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Which Fish Benefit from the Combined Influence of Eutrophication and Warming in the Dnipro River (Ukraine)?

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Abstract: The effects of climate warming and eutrophication on aquatic organisms are well established, but we lack a deep understanding of the selective mechanisms of fish communities towards eutrophication and warming in tandem. The aim of the study was to identify fish traits that were positively related to eutrophication and ongoing warming. The research was conducted for 19 years in the Dnipro River channel and floodplain water system of the "Dnipro-Orylskiy" Nature Reserve. Both categorical and continuous fish traits were considered. The study area is characterized by a more intense warming trend than the average for Europe, which reflects an increase in the maximum summer air temperature. At the same time, the concentration of chlorophyll-a had a monotonic tendency to decrease during the study period. Phytophilic, limnophilic, and freshwater fish species are increasing in abundance, while rheophilic and lithophilic fish are decreasing due to global warming. Fish species with greater vulnerability and resilience have selective advantages in terms of global warming. Pelagic fish species are the most resistant to eutrophication, while benthopelagic and phytolithophilic fish species are the most sensitive. Brackish-water demersal self-settled species of marine origin have a competitive advantage over other native freshwater species in the face of increasing symptoms of eutrophication and a warming climate.

Keywords: fish; community; traits; Dnipro; eutrophication; global warming

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Citation: Zymaroieva, A.; Bondarev, D.; Kunakh, O.; Svenning, J.-C.; Zhukov, O. Which Fish Benefit from the Combined Influence of Eutrophication and Warming in the Dnipro River (Ukraine)? *Fishes* **2023**, *8*, 14. https://doi.org/10.3390/fishes8010014

Academic Editor: Manuel Otilio Nevárez Martínez

Received: 18 November 2022
Revised: 18 December 2022
Accepted: 22 December 2022
Published: 26 December 2022

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1. Introduction

Eutrophication has affected most of the world's freshwater ecosystems to varying degrees [1–4] and is usually caused by an increasing amount of nutrients entering aquatic ecosystems from urban and industrial wastewater, erosion runoff, and leaching from agricultural areas [5]. Since eutrophication increases primary production and alters the distribution, taxonomic diversity, and relative abundance of primary producers in the aquatic environment, it influences the composition and location of resources, the flow of energy, and biomass throughout the food webs [6,7]. Such ecological changes influence populations of freshwater biota, and particularly fish. Eutrophication can lead to undesirable shifts in the composition of fish communities [8].

Severe environmental stresses such as climate change are also altering key ecological mechanisms that determine the abundance and distribution of freshwater fish communities around the world [9–11]. The warming climate is causing complex changes in the

structure of fish communities through direct and indirect effects on fish metabolism, biotic interactions, and geographic distribution [12]. Global warming causes the spread of several species, including invasive species that may compete with local or native species for space and food in newly colonized ecosystems. Thus, with the warming of water in lakes, the number of strictly herbivorous fish in fish communities decreases, but the number of omnivorous fish increases [13]. Another consequence of climate change is the increased frequency and severity of extreme heat waves in the last decade, which have caused massive fish kills [2,12,14,15]. Often, heat waves are accompanied by violent algae blooms, which increase the negative effect on aquatic organisms [2,16].

The effects of climate change or eutrophication on freshwater biota are difficult to separate because of the simultaneous effects and their interdependence. Thus, eutrophication symptoms in freshwaters are becoming more severe due to climate change, which in turn creates conditions that increase the nutrient load in aquatic ecosystems and enable fast algal blooms [2,17–20]. On the other hand, recent research implies that eutrophication itself may facilitate climate change by decreasing seagrass beds' capacity to store carbon [2,21] and releasing methane and nitrous oxide into the atmosphere [3,22]. The negative effects of climate change and eutrophication on fish communities and the positive feedback loop between these threats are compelling, but how fish respond to the combined effects of these threats remains less clear.

The Dnipro is the third largest river in Europe and covers 48% of the territory of Ukraine. Accelerated eutrophication from municipal and agricultural discharges, industrial pollution, and radionuclide contamination of reservoir bottom sediments are the most important causes of the Dnipro River biota transformation. The Dnipro-Zaporizhzhya-Kryvyi Rih triangle was recognized as a territory heavily affected by pollutants generated by many activities, including heavy industry, oil refining, metallurgy, petrochemistry, mining, and energy [23]. Nutrient input into the Dnipro River increased by approximately ten times from the 1960s until the 1990s as fertilizer usage was drastically extended in the agricultural sector [24,25]. In the 1970s, the Dnipro suffered from particularly severe eutrophication compared to other freshwater bodies of the USSR due to the strong cyanophyte blooms that occurred in the Dnipro reservoirs [26]. The main reasons for the ecosystem transformation of the Dnipro River are the construction of a dam system and regulation of water flow, eutrophication, recreation, and overfishing. These processes began to develop in different periods, but at present, their impacts are interrelated. The creation of the Dnipro-Orylskiy Reserve made it possible to minimize the negative impact of recreation and fishing. Therefore, the evaluation of the temporary dynamics of fish communities within the Dnipro-Orylskiy Reserve provides an opportunity to find out the nature of the impacts of flow regulation, climate change, and eutrophication.

Functional traits of organisms are used for developing models to predict the response of ecological communities to abiotic and biotic perturbations [27,28]. The understanding and prediction of ecological processes based on species traits are believed to be the "Holy Grail" in ecology [29]. Fish traits related to growth, maturation, and longevity respond most strongly to the environment. The traits vary with temperature at large spatial scales and with depth and seasonality at more local scales [30]. The relationship between eutrophication and fish traits has only been studied in a few studies, mostly in lakes, with contrasting results [31]. There have been no studies of the combined effect of climate and eutrophication on fish trait variations in the highly anthropogenically transformed Dnipro River.

The study material was juvenile fish caught from 1998 to 2015 in the Dnipro River channel and floodplain water system within the territory of the "Dnipro-Orylskiy" Nature Reserve. The research with juveniles is reasonable because the response of young fish communities to environmental changes is relatively fast, both in the case of negative and positive impacts [32–34]. Larval and juvenile phases of fish development are more sensitive to abiotic conditions and are indicators of spawning success and efficiency [35]. The species composition of adult fish communities is similar to that of juveniles [36]. The ecological

monitoring of young fish can be especially useful in large and medium-sized rivers, where the representative sampling of adult fish is almost impossible [37]. Many fish species aged over one year migrate to deeper parts of rivers, but their young fish concentrate in shallow waters [38–40], where they can easily be collected, regardless of the size of the river. In large rivers, young fish are easier to sample than adults, so the actual structure of fish communities in certain places is assumed to be better estimated by sampling young fish [41]. The unified method of accounting and the strategy of monitoring young fish populations can be applied to the whole river with the same catch efficiency, but this is impossible for older fish [42].

So, in this study, we aim to find out which fish traits are positively related to eutrophication and ongoing climate change. We hypothesize that in heavily regulated aquatic ecosystems of the Dnipro River, climate change and eutrophication have affected fish community structure, life history, feeding habits, reproduction, migration, and other attributes, resulting in significant changes in ecosystem functioning.

2. Materials and Methods

2.1. Study Sites

The research was conducted in the waters of the "Dnipro-Orylskiy" Nature Reserve (Figure 1). The Reserve was created in 1990. The area is 3766 hectares, of which the water bodies are 203 hectares [43]. Intensive changes in the relief on the territory of the "Dnipro-Orylskiy" Nature Reserve occurred after the construction of the Dnipro Hydroelectric Station dam in 1932. This led to an increase in the water level of the study territory by 1.5–2 m, which corresponds to an average level of 49.7 m above sea level. During the Second World War, the dam was destroyed (1941), which returned the water level to its previous state. After the dam was rebuilt in 1950, the water level rose again. After the start of the second Dnipro Hydroelectric Station block in the 1960s and the construction of the Dniprodzerzhinsk (Kamianske) Hydroelectric Power Plant, the water level was raised even more—to 51.4 m above sea level. Thus, after the construction of the Dnipro reservoir cascade, the total Dnipro level rise in the "Dnipro-Orylskiy" Nature Reserve area, compared to its natural level, was 3.0–3.5 m, which led to the inundation of part of the floodplain, changes in the configuration of banks and the area of water bodies. The studied water bodies are the Dnipro riverbed and floodplain water system.

The biotopes studied can be grouped into five groups.

Water reservoirs of the Mykolaevka ledge system. The system of floodplain ponds is located in the narrowest part of the floodplain terrace. The ponds extend a narrow strip along the channel of the Dnipro. The maximum distance of water bodies from the Dnipro riverbed within the Reserve is about 300–1000 m. Water bodies are characterized by significant levels of flow and water level differences during the day, which depends on the conditions of the reservoir operation. Part of the water bodies that are connected to the specified area by separate streams is outside the Reserve. The area of shallow water areas (littoral zone) is minimal due to steep banks, which are typical for the reservoirs in this area. Maximum depths are 5–6 m. In recent years, the reservoirs in the central part of this section have begun to be actively silted and overlapped by sandy sediments due to the accumulation of excessive bottom deposits caused by disturbance of the reservoir water regime. Samples were taken from five sites. The macrophyte community is represented by 30 species, dominated by *Myriophyllum spicatum* L., *Nuphar lutea* (L.) Smith, *Phragmites australis* (Cav.) Trin.ex Steud., *Trapa borysthenica* V. Vassil., *Typha angustifolia* L., and *Ceratophyllum demersum* L. Such plant species as *Veronica anagallis-aquatica* L., *Alisma plantago-aquatica* L., and *Bolboschoenus maritimus* (L.) Palla were found exclusively in this group of water bodies.

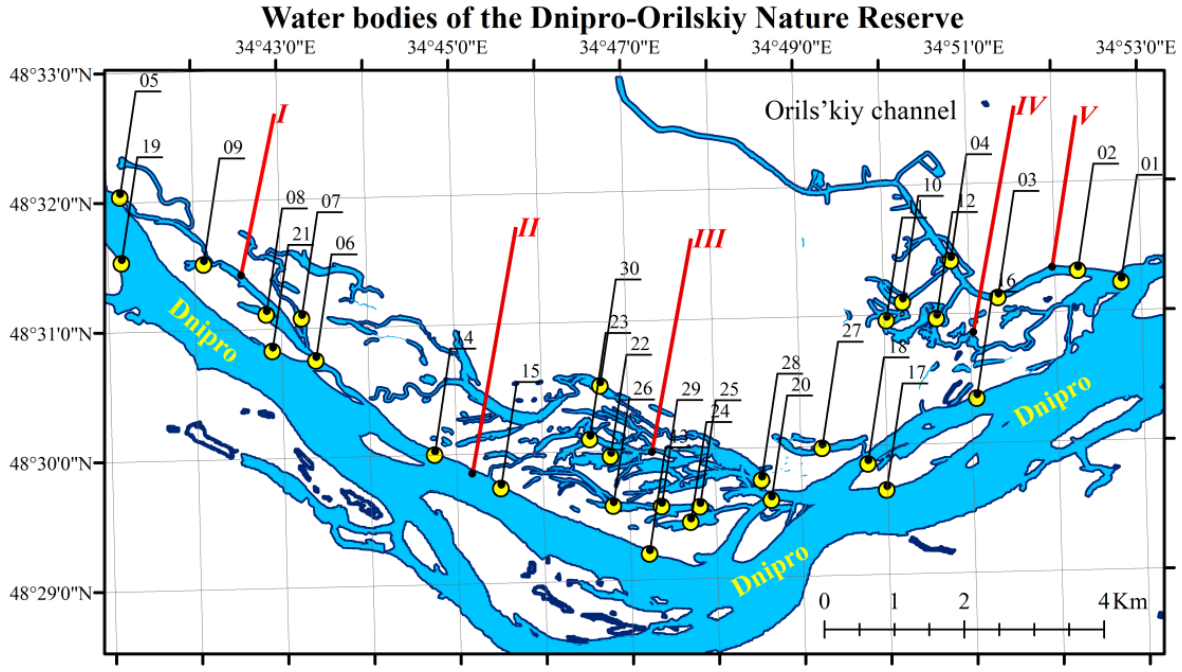


Figure 1. Main groups of water bodies and the location of fish sampling points. I is the Mykolaevka ledge system: 5—Upper duct, 6—Lower duct, 7—Lake Ostupus, 8—Rybachiy Bay, left spur, 9—Rybachiy Bay; II is the Dnipro River channel part: 13—Near the Korchevatka flow path, 14—Near the Oak Grove, 15—Near the guard station, 16—Near the flow into Lake Solone, 17—Kamyanisty Island from the side of the main channel, 18—Kamyanisty Island from the side of the secondary channel, 19—Korchuvaty Island, 20—Kryachny Island, 21—Near the mouth of the Konoplyanka river; III is the Taromske ledge system: 22—Lake Humutzi, 23—Lake Lytvynove, 24—Lake Lopata, 25—Mala Hatka Lake, 26—Gorbove Lake, 27—Lake Solone, 28—Lake Somivka, 29—Lake Richische, 30—Lake Sokylki; IV is the Obukhiv floodplain system: 10—Lake Kovbasyane, 11—Near Yalowske Island, 12—Yalowske Lake; V is the mouth of the Oril River: 1—Obukhivsky Island, 2—Left bank of the Orill River, 3—Right bank of the Orill River, 4—Near the entrance to Lake Kovbasiane.

