Large enclosure experiment (LakeLab in Lake Stechlin) to study effects of browning and nutrient loading on lake plankton: light, nutrients, phytoplankton cell size, and community structure (project MARS-2015)

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DATA

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RESEARCH ARTICLE

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Title

Cell size explains shift in phytoplankton community structure following storm-induced changes in light and nutrients

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METHODS

Enclosure experiments: Design and Set-up

An enclosure experiment was carried out between June and July 2015 at the LakeLab, a large enclosure facility deployed in the deep stratified clear-water Lake Stechlin, North-Eastern Germany (Figure 1). A total of 21 enclosures were used, each ca. 20 m deep and 9 m in diameter, enclosing a water volume of ca. 1300 m³ (Giling et al. 2017). A gradient design was chosen to maximize the number of predictor levels, instead of replication at each level (Kreyling et al. 2018, Bergström & Karlsson 2019, Gerhard et al. 2023). This design is well suited to capture non-linear responses of phytoplankton and cyanobacteria to nutrient enrichment (Ptacnik et al. 2008, Carvalho et al. 2013, Lyche Solheim et al. 2024).

The experiment was designed to test for effects of a single heavy rain event by simulating one major initial pulse of nutrients and browning (Figure 2). Seven nutrient levels were fully crossed with three browning levels. The intended concentrations of total phosphorus (TP) covered a broad gradient from oligo-meso- to eutrophic conditions including the critical threshold for cyanobacteria response to nutrient enrichment (Carvalho et al. 2013). An arithmetic progression ($a_n = 18 + n^2$) was applied to select the intended TP concentrations, starting with the lake epilimnion TP (18 μ g L⁻¹). Phosphorus (P) and nitrogen (N) were added as orthophosphoric acid (H_3PO_4) and ammonium nitrate (NH₄NO₃). Nitrogen was added to ensure a ratio of bioavailable N to P as in the lake water, which was close to the Redfield ratio (7:1 by mass). Browning was achieved by adding HuminFeed (HF; HuminTech GmbH, Grevenbroich, Germany), a highly soluble natural commercial product that has the advantage of strongly staining water without adding significant amounts of bioavailable carbon or nutrients (Scharnweber et al. 2021). Three browning levels corresponded to browning levels in natural lakes: A) low = clear or oligohumic (<5 mg Pt L⁻¹, no addition of HF); B) medium = mesohumic (67 mg Pt L⁻¹, addition of 5 mg HF L⁻¹); C) high = polyhumic (133 mg Pt L⁻¹, addition of 10 mg HF L⁻¹). The experiment lasted 7 weeks from early June to late July 2015.

In situ **measurements, sampling and abiotic variables**

The 21 enclosures used in the experiment were equipped with temperature (YSI Inc., Yellow Springs, OH, USA) and PAR (LI-COR Inc., Lincoln, NE, USA) sensors mounted on profilers recording hourly vertical profiles at 0.5 m depth steps (Giling et al. 2017, Lyche Solheim et al. 2024). The light attenuation coefficient was estimated as the slope of the linear regression between ln(PAR) and depth. Depth-integrated water samples from the epilimnion (6-7 m) were collected by hose samplers once a week from 5 June until 21 July 2015. Concentrations of total phosphorus (TP), soluble reactive phosphorus (SRP), total nitrogen (TN), ammonium, nitrite and nitrate were determined by flow injection analysis following ISO procedures (FIAStar 5000, FOSS, Höganäs, Sweden).

Biotic variables

We analyzed phytoplankton species composition and biovolume from epilimnetic water samples (250 mL) taken weekly from 5 June to 21 July and fixed with acidic Lugol's solution. Species were identified and enumerated under an inverted microscope (Nikon Diaphot, Tokyo, Japan, and Leica DMI3000 B, Wetzlar, Germany). Species-specific cell volumes (referred to as cell size below) were estimated from approximations of geometric shapes (European Committee for Standardization 2015). Species-specific biovolumes were then determined as the product of species-specific cell volume and cell abundance. Mesozooplankton were sampled by vertical net tows (90 µm mesh size) from 1.5 m above the sediment to the water surface and preserved in sugar-formalin solution (final concentrations of 50 and 4%, respectively). Biomass of the mesozooplankton species was determined by identifying, counting and sizing specimens under an inverted microscope. Biomass was calculated based on length measurements of 10-30 specimens per taxon and length-dry mass relationships established for Lake Stechlin and other populations (Bottrell et al. 1976, Kasprzak 1983). Biomass carbon was assumed to be 50% of dry mass (Winberg 1971).

LakeLab enclosure facility

Figure 1 | LakeLab enclosure facility deployed in the deep stratified clear-water Lake Stechlin, North-Eastern Germany (Photo: Peter Casper, IGB).

Figure 2 | LakeLab enclosures showing brown and clear treatments during the experiments (Photo: Jens C. Nejstgaard, IGB).

