

<https://doi.org/10.5281/zenodo.8290059>

Primary productivity in rivers and streams - the Danube example

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CITATION

Dokulil, M. (2023) Primary productivity in rivers and streams - the Danube example. In: Teubner K., Trichkova T., Cvijanović D., eds. *Tackling present and future environmental challenges of a European riverscape*. IAD Proceedings, 1: 8290059.

DOI: [10.5281/zenodo.8290059](https://doi.org/10.5281/zenodo.8290059)

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Abstract Phytoplankton production in riverine systems is regulated by hydrologic processes and coupled light availability during transit. Resulting net primary production is a fundamental ecological process that reflects the amount of carbon synthesized within river ecosystems, which is ultimately available to consumers. Nutrients affect the physical, chemical, and biological components of large rivers and hence the response of the ecosystem. The direct consequences of nutrient loading are an increased primary productivity. The ultimate driver of aquatic primary production in streams, however, is light availability. Rivers also function to transport nutrients to downstream ecosystems, and some of the impacts of nutrients on large rivers are transported to downstream lakes, reservoirs, estuaries, and coastal waters affecting phytoplankton biomass and production in these systems. Here, data on chlorophyll-a as a measure of biomass, photosynthetic activity, and primary production have been analysed using fast repetition rate fluorescence for phytoplankton from a cruise on the River Danube in 2007. The profile of the river corridor for phytoplankton is compared to chlorophyll-a and calculated primary production from the phyto-benthos extracted from the data report.

Received: 05. April 2023
Accepted: 18. July 2023
Published: 12. Sept 2023

Keywords: Phytoplankton, photosynthesis, production, fluorescence, phytobenthos

1 Introduction

Growing attention, focusing on the metabolic dynamics of inland waters in the 1950s, led to rapid development of techniques to estimate primary production (PP). In rivers interests were closely linked to the oxygen conditions and aeration rates. Both perceptions were amalgamated by Odum (1956, 1957) to estimate primary productivity in flowing waters from daily oxygen changes in the open water. The

laborious and time-consuming method never gained great popularity. Other procedures similar to techniques used for lakes such as enclosures (McConnell and Sigler, 1959) or CO₂ changes (Wright and Mills, 1967) were exceptions. Renewed interest in stream and river metabolism came through the introduction of novel sensor techniques offering continuous in-situ measurements (Rode et al., 2016), allowing to return

to the free water dissolved oxygen estimates. Data collected by continuous measurements of diel O₂ or CO₂ changes can be used to calculate primary production for the entire stream or river community (Staeher et al., 2010; Peeters et al., 2016). Needoba et al. (2012) provide a detailed practical approach to sensor applications. In a few cases remote sensing from satellites has already applied to estimate PP via models (Vis et al., 2007; Ward et al., 2016).

Investigations in the Danube started in the summer of 1961 (Knöpp, 1966), applying the classical oxygen light-dark bottle technique to a river. This method and associated parameters were described by Knöpp (1968) and compared to carbon-14 measurements in the laboratory (Müller and Knöpp, 1971). In-situ measurements using carbon-14 were performed in two impoundments of the Danube in

Austria (Frantz and Sas-Hubicki, 1972). Primary productivity of potamoplankton in the River Danube has been summarized for the Austrian Stretch (Dokulil, 2006a) and compiled for the river corridor (Dokulil, 2006b; 2014).

Estimates of primary production and chlorophyll-a are presented here for phytoplankton and phyto-benthos, using data from the River Danube obtained during August and September 2007 while cruising down the river during Joint Danube Survey 2 (JDS2). The aim of the study is (1) to present estimates of potamoplankton production, using the novel method of fast repetition rate fluorescence and (2) to compare these data to phyto-benthos production approximated from chlorophyll-a. Additionally, surface water temperature and light conditions are given as important background information.

2 Material and methods

Qualitative and quantitative investigations were carried out along the Danube as part of the Joint Danube Survey 2 (JDS2) in August/September 2007 to reveal longitudinal variations. Samples were taken at 78 locations in the middle of the river from the surface with a black bucket (8 L) and used for all further analyses.

2.1 TRANSPARENCY AND LIGHT MEASUREMENTS

Photosynthetic available radiation (PAR) in the range of 400 – 700 nm was measured above the water with a 2π flat Li-Cor sensor in units of μ Einstein m⁻²s⁻¹ equivalent to μmol photons at each station. Sub-surface PAR (E₀) was calculated from the measurements in air, assuming 10% reflection and reported as mol photons m⁻²h⁻¹.

