

# Community analysis of Belarusian lakes: correlations of species diversity with hydrochemistry

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**Abstract** Our purpose was to explore relationships of freshwater planktonic and benthic community species richness with water chemistry parameters using a dataset of biological, chemical, and physical data from 550 lakes. This was done using multivariate (ordination), graphical, and correlation analyses. Although the lakes are rather similar in location (Belarus) and in being mostly eutrophic, they do show variations in water chemistry. We ordinated lakes by water chemistry variables, and then looked for correlations between the ordination axes and species richness in 10 taxonomic groups: Cyanobacteria, Chlorophyta, Bacillariophyta, Cladocera, Copepoda, Rotatoria, Mollusca, Trichoptera, Chironomidae, and aquatic macrophytes. The first four Principal Components Analysis (PCA) axes explained about 67% of the total variability in water

chemistry. The axes represent water hardness (DIC, dissolved inorganic carbon), organic content (DOC, dissolved organic carbon), nutrients, and chlorides and sulfates. The PCA ordination revealed environmental gradients, but not the distinctive clusters of lakes. Species richness was most strongly correlated with the first PCA axis (DIC), which accounted for 29% of the total variation in water chemistry. Species richness was positively correlated with DIC for eight of 10 taxonomic categories. The second PCA axis (DOC), which accounted for 20% of total variation in water chemistry, was correlated with species richness in the three phytoplankton groups, and with chironomid species richness. The third PCA axis (nutrients, especially nitrogen, 11%) was correlated with species richness of copepoda, chironomids, and macrophytes. The fourth PCA axis (chloride and sulfate) accounted for only 7% of the total variance in water chemistry, and was significantly negatively correlated with species richness of rotifers, molluscs, and chironomids. In addition to these linear correlations, there were several significant non-linear relationships. DIC variables showed curvilinear (hump-shaped) relationship with benthos (all groups combined) and especially with molluscs, and DOC variables—with phytoplankton and benthos. Each community, and often separate taxonomic groups within community have their own optimal ranges of chemical concentrations, and various water chemistry variables showed significant curvilinear relationships with biodiversity, suggesting that the diversity of different

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major aquatic groups may be influenced by different chemicals.

**Keywords** Phytoplankton · Zooplankton · Zoobenthos · Hydrochemistry · Biodiversity

## Introduction

Lake chemical parameters play critical roles in aquatic ecosystems affecting water quality, productivity of aquatic communities, and biodiversity. However, effects of only a few water chemistry parameters (e.g., phosphorus, alkalinity, or pH) on biodiversity have been studied extensively (Økland, 1983; Økland & Økland, 1986; Brezonic et al., 1984; Arvola et al., 1990; Jeppesen et al., 2000; Vestergaard & Sand-Jensen, 2000; Declerck et al., 2005). Moreover, some communities (e.g. phytoplankton) have been studied more often than other communities (e.g. zoobenthos). The same is true for taxonomic groups within a community. For example, for the community of benthic invertebrates, much more information is available on the effects of chemical parameters on the species richness of gastropods (Økland, 1983; Lodge et al., 1987; Pip, 1987; Savage & Gazey, 1987), than chironomids.

In some cases, the impact of water chemistry on biodiversity is controversial. Arvola et al. (1990) found a significant positive correlation between rotifers species richness and pH in acid to neutral Finish lakes (pH range 4.9–7.0). In contrast, Sharma (2005) found a negative relationship between rotifers diversity and pH in acid to alkaline flood plain Indian lakes (pH range 5.5–9.5). According to Kondoh (2001) hypotheses, the species richness is highest at an “intermediate” level of disturbance or primary productivity (Dodson et al., 2000), indicating a unimodal response of communities. Jeppesen et al. (2000) showed that, in 71 Danish lakes, species richness of zooplankton and submerged macrophytes declined significantly with increasing total phosphorus concentration (indicator of primary productivity), while fish, phytoplankton, and floating-leaf macrophytes were unimodally related to total phosphorus. Therefore different communities or taxonomic groups may have different optimal requirements for highest diversity.

Most biodiversity studies focus on one or few communities due to the scarcity of data on diversity patterns across organism groups of different trophic levels (Allen et al., 1999; Declerck et al., 2005). Understanding the relationship between biodiversity and water chemistry across various communities is of critical importance for many issues of freshwater management, conservation, and restoration of aquatic ecosystems.

To assess the effect of water chemistry on lacustrine species richness, we used biological and hydrochemical data on 550 glacial lakes in the Northern Belarus. The dataset has unique features: all the lakes belong to the same geographic region, were formed during the last glaciation, and most importantly, they were studied using the same methods. This data set allowed us to explore even subtle correlations between species richness and abiotic parameters that would not have been possible to detect with a smaller or more heterogeneous dataset (Karatayev et al., 2005).

Variables related to lake morphometry are linearly correlated with biodiversity. For example, larger lakes have more species (Karatayev et al., 2005). However, we hypothesize that, in contrast to lake morphometry, some hydrochemical parameters show a curvilinear (hump-shaped) relationship to biodiversity, with the highest biodiversity at an intermediate chemical concentration. For example, the relationship between productivity and species richness suggest that biodiversity might have a curvilinear relationship to productivity surrogates, such as phosphorus or nitrogen (Dodson et al., 2000). Several authors have reported that various communities have significant differences in peak biodiversity relative to the same chemical parameter (e.g. Brezonic et al., 1984; Arvola et al., 1990; Declerck et al., 2005). One of our goals is to use our biodiversity data to generate additional hypotheses about the possibility that different taxa have different responses to water chemistry.

## Methods

### Site description

This study was based on the analysis of 550 lakes in northern Belarus, formed at approximately same time

during last glaciation. These lakes comprise 51% of the total number of Belarusian lakes. A database containing information on the lake location, characteristic of the drainage basin, lake morphology, hydrochemistry, and hydrobiology was made for each of the study lakes. All lakes were sampled once during 1971–1991 in summer season from mid June to mid August by the Lakes Research Laboratory and the General Ecology Department of the Belarusian State University. A similar snapshot method was successfully used in other studies (Stemberger et al., 2001; Dodson et al., 2005). During 1997–1998 the lake data were digitized as a contribution to the Limnoflora-Limnofauna Belarusi (Karatayev et al., 2005).

