

===== **General comment** =====

This manuscript investigates seasonal patterns of phytoplankton biomass development in German rivers through the concept of "realized eutrophication" (α_{realized}), defined as the ratio between observed and potential chlorophyll-a concentrations for a given phosphorus concentration. By combining long-term monitoring data from 133 river sites with clustering approaches, the authors identify distinct seasonal archetypes and relate them to nutrient dynamics, light availability, hydrological conditions, and the presence of upstream lakes. The study addresses an important question in river ecology and eutrophication management: why some rivers convert available nutrients into phytoplankton biomass more efficiently than others, and how these controls vary seasonally.

The manuscript is generally well written and easy to follow. The figures are clear and informative, Section 3 presents a large amount of information in a structured and engaging manner, and the Discussion is particularly well organized. The identification of distinct seasonal eutrophication archetypes provides a useful framework for interpreting large-scale patterns in river networks and may have practical implications for river management.

[We thank the reviewer for the positive acknowledgement of our work!](#)

However, several conceptual and methodological issues require clarification before the conclusions can be fully supported. First, the manuscript places strong emphasis on the role of upstream lakes, light availability, and nutrient stoichiometry as controls on phytoplankton development, yet some of the underlying mechanisms remain insufficiently discussed. In particular, the distinction between natural lakes and reservoirs deserves greater attention, as does the potential contribution of other primary producers such as periphyton and macrophytes to nutrient uptake and ecosystem functioning.

[See RC1.01, RC1.04, and RC1.05 for a detailed response.](#)

Second, some methodological choices require additional justification. The estimation of underwater PAR is insufficiently described despite being a key explanatory variable throughout the study. Moreover, the proposed metric of realized eutrophication relies on fixed assumptions regarding phytoplankton stoichiometry and chlorophyll content, which may not adequately reflect the variability observed across species, communities, and environmental conditions. The limitations of this metric should therefore be discussed more explicitly.

[See RC1.06 and RC1.07 for a detailed response.](#)

Third, I encourage the authors to be more cautious when interpreting nutrient ratios and deriving management implications. Nutrient stoichiometry alone does not demonstrate nutrient limitation, and the evidence supporting nutrient co-limitation, light limitation, or grazing control remains largely indirect. Similarly, recommendations regarding dual nutrient management or riparian shading should be presented with appropriate acknowledgement of the observational nature of the analyses.

See RC1.08 for a detailed response.

Overall, I believe this study has the potential to make a valuable contribution to the understanding of eutrophication processes in river networks. Addressing the points below would strengthen both the mechanistic interpretation of the results and the robustness of the conclusions.

===== **Major issues** =====

L38–39:

Please clarify in what sense this statement applies. The effect of lake presence on downstream river phytoplankton dynamics is a central component of the study and should therefore be explained more explicitly at this early stage.

[RC1.01](#)

We agree that our statement requires further clarification. In the revised version of the manuscript, we will therefore explain that downstream transport of phytoplankton originating from lakes is a known phenomenon. We will also add additional references for this statement.

L65:

This pattern is not specific to Germany. It is generally observed in river systems where phosphorus originates predominantly from point sources and nitrogen from diffuse sources. In addition, the authors should acknowledge that these seasonal patterns may vary longitudinally within a river network. For example, phosphorus concentrations may peak during high-flow periods in headwater sections dominated by non-point sources, whereas maxima may occur during low-flow periods downstream where wastewater treatment plant inputs become dominant and river dilution capacity is reduced.

[RC1.02](#)

We thank the reviewer for these two observations. We will (1) replace “In Germany, (...)” with “In river systems where phosphorus originates predominantly from point sources and nitrogen from diffuse sources, (...)” and to (2) add a sentence acknowledging potential longitudinal changes of the described pattern.

L75–84:

There is no doubt that light availability and underwater light climate are key controls on phytoplankton growth. However, the importance of riparian shading should be discussed in relation to river size. While shading can strongly regulate primary production in streams and narrow rivers, its influence is often much weaker in larger river sections where the channel width exceeds the effective reach of riparian vegetation.

[RC1.03](#)

We agree that a note on the link between shading and channel width would already be appropriate in the introduction. We will add this to the introduction in a similar way as in the Discussion section (L391-394).

