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Deep oxygen status of Lake Geneva: a zombie lake or a prematurely pronounced death?

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We revisit the dominant narrative surrounding Lake Geneva, the largest lake in Western Europe, that phosphorus management, despite being remarkably successful, has failed to improve the lake's deep-water dissolved oxygen status. We show that this narrative does not reflect the underlying mechanisms. Instead, our analyses demonstrate that phosphorus management has substantially built the lake's resilience to deep deoxygenation. Reducing lake deoxygenation to a simple consequence of climate warming obscures the complex interplay of processes governing oxygen dynamics and may ultimately lead to counterproductive and misdirected management actions.

Abstract

Lake Geneva has become an emblematic example of a lake trapped in an apparent "zombie" state, where deep-water hypoxia persists despite decades of declining phosphorus concentrations. The persistence of oxygen depletion has largely been attributed to climate-driven reductions in deep winter mixing, assuming a limited responsiveness to successful nutrient management. The analysis of the 53-year record of dissolved oxygen profiles reveals that hypolimnetic oxygen consumption has declined markedly since 2000, but only in the deepest waters (>275 m), where oxygen depletion is most critical for hypoxia development. A mechanistic oxygen-consumption model indicates that the decline is primarily attributable to reduced sediment oxygen uptake rather than changes in water-column mineralization. In parallel, recurrent deep-water oxygen replenishment occurring below the depth of winter convective mixing points to an additional oxygen source, possibly associated with river underflows. Together, these processes partially offset the documented decline in deep winter mixing caused by climate warming, indicating that phosphorus management has improved the lake's resilience to deoxygenation. These findings remind that long-term oxygen dynamics cannot be inferred from changes in mixing alone and highlight the importance of considering both oxygen consumption and alternative oxygen-supply pathways when assessing lake responses to climate change.

Introduction

As old as Limnology itself is the recognition that deep-water oxygen conditions reflect the overlying physical and biological processes of lakes (Forel 1892; Delebecque 1898; Birge 1906). The link between lake productivity and the deep-oxygen deficit was identified shortly thereafter (Thienemann 1928; Hutchinson 1938; Imboden 1974). Because water holds 50,000 times less oxygen than air, small changes in deep dissolved oxygen (DO) can severely constrain aquatic life, making deep oxygen deficit one of the most detrimental consequences of eutrophication (Lardner-Cornett 1982).

The accelerating spread of lake eutrophication, peaking in the mid-20th century in North America and Western Europe, has led to many lakes' bottom waters to turn hypoxic (DO $<$ 2 mg L^{-1}, Vaquer-Sunyer and Duarte 2008) or anoxic (e.g., DO $<$ 0.5 mg L^{-1}, Diaz and Rosenberg 2008). The rate at which lakes of the North shifted slowed down by the end of the 20th century (Jenny et al. 2016), thanks to eutrophication-control measures. Yet, even after successful reoligotrophication, deep-lake deoxygenation remains a major concern, as climate warming, while rarely sufficient to induce deep hypoxia on its own, can exacerbate existing DO deficits in many temperate lakes (Jane et al. 2023; Nkwalale et al. 2026).

Lake Geneva (Switzerland-France) has been one of the iconic lakes whereby the topic of deep oxygenation has crystallized, thanks to (i) an exceptionally long data record (Fig. 1), (ii) a textbook eutrophication history for lakes of the North and (iii) an extreme sensitivity of the winter mixing to climatic conditions. The first measurements in Lake Geneva date back to the late 19th century (Forel 1892), while monitoring records span up to six decades (Fig.1). Early signs of ecosystem change were reported at the dawn of the 20th century, and the process accelerated in pace with the post-World War II economic growth (Lachavanne 1980; Fig.1B). Within 40 years, the total phosphorus concentrations (TP) increased from a base

63 level < 8 µgP L^{-1} (Berthon et al. 2014) to 90 µgP L^{-1} (Loizeau and Dominik 2005) in the
64 early 1980s (Fig. 1B), accompanied with the typical cascade of changes in the littoral and
65 planktonic primary producers, decreased water transparency, fish communities shifting from
66 salmonids to percids and cyprinids (Lachavanne 1980). The orthocline DO profiles turned to
67 negative heterograde profiles from the mid-1950s and persisted so since then (Fig. 1C-D),
68 with appearance of deep hypoxic waters dated to 1950 (Jenny et al. 2014; Fig 1B). Local and
69 collective activisms, legal and political actions in 1960-1980 enforced the deployments of
70 multiple levers of P-control, from regulating P content in manufactured detergents to
71 implementing waste-water treatment infrastructures (Elsig 2018). Yet, despite a spectacular
72 decline in TP over the past 55 years (Fig. 1B), hypoxic bottom waters have remained the rule
73 rather than the exception (Fig. 1D).

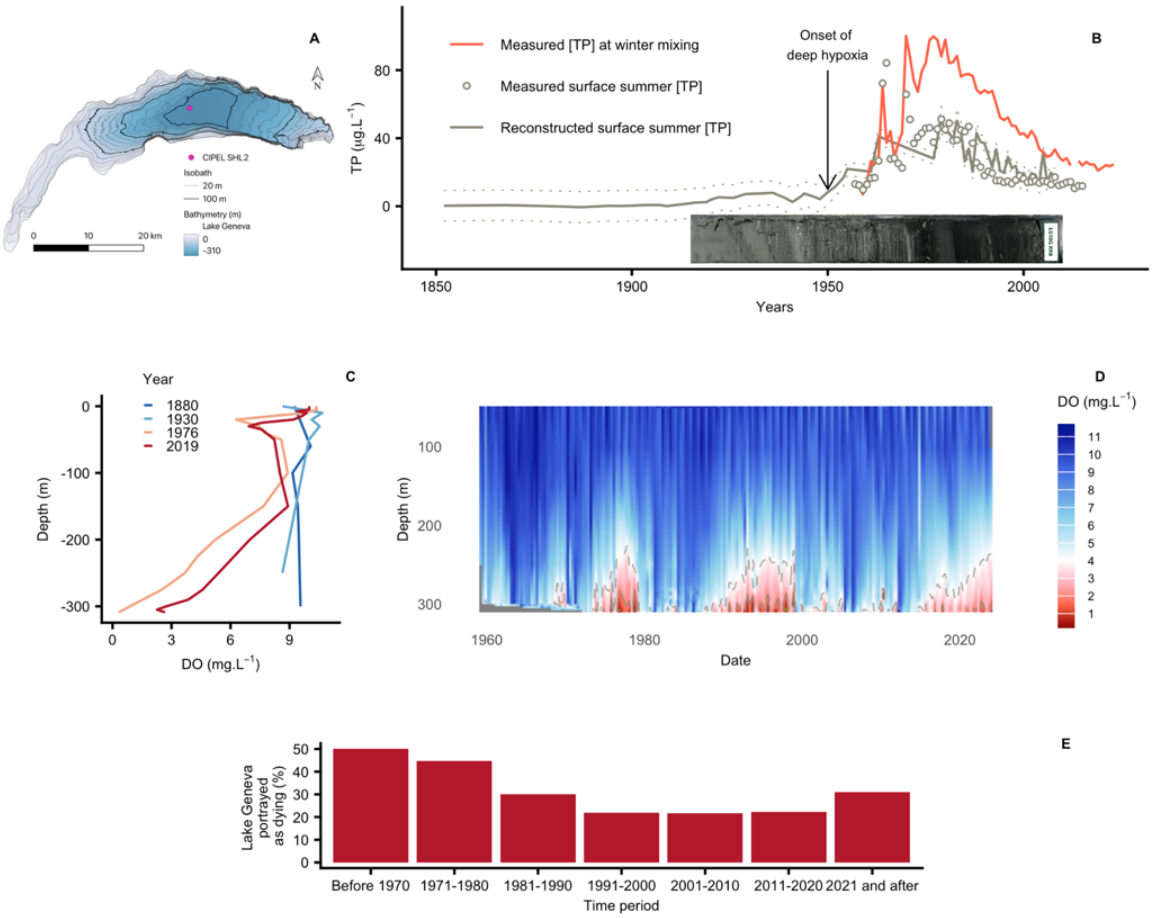


Figure 1: Historical changes in Lake Geneva TP and DO concentrations. A) Map, with the location of the historical monitoring point (SHL2). B) Pre-instrumental and historical changes in TP at mixing across the water column and summer surface concentrations. Image of a sediment core taken at the lake's deepest point for which the appearance of the annual varves indicates the onset of deep hypoxia (Jenny et al. 2014; Bruel et al. 2021). C) Measured fall DO profiles of 11-30-1880 (F.A. Forel), 08-30-1930 (P. Vivier), 10-11-1976 and 10-14-2019. D) DO at depths ≥ 50 m from 1958-2023. Deep DO replenishment by complete mixing occurred in the springs of 1960, 1970, 1971, 1985, 1986, 1999, 2006 and 2012. E) Proportion of the local and national press articles on the topic of DO in Lake Geneva depicting the lake as 'dying', 'suffocating' or 'asphyxiating' (see SI 1 for more details on methods).

The geomorphology of Lake Geneva makes it oligomictic with a mixing regime particularly sensitive to climate variability: the lake does not freeze over, and winter convective cooling and windstorm do not mix the lake to the bottom every year. For the period 1981-2012, Lake Geneva got mixed on average down to ca 180 m (for a 310 m max depth, Fig. 1D), representing 78% of the total lake volume, with a complete overturn on average every 5 years (Schwefel et al. 2016). Together with a reduced frequency of cold winters, both the mean winter mixing depth and percent of winters of complete mixing are expected to decrease (from 180 to 136 m and 22 to 19% respectively for 2046-2076; (Schwefel et al. 2016), further limiting deep DO replenishment at depths.