2.2 CHLOROPHYLL-A AND PIGMENT ANALYSIS

On-board analysis included the immediate in vivo measurement of photosynthetic pigments by delayed fluorescence (DF) according to Gerhardt and Bodemer (1999). The DF-kinetic photometer detects 'photosynthetic active' chlorophyll-a from the P680 reaction center estimated from the fluorescence decay curve in the dark following a strong light pulse.

Results are directly proportional to the quanta absorbed and therefore provide an estimate of physiological acclimation to environmental conditions. Chlorophyll-a (chl-a) provides a good estimate of phytoplankton biomass ($r^2 = 0.86$, $F = 455.5$, $p < 0.001$). Phyto-benthos total chlorophyll-data were obtained from Makovinska et al. (2008) and converted to mg m⁻².

2.3 PHOTOSYNTHETIC PARAMETERS OF PHYTOPLANKTON

Active fluorescence measurements were acquired in the laboratory, using a Fast Repetition Rate Fluorometer (FRRF, Fasttracka, Chelsea Instruments Co Ltd.). Samples were immediately protected against ambient light. At each sampling location, at least one, in most cases three replicates were taken. The quantum efficiency of photosystem 2 was calculated from variable fluorescence ($F_v = F_m - F_0$) normalised to F_m , indicating the proportion of functional PSII reaction centers (Geider et al., 1993). Fluorescence-based productivity was calculated following the model of Kolber and Falkowski (1993) and further elaborated following procedures described in Smith et al. (2004) and Kaiblinger and Dokulil (2006). For more detailed information on methodology consult Liška et al. (2008). Phyto-benthos primary production was approximated by a simple predictive model (Morin et al., 1999).

3 Results and discussion

Surface water temperature (SWT) fluctuated around a mean of 21°C (17.4-24.9°C) throughout the entire river stretch (Figure 1A). This relative uniformity contrasts with the theory of asymptotic increase towards downstream (Ward, 1985). The elaboration of longitudinal profiles by Fullerton et al. (2015) revealed five different classes of which one is 'uniform' like the Danube profile. Reasons related to the uniformity are not fully clear but could be discharge, and tributary temperature. In the upstream section the main factor could be the river dam, while more uniform terrain might have influenced temperature in middle and downstream sections. Photosynthetic radiation (PAR) varied between 0.06 and 9.2 mol photons m⁻² h⁻¹ (average 1.9). These data (Figure 1A) and the efficiencies derived from them (Figure 1D) must be treated with caution since they have been measured at different times of the day in the 78 sampling locations.

Active chlorophyll-a profiles for both phytoplankton and phytobenthos are shown in Figure 1B. Average plankton chlorophyll-a was 6.3 mg m⁻³ (range 0.8-28.8), which was less than the average of 10.3 mg m⁻² for the algal benthos (range 0.8-21.8). Both profiles separated into three distinct regions. The section from km 2600 upstream of Iller in Germany to about km 1632 below Budapest in Hungary was characterized by a of mean 2.1 mg m⁻³ plankton-chl-a and 9.6 mg m⁻² benthos-chl-a, with ranges 0.8-5.9 and 3.5-17.3 respectively. The middle stretch from km 1632 to km 1097 Velika Morava was defined by a marked increase of phytoplankton chlorophyll-a to 28.8 mg m⁻³ at km 1200 below the Tisza tributary (average 14.8, minimum 3.1 mg m⁻³, while phytobenthos chlorophyll-a reached a minimum of 0.8, an average of 8.7 and a maximum of 18.8 mg m⁻² (Figure 1B). Phytoplankton in the downstream stretch is similarly low as in the upstream stretch (average 3.9 mg m⁻³ 0.8 – 10.6 mg m⁻³), while phytobenthos is even higher than in the upstream averaging 13.1 mg m⁻² and ranging from 6.5 to 21.8 mg m⁻². Calculated for the observed river profile mean phytobenthos chlorophyll-a (10.3 mg m⁻²) exceeds phytoplankton chl-a (6.3 mg m⁻³) by 40%.

