

# Effect of Extreme Climate Events on Lake Ecosystems

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The Earth is facing a major change in climate due to ongoing global warming [1], and as a result of this warming, the occurrence of more extreme weather is also expected to increase. Accordingly, the impacts of extreme climatic events on lakes have been receiving more and more attention in recent years. Furthermore, advances in real-time high-resolution monitoring, together with an increase in the use of in-situ monitoring platforms on many lakes across the globe, now make it possible to track even the short-term effects of such events in lakes with differing characteristics and local climates. Such high-resolution data can also be used to better validate dynamic models of lake processes, models which are essential if the projected effects of global warming on lake ecosystems are to be quantified.

Extreme climatic events include heatwaves, storms, extreme calm periods, sudden and intense rainfall, and droughts. These changes in local weather have the potential to result in physical, chemical, and biological changes within lakes. In deep lakes, for example, heatwaves and calm periods lead to stronger stratification and, if the lakes are nutrient enriched, often to higher levels of cyanobacterial biomass [2–5]. Similar conditions can lead to temporary stratification of shallow lakes and this, in turn, can result in higher internal loading of phosphorus and thus eutrophication [6]. Storms often deepen the mixed layer depth and, combined with rain, it may enhance the input of dissolved and particulate matter and ultimately increase eutrophication [7]. Extreme drought may result in reduced water level, higher salinity, and higher nutrient concentrations [8], and extreme rain may result in increases in the flux of dissolved organic carbon from catchments [9]. Such effects may be of short-term duration, but if severe, they may have long-lasting consequences, particularly in lakes with longer retention times [10].

There is no universally accepted approach to define extreme events for lake studies. Extremes in climatic and hydrological datasets are generally defined by the use of thresholds based on, for example, a top or bottom percentile of the observed data from the site [11]. This type of threshold approach does allow for a systematic identification and assessment of events but has the drawback that the absolute threshold values will differ depending on location and the local climate. Nevertheless, thresholds based on local meteorological data have been used to identify potential extreme events within lakes (e.g., [12]). Definitions based on within-lake physical changes can, however, be more complex due to inconsistency in the metrics used to define such extremes [13]. Other commonly used and equally valid approaches focus on the effects of, for example, named storms (e.g., [14]) or



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studies on extreme or episodic responses within the lakes, even though the meteorological conditions that trigger the response may not in itself be over any extreme threshold [10]. This Special Issue includes all of these approaches and addresses effects of extreme events based on field studies, controlled experiments, and modelling.

While winter storms are generally common in western Europe, the rarer summer storms may have more pronounced impacts on lake physics. Using a 13-year high frequency dataset of weather and lake thermal structure from the west of Ireland, Andersen et al. [15] quantified the effects of storms (defined using local wind speeds) on the physical conditions in a monomictic, deep lake situated close to the Atlantic Ocean. In winter, changes were distributed over the entire water column, whereas in summer, when the lake was stratified, storms only impacted the smaller volume above the thermocline. During an average summer storm, the lake number dropped by an order of magnitude, the thermocline deepened by an average of 2.8 m, water column stability decreased, and the epilimnion temperature decreased by a factor of five compared to the average change in response to winter storms (0.5 °C vs. 0.1 °C). The results suggest that any projected increase in summer storm frequency may have important implications for lake physics and biological pathways.

In the Arctic and Alpine areas, the frequency of glacial lake outburst floods (GLOF) is increasing due to climate change, and this may also have strong effects on circulation patterns and biota in downstream aquatic ecosystems. Ross et al. [16] explored the response of circulation and zooplankton abundance in a Patagonian fjord to GLOF events between 2008 and 2014 based on measurements of current velocities, density, in-situ zooplankton samples, and volume backscatter (Sv) derived from an acoustic profiler. They found an increase in Sv in late winter and spring, which coincided with a high species richness of zooplankton. In addition, diel vertical migrations were recorded during this seasonal increase. These events combined with wind forcing that deepened the pycnocline led to peaks in zooplankton abundance, indicating that mixing conditions could favor secondary production.

