Received: 5 May 2023 | Accepted: 30 June 2023

DOI: 10.1111/gcb.16919

Global Change Biology WILEY

RESEARCH ARTICLE

The recovery of crustacean zooplankton from acidification depends on lake type

Francesca Pilotto | **Bjørn Walseng** | **Thomas C. Jensen** | **Ann Kristin Schartau**

Norwegian Institute for Nature Research (NINA), Oslo, Norway

Correspondence
Francesca Pilotto, Norwegian Institute for Nature Research (NINA), Oslo, Norway.
Email: francesca.pilotto@nina.no

Funding information
Norsk institutt for naturforskning

Abstract

Acidification has harmed freshwater ecosystems in Northern Europe since the early 1900s. Stricter regulations aimed at decreasing acidic emissions have improved surface-water chemistry since the late 1980s but the recovery of biotic communities has not been consistent. Generally, the recovery of flora and fauna has been documented only for a few lakes or regions and large-scale assessments of long-term dynamics of biotic communities due to improved water quality are still lacking. This study investigates a large biomonitoring dataset of pelagic and littoral crustacean zooplankton (Cladocera and Copepoda) from 142 acid-sensitive lakes in Norway spanning 24 years (1997–2020). The aims were to assess the changes in zooplankton communities through time, compare patterns of changes across lake types (defined based on calcium and humic content), and identify correlations between abiotic and biological variables. Our results indicate chemical and biological recovery after acidification, as shown by a general increase in pH, acid neutralizing capacity, changes in community composition and increases in the total number of species, number of acid-sensitive species and functional richness through time. However, the zooplankton responses differ across lake types. This indicates that the concentration of calcium (or alkalinity) and total organic carbon (or humic substances) are important factors for the recovery. Therefore, assessment methods and management tools should be adapted to the diverse lake types. Long-term monitoring of freshwater ecosystems is needed to fully comprehend the recovery dynamics of biotic communities from acidification.

KEYWORDS
acid-sensitive species, browning, cladocerans, climate change, community composition, copepods, functional richness, microcrustaceans, Northern Europe, pH

1 | INTRODUCTION

Acidification, caused by deposition of sulfur and nitrogen oxides, has impacted ecosystems and biodiversity in Europe and North America since the early 1900s, and has emerged as an environmental problem in China from the late 1970s (Larssen et al., 2006; Liu et al., 2020). In freshwater ecosystems, acidification has led to a decline and local extinction of acid-sensitive species at different trophic levels (Keller & Pitblado, 1984; Muniz, 1990). In Europe and North America, the reduction of acidic emission, induced by stringent national and international regulations, prompted the recovery of surface-water chemistry from the late 1980s in several of the affected regions (Keller, 1992;

Skjelkvåle et al., 2005; Stoddard et al., 1999). In Europe, and especially in Norway and Sweden, large resources have been invested in liming to enhance the water quality and enable a fast recovery process; several liming projects are still running (Henrikcson et al., 1995; Laudon et al., 2021). The recovery of surface-water chemistry has not always been followed by an unambiguous recovery of biotic communities. The trajectories of biotic recovery after degradation depend on several factors, e.g., the persistence of the key pressures that led to degradation, the presence of environmental constraints and the ability of populations to re-colonize the system.

Zooplankton plays a crucial role in lacustrine ecosystems by acting as trophic link between microbes and phytoplankton and higher trophic levels, such as macroinvertebrates and fish. Thus, it serves as important food resource for several species of freshwater fish, and it regulates phytoplankton growth (Declerck & de Senerpont Domis, 2023). Zooplankton has been heavily affected by acidification (Brett, 1989). Gray and Arnott (2009) showed that zooplankton response to the recovery of surface-water chemistry could vary from limited recovery of species richness in heavily acidified lakes to full recovery in moderately acidified lakes. The recovery of zooplankton from acidification seems to be more strongly affected by physico-chemical variables, such as persisting low pH, calcium concentration (Ross & Arnott, 2022), and content of organic matter (Leach et al., 2019), than by recolonization from external sources (Keller et al., 2002). Climate change has also been shown to affect several facets of zooplankton communities, such as species distribution, body size, abundances, diversity, food web interactions, and phenology (Carter & Schindler, 2012; Vadadi-Fülöp et al., 2012). Warmer temperatures in late winter and spring cause earlier ice breakup (Woolway et al., 2020), which has been associated with increases in phytoplankton species richness and biomass in cold oligotrophic lakes (Weyhenmeyer et al., 2013) with possible effects on zooplankton communities. Thus, climate changes may also affect recovery dynamics after acidification, especially at high latitudes and elevations, where climatic change is faster and affects a larger proportion of species (Antão et al., 2022; Pepin et al., 2022; Previdi et al., 2021).

Studies of zooplankton recovery have mainly focused on pelagic communities (e.g., Gray & Arnott, 2009; Jiang et al., 2023), with a few exceptions including littoral communities (e.g., Walseng et al., 2003). Littoral zooplankton, which represent ca. 70% of the crustacean zooplankton diversity in a lake (Walseng et al., 2006), has also been used as indicator of recovery but primarily in limed lakes (Hesthagen et al., 2011; Wærvågen & Nilssen, 2003; Walseng et al., 2001; Walseng & Karlsen, 2001). Large scale assessments of the long-term dynamics of concurrent pelagic and littoral zooplankton communities in response to improved water quality are still lacking.

Understanding biological recovery from acidification is also relevant within the context of the EU Water Framework Directive

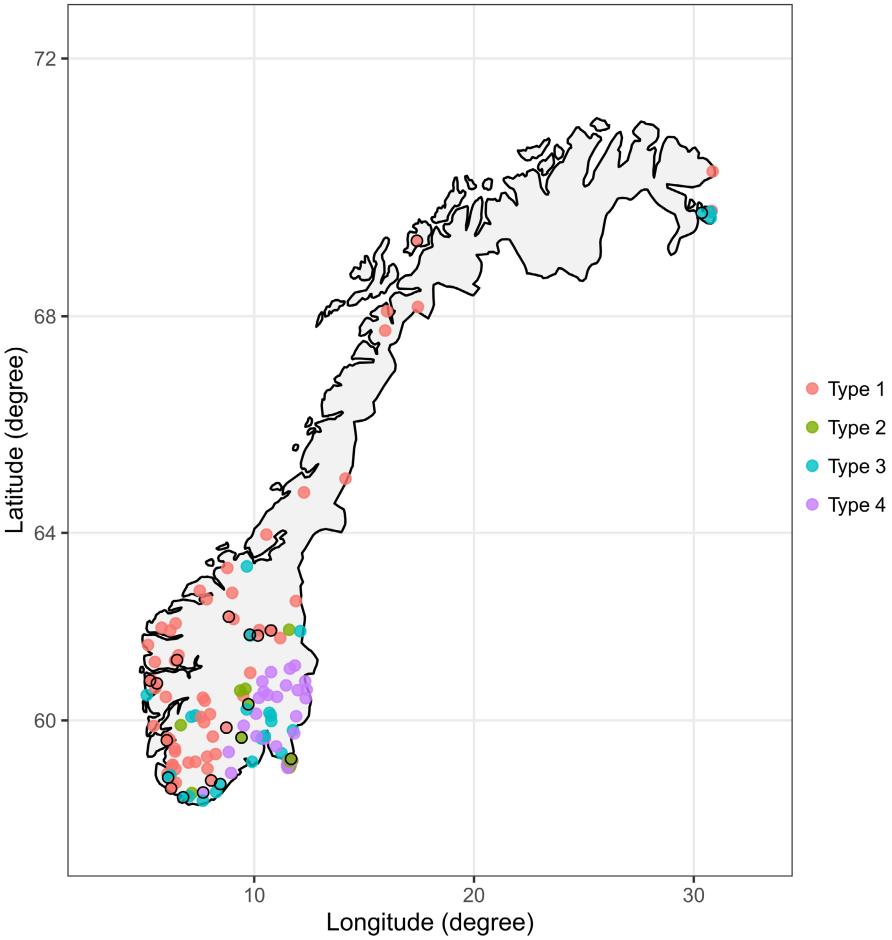

FIGURE 1 Geographical distribution of the studied lakes. Colours correspond to the lake types (see Table 1). Dots with black circle show lakes of subset1 (i.e., with at least 20 years of monitoring).

