

Time-series analysis of zooplankton diversity in upper reaches of the Ob River

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Abstract

Long-term data sets on various ecosystem parameters serve as the basis for environmental monitoring. Time series analysis is used to identify the structure of dynamic series and their prediction. The demographic characteristics of zooplankton are well suited to analyze seasonal and interannual changes in ecosystems. Since the dynamics of species richness and river flow are often interdependent, we studied zooplankton biodiversity in the upper reaches of the Ob River in relation to the phases of the water regime. A six-year sampling of zooplankton was performed from surface water from the Ob River at two stations near the city of Barnaul. In total, 203 species and forms of zooplankton were detected. In all phases of the water cycle, Rotifera dominated in species number. To analyze the species diversity of zooplankton, we used 20 indices, of which 10 were not random on both coasts and could be used in monitoring. The species diversity of zooplankton in a sample, according to Margalef and Menhinick indices, was the highest during the recession of the second flood wave. The generalized measures of diversity (Williams polydominance and Shannon indices, and Fischer alpha) showed their maximum during the recession of the second wave of high water and in the summer low water period. Statistically significant declines in trends of some species diversity are evidence of small changes in the structure of the zooplankton. Time series analysis in the assessment of community biodiversity helps to select indices suitable for predicting ecosystem state, as well as to identify related changes in the community.

Keywords

Biodiversity indices, time series, zooplankton, hydrological seasons

Introduction

In ecology, assessment and conservation of biodiversity are among the central problems. Species diversity is often used as a synonym for the number of species. In fact, it encompasses several components. Biodiversity can be described in terms of composition and structure of the biota, differences in functional characteristics of species, or their interaction (Hooper et al. 2005). The number of species and the indices of species richness can represent the composition of the biota, whereas its structure could be expressed by indices of heterogeneity (dominance or evenness). Both components can be considered through generalized measures of diversity. Long-term datasets on various ecosystem parameters (including biodiversity) serve as the basis for environmental monitoring. These parameters help to understand the drivers of biodiversity changes, as well as to assess the impact of rare events and the interaction between short-term and long-term trends (Haase et al. 2018).

Long-term studies allow us to distinguish changes that can be attributed to external factors (e.g., anthropogenic activities) from underlying natural changes (Magurran et al. 2010; Mirtl et al. 2018). Long-term studies often account for only the number of species and their abundance (Wang et al. 2016; Dexter et al. 2020). However, it is hard to stick to the same sampling method for decades, and diversity indices turn out to be more informative than just the number of species (Magurran et al. 2010). Time series analysis is performed to identify the structure of long-term datasets and to implement their prediction because long-term investigations (several tens and hundreds of years) with spatial coverage are currently limited (Berline et al. 2012; Mackas et al. 2012; Koslow and Couture 2013; Ouba et al. 2016).

The drivers affecting ecological processes in rivers vary in different climatic and biogeographical regions. Of course, a taxonomic description of natural communities is not sufficient to reveal their response to stress (Baird et al. 2011). Along with species number, other indicators should be employed (e.g. indices of species diversity). This work aims to study the seasonal and interannual dynamics of the diversity of zooplankton species in order to develop recommendations on applying indices for monitoring the state monitoring.

Materials and methods

Study site

The Ob River is formed at the confluence of the Biya and Katun (which basins are located in the Altai Mountains) and flows into Ob Bay of the Kara Sea. The total length of the river is 3,618 km. The river regime is characterized by low and prolonged spring-summer floods, increased summer-autumn runoff, and decreased low water. In the low-water summer-autumn period, flow velocity in the study site is

0.7-1.0 m/s; in high water it reaches 1.5-2.1 m/s. The discharge of the Ob River near Barnaul (Russia) varies from 230-350 at 4,000-6,000 m³/s. According to chemical composition, river water refers to bicarbonate class of the calcium group (Kotovshchikov and Dolmatova 2018).

Since species richness dynamics and river flow are often interdependent, zooplankton biodiversity was studied in terms of water regime phases (see the characteristics of phases in Table 1).

