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Original Articles

Long-term shifts in water quality show scale-dependent bioindicator responses across Russia – Insights from 40 year-long bioindicator monitoring program

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A R T I C L E I N F O

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A B S T R A C T

Scale-related assessment strategies are important contributions to successful ecosystem management. With varying impact of environmental drivers from local to regional scales, a focal task is to understand scale-dependent responses when assessing the state of an ecosystem. In this study we use large-scale monitoring data, spanning 40 years and including four aquatic bioindicator groups (phytoplankton, zooplankton, periphyton, zoobenthos) to expose the long-term changes of water quality across Russia. We include four hierarchical spatial scales (region, basin, waterbody and observation point) to identify the relative importance of different spatio-temporal scales for the variation of each bioindicator and patterns of co-variation among the bioindicators at different hierarchical levels. We analysed the data with Hierarchical Modelling of Species Communities (HMSC), an approach that belongs to the framework of joint species distribution models. We performed a cross validation to reveal the predictive power of modelled bioindicator variation, partitioned explained variance among the fixed effects (waterbody type, and influence of human population density) and the random effects (spatial and spatio-temporal variation at the four hierarchical scales), and examined the co-variation among bioindicators at each spatio-temporal scale. We detected generally decreasing water quality across Russian freshwaters, yet with region and bioindicator specific trends. For all bioindicators, the dominating part of the variation was attributed the largest (region) and smallest (observation point) hierarchical scales, the region particularly important for benthic and the observation point for pelagic bioindicators. All bioindicators captured the same spatial variation in water quality at the smallest scale of observation point, with phytoplankton, zooplankton and periphyton being associated positively to each other and negatively to zoobenthos. However, at larger spatial scales and at spatio-temporal scales, the associations among the bioindicators became more complex, with phytoplankton and zooplankton showing opposite trends over time. Our study reveals the sensitivity of bioindicators to spatial and temporal scales. While delivering unidirectional robust water quality assessments at the local scale, bioindicator co-variation is more complex over larger geographic scales and over time.

1. Introduction

Safeguarding good environmental status of aquatic ecosystems is one of the global ecological challenges. Ever-increasing human impacts such as eutrophication, artificial land- and seascapes modifications, pollution and contamination, in combination with the continuous superimposed effects of a changing climate, alter the ecological integrity and biodiversity of rivers, lakes and coastal systems (e.g. Sala et al., 2000; Dudgeon et al., 2006; Halpern et al., 2007). The gained goods and services from aquatic ecosystems are pervasive and fundamental for human wellbeing (Covich et al., 2004). For effective management and conservation, scale-related assessment strategies are needed, from local waterbodies to broad geographic regions, which comprise a collective of connected and individual ecosystems and encompass environmental variation (Frissell and Bayles, 1996; European Comission, 2000; UNEP, 2002). National and international strategies to protect and

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manage the integrity of aquatic systems, such as the U.S. Clean Water Act or the European Water Framework Directive (WFD), are based on the concept that the state of biological communities reflects the water quality and the impacts they are exposed to (European Comission, 2000; Fore, 2003). The utilisation of such bioindicators is well established and their integration in ecological studies and management tools has tremendously increased in the past decades (Siddig et al., 2016). The principle behind their application is stemming from the assumption that species communities reflect the cumulative effects of environmental changes, both over short and long-term periods of exposure, and hence are represented in community attributes such as species richness, diversity, composition, abundance or biomass (Burger, 2006). Aquatic communities are rapidly responding to physical and chemical disturbance by human impacts, making them highly suitable for ecological monitoring (Ector and Rimet, 2005).

While abiotic measures such as chemical pollution only provide momentary quantitative data on specific substances, present organisms are exposed to the entirety of pressures and substances and reflect immediate as well as long-term cumulative and synergistic effects in real world situations (De Pauw and Vanhooren, 1983). Depending on the group of included bioindicators, it is possible to target different aspects and timeframes of ecosystem health. Phytoplankton communities, on the one hand, are the first to be affected by eutrophication pressures and excess nutrients, showing fast responses due to their short generation times. On the other hand, the mainly stationary and longer-lived zoobenthos is permanently exposed to its surrounding conditions and the most frequently used bioindicator group, including diverse taxa with a wide range of tolerances, providing good indications for the current state and longer-term ecosystem changes affecting the benthos. It depends not only on direct effects like eutrophication but also on secondary consequences of organic enrichment such as oxygen depletion (Pearson and Rosenberg, 1978; Cairns and Pratt, 1993; Solimini et al., 2006). However, most of the work comprising bioindicators generally include only one taxonomic group with an increasing trend of using single bioindicator species to determine the overall ecosystem state (Siddig et al., 2016). Considering the complexity of the total environment, there is no single species which is able to provide an overall environmental state (Lindenmayer and Likens, 2011). For most accurate determination of aquatic ecosystem health through bioindicators, the integration of several taxa including different life history strategies over varying times scales is necessary (Carignan and Villard, 2002; Ector and Rimet, 2005). In the present study we include four multimetric bioindicators across phyla and trophic levels, from autotrophic phytoplankton and periphyton to zooplankton and zoobenthos, covering benthic and pelagic realms, to expose the broad trend in changing water quality across Russia since the 1970s.

