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Article

Effects of temperature patterns on the spawining phenology and niche overlap of fish assemblages in the water bodies of the Dnipro River basin

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Abstract
The effect of the temperature on the spawining phenology of the fish assemblages and the role of the exogenious and endogenious factors in temporal niche overlaping of fish assemblages were investigated in different water body types of the Dnipro River basin within the "Dnipro-Orilskiy" Nature Reserve (Ukraine in the years 1997-2018. The period of spawning (beginning and end) of the *Blicca bjoerkna*, *Carassius gibelio*, *Scardinius erythrophthalmus, Abramis brama, Perca fluviatilis, Rutilus rutilus*, and *Esox lucius* was estimated. Community niche overlap was estimated by calculating the pairwise Pianka index. The temperature was discused as an exogenous factor effecting on the fishes spawn timing. From 1998 to 2018 the average temperature in the study area continued to rise. The annual course of the temperature takes the sinusoidal waveform, which can be described by a fourth-degree polynomial. The residuals of the corresponding polynomial trend are specific for each year. The regular components of the residuals variation were revealed by dbMEM-variables. Fishes spawning occurred within the narrow water temperature ranges, which are specific for each fish species. There are statistically significant differences between ponds in water temperatures at which the spawning start occurred. The water temperature at which the spawning start occurred is linearly dependent on the time of the spawning start. There were temporal overlaps between spawning of the different species. The deviation of the Pianka mean niche overlap indexes from random alternatives does not depend on the habitat type. The decreasing trend of the Pianka mean niche overlap indexes was observed during the study period. There is no statistically significant correlation between the average annual air temperature and the level of the niche overlap. The degree of niche overlapping depends on broad-, medium-, and fine-scale temperature patterns.

Key words: spawning, niche overlap, global warming, competition, temperature patterns.

Introduction

The climate changes effect considerably on the timing of seasonal activities such as migration, flowering or breeding (Root et al. 2003; Parmesan 2006). In many organisms there are developed strategies for reliable warning signals that vary in strict accordance with the "ultimate" factors for controlling seasonal activity (Gwinner 1981). These cues actually control the annual cycles of influence on physiological processes called "proximate causes" (Baker 1938). Although ultimate factors affect the forecasted annual cyclical biological processes, natural selection promotes the development of mechanisms that allow organisms to anticipate changes in environmental conditions on the basis of their internal biological clock and the external opportunities to perceive warning signals (Immelmann 1971). The photoperiod as the environmental stimulus is the most considerable proximate causes controlling phenology in animals (Sbragaglia et al. 2018). The synchronization of annual biological processes in fish is under synergistic effect of the photoperiod, temperature and food availability (Falcón et al. 2010; Cowan et al. 2017). A key role of local temperatures behind interannual variability of plant and animals phenophases was revealed (Gordo & Sanz 2005). Temperature is an important trigger of the annual temporal organization of biological processes due to its influence on embryonic development, hatching, emergence, growth and life-history traits (Jonsson & Jonsson 2009). The pre-breeding intrinsic foraging ability is critical in determining breeding phenology (Daunt et al. 2006). An offspring production by vertebrates is timed to coincide with the annual peak of resource availability in highly seasonal environments (Post & Forchhammer 2008). The inter-annual variations in freshwater fish abundances were shown to be driven by inter-annual variations in temperature through variations in migration timing (Kuczynski et al. 2017).

Phenology is the temporal aspect of natural history (Forrest & Miller-Rushing 2010). The species during their evolutionary process are able to adapt only to the recurring changes in the environment which are caused by geophysical cycles such as photoperiodism (Bradshaw & Holzapfel 2007, 2010), temperature, and precipitation (Foster & Kreitzman 2009). That is why phenology being seasonal timing of recurring biological processes is discussed as a result of the complex affect of the environment factors, species-specific, and timing processes (Helm et al. 2013). The timing of life-cycle events determines the survivorship, reproductive success and fitness of many species (Lane et al. 2012; Fletcher et al. 2013). The endogenous timekeeping mechanisms enable animals to track, anticipate and prepare for the seasons (Paul et al. 2008). Environmental factors which in the process of evolution have formed selective pressures that restrict certain biological event within a defined time period can be classified as ultimate causes (Baker 1938; Thompson 1950). Most types of seasonal activity cannot begin as soon as the ultimate causes reach critical levels since a relatively long period is required for these causes to take effect, which is particularly evident in the case of reproduction (Bondarev et al. 2018).

Freshwater fish species play a considerable role in the functioning of freshwater ecosystems (Holmlund & Hammer 2009; Sokolov & Zhukov 2014, 2016, 2017). In seasonal environments resources can be temporally partitioned (Schoener 1974). Mismatches in the timing of phenological events due to climate change may have effect on communities (Daunt et al. 2006). Freshwater fish commonly exhibit the seasonal variability in spawning time within comminities (Peterson & VanderKooy 1995; Pusey et al. 2001). Reproductive phenology affects fish community composition (Turner et al. 2010). Photoperiod plays a role in reproductive readiness while temperature is a proximal cue for initiating spawning (Stacey 1984). A key determinant of reproductive success and specific timing of spawning of fish species depends on how well current conditions predict future conditions (Turner et al. 2010). The mean overlap in resources temporal utilization of the community may be significantly larger than expected from null models revealing that competition is not important in the temporal organization of the community (Tokeshi 1986). If the community niche overlap is higher than may be expected at random revealing the community dynamics constrained by environmental and physiological factors (Reinhardt et al. 2013). Species partition a niche to reduce competition (Pianka 1974). When competition is a dominant factor structuring communities the lower niche overlap may be expected (Albrecht & Gotelli 2001).

Ecological structures and processes occur across multiple spatiotemporal scales (Nash et al. 2014). Ecological systems are hierarchically structured and may be decomposed into structural and process components (La Notte et al. 2017). These components can be defined over a range of spatial and temporal scales (Allen et al., 2014). The elucidation of the mechanisms underlying observed spatial and temporal patterns and different scale levels is a key to prediction and understanding to the development of principles of management (Levin 1992). The complexity is needed to be accounted for modelling temporal patterns in time series (Baho et al. 2015). In time series modelling redundancy analysis is increasingly used both for ecological (Angeler et al. 2009; Black et al. 2010; Garcia et al. 2012) and climatological (Wang & Zwiers 2001; Kunah et al. 2019) investigation. Redundancy analysis is the canonical form of principal component analysis (Rao 1964). The principal coordinates of neighbour matrix method (PCNM) is a powerful approach able to detect temporal structures of varying scale in time series data (Borcard & Legendre 2002; Borcard et al. 2004; Dray et al. 2006). PCNM after conversion the time vector produces a series of temporal variables with distinct sine-wave properties. PCNM-variables can be used in redundancy analysis to model the oscillation of response variables. The importance of each PCNM-variable can be assessed in terms of adjusted variance explained and thus the strength of the temporal patterns determined (Angeler et al. 2009). This approach has become popular for assessing hierarchical dynamics and resilience of ecological systems (Angeler et al. 2011; Spanbauer et al. 2014). The PCNM-based approach has been further elaborated in distance-based Moran’s eigenvector maps (MEM) (Dray et al. 2006; Baho et al. 2015). MEM are able to increase the proportion of explained variation compared to the original PCNM approach and are more robust in dealing with correlation structures (Dray et al. 2006; Baho et al. 2015).

The phenological observations of freshwater organisms are very few in number (Parmesan 2007). Very few studies were devoted to investigate the impact of climate change on the phenology of freshwater fish species (Woodward 2009). The objective of this research was to study the effect of the temperature on the spawining phenology of the fish assemblages and assess a role of the exogenious and endogenious factors in temporal niche overlaping of fish assemblages in different water body types of the Dnipro River basin within the “Dnipro-Orilskiy" Nature Reserve (Ukraine).

We hypothesized that:

1) Both the average annual temperature and the temporal patterns of the temperature oscillation with the different specific periods are able to effect on the fish spawining phenology as exogenous factors.
2) The niche overlap decreasing and the role of the endogenous factors for structuring communities increasing are the fish community response on the global trend of the climate warming.

Material and methods

Physico-geographical features of the "Dnipro-Orilskiy» Nature Reserve

In order to preserve the unique landscape of the Valley of the Middle Dnipro and the River Oril with its characteristic complex of flora and fauna the “Dnipro-Orilskiy" Nature Reserve was created in 1990. Today it is the only strict nature reserve (zapovednik) in the Dnipropetrovsk region of Ukraine. The reserve protects the landscapes and the biodiversity of the valley of the Dnipro and its tributary the River Oril. The total area of the reserve is 3,766.2 hectares, and about 30% of this is covered by water, most of which is unique floodplain lakes (Bondarev & Zhukov 2017).

The reserve is located on the upper area of the Dnipro reservoir, which has suffered considerable anthropogenic transformation (Sharamok et al. 2017). This has created the need for comprehensive ichthyological research to determine the direction and depth of the processes that occur in populations of fish influenced by the actions of the aggregate anthropogenic factors (Bondarev et al. 2018). Research on the fish fauna of the reserve enables us not only to identify the composition of the fish fauna and the character of its distribution in the water bodies but also to reveal the direction of the processes that are taking place in the ecosystem in general (Bondarev et al. 2018).

Biotopes

Information about fish spawning was collected in the following locations (Fig. 1).

Nikolayev system of water bodies. The system of flood waters, located in the narrowest part of the floodplain terraces. The water bodies extend in a narrow strip extending along the flow the Dnipro. The maximum distance from the Dnipro within the reserve is about 300–1000 meters. Characterized by high level of flow and drop in the water level during the day, depending on the operating conditions of the reservoir. Part of the water body, connected with individual channels specified area, is located outside the reserve. Shallow areas (littoral zone) are minimal. Maximum depth is 5.6 meters. In recent years, the water in the central part of this area have been actively silted up with sandy sediment due to the accumulation of excess sandy deposition in areas outside the reserve and the formation of new sand spits and islands.

River Protoch system and Obukhov floodplain. Most of the ponds are poorly flowing, shallow waters which are remnants of the lower parts of the Protovch creek which united the Dnipro with the old course of the Orel. The ponds were flooded due to the formation of the reservoir. The water regime of the Protoch system and the Obukhov floodplain is under significant influence of the water regime of the reservoir. The water bodies are characterized by significant silting (in some places the thickness of silt accumulation reaches 0.6-1.0 m) and growth of higher aquatic vegetation. The system is connected with the

Dnipro and the estuary of the Orel by narrow streams. The greatest distance between the Dnipro and the Orel within this section is about 2 km.