Table 1. Hydrological characteristics of the Ob River (Barnaul) for different years of investigation

Hydrological seasons				2013	2014	2015	2016	2017	2018	
Average water discharge m ³ /s (per year; April-November)				2005; 2760	1594; 2129	1516; 2044	1684; 2285	1535; 2064	1582; 2166	
Onset of ice drift, date				12.4	2.4	17.4	6.4	12.4	15.4	
Winter low water period (days; I L; T(l), T(r))				100; 1; 0.2, 0.2	122; 23; 0.1, 0.1	137; 16; 0.2, 0.2	116; 17; 0.2, 0.2	129; 32; 0.2, 0.3	134; -5; 0.2, 0.2	
Transition period (days; L; II T(l), T(r))				23; 193; 0.4, 0.7	13; 169; 0.5, 0.8	18; 144; 0.4, 0.6	19; 146; 0.3, 0.5	15; 204; 0.3, 0.8	7; 182; 0.4, 0.2	
Spring-summer seasonal flood	1 st flood wave (days; L; T(l), T(r))	Rise	III-A	19; 471; 8.7, 8.0	8; 354; 5.1, 4.6	17; 560; 8.6, 8.5	26; 398; 6.7, 6.4	9; 500; 5.6, 5.2	16; 441; 1.8, 1.4	
		Recession	III-B	21; 411; 11.0, 11.1	47; 239; 10.0, 9.9	17; 500; 15.0, 15.3	27; 366; 9.9, 9.9	17; 501; 9.7, 9.8	40; 436; 6.9, 6.9	
	Second flood wave (days; L; T(l), T(r))	Rise	IV-A	38; 474; 14.1, 14.6	11; 542; 12.3, 13.0	15; 496; 13.4, 13.8	24; 522; 14.0, 15.2	13; 491; 13.6, 13.7	25; 512; 15.9, 16.4	
		Recession	IV-B	16; 466; 17.4, 17.4	33; 526; 18.8, 19.9	17; 458; 18.3, 18.5	22; 491; 19.8, 20.2	21; 445; 15.1, 5.7	15; 470; 19.1, 20.0	
	Duration, days				94	99	66	99	60	96
	Floodplain inundation, days (III+IV)				0+10	0+25	19+3	0+23	11+6	0+16
Summer-autumn low-water period	Summer low water period (days; L T(l), T(r))			V 57; 330; 19.3, 19.4	57; 234; 19.7, 19.6	80; 202; 20.1, 20.1	62; 257; 18.8, 18.8	84; 232; 21.5, 21.6	60; 222; 19.5, 19.5	
	Autumn low water period (days; L; T(l), T(r))			VI-A 41; 173; 10.1, 10.0	58; 124; 9.8, 9.7	42; 129; 7.0, 7.0	42; 94; 12.7, 12.6	55; 140; 10.2, 10.1	51; 85; 12.7, 13.0	
	Late autumn low water period (days; L; T(l), T(r))			VI-B 50; 111; 3.2, 4.0	16; 103; 0.9, 1.0	22; 87; 2.0, 1.8	28; 103; 2.2, 2.5	22; 72; 2.2, 2.5	17; 42; 2.2, 2.5	
	Duration, days				148	131	144	132	161	128

Note: L – is the average level relative to the zero gauge, cm (the floodplain flood begins at 520 cm water level); T – is the chronological average water temperature, °C, (l) on the left bank, (r) at the right bank.

In the winter low-water period (I, November–March), the level, discharge, and temperature of water are low. At the end of March, even before the onset of ice drift, the restructuring of zooplankton community begins (transition level II, March–April). With an increase in water discharge and level, the water temperature does not exceed 1 °C. In the first wave of high water (III, April–May), when snow melt begins in the plain, the discharge of water increases sharply. Both air temperature and water temperature in the river rise. During the second wave of high water (IV, May–July), when snow and glaciers melt in the mountains, maximum discharge and runoff usually occur. The water temperature during the second flood wave is much higher (15.1–20.2 °C) than at the rise of the wave (12.3–15.9 °C). Low water in summer–autumn (V, June–September) is the most favorable for the development of zooplankton (water temperature reaches 18.8–21.6 °C). In autumn (VI-A, September–October), water level falls, causing a sharp drop in water temperature (to 7.0–13.0 °C). The late autumn low-water period (VI-B, October–November) is characterized by low water discharge, low water level, and even greater temperature drop (0.9–4.0 °C).