During the 1950s to the 1970s the anthropogenic footprint on aquatic ecosystems was strong with many of Russia's largest rivers, such as the Volga or the Yenisei, being managed and transformed into cascades of reservoirs to provide irrigation and hydroelectric power. Taming the natural flow regime and creating reservoirs increased the susceptibility to higher organic deposition, more stagnant waters and accumulation of pollutants. With the dissolution of the Soviet Union in 1991, the anthropogenic impact on aquatic ecosystems weakened due to the decreased economic and industrial performance, but did not lead to a significant improvement during the following years (Kimstach et al., 1998). Despite decreasing chemical pollution through organochloride pesticides (Zhulidov et al., 2000), the previously existing water quality problems from ecotoxic substances such as inorganic and organic metal compounds (Moiseenko et al., 2008; Qdais et al., 2018) as well as the increasing nutrient inputs from growing population, agriculture, and industry, causing eutrophication, remain and are for the latter still growing (Kimstach et al., 1998; Timoshkin et al., 2018). Hence, in this study we hypothesise an overall decreasing trend of Russian water quality with all included bioindicator groups. In particular in areas with modified flow regimes and high population densities, we expect to find signals of increasing eutrophication, lowering the water quality.

We take advantage of a large-scale and long-term sampling network, spanning a geographic region of more than 7000 km over a 40-year time period, and including community monitoring data across Russia's freshwater systems, both in natural and urban environments. Using a hierarchical joint species distribution modelling approach, applied on bioindicator data, we test the hypothesis of a directional change in ecological quality of aquatic systems over the past four decades. We further examine patterns of co-variation among the different bioindicator groups at the included hierarchical levels, both related to permanent spatial variation, as well as to spatio-temporal variation. Considering four hierarchical spatial scales, namely region, water basin, waterbody, and observation point, enables us to disentangle scale-related variation of aquatic ecosystem health over a multi-decadal time frame and add to the understanding of spatial and temporal dependencies among bioindicators.

