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How warming and other stressors affect zooplankton abundance, biomass and community composition in shallow eutrophic lakes

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Abstract

We aimed to investigate the influence of environmental factors and predict zooplankton biomass and abundance in shallow eutrophic lakes. We employed time series of zooplankton and environmental parameters that were measured monthly during 38 years in a large, shallow eutrophic lake in Estonia to build estimates of zooplankton community metrics (cladocerans, copepods, rotifers, ciliates). The analysis of historical time series revealed that air temperature was by far the most important variable for explaining zooplankton biomass and abundance, followed, in decreasing order of importance, by pH, phytoplankton biomass and nitrate concentration. Models constructed with the best predicting variables explained up to 71% of zooplankton biomass variance. Most of the predictive variables had opposing or antagonistic interactions, often mitigating the effect of temperature. In the second part of the study, three future climate scenarios were developed following different Intergovernmental Panel on Climate Change (IPCC) temperature projections and entered into an empirical model. Simulation results showed that only a scenario in which air temperature stabilizes would curb total metazooplankton biomass and abundance. In other scenarios, metazooplankton biomass and abundance would likely exceed historical ranges whereas ciliates would not expand. Within the metazooplankton community, copepods would increase in biomass and abundance, whereas cladocerans would lose in biomass but not in abundance. These changes in the zooplankton community will have important consequences for lake trophic structure and ecosystem functioning.

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1 Introduction

The ongoing global climate warming is expected to deeply alter lacustrine zooplankton biomass and abundance (Gerten and Adrian 2002; Strecker et al. 2004; Brucet et al. 2010; Zingel et al. 2018). As demonstrated already more than three decades ago in Lake Windermere (UK), year-to-year zooplankton biomass fluctuations are mostly determined by water temperature (George and Harris 1985). It has been shown experimentally that water temperature also influences zooplankton structure and composition (Iglesias et al. 2011), and that warming selects for smaller sized and fast-growing, r-trait zooplankters (Rasconi et al. 2015). Some authors have argued that the warming effect could also be indirect because heating enhances fish predation pressure that would cause a reduction of large-bodied zooplankters (Moss et al. 2004). Indeed, besides its direct effects on zooplankton metabolic rates and survivorship, temperature affects physical and chemical properties of water (such as salinity and dissolved oxygen availability) which affects fish, phytoplankton and macrophyte community composition that influence zooplankton biomass (Brucet et al. 2010). In lacustrine systems devoid of large perturbations in the fish community, fish and temperature effects on zooplankton are consequently not competing predictors as fish influence is nested in temperature dependence. Considering the crucial position of zooplankton in lake food webs between primary producers and fish, stressors affecting zooplankton might provoke trophic cascades that impact the whole food web functioning.

Growth of human population and globalization are expected to further exacerbate the anthropogenic pressure on ecosystems by adding supplementary stressors to the temperature rise such as eutrophication (Straile 2015), land use changes, water column brownification, alkalization and invasive alien species (Jeppesen et al. 2014). These multiple stressors may have potential synergistic or antagonistic effects that impact ecosystems, and hence zooplankton, differently compared with single stressors (Moss et al. 2011; Mack et al. 2019). Because of their high surface to volume ratio, shallow lakes are considered particularly at risk and may act as early responders and amplifiers for a variety of environmental stressors (Mooij et al. 2005; Smol 2016), including water temperature (Mooij et al. (2005). This sensitivity is further increased in shallow lakes situated at higher latitudes as global warming is already modifying ice phenology and thus hydrological and thermal regime, carbon processing and lake metabolism (Jeppesen et al. 2014). For these reasons, we selected Lake Võrtsjärv (Estonia) as a model water body to test the global change effects on zooplankton.

During the last four decades, the large and shallow Lake Võrtsjärv experienced major shifts in its water chemical composition and temperature, nutrient concentration, and abundance of planktonic primary producers and consumers (Cremona et al. 2018; Janatian et al. 2019). Despite a decrease in nutrient loading following the collapse of the Soviet Union, phytoplankton biomass kept growing in the lake. Microbial ciliate biomass surged whereas larger metazooplankton biomass and abundance declined. The exact reasons behind these massive changes remain largely unknown to date partly because the number of co-occurring and interacting variables seems to defy a descriptive modelling approach. A quantitative study to explore the dynamic relationships between environmental stressors and zooplankton metrics in Võrtsjärv was still lacking. With the advent of machine learning algorithms, it is now possible to handle a large number of variables simultaneously in order to select the most sensible ones (Zuur et al. 2007). Additionally, empirical models offer several predictive tools that are suitable for ecological model simulations (Feld et al. 2016). Here, we aimed (1) to describe the dependence of metazooplankton (cladocerans, copepods, rotifers) and ciliate abundance and biomass on a set of key environmental parameters, and (2) to predict the biomass and abundance of those groups through 2050 using IPCC scenarios and Võrtsjärv as a case study. Our working hypothesis was that warming has acted as the main driver behind changes of zooplankton abundance, biomass and composition (Mooij et al. 2005; Haberman and Haldna 2017), with other stressors playing only a minor role.