The concentration of dissolved organic carbon (DOC) in freshwater catchments has implications for the carbon availability in downstream lakes and for water supplies. Jennings et al. [17] used high-frequency fluorescence data, a proxy for DOC, to investigate the relationship between stream discharge and DOC in a blanket peat catchment during extreme high flows, as well as the relationship between inflow and in-lake DOC concentrations. They found that for approximately 2/3 of extreme events, there was a decrease in stream DOC concentrations on the rising limb of the hydrograph rather than an increase. Events where DOC concentrations increased dominated only in spring and summer. In comparison to the stream, concentrations in the downstream lake were less variable, and peaks and troughs were damped and lagged. Warner et al. [18] also evaluated the effects of extreme events on the quality of DOC that exported to lakes by measuring changes in DOC concentration and quality in boreal lakes following storm events in different seasons. They found differences in the response of DOC quality metrics between an early summer and an autumn storm, with changes in DOC quality being dependent on lake features. During the early summer storm, greater changes in various DOC quality metrics were observed in deep lakes with longer residence times, whereas during the autumn storm, lakes with large watershed area to lake area ratios experienced the greatest changes. Land cover was highly correlated with changing DOC quality metrics in the early summer storm but did not play a significant role in the autumn storm response. They concluded that seasonal differences in the effects of storms on boreal lakes are mediated by a combination of lake and watershed characteristics as well as seasonal differences in climate such as solar radiation and antecedent weather conditions.

Calderó-Pascual et al. [19] conducted a study in Lough Feeagh, Ireland, during an exceptional heatwave in 2018, which broke long-term temperature and drought records. These calm, stable conditions were abruptly interrupted by a second extreme storm event in late June. Using high-frequency monitoring data, coupled with fortnightly biological sampling, they showed that the storm resulted in an intense mixing event that changed

the stratification pattern of the lake, even though stratification re-established quickly after the storm as the heatwave continued. During the storm, there was a three-fold reduction in Schmidt stability, with a mixed layer deepening of 9.5 m coinciding with a two-fold reduction in chlorophyll *a* and a three-fold increase in total zooplankton biomass. Epilimnetic respiration increased and net ecosystem productivity decreased. The ratio of total nitrogen:total phosphorus in the lake surface waters versus that in the inflow rivers followed different patterns after the storm, a change that led to cascading effects on higher trophic levels and emphasized the key role that extreme weather may have on lake ecosystems.

In the same lake and during the same time period, Hoke et al. [20] studied the bacterial community composition using high-throughput sequencing to explore the bacterial community composition in this humic oligotrophic lake and to assess the impacts on composition dynamics related to extreme weather events. Filtration was used to separate free-living and particle-associated bacterial communities and amplicon sequencing was performed for the 16S rRNA V4 region. Two storms, six high discharge events, and one drought period occurred during the sampling period. They found that the particle-associated community was more likely to respond to physical changes, such as mixing, while the free-living population responded to changes in nutrient and carbon concentrations. Generally, however, a high stability of the bacterial community was observed, suggesting that the bacterial community is relatively resilient to extreme weather events.

Using an experimental mesocosm approach, Cao et al. [21] studied the effect of simulated extreme precipitation on submerged macrophytes based on three different community treatments. These included six species of various growth forms in various combinations. Two levels of extreme precipitation treatment were simulated, one simulating a sudden increase of water level from 75 cm to 150 cm within one day and the other a gradual increase to the same water level within 3 months. They found that the macrophyte community biomass was resilient to the disturbances, while species-specific variations in responses, in terms of biomass, maximum height, and sexual reproduction, were found. They concluded that freshwater ecosystems with high coverage of submerged macrophytes may be overall resilient to extreme precipitation under nutrient-limited conditions, especially communities with diverse growth forms.

Three papers in this issue deal with the ecological effects of a 5 °C simulated heatwave. Using the world's longest-running shallow lake experiment facility, investigations were conducted in mesocosms adapted to three different temperature treatments (ambient, IPCC A2 scenario, and A2+50% and two levels of nutrient loadings (high and low)) for 11 years prior to the initiation of the additional 5 °C heatwave. Thus, each mesocosm was adapted to different conditions prior to the onset of the experiment. Filiz et al. [22], Işkın et al. [23], and Jeppesen et al. [24] studied the effects of the simulated one-month summer heatwave in the A2 and A2+50% mesocosms on phytoplankton, zooplankton, and metabolism, respectively. Filiz et al. [22] found major differences in the phytoplankton community and biomass between the low and high nutrient mesocosms, while the effects of the temperature treatments as well as the heatwave were modest and clearest in the high temperature scenario in the low nutrient treatments. Stability analyses revealed that the high nutrient mesocosms were less affected by the heatwave press disturbance, most likely because the dominant algae group, cyanobacteria, is rather tolerant to variations in temperature. The authors concluded that the phytoplankton community was strongly affected by the nutrient level but less sensitive to the heatwave-induced changes in temperature in these systems that had already adapted to long-term temperature differences prior to the experiment.