Both sources (vertical mixing) and sinks (oxygen uptake) control deep DO in lakes (Bella 1970). However, the designated culprit for Lake Geneva deep oxygen deficit has moved from eutrophication (from the 1960s onwards, cited in Loizeau and Dominik 2005) to climate warming (Müller et al. 2012; Jenny et al. 2014; Deyle et al. 2022; Soares et al. 2025), while the persistent deep DO depletion is interpreted as a limited responsiveness to four decades of successful TP management. As a consequence, echoing scientific discourse, Lake Geneva has been portrayed by the local and national media as ‘dying’, ‘suffocating’, and ‘asphyxiating’ (SI 1, Fig. 1E) for even longer than the two authors of this article have been alive — depictions that, if accurate, would indeed warrant its characterization as a ‘zombie lake’—. One limitation, however, is that, except for Müller et al. (2012), none of the previously cited studies have specifically scrutinized the long-term dynamics of DO consumption in Lake Geneva. While the climate-driven decline in winter mixing efficiency is well-documented, we aim here at quantifying the depth-dependent DO consumption in the hypolimnion of Lake Geneva across the last 50 years. If deep-water DO consumption has been responding to re-oligotrophication, it may partially offset the reduced frequency of deep convective mixing, suggesting that the lake may have been prematurely pronounced dead.

Material and Methods

Lake Geneva is a large (580 km^2) deep (310 m and 153 m max and mean depths respectively) subalpine, clearwater lake, at the border between Switzerland and France, with 1.1 M inhabitants within 10 km from the lake's shoreline. The analysis conducted herein relies on the DO concentrations measured at the deepest point of Lake Geneva (SHL2, Fig.1A) through the regular monitoring program. From 1971 onward, DO was measured at least monthly, increasing up to 18-20 times per year from 1981 (Rimet et al. 2020). DO was measured exclusively using the Winkler's method on water sampled at fixed depths with a Niskin bottle until 1991. Since 1991, DO has been measured using vertical profiling using multiparameter probes (Eco Meerestechnik Elektronik GmbH, SST and RBR probes since 2002) with results post-calibrated against the Winkler's method on sampled water. Data (1971-2023) were retrieved from the Observatory Information System for Lake Environmental Research (*https://si-ola.inrae.fr*) in November 2025. The analysis focuses on the hypolimnetic DO dynamics at the depths ≥ 50 m whereby DO had been measured consistently over time.

Hypolimnetic oxygen depletion is caused by mineralization of the settling organic matter in the water column and oxygen uptake by the sediment. Typically, DO consumption where water column mineralization (WCM) dominates is considered as substrate-limited and can be modelled by a zero-order, linear process (Beutel 2003, eq.1) as

$$\frac{d(\mathrm{DO})}{dt} = -k\,, \qquad (1)$$

with DO in $mg \cdot L^{-1}$, time t as day and k the consumption rate in $mg \cdot L^{-1} \cdot d^{-1}$.

Where sediment oxygen uptake (SOU) becomes predominant, the DO consumption becomes a diffusion-limited process at the sediment–water interface that depends on the

maximum value of DO. The DO dynamics therefore better fits a first-order, exponential decay (Beutel 2003, eq. 2):

$$\frac{d(\mathrm{DO})}{dt} = -K_{\mathrm{exp}}\,\mathrm{DO}, \qquad (2)$$

with K_{exp} the exponential decay in d^{-1}. Modelling DO consumption using a zero-order equation (1) where sediment uptake is the main process explaining the oxygen decay may lead to a dependence of DO consumption to the absolute ambient DO (SI 2).

For depths in 50-250 m, the consumption rate is computed through a linear fit to DO (eq. 1). At depths ≥ 250 m, the consumption dynamics is modelled as an exponential decay (eq. 2). To enable comparison of the DO uptake dynamics across depths (k is $in\ mg \cdot L^{-1} \cdot d^{-1}$ while K_{exp} is in d^{-1}), consumption rates beyond 250 m are simulated using the computed K_{exp} and the average DO after mixing for each depth. Although more consistent with the dominant processes at play, using different fits across depths yields coherent patterns of DO consumption across depths and times, that are also independent from the efficiency of DO replenishment at depth (SI.2). However, all conclusions hold regardless of the method chosen (SI 3-4). DO consumption rates are computed for each depth layers since 1971 during the stratified period (i.e. from March to September included) and compared over time and depth. Continuous changes in DO consumption rates over time are tested using Mann-Kendall's tau, and significant changes across periods between complete deep mixings are tested using a Kruskal-Wallis test.

To evaluate the processes contributing observed changes in hypolimnetic DO consumption for Lake Geneva, we resort to the one-dimensional topographic vertical model formalized in Livingstone and Imboden (1996). In its simplest version, the model simulates the DO consumption rate $k(z)$ (in mg L^{-1} d^{-1}) at depth z as the sum of the consumption due to WCM and SOU (eq.3). The model applies where z is deep enough in the hypolimnion to

allow the production and vertical transport of DO to be neglected (herein ≥50 m during the stratification period).

$$k(z) = WCM(z) + SOU(z).\alpha(z) \quad (3)$$

where $WCM(z)$ is the DO consumption rate associated with the water column mineralization ar at depth z, $SOU(z)$ the sediment oxygen uptake and $\alpha(z)$ the morphometric function representing the sediment area to water volume ratio at depth z. $WCM(z)$ is first set as constant across the hypolimnion, at values representative for a eutrophic and oligotrophic water column of the deep subalpine Swiss lakes (0.0064 and 0.005 mg L^{-1} $d^{-1,}$ respectively, for the high and low constant scenarios (Steinsberger et al. 2020). $WCM(z)$ is thereafter modelled (eq. 4) as a decaying function of depth, as in Schwefel et al (2018) that adds a slow-degrading part of organic matter WCM_1 to a fast degrading fraction WCM_2.

$$WCM(z) = WCM_1 + WCM_2.e^{-(z-z_0)/(z_\tau)} \quad (4)$$

WCM_1 and WCM_2 are set at 0.002 mg L^{-1} $d^{-1}$and 0.006 d^{-1}, consistent with Schwefel et al.'s (2018) micromeasurements (scenario WCM_2013-2017). Thereafter, WCM_2 is reduced to 0.002 d^{-1} to mimic a decreasing organic matter settling flux (scenario "low-depth-dep").

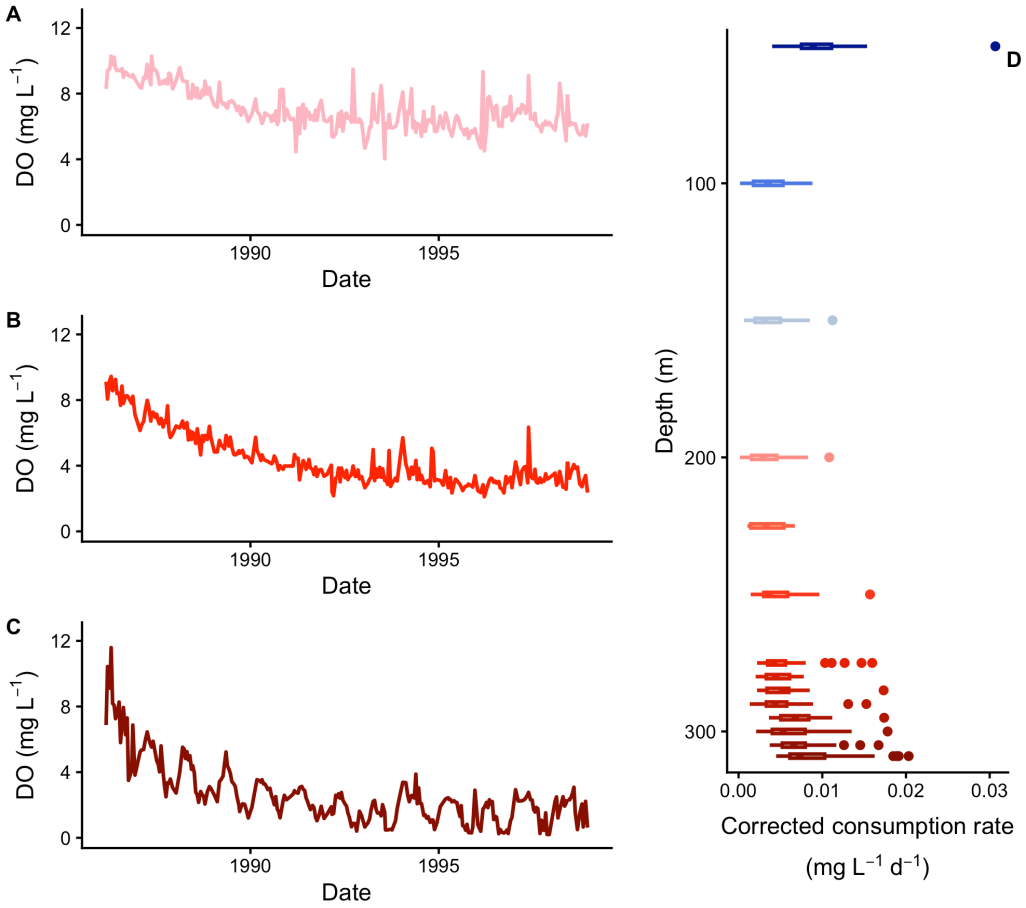
$SOU(z)$ is also modelled as depth-dependent, with a slow and fast degradation component, as in Schwefel et al. (2018), following

$$SOU(z) = SOU_1 + SOU_2.e^{-(z-z_0)/(z_\tau)} \quad (5)$$

with SOU_1 set to 0.18 mg L^{-1} $d^{-1}$and SOU_2 to 1.45 d^{-1}. z_0, and z_τ are set to 30 m as for Schwefel et al. (2018) (scenario SOU_2013-2017). Further scenarios of the hypolimnetic DO consumption include doubling and halving the sediment oxygen uptake at all depths ("high" and "low sediment flux" scenarios respectively).

Results

As expected given the lake morphometry, the DO dynamics varies with depth, including below the average depth of annual mixing (i.e., 180 m). For depths within 100-250m, following complete overturn (e.g., 1986 in Fig. 2), DO concentrations reaches a local extremum (9 mg L^{-1} in March 1986) and subsequently declines almost linearly over time, consistent with a substrate-limited consumption. A similar linear decrease resumes after partial replenishment of DO during the winter of 1996, when convective mixing extends to depths ≥ 200 m. At depths ≥ 250 m, the post-replenishment decline in DO follows an exponential decay pattern (Fig. 2B and C), as expected when DO consumption is controlled by diffusive fluxes across the sediment–water interface. At 275 m, this decay approaches an asymptotic concentration that remains higher than that observed at 309 m. However, at the deepest layers (≥ 290 m), the decline is punctuated by recurrent DO recharge events of approximately 1-2 mg L^{-1} each spring (Fig. 2C), that maintains the deepest waters to above the strict DO limit of anoxia at all times, even after prolonged absence of deep mixing (Fig 1D and Fig 2C). Such seasonal deep DO recharge events are not observed at depths shallower than 275 m (Fig. 2B).



