

Water-level fluctuations and nutrient enrichment interact to alter ecosystem structure in distinct ways at different water depths

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Funding information

EU INTERREG IVA Cross-border Programme

Abstract

1. Aquatic ecosystems are often impacted by several human-derived pressures simultaneously. A key challenge for ecologists is to develop mechanistic understanding of the cumulative effects of multiple stressors on freshwater biodiversity.
2. We established an outdoor mesocosm experiment to examine the individual and combined effects of two key stressors on lake ecosystems globally—nutrient enrichment and amplified water-level fluctuations—on benthic algal and macroinvertebrate assemblages along a gradient in littoral water depth.
3. We found that nutrient enrichment and water-level fluctuations not only altered the structure of littoral communities when acting individually, but also interacted to dynamically alter biomass and community structure in different ways at different depths. As expected, enrichment increased benthic algal biomass significantly in very shallow waters. Yet, when enrichment co-occurred with water-level fluctuations, this pattern was reversed, with algal biomass increasing significantly in deeper waters, but not in the shallows that were exposed to fluctuating water levels. This pattern occurred across all algal groups that we examined except for green algae. Green algae biomass increased with nutrient enrichment, was greatest in the shallows, and remained unaffected by fluctuating water levels.
4. Water-level fluctuations modified the functional feeding group structure of benthic macroinvertebrate communities, reducing relative densities of collector-gatherers and increasing those of predators. However, these changes occurred only in the shallow-most regions exposed directly to fluctuating water levels.
5. Our results reveal how two globally important stressors of standing water systems can interact in different ways in different ecological contexts and show how stressors can combine to have unanticipated impacts that vary in space. Our findings underscore the potentially highly multifaceted and complex nature of stressor combinations that present a major and growing challenge to ecosystem management, particularly in light of accelerating global environmental change.

KEYWORDS

littoral, mesocosm, nutrient enrichment, pond, water-level fluctuations

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1 | INTRODUCTION

Freshwater ecosystems are fundamental to sustaining human well-being (Aylward et al., 2005; Carpenter et al., 2011). They are, however, exposed to substantial and ever-increasing anthropogenic pressure across the globe (Dudgeon, 2014; Dudgeon et al., 2006; Reid et al., 2019). Anthropogenic stressors disturb freshwater ecosystems in a variety of ways (Craig et al., 2017; Ormerod et al., 2010; Vörösmarty et al., 2010). Such stressors do not always interact predictably and frequently have unanticipated consequences (Christensen et al., 2006; Darling & Côté, 2008; Jackson et al., 2016; Mantyka-Pringle et al., 2014). What is becoming clear is that ecosystems are increasingly impacted by several pressures simultaneously (Reid et al., 2019). Accordingly, developing a mechanistic understanding of how key pressures can interact has become a central challenge for ecologists.

Two of the most important stressors on lake ecosystems globally are anthropogenic nutrient enrichment (Donohue, Jackson, et al., 2009; Heisler et al., 2008; Zhang et al., 2019) and amplified water-level fluctuations (Evtimova & Donohue, 2016; Wantzen et al., 2008; Zohary & Ostrovsky, 2011). Large influxes of nutrients resulting from anthropogenic activities such as agriculture, industry and septic treatment are a major threat to freshwater communities (Smith et al., 2006). In lakes, nutrient enrichment alters both community structure and function in the water column and the benthos (Donohue et al., 2009a, 2009b; Dubey & Dutta, 2020; Zhang et al., 2019). Ecological consequences of modifications to natural patterns of water-level fluctuations are, however, less well-understood.

Most lakes experience natural fluctuations in water levels across seasons (Keough et al., 1999; White et al., 2008), yet freshwater extraction from lakes can significantly alter the magnitude of water-level fluctuations and drive shifts in seasonality and/or frequency of these normally predictable disturbances (Wantzen et al., 2008). Such alterations to natural water fluctuation regimes can have substantial ecological consequences for lake ecosystems (Evtimova & Donohue, 2016; Wantzen et al., 2008; Zohary & Ostrovsky, 2011). The negative effects of altered water-level fluctuations disproportionately affect littoral zones, where the majority of lacustrine