### Sampling method

The abiotic and biotic characteristics used in this study included hydrochemistry and species richness of phytoplankton, zooplankton, zoobenthos, and macrophytes collected from multiple sites (from 6 in smallest to 25 in largest lakes) within each lake. Hydrochemical parameters included water transparency (Secchi depth), color, pH, concentration of hydrocarbonates, sulfates, chlorides, calcium, magnesium, total dissolved solids (TDS), iron, silicon, ammonia, nitrites, phosphates and bichromate, and permanganate oxidizability. All hydrochemical parameters were analyzed using standard procedure (Unified methods of study of the water quality, 1974). The species richness was analyzed separately for 10 major freshwater taxonomic groups: Cyanobacteria, Chlorophyta, Bacillariophyta, Cladocera, Copepoda, Rotatoria, Mollusca, Trichoptera, Chironomidae, and aquatic macrophytes.

Phytoplankton samples were collected in a 1 l Ruttner bathometer and preserved with Lugol's solution. Zooplankton was collected with a 10 l Vovk plankton sampler (Kisselev, 1969), filtered through 50  $\mu\text{m}$  silk mesh and preserved with 4% neutral buffered formalin. Samples were collected at 2 m depth intervals in the epilimnion and in deep lakes at 5 m depth in the hypolimnion. In addition a plankton net was towed in the littoral zone of each lake horizontally for about 100 m and vertically in the deepest part, if the lake maximum depth was  $>3$  m. Benthic invertebrates were collected using an Eckman (on soft substrate) or Petersen (on hard

substrate) dredge with sampling area = 0.025  $\text{m}^2$ , washed through a 500  $\mu\text{m}$  mesh and preserved with 10% neutral buffered formalin. In addition, benthic species composition along a 100 m stretch of the littoral zone (down to 1.5 m depth) was examined by checking substrates (rocks, submerged woods, etc.) and dip-nets. In benthic samples, all organisms collected were identified. Zooplankton samples were split, and only 30% of the total collected was identified. Number of individuals counted varied from few individuals to few thousands per sample.

All organisms collected were identified to the lowest possible level using only morphological criteria. Phytoplankton and zooplankton species in most cases were identified to species with the exception of selected groups that were identified to genera (e.g. some cyclopoid copepods). Most of benthic taxa were also taken down to species, however chironomid larvae were identified to mostly larval groups (some down to species or genus levels). Pisidiidae were identified to genus, and Oligochaeta were lumped. All other groups were identified to the species level. The level of identification was consistent across all lakes studied. Rarefaction of species richness data would have been desirable, but for each lake either the entire sample, or a standard fraction of the entire sample were observed. The number observed was not recorded in the original data and therefore the data cannot be corrected by rarefaction.

### Data analysis

We used Principal Component Analysis (PCA) on a correlation matrix (STATISTICA version 6, StatSoft, Inc. 2001). PCA is based on algebraic and linear relationships among the values of component variables (McCune & Grace, 2002) and works best, when the data matrix contains few zeros. Our approach was to use PCA on the chemistry data alone to create independent hydrochemical axes, and then look for strong correlations between the PCA axes and species richness.

Since distribution of lakes within a lake district along majority of abiotic and biotic parameters is often skewed due to disproportionally high abundance of lakes that are small and shallow (e.g. Jeppesen et al., 2000; Auer et al., 2004; Søndergaard et al., 2005), before ordination, all raw data were fourth-root-transformed (except for pH), and

normalized (to a mean of zero and standard deviation of 1.0). Fourth-root transformation is less severe than log-transformation, but is effectively equivalent (Clarke & Warwick, 2001). Correlation analysis was used to find the relationship between log species richness (the dependent variable) and the PCA axes. For this analysis, we calculated the correlation coefficients of the log-transformed number of species in each lake, for each taxonomic group, with the score of the lake along the PCA axes.

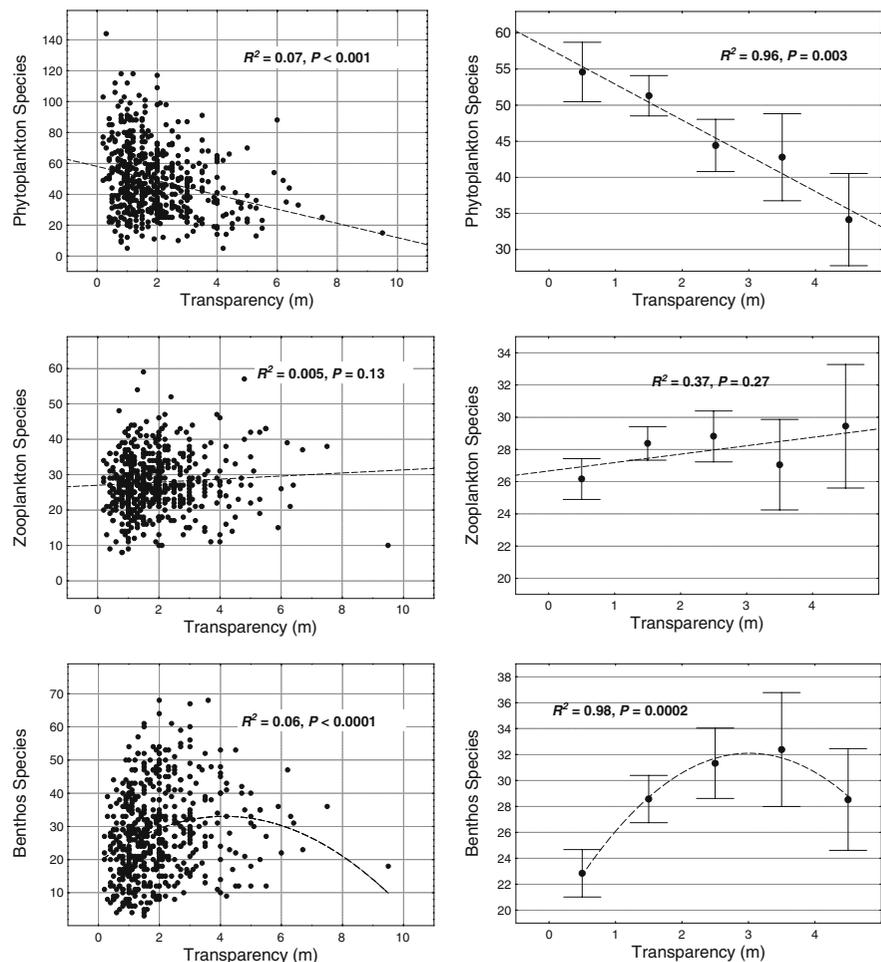
### Grouping of data

Different lake types were unequally represented in the dataset. Most of the lakes were very similar chemically (trophically), producing a large cloud of points with a tail representing a few lakes with different water chemistry (Figs. 1–4). Thus,

