

Consistent, long-term change in rotifer community composition across four Polish lakes

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Abstract Few studies exist documenting changes in rotifer communities over long time intervals. Here, we explore seasonal and long-term variation in rotifer communities in four Polish lakes sampled in 1976 and again in 1997. Rarefied, asymptotic species richness did not differ significantly across study years, although values in 1997 tended to be higher. Simpson's and Shannon–Wiener diversity measures provided inconsistent temporal results, with only the former indicating significantly higher richness in 1997. Sorensen's coefficient of community similarity was as high among lakes in 1976 (0.81) and in 1997 (0.76) as within lakes across the 21-year span (0.77). Nonlinear redundancy analysis of species' abundances revealed large, consistent seasonal changes across lakes, smaller consistent shifts between

sampling periods, and small differences between lakes. Collectively, these metrics indicate that species composition was relatively stable among lakes within years and within lakes between years, while species' abundance patterns were far more variable and most affected by season.

Keywords Biodiversity · Rotifer communities · Ordination · Species richness

Introduction

Species richness patterns and biodiversity indicators have been widely utilized in terrestrial ecology (e.g., Moreno & Halfpeter, 2000; Mac Nally & Fleishman, 2004; Majer et al., 2007; Mgobozi et al., 2008). These metrics have also been used extensively in freshwater systems (Dumont & Segers, 1996; Arnott et al., 1998; Muirhead et al., 2006; Walsh et al., 2007; Kuczyńska-Kippen, 2007). However, few studies have explored biodiversity variation at different temporal and spatial scales (but see Arnott et al., 1998).

Patterns of variation in any community can be determined and affected by which community metrics are utilized. Species richness can be estimated using both parametric or non-parametric models and non-asymptotic or asymptotic accumulation curves (e.g., Colwell & Coddington, 1994; Hortal et al., 2004; Jiménez-Valverde & Lobo, 2005). These methods attempt to predict richness by extrapolation

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Table 1 Study lake characteristics and trophic description, recorded by Ejsmont-Karabin et al. (2004)

Lake	Depth (m)		Area (ha)	Description
	Mean	Maximum		
Majcz Wielki	6.0	16.4	164	Dimictic, mesotrophic
Inulec	4.6	10.2	178	Often stratified, eutrophic
Głębokie	11.8	34.3	47	Dimictic, meso-eutrophic
Zelwążek	3.7	7.4	12	Polymictic, hypertrophic

from sample-based rarefaction curves (Colwell et al., 2004; Hortal et al., 2006). Two non-parametric estimators, Chao2 and Jackknife2, work best at small spatial scales, thereby decreasing the likelihood of underestimating species richness (Hortal et al., 2006). These estimators project only the expected total number of species, and do not consider relative abundance within communities or temporal shifts in species identities within communities. Patterns of relative abundance (dominance) are typically assessed separately using metrics such as Simpson's Index of Diversity or the Shannon–Wiener Index (see Krebs, 1999).

A number of metrics are also available to compare the similarity of community composition between systems or temporally within systems. Similarity indices consider joint occurrences, discrete occurrences, and joint species absences to determine a coefficient of species overlap between two communities. Sorensen's coefficient weighs matches in species composition between two samples more heavily than mismatches (Krebs, 1999). One may also assess similarity in community composition over space or time using multivariate techniques including nonlinear Redundancy Analysis (RDA). This technique may utilize either species presence/absence or species abundance data.

In this study, we assess among (4 lakes) and within (temporal) lake variation in rotifer species richness and community similarity using a variety of biodiversity measures. Temporal analyses considered both seasonal and long-term (21-year span) variation in community composition with the goal to determine significant and consistent patterns of change occurred in rotifer communities. Study sites were located in four lakes in the Masurian lake region of north-east Poland. This is a well-studied region of the Jorka River watershed that is variable in both lake characteristics and anthropogenic stressors (e.g., Węgleńska

et al., 1983; Ejsmont-Karabin & Kruk, 1998; Ejsmont-Karabin et al., 2004). Our particular study lakes include Majcz Wielki, Inulec, Głębokie, and Zelwążek, which span a range of depth, mixing and trophic states (Table 1). We utilize a combination of biodiversity measures to explore seasonal, long-term and between lake variation in rotifer community composition to determine the most accurate assessment of change in our study system.