biological diversity is concentrated (Vadeboncoeur et al., 2011). Water-level fluctuations impact littoral zones directly as a result of desiccation or exposure to extreme temperatures and wind (Balogh et al., 2008) and indirectly as a result of consequent resource scarcity or increased competition for habitat in littoral communities (Gasith & Gafny, 1998). In the short-term, water-level fluctuations may reduce biotic abundance and diversity (Fischer & Öhl, 2005; Fisher & Lavoy, 1972), leading to reductions in or loss of multiple ecosystem functions over longer timescales, including productivity, carbon storage and nutrient cycling (Aroviita & Hämäläinen, 2008; Cantonati et al., 2009). Even though the pressure on lakes resulting from anthropogenically altered water-level fluctuations is growing, and is predicted to be exacerbated considerably by ongoing climate change (Gronewold & Rood, 2019; Woolway et al., 2020), little is known about the combined impacts of amplified water-level fluctuations and other major global stressors of freshwater ecosystems such as nutrient enrichment.

To address this, we established a mesocosm experiment in outdoor ponds, where we manipulated water levels and enriched the ponds with nutrients to determine how these pressures both independently and collectively influence littoral benthic communities along a gradient in water depth. Specifically, we tested whether: (1) water-level fluctuations interact with nutrient enrichment to alter the structure and/or functioning of phyto-benthic algae and benthic macroinvertebrate communities; and (2) the combined effects of water-level fluctuations and nutrient enrichment vary along a gradient in littoral water depth.

2 | MATERIALS AND METHODS

2.1 | Experimental design and setup

We conducted an 8-week factorial experiment in 28 outdoor mesocosms located in the Trinity College Dublin Botanical Gardens (53°18'44"N, 06°15'25"W). The 750-L purpose-built mesocosms faced south and were 1 m (depth) × 1 m (width) × 1.5 m (length) with a sloped bottom (~33°, corresponding to a relatively steep shore in Irish lake systems; Figure 1). Mesocosms were constructed by digging

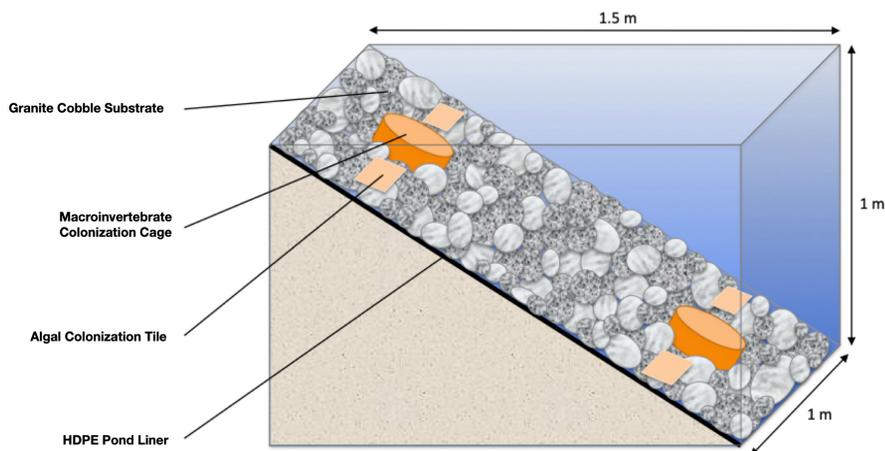


FIGURE 1 Design of our experimental mesocosms (see Methods for detailed description).

into topsoil, and insulating and lining with polyvinyl chloride (PVC) pond liner. Granite gravel and cobble substrate were used to cover the liner to a depth of 10 cm. The mesocosms were then exposed to natural climatic variation for the duration of the experiment.

Each mesocosm was equipped with two macroinvertebrate colonisation cages constructed from 25 cm (diameter) × 10 cm (height) PVC perforated with 1-cm holes spaced every 4 cm over their surface, filled with gravel and placed into the substrate so that the top of the colonisation cages were level with the substrate (Evtimova & Donohue, 2014; García & Donohue, 2010). One cage was placed at each of two fixed water depths (that is, 0.1 m and 0.8 m), together with two 15 × 15 cm ceramic algal colonisation tiles at each depth (Figure 1).