197

198 *Figure 2. DO dynamics in the hypolimnion of Lake Geneva. DO at fixed depths for the 1986-*
199 *1999 period when no complete winter overturn happened. (A) 200 m, (B) 275 m and (C) 309*
200 *m. (D) DO annual consumption rates in the hypolimnion. Boxplots include all computed*
201 *annual consumption rates in 1971-2023.*

202 The annual consumption rate also varies following a C-shaped relationship to depths,
203 being maximal right under the metalimnion (0.01 mg L^{-1} d^{-1} at 50 m on average) and up to 35
204 m above the maximum lake depth (from 0.008 to 0.01 mg L^{-1} d^{-1} at 275-310 m). DO
205 consumption rates are minimum, and 5-10 times lower within the 150-250 m depth layer (Fig.
206 2D).

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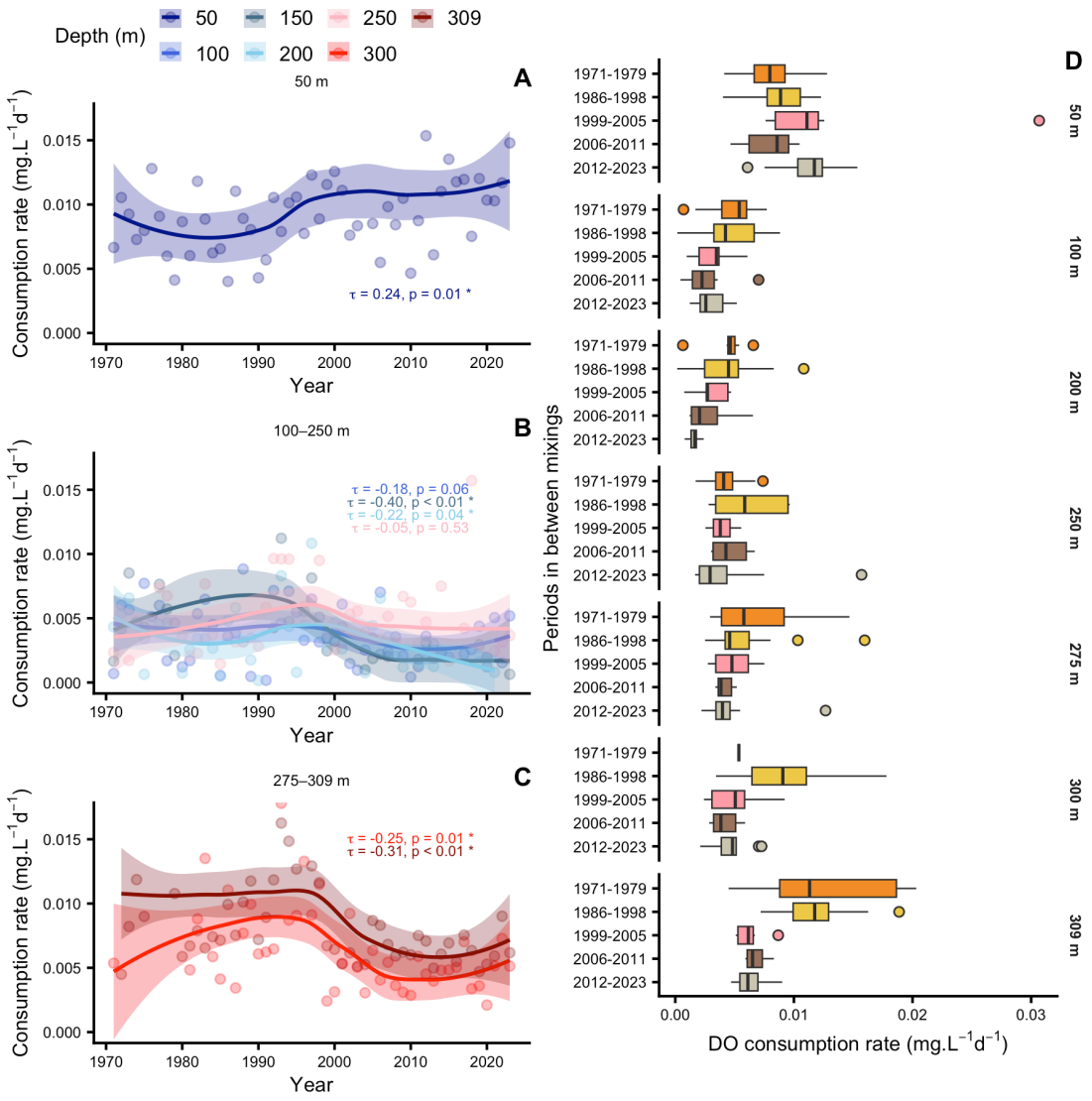


Fig.3. Changes in hypolimnetic DO consumption rates over time and depths. Annual DO consumption rates for 1971-2023 at (A) 50 m, (B) 100-250m and (C) >275 m. Lines represent smoothed temporal trends, and results from the Mann-Kendall trend test are provided. (D) Boxplots of DO consumption rates at fixed depths for periods between full mixing.

Across the last four decades, hypolimnetic DO consumption rates have remained low and slightly decreasing for depths within 100 - 200 m (Fig 3A, B). For depths ≥ 200m, the standardized DO consumption rate decreased significantly over time (Fig.3.B,C,D); especially after the year 2000. The decrease in annual DO consumption is particularly marked for depths ≥ 275 m (Fig. 3C,D), and, at depths≥ 300 m, is only half that of the 1970-1999 period after

2000 (Kruskal-Wallis test, W= 17 and 24, *p-values*=2.10^{-3} and 6.10^{-5} at 300 and 309 m respectively). In contrast, after a transient minimum in the early 21^{st} century, the most recent DO consumption rates at 50 m are now higher than any previously recorded (Fig. 3A and D).

The simplified one-dimensional model reproduces well the overall C-shaped vertical DO consumption pattern in lake Geneva's hypolimnion (Fig.4). The different WCM and SOU scenarios vary in the depth layers at which they influence the DO consumption (Fig.4A,B). Modifying the WCM using a depth-constant rate leads to a change in the DO consumption rate across the whole hypolimnetic layer that does not reflect the observed dynamics of depth-dependent changes in DO consumption rates. Lowering the WCM through a depth-dependent rate leads to a decreased consumption rate within the top 50 m of the hypolimnion, with no differences below 150 m (Fig. 4C). In contrast, lowering in SOU decreases DO consumption rates simultaneously in the uppermost 50 m and lowermost 30 m (Fig. 4D). The observed DO consumption trends over the last four decades in Lake Geneva are therefore better reflected by the simulations of a decreasing SOU (Fig. 4D) rather than of a decreasing WCM (Fig. 4C), except for the uppermost 50 m of the hypolimnion for the period since the last complete mixing (2012). None of the scenarios reproduces the recent increased DO consumption rate in the uppermost hypolimnion.

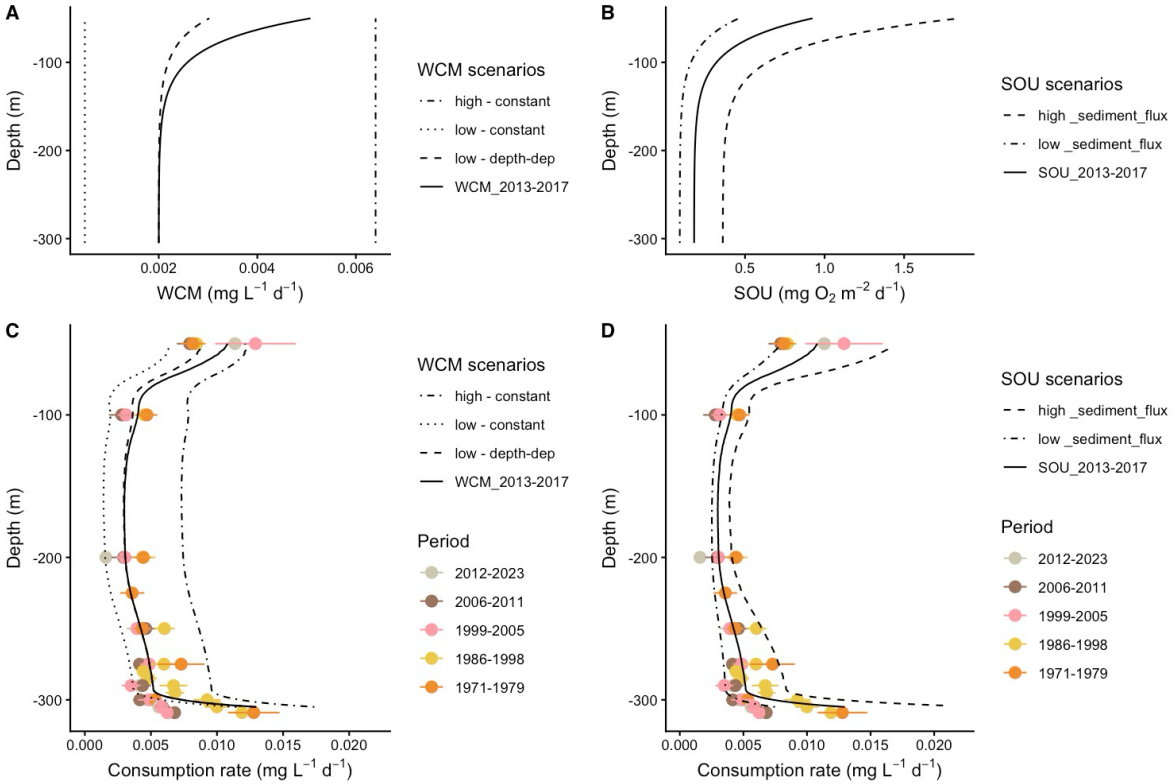


Fig. 4. Estimates of the contribution of water column mineralization versus sediment oxygen uptake to observed changes in hypolimnetic DO consumption over time (A) four scenarios for water column mineralization, (B) three scenarios for sediment oxygen uptake. Modelled (lines) versus observed (colored data points) vertical and temporal changes in hypolimnetic DO due to (C) changes in WCM and (D) due to changes in SOU.