2. Material and methods

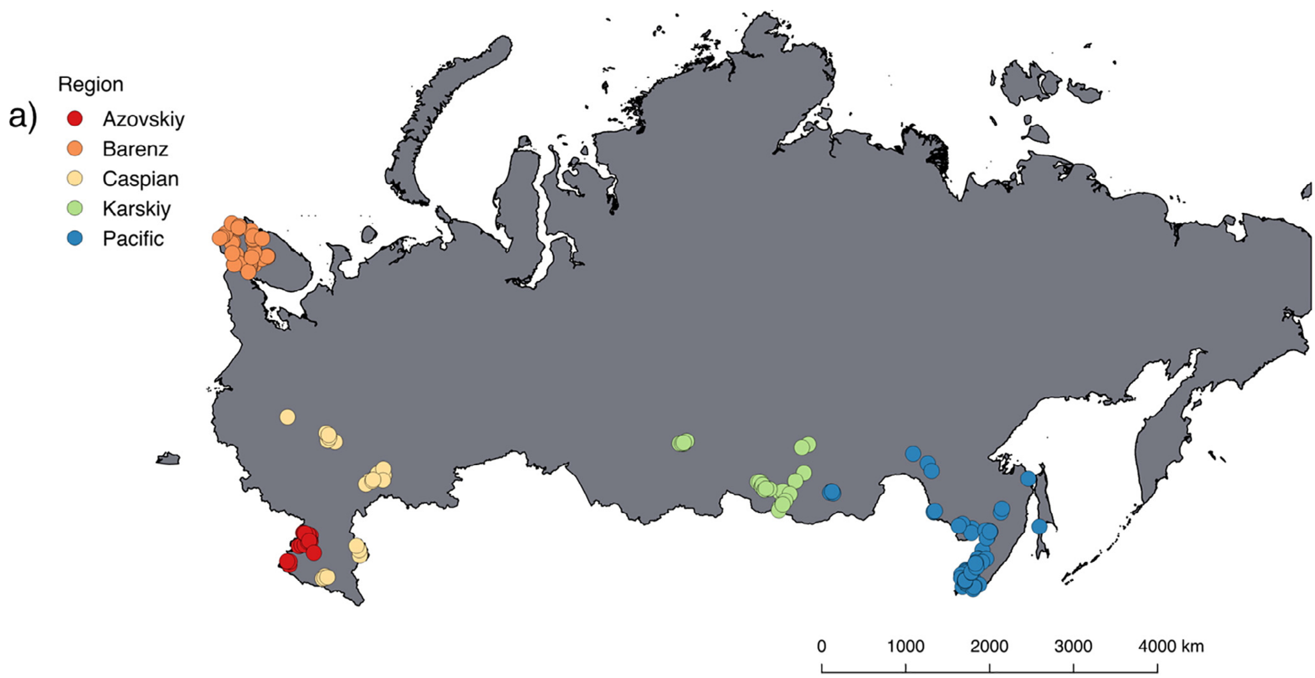
2.1. Sampling scheme

The data sampling scheme followed a hierarchical structure. The largest spatial unit represents the hydrological region, classified as (1) the Azovskiy Sea basin (hereafter Azovskiy region), (2) the White and Barenz Sea basin (hereafter Barenz region), (3) the Caspian Sea basin (hereafter Caspian region), (4) the Karskiy Sea basin (hereafter Karskiy region), (5) the Pacific Ocean basin (hereafter Pacific region) (Fig. 1a). Each hydrological region includes several river basins with each basin containing several waterbodies (e.g. river or lake) (Fig. 1b). From each waterbody, samples were obtained from one or more observation points (Fig. 1b).

All data were obtained from the Russian surface water quality monitoring network of the Russian Federation (until 1991 of the USSR). The national network of surface water monitoring of the Federal Service for Hydrometeorology and Environmental Monitoring of Russia (Roshydromet) carries out annual observations of surface water quality and the status of aquatic ecosystems on bioindicators from 1974 to the present (Buyvolov et al., 2016). Scientific and methodological support as well as control and data quality assurance is provided by the Institute of Global Climate and Ecology of Roshydromet and the Russian Academy of Sciences. The annual report of surface water ecosystems of Russia and their status is presented on the website of the Institute (Khromov, 2016).

In each sampling location, we utilize data on four bioindicator groups, namely phytoplankton, zooplankton, periphyton and zoobenthos. Phytoplankton and zooplankton were collected by water and net sampling respectively, while periphyton and zoobenthos were collected by scrape and grab samples. The sampling methods follow the techniques in Rukovodstvo po gidrobiologicheskomu monitoring presnovodnykh ehkosistem (1992). Each of the bioindicators is derived from community data of the respective group. Out of these, the Trent Index (Biotic Index) (Woodiwiss, 1964) was calculated for zoobenthos, and it correlates positively with water quality. The Saprobic Index (Sládeček, 1973) was used for the remaining three groups, and it correlates negatively with water quality.

Several measurements (typically 1–6) were taken from each sampling location (observation point) each year. Out of these, the minimum and maximum values of the bioindicators were stored. The sampling interval for the sites depended on the grade of pollution. Areas with very little pollution, located far away from urban centres, were mainly sampled only once per year. In this case, the sampling was conducted during the vegetation peak in the summer, and thus the measured indices were registered as maximum values, the minimal values being considered as missing. For areas known to be affected by pollution, and located close to industrial centres, the sampling interval was at least



b)

Region	Basins	Waterbodies	Observation points	Number of observations
Azovskiy	2	10	22	371
Barenz	9	33	48	888
Caspian	2	20	29	626
Karskiy	3	20	35	969
Pacific	7	40	64	1365
Total	23	123	198	4219

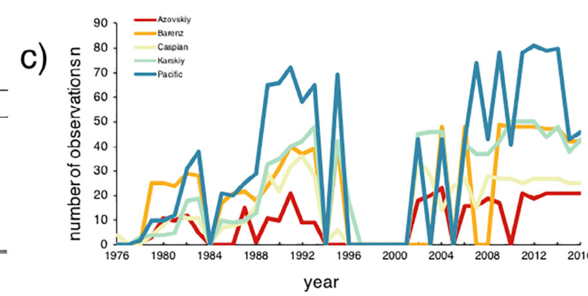


Fig. 1. a) Study region and geographic distribution of sampling in Russia. Shown are colour coded observation points grouped into five hydrological regions: Azovskiy (red), Barenz (orange), Caspian (yellow), Karskiy (green), and Pacific (blue). b) Number of basins, waterbodies, observations points and observations included in each of the five regions. c) Variation in the number of observations included in the analysis for each region over the years.

every two months. The minimum values, if recorded, show how much water quality indices improve (or deteriorate for zoobenthos) during the transition seasons, when community change slows down. The differences between the maximum and minimum values of bioindicators show the contrast of the conditions for the formation and maintenance of communities and, as a rule, are associated with the seasonal conditions and the level of varying water pollution. Unfortunately, it was not possible to reconstruct the number of samples taken behind each minimal or maximal value.