The substantial increase and decrease in phytoplankton chlorophyll-a in the middle river section is a recurring phenomenon in longitudinal surveys summarised in Dokulil (2015, Fig. 2). Still small in 1961, the peak increased until 2001 because of enhanced nutrient input from the catchment. Due to the reduction in nutrients largely by sewage treatment, the bump of the chl-a

concentrations was much smaller in 2007. The decline was mainly caused by the discharges from the Tisza and Sava rivers leading to high loss rates by dilution. Losses by grazing turned out to be negligible (Dokulil, 2015). This pattern was replaced by alternating sections of low and high concentrations in August/September 2013 during the JDS3 cruise (Dokulil, 2015; Dokulil and Donabaum, 2014). Chlorophyll-a concentrations of the phytobenthos from this cruise, ranging from 1 to 72 mg m⁻² (mean 24.4) were higher than in previous surveys (see above). The lowest values occurred in the region of maximum phytoplankton development. Monthly sampling from April to September 2019 during JDS4 revealed again the highest chlorophyll-a concentrations in the middle section of the river (Stanković et al., 2021).

The phytoplankton development in the middle section is largely caused by a large increase in daily column production (Figure 1C). Rates converted from fluorescence signals to carbon-uptake ranged from 0.21 to 253 mg C m⁻² d⁻¹ with average rates for the three sections of 13.6, 51.8 and 5.7 mg C m⁻² d⁻¹ defined above. The respective calculated rates for the phytobenthos were 102, 93 and 131 mg C m⁻² d⁻¹ indicating at least in their magnitude much greater importance for river quality than phytoplankton. These findings partly contradict the statement by Vannote et al. (1981) that the leading role in primary production is governed by phytoplankton in large rivers.

Specific PP calculated as mg C (mg Chl-a⁻¹) E⁻¹ m⁻² (Figure 1D) is a measure of photosynthetic efficiency (Kapfer et al., 1997) with values usually between 2 and 37 (Reynolds, 2006; p. 106). Values for phytoplankton from 0.5 to 46.7 (mean 11.0) were in the same range as those for phytobenthos (1.1 to 50.1; mean 12.0). Falling into the same order of magnitude, these data indicate that both assemblages are equally efficient. Results for benthos production calculated from a simple model seem to be at least in the correct magnitude.

Patterns of phytoplankton biomass and production in larger rivers with a summary of measurements from several rivers were provided by Reynolds and Descy (1996). The authors defined river order and sections where production is higher than respiration like what has been shown above for the Danube. Turbidity, turbulences and hence irradiance fluctuations in rivers were identified as factors selecting for successful algal species (Dokulil, 1994; Reynolds et al., 1994). Potential

effects of nutrient enrichment on production of streams and rivers were identified in [Dodds \(2006\)](#).

Comparable estimates of primary production are available for several large European rivers. Annual average PP was $10.3 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (range 1.3 – 23.4) or $3400 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the River Spree in 1992 assessed by daily oxygen changes ([Böhme, 1994](#)). Circadian oxygen changes in the River Elbe corridor (German km 0 to 600) yielded 5.5 to $14.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, equal to 1830 – $4660 \text{ mg C m}^{-2} \text{ d}^{-1}$, while chlorophyll-a increased from 50 to $250 \mu\text{g L}^{-1}$. Estimates from diurnal oxygen curves with L/D bottle results agreed largely ([Böhme et al., 2002](#)). Chlorophyll-a concentrations in the River Rhein at Bimmen ranged from 2 to $62 \mu\text{g L}^{-1}$ in 2006/07 (IKSR, 2009). Results from 2018 increased from an average of $2.1 \mu\text{g chl-a L}^{-1}$ (max 5) downstream of Lake Constance to a mean of $29 \mu\text{g chl-a L}^{-1}$ (max 96) at Bimmen (km 680) near the German-Dutch border (IKSR, 2020). Maximum production rates at Bimmen were estimated from a simulation as $1.04 \text{ g C m}^{-2} \text{ d}^{-1}$ [Schöl et al. \(2002\)](#) while earlier

