

Spatial and temporal variation of metabolism in inland water transects under changing water regime conditions

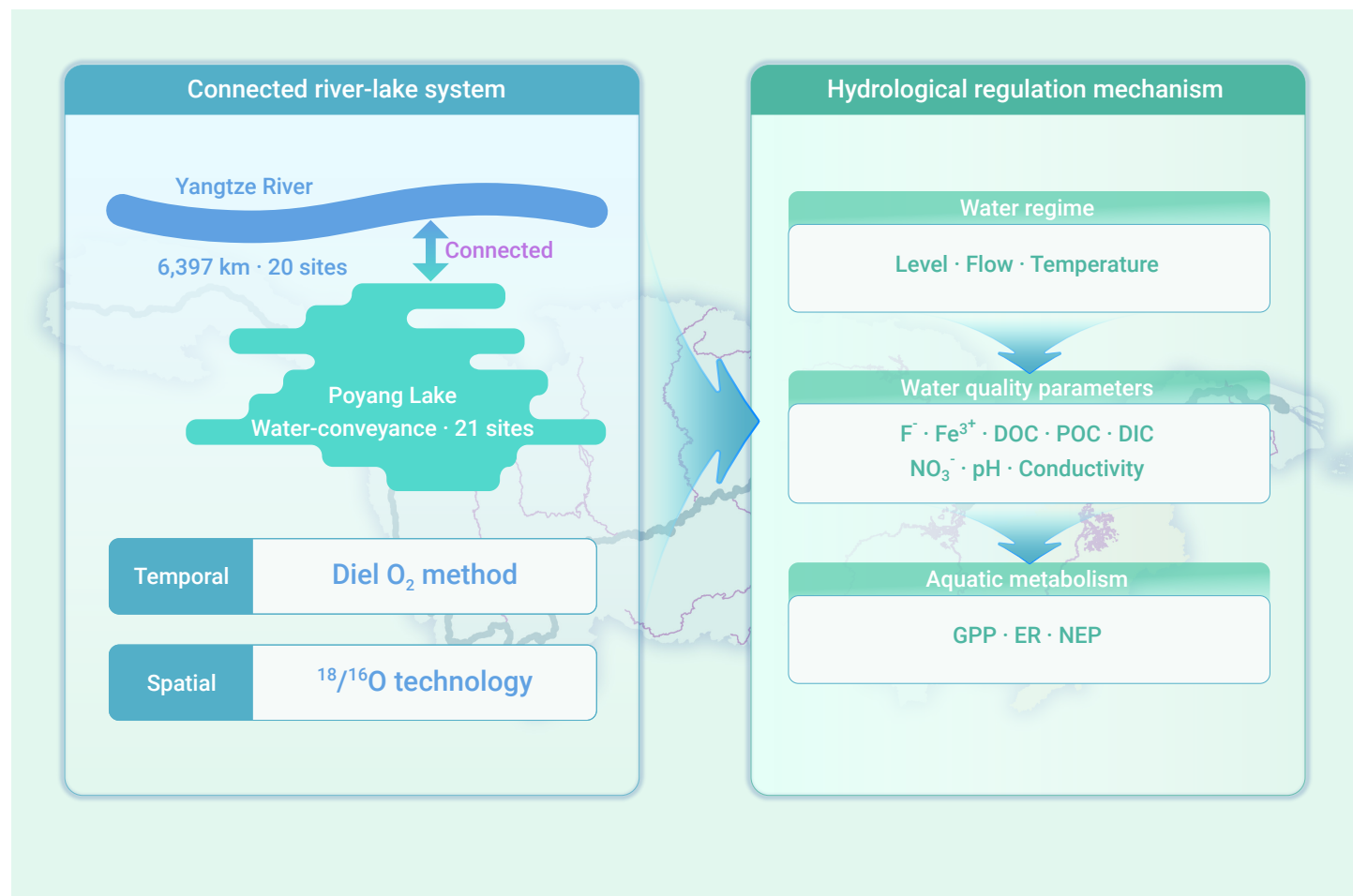
Yao Lu,^{1,3} Yang Gao,^{2,3,*} Dag Olav Hessen,⁴ Junjie Jia,^{2,3} Shuoyue Wang,^{2,3} Xianrui Ha,^{2,3} Huamao Yuan,^{1,3} and Jinming Song^{1,3}

*Correspondence: gaoyang@igsrr.ac.cn

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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- Gross primary productivity (GPP) and ecosystem respiration (ER) were measured using two complementary methods.
- Water regime indirectly regulated metabolism via water-quality variables, with 55-day seasonal hysteresis.
- Depletion of organic carbon supplied by the watershed and CO₂ emissions increased at high GPP.

Spatial and temporal variation of metabolism in inland water transects under changing water regime conditions

Yao Lu,^{1,3} Yang Gao,^{2,3,*} Dag Olav Hessen,⁴ Junjie Jia,^{2,3} Shuoyue Wang,^{2,3} Xianrui Ha,^{2,3} Huamao Yuan,^{1,3} and Jinming Song^{1,3}

¹Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266404, China

²Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, CAS, Beijing 100101, China

³College of Resources and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

⁴Department of Biosciences, University of Oslo, Oslo N-0316, Norway

*Correspondence: gaoyang@igsnr.ac.cn

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Investigating the regulatory mechanisms of inland water metabolism can elucidate its role in biogeochemical cycling and CO₂ emissions. However, the underlying processes remain poorly understood, especially for systems with severe water regime fluctuations or large spatial heterogeneity in water regime, such as rivers and water conveyance-type lakes. The diel O₂ method and the ¹⁸/16O technology are combined in this study to estimate the metabolism of such inland water systems along transects, covering temporal and spatial resolutions. The Yangtze River and Poyang Lake (a large water conveyance-type lake connected to the Yangtze River) were used to examine how hydrological dynamics and water quality parameters regulate aquatic metabolism. The lake metabolic rates estimated by ¹⁸/16O technology were as follows: gross primary productivity (GPP) was 16.0±16.0 g O₂ m⁻² d⁻¹ (mean ± SD), ecosystem respiration (ER) was 18.0±17.8 g O₂ m⁻² d⁻¹, and net ecosystem productivity (NEP) was -2.0±2.8 g O₂ m⁻² d⁻¹, suggesting net heterotrophy. Water regime (including water level, flow, and water temperature) was strongly associated with metabolic rates, with water quality parameters (especially F⁻, Fe³⁺, DOC, POC) potentially mediating these relationships. On an annual timescale, metabolism exhibited seasonal hysteresis relative to water regime, with metabolic processes lagging hydrological changes by 55 days. Peaks in GPP and ER occurred during flow recession phases rather than at peak flows. This study demonstrates that water regime fluctuations indirectly regulate aquatic metabolism by modulating water quality parameters, with regulatory mechanisms differing between temporal and spatial scales. These findings deepen our mechanistic understanding of hydrological regulation on aquatic metabolism and provide critical information for predicting CO₂ emissions from hydrologically dynamic inland waters under future environmental change.

INTRODUCTION

Inland waters (rivers, lakes, ponds and wetlands), play an important role in biogeochemical cycling (i.e., carbon, nutrients, etc.) and climate regulation via greenhouse gas release.^{1,2} Compared with oceans, inland waterbodies vary greatly among individual waterbodies, with some having extremely high phytoplankton biomass and rates of metabolism.³ Such systems act as important conduits of carbon dioxide (CO₂) and methane (CH₄), and thus play an important role in carbon cycling and climate.⁴ Hence progressively more attention has been devoted to the role of inland waters in this context. Inland waterbodies transport, mineralize, and bury approximately 2.7 Pg C yr⁻¹, which is similar to that of the capture and storage in terrestrial ecosystems of C emitted from human activities (2.8 Pg C yr⁻¹),⁵ and the carbon buried in their sediments exceeds that of the ocean floor.⁶ Therefore, a more comprehensive understanding of inland water metabolism is increasingly being employed as a means to assess the health of aquatic environments and to quantify the biogeochemical flux of organic carbon, oxygen, and other important nutrients at both regional and global scales.⁷ Aquatic metabolism can be broadly defined as the difference between primary production and aerobic respiration within an aquatic system,⁸ which can be quantified by gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem productivity (NEP), where NEP = GPP - ER.⁹

The magnitude of GPP, ER, and NEP varies between inland waters and is

also affected by the chosen methodology.⁹ Traditional incubation techniques such as the "light and dark bottles method" and radioisotope or stable isotope labelling (e.g. ¹⁴C and ¹³C) are significantly affected by incubation bias and "container effects".¹⁰ With advances in sensor technology, Odum¹¹ proposed the "diel O₂ method" for open water metabolism estimation, which enabled continuous in-situ monitoring and provided an effective alternative to traditional approaches. In recent years, this method has been improved in sensor selection, model improvement, and error control.^{12,13} However, the diel O₂ method is primarily applicable to point-scale monitoring and has spatial scale limitations. Advances in ¹⁸/16O technology have improved the convenience of multi-site metabolic estimation, thereby facilitating enhanced spatial resolution of metabolic estimates.¹⁴ However, it should be noted that the steady-state assumptions underlying this technique render it suitable only for low-productivity systems, and sampling is preferably conducted around midday.¹⁵

Based on methodological developments, metabolic studies in inland waters have advanced our understanding of aquatic ecosystem processes, particularly in linking environmental drivers to metabolic rates.^{16,17} Relationships have been established between GPP/ER and key environmental drivers, including solar radiation,⁷ organic matter and nutrient concentrations,¹⁸ water temperature,^{19,20} lake morphometry, water level fluctuations,²¹ and watershed vegetation coverage.²² The coupling relationship between GPP and ER under different nutritional conditions has also been widely verified.²³

Water hydrologic variability exerts multifaceted controls on aquatic metabolism through physical and chemical pathways. Physically, flow velocity enhancements may resuspend nutrients from sediments, temporarily stimulating GPP.²⁴ Chemically, hydrological pulses alter dissolved organic matter (DOM) and nutrient loading, which modulate the balance between autotrophy and heterotrophy. For instance, terrestrial DOM inputs can elevate ER by providing labile carbon substrates, while nitrogen and phosphorus subsidies may decouple GPP and ER seasonally.²⁵ Furthermore, water temperature fluctuations driven by hydrological regimes directly affect enzyme kinetics, with warmer temperatures accelerating ER disproportionately relative to GPP.²⁶

In summary, while metabolic rates in stable inland waters typically peak when high temperature, solar radiation, and nutrient concentrations coincide,²⁵ this "ideal" model is often disrupted in hydrologically dynamic systems through three principal pathways. First, hydrodynamic forcing alters biomass concentration, mixed-layer depth, and gas exchange through flow velocity and water level changes, thereby affecting photosynthesis and respiration.^{27,28} Second, dynamic hydrological conditions increase suspended particulate concentrations, reduce light transmittance, and weaken photosynthesis.^{29,30} Third, allochthonous substrate supply occurs when hydrological pulses introduce exogenous dissolved and particulate organic carbon from the watershed, thereby stimulating heterotrophic respiration and promoting net heterotrophy.²⁵ Moreover, anthropogenic activities such as dam construction can alter flow velocity and turbidity, indirectly modulating these metabolic pathways.³¹ Together, these three pathways establish a unique interconnection among water regime, water quality factors, and aquatic metabolism.