Water area of the Dnipro River channel part. The group of biotopes includes part of the upper section of the Dnipro Reservoir, where the river flow regime is partially retained. The water regime is characterized by a significant level of flow and movement of sand masses, which is associated with active channel processes in this part of the reservoir. Depths fluctuate within 2–7 m. Samples were collected from nine sites. The macrophyte community is represented by 32 species, dominated by *Myriophyllum spicatum* L., *Phragmites australis* (Cav.) Trin.ex Steud., *Potamogeton crispus* L., *Typha angustifolia* L., and *Nuphar lutea* (L.) Smith. No unique macrophyte species were found for this group of water bodies.

Water bodies of the Taromske ledge system. The system of floodplain ponds is located in the low part of the floodplain terrace. All lakes are separated from the Dnipro riverbed by a sand wall. The lakes are connected to each other and to the channel of the Dnipro by numerous waterways. Most lakes have a significant littoral zone that is actively overgrown with aquatic macrophytes. Depths fluctuate between 1–10 m. Water is exchanged through the operation of the reservoir and spring floods. The maximum distance of individual ponds from the Dnipro riverbed is about two kilometers. Currently, due to the unbalanced functioning of the reservoir, the water bodies in this area are actively swamped and silted. In some areas, the thickness of silt sediments reaches 0.3–0.7 m. Samples were collected from nine sites. The macrophyte community is represented by 56 species, dominated by *Phragmites australis* (Cav.) Trin.ex Steud., *Typha angustifolia* L., *Ceratophyllum demersum* L., *Stratiotes aloides* L., *Lemna trisulca* L., *Trapa borysthenica* V. Vassil. Plants like *Cyperus flavescens* Reichenb and *Sparganium erectum* L. were only found in this group of water bodies.

Water bodies of the Obukhiv floodplain system. Most of them are weakly flowing, shallow water bodies, being the remnants of the lower part of the channel of the Dnipro River, which connected the Dnipro with the floodplain system of the Oril River. They were flooded as a result of the reservoir's formation. They function under the significant influence of the reservoir water regime. They are characterized by significant sedimentation (in some areas, silt thickness reaches 0.6–1.0 m) and an overgrowth of aquatic macrophytes. They are connected to the Dnipro River and the mouth of the Oril River by narrow channels. The largest distance to the Dnipro River within this section is about 2 km. Samples were collected at three sites. The macrophyte community is represented by 56 species, dominated by *Phragmites australis* (Cav.) Trin.ex Steud., *Ceratophyllum demersum* L., *Typha angustifolia* L., *Lemna trisulca* L., *Ceratophyllum submersum* L., and *Sium latifolium* L. Such plant species as *Caltha palustris* L., *Galium palustre* L., and *Solanum dulcamara* L. were found exclusively in this group of water bodies.

The mouth of the Oril River. The estuary section of the Orel River was artificially created in the early 1960s of the 20th century by diverting the natural channel of the Orel River into the Dnipro (Zaporozhye) reservoir. This need arose during the large-scale hydro construction and creation of a cascade of reservoirs on the Dnipro River. The main purpose of this activity was to preserve the ways of natural spawning migration and sustainable fish reproduction in the water area of the upper section of the Dnipro (Zaporozhye) reservoir. For the most part, this artificial canal was laid along the remnants of the Prototch River system, which had a narrow strip of water flowing in the opposite direction along the Dnipro River from Obukhovka village. The functioning of the hydrological regime of the reservoir largely depends on the daily regulation of the water level in the reservoir. This is especially true during the summer when the almost daily reverse flow is observed as the reservoir's water level drops. In the spring period, the natural flow of the Oril is expressed to a much greater extent, and the impact of the reservoir is reduced. The site is characterized by a limited area of coastal biotopes, which is explained by its artificial origin. The water reservoir is in close contact with the water area of the Obukhovskaya floodplain. The longest distance from the Dnipro riverbed is about 2 km. The total length of the site within the Reserve does not exceed 5 km. Obukhovka village and a significant number of recreation centers are located on the left bank of the Oril, which considerably increases the anthropogenic load on the water area of this area. Maximum depths reach 8-10 m (exactly near the inflow point). In higher water areas, the depth does not exceed 4 m. Samples were collected from four sites. The macrophyte community is represented by 25 species, dominated by *Myriophyllum spicatum* L., *Vallisneria spiralis* L., *Potamogeton perfoliatus* L., *Phragmites australis* (Cav.) Trin.ex Steud., *Potamogeton crispus* L., and *Elodea canadensis* Michx. No unique macrophyte species were found for this group of water bodies.

2.2. Fish Sampling

Ichthyological sampling was conducted using the protocol for studying the quantitative and qualitative composition of fish communities [44]. Fish sampling was carried out in various biotopes of coastal zones. Flat bottoms allowed the use of seine nets [45]. The main advantages of using seines are low selectivity and simplicity of manipulation during the catch [46–48]. Catching was done in the coastal zone with a 15-m-long and 2-m-high beach seine with a bag (mesh size 3 mm). One end of the beach seine was held on the shore. The other was fully stretched perpendicular to the shore. The closing of the seine was carried out on the shore. Each haul covered an area of about 50–300 m^2. The depth at the catch locations did not exceed 1.7 m. Five hundred seventy samples were collected in the analyzed reservoir area over the course of the study. Samples contained both adult and juvenile fish. Only juvenile fish are reported in the study. The fish was considered a juvenile until the moment when it became scaly, morphologically resembled an adult, and reached sexual maturity [49]. The age of the fish was determined based on the work of N. I. Chugunova [50]. Fish were sampled between 189 and 274 days from the start of the year, with the second and third quartiles ranging from 217 to 227 days from the start of the year

(Figure 2a). The results of fish catches are presented as the number of fish individuals per 100 m^2.

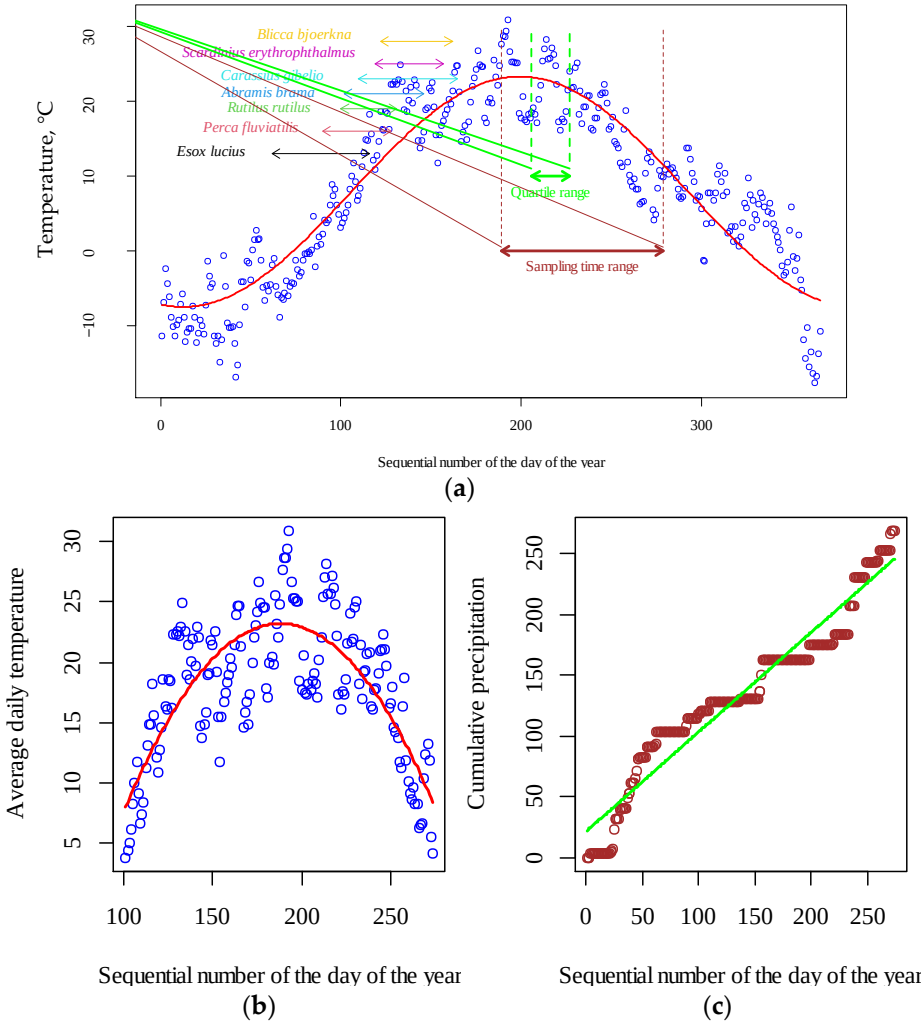


Figure 2. Seasonal course of temperatures and cumulative precipitation: (**a**) is the annual temperature pattern, the spawning time range of the dominant fish species, and the sampling time range (the quartile range indicates the range that corresponds to quartile 2 and 3, in other words, in this time range 50% of the fish collections were made); (**b**) is the average daily temperature variations (°C) from day 100 to day 275 of the year (blue circles) and the parabola that approximates the temperature trend (red line); (**c**) is the cumulative precipitation (mm) from day 1 to day 275 of the year (brown circles) and the straight line approximating the cumulative precipitation trend (green line).

2.3. Fish Traits

Categorical and continuous traits of species were considered in this study. Migration, preferred habitats, preference for water flow rate, the zone of water bodies for feeding and spawning, and preference for water salinity were considered as the categorical fish traits (Appendix A: Table A1). Trophic level, resilience, and vulnerability were considered to be the continuous traits of the fish.

Migration (M) is a parameter providing information about the type of migration of fish species [51]. Migration is the movement of a large number of individuals from one place to another to meet feeding or breeding needs [52] and is classified into the following categories: potamodromous (pot) are migratory fish species that spend the entire life cycle in freshwater bodies [53]; diadromous (dia) migratory fish species spend a part of the life cycle in fresh water, and a part in salt water [54,55]; and no migration (nom) is a species with no migratory movements [56]. Diadromous fishes are considered sensitive because

of their highly specialized lifestyle involving migration between marine and freshwater habitats [57,58]. Potamodromous fish primarily migrate in freshwater and are therefore considered less sensitive [59].

Fish are divided into pelagic, benthopelagic, and demersal according to their preferred habitat (H) [60]. The pelagic (pel) species live and feed in the pelagic (free water) zone [61]. The benthopelagic (ben) species live and feed near the bottom as well as midwaters or near the water surface [51,62]. Demersal (dem) species live and feed near the bottom [63,64]. The benthopelagic fish are regarded as a part of the demersal fish, which also include strictly benthic fish.

Fish are divided into rheophilic, limnophilic, and eurytopic according to a preference for water velocity (R) [65]. The rheophilic (rhe) fish prefer to live in a habitat with high- flow conditions and clear water [66]. The limnophilic (lim) fish prefer to live in a habitat with slow flowing to stagnant conditions [67,68]. The eurytopic (eur) fish exhibit a wide tolerance of flow conditions, although they are generally not considered to be rheophilic [56,69].

Fish are classified as water column or benthic based on their preferred feeding habitat (FH) [70]. The water column fish (wc) feed in the water column and usually do not go to the bottom to search for food. Benthic fish (ben) prefer to live near the bottom, from where they take food. They usually do not go to the surface for feeding purposes [71,72].

Habitat-related parameters describe the preferred habitat for the reproduction of a fish species (RH) [73]. The fish species preferring to spawn on rock and gravel substrates are referred to as lithophilic (lit) [73]. Phytophilic fish (phy) spawn on plants submerged in water [74–76]. Phyto-lithophilic species (pli) spawn on submerged plants or on rock-gravel substrates [77]. Psammophilic species (psa) are sandy spawners. Other species (oth) can spawn in a variety of different substrates, including mollusk shells [78].

Fish can be divided by their preference for water salinity (S) into freshwater (fre), freshwater-brackish (fbr), and freshwater-brackish-marine (fbm) [79,80]. The categorical traits of fish data were obtained from the freshwaterecology.info database [56].

The trophic level (TrL) indicates the position of fish in the respective food chains [81]. The trophic level in the food chain is denoted by a whole number (primary producers and detritus are denoted by 1), but a particular species usually have a complex diet, so its trophic level is denoted by a fractional number, and the variable that represents the trophic level of that species is a continuous variable [82].