2 Material and methods

2.1 Study site

With a surface area of 270 km^2, Lake Võrtsjärv is the second largest lake in the Baltic countries after Lake Peipsi. It is a shallow (mean depth = 2.8 m) and eutrophic (total phosphorus TP = 48 µg L^{-1}, total nitrogen TN = 0.91 mg L^{-1}) water body that is ice-covered for 135 days per year on average (Nõges et al. 2010; Nõges and Tuvikene 2012). During most of the ice-free season, the lake water column is continuously mixed, resulting in a high turbidity and a Secchi depth less than 1 m. Phytoplankton is by far the largest contributor to Võrtsjärv primary production although macrophytes can be important along the shoreline and in the southern tip of the lake. The dominant phytoplankton species are non-N_2-fixing cyanobacteria *Limnothrix planktonica* (Wolosz.) Meffert, *L. redekei* (Van Goor) and *Planktolyngbya limnetica* (Lemm.) Kom.-Legn. The poor edibility of the dominating filamentous cyanobacteria for crustacean zooplankton causes scarcity of large zooplankters in Võrtsjärv (Haberman 1998). The dominant crustaceans are the cladocerans *Bosmina longirostris* (O. F. Müller), *Chydorus sphaericus* (O. F. Müller) and the juvenile forms of copepod genera *Mesocyclops* and *Thermocyclops*. The main rotifer species are *Anuraeopsis fissa* (Gosse), *Keratella cochlearis* (Gosse), *Keratella quadrata frenzeli* (Eckstein), *Keratella tecta* (Gosse), *Trichocerca rousseleti* (Voigt), *Polyarthra luminosa* Kutikova. Protozooplankton taxa are mostly small-bodied ciliates—oligotrichs from *Rimostrombidium*, *Limnostrombidium*, *Pelagostrombidium* and *Halteria* genera.

During the 1979–2017 period, the rise in lake water temperature (+ 1.2 °C on average) was more moderate than the increase in air temperature (avg. + 2.77 °C). Võrtsjärv water column became slightly more basic, with a rise in pH by 0.5 units during the same period. Although the dissolved oxygen concentrations (O_2) slightly increased (avg. + 4%), the chemical oxygen demand measured by the permanganate method (CODmn) increased even more (avg. + 26%), showing an accumulation of organic matter in the water column that could be partly attributed to a brownification trend (Nõges et al. 2011) and partly to the increasing phytoplankton biomass. Despite considerably diminished nutrient loads since the early 1990s (avg. − 47% for TN and − 27% for TP, in Võrtsjärv) resulting from a sharp decline in fertilizer use and improving water treatment in the independent Republic of Estonia, the phytoplankton biomass concurrently nearly tripled (avg. + 172%). Metazooplankton average abundance and biomass declined respectively from 0.55×10^6 to 0.39×10^6 ind. m^{-3} (− 29%) and from 0.74 to 0.6 g m^{-3} (− 19%) between 1979 and 2017 (Supplementary Fig. 1). Ciliate biomass surged more than fivefold, from 0.7 to 3.8 g m^{-3}, although their average abundance decreased by 11% during the last three decades (from 105 × 10^6 to 92 × 10^6 ind m^{-3}). The numerically largest groups in metazooplankton were rotifers (≈ 74%), copepods (≈ 12%) and cladocerans (≈ 13%) whereas in the biomass rotifers were underrepresented (≈ 22%) compared with copepods (≈ 28%) and cladocerans (≈ 50%, Supplementary Fig. 2). The beginning of the twenty-first century has seen a relative decrease of rotifer biomass compared with cladocerans and copepods.

2.2 Data collection

Although ecological monitoring on Lake Võrtsjärv dates back to the early 1960s, we started our analysis from 1979 because of an increase in data reliability and regularity starting from that year. The following variables were measured on a monthly basis: biomass and abundance of total metazooplankton (B_{meta}, A_{meta}), rotifers (B_{roti}, A_{roti}), copepods (B_{cope}, A_{cope}), cladocerans (B_{clad}, A_{clad}), protozooplankton (ciliates B_{cili}, A_{cili}), biomass of phytoplankton (B_{phyto}), water and air temperature (T_{wat}, T_{air}), water level (WL), pH, dissolved oxygen (O_2), chemical oxygen demand by permanganate (CODmn), alkalinity (HCO_3), total nitrogen (TN) and phosphorus (TP), nitrate (NO_3), ammonium (NH_4) and phosphate concentrations (PO_4). The sampling and analysis methods for most of the variables are described in Nõges et al. (2010, 2016) whereas air temperature time series were obtained from Estonian Environment Agency (https://www.keskkonnaagentuur.ee/en). As Võrtsjärv water and air temperature are strongly positively correlated to each other (Fig. 1), we used air temperature as an independent variable in our modelling. The main reason for this choice was that site-specific air temperature predictions (which can be downscaled from climate models) were more readily available than water temperature predictions.

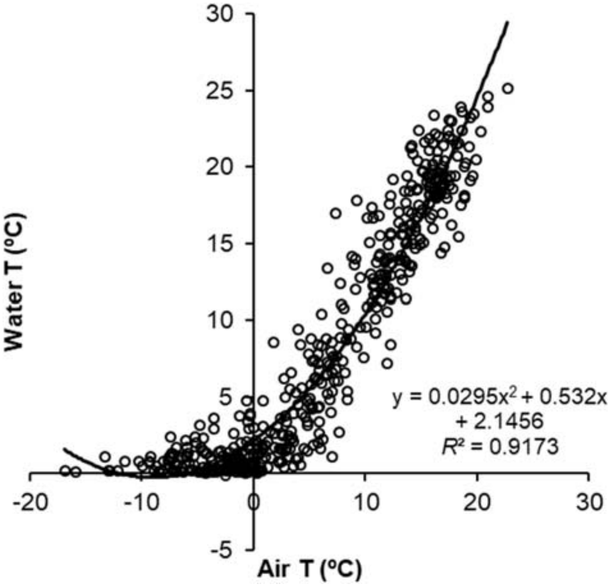

Fig. 1 Biplot of monthly air and water temperature in Lake Võrtsjärv (1979–2017)

