

Heatwave-induced functional shifts in zooplankton communities result in weaker top-down control on phytoplankton

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Abstract

Freshwater ecosystems are increasingly affected by rising annual mean temperatures and extreme heatwaves. While heatwaves are expected to have more immediate effects than mean temperature increases on local communities, comparative experimental studies are largely lacking. We conducted a one-month mesocosm experiment to test the effect of different warming scenarios, constantly raised temperatures (+3°C), and recurring heatwaves (+6°C) on plankton communities. We specifically tested how shifts in zooplankton trait composition and functional groups are reflected in ecosystem functioning (top-down control on primary producers). We found that heatwaves had a stronger and more immediate effect on trait and functional group compositions. Heatwaves were associated with larger body sizes, and the decrease in micrograzers resulted in weaker top-down control, leading to elevated algal biomass. Altogether, our results highlight the importance of the indirect effects of heatwaves via inducing shifts in zooplankton functional groups and trait composition which may foster periodic algal blooms.

1 **Title: Heatwave-induced functional shifts in zooplankton communities result in weaker**
2 **top-down control on phytoplankton**

3 **Running head: Climate change effect on plankton communities**

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17

18 **Author Contribution statement**

19 CFV and ZH came up with the original concept, research questions, and experimental
20 design. All authors participated in conducting the experiment, collecting the samples, and
21 taking part in laboratory work. THHN and VK performed zooplankton identification while
22 PD carried out the water chemistry analyses. THHN, ZH, CFV, and KP analyzed the data.
23 The first draft was written by THHN, CFV, and ZH. All authors edited subsequent versions
24 of the manuscript.

25

26 **Data availability statement:** Data will be made available in the Dryad data repository.

27

28 **Abstract**

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30 and extreme heatwaves. While heatwaves are expected to have more immediate effects than
31 mean temperature increases on local communities, comparative experimental studies are
32 largely lacking. We conducted a one-month mesocosm experiment to test the effect of
33 different warming scenarios, constantly raised temperatures (+3°C), and recurring heatwaves
34 (+6°C) on plankton communities. We specifically tested how shifts in zooplankton trait
35 composition and functional groups are reflected in ecosystem functioning (top-down control
36 on primary producers). We found that heatwaves had a stronger and more immediate effect
37 on trait and functional group compositions. Heatwaves were associated with larger body
38 sizes, and the decrease in micrograzers resulted in weaker top-down control, leading to
39 elevated algal biomass. Altogether, our results highlight the importance of the indirect effects
40 of heatwaves via inducing shifts in zooplankton functional groups and trait composition
41 which may foster periodic algal blooms.

42

43 **Keywords:** climate change, warming, heatwave, species interactions, functional traits,
44 microzooplankton, top-down control.

45

46 **Introduction**

47 Heatwaves, periods of acute temperature increase, are expected to occur with
48 increasing intensity, duration, and frequency under climate change (IPCC, 2013). Compared
49 to rising mean temperature, heatwaves might exert a stronger and more immediate effect on
50 communities (Stillman, 2019; Vasseur et al., 2014). However, most experimental studies in
51 freshwater ecology have so far applied static warming treatments in their design (Thompson
52 et al., 2013; Woodward et al., 2016). While the number of studies focusing on the effect of
53 heatwaves on aquatic ecosystems is rising, the majority of these studied single temperature
54 scenarios (but see Striebel et al., 2016; Zhang et al., 2018). This limits our comprehensive
55 understanding of how aquatic ecological communities respond to different warming
56 scenarios, including heatwaves and increasing mean temperatures.

57 Changing temperature regimes can alter population dynamics and species
58 interactions, leading to changes in community composition and ecosystem-level processes
59 (Ohlberger, 2013; Tylianakis et al., 2008). As aquatic species exhibit narrower thermal safety
60 margins compared to terrestrial taxa (Pinsky et al., 2019; Sunday et al., 2012), they may be
61 particularly vulnerable to sudden temperature changes, resulting in high community turnover
62 (Comte & Olden, 2017). Effects of extreme temperatures may be especially strong in shallow
63 lakes, where thermal refugia (e.g., hypolimnetic refuge) are scarce.

