# Slowing down in recovery of phytoplankton community due to recurrent heatwaves

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# Introduction

Climate change is an urgent global challenge characterized by significant alterations in weather patterns, rising global temperatures, and increased frequency of extreme weather events (IPCC 2023). One of the most concerning aspects of climate change is the increasing frequency and intensity of extreme events, such as hurricanes, floods, droughts, and heatwaves (Fischer *et al.* 2021).

Particularly, heatwaves (HWs) have been projected to increase in frequency and severity globally (Perkins *et al.* 2012), including in freshwater ecosystems (Woolway *et al.* 2021, 2022).

The projected increase in HWs frequency and intensity is growing concerns, as evidence of the detrimental effects of HWs on freshwater populations, communities, and ecosystems keeps accumulating (Correa-Araneda *et al.* 2020; Mouthon & Daufresne 2006; Polazzo *et al.* 2022; Woodward *et al.* 2016). Yet, the effects of HWs on ecological stability, and of extreme climatic events in general, have been hardly assessed (Polazzo *et al.* 2022). The few studies that did look at the effects of HWs on stability have shown that HWs can negatively affect multiple dimension of functional and compositional stability, such as resistance, recovery and temporal stability in freshwater ecosystems (Polazzo *et al.* 2023; Ross *et al.* 2021).

Additionally, HWs may determine abrupt shift in aquatic ecosystems (Bertani *et al.* 2016; Meunier *et al.* 2024; Turner *et al.* 2020; Wernberg *et al.* 2016). Abrupt shifts, critical transition or tipping points, are all concepts related to the behaviour of some systems in which multiple stable states are possible, and describe the transition from one state to another one (Scheffer *et al.* 2001; Scheffer & Carpenter 2003). The ability of a system to absorb perturbations without transitioning to an alternative equilibria is a way to measure the ecological resilience of that system (Holling 1973).

At present, evidence for HW – driven abrupt shifts or collapses is limited in freshwater systems (Bertani *et al.* 2016; Filiz *et al.* 2020; Polazzo *et al.* 2022). Scarce support for HW related collapse may be linked to the fact that most empirical studies analyse a single HW event (Polazzo *et al.* 2022). A single HW event, although detrimental, might not be sufficient to determine an abrupt shift in freshwater systems. Indeed, freshwater organism experience large daily and seasonal temperature fluctuations, and are thus adapted to large temperature changes (Woodward *et al.* 2016). Yet, since HWs are projected to become more frequent in the future, concern is rising about whether and how natural communities can face multiple recurring HWs and keep performing their functions.

There is currently a lack of knowledge and understanding about how recurrent HWs can influence community and ecosystem stability. The few available studies considering recurrent HWs have focused on other aspects of HW’s effects of freshwater organisms (Hermann *et al.* 2023, 2024).

There are two major ecological frameworks that can be applied to systems facing repeated perturbations to gain insight about their resilience: critical slowing down and community rescue.

Critical slowing down is a mechanism related to the abrupt shift in functioning or composition communities and ecosystems show when experiencing a gradually increasing pressure or when exposed to repeated perturbations (Veraart *et al.* 2012). The exact shifting point is notoriously difficult to predict (van Nes & Scheffer 2007). Therefore, the focus has shifted to deducing processes from patterns. This involves identifying observable signals in measurable aspects of a biological system that indicate changes in the underlying processes, which may result in a critical transition. In the last two decades, the phenomenon known as critical slowing down has been indicated as a possible early warning signal (EWS) of an approaching abrupt shift, derived from dynamic systems theory (Rietkerk *et al.* 1996; Strogatz 2019). The theory suggests that early warning signals could be based on the idea that recovery rates from disturbances tend to zero as a system approaches a transition point. However, there is limited evidence to support this occurring in complex systems. Oppositely, community rescue happens when ecological or evolutionary processes restore recovery under stressful conditions that would have been detrimental to the community in its original form, thereby preventing community or ecosystem functioning from collapsing in a worsening environment. Although empirical examples of community rescue are scarce (Fugère *et al.* 2020), it is considered a key mechanism that enhances stress resistance in communities and helps maintain aggregate community properties, such as biomass, under stressful conditions.