To reduce the unevenness of data availability over space and time as well as between the bioindicators, we included only those observation points, which have been sampled both before and after the year 2000, ensuring the robustness of our analysis. The total number of selected data points was n = 4219 (Fig. 1b, c). Overall, 92% of these data originates from rivers or streams and 8% from lakes. The number of biological parameters recorded varied among the bioindicators. The proportion of data points that include the measurement is 58% for *phytoplankton min*, 72% for *phytoplankton max*, 55% for *zooplankton min*, 67% for *zooplankton max*, 19% for *periphyton min*, 24% for *periphyton max*, 48% for *zoobenthos min* and 78% for *zoobenthos max*.

2.2. Statistical analyses

We analysed the data with Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017), an approach that belongs to the class of joint species distribution models (JSDM; Warton et al., 2015). As fixed factors we included (1) the five hydrological regions, (2) the interactions between the regions and the linear effect of the year, (3) the population sum (CIESIN and CIAT, 2005) within a 5 km radius around the observation point, serving as proxy for human impact, and (4) a classification of the study sites to lakes and rivers. As community-level random effects, we included the basin, the waterbody, the observation point, and the interaction effect of the respective random terms with year. Prior to the analysis, we standardized the value of each index to zero mean and unit variance over all data. As a response variable, we used the vector of the eight standardized bioindicator values, i.e. the min and max values for each of the four bioindicators. We assumed that the error variance was normally distributed. To explore the predictive power of the model, we performed a two-fold cross validation. We followed Ovaskainen et al. (2017) to partition the explained variation among the fixed and random effects. Further following Ovaskainen et al. (2017), we examined patterns of co-variation among the response of bioindicators at the levels where the random effects were set, i.e. river basin, waterbody, observation point, and their respective interaction with year.

3. Results

3.1. Variance partitioning

Averaged over the eight bioindicators, the explanatory power of the model was 0.93 and the cross-validation – based predictive power was

Table 1
Explanatory and predictive powers of the fitted joint species distribution models. Both explanatory and predictive power was measured by the R^2 of the linear mixed model, explanatory power being based on the model fitted to all data and predictive power by the two-fold cross-validation. The codes for the bioindicators, each sub-divided in min and max values, are F (phytoplankton), Z (zooplankton), P (periphyton) and B (zoobenthos).

Bioindicator	Explanatory power	Predictive power
F (min)	0.91	0.79
F (max)	0.89	0.80
Z (min)	0.96	0.78
Z (max)	0.93	0.80
P (min)	0.95	0.83
P (max)	0.92	0.82
B (min)	0.92	0.75
B (max)	0.94	0.77

0.79 (Table 1). While the difference between these two suggests that the complexity (in terms of the inclusion of several hierarchical levels) of the model resulted to some level of overfitting, the model had a high power to predict also independent data, suggesting a high signal in the data and robustness of the analyses. The proportion of variance within each bioindicator group (including responses of minimum and maximum values) was similar but differed markedly between groups (phytoplankton, zooplankton, periphyton, zoobenthos). Out of the explained variance, variation attributed to region was 20% (on average over the eight bioindicators) with highest importance for the zoobenthos bioindicator (Fig. 2). The human population density in the vicinity of the sampling site accounted on average for 5.6% of the explained variance and had the highest impact on periphyton. Among the random effects, the observation point was most important, accounting on average for 36% of the explained variance and being most pronounced for the planktonic bioindicators (Fig. 2). Thus, the dominating part of the permanent spatial variation among the bioindicators was expressed at the largest and smallest hierarchical spatial scales of hydrological region and observation point respectively (Fig. 2). While most variation at these levels was spatial rather than spatio-temporal, much of the variation at the intermediate scales of basin and waterbody was of spatio-temporal nature (Fig. 2). In particular, spatio-temporal variation at the basin level explained 11% of the variation, and thus almost four times as much as the permanent spatial effect at the basin level (2.9%).

3.2. Model-fitted temporal trends of bioindicators

We observed several region- and bioindicator-specific trends with a high level of statistical support (Fig. 3, Table 2), generally suggesting decreasing water quality in the Caspian, Karskiy and Pacific regions, as indicated by trends in phytoplankton, periphyton and zoobenthos. The minimal and maximal values of each bioindicator followed typically the same trends within each region, suggesting the robustness of our results. Interestingly, the phytoplankton and zooplankton bioindicators showed however opposing trends for the long-term changes in water quality at the level of region (Table 2, Fig. 3).

