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Changes in Dissolved Oxygen Recovery Patterns Following Prolonged Thermal Stress in Shallow Lakes

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Abstract: While the decline in dissolved oxygen is the most direct link between lake temperature and aquatic life, studies of the recovery after a long warm period are much less extensive. A 70-day outdoor mesocosm experiment was designed to simulate shallow lakes subjected to extended periods of thermal stress for 28 days by increasing the temperature of 12 mesocosms by either +3 °C or +5 °C above ambient, with four replicates for each temperature, along with an ambient control, followed by a recovery period of 42 days. By day 28, minimum dissolved oxygen had fallen from 7.9 mg L^{-1} to 4.6 mg L^{-1} at +3 °C and 2.5 mg L^{-1} at +5 °C, which is 39% and 67% below the control, and bottom-water saturation reached 41% and 18%. The SOD increased in a linear fashion with water temperature (0.22 g O_2 m^{-2} d^{-1} $°C^{-1}$; $R^2 = 0.97$). The recovery to 90% of the control levels was 20 and 34 days after the end of heating at +3 °C and +5 ° C, respectively, and the initial recovery rate was 7% and 23% slower than the previous decrease. The +5 °C mesocosms were still 5% lower at day 70. The recovery is thus slower than the depletion and this asymmetry becomes larger as the thermal stress is increased.

Keywords: Dissolved Oxygen; Thermal Stress; Shallow Lakes; Hypoxia; Recovery.

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I. Introduction

Dissolved oxygen sets the habitable limits of lakes. Oxygen loss and its return when it does, affects fish, causes nutrient releases from sediment, and restructures the food web – the timing of oxygen loss and the rate of its return are key to lake health. Shallow lakes are very sensitive as they have limited water capacity and are in direct contact with the sediment, thus warming has an immediate effect on the oxygen demand. Eleven years of experiments in shallow lake mesocosms, pre-adapted for this purpose, have established that it is the joint effect of temperature and nutrient loading and heat waves on nutrients, oxygen and ecosystem metabolism that is most important, rather than any one of these factors alone (Jeppesen et al., 2021).

Thermal structure and oxygen are intrinsically coupled in larger systems as indicated by long records. Thermal and oxygen observations carried out in lake Kariba for 60 years showed that the oxygen regimes vary between the riverine and lacustrine sub-basins of this single water body and are time varying (Calamita et al., 2019). Failure of the oxygen supply may also be sudden. A large shallow lake, after a drought, experienced a sudden inflow of carbon which resulted in whole-lake anoxia and a massive fish kill Kragh et al., (2020): This is a very short time for a shallow system to go from normal oxygen conditions to lethal conditions.

These physical relationships are modified by biological factors. If primary producer communities are disturbed, the associated aquatic fauna is likely to be affected by the thermal limits Booth et al., (2023) and disturbance cannot be divorced from community structure. The resistance and resilience of the lake surface temperature and oxygen saturation have been demonstrated to be dependent on the amount of chlorophyll a before extreme storms (Thayne et al., 2023). Both drivers and implications have been associated with oxythermal habitat loss in long-term trends for Cisco in Lake Mendota (Magee et al., 2019).

These studies provide a detailed description of the oxygen loss, but little information on its return at the end of a long warm period. In particular, it is not known whether recovery follows a similar pattern to a decline or a more gradual course and what this may depend on when considering the severity of stress. In this paper, it will be answered using a controlled experiment. There were four aims: (i) to measure the amount of oxygen lost in extended heating, (ii) to establish the vertical oxygen distribution pattern at

maximum stress, (iii) to relate oxygen demand to temperature, and (iv) to compare recovery rates with decline rates.

The rest of the paper is organized as follows. Section II presents a review of the existing literature on oxygen depletion models, the long-term recovery experience, and seasonal oxygen systems. Section III gives information about the experimental design of the twelve outdoor mesocosms, thermal stress treatments, and the methodology applied in the analysis of oxygen dynamics and sediment oxygen demand. Section IV provides the empirical findings related to the rate of oxygen depletion, stratification dynamics, sediment respiration, and recovery patterns. Section V gives an explanation of the mechanisms of asymmetrical recovery and its ecological/management implications. Finally, section VI provides a summary of the main findings.