(2000/60/EC), where the assessment of ecological status should be based on the deviation from reference conditions. For Norwegian waterbodies, which have been subjected to acidification for a long period, reference data for biota are generally lacking. Introduction of freshwater types, based on a set of hydro-morphological (e.g., lake depth) and chemical parameters (e.g., calcium), which ensure that lakes belonging to the same type are sufficiently similar under natural conditions, is a method used when it is not possible to establish site-specific reference values. For Norwegian lakes and rivers, the concentration of calcium (or alkalinity) and total organic carbon (or humic substances) has been shown to be important structuring factors for the biological communities, influencing both reference conditions and the sensitivity to different environmental pressures (Direktoratsguppen vanndirektivet, 2018; Hesthagen et al., 2008; Schneider, 2011). Very low concentrations of dissolved ionic calcium can limit crustacean zooplankton populations, as it is used for building and hardening their exoskeleton (Giardini et al., 2015). Humic substances can reduce zooplankton production (Kelly et al., 2014) but they can also buffer against the detrimental effects of aluminum in acidified water bodies (Besser et al., 2019; Herrmann, 2001; Locke, 1991) and thus reduce the impacts of acidification on biota. A better understanding of the long-term dynamics of zooplankton communities at different lake types is needed to assess the recovery from acidification and its interactions with climate change.

In this study we investigated a large biomonitoring dataset including 142 Norwegian acid-sensitive lakes spanning 24 years (1997–2020; Figure 1). By using different subsets of data (see Section 2), we addressed three main aims. First, we aimed to assess the changes in crustacean zooplankton (Cladocera and Copepoda; hereafter zooplankton) communities, as described by species composition, species richness, number of acid-sensitive species, and functional diversity, over 24 years. Second, we aimed to compare patterns of changes across lake types (defined based on calcium and organic matter concentrations). Third, we wanted to identify the correlations between abiotic variables and zooplankton diversity metrics. In line with previous assessments, we expected that physico-chemical recovery would lead to changes in zooplankton communities, namely, increases in number of species, number of acid-sensitive species and functional diversity. As calcium and organic matter concentration strongly influence zooplankton communities (Leach et al., 2019; Ross & Arnott, 2022), we also expected the changes in zooplankton communities to vary across the different lake types, with stronger recovery at lakes with higher concentrations of calcium and mixed responses at lakes with higher concentrations of humic substances.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling scheme

All data included in this study are from national monitoring programs that are performed by the Norwegian Institute for Nature Research (zooplankton) and the Norwegian Institute for Water Research (water chemistry) or from research projects (see Table S1 for references). Most of the studied lakes are minimally affected by anthropogenic environmental pressures besides acidification. The data span the period 1997–2020, that is a period with reduced deposition of acid compounds and most pronounced recovery of water chemistry. The frequency of the samplings differed across the sampling programs but it was constant through time for each lake: some lakes ($n=34$) were sampled in three sampling occasions per year during the period June–September, while the other lakes ($n=108$) were sampled only twice during the same period. For all lakes, the sampling period was adjusted to the length of the ice-free season of the lake. The lakes are oligotrophic with very low phytoplankton biomass (mean Chla $<2.5\,\mu g/L$) and represent a wide range in latitude (58.12° N–70.34° N), altitude (10–1400 m), lake surface area (0.02–43.83 km^2) and chemical conditions (Figure S1; Table S1). None of the studied lakes has been treated with liming. All lakes are acid-sensitive, low-alkalinity lakes ($<0.2\,\mu eq\,L^{-1}$) and include unacidified reference lakes, naturally acidic lakes, anthropogenically acidified lakes and lakes affected by both natural acidity and anthropogenic acidification. Lakes were classified into four lake types based on inter-annual averages of the concentration of calcium and organic matter (Table 1; Direktoratsguppen vanndirektivet, 2018). Calcium input to lakes derives primarily from chemical weathering and depends on the geologic environment (Wright & Henriksen, 1978). For lakes with more than 20 years of data, the classification was based on inter-annual averages for the period up to 2010.

2.2 | Biotic data

At each sampling date, one pelagic sample and two littoral samples were collected during daytime. Pelagic samples were collected

TABLE 1 Number of lakes per lake type. Low calcium: 1–4 mg Ca L^{-1}; very low calcium: <1 mg Ca L^{-1}; clear-water lakes: <5 mg C L^{-1}; humic lakes: >5 mg C L^{-1} (Direktoratsguppen vanndirektivet, 2018).

Lake type	Calcium	Organic material	Full dataset (total number of lakes)	Subset1 (number of lakes with 20 years of monitoring)	Subset2 (number of lakes with at least 3 years of monitoring)
Type 1	Very low	Clear	67	12	33
Type 2	Very low	Humic	19	3	6
Type 3	Low	Clear	26	4	13
Type 4	Low	Humic	30	1	12

vertically from just above the sediment up to the surface, using a standard zooplankton net with mesh size of 90 μm and a diameter of 30 cm. Littoral species were sampled horizontally at low speed, both inside and outside the aquatic vegetation belt whenever possible, using a net haul with mesh size of 90 μm and a diameter of 27.5 cm. All crustaceans except small copepodites and nauplii of copepods were identified to species. Cladocerans were identified according to Bledzki and Rybak (2016) and Flößner (1972, 2000); copepods were identified following Bledzki and Rybak (2016), Einsle (1993, 1996), Kiefer (1978) and Sars (1903, 1913).

As the sampling method for zooplankton was semi-quantitative, we used presence-absence data in the statistical analysis. We obtained yearly presence-absence data by pooling all the littoral and pelagic samples that were collected during each year.

2.3 | Abiotic data

Water samples for chemical analyses were collected and analyzed by the Norwegian Institute for Water Research using national, accredited methods: *EN ISO/IEC 17025: 2005*, with the exception of water samples for the project INTERREG Enningdalselven (see Table S1), which were collected by the Norwegian Institute for Nature Research and analyzed by the analysis center of Trondheim municipality using the same accredited methods. We computed yearly averages of the physico-chemical variables that were most consistently recorded at the studied lakes: pH, acid neutralizing capacity (ANC), nitrate (NO_3^-), total organic carbon (TOC), calcium, and conductivity.

For each lake, we gathered monthly climatic data (monthly average maximum temperature) from TerraClimate (Abatzoglou et al., 2018) for the period from 1958 (i.e., the first year in the TerraClimate dataset) to 2020. For each year, we computed the average values of maximum temperature during the spring period (March–May) and during the growing season (June to October). We selected those two time periods because seasonal dynamics of community successions are influenced differently by climatic variables (Bellier et al., 2022). Similarly, we computed the historical average values of maximum temperature during spring and during the growing season for the period 1958–1990. We then expressed the yearly average values of spring and growing season maximum temperature of the studied period (1997–2020) as anomalies, that is, difference between observed values and historical average values.

To avoid collinearity, we did not include the variables that were highly correlated ($|r| > .6$) with others in the models. We excluded ANC and calcium because they correlated with pH, altitude because it correlated with conductivity, and latitude because it correlated with longitude (Table S2).