The mesocosms were inoculated with algae and benthic macroinvertebrates from four lakes: Lough Derravaragh (53°39'24"N, 07°21'57"W); Lough Ennell (53°28'10"N, 07°24'04"W); Lough Lene (53°39'45"N, 07°13'56"W); and Lough Owel (53°34'08"N, 07°23'11"W). These lakes were selected based on similarity of water chemistry to the water used to fill the ponds, which was tap water derived from Lough Poulaphouca (53°7'24"N, 06°30'21"W). Macroinvertebrates were collected from stony littoral substrates in each lake using a 500-µm pond net. Rocks and hard surfaces were wiped at each site to capture invertebrates clinging to hard surfaces. Macroinvertebrates were pooled and an equal volume of well-mixed inoculum added to each pond. The densities and richness of invertebrate assemblages in the mesocosms were similar to those found in nearby natural systems (Donohue et al., 2009a, 2009b). Benthic algae-covered stones also were collected from each donor lake and introduced into mesocosms 3 weeks before the commencement of the experiment such that each mesocosm contained approximately the same colonised stone surface area from each of the donor lakes. To ensure high initial biodiversity, mesocosms were allowed to settle untouched for 3 weeks before the commencement of the experiment on 18 June 2012.

Mesocosms were assigned randomly to one of the following four treatments, each of which was replicated seven times: (1) with water-level fluctuations; (2) with nutrient enrichment; (3) with water-level fluctuations and nutrient enrichment; and (4) no water-level fluctuations or nutrient enrichment (control). Nutrient enrichment was done by adding solutions of ammonium nitrate ($\text{H}_4\text{N}_2\text{O}_3$) and sodium phosphate monobasic ($\text{H}_2\text{NaO}_4\text{P}$) weekly to mesocosms to increase water column concentrations by 2 g N and 0.1 g P. This equates to increases of 2.7 mg N/L and 0.13 mg P/L, which correspond to the upper level of nutrient loadings experienced by eutrophic lake and pond systems in Ireland and significantly greater than those in the lakes from which the organisms used to inoculate the ponds were collected (Environmental Protection Agency, 2023). For water-level fluctuation treatments, water levels in the ponds were lowered by approximately 45 cm and kept at low levels for 3 days and were then refilled gradually over the course of several hours to maximum capacity for 3 days. This water fluctuation regime was repeated weekly and was chosen to simulate short-duration water-level fluctuations of relatively large magnitude found in natural Irish lakes

(Evtimova, 2013). Water level was manipulated using a submersible electric pump and was lowered a few centimetres at a time over the course of several hours. To minimise confounding factors associated with the removal of water from treatments with fluctuations and the replacement with fresh water upon refilling, water was replaced in all ponds, irrespective of experimental treatment, at the same rate. In all circumstances, tap water used for refilling mesocosms was allowed to settle for at least 48 h in one of two 2,600-L tanks before use, to allow residual chlorine-based compounds to settle out.

2.2 | Sampling and laboratory analyses

Phytobenthic algal biomass was assessed *in situ* with a benthic fluorometer (BenthosTorch; bbe Moldaenke GmbH). In addition to providing reliable estimates of total microalgal biomass (Aberle et al., 2006; Kahlert & McKie, 2014), this method enables the differentiation of component microalgal populations (diatoms, cyanobacteria and chlorophytes) based on their fluorescence excitation spectra. Because the distribution of epilithic microalgae is highly heterogeneous at small scales (Hutchinson et al., 2006), we used mean values, averaged across three haphazardly-spaced readings per tile, where each individual reading quantified algal biomass from a 1-cm² area (Rosero-López et al., 2021), in all analyses.

At the conclusion of the experiment, benthic macroinvertebrates were collected from the colonisation cages by removing the cages and preserving their contents with 90% ethanol. All macroinvertebrates were quantified and identified to the lowest taxonomic level practicable using standard taxonomic references, and categorised to functional feeding groups following Merritt and Cummins (1978). This scheme uses autecological traits to separate macroinvertebrate species into 10 primary classes of functional feeding groups.

