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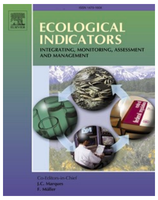

Expanding the European water Framework Directive indicators to address long-term climate change impacts on lakes using mechanistic lake models

L.M.V. Soares[a,c,1,*], M. Thouillot[a,1], V. Frossard[a], O. Desgué-Itier[a], C. Barouillet[a], Y. Baulaz[a], J.-C. Clément[a], I. Domaizon[a], J.-M. Dorioz[a], C. Goulon[a], J. Guillard[a,b], S. Jacquet[a], E. Réalis[a], V. Tran Khac[a], J.-P. Jenny[a]

[a] Université Savoie Mont Blanc, INRAE, CARRTEL 74200 Thonon-les-Bains, France
[b] Pole ECLA, OFB, INRAE, USMB 74200 Thonon-les-Bains, France
[c] Helmholtz Centre for Environmental Research (UFZ), Department of Lake Research 39114 Magdeburg, Germany

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ABSTRACT

Climate change is altering lake ecosystems at an unprecedented rate, disrupting thermal regimes, biogeochemical cycles, and key ecological functions essential for human use such as drinking water, fisheries, and recreational activities. However, climate effects are often studied in isolation and over short time periods, which limits our ability to quantify the extent and speed of multifaceted ecological changes as well as our understanding of how lakes will evolve under climate change. We present a framework that integrates computer modelling, long-term forecasting, and multi-decadal limnological data to comprehensively evaluate 25 key metrics within the European Water Framework Directive related to lake functioning and ecological status through to 2100. Long-term projections of the effects of climate change were based on lake priority uses: 1) overall functioning, which supports aesthetic value and general attractiveness, 2) drinking water supply, and 3) stock of salmonids. Our findings reveal that although key thermal regime changes have already occurred, higher water temperatures will progressively push deeper salmonid habitat on both annual and seasonal scales. Favourable conditions for salmonids reproduction will exceed tolerance limits by 2050, and fishery management adjustments are needed. Conversely, drinking water supply should remain unaffected until 2100, assuming stable nutrient inputs and pollution levels. This approach offers a tool for forecasting climate change's impacts on lakes, allowing decision-makers to anticipate measures to ensure long-term ecological and human benefits.

1. Introduction

Lakes are critical ecosystems, that support a wide range of species and provide significant cultural and recreational value to communities worldwide (Sterner et al., 2020). Although they cover less than 3 % of global inland area (Downing et al., 2006), lakes are home to high biodiversity and disproportionately contribute to ecosystem services across the planet. As climate change intensifies, lakes face unprecedented challenges at the global scale, including increased temperatures, alterations in geochemical cycles, and shifts in hydrological regimes which frequently result in a cascade of ecological and environmental consequences (Woolway et al., 2022). The multifaceted nature of these impacts renders lake ecosystems particularly vulnerable, requiring adaptive management strategies to ensure the sustainability of essential functions and services (Janssen et al., 2021).

Lake managers are confronted with the urgent task of adapting their practices to accommodate climate change pressures while ensuring the continuity of water uses for human needs. The European Water Framework Directive (WFD) is designed as a way for managers to achieve or maintain good ecological status of water bodies that may be altered by anthropogenic forcing among which climate change is expected to be of growing importance in the future. Good ecological status is appreciated through reference values for different lakes characteristics that supports the computation of ecological quality ratio (EQR) that are the actual lake characteristic over its reference. EQR hence represents the core operational metrics for which different lake characteristics can be compared enabling to quantify the completion to the WFD for individual water bodies. Yet, a comprehensive, multi-faceted study that

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* Corresponding author.
E-mail address: laura.soares@ufz.de (L.M.V. Soares).

[1] These authors are assessed as having contributed equally to this article.

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considers climate impacts on different water uses under different time horizons remains a challenge for effective adaptation to align with the WFD's objectives. There is also an increasing need to develop long-term strategies that can anticipate the different horizons of disturbances, as climate change impacts can unfold over decades and even centuries (Smol, 2019). In the face of continued climate pressures in future projections (Huang et al., 2024), which induce severe implications on ecosystem sustainability at a global scale (Heino et al., 2021), predicting the extent and speed of multifaceted climate-related lake ecological changes is urgently needed.

Lake Annecy, located in the French Alps, is an emblematic site for climate change investigations. Lake managers assumed a pioneering role in the fight against pollution during the 1930s and 1940s, when the demographic and economical development led to the first symptoms of eutrophication, including increased lake primary production (Perga et al., 2010) and bottom hypoxia (Jenny et al., 2014). Phosphorus abatement was early undertaken, through the set-up of wastewater collectors and sewage treatment as soon as 1967. As a result, eutrophication was limited to a mesotrophic state at the end of the 1960s and the lake was recognised as one of the cleanest lakes in Europe, successfully achieving a regional socio-economic importance. It includes 1,323 km of collectors, 100 pumping stations, and 12 wastewater treatment plants (https://www.sila.fr/nos-missions/assainir-vos-eaux/). These infrastructures demonstrate stakeholders' commitment to protecting the environment through an efficient sanitation network. Gradually implemented since the 1960s, they have contributed to the lake's significant restoration, ensuring that low phosphorus levels will be maintained. Currently, climate change is the most important threat to the lake in comparison to other anthropic pressures.

Here, we present a novel methodology grounded in the integration of long-term monitoring data and predictive modeling to project the evolution of key climate-related limnological changes in Lake Annecy from 1968 to 2100 constrained by Shared Socioeconomic Pathways (Riahi et al., 2017) and Representative Concentration Pathways (Van Vuuren et al., 2011) scenarios (SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5). This method is designed as a multi-faceted approach that integrates process-based modelling, long-term forecasting, and multi-decadal limnological data spanning a long timeframe to comprehensively evaluate key ecosystem metrics related to lake functioning and ecological status. Our approach incorporates 101 metrics related to key lake variables, which we classify into three categories: (1) ecological properties to support aesthetic and cultural attractiveness, (2) drinking water supply, and (3) fish community.

Modelling emerges as an essential tool to investigate the long-term dynamics of lake systems. In recent years, mechanistic lake models have seen widespread application to enhance the understanding of aquatic ecosystem dynamics, evaluate different environmental scenarios, and forecast ecosystem responses to climate change (Piccolroaz

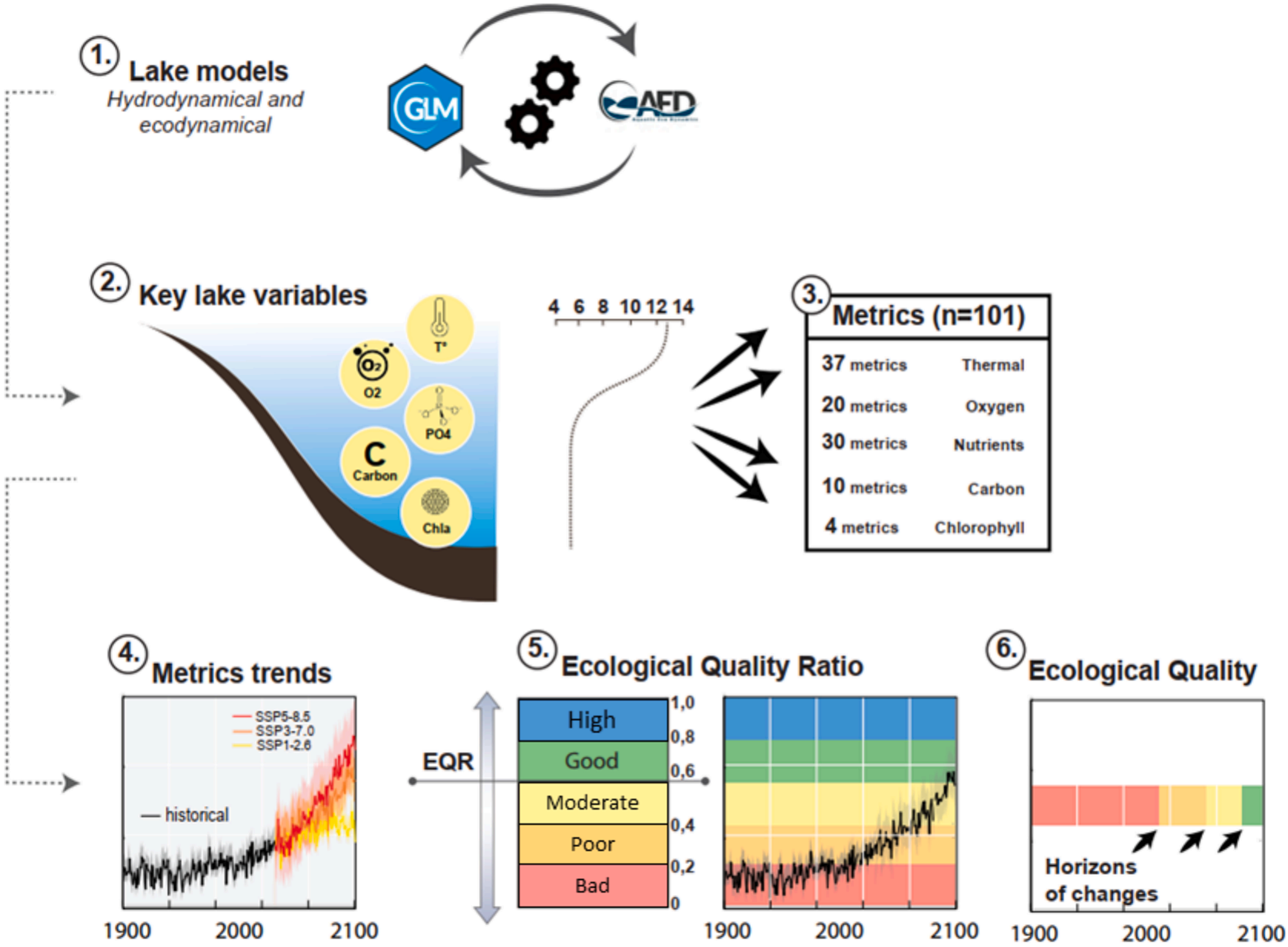

Fig. 1. Overview of the framework used to study long-term dynamics in Lake Annecy under three Socio-Economic Pathways and Representative Concentration Pathways (SSP1-RCP2.6, SSP3-RCP7.0, SSP5-RCP8.5). Using GLM and AED lake models, this framework simulates the evolution of key lake variables, identifies metric trends, calculates ecological quality ratios, and predicts future changes based on different climate scenarios. A total of 101 variables were simulated, with 25 key metrics from the European Water Framework Directive evaluated in relation to lake functioning and ecological status through to 2100.

et al., 2024). Here we employed a hydrodynamic one-dimensional model (General Lake Model – GLM) coupled with a biogeochemical model (Aquatic EcoDynamics – AED2) to simulate the physico-chemical and biological evolution of Lake Annecy.