While extensive data are available for stable lentic systems and rivers,^{32,33} the complexity of waterbodies with pronounced hydrological variability

remains underexplored. A prime example is water conveyance-type lakes, which experience rapid shifts in water level, flow velocity, and residence time, directly altering light availability, nutrient stoichiometry, and organic matter loading — key drivers of gross primary production (GPP) and ecosystem respiration (ER).^{34,35} Such dynamic interactions position water conveyance-type lakes as critical subjects for investigating the interplay between hydrological regimes, water quality parameters, and aquatic metabolism. However, methodological constraints in resolving how water regime dynamics regulate metabolic processes often necessitate trade-offs between temporal and spatial resolution, limiting mechanistic insights.³⁶ The Yangtze River was selected as the study area. It is the world's third longest river and China's longest, and feeds into China's largest freshwater lake (i.e., Poyang Lake). Together, they form two interconnected water bodies characterized by severe fluctuations in water regimes. Monitoring temporal and spatial changes in metabolism and water quality factors (including physical indicators, chemical indicators, and biological indicators of water bodies), and exploring the influence of water regimes (i.e., water level, water flow, and water temperature) is thus of major importance. Our central scientific question addresses how hydrological regime fluctuations influence aquatic metabolism in water conveyance-type lakes and rivers. We hypothesize that water regime fluctuations indirectly regulate metabolism through their effects on water quality parameters, particularly carbon substrates and nutrients. The specific objectives of this study were: (1) to quantify lake metabolism in large inland waterbodies by applying two complementary techniques: the diel O₂ method for maximizing temporal resolution and the ¹⁸O/¹⁶O technology for maximizing spatial resolution; (2) to ascertain spatial and temporal correlations among water regime, water quality, and metabolic parameters, focusing on water regime impact mechanisms. This study aims to elucidate the mechanistic links between hydrological dynamics and aquatic metabolism, advancing our understanding of carbon cycling in highly dynamic inland waters.

MATERIALS AND METHODS

Study site

As the largest river in Eurasia and the third largest globally,³⁷ the Yangtze River plays a vital role in China's hydrology and ecology. Originating from the Qinghai-Tibet Plateau and emptying into the East China Sea, this 6,397 km-long river drains a vast basin of approximately 1.8×10⁶ km² (Figure 1A).³⁸ Its annual water discharge (900 km³ yr⁻¹) and sediment load (478 Mt yr⁻¹) rank fifth and fourth worldwide respectively.^{37,39} The river's hydrology reflects strong climatic gradients along its course. The headwaters experience a harsh alpine climate with extreme cold (-4.4°C mean annual temperature), aridity, and intense aeolian processes. In contrast, the middle and lower reaches lie within a subtropical monsoon zone characterized by warmer conditions (16–18°C mean annual temperature) and pronounced seasonality, with summer highs reaching 40°C and winter lows dipping to -4°C.⁴⁰ These climatic variations drive the river's distinct hydrological regime, marked by summer high flows and significant spatial variability in water characteristics.

Poyang Lake, the largest freshwater lake in China, is located within the middle reaches of the Yangtze River (latitude 28°40'–29°46' N, longitude 115°49'–116°46' E) (Figure 1). With a watershed area of 16.22×10⁴ km² and an annual runoff of 152.5 km³, it accounts for 9% and 16.3% of the entire Yangtze River basin, respectively.⁴¹ The Poyang Lake basin lies within a typical subtropical monsoon climate zone, with an average annual rainfall of approximately 1,622 mm. A significant portion of this rainfall, between 42% and 53%, occurs from April to June.^{42,43} This seasonal rainfall pattern leads to considerable inter-annual variation in the lake's inflow, giving it the characteristics of a water conveyance-type lake.^{34,44} The lake experiences substantial water level fluctuations. During the summer months (July–September), the water level can reach around 18 m, while in the winter (November–February of the following year), it drops to approximately 9 m.²⁸ The central main channel area serves as a typical pelagic zone, characterized by relatively greater depth. On the east and west sides of the main channel, there are seasonal water-storage grooves, hereinafter referred to as “sub-lakes”.⁴⁵ In terms of hydrodynamic features, Poyang Lake maintains complete vertical mixing throughout the year due to its shallow depth and strong mixing forces, and exhibits no thermal or dissolved oxygen (DO) stratification.⁴⁶ Poyang Lake exhibits mesotrophic status with significant spatial variation. Trophic

levels are lower in the main channel and higher in sub-lakes.

Sample collection and determination

In 2022, field sampling activities were conducted from the upper reaches of the Yangtze River to the lower reaches in June 27 to July 22, and collected samples from Poyang Lake from July 23 to August 1. A total of 20 sampling points was established in the main stream of the Yangtze River, and repeated samples were collected at a distance of 100 m before and after each sampling point (Table S1). We have arranged a total of 21 points in Poyang Lake, of which 8 points (from sample 1 to 8) are located in sub-lakes and 13 points (from sample 9 to 21) are located in the main lake (Figure 1). At each sampling point, a 200 ml polyethylene plastic bottle was opened to collect each surface water sample (25 cm) and wrapped in a sealing film. A hand-held DO meter (Pro20, YSI Inc., Ohio, USA) was used to measure DO (accuracy: ±1% of reading) and water temperature (accuracy: ±0.01°C). During the sampling period, the instrument was calibrated weekly using zero point calibration and water saturated air calibration. This ensured accurate and reliable dissolved oxygen measurements throughout the study. An Ultrameter II pH meter (6P, Myron L company, Carlsbad, CA, USA) was used to measure salinity (accuracy: ±2% of reading), electrical conductivity (COND, accuracy: ±2% of reading), redox potential (ORP, accuracy: ±20 mV), and water acidity (pH, accuracy: ±0.2 units).

When collecting ¹⁸O-DO samples at each sampling point, the 12 mL precombusted borosilicate vials were opened at 25 cm depth underwater, following the protocol of which designates this depth as representative of the surface mixed layer for oxygen isotope mass balance calculations.¹⁴ After tightening the cap, an injection needle was used to add 50 µL of HgCl₂ saturated solution to inhibit microbial activity and prevent post-collection changes in DO concentration and isotopic composition during storage. Finally, high vacuum grease was applied to the pinholes to seal and caps were wrapped with parafilm.¹⁴ For every POC sampling, in situ water samples were immediately filtered through Whatman glass fiber filters (GF/F, 0.7 µm and Φ47 mm), which were combusted at 450°C for 5 h and packed in aluminum foil before sampling. To remove particulate inorganic carbon (PIC) prior to analysis, all POC samples were acidified for 8 hours in a desiccator containing an open container of 10% hydrochloric acid (HCl) at its base. For each partial pressure of carbon dioxide (pCO₂) sampling, a rubber tube was used to pour water from the bottom of a 100 mL brown vial containing 14 g of KCl. The air was slowly pushed out, and the butyl rubber stopper was tightly plugged (ensure no air bubbles), and then a capper was used to compress the aluminum cap and was wrapped with a parafilm.⁴⁷

After field sampling, all collected water samples were immediately transferred to Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences (IGSNRR, CAS) and stored in the dark at 4°C until analysis. For a 12 mL headspace bottle sample, about half of the water was drawn out to form a vacuum, and then the bottle body was shaken on a shaker to allow the gas to enter the headspace and was separated and purified.²⁸ After these pretreatments, the samples were used to test for the following indicators (Table S2): (1) δ¹⁸O-DO was determined using Stable gas isotope mass spectrometer (253-plus, Thermo Fisher Scientific, USA). The analytical precision, determined from replicate analyses of internal laboratory standards, was ±0.3‰ (1σ), and sample reproducibility, assessed through duplicate samples collected at approximately 10% of the sampling sites, yielded a mean standard deviation of ±0.4‰. (2) dissolved inorganic carbon (DIC), dissolved organic matter (DOC), dissolved total nitrogen (DTN), and particulate organic carbon (POC) concentrations were determined using a TOC analyzer (Shimadzu, Japan). The detection limits were 0.001 mg L⁻¹. (3) Nitrate nitrogen (NO₃-N) was determined using a segmented continuous flow analyzer (Futura, France). The detection limits were 0.01 mg L⁻¹. (4) K⁺, Ca²⁺, Na⁺, Mg²⁺, and dissolved silicon (DSi, in the form of SiO₂) were determined using an inductively coupled plasma optical emission spectrometer (ICP-OES, Thermo Fisher Scientific, Darmstadt, Hesse, Germany). The detection limits were 0.01 mg L⁻¹. (5) Cl⁻ and SO₄²⁻ were determined using an ion chromatograph (Thermo Scientific Aqion IC, USA). The detection limits were 0.01 mg L⁻¹. (6) δ¹³C-DIC was determined using a Finnigan MAT-252 mass spectrometer (Thermo Fisher Scientific, Darmstadt,