2.3 | Data analyses

All statistical analyses were done in R 4.1.3 (R Core Team, 2022). We used mixed-model analysis of variance (ANOVA) based on Type III sums of squares to test how water-level fluctuations and nutrient enrichment affected univariate response variables (that is, total chlorophyll-*a*, biomass of cyanobacteria, green algae and diatoms, total benthic macroinvertebrate density and the proportions of individual macroinvertebrate functional groups). Our statistical model comprised three fixed factors: water-level fluctuations (two levels: present and absent), nutrient enrichment (two levels: enriched and ambient) and water depth (two levels: shallow [0.1 m] and deep [0.8 m]). Mesocosm number was incorporated as a random effect to account for variation among mesocosms. Models were implemented using the 'lmer' function in the package *lme4* (Bates et al., 2015) and *p*-values were calculated to confirm the significance of the relationships using the *lmerTest* package (Kuznetsova et al., 2017). *Post hoc* tests were performed using the package *emmeans* (Lenth, 2022) to assess pairwise comparisons among levels of significant terms.

We used permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001; McArdle & Anderson, 2001) with the same fixed factors as the univariate analyses to test for treatment effects on the overall structure of phyto-benthic and macroinvertebrate communities. These analyses were based on Bray–Curtis similarity matrices and were done with 9,999 permutations of the residuals using the function ‘adonis2’ in the *vegan* package (Oksanen et al., 2022). We used similarity percentage (SIMPER) analysis to explore the effects of our experimental treatments on macroinvertebrate community composition (Oksanen et al., 2022).

3 | RESULTS

3.1 | Phyto-benthic algae

Phyto-benthic biomass was influenced by the three-way interaction of water-level fluctuations, nutrients and water depth (ANOVA, $F_{1,23}=24.06$, $p \leq 0.001$). *Post hoc* tests indicate that water-level fluctuations modified the effects of nutrient enrichment across the depth gradient, even though they alone did not affect algal biomass. Specifically, nutrients increased algal biomass at the shallow-most sampling depth (i.e., 0.1 m) in ponds lacking water-level fluctuations. In ponds with fluctuating water levels, however, algal biomass was significantly greater in nutrient-enriched ponds at the deeper focal sampling depth (0.8 m) but was unaffected by nutrient enrichment at the shallow depth (Figure 2a).

We also found a significant three-way interaction among water-level fluctuations, nutrients and depth on the overall community structure of the phyto-benthos (PERMANOVA; pseudo- $F=4.95$, $p=0.009$; Table S1). In terms of individual algal groups, water-level fluctuations, nutrients and depth all interacted to moderate the

biomass of both cyanobacteria (ANOVA: $F_{1,23}=17.28$, $p \leq 0.001$; Figure 2b) and diatoms (ANOVA, $F_{1,23}=16.53$, $p \leq 0.001$; Figure 2d), with patterns consistent to that of overall phyto-benthic biomass (Figure 2a). Biomass of green algae diverged from this pattern, however, because it was not affected by a three-way interaction among water-level fluctuations, nutrients and depth. Rather, biomass of green algae increased significantly with nutrient enrichment (ANOVA, $F_{1,23}=8.12$, $p=0.009$), was highest at the shallow-most sampling depth (ANOVA, $F_{1,23}=12.37$, $p=0.002$), and was unaffected by water-level fluctuations (Figure 2c).

3.2 | Macroinvertebrates

Twenty-seven taxa of benthic macroinvertebrates representing 18 families were found in the experimental ponds at the end of the experiment (Table S2). Densities of benthic macroinvertebrates were significantly greater in nutrient enriched ponds compared to the controls (ANOVA; $F_{1,23}=5.26$, $p=0.003$; Figure 3a). In addition, water-level fluctuations and water depth interacted to modify benthic macroinvertebrate densities (ANOVA; $F_{1,23}=19.24$, $p < 0.001$). Specifically, mesocosms with water-level fluctuations had reduced macroinvertebrate densities at the shallow-most sampling depth (Figure 3a).

