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Ecological feedbacks modulate lake surface oxygen responses to heatwaves

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Abstract Climate warming intensifies lake heatwaves (LHWs) and deoxygenation, yet short-term surface dissolved oxygen (DO) responses to LHWs remain unclear. This study integrates 25-year *in-situ* observations (2000–2024) and 73-year lake surface water temperature (WT) dataset (1950–2022) from Lake Taihu, a eutrophic shallow lake, with explainable machine learning models to decode seasonally divergent surface DO responses to LHWs. We reveal that surface DO during LHWs was generally lower than normal in winter, but higher in summer. Explainable machine learning revealed that DO is mainly influenced by WT in winter, higher temperatures reduced oxygen solubility, and ultimately led to lower DO during heatwaves. However, reduced ammonia nitrogen and turbidity during summer heatwaves inhibited oxygen consumption by nitrification and increased oxygen production from photosynthesis, ultimately resulting in DO increasing. These results highlight the complex impact of LHWs on DO, underscoring the need for tailored management strategies in a warming climate.

Keywords Lake heatwaves, Dissolved oxygen, Machine learning, Eutrophic Lake Taihu

1. Introduction

Lakes cover only approximately 3% of the Earth's total land surface area (Downing et al., 2006), but store 87% of the planet's liquid surface freshwater (Messager et al., 2016). Lakes are essential to human life, serving as a critical source of safe drinking water and supporting some of the most biodiverse ecosystems (Schallenberg et al., 2013; Ho and Goethals, 2019), while they are sensitive to climate change (Woolway et al., 2021a). Some recent studies indicate that the frequency, duration, and intensity of heatwaves have accelerated on global land, ocean, and lakes under global warming (Hobday et al., 2016; Zheng and Wang, 2019; Woolway et al., 2020, 2021b; Wang et al., 2022; Wang C et al., 2023; Wang X, et al., 2023).

Lake heatwaves (LHWs) can be defined, similar to marine heatwaves (Perkins and Alexander, 2013; Hobday et al., 2016), as a period when five consecutive days exceed the 90th percentile of lake surface water temperature (WT) for each calendar day (see the "LHW definitions" section in Sect. 2). There is increasing evidence that the record-breaking terrestrial heatwave can lead to increased exposure to climate-related hazards and increased health risks (Cai et al., 2022; Zhang et al., 2023; Liang et al., 2024). Marine heatwaves and deoxygenation are also well-documented as a significant threat to marine ecosystems, with substantial evidence showing their adverse impacts on aquatic life and water quality (Li et al., 2020, 2024; Yao and Wang, 2022). Similarly, LHWs characterized by periods of abnormally high WT have emerged as a growing concern for lakes and their ecosystems globally (Woolway et al., 2021b; Wang X, et al., 2023). The intensity and duration of these LHWs are expected to increase, with some lakes potentially entering a state of permanent LHWs in the future (Woolway et al., 2020). As an important and fragile component of the Earth's ecosystem, lake ecosystems are highly sensitive to temperature changes (Woolway et al., 2021b) and are consequently profoundly impacted by LHWs. These events lead to a significant increase in WT, which can rapidly alter the lakes' physical and chemical properties (Anderson et al., 2021). Meanwhile, elevated WT may even exceed the critical temperature, allowing the normal physiological functions for species (Dokulil et al., 2021), affecting the organisms that rely on these environments, potentially leading to irreversible damage to the entire lake ecosystem (Wang et al., 2024).

Oxygen is a necessity for the survival of almost all living organisms on Earth (Huang et al., 2018; Liu et al., 2020a; Ding et al., 2022). Dissolved oxygen (DO) is defined as the amount of free, non-compound oxygen dissolved in water (Chi et al., 2020). As a critical indicator for assessing lake water quality, DO is of vital importance for maintaining the health of lake ecosystems (Qin et al., 2013). A reduction in DO can result in the loss of essential habitats for aquatic life (Schindler, 2017), potentially leading to a decline in certain fish species (Plisnier et al., 2023). The occurrence of LHWs is bound to have a significant impact on DO (Zhang et al., 2025). Long-term monitoring data reveal a persistent decline in DO across both surface and deep water of

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temperate lakes worldwide, with thermal-driven reduction in oxygen solubility emerging as the principal factor associated with climate change (Jane et al., 2021). However, comparative studies across different climatic regions remain limited, particularly for subtropical lakes where warming rates and ecological responses may differ from those in temperate systems (Zhang et al., 2015; Jane et al., 2021). Nevertheless, there are still many gaps in our understanding of how DO responds to LHWs events characterized by short durations but extremely high temperatures under current climate change, as the process is highly complex (Woolway et al., 2021b; Zhang et al., 2025). DO are influenced by the physical, chemical, and biological dynamics within lakes (Guo et al., 2021). In lake ecosystems, DO concentration is mainly determined by oxygen replenishment (production) and depletion processes (Jane et al., 2021). The replenishment processes include atmospheric diffusion, photosynthesis of aquatic organisms, and runoff (Ali et al., 2022), while the depletion processes include respiration of aquatic organisms and nitrification by microorganisms (Breitburg et al., 2018; Zhi et al., 2023). Increased temperatures can accelerate the rate of oxygen consumption by respiration (Yvon-Durocher et al., 2010; Breitburg et al., 2018) and reduce the solubility of oxygen in the water, diminishing the lake's oxygen storage capacity (Akiya and Savage, 2002; Breitburg et al., 2018). However, there is evidence that phytoplankton blooms are increasing globally, as elevated temperatures promote the growth of cyanobacteria and other algae, which enhances oxygen production through photosynthesis (Paerl and Huisman, 2008; Ho et al., 2019). High temperatures and eutrophication during the LHWs can promote cyanobacterial blooms, leading to DO supersaturation, especially in some eutrophic lakes (Kosten et al., 2012; Blaszczak et al., 2023). This dual role of warming, both depleting and potentially elevating DO under specific conditions (Jane et al., 2021; Zhang et al., 2025), highlights the need for region-specific studies, particularly in subtropical eutrophic lakes like Taihu, where biological feedbacks may have great influences on oxygen dynamics. The complex interplay of these factors makes the impact of lake LHWs on DO in water still unclear (Zhang et al., 2025). Therefore, a systematic and comprehensive analysis of the key processes and mechanisms affecting DO during LHWs is urgently needed.

To address this gap, we utilized both *in-situ* water quality observations and WT simulation datasets from Lake Taihu to analyze the spatiotemporal variation patterns of DO and LHWs. Lake Taihu is a typical eutrophic lake situated in a subtropical climate zone characterized by hot summers and cold winters (Zhang et al., 2020). Since the 1990s, rapid population and economic growth have led to severe eutrophication (Qi et al., 2020). In recent decades, frequent algal bloom events and other ecological problems, combined with the impacts of climate change, have made Lake Taihu a representative research site for global ecologists, limnologists, and environmental scientists (Qin et al., 2019; Xiao et al., 2022). Its conditions mirror those of other shallow subtropical eutrophic lakes worldwide, such as Lake Okeechobee (Kiwanuka et al., 2025) and Lake Victoria (Jin et al., 2025), which also experience pronounced warming and algal blooms, yet Taihu offers a unique opportunity to explore LHW impacts in a highly nutrient-rich system. Recent studies have shown that climate warming not only increases the frequency and intensity of LHWs but also promotes significant algal growth in Lake Taihu (Zhang et al., 2018; Wang et al., 2023), thereby creating a natural laboratory to investigate ecological feedbacks that regulate lake oxygen responses to LHWs. Specifically, we developed and validated Machine Learning Regression Models of DO in eutrophic Lake Taihu, using variables including WT, ammonia nitrogen (AN), turbidity (TBD), algal density (AD), total phosphorus (TP), total nitrogen (TN), and chlorophyll a (CHLA). This investigation provides critical insights into the impacts and mechanisms of LHWs on DO, contributing to a better understanding of the effects of LHWs on lake ecosystems and supporting the sustainable development of the lake communities.