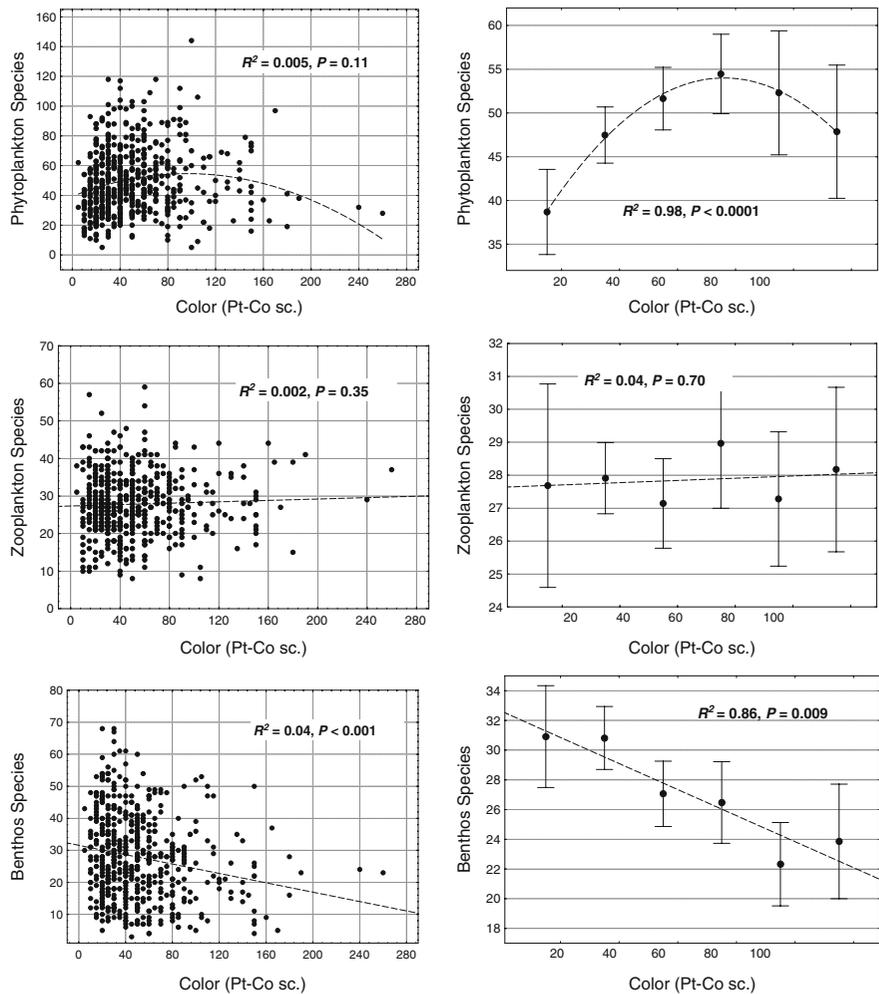
correlations between biodiversity and water chemistry were dominated by the many similar lakes, and the relationship across the entire range of water chemistry was obscured. In order to visualize the relationship between biodiversity and water chemistry, we grouped biodiversity data at equal intervals across the whole range of each chemical parameter, and then the average and confidence intervals were calculated for each group. This is a hypothesis-generating method only.

We evaluated curvilinearity by testing the significance of a quadratic model (i.e. linear regression including a second order term) against a linear model. The significance of the inclusion of the quadratic term provides a convenient statistical test for a declining slope (Caley & Schluter, 1997; Karlson & Cornell, 1998). To check if the quadratic model explains significantly more variation than linear, we

**Fig. 1** Associations between water transparency and the species richness of phytoplankton, zooplankton, and zoobenthos communities in Belarusian lakes. Raw data (left column) and grouped data (right column). Coefficients of determination and their significance are given. Vertical bars denote 95% confidence intervals



**Fig. 2** Associations between water color and the species richness of phytoplankton, zooplankton, and zoobenthos communities in Belarusian lakes. Raw data (left column) and grouped data (right column). Coefficients of determination and their significance are given. Vertical bars denote 95% confidence intervals



performed an *F*-test of the residual variation from the linear model and the quadratic model (Zar, 1996).