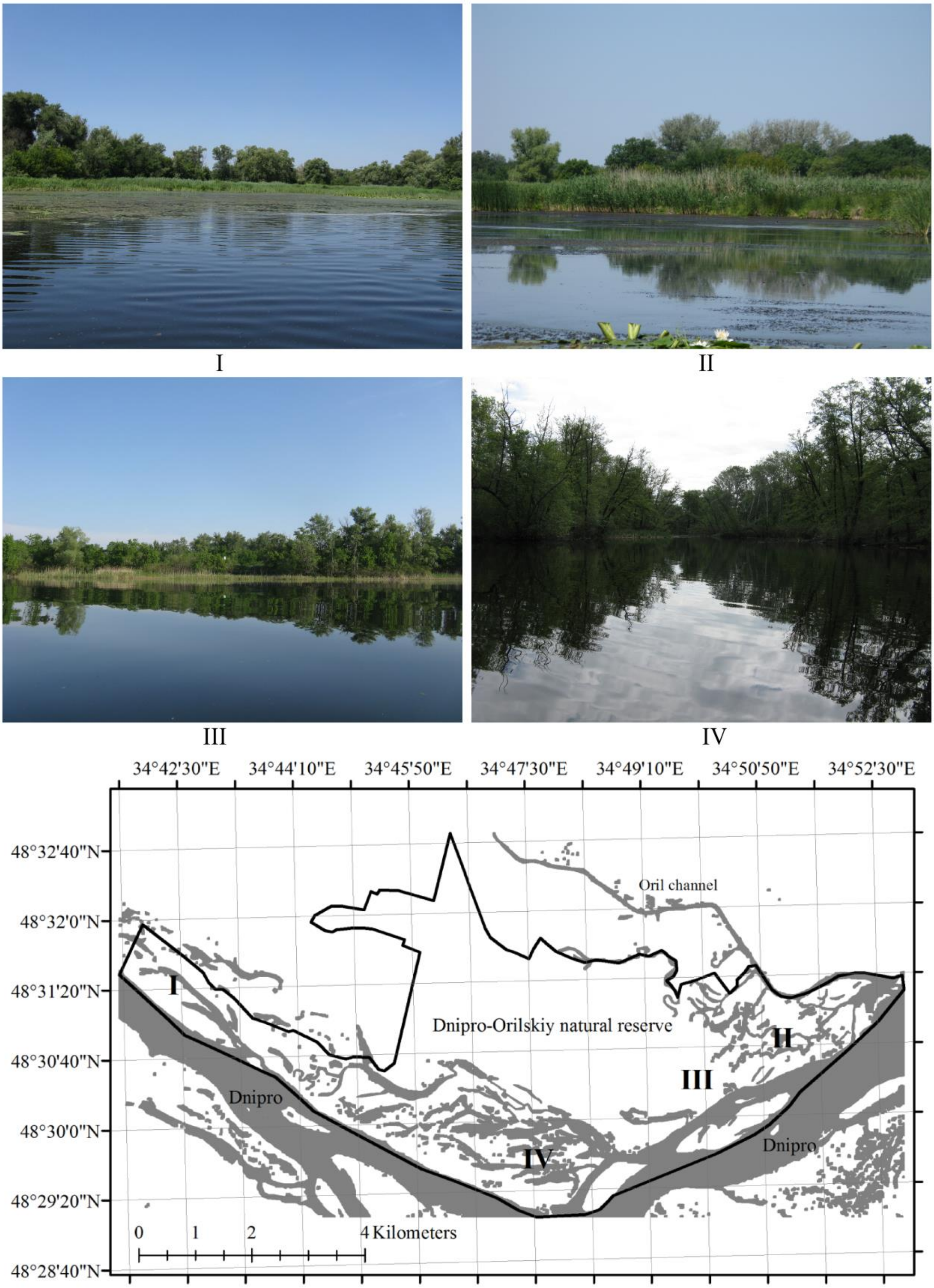

Figure 1. Map of the "Dnipro-Orilskiy»Nature Reserve and spawning locations. I – Nikolayev system of water bodies; II – river Protoch system and Obukhov floodplain; III – the channel of the river Dnipro; IV – water bodies of the Taromske ledge.

The channel of the Dnipro. Includes the area of the upper Dnipro reservoir, which partially retains a river regime. The area studied is along the left bank between Krachynyy and Kamyanisty islands. Biotopes are characterized by high level of changing in water levels and moving sand masses associated with active formation of channel process at the site of the reservoir. Depths range between 2–7 meters. Between these islands is part of the rock ridge that stretches from the right bank of the Dnipro left bank.

Water bodies of the Taromske ledge. The system of flood waters, located in the lowest part of the floodplain terraces is a unique floodplain biogeocoenosis in the steppe Dnipro region. According Pervukhin's (1979) genetic classification it is an example of the oxbow lakes formed in the Dnipro floodplain. All lakes are separated from the Dnipro bed by a belt of sand and connected by multiple channels, directly related to the channel of the Dnipro. Most ponds have a significant littoral zone that is actively covered with higher aquatic vegetation. Depths range between 1–10 meters. Water exchange is carried out through the operation of the reservoir and spring floods. Maximum distance of these ponds from the Dnipro river is about two kilometers. At present, the ponds of the specified area are actively swamping and silting due to unbalanced operation of the reservoir. In some parts the thickness of silt reaches 0.3–0.7 m.

Methods spawning phenology

The materials that formed the basis of this research were collected from the waters of the reserve in the years 1997-2018. Sampling was conducted using a standard set of fishing gear (nets with mesh size 30 to 90 mm) in different parts of the waters of the reserve. All work associated with the removal of fish from natural water bodies was conducted in accordance with current norms and regulations by standard ichthyological methods (Arsan et al. 2006; Chugunova 1952; Pravdin 1966).

During the research we conducted full or part-biological analysis of fish. We determined the species, size, weight, gender, stage of maturity of sexual products, and selected samples to determine the age and fertility. Determining the stage of maturity of sexual products actually allowed us to track phenological dates of the beginning of spawning of some fish species. All data was recorded in a special journal. Additionally, tracking of weather conditions, fluctuations in water level and water temperature was determined.

In addition, to obtain data on the characteristics and intensity of fish spawning we made visual observation and conducted planned survey routes through spawning grounds with stops every 20, 50, 100 m to check the vegetation and presence of fish eggs. If roe was found, the place of its location was described in detail. We noted the name of the water body, depth, water temperature, time of day, type of vegetation and richness of the spawning (Koblitskaya 1963).

Assessment of spawning events

The period of spawning (beginning and end) of the *Blicca bjoerkna* (Linnaeus, 1758), *Carassius gibelio* (Bloch, 1782), *Scardinius erythrophthalmus* (Linnaeus, 1758), *Abramis brama* (Linnaeus, 1758), *Perca fluviatilis* Linnaeus, 1758, *Rutilus rutilus* (Linnaeus, 1758), and *Esox lucius* Linnaeus, 1758 was estimated by the usual calendar. According to astronomical solar calendar, dates were converted into variables that represent the number of days from January 1 of each year to the spawning event (beginning and end).

Meteorological data

We used the data from the meteorological observatory of the city Dnipro.

Statistical analyses

The symmetric distance-based Moran's eigenvector maps analyses (MEM; Dray et al. 2006) were carried out to extract a set of orthogonal temporal variables (dbMEM-variables) that are derived from the time vector comprised of 360 time steps from Julay 1 of the previous year to June 31 of the current year. MEM requires detrending of the data to remove linear trends prior to analysis (Blanchet et al. 2013; Legendre & Legendre 2012; Baho et al. 2015). To do this foth-order trend was prediously extracted from the temperature data. dbMEM-variables can be used as explanatory variables to model temporal patterns of the temperature courses. In MEM all variables depict sine-wave patterns (Legendre & Legendre 2012). These extracted temporal variables are then used as explanatory variables in the time series models based on redundancy analysis (RDA). dbMEM-variables are linearly combined in the RDA models to extract temporal structures from the temperature time series. The significant RDA axes were tested through permutation tests. These

RDA axes are independent from each other. The R software generates linear combination (lc) score which present the modelled temporal patterns that are associated with each RDA axis.

Community niche overlap was estimated by calculating the pairwise Pianka index (Pianka 1973; 1974) for all species during a single year at each water body using the range date of the spawning from the start to end. As niche overlap was found only for one resource – the time then Pianka's index was calculated as followed:

$$O_{ij} = \frac{p_i p_j}{\sqrt{p_i^2 p_j^2}},$$

where O_{ij} – the niche overlap between species *i* and *j*, p_i and p_j – the proportion of time when spawing of the species *i* and *j* occurs. For all species pairs the average Pianka index was calcutated for a single year at each water body as a measure of the community niche overlap.

To determine whether the observed community overlap was different than what should be expected at random, we created a null model (Reinhardt et al. 2013). The null model of community niche overlap was built by random generations of the start and finish date with mean and standart deviation are equal with corresponding spawning statisticsc of the fish species in each water bodies. This procedure was repeated 999 times to generate a distribution of random community niche overlaps for each site and water bodies.

Statistical analyses were carried out in R 3.0.2 (RDevelopment Core Team, 2012) using the following packages: vegan (v. 2.5-2, https://CRAN.R-project.org/package=vegan) for the multivariate analysis (Oksanen et al. 2018), adespatial (v. 0.3-2. https://CRAN.R-project.org/package=adespatial) for the forward selection and for the generation of temporal filters (Dray et al. 2018), spaa (Jinlong Zhang (2016). spaa: SPecies Association Analysis. R package version 0.2.2. https://CRAN.R-project.org/package=spaa) for the computing niche overlap between each pair of species. To test if Pianka index are significantly different from a null model, a randomization test was performed using the function randtest() from the ade4 package (Dray & Dufour 2007).

Results

From 1998 to 2018 the average temperature in the study area continued to rise (Fig. 2). This trend is not monotonous: the local minimum temperature was observed in the period 2003-2009 (except in 2007).

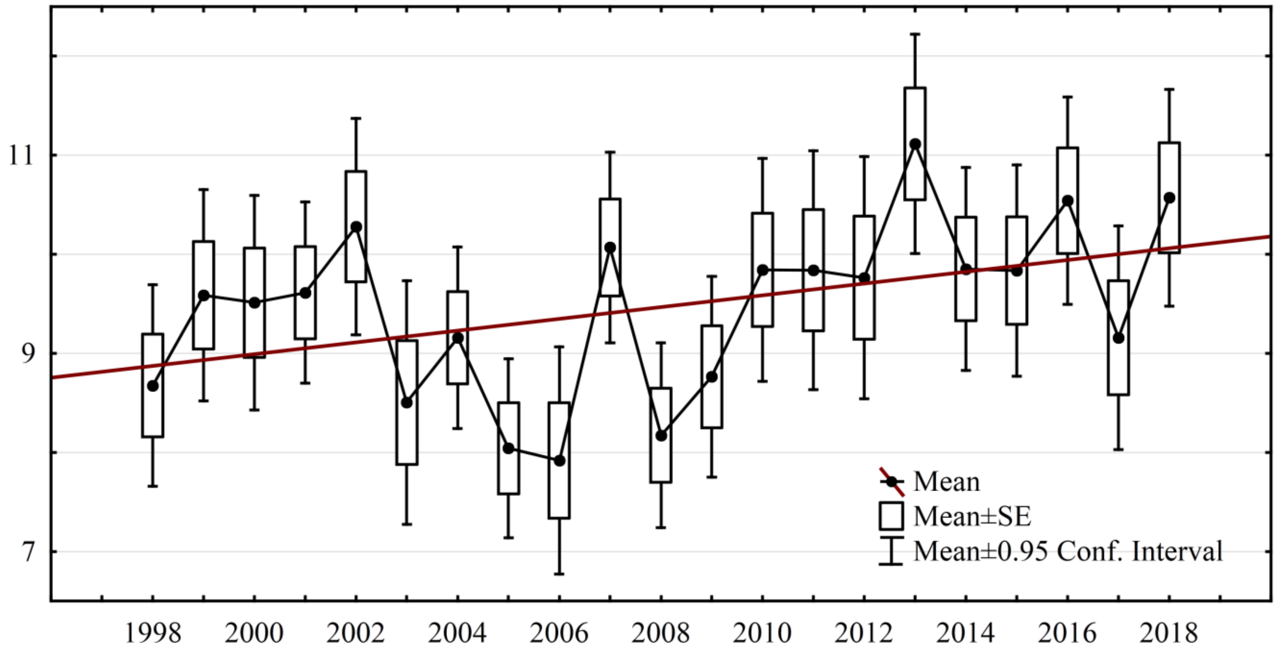

Figure 2. The dynamics of air temperature from 1998 to 2018. The line indicates an approximation of the average annual temperature trend *Temp* = 8.81 + 0.059 *t*, where *Temp* – average annual temperature, *t* – the order of year: 1 – 1998, 2 – 1999, etc.