Also for zooplankton, the nutrient effect was much stronger than that of temperature in this experiment [23]. Before the heatwave, taxon richness was higher and functional diversity and evenness were lower in the high nutrient tanks. Lower biomass of large Cladocera and lower zooplankton:phytoplankton ratios indicated higher fish predation in these tanks as well. None of these metrics were affected by temperature. However, the zooplankton community structure indicated a higher predation pressure from fish at low nutrient concentrations during the heatwave, while the opposite pattern was found at

high nutrient loading at the highest temperature, the latter likely reflecting observed fish kills in these tanks. Stability analyses also suggested modest effects of the heatwave as total zooplankton biomass showed overall high resistance.

The metabolism metrics were also affected by nutrients but also by long-term temperature adaptation compounded by the heatwave [24]. Nutrients had a substantial effect on both gross primary production (GPP), ecosystem respiration (ER), net ecosystem production (NEP), and bacterioplankton production (BACPR), and positive effects of temperature on ER and BACPR were also found. The heatwave had a positive effect on GPP and ER. All of these metabolic process variables also responded to a cool and cloudy-low irradiance event in the middle of the heatwave, resulting in a severe drop in  $O_2$ , not least in the heated mesocosms. In the same experiment, substantial effects associated with the heatwave were also found on the biomass of bacterioplankton, heterotrophic flagellates, and ciliates, respectively [25], and to some degree also on the greenhouse gas (GHG) dynamics [26]. The results from this experiment collectively indicated that microbial communities and ecosystem processes are more sensitive to a short-term heatwave than larger-bodied and more slow-growing organisms such as zooplankton [24].

Modelling experiments allow exploration of the impacts of extreme climatic events under current and future conditions. Gal et al. [27], using a weather generator, constructed 30-year scenarios that included no change in climate conditions, a gradual progressive change, increased frequency of heatwaves, and a merging of the latter two. They elucidated the effect on a lake's physical properties applying an ensemble of one-dimensional (1-D) hydrodynamic lake models. Such 1-D models have been shown recently to reproduce the overall direction and magnitude of change during extreme events with accurate timing and little bias, although with some increase in uncertainty during events [28]. The study of Gal et al. [27] revealed that the gradual increase scenario had the largest impact on annual water temperatures and on the length of the stratification period; however, increased heatwaves had a large effect on the summer lake conditions and introduced a larger degree of variability in water temperature. They also highlighted that the use of an ensemble of models provided results with a higher degree of confidence, and they therefore advocate for the need to include heatwaves in climate studies to better understand the possible consequences for lake ecosystems.

Chen et al. [29] used a 1-D hydrodynamic ecosystem-model to determine the influence of extreme climate events on a temperate and temporarily summer stratified lake in Denmark. After calibration and validation, they ran a range of extreme warming scenarios that affected the air temperature inputs to the model and were based on data from the heatwave seen over northern Europe in May–July 2018, mimicking situations of extreme warming returning every year, every three years, every five years in summer, and all year round, respectively. They found only modest impacts of the extreme climate events on internal nutrient loading; however, there were much stronger effects on the summer average of chlorophyll *a* and peak cyanobacteria biomass, which were up to 39% and 58% higher than during the baseline, respectively. The phytoplankton blooms occurred up to 15 days earlier and lasted up to 15 days longer during the heatwave years relative to the baseline, illustrating the strong effect that more frequent and longer-term heatwaves may have on temperate lakes.

This special issue highlights that lakes can be severely affected by extreme events but also that resistance to such events and fast recovery may occur. Generally, however, knowledge of the effects of extreme climatic events on lakes is modest and they need to be explored further, especially given the projected changes in such events due to global warming. This lack of knowledge includes how series of concurrent or sequential extreme events, such as multiple storms or mixtures of storms and heatwaves, which may come with higher frequency in the future, will affect ecosystem response and resilience. High frequency field sampling, experiments, and (real time) modelling are promising tools to identify short-term responses to extreme events and a series antecedent conditions encompassing the effects of ecosystem resilience. For effects of extreme climatic events



with longer duration, such as the 8.2K cooling period, the mid-Holocene warming period, and the Little Ice age, paleoecological studies can provide valuable insight into responses, resilience, and resistance (e.g., [30–35]), and in some cases they have revealed long-lasting effects following such extremes. [34]. Moreover, long term monitoring, including use of in-situ stations with sensor measurement of multiple parameters, can provide evidence of on-going changes at the decadal time scale and in some instances shown sharp changes, for instance from a colder period in the 1970s to a warmer period after 1980 (e.g., [35,36]). A fruitful way forward is to combine these various approaches to obtain more solid information about lake responses to extreme events.

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