64 Zooplankton plays a crucial role in aquatic food webs by transferring energy from
65 primary producers to higher trophic levels. Shifts in dominant species or trait composition
66 can alter energy flow in these ecosystems (Hébert et al., 2016; Ye et al., 2013), e.g., changes
67 in abundance and community size structure affect their overall grazing impact on
68 phytoplankton (Carpenter et al., 1985). Physiology, behaviour, and life history traits
69 (Litchman et al., 2013) can be similarly important when predicting the responses of
70 zooplankton communities to environmental change. Hence zooplankton, with a high
71 diversity of traits and ecological strategies (Barnett et al., 2007) and their key position in
72 aquatic food webs, provide an excellent model for understanding the mechanisms of
73 community reorganization in response to different warming scenarios.

74 Trait-based approaches are powerful tools for addressing the mechanisms of
75 ecosystem change beyond community shifts (Litchman & Klausmeier, 2008). By focusing
76 on key traits, we can forecast functional community reorganization under warming scenarios
77 and link this to changes in ecosystem functioning (Litchman et al., 2006; Schleuning et al.,
78 2020). For example, decreasing body size of ectothermic organisms is a universal response
79 to warming in freshwater systems at both population and community levels (Daufresne et
80 al., 2009), which can weaken the strength of trophic cascades by reducing top-down control
81 (DeLong et al., 2015). These changes can alter the magnitude and direction of energy flow,
82 eventually reflected in the provision of ecosystem services.

83 The aim of this study was to record and contrast the responses of zooplankton
84 communities to warming scenarios of constantly elevated mean temperatures versus
85 heatwaves, and to link community-level shifts to changes in the strength of top-down control
86 on phytoplankton. Warming treatment was designed with a constantly elevated average
87 temperature compared to the ambient (control) treatment, whereas heatwave treatment was
88 designed as pulses of higher temperature for pre-determined time periods. We expected that,

89 from these two temperature treatments, heatwaves would have a stronger and more
90 immediate effect on community composition and ecosystem functioning. In line with this,
91 we predicted that heatwaves would be associated with small body size, as populations of
92 smaller-sized species would respond faster to sudden temperature changes due to their short
93 generation times. The dominance of smaller zooplankton species may imply weaker top-
94 down control on primary producers, hence we expected increased phytoplankton biomass,
95 especially in response to heatwaves.

96

97 **Material and Methods**

98 *Experimental design and environmental parameters*

99 We conducted a one-month outdoor mesocosm experiment between June and July
100 2020 at the Balaton Limnological Institute of the Centre for Ecological Research. Twelve
101 mesocosms were filled with water directly from Lake Balaton two days before the start of
102 the experiment. The water level was set to 1.20 m, resulting in an experimental volume of
103 3,000 L (inner diameter of mesocosms: 2 m; maximum depth: 1.5 m). The water column of
104 each mesocosm was constantly mixed with an airlift system (with 0.6 m³ h⁻¹ carrying
105 capacity) to prevent vertical stratification (Striebel et al., 2013) hence representing shallow
106 lake ecosystems that are regularly mixed by the wind. Besides, it also ensured that dissolved
107 oxygen levels were saturated in all mesocosms during the experiment, which was followed
108 with daily DO measurement with a sensor. The airlift consisted of a PVC pipe hanging in
109 the center of each mesocosm, in which compressed air released from a tube produced a gentle
110 upward current. As the primary focus of the experiment was to study the responses of pelagic
111 plankton communities, we did not include fish, macrophytes, or sediment in the mesocosms.
112 Mesocosms were covered with a mosquito mesh to prevent larger debris from falling into
113 the tanks and the colonization of macroinvertebrates that could influence the nutrient level
114 and species interactions in the water.

115 Three treatments, each replicated four times, were randomly assigned to the 12
116 mesocosms: (1) ambient environmental conditions (C - control); (2) warming set to a
117 constant elevation of 3°C above the control conditions (W - warming); and (3) recurring 1-
118 week 6°C heatwaves (H - heatwaves) during weeks one and three (**Figure 1a**). Both warming
119 scenarios (W and H) received an identical total energy input but in different pulses, and both
120 started on the first day of the experiment. Water temperature throughout the experiment was

121 recorded automatically in 10-minute intervals. Regular nutrient measurements (detailed in
122 the **Supplemental Information**) were carried out to monitor and, if necessary, ensure
123 relatively constant levels of basal resources by nutrient addition, which was eventually not
124 necessary as they were comparable across treatments (**Figure S1**).