## Results

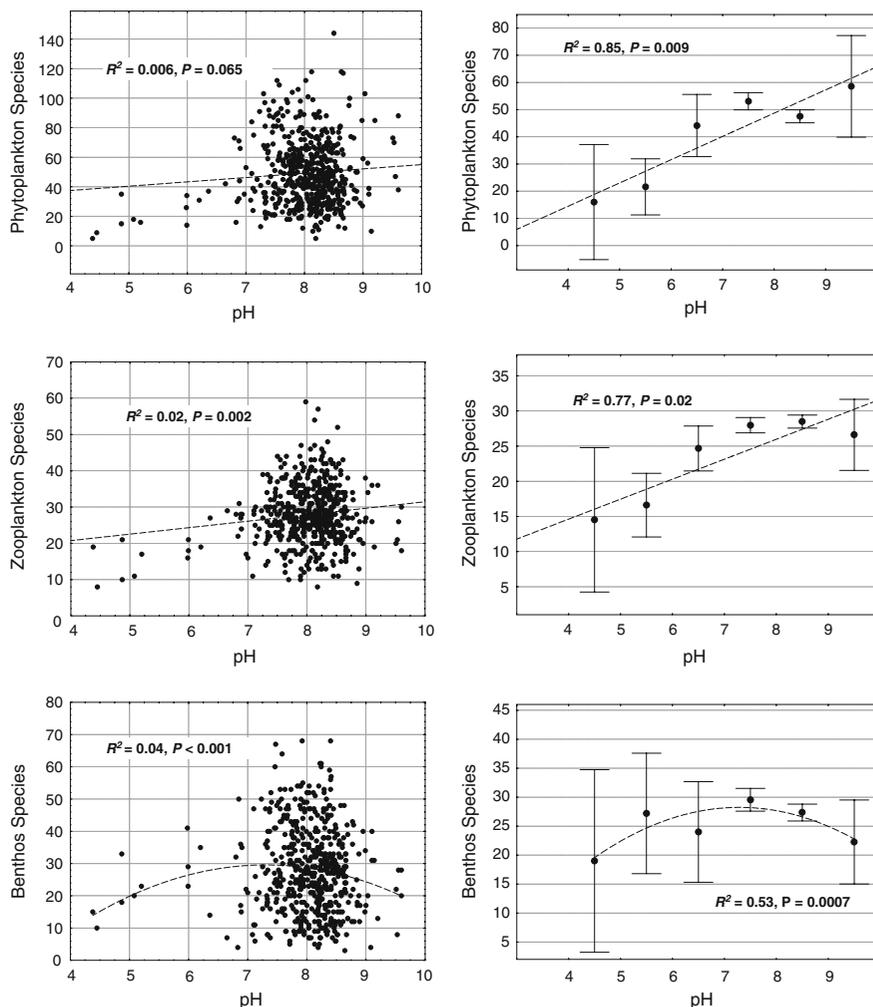
### Data set description

The whole range of variation for most of hydrochemical parameters studied was quite large (Table 1), however this large range was almost always due to the presence of outliers, with the bulk of lakes falling into a more narrow range. For example, although the water clarity (Secchi depth) in Belarusian lakes in summer varied from 0.2 to 9.5 m, lakes with low transparency (0.5–3 m) were disproportionately abundant and formed 82% of all lakes

studied. Water color varied from 5 to 260° Pt-Co scale, but in most lakes (87%) color varied between 10 and 90°. Although a few Belarusian lakes were acidic with  $\text{pH} < 5$  (1%), more than 92% were neutral or slightly alkaline ( $\text{pH} 7\text{--}9$ ). Although concentration of total dissolved solids in all Belarusian lakes studied varied from 18.3 to 538.5  $\text{mg l}^{-1}$ , in most lakes (80%) concentration of dissolved solids was between 100 and 250  $\text{mg l}^{-1}$ .

The highest diversity was found in phytoplankton. During the whole study, 695 species and higher taxa were identified in this community, including 257 species of green algae, 225 species of diatoms, and 94 taxa of cyanobacteria. Total 499 species and higher taxa were found in benthic community, including 101 species of chironomids, and 69 of molluscs. The lowest species richness (299 species and higher taxa)

**Fig. 3** Associations between pH and the species richness of phytoplankton, zooplankton, and zoobenthos communities in Belarusian lakes. Raw data (left column) and grouped data (right column). Coefficients of determination and their significance are given. Vertical bars denote 95% confidence intervals



was found in zooplankton community. Both mean and median species richness of planktonic algae per lake was almost twice as high as the diversity of planktonic and benthic invertebrates.

#### Large scale correlates revealed by PCA

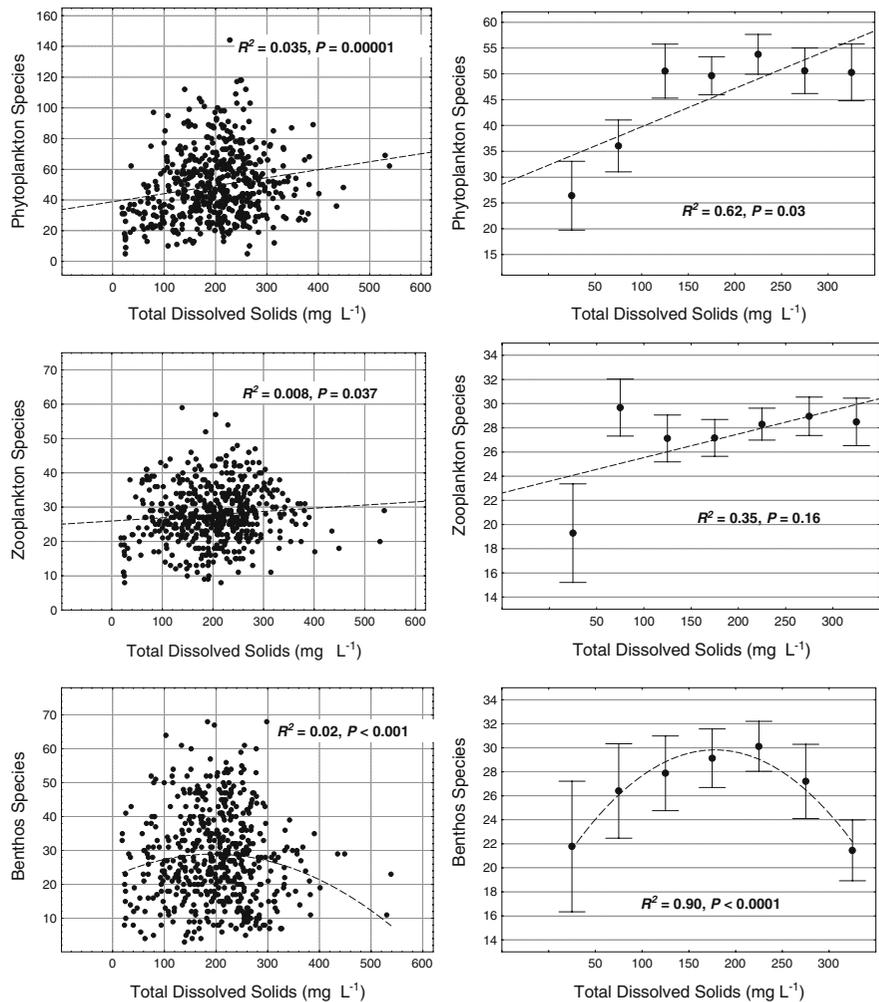
The first four PCA axes represented 67% of the total variability in the hydrochemical data (Table 1). Water hardness (DIC—dissolved inorganic carbon) was strongly correlated with the first PCA axis. Parameters indicating dissolved organic content (DOC) in the water (*e.g.*, color and oxidizability) were negatively correlated with the second PC axis, while water transparency correlated positively with PC 2. Strong negative correlates with the third PCA axes included nitrites and ortho-phosphates

(nutrients), and positive correlates with the fourth PCA axes—chlorides and sulfates.