2. Methods

A long-term, multi-faceted approach, integrating computer modelling, long-term forecasting, and multi-decadal limnological data, is used to comprehensively evaluate key ecosystem metrics related to lake functioning and ecological status through to the horizon of 2100 (Fig. 1).

2.1. *Study site*

Lake Annecy is the third deepest French lake with a maximum depth of 65 m and an area of 27 km^2. It is a perialpine lake, located at an altitude of 447 m, within a continental temperate climate. Of glacial origin, it is monomictic and oligotrophic since the 1990s following an earlier period of eutrophication. Its main tributaries are the Eau morte, the Ire, the Laudon and the Bornette rivers (Fig. 2), and its main outlet is the Thiou river, discharging into the Fier river, a tributary of the Rhône river. The catchment area covers 273 km^2, with a maximum altitude of 2351 m.

Discrete water samples are taken at the deepest part of the lake (referred to as Grand lac) from the surface to the bottom (at 0, 3, 5, 10, 15, 20, 30, 40, 45, 50, 60, and 65 m depth) every two weeks, except from November to February, when sampling is performed monthly (Rimet et al., 2020). The collection of physical, chemical and biological data has been conducted since 1966 by the Centre Alpin de Recherche sur les Réseaux Trophiques des Ecosystèmes Limniques (CARRTEL) and financed by the water manager (SILA). Fisheries catches in Lake Annecy (angling and commercial fishery) are focused mainly on two salmonids, the European whitefish (*Coregonous lavaretus*) and the Arctic charr (*Salvelinus alpinus*), with total exploitation of 20 and 2 tons per year, respectively (Goulon and Guillard, 2022; Lemaire et al., 2020). These species are of major heritage interest and are important to the local economy (Bourinet et al., 2023).

2.2. *Hydrodynamic and biogeochemical models*

The GLM model v. 3.1.1 (https://github.com/AquaticEcoDynamics/GLM) previously calibrated for Lake Annecy (Desgué-Itier et al., 2023) was coupled with the AED model v. 2.0 (https://github.com/AquaticEcoDynamics/glm-aed) to simulate the evolution of hydrodynamics, dissolved oxygen, carbon, nitrogen and phosphorus cycles, organic matter, as well as phytoplankton biomass (Fig. S1). Model coupling is a dynamic process which allows GLM to provide thermal conditions to AED for the computation of temperature dependent biogeochemical processes. AED integrates the main aquatic processes such as chemical reactions equilibrium and kinetics along the water column, and exchanges at the water-atmosphere and water-sediment interfaces. The one-dimensionality was needed for this long-term study given its good balance between accuracy and computational cost. Although the simulation of large deep lakes often calls for the use of 3D models (or in some cases 2D models) due to heterogeneous hydrometeorological conditions over extensive water surface areas, 1D models can be sufficient to represent long-term dynamics (Dresti et al., 2021). Particularly for Lake Annecy, 1D models have been found to provide accurate reproduction of the mixing dynamics (Desgué-Itier et al., 2023).

2.3. *GLM-AED input data*

Required data for the simulations (bathymetry, climatic variables, tributaries discharge and water quality) were collected from the lake manager (Syndicat Mixte du Lac d'Annecy, https://www.sila.fr/) and government agencies: SAFRAN (https://www.umr-cnrm.fr/), MétéoSuisse (https://www.meteosuisse.admin.ch/), HydroPortail (https://www.hydro.eaufrance.fr/), and Naiades (https://naiades.eaufrance.fr/). Limnological monitoring data from the Grand Lac station (Rimet et al., 2020) was used for model calibration and validation.

The model was constrained by statistically bias-adjusted and down-

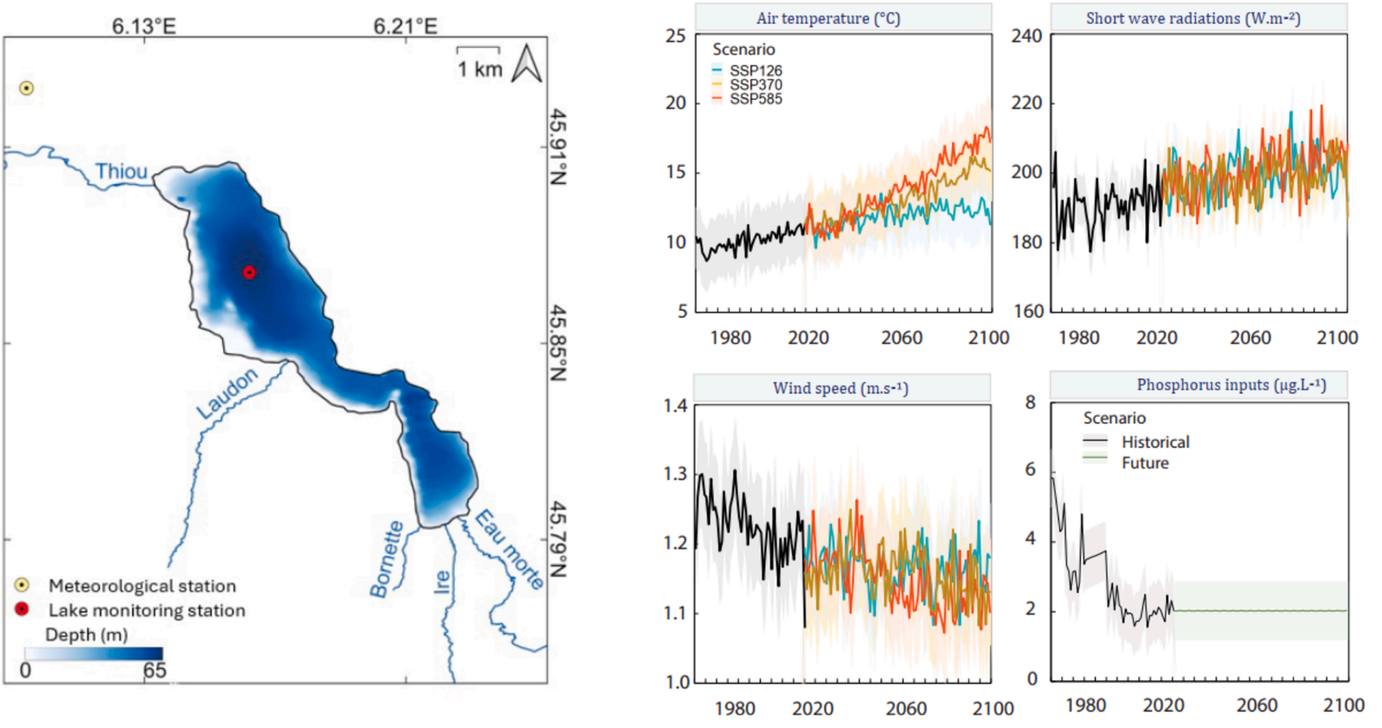

Fig. 2. Lake Annecy and location of the meteorological and monitoring stations. Major input data used in the GLM-AED model: air temperature (°C), short wave radiation (W m^{-2}) and wind speed (m s^{-1}) for three SSP-RCP scenarios (SSP1-RCP2.6, SSP3-RCP7.0 and SSP5-RCP8.5), as well as phosphorus inputs (µg/L).

scaled climate projections (Lange, 2019; Cucchi et al., 2020) using the ISIMIP3BASD method from phase 3b of the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP3b). These projections were derived from the outputs of phase 6 of the Coupled Model Intercomparison Project (Eyring et al., 2016, CMIP6). The IPSL-CM6A-LR model was chosen for this study because it showed the best fit to observations from the closest meteorological station to the lake (air temperature: RMSE = 4.27 °C, NMAE = 1.57 °C, $r = 0.81$; shortwave radiation: RMSE = 76.8 W m^{-2}, NMAE = 2.4 W m^{-2}, $r = 0.69$). The climatic projections of air temperature, shortwave radiation, and windspeed covered a historical subset (1965–2014) and three future scenarios for the period 2015–2100 (SSP1-RCP2.6, SSP3-RCP7.0 and SSP5-RCP8.5; see Fig. 2). These data were extracted at a daily resolution for the grid cell (55 km × 55 km) containing the lake. Locally downscaled cloud cover fraction, air relative humidity, and precipitation often show limited accuracy. To address this, these variables were extracted from meteorological observations with daily means calculated and then annually replicated from 1965 to 2100 as we currently lack clear expectation for their fate under future scenarios. This approach of reducing model input variables to only those with a high confidence level was previously applied to Lake Annecy and was found to be well-adapted to long-term simulations by overcoming limitations on their scaling and by their negligible effects on the hydrodynamic processes (Desgué-Itier et al., 2023). Details on the simplifications and assumptions adopted are provided in Desgué-Itier et al. (2023).

Daily discharge of the tributaries representing around 75 % of the total discharge into the lake (Nomade, 2005) were obtained for the period 1987–2022 (Hydro Portail, 2022). A coefficient of 1.33 was applied to the sum of their discharges, corresponding to the missing 25 % coming from the secondary tributaries, to estimate the total inflow discharge from all the tributaries. Average daily discharge was calculated for an average year and this typical year was replicated over the period 1965–2100. This rather unrealistic assumption does not account for precipitation variation over time. Still, it may have limited impact on model simulations since the lake's water level is highly regulated. For instance, over the last decades, its variation was negligible reaching only 0.9 m under exceptional circumstances, which represents 1.4 % of the maximum depth of the lake (Jalinoux, Pasquini, F. and SILA, 2015). In addition, inflow and outflow discharges were neglected in previous modelling applications in Lake Annecy without deterioration of the results of the temperature simulation (Desgué-Itier et al., 2023). Inflow and outflow discharges were taken as equal over the period 1965–2100.