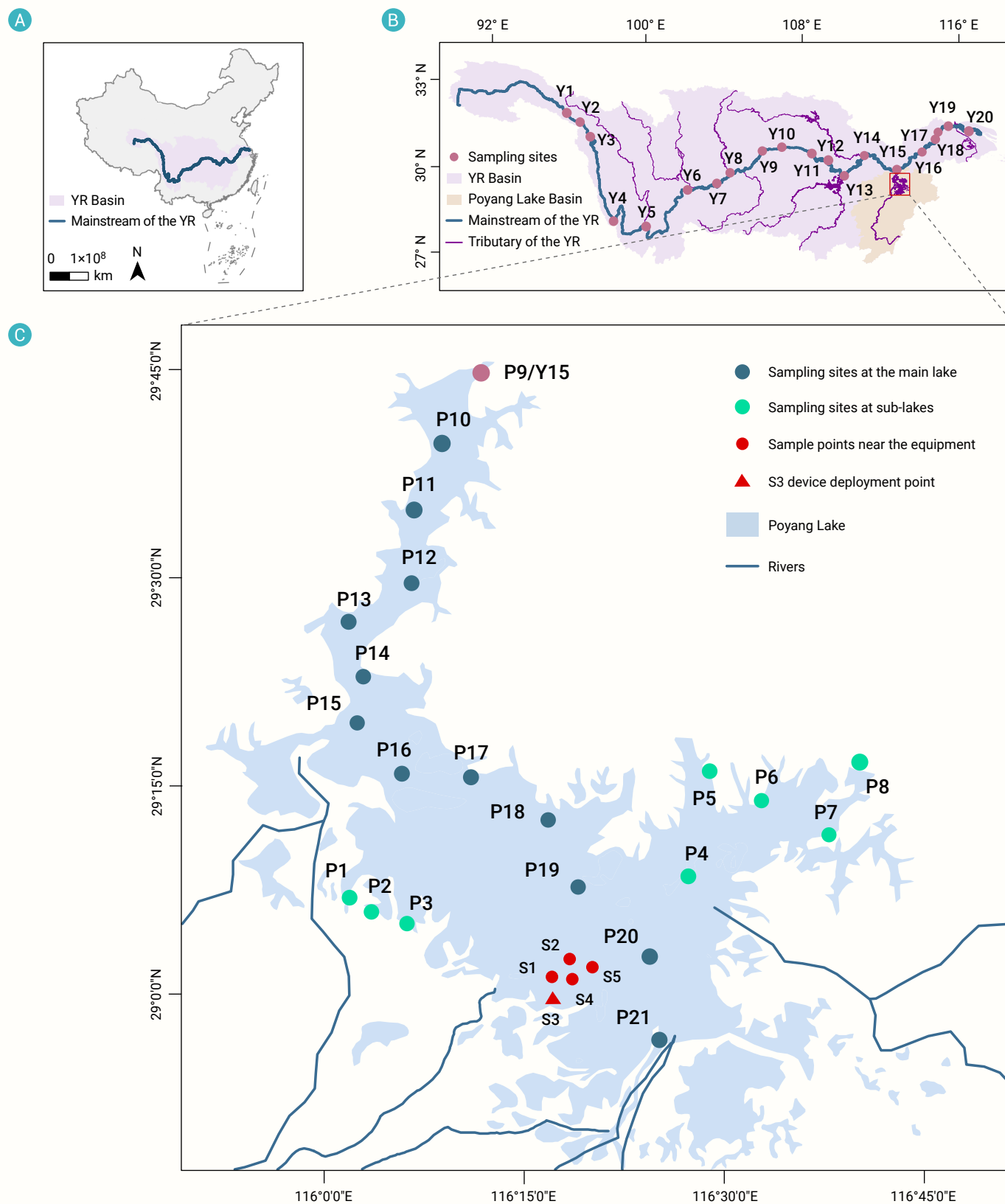


Figure 1. Sampling point locations (A) The location of the Yangtze River Basin in China; (B) Yangtze River; (C) Poyang Lake. See Table S1 for detailed information on Yangtze River sample site locations. YR: the Yangtze River.

Hesse, Germany). The analytical precision, determined from replicate analyses of internal laboratory standards, was $\pm 0.1\%$ (1σ), and sample reproducibility was $\pm 0.2\%$ (1σ) based on duplicate samples. (7) $p\text{CO}_2$ was determined using an gas chromatograph (Agilent7890A, Thermo Fisher Scientific, USA).

Diel O₂ method

Oxygen (O₂) is primarily regulated by the balance between primary production and aerobic respiration,⁴⁸ hence the production of DO by photosynthesis occurs only during day, while the consumption of DO occurs through day and night.^{11,12} Temporal changes in DO concentrations over a 24-h period, will

allow for quantification of NEP, ER, and GPP.⁴⁹

In September 2021, we deployed a water quality in-situ detection instrument (YSI EX02 multiparameter water quality sonde, USA) at 1 m underwater in Nanjishan area (latitude: 28°58'W, longitude: 116°20' E) of South Poyang (Figure 1). The sensor was deployed at a site near the main channel of Poyang Lake, specifically in the transition zone between the main channel and the sub-lakes. This location was selected because it maintains good hydrological connectivity with the main channel throughout the year, making it suitable for capturing the metabolic dynamics of the lake's primary water body. However, we recognize that this single station does not represent the extreme metabolic rates observed in the isolated sub-lakes, which were separately captured through the spatial survey using the ¹⁸/¹⁶O technology. Based on the vertical temperature profiles, no distinct mixed layer was observed in Poyang Lake. The anchoring system was fine-tuned weekly via vertical adjustments of the mooring rope length to maintain the sensor at 1 m below the water surface. Dissolved oxygen (accuracy: ±1% of reading), chlorophyll (accuracy: ±0.1 µg/L), water temperature (accuracy: ±0.01°C), and salinity (accuracy: ±1% of reading) were monitored in real time every 30 min. We verified the location, cleanliness, battery capacity, and data integrity of the instrument weekly to reduce the risk of data loss due to baseline drift, biofouling, hardware degradation, storage limitations, or power outages. Metabolic calculations followed the methods of Staehr et al.¹² and Needoba et al.²⁷ Field measurements showed Poyang Lake's winds typically fall within this range. Before model analysis, all data were manually inspected to identify gaps, anomalies missed by automated checks, sensor drift, or non-physical repeated values.

DO measured in mg L⁻¹ can be converted to volumetric concentration (mL L⁻¹) at standard temperature and pressure (0°C, 1 atm) by:

$$O_2 (\text{mL L}^{-1}) = O_2 (\text{mg L}^{-1}) \times \frac{22.4}{31.9} \quad (1)$$

DO solubility is also reported in relation to atmospheric equilibrium:

$$O_{2\% \text{Sat}} = \frac{O_{2\text{meas}}}{O_{2\text{sat}}} \times 100 \quad (2)$$

where $O_{2\text{meas}}$ is the measured value, corrected for salinity and temperature, and $O_{2\text{sat}}$ is the computed equilibrium concentration oxygen with respect to the atmosphere at sea level as a function of water temperature and salinity. The elevation of the study site (15 m) would theoretically cause a 0.9% increase in $O_{2\% \text{Sat}}$ values compared to sea-level calculations, which was considered negligible given other sources of variability.

For routine computation of $O_{2\text{sat}}$, we followed the recommended procedure of Needoba et al.²⁷

$$\ln O_{2\text{sat}} (\text{mL L}^{-1}) = A_0 + A_1 T_s + A_2 T_s^2 + A_3 T_s^3 + A_4 T_s^4 + A_5 T_s^5 + S(B_0 + B_1 T_s + B_2 T_s^2 + B_3 T_s^3) + C_0 S^2 \quad (3)$$

where T_s is a scaled temperature function, S is salinity (mg L⁻¹), and A , B , and C are coefficients. The coefficients A , B , and C are originally from: $A_0 = 2.00907$, $A_1 = 3.22014$, $A_2 = 4.05010$, $A_3 = 4.94457$, $A_4 = -2.56847 \times 10^{-1}$, $A_5 = 3.88767$, $B_0 = -6.24523 \times 10^{-3}$, $B_1 = -7.37614 \times 10^{-3}$, $B_2 = -1.03410 \times 10^{-2}$, $B_3 = -8.17083 \times 10^{-3}$, $C_0 = -4.88682 \times 10^{-7}$. The formula is explicitly designed to cover the entire salinity range without loss of accuracy, including freshwater ($S = 0$). As Poyang Lake in this study is a freshwater lake, $S=0$ was adopted.

T_s is calculated by:

$$T_s = \ln \left[(298.15 - t) \times (273.15 + t)^{-1} \right] \quad (4)$$

where t is the measured temperature (°C).

Followed the procedure of Needoba et al., Air-water diffusion can be calculated by:

$$F_{O_2} = \left(1 - \frac{O_{2\% \text{Sat}, t1} + O_{2\% \text{Sat}, t2}}{200} \right) \times k_{O_2} \times dt \quad (5)$$

where dt is the time interval between two consecutive measurements, and $O_{2\% \text{sat}}$ is the percent oxygen saturation calculated for the intervals of time t_1 and t_2 . The k_{O_2} was calculated using the method from the ¹⁸O technique, as detailed in Section ¹⁸/¹⁶O technology.

NEP (in this case the production and consumption of DO caused by biological processes) for each time interval (t) is calculated from the change in DO_{HBF} for each time interval (t).

$$NEP_t = (DO_t - DO_{t-1}) \times h - F_{O_2} \quad (6)$$

where h is depth of the mixed layer (m), which was about 2 m at the device. For the period when there is no daylight, it is assumed that the only process altering the NEP is aerobic respiration.

The hourly ER ($\text{g O}_2 \text{ m}^{-2} \text{ h}^{-1}$) is

$$\text{Hourly ER} = \frac{\text{Sum of } NEP_n}{\text{Hours of night}} \quad (7)$$

where NEP_n is the hourly NEP during the night.

The daily oxygen respiration is determined by:

$$\text{Daily ER} = 24 \times \text{Hourly ER} \quad (8)$$

The daily GPP ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) is the sum of the NEP ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), plus a correction for the DO removed by ER during the day:

$$GPP = NEP + (\text{Hours of daylight} \times \text{Absolute value of hourly ER}) \quad (9)$$

Throughout this study, we used O_2 as the unit of measure for metabolic estimates. With no topographic or vegetation shading near the equipment deployment site or across most of the water area, daylight hours were determined using calculated sunrise/sunset times based on latitude and longitude.

¹⁸/¹⁶O technology

The ¹⁸/¹⁶O technology assumes that the isotopic composition of O_2 molecules in the atmosphere and the isotopic fractionation effect of each metabolic link are constant.¹⁴ This assumption is valid in both rivers and lakes, so this study applied it to the Yangtze River and Poyang Lake. The final metabolic rates obtained from the ¹⁸O/¹⁶O mass balance model are reported on an areal basis ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). This result is mathematically independent of mixing depth; therefore, no correction or estimation for mixing depth was applied in our metabolic calculations. Below is the equation for estimating GPP, ER and NEP of inland water using ¹⁸/¹⁶O technology.

Saturated DO concentration (DO_{sat} , mg L⁻¹):

$$DO_{\text{sat}} = (e^e) \times 1.423 \quad (10)$$

$$C = -173.4292 + 249.6339 \times \left(\frac{100}{T} \right) + 143.3483 \times \ln \left(\frac{T}{100} \right) - 21.8492 \times \left(\frac{T}{100} \right) + S \times \left[-0.033096 + 0.014259 \times \left(\frac{T}{100} \right) - 0.0017 \times \left(\frac{T}{100} \right)^2 \right] \quad (11)$$

where C (ml $\text{O}_2 \text{ L}^{-1}$) is a molar volume of O_2 (mL $\text{O}_2 \text{ L}^{-1}$) at specific temperature (T , Kelvin) and salinity (S , ng L⁻¹).