125

126 *Chlorophyll a*

127 After thorough mixing of water column, a vertically integrated water sample was
128 collected with a PVC tube sampler for chlorophyll *a* (Chl*a*) and nutrient measurements
129 pooled from three random locations in each mesocosm and filtered through a 100- μ m
130 plankton mesh to obtain water free of large zooplankton. To measure Chl*a* concentration, a
131 proxy for phytoplankton biomass, 500-850 mL of water (depending on algal densities) was
132 filtered through glass microfiber filters (Whatman GF/F) twice a week. Subsequently, the
133 spectrophotometric determination was carried out after hot methanol extraction, using the
134 absorption coefficients determined by Iwamura et al., (1970). Data was converted to
135 phytoplankton dry weight (μ g dry weight L⁻¹) by a multiplication factor of 100 for
136 subsequent analyses (Reynolds, 2006).

137 Additionally, to obtain higher-frequency data on Chl*a*, and hence phytoplankton
138 dynamics, we measured Chl*a* fluorescence daily (maximum fluorescence yield; **Figure 1b**)
139 with a handheld fluorometer (AquaPen AP 110-C, Photon System Instruments). We took
140 samples from each mesocosm every morning during the experiment from the central surface
141 water of the mesocosms (next to the airlift, where water was well-mixed). Measurements
142 were carried out after a 30-minute dark adaptation period to avoid potential bias resulting
143 from short-term physiological changes. Chl*a* fluorescence was measured using the OJIP
144 protocol (Stirbet & Govindjee, 2011). We assessed the overall precision of Chl*a* fluorescence
145 measurements by testing the relationship between Chl*a* concentration and fluorescence via
146 linear regression (**Figure S2, S3**).

147

148 *Zooplankton*

149 To determine initial densities and community composition, zooplankton were
150 sampled at the start of the experiment (day 0, before the start of the warming treatments).
151 Subsequently, samples were collected twice a week with a Schindler-Patalas plankton trap

152 (volume: 10 L, with a net mesh size: 45 μm) from three randomly chosen locations of the
153 mesocosms, which represented different vertical layers, hence resulting in a depth-integrated
154 sample, and preserved in 70% ethanol. We counted and identified zooplankton with an
155 inverted microscope at 20 \times magnification. For microcrustaceans, we used the average body
156 lengths obtained from the regular monitoring data of Lake Balaton (provided in **Table S1**),
157 and then we converted body length to biomass (dry weight), following published length-
158 weight relationships (McCauley, 1984). As similar data were not available for Rotifera, here
159 literature data (Cieplinski et al., 2018; Gosse, 1851; Roche, 1993; Skorikov, 1986) was used
160 as average body length and biomass (dry weight) was calculated similarly based on length-
161 weight relationships (Finlay & Uhlig, 1981). Traits were assigned to each species, including
162 body length, body mass, reproduction mode, feeding mode, generation time, and clutch size,
163 according to **Table S1**.

164

165 *Biomass ratios as indices for changes in top-down control*

166 Biomass ratio of organisms at higher and lower trophic positions can be used as a
167 measure of the strength of top-down control (Shurin et al., 2012). We, therefore, calculated
168 the ratio between zooplankton (ZP, $\mu\text{g dry weight L}^{-1}$) and phytoplankton (PP, $\mu\text{g dry weight}$
169 L^{-1}) biomass, referred to as ZP:PP, and tested its potential response to the different warming
170 treatments. As a further measure of changes in the trophic structure and functioning, we also
171 analyzed the temporal trend of the biomass ratio of the two dominant functional groups, the
172 small-bodied micrograzer Rotifera and the larger omnivorous Copepoda across treatments
173 (R:C).

174

175 *Data analysis*

176 To visualize the temporal dynamics of Chl a , zooplankton biomass (ZP), and ratios
177 of zooplankton:phytoplankton (ZP:PP) and Rotifera:Copepoda (R:C) in the different
178 treatments, we fitted generalized additive models (GAMs) on the respective data for each
179 treatment over the experimental duration. For this, we used the “geom_smooth” function of
180 the package “ggplot2” (Wickham, 2016), with $k=7$ for Chl a and $k=4$ for the other datasets.
181 To test for treatment-specific differences for ZP, ZP:PP, and R:C, we performed non-
182 parametric Kruskal–Wallis (KW) tests for each sampling date after the double square root

183 transformation of data. Subsequently, we applied Dunn's *post hoc* test to reveal pairwise
184 differences (p-values were adjusted with the Holm method) using the package “FSA”.