The water temperature of the tributaries was calculated from air temperature and discharge monitoring data using the Air2Stream model (Toffolon and Piccolroaz, 2015). Dissolved oxygen (DO) concentrations in the tributaries were estimated from water temperature, by taking oxygen saturation as 100 % (Jones et al., 2018). These variables were calibrated and validated against monthly monitoring data in the main tributary from 2002 to 2021 (Naiades, 2022), and produced generally accurate estimates ($R^2 = 0,74$ and RMSE < .1,49 °C for water temperature; $R^2 = 0,56$ and RMSE < 0,98 mg L^{-1} for DO). Water temperature and DO were calculated for the three future climate scenarios.

The daily chlorides (used to calculate salinity), nitrates, ammonium, phosphates, reactive silica and dissolved organic carbon concentrations in the main tributary of the lake (Eau morte) were obtained by linear interpolation from monthly measurements from 2007 to 2021. Then, a factor of 2.22 was applied to these monitoring data, which represent ~ 45 % of the total inflow, in order to estimate missing inflows from the other tributaries. This method has been used in other studies (Burger, Hamilton and Pilditch, 2008; Özkundakci et al., 2011), but such a sampling frequency does not capture extreme events such as floods. The unavailability of data before 2007 was overcome by reconstructions of total phosphorus (TP) concentration, based on paleolimnological studies, using fossil diatoms assemblages to estimate annual averages of nutrient enrichment (Berthon et al., 2013). Daily variations relative to the annual average of phosphate, nitrate, ammonium, and reactive silica were calculated based on field monitoring to establish an intra-annual pattern. Then, daily inflow concentrations were calculated according to PO_4/TP, NO_3/TP, NH_4/TP and RSi/TP ratios in the Eau morte river for the period 2007–2021. In the absence of available data on organic nutrients, concentrations were calculated from inorganic nutrients concentrations, by separating dissolved and particulate fractions. Over the period 2021–2100, it was hypothesised that nutrients inputs would remain equal to those measured in 2020, consistent with observed restoration and existing treatment systems of the lake managers (SILA, 2023).

2.4. Model calibration and validation

The GLM-AED model was calibrated and validated for the state variables considered most important for lake water quality: water temperature and dissolved oxygen, total phosphorus and chlorophyll-a concentrations (Wetzel, 2001). A manual then automated calibration, based on the CMA-ES (Covariance Matrix Adaptation Evolution Strategy) optimisation algorithm (Hansen, 2016), were performed to reproduce as best as possible the amplitude, seasonal and interannual variations, and long-term trends for each variable. Temporal and seasonal variability for other nutrients (ammonium, nitrates) and for total organic carbon were reproduced with a higher uncertainty due to the absence of calibration for these variables.

The model was calibrated on a 10-year period, from January 1st 1992 to December 31st 2001, then validated on 1966–1991 and 2002–2020. Several metrics were calculated to evaluate model performance (Root Mean Square Error – RMSE, Normalised Root Mean Square Error – rRMSE, Mean Absolute Error – MAE, Pearson correlation coefficient – r and Percent Bias – PBIAS) by comparing model results to observations taken from the Grand Lac monitoring station over the whole monitoring period (1966–2020). For water temperature, dissolved oxygen, total phosphorus, nitrates and ammonium, the metrics were calculated for the mean values of surface (0–5 m) and bottom (60–65 m) layers as well over the entire water column, while for chlorophyll-a they were calculated exclusively for the euphotic zone (0–30 m).

2.5. Long-term trends by 2100

Daily model results for water temperature, dissolved oxygen, total phosphorus, chlorophyll-a, nitrates, ammonium, and total organic carbon concentrations were aggregated into annual averages over the entire study period (1968–2100). The two first years (1966–1967) correspond to the spin-up phase of the model, thus they were discarded from results to limit the impact of initial conditions. A non-parametric Mann-Kendall test with a 95 % confidence level was used to calculate trends in water temperature. It has been widely applied to assess randomness in relation to trends within climatological and hydrological time series data (Hamed, 2008). The analyses were carried out with R (version 4.3.2, R Core Team, 2023).

2.6. Ecological indicators of climate change impacts on lake water uses

As part of the collaboration between SILA and INRAE, a technical committee was established, consisting of experts, elected officials, and stakeholders, to oversee the study. During meetings and discussions, the stakeholders' priority uses were defined, ensuring that the study's focus was aligned with their practical needs and concerns. These priorities, such as lake functioning for aesthetic value, drinking water supply, and salmonid stock, shaped the study's approach and the selection of metrics, enhancing its practical relevance. The model outputs provided 101 variables that predict the likely state of the lake until 2100. From those, 25 metrics were calculated to describe the effects of climate on Lake Annecy that impact the greatest number of lake users. They are related either to non-extractive values that depend on ecosystem processes and ecological quality, i.e 1) overall lake functioning, which supports its aesthetic value and general attractiveness, or to goods extracted from lakes, i.e. 2) drinking water supply, and 3) stock of salmonids community.

2.6.1. *Overall lake functioning*

The following ecological indicators developed in the context of the WFD were investigated in face of their support to the aesthetic value and general attractiveness of the lake: water temperature and related thermal dynamic indices (water column stability, stratification onset and end dates, stratification duration, thermocline depth, metalimnion temperature, and water mixing maximum depth and date); oxygen concentration; nutrients concentration; chlorophyll-a concentration; and Trophic Status Index (TSI; Carlson, 1977) calculated from chlorophyll-a and total phosphorus concentrations. Changes in these water quality variables are not only a scientific assessment of the ecological status of the lake, but also translate into changes in recreational use patterns and the well-being of lake users (Egan et al., 2009).

2.6.2. *Drinking water supply*

The conservation of drinking water supply was evaluated based on water quality standards of $NO_3 < 50$ mg L^{-1} and $DO > 5$ mg L^{-1} ('Directive (EU) 2020/2184′, 2020). In addition, the temporal evolution of the distance of the chlorophyll-a peak to the water intake (currently at 30 m depth) was evaluated to investigate any risk of additional costs in the ultrafiltration treatment of organic matter produced by the phytoplankton (Schäfer et al., 2001).

2.6.3. *Preservation of salmonids*

Preservation of salmonids, fish of patrimonial interest for biodiversity conservation in the lake, was evaluated as the ability to maintain their habitat and reproduction favourable conditions. Suitable habitat for salmonids was assessed based on the Directive 2006/44/EC of the European Parliament and of the Council of 6 September 2006 on the quality of fresh waters needing protection or improvement in order to support fish life (2006), as $NH_4 \leq 0.04$ mg L^{-1} and $DO > 7$ mg L^{-1}. Additional parameters were evaluated due to their significant influence on habitat conditions of salmonids, including an optimal range between 7 °C and 13 °C for adult growth and a tolerance range between 5 °C and 18 °C in which no stress-related behaviour occurs and survival of adults can be assured. Finally, monthly habitat suitability was evaluated based on thermal preferences and oxygen requirement above 4 mg L^{-1} (Davis, 1975). Favourable conditions for reproduction were evaluated for two species, with reproductive cycles physiologically driven by water temperature (Sunday, 2020; Stewart et al., 2024): *Coregonus lavaretus* (European whitefish), that is the most representative in catch number and mass in Lake Annecy, and *Salvelinus alpinus* (Arctic charr) which is extremely sensitive to pollution and water temperature (cold oxyphilous stenotherm) and particularly vulnerable to the degradation of water quality in deepwater lake environments (Caudron et al., 2014). For both species, reproduction takes place between late November and January at different depths in the lake. European whitefish is a littoral spawner (0–2 m depth) while artic charr is a deep spawner (30–40 m depth) but they exhibit similar thermal ranges for embryogenic development spanning 2 °C to 8 °C (Hartmann, 1984; Gillet, 1991).

2.7. *Reference benchmarks for lake water quality*

The Ecological Quality Ratio (EQR) approach (De Bund and Solimini, 2007) was applied to elucidate the temporal evolution of the ecological quality within the context of the Water Framework Directive (WFD, 'Directive 2000/60/EC', 2000), by defining quality classes corresponding to the ratio between the observed state and the reference condition of a good ecological state. This ratio expressed between 0 and 1 classifies the system state as high (values close to 1), good, moderate, poor, or bad (values close to 0). This method was applied to 25 metrics to reveal the long-term effects of climate change on the priority uses of the lake. The reference state of nutrient concentration at surface and TSI are based on standard values (MEEM, 2016). For the remaining metrics, the reference state was defined as the average value over the initial 30-year period (1968–1998) since this time-span is commonly used (notably by the IPCC) in prospective studies as reference periods where trends can be identified. While the reference period doesn't necessarily represent optimal conditions, it allows the assessment of changes over time. The thresholds of each class were defined at 0.2 intervals, i.e. high when $EQR > 0.8$, good when $0.6 < EQR < 0.8$, moderate when $0.4 < EQR < 0.6$, poor when $0.2 < EQR < 0.4$, and bad when $EQR < 0.2$. For the hydrodynamic metrics, the thresholds were arbitrarily defined as high when $EQR < 0.6$, good when $0.6 < EQR < 0.7$, moderate when $0.7 < EQR < 0.8$, poor when $0.8 < EQR < 0.9$, and bad when $EQR > 0.9$. The threshold values for each metrics are provided in Table S1.