Resilience describes the ability of a species population to recover after a perturbance [83] and can be rated as low, medium, or high [84]. The population doubling time is a good indicator of resilience [85]. Intrinsic vulnerability (V) to fishing can be assessed from knowledge of the life history and ecological traits of the fish [86]. Large fish with slow growth, a long life span, and late reproduction are most vulnerable [87]. FishBase provides continuous vulnerability values ranging from extremely low to extremely high (0-100). Continuous trait data from the FishBase database was loaded using the rfishbase library [88].

2.4. Landsat 5/TM, 7/ETM, and 8 OLI Data

Remote sensing data can be used to effectively monitor temperature and chlorophyll-a concentrations in water bodies [89]. Landsat 5/TM, Landsat 7/ETM, and Landsat 8 OLI satellites were launched on 1 March 1984, 15 April 1999, 11 February 2013, respectively. The USGS has reprocessed the Landsat archive and released Collection 2 in December 2020. Improved surface control and elevation datasets were implemented, some improvements were made to the geometric and radiometric calibration, and the atmospheric correction algorithm was upgraded. Landsat 5/TM, Landsat 7/ETM, and Landsat 8 OLI Collection 2 Level 2 products were obtained from the USGS website through the EarthExplorer tool [90]. Satellite images were geometrically corrected, radiometrically calibrated, and atmospherically corrected and can be used directly after processing according to the following formula:

$$b_\lambda = 0.0000275 \times \text{Pixlel Value} - 0.2, \quad (1)$$

The surface temperature (°C) was estimated using the spectral bands b6 (Landsat 5/TM, Landsat 7/ETM) and b10 (Landsat 8 OLI) using the formula:

$$T = b6 \text{ (or } b10) \; 0.00341802 - 124, \tag{2}$$

Table A2 presents the dates of the Landsat 5/TM, Landsat 7/ETM, and Landsat 8 OLI images used in the study.

2.5. Remote Sensing Estimation of Chlorophyll-a Concentration

Chlorophyll-a (Chl-a) is a photosynthetic pigment present in all algal groups of inland water bodies. The broad bands of Landsat satellite data cannot spectrally distinguish the spectral features associated with Chl-a absorption. The Chl-a absorption in the red range of 670 nm is only half contained in the red band of Landsat data. The absorption peak near 700 nm is completely absent in the Landsat red band. This means that the Chl-a cannot be estimated from the Landsat bands similar to the application of the field spectral regression analysis. Therefore, different methods were used to estimate Chl-a levels from Landsat data [91]. The studies showed that combinations of bands, including ratios, multiplication, and/or mean, can provide useful relationships for estimating Chl-a concentrations [92,93]. The most successful regression was found at the band ratios b4/b3 (for Landsat 5/TM and Landsat 7/ETM) or b5/b4 (for Landsat 8 OLI) to retrieve Chl-a concentrations for the lake as follows:

$$Ch_a = k \cdot b_{0.76\text{-}0.90}/b_{0.63\text{-}0.69} + c, \tag{3}$$

where $b_{0.76–0.90/b0.63–0.69}$ is the spectral ratio, k and c are regression coefficients. The regression coefficients varied slightly from paper to paper, which may also be due to the different range of spectral ratios used to derive the coefficients of the regression model. The spectral ratio ranged from 0.1–0.25 [94], 0.3–0.68 [91], and 0.78–1.0 [95]. The spectral ratio in our study was in the range 0.88–1.51. On this basis, the following model was chosen [95]:

$$Ch_a = 98.87 \cdot b_{0.76\text{-}0.90}/b_{0.63\text{-}0.69} - 59.40. \tag{4}$$

This model's estimates of chlorophyll concentration range from 40–136 µg/g (mean ± st.error was 81.5 ± 0.99 µg/g). These estimates are consistent with those obtained in laboratory studies of water in the Dnipro River [96,97]

2.6. Climatic Data

During the study period, the sampling was carried out in the range of 189–274 days from the beginning of the year, i.e., during the summer and early autumn. Obviously, the climatic characteristics at the moment of sampling or at any given date are not identical between years. Therefore, to describe the fish community dynamics, it is necessary to rely on characteristics of climatic regimes, which reflect annual or seasonal patterns but are independent of specific dates. Therefore, to describe the ecological properties of the environment, we applied indicators derived from the analytical descriptions of trends in the variability of air and water temperature, precipitation, and chlorophyll-a concentrations.

The annual course of the temperature follows a sinusoidal pattern (Figure 2a). In the period of the year from 100 to 275 days, the temperature trend could be described with the use of a parabola (Figure 2b).

The quadratic equation is a model of a parabola and has the form:

$$T = k_t \cdot Order^2 + a \cdot Order + b, \tag{5}$$

where T is the average daily temperature (°C), Order is the sequence number of days since the beginning of the year, k_t, a, b are regression coefficients. Based on regression coefficients, we can estimate the quantitative properties of the parabola, which have a physical meaning

and can be used as quantitative variables to describe the temperature regime of the year. The first derivative of the quadratic function over time (t) has the form:

$$\frac{d\mathrm{T}}{d\mathrm{t}} = 2k_t\ \mathrm{Order} + a, \tag{6}$$

The coefficient $2k_t$ is the slope of the line, which represents the rate of temperature change during the time range under study: the greater the coefficient modulo, the faster is the heating of atmospheric air before the temperature trend reaches the maximum, and the faster is the cooling after the temperature trend reaches the maximum. The time of maximum onset corresponds to the moment when the derivative is equal to zero (Extr):

$$\frac{d\mathrm{T}}{d\mathrm{t}} = 2k_t\ \mathrm{Order} + a = 0, \tag{7}$$

$$\mathrm{Order} = -\frac{a}{2k_t} \tag{8}$$

At this point, the temperature trend reaches its maximum:

$$\mathrm{Max} = \frac{a^2 - a}{2k_t} + b \tag{9}$$

The quadratic model can be parameterized by R^2, which characterizes the degree of deviation of temperature indicators from the trend. Thus, we used four indicators as predictors of fish community structure dynamics: temperature trend rate ($2k_t$), time of summer temperature maximum (Extr), temperature value when the trend reaches its maximum (Max), and degree of temperature regime variability (R^2).

Cumulative precipitation (the sum of precipitation since the beginning of the year on a given date) showed a linear trend (Figure 2c), which can be described by a linear dependence:

$$\mathrm{P_c} = k_p \cdot \mathrm{Order}, \tag{10}$$

where $\mathrm{P_c}$ is the cumulative precipitation (mm), Order is the sequence number of days since the beginning of the year, k_p, is regression coefficient. The explanatory power of the regression model can be characterized by R^2. Precipitation evened out in time gives a high value of R^2, and periods of heavy precipitation and droughts give a decrease in this indicator.

Data on average daily atmospheric air temperature and daily precipitation in the city of Dnipro were obtained from NOAA Weather Data [98].

2.7. Chlorophyll-a Concentration and Water Temperature Correction

The estimates of chlorophyll-a concentration and water temperature were made on different dates during a particular year. Obviously, a scaled indicator that can be compared between years should be used as an explanatory variable for the fish community. Estimates of maximum chlorophyll-a concentrations throughout the year and water temperature at the peak of the seasonal trend can be used as explanatory variables. Daily air temperature measurements are available over the study period, so the date of the local maximum air temperature can be used to determine when local maximum chlorophyll-a concentrations and water temperatures occur. The chlorophyll-a concentration and water temperature of the water bodies exhibit a seasonal pattern that can be described by a quadratic equation (Figure 3). The coefficients of the quadratic equation allow us to find that the maximum chlorophyll-a concentration during the study period was observed at $3.59/(2 * 0.0089) = 201.7$ days.

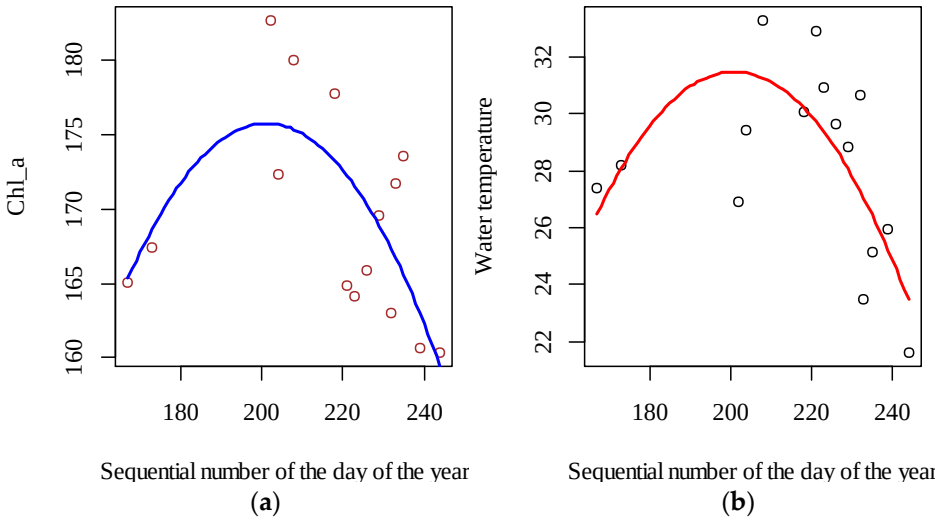


Figure 3. Seasonal course of chlorophyll-a concentration and water temperatures (°C) from day 167 to day 244 of the year: (**a**) is the chlorophyll-a (mg/m^3) (brown circles) and the parabola that approximates the trend (blue line): Chl_a = −0.0089 Order^2 + 3.59 Order −185.2, $R_{ad}{}^{j2}$ = 0.40; (**b**) is the water temperature (°C) (black circles) and the parabola approximating the trend (red line): Chl_a = −0.0043 Order^2 + 1.75 Oder −143.9, $R_{adj}{}^2$ = 0.44.

The air temperature maximum was on average observed on day 197 of the year during the study period. Thus, if other factors are omitted, we can assume that the maximum chlorophyll-a concentration was observed 4.7 days later than the seasonal maximum air temperature. Thus, based on the information about the seasonal course of air temperatures, which are constantly fixed, it is possible to estimate the onset of the seasonal maximum of chlorophyll-a concentration in water. Similarly, based on the quadratic dependence coefficients, we can find that the maximum water temperature was observed at 1.75/(2 × 0.0043) = 203.5 days. Thus, if we neglect other factors, we can assume that the maximum water temperature was observed 6.5 days later than the seasonal maximum air temperature.

The date of the satellite image, on the basis of which the chlorophyll-a concentration and water temperature were estimated, and the date of the maximum of these indicators form the shift (Δx, days) that distances the observed indicator from the annual maximum. Knowing the shape of the time dependence of a given indicator and assuming it is constant between years, a correction factor (Δy, mg/m^3 for chlorophyll-a concentration, or °C for water temperature) can be found to calculate the annual maximum of the indicator based on information about the time of the maximum indicator and the time of the space survey (see the Appendix B for details):

$$\Delta y = -\mathrm{k}\,\Delta x^2, \tag{11}$$

where Δy is the correction factor to estimate the annual maximum of the index from the observed value, k is the coefficient of the quadratic term of the parabolic dependence, Δx is the time shift between the date of the space survey and the date of the annual maximum of the index.

2.8. Data Analysis

The gamma diversity of the fish metacommunity and its partitioning into alpha- and beta-components was performed using the Divest function from the *entropart* library [99] for the order of diversity was 1, which corresponds to the number of species as a measure of the diversity.

Multivariate data analysis techniques enabled the discovery of relationships between species abundance, environmental factors, and species traits [100]. RLQ and fourth corner analysis are effective for estimating the covariance between environmental variables

and traits [101] are the most integrated methods for analyzing trait-environment relationships [102]. RLQ analysis is an extension of coinertia analysis that provides an examination of multivariate associations by finding a combination of traits (Q-matrix) and environmental variables (R-matrix) with maximum covariance that is weighted by the abundance of species at sites (L-matrix) [103]. R-, L-, and Q-matrix analysis was performed separately before performing the RLQ analysis [104]. Correspondence analysis was applied to the species matrix [105]. The trait data matrix and environmental factor matrix contained both quantitative and categorical variables. Hill and Smith's analysis [106] considers a combination of different types of variables, so it was used to analyze R- and Q-matrices. The RLQ analysis combined three separate ordinations and revealed the principal associations between the R- and Q-matrices weighted by the L-matrix [107]. In the RLQ analysis, the site scores in the R-matrix constrain the site scores in the L-matrix, and the species scores in the Q-matrix constrain the species scores in the L-matrix. The axis maximizing the covariance in the L-matrix is then selected, providing a compromise between the best joint combination of site scores on their ecological characteristics, the best combination of species scores on their traits, and the simultaneous ordination of sites and scores. The total significance of the relationship between ecological variables (R-matrix) and species traits (Q-matrix) was evaluated using a Monte Carlo test with 999 permutations on the total inertia of RLQ analyses [103]. The fourth-angle method was used to test the significance of all possible pairwise associations between individual traits and environmental variables. The Pearson product-moment correlation coefficient (r) was used to compare the two variables [108]. The significance of the relationship measure was assessed by permuting the R and Q table rows simultaneously (999 runs) [103]. RLQ and fourth-angle analyses were performed in the R ade4 package [109].

