three contrasting stratified lakes. *Limnology Oceanography* 59: 1228–1240.

- Odum, H. T., 1956. Primary production in flowing waters. *Limnology Oceanography* 1: 102–117.
- Ostrovsky, I., A. Rimmer, Y. Z. Yacobi, A. Nishri, A. Sukenik, O. Hadas & T. Zohary, 2013. Long-term changes in the Lake Kinneret ecosystem: the effects of climate change and anthropogenic factors. In Goldmann, C. R., M. Kumagai & R. D. Roberts (eds), *Climatic change and global warming of inland waters: impacts and mitigation for ecosystems and societies J*, 1st ed. Wiley, New York: 271–293.
- Padisak, J., L. Krienitz, R. Koschel & J. Nedoma, 1997. Deep-layer autotrophic picoplankton maximum in the oligotrophic Lake Stechlin, Germany: origin, activity, development and erosion. *European Journal Phycology* 32: 403–416.
- Pálmai, T., B. Szabó, K. K. Kotut, L. Krienitz & J. Padisák, 2020. Ecophysiology of a successful phytoplankton competitor in the African flamingo lakes: the green alga *Picocystis salinarum* (Picocystophyceae). *Journal of Applied Phycology*. <https://doi.org/10.1007/s10811-020-02092-6>.
- Peeters, F., D. Atamanchuk, A. Tengberg, J. Encinas-Fernández & H. Hofmann, 2016. Lake metabolism: comparison of lake metabolic rates estimated from a diel CO₂ and the common diel O₂-technique. *PLoS ONE* 11: e0168393.
- Price, G. D., S. I. Maeda, T. Omata & M. R. Badger, 2002. Modes of active inorganic carbon uptake in the cyanobacterium, *Synechococcus* sp. PCC7942. *Functional Plant Biology* 29: 131–149.
- Raven, J. A. & J. Beardall, 2016. The ins and outs of CO₂. *Journal of Experimental Botany* 67: 1–13.
- Raven, J. A., M. G. Giordano, J. Beardall & S. C. Maberly, 2012. Algal evolution in relation to atmospheric CO₂: carboxylases, carbon-concentrating mechanisms and carbon oxidation cycles. *Philosophical Transactions Royal Society B* 367: 493–507.
- Regaudie-de-Gioux, A., S. Lastermas, S. Agusti & C. M. Duarte, 2014. Comparing marine primary production estimates through different methods and development of conversion equations. *Frontiers in Marine Science* 1: 1–14.
- Reynolds, C. S., 1972. Growth, gas vacuolation and buoyancy in a natural population of a planktonic blue-green alga. *Freshwater Biology* 2: 87–106.
- Reynolds, C. S., 1983a. A physiological interpretation of the dynamic responses of populations of a planktonic diatom to physical variability of the environment. *New Phytol.* 95: 41–53.
- Reynolds, C. S., 1983b. Growth-rate responses of *Volvox aureus* EHRENB. (Chlorophyta, Volvocales) to variability in the physical environment. *British Phycology Journal* 18: 433–442.
- Reynolds, C. S., 1988. Potamoplankton: paradigms, paradoxes, prognoses. In Round, F. E. (ed.), *Algae and the Aquatic Environment*. Biopress, Bristol: 285–311.
- Reynolds, C. S., 1989. Physical determinants of phytoplankton succession. In Sommer, U. (ed.), *Plankton Ecology. Succession in Plankton Communities*. Springer, Berlin: 9–56.
- Reynolds, C. S., 1994a. River plankton: the paradigm regained. In Harper, D. M. & A. J. D. Ferguson (eds), *The Ecological Basis of River Management*. Wiley, Chichester.
- Reynolds, C. S., 1994b. The long, the short and the stalled: on the attributes of phytoplankton selected by physical mixing in lakes and rivers. *Hydrobiologia* 289: 9–21.
- Reynolds, C. S., 1996a. The plant life of the pelagic. *Verhandlungen Internationale Vereinigung Limnologie* 26: 97–113.
- Reynolds, C. S., 1996b. The 1996 founders' lecture: potamoplankters do it on the side. *European Journal Phycology* 31: 111–115.
- Reynolds, C. S., 1997. Vegetation processes in the pelagic: a model for ecosystem theory. In Kinne, O. (ed.), *Excellence in Ecology*. Ecology Institute Publisher, Oldendorf.