Discussion

Our analysis underscores that deep-lake DO dynamics are governed by a broader suite of processes than vertical mixing alone, calling for a more nuanced understanding of the past and future evolution of deep hypoxia. DO consumption in Lake Geneva has declined substantially over the four decades of phosphorus reduction, but that this response is confined to specific depths. DO consumption rates decreased markedly since 2000, almost exclusively

248 below 275 m depth. This decline is most consistent with reduced sediment oxygen demand
249 driven by lower TP loading, whereas DO consumption associated with water-column
250 mineralization appears to have remained comparatively stable over time.

251 At first sight, evidence of a decline in DO consumption appears to contradict previous
252 findings of Müller et al. (2012) and Schwefel et al. (2016), who reported no significant
253 change in the areal hypolimnetic mineralization rate (AHM) since the eutrophication peak.
254 AHM is computed as the total quantity of DO consumed in the whole hypolimnion during the
255 annual stratification, divided by the maximum hypolimnion surface (similar to Hutchinson's
256 (1938) areal hypolimnetic oxygen demand, AHOD). As such, AHM does not explicitly
257 account for the depth dependence of DO consumption. In large lakes with high mean
258 hypolimnion depth, WCM largely dominates the AHM (Livingstone and Imboden 1996;
259 Rhodes et al. 2017), i.e., WCM accounts for 77 % of the AHM of Lake Geneva (Schwefel et
260 al. 2018). Our results point to relatively stable WCM over the last decades, which agrees with
261 the absence of detectable long-term trends in AHM. However, the deepest 30m of the water
262 column, where substantial changes in DO consumption occurred, correspond only to <3% of
263 the hypolimnetic volume, and therefore contribute little to whole-hypolimnion metrics such as
264 AHM. Yet, these deepest layers are precisely where DO consumption is the greatest, i.e., 2-3
265 times as large as at mid-hypolimnetic depths, and most strongly influence the onset and
266 expansion of deep-water hypoxia. Consequently, while AHM provides a useful integrative
267 measure of hypolimnetic metabolism, it may be less informative on changes in the processes
268 governing deep hypoxia in large lakes such as Lake Geneva.

269 The C-shaped relationship between depth and hypolimnetic DO consumption results
270 from the combined effects of lake hypsometry and the depth dependence of SOU (Schwefel et
271 al. 2018). On the one hand, the geomorphology of Lake Geneva produces a very low sediment
272 area-to-water volume ratio down to the 250 m depth (< 0.01 m^{-1}). On the other hand, high-

resolution *in situ* measurements showed that SOU is greatest in the upper hypolimnetic depths and declines toward intermediate depths (Schwefel et al. 2018), reflecting the progressive decrease in organic matter sedimentation with increasing distance from the productive surface waters (as modelled in Fig 4). At depth > 150 m, the degradation of labile organic matter is mostly complete by the time of sediment burial (Steinsberger et al. 2020). Volumetric DO consumption rates are maximum in the upper hypolimnion, despite the low sediment area-to-volume ratio, owing to the high SOU at such shallow depths. In contrast, high DO consumption rates in the c.a. 35 m above the lake maximum depth (275 -310 m), despite low SOU, are due to the very high sediment area-to-water volume ratio at these depths.

SOU is the component of hypolimnetic DO consumption that has been the most responsive to TP abatement in the lake. This is consistent with previous findings by Mathias and Barica (1980), showing that sediment oxygen consumption was three times faster in eutrophic lakes compared to oligotrophic lakes, for similar water column mineralization rates. DO consumption at the sediment-water interface (i.e., SOU) is the sum of the oxygen demand for the oxidation of the reduced compounds diffusing up from the sediment and of the water DO diffusion in the sediment. The flux of reducers is very low at every hypolimnetic depth in Lake Geneva (Steinsberger et al. 2017). If the flux of reducers may respond mostly to changes in the organic carbon mass accumulation (Steinsberger et al. 2017), the few results for Lake Geneva (a sediment core taken at the deepest point in 2011) do not show clear evidence for a significant decrease in organic carbon accumulation rate over the last 30 years (SI 5). Therefore, instead of a lower flux of reducers, the decrease in SOU most likely comes from a decrease in the DO diffusion across the sediment-water interface (Schwefel et al. 2018).

Reducing the DO diffusion flux across the water sediment interface requires a deepening of the oxygen depleted layer in the sediment, which happens when the mineralization of organic matter in the sediment declines (Schwefel et al. 2018). The

298 reduction in TP concentrations in the lake has had only limited effects on overall primary
299 production (Tadonléké et al. 2009), consistent with a stable WCM and organic carbon mass
300 accumulation. Yet, the decreasing lake water TP concentrations drove substantial qualitative
301 shifts in the phytoplankton community (CIPEL 2025). The phytoplankton communities may
302 have maintained maximum biomass production despite reduced P availability by
303 compensating through more efficient P utilization (Müller et al. 2019). Indeed, during the re-
304 oligotrophication phase of deep Swiss lakes, the molar C:P ratio of settling organic matter has
305 decreased (Müller et al. 2019). Because organic matter degradability declines with increasing
306 C:P ratios (Rosemond et al. 2015), reduced DO consumption in Lake Geneva sediments may
307 therefore be driven by changes in the quality of settling organic matter, rather than by a
308 decrease in sediment organic matter flux alone (Rosemond et al. 2015).

309 Despite long periods in between complete mixings (1986-1999 and 2012 -), the
310 deepest waters have not reached strict anoxia, due to a seasonal, approximately 1-2 mg L^{-1}
311 DO increase every year between late winter and early spring far below the lowermost limit of
312 the deep convective mixing (Fig. 2). DO fluctuations at depths highlights the existence of a
313 supply, additional to vertical deep mixing, that would inject annual approximately 8.5 10^3 t of
314 DO below the 250m depth. Below the 200 m depth, the DO dynamics following a full
315 replenishment event would therefore be better described by adding up a constant supply term
316 to the first-order decay model that we've used so far:

317 $$\frac{d(\mathrm{DO})}{dt} = -K_{\mathrm{exp}}\,\mathrm{DO} + S, \qquad (6)$$

318 whose analytical solution is

319 $$\mathrm{DO}(t) = \left(\mathrm{DO}_0 - \frac{S}{K_{\mathrm{exp}}}\right)\exp\left(-K_{\mathrm{exp}}t\right) + \frac{S}{K_{\mathrm{exp}}} \qquad (7)$$

where DO_0 is the initial oxygen concentration immediately after replenishment, K_{exp} (yr^{-1}) is the first-order decay constant representing the net oxygen consumption rate, and $S = k\,DO_\infty$ (mg L^{-1} yr^{-1}) is the annual oxygen supply. The equilibrium concentration approached asymptotically at large t is $DO_\infty = S/k$. The best fit suggests DO_∞ to be 1.4 or 2.4 mg L^{-1} for the periods 1986 -1996 and 2012- 2022 respectively. It is worth mentioning the equilibrium concentration DO_∞ has increased substantially between the two periods at all depths, with the recent period consistently yielding higher asymptotic values. Using the k value for the period 1986 -1996 and 2012- 2022 derived from the previous seasonal analysis ($k_{1986\text{-}1996}$ = 2.8 x10^{-3} d^{-1} and $k_{2012\text{-}2022}$ =1.5 x 10^{-3} d^{-1} thereafter converted into yr^{-1}), we infer a yearly supply at lake bottom of 1.4 and 1.3 mg L^{-1} respectively which agrees well with the observed yearly DO replenishment and is thus consistent with the presence of a source term that remains to be understood.

Three injection mechanisms can be considered. First, surface heat loss could drive convective plumes to the lake bottom (Bill et al. 1978; Larrieu et al. 2025), but DO and temperature profiles show no mixing below 200 m since 2012, and a turbulent flux signal would weaken with depth rather than accumulate at the bottom as observed. Second, Peng et al. (2024) attributed part of the deep oxygenation of the cold winter of 2012 to dense water cascading from the Petit Lac into the Grand Lac. This may have contributed to the near-complete mixing that year, but cannot explain the recurrent seasonal replenishment during the following period of incomplete mixing: Rhône River temperatures at Geneva, used as a proxy for Petit Lac surface temperature, show surface waters have remained warmer than bottom waters at 300 m since 2012. Because density in Lake Geneva's surface layer is almost entirely temperature-controlled, this excludes cascading as well as lateral intrusions, which would settle within the winter thermocline (Bouffard et al. 2025).

Third, underflows from the Rhône river offer a physically plausible and seasonally recurring mechanism. In winter, the Rhône River can generate negatively buoyant inflows that plunge and propagate as gravity currents along the lake bed through the 14 km "Rhône" canyon (Lambert and Giovanoli 1988). The penetration depth of these currents depends on entrainment processes that progressively dilute the inflow, reducing its density excess both at the plunge point and during downstream propagation. As a result, entrainment ultimately controls the depth at which oxygenated water is injected into the lake interior (Fink et al. 2016; Dresti et al. 2022). To estimate the order of magnitude of this contribution, we combined daily Rhône River observations (discharge, temperature, conductivity, and suspended-matter concentration) with SHL2 profiles from Lake Geneva (1981-2016) in a simplified underflow model (see SI 6 for details). Simulations indicate that the underflow reaches depths of at least 250 m on approximately 4% of days with plunging flow, and reaches 300 m on 2.5% of those days. These events occur exclusively during winter (January-April). Averaged over the 36-year period, the oxygen surplus delivered below 250 m amounts to approximately 4.3×10^3 t DO yr^{-1}, equivalent to about 0.8 mg L^{-1} yr^{-1} when distributed over the 5.5 km^3 of water below 250 m depth. This represents roughly half of the annual oxygen supply required to sustain observed deep-water oxygen dynamics (8.5×10^3 t DO yr^{-1}), suggesting, that Rhône underflows can account for a substantial fraction of the replenishment.