3. Results

3.1. Temporal Variability of Climatic Regime and Eutrophication Level of Water Bodies

The principal component analysis of the environmental variables identified two principal components with eigenvalues exceeding unity (Table 1).

Table 1. Descriptive statistics of the environmental explanatory variables (n = 570) and results of the principal component analysis (only statistically significant correlation coefficients of the principal components and variables are presented for $p < 0.05$).

Variable	Mean ± st. Error	Minimum	Maximum	PC1, λ = 5.0, 62.5%	PC2, λ = 1.7, 21.8%
Chlorophyll-a *, µg/L	81.47 ± 0.99	39.94	136.25	0.50	0.81
Water temperature*, °C	30.43 ± 0.09	25.28	35.26	0.59	0.74
$k_t \times 10^{-3}$ **	−1.57 ± 0.011	−1.96	−1.03	−0.84	–
Date of maximum air temperature	197.1 ± 0.13	190	204	−0.79	−0.29
Maximum of the air temperature trend	22.47 ± 0.042	19.73	24.03	0.90	−0.30
R^2 of the air temperature trend	0.58 ± 0.004	0.43	0.70	0.91	−0.22
Precipitation intensity (k_p)	1.12 ± 0.014	0.43	1.99	−0.83	0.42
R^2 of the precipitation trend	0.92 ± 0.001	0.85	0.98	−0.83	0.39

* estimation of the maximum value for the annual trend extremum; ** rate of temperature change during the study time range.

Principal component 1 explained 62.5% of the variation in traits and reflected the opposite trend in the atmospheric temperature and precipitation. The increase in the maximum seasonal temperature trend was associated with an increase in air temperature variation and the rate of the seasonal change in temperature and precipitation, as well

as the acceleration of the date of the seasonal temperature maximum. The principal component 1 described a tendency for the water temperature to increase following an increase in atmospheric temperature and an increase in the level of eutrophication of water bodies. The time factor (year) explained 69.8% of the variation in the principal component 1 (F = 210.6, $p < 0.001$), and the reservoir type explained only 19.9% of the variation (F = 203.8, $p < 0.001$). The principal component 1 exhibited a temporal trend (Figure 4a), which could be described by the equation:

$$PC1 = 0.12\ Year - 246.6\ (R^2 = 0.45, p < 0.001), \quad (12)$$

where PC1 is the scores of the principal component, Year is time as a continuous variable.

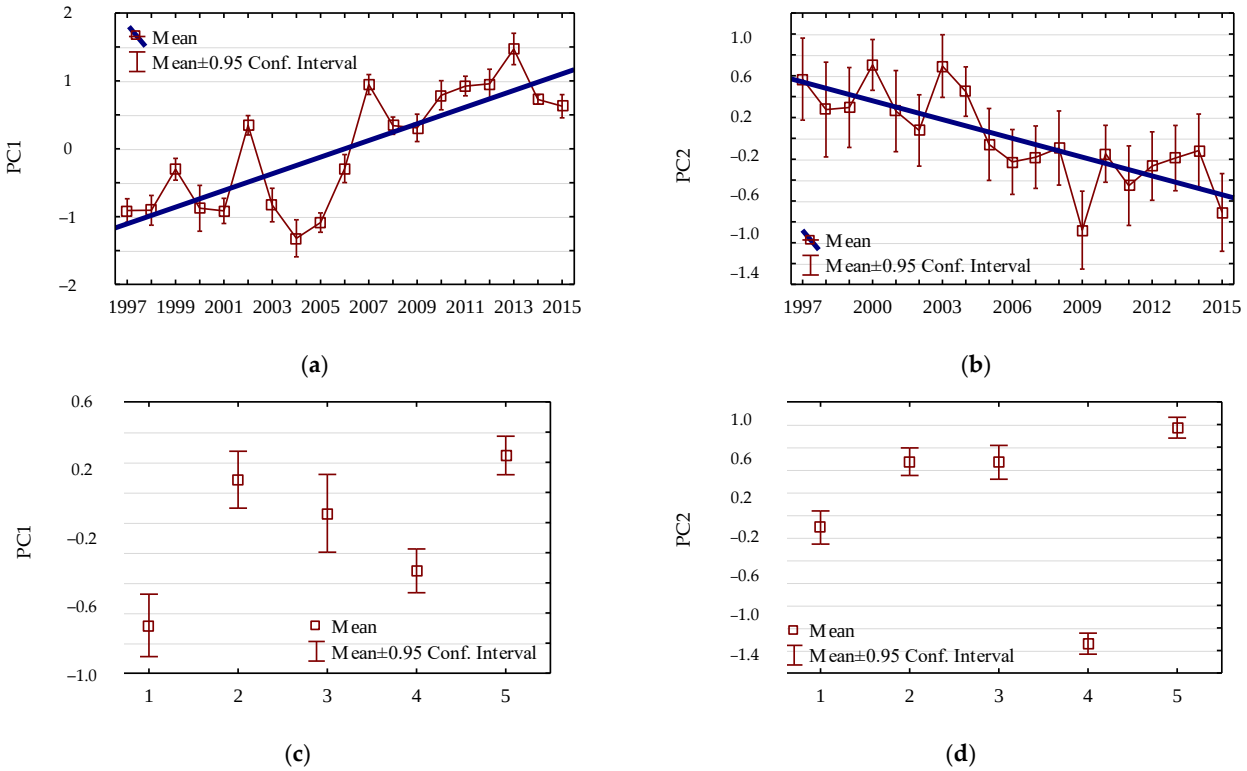


Figure 4. The dynamics of PC1 and PC2 (scores mean ± 95% confidence intervals). (**a**,**b**): the abscissa axis is years (1997–2015, the blue line shows a linear time trend); (**c**,**d**): 1 is the mouth of the Oril River, 2 are the water reservoirs of the Mykolaevka ledge system, 3 are the water bodies of the Obukhiv floodplain system, 4 is the water area of the Dnipro River channel part, and 5 are the water bodies of the Taromske ledge system.

The water bodies of the mouth of the Oril River and the water area of the Dnipro River channel part differ significantly from all other water bodies by the values of principal component 1 (planned comparison F = 363.5, $p < 0.001$ and F = 315.5, $p < 0.001$, respectively) (Figure 4c). This difference indicated the lower water temperatures and chlorophyll-a concentrations in these reservoirs under equal climatic conditions.

The principal component 2 reflected a trend in the variability of water temperature and chlorophyll-a concentration. The concentration of chlorophyll-a increased with an increase in water temperature and an increase in the rate of seasonal change and variation in precipitation, as well as a lag in the timing of the seasonal maximum temperature. In the variation of principal component 2, the time (year) factor explained only 15.4% of the variation (F = 29.4, $p < 0.001$), and the reservoir type factor described 68.3% (F = 458.1,

$p < 0.001$). The principal component 2 exhibited a temporal trend (Figure 4b), which could be described by the equation:

$$PC2 = -0.06\ Year - 120.5\ (R^2 = 0.11, p < 0.001), \quad (13)$$

where PC2 is the scores of the principal component, Year is time as a continuous variable.

The water bodies of the Dnipro River channel and mouth of the Oril River differ from all other water bodies by the decreased values of principal component 2 (Figure 4d), which indicate a regularly lower concentration of chlorophyll-a and lower water temperature in these water bodies.

3.2. Fish Community Diversity

A total of 33,622 individuals representing 38 fish species were recorded over the period of the study (Appendix C: Table A3). The most abundant species in the reservoirs of the mouth of the Oril River were *Alburnus alburnus*, *Esox lucius*, *Rutilus rutilus*, *Syngnathus abaster*, and *Proterorhinus marmoratus*, in the reservoirs of the Mykolaevka ledge system were *Rutilus rutilus*, *Proterorhinus marmoratus*, *Scardinius erythrophthalmus*, and *Petroleuciscus borysthenicus*, in the reservoirs of the Obukhiv floodplain system were *Rhodeus sericeus*, *Alburnus alburnus*, *Rutilus rutilus*, *Pungitius platygaster*, and *Scardinius erythrophthalmus*, in the reservoirs of the Dnipro River channel part were *Rutilus rutilus*, *Proterorhinus marmoratus*, *Alburnus alburnus*, *Rhodeus sericeus*, and *Neogobius fluviatilis*, in the reservoirs of the Taromske ledge system were *Rutilus rutilus*, *Petroleuciscus borysthenicus*, *Rhodeus sericeus*, *Esox lucius*, *Scardinius erythrophthalmus*.

Alpha diversity of the fish metacommunity was 22.1 species and ranged from 22.0–22.2 species in 95% of cases (Appendix C: Figure A2). Gamma diversity was 38.2 species and ranged from 37.1–38.3 species in 95% of cases. Beta diversity was 1.73 and ranged from 1.67–1.74 in 95% of cases. Twenty-nine species occurred at least 12 times. These species were used for further analysis.

3.3. Fish Community Ordination

An eigenvalues decomposition table gives the eigenvalues and their square root (Covar) (Table A4). The eigenvalues showed that the first two axes extracted from the RLQ analysis described 98.7% inertia, indicating the major relationships between fish traits and environmental variables can be explained using the first two RLQ axes. The covariance is equal to the product of the correlation between the environmental scores of sites and the species trait scores and the standard deviations of the environmental score and the species trait score. The maximum possible values of inertia (Table A5) were obtained by a simple analysis of the original tables of environmental properties and species traits, which define the basic structures of the corresponding dataset. A comparison of the amount of variance covered by the RLQ analysis (inertia) with the maximum possible value of inertia provided by the simple analysis showed that an important part of the information contained in each original structure is preserved in the co-structure.

A multivariate test based on Model 6 showed the statistical significance of the global importance of the relationships between the traits of species and the properties of the environment (Figure 5, I and II). A four-corner analysis allowed us to assess the statistical significance of the pairwise correlation between species traits and environmental factors (Figure 5, III), species traits and RLQ-axes (Figure 5, IV), and environmental factors and RLQ-axes (Figure 5, V). Water temperature and chlorophyll-a concentration were negatively correlated with the abundance of rheophilic and lithophilic species. The temperature constant kt was positively correlated with the abundance of no migration, limnophilic species and inversely correlated with the rheophilic species abundance. The timing of summer temperature extremes (Extr) was positively correlated with the abundance of rheophilic and lithophilic fish species. The value of the summer maximum temperature (Max) and temperature variation (Rt^2) correlated positively with the abundance of no migration and limnophilic species. The rate of the increase of precipitation intensity

(k_p) and the precipitation variation (Rp^2) were negatively correlated with the abundance of no migration species. The constant k_p was positively correlated with the brackish-marine species.