- Reynolds, C. S., 2002. On the interannual variability in phytoplankton production in freshwater. In Williams, P. J., D. N. Thomas & C. S. Reynolds (eds.), *Phytoplankton Productivity. Carbon Assimilation in Marine and Freshwater Ecosystems*. Blackwell Science, Oxford.
- Reynolds, C. S., 2012a. Pelagic ecology. In El-Shaarawi, A. H. & W. W. Piegorsch (eds), *Encyclopedia of Environmetrics*, 2nd ed. Wiley, New York.
- Reynolds, C. S., 2012b. Benthic ecology. In El-Shaarawi, A. H. & W. W. Piegorsch (eds), *Encyclopedia of Environmetrics*, 2nd ed. John Wiley, New York.
- Reynolds, C. S. & J.-P. Descy, 1996. The production, biomass and structure of phytoplankton in large rivers. *Archiv fur Hydrobiologia* 10: 161–187.
- Reynolds, C. S. & M. S. Glaister, 1989. Remote sensing of phytoplankton concentrations in a UK River. *Proceedings on NERC Airborne Campaigns Workshop* 1989: 131–140.
- Reynolds, C. S. & M. S. Glaister, 1993. Spatial and temporal changes in phytoplankton abundance in the upper and middle reaches of the River Severn. *Archiv fur Hydrobiologia* 101: 1–22.
- Reynolds, C. S. & A. E. Irish, 1997. Modelling phytoplankton dynamics in lakes and reservoirs: the problem of in situ growth rates. *Hydrobiologia* 349: 5–17.
- Reynolds, C. S., G. P. Harris & D. N. Gouldney, 1985. Comparison of carbon-specific growth rates and rates of cellular increase of phytoplankton in large limnetic enclosures. *Journal Plankton Research* 7: 791–820.
- Riedler, P., K. Abderrah, U. Artmann, et al., 1999. Benthische und pelagische Primärproduktion im Regelsbrunner Altarmsystem. *Linzer biologische Beiträge* 31: 763–781.
- Rodionov, S. N., 2004. A sequential algorithm for testing climate regime shifts. *Geophysical Research Letters* 31: 9204.
- Rousseaux, C. S. & W. W. Gregg, 2014. Interannual variation in phytoplankton primary production at a global scale. *Remote Sensing* 6: 1–19.
- Ruttner, F., 1921. Das elektrolytische Leitvermögen verdünnter Lösungen unter dem Einflusse submerser Gewächse I Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche. Klasse 130: 71–108.
- Ruttner, F., 1948. Zur Frage der Karbonatassimilation der Wasserpflanzen. I. Teil: die beiden Haupttypen der Kohlenstoffaufnahme. *Österreichische Botanische Zeitschrift* 94: 265–294.
- Ruttner, F., 1949. Zur Frage der Karbonatassimilation der Wasserpflanzen. II. Teil Das Verhalten von *Elodea canadensis* und *Fontinalis antipyretica* in Lösungen von Natrium- bzw. Kaliumbikarbonat. *Österreichische Botanische Zeitschrift* 95: 208–238.

- Sakshaug, E., 1993. The relationship between phytoplankton growth rate and production with emphasis on respiration and excretion. ICES Marine Science Symposia 197: 63–68.
- Sakshaug, E., A. Bricaud, Y. Dandonneau, P. G. Falkowski, D. A. Kiefer, L. Legendre, A. Morel, J. Parslow & M. Takahashi, 1997. Parameters of photosynthesis: definitions, theory and interpretation of results. *Journal of Plankton Research* 19: 1637–1670.
- Sathyendranath, S. & T. Platt, 1993. Remote sensing of water-column primary production. ICES Marine Science Symposia 197: 236–243.
- Sellers, T. & P. A. Bukaveckas, 2003. Phytoplankton production in a large, regulated river: a modeling and mass balance assessment. *Limnology Oceanography* 48: 1476–1487.
- Singh, A. K., R. Kumari & A. Kumar, 2018. The contribution of phytoplankton to the primary production in Floodplain Lakes (Chauras) of North Bihar, India. *International Journal of Ecology and Development Research* 4: 44–52.
- Staehr, P. A., D. Bade, M. C. Ven de Bogert, G. R. Koch, C. Williamson, P. Hanson, J. J. Cole & T. Kratz, 2010. Lake metabolism and the diel oxygen technique: state of the science. *Limnology Oceanography: Methods* 8: 628–644.