2. Materials and methods

2.1 Study area

Lake Taihu, the third-largest freshwater lake in China (area: 2,338 km^2, average depth: 1.9 m, maximum depth: 2.6 m), is a typical shallow eutrophic lake located in the highly urbanized and densely populated Yangtze River Delta (Liang et al., 2022). Lake Taihu not only provides drinking water for over 20 million people but also plays a crucial role in tourism, fisheries, and shipping. Situated in a subtropical monsoon climate zone, Lake Taihu had an annual mean temperature of 16.2 °C from 2010 to 2018, with an annual total precipitation of 1122 mm and an annual average wind speed of 2.6 m/s (Zhang et al., 2020).

2.2 Data

The China Regional Lake Surface Water Temperature Dataset (Wang X, et al., 2023), provided by National Tibetan Plateau/Third Pole Environment Data Center (http://data.tpdc.ac.cn/), contains hourly data spanning January 1, 1950 to December 31, 2022. This data is verified with satellite products of lake surface WT and *in-situ* observation data of 10 lakes in China, and these lakes include Lake Taihu, Thousand Island Lake, Poyang Lake, Hulun Lake, Nam Co, Lugu Lake, Erhai Lake, Fuxian Lake, Chenghai Lake, and Dianchi Lake. The average correlation coefficient is 0.97, and the root mean square error is 1.39 °C, confirming the credibility of the dataset. In Lake Taihu, the correlation coefficient between this dataset and *in-situ* observation data is 0.98, and the average root mean square error is 1.63 °C (Appendix Fig. S1).

The *in-situ* water quality data of Lake Taihu (Fig. S2), sourced from the National Ecosystem Science Data Center, includes parameters such as WT, DO, collected monthly. The data spans from January 2000 to December 2019 (http://rs.cern.ac.cn/data/meta?id=39210).

Real-time surface water quality data (Fig. S2) released by the China National Environmental Monitoring Centre includes variables (WT, DO, TBD, AN, TP, TN, CHLA, and AD) used in constructing our machine learning regression model. The water quality data were released every 4 h, covering the time period from April 1, 2014, to March 15, 2019, and from April 30, 2020, to the present (https://szzdjc.cnemc.cn:8070/GJZ/Business/Publish/Main.html).

2.3 How these data (datasets) are used

The data used in calculating the trends of WT (Fig. 1A) and LHWs (Fig. 1C–F) were obtained from the China Regional Lake

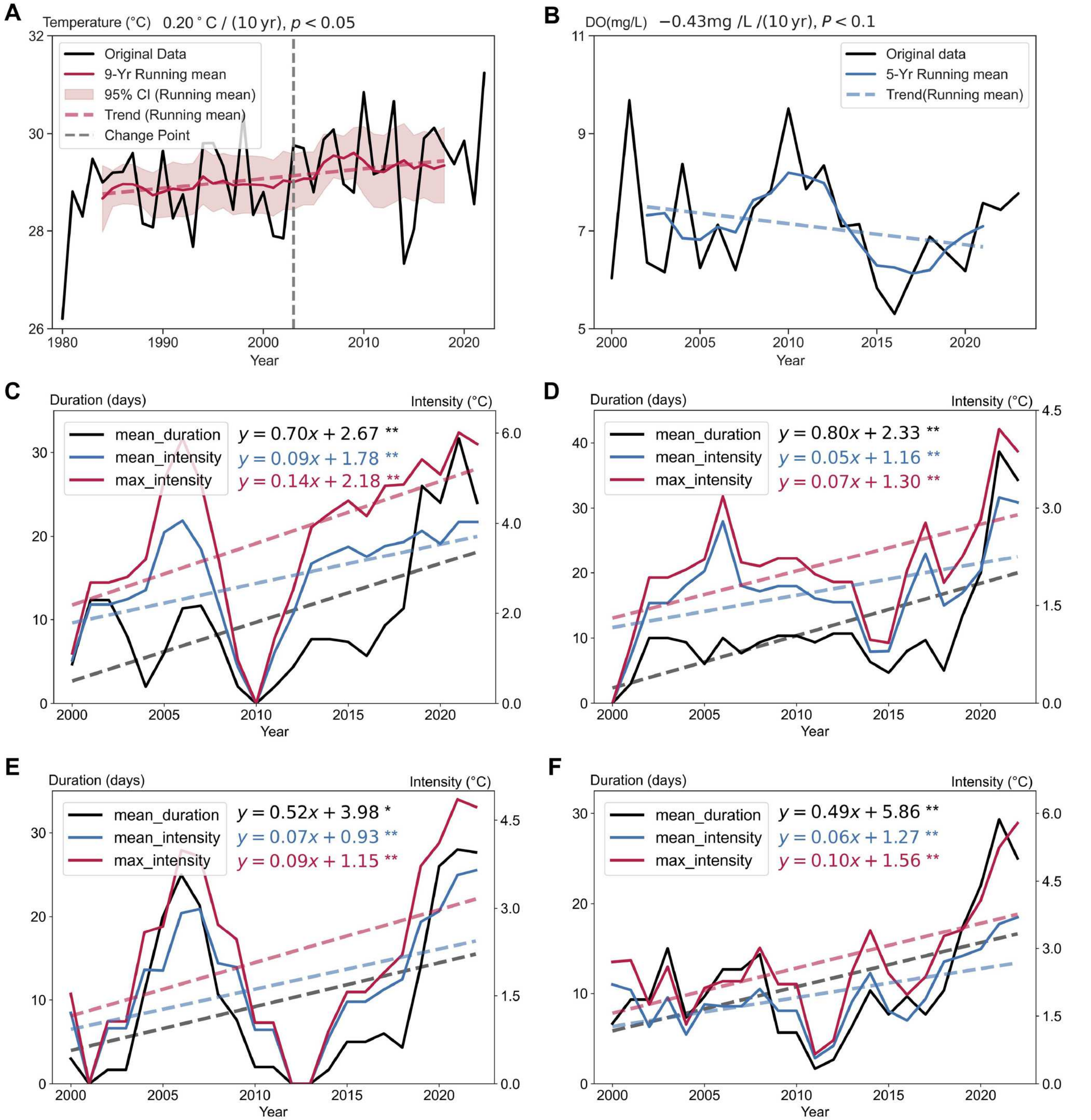

Fig. 1 (A) Trend of WT in August in Lake Taihu from 1980 to 2022. The black solid line represents the original data, while the red solid line shows the 9-year running mean. The red dashed line indicates the trend after applying the running mean, and the shaded area denotes the 95% confidence interval. The grey dashed line marks the year of the abrupt change (2003). (B) Trend of DO in August in Lake Taihu from 2000 to 2023. The black solid line represents the original data, while the blue solid line shows the 5-year running mean. The blue dashed line indicates the trend after applying the running mean. (C–F) Characteristics of annual LHWs in Lake Taihu from 2000 to 2022. The figure displays the duration (black), mean intensity (blue), and maximum intensity (red) of LHWs, with solid lines representing three-point smoothing values and dashed lines indicating linear trend fitting (C: spring, D: summer, E: autumn, F: winter). The "*" on the fitted line expression represents that $P \leqslant 0.1$, and the "**" represents that $P \leqslant 0.05$.

Surface Water Temperature Dataset. And when calculating the trend of DO (Fig. 1B) from 2000 to 2023, considering the different time spans of different data, we used data for splicing, specifically: (1) From 2000 to 2019: *In-situ* monthly water quality data (from the National Ecosystem Science Data Center). (2) From 2020 to 2023: Real-time surface water quality data (from the China National Environmental Monitoring Centre).