185 To test the effect of treatments on daily Chla fluorescence, we excluded the first days
186 (days 0-3) when Chla still showed a decreasing trend in all treatments. Then, we split the
187 dataset into two periods: days 4-14 including the first heatwave (until day 7) and its direct
188 aftermath (days 8-14) and days 16-28 including the second heatwave (days 15-21) and its
189 direct aftermath (days 22-28) For each dataset, we used a generalized additive mixed model
190 (GAMM) with treatment as the main linear predictor, adding time with varying shapes of
191 smooth according to individual mesocosms and a temporal autocorrelation within individual
192 mesocosms to account for random effects. In case of a significant treatment effect, we
193 performed a pairwise test for multiple comparisons based on the GAMM with single-step p-
194 value adjustment with the package “multcomp” (Bretz et al., 2010).

195 To test how environmental predictors, or in our case, treatments, can filter species
196 traits based on species abundances, we performed RLQ analyses (Dolédec et al., 1996) with
197 the package “ade4” (Dray & Dufour, 2007) separately for each date. The RLQ method
198 performs a double inertia analysis including three data matrices (environmental variables by
199 samples - R; species by samples - L table; and traits by species - Q table) and produces their
200 simultaneous ordination. Fourth-corner statistics were computed based on 9999
201 permutations by permuting both sites and species (with “modeltype=6”), to avoid Type I
202 error (Dray et al., 2014). We used the log(x+1) transformed biomass of zooplankton species
203 and the traits presented in **Table S1**.

204 To quantify the direct and indirect trophic relationships between the main organism
205 groups across treatments, we applied a structural equation model (SEM) on the copepod
206 (double-square-root transformed) and rotifer (cubic-root transformed) biomasses and Chla
207 fluorescence (untransformed). We started with an initial SEM that included all the plausible
208 pathways between plankton groups and the treatments using the R package “piecewiseSEM”
209 (Lefcheck et al., 2015). Each relationship within the SEM was estimated with linear mixed-
210 effects models with a temporal autocorrelation structure of order 1 (AR-1) and mesocosm
211 number as a random factor. We expected that any top-down effect on phytoplankton would
212 manifest with a time lag. Therefore, separate SEMs were fitted using the Chla values on the
213 zooplankton sampling days and the values 0 to 6 days after the samplings. The SEM yielding

214 the highest explanatory power for Chla (based on R^2) was selected to describe the causal
215 network between the three organism groups and the treatments.

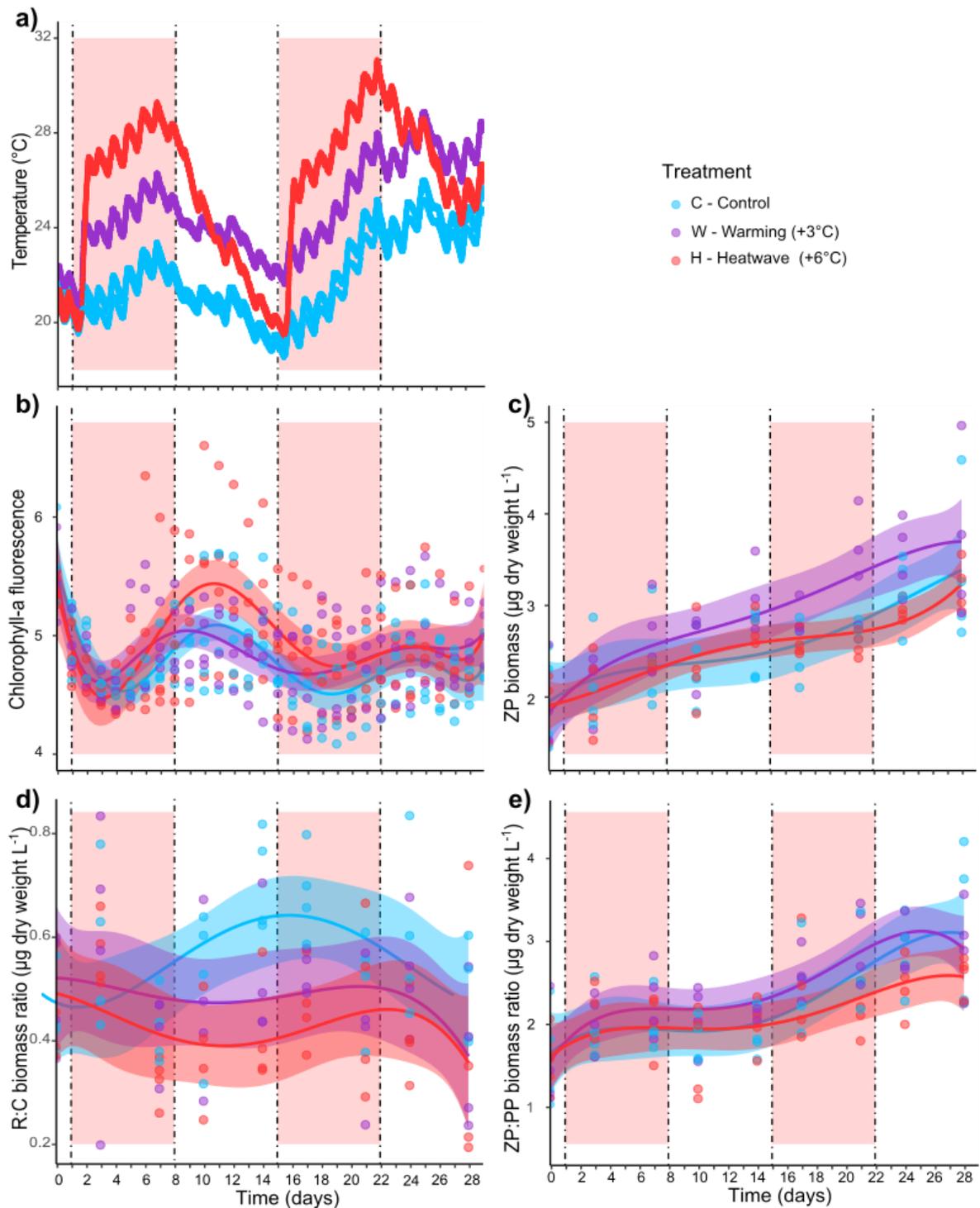
216 All statistical analyses were performed using R version 4.0.2 (R Core Team, 2020).