The annual course of the temperature takes the sinusoidal waveform, which can be described by a fourth-degree polynomial (Figure 3, A). This curve describes a trivial change of temperature in different seasons. The residuals of the corresponding polynomial trend are specific for each year (Figure 3, B). The regular components of the trend residuals were revealed by dbMEM-variables.

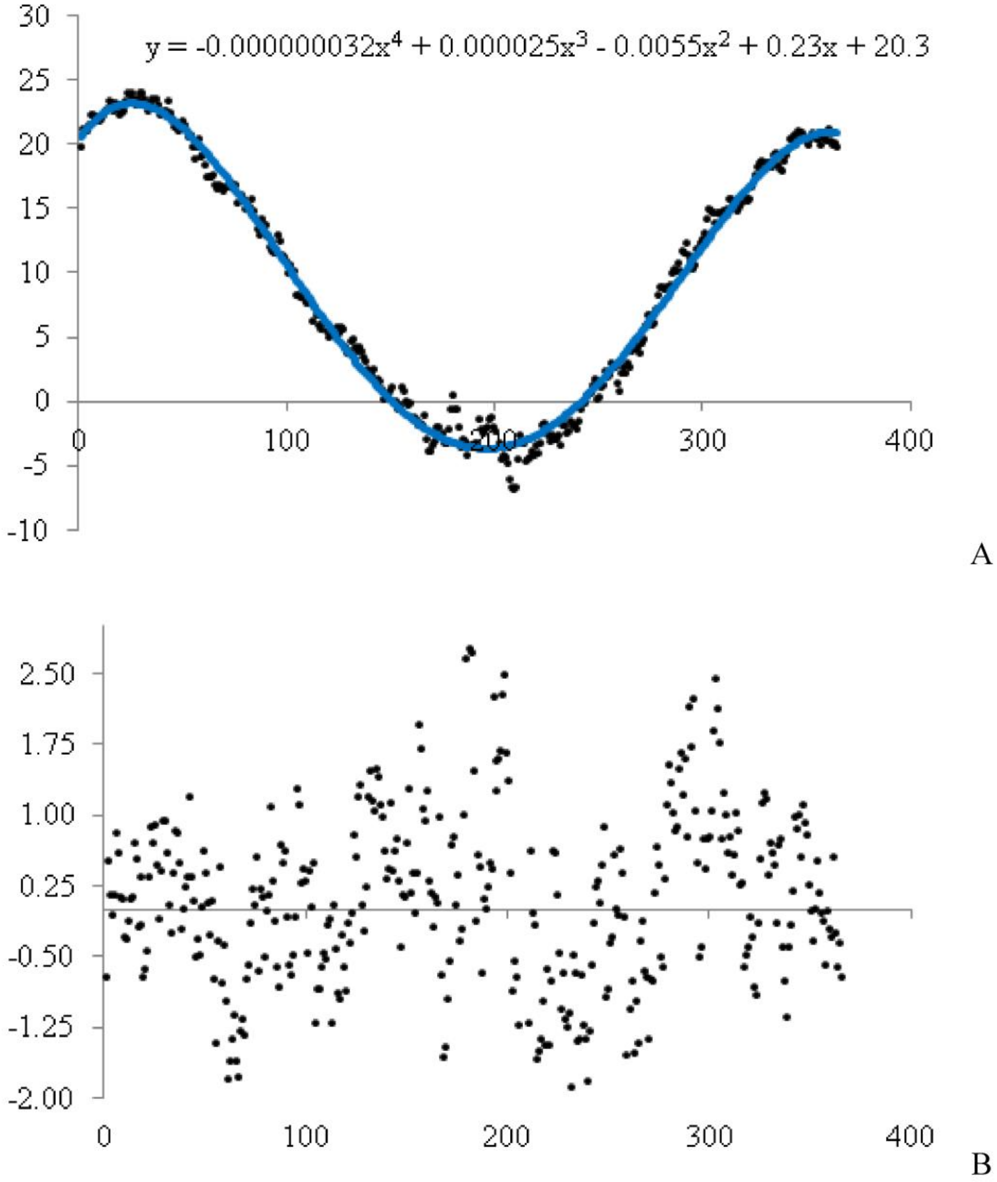

Figure 3. Annual course of the temperature (A) and residuals of the trend line (B). The abscissa axis – the number of days from 1 July of the previous year to June 31 of the next year, the ordinate axis – the average temperature for the period 1998–2018 (A). Line indicates the graph of the polynomial of the fourth degree.

A set of 104 orthogonal dbMEM variables that together describe 72% (F = 10.02, p <0.001) variation of the polynomial trend residuals was derived from the daily time series. Scalogram indicates that the distribution of variation explained by individual dbMEM variables (ordered by decreasing temporal scale from broad- to fine-scaled variables) is left skewed (Figure 4).

The forward selection procedure allowed us to extract 85 dbMEM-variables which explain statistically significantly the variation of the polynomial trend residuals. Of these, the first 10 dbMEM-variables were interpreted as a broad-scale component of the temperature variation. These variables explains 22.7% of total variation of the polynomial trend residuals (F = 11.74, p <0.001). Constrained RDA of the polynomial trend residuals with broad-scale variables as predictors revealed three RDA-axis, which reflect the broad-scale patterns of annual temperature deviations from the typical temperature trend (Figure 5).

RDA-axis 1 reflects the systematic presence of sharp temperature drop in January and February. The positive RDA-axis 1 scores show a strong cold snap in early January, which is accompanied by significant and sudden warming in late January or early February. The negative RDA-axis 1 scores show the inverse relationship: the warming in the beginning of January and the cold snap at the end. Also this axis reflects a sharp change in temperature in the course of the middle of the spring – in late April or early May. The characteristic period being most typical for this axis has duration of 120 days. RDA-axis 2 represents the occurrence of a series of sharp temperature drops in winter and a sharp temperature drop in the spring. The characteristic periods being typical for this axis, have duration of 90–120 days. RDA-axis 3 reflects the presence of the oscillation process with close to a sinusoidal long period of 60-90 days.

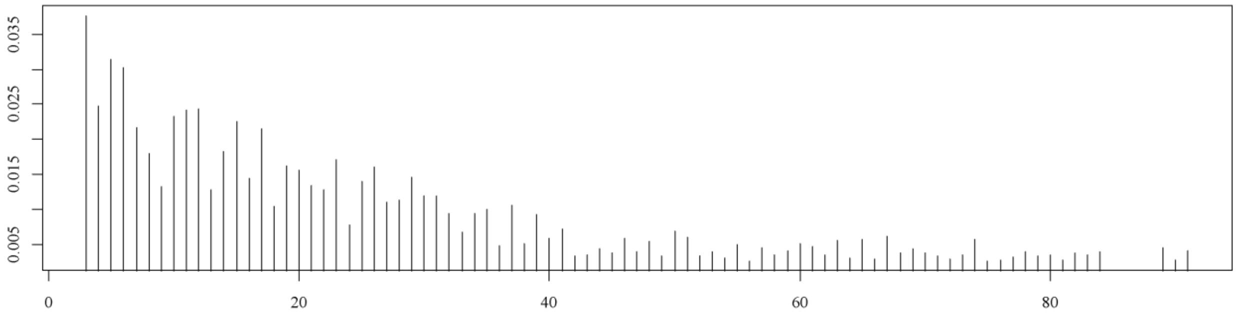

Figure 4. Scalogram illustrating the scaling of temporally structured variation in polynomial trend residuals data. The abscissa axis – dbMEMs ordered decreasingly according to the scale of temporal patterns they represent (dbMEM 1 represents the broadest scale, dbMEM 104 the finest scale). The ordinate axis – value of R^2_{adj} is the variation explained by individual dbMEM variables.

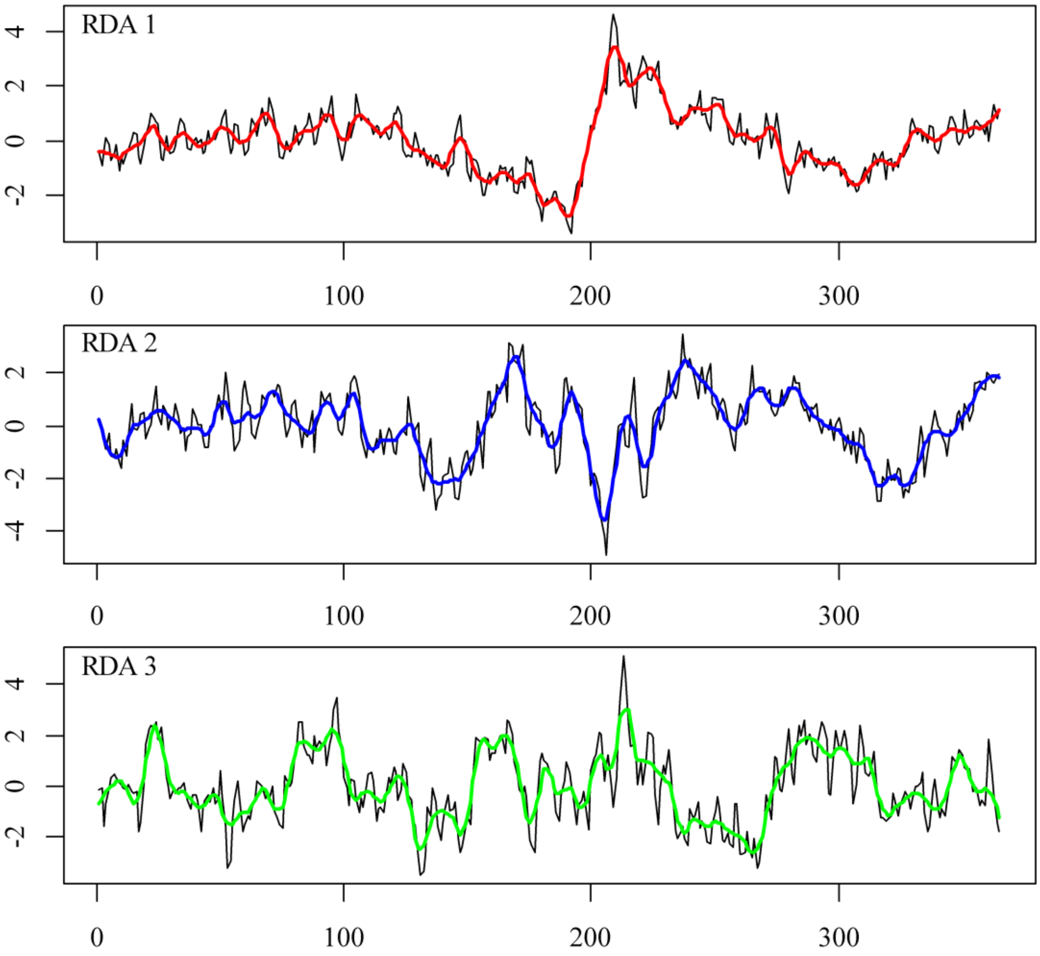

Figure 5. Broad-scale components RDA 1-3 of the annual temperature variation. Black line – the original data, colored lines – smoothed data. The abscissa axis – the number of days from 1 July of the previous year to June 31 of the next year

dbMEM-variables 11-40 were considered as reflecting the meso-scale component of the temperature variation. These variables explain 29.7% of total variation of the polynomial trend residuals (*F* = 6.13, *p* <0.001). Constrained RDA of the polynomial trend residuals with meso-scale variables as predictors revealed three RDA-axis, which reflect the meso-scale patterns of annual temperature deviations from the typical temperature trend (Figure 6). The characteristic periods being the typical for meso-scale RDA-axis 1 has a duration of 45 days, for RDA-axis 2 – 28 and 45 days, for RDA-axis 3 – 18 and 36 days.