Methods

Zooplankton samples were collected approximately every 4 weeks at the deepest area (i.e., pelagic habitat) in each of our four study lakes. Samples were collected from March through November in 1976, and from April through November in 1997. In each case and for each lake, rotifer samples were collected with a 5-l sampler at 1-m depth intervals. These samples were then concentrated using a 30- μ m mesh plankton net and preserved with Lugol's solution and then 4% formalin (Węgleńska et al., 1983; Ejsmont-Karabin et al., 2004). Rotifers were identified and counted in five subsamples, encompassing 25% of the entire sample. At least 2,000 individuals were identified in each sample, which is about six times higher resolution than the norm in aquatic science. Our study provides a rare opportunity to address long-term changes in biodiversity without confounding issues related to changes in taxonomists over time, as a single investigator, J. Ejsmont-Karabin, conducted all sampling and species identifications.

Species richness estimates

Species lists were generated for each lake in 1976 and 1997. Presence/absence data from different depths

were merged if multiple samples were collected at one site; in such cases, if a species was recorded at any depth, it was considered present at the site. Sample-based species accumulation curves were constructed to estimate species richness for each lake by year combination. To do this, samples from each location in a lake were randomized without replacement, sampled (from $n = 1$ to m where m is the number of samples available), and the cumulative number of different species was recorded (Muirhead et al., 2006). This procedure was repeated for 100 bootstrap iterations to derive a mean species richness (\pm SE) value. Actual (versus sampled) species richness was estimated for each lake in each year by calculating Chao2 and Jackknife2 asymptotic estimates using the software EstimateS (Colwell, 2006). Both of these estimates reduce underestimation of actual species richness from sampling and are particularly accurate for incidence data (Hortal et al., 2006; Muirhead et al., 2006).

To determine whether inter-lake or inter-annual differences were significant, rarefied species richness values (\hat{S}_{MaoTao}) were calculated. \hat{S}_{MaoTao} is the expected number of species based on the accumulation curve for the total observed species (S_{obs}) (Colwell et al., 2004). Richness was standardized by rarefying to a common sample size. In this study, data was rarefied to our minimum sample size, $n = 14$, and compared statistically using the 95% CI of the calculated \hat{S}_{MaoTao} .

Community evenness and similarity

Nonparametric indices (Jackknife2 and Chao2) were used to estimate actual species richness per lake, per year. We utilized Simpson's and Shannon–Wiener diversity indices to assess evenness within lakes (see calculations in Krebs, 1999). Samples collected from different depths were merged for these analyses. Analysis of variance (ANOVA) was used to determine the effects of year and lake on each diversity index and sampled species richness. Post-hoc contrasts were assessed with LSMeans if significant interactions occurred among main effects.

Sorensen's coefficient was used to measure similarity within lakes over the 21-year span, as well as between lakes in each time period using the labdsv package of R Statistical Data Analysis software (Roberts, 2006; see calculations in Krebs, 1999).

Samples from different depths at a single location were merged for this calculation.