217

218 **Results**

219 Temperature varied between 18.5–26.0 °C in C, 18.9–28.9 °C in W, and 19.4–31.1
220 °C in H during the four weeks of the experiment (**Figure 1a, Figure S4**). We found
221 significantly higher Chla fluorescence in treatment H than in W and C during and after the
222 first heatwave (day 4-14) according to the GAM model and the pairwise test (H-C estimate:
223 0.27, $p=0.001$; H-W estimate: 0.24, $p=0.005$). Differences were not significant in the second
224 experimental period (day 15-28). A peak in Chla fluorescence was observed in treatment H
225 after the first heatwave (**Figure 1b**). This difference disappeared by the second part of the
226 experiment (no significant treatment effect).

227 In our experiment, the copepods *Mesocyclops leuckarti* and *Eudiaptomus gracilis*,
228 and the rotifer *Polyathra remata* dominated zooplankton, by accounting for 19.0 ± 24.6 , 13
229 ± 9.8 and 4 ± 6.6 % (mean \pm SD) of total biomass over the experiment. We found an overall
230 increase in zooplankton biomass over time, largely comparable across treatments (**Figure**
231 **1c**). We found statistically significant differences between W and H (KW test: $\chi^2=7.65$,
232 $df=2$, $p=0.02$, W-H: $p<0.01$) only at the end of the second heatwave (day 21, **Table S2**). We
233 found overall higher zooplankton biomass in W than in H and C, while the temporal trends
234 in H and W were similar (**Figure 1c**). Overall, the R:C biomass ratio decreased significantly
235 as a response to H, which became evident after the first heatwave (KW test: $\chi^2=7.04$, $df=2$,
236 $p=0.02$, H-C: $p<0.01$) and lasted until the first part of the second heatwave (significant
237 differences between H and C on days 14 and 17; **Figure 1d, Table S2**). We found an
238 increasing trend in the ZP:PP biomass ratio with significant differences (KW test: $\chi^2=4.77$,
239 $df=2$, $p=0.03$, H-W: $p<0.03$) between W and H at the end of the second heatwave (day 21;
240 **Figure 1e, Table S2**).