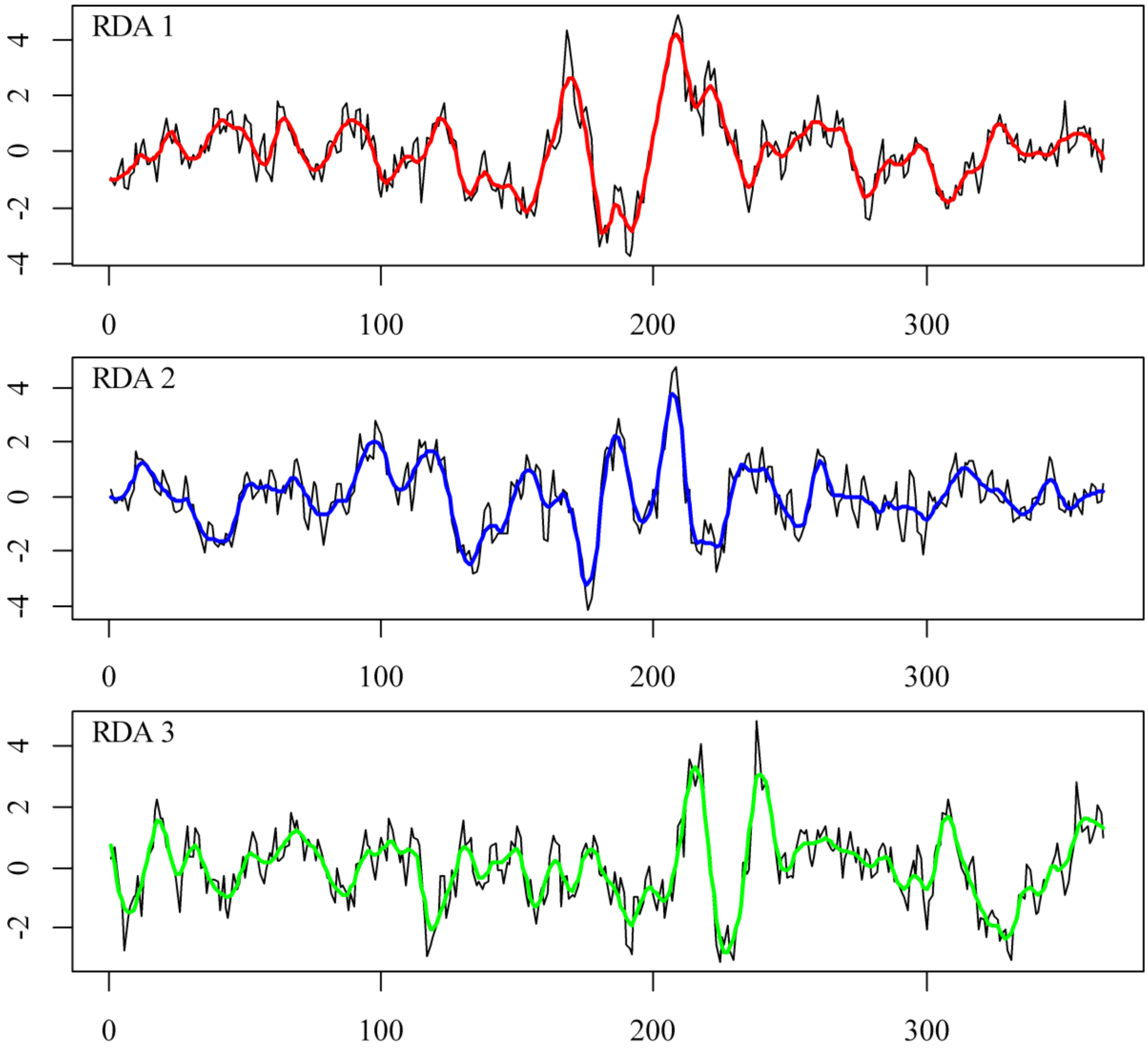

Figure 6. Medium-scale components RDA 1-3 of the annual temperature variation. Black line – the original data, colored lines – smoothed data. The abscissa axis – the number of days from 1 July of the previous year to June 31 of the next year.

dbMEM-variables 41-85 were considered as as reflecting the fine-scale component of the temperature variation. These variables explain 6.6% of total variation of the polynomial trend residuals (*F* = 1.56, *p* <0.001). Constrained RDA of the polynomial trend residuals with fine-scale variables as predictors revealed three RDA-axis, which reflect the fine-scale patterns of annual temperature deviations from the typical temperature trend (Figure 7). The characteristic periods being the typical for fine-scale RDA-axis 1 have duration 22, 33 and 72 days, for RDA-axis 2 – 14 and 18 days, for RDA-axis 3 – 15, 28 and 60 days.

The *Esox lucius* spawn was the first among of all the studied species of fish. The *Esox lucius* spawning started from 66 to 96 day of the year and finished from 78 to 113 days of the year (Table 1). The onset of the *Perca fluviatilis* spawning varied from 98 to 115 days of the year and termination varied from 124 to 103 days of the year. Next in order of time the *Rutilus rutilus* spawning was occurred. The spawning start of this species took place from 106 to 123 day of the year and spawning finish was from 115 to 131 days of the year. The timing of the onset of *Abramis brama* spawning occurred from 113 to 134 days of the year. The timing of the end of spawning took place from 123 to 141 days of the year. After *Abramis brama* the *Carassius gibelio* spawning took place. For this species spawning started from 114 to 136 days of the year and finished from 130 to 160 days of the year. The *Blicca bjoerkna* spawning began from 122 to 142 days of the year and finished from 141 to 160 days of the year. The *Scardinius erythrophthalmus* spawning started from 126 to 150 days of the year and finished from 139 to 157 days of the year.

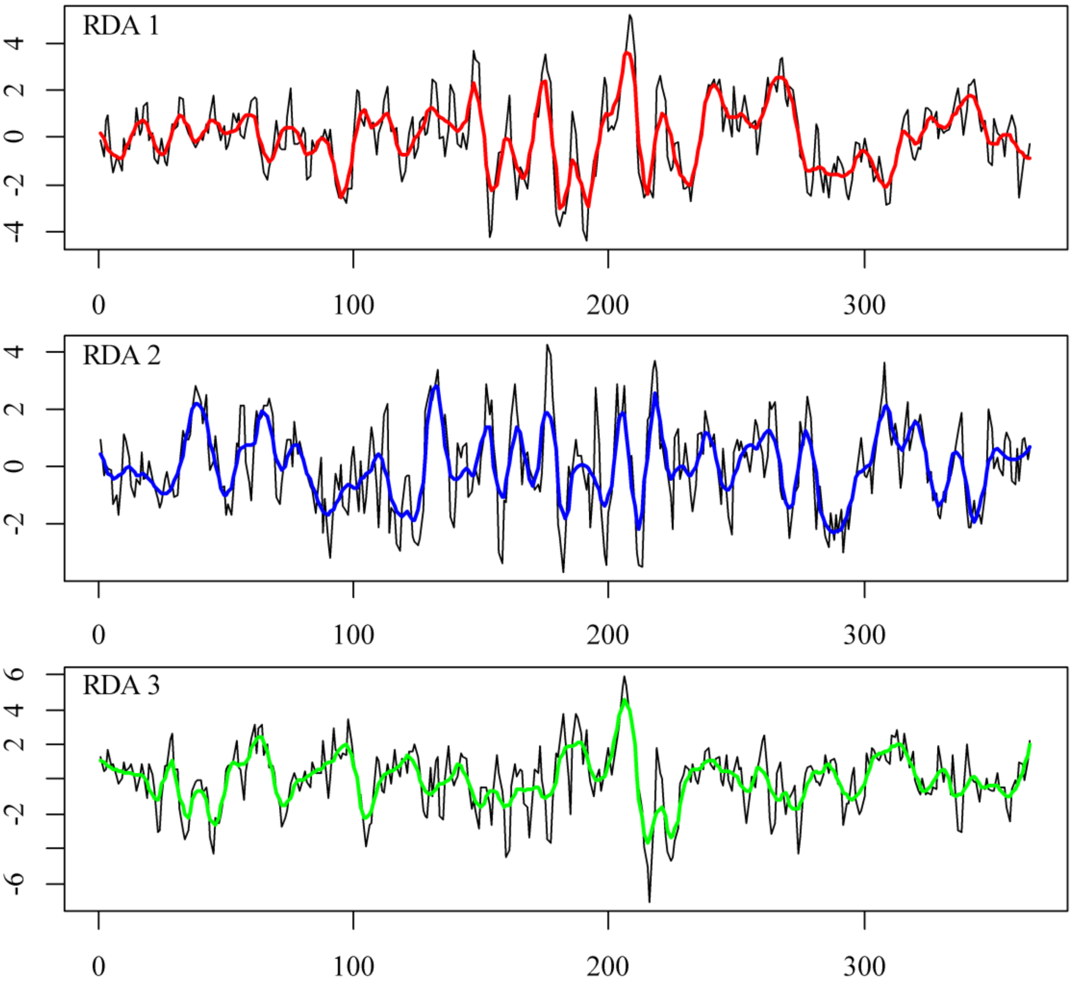

Figure 7. Fine-scale components RDA 1-3 of the annual temperature variation. Black line – the original data, colored lines – smoothed data. The abscissa axis – the number of days from 1 July of the previous year to June 31 of the next year.

The spawning period for the studied fish is ranged from 66–96 days of the year to 141–160 days of the year. The spawning duration is 55–85 days. The variability of the start or end of the spawning period is highest at the beginning or end of the whole spawning range (Figure 8). It is important to note the variation of the spawning start time is larger than that of end time (Wilcoxon Matched Pairs Test $Z = 4.41$, $p < 0.001$).