2.3 Data treatment

We divided our statistical analysis into five successive steps: (1) data preparation, (2) exploratory and (3) quantitative analyses (Feld et al. 2016), (4) predictor simulation and (5) response variable simulation according to scenarios. All the computation was done using R software versions 3.5.2., 3.5.3. and 3.6.1. (R Core Team 2019). All the plankton-related variables except phytoplankton biomass were further used as dependent variables (hereafter "response variables") whereas physical and chemical variables plus phytoplankton biomass were entered as predictive variables (hereafter "predictors"). For the response variable simulation (fifth and last step), we conducted an uncertainty analysis by using three different sets of predictor values representing "low", "mid" and "high" scenarios (see predictor simulation section).

2.3.1 Data preparation

For the variables that were sampled during the whole study timeframe (1979–2017), the number of observations (*n*) reached a maximum of 468. However, nutrients started being monitored only in 1989, CODmn in 1991, and ciliate biomass and abundance in 1995. Missing data was labelled as "NA" for R and further ignored for the rest of the analysis. Nevertheless, we managed in all cases to exceed the rule of thumb requirements of a 10 to 1 ratio between the number of observations and that of predictors (Harrell 2001). Both predictors and response variables were, when necessary, log- or square root transformed in order to approach normal distribution.

2.3.2 Data exploration

For selecting the most meaningful predictors for each response variable, we employed Boosted Regression Trees (BRT) following a collinearity analysis. We calculated the Variable Inflation Factor (VIF, Zuur et al. 2007) using the *usdm* package and setting the VIF threshold at 8, excluding from the analysis variables that exceeded this threshold. We conducted the BRT analysis (tree complexity 2, learning rate 0.0001, bag fraction 0.6) with the R packages *gbm* (Greenwell et al. 2018) and *dismo* (Hijmans et al. 2016). For a better interpretation of the results of multiple regression analysis, it is recommended to keep the number of predictors small enough (Qian 2017). Additionally, a limited set of predictors is more reliable and easier to integrate into the simulation of future ecological conditions. Consequently, only the predictors that ranked first and second for each response variable in the variable importance output of BRT analysis were kept for the following quantitative analysis. When encountering two concurrent, equally ranked predictors, we prioritized abiotic over biotic predictors because the former being generally more ecologically informative than the latter (Cremona et al. 2018).

2.3.3 Data quantification

We employed a multivariate analysis resting on generalized least squares (GLS) models for predicting response variables. As our dataset consisted of time series from a single site, we wanted to test the dependence between time points using the autocorrelation function (ACF, Crawley 2013) that is available in the package *nlme* (Pinheiro et al. 2018). Initially, we checked GLS model performance without autoregressive factor and then with the addition of autoregressive factors of increasing complexity, firstly with first-order AR1 and then with second-order autoregressive moving-average models (ARMA2). For the response variable simulation step, we selected the most performant model regarding Akaike's information criteria (AIC, Akaike 1973), Bayesian information criteria (BIC, Schwarz 1978), root-mean-square error (RMSE) and compliance with residual normal distribution and homoscedasticity. The potential interaction between the two predictors of each response variable was classified according to Feld et al. (2016) simplified typology of Piggott et al. (2015). In short, a very weak interaction term indicated additive effects (no interaction). In case the predictors and interaction coefficients all had the same sign, the interaction was considered synergistic. If predictors had the same sign but interaction coefficient had a different sign, the interaction was antagonistic. If individual predictor coefficients had opposite signs, then the interaction was opposing, irrespective to the sign of its coefficient.

For the forecasting part of the study, only these response variables were used for which at least one-third of the variance ($R^2 = 0.33$) was explained by the GLS model.

2.3.4 Predictor simulation

To forecast predictor dynamics in the near future (2020–2050), we used two different techniques depending on the type of predictor. For predictors other than air temperature, we used automated forecasting function "auto.arima" from R package *forecast* (Hyndman et al. 2018). The auto.arima function returns the best autoregressive integrated moving average (ARIMA) model according to AIC and BIC scores. For pH, we considered that the pH would eventually reach a plateau of 9.5. Indeed, averages above this value are unrealistic in Võrtsjärv because they would necessitate a 10-fold increase in primary production (Peeter Nõges, unpublished data). We used the monthly 20th, mean and 80th percentiles of predictor posterior distribution for low, mid and high scenario values respectively. Thus, if ARIMA model for pH returned a 20th percentile value of 7.9, a mean of 8.0 and an 80th percentile of 8.2 for January 2025, these values were employed as predictive values for this date in the low, mid and high scenarios, respectively. For air temperature projections, we employed output from IPSL-CM5 global climate model under three different future scenarios (RCP4.5, RCP6.0 and RCP8.5) downscaled to central-south Estonia. Air temperature data was bias-corrected using the linear scaling method of Shrestha (2015) and observed air temperature in Võrtsjärv region (1979–2017) as the reference.

