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LETTER

Unraveling Lake Geneva's hypoxia crisis in the Anthropocene

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Scientific Significance Statement

Recent decades have witnessed widespread deoxygenation of temperate lakes. The intricate interplay between climate change and nutrient loading and its impact on oxygen dynamics still lacks clear understanding. We develop a paleo-data-model coupling approach to investigate long-term variations of dissolved oxygen conditions in Lake Geneva over the period 1850–2100. Our approach provides first estimates of oxygen baseline conditions and quantifies duration of hypoxia since pre-disturbance. Over the 19th and 20th centuries, an increase in DO consumption rates (from 0.3 to 2.5 g $O_2 m^{-2} d^{-1}$) following nutrient over-enrichment caused the onset of hypoxia, and its intensity and duration were governed by the combined influence of climatic forcing and high phosphorus concentration. In the future, hypoxia will be primarily disrupted by reduced frequency of full mixing events.

Abstract

Despite global evidence of lake deoxygenation, its duration, timing, and impacts over decadal to centennial timescales remain uncertain. This study introduces a novel model approach using 150 yr of limnological and paleolimnological data to evaluate the anthropogenic impacts on deep oxygen in Lake Geneva. Results highlight an increase in oxygen consumption rates due to cultural eutrophication, initially triggering historical hypoxia, subsequently exacerbated by reduced winter mixing induced by climate change. Simulations of

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Data Availability Statement: The model setup to reproduce the simulations as well as daily vertical profiles of model outputs are available at https:// doi.org/10.57745/L4RABJ. GLM model and AED2 model are open-source and publicly available at https://github.com/AquaticEcoDynamics/glm-aed and https://aquaticecodynamics.github.io/aed-science/. The model is constrained by IPCC climatic scenarios SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5 obtained from ISIMIP projections (https://data.isimip.org) and validated according to 63 yr of observation data collected and stored by the Lake Observatory OLA (https://si-ola.inra.fr).

Additional Supporting Information may be found in the online version of this article.

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More than a century of research, starting at the beginning of limnology as a discipline (Forel 1895), has addressed oxygen dynamics in lakes using empirical, theoretical, and predictive approaches. A hypoxia crisis characterized by a worldwide spread of declining dissolved oxygen (DO) is a major threat to freshwater and marine environments attributed to excessive nutrient inputs (Jenny et al. 2020) and anthropogenic climate change (Grant et al. 2021). In the Anthropocene, as human activity significantly modifies the planet's climate (Witze 2024), abrupt, large, and persistent shifts (i.e., crises) in the functioning and structure of ecosystems have made both reliable prediction and managed reversal of change exceptionally difficult (Huang et al. 2022). Complex interactions among these regulators, which may act as triggers, contributors, or amplifiers of oxygen depletion, cause nonlinear long-lasting responses in ecosystems that are still largely difficult to predict (Deyle et al. 2022). Given that oxygen depletion has substantial implications for critical lake ecosystem services mediated by oxygen-sensitive biogeochemical processes, identifying the drivers and mechanisms of changes in oxygen dynamics is critical for understanding lake ecosystem functioning as a whole and mandatory for managing water quality.

Despite multiple concurrent observations on the oxygen decline in lakes worldwide, the interpretations of the drivers and the underlying mechanisms differ between long- and short-timescale approaches. On one hand, clear evidence of persistent oxygen depletion, based on a limnological synthesis of data from 393 temperate-zone lakes, indicates that the decline in the hypolimnion is associated with stronger and longer thermal stratification and decrease of water clarity during the past 40 yr (Jane et al. 2021). On the other hand, paleolimnological synthesis of data from 365 lakes worldwide suggests that increased human activity and nutrient loading, but not climate, has led to the onset of hypoxia during the last 300 yr (Jenny et al. 2016). To reconcile the apparent contradiction, comprehensive systematic long-term, temporally continuous data, are needed to fill a critical knowledge gap, and will be mandatory for unraveling the precise role of external drivers of ecosystem patterns, particularly complete mixing events and phosphorus input. Here, we develop an explicit integration of (1) a process-based lake model (Dresti et al. 2021), with (2) in situ monitoring data for model calibration, and (3) paleolimnological proxies stored in lake sediments to provide the missing long-term perspective in continuous temporal information. The pioneering approach presented here harmonizes disparate data sources that enabled

a novel modeling application over a centennial period and strongly changing lake ecosystem conditions.

