

Community analysis of Belarusian lakes: relationship of species diversity to morphology, hydrology and land use

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In the glacial lake district of northern Belarus, limnologists collected extensive biological, chemical and physical data on 550 lakes (51% of all Belarusian glacial lakes). This large data set provided a unique opportunity to examine subtle relationships with great statistical power. Our purpose was to use multivariate and correlation analyses to explore relationships of species richness with morphological and hydrological parameters. A multivariate analysis of the environmental data suggests that the Belarusian lakes can be separated along gradients of size, hydraulic residence time and watershed development (land use). In most instances, species richness for major planktonic and benthic groups was correlated significantly with lake size and land use. Species richness values were correlated less with watershed size or hydraulic residence time. In each community, there was a group of species characterized by higher correlations with principal component analysis (PCA) axes. These groups are as follows: for phytoplankton—diatoms, for zooplankton—rotifers, and for zoobenthos—molluscs. For lakes both in pristine and developed watersheds, we found small but significant negative species–area correlations for littoral crustaceans. A survey of the relevant literature shows scale dependence for the correlation between species richness and lake size. For pelagic crustaceans, the species–area correlation was significant (and positive) for lakes with developed watersheds but not for pristine watersheds.

INTRODUCTION

Lake basin morphology, hydrology and watershed characteristics play critical roles in the functioning of aquatic communities affecting lake trophic status and water quality. However, our knowledge of the impact of these parameters on biodiversity is controversial. Järnefelt (Järnefelt, 1956) and Ruttner (Ruttner, 1952) did not find any correlation between phytoplankton species richness and lake surface area. In contrast, other authors found a positive correlation between the size of a lake and diversity of fish (Barbour and Brown, 1974; Jackson and Harvey, 1985), zooplankton (Dodson, 1991, 1992), phytoplankton (Smith *et al.*, 2005) and snails (Bronmark, 1985). This complexity of results could be due to different responses to the same factor (Dodson *et al.*, 2000), or it may be that results are scale dependent. Dodson

(Dodson, 1992) indicated that the correlation between zooplankton biodiversity and lake size could be found only over several orders of magnitude of size. Fewer data are available on the impact of watershed characteristics on species richness of aquatic communities. According to Strayer (Strayer, 1983, 1993), there is a positive correlation between the unionid species richness and stream watershed area. Hoffman and Dodson (Hoffman and Dodson, 2005) observed that the zooplankton species–area relationship occurred for lakes in developed watersheds but not for pristine lakes.

Two approaches are typically used in limnological research: long-term monitoring on few lakes and short-term studies on many lakes (Horne and Goldman, 1994). Both approaches have advantages and disadvantages. While detailed long-term studies on few lakes may

eliminate problems connected to the seasonal variations in species diversity, unique characteristics of each lake may strongly affect the general pattern. In contrast, although in ‘snapshot’ studies seasonal variation of species richness may not be synchronized in all lakes, a large number of lakes sampled may average the uniqueness of each lake and help to reveal general relationships between species diversity and various morphological parameters (Stemberger *et al.*, 2001). However, large and long-term studies are scarce.

This article is based on the analysis of 550 glacial lakes in northern Belarus. Each lake was visited once during 1971–1996 by the Lakes Research Laboratory and the General Ecology Department of the Belarusian State University (Fig. 1). In 1997–1998 under a grant from the Belarusian Committee of Ecology ‘Development of an Informational System—Limnoflora-Limnofauna Belarusi’ (lead by Alexander Karatayev), computerization and summarization of these data was initiated. As a result, a large database was created, containing data on morphology, hydrochemistry and hydrobiology for the studied lakes.

The data set used in our analysis is unique from several perspectives: (i) all lakes used in the analysis were studied using the same methods and (ii) all lakes were from the same geographic region, were formed during the last glaciation and belong to a single lake district. This data set gives us a very sensitive tool to reveal even subtle correlations between species richness and morphological and hydrological parameters of the lakes studies that would not have been possible to detect with a smaller or more heterogeneous data set. This

database has been used previously to study the patterns and mechanisms of zebra mussel dispersal (Kraft *et al.*, 2002; Karatayev *et al.*, 2003).