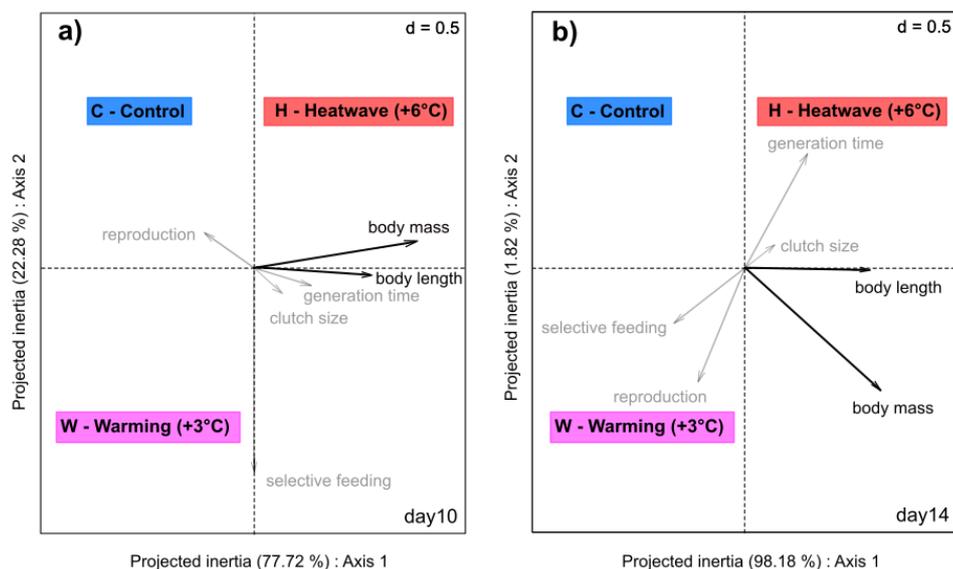


241

242 **Figure 1.** Temporal patterns in (a) observed water temperature (°C), (b) log-transformed
 243 chlorophyll *a* (Chla) fluorescence (proxy of phytoplankton biomass), (c) zooplankton (ZP)
 244 biomass (dry weight, $\mu\text{g L}^{-1}$) (c), (d) biomass ratio of Rotifera (R) to Copepoda (C), and (e)
 245 biomass ratio (dry weight, $\mu\text{g L}^{-1}$) of total zooplankton (ZP) to phytoplankton (PP) in the
 246 three (colour-coded) treatments. Biomass data were double-square-root transformed for the

247 analyses. Solid trend lines and error bands represent fitted GAMs \pm SE. Red backgrounds
248 indicate the lengths of the two experimental heatwaves (H, +6°C).

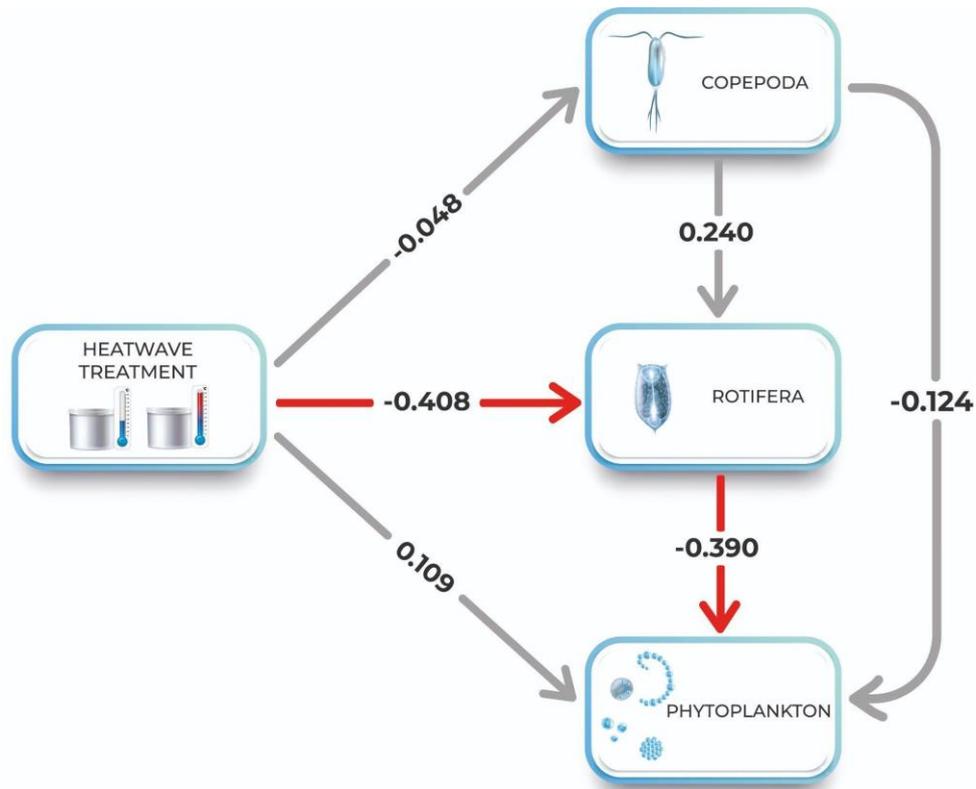
249 We found significant relationships between traits and treatments revealed by fourth-
250 corner analysis (related RLQ plots presented in **Figure 2**), with body-size related traits (body
251 mass, body length) responding positively to H. Specifically, body mass (day 10, $p=0.048$)
252 and body length (day 14, $p=0.046$) were positively associated with H in the period after the
253 first heatwave (**Figure 2**). At the same time, both traits were negatively associated with the
254 control treatment on day 14 (body length: $p=0.031$; body mass: $p=0.046$). During and after
255 the second heatwave, we did not find any significant treatment effects.