#### Different correlates for different groups

Zooplankton diversity (especially copepods and rotifers), phytoplankton (especially Bacillariophyta), molluscs in benthos, and macrophytes showed highest positive correlation with PC 1 (DIC) (Table 1). Phytoplankton diversity (especially Chlorophyta) correlated negatively with PC 2 (*i.e.* positively with DOC), while total benthos diversity (and especially Chironomidae) was negatively correlated with DOC. Benthos diversity was negatively correlated with PC 3 (*i.e.* positively with nutrient concentration). Zooplankton and zoobenthos diversity were negatively correlated with PC 4 (chlorides).

**Fig. 4** Associations between total dissolved solids and the species richness of phytoplankton, zooplankton, and zoobenthos communities in Belarusian lakes. Raw data (left column) and grouped data (right column). Coefficients of determination and their significance are given. Vertical bars denote 95% confidence intervals



For analysis of the impacts of individual hydro-chemistry variables on biodiversity, we selected parameters that showed the highest correlation with the species richness (Table 2). Different communities showed different, sometimes opposite responses to the same parameter. Transparency was negatively correlated with the phytoplankton species richness and positively with zoobenthos (Fig. 1). No high correlation was found between zooplankton diversity and water clarity. Water color was negatively correlated with zoobenthos species richness, and positively with phytoplankton, however no significant correlations were found among water color and number of species in zooplankton (Fig. 2). There was a weak but significant correlation between zooplankton, phytoplankton and macrophyte diversity and pH (Table 2, Fig. 3). However, no consistent linear correlation was

found between total zoobenthos diversity and lake pH (thus there were some positive correlations for molluscs and negative for trichopterans, Table 2). The amount of hydrocarbonates and correspondingly TDS in the water were positively correlated with phytoplankton and zooplankton diversity (mainly due to correlation with the species richness of rotifers), and macrophytes (Table 2, Fig. 4). While total number of species in zoobenthos was not linearly correlated with TDS, molluscs showed positive correlation with hydrocarbonates and TDS, and trichopterans showed negative correlation with both these parameters (Table 2). Calcium content in the water was positively correlated with the diversity of all groups in phytoplankton, total richness of zooplankton, molluscs in benthos, and macrophytes (Table 2). Oxidizability was positively correlated

**Table 1** Averages and ranges of hydrochemical variables and species richness of aquatic organism groups in the 550 Belarusian lakes, with Pearson correlation coefficients between hydrochemical variables and the PCA axes on these variables ( $N = 311$ ), and Pearson correlation coefficients between species richness and these hydrochemical PC axes. Percent of

total variation explained by the PCA axes is given in parentheses. The highest loadings for each PC axis are in bold. To summarize the variables correlated with axes, we named PC 1 as DIC (dissolved inorganic carbon), PC 2—DOC (dissolved organic carbon), PC 3—nutrients (especially nitro- gen), and PC 4—chloride

Parameter	<i>N</i>	Mean $\pm$ 1 SE	Range	PC 1 (29.4%) DIC	PC 2 (20.6%) DOC	PC 3 (10.8%) Nutrients	PC 4 (6.8%) Chloride
Transparency, m	548	1.92 $\pm$ 0.05	0.2–9.5	–0.154	<b>0.754</b>	–0.195	0.130
Color, Pt-Co sc.	548	50.9 $\pm$ 1.5	5–260	–0.108	<b>–0.860</b>	0.186	0.000
pH	542	8.013 $\pm$ 0.028	3.65–9.60	0.603	0.023	0.128	–0.459
Hydrocarbonates (HCO <sub>3</sub> ), mg l <sup>–1</sup>	550	139.7 $\pm$ 2.5	4.6–367.3	<b>0.968</b>	0.010	0.022	–0.131
Sulfates (SO <sub>4</sub> ), mg l <sup>–1</sup>	537	9.93 $\pm$ 0.32	0.8–98.5	0.455	–0.165	0.160	<b>0.505</b>
Chlorides (Cl), mg l <sup>–1</sup>	547	6.76 $\pm$ 0.25	0.1–58.4	0.614	–0.071	–0.069	<b>0.542</b>
Calcium (Ca), mg l <sup>–1</sup>	549	33.15 $\pm$ 0.56	2.8–89.6	<b>0.949</b>	–0.066	0.046	–0.044
Magnesium (Mg), mg l <sup>–1</sup>	548	10.36 $\pm$ 0.21	0.4–24.0	<b>0.851</b>	0.096	0.010	–0.101
Total dissolved solids, mg l <sup>–1</sup>	550	199.4 $\pm$ 3.4	18.3–538.5	<b>0.984</b>	–0.002	0.021	–0.047
Ferrum total (Fe), mg l <sup>–1</sup>	548	0.226 $\pm$ 0.014	0.005–2.790	–0.134	–0.614	–0.449	0.001
Silicon (Si), mg l <sup>–1</sup>	523	0.626 $\pm$ 0.034	0.005–8.240	0.403	–0.092	–0.429	0.145
Ammonia nitrogen (NH <sub>4</sub> ), mgN l <sup>–1</sup>	539	0.226 $\pm$ 0.011	0.005–2.180	0.005	–0.304	<b>–0.520</b>	0.339
Nitrites (NO <sub>2</sub> ), mgN l <sup>–1</sup>	497	0.004 $\pm$ 0.001	0.0005–0.508	0.039	–0.204	<b>–0.687</b>	–0.166
Phosphates (PO <sub>4</sub> ), mgP l <sup>–1</sup>	543	0.0269 $\pm$ 0.0025	0.0005–0.8000	0.078	–0.239	<b>–0.572</b>	–0.299
Oxidizability (mgO l <sup>–1</sup> )							
Permanganate	549	11.57 $\pm$ 0.28	1.0–46.5	–0.058	<b>–0.857</b>	0.185	–0.137
Dichromate	324	40.06 $\pm$ 1.04	5.0–108.0	–0.043	<b>–0.792</b>	0.334	0.079
<i>Species</i>							
All phytoplankton	541	49.3 $\pm$ 0.95	5–144	0.157**	–0.304***	–0.012	–0.075
Cyanobacteria	541	8.7 $\pm$ 0.21	0–29	0.026	–0.192**	0.022	–0.119
Chlorophyta	541	18.2 $\pm$ 0.46	0–65	0.149*	–0.316***	–0.005	–0.013
Bacillariophyta	541	13.8 $\pm$ 0.28	0–41	0.193***	–0.182**	–0.004	–0.137*
All Zooplankton	532	27.8 $\pm$ 0.35	8–59	0.142*	–0.043	0.023	–0.228***
Cladocera	530	12.2 $\pm$ 0.21	2–27	0.027	–0.023	–0.002	–0.098
Copepoda	530	4.9 $\pm$ 0.10	1–14	0.205***	–0.014	0.132*	–0.182**
Rotatoria	530	10.8 $\pm$ 0.17	0–25	0.182**	–0.095	0.044	–0.266***
All benthos	539	27.8 $\pm$ 0.57	3–68	–0.044	0.120*	–0.202**	–0.132*
Mollusca	533	5.1 $\pm$ 0.15	0–15	0.165**	0.002	–0.103*	–0.130*
Trichoptera	531	2.0 $\pm$ 0.09	0–14	–0.149*	0.053	–0.080	–0.101
Chironomidae	534	11.6 $\pm$ 0.25	0–29	–0.154**	0.137*	–0.221***	–0.126*
All macrophytes	517	10.1 $\pm$ 0.19	0–23	0.163**	0.028	0.125*	0.010