Lake Geneva is unlikely to return to the predominantly oxic conditions that characterized the pre-industrial era (Deyle et al. 2022). Yet, oxygen consumption rates at depth have declined significantly since 2000, and there is growing evidence of a continuing decrease in oxygen demand throughout the mid-hypolimnion. This reduction in SOU may help sustain acceptable oxygen conditions for longer periods as complete overturn events become increasingly rare. Furthermore, should TP concentrations decline beyond the

threshold at which primary production is expected to decrease substantially (Müller et al. 2019), DO consumption within the water column could also decline, further enhancing the lake's resilience to climate-driven reductions in deep convective DO resupply. Despite a mixing regime that is particularly sensitive to climate warming, bottom-water deoxygenation currently affects less than 1% of the total hypolimnetic volume (Fig. 5A). Remarkably, this remains true even after 14 consecutive years without full-depth oxygen replenishment through winter mixing, making Lake Geneva one of the Swiss lakes with the smallest volumetric proportion of hypoxic waters (Fig. 5B).

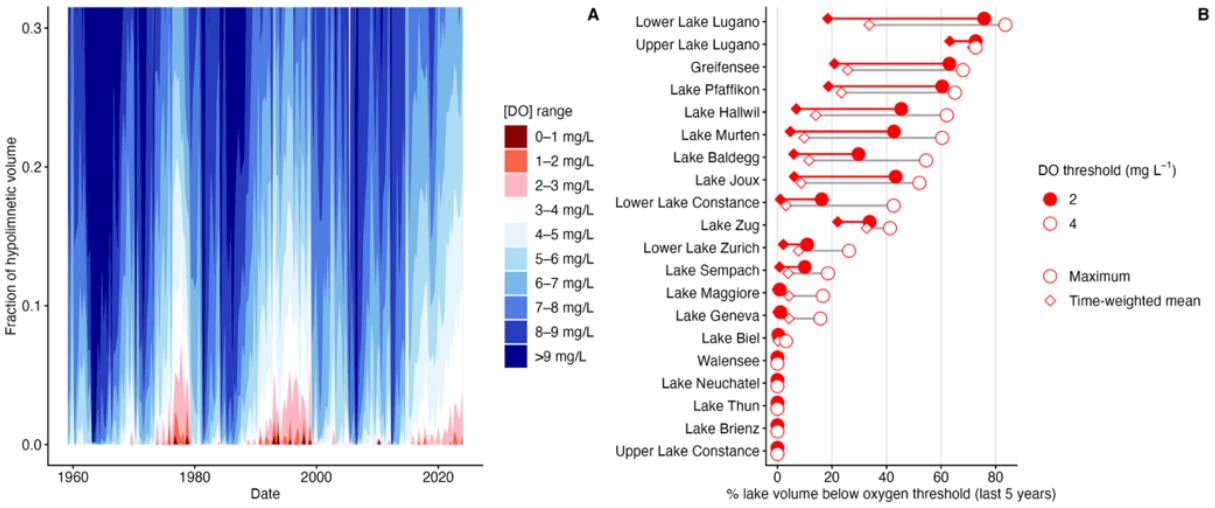


Figure 5. Shifting perspective to volumetric hypoxia. A) Changes in Lake Geneva's hypolimnetic DO seen as fraction of hypolimnetic volume. B) Percent of the volume of the 20th largest Swiss lakes with DO below the hypoxic threshold (2 mg L-1) and below the legal criterion for lake water quality in Switzerland (Leaux, 4 mg L^{-1}). Data from Barenbold et al, 2026, with compilations made over the latest five years (except for Lake Zurich, where consistent data were available only for 2019-2021).

The lake's iconic status as the largest lake in Western Europe and the substantial socioeconomic stakes associated with it may have amplified public and scientific attention to

its oxygen dynamics. This magnifying-glass effect has likely contributed to the persistence of a "zombie lake" narrative that does not reflect the lake's current ecological status, and may even foster public numbness or environmental doomism. A more appropriate metaphor may be that of a convalescent patient: still vulnerable, yet responding positively to treatment. Lake Geneva remains exposed to multiple pressures, amongst which climate warming, invasive species and micropollutants. Acknowledging the TP management success does not imply that monitoring and management efforts should be relaxed. Rather, recognizing its long-term benefits provides an opportunity to foster environmental optimism (Smith et al. 2025) and redirect attention and resources toward emerging threats and while maintaining vigilance over the lake ecological status.

Acknowledgements

ME Perga thanks the Musée du Léman and A.S. Deville, for creating the opportunity to revisit the long-term DO data for Lake Geneva. Copilot has been used in the preparation for this manuscript for language editing.

Data availability statement

Data and codes will be shared through a Zenodo link upon acceptance.

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Supplementary Material 1: an analysis of the way Lake Geneva has been portrayed in the local and national media (France and Switzerland) since 1957.

A Swiss (e-newspaperarchives.ch) and a European (Europresse) media databases were used to identify local and national newspaper articles dealing with the issue of oxygen concentrations in Lake Geneva. Search words were “Lake Geneva” and “oxygen concentrations” or “oxygen deficit” in both French and German languages. After checks for false-positives and doubles, the searches retrieved 133 articles from the e-newspaperarchives and 34 from the Europresse database. All articles were entirely read and classified as portraying the lake as “dying” when the following terms were present in the title or text (in French or German) and referring to Lake Geneva: “dying”,”death” , “suffocation”, “suffocating”, “apnea”, “asphyxia”,”asphyxiated”, “death-bed”,”sick”, “desperate”.

The dataset is available in the Zenodo reference related to this article.

Supplementary Material 2 : Dependence of DO consumption rates to the efficiency of deep mixing.

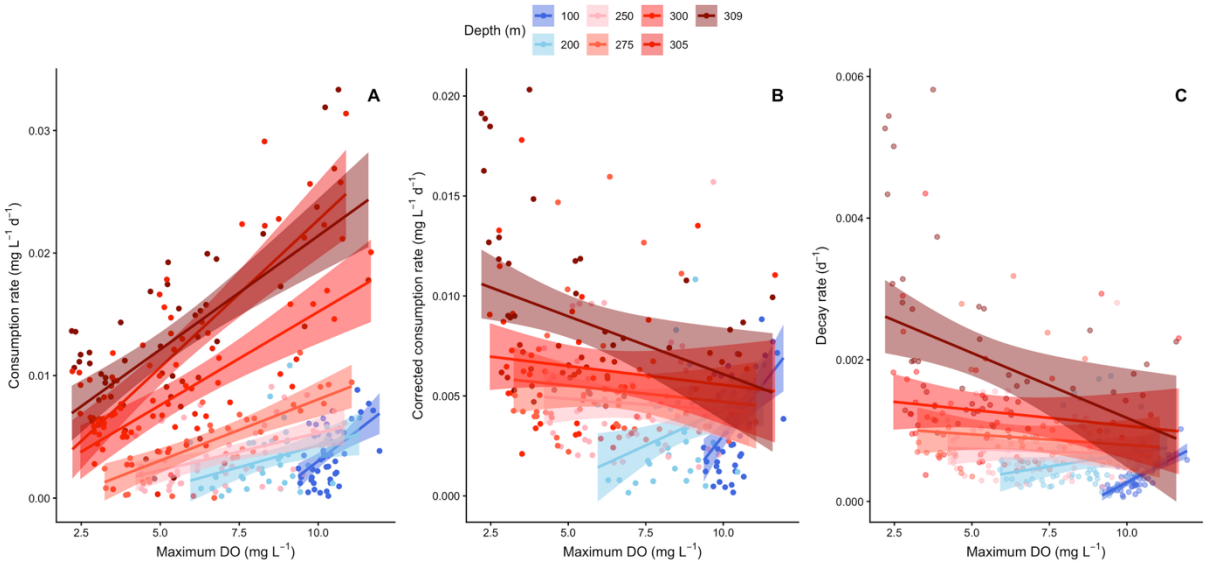


Fig. SI2. Relationships between maximum annual DO concentrations at fixed depths and the A. consumption rate computed from a zero-order equation (linear consumption model), B. consumption rate computed from a zero-order equation (linear consumption model) for depths<250m and from a first-order decay for deeper depths (aka corrected consumption rate as used throughout the paper), C. from a first order-decay at all depths. The mixed metric (B) is the one that is the least dependent on the max DO concentration, i.e., winter mixing efficiency.

Supplementary Material 3: Vertical variability of the metrics used to compute the hypolimnetic DO dynamics.

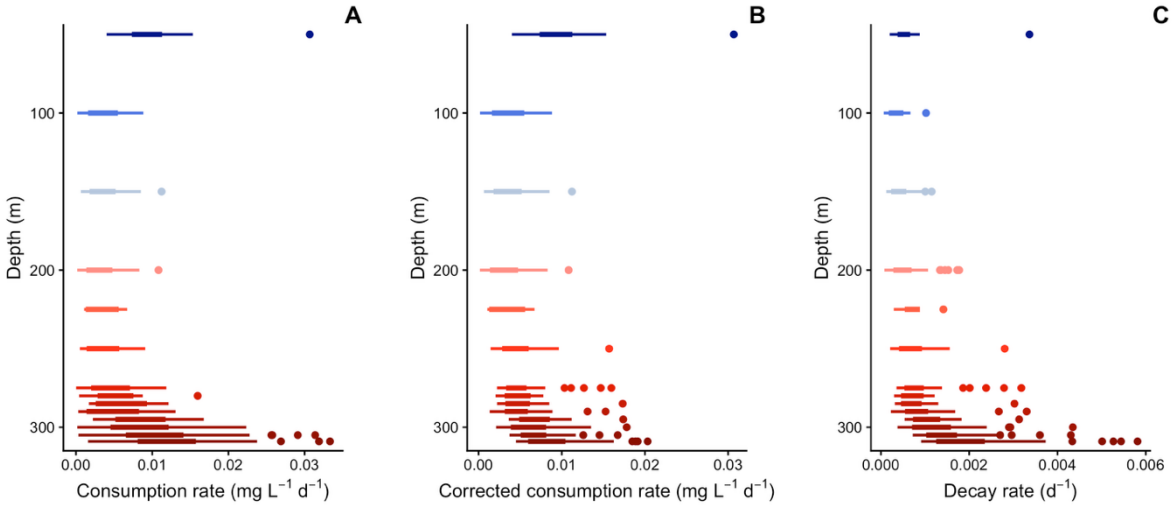


Fig. SI 3. Vertical variability of the metrics to compute the hypolimnetic DO dynamics. A. Consumption rate computed from a zero-order model, B. corrected consumption rate computed from a zero-order model down to 250m and a first order decay below (used throughout the study, C. decay rate computed from a first order equation. The vertical variability in hypolimnetic DO dynamics is very similar whatever used metrics.