Both water-level fluctuations and depth (PERMANOVA; pseudo- $F=6.49$, $p \leq 0.001$) and nutrient enrichment and depth (PERMANOVA; pseudo- $F=2.61$, $p=0.021$) interacted to moderate benthic macroinvertebrate community structure (Table S1). Reductions in Chironominae at the shallow-most sampling depth in ponds with water-level fluctuations primarily drove the observed differences in macroinvertebrate communities (Table S3). Increases in the densities of *Gammarus duebeni*, coupled with reductions in the

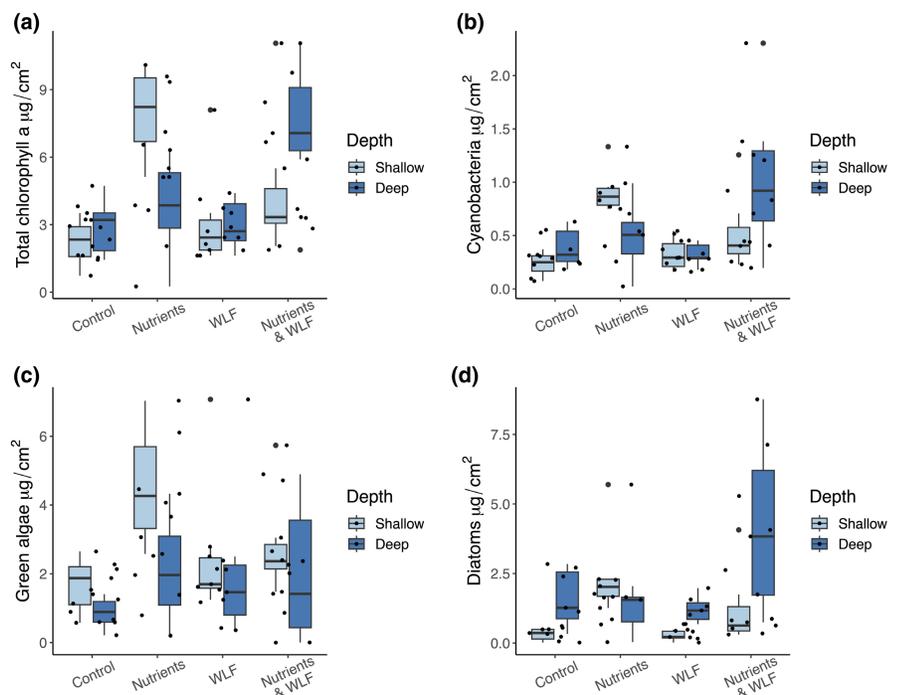


FIGURE 2 Concentrations ($\mu\text{g}/\text{cm}^2$) of phyto-benthic (a) chlorophyll-a, (b) cyanobacteria, (c) green algae and (d) diatoms in our experimental treatments at both the shallow (0.1 m) and deeper (0.8 m) sampling depths at the end of the experiment. Note that the scale of the Y-axis varies across the four panels.

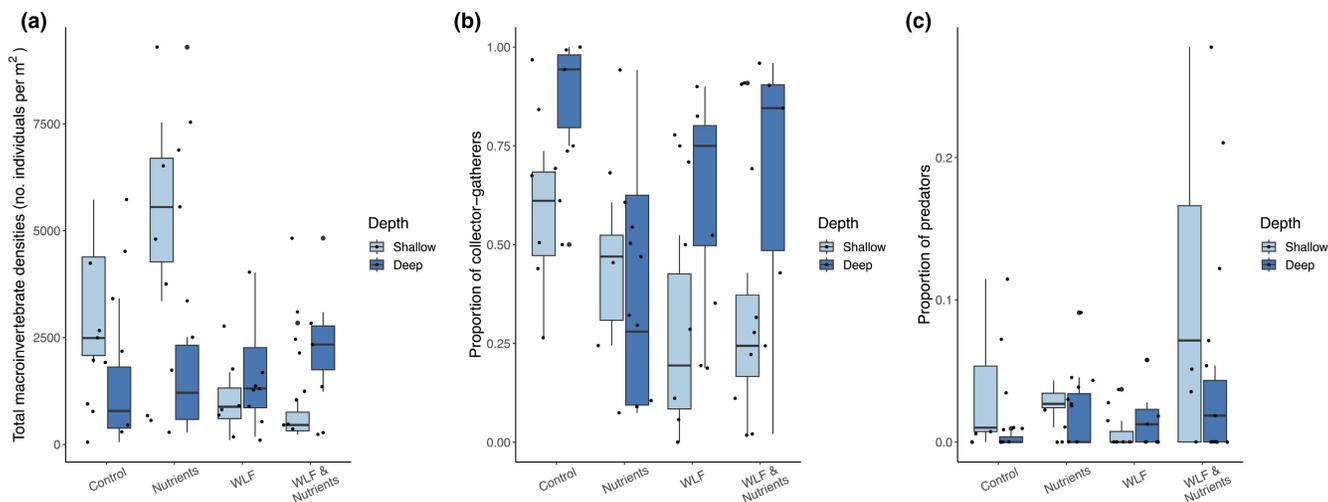


FIGURE 3 (a) Total densities of benthic invertebrates and the proportions of (b) collector-gatherers and (c) predators in our experimental treatments at both the shallow (0.1 m) and deeper (0.8 m) sampling depths at the end of the experiment. Note that the scale of the Y-axis varies across the three panels.