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

with the phytoplankton species richness and negatively with zoobenthos (Fig. 5). Correlations between oxidizability of water and number of species in

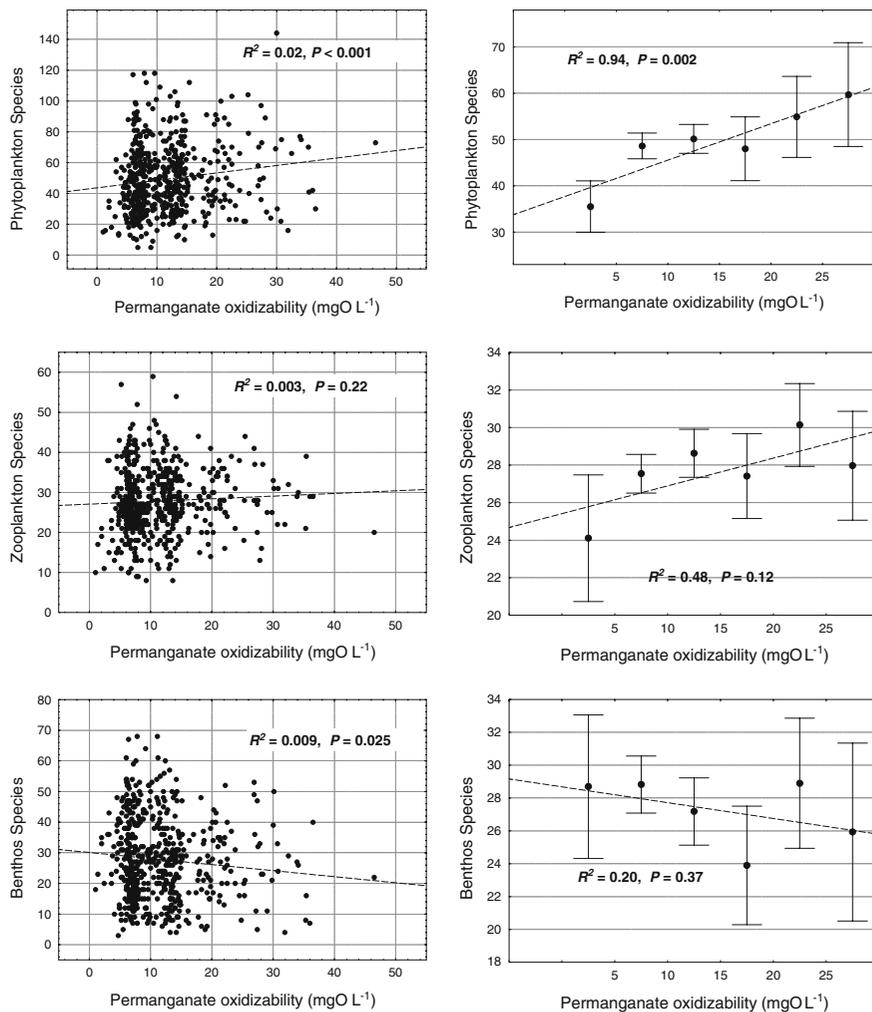
zooplankton were mostly non-significant, except for rotifers (Table 2). Diversity of the majority of phytoplankton groups positively correlated with

**Table 2** Pearson coefficients of correlations  $r$  between the log-transformed number of species (species richness, raw data) in lake communities with log-transformed (except pH) hydrochemical parameters

Community	Transparency	Color	pH	HCO <sub>3</sub>	Ca	TDS	Permanganate oxidizability	Cl	NH <sub>4</sub>	NO <sub>2</sub>	PO <sub>4</sub>
All phytoplankton	-0.240***	0.129**	0.150**	0.278***	0.298***	0.289***	0.166***	0.200***	0.037	-0.024	0.127**
Cyanobacteria	-0.233***	0.076	0.187***	0.164***	0.171***	0.166***	0.104*	0.113*	0.05	-0.014	0.064
Chlorophyta	-0.329***	0.193***	0.124**	0.234***	0.244***	0.248***	0.200***	0.226***	0.059	0.005	0.114*
Bacillariophyta	-0.074	0.050	0.160***	0.294***	0.320***	0.294***	0.112*	0.069	-0.014	-0.038	0.093
All zooplankton	0.081	0.051	0.179***	0.206***	0.208***	0.187***	0.107*	-0.06	-0.05	0.100*	0.036
Cladocera	0.165***	0.045	0.057	0.059	0.068	0.039	0.040	-0.125**	-0.012	0.130**	-0.033
Copepoda	0.065	0.019	0.248***	0.091*	0.087	0.063	0.072	-0.102*	0.035	0.163**	-0.095*
Crustacean	0.150***	0.030	0.106*	0.070	0.078	0.048	0.051*	-0.135**	0.012	0.155**	-0.058
Rotatoria	-0.058	0.053	0.180***	0.292***	0.289***	0.288***	0.138**	0.065	-0.106*	-0.03	0.110*
All Benthos	0.246***	-0.196***	0.015	-0.049	0.049	0.040	-0.096*	-0.03	0.011	-0.057	0.123*
Mollusca	0.181***	-0.091*	0.143**	0.226***	0.237***	0.217***	-0.012	0.066	-0.012	0.016	0.074
Trichoptera	0.154***	-0.091*	-0.140**	-0.116*	-0.088	-0.113*	-0.038	0.021	-0.019	-0.121*	-0.018
Chironomidae	0.213***	-0.204***	-0.034	-0.049	-0.052	-0.060	-0.108*	-0.141**	-0.037	-0.027	0.097*
All macrophytes	-0.024	-0.026	0.194***	0.149**	0.170***	0.138**	0.063	-0.047	0.031	-0.117*	0.128**