2.4 | Data analysis

Based on the yearly presence of zooplankton data, we computed four metrics for each lake and sampling year: species composition (SpComp), the total number of species (NSp), the number of species sensitive to acidification (AcIn), as defined by the Norwegian classification system for the assessment of the ecological status (Direktoratsguppen vanndirektivet, 2018), and functional richness.

For the species composition, we ran a principal component analysis (PCoA) on the Jaccard dissimilarity between pairs of samples. The Jaccard dissimilarity is suitable for binary data, such as presence-absence data. We then extracted the first axis of the PCoA and used it as proxy for species composition. We used the function vegdist in the R package “vegan” (version 2.6.4; Oksanen et al., 2019), and cmdscale in the R package “stats” (version 4.2.2; R Core Team, 2019) for computing the dissimilarity matrix and PCoA.

For the functional richness, we gathered the following species-specific trait data from the literature and expert opinion (Table S3): body size (maximum size of females and males), habitat (littoral/pelagic), and feeding habits (predator, omnivore, herbivore/macrofiltrator, bacteriovorus/microfiltrator, detritivore, ectoparasite of Hydra). Trait data were obtained for all dominant and common species (i.e., habitat and feeding habits: 96 out of the 104 studied species; maximum size of females: 76 species; maximum size of males: 72 species). Based on the trait information and the community taxonomic composition (presence-absence data) of samples, we computed functional diversity for each sample as functional richness (FRic), that is, the volume of the convex hull that includes all species in the sample in the multidimensional trait space, using the function dbFD in the R package FD (version 1.0.10.1; Laliberté & Shipley, 2014). To allow for comparisons across samples, we computed FRic based on the global multidimensional trait space, that is, the trait space including all species and traits sampled in the whole study area and study period. As FRic is dependent on taxonomic richness, we computed the standardized effect size of FRic (sFRic) by applying a null model approach. We computed the null distribution of FRic after randomizing species identities in the community composition matrix (99 randomization) and keeping the sample taxonomic richness (Kuczynski et al., 2018). We then obtained sFRic as

$$\text{sFRic} = \frac{\text{FRic} - \text{mean}\left(\text{FRic}_{\text{null}}\right)}{\text{SD}\left(\text{FRic}_{\text{null}}\right)}$$

where FRic is the observed functional richness of the sample and $\text{FRic}_{\text{null}}$ is the null distribution of functional richness. A positive or negative sFRic value indicates that the observed FRic is higher (functional over-dispersion) or lower (functional under-dispersion) than expected for the taxonomic richness of that sample.

We used generalized additive models (GAM; Wood, 2006) and hierarchical generalized additive models (HGAM; Pedersen et al., 2019) to identify the trends of biotic metrics through time (GAM) and across lake types (HGAM), and to identify correlations between biotic metrics and abiotic variables in the four lake types (HGAM). GAM and HGAM are non-linear models and were fitted using the function *gam* in the R package “mgcv” (version 1.8.41; Wood, 2012).

We used three different sets of data to address the three study aims (Table 1). To identify the trends of biotic metrics through time, we ran a series of GAMs for the 20 lakes that were monitored for at least 20 years during the study period (hereafter "subset1"). A GAM was run for each response variable (i.e., biotic metrics) and included: (1) a smooth of year, (2) lake-specific random smooths to account for the replicated sampling design, and (3) random effects for year (as factor) to account for the year-to-year variation. We chose the distribution family according to the distribution of the data and that of the model residuals, which was obtained using the function *appraise* in the R package "gratia" (version 0.8.1; Simpson & Singmann, 2022). We used quasipoisson distribution for NSp, scaled t distribution for AcIn, pH, TOC, conductivity, calcium, and temperature anomalies, gaussian distribution for SpComp, FRic, sFRic, ANC, and NO_3^-.

A series of HGAMs was run to identify the trends of abiotic variables and biotic metrics through time in the four lake types. For this purpose, we expanded the subset1 with additional 44 lakes that were monitored at least for 3 years (hereafter "subset2") to increase the number of lakes within the lake types. Those models were also run for each response variable and included: (1) lake type as parametric term, (2) a type-specific smooth for year, (3) lake-specific random smooths to account for the replicated sampling design, and (4) random effects for year (as factor) to account for the year-to-year variation.

Finally, HGAM were also used to identify correlations between biotic metrics and abiotic variables in the four lake types, across the full dataset (all lakes, $n=142$). As above, HGAM models were run for each response variable separately and included: (1) lake type as parametric term, (2) type-specific smooths of each abiotic variable, and (2) lake-specific random effects to account for the replicated sampling design. For these models, TOC, NO_3^-, and conductivity were log-transformed to improve the distribution of model residuals, and all abiotic variables were scaled to mean = 0 and standard deviation = 1.

Changes in the selected abiotic variables through time were assessed using GAM and HGAMs, as described above for biotic metrics. The results are shown in the Data S1.

3 | RESULTS

Our dataset included 104 species, 31 of which are classified as sensitive to acidification (Direktoratsguppen vanndirektivet, 2018). The number of species per sample ranged between 6 and 48 (mean:

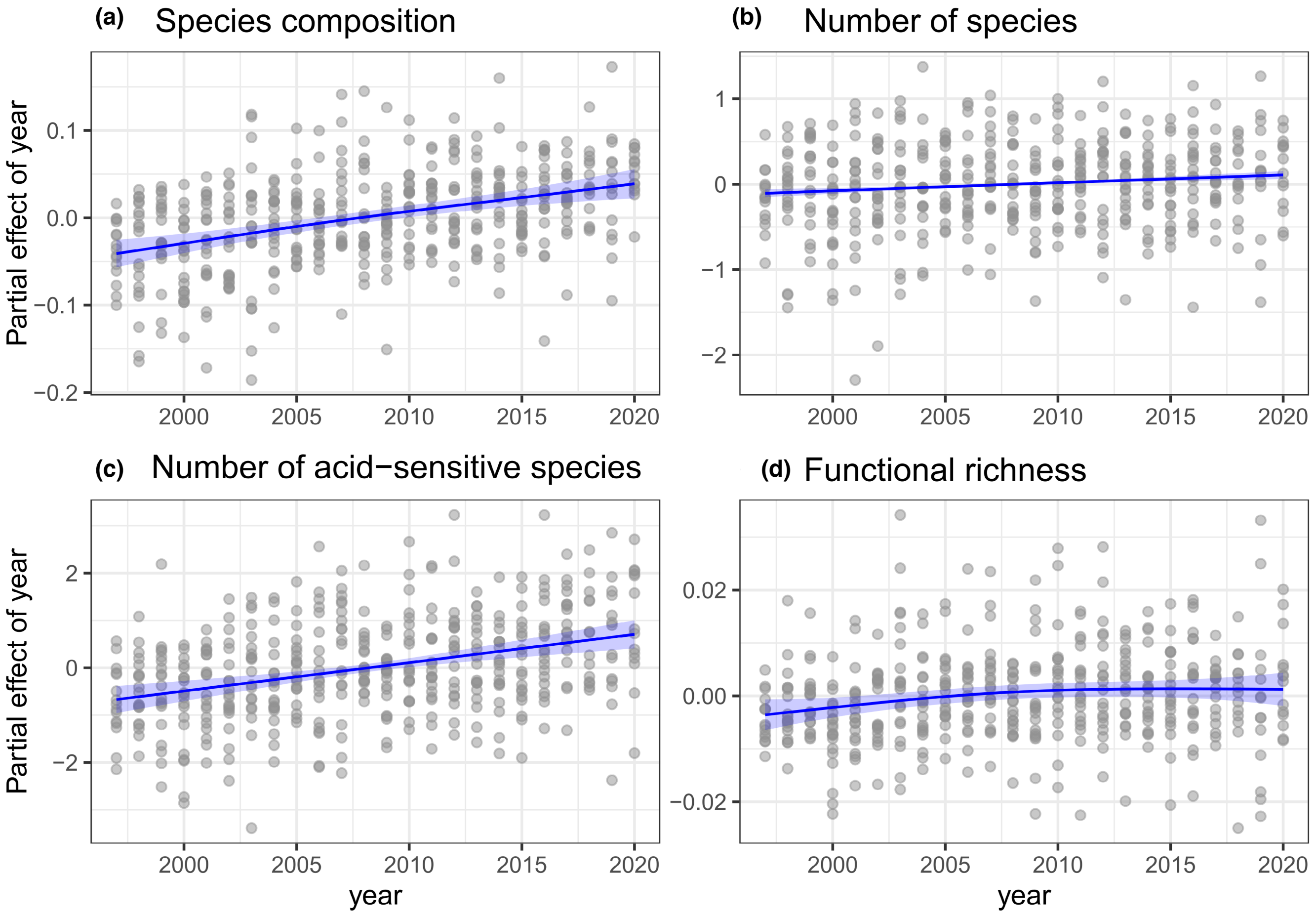

FIGURE 2 Changes in (a) species composition (i.e., first axis of the PCoA), (b) number of species, (c) number of acid-sensitive species, and (d) functional richness through time, at the lakes within subset1, as resulting from GAM. The *y*-axis represents the partial effect of "year" on the response variable. The dots show the marginal residuals. The shaded areas indicate the 95% confidence intervals of the smoothers. All smoothers are significant ($p<.05$; Table S4).

23.0), and the number of acid-sensitive species ranged between 0 and 17 (mean: 3.2).

3.1 | Temporal trends in yearly surveyed lakes

Between 1997 and 2020, we recorded a significant increase in pH and ANC (Figure S2). The values of pH ranged on average from 5.6 ± 0.5 (mean ± SD) in the first 5 years of survey to 5.9 ± 0.5 in the last 5 years of survey. We also recorded a significant change in species composition, a significant increase in the total number of species (+12% on average between the first and last 5 years of the study) and the number of acid-sensitive species (+43% on average between the first and last 5 years of the study; Figure 2a–c; Table S4). We found that 24 species of Cladocera (out of 45 species occurring in lakes of subset1, i.e., 53%) and 11 species of Copepoda (out of 29, i.e., 38%) were present in more lakes during the last 5 years compared with the first 5 years of the study. Some of the acid-sensitive species occurred regularly after they first were found (e.g., *Dapnia longispina*), while other species occurred less regularly (e.g., *Alona intermedia*, *Paralona pigra*, *Leptodora kindti*, *Megacyclops gigas*) (Figure S3). Functional richness increased consistently with the number of species (Figure 2d; Table S4), which resulted in no significant changes in sFRic (Figure S4).

3.2 | Temporal trends in the four lake types

The values of pH and ANC significantly increased at all four lake types (except pH at lakes of type 2; Figure S5): the values of pH ranged from 5.6 ± 0.5 (first 5 years) to 6.0 ± 0.4 (last 5 years) at lakes of type 1, from 5.0 ± 0.2 to 5.3 ± 0.2 at lakes of type 2 (not significant change), from 5.9 ± 0.4 to 6.3 ± 0.1 at lakes of type 3, and from 5.6 ± 0.4 to 6.2 ± 0.4 at lakes of type 4.

Species composition significantly changed at lakes of types 1 and 3 (Figure 3; Table S5). The number of species significantly increased at lakes of type 1 (+30% on average between the first and last 5 years), type 3 (+7%) and type 4 (+27%), as did the acid-sensitive species (type 1: +128%, type 3: +47%, type 4: +77%). At lakes of type 4, the described trends of the biotic metrics were evident up

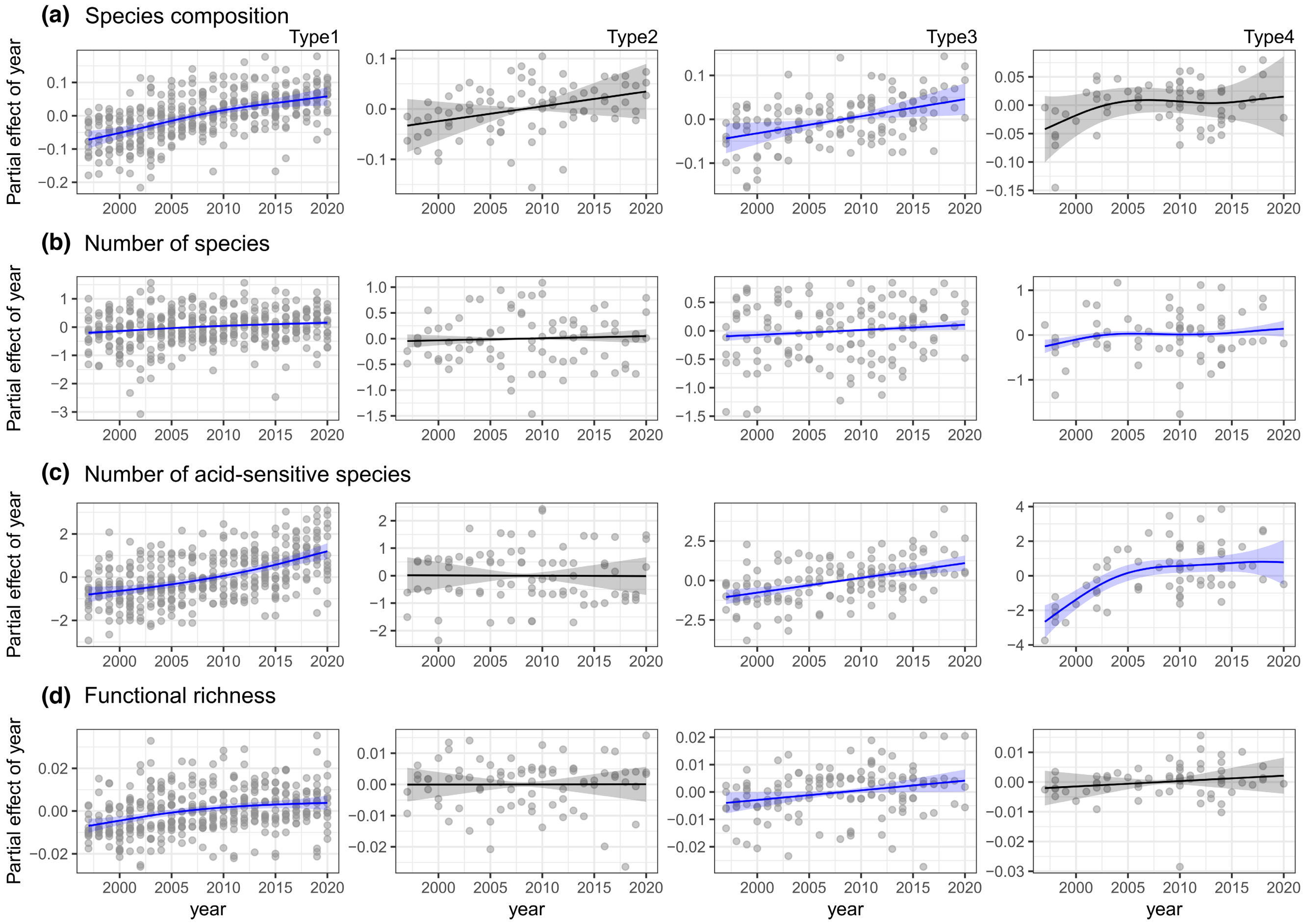

FIGURE 3 Changes in (a) species composition (i.e., first axis of the PCoA), (b) number of species, (c) number of acid-sensitive species and (d) functional richness through time, at lakes that were sampled at least in 3 years (subset2), as resulting from HGAM. The *y*-axis represents the partial effect of "year" on the response variable. The dots show the marginal residuals. The shaded areas indicate the 95% confidence intervals. Blue: significant smoother ($p < .05$); grey: non-significant smoother ($p > .05$; Table S5).

until 2005 and plateaued afterwards (Figure 3). Functional richness showed a positive trend at lakes of types 1 and 3 (Figure 3d), but the standardized effect size of functional richness (sFRic) did not show any significant trend through time in any lake type (Figure S6).