It is possible that either critical slowing down or community rescue may occur in communities that have been exposed to recurrent HWs. A community may sustain and / or recover following a first HW. However, the recovery following a subsequent HW might be impaired, and additional HWs may impede further recovery as a result of accumulating stress, driving the community to collapse. It is also possible to envisage a community rescue. A first HW can determine a decline in community functioning, which may be recovered through a compositional change that promotes stress-tolerant species (Fugère *et al.* 2020). This new community composition might then be more resistant to a following HW, and thus determine higher community stability. The same process may occur as a result of adaptation or evolutionary processes, where more resistant genotypes are selected and result in a more resistant and stable community to subsequent HWs. Thus, both framework are plausible and have been documented in communities undergoing repeated perturbations (Fugère *et al.* 2020; Veraart *et al.* 2012). Critically though, the result in terms of community resilience would be opposite, where community rescue is stabilising and thus increases resilience, whereas critical slowing down is destabilising and indicates a decrease in resilience.

It is crucial to emphasise that a recent meta-analysis has demonstrated that critical transitions are not commonly observed in empirical data (Hillebrand et al., 2020). Nevertheless, it is not necessary for a community to tip in order to show a slowing down in recovery. van Nes & Scheffer (2007) suggested that critical slowing down may not only be related to a critical transition or tipping point, but could also generically indicate an increased sensitivity of the system to repeated perturbations. Critical slowing down may thus provide important information in cases where the threshold leading to a critical transition is not reached, and thus working as an EWS, but may be informative even in systems that do not have multiple stable states at all.

With this article we wanted to test which of these two major ecological frameworks is more likely to appear in a phytoplankton community exposed to recurring HWs.

For this we used data coming from an outdoor pond mesocosm experiment (2021 Spain) where a semi-natural phytoplankton community was exposed to three subsequent heatwaves of increasing intensity, and the change in the short-term recovery after each HW was assessed.

# Materials and Methods

## Mesocosm experiment

We performed an outdoor mesocosm experiment at the facilities of the IMDEA Water Institute (Alcalá de Henares, Madrid, Spain) between April and July 2021. The 8 mesocosms used in this study were filled with 40 cm of sediments and 850 L of water from an artificial lagoon. The biological community of the mesocosms was composed of phytoplankton, zooplankton, and macroinvertebrates, and was allowed to establish and homogenize among experimental units for 2 months prior to the start of the experiment. Four of the test mesocosms were used to simulate the HW scenario (n = 4): three repeated HWs (Figure 1); while four mesocosms were kept at ambient temperature for the whole experimental duration and were used as controls. The HWs treatment consisted of three HWs lasting 7 days each and separated one another by 7 days of ambient temperature. In the HWs treatment, the temperature was +8°C above the control temperature, which meant that the HW absolute temperature progressively increased from the first to the third HW, as the water temperature in the control mesocosm warmed as result of seasonality.

All temperature manipulations and recordings were carried out using a transportable temperature and heatwave control device (TENTACLE) applicable for aquatic micro-and mesocosm experiments (Hermann *et al.* 2022). Additionally, we place a Hobo logger (Onset Computer Corporation, Bourne, MA, USA) in one control mesocosm and in one mesocosm undergoing the HWs treatment to have an independent water temperature measurement.

## Phytoplankton sampling and biomass quantification

The phytoplankton community was sampled on days -4, 3, 10, 15, 24, 30, and 38 to the start of the first HW. Samplings were performed by taking depth-integrated water samples with a polyvinyl chloride (PVC) tube (six sub-samples per mesocosm mixed in a bucket). Next, for phytoplankton samples, 250 ml of this water sample were introduced into glass amber bottles and 10% Lugol’s iodine was added for preservation. Phytoplankton taxa identification and counts were perfomed on a 1 mL subsample by means of an inverted microscope and a Sedgewick-Rafter counting cell (Graticules Optics).

Every phytoplankton taxon was digitally photographed with scale reference using a camera Samsung 12 mp (4032 X 3024, JPG format), and measuredusing Image J software (Schneider *et al.* 2012). The biovolume (μm3/org) of the phytoplankton individuals was calculated using geometric models according to Hillebrand *et al.* (1999) and Sun & Liu (2003). Biovolume was transformed to fresh weight using the following ratio 1 μg = 106 μm3,assuming specific weight of water = 1.