II. Literature Review

Predicting Oxygen Depletion

The prediction of oxygen loss has progressed to simple models which are transferable. In a simple model for predicting oxygen depletion in lakes due to climate change, it is shown that oxygen depletion can be predicted from only a few physical and trophic variables, not from complex simulations (Nkwalale et al., 2023). Such models are important for management but are based on 'depletion' and, as such, provide little insight into how oxygen returns which is the impetus for this study's focus on recovery.

Long-Term Recovery Evidence

Evidence of recovery has been found primarily on a long time-scale. However, over the last three decades, Chinese freshwater ecosystems showed a recovery in dissolved oxygen levels, suggesting that dissolved oxygen can be restored if pressures can be reduced (Zhang et al., 2022). These multi-decade recoveries are in contrast to those from event-scale processes, such as heatwaves and thermal pulses, for which there are limited controlled data.

Seasonal Regimes and Applied Consequences

There is also a change in oxygen regimes throughout the year. For a shallow, winter ice-covered lake, dissolved oxygen was demonstrated to be a function of changes in light, thermal and ice regimes Zdorovennova et al., (2021) and thus oxygen in shallow lakes is quickly affected by changes in the physical environment at both the warm and cold end. The impact of heat stress on the sustainability of traditional freshwater pond fishery systems under climate change (CC) Orság et al., (2023) indicates that there are direct economic implications of oxygen and temperature stress for managed shallow waters. Combined, these studies show that oxygen can be predicted, recovered and used, but not how fast it can be recovered compared to how fast it is used up for the same system.

III. Experimental Design and Methods

Mesocosms and Thermal Stress Treatments

This study was carried out in twelve mesocosms in the outdoor freshwater culture facility, each holding 1000 L of water with a water-column depth of about 1.0 m. The same community of established macrophytes and plankton, and a 10 cm sediment layer, were present in each mesocosm and had been taken from a single shallow pond. The use of a common source ecosystem enabled the use of similar initial biological and environmental conditions for all of the experimental units. Mesocosms were set up in the outdoor environment of the lab in order to let the existing aquatic communities and sediment components settle prior to the start of the experiment. The 12 mesocosms were then randomly distributed among the 3 experimental treatments with four independent replications per treatment (Table 1). The experimental treatments were an ambient control, prolonged moderate warming (+3 °C), and prolonged intense warming (+5 °C). The two warming treatments experienced a rise in temperature of about 3 °C and 5 °C above

ambient temperature, respectively, whereas the control treatment was not subjected to any additional heating. Temperature was controlled from the first experimental day and continued to be controlled for the entire duration of the experiment (days 1-28) to represent chronic thermal stress exposure. The desired differences in temperature between treatments were maintained during the exposure period with the use of heating equipment. The mean (across the four replicates) water temperatures measured during the heating phase were 22.0 °C, 25.1 °C and 27.0 °C for the control, +3 °C and +5 °C treatment, respectively. All the heaters were then turned off after 28 days of heating, and the mesocosms were allowed to slowly move back to ambient natural temperature conditions. Experimental units were then monitored for another 42 days post thermal exposure (from D29 to D70) to assess recovery of dissolved oxygen conditions after the end of the thermal exposure. By using this experimental setup, the effect of various intensities of warming could be compared, and recovery over time could be evaluated.

Table 1: Experimental Design

Treatment	Heating above ambient	Heating period	Replicates	Mean water temperature during heating (°C)
Control	None	–	4	22.0
Prolonged +3 °C	+3 °C	Days 1–28	4	25.1
Prolonged +5 °C	+5 °C	Days 1–28	4	27.0