In-situ monthly water quality data (from the National Ecosystem Science Data Center) were primarily used to analyze the spatial variation of DO during LHW events (Fig. 2A and B). Specifically, months with at least one LHW event were categorized as "LHW conditions". Months without any LHW event were categorized as "normal conditions". The spatial differences in DO under LHWs were calculated by subtracting DO values under normal conditions from those during LHW conditions, followed by interpolation to generate the spatial

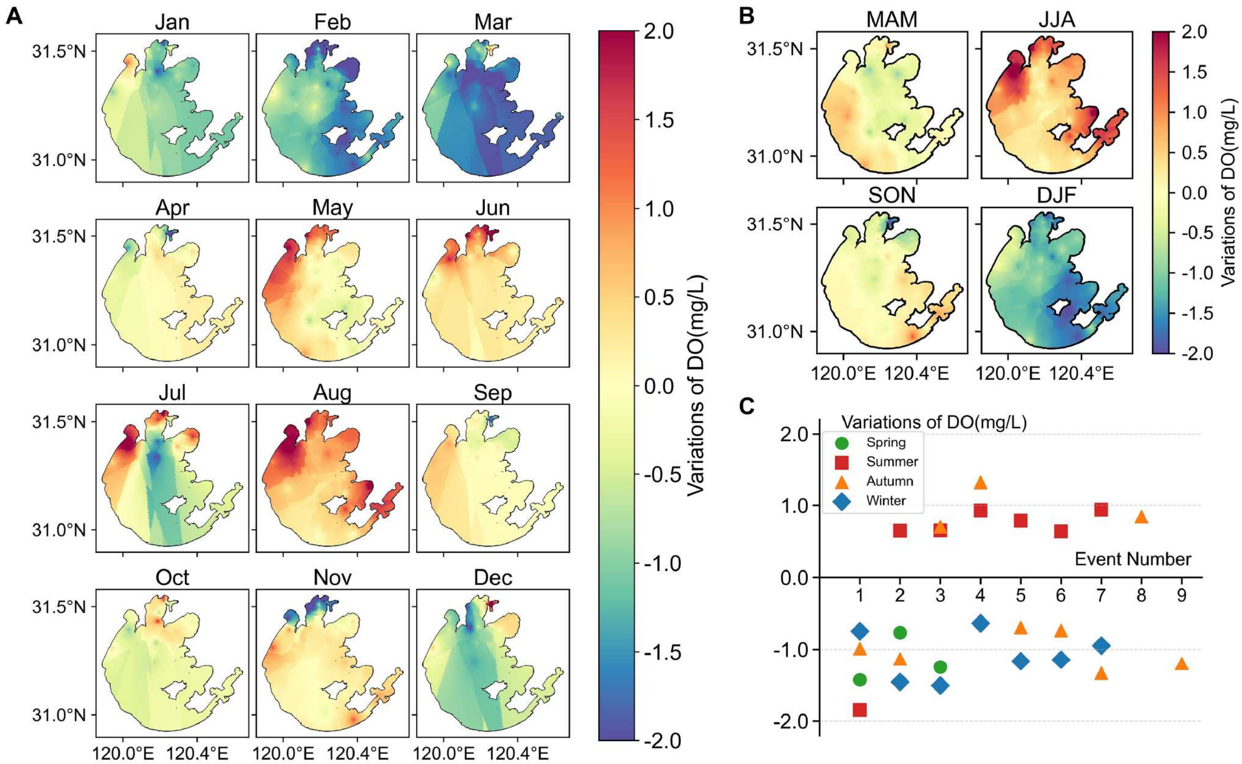

Fig. 2 (A) Spatial distribution of the DO differences (DO under LHWs conditions minus DO under normal conditions, and normal conditions mean periods when LHWs do not occur) during LHWs in Lake Taihu. The twelve subplots from left to right, top to bottom, correspond to January to December. (B) Spatial distribution of the DO differences (same as (A)) during LHWs in Lake Taihu. The four subplots are arranged from left to right, top to bottom, corresponding to spring, summer, autumn, and winter, respectively. (C) Seasonal differences (same as (A) and (B)) in DO during LHWs in Lake Taihu (green: spring, red: summer, orange: autumn, blue: winter).

patterns.

High-frequency real-time surface water quality data (from the China National Environmental Monitoring Centre) were used to validate the robustness of the observed DO trends (Fig. 2C). While this dataset covers fewer monitoring stations, its temporal resolution (4-hourly) complements the monthly data by reducing potential randomness associated with infrequent sampling.

2.4 LHW definitions

The identification of LHW events follows the marine heatwave framework proposed by Hobday et al. (2016). Specifically, a LHW event is defined as: a lake surface WT exceeding the 90th percentile of seasonal variation in climatological reference data for at least five consecutive days. The percentile approach is adopted because natural temperature variability exhibits significant differences across regions and temporal scales; using relative (percentile) thresholds ensures a consistent definition of extreme events under varying climatic conditions. Furthermore, the five-day minimum duration criterion aligns with sensitivity analysis results from Hobday et al. (2016): shorter thresholds capture numerous transient warming events with weaker ecological significance (especially in warmer regions), while longer thresholds result in insufficient event counts. Thus, a period of five days represents a balance point that captures persistent warming events while ensuring ecological relevance.

When identifying LHWs, the climatological mean (T_m) was calculated over a reference period, to which all values were relative.

$$T_m(j) = \left\{T(y) \mid y_s < y < y_e\right\} \tag{1}$$

where j is the day of the year, and T is the daily temperature. y_s and y_e are the start and end of the climatological base period. For this study, we used the period from 1980 to 2009 as the baseline climatology while calculating LHWs, which means y_s=1980 and y_e=2009.

In calculating the threshold for the LHWs, P_{90} is the 90th percentile, and $T_{90}(j)=P_{90}(X)$, with X denoting the climatological mean state, i.e., $X = \left\{T(y, d) \mid y_s \le y \le y_e, d = j\right\}$.

The start date of the LHWs was calculated as t_s: $T(t_s)>T_{90}(j)$ and $T(t_{s-1})<T_{90}(j)$, and the end date of the LHWs was calculated as t_e: $T(t_e)>T_{90}(j)$ and $T(t_{e+1})<T_{90}(j)$. Furthermore, t_s and t_e also need to meet the conditions $t_e-t_s\geqslant 5$.

The duration (D) is defined as the duration between the start and end dates of an event.

$$D = t_e - t_s \tag{2}$$

Intensity (I_{max}, I_{mean}): I_{max} and I_{mean} represent the highest temperature anomaly value and mean temperature anomaly during the LHW, respectively.

$$I_{max} = \max(T(t) - T_m(j)) \tag{3}$$

$$I_{mean} = \mathrm{mean}(T(t) - T_m(j)) \tag{4}$$

2.5 Construction of DO models

We used Random Forest (RF), eXtreme Gradient Boosting

(XGboost), Gradient Boosting Decision Tree (GBDT), and Extremely Randomized Trees (ET) algorithms to construct DO models in Lake Taihu and analyze the impact of LHWs on DO. The driving factors included WT, AN, TBD, AD, TP, TN, and CHLA. The evaluation metrics we used for DO models are shown in Text S1. Hyperparameters were optimized using GridSearchCV with 5-fold cross-validation on the training set; the candidate parameter ranges and the final selected values for each model are listed in Table S1. After tuning, each model was refitted on the full training set and subsequently evaluated on the independent test set. The detailed model performance evaluations are provided in Table S2. In the fields of machine learning, model interpretability is a crucial topic. Although complex models such as deep neural networks and ensemble models (e.g., RF, XGBoost) excel in predictive performance, they are often regarded as "black boxes", making it difficult to understand their internal decision-making processes. SHapley Additive exPlanations (SHAP) addresses this issue. It is based on the Shapley value, a game theory concept used to fairly distribute costs among participants in a coalition game (Shapley, 1953). By applying this principle, SHAP quantifies the contribution of each feature to the model's prediction, thus explaining the model's output. This makes the decision-making processes of deep neural networks and ensemble models more transparent and understandable. Using the SHAP approach, we can evaluate the influence of each variable on DO.