The purpose of this article is to search for correlations between aquatic species diversity and large scale physical (morphometric) factors: lake size and morphology, hydrology and watershed characteristics. This article is intended to be the first in a series of articles using the Belarusian data set for which we will analyse relationships of abiotic and biotic components of aquatic ecosystems. Chemical parameters will be considered in our next article. Specifically, our goals of the current article are to address the following questions:

Which large-scale abiotic factors (lake morphology and watershed characteristics) are strongly associated with the biodiversity of aquatic communities in Belarus lakes?

Are species–area relationships similar among phytoplankton, zooplankton, zoobenthos and macrophytes as well as among major taxonomic groups in each community?

Is there a monotonic species–area relationship for crustacean zooplankton of lakes in developed watersheds but not for pristine lakes? This pattern was predicted to be a general expectation for crustacean zooplankton by Hoffman and Dodson (Hoffman and Dodson, 2005).

METHOD

There are more than one thousand glacial lakes in the Republic of Belarus (Kurlovich and Serafimovich, 1981). Almost all these lakes found mainly in northern Belarus



Fig. 1. Map of studied Belarusian Lakes.

(Belarusian Lakeland) between 51°37' and 57°47'-N and 23°37' and 30°45'-E (Fig. 1). More than 85% of studied lakes belong to the Zapadnaya Dvina River basin; 6% to the Neman River basin and the rest—to the basins of Pripyat (4%), Zapadniy Bug (2%), Dnieper (2%) and Lovat (1%) rivers. The 550 lakes studied account for 51% of the total number of Belarusian lakes (1072).

The large-scale abiotic factors used in this study included characteristics of the drainage basin, lake morphology, hydrochemistry and hydrobiology. There were total of 19 variables in the database, however, some of them were calculated from the primary variables and therefore were not used in the analysis. The morphometric variables used included lake area, volume, maximal depth, area of watershed, percent of developed area of the watershed (assessed from the maps by geographic staff of the Lakes Research Laboratory), hydraulic residence time and shoreline development. Lake and watershed surface area were estimated from maps (1:25,000 scale). Lake maximum depth was measured, and volume was estimated from bathymetric maps that were made based on the field study. Hydraulic residence time (time required to refill or empty lake with its natural flow) was calculated based on the field observation of the water entering or discharging from the lake (based on measurements at the time of sampling). Drainage ratio was calculated as a ratio between watershed area and lake surface area. Shoreline development was estimated as a ratio of the length of the lakeshore (estimated from the map) to the circumference of a circle of area equal to that of the lake surface.

Hydrobiological studies included the species composition, numbers and biomass of phytoplankton, zooplankton and zoobenthos from multiple sites within each lake. There were as few as six sites for the smallest lakes and up to 12 sites for the largest lakes. We used a snapshot method, sampling each lake once during summer season from mid June to mid August. This approach was successfully used in other studies (Stemberger *et al.*, 2001; Dodson *et al.*, 2005). Choice of sampling sites within lakes was made to maximize the diversity of habitat types sampled (macrophyte beds, open water and bays) as described by Mordukhai-Boltovskoy (Mordukhai-Boltovskoy, 1975) and Rosenberg *et al.* (Rosenberg *et al.*, 2001). Phytoplankton samples were collected with Ruttner 1 L sampler and preserved immediately after sampling with Lugol's solution. Zooplankton samples were collected using a 10-L sampler, filtered through 50- μ m silk mesh and preserved with 4% formalin. Zoobenthos was collected using an Eckman dredge on soft substrate and a Petersen dredge on hard substrate. Both dredges had a sampling area of 0.025 m². All benthic samples were washed through a 500- μ m mesh. After

sampling, all macroinvertebrates were transferred to containers with 10% neutral buffered formalin and labelled. All aquatic organisms were identified to the species level when possible.

For the majority of the lakes, we have the primary data on species composition in each lake. However, for some lakes the primary data were lost, and just the total number of species was used in the analysis. These latter lakes were not used in the detailed analysis of zooplankton community structure [e.g. for comparing pelagic versus littoral zooplankton and checking the Hoffman-Dodson hypothesis (Hoffman and Dodson, 2005)].