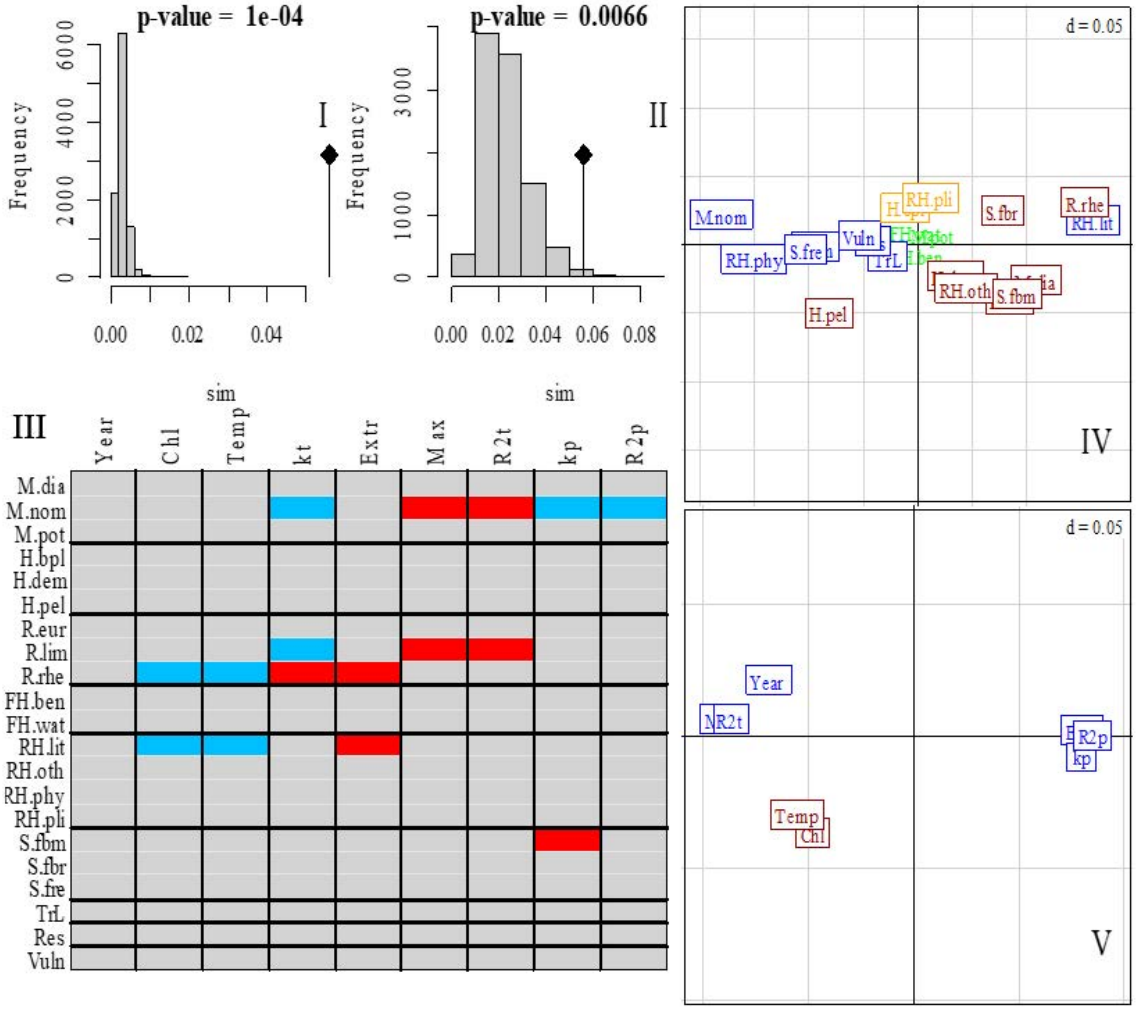


Figure 5. Results of RLQ-analysis: (**I**) is a global test of the significance of the relationship between species traits and environmental properties based on model (**II**) (the histogram shows the distribution of simulated values of total inertia (sim) for the permuted values of sites compared to the observed value of total inertia), (**II**) is a test of the global significance of the relationship between species traits and environmental properties based on model (**IV**), (**III**) is fourth-corner analysis with 999 permutations, which demonstrates the pairwise correlations between species traits and environmental variables. The *p*-values were adjusted for multiple comparisons using the false discovery rate. The gray cells indicate no statistically significant correlation, the red cells indicate positive correlations, and the blue cells indicate negative correlations significant for $p < 0.05$, (**IV**) is the correlation of species traits and RLQ axes 1 and 2, (**V**) is the correlation of environmental properties and habitat types and RLQ axes 1 and 2. The green color indicates no correlation, the blue color indicates a statistically significant correlation with axis 1, the orange color indicates a significant correlation with axis 2, and the dark red color indicates a significant correlation with both axes. Migration—pot are potamodromous, dia are diadromous, and nom are no migration fish species; habitat preference—pel are pelagic, bpl are benthopelagic, and dem are demersal fish species; water velocity preferences—rhe are rheophilic, lim are limnophilic, and eur are eurytopic fish species; preferred feeding habitat—wc are water column, ben are benthic fish species, reproduction habitat—lit are lithophilic, phy are phytophilic, pli are phyto-lithophilic, spa are psammophilic, and oth are other fish species; salinity—fre are freshwater species, fbr are freshwater-brackish species, fbm are brackish-marine species.

The RLQ-axes 1 was positively correlated with rheophilic and lithophilic species and negatively correlated with limnophilic, phytophilic, freshwater no migration species, and resilience and vulnerability (Figure 5 IV, V). The RLQ-axes 2 was correlated positively with phyto-lithophilic and benthopelagic fishes and was correlated negatively with pelagic, eurytopic, and brackish-marine species. The RLQ-axes 1 was positively correlated with the Extr, Rp^2, kt, and kp and was negatively correlated with the Max and Rt^2. The RLQ-axes 2 was positively correlated with time and was negatively correlated with the water temperature and chlorophyll-a concentration.

3.4. Interpretation of Clusters in Terms of Species Traits

Clustering by agglomerative nesting was performed based on RLQ-axis scores. The Kelley-Gardner-Sutcliffe penalty function showed that the five-cluster solution was the best for a hierarchical cluster tree (Figure 6).

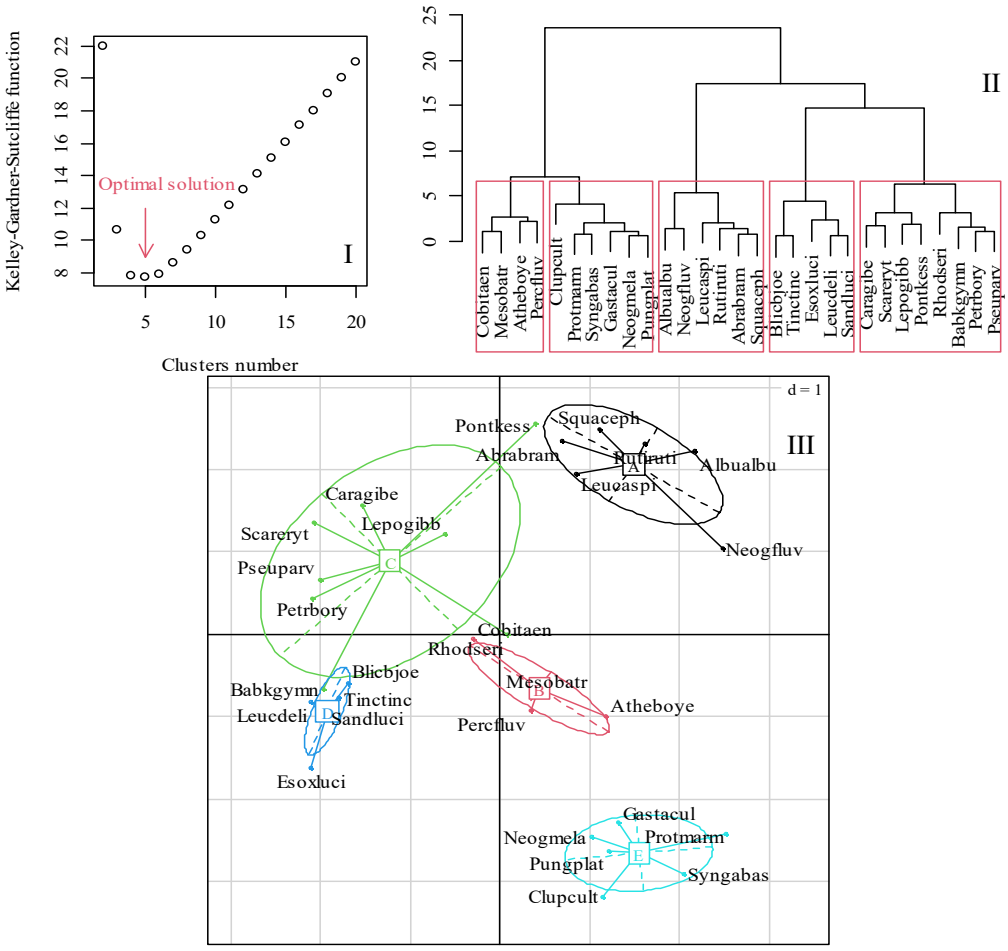


Figure 6. (**I**): Location of species in the RLQ space of axes 1 and 2 ((**II**): box is a hierarchical cluster analysis). (**III**): The species are grouped into clusters A, B, C, D and E: *Abrabram—Abramis brama*; *Albualbu—Alburnus alburnus*; *Atheboye—Atherina boyeri*; *Babkgymn—Babka gymnotrachelus*; *Blicbjoe—Blicca bjoerkna*; *Caragibe—Carassius gibelio*; *Clupcult—Clupeonella cultriventris*; *Cobitaen—Cobitis taenia*; *Esoxluci—Esox lucius*; *Gastacul—Gasterosteus aculeatus*; *Lepogibb—Lepomis gibbosus*; *Leucdeli—Leucaspius delineatus*; *Leucaspi—Leuciscus aspius*; *Mesobatr—Mesogobius batrachocephalus*; *Neogfluv—Neogobius fluviatilis*; *Neogmela—Neogobius melanostomus*; *Percfluv—Perca fluviatilis*; *Petrbory—Petroleuciscus borysthenicus*; *Pontkess—Ponticola kessleri*; *Protmarm—Proterorhinus marmoratus*; *Pseuparv—Pseudorasbora parva*; *Pungplat—Pungitius platygaster*; *Rhodseri—Rhodeus sericeus*; *Rutiruti—Rutilus rutilus*; *Sandluci—Sander lucioperca*; *Scareryt—Scardinius erythrophthalmus*; *Squaceph—Squalius cephalus*; *Syngabas—Syngnathus abaster*; *Tinctinc—Tinca tinca*.

The cluster partitioning was interpreted in terms of species traits (Figure 7). Cluster A included 6 species: *Abramis brama*, *Alburnus alburnus*, *Leuciscus aspius*, *Neogobius fluviatilis*, *Rutilus rutilus*, and *Squalius cephalus*. The peculiarity of this cluster was that all species included in it were benthopelagic and rheophilic, which preferred brackish-water conditions. Cluster B included 4 species: *Atherina boyeri*, *Cobitis taenia*, *Mesogobius batrachocephalus*, and *Perca fluviatilis*. The peculiarity of this cluster was that the proportion of phyto-lithophilic species for it was the highest, as well as the relatively high trophic level of the species composing it. Cluster C included 8 species: *Babka gymnotrachelus*, *Carassius gibelio*, *Lepomis gibbosus*, *Petroleuciscus borysthenicus*, *Ponticola kessleri*, *Pseudorasbora parva*, *Rhodeus sericeus*, and *Scardinius erythrophthalmus*. Nonmigratory, benthopelagic, limnophilic, freshwater species predominate among this cluster. Cluster D included 5 species: *Blicca bjoerkna*, *Esox lucius*, *Leucaspius delineatus*, *Sander lucioperca*, and *Tinca tinca*, which were potadromus, demersal and bentopelagic, phytophilic species. These species had the highest trophic, resilience, and vulnerability level. Cluster E included 6 species: *Clupeonella cultriventris*, *Gasterosteus aculeatus*, *Neogobius melanostomus*, *Proterorhinus marmoratus*, *Pungitius platygaster*, and *Syngnathus abaster*. The species of this cluster were diadromous, predominantly demersal, and brackish-marine species, half of which are invasive to the Dnipro.

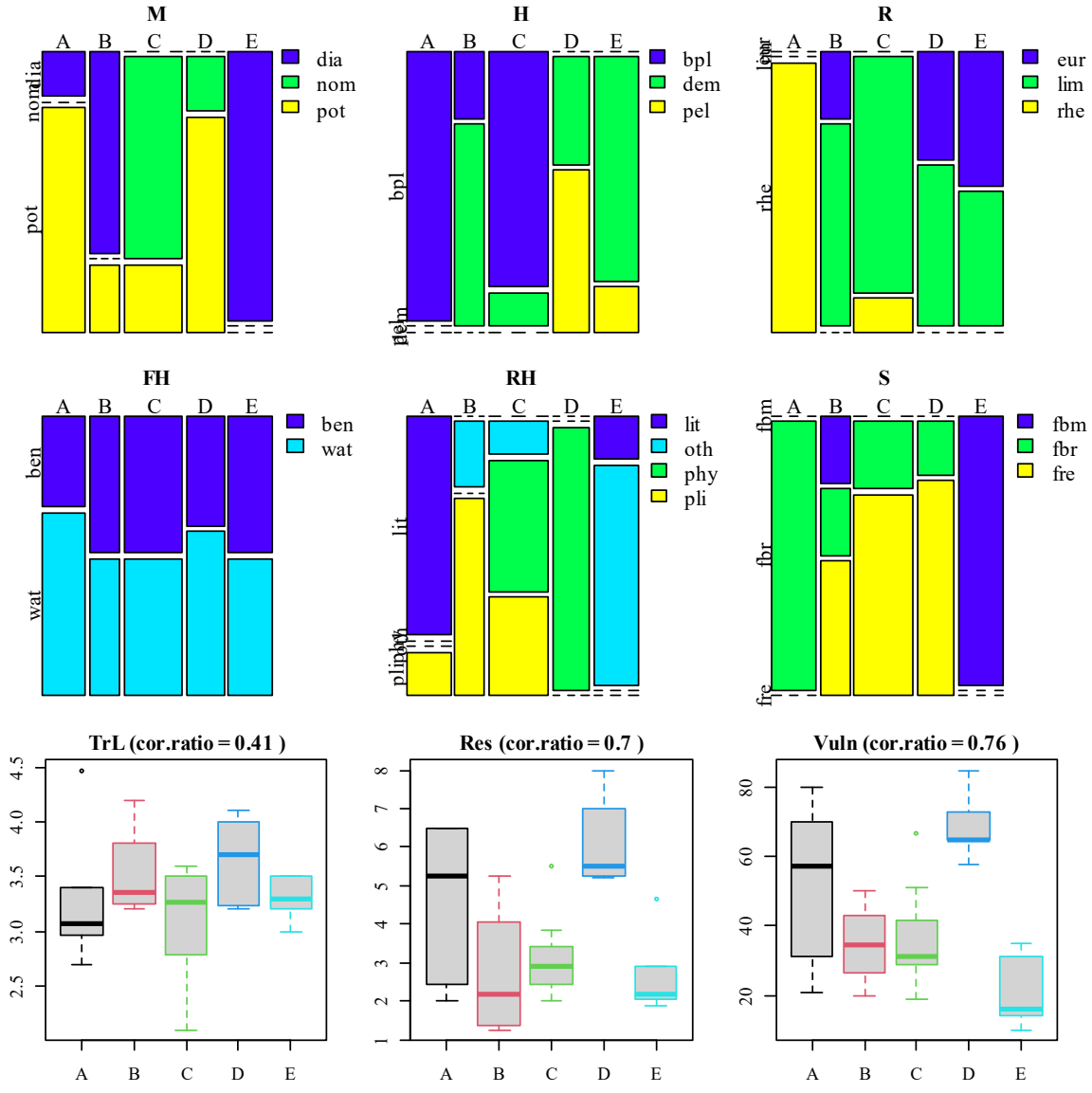


Figure 7. Distribution and variation of species traits in clusters: M—pot are potamodromous, dia are diadromous, and nom are no migration fish species; H—pel are pelagic, bpl are benthopelagic, and

dem are demersal fish species; R—rhe are rheophilic, lim are imnophilic, and eur are eurytopic fish species; FH—wc are water column, ben are benthic fish species, RH—lit are lithophilic, phy are phytophilic, pli are phyto-lithophilic, spa are psammophilic, and oth are other fish species; S—fre are freshwater species, fbr are freshwater-brackish species, fbm are brackish-marine species; TrL is the trophic level; Res is the resilience, Vuln is the vulnerability.