densities of Chironominae, were the primary drivers of shifts in community composition caused by nutrient enrichment at the shallow-most sampling depth, with increases in densities of *Asellus aquaticus* contributing most strongly to nutrient-driven shifts in community composition at the deeper sampling depth (Table S4).

Water-level fluctuations and water depth interacted to modify the functional feeding group structure of benthic macroinvertebrate communities (PERMANOVA; pseudo- $F=10.49$, $p\leq 0.001$; Table S1). In terms of individual functional feeding groups, we found a significant two-way interaction between water-level fluctuations and depth on the relative densities of collector-gatherers (ANOVA; $F_{1,23}=4.63$, $p=0.042$). *Post hoc* tests indicate that water-level fluctuations in isolation reduced the proportion of collector-gatherers at the shallow-most sampling depth (Figure 3b). We also found a significant three-way interaction among water-level fluctuations, nutrients and depth on the relative densities of predators (ANOVA; $F_{1,23}=4.90$, $p=0.037$). Predators increased significantly in mesocosms exposed to combined water-level fluctuations and nutrient enrichment at the shallow-most sampling depth (Figure 3c).

4 | DISCUSSION

Lake communities are increasingly exposed to multiple anthropogenic stressors simultaneously. Our results highlight how such stressors may interact in some ecological contexts but not in others. We found that water-level fluctuations and nutrient enrichment both impacted the structure of our focal experimental communities when acting individually, and frequently interacted with each other to affect various components of the ecosystem in distinct ways at different water depths. These findings underscore how novel effects produced by combinations of globally important stressors in different ecological contexts contribute to the enormous challenge of predicting the ecological consequences of anthropogenic pressures

on lake ecosystems. The potential for unanticipated consequences resulting from multifaceted disturbances demonstrates that impacts of stressors cannot be considered in isolation when they co-occur with additional pressures.

Our results show that nutrient enrichment can have unexpected consequences for lake communities when co-occurring with other stressors such as water-level fluctuations, and that these impacts also vary significantly along the depth gradient. We found that, in isolation, nutrient enrichment increased the biomass of all classes of algae at the shallow-most sampling depth. However, in nutrient-enriched systems with water-level fluctuations, this pattern was reversed, with all algal groups except green algae occurring at higher biomass at the deeper sampling depth in our ponds. Green algae are relatively tolerant of desiccation (Holzinger & Karsten, 2013), which is likely to explain their lack of response to water-level fluctuations in our experimental ponds. Aside from green algae, however, our results suggest that littoral zones exposed by water-level fluctuations may be desiccating to such an extent that motile primary producers are either forced to move downslope, or simply die on the exposed shore. Intermittently higher light availability at the deeper sites caused by water-level fluctuations also may contribute to this apparent shift (Loiselle et al., 2005). As anthropogenic pressures on aquatic systems continue to increase, understanding the interactions between water-level fluctuations and nutrient enrichment will only become even more important.

We found that water-level fluctuations reduced the total densities of macroinvertebrates at the shallow-most sampling depth in our experimental ponds. However, consistent with the findings of Evtimova and Donohue (2014, 2016), we also found that water-level fluctuations increased the relative densities of predators in these shallow littoral regions exposed to fluctuating water levels. Predatory chironomids such as Tanytopodinae are relatively mobile and their distribution strongly depends on prey availability (Real & Prat, 1992; Vodopich & Cowell, 1984). *Gammarus* also are very

mobile and can act as opportunistic predators (Kelly et al., 2002; Macneil et al., 1997, 2002). Perhaps the predators in our experimental ponds benefited from the inability of less mobile prey to move efficiently owing to water-level fluctuations. This could explain the reductions in relative densities of collector-gatherers we observed in the shallows of mesocosms with water-level fluctuations. Simultaneously, fluctuating water levels also may have reduced the availability of organic matter particles on which collector-gatherers feed. Collectively, these findings highlight how amplified water-level fluctuations can impact the trophic structure of littoral communities and suggest that collector-gatherers and predators may be particularly useful as indicator groups for monitoring the ecological impacts of water-level fluctuations.