Field sampling

Zooplankton samplings were carried out in the period of 2013–2018 from the surface water layer of the Ob River near Barnaul (53°19'20" N, 83°48'15" E) at two stations located 234 km away from the Biya and Katun confluence. When sampling, we measured water temperature and transparency. In addition, water samples were taken for hydrochemical analysis (total hardness, permanganate oxidizability, oxygen consumption BOD₅, total mineralization, mass concentrations of phosphates, nitrates, ammonium, sulfates, chlorides, bicarbonates, calcium, magnesium, sodium, and potassium).

The collected zooplankton was filtrated through 100 L of water using an Apstein net (with a mesh size of 62×62 µm). Overall, we analyzed 283 zooplankton samples. The least number of samples were taken in winter (6) and in the transition period (12). In spring–summer flood, 108 samples were collected (50 in the first wave, 58 – in the second), while during the summer–autumn low-water season – 157 (i.e. in summer, autumn and late autumn– 95, 44, and 18, respectively). The taxonomic composition of three groups of zooplankton was analyzed with MBS-10 (Cladocera and Copepoda) and a Nikon Eclipse 80i microscope (Rotifera).

Data analysis

We employed six indicators (the average number of species in samples during a certain phase of the water regime (Si) and the average number of main groups of zooplankton (SR_{rot}, SC_{cl}, SC_{cop}), the Menhinick (DMn), and Margalef (DMg) indices as characteristics of the richness of the zooplankton species. The dominance level in the community was measured through the use of four indices, i. e. the Berger-

Parker (DBP), McIntoch (DMI) and Simpson ones calculated from number of individuals ($DS(N)$) and biomass ($DS(B)$). The community uniformity was studied using five equalization indications, i.e., the McIntoch (EMI), Simpson ($ES(N)$, $ES(B)$) and Pielou ($EP(N)$, $EP(B)$) indices. Based on the generalized measures of species diversity, we quantified five indicators, i.e. the Williams polydominance index ($S_{\lambda(N)}$, $S_{\lambda(B)}$), the Shannon diversity index ($H(N)$, $H(B)$) and Fisher's alpha (α).

To identify temporal patterns of changes in zooplankton biodiversity, time series was made using PAST 4.0 and Statgraphics Plus 5.0. The missing data were eliminated by applying the arithmetic mean of all values in a certain phase for other years. To test the white noise hypothesis or random distribution of data (i.e. the data series do not contain any regular components), we implemented randomization tests. To identify stable long-term changes in biodiversity, a nonparametric Mann- Kendall trend test was made for the selected trend-cyclic component of dynamic series. For the construction of the averaged seasonal cycles, an additive method for calculating the seasonal components was applied. Due to the limited datasets, we did not perform the cyclic component analysis. Spearman rank correlation coefficients were used in analyzing the relationship between zooplankton species diversity and environmental factors.

Result

During the study period, a total of 203 species and forms of zooplankton were detected (177 on the left bank and 192 – on the right bank). The largest number of zooplankton species and forms falls on the left coast during the summer low water period (Fig. 1A) and on the right one, during recession of the second wave in spring- summer flood (Fig. 1B). In all phases of the water cycle, Rotifera dominated in species number, the proportion of Cladocera increased during recession of the second flood wave (IV-B) and in the summer low-water season (V). The juvenile stages of Copepoda development prevailed, whereas the adult species were rare. Differences in the species composition of zooplankton (Fig. 1C) were not observed on both coasts. Among the 20 calculated indicators of zooplankton biodiversity in the Ob River, 10 demonstrated a non-random distribution within both banks of the river. Therefore, they can be used to assess dynamics, forecasting, and monitor.