Saturated DO concentration corrected based on atmospheric pressure or altitude:

$$DO_{\text{sat}} \text{ corrected for pressure} = DO_{\text{sat}} \times \text{correction factor} \quad (12)$$

$$\text{correction factor} = \frac{BP \times 0.0987 - 0.0112}{100} \quad (13)$$

$$\text{correction factor} = \frac{0.0000005 \times \text{altitude}^2 - 0.0118 \times \text{altitude} + 99.979}{100} \quad (14)$$

where BP is barometric pressure (mmHg). The unit of altitude is meters (m).

Measured DO concentration (DO_{meas} , mg L⁻¹):

$$DO_{\text{meas}} = DO (100\%) \times DO_{\text{sat}} \quad (15)$$

Schmidt coefficient (Sc) based on water temperature:

$$Sc = 0.0476T^3 + 3.7818T^2 - 120.1T + 1800.6 \quad (16)$$

Piston velocity 1 (k_{500} , m h⁻¹):

$$k_{600} = \frac{2.07 + 0.215U_{10}^{1.7}}{100} \quad (17)$$

Piston velocity 2 (k_{O_2} , $m \cdot h^{-1}$):

$$k_{O_2} = k_{600} \times \left(\frac{Sc}{600} \right)^{-\frac{2}{3}} \quad (18)$$

Atomic fraction (AF):

$$AF = \frac{R_{sample}}{1 + R_{sample}} \quad (19)$$

$$R_{sample} = \frac{\delta^{18}O}{1000} \times 0.0020052 + 0.0020052 \quad (20)$$

AF_{DO} , AF_{H_2O} and AF_{atm} represent the AF of ^{18}O in DO , water and atmospheric O_2 , respectively. R_{sample} is the ratio of heavy isotope to light isotope in the sample.

GPP ($g \cdot O_2 \cdot m^{-2} \cdot d^{-1}$):

$$GPP = k_{O_2} \times \frac{DO_{meas} \times (b - c) - DO_{sat} \times (a - c)}{d - c} \quad (21)$$

$$a = AF_{atm} \times \alpha_s \times \alpha_g \quad (22)$$

$$b = AF_{DO} \times \alpha_g \quad (23)$$

$$c = AF_{DO} \times \alpha_c \quad (24)$$

$$d = AF_{H_2O} \times \alpha_p \quad (25)$$

$$\alpha_s = 1.0007; \alpha_g = 0.9972; \alpha_c = 0.9900; \alpha_p = 1.0000 \quad (26)$$

ER ($g \cdot O_2 \cdot m^{-2} \cdot d^{-1}$):

$$ER = k_{O_2} \times \frac{DO_{meas} \times (b - d) - DO_{sat} \times (a - c)}{d - c} \quad (27)$$

NEP ($g \cdot O_2 \cdot m^{-2} \cdot d^{-1}$):

$$NEP = GPP - ER \quad (28)$$

zation (WMO) Resolution 40 (Cg-XII, 1995).

RESULTS

Water quality parameters distribution

Spatially, we observed striking differences in water quality parameters between the Yangtze River and Poyang Lake. The distribution of the five parameters (i.e., COND, SO_4^{2-} , Ca^{2+} , DIC, and $\delta^{13}C-DIC$) were similar, gradually decreasing from the first, second to third section of the Yangtze River while increasing in the fourth section. The concentrations of these parameters in Poyang Lake were significantly lower than those in Yangtze River, while no significant differences were observed among the three groups of EQU (sampling points near the monitoring equipment), SUB (sub-lake sampling points), and MAIN (main channel sampling points) (Figures 2A, D, F, J & R).

The oxidation-reduction potential (ORP) gradually increased from the first, second, to third sections of the Yangtze River, where no significant differences were observed from the first section to the fourth section in Poyang Lake (Figure 2B). pH gradually decreased from the first, second, to third sections, and increased slightly during the fourth section (Figure 2C). NO_3^- concentrations were high in the second and third sections, but no significant differences were observed between the first and fourth sections and in Poyang Lake (Figure 2E). Yangtze River water was low in Fe^{3+} , but Fe^{3+} concentration significantly increased in Poyang Lake, where it was relatively low in the main channel (Figure 2G). DSI was stable (i.e., 6 mg L^{-1}) in the Yangtze River. The DSI of Poyang Lake differed significantly at all sampling points except for the main channel (Figure 2H). DOC was low in the Yangtze River, but it gradually decreased in the first three river sections, while DOC in Poyang Lake was significantly higher than that in the Yangtze River (Figure 2I). POC was high in the first section of the Yangtze River and low in the second to fourth sections, while significant differences were observed among the different Poyang Lake sampling points (Figure 2K). Particulate inorganic carbon (PIC) was extremely high in the first section of the Yangtze River, while decreasing towards zero in the second to fourth sections of the river, with significant differences in Poyang Lake (Figure 2L). Yangtze River pCO_2 was aggregated and supersaturated (i.e., above mean atmospheric pCO_2 : $413 \mu\text{atm}$), while in Poyang Lake, it was dispersed, where sub-lake sampling point values were much higher than atmospheric pCO_2 (Figure 2M). Except for the low DO observed in the sub-lakes, the other sampling points exhibited no significant differences (Figure 2N). $\delta^{18}O-DO$ in Yangtze River was significantly higher than that of Poyang Lake (Figures 2O & S1). Specifically, $\delta^{18}O-H_2O$ was the highest (while $D-H_2O$ was lowest) in the third and fourth sections of the Yangtze River, while being the lowest in the second section. $\delta^{18}O-H_2O$ in Poyang Lake was significantly higher than that of that in Yangtze River (Figures 2P & Q).

Spatial distribution of metabolic parameters

For large rivers, dramatic elevation and climate differences within different river sections can significantly affect the water regime. We divided the Yangtze River into four sections (Figure 3 & Table S1). Although the sampling stations on the Yangtze River represent a successively increasing flow velocity (i.e., from an upstream to a downstream direction), water levels varied significantly and exhibited no obvious trend. The water level (approx. 25 m) and the flow rate (approx. $1,373 \text{ m}^3 \text{ s}^{-1}$) at sampling points Y1–Y5 were both low. At sampling points Y6–Y9, water levels abruptly decreased (by approx. 196 m), where it reached its deepest point (271 m) at the XJB station (i.e., sampling point Y6), while the flow rate further increased (approx. $9,860 \text{ m}^3$). The Hukou hydrological (HK) station is situated in a tributary of the Yangtze River, whose discharge rate is much lower than that of the main stream ($7,930 \text{ m}^3$). After sampling point Y11, the water level steeply decreased again to approximately 24 m, while the flow rate significantly increased until reaching its maximum value ($42,500 \text{ m}^3$) at sampling point Y16.

Metabolic rates (GPP, ER, and NEP) differed significantly among the four sections of the Yangtze River (Figure 3B). The GPP of the Yangtze River (shown by the orange column in Figure 3B) was low in the first section (i.e., Y1–Y5, by approx. $1.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), of which the GPP of sampling point Y3 was the lowest overall ($0.8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). The second section of the Yangtze River (Y6–Y10) exhibited a slight but relatively stable decrease in GPP (approx. $1.4 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). The third section (Y11–Y18) had two GPP peaks, of

Statistics and mapping

All statistical analyses were performed using R version 3.4.3. Pearson correlation coefficients were computed using the PerformanceAnalytics and corplot packages, and the results were visualized as heatmaps with significance levels (p-values) reported. Redundancy analysis (RDA) was carried out using the rda function in the vegan package; explanatory variables were pre-screened by variance inflation factor ($VIF < 10$) to mitigate multicollinearity, and the significance of the overall model as well as individual ordination axes was assessed via 999 unrestricted permutation tests. Structural equation modeling (SEM) was implemented with the lavaan package, using maximum likelihood estimation combined with bootstrap resampling (1000 iterations) to obtain robust standard errors for the path coefficients. The final SEM exhibited a good fit to the data ($\chi^2 = 73.07$, $df = 21$, $p = 0.58$; $\chi^2/df = 3.48$). All graphical outputs, including correlation heatmaps, RDA ordination plots, and SEM path diagrams, were generated using the ggplot2 and semPlot packages.

Other data sources

Water level and flow data are from China National Water Regulatory Network (<http://xxfb.mwr.cn/>). The wind speed data was obtained from the National Oceanic and Atmospheric Administration (NOAA)—National Centers for Environmental Information (NCEI) (available at: <https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.ncdc:C00516>). We used daily average (24h) 10-meter wind speed data from the nearest meteorological station to each sampling location, with Changbei Station representing Poyang Lake. These data are shared under the World Meteorological Organi-