Methods

Lake Geneva

Lake Geneva is a large deep perialpine lake located at the border between France and Switzerland, at 372 m above sea level (46.45°N, 6.53°E). It is the largest lake in western Europe with a mean depth of 153 m and a maximum depth of 309 m. Its surface area is 582 km², its volume is 89 km³, and its hydraulic retention time is around 11.4 yr. It is thermally stratified from spring to early fall with a thermocline located at about 15 m depth in summer. Complete water mixing promoting deep reoxygenation occurs during very cold winters only once per 5-10 yr on average according to monitoring since the 1950s (Schwefel et al. 2016). This water body is one of the most thoroughly monitored and well-known lakes in the world, with a rich high-quality database of monitoring data for over 60 yr. In addition, since the 1950s, it has experienced a history of anthropogenic eutrophication followed by re-oligotrophication similar to that of several other lakes over about the same time period (Dresti et al. 2021). And like other lakes, Lake Geneva faces the ongoing effects of climate change with significant warming trends and strengthening thermal stratification (Desgué-Itier et al. 2023).

Coupling process-based model, in situ monitoring data, and paleolimnological proxies

The methodological framework applied here (Fig. 1) incorporates recent observations and geological data into a state-ofthe-art one-dimensional vertical process-based model-Aquatic EcoDynamics coupled to General Lake Model, GLM-AED2 model (GLM: v.3.1.1, AED2: v.2.0)-to perform continuous simulations of lake biogeochemistry, with a focus on the dynamics of bottom oxygen concentration, driven by both climatic forcing and nutrient loading in Lake Geneva. AED2 model was selected because it includes the key processes of water quality dynamics that depend on both the climatic environment and nutrient loads. It must be coupled to a host physical (hydrodynamic) driver model, here GLM, to connect the role of thermal stratification and vertical mixing on lake ecosystem dynamics, which take into account the dominant biogeochemical processes in the water column and the fluxes between the air-water and water-sediment interfaces. The estimation of hypoxia in 1D models is conservative due to the omission of spatial processes that may lead to a certain replenishment of oxygen within the hypolimnion.

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Fig. 1. Hypoxia zone in Lake Geneva based on field monitoring (1957–2020), sediment archives (1850–2018), and climatic projections (1850–2100) combined to inform a state-of-the-art process-based model that simulates continuous long-term changes in lake phosphorus and hypoxia from 1850 to 2100. The hypoxia area in the map represents data from the 1990s, the most critical period of deoxygenation in the lake.

Model forcing data consist of (a) climatic models of air temperature, shortwave radiation, and wind speed derived from the ISIMIP framework (Golub et al. 2022) comprising a historical period (1850–2014) and future simulations (2015–2100) of three projections based on socioeconomic pathways and forcing levels of the representative greenhouse gas concentration pathways (SSP1–RCP2.6, SSP3–RCP7.0, and SSP5–RCP8.5; Golub et al. 2022); (b) field measurements of discharge, temperature, and nutrients collected in the main tributary of the lake (Rhone River) over 47 yr (1974–2020; Eawag and FOEN 2022); (c) paleolimnological proxies, that is, preserved *Daphnia* subfossils (Cladoceran) extracted from well-dated sediment cores that allow the development of a *Daphnia*-based transfer function to predict volume-averaged total phosphorus (TP) concentration in the lake water from 1850 to 2018 based on their strong relationship, also referred to as *Daphnia*-inferred TP (Berthon et al. 2014); and (d) lake-specific hypsography based on 10-m lake isobath (Stockwell et al. 2021).