Seasonal dynamics of biodiversity indices

Five indicators of species richness suggest a nonrandom distribution of data, i.e. the number of species in a sample, the number of Rotifera and Cladocera species, the Menhinick and Margalef indices. During low water (I), the transition period (II), and the first wave of high water (III), species richness of zooplankton is low (Fig. 2A). With rise of the second flood wave (IV-A), this indicator increases, reaching its maximum during recession (IV-B) followed by its decline (VI). On the right bank, with its well-developed floodplain, seasonal indices of zooplankton species

are higher during the entire period, which is favorable for its development (water temperature above 10 °C). During the low-water period of autumn (VI-A), species richness of zooplankton remains high on the right bank, but significantly drops near the left bank. Simpson and Pielou indices of evenness (in number of individuals) are maximal during the transition period (II) (Fig. 2B) when the number of winter zooplankton falls, and the summer species are not abundant yet. As a result, the equalization of the community is reduced. It becomes the least during the recession of the second flood wave (IV-B), which indicates extreme habitat conditions for zooplankton during this period.

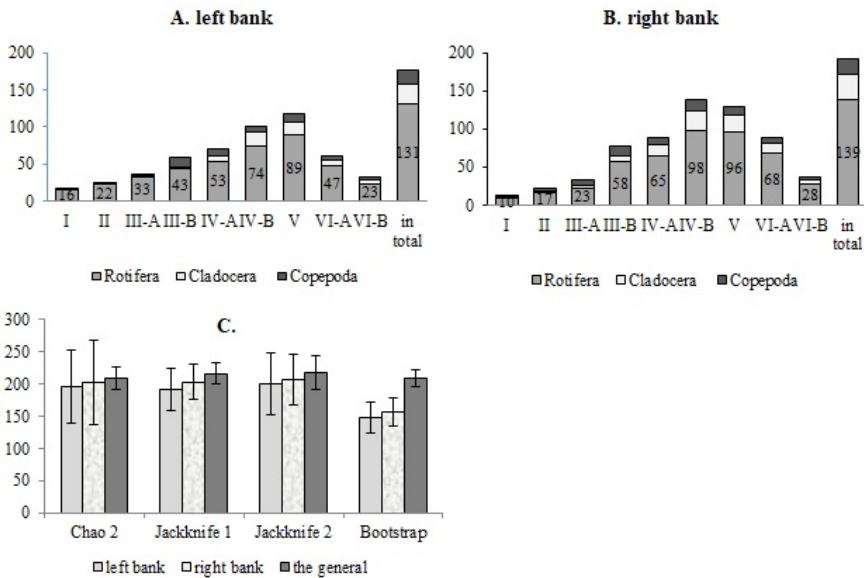


Figure 1. The number of species and forms of zooplankton in the Ob River (A, B); quantitative assessment of the species composition of zooplankton based on resampling (C) recorded in the period 2013-2018. I – winter low-water period; II – transition period; III-A – rise of the first flood wave; III-B – decrease of the first flood wave; IV-A – rise of the second flood wave; IV-B – recession of the second flood wave; V – summer low water period; VI – autumn low water period; VI – late autumn low water period.

According to the generalized measures of diversity, the datasets for three indicators are not random: the Williams polydominance and Shannon indices (in number of individuals) and the alpha Fisher diversity measure. The Shannon (Fig. 2C) and Williams polydominance indices show similar seasonal dynamics. During the winter low-water period (I), these values are high for the left coast and low for the right coast. In the transition period (II) and the first flood wave (III), the diversity is low; its increase is observed during the second wave (IV). The highest indices are marked in the low-water summer period (V). In the low-water season (VI),

a tendency towards a decrease in index values is observed. However, on the right bank they remain quite high, unlike the left bank showing a drastic drop. From the Fischer alpha indicators (Fig. 2D) it follows that both river banks are distinguished by the richest diversity of zooplankton during the recession of the second flood wave (IV-B). Similar dynamics in species richness is evidence of stronger influence of species number, rather than abundance.

There is a significant similarity in the seasonal cycle of species richness indices and general measures of diversity with changes in water temperature during the open water period (Fig. 2E). In seasonal dynamics, the water temperature on both coasts is almost identical. Its minimum was recorded in the winter low water period, with a further gradual increase to maximum in summer followed by a sharp drop. According to hydrochemical analysis, nitrates demonstrate the best correlation of the seasonal cycle with water temperature and indices of zooplankton species diversity, but in reverse order: maximum values in winter, gradual fall (up to minimum) until summer, and finally sharp rise.