During the study period, a trend to reduce the *Esox lucius* and *Carassius gibelio* spawning start and end time was identified (Figure 9). There was a tendency to increase the *Blicca bjoerkna, Scardinius erythrophthalmus, Abramis brama* and *Rutilus rutilus* spawning time parameters. There was no statistically significant trend indicating changes in the *Perca fluviatilis* spawning timing.

Fishes spawning occurred within the narrow water temperature ranges, which are specific for each fish species (Table 2). There are statistically significant differences between ponds in water temperatures at which the spawning start occurred. Also, the water temperature at which the spawning start occurred is linearly dependent on the time of the spawning start, as evidenced by the results of the regression and correlation analysis.

Table 1. Descriptive statistics of the fish spawning characteristics for the period 1997-2018 ($N = 84$).

Species	**Biotope**	***Start***					***End***				
		Mean	***CV***	***Min***	***Max***	***Median***	***Mean***	***CV***	***Min***	***Max***	***Median***
Blicca bjoerkna	1	134.0	2.75	127	141	135	154.6	2.29	150	160	155
	2	127.7	1.95	122	131	128	143.8	1.55	141	148	143
	3	134.6	2.69	127	142	135	156.0	2.02	150	160	157
	4	130.1	2.83	122	138	131	148.7	1.92	144	154	148
Carassius gibelio	1	125.9	3.54	119	136	125	149.7	3.78	140	160	149
	2	119.0	4.69	113	132	117	140.4	4.16	130	153	139
	3	128.0	3.23	121	136	127	140.4	4.11	132	153	141
	4	124.0	4.87	116	135	122	145.0	4.61	137	160	143
Scardinius erythrophthalmus	1	140.1	3.18	131	148	140	151.5	1.51	148	156	152
	2	132.6	3.50	126	144	132	142.4	1.59	139	147	142
	3	142.1	2.84	136	150	142	153.2	1.62	148	157	154
	4	135.8	3.39	128	146	135	148.7	2.16	144	155	148
Abramis brama	1	125.7	3.75	116	134	126	135.2	2.06	129	139	135
	2	118.9	1.98	113	123	119	127.3	2.08	123	131	127
	3	127.3	3.46	120	134	128	136.7	2.12	130	141	137
	4	119.7	3.74	114	131	119	132.0	1.92	126	136	132
Perca fluviatilis	1	108.0	3.29	102	113	109	115.4	2.40	110	120	115
	2	102.2	2.86	98	108	102	107.7	2.81	103	113	108
	3	109.6	2.89	105	115	110	117.8	3.14	110	124	118
	4	103.9	3.29	98	111	104	110.8	2.19	106	114	110
Rutilus rutilus	1	116.9	3.23	110	123	118	125.0	1.88	120	130	125
	2	112.7	3.29	106	120	113	118.5	2.35	115	124	118
	3	117.7	3.56	111	123	119	125.3	1.86	122	131	125
	4	113.7	3.18	107	121	115	121.8	1.51	119	125	122
Esox lucius	1	83.9	6.51	71	93	84	96.4	5.32	86	104	97
	2	75.8	6.48	66	85	76	90.1	6.88	78	100	92
	3	90.0	4.33	83	96	90	106.4	4.96	97	113	107
	4	81.2	8.01	66	90	83	97.0	6.45	82	108	98

There were temporal overlaps between spawning of the different species, which can be estimated by the Pianka mean niche overlap index. In many cases, the measured Pianka mean niche overlap indexes were statistically significant different from the random alternatives (Figure 10).

The deviation of the Pianka mean niche overlap indexes from random alternatives does not depend on the habitat type (Table 3). The decreasing trend of the Pianka mean niche overlap indexes was observed during the study period (Figure 11). Thus there is no statistically significant correlation between the average annual air temperature and the level of the niche overlap ($r = 0.004$, $p = 0.97$). The degree of niche overlapping depends on broad-scale patterns of the temperature variation (broad-scale RDA 2 and 3), medium-scale (RDA 1 and 3) and fine-scale pattern (RDA 3).

There is a negative correlation between the start and finish time of spawning (Table 4). Therefore, for further statistical analysis in order to avoid the multicollinearity between the start and finish time of spawning as the variable of the time of the spawning finish the residuals of the regression models were used, in which the time of spawning start and biotope type were used as predictors of the time of spawning finish.

In the future, a matrix that contains data for each studied species about the spawning start and the residuals of the regression models we will call the as spawning matrix.

Table 2. Descriptive statistics of the water temperature at which the spawning start of the fishes "Dnieper-Orilsky" took place (1998-2018).

Species and ANOVA of the biotope effect	**Biotope**	***Start***					***Regression and correlation with starting day number***
		Mean	***CV***	***Min***	***Max***	***Median***	
Blicca bjoerkna $F = 6.52$, $p < 0.001$	1	15.5	3.77	14.2	16.2	15.4	$6.51+0.068*x$, $r = 0.58$, $p < 0.001$
	2	14.8	4.62	13.6	15.8	15.1	$4.61+0.082*x$, $r = 0.61$, $p < 0.001$
	3	15.5	3.21	14.5	16.6	15.5	$1.12+0.11*x$, $r = 0.78$, $p < 0.001$
	4	15.2	3.51	14.1	16.1	15.2	$4.93+0.079*x$, $r = 0.58$, $p < 0.001$
Carassius gibelio $F = 5.41$, $p < 0.001$	1	13.9	6.72	12.0	15.9	13.9	$8.58+0.047*x$, $r = 0.33$, $p = 0.14$
	2	12.8	6.43	11.5	14.7	12.6	$2.61+0.086*x$, $r = 0.67$, $p < 0.001$
	3	13.3	6.62	12.2	15.7	13.2	$1.61+0.09*x$, $r = 0.49$, $p = 0.021$
	4	13.7	8.69	12.0	16.0	13.4	$1.04+0.10*x$, $r = 0.75$, $p < 0.001$
Scardinius erythrophthalmus $F = 7.23$, $p < 0.001$	1	15.8	7.36	14.3	18.1	15.5	$-15.49+0.23*x$, $r = 0.78$, $p < 0.001$
	2	15.2	7.08	13.0	17.5	15.0	$-6.97+0.17*x$, $r = 0.62$, $p < 0.001$
	3	16.7	6.76	15.1	18.3	16.9	$-5.80+0.16*x$, $r = 0.54$, $p = 0.010$
	4	15.7	5.70	14.0	17.1	15.5	$-6.93+0.17*x$, $r = 0.69$, $p < 0.001$
Abramis brama $F = 9.34$, $p < 0.001$	1	13.4	4.66	12.5	14.9	13.4	$1.77+0.092*x$, $r = 0.69$, $p < 0.001$
	2	12.6	3.96	11.9	14.1	12.6	$1.09+0.096*x$, $r = 0.47$, $p = 0.030$
	3	13.3	5.42	12.0	14.5	13.3	$-0.68+0.11*x$, $r = 0.67$, $p < 0.001$
	4	12.8	4.63	12.1	14.1	12.4	$2.80+0.083*x$, $r = 0.64$, $p < 0.001$
Perca fluviatilis $F = 40.62$, $p < 0.001$	1	8.2	3.96	7.5	8.6	8.1	$4.47+0.034*x$, $r = 0.37$, $p < 0.095$
	2	7.4	4.07	6.9	8.1	7.5	$3.59+0.037*x$, $r = 0.36$, $p < 0.11$
	3	8.3	3.00	7.8	8.6	8.3	$3.37+0.048*x$, $r = 0.57$, $p = 0.007$
	4	7.6	4.64	7.0	8.3	7.4	$1.39+0.059*x$, $r = 0.58$, $p = 0.006$
Rutilus rutilus $F = 7.63$, $p < 0.001$	1	10.2	4.74	9.0	11.1	10.1	$0.58+0.082*x$, $r = 0.64$, $p = 0.002$
	2	9.4	6.59	8.7	10.8	9.0	$-4.09+0.12*x$, $r = 0.67$, $p < 0.001$
	3	9.9	4.58	9.1	10.7	9.9	$1.17+0.073*x$, $r = 0.68$, $p < 0.001$
	4	9.7	5.24	8.9	10.4	9.7	$-3.98+0.121*x$, $r = 0.85$, $p < 0.001$
Esox lucius $F = 14.31$, $p < 0.001$	1	6.0	8.03	5.1	6.7	6.1	$1.62+0.053*x$, $r = 0.59$, $p = 0.005$
	2	5.4	11.69	4.3	6.6	5.1	$0.80+0.060*x$, $r = 0.47$, $p = 0.03$
	3	6.1	10.01	4.4	6.7	6.4	$-3.17+0.10*x$, $r = 0.66$, $p < 0.001$
	4	5.1	13.35	4.0	6.0	4.9	$0.37+0.058*x$, $r = 0.56$, $p = 0.009$

The partitioning of the spawning matrix into broad-, medium and fine-scale temperature temporal components and biotope type revealed that these predictors are able to explain 62.9% of the spawning timing variability (Figure 12). The biotope type variable has the most important role in determining the spawning timing and explains 44.8% of the variation embraced by the spawning matrix. The broad-scale temperature temporal component explains 9.8 % of the variability of the spawning timing, medium-scale component – 7.5 %, and fine scale – 7.7 %. Thus, the lower to the level variation fine-scale temporal patterns have a similar impact on spawning timing, as well as broad-scale patterns.

The principal component analysis allowed to extract from spawning matrix a set of five principal components whose eigenvalues are greater than 1 (Table 5). The principal component 1 represents the correlated variations of the starting date of spawning between the studied fish species. Also, this component indicates that the earlier spawning of the all fish species is associated with the later ending of the *Carassius* *gibelio* and *Scardinius erythrophthalmus* spawning. The principal component 2 is sensitive to the timing of the spawning finish. This principal component reveals that the *Perca fluviatilis* end of the spawning is out of phase with the end of the spawning of the other fish species. The date of spawning beginning of such species as *Blicca bjoerkna*, *Carassius gibelio*, *Scardinius erythrophthalmus*, and *Rutilus rutilus* were in coherence with the terms of the end of the all fish spawning. The principal component 3 is the most sensitive to the *Esox lucius*, *Blicca bjoerkna*, and *Abramis brama* end of the spawning. The principal component 4 is the most sensitive to the *Scardinius erythrophthalmus* and *Rutilus rutilus* end of the spawning. The principal component 5 is the most sensitive to the *Perca fluviatilis* end of the spawning.

Table 3. Pianka mean niche overlap indexes deviation from random alternatives in dependence of temperature patterns and biotope type according GLM-analysis ($R^2 = 0.37$, $F = 4.74$, $p < 0.001$).

Predictors	***F*-ratio**	***p*-level**	***Beta*-regression coefficients**
Intercept	23.23	< 0.001	–
Biotope type	0.87	0.46	–
Broad-scale temperature patterns			
RDA 1	0.43	0.52	–0.07±0.10
RDA 2	9.47	< 0.001	–0.30±0.10
RDA 3	1.26	0.27	–0.13±0.12
Medium-scale temperature patterns			
RDA 1	2.26	0.14	0.17±0.11
RDA 2	0.02	0.89	0.02±0.11
RDA 3	0.12	0.73	–0.03±0.10
Fine-scale temperature patterns			
Fine_1	0.09	0.76	–0.03±0.11
Fine_2	0.13	0.72	0.05±0.14
Fine_3	0.01	0.91	0.01±0.10

Table 4. Dependence of the finish time of spawning from the start time of spawning and biotope type according to GLM-analysis.