A GLM-AED2 model was run on an hourly time step from January 1, 1850 to December 31, 2020. A continuous run throughout the complete period was performed to ensure the annual carryover of heat stored in the hypolimnion between full turnovers. A detailed description of the data and model applied in this study is provided in the Supporting Information. The model's ability to reproduce the bottom oxygen and hypoxia regime over different temporal scales was assessed by comparison against field measurements from probe sensors and analysis of water samples collected in the deepest point of the lake every 2 weeks (Rimet et al. 2015). The calibration procedure was performed over a period with a large gradient of TP (38–60 μ g L⁻¹) to test the model's ability to represent substantial long-term trends in major state variables. Hypoxia regime was further validated using paleolimnological records of water hypoxia, expressed as annual volume of hypoxic waters, derived from a varve index, that is, annually laminated sediments (Jenny et al. 2014). The performance assessment of the model's ability to represent the hypoxia regime over different temporal scales confirms the reliability of the methodological framework in providing robust modeled longterm trends of bottom oxygen in terms of general behavior, amplitude, and timing. A detailed description of the calibration and validation procedures, as well as the assessment of model performance are provided in the Supporting Information.

Characterizing long-term hypoxia

Simulated daily oxygen concentrations throughout the water column from 1850 to 2100 are summarized as annual values to characterize the hypoxia regime, matching the same frequency as the paleolimnological data. We characterized hypoxia intensity by calculating the annual average of daily minimum values from modeled oxygen concentrations throughout the water column, that is, the concentration nearest the sediments. Hypoxia duration was calculated as the number of days per year for which hypolimnetic minimum concentrations were below specific thresholds. We tested the often-used thresholds of $1-4 \text{ mg L}^{-1}$ and found a better match with the paleolimnological proxy at 1 mg L^{-1} , but the other thresholds presented similar patterns.

Disentangling the drivers of historical hypoxia

We investigated the primary drivers of hypoxia by disentangling the effects of climatic forcing and nutrientenrichment in order to isolate the influence of each, both of which have been considered important for the oxygen content in the bottom of the lake. We did this by running the model with very low external phosphorus input, taking it at its natural background, that is, repeating intra-annual variation of year 1850 over the simulation period, while all the remaining forcings were unchanged. As a specific model's parametrization fitted for background TP concentrations and related lower mineralization rates was prevented by the absence of field monitoring under predisturbance conditions, model outputs are at uncertain confidence.

For analyzing the effects of climate on lake hydrodynamics, thereby affecting DO replenishment in the hypolimnion, winter complete mixing was characterized when temperature and oxygen concentration differences between the surface and the bottom of the lake remained below 2°C and 2 mg L-1 for at least 5 consecutive days. Although those thresholds are rather arbitrary, the combination of both criteria allows a better assessment of winter mixing events. The temperature threshold is in the range of often-used values from 1° C (Perroud et al. 2009) to 3° C (Schwefel et al. 2016) found in previous studies in Lake Geneva.

Future projections of lake hypoxia

We used climatic projections for predicting changes in solar radiation, air temperature, and wind speed in three different future scenarios (SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5). Long-term future projections of phosphorus inputs into the lake from 2020 to 2100 were based on the replication of current conditions. All the remaining input data adopted for the historical modeling were assumed constant. Future projections were compared to historical conditions in terms of the areal hypolimnetic mineralization rate (AHM, g $O_2 m^{-2} d^{-1}$) over the whole hypolimnion, which describes the processes of (1) organic matter mineralization in the water column, (2) sediment oxygen uptake, and (3) flux of reduced compounds from the sediment, being a strong indication of the nutrient effects in the bottom of the lake. It was computed from modeled volume-weighted mean DO concentrations between 15 and 309 m depth on a daily basis as the difference between the annual maximum concentration (February to April) and the minimum concentration at the end of summer stratification (late October/November) divided by the number of days of summer stratification (Müller et al. 2019). AHM depends on the oxygen concentration attained by the end of spring overturn, $[O_2]_{max}$, the minimum hypolimnetic concentration at the end of the stratification period, $[O_2]_{min}$, the mean hypolimnion depth, z_{hypo} , and the duration of the stratified period Δt_{strat} (Müller et al. 2019):

$$AHM = \frac{z_{hypo}}{\Delta t_{strat}} \times ([O_2]_{max} - [O_2]_{min})$$
(1)