Rotifer species abundance patterns were assessed in relation to lake, sampling period, and Julian date using nonlinear RDA (Makarek & Legendre, 2002). Unlike some of the other ordination analyses, RDA constrains the community data such that the corresponding ordination distances are a linear combination of terms in a multifactorial analysis-of-variance model. The use of traditional, linear RDA is problematic owing to colinearities between explanatory variables, and a nonlinear relationship between response and explanatory variables. Nonlinear RDA accounts for these problems by fitting of a polynomial model to the data and reduces the effects of colinearities by centering explanatory variables on their respective means before model parameters are calculated (Makarek & Legendre, 2002). Thus, the use of nonlinear RDA still allows testing the a priori effects of environmental explanatory variables, but accounts for common errors with linear RDA. In this analysis, lake and sampling period were considered as factors and seasonal effects as a continuous variable represented by Julian date. Sites and depths were merged to obtain an integrated density (individuals per l). Species abundance was transformed prior to the RDA using the Hellinger transformation (Legendre & Gallagher, 2001). Tests of significance for each of the factors and RDA axes were assessed using a permutation approach (Legendre & Legendre, 1998). All transformations and analyses were carried out in the R package vegan (Oksanen et al., 2007; R v 2.7.1, R Development Core Team, 2008). The RDA was performed with Program Polynomial RdaCca (Makarek & Legendre, 2001, 2002).

Results

A total of 72 species were identified, of which 22 were ubiquitous in all the lakes in both years. The greatest number of species was observed in Lakes Głębokie (1976 and 1997) and Lake Inulec (1976) (Table 2). Lake Głębokie also had the highest total richness (57 species), and highest saturation richness in 1997 based upon Chao2 and Jackknife2 estimates (Table 2). Lake Żelwazek had the lowest richness overall (45 species) and for any given year (15

Table 2 Observed and estimated rotifer species richness in four Polish lakes

Lake	Year	Samples	# Species per year	Total # species sampled	\hat{S}_{MaoTao} (95% CI)	Chao2 (95% CI)	Jackknife2	Simpson Index	Shannon–Weiner Index
Majcz Wielki	1976	26	45	53	41 (36–46)	46 (45–51)	45	0.68	1.96
	1997	14	41					0.89	2.59
Inulec	1976	30	47	53	41 (33–49)	51 (43–86)	56	0.61	1.67
	1997	14	37					0.73	1.97
Głębokie	1976	35	47	57	41 (34–47)	54 (49–74)	61	0.78	2.24
	1997	28	47					0.81	2.20
Zelwążek	1976	15	36	45	37 (30–44)	41 (38–58)	46	0.67	1.95
	1997	14	39					0.81	2.45

\hat{S}_{MaoTao} richness was rarefied to $n = 14$ samples, while total number of species, and Chao2 and Jackknife2 estimates are for whole lake species richness

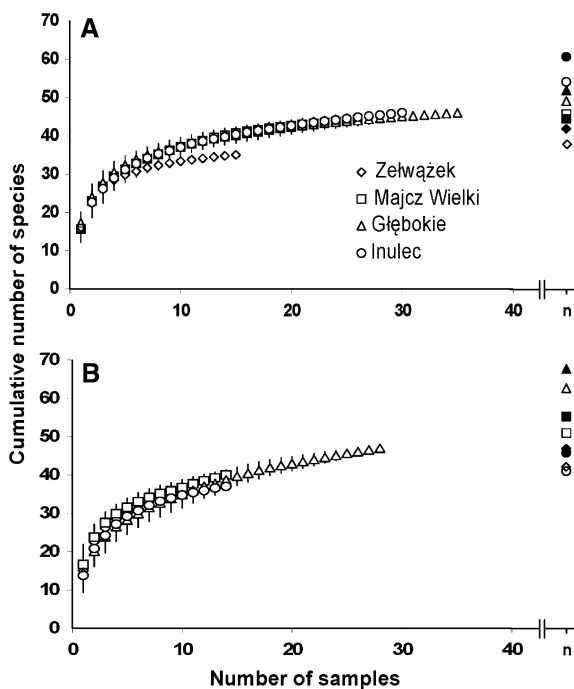


Fig. 1 Mean (\pm SE) species richness as a function of number of samples surveyed, based upon 100 bootstrap simulations in 1976 (A) and 1997 (B). Error bars smaller than symbols are not shown. Saturation richness estimates based upon Chao2 (open symbols) and Jackknife2 (solid symbols) are shown in the right side of both panels

species; 1976), as well as the lowest predicted saturation richness measures in 1976 (Table 2).