3. Results

3.1. *Model performance*

Overall, the GLM-AED model was able to reproduce the state variables over the simulation period (1966–2020) (Table 1). The RMSE of 1.04 °C and Pearson correlation coefficient of 0.91 for simulated water temperature over the whole water column reveal the ability of the model to reproduce thermal dynamics and interannual variability. A negative bias (–4.01 %) indicates that the model underestimated temperature values over the simulation period. Dissolved oxygen concentration in the surface layer and over the entire water column were reproduced with high accuracy (RMSE of 1.3 and 2.2 mg L^{-1} respectively), but the model was unable to correctly capture diffusion of hypoxic conditions in the bottom layers away from the sediment interface (RMSE of 4.55 mg L^{-1}, PBIAS of 55.75 %). Conversely, interannual variability was well captured (*r* above 0.6), revealing that the occurrence of hypoxia events

Table 1

Performance metrics for water temperature, dissolved oxygen, total phosphorus, and chlorophyll-a calculated between model output and monitoring data between 1966 and 2020; the metrics for chlorophyll-a were calculated for the layer 0–30 m; n = number of observation data.

Performance metrics	Surface layer (0–5 m)	Bottom layer (60–65 m)	Water column (0–65 m)
Water temperature			
n	571	563	27,472
RMSE (°C)	2.54	**1.28**	**1.04**
RRMSE (%)	11.67	4.29	13.55
MAE (°C)	1.87	1.17	0.86
r	0.94	0.07	0.91
PBIAS (%)	–10.89	–21.36	–4.01
Dissolved oxygen			
n	570	553	46,636
RMSE (mg L^{-1})	**1.3**	4.55	**2.2**
RRMSE (%)	10.86	30.98	21.87
MAE (mg L^{-1})	0.99	3.67	1.6
r	0.45	0.67	0.67
PBIAS (%)	6.85	55.75	13.97
Total phosphorus			
n	523	528	4,097
RMSE (μg L^{-1})	3.67	27.21	6.54
RRMSE (%)	**12.78**	**12.01**	**8.17**
MAE (μg L^{-1})	2.72	12.05	3.66
r	0.54	0.22	0.42
PBIAS (%)	16.96	–44.45	–10.67
*Chlorophyll-a**			
n	364	–	–
RMSE (μg L^{-1})	1.67	–	–
RRMSE (%)	11.16	–	–
MAE (μg L^{-1})	1.14	–	–
r	0.41	–	–
PBIAS (%)	–39.27	–	–

* Calculated for the euphotic layer (0–30 m).

was nonetheless modelled with good accuracy. Total phosphorus concentration was simulated with rRMSE below 15 % in the different layers, but the model showed reduced performance for the bottom layer. Chlorophyll-a concentration was simulated with good accuracy (rRMSE of 11.16 % and *r* of 0.41).

3.2. *Response of Lake Annecy to climate change scenarios*

3.2.1. *Lake functioning*

Water temperature is expected to increase from the surface to the bottom of the lake by 2100 (Fig. 3). Projections reveal surface warming rates from 0.16 °C dec^{-1} (SSP1-RCP2.6) to 0.75 °C dec^{-1} (SSP5-RCP8.5), whereas bottom layers are projected to warm from 0.13 °C dec^{-1} (SSP1-RCP2.6) to 0.43 °C dec^{-1} (SSP5-RCP8.5). This represents a total warming of 1.3–6.0 °C at the surface and 1.0–3.4 °C in bottom layers in the end of the century in comparison to 1968–1998. The higher warm rate at the surface compared to the bottom accentuates the thermal stratification of the lake during summer resulting in stronger stability of the water column (Fig. S2). The onset date of stratification is not expected to change significantly by 2100, but a later end date will result in longer stratification by 2050, reaching a plateau over 2050–2100 (Fig. S3). A summary of the main changes in Lake Annecy is provided in Table 2.

The thermocline has experienced a significant deepening of 4.0 m between 1968 and 2000, but no significant trend is expected by 2100 according to the three scenarios. However, the metalimnion shows a marked deepening and warming by 2100 (from + 0.2 to + 0.6 °C per decade in comparison to the reference period; Fig. S4). Annual complete winter mixing of the water column is maintained until 2100 for all 3 scenarios, despite milder winters (Fig. S5).

The simulation of dissolved oxygen reveals high concentrations in the surface layers until 2100 (annual average DO > 10 mg L^{-1}) despite a deoxygenation process due to the impact of water temperature increase on oxygen solubility. In the deep layers, the annual average concentrations are higher than 2.0 mg L^{-1} (Fig. S6). Overall, nutrient concentrations in the surface layers are far below the WFD thresholds for “very good status”, with the exception of total phosphorus, which average concentration exceed the threshold until the early 1970s (Fig. S7). By 2100, simulated annual average concentrations are 6.7 μg L^{-1} for total phosphorus, 0.14 mg L^{-1} for nitrate, and 0.02 μg L^{-1} for ammonium. A minor variation between the three future scenarios is observed due to the assumption of constant nutrient inputs. The model simulations indicate low concentrations of chlorophyll-a from the 2000s (annual average of 1.3 μg L^{-1}) that are below the threshold of 2.6 μg L^{-1}, characteristic of oligotrophic lakes (Fig. S8). Since phytoplankton growth is strongly correlated with phosphorus availability, the model output suggests that chlorophyll-a trends are extremely similar between the three future scenarios. The simulated TSI estimated from chlorophyll-a and total phosphorus concentrations in the surface layers reveals a clear improvement since the 1990s while the lake is classified as oligotrophic during the complete simulation period (Fig. S9).

Table 2
Summary of metrics (annual averages) related to climate change impacts on lake functioning, drinking water supply, and stock of salmonids, for the reference period (1968–1998) and future scenarios (2070–2100) SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5.

Metric	1968–1998	2070–2100		
	Reference	SSP126	SSP370	SSP585
Surface temperature (°C)	11.5	13.6	15.2	16.6
Bottom temperature (°C)	4.2	5.2	6.5	7.7
Metalimnion temperature (°C)	7.2	8.8	10.1	11.2
Distance of the Chl-a peak to the water intake (m)	23.4	24.2	21.7	17.1
Depth of optimal temperature for salmonids (m)	13.7	18.0	20.5	23.9
Depth of tolerable temperature for salmonids (m)	10.8	13.1	14.1	15.5
Suitable water volume for reproduction: *Coregonus lavaretus* (%)	99	100	68	19
Suitable water volume for reproduction: *Salvelinus alpinus* (%)	97	81	68	19

3.2.2. *Drinking water supply*

Relatively stable concentrations of chlorophyll-a are expected under future projections. However, the model predicts significant variations in the depth of its peak concentration, particularly after 2050. No significant variation is predicted for the most optimistic scenario (SSP1-RCP2.6), with the peak remaining 25.0 m far from the water intake, while a clear deepening is expected for the most pessimistic climate scenario (SSP5-RCP8.5), with the peak reaching depths 15.5 m far from

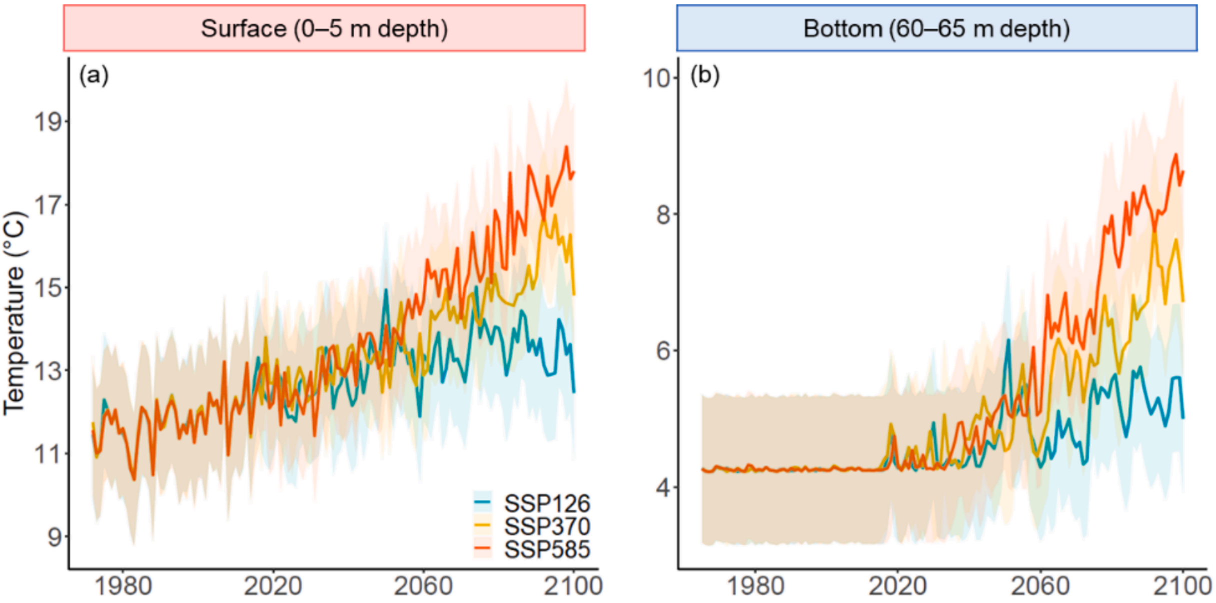

Fig. 3. Annual average water temperature at (a) the surface (0–5 m depth) and (b) the bottom (60–65 m depth) over 1968–2100 in Lake Annecy according to the scenarios SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5.

the water intake (Fig. 4). The daily nitrate (0.11–0.14 mg L^{-1}) and dissolved oxygen (> 5 mg L^{-1}) concentrations are expected to remain in accordance with the regulatory WFD thresholds for the three scenarios tested.

3.2.3. Salmonids habitats and reproduction

Higher water temperatures, in particular near the surface, will progressively push salmonid habitat deeper on both annual and seasonal scales. The upper limit of the depth range in which temperatures are below 13 °C is expected to deepen from 13.7 m (1968–1998 average) to 16.0–27.3 m by 2100 (Fig. 5). Similarly, the upper limit of the depth range in which temperatures are below 18 °C is projected to deepen from 10.7 m (1968–1998 average) to 12.5–16.7 m by 2100. Optimal temperatures for growth (7–13 °C) are expected to be maintained throughout the water column from December to April, but from May to November, a substantial restriction of optimal thermal habitat is observed. When combined with oxygen concentration, salmonid habitat is projected to be even more restricted by the end of the century. Indeed, good conditions for aquatic life require oxygen concentrations above 4 mg L^{-1}, and will be impacted by deep-layer hypoxia during a large part of the year (Fig. 6). Water quality standards from regulation regarding ammonium will not be impacted by 2100, as it is expected to remain below the thresholds according to the three scenarios tested assuming nutrient stability.