2.3.5 Response variable simulation

For each response variable, forecasted values of predictors were employed as inputs into the GLS model for numerically forecasting time series in the near future (2020–2050) period, depending on the three aforementioned scenarios. A bias-correcting procedure was done on GLS model outputs using multiplicative or empirical quantile mapping (EQM) method depending on the type of data. Bias-correction computation was proceeded with the R package *hyfo* (Xu 2018).

3 Results

3.1 Data exploration

Statistical analysis by BRT revealed that air temperature was ranked as the most important predictor for seven response variables out of ten (A_{meta}, B_{meta}, A_{roti}, A_{cope}, B_{cope}, A_{cili}, B_{cili}, Table 1). Additionally, air temperature was ranked second or third most important predictor for the three remaining response variables. For six response variables out of ten, air temperature alone explained 45–85% of the variance. Although pH was never ranked first in the analysis, it was the second most important predictor for five response variables (B_{meta}, A_{cope}, B_{cope}, A_{cili}, B_{cili}). The next most important predictors by decreasing order of importance were the biomass of phytoplankton (B_{phyto}), nitrate (NO_3) and HCO_3. The remaining predictors which were related to phosphorus and nitrogen (TP, TN:TP, TN), oxygen (O_2, CODmn) or water level (WL) were all poorly ranked and did not contribute substantially to explain response variable variance.

3.2 Data quantification

GLS models comprising the two best predictors from BRT analysis and a first- to second-order autoregressive module explained in some cases more than two-thirds of the variance of response variables (Table 2). The best explanatory power was obtained for the biomass of copepods (B_{cope}, $R^2 = 0.71$) and the weakest for the biomass of rotifers (B_{roti}, $R^2 = 0.09$). Models constructed with air temperature, pH and their interaction explained a greater proportion of whole metazooplankton, copepod and ciliate biomass ($R^2 = 0.58$, 0.71 and 0.58 respectively) than of their abundance ($R^2 = 0.38$, 0.50 and 0.53 respectively). A similar inconsistency was observed in case of cladoceran biomass and abundance ($R^2 = 0.65$ vs 0.52) although the abundance was predicted best by B_{phyto} and air temperature while the biomass by nitrates and air temperature. The GLS model did not predict a large share of variation in biomass and abundance of rotifers ($R^2 < 0.17$) despite the use of high-ranking predictors from the BRT analysis. Consequently, A_{roti} and B_{roti} were the only response variables that were not kept for the forecast part of the analysis. The analysis of the significant interactive terms of predictors revealed that the two main predictors (air temperature and pH) had opposing (A_{meta}, B_{cope}) or antagonistic (A_{cili}, B_{cili}) interactions. The combined effects of temperature and pH were consequently weaker than their individual effect for ciliates while the two variables worked in opposing ways for the biomass of copepods and the abundance of metazooplankton. For cladoceran abundance, the interaction between phytoplankton and temperature was antagonistic whereas nitrate and temperature worked in opposite ways for their biomass. For the four remaining response variables (B_{meta}, A_{roti}, B_{roti}, A_{cope}), the interaction was not statistically significant and the predictor effect was thus only additive (Table 3).

3.3 Response variable simulation

Our model forecasted that the average total metazooplankton abundance and biomass would increase strongly in the warming scenario (RCP8.5), increase markedly in the moderate warming scenario (RCP6.0) and decrease in the lower warming scenario (RCP4.5) compared with historical values (Fig. 2). However, within the metazooplankton community, although cladoceran abundance would rise in the moderate and high scenarios, their biomass would

Table 1 Boosted regression trees (BRT) results for predicting zooplankton abundance and biomass in Lake Võrtsjärv

Variable	Explained variance (%)	Top 5 variable relative influence (%)	Strongest interactions[a]
A_{meta}	67	T_{air} (46), B_{phyto} (10), pH (10), HCO_3 (8), CODmn (8)	HCO_3-T_{air} (4.13), CODmn-T_{air} (3.94), CODmn-pH (2.14)
B_{meta}	70	T_{air} (58), pH (13), B_{phyto} (10), NO_3 (8), HCO_3 (3)	pH-T_{air} (3.4), NO_3-pH (0.87), TN:TP-T_{air} (0.8)
A_{clad}	74	B_{phyto} (59.1), NO_3 (10.8), T_{air} (9.3), pH (8.6), TN (5.8)	B_{phyto}-T_{air} (25.5), NO_3-T_{air} (14), B_{phyto}-TN:TP (12.7)
B_{clad}	80	NO_3 (49.9), T_{air} (16.4), B_{phyto} (12.2), pH (10.1), TN:TP (5.1)	NO_3-T_{air} (16.6), NO_3-pH (4.1), B_{phyto}-T_{air} (2.6)
A_{roti}	62	T_{air} (23.2), B_{phyto} (12.1), HCO_3 (12), CODmn (9.4), TP (8.3)	PO_4-TP (9.6), HCO_3-WL (9.4), TN:TP-TP (5.5)
B_{roti}	64	B_{phyto} (17.2), T_{air} (17), HCO_3 (11), pH (10.7), CODmn (10.3)	B_{phyto}-T_{air} (3.4), NO_3-T_{air} (3), HCO_3-CODmn (1.1)
A_{cope}	70	T_{air} (78.6), pH (4.7), B_{phyto} (4.5), WL (3.7), CODmn (2.5)	CODmn-T_{air} (82.1), B_{phyto}-T_{air} (35.6), WL-T_{air} (29.8)
B_{cope}	80	T_{air} (84.9), pH (3.3), WL (2.5), B_{phyto} (2.2), O_2 (1.5)	B_{phyto}-T_{air} (1.4), pH-T_{air} (1.1), WL-T_{air} (0.6)
A_{cili}	73	T_{air} (55.7), pH (18.7), WL (6.5), B_{phyto} (4), HCO_3 (4)	WL-T_{air} (2.5), PO_4-T_{air} (1.6), pH-T_{air} (1.2)
B_{cili}	77	T_{air} (45), pH (30.3), NO_3 (4.3), WL (3.8), B_{phyto} (3.4)	pH-T_{air} (4.3), PO_4-T_{air} (2.2), O_2-T_{air} (1.4)