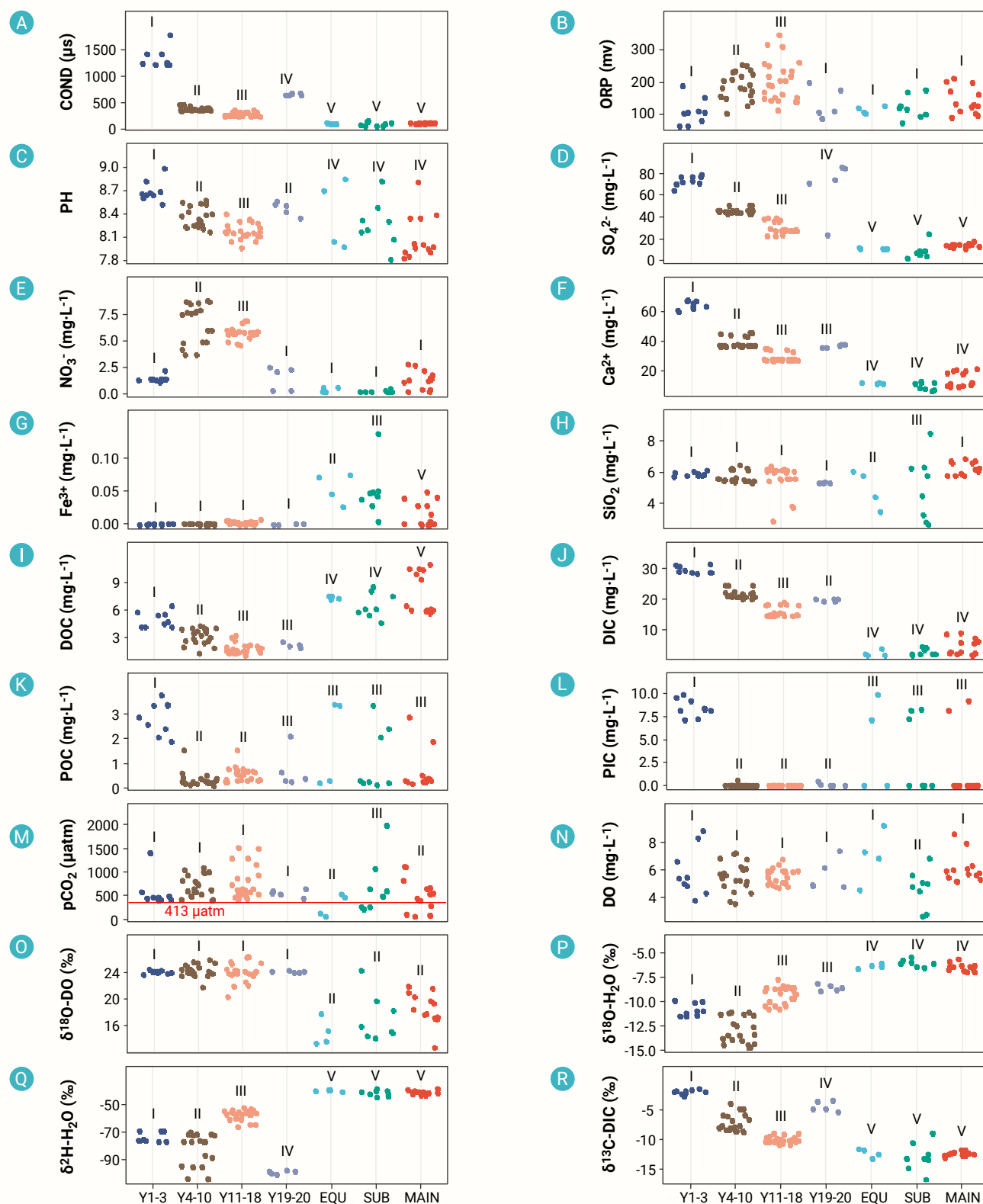


Figure 2. Water quality parameters at each sampling point (divided into seven categories) Y1–Y3 represents the first section of the Yangtze River; Y4–Y10 represents the second section of the Yangtze River; Y11–Y18 represents the third section of the Yangtze River; Y19–Y20 represents the fourth section of the Yangtze River; EQU represents sampling points near the monitoring equipment; SUB represents sub-lake sampling points; MAIN represents main channel sampling points. Same capital Roman numerals indicate no significant difference between groups, whereas different Roman numerals indicate significant differences.

which the first peak ($3.9 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) occurred at sampling point Y13 and the second peak ($3.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) occurred at sampling point Y18. GPP then abruptly decreased at sampling points Y19–Y20 (by approx. $1.3 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). The trend in Yangtze River NEP (shown by the blue column in Figure 3B) was opposite to that of GPP. NEP was high in the first section of the Yangtze River

(Y1–Y5, by approx. $-2.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), with the highest value recording at sampling point Y3 overall ($-1.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). NEP in the second section of the Yangtze River (Y6–Y10) had hardly changed compared with the first section, but was more stable (approx. $-2.4 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). In the third section of the Yangtze River (Y11–Y18), NEP exhibited two troughs, where Y13 was the first

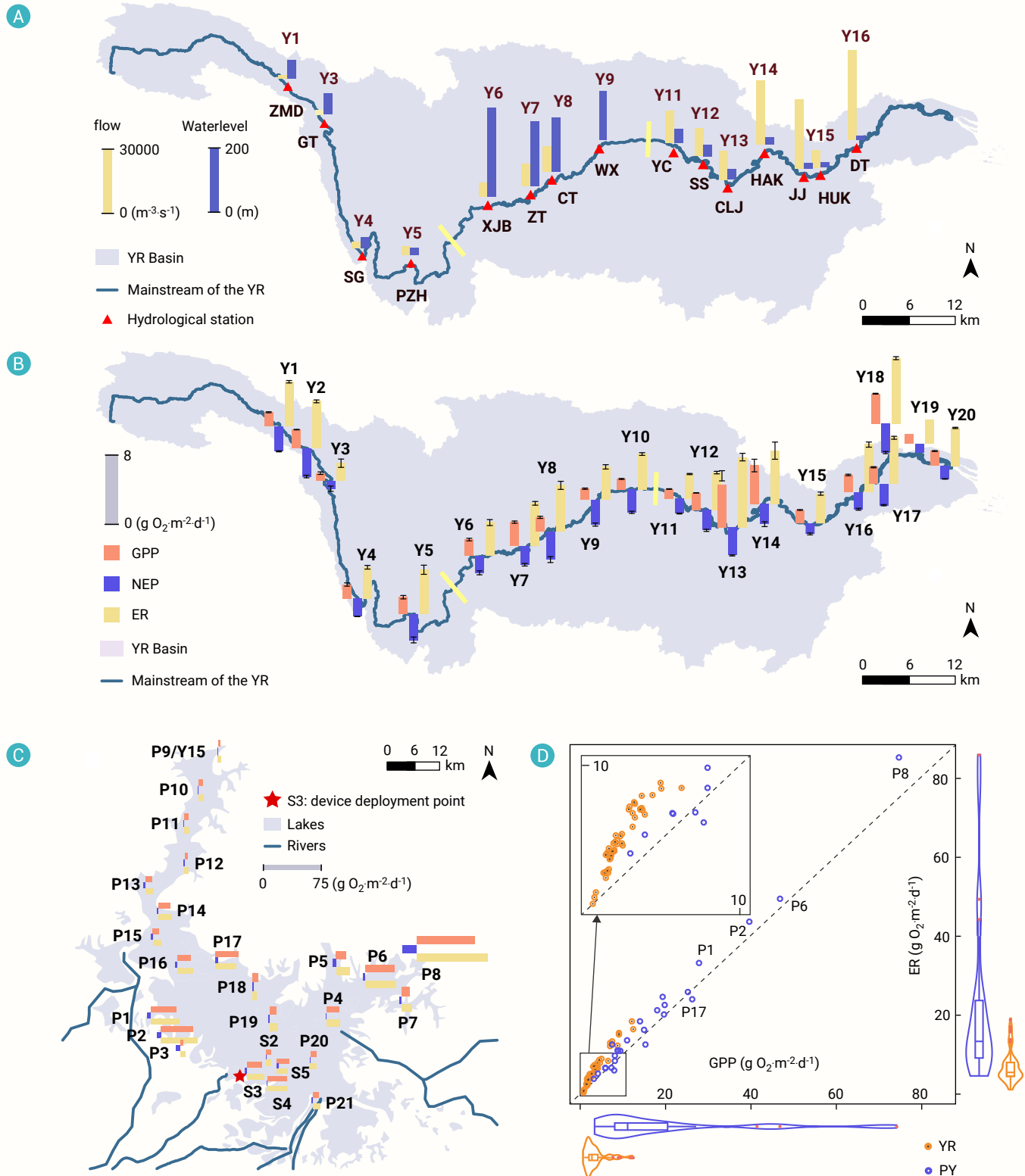


Figure 3. Water levels at different stations on the Yangtze River (A) and metabolic indicators of the Yangtze River and the Poyang Lake obtained using ^{18}O technology (B–D). The yellow line represents the three-section division of the Yangtze River (Table S1). YR: the Yangtze River; PY: the Poyang Lake. See Figure S1 for conventional bar plots of metabolic indicators.

trough ($-3.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and Y18 was the second trough ($-3.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). NEP then rebounded sharply in the section from Y19 to Y20, reaching approximately $-1.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$.

For large water conveyance-type lakes, there are obvious differences of water regimes and metabolic processes between the fast flowing and deep depth main channels and the slow flowing and shallow depth sub-lakes. GPP

in Poyang Lake was lower (approx. $8.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the main channel (P9–P21) under a higher flow velocity and a deeper water depth, but was higher (approx. $28.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the sub-lakes under slower flow velocities and shallower water depths (P1–P8). GPP near the monitoring equipment was approximately $15.8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, which was higher than the average level in July and August ($10.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) obtained from diel O_2 method.

Overall, Poyang Lake NEP was slightly higher ($-2.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) than that of the Yangtze River ($-2.3 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), where the NEP in the main channel (P9–P20) was higher (approx. $-1.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) while the NEP was lower (approx. $-4.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in the sub-lakes (P1–P8). NEP near the monitoring equipment was approximately $-0.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, which was higher than the average level in July and August ($-1.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) obtained from diel O_2 method. Overall, the metabolic rates derived from the $^{18/16}\text{O}$ technology exhibited exceptionally high spatial variability. Across all sampling sites, GPP ranged from 2.9 to $72.7 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, and ER ranged from 4.4 to $84.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, representing approximately a 25-fold and 19-fold difference between the lowest and highest values, respectively (Figure 3D). GPP (average $16.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and ER (average $18.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) in Poyang Lake was significantly higher than those of the Yangtze River ($1.8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and $4.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), especially in the sub-lakes (Figure 3D).

Metabolic time series

Observations from high-frequency diel O_2 time series revealed typical periodic changes in the water conveyance-type lake. The average GPP and ER values of Poyang Lake derived from the diel O_2 method were $14.6 (\pm 15.6) \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and $18.2 (\pm 16.7) \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively, and the average NEP value was $-3.6 (\pm 4.1) \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, implying a net heterotrophy at the system level. Both GPP and ER began to rise in late July, peaked in mid-August, and then dropped sharply while fluctuating steadily between 0 and $8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in early October (Figure 4A). During the months when GPP and ER were high (i.e., July–August), NEP was low while remaining stable for the remainder of the year.

The annual average of chlorophyll concentration at the monitoring station was $8.5 \mu\text{g L}^{-1}$. Chlorophyll peaked twice, first increasing slightly (i.e., to $16.7 \mu\text{g L}^{-1}$) between the end of July and early October, followed by a higher peak between December and February ($26.0 \mu\text{g L}^{-1}$) (Figure 4B). The mean DO value was 4.8 mg L^{-1} , with the highest value of 8.2 mg L^{-1} in February and March and the lowest value during August and September (Figure 4C). The water temperature range was 4.1 – 36.1°C , with fluctuation trends opposite to that of DO, reaching its lowest point in February and March and its highest in August and September (Figure 4D). From September 2021 onwards, the water level gradually decreased, reaching its lowest level in January of the following year (7.4 m) before peaking in July (19.0 m) and decreasing thereafter (Figure 4E). Water flow fluctuations roughly coincided with water levels, peaking in early July ($26,500 \text{ m}^3 \text{ s}^{-1}$) (Figure 4F).