Aquatic macroinvertebrates are important drivers of ecosystem processes. Alterations to the functional composition of macroinvertebrate communities as seen in our mesocosms can, for example, have significant consequences for energy flows and processes such as the rate of leaf litter decomposition and therefore nutrient cycling in aquatic environments (Frainer et al., 2018). As the frequency and severity of anthropogenic stress increases, the impacts of disturbances on macroinvertebrates may accumulate to further alter community composition, and are likely to have disproportionately strong effects on rare taxa (Haghkerdar et al., 2019). Multiple disturbances also can modify structural characteristics of food webs in aquatic environments. For example, significant variation in the stability of detritus-based food webs has been observed in response to species extinction scenarios (Calizza et al., 2015). Because macroinvertebrates also are an important food source for higher trophic levels in aquatic and riparian habitats (Sato et al., 2016), any alterations to community composition could have even wider-reaching consequences for both nearby aquatic and terrestrial systems.

A common criticism of mesocosm experiments is that their extent or duration may not accurately represent the responses of communities and ecosystems to natural disturbances (Carpenter, 1996). The 8-week duration of our experiment may not, for example, allow sufficient time for substantial effects to be manifested, particularly at higher trophic levels, such as the predatory macroinvertebrates in our ponds. Even so, our pond mesocosms were exposed to natural climatic fluctuations for the duration of the experiment and contained realistic biotic assemblages representative of nearby lakes. This relatively high level of realism in our experiment provides much-needed mechanistic insights into the likely individual and combined impacts of water-level fluctuations and nutrient enrichment in the littoral zone, which can now be tested in the field at larger scales in both space and time. However, the spatial extents, periods, durations, frequencies and intensities of disturbances can all combine to affect ecosystems in distinct ways (García & Donohue, 2010, 2011; Miller et al., 2011; Mrowicki et al., 2016; Yang et al., 2019). As yet, we know remarkably little about the consequences of different temporal patterns and magnitudes of water-level fluctuations for lake ecosystems. The results of experiments like ours run over longer periods of time are, therefore, needed to provide mechanistic information on the interactions between multiple important stressors of lacustrine

ecosystems, and critically, how time and the temporal pattern of disturbances influence these ecological drivers.

The future status of freshwater ecosystems will be determined by the interplay of the stressors examined here, and the many other key elements of global environmental change. Our results show that amplified water-level fluctuations can alter the productivity and biological diversity of littoral zones. These findings align with previous studies indicating that alterations in precipitation patterns and hydrological regimes have substantial effects on algal and macroinvertebrate communities, which are expected to intensify with climate change (DeColibus et al., 2017; Epele et al., 2022). Given that amplified water-level fluctuations in lakes also are likely to be exacerbated even further by predicted increases in climatic variability (IPCC, 2018, 2023), our need to understand the ecological consequences for these systems will only grow more critical. As our demand for water continues to increase, further examinations of how water-level fluctuations interact with other anthropogenic and/or natural stressors to influence lake biota are urgently needed.

AUTHOR CONTRIBUTION

Conceptualisation, developing methods: ID. Data analysis: CG. Preparation of figures and tables: CG. Conducting the research: DM, ID. Data interpretation, writing: ID, DM, CG.

ACKNOWLEDGEMENTS

We thank Lindsay Hislop for her assistance with the experiment. This study was funded by the EU INTERREG IVA Cross-border Programme managed by the Special EU Programmes Body under the project 'Development of targeted ecological modelling tools for lake management; DOLMANT' (ref. no. 002862). Open access funding provided by IReL.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known conflicts of interests that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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How to cite this article: Gorman, C. E., McClean, D., & Donohue, I. (2024). Water-level fluctuations and nutrient enrichment interact to alter ecosystem structure in distinct ways at different water depths. *Freshwater Biology*, 69, 416–424. <https://doi.org/10.1111/fwb.14220>