Supplementary Material 4 : Variability over time of DO hypolimnetic dynamics and whether it depends on the metric used to compute the hypolimnetic DO dynamics.

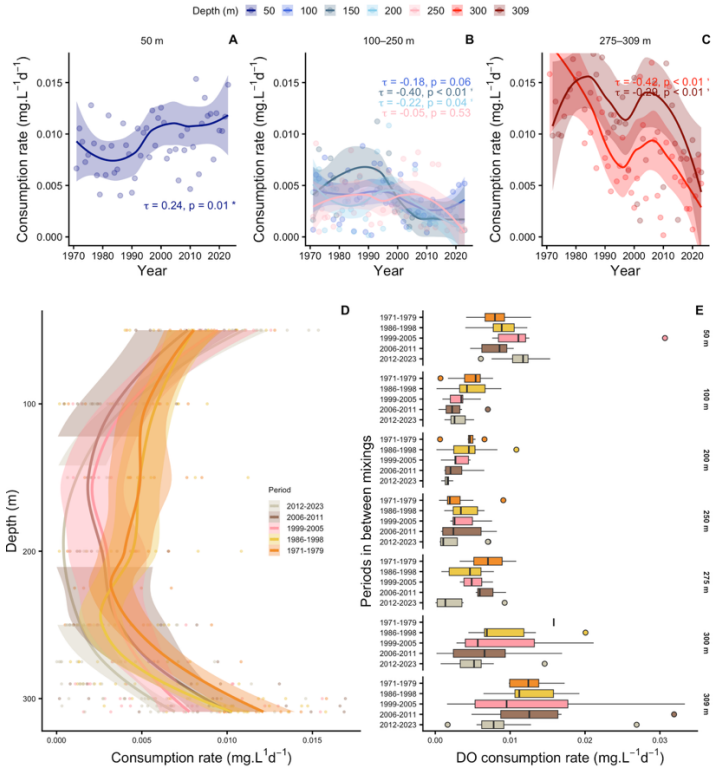
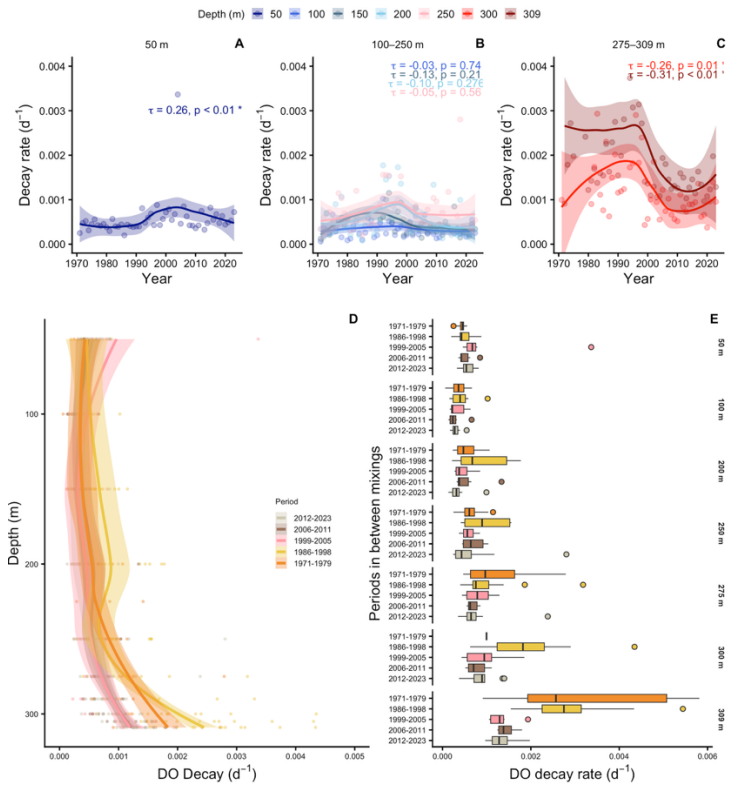


Fig. SI 4.1. Variability over time of DO hypolimnetic dynamics, as computed from a linear consumption rate at all depths. Annual DO consumption rates at 50m (A), 100-250m (B) and >275 m (C). Results of the Mann Kendall's trend tests are indicated. (D) Depth-resolved annual DO consumption rates discretised for periods in between full mixings. Lines represent smoothed vertical trends. (E) Boxplots of DO consumption rates ate fixed depths for periods in between full mixing.



590

591 *Fig. SI 4.2. Variability over time of DO hypolimnetic dynamics, as computed from a decay*

592 *rate at all depths. Annual DO decay rates at 50m (A), 100-250m (B) and >275 m (C). Results*

593 *of the Mann Kendall's trend tests are indicated. (D) Depth-resolved annual DO decay rates*

594 *discretised for periods in between full mixings. Lines represent smoothed vertical trends. (E)*

595 *Boxplots of DO decay rates ate fixed depths for periods in between full mixing.*

596

Supplementary Material 5: Total Organic Carbon accumulation rate.

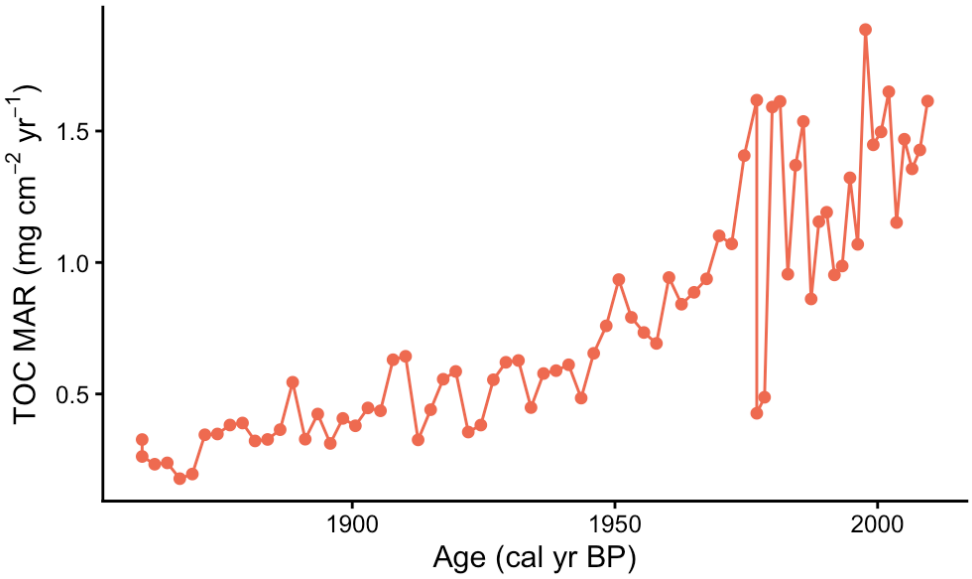


Fig. SI 5. Total Organic Carbon mass accumulation rate at lake Geneva's deepest point from ca 1850 to 2010, as measured in sediment core LEM11P4-B (Perga, unpublished data)

Supplementary Material 6: Contribution of the Rhône to deep DO injection.

The contribution of the Rhône underflow to the deep oxygen supply was estimated with a simplified, one-dimensional model of the plunging river driven by observations (Blanckaert et al. 2024). The model follows the Rhône water from its mixing with the surface water of the lake at the plunge point, down the delta and canyon slope, until it reaches its level of neutral buoyancy, and records the oxygen it brings in excess of the oxygen already present at that depth. It was run daily over 1981–2016, the period covered by the SHL2 profiles of temperature, conductivity and DO.

River inputs are the discharge, temperature, conductivity, suspended-matter concentration (TSM) and DO of the Rhône at Porte du Scex (NAWA programme, one sample every 14 days), linearly interpolated to daily values. The daily mean discharge of the same station (FOEN station 2009; Höge et al. 2023) and a cross-validated reconstruction of the daily TSM were used in sensitivity tests. The SHL2 profiles were interpolated to a 20 m depth grid and to daily values, and the volume of each layer was derived from the hypsography of the lake. The conductivities of the lake and of the river were both referred to 25 °C.

Density was calculated from temperature and salinity with the equation of state of Chen and Millero (1986), $\rho_{CM}(T, S)$, the salinity being derived from the conductivity ($S = 0.871\ \kappa_{20}$, in mg L^{-1}, with $\kappa_{25}/\kappa_{20} = 1.104$; Giovanoli and Lambert 1985), and increased for the suspended particles (particle density of 2650 kg m^{-3}):

$$(S1)\ \rho = \rho_{CM}(T,S) + 0.63\,\frac{\mathrm{TSM}}{1000}, \quad S = 0.871\,\kappa_{20}$$

At the plunge point, the river discharge Q_r mixes with the surface water of the lake (Blanckaert et al. 2024),

$$(S2)\ Q_p = Q_r\,(1+\gamma), \quad X_p = \frac{X_r\,Q_r + X_0\,(Q_p - Q_r)}{Q_p}$$

where γ is the plunge mixing coefficient and X is the temperature, conductivity, suspended-matter concentration (TSM) or DO, which are mixed conservatively.

The plunging flow is then followed level by level down the thalweg, with a vertical resolution of 20 m, until its density becomes lower than that of the lake. At each level, the reduced gravity g′ and the thickness of the current h are

$$(S3)\ g' = g\,\frac{\rho_p - \rho_l}{\rho_l}, \quad h = \left(\frac{Q^2}{Fr^2\,g'\,W^2}\right)^{1/3}$$

with W the width of the current and Fr its densimetric Froude number. The entrainment of lake water over the distance ds travelled along the bed is

$$(S4)\ dQ = a(Ri)\,\frac{Q}{h}\,ds, \quad a(Ri) = \frac{0.08 - 0.1\,Ri}{1 + 5\,Ri}, \quad Ri = Fr^{-2}$$

(Turner 1986; Cenedese 2024; as used by Giamagas et al. 2026). Ri was derived from the local slope S of the thalweg with the normal-state balance of a gravity current,

$$(S5)\ Ri\,S = a(Ri) + C_d$$

where C_d is the bed drag coefficient, so that gentle slopes entrain less. The entrained water (temperature, conductivity and DO of the new level) is mixed conservatively with the current and the density is recomputed. The depth–distance relationship of the thalweg was built from the published description of the canyon (about 120 m depth 1.2 km from the mouth, 156 m at 3 km and 280 m at 14 km; Blanckaert et al. 2024) and from the position of the plunge point (200–250 m from the mouth, at about 20 m depth; Giovanoli and Lambert 1985). Examples of the descent of the plunging flow are shown in Fig. SI 6.1.