## Ecosystem functioning proxies

We measured chlorophyll – *a* (chl *a*) as proxy for primary productivity, as it represents the living part of the phytoplankton biomass. Chl *a* was measured on days -4, 3, 7, 10, 15, 24, 30, and 38 in situ by using a portable multi-meter (YSI Pro DSS 626,973–01). We also measured dissolved oxygen (DO) during the experimental period. Oxygen is essential to all aerobic organisms, and its dynamics in freshwater involve interconnected physical and biological processes that form the basis of the functioning of freshwater ecosystems. DO was measured on days -4, 3, 7, 10, 15, 24, 30, and 38in situ by using a portable multi-meter (YSI Pro DSS 626,973–01).

## Statistical analysis

To investigate the effect of heatwave treatment on oxygen levels in mesocosms, we employed a linear mixed-effects model (LMM) using the lmer function from the “lme4” package (Bates *et al.* 2015). The model included HW, time, and their interaction as fixed effects, with mesocosm identifier as a random effect to account for the repeated measures within each mesocosm. The model diagnostics were performed using the “check\_model” function from the performance package (Lüdecke *et al.* 2020) to ensure the assumptions of the LMM were met. When an interaction effect between HW and time was found we performed a post-hoc comparisons across different days using the “emmeans” package (Lenth *et al.* 2024) to perform estimated marginal means (EMMs) analysis.

The same approach was used to analyse the effects of the HWs on chl *a.*

To quantify whether there was a slowing down in recovery after each HW, we first calculated the difference in DO or chlorophyll-a concentration between control and HW mesocosms. We then used the value of the slope of the linear regression between two subsequent time points (during and after a HW) as a measurement of recovery. For that, we calculated the slope between day 3 and 10 (during and after the first HW), 15 and 24 (during and after the second HW), and 30 and 38 (during and after the third HW). A positive slope was interpreted as sign of recovery, whereas a negative slope as a sing of missing recovery. In case of critical slowing down, we would expect the slope of recovery to become increasingly less positive, and perhaps eventually negative. In case of rescue, we expect the slope to become close to zero after the first HW, as this would suggest a smaller effect of the second and third HW determined by a change in the community, that may have shifted towards a more resistant composition.

To investigate the effects of the HWs on community composition, we performed a non-parametric permutational multivariate analysis of variance (PERMANOVA, function adonis2 of the R package “vegan” (Oksanen *et al.* 2019) with 999 permutations and based on Bray–Curtis distances.

All statistical analysis and figures have been done in R (R version 4.2.2; R Core Team 2022). Data and code to reproduce the analysis and figures is available at <https://github.com/FrancescoPola/rescue_critical_slowing>.

# Results

During the experiment, water temperatures ranged between 13.1 and 27.6 °C (Amb), and 13.2 and 35.7 °C (HW) (Fig. 1). Throughout the whole experiment the average ambient water temperature was 20.18 °C and ranged between 13 °C and 29.64 °C (Fig. 1). Except for a few temporary declining temperature periods, the ambient water temperature gradually increased during the experiment. The average HW water temperature was 24.19°C, and ranged between 13.21°C and 35.73°C.

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Figure 1. Water temperature dynamics over time in ambient mesocosms (blue line) and HWs mesocosms (orange line).

Dissolved oxygen declined sharply after the first HW but recovered quicky returning to values higher than the control between the first and the second HW (Fig. 2). The second HW determined a similar decreased in DO, which was however completely recovered, and between the second and third HWs, although with a less steep recovery trajectory, DO returned to control levels. The third HW drastically decreased DO during its course and on and after the last HW (day 38), DO further declined, showing no sign of recovery (Fig. 2). The trend was also confirmed by the calculated slopes of the recovery, which became less and less positive after the first two HWs, and eventually turned negative after the third HW (Fig. 2).

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Figure 2. Dissolved oxygen dynamics over time. (a) shows the difference in DO between mesocosm undergoing the HWs treatment and the control (dashed line at zero). The red areas show the three heatwaves. (b) shows the slopes of the linear regression connecting two subsequent time point (during and after a HW) of the difference between DO in control and HW mesocosms. In (b), the first panel shows the slope between day 3 and 10, the second panel shows the slope between day 15 and 24, and the third panel shows the slope between day 30 and 38.