Species	**Start**	**Biotope type**			R^2_a	***F*-ratio**	***p*-level**
		1	**2**	**3**			
Blicca bjoerkna	–0.63±0.10	0.53±0.10	–0.97±0.11	0.74±0.10	0.52	24.10	< 0.001
Carassius gibelio	–0.68±0.13	0.27±0.11	–0.36±0.13	–	0.38	13.89	< 0.001
Scardinius erythrophthalmus	–1.07±0.10	0.29±0.09	–0.78±0.11	0.41±0.10	0.62	34.78	< 0.001
Abramis brama	–0.89±0.08	0.22±0.08	–0.74±0.08	0.44±0.08	0.68	45.21	< 0.001
Perca fluviatilis	–0.68±0.12	0.30±0.12	–0.67±0.13	0.68±0.13	0.33	11.43	< 0.001
Rutilus rutilus	–0.80±0.08	0.37±0.09	–0.69±0.09	0.32±0.09	0.60	31.98	< 0.001
Esox lucius	–0.57±0.14	–	–0.39±0.15	0.49±0.16	0.17	5.12	< 0.001

The principal components 1, 2 and 5 did not demonstrate a statistically significant linear trend in time variation (Figure 13). A linear trend in time variability was found for the principal components 3 and 4.

The principal components 1 and 2 are sensitive to the environmental conditions of the habitats (Figure 14). In turn, the principal components 3, 4 and 5 are practically unrelated with the environmental conditions of the habitats. Also, the principal components are sensitive to temperature patterns of different scales (Table 6).

The spawning time of fish presented by the principal components 1–5 determines 47.9 % of the niche overlap (Table 7). The principal components 3 and 4 reflect the main structural characteristics of fish communities affecting niche overlap. The mean annual temperature and time trend determine the variation of spawning time, which in turn effects on the niche overlap. This result is derived from that the effect of the principal component 4 on niche overlap is not statistically significant if temperature and time patterns are used as covariates. Therefore, the principal component 4 reflects the response of the spawn activities within fish community to external factors. Taking into account the temperature trend as covariate increases the explanatory ability of the principal component 3 to explain niche overlap. This indicates that the principal component 3 is depended on the internal factors which are determined by the competitive relationship of the species within community.

Table 5. Principal components analysis of the spawning matrix ($N = 82$, significant correlation coefficients with $p < 0.05$ are presented only)

Variables	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Start					
Blicca bjoerkna	–0.78	0.33	–	–0.23	–
Carassius gibelio	–0.73	0.28	–	0.34	–
Scardinius erythrophthalmus	–0.61	0.59	–	–0.29	–
Abramis brama	–0.83	–	–0.28	–	–
Perca fluviatilis	–0.89	–	–	0.24	–
Rutilus rutilus	–0.79	–0.29	–	–	–
Esox lucius	–0.62	–	0.53	0.37	–
End, residuals					
Blicca bjoerkna	–	0.23	–0.64	–	–0.48
Carassius gibelio	0.24	0.80	–	–	–
Scardinius erythrophthalmus	0.31	0.59	–	0.46	–
Abramis brama	–	0.32	–0.61	–	–
Perca fluviatilis	–	–	0.36	–	–0.84
Rutilus rutilus	–	0.23	–0.30	0.48	–
Esox lucius	–	0.23	–0.64	–	–0.48
Statistics					
Eigenvalue	4.19	2.18	1.60	1.14	1.09
% Total	29.94	15.58	11.42	8.14	7.79
Cumulative Eigenvalue	4.19	6.37	7.97	9.11	10.20
Cumulative %	29.94	45.52	56.94	65.08	72.87

The temperature patterns determine 18.5% of the overlapping niches variability (Table 8). The fine- and broad-scale patterns have the most important role to explain niche overlap. The influence of the temperature on the niche overlap is not statistically significant if take into account the spawning matrix as covariate. Consequently, the temperature effect on the niche overlap is mediated by the influence of the temperature on the dynamics of the spawning processes of individual fish species.

The correlation indexes are the linear generalizations of the relationship between variables, which may be more complex and non-linear. This assumption is confirmed by the reproduction of the variability of the Pianka index within the spatial range of the principal components 3 and 4 (Figure 15).

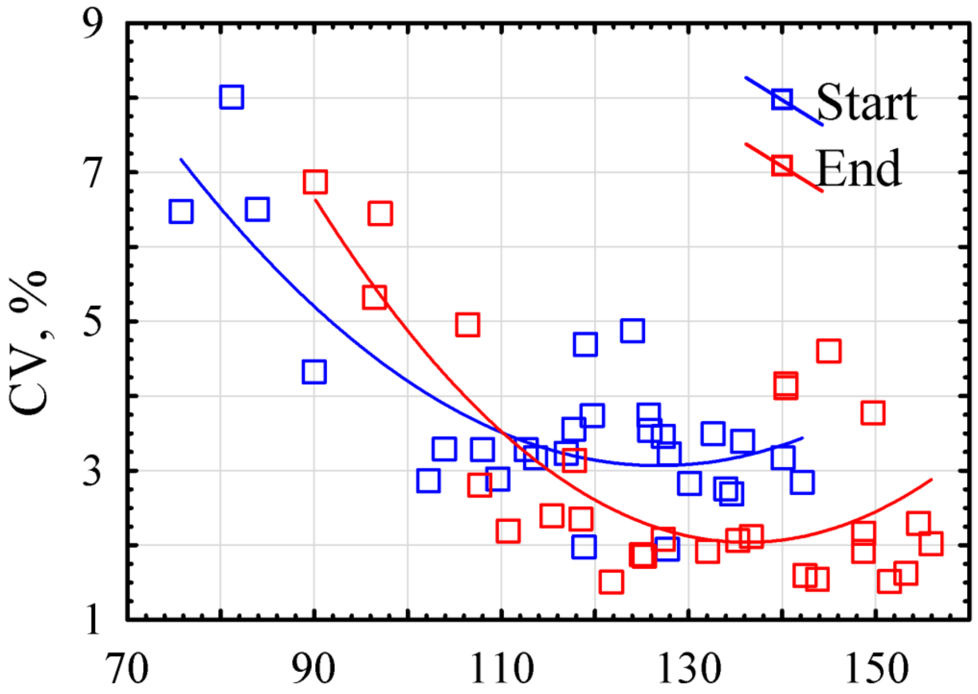

Figure 8. Dependence of the coefficient of variation of the spawning start time from the average time of the spawning onset and the coefficient of variation of the end of the spawning from the average time of the end of the spawning. The abscissa axis – days of the year; the ordinate axis – coefficient of variation (blue dot – spawning start time, red dot – spawning end time); lines – second order approximation polynomials.

Discussion

The increase in the average annual temperature is a marker of the global climate change (Jones et al. 2001). In turn, the variation in the fish timing of spawning can be indicators of climate change (Schneider et al. 2010). Substantiated evidence shows that the global average temperature has increased by 0.90 ± 0.05°C since mid-1950 and will increase by another 1-3°C by the end of this century (Hansen et al. 2010; Rohde 2013). The analysis of data for Ukraine for last 100–130 years showed the annual temperature increase by 0.6±0.2ºC/100 years which is approximately coincided with a level of global warming (Boychenko et al. 2016). However, this indicator is readily apparent only over a large time interval. The other aspects of climate warming, such as changing the precipitation rhythm, the dynamics of temperature conditions, increasing the frequency and amplitude of climatic anomalies have significant environmental effects (Cai et al. 2014). In Ukraine the decrease of amplitude of a seasonal course of temperature by ~0.4–0.5ºC was detected. The significant warming in the cold period of year and for spring was revealed but there was no significant warming for summer months (Boychenko et al. 2016). In the context of the significant fluctuations in environment which is characterized in general by the climate change concepts (Füssel & Klein 2006), the impact of annual mean temperature rise on the living organisms is difficult to reveal on the relatively short time series (Walther et al. 2002; Parmesan & Yohe 2003). This situation is complicated by the fact that there are a limited number of phenological observations data on the spawning over an extended period of time (Parmesan 2007; Woodward 2009).

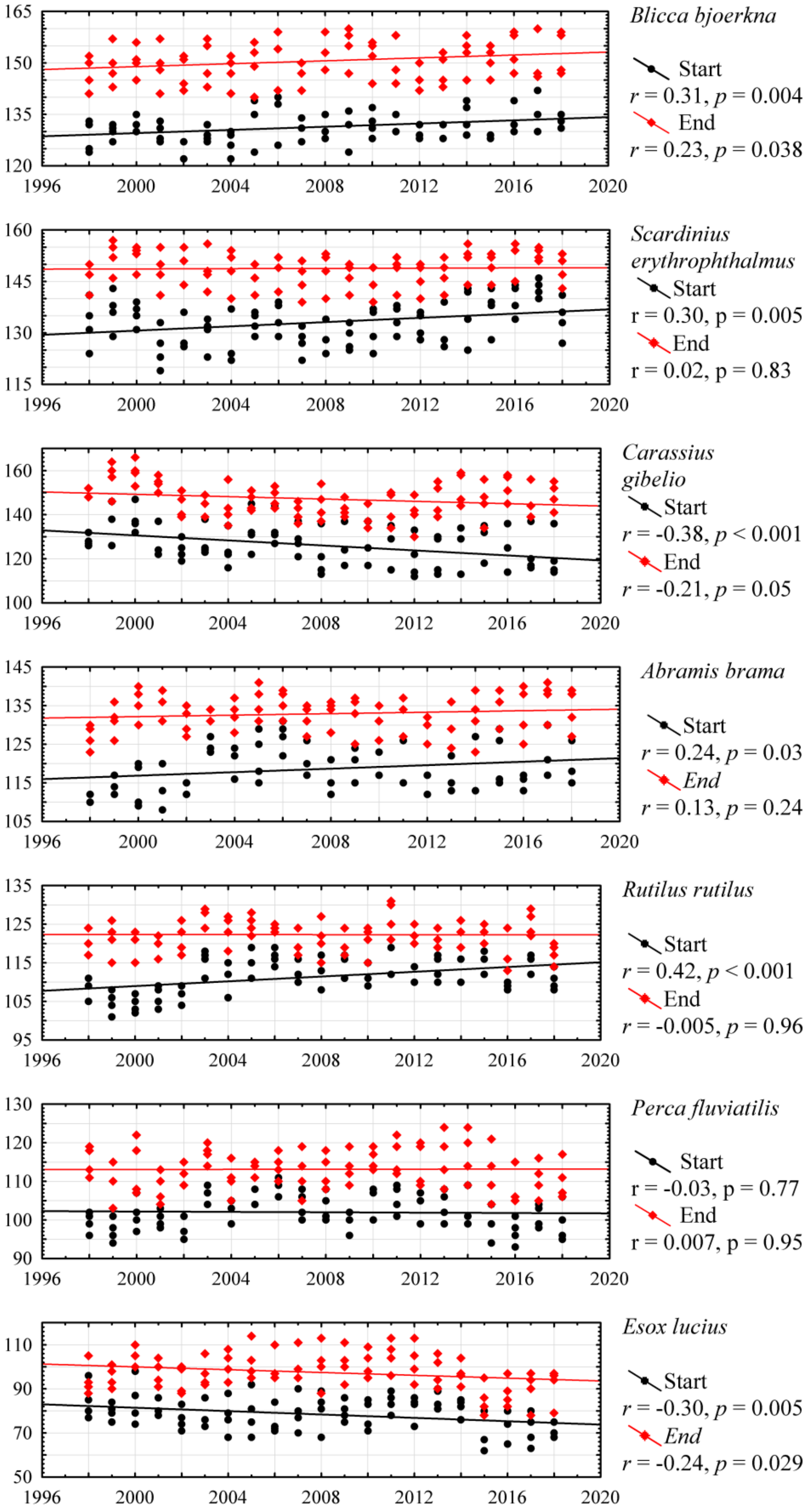

Figure 9. Dynamics of the spawning start and end of fish in the "Dnipro-Orilskiy" nature reserve. The abscissa axis – years; the ordinate axis – spawning start and end, days of the year (black dot – spawning start time, red dot – spawning end time); lines – linear trend approximation

Table 6. Fitting predictors index onto an ordination, the cosine between angle of principal components direction and predictors.