Interannual dynamics of biodiversity indices

Comparison of actual and forecasted (from the average seasonal cycle) data enables us to reveal the features of a particular year. In the high water year of 2013, during the recession of the richness second flood wave, the indices of the zooplankton species (Fig. 3A) and the Fisher alpha were lower than usual. As a result, maximum species richness was marked in the low-water summer period. The highest level of equalization of the community was not only in the transition period, but also in the fall (Fig. 3B).

In 2014, the first flood wave was rather weak. Naturally, a higher level of the community was observed (Table 1). In 2014 and 2018, the species richness was higher during the second flood wave than in the seasonal rise (Fig. 3A). In 2014, this effect was caused by an extremely high and prolonged flood. In 2018, with a high water level during the rise of the second flood wave, the water temperature increased (compared to other years), providing favorable conditions for the development of a large number of species of zooplankton. In 2015 and 2017, the shift of the maximum in the Williams polydominance and Shannon indices from the recession summer low water to the period of the second seasonal flood wave was recorded on the right bank (Fig. 3C). It was associated with spring-summer seasonal flood peculiarities of spring and summer. Floodplain inundation occurred during the first flood wave (Table 1) and provided good conditions for the development of zooplankton. This was especially evident in 2015, when the water temperature during the recession of the first wave in the high-water period was higher (approximately 15 °C) than usual (approximately 10 °C). In 2017, seasonal indices of zooplankton richness were maximal in summer due to early, not prolonged, and lowest runoff from spring-summer floods.

A feature of 2016 was a shift in the peak of species richness near the right river-bank in the autumn low-water season (Fig. 3A). The Shannon index (Fig. 3C) that time apparently increased because of optimal for zooplankton development until the end of September (17.4 °C).