Measurements and Analysis

The concentration of dissolved oxygen (DO) and water temperature were measured continuously from the beginning of the experiment to the end with optical sensors placed at three representative depths of the water column: surface, mid-depth, and bottom. Records were taken every 15 minutes to provide short-term oxygen level fluctuations and variations with depth. The high-frequency monitoring method gave the detailed information to understand the temporal change of oxygen depletion during heating and oxygen recovering after the end of thermal stress. Recorded dissolved oxygen (DO) and percent oxygen saturation (O2S) were used to determine the duration of severe oxygen depletion and hypoxic conditions, accounting for the 1-hour maximum lag time in data. To find periods of severe oxygen depletion and potential hypoxic conditions, daily minimum DO and percent oxygen saturation (O2S) were calculated from the recorded measurements, allowing for a 1-hour maximum lag time. Dark incubation experiments were used to measure sediment oxygen demand (SOD) of intact sediment cores. The dark incubation method did not allow the production of photosynthetic oxygen, thus providing a measure of the oxygen consumed during sediment respiration and other biological processes. SOD was presented in terms of g O_2 m^{-2} d^{-1}. Recovery time was defined as the number of days after the end of the heating period needed for the daily minimum DO to reach 90% of the control mean. The threshold is used to facilitate comparisons of recovery rates in the two warming treatments. Differences among the experimental treatments were evaluated by statistical analyses. Differences in the dissolved oxygen conditions and the sediment oxygen demand among the different treatments were analyzed using one-way analysis of variance (ANOVA). The relationship and the rate of change of the water temperature and sediment oxygen demand were determined by linear regression analysis. A p value of <0.05 was used to define statistical significance. These measurements and analytical procedures, combined, enabled the quantitative assessment of the impact of extended thermal stress on changes in dissolved oxygen (DO) dynamics, sediment oxygen consumption (SOC), and post-heatwave recovery in shallow freshwater mesocosms.

IV. Results

Oxygen Decline During Prolonged Heating

Oxygen concentration in the control mesocosms remained almost stable and decreased from 7.9 to 7.6 mg L^{-1} (Figure 1). During the heated treatments, the amount of oxygen was also reduced over the 28 days. By day 28 it had reached 4.6 mg L^{-1} at +3 °C and 2.5 mg L^{-1} at +5 °C, which is 39% and 67% below the control. The mean decline rate was 0.118 mg L^{-1} d^{-1} at +3 °C and 0.193 mg L^{-1} d^{-1} at +5 °C, compared with

0.011 mg L^{-1} d^{-1} in the control. Since the drop was not stabilized, the level of oxygen deficit was determined not by an immediate change to an equilibrium level, but by the duration of the heating period.

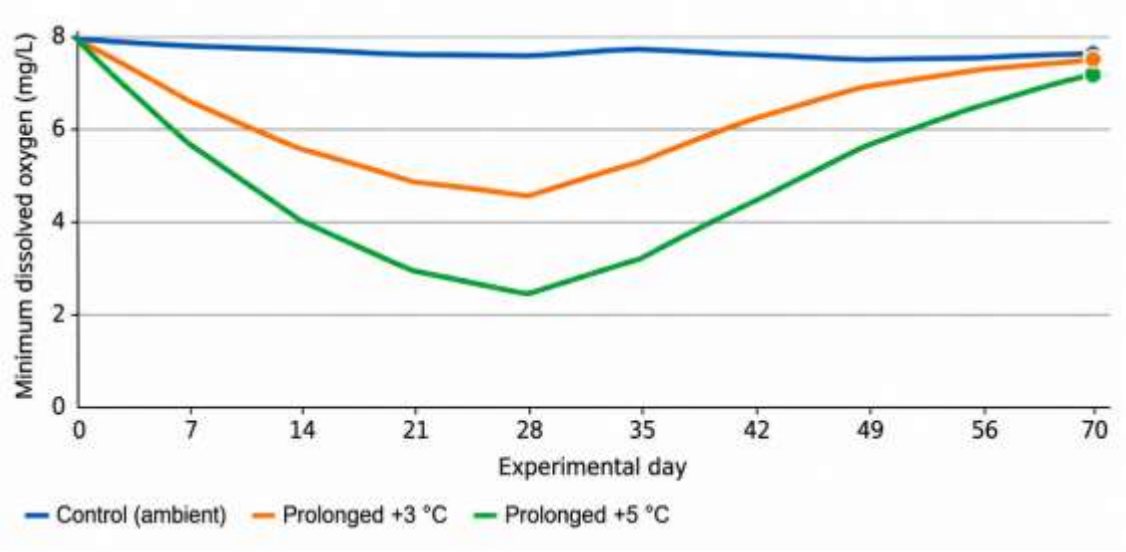

Figure 1: Daily Minimum Dissolved Oxygen During and After Prolonged Thermal Stress (Heating Days 1–28)