We used principal component analysis (PCA) (STATISTICA version 6, StatSoft, Inc., 2001) combined with correlation analysis to detect links between species richness and morphometric variables in the study. Because the data were highly skewed due to a large number of small lakes, and few large lakes with large watershed, the data were non-normally distributed. Before ordination, all raw data were log-transformed [except for the percent of developed area which were arcsine square root transformed as suggested for percentages (Zar, 1996)] and normalized (to a mean of zero and standard deviation of 1.0). PC axes were rotated using orthogonal varimax rotation, which was found to be the best under most circumstances to maximize the variances of the squared raw factor loadings across variables for each factor (McGarigal *et al.*, 2000). Correlation analysis indicated which morphometric variables were the best correlated with each PC axis. Correlation analysis was used to find the relationship between log species richness (the dependent variable) and the PC axes. For this analysis, we calculated the correlation coefficients of the log-transformed number of species in each lake with the score of the lake along the PC axes.

The species–area relationship is described by power function $S = C \times A^z$, approximated with double logarithmic transformation $\log S = \log C + z \log A$ (Preston, 1962; MacArthur and Wilson, 1967; Connor and McCoy, 1979), where S is the number of species present, C is a constant which varies with the taxonomic group under study, A is the area of the island, and z represents the slope and the intercept of the log–log relationship between species richness and area. We calculated the slopes and coefficients of determination of linear regression between the log-transformed number of species in major groups (dependent variable) and log lake area (independent variable) using the least squares estimation in the Multiple Regression routine in STATISTICA 6.0 software. To determine whether the statistical significance of the species–area relationship for planktonic communities is scale dependent, we compared correlation coefficients of studies in which surface ranged from

as little as three orders of magnitude to as much as 16 orders of magnitude, including this study and data from Dodson (Dodson, 1992), Dodson *et al.* (Dodson *et al.*, 2000), and Smith *et al.* (Smith *et al.*, 2005). Only significant correlations were included in the analysis.

For our analysis, we used only the lakes for which we had detailed data on the species composition (422 lakes). To test whether there is a difference in species–area relationships between pelagic and littoral crustacean zooplankton, all species were combined into littoral and pelagic groups. Assignment of species to littoral or pelagic zone follows common usage (e.g. Straškraba, 1967; Dodson, 1991). Littoral species are *Sida crystallina*, *Ophryoxus gracilis*, *Drepanotrix dentata*, *Streblocerus serricaudatus*, *Lathonura rectirostris*, *Acropenus harpae*, *Peracantha truncata*, *Anchistropus emarginatus*, *Monospilus dispar*, *Graptoleberis testudinaria*, *Kurzia latissima*, *Oxyurella tenuicaudis*, *Polyphemus pediculus*, *Ectocyclops phaleratus*, *Microcyclops bicolor*, *Paracyclops fimbriatus*, and *Canthocamptus staphylinus*, all species of *Simocephalus*, *Macrobrachium*, *Ilyocryptus*, *Eurytercerus*, *Camptocercus*, *Leydigia*, *Alonopsis*, *Chydorus* (except pelagic *Chydorus sphaericus*), *Rhynchotalona*, *Pleuroxus*, *Alonella*, *Eucyclops* and *Macrocyclus*.

Pelagic species are *Diaphanosoma brachyurum*, *Holopedium gibberum*, *Scapholeberis mucronata*, *Chydorus sphaericus*, *Bythotrephes longimanus*, *Leptodora kindtii*, *Limnocalanus macrurus* and *Heterocope appendiculata*, all species of *Daphnia*, *Ceriodaphnia*, *Alona*, *Bosminopsis*, *Bosmina*, *Acanthocyclops*, *Mesocyclops*, *Eudiaptomus* and *Eurytemora*. In some lakes, *Cyclops* were not identified to species level; in these lakes, we counted them as one pelagic and one littoral *Cyclops* species.

To test the Hoffman-Dodson hypothesis (Hoffman and Dodson, 2005), all lakes based on the use of their watershed were grouped into developed (more than 20% of the drainage basin subjected of agricultural activity or urban territories) and undeveloped (less than 20% represented by urban or agricultural land use). Only crustacean pelagic zooplankton was used in this analysis. As we had only 4.2% of all lakes in our database with less than 1% development (18 lakes only), we chose the 20% boundary to distinguish between developed and undeveloped lakes. This ‘undeveloped’ group had 62 lakes (14.7% of total), and the ‘developed’ group had 357 lakes. The larger number was important for the increased statistical power it provided. To test the equality between two regression coefficients, we used Student’s *t*-test (Zar, 1996).