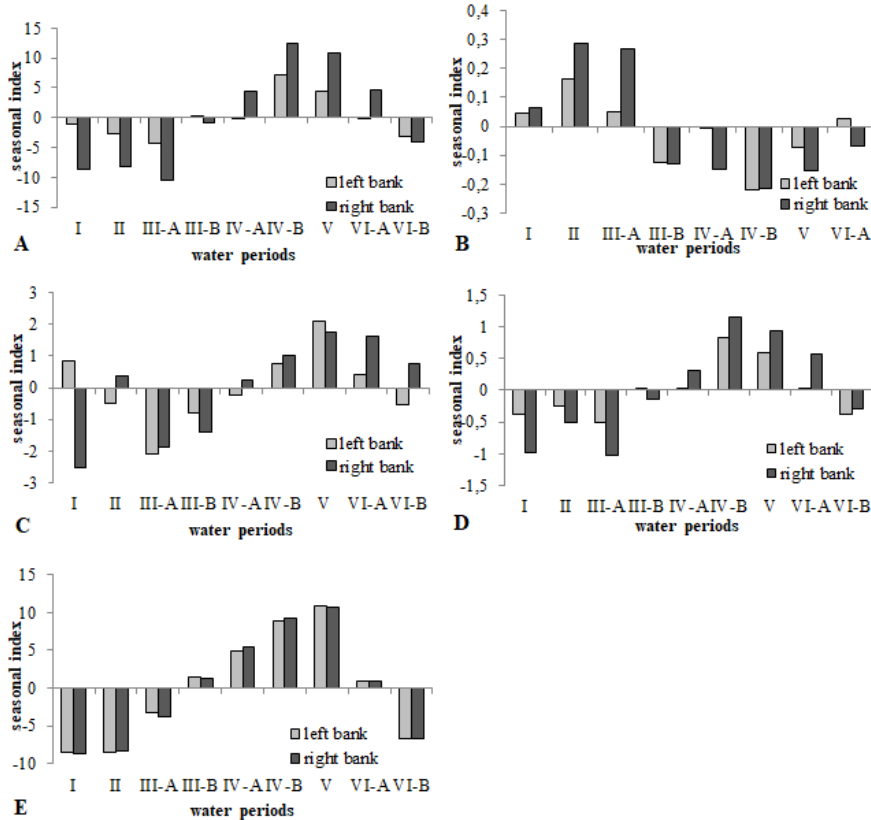


Figure 2. Schematic averaged seasonal cycle of zooplankton biodiversity indices of the Ob River (Barnaul) for 2013-2018. A – the average number of species in a sample; B - Simpson evenness; C – the Williams polydominance index; D – the Fischer alpha; E – the water temperature. I – winter low-water period; II – transition period; III-A – rise of the first flood wave; III-B – decrease of the first flood wave; IV-A – rise of the second flood wave; IV-B – recession of the second flood wave; V – summer low water period; VI – autumn low water period; VI – late autumn low water period.

Relationship with environmental factors

Almost all indicators (except the Williams polydominance index) correlate well with changes in water temperature (Table 2). The temperature of the growing water has a beneficial effect on the richness and diversity of the zooplankton. The structure equalization weakens with an increase in temperature, which indicates the presence

of dominant species in the community. Changes in sulfate concentrations are most prominent on the left bank, whereas nitrates and chlorides are most prominent on the right bank. During the study period, no excess MPC was observed in hydrochemical parameters.

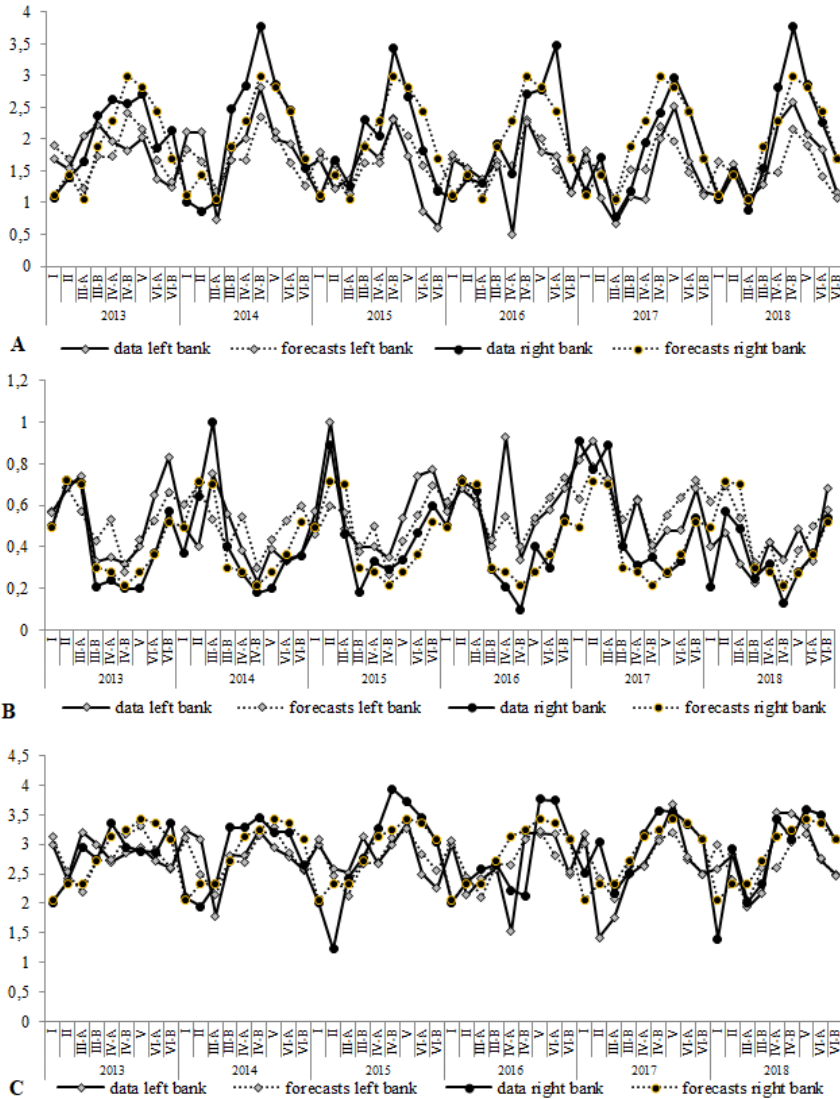


Figure 3. Dynamics of biodiversity indices accounting for a seasonal component: A, Margalef index; B – the Simpson evenness; C, Shannon index. I – winter low water period; II – transition period; III-A – rise of the first flood wave; III-B – decrease of the first flood wave; IV-A – rise of the second flood wave; IV-B – recession of the second flood wave; V – summer low water period; VI – autumn low water period; VI – late autumn low water period.