Vertical Oxygen Structure at Peak Stress

The highest loss of oxygen was found close to the sediment (Figure 2). The saturation of bottom water was controlled at 84% after heating, but was only at 41% at +3 °C and at 18% at +5 °C, which is very hypoxic. The vertical gradient was less affected and became narrower with cooling (98%, 82% and 71% for the control, +3 °C and +5 ° C, respectively). The pattern suggests that oxygen is consumed mostly in the sediment and bottom water and not at the surface.

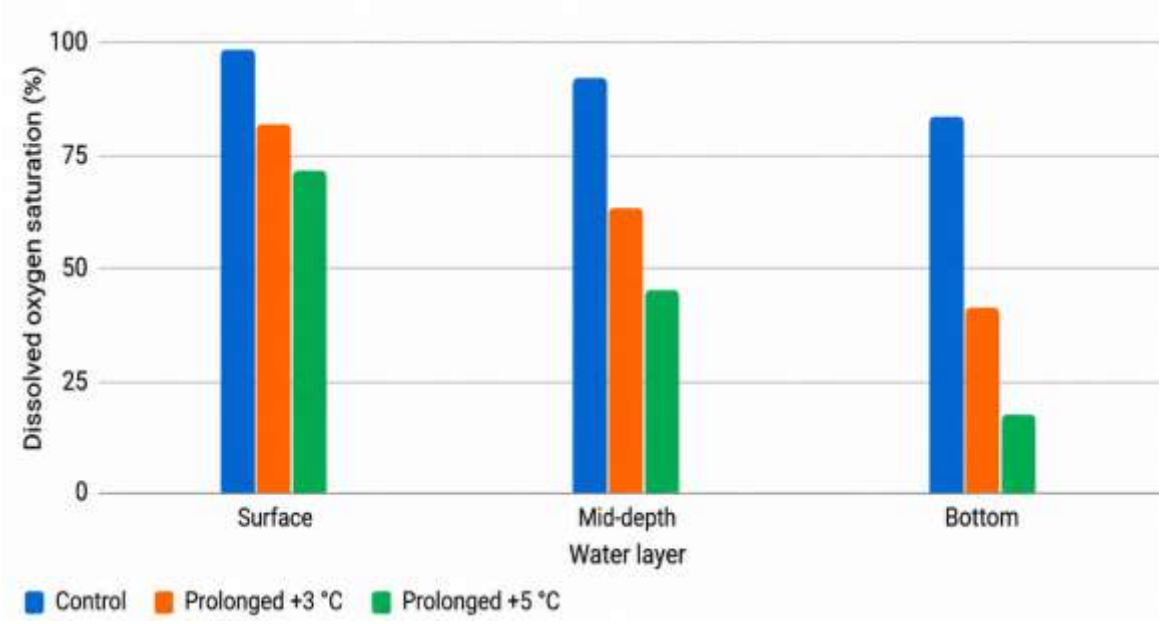

Figure 2: Ecological Impacts of Prolonged Thermal Stress on Dissolved Oxygen Dynamics and Water Quality in Freshwater Systems

Table 2: Oxygen Metrics at the End of Heating and at the End of the Experiment

Metric	Control	+3 °C	+5 °C
Minimum oxygen, day 28 (mg L^{-1})	7.6	4.6	2.5
Bottom saturation, day 28 (%)	84	41	18
Mean decline rate, days 0–28 (mg L^{-1} d^{-1})	0.011	0.118	0.193
Initial recovery rate, days 28–49 (mg L^{-1} d^{-1})	–	0.110	0.148
Days to 90% of control after heating	–	20	34
Minimum oxygen, day 70 (% of control)	100	99	95