RESULTS

Belarusian lakes are typically small and shallow, with an average drainage area of around 90 km² (Table I). Surface area of the lakes varied over three orders of magnitude from 0.05 to 57.7 km², but small lakes, with the

Table I: Morphological parameters and species richness in Belarusian lakes

Parameter	N	Mean ± SE	Median
Lake area (km ²)	550	1.8 ± 0.20	0.5
Lake volume (10 ⁶ m ³)	549	7.3 ± 0.87	1.8
Maximum depth (m)	548	9.7 ± 0.36	6.8
Watershed area (km ²)	549	90.1 ± 11.79	11.2
Drainage ratio (watershed area/lake surface area)	549	93.0 ± 12.8	16.1
Developed watershed area (%)	545	58 ± 1.2	62
Hydraulic residence time (years)	535	2.4 ± 0.20	1.1
Shoreline development	545	1.7 ± 0.02	1.6
Number of species			
All Phytoplankton	541	49.3 ± 0.95	46
Cyanobacteria	541	8.7 ± 0.21	8
Chlorophyta	541	18.2 ± 0.46	16
Bacillariophyta	541	13.8 ± 0.28	13
All Zooplankton	532	27.8 ± 0.35	27
Cladocera	530	12.2 ± 0.21	12
Copepoda	530	4.9 ± 0.10	5
Crustacean total	422	16.0 ± 6.31	16
pelagic	422	11.3 ± 3.80	11
littoral	422	5.7 ± 3.42	6
Rotatoria	530	10.8 ± 0.17	11
All Benthos	539	27.8 ± 0.57	27
Mollusca	533	5.1 ± 0.15	5
Odonata	531	0.7 ± 0.04	0
Trichoptera	531	2.0 ± 0.09	2
Chironomidae	534	11.6 ± 0.25	11
All Macrophytes	517	10.1 ± 0.19	10

surface area ≤5 km² were disproportionately abundant and formed more than 92% of all lakes studied. Maximum depth varied from 0.4 to 53.6 m. Volume of lakes, drainage area and drainage ratio varied over four orders of magnitude.

A total of 695 species and higher taxa were found in phytoplankton, 298 in zooplankton and 499 in the zoobenthos community. The average diversity of phytoplankton per lake was almost twice that of zooplankton and zoobenthos diversity (Table I).

The first three PCA axes explained 80% of the total variability in the lake and watershed data (Table II). The next four axes explained <20% of total variability, had eigen values <1, weak correlations (<0.68) with the morphometric parameters and therefore were not presented. Lake morphology variables (e.g. volume, area and depth) were strongly correlated with the first PCA factor. Strong correlates with the second PCA axis

Table II: Factor loadings based on Pearson correlation coefficients between a variable and the factor axes for principal component analysis (PCA) of Belarusian lakes

Parameters	Factor 1 (37.7%)	Factor 2 (26.8%)	Factor 3 (15.8%)
Log lake area	0.906	-0.142	-0.163
Log lake volume	0.971	0.121	0.094
Log depth max	0.457	0.463	0.533
Log shoreline development	0.505	-0.212	0.369
Log watershed area	0.533	-0.803	0.033
Arcsin developed area	-0.118	-0.028	0.878
Log hydraulic residence time	0.187	0.947	0.027

All the variables used were standardized prior to the analysis. PCA axes were rotated using orthogonal varimax rotation. Percent of total variation explained by the PCA axis is given in parentheses. Bold text indicates loadings are significant at $P < 0.01$.

included hydraulic residence time (positive correlation) and watershed area (negative). The proportion of the drainage basin that was developed was strongly correlated with the third axis (Table II). Final communality estimates for three first PCA axes ranged from 0.44 for shoreline development to 0.97 for lake volume and averaged 0.80 for all variables used in the analyses. PCA did not reveal any distinctive lake clusters (Fig. 2).