The LMM found a significant interaction between HW and time, suggesting a time dependent effect of the HWs (Table 1).

Table 1. Results of the LMM analysing the effects of HW and time on DO.

| **term** | **estimate** | **std.error** | **statistic** | **df** | **p.value** |
| --- | --- | --- | --- | --- | --- |
| (Intercept) | 2.435 | 0.039 | 62.613 | 26.146 | 0.000 |
| HW | 0.060 | 0.055 | 1.090 | 26.146 | 0.286 |
| Day | 0.003 | 0.002 | 1.957 | 46.000 | 0.056 |
| HW:Day | -0.007 | 0.002 | -2.689 | 46.000 | **0.010** |

The post-hoc analysis showed that there was a significant difference in DO between control mesocosms and mesocosms undergoing HWs from day 24 onward. After day 24, the DO concentration was always significantly lower in mesocosms experiencing the HWs (Table 2).

Table 2. Results of the post-hoc test (estimated marginal means (EMMs) analysis) the LMM assessing the effects of HWs and time on DO.

| **contrast** | **Day** | **estimate** | **SE** | **df** | **t.ratio** | **p\_value** |
| --- | --- | --- | --- | --- | --- | --- |
| Control - HW | -4 | -0.087 | 0.063 | 35.683 | -1.381 | 0.176 |
| Control - HW | 3 | -0.040 | 0.050 | 19.228 | -0.802 | 0.432 |
| Control - HW | 10 | 0.007 | 0.040 | 8.677 | 0.182 | 0.86 |
| Control - HW | 15 | 0.041 | 0.036 | 6.142 | 1.122 | 0.304 |
| Control - HW | 24 | 0.101 | 0.041 | 9.486 | 2.490 | **0.033** |
| Control - HW | 30 | 0.142 | 0.049 | 18.925 | 2.869 | **0.010** |
| Control - HW | 38 | 0.195 | 0.065 | 37.548 | 3.023 | **0.004** |

Chlorophyll - *a* showed a slight decline after the first two HWs. Though, after the third HW, chlorophyll – *a* concentration abruptly declined in mesocosms experiencing the HWs compared to control levels (Fig. 3). This trend was highlighted also by the calculated slopes of recovery. After the first and second HWs, the slope was slightly negative. Yet, after the third HW, the slope became more negative, decreasing its value by roughly one order of magnitude.

The LMM analysis showed that the HW treatment had a significant effect on chlorophyll- a concentration (Table 3).

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Figure 3. Chlorophyll *- a* concentration dynamic over time. (a) shows the difference in Chlorophyll *- a* between mesocosm undergoing the HWs treatment and the control (dashed line at zero). The red areas show the three heatwaves. (b) shows the slopes of the linear regression connecting two subsequent time point (during and after a HW) of the difference between Chlorophyll *- a* in control and HW mesocosms. In (b), the first panel shows the slope between day 3 and 10, the second panel shows the slope between day 15 and 24, and the third panel shows the slope between day 30 and 38.

Table 3. Results of the LMM analysing the effects of HW and time on Chlorophyll *- a.*

| **term** | **estimate** | **std.error** | **statistic** | **df** | **p.value** |
| --- | --- | --- | --- | --- | --- |
| (Intercept) | 0.657 | 0.214 | 3.071 | 25.799 | 0.005 |
| HW | -0.650 | 0.303 | -2.148 | 25.799 | **0.041** |
| Day | 0.011 | 0.010 | 1.108 | 46.000 | 0.274 |
| HW:Day | -0.020 | 0.014 | -1.440 | 46.000 | 0.157 |

The relative biomass of different phytoplankton groups in mesocosms undergoing the HWs treatment showed a gradual turnover across the experiment, and became gradually more and more dissimilar to control mesocosms (Fig. 4). The increased compositional dissimilarity was confirmed by the PERMANOVA analysis, which highlighted significantly different compositions between control and HW mesocosms on day 10, 30, and 38 (Table 4).

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Figure 4. Mean relative biomass of different phytoplankton taxa in control and HWs mesocosms in different time points of the experiment.