Temperature Dependence of Sediment Oxygen Demand

The increase in sediment oxygen demand was found to be significantly positive with temperature (Figure 3). Mean SOD was 1.01 g O_2 m^{-2} d^{-1} in the control, 1.57 at +3 °C and 2.11 at +5 °C, which is 56% and 109% higher, and the treatment effect was highly significant (ANOVA, $F_{2,9} = 99.5$, $p < 0.001$). Across all twelve mesocosms, SOD increased linearly with mean water temperature at 0.22 g O_2 m^{-2} d^{-1} per °C ($r = 0.98$, $R^2 = 0.97$, $p < 0.001$). Replicates were grouped tightly within each treatment indicating uniformity of the response.

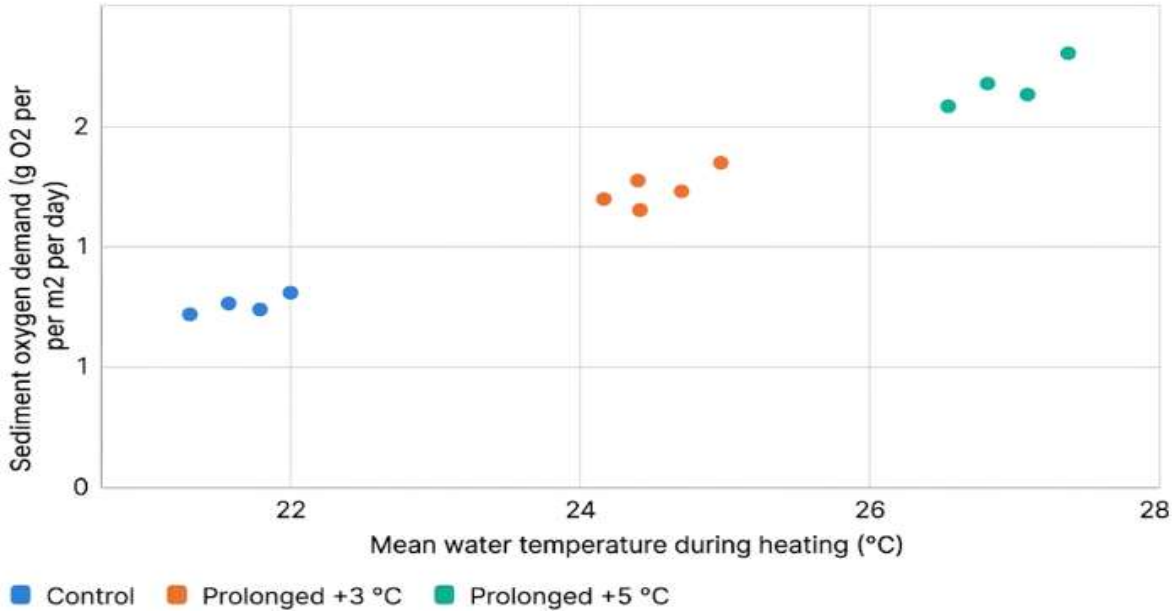

Figure 3: Thermal Dependence of Sediment Oxygen Demand Under Prolonged Heatwave Conditions

Recovery After Heating

Once the heat was turned off, oxygen levels started to rise rapidly in both treatments (Table 2, Figure 1). These mesocosms had 90% of the oxygen of control after 20 days of heating in the +3 °C mesocosms and after 34 days of heating in the +5 °C mesocosms. The initial recovery rate over days 28 to 49 was 0.110 mg L^{-1} d^{-1} at +3 °C and 0.148 mg L^{-1} d^{-1} at +5 °C. Relative to the preceding decline, recovery was therefore 7% slower at +3 °C (0.110 versus 0.118) and 23% slower at +5 °C (0.148 versus 0.193). While absolute recovery was faster at +5 °C, recovery was from a much deeper deficit, resulting in 14 days longer. Minimum oxygen did not reach the +3 °C control level at day 70, but only had a 4% difference compared to the +5 °C control level (7.2 mg L^{-1} versus 7.6 mg L^{-1}), indicating that recovery was not complete under the more stressed condition.