We found numerous small although highly significant correlations between PCA axes and species richness in all communities studied (Table III). Phytoplankton diversity (especially Bacillariophyta) and benthos (especially chironomids) showed highest correlation with PC 1 (lake volume and area). Phytoplankton diversity (especially

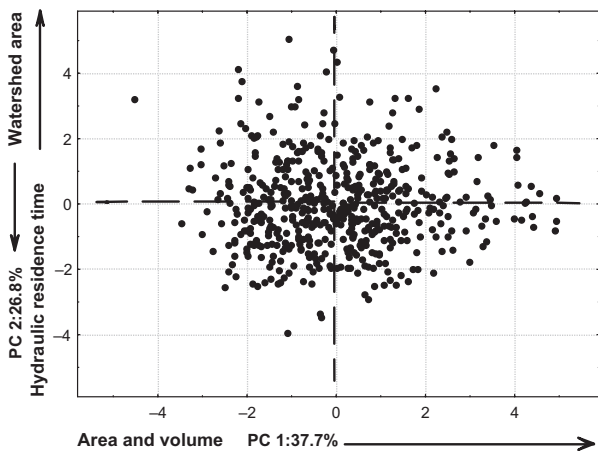


Fig. 2. Projection of the studied lakes on the factor-plane (factors 1 × 2).

Table III: Coefficients of correlations r (and their significance) between the number of species (species richness) in lake communities with morphometric principal component analysis (PCA) axes

Community	PC 1	PC 2	PC 3
All phytoplankton	0.15*	0.20*	0.15*
Cyanobacteria	0.17*	0.03	0.06
Chlorophyta	0.03	0.14*	0.13**
Bacillariophyta	0.25*	0.32*	0.11**
All Zooplankton	0.02	0.06	0.15*
Cladocera	0.03	-0.009	0.05
Copepoda	-0.04	-0.07	0.009
Rotatoria	0.06	0.17*	0.26*
All Benthos	0.29*	0.08	0.14**
Mollusca	0.20*	0.17*	0.24*
Odonata	-0.09***	0.06	0.08
Trichoptera	0.11**	0.01	-0.003
Chironomidae	0.37*	0.01	0.04

PC 1 represents lake morphology; PC 2 represents hydraulic residence time and PC 3 represents percent development of the watershed. * $P < 0.001$. ** $P < 0.01$. *** $P < 0.05$.

diatoms) was correlated with PC 2 (hydraulic residence time). Rotifers and molluscs were correlated with PC 2. Other zooplankton and zoobenthos were not correlated with PC 2. Total species richness of all communities was correlated with PC 3 (percent of developed areas on the watershed).

The total species richness of phytoplankton and zoobenthos was positively correlated with lake surface area (Table IV). In contrast, total zooplankton and macrophytes species richness was negatively correlated with lake area. Different taxonomic groups in each community had different correlations. For phytoplankton, the highest correlation between diversity and lake surface area was found for the Bacillariophyta. Among benthic invertebrates, chironomids had the largest correlation with lake area ($R^2 = 0.14$). For the zooplankton community, the highest negative correlation ($R^2 = 0.06$) was found for littoral crustaceans.

We found that the log species–area relationships for planktonic communities is strongly scale dependent when comparing across studies on waterbodies with different surface areas (this study; Dodson, 1992; Dodson *et al.*, 2000; Smith *et al.*, 2005) (Fig. 3). Correlation coefficients ranged from as low as 0.07 for studies where surface area ranged 3 orders of magnitude, to 0.74 for the study where surface area ranged over 15 orders of magnitude.

Table IV: Slope values z , coefficients of determination (R^2) and their significance (in parentheses) of species–area relationships for different communities in Belarusian lakes

Taxa	N	z (mean \pm SE)	R^2 (P)
All Phytoplankton	541	0.106 \pm 0.017	0.07 (<<0.001)
Cyanobacteria	541	0.121 \pm 0.020	0.07 (<<0.001)
Chlorophyta	541	0.073 \pm 0.023	0.02 (0.002)
Bacillariophyta	541	0.135 \pm 0.017	0.11 (<0.001)
All Zooplankton	532	-0.023 \pm 0.011	(-)0.01 (0.038)
Cladocera	530	-0.034 \pm 0.015	(-)0.01 (0.025)
Copepoda	530	-0.074 \pm 0.019	(-)0.03 (<0.001)
Crustacean total	422	-0.096 \pm 0.019	(-)0.06 (<0.001)
Pelagic	422	-0.046 \pm 0.014	(-)0.02 (0.0015)
Littoral	422	-0.127 \pm 0.024	(-)0.06 (<0.001)
Rotatoria	530	0.010 \pm 0.014	0.001 (0.48)
All Benthos	539	0.125 \pm 0.019	0.08 (<0.001)
Mollusca	533	0.131 \pm 0.036	0.03 (<0.001)
Odonata	531	-0.025 \pm 0.018	(-)0.004 (0.16)
Trichoptera	531	0.020 \pm 0.025	0.001 (0.42)
Chironomidae	534	0.164 \pm 0.018	0.14 (<0.001)
All Macrophytes	517	-0.061 \pm 0.018	(-)0.02 (0.001)