measurements ranged from 2.1 to $4.3 \text{ g C m}^{-2} \text{ d}^{-1}$ ([Admiraal et al., 1994](#)). A comparison of the longitudinal phytoplankton development in the rivers Rhine and Elbe 2009–2011 ([Hardenbicker et al., 2016](#)) revealed maximum chlorophyll-a concentrations below $5 \mu\text{g L}^{-1}$ in the River Rhine (km 170 to 854) in 2010. In contrast, high and increasing chlorophyll-a concentrations with maximum values of 174 and $123 \mu\text{g L}^{-1}$ (2009 and 2011) were observed in the River Elbe (km 4 to 582). Annual average PP in the River Meuse in Belgium was $1.68 \text{ g C m}^{-2} \text{ d}^{-1}$, range 0.18 to 4.35 in 1984. Maximum chlorophyll-a reached $89.6 \text{ mg chl-a m}^{-3}$ ([Descy et al., 1988](#)). This paper listed also earlier measurements from several European rivers. Measurements in cascading reservoirs of the River Volga by the oxygen light-dark bottle technique were on average between 1.0 and $3.51 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (equivalent to 300 – $1700 \text{ mg C m}^{-2} \text{ d}^{-1}$) for the 10 reservoirs, with average chl-a concentrations from 6.5 to $22.6 \mu\text{g L}^{-1}$ ([Mineeva et al., 2016](#)).