A_{cili}, abundance of ciliates (ind. m^{-3}); A_{clad}, abundance of cladocerans (ind. m^{-3}); A_{cope}, abundance of Copepods (ind. m^{-3}); A_{meta}, abundance of metazooplankton (ind. m^{-3}); A_{roti}, abundance of rotifers (ind. m^{-3}); B_{cili}, biomass of ciliates (mg m^{-3}); B_{clad}, biomass of cladocerans (mg m^{-3}); B_{cope}, biomass of copepods (mg m^{-3}); B_{meta}, biomass of metazooplankton (mg m^{-3}); B_{phyto}, biomass of phytoplankton (mg m^{-3}); B_{roti}, biomass of rotifers (mg m^{-3}); COD_{mn}, chemical demand of oxygen (mg L^{-1}); HCO_3, alkalinity (mg L^{-1}); NO_3, nitrate concentration (mg L^{-1}); O_2, dissolved oxygen concentration (mg L^{-1}); PO_4, phosphate concentration (μg L^{-1}); T_{air}, air temperature (°C); TN, total nitrogen concentration (mg L^{-1}); TP, total phosphorus concentration (μg L^{-1}); TN:TP, total nitrogen to total phosphorus ratio

[a] Dimensionless unit, higher value signifies stronger interaction

Table 2 Generalized least squares (GLS) model results with pre-selected descriptor variables

Response variable	Descriptor variables	Model code entry[a]	AIC	BIC	*df*	R^2	RMSE
A_{meta}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{ARMA(2,2)}$	1300	1337	9	0.38	1.19
B_{meta}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{ARMA(2,2)}$	1316	1353	9	0.58	1.07
A_{clad}	B_{phyto}, T_{air}	$\text{Log(y)} = (B_{phyto})^{1/2} * T_{air} + \text{AR(1)}$	2634	2659	6	0.52	4.3
B_{clad}	NO_3, T_{air}	$\text{Log(y)} = NO_3 * T_{air} + \text{AR(1)}$	996	1019	6	0.65	1.06
A_{roti}	T_{air}, HCO_3	$\text{Log(y)} = T_{air} * HCO_3 + \text{ARMA(2,2)}$	1749	1786	9	0.16	1.94
B_{roti}	T_{air}, HCO_3	$\text{Log(y)} = T_{air} * HCO_3 + \text{ARMA(2,2)}$	1294	1331	9	0.09	1.09
A_{cope}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{AR(1)}$	2610	2634	6	0.50	4.3
B_{cope}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{AR(1)}$	1190	1214	6	0.71	0.86
A_{cili}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{ARMA(2,2)}$	731	763	9	0.53	0.97
B_{cili}	T_{air}, pH	$\text{Log(y)} = T_{air} * \text{pH} + \text{ARMA(2,2)}$	758	790	9	0.58	1.05

[a] In R notation of functions, a plus (+) sign corresponds to additive effects, while an asterisk (*) sign both additive effect and interactions are considered. Only models that attained the best performance (AIC, BIC, RMSE) are displayed here. Model choice (AR: first-order autoregressive term; ARMA: second-order autoregressive moving-average) is explained in the methods section

collapse in all scenarios with a drop from 25% (low scenario) to 90% (high scenario). This parallel rise in abundance and drop in biomass means that the individual size of cladocerans would shrink in the 2020–2050 period. Copepods, on the other hand, would exhibit a rise in abundance irrespective of the scenario (Fig. 3). In the low scenario, their abundance would stagnate whereas it would nearly triple in the high warming scenario. Protozooplankton dynamics would not mirror that of metazooplankton in the modelled scenarios. The model simulated that ciliate abundance would increase the most in the low warming scenario, owing to a large number of seasonal peaks, but would reach a lower average in moderate and high warming scenarios. Similarly, ciliate biomass would rise markedly above the last decade average only in the case of a high scenario. In mid and low scenarios, the model simulated a stagnation of ciliate biomass around the average historical values of the early 2000s because of the antagonistic effects between air temperature and pH on ciliates.