The relationship is described by power function $S = kA^z$, approximated with double logarithmic transformation $\log S = \log k + z \log A$.

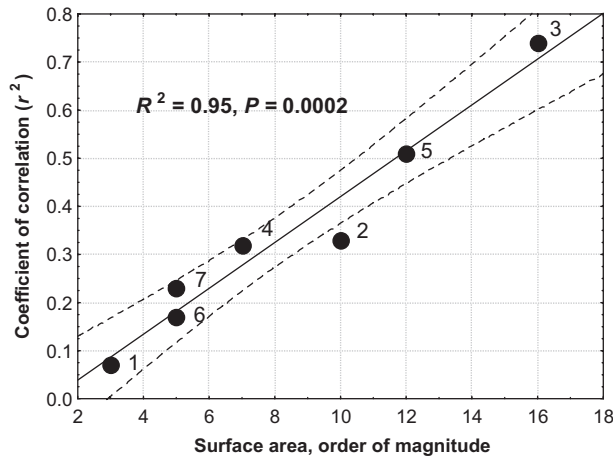


Fig. 3. Relationship between correlation coefficients for log species–area relationships for planktonic communities and ecosystem surface area. Data points are 1, phytoplankton, this study; 2, zooplankton (Dodson, 1992); 3, phytoplankton, pooled data (Smith *et al.*, 2005); 4, phytoplankton, experimental systems (Smith *et al.*, 2005); 5, phytoplankton, natural ecosystems (Smith *et al.*, 2005); 6, cladocerans (Dodson *et al.*, 2000); and 7, rotifers (Dodson *et al.*, 2000). Only significant correlations (at $P < 0.05$) were used. Linear regression with 95% confidence intervals, coefficient of determination and its significance are given.

The highest z -value (which relates log area to log species richness) was 0.16 for Chironomidae. The benthos in total had a higher z -value than plankton communities. For the phytoplankton, Bacillariophyta and Cyanophyta had z -values > 0.12 . The lowest, predominantly negative z -values were found in zooplankton community (Table IV).

For lakes both in pristine and developed watersheds we found small, but highly significant negative species–area correlations for littoral crustaceans (Fig. 4). For pelagic crustaceans, the correlation was significant for lakes with developed watersheds only, and the slope was lower but not significantly different from that for littoral species ($b_{\text{pelagic}} = -0.052 \pm 0.015$, $b_{\text{littoral}} = -0.122 \pm 0.026$, $df = 710$, $t = 1.54$, $t_{0.05(2),710} = 1.963$, $P = 0.12$; Student's t -test).