3. Results

3.1 Temporal and spatial characteristics of DO and LHWs in Lake Taihu

As illustrated in Fig. S3A, DO is lowest during summer, predominantly falling within the interquartile range of 6.4 to 8.4 mg/L (25th to 75th percentile), with a recorded minimum of approximately 3.4 mg/L and a peak of around 11.3 mg/L. In contrast, winter exhibits the highest DO levels, primarily concentrated within the range of 10.2 mg/L to 11.8 mg/L, with a recorded minimum of approximately 7.8 mg/L and a maximum of roughly 13.7 mg/L. This seasonal variation is predominantly driven by reduced oxygen solubility resulted by elevated temperatures during summer, in contrast to cooler temperatures and enhanced oxygen solubility in winter. The seasonal analysis also reveals that DO in Lake Taihu fluctuates more dramatically in summer, while the changes are relatively stable in winter. This suggests that factors beyond WT may significantly influence DO in the summer, leading to considerable fluctuations. In contrast, WT emerges as the predominant factor governing DO during the winter. The lower WT in winter could maintain higher concentrations of DO. From the perspective of the spatial distribution, DO in the northern part of Lake Taihu is higher in summer and lower in the western part of the lake (Fig. S3B).

We refer to the approach used by Jane et al. (2021). In their study of deoxygenation trends in global temperate lakes, they used late summer WT and DO data for Northern Hemisphere lakes. In this study, we used August data to calculate the long-term trends of WT and DO for Lake Taihu, which showed that from 1980 to 2022, WT increased significantly at a rate of 0.20 °C per decade (Fig. 1A) and DO decreased significantly at a rate of 0.43 mg/L per decade (Fig. 1B) from 2000 to 2023 in Lake Taihu. This rate is notably higher than that reported for many temperate lakes, where recent studies documented reductions of 0.45 mg/L in surface waters and 0.42 mg/L in deep waters from 1980 to 2017 (37 yr), equivalent to approximately 0.12 and 0.11 mg/L per decade, respectively (Jane et al., 2021). As for the LHWs, our results indicate that the LHWs in Lake Taihu have undergone varying degrees of significant upward phase in all seasons from 2000 to 2022, with LHW enhancement including duration, average intensity, and maximum intensity. In spring (Fig. 1C), the mean duration, mean intensity, and maximum intensity of LHWs increased significantly, with the mean duration of LHWs increasing by 0.70 d/y (P<0.05), the mean intensity increasing by 0.09 °C/y (P<0.05), and the maximum intensity increasing by 0.14 °C/yr (P<0.05). In the summer (Fig. 1D), the mean duration, mean intensity, and maximum intensity of LHWs increased significantly (P<0.05), with growth rates of 0.80, 0.05, and 0.07 °C/yr respectively. In autumn (Fig. 1E), the mean duration of LHWs increased significantly with a growth rate of 0.52 d/y (P<0.1), while the mean intensity and maximum intensity increased significantly (P<0.05) with growth rates of 0.07 and 0.09 °C/yr respectively. In winter (Fig. 1F), the mean duration, mean intensity, and maximum intensity of LHWs increased significantly (P<0.05), with the mean duration of winter LHWs increasing by 0.49 d/yr, the average intensity of LHWs increasing by 0.06 °C/yr, and the maximum intensity increasing by 0.10 °C/yr.

3.2 Changes of DO during the LHWs in Lake Taihu

We used monthly water quality data of Lake Taihu, sourced from the National Ecosystem Science Data Center, to explore the spatial variation of DO during the LHWs. This was done by categorizing LHWs conditions if LHWs occurred in that month, and conversely as normal conditions if not a single heatwave occurred in that month, after which the spatial change in DO under LHWs conditions was obtained by subtracting DO from the normal conditions by the LHWs condition and interpolating. We used this monthly data because it is more densely populated with stations, and it can help avoid randomness. To argue for the above results, we then used the data with a frequency of 4-hourly observations, but fewer stations-National Real-time Water Quality data sourced from the China National Environmental Monitoring Centre. The observed results (Fig. 2A and B) align with the spatial distribution patterns of DO variations in Lake Taihu during LHW events. During spring (March, April, and May), there is a decrease in DO in the northeast region of the lake during LHWs, while the west region experiences an increase (see Fig. 2A, May). In the summer, especially in August, DO across Lake Taihu rises significantly during LHWs, with pronounced increases observed in the northwest and southeast regions, where differences range between 1.2 mg/L to 2.0 mg/L. Although the phenomenon of DO rise during LHWs looked surprising, some previous studies have demonstrated that this phenomenon is not rare in eutrophic lakes or lakes located in warmer zones (Jane et al., 2021; Zhang et al., 2025), and eutrophic Lake Taihu happens to be in the warmer subtropics. In autumn, the impact of LHWs on DO is less pronounced. There is a slight decrease in the northern parts of Lake Taihu and a modest increase in the southern parts, with differences being less than 0.4 mg/L. In winter, DO decreases during LHWs, with the degree of reduction intensifying from the northwest to the southeast. The most severe declines occur in the southeastern region, where the difference ranges between 1.6 mg/L to 2.0 mg/L.

We analyzed monitoring data from the Lake Taihu station, located within the state-controlled surface water section, to compare DO during LHWs and normal conditions. Figure 2C indicated that DO in Lake Taihu was generally higher during LHWs compared to normal conditions in summer, with an average increase of 0.57 mg/L. It is noteworthy that only one instance presented a decrease in DO during the LHW, which recorded a decline of 1.42 mg/L.Our observation results (see Fig. S4) at Lake Taihu in August 2024 also validate the summer results above, which show an increasing trend in DO with increasing WT. In contrast, DO in Lake Taihu exhibited a reduction in comparison to periods without LHWs during spring and winter, with an average decrease of 0.82 mg/L and 0.74 mg/L, respectively. During autumn, the impact of LHWs on DO was mixed: there were three instances where DO increased, with an average rise of 0.81 mg/L, and six instances where it decreased, with an average reduction of 0.67 mg/L.

3.3 Model performance evaluations

The study employed several machine learning models, which were meticulously tuned and evaluated using 5-fold cross-validation. To ensure robust performance assessment, Grid-SearchCV was applied. The total sample size consisted of 36832 samples collected throughout the year, with 7928 samples from the summer season and 10677 samples from the winter season, and the training set accounts for 80%, and the validation set accounts for 20%. The correlation matrices between predictor variables, DO, and predictors are shown in Fig. S5

The accuracy metrics for the various backbone models are summarized in Table S2. Among the models, the RF consistently outperformed others across all evaluation metrics in both the year-round and winter datasets. Conversely, the ET model demonstrated superior performance in the summer dataset. The overall performance of the models ranked in descending order is as follows: RF, ET, XGBoost, and GBDT. When comparing the seasonal models, the winter model exhibited the best performance, followed by the year-round model, with the summer model showing the least accuracy.

Comparisons of the DO derived from *in-situ* measurements and that retrieved by the RF models (RF_{year}, RF_{summer} and RF_{winter}), ET models (ET_{year}, ET_{summer} and ET_{winter}), GBDT models ($GBDT_{year}$, $GBDT_{summer}$ and $GBDT_{winter}$), and XGBoost models ($XGBoost_{year}$, $XGBoost_{summer}$ and $XGBoost_{winter}$) are shown in Fig. S6. The models consistently overestimated DO at lower concentrations and underestimated it at higher concentrations, while performing most accurately in the mid-range. Notably, prediction accuracy varied across different seasons. For the year-around model, the best results were observed when DO was between 8 and 12 mg/L. The R values range from 0.85 to 0.89 in the year-around models, though the mean squared error (MSE) remained between 0.82 and 1.12 mg/L. In the winter model, predictions were most accurate at DO between 11 and 13 mg/L, where the R values ranged from 0.83 to 0.91, and the model achieved a particularly low MSE of just 0.18 mg/L to 0.32 mg/L. On the other hand, the summer model exhibited the greatest deviations. However, even here, the model performed reasonably well when DO were in the 7 mg/L to 9 mg/L range, producing R values between 0.66 and 0.71, though with a higher MSE, ranging from 1.46 mg/L to 1.64 mg/L.