3.3. Scale related co-variation among bioindicators

At the level of observation point, we observed positive associations among those bioindicators for which the values increase with decreasing water quality (Fig. 4a; phytoplankton, zooplankton and periphyton). Further, these three bioindicators showed negative associations with zoobenthos (Fig. 4a), for which the values increase with increasing water quality. Thus, at the level of observation point, all bioindicators yielded consistent results on water quality. However, at the higher spatial scales of waterbody and basin, the clear directional associations among the bioindicators vanished (Fig. 4b, c). All bioindicators yielded a consistent assessment of water quality at the level of observation point also regarding spatio-temporal variation, although not with 95% statistical support for all pairs of bioindicators (Fig. 4d). At the higher spatial scales of waterbody and basin, the spatio-temporal associations among the bioindicators became more complex (Fig. 4e, f). Interestingly, we found zooplankton and phytoplankton co-vary negatively spatio-temporally not only at the region-level (Tab. 2, Fig. 3) but also the basin level (Fig. 4f), thus yielding contrasting assessments of variation in water quality. Hence, our results showed differing patterns of covariation among the bioindicators depending on the spatio-temporal scale examined.

4. Discussion

Biomonitors respond to multiple pressures ranging from local point source impacts to larger scale regional effects, reflecting the environmental conditions they are exposed to. Different species groups being used as bioindicators are capable of mirroring different ecosystem pressures, such as organic enrichments through eutrophication processes or chemical pollution, and may respond at a different pace to pressures depending on their life-history and longevity (Niemi and McDonald, 2004). Hence, considering the abilities of the selected bioindicators for detecting ecosystem change is important when planning or conducting bio-monitoring programs. Here we have taken the advantage of a long-term and large-scale monitoring program involving multiple trophic groups to examine how bioindicators with different characteristics respond to environmental stress at different spatio-

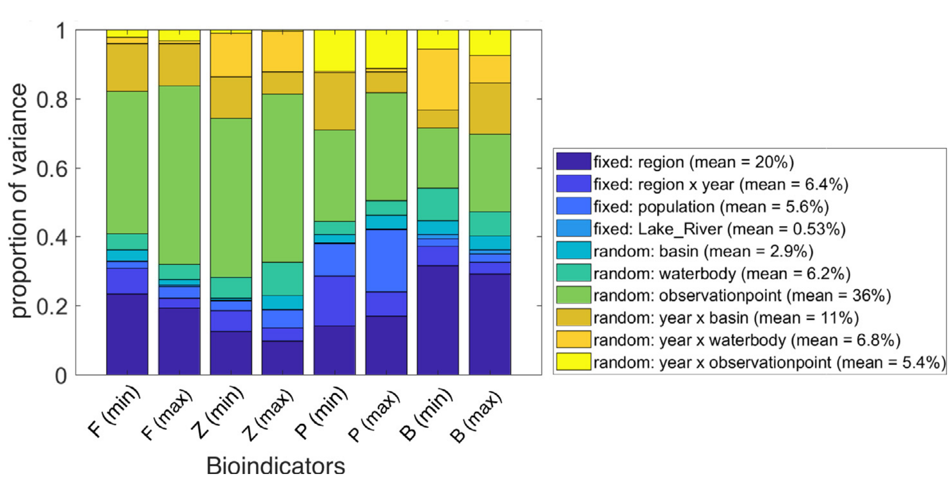


Fig. 2. Results on variance partitioning. Variation in bioindicator values is partitioned into responses to fixed and random effects. Fixed effects include region, region x year, human population density, and differentiation between lake and river. Random effects include the spatial scales of basin, waterbody and observation point, as well as the interaction of the respective spatial scales with year. The bar-plot shows bioindicator-specific results whereas the legend shows averages over all bioindicators. The codes for the bioindicators, each sub-divided in min and max values, are F (phytoplankton), Z (zooplankton), P (periphyton) and B (zoobenthos).