3.3 | Correlations between biotic metrics and abiotic variables in lake types

The correlations between biotic metrics and abiotic variables varied across lake types (Table 2; Figures S7–S9).

At lake type 1, all biotic metrics increased with increasing pH, TOC, and conductivity (except functional richness) and from east to west (except functional richness; note that the lakes of types 1, 3 and 4 that are most to the east are also those that are most to the north; Figure 1 and Table S2). All metrics showed a correlation with NO$_3^-$ (non-linear correlation for number of species and acid-sensitive species, negative correlation for species composition and functional richness). Species composition changed with spring temperature anomalies.

At lake type 2, biotic metrics showed no correlations with abiotic variables.

TABLE 2 Correlations between metrics and abiotic variables in the four lake types as resulting from HGAM (full dataset).

		Species composition		Number of species		Number of acid-sensitive species		Functional richness	
Lake type	Variable	*p*	*d*	*p*	*d*	*p*	*d*	*p*	*d*
Type 1	pH	.031	+	<.001	+	<.001	+	.014	+
Type 2	pH	.123		.108		.119		.122	
Type 3	pH	.253		.004	+	<.001	+	.261	
Type 4	pH	.587		.292		<.001	+	.316	
Type 1	NO$_3$[a]	.015	−	<.001	−+	<.001	+−	.050	−
Type 2	NO$_3$[a]	.673		.983		.390		.837	
Type 3	NO$_3$[a]	.408		.706		.563		.157	
Type 4	NO$_3$[a]	.695		.826		.001	+−	.872	
Type 1	TOC[a]	<.001	+	<.001	+	.015	+	<.001	+
Type 2	TOC[a]	.969		.899		.717		.557	
Type 3	TOC[a]	<.001	+	<.001	+	.003	+	.002	+
Type 4	TOC[a]	.358		.707		.382		.447	
Type 1	Conductivity[a]	<.001	+	.001	+	.048	+	.111	
Type 2	Conductivity[a]	.752		.871		.918		.954	
Type 3	Conductivity[a]	.186		.054	+	<.001	+	.144	
Type 4	Conductivity[a]	.082		.242		.027	+	.852	
Type 1	Longitude	<.001	−	<.001	−	.002	−	.057	
Type 2	Longitude	.265		.756		.661		.183	
Type 3	Longitude	<.001	−	.001	−	.028	+−	.003	−
Type 4	Longitude	.641		.553		.281		.686	
Type 1	TSpring	.012	+	.062		.281		.404	
Type 2	TSpring	.751		.461		.143		.059	
Type 3	TSpring	.885		.812		.298		.539	
Type 4	TSpring	.451		.107		.149		.379	
Type 1	TGrowing	.659		.144		.714		.343	
Type 2	TGrowing	.102		.379		.862		.333	
Type 3	TGrowing	.552		.960		.340		.039	+
Type 4	TGrowing	.028	+	.022	+	.046	+	.621	
Lake code		<0.001		<0.001		<0.001		<0.001	
R^2(adj)		.88		.81		.83		.7	
Deviance explained		89.60%		83.60%		76.30%		73.80%	

Note: The statistical significance (*p*) and direction (*d*) of the smooths are shown (*d*: +, positive correlation; −, negative correlation; +−, non-monotonic correlation).

[a]The variable was log-transformed. TSpring and TGrowing: temperature anomalies in spring and in the growth season.

At lake type 3, species composition changed with TOC and longitude. The number of species and acid-sensitive species increased with increasing pH, TOC, conductivity, and from east to west. Functional richness increased with increasing TOC, with temperature anomalies in the growth season and from east to west.

Finally, at lake type 4, species composition changed with temperature anomalies in the growing season. The number of species and acid-sensitive species increased with increasing temperature anomalies in the growth season. The number of acid-sensitive species also increased with increasing pH and conductivity and showed a non-monotonic correlation with NO_3^-.

4 | DISCUSSION

Our results document both chemical and biological recovery after acidification in Norwegian lakes during the studied period (1997–2020), as shown by a general increase in pH, acid neutralizing capacity, and all biotic metrics through time. Evidence of biological recovery in Europe has been sparse (Gray & Arnott, 2009) and have mostly focused on recovery after liming (Wærvågen & Nilssen, 2003; Walseng et al., 2001; Walseng & Karlsen, 2001), in contrast to our study where recovery is primarily a result of the reduction of acidifying compounds.

Our study, in addition to pelagic zooplankton, did also include littoral species, constituting more than two thirds of the total number of crustacean zooplankton in a lake (Walseng et al., 2006); thus, our results stand out as a robust document of recovery. Previous studies have mainly focused on pelagic zooplankton (see Gray & Arnott, 2009) and have been conducted within restricted geographical areas, primarily in systems that were acidified because of local industrial activities (e.g., Jiang et al., 2023), rather than as a result of long-range transboundary pollutions. For example, pelagic zooplankton has been used to assess the degree of biological recovery in 46 lakes in Ontario (Killarney Park, Canada) after reduced emissions over 30 year (1971–2000) (Holt & Yan, 2003). That study documented changes in species composition along a gradient from strongly acidified to neutral lakes but no changes in species richness were found. In contrast, our study, ranging over a shorter period, could document recovery both as changes in species composition and increase in species richness, mainly caused by acid-sensitive species. The inclusion of both pelagic and littoral species when assessing zooplankton recovery after acidification or, more in general, when investigating changes in biodiversity, provides stronger signals than using pelagic species only (Walseng, 2002). In our study, we used presence-absence data because the sampling method was semi-quantitative. The use of quantitative data of species abundance could have tracked more nuanced changes in the zooplankton community, for example increases in the relative abundance of acid-sensitive species or changes in species dominance, and thus it could have strengthened our results further.

By expanding our dataset with lakes that had been surveyed for 3 years or more, we could also document recovery across four different lake types. For all lake types, the trend analysis showed a significant increase in pH and/or ANC. Such an increase in pH was associated with higher number of total species and acid-sensitive species in all lake types except in humic lakes with very low calcium concentration (type 2).

At lakes of type 2, the zooplankton communities showed no changes through time and no correlations with abiotic variables. This might be an artifact due to the limited representation of those lakes in our dataset. However, the lack of biotic responses in those lakes may also be caused by the persistent low pH (average values during the last 5 years of sampling: 5.3 ± 0.2, no significant increases during the study period) and the combination of low calcium and high humic content. Low calcium concentration has been shown to limit the recovery of zooplankton after acidification independently of improvement in pH (Ross & Arnott, 2022) and, when associated with high content of humic matter, it even causes declines in zooplankton biomass (Leach et al., 2019). On the other hand, humic substances can buffer against detrimental effects of aluminum (Besser et al., 2019; Herrmann, 2001; Locke, 1991). Humic lakes may therefore have been less impacted by acidification, and strong signs of recovery is therefore not expected. While this seems to be the case in lakes of type 4 (humic lakes with low calcium concentration), the low number of species and acid-sensitive species at lakes of type 2 (Figure S10) indicates little progress in recovery from acidification so far.