PARAMETERS

Data_Figure1

Temporal dynamics of the light attenuation coefficient (a-c) and mean PAR during daytime (d-f), SRP (g-i), DIN (j-l) and mesozooplankton biomass (m-o) in enclosures receiving no (A: 0 mg HF L^{-1} ; left column: a, d, g, j, m), intermediate (B: 5 mg HF L⁻¹; middle column: b, e, h, k, n) or high (C: 10 mg HF L⁻¹; right column: c, f, i, l, o) levels of cDOM in the form of HuminFeed (HF). The experimental P enrichment (addition of 0, 1, 4, 9, 16, 25 and 36 µg P L−1) is represented by the color gradient from dark blue to yellow.

Date (Year, Month, Day in format YYYY-MM-DD)

Treatment label (A = control, B = low HF, C = high HF combined with the Phosphorus level 1-7 = ambient-high)

HF level $(A = control, B = low HF, C = high HF)$

P level (Phosphorus level, 1-7 = ambient-high)

Attenuation /m1 (Attenuation coefficient of the Photosynthetic Active Radiation (PAR 400-700 nm), in m- $\mathbf{1}_{\mathcal{L}}$

PAR_umol_/m2_/s1 (mean epilimnion Photosynthetic Active Radiation (PAR 400-700 nm) during daytime, in µmol photons m^{-2} s⁻¹)

SRP_µg_/L1 (Soluble Reactive Phosphorus, in μ g L⁻¹)

DIN_μg_/L1 (Dissolved Inorganic Nitrogen, in μg L^{-1})

Mesozoo_mg_C_/m3 (mesozooplankton biomass, in mg C m⁻³)

Data_Figure2

Cell-size distribution of the relative biovolume of phytoplankton species in enclosures receiving no (A: 0 mg HF L^{-1} ; left column: a, d, g, j, m, p); intermediate (B: 5 mg HF L^{-1} ; middle column: b, e, h, k, n, q) or high (C: 10 mg HF L^{-1} ; right column: c, f, i, l, o, r) levels of cDOM before the simulated storm event on 5 June (ai) and at the end of the experiment six weeks later, on 21 July (j-r); sum of the relative biovolumes over seven nutrient enrichment levels (addition of 0, 1, 4, 9, 16, 25 and 36 μ g P L⁻¹) per browning level (a-c, j-l); Generalized Additive Models (GAMs) for each browning level on logit-transformed relative biovolumes of species within each of seven P enrichment levels (d-f, m-o); means and, in gray, 95% confidence intervals (barely visible) of the first-order derivatives across nutrient levels (g-i, p-r).

Date (Year, Month, Day in format YYYY-MM-DD)

Treatment_label (A = control, B = low HF, C = high HF combined with the Phosphorus level 1-7 = ambient-high)

HF level $(A = control, B = low HF, C = high HF)$

P level (Phosphorus level, $1-7 =$ ambient-high)

Size_interval (phytoplankton species cell size intervals of 1 log₂ μ m³ over the range 1-15 log₂ μ m³) **Relative** biovolume (relative biovolumes of species categorized by size intervals of 1 log₂ μ m³ within each enclosure at a given date)

Data_Figure3

Estimated probability of species occurrences as a function of the interaction between cell-size range (smallcelled vs large-celled species) and PAR (a), elapsed time (b) and zooplankton biomass (c) as standardized predictors.

Date (Year, Month, Day in format YYYY-MM-DD)

Treatment label (A = control, B = low HF, C = high HF combined with the Phosphorus level 1-7 = ambient-high)

Species code (species observed in the enclosures)

Standard. Day (standardized predictor of day of experiment)

Standard. PAR (standardized predictor of mean PAR in the epilimnion during daytime)

Standard. Mesozoo (standardized predictor of mesozooplankton biomass)

Cluster (small-celled species: cell size ranging between $0-8 \log_2 \mu m^3$ or species with moderate cell ranging between size 8-15 $log_2 \mu m^3$)

Data_Figure4

Predicted relationships between cell size and relative phytoplankton biovolume along gradients of standardized PAR (**a**) and zooplankton biomass (i.e. putative grazing pressure) (**b**). Bands represent 95% confidence intervals. The three lines per plot indicate species with cell sizes of 3, 7 and 11 $\log_2 \mu m^3$, corresponding to 8, 128 and 2048 μ m³.

Date (Year, Month, Day in format YYYY-MM-DD)

Treatment label (A = control, B = low HF, C = high HF combined with the Phosphorus level 1-7 = ambient-high)

Species Bio code (species included in the biovolume models, observed at least three times during the experiment, sp $Bio#1$ to sp $Bio#120$

Relative biovolume (relative biovolumes of species within each enclosure i.e. proportion of the total biovolume at a given date)

Standard. PAR (standardized predictor of mean PAR in the epilimnion during daytime) Standard. Mesozoo (standardized predictor of mesozooplankton biomass)

Standard. log2Size (standardized log₂ species cell size)

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