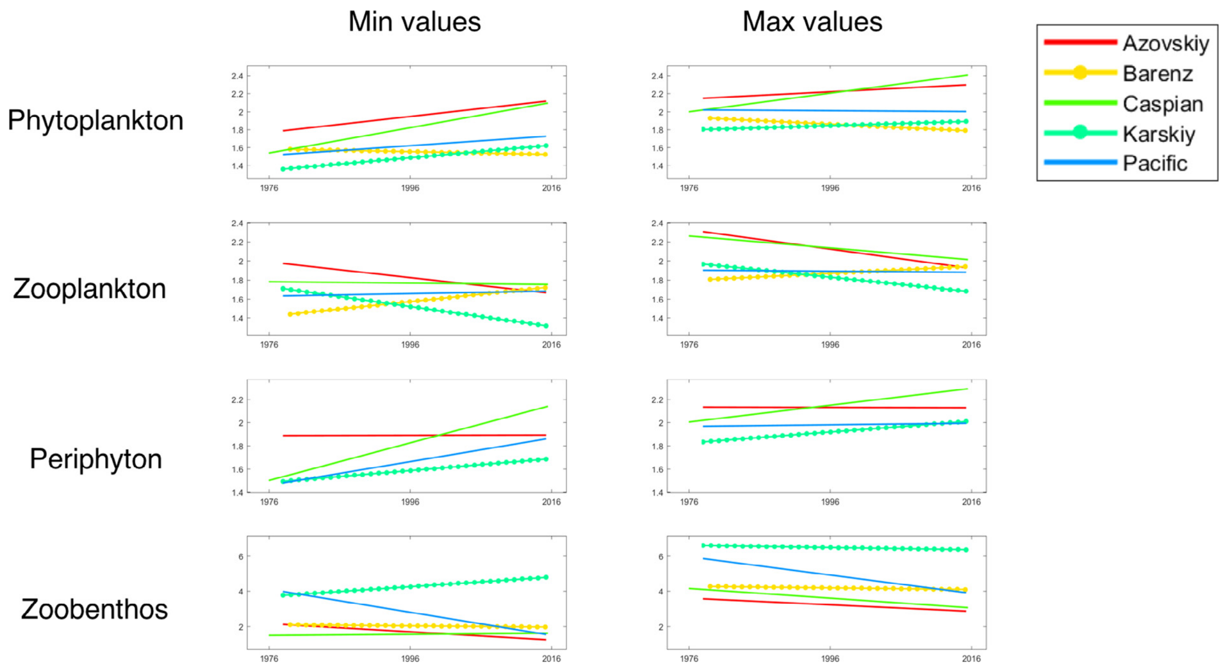


Fig. 3. Model-fitted trends observed in the four bioindicators including their subdivision in min and max values in the five study regions. The lines show the posterior mean predictions, different line types corresponding to different regions. The spans of time covered by the lines vary slightly according to the availability of data from each region. Note that an increase in bioindicator values for phytoplankton, zooplankton and periphyton corresponds to poorer water quality, following the Saprobic index, while an increase in values for zoobenthos corresponds to better water quality, following the Trent index.

Table 2
Trends observed in different bioindicators in different study regions. Cases shown by 1 correspond to such increasing trend and -1 to such decreasing trends for which the level of statistical support was at least 95% posterior probability. Colours highlight the decrease and increase in water quality to associated bioindicator, with red indicating deterioration of the bioindicator and green indicating improvement. The trends are illustrated in Fig. 3. The codes for the bioindicators, each sub-divided in min and max values, are F (phytoplankton), Z (zooplankton), P (periphyton) and B (zoobenthos).

Bioindicator	Azovskiy	Barenz	Caspian	Karskiy	Pacific
F (min)	1	0	1	1	1
F (max)	0	-1	1	0	0
Z (min)	-1	1	0	-1	0
Z (max)	-1	1	-1	-1	0
P (min)	0	no data	1	1	1
P (max)	0	no data	1	1	0
B (min)	0	0	0	1	-1
B (max)	0	0	-1	0	-1

temporal scales.

The results from our variance partitioning reflect the expectation that the efficiency of bioindicators may vary among spatial scales (Stemberger et al., 2001). We found the pelagic bioindicators (phytoplankton and zooplankton) to display high explained variance at the level of observation point, suggesting that they are best in reflecting local conditions. However, in moving waters such as rivers and streams, plankton bioindicators may also be indicative of conditions upstream, and may therefore also reflect geographically broader scale conditions (Stevenson et al., 2010). Our spatio-temporal results are in line with this expectation, especially for phytoplankton at the regional level (Fig. 2). For the benthic bioindicators (periphyton and zoobenthos), we found substantial spatial and spatio-temporal variation at larger spatial scales, which can be attributed to their longevity and the accumulative effects of environmental conditions over multiple years compared to short-term local conditions. The effect of region was greatest for zoobenthos, reflecting large-scale processes such as climatic drivers or increasing organic matter through nutrient inputs from entire drainage basins.