Predictors	Principal component and variation explained					R^2	*p*-level
	PC1	PC2	PC3	PC4	PC5		
Overlap*	0.32	–0.13	0.45	0.78	–0.26	0.51	<0.001
Mean annual temperature	0.38	0.29	0.44	–0.73	–0.20	0.23	<0.001
Broad-scale temperature patterns							
RDA 1	0.71	0.55	0.07	0.02	–0.43	0.15	0.03
RDA 2	0.19	0.78	–0.12	–0.32	0.49	0.37	<0.001
RDA 3	0.51	–0.13	0.51	0.45	0.51	0.11	0.10
Medium-scale temperature patterns							
RDA 1	0.37	0.18	–0.83	0.36	–0.14	0.15	0.02
RDA 2	–0.12	–0.75	0.47	0.27	0.35	0.25	<0.001
RDA 3	0.21	0.01	–0.97	–0.06	–0.08	0.18	0.01
Fine-scale temperature patterns							
RDA 1	–0.13	–0.55	–0.12	0.07	–0.81	0.15	0.03
RDA 2	–0.13	–0.09	–0.03	–0.99	0.00	0.27	<0.001
RDA 3	–0.12	0.49	0.32	0.72	0.35	0.08	0.29

Symbols: * – Pianka mean niche overlap indexes deviation from random alternatives

Table 7. Redundancy analysis of the Pianka mean niche overlap index deviation from random alternative.

Constrained variables	R^2	*p*-value	Conditional: Temperature*		Conditional: Temperature+Time**	
			R^2	*p*-value	R^2	*p*-value
PC1	0.042	0.030	0.070	0.011	0.048	0.033
PC2	–0.004	0.418	–0.010	0.616	–0.011	0.647
PC3	0.093	0.006	0.196	0.001	0.077	0.004
PC4	0.300	0.001	0.160	0.002	0.016	0.162
PC5	0.024	0.069	0.000	0.325	0.083	0.010
Total	0.479	0.001	0.389	0.001	0.218	0.001

Symbols: * – mean annual temperature; ** – year sequence

Table 8. Redundancy analysis of the effect of the temperature patterns on the Pianka mean niche overlap index deviation from random alternative.

Constrained variables	R^2	*p*-value	Conditional: Spawning*		Conditional: Spawning+Time**	
			R^2	*p*-value	R^2	*p*-value
Broad	0.090	0.017	0.010	0.204	0.019	0.125
Medium	0.031	0.151	–0.010	0.682	–0.009	0.635
Fine	0.105	0.018	–0.014	0.819	–0.017	0.917
Total	0.185	0.003	0.024	0.221	0.022	0.204

Symbols: * – spawning matrix; ** – year sequence

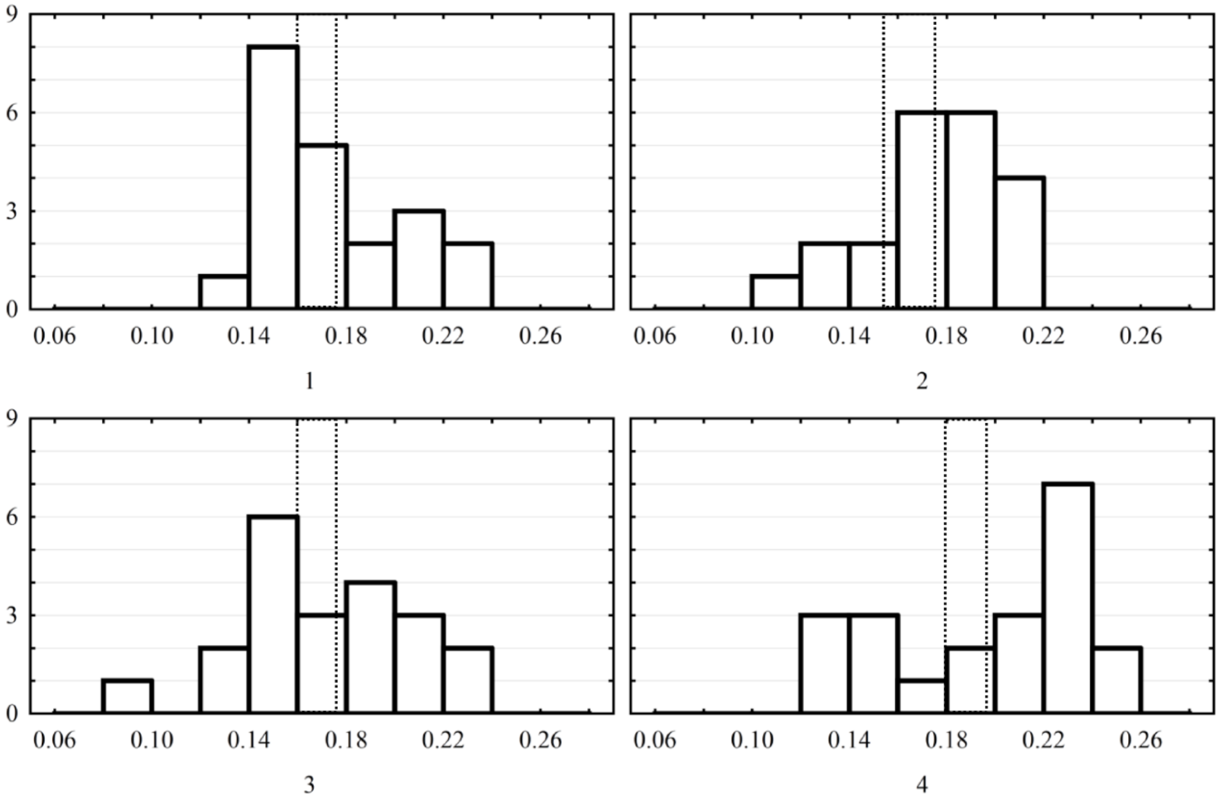

Figure 10. Distribution histograms of the Pianka mean niche overlap indexes in different types of habitats: 1 – Nikolayev system of water bodies; 2 – river Protoch system and Obukhov floodplain; 3 – the channel of the river Dnipro; 4 – water bodies of the Taromske ledge.

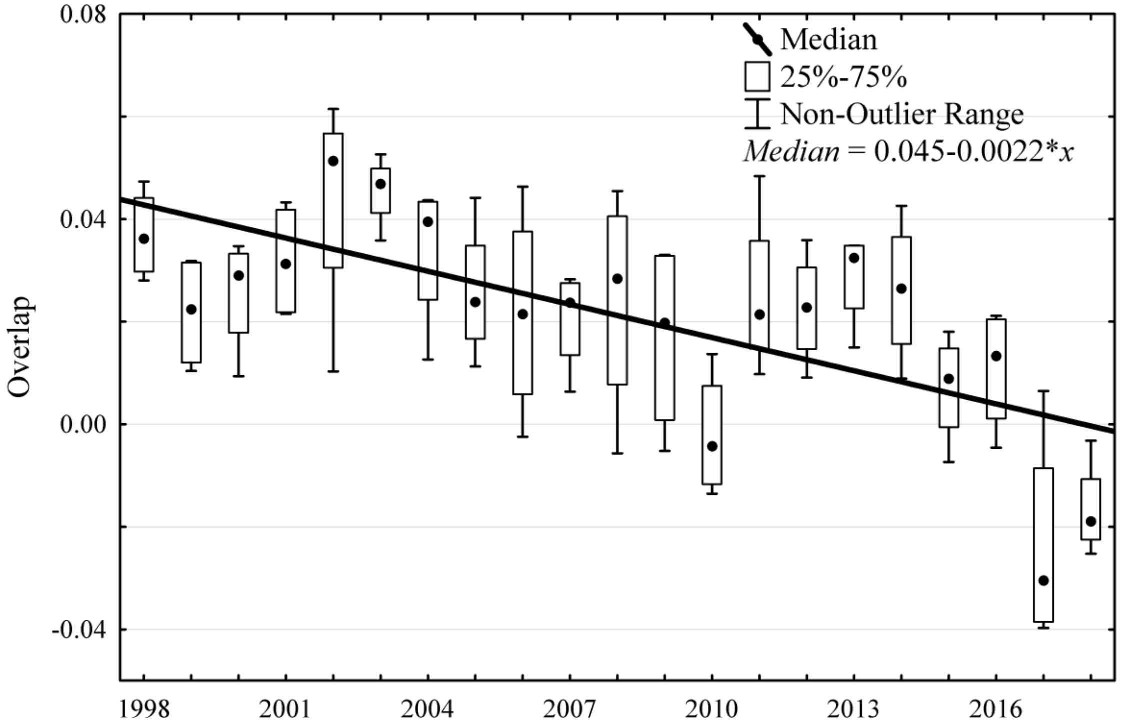

Figure 11. Temporal trend of the Pianka mean niche overlap indexes deviation from random alternatives (1998–2018). The abscissa axis – years, the ordinate axis – the Pianka mean niche overlap indexes deviation from random alternatives, line – the linear approximation of the temporal trend ($R^2 = 0.32$, $p < 0.001$).

The phenology concept is based on the principle that biological systems are able to adapt to repeated changes of the environmental systems (Turner et al. 2010; Helm et al. 2013). Obviously, biological systems cannot adapt to unpredictable environmental changes. This approach makes it relevant to find repeated patterns of the environmental regimes and evaluate their effects on phenology. Temperature effects on the fish biological properties connected with the reproduction of fish, the definition of the sex, gametogenesis dynamics, gametes quality, fertility, age, sexual maturity and the duration of the reproductive period (Billard 1978, 1986; Jafri 1989; Sandström et al. 1995; Alavi & Cosson 2005; Lahnsteiner & Mansour 2012; Domagała et al. 2013). The temperature in temperate latitudes shows the seasonal dynamics. The period of the temperature course is one year. Annual timekeeping mechanisms promote animals to adapt for the seasonal changes (Paul et al. 2008). Phenology events can be explained by the oscillating processes with higher frequency and therefore shorter time period. The dbMEM-approach is a quite flexible method for detecting of the multiscale temporal pattern (Dray et al. 2006). Using this method, the broad-, medium-, and fine-scale temperature patterns were extracted. These patterns are most sensitive to temperature changes in winter and spring, which are very important for describing temperature regime before and during spawning.