4 Discussion

Using a 38-year-long time series, we discovered that few environmental variables, chiefly temperature and pH, were important variables for predicting zooplankton abundance and biomass in Võrtsjärv. Projected future warming in Võrtsjärv will lead, according to our model simulation, to an increase in total biomass and abundance paralleled to a further restructuring of zooplankton community that will benefit copepods at the detriment of cladocerans. After more than two decades of rise in biomass, protists are projected to reach a plateau and even fall back to the values observed at the turn of the century. Our modelling findings echo literature observations regarding climate warming which, combined with the alkalization of shallow lakes, is expected to deeply alter lacustrine zooplankton communities (Moss et al. 2011; Jeppesen et al. 2014). pH appeared in our analysis as one of the most influential variables for predicting zooplankton abundance and biomass. It is unclear whether the positive effect of pH on zooplankton was direct or if it reflected an increase in algal primary production which ultimately benefited zooplankton. Considering that pH ranked as a more influential variable than algal biomass in the BRT model, we can infer that pH effects were both direct and indirect. The positive effects of pH on zooplankton seem to take place within a 7.5–9 range

Table 3 Details of GLS model coefficients and correlations

Response variable	Fixed effects	Estimate	Standard error	*t* value	*p*	Interaction
A_{meta}		2.0426597	1.5178898	1.345723	0.1790	
	T_{air}	−0.1859277	0.1225340	−1.517357	0.1299	
	pH	1.1951645	0.1848116	6.466935	0.0000***	
	T_{air}:pH	0.0313339	0.0151221	2.072063	0.0388*	Opposing
B_{meta}		−15.494281	1.5069015	−10.282212	0.0000***	
	T_{air}	0.215435	0.1240374	1.736856	0.0831	
	pH	1.691025	0.1868121	9.052010	0.0000***	
	T_{air}:pH	−0.015823	0.0152917	−1.034744	0.3013	–
A_{clad}		−0.5743766	0.5485344	−1.047111	0.2956	
	B_{phyto}	2.0028605	0.1924483	10.407263	0.0000***	
	T_{air}	0.4139760	0.0629455	6.576736	0.0000***	
	B_{phyto}:T_{air}	−0.0630724	0.0177083	−3.561740	0.0004***	Antagonistic
B_{clad}		−3.786633	0.11663269	−32.46631	0.0000***	
	NO_3	−0.587169	0.06503875	−9.02798	0.0000***	
	T_{air}	0.089813	0.01253839	7.16306	0.0000***	
	NO_3:T_{air}	0.010716	0.00516530	2.07454	0.0388*	Opposing
A_{roti}		11.181387	0.7397945	15.114180	0.0000***	
	T_{air}	0.173952	0.0716293	2.428497	0.0156*	
	HCO_3	−0.000539	0.0028593	−0.188642	0.8505	
	T_{air}:HCO_3	−0.000409	0.0003528	−1.158549	0.2473	–
B_{roti}		−2.7694577	0.4694393	−5.899501	0.0000***	
	T_{air}	0.0037402	0.0416228	0.089859	0.9284	
	HCO_3	−0.0000283	0.0016799	−0.016854	0.9866	
	T_{air}:HCO_3	0.0001782	0.0002058	0.865904	0.3870	–
A_{cope}		−22.245353	6.145725	−3.619647	0.0003***	
	pH	3.225226	0.779640	4.136815	0.0000***	
	T_{air}	1.026114	0.545509	1.881020	0.0606	
	pH:T_{air}	−0.073165	0.067344	−1.086430	0.2779	–
B_{cope}		−8.457032	1.2459207	−6.787777	0.0000***	
	T_{air}	−0.221615	0.1118503	−1.981355	0.0481*	
	pH	0.608041	0.1580905	3.846154	0.0001***	
	T_{air}:pH	0.042824	0.0137934	3.104700	0.0020**	Opposing
A_{cili}		1.5372570	1.9737848	0.778837	0.4368	
	T_{air}	0.5500547	0.1715914	3.205607	0.0015**	
	pH	1.0251586	0.2460942	4.165716	0.0000***	
	T_{air}:pH	−0.0553836	0.0209392	−2.644964	0.0086**	Antagonistic
B_{cili}		−4.548500	2.0651239	−2.202531	0.0285*	
	T_{air}	0.651256	0.1791644	3.634963	0.0003***	
	pH	1.314815	0.2572185	5.111666	0.0000***	
	T_{air}:pH	−0.066555	0.0218499	−3.046001	0.0025**	Antagonistic

p significance are as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. Only interactions that reach statistical significance are displayed out

above which there is a loss of grazing and zooplankton diversity (Kalff 2002). A further increase in pH in Võrtsjärv, although highly improbable (see Section 2.3.4), might thus cross a threshold which is detrimental to zooplankton physiological requirements.

The model simulated a concurrent decline of cladoceran biomass and rise in their abundance, hinting to a reduction in the body size of those zooplankters. These predictions concord with the previous in situ observations (Gillooly and Dodson 2000) that revealed a decrease in limnetic cladoceran body size from cold to tropical regions (Iglesias et al. 2011). Additionally, it has been observed that temperature rise was responsible for the decrease in density of large-

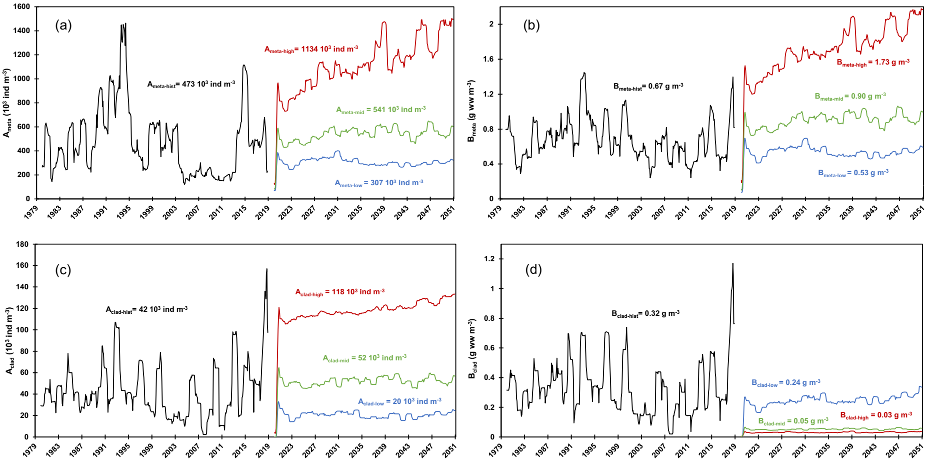

Fig. 2 Historical (black) and model-simulated, yearly-averaged output for high (red), mid (green) and low (blue) scenarios of abundance and biomass of metazooplankton (**a**, **b**) and cladocerans (**c**, **d**). The value next to each variable corresponds to the statistical average for the historical or simulated time series