At clear-water lakes (i.e., types 1 and 3), browning (i.e., increase in TOC) was associated with an increasing number of species, including the acid-sensitive species. This association did not emerge for humic lakes and is likely the consequence of increased food availability. Browning causes shifts in dominant species and biomass of phytoplankton, with positive effects on phytoplankton biomass in clear-water lakes and negative effects in humic lakes (Bergström & Karlsson, 2019; Isles et al., 2021). Browning can also enhance the supply of essential fatty acids for zooplankton (Lau et al., 2021). Increased TOC can also stimulate microbial activity, increasing the number of heterotrophic bacteria (Jansson et al., 2007), serving as an additional food source for microfiltrators. The increase in lake productivity is also associated with increased zooplankton functional diversity (Vogt et al., 2013). In line with this, we found that the increase in species richness at lakes of types 1 and 3 was associated with a consistent increase in functional richness which resulted in no net changes in sFRic (Figure S6), indicating that the newly established species introduced additional traits into the communities. This suggest that the newly established species filled empty ecological niches, which may enhance ecosystem functions, without increasing functional redundancy. In clear-water alpine lakes, as some of our lakes within types 1 and 3, increased TOC-concentration may protect zooplankton from damaging UV-exposure. Under those conditions, browning can contribute to increased species richness (Nevalainen et al., 2018), especially in the shallow littoral areas where most of the species live.

In contrast to the other lake types, in humic lakes with somewhat higher calcium concentration (type 4), the increases in total number of species and in acid-sensitive species were steeper at the beginning of the study period and plateaued afterwards. This suggests that those lakes recovered from acidification faster than the others. Indeed, these lakes had the highest taxonomic richness, number of acid-sensitive species and acid neutralising capacity (Figures S1 and S10) across the studied lakes. As anticipated above, humic substances can buffer against the detrimental effects of acidification (Besser et al., 2019; Herrmann, 2001; Locke, 1991). Thus, zooplankton communities in these lakes might have been less impacted compared to other lake types. Moreover, in our study, lakes of type 4 are primarily located in southeast Norway, which is the region with the most diverse species pool of zooplankton (Hessen et al., 2019). Therefore, those lakes are likely exposed to a higher recolonization potential. The combination of lower impacts from acidification, faster improvements of physico-chemical conditions and higher recolonization potential may have contributed to a fast recovery at those lakes.

The increases in the number of species at lakes of type 4 were also associated with increases in temperature anomalies during the growing season. In cold oligotrophic waters, as the studied lakes, warming is associated with increases in primary productivity, which benefits organisms at higher trophic levels, at least until a certain threshold where warming alters the nutritional quality of phytoplankton, which in turn can affect zooplankton growth and reproduction (Lau et al., 2021). Although a decline in food quality is expected under climate warming, zooplankton growth is mostly constrained by food quantity in oligotrophic lakes (Persson et al., 2007). Warming can also promote range expansion of warm-adapted species and declines in cold-adapted species (Antão et al., 2022), potentially affecting zooplankton species composition, richness, and functional diversity in lakes. Thus, the effects of warming could interact with the effects of the recovery of water chemistry in shaping zooplankton communities. Our results seem to support this prediction, at least at lakes of type 4.

To conclude, our results showed that zooplankton communities have been recovering after acidification, but recovery is slow at certain lake types. This indicates that assessment methods and management tools should be tailored to the specificity of the different lake types. In Norway and worldwide, freshwater ecosystems and their biodiversity and functions are threatened by several pressures (Darwall et al., 2018). Lake acidification itself cannot be considered a solved problem. Increasing concentration of atmospheric CO_2 and brownification can cause increasing pCO_2 in lake surface water (Couturier et al., 2022; Weiss et al., 2018), which can lead to pH declines and thus to the re-acidification of lakes. Continuous monitoring is needed to understand the trajectories of recovery and their interplay with existing and emerging pressures.

AUTHOR CONTRIBUTIONS

Francesca Pilotto and Ann Kristin Schartau conceived the ideas and the study. Bjørn Walseng, Thomas C. Jensen, and Ann Kristin Schartau collected and curated the data. Francesca Pilotto performed data analysis and led manuscript writing. All authors participated with intellectual contributions and revised the manuscript.

ACKNOWLEDGMENTS

This research was funded by The Norwegian Institute for Nature Research. The Norwegian Environment Agency funded sampling and species identification as well as chemical analyses through national monitoring programs in the period 1997–2020. A CC BY or equivalent licence is applied to any Author Accepted Manuscript (AAM) version arising from this submission, in accordance with the grant's open access conditions.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available at https://vannmiljo.miljodirektoratet.no (Miljødirektoratet, NLOD license). The data from https://vannmiljo.miljodirektoratet.no that were used in this study are available at the repository osf.io [https://osf.io/vb5rp].

ORCID

Francesca Pilotto https://orcid.org/0000-0003-1848-3154
Bjørn Walseng https://orcid.org/0000-0002-8572-9970
Thomas C. Jensen https://orcid.org/0000-0003-2777-2759
Ann Kristin Schartau https://orcid.org/0000-0001-6875-6136

REFERENCES

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958–2015. *Scientific Data*, *5*(1), 170191. https://doi.org/10.1038/sdata.2017.191

Antão, L. H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, Ø. H., Heliölä, J., Henttonen, H., Huitu, O., Korpimäki, E., Kuussaari, M., Lehikoinen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., … Laine, A.-L. (2022). Climate change reshuffles northern species within their niches. *Nature Climate Change*, *12*(6), 587–592. https://doi.org/10.1038/s41558-022-01381-x

Bellier, E., Engen, S., & Jensen, T. C. (2022). Seasonal diversity dynamics of a boreal zooplankton community under climate impact. *Oecologia*, *199*(1), 139–152. https://doi.org/10.1007/s00442-022-05165-0

Bergström, A.-K., & Karlsson, J. (2019). Light and nutrient control phytoplankton biomass responses to global change in northern lakes. *Global Change Biology*, *25*(6), 2021–2029. https://doi.org/10.1111/gcb.14623

Besser, J., Cleveland, D., Ivey, C., & Blake, L. (2019). Toxicity of aluminum to *Ceriodaphnia dubia* in low-hardness waters as affected by natural dissolved organic matter. *Environmental Toxicology and Chemistry*, *38*(10), 2121–2127. https://doi.org/10.1002/etc.4523

Bledzki, L. A., & Rybak, J. I. (2016). *Freshwater crustacean zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) key to species identification, with notes on ecology, distribution, methods and introduction to data analysis*. Springer.

Brett, M. T. (1989). Zooplankton communities and acidification processes (a review). *Water, Air, and Soil Pollution*, *44*(3), 387–414. https://doi.org/10.1007/BF00279267

Carter, J. L., & Schindler, D. E. (2012). Responses of zooplankton populations to four decades of climate warming in lakes of southwestern Alaska. *Ecosystems*, *15*(6), 1010–1026. https://doi.org/10.1007/s10021-012-9560-0

Couturier, M., Prairie, Y. T., Paterson, A. M., Emilson, E. J. S., & del Giorgio, P. A. (2022). Long-term trends in pCO_2 in lake surface water following rebrowning. *Geophysical Research Letters*, *49*(11), e2022GL097973. https://doi.org/10.1029/2022GL097973

Darwall, W., Bremerich, V., Wever, A. D., Dell, A. I., Freyhof, J., Gessner, M. O., Grossart, H.-P., Harrison, I., Irvine, K., Jähnig, S. C., Jeschke, J. M., Lee, J. J., Lu, C., Lewandowska, A. M., Monaghan, M. T., Nejstgaard, J. C., Patricio, H., Schmidt-Kloiber, A., Stuart, S. N., … Weyl, O. (2018). The Alliance for freshwater life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(4), 1015–1022. https://doi.org/10.1002/aqc.2958

Declerck, S. A. J., & de Senerpont Domis, L. N. (2023). Contribution of freshwater metazooplankton to aquatic ecosystem services: An overview. *Hydrobiologia*, *850*(12), 2795–2810. https://doi.org/10.1007/s10750-022-05001-9

Direktoratsguppen vanndirektivet. (2018). *Veileder 02:2018 Klassifisering av miljøtilstand i vann*. Økologisk og kjemisk klassifiseringssystem for kystvann, grunnvann, innsjøer og elver.