256

257 **Figure 2.** RLQ plots for the relationships between zooplankton traits and experimental
258 treatments after the first heatwave, on day 10 (a) and day 14 (b). Traits having at least one
259 significant ($p < 0.05$) relationship with at least one treatment based on fourth-corner analyses
260 are shown with black arrows, while others are in grey. (Grid size: $d=0.5$)

261 Treatment H exerted a direct and significant negative effect on Rotifera biomass
262 based on the SEM (standardized beta estimate: -0.408 , $p < 0.05$, **Figure 3, Table S3**). Besides,
263 the SEM revealed a direct negative effect of Rotifera on Chl a fluorescence, which appeared
264 with a time lag of 2-5 days (**Figure 3, Table S3**). This relationship was strongest directly
265 after the first heatwave and diminished over time. The results obtained for W were not
266 significantly different from those obtained for treatment C (**Table S3**).



268

269 **Figure 3.** A structural equation model (SEM) of the linkages between the dominant
 270 zooplankton groups, Rotifera and Copepoda (biomass), and phytoplankton (Chl*a*
 271 fluorescence) in the heatwave treatment during the first two weeks of the experiment. The
 272 model presented here is based on a time lag of 5 days between Chl*a* and zooplankton. Solid
 273 red arrows represent direct, significantly negative pathways ($p < 0.05$), while grey arrows
 274 stand for non-significant direct pathways. Numbers represent standardized parameter
 275 estimates. The amount of variation explained by the model (along with others with different
 276 time lags) is presented in **Table S3**.

277

278 Discussion

279 The results of this study supported our expectation that heatwaves exert stronger and
 280 more immediate effects on community composition than a constantly warmer temperature
 281 of the same energy input. However, contrary to our expectation, heatwaves had a negative
 282 impact on the biomass of small-bodied zooplankton (Rotifera) in our study. This result has
 283 important implications for ecosystem functioning, as the decline in small-bodied grazers in

284 turn resulted in reduced top-down control of phytoplankton and contributed to elevated algal
285 biomass in treatment H during the first heatwave.

286 The positive association between body size and heatwaves was counterintuitive as
287 most existing studies reported zooplankton body size to decline with warming, spanning
288 from population to community levels (Brans et al., 2017; Bruce et al., 2010). However, these
289 studies largely derived their conclusions from natural temperature gradients (where species
290 can adapt over time) or experiments with constant warming setups. Heatwave effects, in
291 contrast, may be less predictable due to stronger pressure on individual physiology,
292 potentially compromising physiological or genetic adaptations (Dam & Baumann, 2017),
293 resulting in increased mortality rates (Stillman, 2019), or sudden changes in species
294 interactions and phenology (Zhang et al., 2018). In our study, the positive association with
295 larger body size resulted from the relative decrease in microzooplankton (Rotifera) to
296 mesozooplankton (Copepoda) biomass in the H vs the other treatments.

297 The decline in Rotifera biomass may be a direct effect of the heatwave through the
298 change in metabolic activity (Lansing, 1942) or decrease in lifespan (Kauler & Enesco,
299 2011). At the same time, our results rather point to the possible relevance of other indirect
300 effects for several reasons. First, the negative effect was only observed after the first
301 heatwave, which peaked at lower temperatures compared to the second one. Second, the
302 most dominant Rotifera was *Polyarthra remata*, a eurythermic summer species (Bērziņš &
303 Pejler, 1989). These altogether point at the possible relevance of indirect trophic effects, such
304 as increased predation by copepods. Both cyclopoid and calanoid copepods are known to be
305 efficient predators of rotifers (Brandl, 2005; Lapesa et al., 2002). Although we did not
306 observe a negative correlation between the biomass of Copepoda and Rotifera, Copepoda
307 could have exerted higher predation rates due to increased metabolic demands in treatment
308 H.