The parameters were set to $\gamma = 1$, $C_d = 0.01$ and $W = 250$ m. Both γ and C_d have a wide range of published or plausible values (γ: 0.65–6.5 in large-eddy simulations, Giamagas et al. 2026, and in field measurements at the Rhône mouth, Blanckaert et al. 2024; C_d: 10^{-3}–10^{-2} for gravity currents). Given this range, we took a rounded value within it for each; a full quantitative approach would require a dedicated investigation of these parameters.

The oxygen delivered at the settling depth, or surplus, is the DO of the current multiplied by its discharge, from which the oxygen contained in the same volume of ambient water at that depth (DO_a) is subtracted, per day:

$$(S6)\ \Sigma = (DO - DO_a)\, Q \times 86400$$

The daily surpluses of the flows settling at or below a given depth were summed per year and divided by the volume of the lake below that depth to obtain an equivalent concentration (5.5 km³ below 250 m). Over 1981–2016, 3.7 % of the 13 108 days with a plunging flow reach 250 m or deeper (2.4 % reach the deepest level of the model, 300 m), all between January and April. From May to September the plunging water settles at a median depth of 20 m, consistent with the Rhône interflow observed at 10–30 m depth in August 1983 (Giovanoli and Lambert 1985). The mean annual surplus delivered below 250 m is 4.3×10^3 t of DO (0.8 mg L^{-1} yr^{-1} over 5.5 km³), about half of the supply of 8.5×10^3 t yr^{-1} estimated from SHL2. It is 6.0×10^3 t yr^{-1} below 200 m, 3.6×10^3 t yr^{-1} below 275 m and 2.9×10^3 t yr^{-1} in the deepest layer (290–310 m, 1.1 km³). Replacing the interpolated river discharge and TSM by the daily discharge and by stochastic reconstructions of the daily TSM that retain the variability of the samples changed the surplus by less than 7 %. Across the sensitivity tests, the surplus below 250 m ranged from 0.2 mg L^{-1} yr^{-1} ($\gamma = 5$) to 1.2 mg L^{-1} yr^{-1} (TSM doubled), with 0.5 mg L^{-1} yr^{-1} for $C_d = 0.001$ and 0.4 mg L^{-1} yr^{-1} for $W = 600$ m. The distribution of the settling depth and the seasonal delivery are shown in Fig. SI 6.2 and the sensitivity tests in Fig. SI 6.3.

This result has however several caveats. First, a large part of the density currents of the Rhône results from partial collapses of the delta (G. Sauter, pers. comm.). These turbidity currents are not directly controlled by river discharge or suspended-matter concentrations and cannot be represented in our model. Their contribution is therefore absent from the calculations, implying that our estimate likely represents a lower bound. Second, results are sensitive to the model parameters and input data. Sensitivity analyses varying the drag coefficient, the entrainment factor, the width of the underflow and the exact suspended-matter concentration of the river, yielded estimates ranging from about 0.2 to 1.2 mg L^{-1} per year (Fig. SI 6.3). Third, DO is modelled as a passive tracer, without consumption during the descent; the estimate given below shows that this is a minor effect for the flows of the model..

DO consumption during the descent. DO was treated as a passive tracer. Its consumption by the sediment along the descent was estimated a posteriori for the flows settling at 250 m or deeper (488 days). For each step of length ds, the DO lost by the current through the sediment oxygen uptake (SOU) of the bed in contact with it (width W) is

$$(S7)\ dDO = -\frac{SOU(z)\,W\,ds}{86400\,Q}, \quad SOU(z) = SOU_1 + SOU_2\,e^{-(z-z_0)/z_\tau}$$

with the depth-dependent SOU of the main text (SOU_1 = 0.18 and SOU_2 = 1.45 g O_2 m^{-2} d^{-1}, $z_0 = z_\tau$ = 30 m; Schwefel et al. 2018). These flows travel a median distance of 15.8 km along the thalweg before reaching 300 m, in a median of 74 h, i.e. about three days, with the velocity U = Q / (h W) of the model. The SOU consumes a median of 0.01 mg L^{-1} (25–75 %: 0.01–0.02 mg L^{-1}), i.e. about 0.1 % of the DO of the current. The mineralization in the water column during the descent (0.005 mg L^{-1} d^{-1}) adds about 0.015 mg L^{-1} but the potential priming as decribed in Bouffard and Perga (2016) is not accounted for. The annual surplus delivered below 250 m is reduced by less than 1 % , so that the consumption during the descent can be neglected for the flows of the model. Given all the uncertainties, we therefore

692 consider this an order of magnitude and not a budget, and the exact numbers require dedicated
693 field work

694 We finally briefly evaluate the Rhône contribution to deep oxygen with a climate
695 perspective. Two long-term trends of the forcing are relevant for the Rhône underflow (Fig.
696 SI 6.4). Between 1982 and 2016, the winter (December–March) temperature of the lake
697 surface increased by 0.032 °C yr^{-1}, faster than that of the river (0.018 °C yr^{-1}), which may
698 reflect the contribution of snow and glacier melt to the Rhône, whereas the water at 300 m
699 warmed only marginally (0.008 °C yr^{-1}). The plunging mixture, made of river and surface
700 water, therefore became warmer (0.024 °C yr^{-1}) and lighter with respect to the deep water of
701 the lake. The weaker warming of the river than of the lake surface increases their density
702 contrast and hence favours plunging at the surface of the lake, but the depth reached by the
703 flow is set by the density of the mixture, which includes the warming lake surface water,
704 relative to that of the deep water. This highlights again the need to correctly quantify the
705 plunge coefficient. These trends agree with the observations compiled for Swiss lakes
706 (Bärenbold et al. 2026): for Lake Geneva, they report an annual-mean warming of about
707 0.6 °C per decade at the surface (95 % interval 0.4–0.8) and 0.13 °C per decade at the bottom
708 (0.04–0.23) for 1980–2023, to be compared with 0.49 (0.34–0.60) and 0.07 (−0.04 to 0.19) °C
709 per decade for the annual means of the lake data used here (1982–2016). The winter
710 suspended-matter concentration of the river decreased by 0.23 mg L^{-1} yr^{-1} (8 mg L^{-1} over the
711 period, from a mean of 35 mg L^{-1}), equivalent to a loss of about 0.005 kg m^{-3} of sediment-
712 induced density, which may be related to the operation of hydropower and to sediment
713 retention in the catchment. Both changes reduce the density excess of the river water with
714 respect to the deep water, which is only of the order of 10^{-2} kg m^{-3} in winter. In the model,
715 removing these trends from the forcing tripled the surplus delivered below 250 m (+200 %;
716 +5 % for the suspended matter, +15 % for the river temperature and +150 % for the

temperature of the lake surface), and continuing the same trends for another 36 years decreased it by about 90 % (Fig. SI 6.5). The modelled delivery is therefore very sensitive to the temperature contrast between the river and the lake surface, and, in the model, the warming of the lake surface (and, to a lesser extent, of the river) tends to reduce the ability of the Rhône water to reach the deepest layers while winter deep mixing also decreases. These tests are illustrative and are not projections.