3.4 Explainable machine learning reveals DO's impact factor

It is well-established that an increase in WT generally leads to a decrease in DO saturation in lakes (Zhang et al., 2025), which should theoretically result in a decline in the actual DO. This relationship is clearly evident during winter LHWs, where reductions in DO align with rising temperatures. However, an intriguing phenomenon occurs during summer LHWs, where DO in the lake can surpass levels observed under normal conditions. This suggests that there is also a mechanism that offsets or even exceeds the negative effects of reduced DO solubility due to elevated WT during LHWs in summer. These observations highlight the necessity to investigate the synergistic effects of WT and additional factors (e.g., AN, TBD, and TN) on DO dynamics. Understanding these interactions is critical, as they may play a significant role in enhancing or dampening the impact of rising temperatures on DO in lake ecosystems.

In this study, we utilized SHAP to interpret 12 machine learning models across three temporal periods (year-round, summer, and winter), encompassing four types of models: RF, XGBoost, ET, and GBDT, and the model performance evaluations are shown in Fig. S6 and Table S2. SHAP is employed to generate feature contribution values for individual predictions, thereby revealing the influence of each predictor variable and offering insights into model behavior across different seasons.

In the year-round model, the global importance of the predictor variables is depicted in Fig. 3A. WT emerges as the most influential predictor, with an absolute global SHAP value of 1.27, followed by AN, TBD, AD, TN, TP, and CHLA. As illustrated by the color gradients in Fig. 3B, the local SHAP values for individual samples further demonstrate that WT exerts a negative influence on DO, while AD and TN contribute positively. This analysis provides a foundation for understanding the seasonal dynamics of DO, wherein WT plays the most significant role. Specifically, WT's negative effect results in higher DO during winter, when WT is the lowest, and lower DO during summer, when WT is the highest. This seasonal fluctuation in WT thus drives an annual cycle in DO patterns. As shown in Fig. 3C and D, the relationship between WT and DO prediction overall follows a parabolic pattern, with a notable inflection point at approximate 30 °C. Below this threshold, the increase in WT decreases DO. However, the slope of this relationship decreases as the temperature approaches 30 °C, suggesting that the sensitivity of DO to rising temperatures diminishes near this point. Beyond 30 °C, the sensitivity increases, and when WT exceeds 35 °C, further increases in temperature result in an increase in DO. In contrast, AN exerts a markedly smaller impact on DO prediction compared to WT. From a local interpretability perspective, the overall trend indicates a negative correlation between AN and DO, although some segmentation patterns are evident in Fig. 3D. Specifically, low concentrations of AN exhibit a positive effect on DO.

In the summer model, the global importance of predictor variables is illustrated in Fig. S7A. AN stands out as the most influential predictor, with an absolute global SHAP value of 0.46, followed by AD, TBD, TP, WT, CHLA, and TN. Furthermore, local SHAP values for individual samples reveal that AN and TBD exert a major negative impact on DO, while AD positively influences DO, as indicated by the color gradient in Fig. S7B. This analysis sheds light on the underlying dynamics of DO in summer,

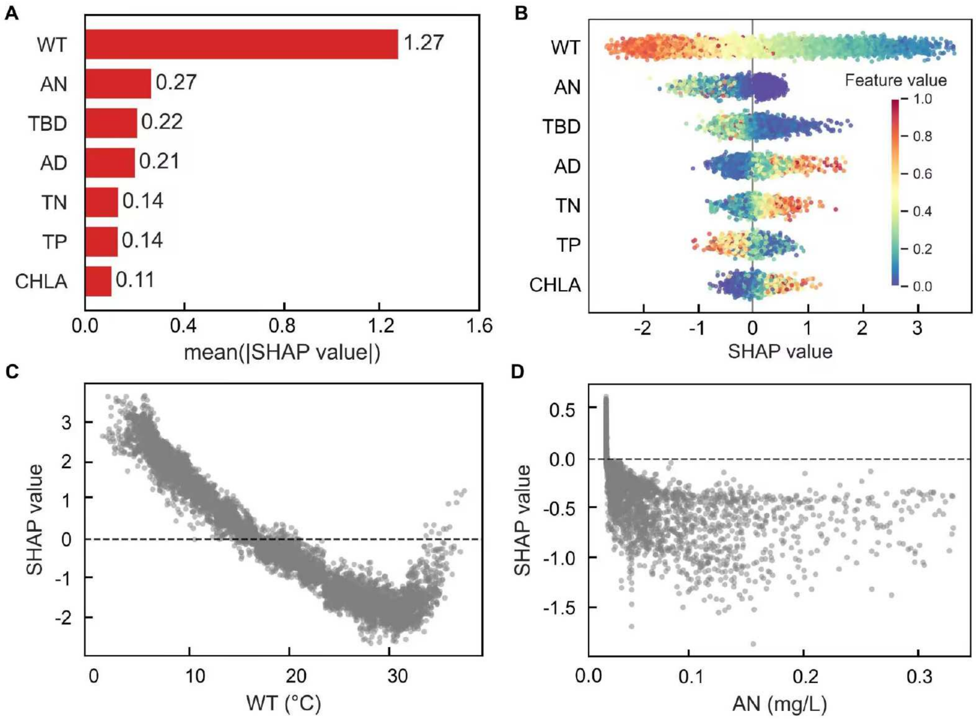

Fig. 3 SHAP Explainer evaluation of global and local impacts on DO predictions for the year-around model. (A) Assessment of the global average feature impact on the model output magnitude; (B) evaluation of local feature impact on the model output, (C) and (D) analysis of the impact of WT and AN on model output, respectively.

highlighting AN as the most critical factor. Specifically, AN consumes DO when participating in nitrification (Zheng et al., 2004). In contrast, AD shows a positive effect, where higher AD indicates greater photosynthetic activity, thus increasing oxygen production and subsequently raising DO. The negative effect of TBD and the positive role of CHLA can be similarly interpreted. Higher TBD indicates an increase in particulate matter, including phytoplankton, which can reduce light penetration and thereby inhibit photosynthesis (Gameiro et al., 2011), leading to lower DO. On the other hand, CHLA reflects the concentration of chlorophyll a, a proxy for the photosynthetic capacity of algae (He et al., 2022). A higher CHLA value suggests more active photosynthesis, which enhances the oxygen-producing capacity of the water.

As illustrated in Fig. S7C and D, the relationship between WT and DO predictions exhibits a one-sided parabolic trend. At temperatures below 30 °C, the sensitivity of DO to WT changes remains minimal, indicating a relatively stable response. However, when the WT surpasses 30 °C, there is a marked increase in the sensitivity of DO to further rises in temperature. This phenomenon suggests that elevated temperatures, particularly during summer LHWs, contribute to a rise in DO, aligning with the observed trend that LHWs can enhance DO in aquatic systems. In contrast, the influence of AN on DO is negative, as highlighted in Fig. S7D. While the general trend indicates a negative correlation between AN and DO, there are notable local variations. Specifically, at lower AN concentration, a positive effect on DO is observed, suggesting that the relationship between AN and DO is more nuanced and may involve complex interactions depending on specific concentration thresholds. These findings highlight the differential impacts of WT and AN on DO dynamics, with WT displaying a temperature-dependent nonlinearity, while AN exerts a predominantly inhibitory effect on DO. In summary, summer fluctuations in these key predictors drive changes in DO, with AN and TBD contributing to oxygen depletion, while AD and CHLA support oxygen generation. This understanding offers valuable insights into the mechanisms influencing DO during the summer months.