Role of other primary producers:

The manuscript largely focuses on phytoplankton as the driver of nutrient dynamics. However, macrophytes and periphyton can also exert strong control on nitrogen and phosphorus cycling, particularly in rivers recovering from eutrophication. Their potential contribution should be acknowledged and discussed more explicitly.

[RC1.04](#)

We thank the reviewer for pointing out this weakness of the manuscript. We will discuss the role of macrophytes and periphyton on nutrient cycling in the revised version of the manuscript. We particularly thank the reviewer for the suggested references, which we find very suitable for this discussion and which we plan to include.

Lakes versus reservoirs:

The authors should acknowledge that many of the "lakes" included in this study are in fact reservoirs. This distinction is important because reservoirs differ from natural lakes in several key respects. Reservoirs are more frequently eutrophic, are often more susceptible to cyanobacterial blooms, and generally exhibit shorter residence times than natural lakes. These characteristics can substantially influence nutrient retention, phytoplankton development, and the transfer of nutrients and biomass to downstream river reaches.

[RC1.05](#)

We agree that our study is limited by differences between lakes, which we will point this out more clearly in the revised version of the manuscript. We considered quantifying differences between lake types, but a distinction between reservoirs and natural lakes is challenging. The HydroLAKES database provides information on lake types, but assignments often have substantial uncertainties (Messenger et al., 2016). Punctual visual assessments confirmed that

many lakes classified as natural are in fact reservoirs, hence we did not conduct a systematic lake type-based analysis.

We note that the ratio of natural to artificial lakes may be spatially heterogeneous across the study area. In northeastern Germany, where the majority of lake-influenced stations (clusters A and B) are located, postglacial natural lakes are also relatively common (Ehlers et al., 2004) and are likely to contribute to in-lake phytoplankton growth.

In our study, lake differences are represented with strong limitations by the parameter τ_{lakes} , which takes residence time estimates from HydroLAKES of all upstream lakes into account. However, we acknowledge that τ_{lakes} does clearly not reflect all of the various differences between lakes that would be relevant for a comprehensive discussion of coupled lake-river systems.

References:

Messenger, M. L., Lehner, B., Grill, G., Nedeva, I., and Schmitt, O.: Estimating the volume and age of water stored in global lakes using a geo-statistical approach, *Nature communications*, 7, 13 603, <https://doi.org/10.1038/ncomms13603>, 2016.

J. Ehlers, L. Eissmann, L. Lippstreu, H.-J. Stephan, and S. Wansa. Pleistocene glaciations of North Germany. *Developments in Quaternary Sciences*, Volume 2, pages 135–146. Elsevier, 2004. doi: 10.1016/S1571-0866(04)80064-2.

L123 (PAR estimation):

The statement "PAR was derived analogously to Hubig et al. (2025)" requires additional explanation. As I understand it, Hubig et al. (2025) estimated underwater PAR using an approach based on Scharfenberger et al. (2019), itself derived from Staehr et al. (2010). This method requires an estimate of the light attenuation coefficient. How was this coefficient calculated in Hubig et al. (2025), and how was it applied in the present study? Was it assumed constant, or was it parameterized as a function of water quality variables such as suspended solids and/or chlorophyll-a?

More generally, this methodology was originally developed for lakes. The authors should discuss its applicability to river systems, where optical conditions and hydromorphology differ substantially. Since PAR is a key driver of phytoplankton growth and ecosystem metabolism, additional methodological details and a discussion of associated uncertainties are warranted.

RC1.06

We agree that the current formulation of the method is potentially misleading. In Scharfenberger et al. (2019), an attenuation coefficient is used to calculate the mean available light (*MAL*) based on photosynthetically active radiation (*PAR*). *PAR* itself is, as in our study and Hubig et al. (2025), calculated from global radiation *E* and two constant factors 0.45 and $\gamma = 4.6 \mu\text{mol J}^{-1}$ according the following equation from Kirk et al. (2010):

$$PAR \approx E \cdot \gamma \cdot 0.45$$

Here, γ is a conversion factor based on the center wavelength of 550 nm of the 400 – 700 nm waveband (McCree et al., 1981). In Scharfenberger et al. (2019), this equation can be found in supplement S2.2. To clarify this, we suggest to include the above equation with a reference to Kirk et al. (2010) in the revised version of the manuscript. We will further add a note that light attenuation in the water column certainly plays a role for the mean available light in a river, but was not quantified in our study. We thank the reviewer for pointing out this lack of clarity in the manuscript.