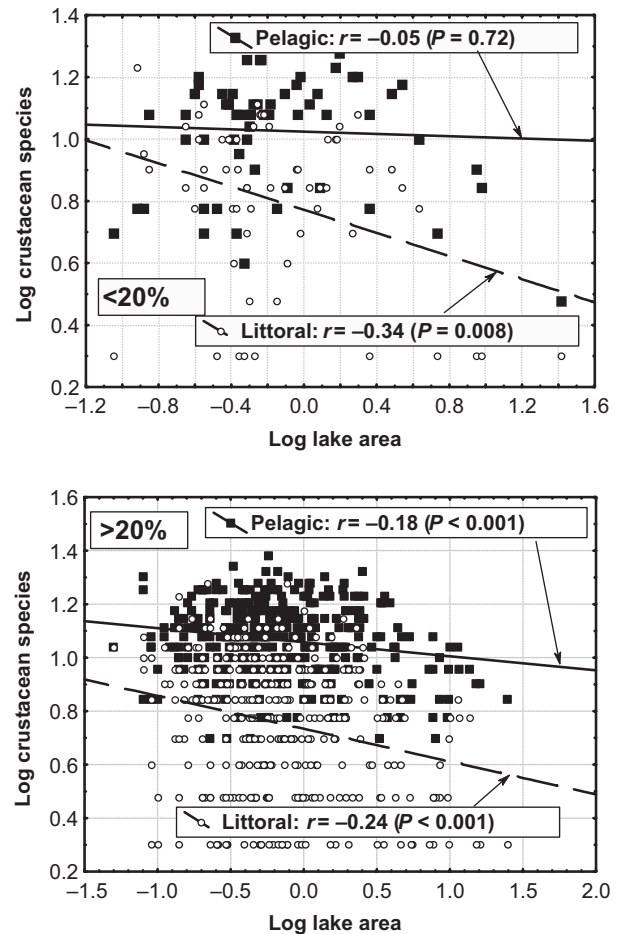


Fig. 4. Log species–area relationships for pelagic and littoral crustacean zooplankton in Belarusian lakes with developed territory less than 20% (upper) and more than 20% of watershed territory (lower). Correlation coefficients and their significance are given.

DISCUSSION

Our analysis of the Belarus data set allowed us to identify several patterns relating large-scale physical environmental factors to lacustrine community diversity. These patterns are of particular interest because they were identified for a huge set of environmentally similar lakes. We found that these lakes differed principally along gradients of lake morphology (especially lake area and lake volume), watershed area (and related hydraulic residence time) and the amount of anthropogenic watershed development (Fig. 2; Table II). Taxon richness was in many instances correlated significantly with one or more of the ordination axes: phytoplankton in general was correlated most strongly with watershed area, rotifers with watershed development and benthos with the first axis (lake area and volume). In each community, there was a group characterized by higher correlations with PCA axes than others. These groups are diatoms (phytoplankton), rotifers (zooplankton) and molluscs (benthos). Correlations between taxon richness and ordination axes were in all cases positive. Species–area relationships were significant, weak and in some cases negative.

Large scale physical factors and species diversity

Phytoplankton taxon richness was affected by all three PCA factors: richness increased most with watershed size but also with lake size and with watershed development. These results are in line with those of related studies (Barbour and Brown, 1974; Bronmark, 1985; Dodson, 1991, 1992). For example, Smith *et al.* (Smith *et al.*, 2005) reported that phytoplankton richness increases regularly with increasing habitat size. Dodson *et al.* (Dodson *et al.*, 2000) reported a similar, but not significant, trend. The increase in richness with increasing lake size is probably due to increases in the number of habitats in larger lakes. The increase in richness related to watershed size and development is more likely due to an often-observed effect of nutrient enrichment (Hoffmann and Dodson, 2005).

Rotifer taxon richness was strongly correlated with watershed development and to a lesser extent watershed size. Neither cladocera nor copepod taxon richness were significantly correlated with any of the PCA factors. Dodson *et al.* (Dodson *et al.*, 2000) reported similar results for the effect of lake size, in that rotifers showed the strongest response. As with the phytoplankton, larger watersheds and increased watershed development probably increase the flow of nutrients into these oligotrophic lakes, which is expected to increase productivity and therefore zooplankton richness (Hoffmann and Dodson, 2005).

Benthos, like phytoplankton, showed strong correlations with all three PCA factors. All categories of

benthic taxa were strongly correlated with lake size, and molluscs were strongly correlated with all three axes. According to Bronmark (Bronmark, 1985), there is a positive correlation between lake area and gastropod diversity. However, to our knowledge, nobody has reported a correlation between chironomid diversity and lakes area.

Species–area relationships among and within aquatic communities

We found that different taxa showed different responses to lake area. Dodson *et al.* (Dodson *et al.*, 2000) also found that not all aquatic communities have the same species–area response. They reported a positive correlation for the species richness of rotifers, cladocerans, macrophytes and fish and lake surface area but not for phytoplankton and copepods.