\* $P < 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\* $P \leq 0.001$

**Fig. 5** Associations between permanganate oxidizability and the species richness of phytoplankton, zooplankton, and zoobenthos communities in Belarusian lakes. Raw data (left column) and grouped data (right column). Coefficients of determination and their significance are given. Vertical bars denote 95% confidence intervals



chlorides, and diversity of zooplankton correlated positively with nitrites (Table 2).

#### Patterns revealed by grouped data

All correlations found between species diversity and chemical parameters were very low, when we used raw data for the analysis (Fig. 1–5). Grouped data often revealed patterns not readily seen in raw data. Thus, we found a negative linear correlation between water clarity and phytoplankton diversity and no linear correlation with zooplankton and benthic richness (Fig. 1). In contrast, we found a curvilinear relationship between benthic diversity and transparency, indicating that species richness of this community may be limited by both high and low transparency (Fig. 1). Water color was negatively

correlated with zoobenthos diversity (Fig. 2). There was a significant negative quadratic term indicating non-linear relationship between phytoplankton species richness and water color (Fig. 2). Similar relationships were found for benthic diversity and TDS as well as pH, and molluscs and TDS, which may be an indicator of unimodal relationship (Figs. 3, 4). Quadratic terms for all these relationships (between benthos and transparency, benthos and pH, benthos and TDS, molluscs and TDS, and phytoplankton and color) were significant ( $0.01 < P < 0.0003$ ,  $t$ -test). Determination coefficients of quadratic regression were much higher than those of linear regression (benthos and transparency:  $R^2 = 0.98$  vs. 0.42; benthos and pH: 0.73 vs. 0.08; benthos and TDS: 0.95 vs. 0.004; molluscs and TDS: 0.95 vs. 0.47; and phytoplankton and color:

**Table 3** Range of hydrochemical parameters at which the highest diversity of each community was found. n.c.p.—no clear patterns were found.

Community	pH	Ca, mg l <sup>-1</sup>	TDS, mg l <sup>-1</sup>	Transparency, m	Color, Pt-Co sc.	Permanganate oxidizability, mgO l <sup>-1</sup>
All phytoplankton	≥6	≥20	≥150	<1	≥ 20	≥5
Cyanobacteria	≥6	≥10	150–300	<1	20–80	≥5
Chlorophyta	≥6	≥20	≥150	<1	≥20	≥5
Bacillariophyta	≥6	≥20	≥150	<3	20–100	≥5
All zooplankton	≥6	≥10	≥100	>2	n.c.p.	≥5
Cladocera	7–8	≥10	≥100	≥2	n.c.p.	≥5
Copepoda	≥7	≥10	≥100	≥2	n.c.p.	n.c.p.
Crustacean	7–8	≥10	≥100	≥2	n.c.p.	≥5
Rotatoria	≥6	≥10	≥100	n.c.p.	n.c.p.	≥5
All benthos	n.c.p.	10–40	100–300	3–4	≤ 20	n.c.p.
Mollusca	≥7	≥20	≥100	2–4	n.c.p.	n.c.p.
Trichoptera	≤7	n.c.p.	≤150	≥2	n.c.p.	<5
Chironomidae	n.c.p.	10–40	100–300	≥2	≤ 20	≤15
All macrophytes	7–8	≥20	≥150	n.c.p.	n.c.p.	≥5
All species	≥7	≥20	150–300	1–4	20–100	≥5

0.98 vs. 0.36). Quadratic regression on grouped data explained significantly more variation than linear regression ( $0.01 < P < 0.0003$ , *F*-test) except for the benthic species, where a pH relationship was marginally significant ( $P = 0.07$ ).

Several taxonomic groups have a significant curvilinear relationship of biodiversity and water chemistry. For these groups, we have indicated the concentration range associated with each taxon (Table 3).

## Discussion

### Large scale correlates of lacustrine diversity

The study lakes differed principally along gradients of dissolved inorganic carbon, organic content (especially oxidizability, color and transparency), nutrients, and concentration of chlorides and sulfates (Table 1). Correlation analysis between hydrochemical PCA axes and diversity in Belarusian glacial lakes identified the most important hydrochemical correlates of plankton and benthic species richness at a large scale (Table 1): dissolved inorganic carbon, dissolved organic carbon, and nutrients (especially nitrogen). These results are in line with those of other

studies. For example, factor analysis of 22 abiotic parameters of 95 Labrador lakes reduced data to six factors including hardness (especially alkalinity, calcium, and magnesium) and dystrophy (especially dissolved organic carbon and color) (Earle et al., 1986). Based on the PCA ordination of 73 small shallow lakes in Wisconsin, Dodson et al. (2005) reported three axes including parameters associated with aquatic vegetation; variables related to the water source, water color, nutrient concentrations (positively) and conductivity (negatively).

In the Belarusian lakes, taxon richness was in many cases significantly correlated with one or more of the ordination axes: phytoplankton (all groups and especially Chlorophyta) was most strongly correlated with DOC, zooplankton (especially copepods and rotifers) with DIC, chlorides and sulfates, and zoobenthos with DIC, amount of nutrients, and chlorides and sulfates. Our results suggest that dissolved carbon and nutrients are the most important hydrochemical drivers of lacustrine diversity.