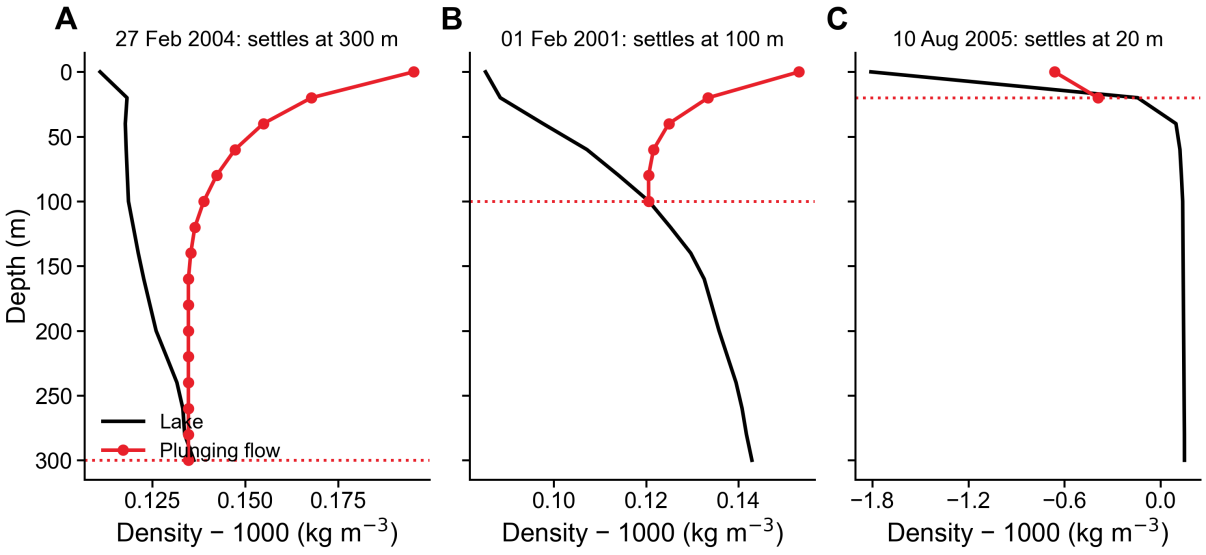
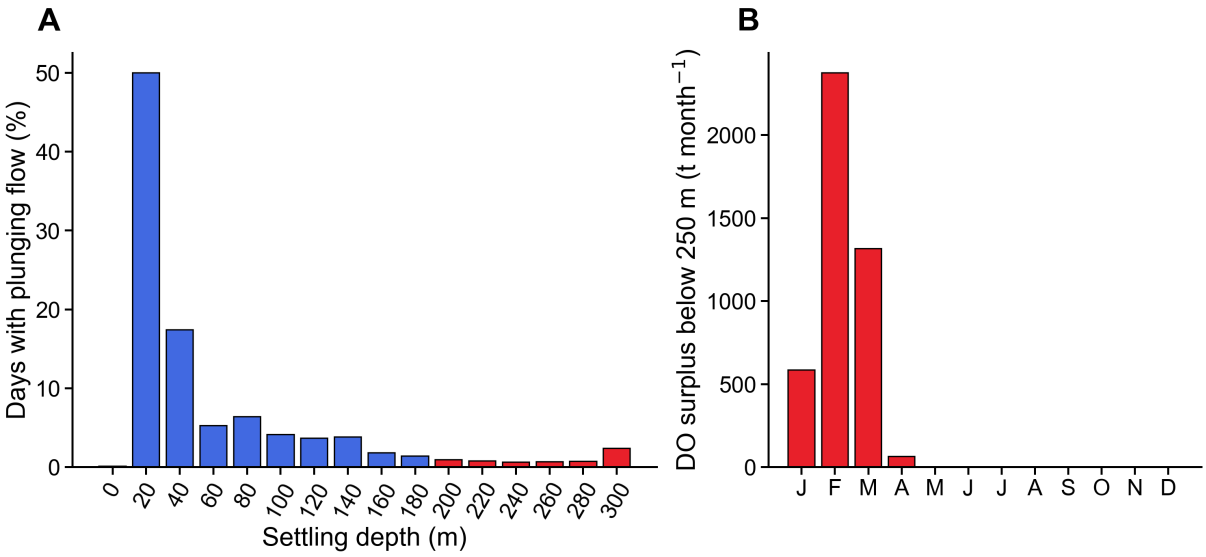
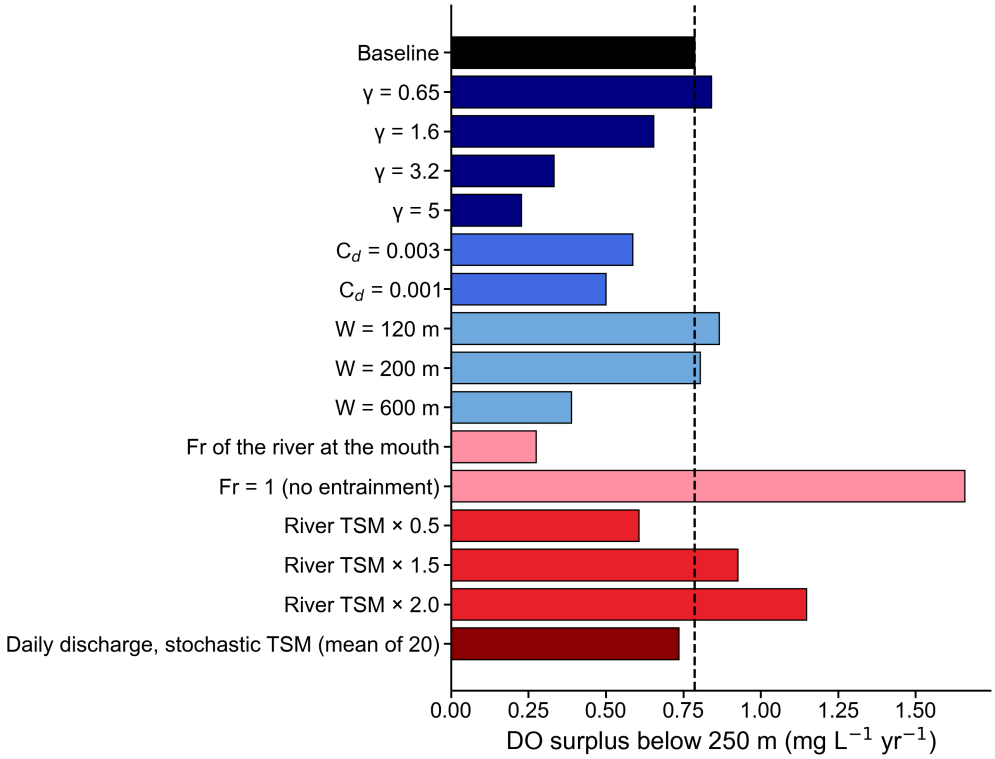


Fig. SI 6.1. Examples of the descent of the plunging Rhône water in the model: density of the lake (black) and of the plunging flow (red) as a function of depth for (A) a winter day with a deep intrusion, (B) a winter day with settling at an intermediate depth and (C) a summer day. The flow settles where its density becomes lower than that of the lake (dotted line).



728

729 Fig. SI 6.2. Rhône underflow model, 1981–2016. (A) Percentage of the days with a plunging
730 flow as a function of the settling depth (red bars: 200 m and deeper) and (B) mean monthly
731 surplus of DO delivered below 250 m.



732

733 Fig. SI 6.3. Sensitivity of the surplus of DO delivered below 250 m (equivalent concentration
734 over 5.5 km³) to the plunge mixing coefficient γ, the bed drag coefficient C_d, the width of the
735 underflow W, the Froude number of the flow, the suspended-matter concentration (TSM) of
736 the river and the temporal resolution of the river data. Dashed line: baseline (γ = 1, C_d = 0.01,
737 W = 250 m).

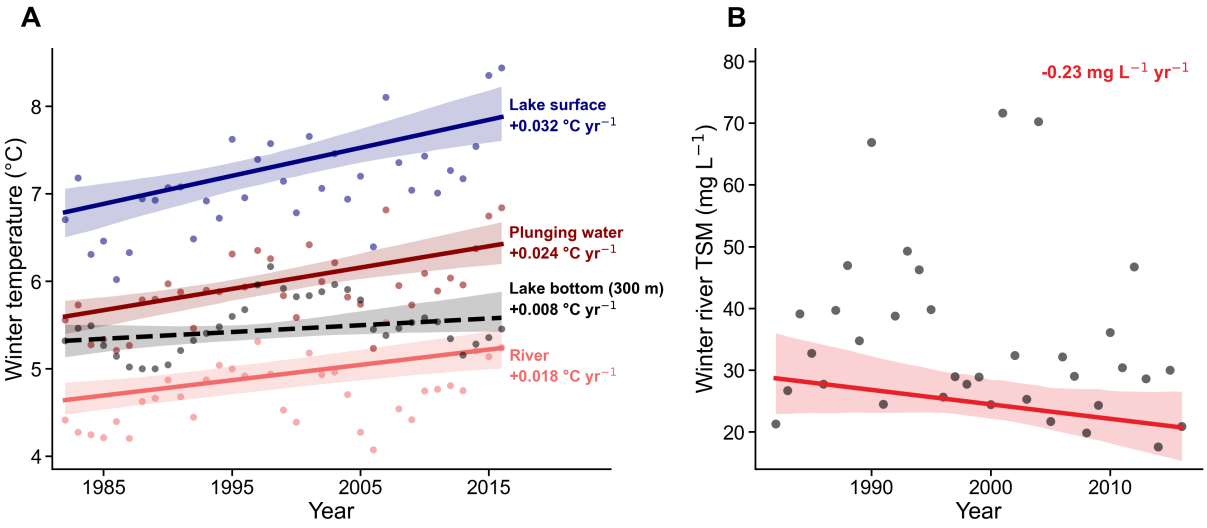


Fig. SI 6.4. Trends of the winter forcing, 1982–2016 (complete winters). (A) Mean winter (December–March) temperature of the lake surface, of the plunging water (mixture), of the Rhône and of the lake bottom (300 m): yearly means (dots), Theil–Sen trends (lines, with their slope) and 90 % bootstrap confidence band of the trend (shading). (B) Mean winter (December–April) suspended-matter concentration of the Rhône, with the same representation.

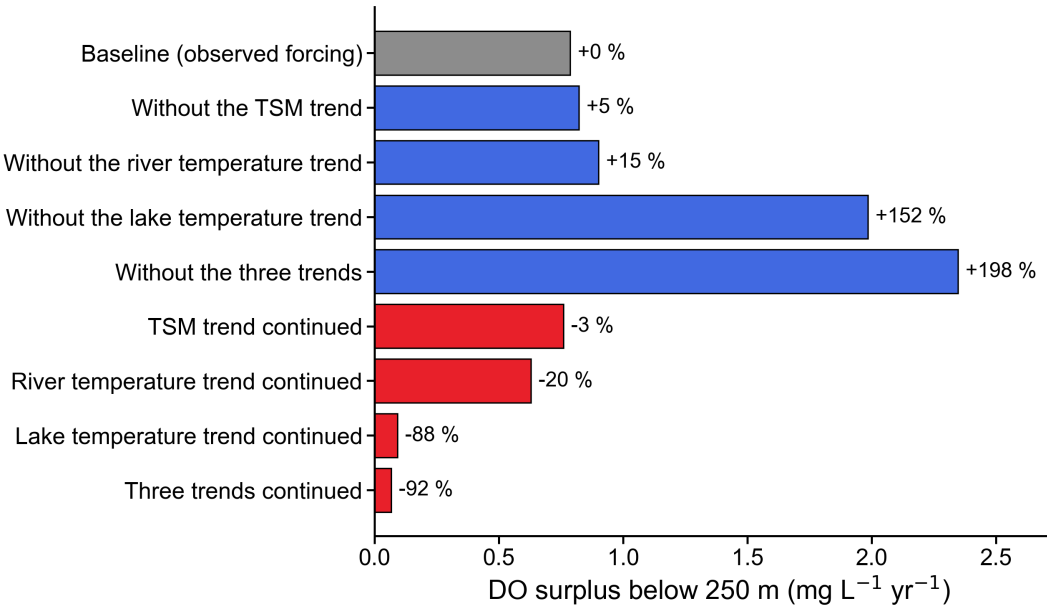


Fig. SI 6.5. Sensitivity of the surplus of DO delivered below 250 m to the trends of the forcing: model run without the observed trends of the winter suspended matter of the river, river temperature and lake temperature (blue), and with the same trends continued for another 36 years (red), compared with the baseline (grey). Numbers: change relative to the baseline.

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