Species saturation curves developed from Monte-Carlo simulations exhibited a large degree of overlap, except for Lake Zelwążek in 1976 (Fig. 1A). Whereas Lake Głębokie had the highest richness

overall, Lake Majcz Wielki accumulated species fastest in 1997; the former lake continued to add new species with additional samples, whereas the latter quickly reached a plateau (Fig. 1B). Estimated species richness was generally higher in 1997 than in 1976, with the exception of Lake Inulec (Table 2; Fig. 1A, B). In addition, Jackknife2 estimates were consistently higher than those for Chao2, except for Lake Majcz Wielki in 1976 (Table 2; Fig. 1A).

In contrast to total species richness and Jackknife2 and Chao2 richness estimates, we observed no significant differences ($P > 0.05$) in rarefied species richness (standardized at $n = 14$ samples) across lakes or time periods (Table 2). Most deviation in richness accumulation curves occurred at larger ($n > 10$) samples sizes. Nevertheless, the highest and the lowest \hat{S}_{MaoTao} values were observed for Lakes Majcz Wielki and Głębokie, respectively.

Overall, all Simpson's and most Shannon–Wiener diversity estimates increased from 1976 to 1997 (Table 2). Similar to results for \hat{S}_{MaoTao} , Lake Majcz Wielki had the highest Simpson's and Shannon–Wiener diversity estimates (Table 2). While Lake Inulec had the largest number of species observed in any year (47 in 1976), it had the lowest observed Simpson and Shannon–Wiener values in the same year (Table 2).

There were no significant effects of year or lake on Simpson's diversity index for each sampling date (although a marginal interaction $F_{3,122} = 2.33$, $P < 0.0782$, was observed; Fig. 2A). By contrast, there was a significant interaction of year and lake on Shannon's diversity index ($F_{3,122} = 4.02$, $P < 0.0092$; Fig. 2B), and on sample species richness

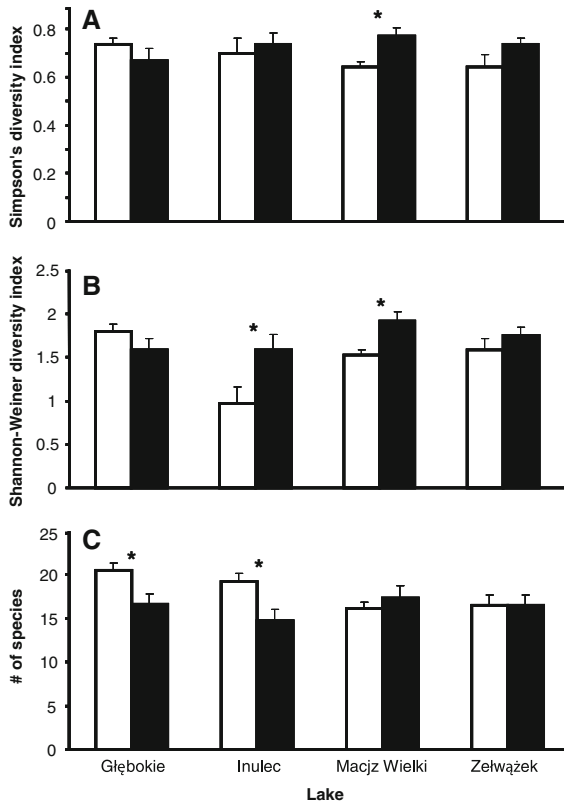
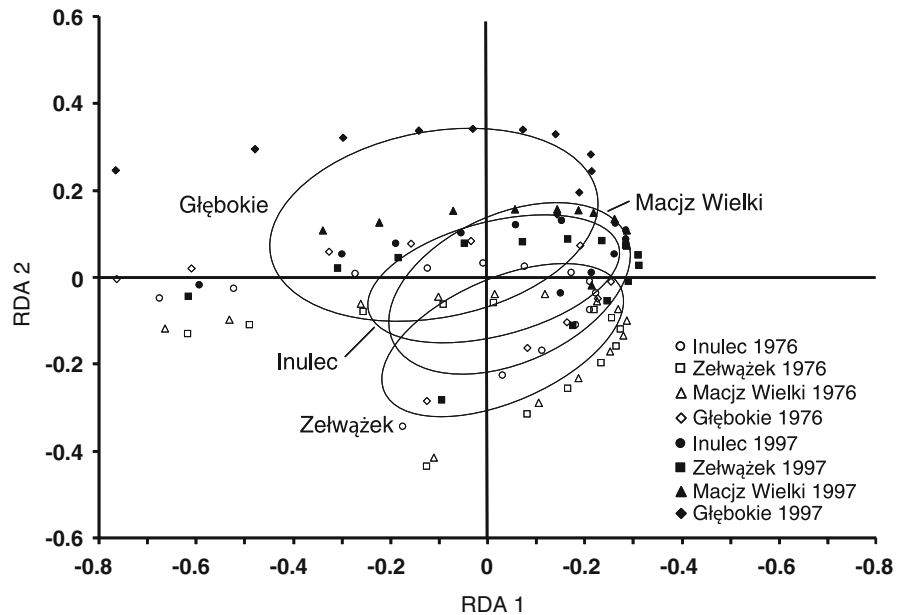