Results and discussion

Historical lake hypoxia

Our modeled daily results capture the phosphorus history in the lake for both natural background and anthropogenic perturbation conditions (Fig. 2a). Baseline conditions of total phosphorus, before the 1950s, revealed the range of inherent natural variability $(3.2 \pm 2.7 \ \mu g \ L^{-1})$. Starting in the mid-20th century, a dramatic TP increase up to 94.8 $\mu g \ L^{-1}$ in model simulation following the demographic and economic development in the region resulted in eutrophic conditions (TP > 24 $\mu g \ L^{-1}$) (Carlson 1977) after 1960 and reached a peak in the 1970s. From then, remediation measures including the construction of wastewater treatment plants and a ban on phosphates in detergents were taken to control phosphorus point sources and diffuse inputs. These resulted in a consistent TP decline termed "re-oligotrophication." The amplitude of the simulated annual averages (15.6–94.8 $\mu g \ L^{-1}$) in the



Fig. 2. The modeled annual long-term trends of (**a**) median total phosphorus, (**b**) hypoxia duration, and (**c**) minimum oxygen concentration throughout the water column over the historical period (1860–2020). Hypoxia duration represents the number of days over the year with a minimum oxygen concentration below 1 mg L⁻¹. Field measurements of TP represent annual median concentration, and field measurements of DO represent the minimum value, both of them throughout the water column. The background color gradient indicates a transition from a well-oxygenated condition to the establishment of hypoxia in the bottom of the lake. The paleolimnological proxy of hypoxia volume in (**b**) and (**c**) corresponds to the right *y*-axis. In 1976, persistent hypoxia was established, showing a sharp shift in duration and magnitude unprecedented in the previous 115 yr (1860–1975). Background colors: blue represents the period under natural conditions and yellow gradient qualitatively represents the intensity of phosphorus and climate change impacts over the period of anthropogenic perturbation.

monitored period was comparable to that of the field monitoring data (10.4–95.1 μ g L⁻¹), being representative of the longterm sharp changes in TP over time.

Model simulations provide important insight into reference oxygen conditions by hindcasting the range of its inherent natural variability before the monitored period (i.e., absence of hypoxia except for a few years where the duration was 133 ± 59 d and 5.5 ± 1.9 mg L⁻¹ of minimum DO throughout the water column), something that is not captured by the paleolimnological proxy (Fig. 2b,c). Since the paleolimnological proxy cannot provide quantitative estimates of oxygen concentrations on a daily or monthly basis, especially below a certain threshold, and does not offer insights into the underlying processes, the combined approach using both paleolimnology and modeling provides a more comprehensive understanding. The reconstructed hypoxia dynamics demonstrated that Lake Geneva was well oxygenated before the second half of the 20^{th} century exhibiting only short-duration, episodic events of hypoxia, that is, not longer than 1 yr. The lake exhibited resilience to the establishment of hypoxia until the 1970s. An early signal of oxygen dynamics change is provided by the paleolimnological proxy in the 1960s. It was only in 1976 that the hypoxia regime experienced a sharp shift in duration and magnitude unprecedented in the previous 115 yr (1860–1975). Indeed, the lake was hypoxic year-round in 25 of the 45 yr between 1976 and 2020 while DO averaged lower than 1 mg L⁻¹ in 32 of those years. In contrast, from 1860 to 1975, the lake did not experience a single year in such conditions.

Drivers of historical hypoxia

By running the model with very low external phosphorus inputs from the affluents at its background conditions, while keeping the trends in historical climatic forcing, we removed the effects of any anthropogenic land use and we assessed the hypoxia regime as influenced solely by climate. Under this condition, very low TP concentrations in the lake

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Fig. 3. Disentangling the effects of solely climatic forcing (dark blue area) on intensity and duration of hypoxia in Lake Geneva based on modeled annual long-term trends of (**a**) median total phosphorus, (**b**) hypoxia duration, and (**c**) minimum oxygen concentration throughout the water column over the historical period (1860–2020). Hypoxia duration represents the number of days over the year with a minimum oxygen concentration below 1 mg L⁻¹. Modeled winter complete mixing (black dotted lines) is defined as the event of temperature and oxygen concentration difference less than 2° C and 2 mg L⁻¹, respectively, between the surface and the bottom of the lake. Red circles indicate winter complete mixing from monitoring data (Gaillard et al. 2022). The background color gradient indicates a transition from a well-oxygenated condition to the establishment of hypoxia in the bottom of the lake. Background colors: blue represents the period under natural conditions and yellow gradient qualitatively represents the intensity of climate change impacts over the period of anthropogenic perturbation.