V. Discussion

The experiment demonstrates that recovery is slower than the decrease of the thermal stress and that the recovery is progressive. The gradual decline is consistent with the hypothesis that warming increases the need for oxygen in shallow systems more quickly than oxygen can be supplied, which has also been observed in mesocosms where warming and heat waves together impacted oxygen and metabolism (Jeppesen et al., 2021). The vertical gradient is increasing with time and the temperature dependence of SOD indicates the major driving force is the sediment. This is in agreement with the suggestion that oxygen depletion could be predicted using a few physical and trophic variables Nkwalale et al., (2023) and with the report that the oxygen regime of the lake is dependent on the thermal regime, as in Lake Kariba Calamita et al., (2019) and in ice-covered shallow lakes where the thermal and light regimes determine the oxygen regime (Zdorovennova et al., 2021).

The most important novel finding is the disparity between the decline and the recovery. The more severe the stress, the further the recovery path moves from the decline path: Recovery was 7% slower than decline at +3 °C but 23% slower at +5 ° C. There may be a few mechanisms. Sedimentary oxygen demand due to accumulation of organic matter and reduced compounds during heating remains after cooling, and a degraded community of primary producers also results in less oxygen demand, consistent with the finding that disturbance of primary producers will lead to a disruption of the thermal limits of the associated fauna Booth et al., (2023) and that chlorophyll a has a significant impact on the resistance and resilience of oxygen saturation following storms (Thayne et al., 2023). Our results show that the rate at which oxygen returns depends on the magnitude of the deficit and are consistent with the longer-term recovery of oxygen, as has been reported in China after 30 years (Zhang et al., 2022).

The conclusions have two messages for management. First, the length of time matters as well as the intensity of thermal stress because the decrease was not even after 28 days. Secondly, no inference can be made on how quickly a lake will recover based on the rate of the decline, so a lake that declined rapidly to hypoxia would take longer to recover to safe levels. These are all important for fish because oxythermal habitat can diminish over time Magee et al., (2019), sudden anoxia can lead to fish kills Kragh et al., (2020) and heat stress can compromise the viability of managed pond fisheries (Orság et al., 2023).

Limitations apply. Mesocosms also do not have the same wind-driven mixing nor the same fish, or an external inflow, as do actual lakes. Further experiments will require multiple durations of one source community and should include a longer recovery period (+5 °C) to ensure complete recovery.

VI. Conclusion

The current research shows that continuous heating of shallow lakes leads to decreased dissolved oxygen concentration and potentially harmful conditions for aquatic life in such environments. The obtained experimental data show significant dependence of oxygen content on temperature, since minimal oxygen concentrations were reduced to 39% under the +3 °C regime and 67% under the +5 °C regime in comparison with control treatment. The most heated water bodies showed especially low values of oxygen in bottom waters, which were just 18% of saturation, meaning hypoxia development. These results show that shallow freshwater bodies are highly vulnerable to prolonged heating, especially those layers which have poor connection with oxygen-enriched water. In addition, it was shown that sediment oxygen demand increased by approximately 0.22 g O_2 m^{-2} d^{-1} for each additional degree of warming. It means that oxygen loss due to sediment respiration is a highly important factor in determining the degree of oxygen depletion. Furthermore, from the recovery patterns, it is evident that the oxygen depletion and replenishment processes were not happening at equal rates. Upon stopping experimental heating, the process of oxygen replenishment took about 20 days in the +3 °C warming treatment and 34 days in the +5 °C warming treatment. The most important fact here is that the oxygen replenishment was incomplete up until 70 days in the case of the strongest warming treatment, which means that the consequences of long-term thermal impact are capable of surviving long after the thermal treatment period. Consequently, shallow lakes may

be subjected to ecologically harmful levels of oxygen even after the recovery of temperature levels to normal. It shows the need to manage the lake ecosystem in accordance with not only thermal but also oxygen levels, as they may take a much longer time to return to normal than the temperature does. Thus, the monitoring of dissolved oxygen concentration in shallow lake ecosystems should be performed continuously, especially at the sediment-water interface.

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