Water temperatures in December and January are expected to remain close to 8.0 °C for the three scenarios until 2050. From then, the reproduction of *Coregonus lavaretus* (at 0–2 m depth) and *Salvelinus alpinus* (at 30–40 m depth) may face the impacts of climate change. Indeed, while the temperature is expected to remain below the threshold by 2100 for the most optimistic climate scenario (SSP1-RCP2.6), temperatures up to 12.6 °C and 12.1 °C are expected at 0–2 m and 30–40 m depth, for *Coregonus lavaretus* and *Salvelinus alpinus*, respectively (Fig. 7).

3.3. Long-term evolution of lake water quality

The deviations from the reference for the metrics regarding the functioning of Lake Annecy and its priority water uses are summarized as annual changes in Fig. 8. The functioning of the lake has already experienced substantial change over the last decades. The changes are relatively rapid and should continue and accelerate during the second half of the 21st century, with pronounced effects on hydrodynamic processes, particularly on the metalimnion temperature and water column stability. The total phosphorus and chlorophyll-a concentrations, and the TSI as consequence, experienced changes in the past that were successfully managed resulting in a high quality state since the 1990s. Dissolved oxygen, nitrate, and ammonium concentrations show similar status to the reference conditions over the study period.

The drinking water supply will not be impacted by future concentrations of nitrate nor dissolved oxygen. However, a poor status is expected due to the reduction of the distance between the chlorophyll-a peak and the water intake in the end of the century. The thermal habitat for salmonid has been facing changes since the 1970s and currently presents a moderate state in comparison to reference conditions but will progressively move to poor or bad conditions. Although current temperature is not affecting salmonids reproduction, conditions will shift into a bad state at the end of the century.

4. Discussion

4.1. Limitations and perspectives

All projections presented here are based on model outputs subjected to different sources of uncertainty. First, intrinsic uncertainties of the 1D model approach arise from the premise that all horizontal processes in the water column are neglected. Thus, space-dependant processes, especially in the littoral zone, are disregarded in the present study. Other models, namely 3D ones, might allow for a better understanding of fine evolution in lake dynamics. In addition, coupling the lake model with a watershed model is recommended for future research to address the long-term climate impacts coming from the catchment. Second, while our calibration and validation processes span 54 years, yielding a robust dataset covering the ecological changes the lake has been facing, some uncertainties persist, including the reliance on global climate models. For instance, climate data were obtained from global models and subsequently downscaled to reflect local topography and climatic conditions. Despite this adjustment, discrepancies between global and local conditions can still introduce uncertainties. Furthermore, the validity of

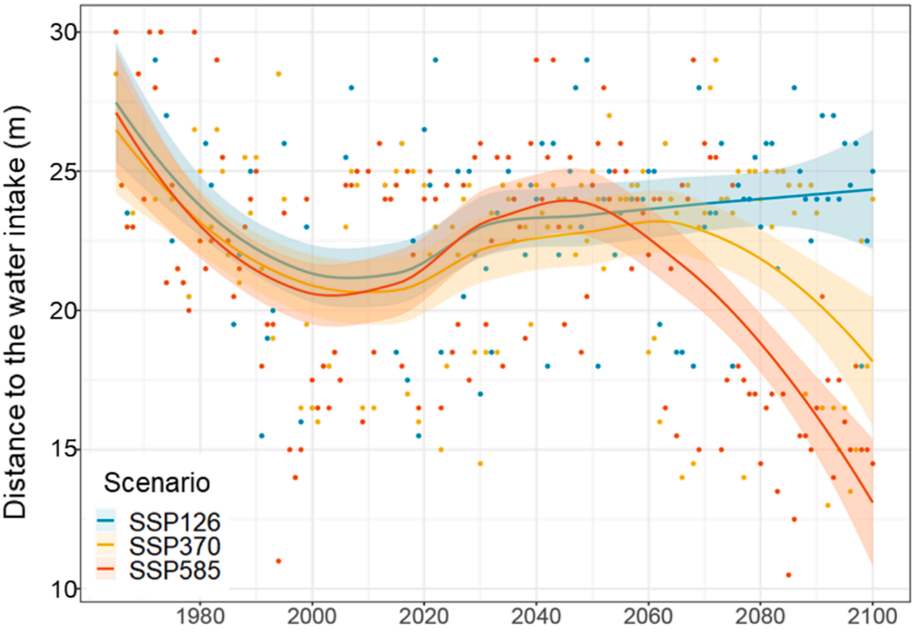

Fig. 4. Annual average distance of the chlorophyll-a peak to the drinking water intake in Lake Annecy over 1968–2100, according to the scenarios SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5.

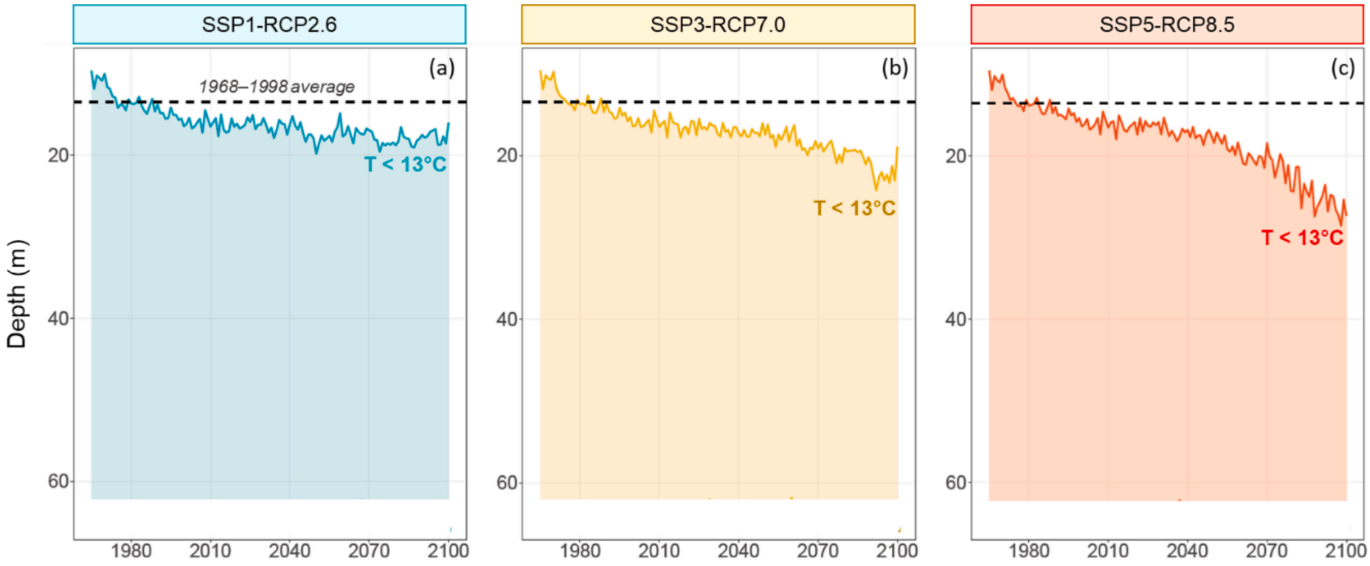

Fig. 5. Annual averages of maximum depths with optimum temperatures (T < 13 °C) for adults of the two main salmonids (*Coregonus lavaretus* and *Salvelinus alpinus*) over 1968–2100 in Lake Annecy according to the scenarios SSP1-RCP2.6 (a), SSP3-RCP7.0 (b) and SSP5-RCP8.5 (c).

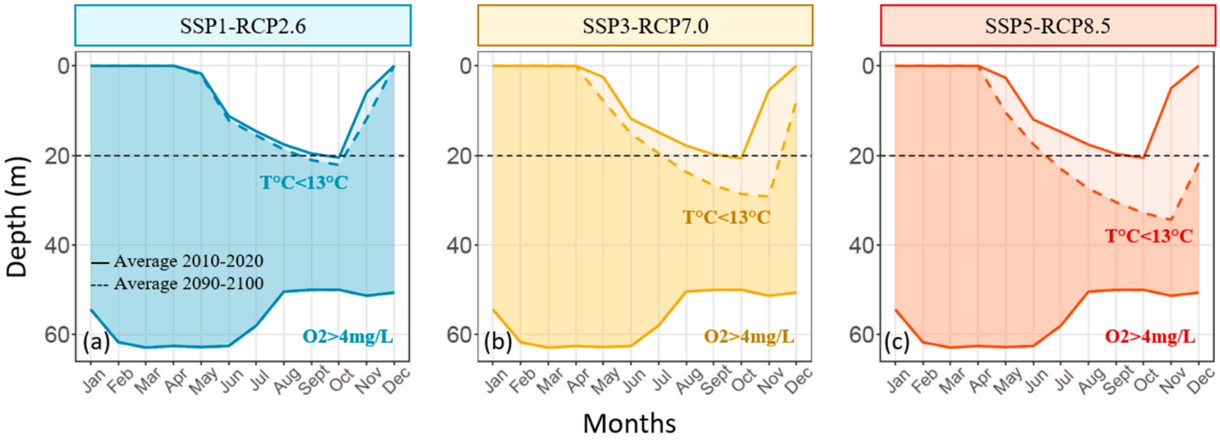

Fig. 6. Depth conditions for adult salmonids optimal habitat. Monthly means of maximal depths where temperature is below 13 °C (threshold for physiological optimum) between 2010 and 2020 (solid lines) and between 2090 and 2100 (dotted lines) for SSP1-RCP2.6, SSP3-RCP7.0 and SSP5-RCP8.5; and depths where dissolved oxygen concentration is above. 4 mg L^{-1} (threshold for survival). The oxygen profile in the hypolimnion is replicated from monitoring data collected between 2010 and 2020.

the projections presented here is dependent on the validity of the aforementioned global climate models, which depends on a myriad of factors in how we respond to climate change. Nevertheless, the combination of state-of-the-art modelling and robust long-term field measurements provides strong insights into potential future changes in the lake dynamics. Third, phosphorus inputs were assumed to remain constant. Although population is expected to keep increasing in the catchment, effective water treatment should be able to handle the increased load, making this assumption reasonable. Nonetheless, this approach overlooks potential changes in watershed phosphorus dynamics. Future studies could benefit from incorporating watershed model simulations and adaptive management strategies into the modelling framework. Finally, many external factors outside the scope of the present study could significantly affect the evolution of lake functioning in the coming decades. These include historical pollutants whose properties can change in higher temperatures, emergent pollutants, trophic resources, shore artificialisation and evolving lake uses. Further studies would be needed to evaluate their impact, and whether they warrant additional adaptations by managers at the lake and catchment levels.