In the winter model (Fig. S8A), WT stands out as the dominant predictor, with an absolute global SHAP value of 0.47. It is followed by AD, TN, TBD, AN, CHLA, and TP. Local SHAP values reveal that WT exerts a significant negative influence on DO, while AD and TN positively contribute to DO, as shown by the color gradient in Fig. S8B. This analysis underscores the critical role of WT in shaping winter DO dynamics. As WT increases, DO saturation declines, directly lowering DO. Conversely, elevated AD and TN suggest enhanced photosynthetic activity and nutrient enrichment, which support phytoplankton and algae growth, thereby boosting oxygen production and raising DO.

The relationship between WT and DO, depicted in Fig. S8C, follows a one-sided parabolic pattern. As WT rises, DO drops, though the decreasing slope indicates a reduced sensitivity to further temperature increases. This trend, coupled with the observed DO decline during winter LHWs in Lake Taihu, highlights temperature-driven reductions in DO saturation as a key mechanism behind DO fluctuations during these events. AN also influences winter DO predictions, but its overall effect is modest, reflected by a global SHAP value of 0.08. Figure S8D shows that although AN generally exhibits a negative correlation with DO, notable local variations occur. At lower AN concentration, a positive effect on DO is evident, indicating that AN's impact on DO may depend on specific concentration thresholds in winter.

3.5 Mechanisms of DO change during LHWs

In this study, we specifically focused on the models of DO in both summer and winter to identify the water quality parameters with the most significant influence on DO. From the models, we selected the top two parameters most strongly influencing DO (excluding WT if it was among the top two, in which case we selected the next significant parameter). For summer, AN and TBD were identified as the most influential factors, whereas in winter, TN and AD were selected for further analysis to examine their relationships with temperature.

Our results, shown in Fig. 4A, revealed a notable inverse correlation between AN and WT during summer. Specifically, as WT increased, AN significantly decreased. This decline may be attributed to the elevated volatilization rate of AN due to rising temperatures (Liu et al., 2020b). Previously Zheng et al. (2004). in constructing a water quality model pointed out that nitrification (AN be converted to nitrate nitrogen) requires the consumption of DO is an important sink of DO, while Wu et al. (2019) exploring the effect of WT on nitrification by ammonia-oxidizing bacteria (AOB) in Lake Taihu found that AOB's abundance was greatest at 20 °C and its growth is inhibited at higher WT (42 °C). This means that higher WT during summer heatwaves in lakes inhibits nitrification and reduces the consumption of DO. Furthermore, SHAP analysis suggested that the decrease in AN contributed positively to the increase in DO, which also suggests that the results of SHAP analysis are compatible with the above conclusions.

Similarly, a significant negative relationship shown in Fig. 4B was observed between TBD and WT in summer. Previous studies have demonstrated that increased suspended matter in water (i.e., elevated TBD) physically blocks light from penetrating the water column, thereby reducing photosynthesis by algal plants and further reducing the source of DO (Takamura et al., 2003; Teng et al., 2007). SHAP analysis also indicated that the reduction in TBD enhanced DO, which suggests that the results of the SHAP analysis can also fit with the findings of the above studies.

In summary, these findings suggest that DO tends to rise during LHWs in the summer. To further investigate this phenomenon, we analyzed changes in WT, AN, and TBD during the LHW in Lake Taihu from July 12 to 16, 2021 (Fig. 4C and D), compared with normal conditions (10 days before the LHW: July 2 to July 11, and 10 days after: July 17 to July 26). The results showed that, in addition to rising WT, both AN and TBD decreased during the LHW, which collectively contributed to an increase in DO.

In winter, alongside WT, TN, and AD emerged as the key factors influencing DO. Notably, a negative correlation was observed between WT and both TN and AD. Specifically shown in

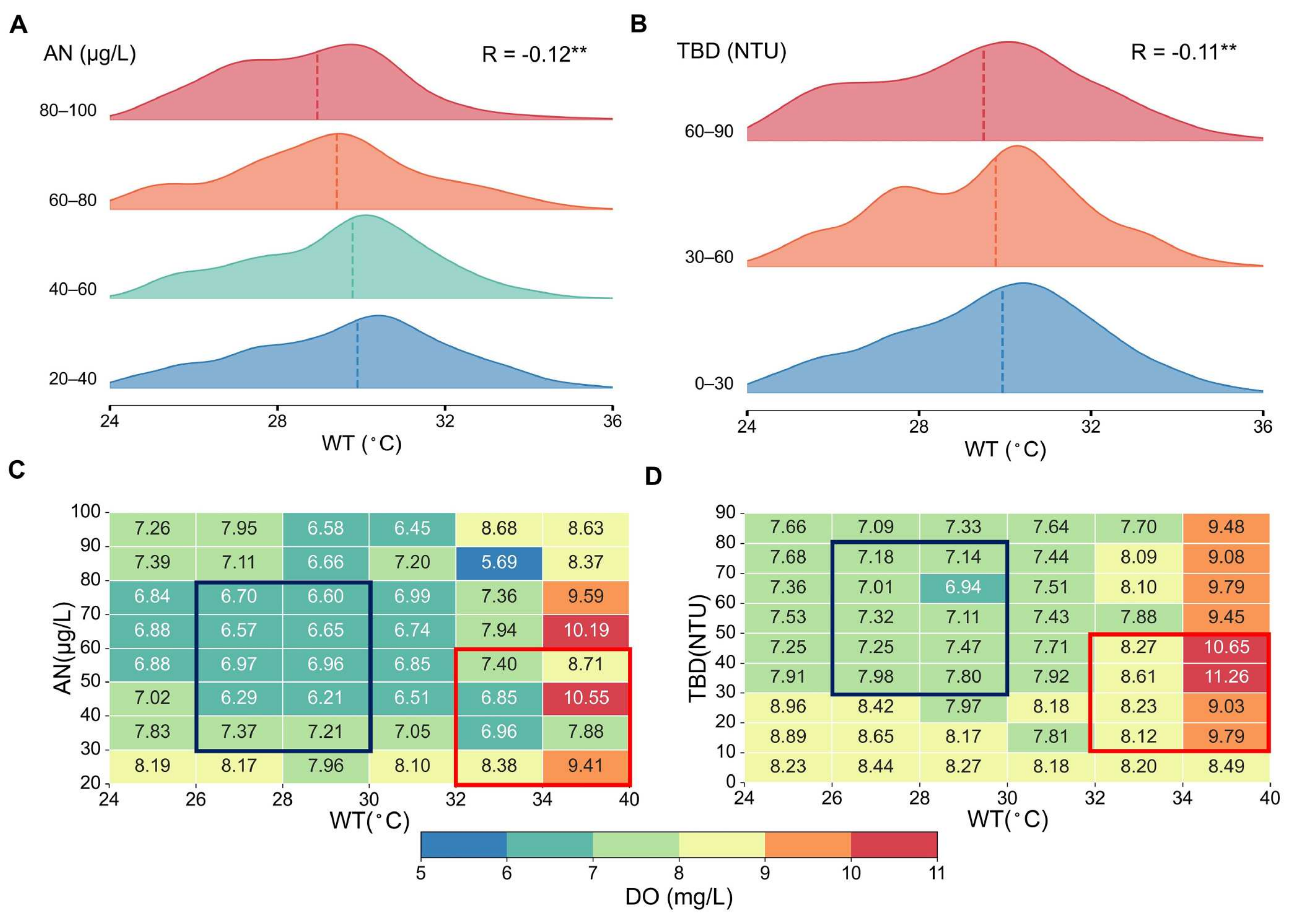

Fig. 4 Response of AN (A) and TBD (B) to elevated WT in summer Lake Taihu, i.e., probability density distributions of AN and TBD across different ranges in WT. The dashed lines indicate the median values. The symbols "*" and "**" next to the correlation coefficient *R* denote significance at the 90% confidence level (P<0.1) and 95% confidence level (P<0.05), respectively. The DO corresponding to different WT and AN (C) concentration ranges, and the DO corresponding to different WT and TBD (D) concentration ranges under LHWs conditions (red box) and normal conditions (blue box).