Table 4. Results of the PERMANOVA analysing the effects of the HWs on phytoplankton community composition in different days of the experiment.

| **Day** | **F** | **R2** | **p\_value** |
| --- | --- | --- | --- |
| -4 | 0.891 | 0.129 | 0.367 |
| 3 | 3.008 | 0.334 | 0.067 |
| 10 | 3.127 | 0.343 | **0.027** |
| 15 | 1.698 | 0.221 | 0.129 |
| 24 | 0.737 | 0.109 | 0.691 |
| 30 | 3.065 | 0.338 | **0.032** |
| 38 | 2.429 | 0.288 | **0.026** |

# Discussion

Our experiment highlights the profound impact of recurring HWs on the resilience of freshwater ecosystems. Our findings align with the growing body of literature that highlights the detrimental effects of HWs on aquatic ecosystems (Hermann *et al.* 2024; Polazzo *et al.* 2023; Ross *et al.* 2021).

Critically, we show that multiple repeated HWs can slow down the rate of recovery of a freshwater ecosystem, which may suggest that repeated extreme events can tip ecosystems to alternative stable states.

The observed trends in dissolved oxygen (DO) levels suggest a pattern of critical slowing down, indicated by the gradual reduction in recovery rate with repeated disturbances (Veraart et al. 2012). Initially, the system exhibited resilience, as evidenced by the quick recovery of DO levels after the first HW. However, the recovery rate decreased progressively after subsequent HWs, and by the third HW, the system failed to recover, indicating a potential loss of resilience and an perhaps the approach towards a tipping point. The significant interaction between HW and time from the linear mixed model (LMM) analysis further supports the notion of a time-dependent deterioration in ecosystem functioning due to recurrent HWs.

Chlorophyll-a concentrations mirrored the DO patterns, with slight declines after the first two HWs and a drastic drop after the third. This suggests that the primary productivity of the phytoplankton community was increasingly compromised with each successive HW. The steeper negative slope in chlorophyll-a recovery after the third HW indicates a critical point where the community's ability to maintain its primary productivity was severely hindered. The significant effect of HWs on chlorophyll-a concentration from the LMM analysis corroborates the observed trend and emphasizes the cumulative stress imposed by recurrent HWs.

The gradual loss of resilience found in our experiment was linked to an increased compositional dissimilarity in the phytoplankton community. Indeed, the turnover in phytoplankton community composition towards increasing dissimilarity with the control mesocosms throughout the experiment indicates a shift towards a new community state. The significant compositional differences detected by the PERMANOVA analysis on days 10, 30, and 38 highlight the extent of this shift. The new community composition did not promote stress-tolerant species able to maintain ecosystem functioning and increase resilience, which led us to exclude any rescue – related change in composition.

On the contrary, the increased compositional dissimilarity linked to the increasingly impaired recovery rate further supports the critical slowing down process. Indeed, critical transitions to alternative stable state are often related to dramatic shift in composition (Bertani *et al.* 2016; Meunier *et al.* 2024; Wernberg *et al.* 2016). Classic example are the shift from clear water state dominated by macrophyte to a turbid water state dominated by phytoplankton in shallow lakes (Scheffer 2009).

We want to emphasise, however, that we did not find any evidence for a critical transition happening in our experimental systems. Although critical slowing down may appear even far away from the tipping point (van Nes & Scheffer 2007), we do not have support for stating that, in out study, a tipping point was approaching. Nervetheless, we want to stress that critical slowing down is a highly relevant phenomenon for stability more generally, independently of whether a transition occurs. Understanting whether and why a system undergoing repeated perturbations loses resilience and recovery potential has deep ecological and management consequences, even in systems that do not exist in multiple stable states.

In our study, the repeated stress caused by increasingy stronger HWs dermined a drastic change in the phytoplankton community composition. The new compositional configuration was unable to maintain and / or recover functional levels similar to unperturbed systems, suggesting an overall increase vulnerability to subsequent perturbations. These results force us to evaluate the consequences of extreme climatic events on the functioning of communities and ecosystems in a future world, where extreme events are likely to become more frequent as well as more sever (Perkins et al. 2012; Woolway et al. 2021, 2022).

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