The consistency in the direction of change among the minimum and maximum values of each bioindicator (Fig. 3, Table 2), as well as their similar explanatory power (Table 1) and partitioned variance (Fig. 2) supports the robustness of our results. Furthermore, considering trends of minimum and maximum values separately provides more detailed information about the changes at the respective ends of the water quality spectrum. This helps to distinguish the deterioration or improvement at the lower and upper limits of the recorded water quality. Minimum values significantly increasing for a Saprobic Index group, as shown for phytoplankton in Table 2, suggest that the baseline of the relatively highest water quality (min) is overall shifting to relatively poorer water quality conditions. If an increase in minimum values coincides with a simultaneous significant increase in maximum values, it implies a general shift to deteriorating water quality at both ends. However, with a non-significant increase in maximum values, as given for phytoplankton in the Azovskiy, Karskiy and Pacific region (Table 2), the results indicate that the shift towards poorer water quality is stronger at the preferable water quality end and can be associated with a deteriorating baseline, where seasonal recovery and improving conditions become worst. Despite some maximum values not showing significantly increasing trends over time, the direction of change remained the same as in the minimum values (Fig. 3, Table 2) supporting our results.

Our study illustrates that Russian freshwater systems follow a mostly declining trend in water quality over the past four decades (Fig. 3, Table 2). Particularly the long-term responses of the autotrophic bioindicators, phytoplankton and periphyton, suggest increasing impacts of eutrophication. These primary producers are directly affected by nutrient concentrations in the waters pushing the community

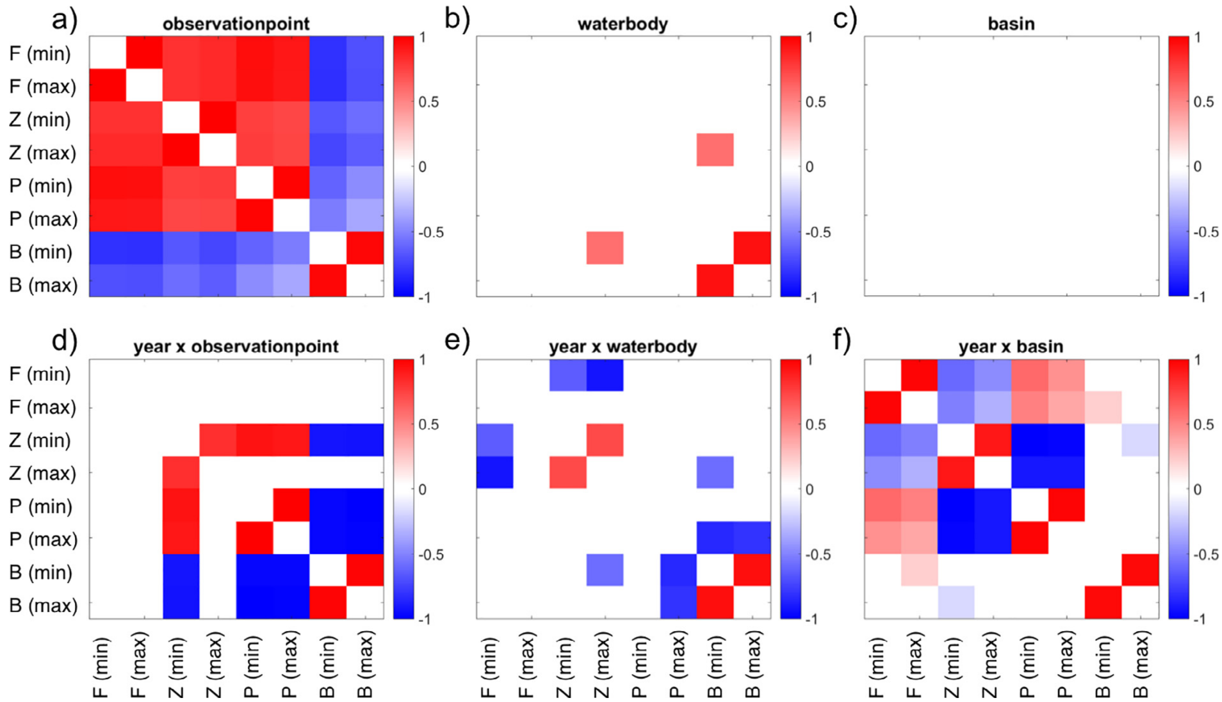


Fig. 4. Residual association plots among the bioindicators at different spatial and spatio-temporal scales. The upper panels (abc) show the permanent spatial associations and the lower panels (def) the spatio-temporal associations at the levels of ad) observations points, be) waterbody and cf) basin. Pairs of bioindicators illustrated by red and blue colour show positive and negative associations, respectively, with statistical support of at least 95% posterior probability. The codes for the bioindicators, each sub-divided in min and max values, are F (phytoplankton), Z (zooplankton), P (periphyton) and B (zoobenthos). Note that an increase in bioindicator values for F, Z and P corresponds to poorer water quality, following the Saprobic index, while an increase in values for B corresponds to better water quality, following the Trent index.