Fig. 5A, TN presented a marked decline as WT increased. This reduction may be attributed to the increased water flow and accelerated biological processes induced by higher temperatures, which potentially lead to nutrient depletion. SHAP analysis further indicated that the decrease in TN contributed negatively to DO, and this is probably because TN serves as a nutrient for phytoplankton. A reduction in nitrogen availability limits phytoplankton photosynthesis, subsequently lowering oxygen production.

Similarly, a significant negative correlation was observed between AD and WT in winter, as shown in Fig. 5B. According to the SHAP analysis, lower AD was associated with decreased DO, and this is possibly because reduced phytoplankton populations hinder photosynthetic oxygen production.

While AN and AD play important roles, WT remains the most dominant factor influencing winter DO. Previous studies have demonstrated that the relationship between WT and DO saturation follows a parabolic trajectory: at lower temperatures, a sharp decline in DO saturation occurs as temperature rises, which then stabilizes as temperatures continue to increase. Thus, during winter, even moderate increases in WT can lead to a pronounced decrease in DO.

These findings collectively suggest that DO tend to drop during winter LHWs. To further investigate this, we examined WT, TN, and AD dynamics during an LHW event in Lake Taihu from December 8 to 15, 2023 (Fig. 5C and D), comparing them to normal conditions (November 28–December 7 and December 16–25). Results indicated that, in addition to elevated WT, both TN and AD declined during the LHW, collectively contributing to changes in DO.

4. Discussions

Our results show a long-term trend of increasing WT and decreasing DO. The results also show that the LHWs in Lake Taihu have undergone varying degrees of significant upward phase in all seasons from 2000 to 2022, including the enhancement of duration, average intensity, and maximum intensity. Warmer lake surface water will have an impact on the physical and chemical properties of the entire aquatic system (Woolway et al., 2020). While a previous study predicted that warming of China's lakes would continue into the 21st century, as well as more intense and prolonged LHWs (Wang X, et al., 2023).

Normally, we would expect rapid deoxygenation of lakes to be due to increased lake temperatures (Jane et al., 2021; Jansen et al., 2024). By comparing DO under LHWs conditions with normal conditions (i.e., during periods when LHWs do not occur), the results, as we expected, showed that DO under LHWs conditions in spring and winter was lower than in normal

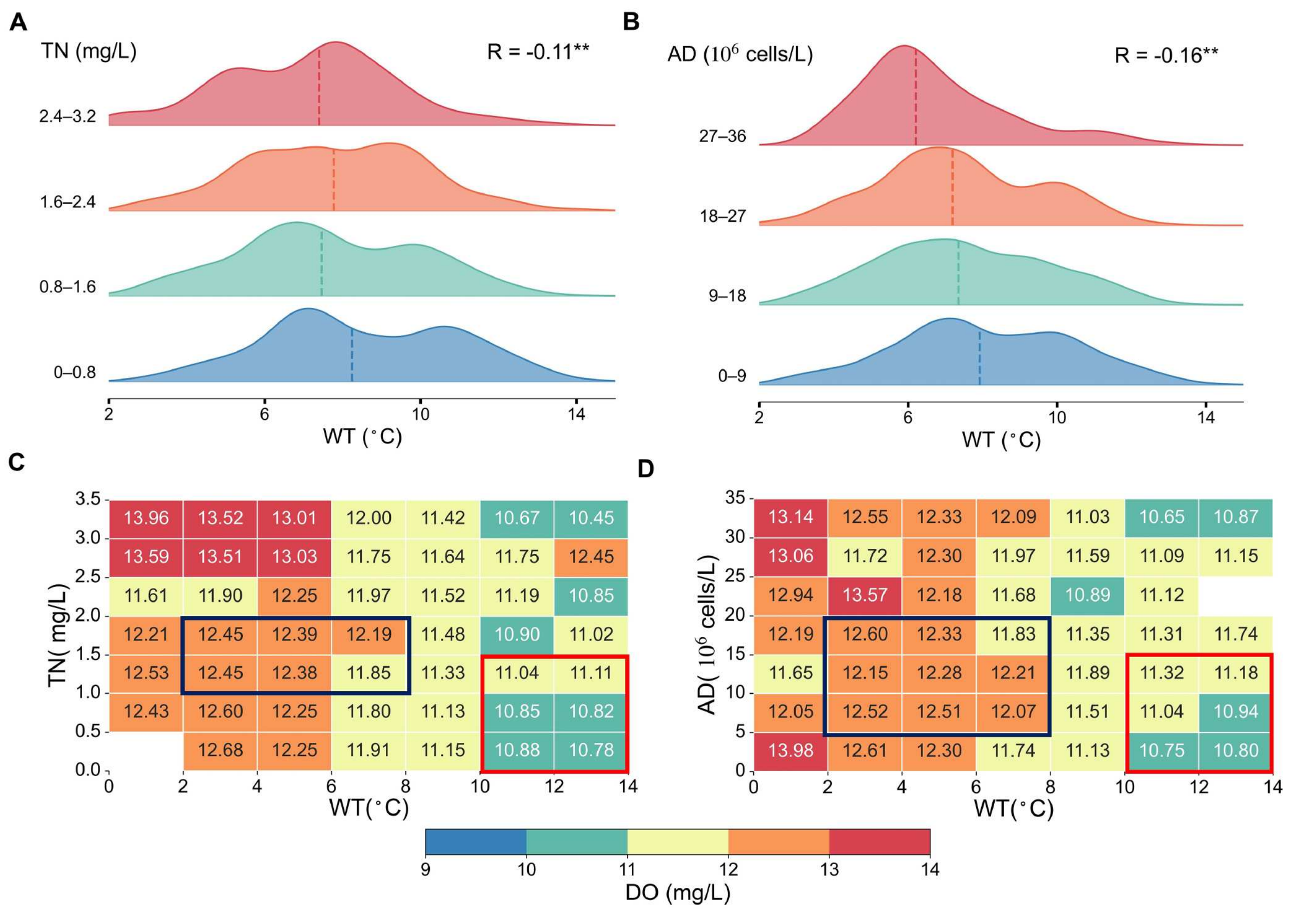

Fig. 5 Response of TN (A) and AD (B) to elevated WT in winter Lake Taihu, i.e., probability density distributions of TN and AD across different ranges in WT. The dashed lines indicate the median values. The symbols "*" and "**" next to the correlation coefficient R denote significance at the 90% confidence level (P<0.1) and 95% confidence level (P<0.05), respectively. The DO corresponding to different WT and TN (C) concentration range, and the DO corresponding to different WT and AD (D) concentration range under LHWs conditions (red box) and normal conditions (blue box).

conditions. However, an interesting phenomenon arose during LHWs in summer, which is that DO under LHWs conditions was higher than DO under normal conditions. This phenomenon is not rare in eutrophic lakes or lakes located in warmer zones (Jane et al., 2021; Zhang et al., 2025). And this is due to the interaction of eutrophication and warming, which causes the rate of oxygen production to exceed the rate of depletion, resulting in supersaturation of the DO concentration, which rises despite the reduced solubility of the gas at this point (Breitburg et al., 2018; Jane et al., 2021; Blaszczak et al., 2023).

To explain the above phenomenon, we developed twelve DO models for Lake Taihu using four distinct machine learning algorithms across annual, summer, and winter periods, and evaluated their performances. The best performers in the year-round, summer, and winter models were RF_{year}, ET_{summer}, and RF_{winter}, respectively. To clarify the influence of each predictor variable on DO predictions, we employed the SHAP approach. The analysis revealed that the primary factors affecting DO in summer were AN and TBD, and they were negative. Although this is a result based on statistical methods, a previous study by Zheng et al. (2004) has shown that AOB consume DO in the process of converting AN to nitrate through nitrification. The negative effects of TBD on DO analyzed by SHAP have also been demonstrated in previous studies, specifically that elevated TBD physically prevents light from penetrating the water column, thereby reducing photosynthesis in algal plants and further reducing sources of DO (Takamura et al., 2003; Teng et al., 2007). In winter, the results of SHAP analysis showed that WT had a primary and negative influence on DO, while TN and AD had secondary but positive influences.