To better observe and infer periodic daily metabolic fluctuation properties and water regimes in more detail, 4-day hourly frequency data (i.e., from 0:00 on September 9 to 24:00 on September 12) are shown separately (Figures 4G–L). GPP exhibited a typical diel pattern: it increased rapidly from sunrise ($0.0 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$), peaked at midday ($3.0 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ between 11:00–12:00), and subsequently declined gradually (Figure 4G). NEP was positive during the day and negative at night. However, no obvious fluctuations were observed at night, when the lowest value was approximately $-2 \text{ g O}_2 \text{ m}^{-2} \text{ h}^{-1}$ (Figure 4G). Chlorophyll exhibited high temporal variability (Figure 4H), with no consistent correlation to NEP across the study period (Pearson's $r = 0.12$, $p = 0.45$). Analogous to the metabolic index, both DO and chlorophyll exhibited extremely good daily single peak fluctuations. However, these peaks occurred later than corresponding GPP and NEP peaks. Specifically, DO peaked at sunset, being approximately 1 h later than the corresponding temperature peak. Within a 4-day period, both metabolic DO and temperature indicator waves were consistent (Figures 4I–J), while the wave size corresponded to a downward trend in water level and water flow (Figures 4K–L).

Pairwise correlations were analyzed using combined water level and flow data from the HK station, along with interannual metabolic rate variations in Poyang Lake derived from the Diel O_2 method (Figure 5). On an annual timescale, water level, flow, temperature, and pH exhibited significant positive correlations. Flow was positively correlated with NEP but negatively correlated with GPP and ER. Water level also showed a positive relationship with NEP. Chlorophyll displayed significant negative correlations with water level, flow, and temperature. Additionally, water temperature was negatively correlated with DO and NEP but positively correlated with GPP and ER (Figure 5A).

On a daily timescale, DO, pH, temperature, NEP, and GPP were all significantly positively correlated—a pattern distinct from the annual scale. Consistent with annual trends, chlorophyll remained negatively correlated with pH and temperature (Figure 5B).

DISCUSSION

Temporal drivers

Temporally, the impact of water regimes on inland water metabolism can be viewed as the cumulative effect of repeated flow pulses, representing cycles of water transport from upstream to downstream. A major flow event may contain multiple smaller flow peaks. On an annual timescale, coincident thermal and precipitation characteristics under a subtropical monsoon climate resulted in a significant positive correlation between water level, flow, water temperature, and pH.⁵⁰ The significant negative correlations of chlorophyll with water level, flow, and temperature are most plausibly due to dilution from increased water volume and hydraulic flushing that reduce algal biomass.⁵¹

In our study area, water temperature showed significant correlations with DO, NEP, GPP, and ER. Specifically, it was negatively correlated with DO and NEP, and positively correlated with GPP and ER. Daily fluctuations in water temperature were more pronounced than those in flow rate and water level (Figure 3). While increasing temperature can accelerate both photosynthesis and respiration, the stimulatory effect on respiration — particularly heterotrophic respiration (ER) — is often more substantial in such systems. This pattern is consistent with findings from Tan et al. (2018),⁵² who studied a small temperate lake that experiences seasonal ice cover and thus a wider annual temperature range than Poyang Lake. However, we acknowledge that in situ temperature effects are partially confounded with the diel light cycle, and our observational design does not allow us to fully separate these two drivers. Therefore, we interpret the observed temperature–metabolism relationships primarily as correlative evidence, which supports (but does not prove) a stronger regulatory role of temperature on respiration in this system. We observed a distinct time lag of approximately 55 days between the hydrological peak (June 24, 2022) and the metabolic peak (August 18, 2022), with maximum GPP occurring during flow recession rather than at peak discharge (Figure 4). We propose that this hysteresis is driven by lagged nutrient mobilization from sediments or delayed phytoplankton community turnover. Nevertheless, we cannot rule out confounding factors, such as gradual temperature increases or light availability changes that covary with the recession period. Moreover, pH negatively correlated with DO and chlorophyll and positively correlated with GPP and ER. Around neutral pH, bicarbonate (HCO_3^-) is the dominant inorganic carbon form; however, CO_3^{2-} will form under increasing pH levels.⁵³ DO significantly and positively correlated with NEP but significantly and negatively correlated with GPP and ER. This is because NEP increased when photosynthesis exceeded respiration, resulting in the large DO consumption by producers.¹²

NEP was higher when GPP was higher during certain periods of the day. This is associated with the constant daily respiration rate assumption under diel O_2 method.¹² Studies have shown that highly productive rivers typically exhibit large increases in diurnal DO concentrations and subsequent nocturnal decreases under relative rate changes in aquatic photosynthesis and respiration.⁵⁴ Therefore, impact mechanisms associated with the water regime–biological factor–metabolism interface differed between under short-term timescales (i.e., hourly units under a daily timescale) and under long-term timescales (i.e., daily units under an annual timescale). On an annual timescale, phytoplankton photosynthesis and respiration both accelerated in summer. However, the increase in respiration was ultimately greater than the increase in photosynthesis under a decrease in NEP. On a diurnal timescale, organic matter accumulated during photosynthesis, and the greater respiration rate of lake organisms at night offset or even exceeded daytime photosynthetic accumulation. The sustained negative NEP indicates that waterbodies with strong hydrological variability receive more energy subsidies (POC and DOC) from their watersheds. These subsidies maintain the ecosystems in a net heterotrophic state, thereby making them important conduits for exporting watershed organic carbon as CO_2 emissions to the atmosphere.

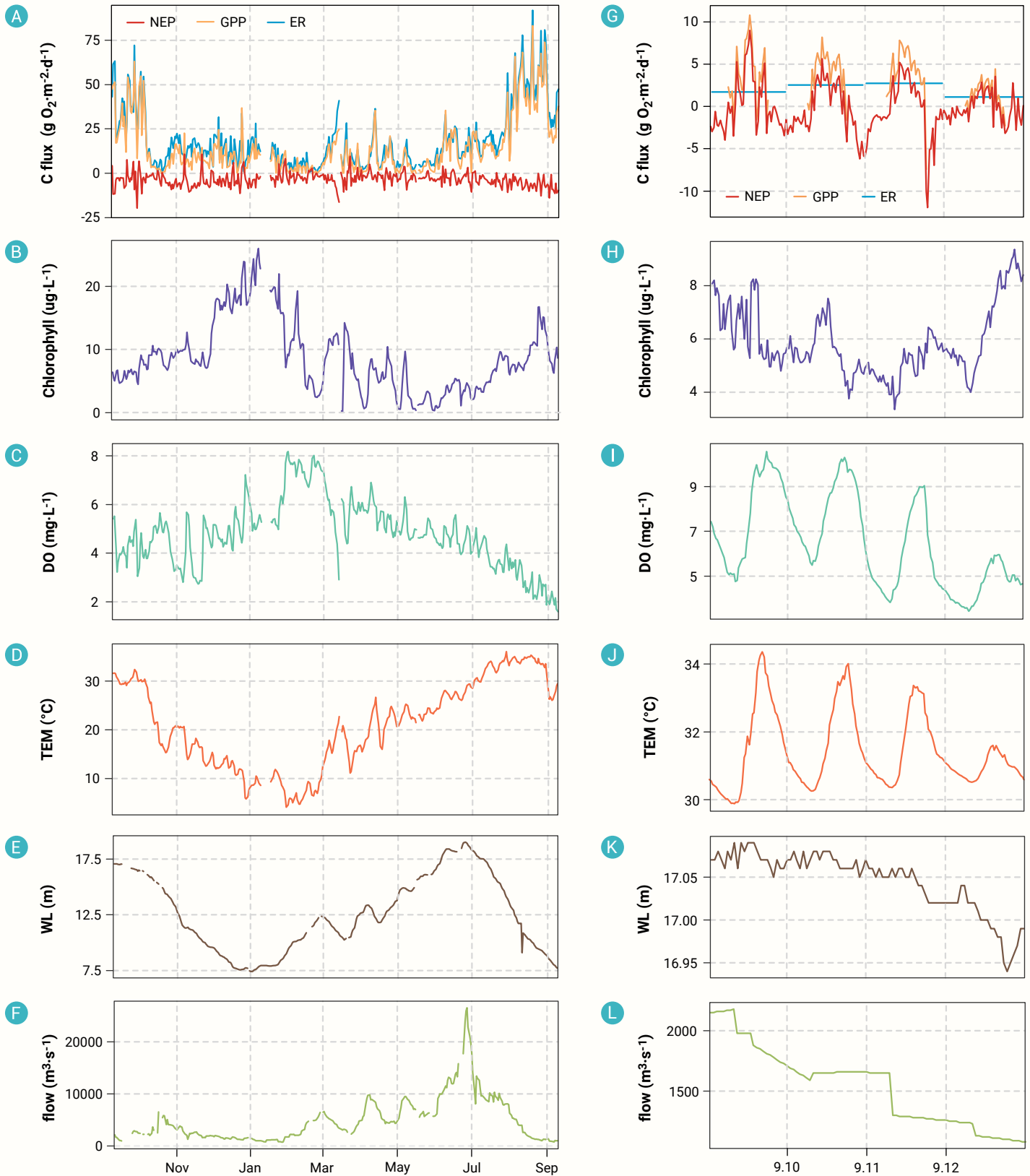


Figure 4. The Poyang Lake water regime and metabolic time series from September 9, 2021, to September 8, 2022 (A to F, daily), and from September 9 to September 12, 2021 (G to L, every half hour) DO: dissolved oxygen; TEM: water temperature; WL: water level.