bodied zooplankton in shallow lakes (Brucet et al. 2010). Although both cladoceran biomass and abundance were positively correlated with temperature in our study, the negative influence of NO_3 on cladoceran biomass is expected to exceed the positive influence of temperature in case of eutrophication. Similarly, the antagonistic interaction between temperature and phytoplankton predictors in the case of cladoceran abundance would mitigate the effect of warming on this zooplankton group. Phytoplankton thriving in eutrophic conditions are generally cyanobacteria which are able to reduce zooplankton grazing capacity (Jeppesen et al. 2014). Nitrate is also associated with poor conditions for zooplankton and reduction in its concentration is one of the core processes of large zooplankter population restoration (Jeppesen et al. 2007). Increased NO_3 concentrations promote cyanobacterial biomass (Burberg et al. 2019). Although, cyanobacteria can contribute a significant part of the cladoceran algal diet in

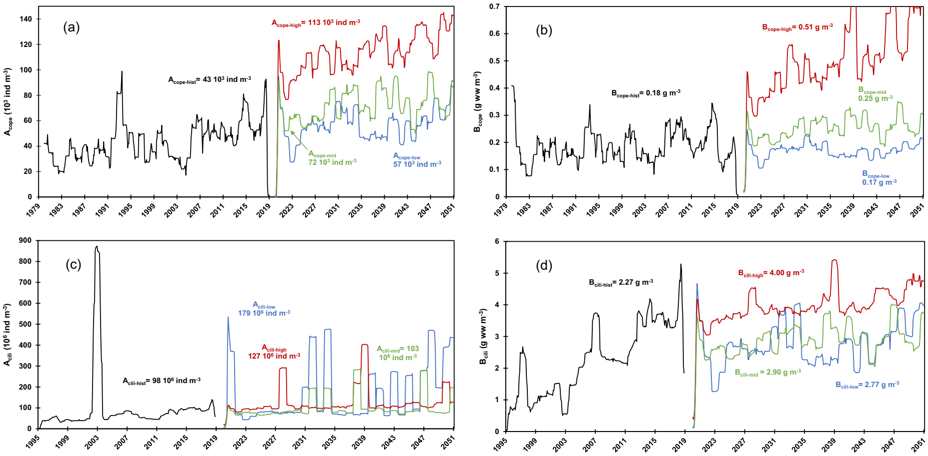

Fig. 3 Historical (black) and model-simulated, yearly-averaged output for high (red), mid (green) and low (blue) scenarios of abundance and biomass of copepods (**a**, **b**) and ciliates (**c**, **d**). The value next to each variable corresponds to the statistical average for the historical or simulated time series

Võrtsjärv (Tõnno et al. 2016), it is generally considered as nutritionally inadequate food source for these grazers. Compared with green algae or cryptophytes, cyanobacteria contain low levels of essential lipids such as highly unsaturated fatty acids and sterols which are important for somatic growth and reproduction for cladocerans (Martin-Creuzburg et al. 2008; Burns et al. 2011). As exemplified by Võrtsjärv case, despite the reduction of in-lake total nitrogen concentration, nitrate concentration has increased in most recent years to a relatively high level as shown by results from the Environmental Monitoring Information System of Estonia (https://kese.envir.ee/kese/) and could be a major stressor for the cladoceran biomass if left unchecked in the future.

Although there is rich published evidence on the temperature effects on ciliate density and biomass, it has been mostly studied in the context of seasonal fluctuations and successions (Gaedke and Wickham 2004; Pace 1982). Zingel et al. (2018) showed in a mesocosm study that ciliates responded quickly and positively to non-seasonal warming. We also reported a synergistic effect between temperature and nutrients with the largest increase in the more eutrophic enclosures (Zingel et al. 2018). However, in the present study conducted in the natural habitat for ciliates, nutrients (NO_3 in that case) ranked only as the third most important variable and explained a mere 4% of B_{cili} variance.