Positive species–area correlations for the total species richness of phytoplankton and zoobenthos were found in the Belarus data set, while zooplankton and macrophytes showed a more complex pattern (Table IV). Although the large sample size (>500 lakes were used in the analysis) increased the power of the test and permitted subtle relationships to be detected, very little variance was explained as a function of lake size. The low explanatory power of lake size is probably due to the rather narrow range of lake sizes in the Belarus study. Hoffmann and Dodson (Hoffmann and Dodson, 2005) stress that three or four orders of magnitude in lake area are needed to detect significant species–area relationships (at least for zooplankton). Smith *et al.* (Smith *et al.*, 2005) found a strong positive correlation between phytoplankton diversity and waterbody area, analysing data from ponds, lakes, oceans and experimental ecosystems with surface area range in 16 orders of magnitude. Shurin *et al.* (Shurin *et al.*, 2000) also reported that surface area was not a major predictor of local richness of zooplankton in their survey, due to the small range in lake areas in their survey. Although this question is still controversial, the species–area relationship for plankton is definitely scale dependent. The value of correlation coefficient depends on the range of the area of the waterbodies studied. This relationship is demonstrated using studies done on waterbodies with the surface area ranged from 3 to 16 orders of magnitude (Fig. 3).

The highest z -values that quantify the scaling of species richness with area were found for benthos and phytoplankton (Table IV). Similar z -values (0.114–0.139) were found for phytoplankton by Smith *et al.* (Smith *et al.*, 2005). As in other studies (Dodson, 1992; Havel *et al.*, 2004), z -values for zooplankton were smaller than reported for other well-studied organisms, such as birds and terrestrial plants.

For zooplankton, we found that Belarusian species–area curves for pelagic species are very different than for littoral (Fig. 4). It was unexpected to find a small but highly significant negative correlation between species richness of littoral zooplankton and lake surface area (Fig. 4). This may be explained by the fact that smaller lakes have a higher proportion of littoral zone to the total area and therefore a wider spread of littoral species across the lake, while in large lakes littoral species are restricted to the near shore areas. In addition, the negative correlation between species richness of littoral zooplankton and lake surface area may be a consequence of the lower species diversity of macrophytes in larger lakes. In lakes with larger open surface area macrophytes suffer more from wind and waves, which may decrease their diversity. These negative effects on aquatic vegetation and its diversity may be stronger in lakes with more developed watersheds where turbidity due to erosion and eutrophication is added to the wind and wave effects.

Species–area relationships and watershed size

Our results show a positive relationship between watershed size and taxon richness of Bacillariophyta, rotatoria and for molluscs. Assuming that lake size is independent of watershed area, lakes with larger watersheds will tend to have higher loading rates of essential phytoplankton nutrients (Horne and Goldman, 1994). Increased nutrient loading in lakes will lead to increased primary productivity, which has already been associated with increased zooplankton species richness (Dodson *et al.*, 2000; Hoffmann and Dodson, 2005), except for the most eutrophic lakes. The same effect may favor increased diatom and mollusc diversity in lakes with larger watersheds. Strayer (Strayer, 1983, 1993) also reported a positive correlation for unionid species richness and stream size estimated as a size of a watershed area.

Species–area relationships in developed and pristine watersheds

Watershed development has been associated with increased species richness. Hoffmann and Dodson (Hoffmann and Dodson, 2005) speculated that increased watershed development resulted in increased flow of phytoplankton nutrients into a lake, and therefore a higher rate of primary productivity. This eutrophication then supports, at least in oligotrophic lakes, an increase in taxon richness. It is also possible that, in addition to the eutrophication effect, higher diversity in lakes in developed watersheds may be due to the dispersal of aquatic organisms associated with the human activity.

Hoffmann and Dodson (Hoffmann and Dodson, 2005) suggested that the positive and monotonic species–area

relationship is characteristic of lakes in developed watersheds but not in pristine lakes, across a large range in lake size. In the Belarus data set (Fig. 4), pelagic zooplankton species richness of undeveloped lakes was not correlated with lake area, in agreement with the prediction of Hoffmann and Dodson (Hoffmann and Dodson, 2005).

In summary, large scale abiotic factors showed significant associations with the aquatic biodiversity in Belarus lakes. The most diverse phytoplankton communities were found in lakes with the largest watersheds, the most diverse zooplankton communities were associated with lakes with developed watersheds, and the most diverse benthic communities were found in the largest lakes. These patterns provide the basis for future research into the relationship between environmental factors and community structure. Species–area relationship for Belarusian lakes was similar to those reported in other studies. In particular, crustacean zooplankton richness was not correlated to lake size in pristine lakes.

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