(TP < 0.8 μ g L⁻¹) were obtained in the model (Fig. 3a). Minimum DO in the lake lower than 1 mg L⁻¹ occurred at a lower frequency (in 21 yr; Fig. 3b) and annual minimum DO of 2.70 mg L⁻¹ on average from 1976 to 2020 (Fig. 3c), against 25 yr and 1.15 mg L⁻¹, respectively, under anthropogenic TP inputs revealed the role of historical anthropogenic phosphorus over-enrichment as a driver of deoxygenation intensity and duration. However, the onset of hypoxia in the absence of eutrophication is explained by climate change.

The resistance mechanism preventing the spread of hypoxia in the 1950s was mixing events sufficiently effective to compensate for high-nutrient levels which maintained hypolimnion oxygenation from the 1950s to 1970. In seasonally stratifying lakes, the dominant process driving the replenishment of dissolved oxygen in the hypolimnion is winter deep mixing (Deyle et al. 2022). Indeed, from 1860 to 1970,

complete mixing occurred during 67 winters (dotted lines in Fig. 3), being the dominant source of DO mass discharges from the surface to the hypolimnion. Since 1970, deep mixing has become intermittent (on average 1 event decade $^{-1}$ for 1971-2020) according to our model results and limnological data. This severely limited the replenishment of bottom oxygen. Despite some mismatches between the timing of modeled and observed mixing events, the frequency is comparable (1.9 event decade⁻¹ in model results against 1.2 event decade⁻¹ in monitoring data for 1971–2020) (Schwefel et al. 2016; Gaillard et al. 2022). As mixing events occur at lower frequency, unprecedented hypoxia in the hypolimnion extended over longer intervals, generally exceeding 1 complete year. The worldwide decreased frequency of mixing is an ongoing process in Lake Geneva which started in the 1970s due to both warming (Vautard et al. 2010) and lower wind speed

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Indicators	Natural (pre-1950)	Hypoxic years (1976–2020)	Future projections (2020–2100)		
			SSP1–RCP2.6	SSP3-RCP7.0	SSP5-RCP8.5
Hypoxia duration (d yr $^{-1}$)	8 (±2)	265 (±144)	46 (±97)	55 (±96)	69 (±102)
Minimum DO (mg L^{-1})	5.5 (±1.9)	1.1 (±2.0)	3.2 (±1.5)	2.5 (±1.6)	2.2 (±1.2)
TP (μ g L ⁻¹)	3.2 (±2.7)	51.2 (±26.3)	15.5 (±1.2)	15.5 (±1.2)	15.5 (±1.2)

Table 1. Modeled mean total phosphorus, mean hypoxia duration, and minimum oxygen concentration throughout the water column.

over almost all continental areas in the northern mid-latitude since 1979 (Vautard et al. 2010). Lake warming is predicted in the future according to numerical simulations and different IPCC emission scenarios (Woolway and Merchant 2019).

Hypoxia under future climate change

Our model projects that changes in the annual duration of bottom hypoxia and the accompanying oxygen concentrations will not be as strong as they were in the past since the shift to hypoxia in 1976. Indeed, the bottom of the lake is expected to experience an annual average daily minimum oxygen concentration of 2.2–3.2 mg L^{-1} , and hypoxia lasting 46–69 d vr^{-1} by the end of the century (Table 1). This is in contrast to the contemporary average of 1.1 mg L^{-1} , with hypoxia lasting 265 d yr⁻¹. As expected, poorer conditions were found in the high-emission scenario (SPP 5-RCP 8.5) and were explained primarily by the magnitude of change in the climatic drivers investigated (air temperature, solar radiation, and wind speed). Although the impacts of future climate warming will not be as strong as the impacts of eutrophication in the past, the projected changes should not be underestimated as they still represent a loss of 42-60% of average daily minimum DO concentration and an additional 38-61 d of hypoxia in comparison to the natural condition (pre-1950). Despite the continued impacts of climate change and a positive feedback mechanism that begets the development of anoxia in subsequent years (Lewis et al. 2024), partial recovery of hypoxia is possible in future projections under low external phosphorus input. The fact that we were unable to detect a full recovery from hypoxia by 2100, the end of our model run, under any climate scenario may mean that climate forcing causes the eutrophication-driven transition to hypoxia to delay recovery so that it takes on a centennial scale (Haas et al. 2019).