The reference conditions used in this study were based on Water Framework Directive standards and historical conditions from the first 30-year period of monitoring data. However, the definition of "reference" conditions is a subject of ongoing debate in lake science (Bouleau and Pont, 2015), necessitating further refinement of our multi-faceted approach. Paleolimnological studies are particularly valuable, as they provide insights into pre-anthropogenic environmental baselines (Bennion and Battarbee, 2007; Soares et al., 2024). Future research should integrate these paleolimnological records to enhance our understanding of anthropogenic impacts, using historically unaltered conditions as baseline data alongside Water Framework Directive references.

4.2. Horizons of change in lake functioning and ecological conditions

Climate change is expected to profoundly alter lake ecosystems over the coming decades, with physical, chemical, and biological processes being affected at various timescales. Recent studies have explored these impacts, often focusing on specific aspects like thermal stratification (Kraemer et al., 2017; Woolway et al., 2021) or fish habitat suitability (Ficke, Myrick and Hansen, 2007). However, few studies have assessed

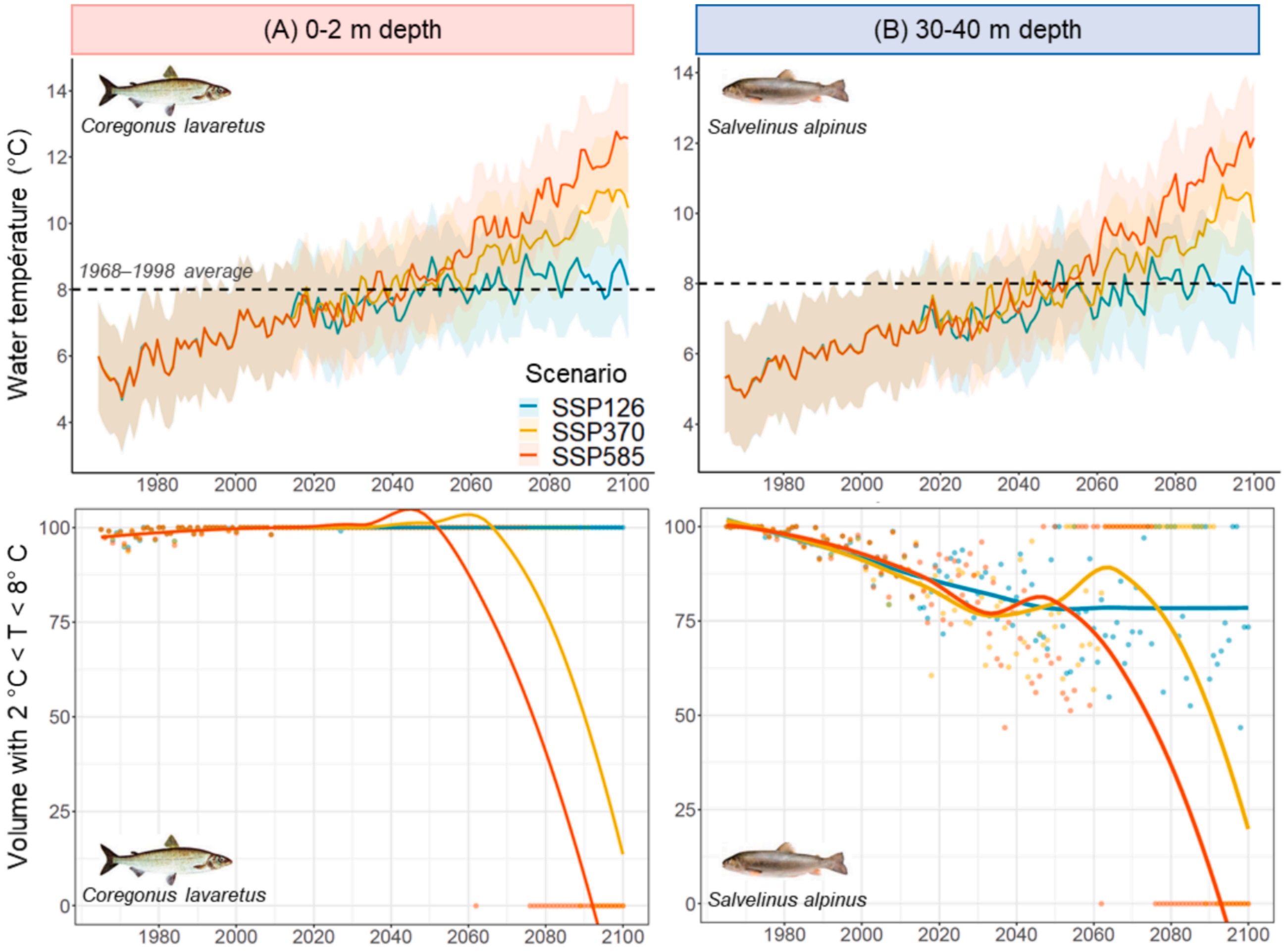

Fig. 7. Annual average temperature and corresponding water volume (%) in December and January at (A) 0–2 m depth for *Coregonus lavaretus*, and (B) 30–40 m depth for *Salvelinus alpinus*, in Lake Annecy between 1968 and 2100 for SSP1-RCP2.6, SSP3-RCP7.0 and SSP5-RCP8.5. The 8 °C threshold (above which high mortality is observed for embryonic development) is exceeded in 2050 under SSP3-RCP7.0 and SSP5-RCP8.5 scenarios.

how these multifaceted changes will interact over long timeframes. Our study integrates physical, chemical, and biological variables over a century in a lake, providing a more comprehensive assessment of ecosystem trajectories under climate change.

Our findings for the perialpine Lake Annecy illustrate a clear progression of ecological changes over distinct time horizons. Surface water temperatures have risen by 1.0 °C since 1980, and projections suggest this trend will continue, with potential increases of up to 6.0 °C by 2100 under a worst-case scenario. This early phase of warming is consistent with global observations of lake surface temperature increase (O'Reilly et al., 2015). However, unlike surface waters, deeper layers (60–65 m) will experience more gradual warming, with significant changes expected only after 2050. This delayed response in deeper waters has also been noted in other studies (Ottosson and Abrahamsson, 1998; Winslow et al., 2015; Desgué-Itier et al., 2023), reinforcing the need to consider depth-specific impacts when forecasting lake ecosystem responses. By 2050, thermal stratification patterns in Lake Annecy will undergo substantial changes. We project a deepening of the summer metalimnion by approximately 4 m, extending to 19 m below the surface, compared to the historical average of 15 m. This shift in stratification depth aligns with observations in other lakes, where longer stratification and deeper thermoclines are becoming more common (Kraemer et al., 2017).

The biological implications of thermal shifts are particularly concerning for salmonids, which are highly sensitive to temperature. For instance, warmer waters are expected to profoundly impact salmonids habitat and reproduction after mid-century. It is projected that the changes in ecological conditions will follow a multi-phase trajectory, with physical changes occurring first followed by biological disruptions. As the salmonids are an important ecological and economic resource, the effects of climate warming will affect the economies that are reliant on those resources, and then human populations. These successive horizons highlight the need for adaptive management strategies that evolve with the changing conditions, ensuring the long-term sustainability of both ecological functions and water uses.

Our simulations further suggest that if phosphorus inputs into the lake remain constant, Lake Annecy may stay as oligotrophic throughout the 21st century. This assumption is valid if nutrient loads from the catchment remain similar to present conditions, which is likely to occur because urbanization is located downstream the lake. The nutrients show minor sensitivity to the different scenarios revealing that local anthropogenic pressures will cause more impact than changes on chemical reactions under higher temperatures, thereby keeping nutrient inputs at current levels is an important strategy to allow for the continued provision of high-quality drinking water and good ecological conditions. Additionally, the appeal of Lake Annecy as a recreational destination, which currently represents a vital economic resource for the area reaching more than 100 M€ per year (SILA, 2013), is not anticipated to decline significantly if pollution levels remain controlled. Indeed, climate change does not appear to impact nutrient levels, which remains constant over the future scenarios. However, lake managers should be vigilant to potential urban densification promoted by global warming around fresh islands and aesthetic spaces, such as the surroundings of Lake Annecy, as well as over-tourism, currently one of the main concerns for the lake, that may lead to the introduction of exotic

Fig. 8. Synthesis of the temporal evolution of the Ecological Quality Ratios and priority water uses in Lake Annecy from 1968 to 2100 under SSP3-RCP7.0.

species (Lockwood et al., 2005) and an intensification of pollution transfer to the lake, therefore making pollutants management even more important (Murray et al., 2010).

4.3. Capacity to maintain drinking water supply

While the ecological changes associated with climate change pose significant challenges for many lake systems (Rinke et al., 2025), the perspective for drinking water supply in Lake Annecy remains cautiously optimistic. Model projections indicate that the provisioning of drinking water is unlikely to be adversely affected by climate change until at least 2100, when considering phytoplankton dynamics. Notably, the depth of the peak chlorophyll-a concentration is expected to remain stable under SSP1-RCP2.6. Despite a deepening trend of the peak of chlorophyll-a concentrations for the other scenarios, it remains at a safe distance from the intake depth used for drinking water supply. Additionally, the possibility of changing the water intake to a deeper layer envisioned by lake managers offers an extra layer of protection, helping to mitigate any unforeseen changes in phytoplankton dynamics that could arise as a result of climate change.