### Different correlates for different groups

In each community, we found at least one group of organisms characterized by high correlations between species richness and PCA axes. In phytoplankton the

strongest correlations were with Chlorophyta and Bacillariophyta; in zooplankton, with Copepoda and Rotifera; and in zoobenthos, with Mollusca and Chironomidae. These groups also showed, in an earlier study, the highest correlations with lake size, hydraulic residence time, and land use (Karatayev et al., 2005). We suggest that these taxonomic groups may be used as the most sensitive organisms (biological indicators) in studies of the impacts of lake chemistry and morphology on the biodiversity.

We found numerous weak, but highly significant correlations between species richness and raw data of chemical parameters studied (Table 2; Figs. 1–5). The correlation coefficients were low, because the majority of the lakes in the study region were so similar: shallow eutrophic lakes with similar water chemistry and watershed characteristics. Similar weak correlations were found by Pip (1987) between species richness of freshwater gastropods and pH, total alkalinity, chloride, phosphorus, and dissolved organic matter for 429 waterbodies in central North America. We hypothesized that this is typical for lakes that belong to the same lake district and are characterized by similar climate, geology, and were formed at the same time. As a result, such a data set gives a unique opportunity to reveal even weak subtle correlations between abiotic parameters and species richness that would not be possible to detect with a smaller or more environmentally heterogeneous dataset.

It is frequently reported that different taxonomic groups showed different, sometimes opposite responses to the same chemical parameter (e.g. Declerck et al., 2005). For example, in our study phytoplankton biodiversity was negatively correlated with water transparency, while zooplankton and zoobenthos species richness correlated positively with water clarity (Table 2). Due to the strong negative correlation between transparency and lake trophic status (Horne & Goldman, 1994), our results suggested that phytoplankton species richness increases with lake eutrophication. Substantial increase in phytoplankton species richness from oligotrophic to eutrophic lakes was also found for 151 Eastern Finish lakes (Ilmavirta et al., 1984). The opposite pattern was observed for zooplankton and benthic species richness, which could be related to the decrease in bottom substrate heterogeneity (increasing proportion of silt substrate with

eutrophication), decreasing depth, light penetration, increasing nutrient levels, etc. Therefore, eutrophication will increase phytoplankton diversity, but may decrease zooplankton and zoobenthos species richness.

Dodson et al. (2000) found a unimodal relationship between primary production and species richness for all communities studied, including phytoplankton, rotifers, cladocerans, copepods, macrophytes, and fish. The unimodal patterns depended on including the most ultra-oligotrophic to the most hyper-eutrophic lakes, if such a wide range of primary productivity is available. As for the Belarusian lakes with their relatively narrow productivity range, it is likely that species richness will appear to be linearly related to eutrophication.

Both raw and grouped data showed significant linear correlation between pH and species diversity of phytoplankton and zooplankton (Fig. 3). Arvola et al. (1990) also found a positive correlation between pH and biodiversity of phytoplankton ( $r^2 = 0.43$  in spring and  $r^2 = 0.52$  in summer) and, to a less extent, zooplankton species richness in lakes in Finland with pH at 4.9–7.0 interval (Arvola et al., 1990). Correlation coefficients reported by Arvola et al. (1990) are higher than ours calculated on raw data from Belarusian lakes for the whole range of pH (3.65–9.60). However, when we limited our analysis to lakes with the pH range similar to that in Finish lakes (<7.0), our raw data also showed much stronger correlation ( $r = 0.67$ ,  $r^2 = 0.45$ ,  $P = 0.0014$ ) than for the whole range of pH ( $r = 0.08$ ,  $P = 0.06$ ). Therefore, a positive correlation between biodiversity of phytoplankton and pH probably exists only in lakes with pH <7.

Acidic waters reduce species richness in all communities. Økland (1983) found a decline in the snail diversity below pH 7.0 and a pronounced decrease at pH <6.0. No gastropods were found in lakes with pH <5.2. Most of diatoms and green algae species disappeared at pH <5.8 and cladocerans at pH <6.0 (Almer et al., 1974). Zooplankton diversity declines below pH 5.0 (Sprules, 1975; Confer et al., 1983). In our study, the lowest pH at which molluscs were found was 4.9, and molluscs' species richness positively correlated with pH (Table 2).

A significant linear correlation between TDS and biodiversity was found only for phytoplankton, due to the strong increase in biodiversity at TDS <125 mg

$l^{-1}$  (Fig. 4). Zoobenthos and molluscan diversity was reduced at both highest and lowest concentration of TDS. This corresponds to a unimodal relationship between molluscs' diversity and conductivity found in other studies (Dussart, 1976; Savage & Gazey, 1987).

In our study, different taxonomic groups appeared to have different optimal ranges for different parameters. For example, optimal water clarity for phytoplankton is  $<1$  m, for zooplankton is  $>2$  m and for zoobenthos between 3 and 4 m (Table 3). Therefore, the highest diversity of the phytoplankton (community scale) could be achieved at the lowest transparency; however on the ecosystem scale, the highest diversity (diversity of all communities combined) requires intermediate clarity (1–4 m). In addition, some taxonomic groups may have a smaller optimum range than the whole community and can therefore be used as bioindicators. For example, biodiversity of molluscs is the highest at calcium concentrations  $\geq 20$  mg  $l^{-1}$ , while the biodiversity of the whole benthic community is highest over the range of 10–40 mg  $l^{-1}$ . Our results support the concept of multidimensionality of taxon richness, which stresses that maximizing biodiversity of different freshwater communities will require different management strategies (Declerck et al., 2005).

#### Unimodal and linear patterns

Mittelbach et al. (2001) found that unimodal, hump-shaped relationships between species richness and productivity are particularly common in aquatic ecosystems (but see Declerck et al., 2005, 2007). However, they could be observed only on a very large range of productivity (Dodson et al., 2000), and would not be easily detectable using multivariate techniques which rely on linear correlations among variables. We found several relationships (e.g. between benthic diversity and transparency, pH, TDS, and phytoplankton and color of water) that were curvilinear (Figs. 1–5). Linear regressions were not able to describe the relationships unambiguously. These curvilinear relationships were revealed by graphing grouped data (Figs. 1–5) and confirmed by the significance of the inclusion of the quadratic term in the regression. We hypothesize that in contrast to morphometric characteristics of lakes, which usually show linear associations with biodiversity (Karatayev

et al., 2005), most of hydrochemical parameters limit biodiversity both at very low and very high concentrations, and the relationship between the concentration and biodiversity will be best described by a unimodal curve.

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