Table 2. Correlation coefficients of zooplankton biodiversity indices with abiotic parameters of the upper reaches of the Ob River (Barnaul) in 2013–2018

	T	Tr	PO	M	Sul	Nit	Chl	Ca	Mg	Na+K
Si	0.88	0.36	-0.60	-0.52	-0.90	-0.83	-0.52	-0.52	-0.69	-0.69
	0.83	0.62	-0.67	-0.33	-0.67	-0.95	-0.74	-0.21	-0.40	-0.17
SRot	0.83	0.19	-0.45	-0.38	-0.83	-0.69	-0.55	-0.38	-0.52	-0.62
	0.86	0.60	-0.71	-0.26	-0.62	-0.98	-0.76	-0.14	-0.36	-0.05
SCl	0.76	0.69	-0.86	-0.26	-0.79	-0.95	-0.81	-0.26	-0.50	-0.55
	0.76	0.60	-0.60	-0.48	-0.71	-0.83	-0.76	-0.36	-0.55	-0.31
DMg	0.90	0.12	-0.40	-0.57	-0.95	-0.71	-0.62	-0.57	-0.74	-0.74
	0.83	0.62	-0.67	-0.33	-0.67	-0.95	-0.74	-0.21	-0.40	-0.14
DMn	-0.81	-0.26	0.24	0.52	0.64	0.60	0.62	0.52	0.57	0.76
	-0.95	-0.43	0.38	0.62	0.71	0.90	0.83	0.50	0.67	0.36
ES(N)	-0.81	0.00	0.12	0.74	0.83	0.50	0.40	0.74	0.74	0.88
	-0.86	-0.36	0.21	0.57	0.60	0.79	0.71	0.45	0.55	0.36
EP(N)	-0.74	-0.19	0.19	0.74	0.76	0.52	0.38	0.74	0.69	0.93
	-0.74	-0.17	0.12	0.52	0.79	0.64	0.50	0.52	0.48	0.48
α	0.90	0.12	-0.40	-0.57	-0.95	-0.71	-0.62	-0.57	-0.74	-0.74
	0.83	0.62	-0.67	-0.33	-0.67	-0.95	-0.74	-0.21	-0.40	-0.17
S λ (N)	0.60	0.10	-0.55	-0.05	-0.74	-0.60	-0.60	-0.05	-0.33	-0.24
	0.40	0.79	-0.98	0.26	-0.14	-0.71	-0.64	0.43	0.12	0.48
H(N)	0.81	0.45	-0.71	-0.17	-0.79	-0.83	-0.67	-0.17	-0.40	-0.50
	0.76	0.76	-0.83	-0.21	-0.36	-0.95	-0.74	0.00	-0.33	0.05

Note: The upper row is corresponds to l station and the lower row – to r station; the correlation coefficients significant at $p < 0.05$ are highlighted in bold; (l) on the left bank, (r) at the right bank; T – temperature; Tr – transparency; PO – permanganate oxidizability; M – total mineralization; Sul – sulfates; Nit – nitrates; Chl – chlorides; Ca – calcium; Mg – magnesium; Na+K – sodium and potassium; Si – number of zooplankton species in a sample; SRot – number of Rotatoria species in a sample; SCl – number of Cladocera species in a sample; DMg – Menhinick index; DMn – Margalef index; ES(N) – Simpson evenness; EP(N) – Pielou index; α – Fischer alpha; S λ (N) – Williams polydominance index; H(N) – Shannon index.