Einsle, U. (1993). *Crustacea: Copepoda: Calanoida und Cyclopoida*. Gustav Fischer Verlag.

Einsle, U. (1996). *Copepoda. Cyclopoida* (Vol. *10*). SPB Academic Publishing.

Flößner, D. (1972). *Krebstiere, Crustacea (Kiemen-und Blattfüsser. Branchiopoda, Fischläusse, Branchiura)*. Die Tierwelt Deutschlands. Gustav Fischer Verlag.

Flößner, D. (2000). *Die Haplopoda und Gladocera (ohne Bosminidae) Mitteleuropas*. Ackhuys Publishers.

Giardini, J.-L., Yan, N. D., & Heyland, A. (2015). Consequences of calcium decline on the embryogenesis and life history of *Daphnia magna*. *Journal of Experimental Biology*, *218*(13), 2005–2014. https://doi.org/10.1242/jeb.123513

Gray, D. K., & Arnott, S. E. (2009). Recovery of acid damaged zooplankton communities: Measurement, extent, and limiting factors. *Environmental Reviews*, *17*, 81–99. https://doi.org/10.1139/A09-006

Henrikcson, L., Hindar, A., & Thörnelöf, E. (1995). Freshwater liming. *Water, Air, and Soil Pollution*, *85*(1), 131–142. https://doi.org/10.1007/BF00483695

Herrmann, J. (2001). Aluminum is harmful to benthic invertebrates in acidified waters, but at what threshold(s)? *Water, Air, and Soil Pollution*, *130*(1), 837–842. https://doi.org/10.1023/A:1013815920101

Hessen, D. O., Jensen, T. C., & Walseng, B. (2019). Zooplankton diversity and dispersal by birds; insights from different geographical scales. *Frontiers in Ecology and Evolution*, *7*, 74. https://doi.org/10.3389/fevo.2019.00074

Hesthagen, T., Fiske, P., & Skjelkvåle, B. L. (2008). Critical limits for acid neutralizing capacity of brown trout (*Salmo trutta*) in Norwegian lakes differing in organic carbon concentrations. *Aquatic Ecology*, *42*(2), 307–316. https://doi.org/10.1007/s10452-008-9191-x

Hesthagen, T., Fjellheim, A., Schartau, A. K., Wright, R. F., Saksgård, R., & Rosseland, B. O. (2011). Chemical and biological recovery of Lake Saudlandsvatn, a formerly highly acidified lake in southernmost Norway, in response to decreased acid deposition. *Science of the Total Environment*, *409*(15), 2908–2916. https://doi.org/10.1016/j.scitotenv.2011.04.026

Holt, C., & Yan, N. D. (2003). Recovery of crustacean zooplankton communities from acidification in Killarney Park, Ontario, 1971–2000: PH 6 As a recovery goal. *Ambio*, *32*(3), 5–207. https://doi.org/10.1579/0044-7447-32.3.203

Isles, P. D. F., Creed, I. F., Jonsson, A., & Bergström, A.-K. (2021). Trade-offs between light and nutrient availability across gradients of dissolved organic carbon lead to spatially and temporally variable responses of lake phytoplankton biomass to browning. *Ecosystems*, *24*(8), 1837–1852. https://doi.org/10.1007/s10021-021-00619-7

Jansson, M., Persson, L., De Roos, A. M., Jones, R. I., & Tranvik, L. J. (2007). Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends in Ecology & Evolution*, *22*(6), 316–322. https://doi.org/10.1016/j.tree.2007.02.015

Jiang, S., Hu, T., Zhao, W., Hu, A., Zhu, L., & Wang, J. (2023). Increasing diversity and biotic homogenization of lake plankton during recovery from acidification. *Science of the Total Environment*, *859*, 160215. https://doi.org/10.1016/j.scitotenv.2022.160215

Keller, W. (1992). Introduction and overview to aquatic acidification studies in the Sudbury, Ontario, Canada, area. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*(S1), 3–7. https://doi.org/10.1139/f92-294

Keller, W., & Pitblado, J. R. (1984). Crustacean plankton in northeastern Ontario lakes subjected to acidic deposition. *Water, Air, and Soil Pollution*, *23*(3), 271–291. https://doi.org/10.1007/BF00283204

Keller, W., Yan, N. D., Somers, K. M., & Heneberry, J. H. (2002). Crustacean zooplankton communities in lakes recovering from acidification. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(4), 726–735. https://doi.org/10.1139/f02-042

Kelly, P. T., Solomon, C. T., Weidel, B. C., & Jones, S. E. (2014). Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. *Ecology*, *95*(5), 1236–1242. https://doi.org/10.1890/13-1586.1

Kiefer, F. (1978). Das Zooplankton der Binnengewasser. Freilebenden Copepoda. *Die Binnengewasser*, *26*, 1–343.

Kuczynski, L., Côte, J., Toussaint, A., Brosse, S., Buisson, L., & Grenouillet, G. (2018). Spatial mismatch in morphological, ecological and phylogenetic diversity, in historical and contemporary European freshwater fish faunas. *Ecography*, *41*(10), 1665–1674. https://doi.org/10.1111/ecog.03611

Laliberté, E., & Shipley, B. (2014). *R-package FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R Foundation for Statistical Computing.

Larssen, T., Lydersen, E., Tang, D., He, Y., Gao, J., Liu, H., Duan, L., Seip, H. M., Vogt, R. D., Mulder, J., Shao, M., Wang, Y., Shang, H., Zhang, X., Solberg, S., Aas, W., Okland, T., Eilertsen, O., Angell, V., … Luo, J. (2006). Acid rain in China. *Environmental Science & Technology*, *40*(2), 418–425. https://doi.org/10.1021/es0626133

Lau, D. C. P., Jonsson, A., Isles, P. D. F., Creed, I. F., & Bergström, A. (2021). Lowered nutritional quality of plankton caused by global environmental changes. *Global Change Biology*, *27*(23), 6294–6306. https://doi.org/10.1111/gcb.15887

Laudon, H., Sponseller, R. A., & Bishop, K. (2021). From legacy effects of acid deposition in boreal streams to future environmental threats. *Environmental Research Letters*, *16*(1), 015007. https://doi.org/10.1088/1748-9326/abd064

Leach, T. H., Winslow, L. A., Hayes, N. M., & Rose, K. C. (2019). Decoupled trophic responses to long-term recovery from acidification and associated browning in lakes. *Global Change Biology*, *25*(5), 1779–1792. https://doi.org/10.1111/gcb.14580

Liu, M., Song, Y., Xu, T., Xu, Z., Wang, T., Yin, L., Jia, X., & Tang, J. (2020). Trends of precipitation acidification and determining factors in China during 2006–2015. *Journal of Geophysical Research: Atmospheres*, *125*(6), e2019JD031301. https://doi.org/10.1029/2019JD031301

Locke, A. (1991). Zooplankton responses to acidification: A review of laboratory bioassays. *Water, Air, and Soil Pollution*, *60*(1), 135–148. https://doi.org/10.1007/BF00293971

Muniz, I. P. (1990). Freshwater acidification: Its effects on species and communities of freshwater microbes, plants and animals. *Proceedings of the Royal Society of Edinburgh, Section B: Biological Sciences*, *97*, 227–254. https://doi.org/10.1017/S0269727000005364