4. Discussion

4.1. The Role of Climatic Factors in the Dynamics of Eutrophication

Two trends in the variability of ecological properties over time were identified through the study. The main factor contributing to the variability of ecological properties is the trend, which can be explained by global climate change. This trend reflects an increase in the maximum summer air temperature and a shift in the time when this maximum is reached to an earlier period. This trend, importantly, shows a monotonous increasing trend throughout the time of the study. This result is in full agreement with the results found for Europe [110]. On average, in Europe, the increase in the maximum summer temperature is 0.4 °C per decade [111,112]. Our result reveals a much more intense warming, which is 1.3 °C per decade. The increase in the summer maximum temperature is accompanied by a decrease in the intensity of precipitation and the degree of its variation. The general trend of increasing atmospheric air temperature leads to an increase in water temperature and chlorophyll-a concentration. Temperature is the leading factor that stimulates an increase in chlorophyll-a concentration, but at temperatures above 30 °C, the dependence plateaus [113]. The global warming trend leads to rapid warming of water in spring and summer, which should be reflected in phenological shifts in the life cycles of fish and their trophic objects [114,115]. The disruption of the phenological coherence of fish and their trophic objects is also stimulated by the increased variability of the temperature regime, which is increasing due to global warming [116]. Additionally, a decrease in the intensity of precipitation and its variability over time is a trend associated with global warming. The principal component 1 reflects the phenomenon of eutrophication, which is caused by climatic conditions. Other things being equal, climate warming stimulates the intensity of blue-green algae growth [117] and oxygen consumption [118].

The variation in chlorophyll-a concentration is a marker of the second important trend in environmental conditions. This trend reflects a monotonic decrease in chlorophyll-a concentration over the study period. The maximum concentration of inorganic nitrogen compounds in the Dnipro River waters was observed in the 1970s. The maximum concentration of inorganic nitrogen compounds in the Dnipro River waters was observed in the 1970s. The concentration of inorganic phosphorus increased in the 1970s and 1980s owing to the widespread use of phosphorus-containing detergents. At a later time, the nutrient content decreased by 2.0–4.5 times and approached the values recorded before the regulation of the Dnipro River or even decreased slightly [119]. This phenomenon was probably caused by a decrease in the intensity of industrial production [120], as well as an increase in the area occupied by higher aquatic plants capable of assimilating nutrients from water [121,122].

The variation in chlorophyll-a concentration correlates positively with precipitation intensity. This dependence indicates that an important source of excess nutrient input that stimulates water blooms is the erosional flushing of soils during intense precipitation. Agricultural production is an important source of nutrients in freshwater reservoirs, causing eutrophication [123,124]. Intensification of agriculture in the catchment area affects the trophic structure of the fish community [125].The legacy stocks of nitrogen and phosphorus in watersheds may be sufficient to sustain algal blooms and turbid water for decades [126]. Loss of nutrients from the soil due to surface runoff accelerates the eutrophication of surface waters [127,128]. Thus, we observe two formally independent complexes of reasons that affect the temporal dynamics of the level of eutrophication in the Dnipro River and floodplain reservoirs. The climatic factors contribute to the acceleration of the occurrence of

eutrophication symptoms at the given level of nutrients in water because of global climate warming. It is natural that this trend tends to increase over the study period. Another trend reflects the variation in the level of eutrophication due to changes in the concentration of nutrients in the water. This trend tends to decrease over time, but this pattern becomes more complex due to the effect of precipitation on the erosion of nutrients that accumulate in the watershed.

4.2. Effects of Global Warming on Fish Communities

Climate warming causes changes in temperature and precipitation regimes, which are the drivers of directional changes in fish community structure. The response of the fish community to global warming was an increase in the abundance of phytophilic, limnophilic and freshwater fish species and a decrease in the abundance of reophilic and lithophilic fish species. The trend of increasing abundance of limnophilic fish species may also be associated with changes in the hydrological regime of the river due to the regulation of its flow [129]. The system of dams that exists on the Dnipro River has turned the river into a sequence of lake-type reservoirs. The building of dams modifies the regime of water flow and nutrient cycling through river networks [130,131]. Significant restructuring of the fish community occurred immediately after the construction of the dams [132–134], but the successional dynamics of the community from predominance of rheophilic species towards the predominance of limnophilic fish species continues to the present day [135]. The difficulty in differentiating between the effects of river flow regulation and global climate change is that these factors have a similar effect on the aquatic ecosystem and change in the same direction over time. Increasing temperatures as a result of global climate change are accelerating the growth of aquatic plants [136]. The accumulation of aquatic plant biomass also occurs as a consequence of the absence of floods after the regulation of the river flow [137,138]. The increase in the phytomass of aquatic macrophytes explains the increase in the abundance of phytophilic fish species. The overgrowth of aquatic plants creates favorable conditions for the spawning of phytophilous fish species [139], while the area suitable for the spawning of lithophilous species decreases [140]. Aquatic macrophytes increase surface area and provide shelter, food, and a variety of ecological niches for juvenile fish [141]. Lithophilic species spawn earlier than phytophilic species [142]. Climate warming in general and earlier warming in spring during and after the spawning period can significantly shift the phenological rhythms of fish and their food objects [143,144], to which previously spawning lithophilic species are more sensitive.

As the temperature rises, the amount of dissolved oxygen in the water decreases, increasing the risk of fish hypoxia [145]. Rheophilic fish species are particularly sensitive to oxygen deficiency [59], so the global warming trend is accompanied by a decrease in their abundance. The lake type of water regime leads to a decrease in water mixing [146], which creates conditions for the overheating of the upper layer of water and the deterioration of oxygen supply in deeper layers of water bodies. Global warming influences the selection of fish species, favoring those with greater vulnerability and resilience.

4.3. Effect of Eutrophication on the Fish Community

Low levels of eutrophication are favorable for benthopelagic, and phyto-lithophilic fish species, which are combined in cluster A. Increased eutrophication causes oxygen deficiency, especially in benthic layers, which deteriorates living conditions for benthopelagic fish species.

The zone of the ordination diagram, which corresponds to the greatest influence of eutrophication, is vacant, indicating the extinction of fish at the extreme levels of eutrophication of water bodies. Additionally, this configuration indicates that eutrophication causes an ambiguous response in the fish community. Pelagic fish species are the most resistant to the effects of eutrophication. Pelagic fish show satisfactory population viability with a constant supply of nutrients to their habitat, as they are not directly affected by the oxygen deficiency occurring in benthic habitats [147]. The upper water layers are best supplied with

oxygen, which allows pelagic species to survive when living conditions due to eutrophication in the bottom layers of water bodies are severely degraded. Additionally, resistant to the effects of eutrophication are the brackish-water demersal species, which make up the majority in Cluster E. All these species became part of the fish faunistic complex of the Dnipro River as a result of self-dispersal from marine refugia. Such species as *Clupeonella cultriventris*, *Gasterosteus aculeatus*, *Neogobius melanostomus* are invasive to the Dnipro [135]. Invasive fishes can cause local populations to decline and species extinction [148], lead to changes in food webs, and even a general biotic homogenization of fish communities [149]. At the same time, non-native species have a number of adaptations that allow them to inhabit a wide range of environmental conditions [150]. Thus, the demersal species can be assumed to have physiological adaptations to oxygen deficiency, which occurs even in conditions without anthropogenically induced eutrophication. The demersal *Neogobius melanostomus* can tolerate exposure to low-oxygen water for several days [151]. Members of this cluster are diadromous, euryreophilic species. Many of them prefer substrates other than plants or rocks for spawning. For example, *Clupeonella cultriventris* is a pelagophilic species spawning in the water column, and the eggs have floatability due to the oil drop attached to the yolk [152]. *Gasterosteus aculeatus* lays eggs in the nests built by males [153]. *Pungitius platygaster* males also construct nests of filamentous algae and submerged plants where females lay eggs [154]. *Neogobius melanostomus* males dig holes, which are used as nests for females to lay eggs [155]. *Proterorhinus marmoratus* makes spawning nests under rocks, clam shells, or other hard objects [156]. The *Syngnathus abaster* males incubate large eggs for 20–25 days in a special pouch, which is formed by two folds on the skin on the underside of the tail [157].

Another group of eutrophication-tolerant fish species consists of freshwater species (cluster D), most of which are phytophilous species. This group is represented exclusively by native species, which are either pelagic or demersal species. Thus, eutrophication-tolerant species are distinguished by the criterion of origin and, accordingly, by the degree of preference for water salinity levels: they are self-settled species from marine reservoirs and native freshwater species. Except for differences in the sources of their origin, the eutrophication-tolerant species possess a spectrum of similar traits. These species are pelagic or demersal. Pelagic species inhabit an environment with a better oxygen supply, which is a critical condition in a water bloom situation. The demersal species have adaptations for living in oxygen-deficient conditions that occur in the benthic layers during a mass bloom of blue-green algae. The eutrophication tolerant species are either limnophilic or eurythropic. Such species, unlike rheophilic species, are preadapted to conditions of oxygen deficiency in water.

5. Conclusions

Our study revealed a more intense warming trend than average for Europe, reflecting an increase in the maximum summer air temperature and a shift in the time of reaching this maximum to an earlier period. An increase in the summer maximum temperature is accompanied by a decrease in the intensity of precipitation and the degree of its variation. We also revealed a tendency for a monotonic decrease in chlorophyll-a concentration during the study period. The fish community of the Dnipro River responds to global warming by increasing the abundance of phytophilic, limnophilic, and freshwater fish species and decreasing the abundance of reophilic and lithophilic fish species. Global warming is causing fish species selection that favors species with less vulnerability and greater resilience. Eutrophication causes an ambiguous response in the fish community. The most eutrophication-resistant fish are pelagic species because they are not directly affected by the oxygen deficiency that appears in benthic habitats. The brackish-water demersal species are also resistant to eutrophication's impacts due to their physiological adaptations to oxygen deficiency. So, self-settled species of marine origin are less sensitive to the level of eutrophication. The increased eutrophication due to more nutrients supplied to the water bodies increases the competitive advantage of this group over other species.

Native freshwater species are more sensitive to increased symptoms of eutrophication as the climate warms.

Author Contributions: Conceptualization, O.Z. and A.Z.; methodology, O.Z. and O.K; software, O.Z.; validation, J.-C.S., A.Z. and O.K.; formal analysis, A.Z.; investigation, D.B.; resources, D.B.; data curation, D.B. and A.Z.; writing—original draft preparation, A.Z.; writing—review and editing, O.Z., J.-C.S.; visualization, O.K.; supervision, O.Z.; project administration, A.Z.; funding acquisition, J.-C.S. All authors have read and agreed to the published version of the manuscript.

Funding: We thank the VILLUM FONDEN for economic support via JCS' VILLUM Investigator project "Biodiversity Dynamics in a Changing World" (grant 16549). We further consider this study a contribution to JCS' Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by Danish National Research Foundation (grant DNRF173).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Ecological traits of fish.