Furthermore, we examined the impact of LHWs on DO by comparing LHWs and normal conditions. Our analysis revealed that DO increased during summer LHWs but decreased during winter LHWs. Specifically, winter LHWs result in lower DO

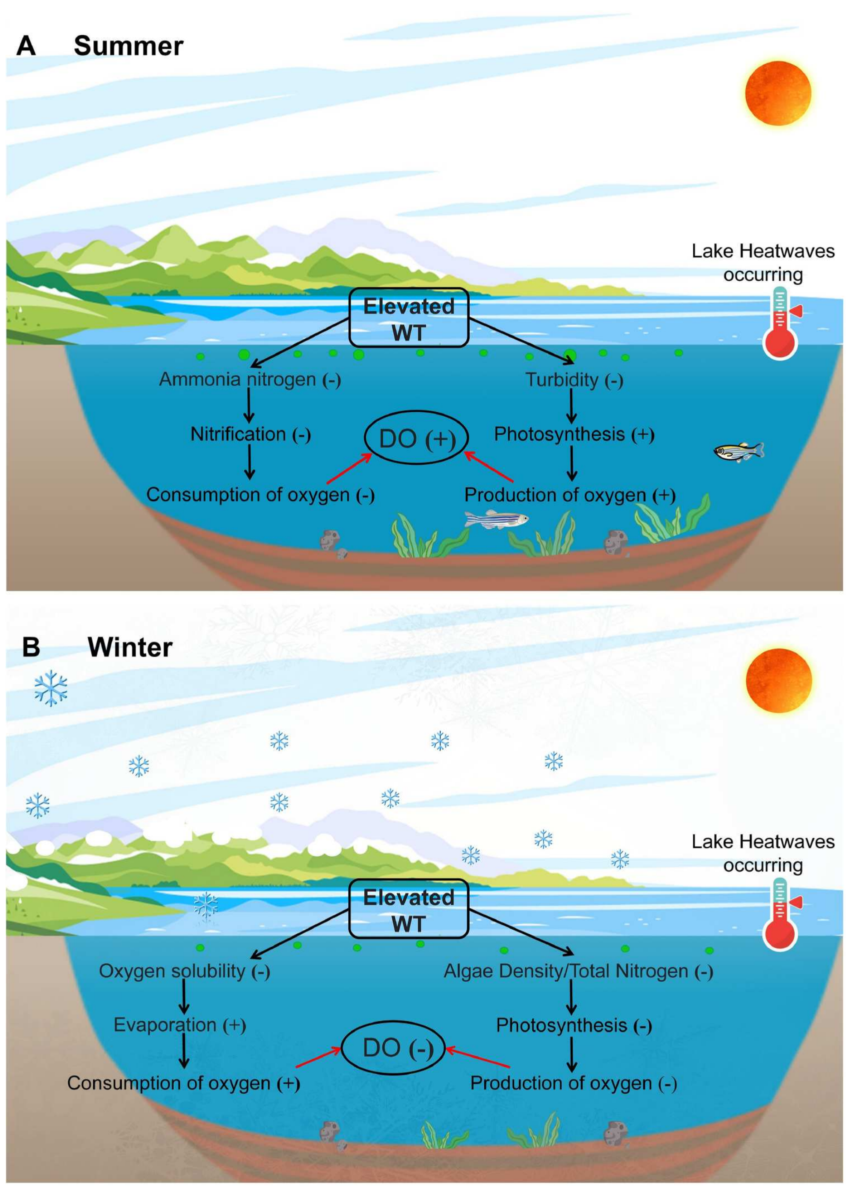

Fig. 6 Schematic diagram of ecological feedback modulation for two typical LHWs: (A) is summer, and (B) is winter. The symbol "+" after the name of a process indicates that the process may be facilitated when LHWs occur, while "−" indicates the opposite.

primarily due to increased WT, which decreases DO saturation. Additionally, the combined effects of increased WT with other key factors—TN and AD, further contributed to the decline in DO. Conversely, summer LHWs were associated with higher DO, primarily due to the dominant influence of AN and TBD. Although LHWs typically reduce DO saturation, the already elevated WT in summer limits this effect. The reduction in AN and TBD at higher temperatures decreases DO consumption and enhances phytoplankton oxygen production, ultimately leading to increased DO. By integrating the findings, we propose a conceptual scheme illustrating the influence of LHWs on DO in Fig. 6.

However, there are obvious drawbacks to the data we used, because of the limited amount of water quality data available to us (Lake Taihu was the only site for which we had access to richer data, reflecting the need to increase the frequency of monitoring of lake data), we referred to Jane et al. (2021) treatment when exploring spatial differences in DO changes during LHWs and calculating long-term trends in DO, using data were all monthly (only August data of each year were used for long-term trends calculation). In addition, Lake Taihu is located in the economically developed eastern coast of China, where industries are well developed. Therefore, a series of anthropogenic impacts, including sewage discharge and domestic water use, cannot be excluded. In recent years, the Chinese government has invested substantial resources in lake restoration, and the ecological environment of Lake Taihu has improved markedly; these anthropogenic influences, therefore, cannot be entirely ruled out. Moreover, natural processes such as wind-induced mixing can enhance air-water gas exchange, and hydrological inflows may alter the lake's thermal and oxygen dynamics. Such natural drivers cannot be fully captured by our machine learning models, and eliminating the interference of these external factors remains an important direction for future research.

5. Conclusions

In this study, we used observational data from Lake Taihu spanning from 2000 to 2019 sourced from the National Ecosystem Science Data Center, complemented by national surface water quality data from 2014 to 2024 released by the China National Environmental Monitoring Centre and a temperature dataset from 1950 to 2022 provided by the National Tibetan Plateau/Third Pole Environment Data Center to analyze the characteristics of LHWs and their impact on DO, and used machine learning and SHAP to explore the mechanisms. The conclusions we have reached are as follows: (1) WT increased significantly at a rate of 0.2 °C per decade from 1980 to 2022. DO decreased significantly at a rate of 0.43 mg/L per decade from 2000 to 2023. The intensity and duration of LHWs in Lake Taihu increased from 2000 to 2022. DO is generally higher during summer LHWs than in normal conditions (i.e., during periods when LHWs do not occur), while it is lower in spring and winter. (2) Machine learning and SHAP suggest that DO increased during summer LHWs because warmer water causes a decrease in AN and TBD, the two main factors affecting DO, with lower AN reducing nitrification to consume oxygen and lower TBD promoting photosynthesis to produce oxygen. (3) The reason that winter LHWs cause a DO decrease is that WT is the main factor controlling DO, and elevated WT during LHWs reduces gas solubility.

These findings highlight the intricate interactions among temperature fluctuations, nutrient dynamics, and LHWs occurrence, which collectively influence DO in Lake Taihu. While this research primarily focuses on the impact of LHWs on DO and its influencing mechanisms in Lake Taihu, expanding the scope to a larger scale will be necessary to confirm the broader applicability of these findings. Future studies should continue to explore the multifaceted relationships between climatic factors and lake responses, with a strong emphasis on developing adaptive management strategies that can withstand the challenges posed by an evolving climate landscape. In particular, our findings suggest that lake management should adopt season-specific measures: (1) During summer, when LHWs generally coincide with higher DO, the priority should be to control algal blooms and nutrient inputs so as to prevent secondary hypoxia; (2) in winter, when LHWs lead to pronounced DO declines, real-time monitoring and early warning systems should be strengthened, and emergency oxygenation or hydrological regulation should be implemented to reduce risks to aquatic life if necessary; and (3) over the long term, nutrient reduction and catchment pollution control should be sustained while building a high-frequency, seasonally targeted monitoring network to cope with the increasing frequency and intensity of LHWs under climate change.

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Supporting information
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Compliance and ethics
The authors declare no conflict of interest.

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