Nevalainen, L., Rantala, M. V., Rautio, M., & Luoto, T. P. (2018). Spatio-temporal cladoceran (Branchiopoda) responses to climate change and UV radiation in subarctic ecotonal lakes. *Journal of Biogeography*, *45*(8), 1954–1965. https://doi.org/10.1111/jbi.13371

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community ecology package*. R package version 2.5-5. https://CRAN.R-project.org/package=vegan

Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, *7*, e6876. https://doi.org/10.7717/peerj.6876

Pepin, N. C., Arnone, E., Gobiet, A., Haslinger, K., Kotlarski, S., Notarnicola, C., Palazzi, E., Seibert, P., Serafin, S., Schöner, W., Terzago, S., Thornton, J. M., Vuille, M., & Adler, C. (2022). Climate changes and their elevational patterns in the mountains of the world. *Reviews of Geophysics*, *60*(1), e2020RG000730. https://doi.org/10.1029/2020RG000730

Persson, J., Brett, M. T., Vrede, T., & Ravet, J. L. (2007). Food quantity and quality regulation of trophic transfer between primary producers and a keystone grazer (Daphnia) in pelagic freshwater food webs. *Oikos*, *116*(7), 1152–1163. https://doi.org/10.1111/j.0030-1299.2007.15639.x

Previdi, M., Smith, K. L., & Polvani, L. M. (2021). Arctic amplification of climate change: A review of underlying mechanisms. *Environmental Research Letters*, *16*(9), 093003. https://doi.org/10.1088/1748-9326/ac1c29

R Core Team. (2019). *R: A language and environment for statistical computing [computer software]*. R Foundation for Statistical Computing https://www.R-project.org/

Ross, A. J., & Arnott, S. E. (2022). Similar zooplankton responses to low pH and calcium may impair long-term recovery from acidification. *Ecological Applications*, *32*(3), e2512. https://doi.org/10.1002/eap.2512

Sars, G. O. (1903). *An account of the Crustacea of Norway: Copepoda Calanoida* (Vol. 4). Bergen Museum, Alb Cammermeyer's Forlag.

Sars, G. O. (1913). *An account of the Crustacea of Norway: Copepoda Cyclopoida* (Vol. 6). Bergen Museum.

Schneider, S. C. (2011). Impact of calcium and TOC on biological acidification assessment in Norwegian rivers. *Science of the Total Environment*, *409*(6), 1164–1171. https://doi.org/10.1016/j.scitotenv.2010.11.019

Simpson, G. L., & Singmann, H. (2022). *gratia: Graceful 'ggplot'-based graphics and other functions for GAMs fitted using "mgcv"* (0.7.3) [Computer software]. https://CRAN.R-project.org/package=gratia

Skjelkvåle, B. L., Stoddard, J. L., Jeffries, D. S., Tørseth, K., Høgåsen, T., Bowman, J., Mannio, J., Monteith, D. T., Mosello, R., Rogora, M., Rzychon, D., Vesely, J., Wieting, J., Wilander, A., & Worsztynowicz, A. (2005). Regional scale evidence for improvements in surface water chemistry 1990–2001. *Environmental Pollution*, *137*(1), 165–176. https://doi.org/10.1016/j.envpol.2004.12.023

Stoddard, J. L., Jeffries, D. S., Lükewille, A., Clair, T. A., Dillon, P. J., Driscoll, C. T., Forsius, M., Johannessen, M., Kahl, J. S., Kellogg, J. H., Kemp, A., Mannio, J., Monteith, D. T., Murdoch, P. S., Patrick, S., Rebsdorf, A., Skjelkvåle, B. L., Stainton, M. P., Traaen, T., … Wilander, A. (1999). Regional trends in aquatic recovery from acidification in North America and Europe. *Nature*, *401*(6753), 575–578. https://doi.org/10.1038/44114

Vadadi-Fülöp, C., Sipkay, C., Mészáros, G., & Hufnagel, L. (2012). Climate change and freshwater zooplankton: What does it boil down to? *Aquatic Ecology*, *46*(4), 501–519. https://doi.org/10.1007/s10452-012-9418-8

Vogt, R. J., Peres-Neto, P. R., & Beisner, B. E. (2013). Using functional traits to investigate the determinants of crustacean zooplankton community structure. *Oikos*, *122*(12), 1700–1709. https://doi.org/10.1111/j.1600-0706.2013.00039.x

Wærvågen, S. B., & Nilssen, J. P. (2003). Major changes in pelagic rotifers during natural and forced recovery from acidification. *Hydrobiologia*, *499*, 63–82. https://doi.org/10.1023/A:1026395602221

Walseng, B. (2002). Plankton versus littoral microcrustaceans (copepods and cladocerans) as indicators of recovery from acidification. *N, Internationale Vereinigung Für Theoretische Und Angewandte Limnologie: Verhandlungen*, *28*(1), 140–143. https://doi.org/10.1080/03680770.2001.11902562

Walseng, B., Halvorsen, G., & Sloreid, S.-E. (2001). Littoral microcrustaceans (Cladocera and Copepoda) as indices of recovery of a limed water system. *Hydrobiologia*, *450*(1), 159–172. https://doi.org/10.1023/A:1017540809917

Walseng, B., Hessen, D. O., Halvorsen, G., & Schartau, A. K. (2006). Major contribution from littoral crustaceans to zooplankton species richness in lakes. *Limnology and Oceanography*, *51*(6), 2600–2606. https://doi.org/10.4319/lo.2006.51.6.2600

Walseng, B., & Karlsen, L. R. (2001). Planktonic and littoral microcrustaceans as indices of recovery in limed lakes in SE Norway. *Water, Air, and Soil Pollution*, *130*(1), 1313–1318. https://doi.org/10.1023/A:1013953806377

Walseng, B., Yan, N. D., & Schartau, A. K. (2003). Littoral microcrustacean (Cladocera and Copepoda) indicators of acidification in Canadian shield lakes. *Ambio*, *32*(3), 208–213. https://doi.org/10.1579/0044-7447-32.3.208

Weiss, L. C., Pötter, L., Steiger, A., Kruppert, S., Frost, U., & Tollrian, R. (2018). Rising pCO_2 in freshwater ecosystems has the potential to negatively affect predator-induced defenses in daphnia. *Current Biology*, *28*(2), 327–332.e3. https://doi.org/10.1016/j.cub.2017.12.022

Weyhenmeyer, G. A., Peter, H., & Willén, E. (2013). Shifts in phytoplankton species richness and biomass along a latitudinal gradient—Consequences for relationships between biodiversity and ecosystem functioning. *Freshwater Biology*, *58*(3), 612–623. https://doi.org/10.1111/j.1365-2427.2012.02779.x

Wood, S. (2012). *mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation*. https://cran.r-project.org/web/packages/mgcv

Wood, S. N. (2006). *Generalized additive models: An introduction with R*. Chapman and Hall/CRC. https://doi.org/10.1201/9781420010404

Woolway, R. I., Kraemer, B. M., Lenters, J. D., Merchant, C. J., O'Reilly, C. M., & Sharma, S. (2020). Global lake responses to climate change. *Nature Reviews Earth & Environment*, *1*(8), 388–403. https://doi.org/10.1038/s43017-020-0067-5

Wright, R. F., & Henriksen, A. (1978). Chemistry of small Norwegian lakes, with special reference to acid precipitation. *Limnology and Oceanography*, *23*(3), 487–498. https://doi.org/10.4319/lo.1978.23.3.0487

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Pilotto, F., Walseng, B., Jensen, T. C., & Schartau, A. K. (2023). The recovery of crustacean zooplankton from acidification depends on lake type. *Global Change Biology*, *29*, 6066–6076. https://doi.org/10.1111/gcb.16919