4.4. Vulnerability of main salmonids to warming

Water temperature influences life at several levels, including metabolism, life cycle, community structure and ecosystem functioning (Daufresne, Lengfellner and Sommer, 2009). It interacts with oxygen, determining together the extent of the suitable zones for fish habitats and reproduction. Our model indicates significant alterations in the temperature and oxygen profiles revealing that global warming could have an effect on salmonids by modifying adult habitat and reproduction conditions. As Lake Annecy is relatively deep and large, it may continue to support key species by offering thermal refuges for adult growth in deeper layers. Low temperature is important also in autumn for other processes, such as vitellogenesis, oocyte development, and for final maturation and ovulation (Pankhurst and King, 2010). For instance, ovulation inhibition occurs at 11 °C and 10 °C for *Salvelinus alpinus* and *Coregonus lavaretus*, respectively (Gillet, 1991). However, the potential threats for populations might be more intense in shallower and smaller peri-alpine lakes because thermal refuges are more limited.

Success of embryonic development of the two main salmonids is especially sensitive, as very high mortality rates are observed in embryos when water temperature is above 8 °C (Stewart et al., 2024; Mari et al., 2021). By the end of the century, a tipping point might occur when the temperature threshold triggering embryonic development is expected to no longer be reached. Indeed, water warming of critical spawning habitats – surface layers for whitefish. (0–2 m) and deep layers for Arctic char (30–40 m) – could surpass the upper thermal limit of 8 °C from mid-century in the two most pessimistic climate scenarios. This result aligns with previous climate projections identifying temperature requirements for reproduction as a critical bottleneck in the life cycle of fish by 2100 (Dahlke et al., 2020).

The biological implications of thermal shifts are particularly concerning for cold-water fish like salmonids, whose thresholds for growth and egg development in terms of temperature, are much lower than other fish species. When combined with physiological requirements with regards to oxygen concentration, it is likely that the water volume suitable for salmonid survival and reproduction in Lake Annecy will significantly decline by 2100. A possible outcome is that fish communities might move towards more warm-adapted species such as perch or pike (Réalis-Doyelle et al., 2022) rather than cold-stenothermic salmonids. It raises the possibility that the impacts could be more complex than what is revealed here, for instance by modifying the structure of metazooplanktonic communities through top-down effects (e.g. Mehner et al., 2008) which may promote cascading effects even though trophic cascades are theoretically weak in oligotrophic lakes. This underscores the urgency for adaptive fishery management strategies for cold water species, as highlighted by Ficke, Myrick and Hansen (2007) and Schindler (2017). Nonetheless, it is likely that species adaptation ability may limit the effects by changing reproduction period and depth, as well as habitat, to stay within physiological limits (Stewart et al., 2024). The extent of such adaptability remains largely uncertain though (Herb et al., 2014; Missaghi et al., 2017; Vigliano et al., 2018).

Narrow temperature ranges for habitat and reproduction in future scenarios underscore the urgency to implement adaptive management to protect fish communities. Future management strategies will likely require new efforts to provide desirable fishing opportunities, enabling them to take better advantage of future conditions. As the effects of climate change interact with other anthropogenic impacts such as land use change and introduction of invasive species, integrated lake-catchment management and cross-disciplinary approach are needed to better understand and manage water uses and lake ecosystem services provided in the Anthropocene.

CRediT authorship contribution statement

L.M.V. Soares: Writing – original draft, Methodology, Formal analysis, Conceptualization. **M. Thouillot:** Writing – original draft. **V. Frossard:** Writing – review & editing, Validation, Conceptualization. **O. Desgué-Itier:** Writing – review & editing, Formal analysis, Conceptualization. **C. Barouillet:** Writing – review & editing, Validation. **Y. Baulaz:** Writing – review & editing, Validation. **J.-C. Clément:** Writing – review & editing, Validation. **I. Domaizon:** Writing – review & editing, Validation. **J.-M. Dorioz:** Writing – review & editing, Validation. **C. Goulon:** Writing – review & editing, Validation. **J. Guillard:** Writing – review & editing, Validation. **S. Jacquet:** Writing – review & editing, Validation. **E. Réalis:** Writing – review & editing, Validation. **V. Tran Khac:** Writing – review & editing, Validation. **J.-P. Jenny:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113220.

Data availability

Metadata and limnological data for the calibration and validation of the model are available in the IS OLA (Observatory on LAkes) data repository https://si-ola.inrae.fr

References

Bennion, H., Battarbee, R., 2007. The European Union Water Framework Directive: opportunities for palaeolimnology. J. Paleolimnol. 38, 285–295.

Berthon, V., et al., 2013. Trophic history of French sub-alpine lakes over the last ~150 years: phosphorus reconstruction and assessment of taphonomic biases. J. Limnol. 72 (3), e34–e. https://doi.org/10.4081/jlimnol.2013.e34.

Bouleau, G., Pont, D., 2015. Did you say reference conditions? Ecological and socio-economic perspectives on the European Water Framework Directive. Environ. Sci. Policy 47, 32–41. https://doi.org/10.1016/j.envsci.2014.10.012.

Bourinet, F., Anneville, O., Drouineau, H., Goulon, C., Guillard, J., Richard, A., 2023. Synchrony in whitefish stock dynamics: disentangling the effects of local drivers and climate. J. Limnol. 82, 2134. https://doi.org/10.4081/jlimnol.2023.2134.

Burger, D.F., Hamilton, D.P., Pilditch, C.A., 2008. Modelling the relative importance of internal and external nutrient loads on water column nutrient concentrations and phytoplankton biomass in a shallow polymictic lake. Ecol. Model. 211 (3–4), 411–423. https://doi.org/10.1016/j.ecolmodel.2007.09.028.

Carlson, R.E., 1977. A trophic state index for lakes. Limnol. Oceanogr. 22 (2), 361–369. https://doi.org/10.4319/lo.1977.22.2.0361.

Caudron, A., et al., 2014. 'Thirty years of reoligotrophication do not contribute to restore self-sustaining fisheries of Arctic charr. Salvelinus Alpinus, in Lake Geneva', Fisheries Research 154, 165–171. https://doi.org/10.1016/j.fishres.2014.01.023.

Cucchi, M., et al., 2020. WFDE5: bias-adjusted ERA5 reanalysis data for impact studies. Earth Syst. Sci. Data 12 (3), 2097–2120. https://doi.org/10.5194/essd-12-2097-2020.

Dahlke, F.T., Wohlrab, S., Butzin, M., Poertner, H.O., 2020. Thermal bottlenecks in the life cycle define climate vulnerability of fish. Science 369, 65–70. https://doi.org/10.1126/science.aaz3658.

Daufresne, M., Lengfellner, K., Sommer, U., 2009. Global warming benefits the small in aquatic ecosystems. Proc. Natl. Acad. Sci. 106 (31), 12788–12793. https://doi.org/10.1073/pnas.0902080106.

Davis, J.C., 1975. Minimal dissolved oxygen requirements of aquatic life with emphasis on canadian species: a review. J. Fish. Res. Board Can. 32, 2295–2332. https://doi.org/10.1139/f75-268.

De Bund, V. and Solimini, A. (2007) Ecological Quality Ratios for Ecological Quality Assessment in Inland and Marine Waters, JRC Publications Repository. https://publications.jrc.ec.europa.eu/repository/handle/JRC36757 (Accessed: 11 October 2024).

Desgué-Itier, O., et al., 2023. Past and future climate change effects on the thermal regime and oxygen solubility of four peri-alpine lakes. Hydrol. Earth Syst. Sci. 27 (3), 837–859. https://doi.org/10.5194/hess-27-837-2023.

'Directive (EU) 2000/60/EC' (2000).

'Directive (EU) 2006/44/EC' (2006).

'Directive (EU) 2020/2184' (2020).

Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., Middelburg, J.J., 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol. Oceanogr. 51 (5), 2388–2397. https://doi.org/10.4319/lo.2006.51.5.2388.

Dresti, C., Fenocchi, A., Copetti, D., 2021. Modelling physical and ecological processes in medium-to-large deep European perialpine lakes: A review. J Limnol 80 (3). https://doi.org/10.4081/jlimnol.2021.2041.

Egan, K.J., Herriges, J.A., Kling, C.L., Downing, J.A., 2009. Valuing water quality as a function of water quality measures. Amer. J. Agr. Econ. 91 (1), 106–123. https://doi.org/10.1111/j.1467-8276.2008.01182.x.

Eyring, V., et al., 2016. Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. Geosci. Model Dev. 9 (5), 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016.

Ficke, A.D., Myrick, C.A., Hansen, L.J., 2007. Potential impacts of global climate change on freshwater fisheries. Rev. Fish Biol. Fish. 17 (4), 581–613. https://doi.org/10.1007/s11160-007-9059-5.

Gillet, C., 1991. Egg production in an Arctic charr (Salvelinus alpinus L.) brood stock: effects of temperature on the timing of spawning and the quality of eggs. Aquat. Living Resour. 4 (2), 109–116. https://doi.org/10.1051/alr:1991010.

Goulon, C., Guillard, J. (2022) 'Monitoring of Lake Annecy fisheries [Suivi halieutique du lac d'Annecy]'. INRAE, SILA, DDT, ALP:36.

Hamed, K.H., 2008. Trend detection in hydrologic data: The Mann-Kendall trend test under the scaling hypothesis. J. Hydrol. 349, 350–363. https://doi.org/10.1016/j.jhydrol.2007.11.009.

N. Hansen 'The CMA Evolution Strategy: A Tutorial'. arXiv 2016.

Hartmann, J., 1984. 11-year cycle of spawning time and growth of the whitefish (Coregonus lavaretus) of Lake Constance. Schweizerische Zeitschrift Für Hydrologie 46 (1), 163–170. https://doi.org/10.1007/BF02538106.

Heino, J., Alahuhta, J., Bini, L.M., Cai, Y., Heiskanen, A.-S., Hellsten, S., Kortelainen, P., Kotamäki, N., Tolonen, K.T., Vihervaara, P., Vilmi, A., Angeler, D.G., 2021. Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. Biol Rev 96, 89–106. https://doi.org/10.1111/brv.12647.