Fig. 2 Effect of lake and year on mean (+SE) species diversity on each date for (A) Simpson's and (B) Shannon's diversity indices as well as (C) sampled species richness. Asterisks (*) marks significant differences between 1976 (open bars) and 1997 (solid bars) within each lake

Fig. 3 Nonlinear Redundancy Analysis (RDA) ordination of rotifer communities between sample lakes and years. Samples from 1976 and 1997 are illustrated with open and solid symbols, respectively. Ellipses represent the 95% CI for each lake across both sampling years



for each sampling date ($F_{3,122} = 3.52, P < 0.0172$; Fig. 2C).

Sorensen's coefficient of similarity was high within lakes and very similar for each of the four systems studied (i.e., 74–78%). Sorensen's values between lakes within years tended to be as high (average 81% in 1976, 76% in 1997) as values within lakes between years (average 77%). For example, between-lake comparisons in 1976 ranged from 78 to 85%, whereas those in 1997 tended to be slightly lower (72–81%).

The nonlinear RDA indicated that rotifer community composition was influenced by all three factors considered (Julian date, year, and lake) and explained greater than 42% ($P < 0.001$) of variation in the data. Seventy-one percent of this variation was accounted for on the first two RDA axes (Fig. 3). Examination of RDA axes one and two illustrates that rotifer community composition exhibited strong seasonal variation, less pronounced long-term variation, and minimal inter-lake differences (Fig. 3).

Discussion

The collection and analysis by a single investigator of samples from four lakes across seasons and over a 21-year span allows us to partition variation in rotifer species richness and community composition. Mean

observed richness varied little (9.6%) within lakes across the 21-year study period. Overall, mean observed richness per sample was slightly higher in 1976 than in 1997 (17.8 vs. 16.3 species, respectively). However, seasonal variation was more extensive, with an average of only 41% of annual species richness recovered on any one sampling date. Observed total species richness in each lake and for both years was always higher than that reported for springs, artificial ponds, tinajas, and cattle tanks sampled in Big Bend National Park, Texas (Walsh et al., 2007). Sampling for this latter study was limited to a single season, mid-summer; thus it is possible that the extensive seasonal variation observed in our study was not captured.