Species	Migration (M)	Habitat Preference (H)	Water Velocity Preferences (R)	Feeding Habitat (FH)	Reproduction Habitat (RH)	Salinity (S)	Trophic Level (TrL)	Resilience (Res)	Vulnerability (Vuln)
Abramis brama (Linnaeus, 1758)	pot	bpl	rhe	ben	pli	fbr	3.1	6.0	62
Acipenser ruthenus Linnaeus, 1758 *	pot	dem	rhe	ben	lit	fbr	3.6	9.5	64
Alburnus alburnus (Linnaeus, 1758)	pot	bpl	rhe	wat	lit	fbr	2.7	2.0	31
Alosa immaculata Bennett, 1835 *	dia	pel	lim	wat	lit	fbm	3.9	1.5	35
Anguilla anguilla (Linnaeus, 1758)	dia	dem	eur	ben	oth	fbm	3.6	7.9	64
Atherina boyeri Risso, 1810	dia	dem	lim	wat	pli	fbm	3.2	1.3	20
Babka gymnotrachelus (Kessler, 1857)	nom	dem	lim	ben	phy	fre	3.5	2.9	29
Ballerus ballerus (Linnaeus, 1758)	pot	bpl	lim	wat	phy	fbr	3.2	3.9	49
Benthophiloides brauneri Beling & Iljin, 1927 *	dia	dem	lim	ben	oth	fbr	3.4	2.4	28
Benthophilus stellatus (Sauvage, 1874)	pot	dem	lim	ben	lit	fbr	3.7	3.4	34
Blicca bjoerkna (Linnaeus, 1758)	pot	dem	lim	ben	phy	fre	3.2	5.5	65
Carassius carassius (Linnaeus, 1758)	pot	dem	lim	ben	phy	fre	3.1	3.2	38
Carassius gibelio (Bloch, 1782)	nom	bpl	lim	ben	pli	fre	2.5	3.9	51
Chondrostoma nasus (Linnaeus, 1758) *	pot	bpl	rhe	ben	lit	fre	2.0	4.0	48

Table A1. *Cont.*

Species	Migration (M)	Habitat Preference (H)	Water Velocity Preferences (R)	Feeding Habitat (FH)	Reproduction Habitat (RH)	Salinity (S)	Trophic Level (TrL)	Resilience (Res)	Vulnerability (Vuln)
Clupeonella cultriventris (Nordmann, 1840)	dia	pel	eur	wat	oth	fbm	3.0	4.7	35
Cobitis taenia Linnaeus, 1758	pot	dem	lim	ben	pli	fre	3.3	1.5	36
Ctenopharyngodon idella (Valenciennes, 1844) *	pot	dem	rhe	wat	oth	fre	2.0	6.0	65
Cyprinus carpio Linnaeus, 1758	pot	bpl	eur	ben	phy	fbr	3.1	4.4	46
Esox lucius Linnaeus, 1758	pot	pel	eur	wat	phy	fre	4.1	8.0	85
Gasterosteus aculeatus Linnaeus, 1758	dia	dem	lim	wat	oth	fbm	3.3	2.1	10
Gobio gobio (Linnaeus, 1758) *	pot	bpl	rhe	ben	psa	fbr	3.1	2.9	31
Gymnocephalus cernua (Linnaeus, 1758)	pot	dem	eur	ben	pli	fbr	3.3	3.2	20
Hypophthalmichthys molitrix (Valenciennes, 1844) *	pot	bpl	eur	wat	oth	fbr	2.0	4.7	55
Hypophthalmichthys nobilis (Richardson, 1845) *	pot	bpl	eur	wat	oth	fre	2.8	5.3	66
Lepomis gibbosus (Linnaeus, 1758)	pot	bpl	lim	wat	pli	fre	3.3	3.0	32
Leucaspius delineatus (Heckel, 1843)	pot	pel	lim	wat	phy	fre	3.2	5.2	58
Leuciscus aspius (Linnaeus, 1758) *	pot	bpl	rhe	wat	lit	fbr	4.5	6.5	70
Leuciscus idus (Linnaeus, 1758) *	pot	bpl	rhe	wat	pli	fbr	3.8	7.0	63
Leuciscus leuciscus (Linnaeus, 1758)	pot	bpl	rhe	wat	lit	fbr	2.9	3.2	48
Lota lota (Linnaeus, 1758)*	pot	dem	eur	ben	lit	fbr	4.1	6.0	66
Mesogobius batrachocephalus (Pallas, 1814)	dia	bpl	lim	ben	oth	fbr	4.2	2.9	33
Misgurnus fossilis (Linnaeus, 1758)	pot	dem	lim	ben	phy	fre	3.4	3.4	31
Neogobius fluviatilis (Pallas, 1814)	dia	bpl	rhe	ben	lit	fbr	3.4	2.4	21
Neogobius melanostomus (Pallas, 1814)	dia	dem	lim	ben	oth	fbm	3.3	2.9	31
Pelecus cultratus (Linnaeus, 1758)	dia	pel	lim	wat	oth	fbr	3.6	4.8	50
Perca fluviatilis Linnaeus, 1758	dia	dem	eur	wat	pli	fre	3.4	5.3	50
Petroleuciscus borysthenicus (Kessler, 1859)	nom	bpl	lim	ben	phy	fre	3.1	2.9	32

Table A1. *Cont.*

Species	Migration (M)	Habitat Preference (H)	Water Velocity Preferences (R)	Feeding Habitat (FH)	Reproduction Habitat (RH)	Salinity (S)	Trophic Level (TrL)	Resilience (Res)	Vulnerability (Vuln)
Ponticola kessleri (Günther, 1861)	nom	bpl	rhe	wat	pli	fbr	3.5	2.9	30
Proterorhinus marmoratus (Pallas, 1814)	dia	dem	eur	ben	lit	fbm	3.5	1.9	15
Pseudorasbora parva (Temminck & Schlegel, 1846)	nom	bpl	lim	wat	phy	fre	3.2	2.0	29
Pungitius platygaster (Kessler, 1859)	dia	dem	lim	ben	oth	fbm	3.5	2.3	14
Rhodeus sericeus (Pallas, 1776)	pot	bpl	lim	ben	oth	fre	2.1	2.0	19
Rutilus rutilus (Linnaeus, 1758)	pot	bpl	rhe	wat	lit	fbr	3.0	4.5	53
Sander lucioperca (Linnaeus, 1758)	nom	pel	eur	wat	phy	fbr	4.0	7.0	73
Sander volgensis (Gmelin, 1789) *	nom	dem	lim	wat	pli	fbr	4.1	7.3	52
Scardinius erythrophthalmus (Linnaeus, 1758)	nom	bpl	lim	wat	phy	fbr	3.6	5.5	67
Silurus glanis Linnaeus, 1758	nom	dem	eur	ben	phy	fbr	4.4	7.3	84
Squalius cephalus (Linnaeus, 1758)	pot	bpl	rhe	wat	lit	fbr	3.0	6.5	80
Syngnathus abaster Risso, 1827	dia	dem	eur	wat	oth	fbm	3.2	2.1	17
Tinca tinca (Linnaeus, 1758)	pot	dem	lim	ben	phy	fre	3.7	5.3	65

*—information on the occurrence of species is given from literary sources (Bondarev, 2015); Migration—pot are potamodromous, dia are diadromous, and nom are no migration fish species; habitat preference—pel are pelagic, bpl are benthopelagic, and dem are demersal fish species; water velocity preferences—rhe are rheophilic, lim are limnophilic, and eur are eurytopic fish species; preferred feeding habitat—wc are water column, ben are benthic fish species, reproduction habitat —lit are lithophilic, phy are phytophilic, pli are phyto-lithophilic, spa are psammophilic, and oth are other fish species; salinity—fre are freshwater species, fbr are freshwater-brackish species, fbm are brackish-marine species.

Table A2. Landsat 5/TM, Landsat 7/ETM, and Landsat 8 OLI images used in the study.

Data	Sequential Number of the Day of the Year	Sampling Time Range		Image	Satellite
21.08.1997	233	219	253	LT05_L2SP_178026_19970821_20200910_02_T1	Landsat 5/TM
23.07.1998	204	213	226	LT05_L2SP_178026_19980723_20200908_02_T1	Landsat 5/TM
11.08.1999	223	221	274	LT05_L2SP_178026_19990811_20211205_02_T1	Landsat 5/TM
13.08.2000	226	214	217	LT05_L2SP_178026_20000813_20200906_02_T1	Landsat 5/TM
01.09.2001	244	212	221	LT05_L2SP_178026_20010901_20200905_02_T1	Landsat 5/TM
16.06.2002	167	204	214	LT05_L2SP_178026_20020616_20211209_02_T1	Landsat 5/TM
06.08.2003	218	212	220	LT05_L2SP_178026_20030806_20200904_02_T1	Landsat 5/TM
21.06.2004	173	231	246	LT05_L2SP_178026_20040621_20200903_02_T1	Landsat 5/TM

Table A2. *Cont.*

Data	Sequential Number of the Day of the Year	Sampling Time Range		Image	Satellite
27.08.2005	239	217	217	LT05_L2SP_178026_20050827_20200902_02_T1	Landsat 5/TM
14.08.2006	226	189	214	LT05_L2SP_178026_20060814_20200831_02_T1	Landsat 5/TM
17.08.2007	229	208	241	LT05_L2SP_178026_20070817_20200830_02_T1	Landsat 5/TM
19.08.2008	232	205	225	LT05_L2SP_178026_20080819_20200829_02_T1	Landsat 5/TM
21.07.2009	202	199	219	LT05_L2SP_178026_20090721_20200827_02_T1	Landsat 5/TM
09.08.2010	221	209	210	LT05_L2SP_178026_20100809_20200823_02_T1	Landsat 5/TM
27.07.2011	208	214	222	LT05_L2SP_178026_20110727_20200822_02_T1	Landsat 5/TM
22.08.2012	235	207	223	LE07_L2SP_178026_20120822_20200908_02_T1	Landsat 7/ETM
17.08.2013	229	206	218	LC08_L2SP_178026_20130817_20200913_02_T1	Landsat 8 OLI
20.08.2014	232	220	227	LC08_L2SP_178026_20140820_20200911_02_T1	Landsat 8 OLI
23.08.2015	235	211	219	LC08_L2SP_178026_20150823_20200908_02_T1	Landsat 8 OLI

Appendix B

The response of the environmental index (chlorophyll-a concentration or surface temperature) is described by the quadratic function $kx^2 + bx + c$ (Figure A1), which reaches its maximum Max at $-b/2k$.

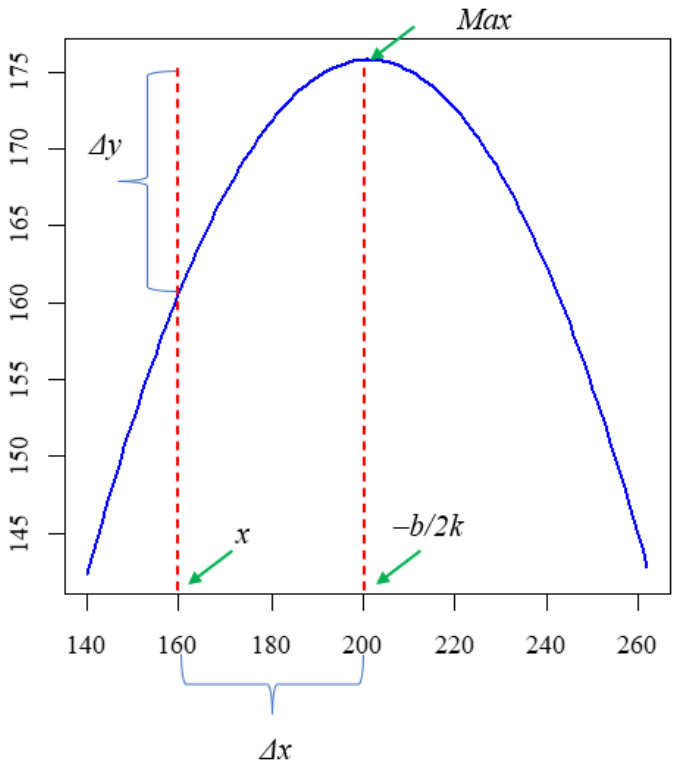


Figure A1. Model of the quadratic dependence of environmental indicators on time $kx^2 + bx + c$, where x is time. At time $-b/2k$ the function reaches maximum Max, which is a key characteristic of the dynamics of the indicator in that year. The different years may be compared in terms of this indicator. The time of space imaging x may be different from time $-b/2k$ in different years by Δx and a correction factor Δy must be found to find Max based on the information about the observed value of the indicator and the shift Δx.