The influence of phosphorus load on oxygen depletion in the bottom lake was assessed by computing the areal hypolimnetic mineralization rate (AHM) over the whole hypolimnion. Our results show AHM oscillation from 0.3 to $1.4 \text{ g } \text{O}_2 \text{ m}^{-2} \text{ d}^{-1}$ over the historical period in the range of previous studies (Müller et al. 2019) with exceptionally high values (1.5–2.6 g $\text{O}_2 \text{ m}^{-2} \text{ d}^{-1}$) during the peak of eutrophication (1967–1996; see the Supporting Information). The logarithmic relation between the number of years without complete mixing and AHM reveals a stronger effect of climate in the future (2020–2100), as a narrower range of AHM would be required to maintain a safe operating space, that is, a boundary that must not be transgressed to prevent an unacceptable environmental change to hypoxia (Fig. 4). If the threshold is crossed, the lake bottom shifts into a detrimental state to the survival of hypolimnetic aquatic life. We therefore conclude that oxygen replenishment during complete mixing events will be the governing driver controlling the severity of hypoxia in deep hypolimnion.

This analysis demonstrates that over the 19th and 20th centuries, hypoxia trajectories have been predominantly driven by the combined effects of climatic forcing and phosphorus concentrations, whereas in the 21st century, it will be primarily under climatic control affecting physical processes that regulate thermal dynamics, and less by nutrient content that influences organic matter and its decomposition if TP loading remains similar to the present, as it was in the model simulations. Given the projected worldwide increase in stratification intensity and duration of deep lakes as a response to climate warming (Shatwell et al. 2019; Woolway et al. 2021; Desgué-Itier et al. 2023) prolonged isolation of the hypolimnion from the atmosphere is expected. As a result, lakes will be increasingly susceptible to hypoxia because of less frequent mixing with more severe consequences expected for the systems with a eutrophic past. Our findings strongly support the need to reduce local phosphorus inputs in stratified lakes to make them more resistant to less frequent mixing events under climate change. The interference of large nutrient changes with climate may also induce other complex phenological changes in lake ecosystems (Straile and Rothhaupt 2024). Furthermore, conducting global-scale lake models without taking into consideration changes in nutrient dynamics is likely to result in flawed predictions by disregarding the role of internal loads and the direct effects of management actions on these processes.

The model projections presented here should be interpreted with some caution as the confidence in future forcing remains of uncertain reliability. For instance, changes in food web composition supported by biological invasion (e.g., quagga mussel populations first detected in Lake Geneva in the 2010s that are expected to increase in European alpine lakes in the next decades; Kraemer et al. 2023) would



Fig. 4. Safe operating space representation for annual bottom lake oxygen conditions in the face of extended climate impacts' duration. DO conditions depends on the interplay between projected winter mixing occurrences (*y*-axis) and areal hypolimnetic mineralization rate (AHM, *x*-axis). The colored background represents the theoretical DO concentrations. Future (2021–2100) represents the intermediate scenario (SSP3–RCP7.0) taking in-lake TP at its current modeled value (15 μ g L⁻¹). The black dotted-line represent the threshold of 4 mg L⁻¹ between well- and poor-oxygenated DO conditions, here defining a safe operating space for bottom conditions. I, II, and III represent the temporal transition from background conditions to maximum eutrophication and re-oligotrophication and then to future scenario. The large dots represent the 90th percentile of AHM and the average time span of all smaller dots of that color.

drastically affect organic matter and nutrient cycling and indirectly critical characteristics of the lake such as transparency (Rohwer et al. 2024), that is, key parameters in our model, that could induce diverging trajectories from the modeled ones. Nevertheless, the combination of modeling, paleolimnological proxies, and field measurements provides strong insights into potential future changes in the hypoxia regime. Our overall results reveal that reducing local phosphorus inputs will likely not be sufficient to prevent hypolimnetic deoxygenation, thus demanding the implementation of additional strategies or engineering approaches to prevent hypoxia. As Lake Geneva shares similar trophic history with other lakes in Europe and North America, our results suggest a common trajectory for lake recovery and challenge for lake management.

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