Although phosphorus did not appear among the top five predictors for A_{cili} or B_{cili}, the BRT model ranked the interaction between PO_4 and temperature as the second strongest in the predictor set. These two results confirm, nonetheless, that nutrients play a role in the increase of ciliate abundance, although their long-term effect is rather limited as exemplified by the concomitant rise in ciliate biomass and reduction in nutrient concentration in Võrtsjärv during the last four decades. Although ciliate growth seems to have benefited from Võrtsjärv warming and alkalization, our model simulation showed that the recent reduction of ciliate biomass is expected to continue even in the moderate warming scenario. This phenomenon is caused by the antagonistic interaction between temperature and pH, which leads to a slump or a decrease in A_{cili} and B_{cili} when the rise in absolute values of individual predictors remains small. It has been demonstrated that global warming may impact unicellular organisms in several ways. First, it is suggested that the carrying capacity and thus the maximum number of cells per volume scales negatively with temperature (Savage et al. 2004) leading to reduced abundances. Forster et al. (2013) showed linear decrease in maximum supported biomass of unicellular ciliates as temperatures increased, due to the temperature-size response of mean cell volume. Atkinson et al. (2003) demonstrated in meta-analysis that protist cell volumes changed with increasing temperature linearly by approximately 2.5% $°C^{-1}$. Second, it has also been shown recently that reduced body size is a universal ecological response to global warming (e.g. Sheridan and Bickford 2011). Different cell size leads inevitably to changes in preference of food items and different risks of predation. In a mesocosm experiment carried out in Võrtsjärv, Zingel et al. (2016) demonstrated an inverse relationship between copepods and large-sized ciliates and showed that this was an important feature adjusting not only the structure of the ciliate community but also the energy transfer between meta- and protozooplankton.

In highly eutrophic Võrtsjärv, copepod assemblage is dominated by small-sized cyclopoid copepods (Haberman 1998). Given their opportunistic omnivorous feeding behaviour, cyclopoids interact with different trophic levels by preying on algae (Hopp and Maier 2005), ciliates (Agasild et al. 2013) and smaller metazooplankters (Hansen and Santer 1996). Cyclopoids copepods are thereby probably less disadvantaged from environmental changes due to warming or eutrophication (i.e. increase of cyanobacteria) than generally non-selective large-bodied cladocerans (e.g. Gliwicz and Lampert 1990). In fact, long-term observations have shown that cyclopoid copepods particularly are the group that benefits most from seasonal temperature increases and climate warming (e.g. Wagner and Adrian 2011; Teubner et al. 2018). Increasing temperature is directly promoting the growth of the more thermophilic cyclopoid species, such as *Mesocyclops leuckarti* and *Thermocyclops crassus* (Maier 1989). In a study involving a whole lake thermal manipulation, thermophilic cyclopoid copepod *T. oithonoides* exhibited an increase in the frequency of reproductive cycles when subjected to higher temperatures (Lydersen et al. 2008). In a recent study from Võrtsjärv, Haberman and Haldna (2017) showed that during the last five decades, the period with a mean water temperature of 10 °C (which is that of marked increase in zooplankton abundance and switch from cold-water to warm-water species) was lengthened by 7 days in spring and 6 days in autumn. Consequently, the hypothesis that temperature rise would further advance the reproduction of thermophilic copepod species as predicted by warming scenarios for copepods in Võrtsjärv appears plausible.

The warming scenarios for cladoceran assemblage most likely reflect the rise of abundance the small-sized *Chydorus sphaericus*, a current dominant cladoceran species in Võrtsjärv (Haberman 1998). *C. sphaericus* is characteristic of eutrophic water bodies and is well adapted to eutrophic conditions with abundant detritus and high cyanobacterial concentrations (Vijverberg and Boersma 1997). Moreover, feeding studies in Võrtsjärv have shown its selectivity towards colonial cyanobacteria supporting their coexistence with cyanobacterial blooms (Tõnno et al. 2016). Overall, the predicted compositional and size structural changes among crustacean zooplankton community imply a weakening of grazing pressure on phytoplankton (e.g. Vakkilainen et al. 2004) and more specialized zooplankton feeding in the course of warming. This in turn will further alter the interactions and energy transfer in the food web.

Rotifer metrics were not included in the scenarios, and we cannot assume that their abundance in Võrtsjärv would increase in warmer conditions. Indeed, a glance at historical data reveals that after reaching a maximum in the mid-1990s, rotifer biomass started to decline and reached a low plateau ($0.1\ \mathrm{g\ m^{-3}}$) at the beginning of the 2010s that coincided with the period of rapid warming (Supplementary Fig. 2). In the last year for which measurements are available (2017), rotifers represented less than 10% of the total metazooplankton biomass. Although warming has been shown to favour smaller zooplankters like rotifers in small fishless ponds (Strecker et al. 2004), their assemblage parameters in Võrtsjärv displayed only weak correlations with environmental variables (Agasild et al. 2007; Virro et al. 2009). The researchers could not distinguish any single essential controlling factor for rotifer community composition and abundance and concluded on a likely important role of interspecific and trophic relationships (Agasild et al. 2007; Virro et al. 2009). As smaller zooplankton groups like rotifers and ciliates constitute the most efficient consumers of phytoplankton in Võrtsjärv (Agasild et al. 2007), inter-group food competition is a plausible explanation for the opposite trends that rotifer and ciliate biomasses followed to date. Consequently, as hinted by the double-decadal decline of rotifer biomass in Võrtsjärv and the parallel rise of ciliate biomass during the 1990–2017 period, we can speculate that the simulated drop or stagnation of ciliate biomass in 2020–2050 would be beneficial to rotifer biomass.

5 Conclusion

Our study, spanning several decades of environmental monitoring in a large shallow eutrophic temperate lake revealed that air temperature and, to a lesser extent, pH, nitrates, and phytoplankton density were the main driving factors of zooplankton biomass. Projections for the next few decades find that stabilization of total metazooplankton biomass and abundance will only occur in a lower warming scenario (RCP4.5). In higher warming scenarios (RCP6.0, RCP8.5), metazooplankton biomass and abundance would exceed historical averages whereas ciliates would stagnate. The restructuring of metazooplankton community would foster copepods at the expense of large-bodied cladocerans.

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