At time x, the function takes the value $kx^2 + bx + c$, which differs from the maximum value by Δy:

$$\text{Max} - (kx^2 + bx + c) = \Delta y, \tag{A1}$$

from where:

$$\left(k\frac{b^2}{4k^2} - \frac{b^2}{2k} + c\right) - kx^2 - bx - c = \Delta y. \tag{A2}$$

After simplification it, we get:

$$\frac{b^2}{4k} - \frac{2b^2}{4k} - kx^2 - bx = \Delta y, \tag{A3}$$

from where:

$$-\frac{b^2}{4k} - kx^2 - bx = \Delta y. \tag{A4}$$

It should be taken into account that:

$$x = -\frac{b}{2k} - \Delta x. \tag{A5}$$

As a result of the substitution, we get:

$$-\frac{b^2}{4k} - k\left(\frac{b^2}{4k^2} + \frac{b * \Delta x}{k} + \Delta x^2\right) - b\left(-\frac{b}{2k} - \Delta x\right) = \Delta y. \tag{A6}$$

After opening the parentheses, we get:

$$-\frac{b^2}{4k} - \frac{b^2}{4k} - b * \Delta x - k\Delta x^2 + \frac{b^2}{2k} + b * \Delta x = \Delta y. \tag{A7}$$

After simplification we get:

$$-\frac{b^2}{4k} - \frac{b^2}{4k} - b * \Delta x - k\Delta x^2 + \frac{b^2}{2k} + b * \Delta x = \Delta y. \tag{A8}$$

from where:

$$-k\Delta x^2 = \Delta y. \tag{A9}$$

Appendix C

Table A3. Fish species abundance in groups of water bodies in the period 1998–2015 (mean ± st. error).

Species	Individuals	Biotope Groups *					Total (n = 570)
		I (n = 76)	II (n = 95)	III (n = 57)	IV (n = 171)	V (n = 171)	
Abramis brama	1357	1.96 ± 0.08	2.12 ± 0.08	2.75 ± 0.09	2.47 ± 0.05	2.50 ± 0.06	2.38 ± 0.03
Alburnus alburnus	1924	2.93 ± 0.14	3.78 ± 0.16	5.82 ± 0.16	2.92 ± 0.11	2.99 ± 0.09	3.38 ± 0.07
Atherina boyeri	682	1.34 ± 0.06	1.07 ± 0.05	1.18 ± 0.05	1.29 ± 0.04	1.11 ± 0.04	1.20 ± 0.02
Babka gymnotrachelus	1246	1.91 ± 0.08	2.25 ± 0.07	2.86 ± 0.09	1.58 ± 0.05	2.65 ± 0.05	2.19 ± 0.03
Ballerus ballerus	14	–	–	–	0.03 ± 0.03	0.05 ± 0.03	0.02 ± 0.01

Table A3. *Cont.*

Species	Individuals	Biotope Groups *					Total (n = 570)
		I (n = 76)	II (n = 95)	III (n = 57)	IV (n = 171)	V (n = 171)	
Benthophilus stellatus	2	–	–	–	0.01 ± 0.01	–	–
Blicca bjoerkna	1791	2.61 ± 0.07	2.98 ± 0.10	5.12 ± 0.12	2.61 ± 0.05	3.35 ± 0.05	3.14 ± 0.04
Carassius carassius	47	–	0.11 ± 0.11	0.18 ± 0.18	–	0.16 ± 0.08	0.08 ± 0.03
Carassius gibelio	1639	2.03 ± 0.13	3.88 ± 0.15	4.46 ± 0.19	2.33 ± 0.09	2.71 ± 0.08	2.88 ± 0.06
Clupeonella cultriventris	104	0.05 ± 0.05	0.05 ± 0.05	–	0.53 ± 0.08	0.03 ± 0.02	0.18 ± 0.03
Cobitis taenia	922	1.59 ± 0.10	1.53 ± 0.09	3.30 ± 0.19	1.20 ± 0.05	1.53 ± 0.07	1.62 ± 0.04
Cyprinus carpio	13	0.05 ± 0.04	–	–	0.05 ± 0.03	–	0.02 ± 0.01
Esox lucius	1900	2.86 ± 0.10	2.55 ± 0.21	3.77 ± 0.15	2.43 ± 0.08	4.74 ± 0.13	3.33 ± 0.07
Gasterosteus aculeatus	140	0.12 ± 0.07	0.59 ± 0.20	0.30 ± 0.21	0.34 ± 0.08	–	0.25 ± 0.05
Gymnocephalus cernua	33	0.03 ± 0.02	0.02 ± 0.01	0.33 ± 0.21	0.03 ± 0.03	0.03 ± 0.03	0.06 ± 0.03
Lepomis gibbosus	519	0.99 ± 0.11	1.08 ± 0.09	1.14 ± 0.14	0.43 ± 0.07	1.19 ± 0.07	0.91 ± 0.04
Leucaspius delineatus	1215	1.66 ± 0.11	1.93 ± 0.12	3.19 ± 0.14	1.34 ± 0.07	2.89 ± 0.09	2.13 ± 0.05
Leuciscus aspius	512	0.86 ± 0.09	0.85 ± 0.08	0.75 ± 0.08	1.28 ± 0.06	0.61 ± 0.05	0.90 ± 0.03
Leuciscus leuciscus	6	–	–	–	0.04 ± 0.02	–	0.01 ± 0.01
Mesogobius batrachocephalus	71	0.17 ± 0.10	0.11 ± 0.11	0.25 ± 0.17	0.20 ± 0.06	–	0.12 ± 0.03
Misgurnus fossilis	14	–	–	0.09 ± 0.09	–	0.05 ± 0.03	0.02 ± 0.01
Neogobius fluviatilis	1012	1.70 ± 0.10	1.13 ± 0.06	1.56 ± 0.14	2.75 ± 0.08	1.27 ± 0.05	1.78 ± 0.05
Neogobius melanostomus	603	2.38 ± 0.16	1.05 ± 0.10	0.63 ± 0.08	1.07 ± 0.06	0.60 ± 0.04	1.06 ± 0.04
Pelecus cultratus	3	–	–	–	0.02 ± 0.01	–	0.01 ± 0.00
Perca fluviatilis	1688	1.96 ± 0.12	2.43 ± 0.10	2.96 ± 0.18	2.23 ± 0.08	4.43 ± 0.11	2.96 ± 0.06
Petroleuciscus borysthenicus	1908	1.70 ± 0.09	3.91 ± 0.08	3.67 ± 0.10	2.08 ± 0.06	4.93 ± 0.06	3.35 ± 0.06
Ponticola kessleri	448	1.09 ± 0.07	0.61 ± 0.06	0.42 ± 0.07	1.22 ± 0.05	0.44 ± 0.04	0.79 ± 0.03
Proterorhinus marmoratus	2067	2.66 ± 0.09	4.26 ± 0.19	4.37 ± 0.23	2.96 ± 0.09	4.12 ± 0.11	3.63 ± 0.06
Pseudorasbora parva	919	1.29 ± 0.09	2.16 ± 0.12	1.63 ± 0.14	1.79 ± 0.08	1.27 ± 0.06	1.61 ± 0.04
Pungitius platygaster	871	2.51 ± 0.11	0.96 ± 0.06	5.44 ± 0.27	0.69 ± 0.05	0.94 ± 0.07	1.53 ± 0.07
Rhodeus sericeus	2187	2.50 ± 0.12	3.72 ± 0.15	5.84 ± 0.25	2.91 ± 0.09	4.75 ± 0.12	3.84 ± 0.07

Table A3. *Cont.*

Species	Individuals	Biotope Groups *					Total (n = 570)
		I (n = 76)	II (n = 95)	III (n = 57)	IV (n = 171)	V (n = 171)	
Rutilus rutilus	2378	2.75 ± 0.11	4.78 ± 0.28	5.79 ± 0.33	3.04 ± 0.10	5.06 ± 0.17	4.17 ± 0.10
Sander lucioperca	26	–	0.03 ± 0.03	–	0.12 ± 0.04	0.02 ± 0.02	0.05 ± 0.01
Scardinius erythrophthalmus	2068	2.26 ± 0.15	4.22 ± 0.34	5.18 ± 0.40	2.31 ± 0.15	4.71 ± 0.23	3.63 ± 0.12
Silurus glanis	41	0.03 ± 0.03	–	0.09 ± 0.09	0.01 ± 0.01	0.19 ± 0.09	0.07 ± 0.03
Squalius cephalus	684	1.03 ± 0.17	0.79 ± 0.18	1.32 ± 0.37	2.37 ± 0.17	0.29 ± 0.09	1.20 ± 0.09
Syngnathus abaster	1242	2.66 ± 0.12	1.89 ± 0.35	2.98 ± 0.44	1.35 ± 0.14	2.68 ± 0.26	2.18 ± 0.12
Tinca tinca	1326	1.92 ± 0.14	1.76 ± 0.11	3.70 ± 0.16	0.87 ± 0.07	3.82 ± 0.15	2.33 ± 0.08

* I is the mouth of the Oril River, II is the Mykolaevka ledge system, III is the Obukhiv floodplain system, IV is the Dnipro River channel part, V is the Taromske ledge system.

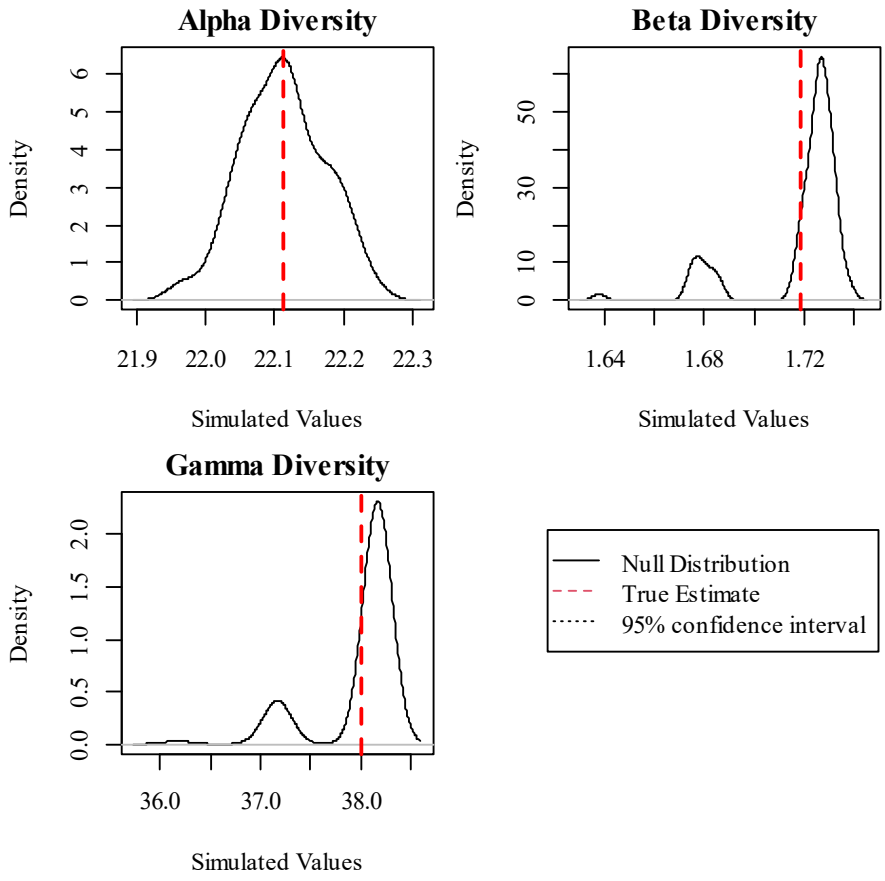


Figure A2. Estimates of alpha, beta, and gamma diversity of the fish metacommunity.

Table A4. Decomposition of the eigenvalues (Covar = sdR × sdQ × Corr). Total inertia: 0.05609.

Eigenvalue Order	Eigenvalue and Projected Inertia	Covar	sdR	sdQ	Corr
1	0.0524 (93.5%)	0.23	2.34	1.64	0.06
2	0.0029 (5.15%)	0.05	1.27	1.72	0.02
3	0.00039 (0.70%)	0.02	0.54	1.50	0.02
4	0.00023 (0.42%)	0.02	0.64	1.00	0.02

Table A5. Comparison of RLQ analysis results with ordinal multivariate data matrix analysis procedures.

Environmental Characteristics (Matrix R)	Inertia	Max Inertia	Ratio
First RLQ axis	5.49	5.50	0.99
First and second RLQ axes	7.10	7.37	0.96
1, 2, and 3 RLQ axes	7.40	7.79	0.95
1, 2, 3 and 4 RLQ axes	7.81	8.15	0.96
Species traits (Matrix Q)	Inertia	Max inertia	Ratio
First RLQ axis	2.71	4.04	0.67
First and second RLQ axes	5.65	6.96	0.81
1, 2, and 3 RLQ axes	7.91	9.29	0.85
1, 2, 3 and 4 RLQ axes	8.91	10.54	0.85
Species matrix (Matrix L)	Corr	Max correlation	Ratio
RLQ axis 1	0.059	0.19	0.32
RLQ axis 2	0.025	0.18	0.14
RLQ axis 3	0.024	0.16	0.15
RLQ axis 4	0.024	0.15	0.16

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