Mean rarefied richness (\hat{S}_{MaoTao}) was very similar across our lakes (40 species \pm 2 SD), though estimated total richness was slightly more variable (Table 2). Estimated \hat{S}_{MaoTao} values for the pelagic habitat of two other Polish lakes, Mikolajskie and Łuknajno, are very similar to those reported here, as are Chao2 and Jackknife2 values (Muirhead et al., 2006). However, total rotifer species richness in the lakes surveyed here is almost certainly underestimated considering that the littoral and psammon habitats surveyed by Muirhead et al. (2006) typically support many more species than the pelagic habitats we examined. Other studies have determined that estimates of species richness increase as more habitats are considered (e.g., Wunderle et al., 2006).

In fact, we targeted the deepest part of our sample lakes for this study. The vast majority of rotifer species sampled were pelagic in nature, but a number of species considered more littoral and benthic, in the genera *Cephalodella* and *Lecane*, were recorded (see Electronic supplementary material). The presence of these species would inflate our species richness estimates for pelagic only species, but that was not our goal and their detection in samples taken from the pelagic still warrants inclusion.

Many studies have compared the utility of Simpson's and Shannon–Weiner diversity indices (e.g., Amman et al., 1997; Muirhead et al., 2006). We found both metrics produced virtually identical overall trends for inter-year and inter-lake trends (Table 2), but significant variation between lakes and between sampling periods was only detected with Shannon–Weiner (Fig. 2). This difference may reflect the differing data types used to generate them and

different relative species abundances in the lakes at different times.

Rotifer community analyses

The four study lakes exhibited a very high degree of community similarity (Sorensen's Coefficient: 0.81 ± 0.04 SD in 1976 and 0.76 ± 0.04 SD in 1997). These findings contrast results obtained by Dumont & Segers (1996), who reported high dissimilarity for rotifer ($\sim 74\%$) and for cladoceran ($\sim 90\%$) communities in mostly temperate lakes. Observed similarity values were substantially higher than those predicted for temperate lakes in general. Dumont & Segers (1996) indicated that their results may have been affected by poor taxonomy, a problem that would not be an issue in our study as all species were identified by the same individual for all lakes in both years. Our calculated Sorensen's coefficients were much higher than all of the values obtained for comparable Texan systems (Walsh et al., 2007). Lower long-term variability of the lakes in this study is consistent with results for 11 other Masurian lakes (see Walsh et al., 2007). Arnott et al. (1998) explored patterns of interannual variation in crustacean zooplankton communities over a 12-year period and suggested that apparent changes in community composition could, in many cases, result from insufficient sampling with attendant sampling errors. Sorensen's coefficient of similarity data between years 1976 and 1997 were very similar (range 74–0.78), and suggests that turnover of species, as reported by Arnott et al. (1998), was not extensive.

RDA detected pronounced seasonal variation in community composition based upon species abundance patterns, and less pronounced long-term and between-system variations (Fig. 3). Fahd et al. (2007) reported that increasing within-year sampling yielded higher species diversity than sampling additional systems within the same region, a result consistent with our observations. A key compositional difference between 1976 and 1997 was a shift away from dominance by species including *Keratella cochlearis*, *Collotheca mutabilis*, and *Synchaeta kitina* and increased dominance by *K. quadrata*, *Trichocerca similis*, *Conochilus unicornis*, *Pompholyx sulcata*, and *Polyarthra* spp. This shift was not apparent with any of the other biodiversity indicators utilized in this study, although the Shannon–Weiner Index did

record a significant increase in richness between 1976 and 1997 for three of the four lakes. It is not clear what factor(s) was responsible for this shift, although it may reflect long-term reductions in water inflow to the lakes owing to climate warming (J. Ejsmont-Karabin, pers. comm.).

In conclusion, we utilized a series of biodiversity measures to analyze temporal and spatial variation in pelagic rotifer communities. While most measures provided consistent results, some differences were apparent. Rotifer community richness and species composition were highly stable and consistent between systems and across a long temporal span. The greatest source of variation in community composition occurred seasonally, with much smaller but still apparent long-term and between-lakes changes.

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