composition towards fast growing, short lived generalists. However, these results are region-specific, the declining trend of water quality being particularly clear for the Caspian and Karskiy regions but also evident for the Pacific and Azovsky regions. Periphyton is not only reflecting the direct effects of eutrophication by filamentous epibionts and fast-growing short-lived algae for example, but also secondary effects of shading when there is a strong increase in phytoplankton production, lowering the euphotic depth and with that autotrophic processes. Most of the measurements in the Azovsky, Karskiy and Caspian region were carried out at the respective major water bodies (e.g. the Yenisei (with the Angara), the Don, the Kuban and the Volga Rivers), as well as in their tributaries. These rivers have a common feature, namely they have all been regulated for water management purposes and largely transformed into cascades of reservoirs during the period of 1951–1970 (UNEP, 1999). In artificially modified rivers where cascades of reservoirs have been created, the stagnant lake-like water in this area favours deposition of minerals and organic matter and contributes to fast warming of the surface water layer. These factors lead to higher primary production compared to unmanaged rivers with natural flow regimes (Kimstach et al., 1998, Mineeva et al., 2008), a phenomenon that has also been observed in other geographical systems (Chapman, 1992). In the Barenz region, where the major rivers are free of reservoirs, we observed an opposite pattern from the other regions, with a negative trend of saprobic phytoplankton max values and increasing zooplankton values (Table 2).

Our results demonstrate a clear unidirectional relationship between bioindicators of different trophic levels for water quality assessments at the local level of observation point. This finding supports the relevance of their application in monitoring anthropogenic impact, as all bioindicators follow the same trend of the quality assumptions of their respective index (i.e. increasing phytoplankton, zooplankton and periphyton values of the Saprobic index along with decreasing zoobenthos values of the Trent index) (Fig. 4a), pointing toward decreasing water quality (Woodiwiss, 1964; Sládeček, 1973). Although all bioindicators provide uniform responses on local water quality, we found their covariation becomes more complex over larger geographic scales. This could be explained by varying magnitudes and directions of change at larger scales and in particular over time, considering changing hydrographic conditions as well as different extents of anthropogenic pressures in sub-regions.

An especially intriguing finding is the opposing trend of phytoplankton and zooplankton as bioindicators over time, apparent in all but the Pacific region where zooplankton did not display any substantial change (Table 2), and at the spatio-temporal random effect at the level of the basin (Fig. 4). One reason for the negative relationship between zooplankton and phytoplankton over time could be because of the strong coupling in their trophic relationship (McCauley and Kalff, 1981): With increasing saprobic values for phytoplankton, indicating higher production of generalists and lower water quality, zooplankton values decrease, hinting water quality improvement. This suggests a possible enhanced suitability and availability of phytoplankton as a food resource for zooplankton, leading to its improvement despite the lower water quality indicated by phytoplankton. A second reason for the negative relationship between zooplankton and phytoplankton over time might be that they react to environmental perturbations at different time scales, with photoautotrophic phytoplankton responding quickly to pressures such as nutrient inputs, while other bioindicators having delayed effects. Thus, simultaneous sampling of all bioindicators may lead to a mismatch in capturing the current water quality signal if conditions are continuously changing. Jeppesen et al. (2011) provided a well-defined argument for the usefulness of zooplankton as bioindicator in lakes. However, our results suggest that the relatively simple measure of the saprobic index of the zooplankton community may not necessarily reflect the general elements of water quality over large spatial scales in rivers. The central role of zooplankton in aquatic food webs and the tight link to lower and higher trophic levels can lead to cases where zooplankton is able to mask poor water quality values through strong top-down control (García-Chicote et al., 2018).

While multimetric bioindicator indices are widely applied and valuable tools for classifying degraded areas from those of good ecological status (Parmar et al., 2016), they alone cannot identify the pressures that have led to the deterioration of water quality (Fore, 2003). Our results provide support for the earlier suggestions that different bioindicator groups differ in the spatio-temporal scales at which they indicate the ecological status of a system (Dale and Beyeler, 2001), and thus, the use of a single bioindicator can lead to an oversimplified assessment of water quality. Considering the information on sensitivity to spatial and temporal scales of the four major aquatic bioindicator groups we included in this study can contribute to successful aquatic ecosystem assessments in the future.

5. Data accessibility statement

The data are provided in the Supporting Information. The spatial and environmental covariates are provided in the file covariates.csv and the bioindicator data in the file bioindicators.csv.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2018.11.027.

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