Spatial drivers

Spatially, water regime impact mechanisms on metabolism were far more complex. Accordingly, the influencing factors discussed below are more diverse. Topography and climate cause great uncertainty for large rivers

whose land area is vast. Although the main channel is relatively stable for water conveyance-type lakes, sub-lakes are easily affected by other factors (e.g., small landform features, local vegetation, and underlying surfaces). To better analyze the spatial relationships and mechanisms among water

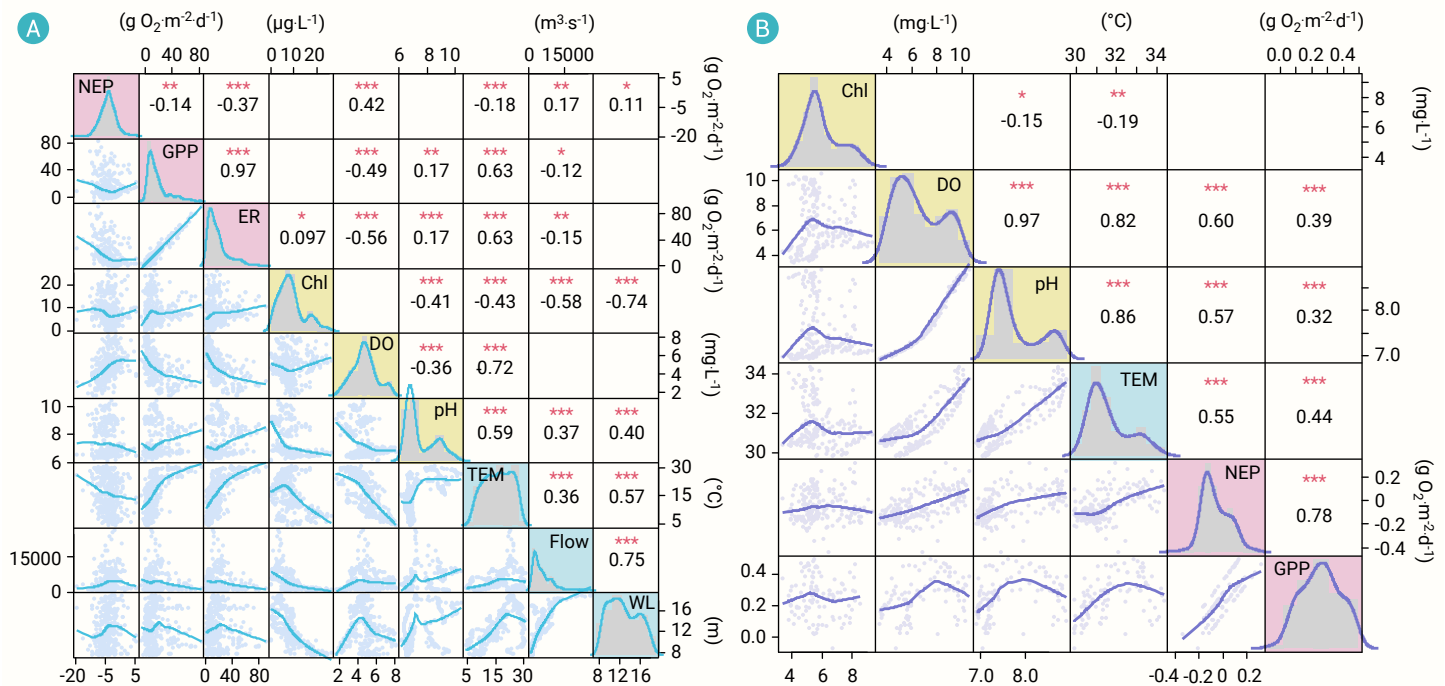


Figure 5. Scatter diagram fitting curves and correlations among metabolic, water regime, and water quality parameters of the Yangtze River, where (A) denotes the daily average value and (B) denotes the hourly average value from September 9 to September 12 * 0.01 < p < 0.05, ** 0.0001 < p < 0.01, and *** p < 0.0001.

regime, water quality, and metabolism, we integrated three datasets: metabolic data from the $^{18}\text{O}/^{16}\text{O}$ technology, water quality parameters from the same samples, and hydrological data from the corresponding Yangtze River stations. We then conducted correlation and redundancy analyses on this combined dataset. The results were subsequently used to construct a structural equation model. Spatially, flow and water temperature positively correlated with GPP and ER. Azevedo et al.⁵⁵ concluded that phytoplankton biomass had a parabolic relationship with water flow, showing a decline at both high and low river water flow, which may be reflected in the lower residence times and lower nutrient and biomass inputs, respectively. Therefore, the Yangtze River and Poyang Lake should reflect the first half of the parabola in July. The sediment load in the upper reaches of the Yangtze River was the largest (0.8×10^8 tons per year), followed by the lower reaches and the middle reaches in descending order.⁵⁶ Reduced sediment loads enhanced solar transmittance, resulting in higher GPP and lower ER in the middle reaches of the Yangtze River (Y10–Y15) (Figure 3B). Both water flow rates and water temperature positively correlated with conductivity and negatively correlated with most ions, except for Fe^{3+} , NO_3^- , and F^- . Due to the gradual increase in water flow from its tributaries, the flow rate of the Yangtze River from its upper to lower reaches is cumulative, while greater rainfall in the middle and lower reaches is caused by their more humid climate conditions.⁵⁷ As the flow rate increased, most ion concentrations were diluted, while concentrations of NO_3^- and F^- increased instead (Figure 3G). This was due to the contribution of pesticides and fertilizers in the middle and lower reaches of the Yangtze River.⁵⁸ High NO_3^- corresponded to lower GPP and ER (Figure S3), and also corresponded to higher pCO_2 (Figures 3E & M). Flow rates negatively correlated with PIC and POC and dissolved carbon, such as DIC and DOC. In other words, carbon concentrations (including POC, PIC, DOC, DIC) were lower in areas with strong flow, especially DIC, resulting from the dilution of incoming water downstream from the Poyang Lake and Dongting Lake basins.⁵⁹

The DOC of Poyang Lake was higher (Figure 3J), because there was more supply of autochthonous DOC (higher GPP and ER) (Figure 3D). DOC significantly and positively correlated with NEP (Figure S3), which was in contrast to findings from other studies.¹⁷ This may reflected the main source of the DOC is algal exudates rather than colored dissolved organic matter (CDOM) from land in Poyang Lake catchments. These two types of DOM differs notably because colored, allochthonous DOC strongly enhances light attenuation, thereby suppressing GPP.⁶⁰ Both sources of DOM may however

support ER.²³ The ER/GPP ratio in the Yangtze River (i.e., the slope in Figure 3D) was 2.5, significantly exceeding the ratio of 1.2 in Poyang Lake. This likely demonstrates that more dynamic waterbodies exhibit higher heterotrophic levels. Their enhanced flow capacity enables greater transport of watershed-derived organic carbon for respiratory utilization, which ultimately makes them significant zones for carbon emissions. Nevertheless, despite the plausibility of this interpretation, our data constitute circumstantial rather than direct evidence for this mechanism.

Water level generally did not correlate with other parameters. In contrast to DIC, DOC significantly and negatively correlated with GPP and ER. This was because high photosynthesis consume more DIC and generate more DOC while microbial respiration consumed DOC (Figure 3J & I).²⁸ Important ions (such as NO_3^-) negatively correlated with GPP and ER, which indicated that nutrients were not the limiting factor of GPP throughout the summer high-water level period under adequate nutrient supplies. The exception was Fe^{3+} , and this is because Fe^{3+} is involved in fundamental enzymatic processes, such as oxygen metabolism, electron transfer, nitrogen assimilation, and DNA, RNA, and chlorophyll synthesis.⁵³ $\delta^{13}\text{C}$ -DIC correlated with GPP and ER and positively correlated with the main ion. Lower $\delta^{13}\text{C}$ -DIC values indicated that terrestrial organic matter respiration was dominant,⁶¹ while an increase in ER positively correlated to an increase in GPP (Figure S3).

Structural equation modeling showed that water temperature indirectly regulated GPP and NEP through their regulation on physical and chemical indicators (Figure 6A). Like the long-term water temperature effect discussed in section Temporal drivers, areas with high GPP also had higher ER, which subsequently decreased NEP. During such times, the state of the waterbody will be more heterotrophic. This means that more organic carbon recharged in the watershed will be consumed and became larger net sources of CO_2 .⁶² The RDA revealed that physical and chemical indicators significantly influenced GPP, with temperature (TEM), F^- , Fe^{3+} , DOC, POC, PIC, and $\delta^{18}\text{O}$ - H_2O showing positive correlations. Higher temperatures accelerate metabolic rates, including photosynthesis and respiration.⁵² The positive correlation between Fe^{3+} and GPP is consistent with the established role of Fe^{3+} in chlorophyll synthesis and electron transport in photosynthesis,⁶³ although our observational data alone cannot confirm a direct causal link. Similarly, the positive correlation between POC and DOC is consistent with their known roles as products of GPP, yet alternative explanations (e.g., shared external inputs) cannot be excluded. Compared with the Yangtze River, physical, chemical, and metabolic indicators at various Poyang Lake sampling points

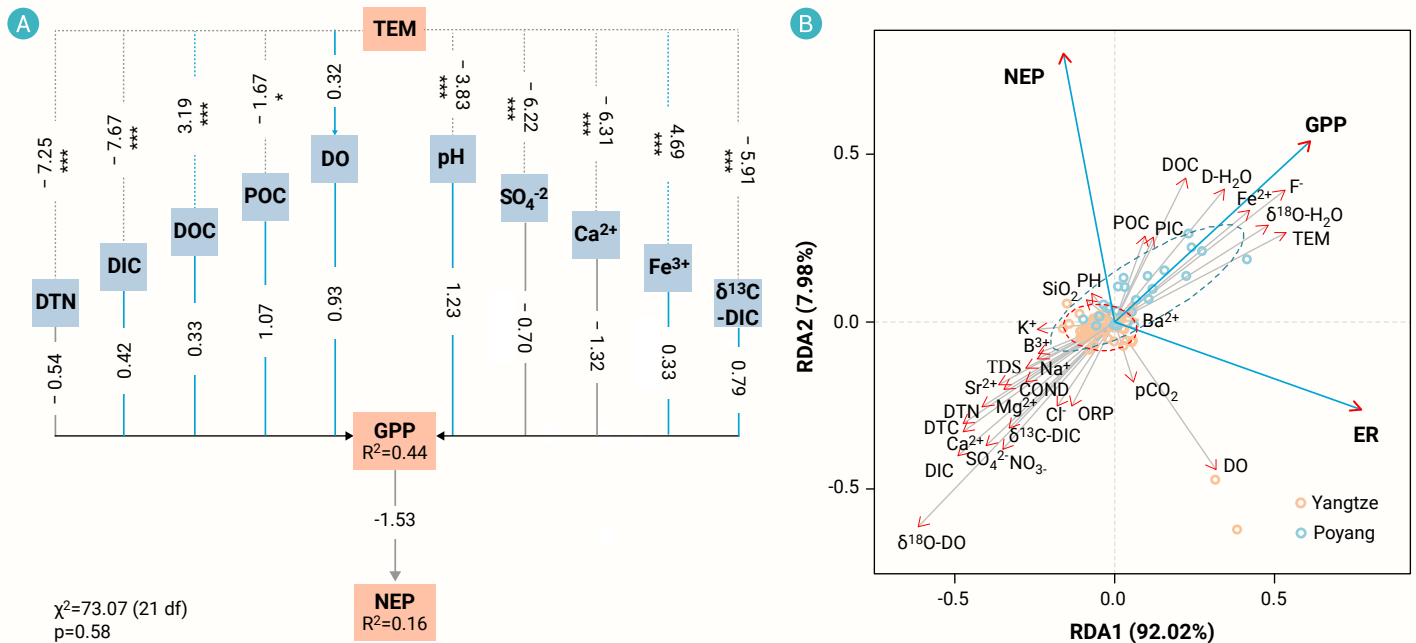


Figure 6. The relationship between water regimes, water quality parameters, and metabolic processes obtained through ^{18}O technology (A) The structural equation used for water regimes, water quality parameters, and metabolic effects. Arrow values denote path coefficients, where blue and gray arrows indicate positive and negative correlations, respectively. Solid lines represent regressions, and dashed lines represent covariances. R^2 represents the proportion of variance explained for each of the model's dependent variables. Nonsignificant pathways were removed from the model until the final model was attained. * $0.01 < p < 0.05$, ** $0.0001 < p < 0.01$, and *** $p < 0.0001$. (B) Redundancy analysis results (scaling = 2). TEM: water temperature; COND: electrical conductivity; ORP: redox potential; DTN: dissolved total nitrogen; PIC: particulate inorganic carbon; POC: particulate organic carbon; DIC: dissolved inorganic carbon; DOC: dissolved organic carbon; DTC: dissolved total carbon.

showed greater spatial variability (i.e., wider dispersion in values across sites), despite the smaller geographic coverage.