- Staehr, P. A., L. Bastrup-Spohr, K. Sand-Jensen & C. Stedmon, 2012. Lake metabolism scales with lake morphometry and catchment conditions. *Aquatic Science* 74: 155–169.
- Staehr, P. A., L. S. Brighenti, M. Honti, J. Cristensen & K. C. Rose, 2016. Global patterns of light saturation and photoinhibition of lake primary production. *Inland Waters* 6: 593–607.
- Sheng, H., Z. M. Yu, M. L. Liu, J. B. He, Y. C. Han & Y. L. Zhang, 2014. The photosynthetic activity of phytoplankton in Qiandao Lake in winter. *Chinese Journal of Ecology* 33: 365–372.
- Sobek, S., L. J. Tranvik, Y. T. Prairie, P. Kortelainen & J. J. Cole, 2007. Patterns and regulation of dissolved organic carbon: an analysis of 7,500 widely distributed lakes. *Limnology Oceanography* 52: 1208–1219.
- Soomets, T., T. Kutser, A. Wüest & D. Bouffard, 2019. Spatial and temporal changes of primary production in a deep peri-alpine lake. *Inland Waters* 9: 49–60.
- Tian, Y., X. Wu, Q. Zhou, O. O. Donde, C. Tian, C. Wang, B. Feng & B. Xiao, 2018. Distribution of aerobic anoxygenic phototrophs in freshwater plateau lakes. *Polish Journal Environmental Studies* 27: 1–9.
- Teubner, K., A. Sarobe, M. R. Vadrucci & M. T. Dokulil, 2001. ¹⁴C photosynthesis and pigment pattern of phytoplankton as size related adaptation strategies in alpine lakes. *Aquatic Science* 63: 310–325.
- Uehlinger, U., 2006. Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period. *Freshwater Biology* 51: 938–950.
- Üveges, V., K. Topolczai, L. Krienitz & J. Padisák, 2012. Photosynthetic characteristics and physiological plasticity of an *Aphanizomenon flos-aquae* (Cyanobacteria, Nostocaceae) winter bloom in a deep oligo-mesotrophic lake (Lake Stechlin, Germany). *Hydrobiologia* 698: 263–272.
- Webster, I. T., N. Rea, A. V. Padovan, P. Dostine, S. A. Rownsend & S. Cook, 2005. An analysis of primary production in the Daly River, a relatively unimpacted tropical river in northern Australia. *Marine Freshwater Research* 56: 303–316.
- Weinberg, A. M., 1961. Impact of large-scale Science on the United States. *Science* 134: 161–164.
- Weinberg, A. M., 1967. Reflections on Big Science. Pergamon Press, Oxford.
- Westlake, D. F., J. Květ & A. Szczepański (eds), 1998. The Production Ecology of Wetlands. University Press, Cambridge.
- Wetzel, R. G. & G. E. Likens (eds), 1991. *Limnological Analyses*, 2nd ed. Springer, New York.
- Williamson, C. E., P. J. Neale, S. Hylander, K. C. Rose, F. L. Figueroa, S. A. Robinson, D.-P. Häder, S. Å. Wängberg & R. C. Worrest, 2019. The interactive effects of stratospheric ozone depletion, UV radiation, and climate change on aquatic ecosystems. *Photochemical & Photobiological Sciences* 1: 717–746.
- Worden, A. Z., J. K. Nolan & B. Palenik, 2004. Assessing the dynamics and ecology of marine picophytoplankton: the importance of the eukaryotic component. *Limnology Oceanography* 49: 168–179.
- Wurtsbaugh, W. A., H. W. Paerl & W. K. Dodds, 2019. Nutrients, eutrophication and harmful algal blooms along the freshwater to marine continuum. *WIREs Water* 6: e1373.
- Xu, H. Y., W. F. Zhou & S. J. Ji, 2016. Review of estimation on oceanic primary productivity by using remote sensing methods. *Chinese Journal of Applied Ecology* 27: 3042–3050. (in Chinese with English Abstract).
- Yacobi, Y. Z., 2006. Temporal and vertical variation of chlorophyll a concentration, phytoplankton photosynthetic activity and light attenuation in Lake Kinneret: possibilities and limitations for simulation by remote sensing. *Journal Plankton Research* 28: 725–736.
- Yokota, K., H. Waterfield, C. Hastings, E. Davidson, E. Kwietniewski & B. Wells, 2017. Finding the missing piece of the aquatic plastic pollution puzzle: interaction between primary producers and microplastics. *Limnology Oceanography Letters* 2: 91–104.

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