309 Increased algal biomass as a response to warming and heatwaves is a commonly
310 observed phenomenon, which may result from direct and indirect (i.e., trophic) effects (Ger
311 et al., 2016; Viitasalo & Bonsdorff, 2022). A moderate increase in temperature increases
312 both the phytoplankton growth rate and the metabolic demands of consumers, shifting to
313 higher feeding rates and, consequently, higher consumer-to-producer biomass (Kratina et al.,
314 2012; O'Connor et al., 2009). Heatwaves, at the same time, may disrupt the predator-prey
315 relationships, thus increasing algal growth (Ross et al., 2022; Vad et al., 2023). Our results
316 highlight the importance of copepods and microzooplankton in trophic cascades. Most
317 freshwater studies on trophic cascades focus on Cladocera-dominated communities

318 (Carpenter & Kitchell, 1993; Sommer, 2008), while in our experiment, zooplankton was
319 largely dominated by Copepoda and Rotifera. In contrast to cladocerans, copepods exert a
320 stronger top-down control on the larger fraction of phytoplankton (Sommer et al., 2001;
321 Sommer & Sommer, 2006) and microzooplankton grazers (Adrian & Schneider-Olt, 1999;
322 Williamson, 1987). This can release small-sized phytoplankton from grazing pressure
323 (Sommer & Sommer, 2006), which was most likely the key mechanism in our experiment
324 as well, where the algal biomass peaks of the H treatment were dominated by small-celled
325 *Chlorella* and *Monoraphidium* species (K. Pálffy, pers. obs.). It is important that elevated
326 phytoplankton biomass appeared without external nutrient input (TP concentration was
327 similar among treatments). Therefore, we argue that it resulted from direct and indirect
328 effects of temperature.

329 An intriguing observation of our study is that the heatwave effect on phytoplankton
330 biomass occurred only after the first heatwave. This effect diminished later on, even though
331 the second heatwave peaked at higher temperatures. It is unlikely that the lack of
332 phytoplankton peaks in the second half of the experiment was related to grazing by Rotifera,
333 as they did not recover in the heatwave treatment (**Figure S5**). A possible explanation is that
334 copepods, with steadily increasing biomass over time (**Figure S5**), performed a diet shift to
335 the more abundant food sources, i.e., phytoplankton over Rotifera (Kiørboe et al., 1996).
336 Omnivorous copepods can become more herbivorous with increasing temperature (Boersma
337 et al., 2016), representing another possible explanation for the disappearance of higher
338 phytoplankton biomass in the heatwave treatment.

339 Mesocosm experiments are useful tools to identify community- and ecosystem-level
340 shifts to climate change by representing a compromise between experimental control and
341 realism (Fordham, 2015; Stewart et al., 2013). In our study, the lack of top-down control
342 due to the absence of higher trophic levels (e.g. fish, macroinvertebrates) likely explains the
343 temporal increase in zooplankton biomass in all treatments. However, by this reduction of
344 trophic complexity, planktonic community shifts and food web interactions could be
345 revealed without confounding factors. Though the one-month duration of our study limits
346 long-term forecasts, it delivers relevant information on the short-term effects of intermittent
347 heatwaves on community dynamics. The relatively short experimental duration may also be
348 the reason for the absence of strong effects in treatment W, which can be considered a press
349 disturbance, typically resulting in permanent restructuring of communities on longer time

350 scales, while the pulse disturbance in treatment H can cause sudden changes followed by a
351 certain extent of recovery (Glasby & Underwood, 1996; Vad et al., 2023).

352 Here we showed that heatwaves could exert a stronger short-term pressure on
353 planktonic communities than a more moderate warming scenario. Most importantly, we
354 showed how heatwave-driven planktonic interactions indirectly lead to increased algal
355 biomasses. At the same time, the lack of lasting effects at this temporal scale implies that
356 communities in shallow lakes may be to some extent resilient to such short-term heat
357 perturbations. As natural systems are facing heatwaves of increasing magnitude and
358 duration, stronger effects on communities and ecosystems are expected in the future. Longer-
359 term studies are required to be able to create more accurate predictive models and thereby
360 improve our forecasting ability, while experimental studies should incorporate temperature
361 fluctuations besides focusing on the predicted increase in mean temperature.

362

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375

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