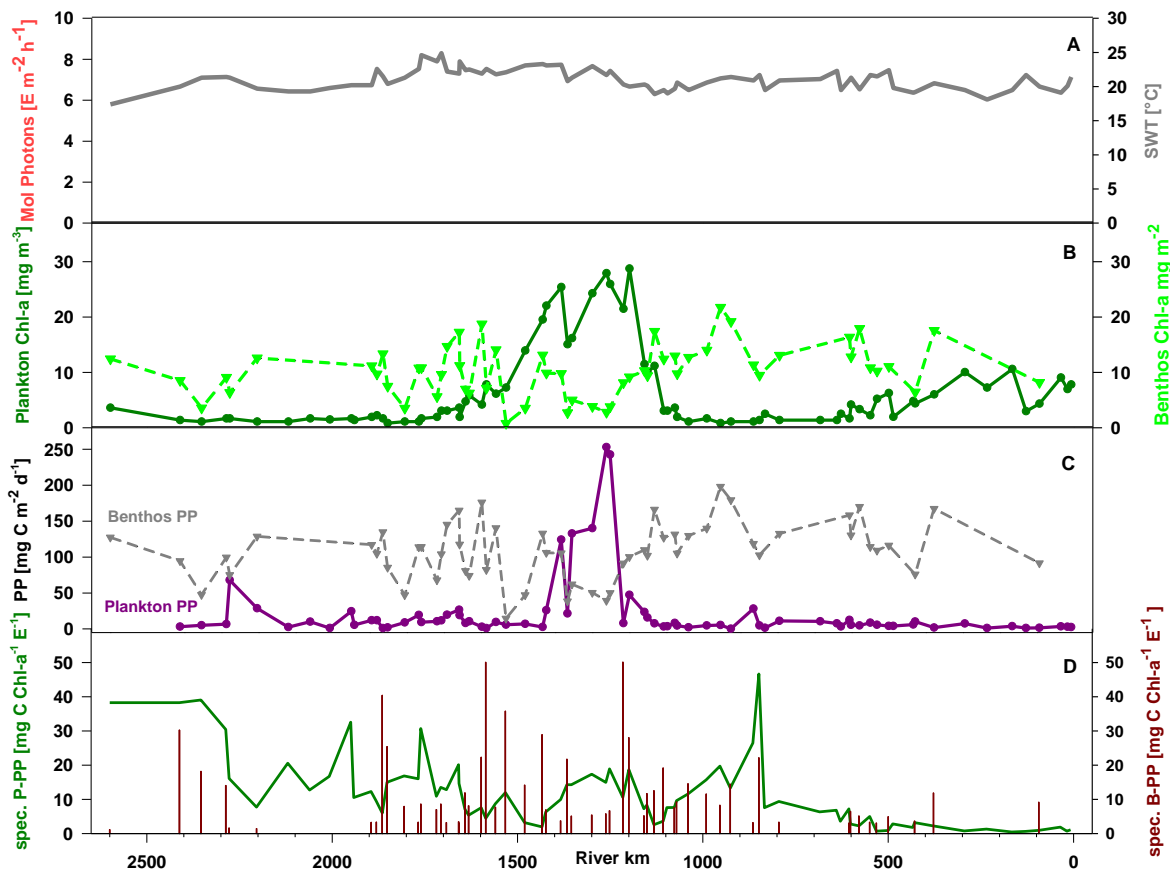


Figure 1: Length profile of the River Danube from north of the city of Regensburg to the Black Sea in August/September 2007 (JDS2). **A.** Surface water temperature (SWT, °C) and incoming radiation (PAR, mol Photons, $\text{E m}^{-2} \text{ h}^{-1}$). **B.** Chlorophyll-a concentration for phytoplankton (mg m^{-3}) and phytobenthos (mg m^{-2}). **C.** Primary production (PP) as $\text{mg C m}^{-2} \text{ d}^{-1}$ for phytoplankton (Plankton PP) and phytobenthos (Benthos PP). **D.** Specific PP per m^2 for both phytoplankton (P-PP) and phytobenthos (B-PP) in units of $\text{mg C (mg Chl-a}^{-1} \text{ E}^{-1})$

Production data on phytoplankton and periphyton from the same environment were not so common in the past (Morin et al., 1999) but became more frequent with the improvement in methodology. Examples include estimates of gross primary production from high frequency measurements along cascading impoundments of the River Saar, which indicated an increase from 180 to 630 mg C m⁻³ d⁻¹ associated with chl-a concentrations between 4.6 and 13.3 µg L⁻¹ (Engel et al., 2018). Another case is mean daily production ranging from 10 to 250 mg C m⁻² d⁻¹ for both phytoplankton and epiphyton in the St. Lawrence River, Canada (Vis et al. 2007). Both assemblages showed a large temporal and inter-annual variability driven by changes in biomass.

Direct estimates of periphyton PP using novel approaches are exemplified from headwater streams of

the Seine in France and the Yenisei in Siberia, Russia. The study on the Grand Morin in France, a tributary to the River Marne, used microelectrodes to measure oxygen release from the system and chlorophyll-a as surrogate for biomass (Flipo et al., 2007). Biomass ranged from 124 to 850 mg chl-a m⁻² and mean gross photosynthesis was 180 to 315 mg C m⁻² h⁻¹. An independent analysis using modelling obtained results in agreement with in situ measurements. A similar agreement between direct measurements using fluorescence and model results was found for periphytic PP in the Yenisei (Kolmakov et al., 2008). Chlorophyll-a concentrations and Gross-PP values varied from 0.83 to 973.74 mg m⁻² and 2–304,425 mg O₂ m⁻² day⁻¹ (0.64–95,133 mg C m⁻² day⁻¹), respectively. GPP was significantly correlated with periphyton chl-a (r=0.8).

4 Conclusions

Patterns in primary productivity and seasonal differences in photosynthesis and respiration in rivers are still not as well understood as in lentic or terrestrial ecosystems. A comprehensive analysis indicated that river production and respiration are controlled by annual light availability and flow while mean annual temperature and precipitation are responsible for variation in terrestrial production (Bernhardt et al., 2018; 2022). These findings in combination with high-resolution data enable the analysis of primary production at river-network scales (Koenig et al., 2019). Moreover, a new approach to evaluate carbon dioxide (CO₂) uptake allows a better insight into river relevance for global carbon budgets.

The analysis presented here implies that measurements of algal production using novel approaches can substantially improve our understanding of river metabolism. Direct estimates from fluorescence signals allow the calculation of uptake, growth, and loss rates of phytoplankton or phytobenthos and their relation, among other interpretations. Measurements of daily oxygen changes in the free water could be used for the interpretation of the metabolism of entire ecosystem.

Continuous monitoring stations utilising high frequency sensor applications at several points in the River Danube and perhaps in larger tributaries should therefore be excellent supplements to regular corridor surveys (<http://www.onlinemonitoring.at/Projekte/Wolfsthal/index.html>). Such stations would not only serve for permanent online data acquisition but can also be used as regular biological sampling places. Remote sensing and model applications can supplement ground measurements. Combinations of these approaches could then serve for both improvements in river science and river quality control in the context of the EC Water Framework Directive.

Acknowledgment Thanks go to anyone involved in preparing, organizing, and accompanying the Joint Danube Surveys two and three, particularly to the fantastic international teams on board and their cooperation. Many thanks to the captains and the crews of the boats for save transport and warmly atmosphere. Special thanks to Christina Kaiblinger (JDS2) and Ulrich Donabaum (JDS3) for their friendship and competent work during the expeditions.

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