References:

J. T. Kirk. Light and photosynthesis in aquatic ecosystems, 3rd Edition, Cambridge University Press, 2010.

K. J. McCree. Photosynthetically active radiation. In Physiological plant ecology I: responses to the physical environment, pages 41–55. Springer, 1981. doi: 10.1007/978-3-642-68090-83.

L172 (realized eutrophication metric):

The concept of "realized eutrophication" is interesting and potentially useful. However, I am not fully convinced by the current implementation.

Several assumptions may limit the robustness of the metric:

- * Phytoplankton phosphorus content varies substantially among species and physiological states. Consequently, the use of a single median value may not adequately represent natural variability.
- * Chlorophyll-a content per unit carbon biomass is also highly variable across taxa and environmental conditions.
- * Because both chlorophyll-a and phosphorus contents are assumed constant, the proposed metric appears to be directly proportional to the Chl-a:TP ratio.

Although this issue does not affect the main conclusions of the study, I find the current formulation potentially misleading. I therefore recommend either retaining the metric while explicitly acknowledging its limitations, or alternatively using the more transparent Chl-a:TP ratio directly.

RC1.07

We agree that the listed points are important limitations of $\alpha_{realized}$. As suggested, we will highlight them more explicitly when introducing the metric. Further, we propose a new Discussion subsection summarizing all limitations of the study, including the limitations of

calculating $\alpha_{realized}$ (For other limitations to be included in the new subsection, please see response to Reviewer 2).

Figure 4 and Section 3.2:

Nutrient ratios alone do not demonstrate nutrient limitation. They indicate stoichiometric imbalance and potential deficiency, but a system may exhibit high nutrient concentrations overall while still displaying skewed nutrient ratios. Demonstrating nutrient limitation requires consideration of absolute nutrient concentrations in addition to stoichiometric relationships. I therefore recommend revising the terminology throughout this section and the manuscript more generally, and distinguishing more clearly between nutrient imbalance and actual nutrient limitation.

RC1.08

We agree that the current version of the manuscript may contain misleading formulations regarding the interpretation of nutrient stoichiometry. We will carefully check the manuscript for the terms “limitation” and “deficiency” and individually decide whether the wording is appropriate or not. If applicable, we will change the wording to “imbalance” or “potential deficiency”. We also plan to critically review the management implications of the manuscript regarding nutrient stoichiometry.

(See Reviewer 2, RC2.08).

L311–315:

Does this result suggest that a substantial fraction of chlorophyll-a, and potentially of the phytoplankton community itself, originates from upstream lakes in clusters A and B? If so, this would be an important finding that deserves further discussion, particularly regarding the downstream transport and persistence of lake-derived phytoplankton populations.

RC1.09

We thank the reviewer for appreciating our results. Yes, we conclude that a substantial fraction of phytoplankton in clusters A and B originates from lakes. To further acknowledge this finding, we will follow the suggestion of the reviewer and broaden our discussion of this finding.

===== Minor issues =====

I haven't spotted any typo, congratulations!

RC1.10

We thank the reviewer for this acknowledgement!

The following references may be useful to strengthen the discussion on river phytoplankton dynamics, eutrophication trajectories, ecosystem metabolism, and large-scale river network functioning:

- * Abonyi, A., Ács, É., Hidas, A., Grigorszky, I., Várbíró, G., Borics, G., and Kiss, K. T. (2018). Functional diversity of phytoplankton highlights long-term gradual regime shift in the middle section of the Danube River due to global warming, human impacts and oligotrophication. **Freshwater Biology**, 63, 456–472.
- * Diamond, J. S., Moatar, F., Cohen, M. J., Poirel, A., Martinet, C., Maire, A., and Pinay, G. (2022). Metabolic regime shifts and ecosystem state changes are decoupled in a large river. **Limnology and Oceanography**, 67.
- * Minaudo, C., Curie, F., Jullian, Y., Gassama, N., and Moatar, F. (2018). QUAL-NET, a high temporal-resolution eutrophication model for large hydrographic networks. **Biogeosciences**, 15, 2251–2269.
- * Pannard, A., Minaudo, C., Leitão, M., Abonyi, A., Moatar, F., and Gassama, N. (2023). Meroplanktic phytoplankton play a crucial role in responding to peak discharge events in the middle lowland section of the Loire River (France). **Hydrobiologia**.