Herb, W.R., et al., 2014. Projecting cold-water fish habitat in lakes of the glacial lakes region under changing land use and climate regimes. Can. J. Fish. Aquat. Sci. 71 (9), 1334–1348. https://doi.org/10.1139/cjfas-2013-0535.

Huang, L., Woolway, R.I., Timmermann, A., Lee, S.S., Rodgers, K.B., Yamaguchi, R., 2024. Emergence of lake conditions that exceed natural temperature variability. Nat. Geosci. 17, 763–769. https://doi.org/10.1038/s41561-024-01491-5.

Hydro Portail, 2022. Données hydrométriques de la banque nationale des données quantitatives relatives aux eaux de surface. Accessed: 26 August 2022. https://hydro.eaufrance.fr.

R. Jalinoux F. Pasquini Sila, Comment et pourquoi le niveau des lacs est-il régulé ?' B. Montuelle A. Clemens Le Tour Des Grands Lacs Alpins Naturels En 80 Questions 2015 Lyon. [Preprint].

Janssen, A.B.G., et al., 2021. Shifting states, shifting services: Linking regime shifts to changes in ecosystem services of shallow lakes. Freshw. Biol. 66 (1), 1–12. https://doi.org/10.1111/fwb.13582.

Jenny, J.-P., Arnaud, F., Alric, B., Dorioz, J.-M., Sabatier, P., Meybeck, M., Perga, M.-E., 2014. Inherited hypoxia: A new challenge for reoligotrophicated lakes under global warming : Holocene hypoxia dynamics in large lakes. Global Biogeochem. Cycl. 28, 1413–1423. https://doi.org/10.1002/2014gb004932.

Jones, H.F.E., et al., 2018. Modelling interactive effects of multiple disturbances on a coastal lake ecosystem: Implications for management. J. Environ. Manage. 207, 444–455. https://doi.org/10.1016/j.jenvman.2017.11.063.

Kraemer, B.M., et al., 2017. Global patterns in lake ecosystem responses to warming based on the temperature dependence of metabolism. Glob. Chang. Biol. 23 (5), 1881–1890. https://doi.org/10.1111/gcb.13459.

Lange, S., 2019. Trend-preserving bias adjustment and statistical downscaling with ISIMIP3BASD (v1.0). Geosci. Model Dev. 12 (7), 3055–3070. https://doi.org/10.5194/gmd-12-3055-2019.

Lemaire, M., Guillard, J., Anneville, O., Lobry, J., 2020. Major biomass fluctuations in lake food webs – An example in the peri-alpine Lake Annecy. J. Great Lakes Res. 46 (4), 798–812. https://doi.org/10.1016/j.jglr.2020.04.007.

Lockwood, J.L., Cassey, P., Blackburn, T., 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20 (5), 223–228. https://doi.org/10.1016/j.tree.2005.02.004.

Mari, L., Daufresne, M., Guillard, J., Evanno, G., Lasne, E., 2021. Elevated temperature and deposited sediment jointly affect early life history traits in southernmost Arctic char populations. Can. J. Fish. Aquat. Sci. 78 (6), 744–751.

Meem 'Guide relatif à l'évaluation de l'état des eaux de surface continentales (cours d'eau, canaux 2016 plans d'eau)'.

Mehner, T., Padisak, J., Kasprzak, P., Koschel, R., Krienitz, L., 2008. A test of food web hypotheses by exploring time series of fish, zooplankton and phytoplankton in an oligo-mesotrophic lake. Limnologica 38, 179–188. https://doi.org/10.1016/j.limno.2008.05.001.

Missaghi, S., Hondzo, M., Herb, W., 2017. Prediction of lake water temperature, dissolved oxygen, and fish habitat under changing climate. Clim. Change 141 (4), 747–757. https://doi.org/10.1007/s10584-017-1916-1.

Murray, K.E., Thomas, S.M., Bodour, A.A., 2010. Prioritizing research for trace pollutants and emerging contaminants in the freshwater environment. Environ. Pollut. 158 (12), 3462–3471. https://doi.org/10.1016/j.envpol.2010.08.009.

Naiades, Données sur la qualité des eaux de surface https://naiades.eaufrance.fr 2022 Accessed: 26 August 2022.

J. Nomade Chronologie et sédimentologie du remplissage du lac d'Annecy depuis le Tardiglaciaire: Implications paléoclimatologiques et paléohydrologiques 2005.

O'Reilly, C.M., et al., 2015. Rapid and highly variable warming of lake surface waters around the globe. Geophys. Res. Lett. 42 (24), 10773–10781. https://doi.org/10.1002/2015GL066235.

Ottosson, F., Abrahamsson, O., 1998. Presentation and analysis of a model simulating epilimnetic and hypolimnetic temperatures in lakes. Ecol. Model. 110 (3), 233–253. https://doi.org/10.1016/S0304-3800(98)00067-2.

Özkundakci, D., Hamilton, D., Trolle, D., 2011. Modelling the response of a highly eutrophic lake to reductions in external and internal nutrient loading. N. z. J. Mar. Freshw. Res. 45 (2), 165–185. https://doi.org/10.1080/00288330.2010.548072.

Pankhurst, N.W., King, H.R., 2010. Temperature and salmonid reproduction: implications for aquaculture. J. Fish Biol. 76 (1), 69–85.

Perga, M.-E., Desmet, M., Enters, D., Reyss, J.L., 2010. A century of bottom-up- and top-down-driven changes on a lake planktonic food web: A paleoecological and paleoisotopic study of Lake Annecy, France. Limnol. Oceanogr. 55, 803. https://doi.org/10.4319/lo.2010.55.2.0803.

Piccolroaz, S., et al., 2024. Lake Water Temperature Modeling in an Era of Climate Change: Data Sources, Models, and Future Prospects. Rev. Geophys. 62 (1), e2023RG000816. https://doi.org/10.1029/2023RG000816.

Réalis-Doyelle, E., Pasquet, A., Fontaine, P., Teletchea, F., 2022. Effects of temperature on the survival and development of the early life stages of northern pike (Esox lucius). Knowl Manag Aquat Ecosyst 423, 10.

Riahi, K., et al., 2017. The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. Glob. Environ. Chang. 42, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009.

Rimet, F., et al., 2020. The Observatory on LAkes (OLA) database: Sixty years of environmental data accessible to the public: The Observatory on LAkes (OLA) database. J. Limnol. 79 (2). https://doi.org/10.4081/jlimnol.2020.1944.

Rinke, K., Mi, C., Magee, M.R., Carey, C.C., 2025. Increasing exposure to global climate change and hopes for the era of climate adaptation: An aquatic perspective. Ambio. https://doi.org/10.1007/s13280-024-02125-1.

Schäfer, A.I., Fane, A.G., Waite, T.D., 2001. Cost factors and chemical pretreatment effects in the membrane filtration of waters containing natural organic matter. Water Res. 35 (6), 1509–1517. https://doi.org/10.1016/S0043-1354(00)00418-8.

Schindler, D.E., 2017. Warmer climate squeezes aquatic predators out of their preferred habitat. Proc. Natl. Acad. Sci. 114 (37), 9764–9765. https://doi.org/10.1073/pnas.1712818114.

SILA (2013) 'Activité touristique sur le territoire statutaire de l'office de tourisme du lac d'Annecy : Quelques données chiffrées (Année 2013)'.

SILA (2023) 'Rapport Annuel 2023 [Annual Report 2023]'. https://www.sila.fr/wp-content/uploads/2024/09/Bilan_2023.pdf.

Smol, J.P., 2019. Under the radar: long-term perspectives on ecological changes in lakes. Proc. r. Soc. B Biol. Sci. 286 (1906), 20190834. https://doi.org/10.1098/rspb.2019.0834.

Soares, L.M.V. et al. (2024) 'Unraveling Lake Geneva's hypoxia crisis in the Anthropocene', Limnology and Oceanography Letters, p. lol2.10435. 10.1002/lol2.10435.

Sterner, R.W., Keeler, B., Polasky, S., Poudel, R., Rhude, K., Rogers, M., 2020. Ecosystem services of Earth's largest freshwater lakes. Ecosyst. Serv. 41, 101046. https://doi.org/10.1016/j.ecoser.2019.101046.

Stewart, T.R., Karjalainen, J., Zucchetta, M., Goulon, C., Anneville, O., Vinson, M.R., Stockwell, J.D., 2024. Winter is not coming: evaluating impacts of changing winter conditions on coregonine reproductive phenology. International Journal of Limnology 60, 17.

Sunday, J., 2020. When do fish succumb to heat? Science 369 (6499), 35–36. https://doi.org/10.1126/science.abd1272.

Toffolon, M., Piccolroaz, S., 2015. A hybrid model for river water temperature as a function of air temperature and discharge. Environ. Res. Lett. 10 (11), 114011. https://doi.org/10.1088/1748-9326/10/11/114011.

Van Vuuren, D.P., et al., 2011. The representative concentration pathways: an overview. Clim. Change 109 (1–2), 5–31. https://doi.org/10.1007/s10584-011-0148-z.

Vigliano, P.H., et al., 2018. Fish thermal habitat current use and simulation of thermal habitat availability in lakes of the Argentine Patagonian Andes under climate change scenarios RCP 4.5 and RCP 8.5. Sci. Total Environ. 636, 688–698. https://doi.org/10.1016/j.scitotenv.2018.04.237.

R.G. Wetzel 'Limnology - Lake and River Ecosystems - 3 3rd edition'. 2001.

Winslow, L.A., et al., 2015. Small lakes show muted climate change signal in deepwater temperatures. Geophys. Res. Lett. 42 (2), 355–361. https://doi.org/10.1002/2014GL062325.

Woolway, R.I., et al., 2021. Phenological shifts in lake stratification under climate change. Nat. Commun. 12 (1), 2318. https://doi.org/10.1038/s41467-021-22657-4.

Woolway, R.I., Sharma, S., Smol, J.P., 2022. Lakes in Hot Water: The Impacts of a Changing Climate on Aquatic Ecosystems. Bioscience 72 (11), 1050–1061. https://doi.org/10.1093/biosci/biac052.