Methodological considerations

The exceptionally wide range in GPP and ER derived from isotopes observed in this study is noteworthy and warrants explicit consideration (the coefficient of variation exceeds 80%). We attribute this pronounced variability to two interacting factors. First, the hydrological connectivity gradient, from the isolated stagnant sub-lakes to the fast-flushing main channel, creates extreme patchiness in water residence time, nutrient availability, and light penetration, directly amplifying spatial heterogeneity in autotrophic and heterotrophic activities. Second, the ^{18}O technology itself, by integrating ambient water and atmospheric O_2 isotope signals, tends to capture the cumulative effects of localized extreme metabolic 'hotspots' that are often smoothed out by the diel O_2 method based on point measurements. This methodological sensitivity makes the spatial heterogeneity more explicitly visible.

In addition, it is important to acknowledge an ongoing methodological debate regarding the ^{18}O technology for estimating aquatic metabolism. Peeters et al.¹⁵ questioned the reliability of this technique, arguing that the steady-state assumptions underlying the isotopic approach are often invalid in natural lakes and can lead to substantial deviations between estimated and true metabolic rates, with uncertainties up to a factor of 2.5 in extreme hypereutrophic scenarios. However, Bogard et al.¹⁷ subsequently published a formal comment challenging this critique, pointing out that Peeters et al.'s conclusions were based on biased scenario constructions and parameterizations that do not represent most lake conditions. Importantly, Peeters et al. themselves acknowledged that the technique "may provide reasonable estimates in systems with low production". Our study sites (Poyang Lake and the Yangtze River in summer) fall within mesotrophic conditions, rather than the extreme hypereutrophic scenarios where the largest deviations were observed. Furthermore, Bogard et al.¹⁷ re-examined Peeters et al.'s¹⁵ simulations and demonstrated that mid-day point sampling provides accurate estimates of daily mean metabolic rates, as modelled and known rates converge around midday. All our ^{18}O samples were collected between 11:00 and 14:00, precisely within this robust sampling window. Collectively, these considerations suggest that our estimates are reliable for the purposes of this study.

More importantly, the primary conclusions of our study rely on large-magnitude differences between systems rather than subtle spatial gradients. The key finding that Poyang Lake exhibits substantially higher GPP (mean $16.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) than the Yangtze River (mean $1.8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) is based on a difference of approximately one order of magnitude. Even under the most conservative assessment, the potential uncertainty (up to a factor of 2.5) identified by Peeters et al.¹⁵ does not undermine this conclusion, as the observed inter-system difference far exceeds this range. In contrast, we acknowledge that the smaller-scale spatial variations in GPP within the Yangtze River (ranging from 0.8 to $3.9 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, approximately a 5-fold variation) should be interpreted with caution, as they may fall within or close to the methodological uncertainty envelope.

Assuming a 1:1 ratio of O_2 produced to CO_2 consumed. Based on diel O_2 technology, the annual average GPP, ER, and NEP of Poyang Lake were 14.6 , 18.2 , and $-3.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively (Figure 5A). Based on ^{18}O technology, the GPP, ER, and NEP of Poyang Lake were 16.0 , 18.0 , and $-2.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively (Figure 3). The metabolism values obtained by the two technologies are close and can confirm each other. The eutrophication of some sub-lakes in Poyang Lake was high, which raised the mean value of GPP, but did not raise the mean value of NEP. The net heterotrophic status of Poyang Lake is consistent with findings from other major water conveyance-type lake systems. In the Amazon floodplain lakes, persistent O_2 undersaturation indicated that ecosystem respiration consistently exceeded autochthonous primary production.⁶⁴ Similarly, in the Mekong River's Tonle Sap Lake, respiration was found to be consistently greater than primary production throughout the flood-pulse.⁶⁵ This convergence suggests that the process by which allochthonous organic matter subsidies from the watershed sustain net heterotrophy may be a common feature of hydrologically dynamic floodplain ecosystems worldwide.

The diel O_2 method itself relies on several key assumptions,^{11,12} which may introduce uncertainties into metabolic estimates. The core equation assumes that: (1) daytime respiration equals nighttime respiration, which, if violated (e.g., due to light-enhanced respiration), may lead to underestimation of both GPP and ER, though NEP remains unaffected; (2) the sensor captures metabolic processes within a well-mixed surface layer, yet vertical and horizontal heterogeneity (e.g., unaccounted hypolimnetic production or littoral influences) can bias areal estimates; (3) physical gas exchange (F) is accurately estimated from wind-based piston velocity (K), though K itself varies

with local turbulence and surface conditions—uncertainty here disproportionately affects R in low-metabolism systems; (4) non-biological oxygen changes (A, e.g., photochemical oxidation, lateral advection) are negligible, which may not hold in optically complex or advectively influenced waters; (5) the mixed layer depth (Z_{mix}) is correctly identified, as errors in Z_{mix} directly scale volumetric rates to areal inaccuracies.

Although the spatial survey (June–August 2022) overlapped with the continuous monitoring period (September 2021 – September 2022), the hydrological and environmental conditions during the survey were not representative of the annual dynamics captured by the time-series analysis. A further limitation is that the single-sensor approach cannot fully capture spatial heterogeneity in metabolic processes across Poyang Lake's dynamic system. This is particularly evident during dry seasons, when reduced hydrological connectivity increases spatial segregation of water masses. Under these conditions, two critical constraints become apparent: (1) isolated water bodies in sub-lakes develop distinct metabolic regimes, and (2) diminished mixing between the main channel and adjacent waters accentuates local heterogeneity. While the $^{18}\text{O}/^{16}\text{O}$ technology helps address some spatial uncertainties (e.g., by integrating processes over larger scales), these seasonal effects substantially constrain the representativeness of single-point measurements across the entire lake system. To better characterize the lake's metabolic heterogeneity in future studies, we recommend a minimum three-station monitoring scheme: retaining the current transition-zone station, adding one station in the main channel to capture riverine influences, and establishing one station in a representative sub-lake to capture the unique dynamics of these isolated habitats.

Combined, the assumptions of the diel O_2 model and the spatial limitations of single-sensor deployment may lead to either over- or under-estimation of metabolism, particularly in a heterogeneous system like Poyang Lake. To better characterize the lake's metabolic heterogeneity and reduce model-dependent errors, we recommend a minimum three-point monitoring scheme in future studies: maintaining the current transitional zone station, adding a main channel station to capture riverine influences, and establishing a station in a major sub-lake to represent these unique habitats. Nevertheless, our sensor was strategically positioned near the main channel, and the collected data establish a crucial baseline for understanding the metabolic behavior of this understudied lake-river transition zone.

CONCLUSION

This study combines two methods for modeling ecosystem metabolism to comprehensively evaluate inland waters and their regulation mechanisms influenced by water regimes from two different perspectives: temporal and spatial. Here, we used diel O_2 method to estimate annual metabolic changes in Poyang Lake over a full annual cycle. Additionally, spatial variations in metabolism were assessed in both the Yangtze River and Poyang Lake during summer using $^{18}\text{O}/^{16}\text{O}$ technology, revealing estimates comparable to those obtained from the diel O_2 method. Overall, higher GPP was accompanied by higher ER, and under such conditions the water body became more heterotrophic, with increased mineralization of watershed organic carbon supplies and subsequent CO_2 emission to the atmosphere. Both the Yangtze River and Poyang Lake exhibited sustained negative NEP (-2.3 and $-2.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively), indicating that the entire Yangtze–Poyang system is net heterotrophic and thus acts as a net CO_2 source to the atmosphere. Using the stoichiometric relationship between NEP and CO_2 evasion (1 mol O_2 consumed $\approx 1 \text{ mol CO}_2$ produced), we estimate a summer-average CO_2 evasion flux of approximately $0.8\text{--}0.9 \text{ g C m}^{-2} \text{ d}^{-1}$ for the system, which is consistent with direct $p\text{CO}_2$ measurements (Figure 3M) showing supersaturation ($p\text{CO}_2 > 413 \text{ atm}$) at most sampling points. This flux is comparable to estimates from other large river–floodplain systems,^{66,67} highlighting the importance of water conveyance-type systems as significant CO_2 sources.

The water regime indirectly regulates waterbody metabolism through water quality parameters regulation processes (especially, F^- , Fe^{3+} , DOC, POC, etc.), of which nutrient ions mainly regulate GPP, and DOM mainly regulates respiration. Over short-term timescales (hourly units under a daily timescale) and long-term timescales (daily units under an annual timescale), influencing mechanisms of the water regime-biological factor-metabolism differed. On an annual timescale, water level and water flow effects on metabolism were periodic and of a hysteresis nature.

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AUTHOR CONTRIBUTIONS

Yao Lu: Conceptualization, Methodology, Investigation, Writing – original draft; Yang Gao: Conceptualization, Methodology, Funding acquisition, Project administration; Dag Olav Hessen: Conceptualization, Validation, Writing – review & editing; Junjie Jia: Conceptualization, Investigation, Project administration; Shuoyue Wang: Conceptualization, Investigation; Xianrui Ha: Conceptualization, Investigation; Huamao Yuan: Supervision, Writing – review & editing; Jinming Song: Supervision, Writing – review & editing. All authors contributed to the manuscript and approved the final version. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

Data are available from the corresponding author upon reasonable request.

SUPPLEMENTAL INFORMATION

It can be found online at <https://doi.org/10.59717/j.tiw.2026.100011>.