Discussion

Similar to large rivers, the diversity of zooplankton in the Ob riverbed is influenced by the upper reaches of the river, lake and watercourses of floodplain, which contribute greatly to its species enrichment (Opperman et al. 2010; Potemkina et al. 2013, Gorski et al. 2013). Floodplain inundation in spring and summer with a thin water layer results in rapid warming, high development of phytoplankton, and, as a consequence, zooplankton (Grosholz and Gallo 2006). The highest abundance and species diversity of zooplankton often occur during the flood phase (Lansac-Toha et al. 2009; Furst et al. 2014; Matsumura-Tundisi et al. 2015; Larsen et al. 2019), and that is also true for zooplankton in the upper reaches of the Ob River. Here, the

maximum species richness was observed during the recession of the second flood wave. For the right bank with the developed floodplain, the seasonal indices were much higher.

The duration and intensity greatly affect the diversity of zooplankton (Thomaz et al. 2007; Napiorkowski et al. 2019; Moacyr et al. 2019). In 2014, extremely high and prolonged Ob flooding caused a very rapid and extensive zooplankton flush and, correspondingly, high species richness and general measures of diversity along with low community equalization. The number of days and the time (in the first or second flood waves) of floodplain inundation also affect the diversity of zooplankton.

Temperature often serves as a driver of changes in the zooplankton community (Havens et al. 2015; Carter et al. 2017; Hu et al. 2019). An increase in water temperature increases the diversity of zooplankton (Deksne and Skute 2011; Wang et al. 2016; Gophen 2020). In addition to a response to seasonal changes, zooplankton populations are also sensitive to interannual temperature fluctuations (Dexter et al. 2020). Temperature had the greatest impact on the temporal patterns of distribution of zooplankton biodiversity in the upper reaches of the Ob River.

In long-term studies, targeted changes over time are among the main issues (Zingone et al. 2019). The Mann-Kendall trend test for some indicators of zooplankton biodiversity in the upper reaches of the Ob River shows statistically significant decreasing trends. For such cases, we performed an additional analysis and excluded data on the 2013 high-water year. The existence of the targeted long-term changes in population structure was supported by additional analysis and the Mann-Kendall trend test application. According to the Menhinick ($Z_{13-18}=5.65$; $Z_{14-18}=3.93$) and Margalef ($Z_{13-18}=4.04$; $Z_{14-18}=2.39$) indices, a steady loss of biodiversity and decreased nitrates ($Z_{13-18}=2.95$; $Z_{14-18}=3.87$) were observed near the left bank. On the right bank, the Margalef indices ($Z_{13-18}=2.77$; $Z_{14-18}=2.79$) and the Fischer Alpha ($Z_{13-18}=3.18$; $Z_{14-18}=2.77$) demonstrated a downward trend. There are small changes in the structure of the zooplankton, probably due to the displacement of the main water flow closer to the left bank.

The higher the diversity, the more stable the response of ecosystems to environmental fluctuations is. Studies of diversity-stability relationships have a long tradition in ecology (Hooper et al. 2005), since in the event of loss of species diversity, ecosystems weaken and can no longer provide people with services of proper quality (Krzon et al. 2017). For better tracking and understanding of the impacts of climate change and anthropogenic activities on aquatic ecosystems, more attention should be paid to long-term research (Lan et al. 2021). Further monitoring of the upper reaches of the Ob River will provide data for a thorough study of interannual changes in zooplankton composition and structure of moderate rivers and exploration of environmental trends over time.

Conclusion

Various parameters and indices are available for assessing water ecosystem diversity. However, we cannot use a unified indicator for all reservoirs and waterways in different biogeographical zones. Time series analysis can be a universal approach that helps to select indices that are appropriate for predicting any ecosystem state. We selected 10 indicators of species diversity could be included in the program of environmental monitoring of the upper reaches of the Ob River. Since the main drivers of seasonal changes in zooplankton diversity are water temperatures, sampling is required throughout the year. Time series analysis determined the usage of minimum indices and reduced the sampling-related efforts and costs. Our analysis testified that small rearrangements in the zooplankton structure probably occurred due to the displacement of the main water flow closer to the left bank of the Ob River.

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