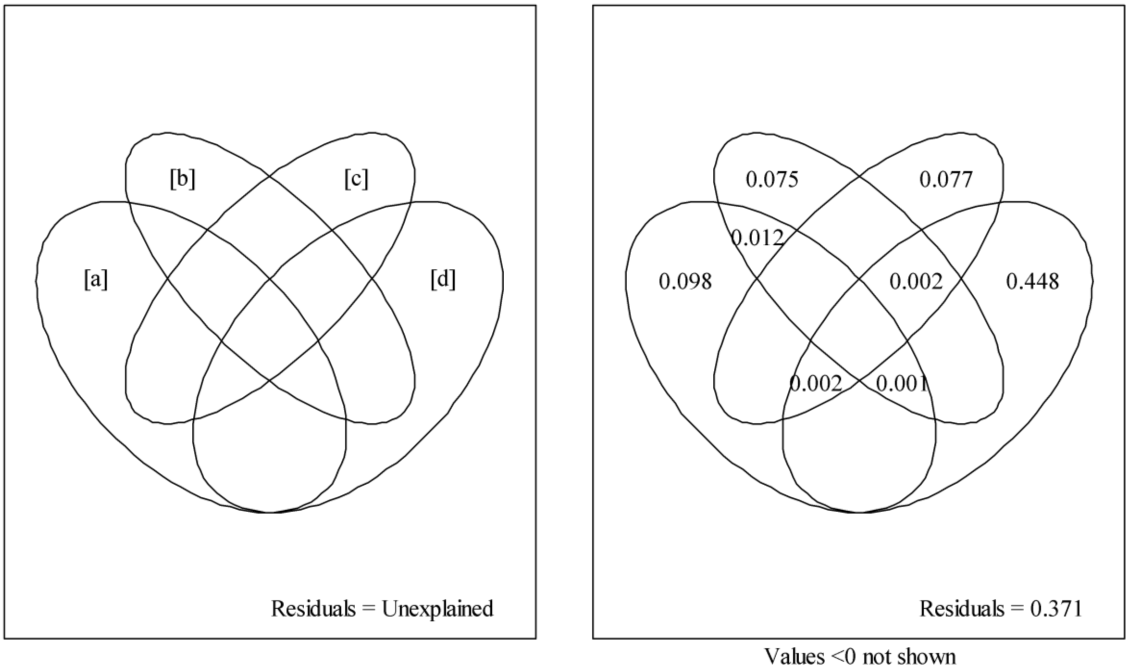

Figure 12. Spawning variance partitioning between broad-, medium-, and fine-scale temporal temperature patterns and biotope type explanatory variables.

Notes: [a] – variation explained solely by broad temperature variables; [b] – variation explained solely by medium temperature variables; [c] – variation explained solely by fine temperature variables; [d] – variation explained solely by biotope type. The intersection of the ellipses corresponds to the variations explained by the respective sources together All the variance fractions shown are significant (*p* <0.001).

Our results reveal a coherent dynamics of the spawning timing of the fish species, which can be explained by the variety factors of a different origin. Species differ in the degree to which their phenologies shift due to climate change (Harrington et al. 1999; Hegland et al. 2009). A coherent dynamics of the spawning timing was shown by means of principal components analysis. The principal components 1 and 2 are the most important to explain the spawning timing which are depended on site-specific properties of the biotope types. This result is due to the spawning of each fish species occurs at considerably different time in different bodies of water of the Dnieper river system. The time differences of the spawning between biotopes do not demonstrate a linear temporal trend. The site-specific differences of the spawning timing between biotopes are coherent for all fish species, and because of this, these differences do not effect on niche overlap. In fact, this indicates that in different waters, there is a fixed time shift of the time of the spawning for all fish species studied. The principal components 3 and 4 reflect the phenology changes which effect on

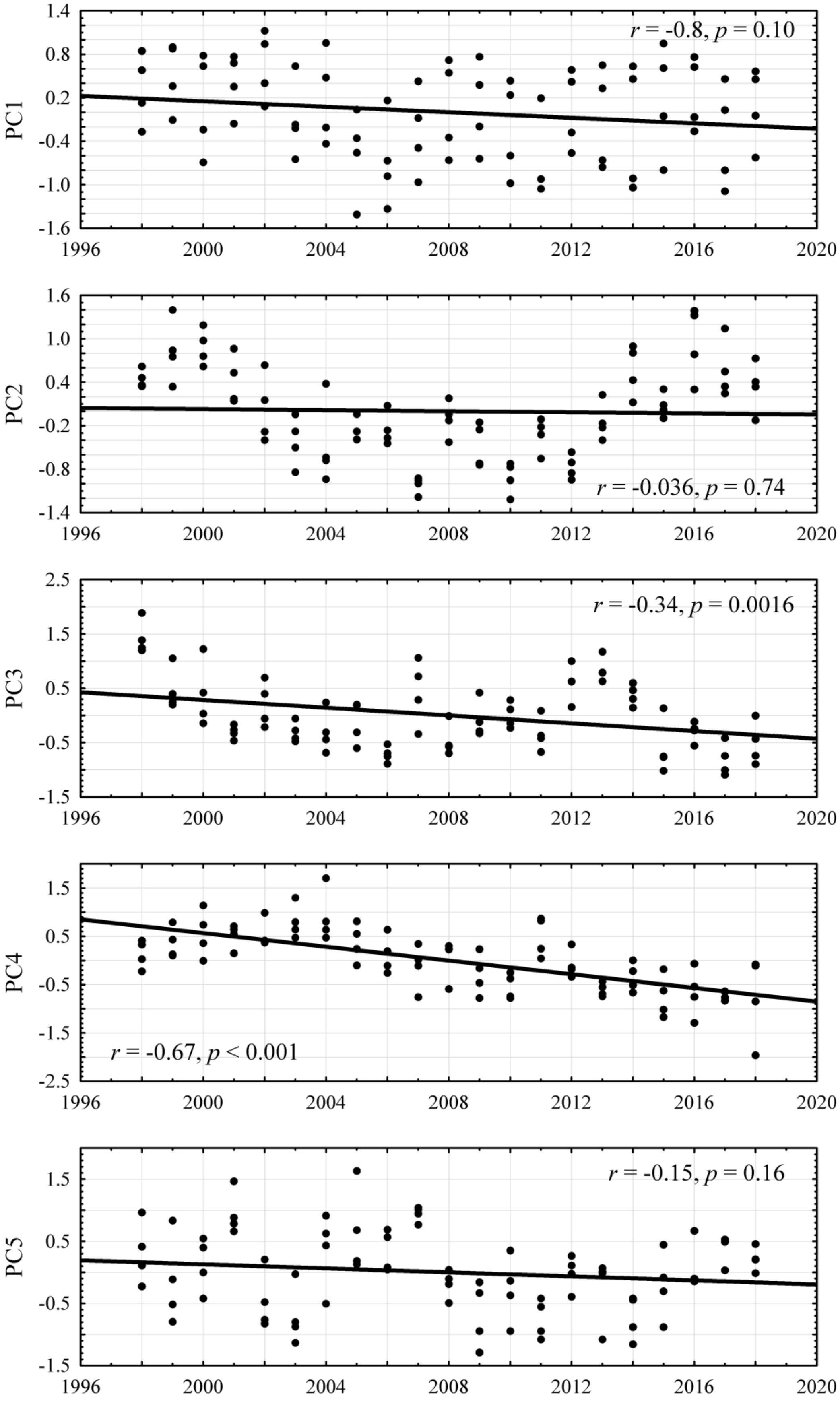

Figure 13. The temporal variation of the principal components 1–5. the *x*-axis – years, the *y*-axis – the scores of the principal components 1–5.

the niche overlapping. As a consequence of different species reacting dissimilarly, even minor climate changes may induce fluctuation responses unbalancing established patterns of synchrony (Durant et al. 2007). Most likely, the changes of the niche overlapping are caused by both exogenous and endogenous factors. The exogenous temperature factors specifically affect the spawning period of the different fish species. The different response of the fish species on equal temperature cues leads to the changes of the niche overlap in the fish community. Endogenous factors are the result of the competition between fish species, leading to incoherent shifts in spawning time and, consequently, to a variation of the niche overlap.

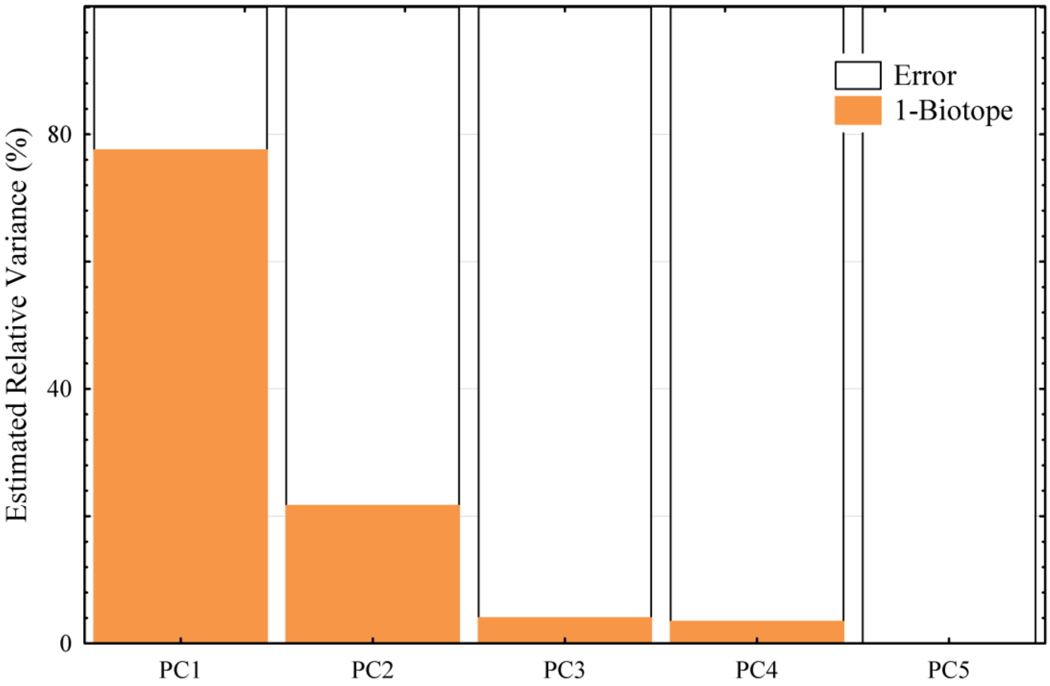

Figure 14. Relative variance of the principal components (in %). Method: ANOVA Method, Type I SS, columns denote cumulative sums of variance components.

The niche overlap demonstrated a clear trend of decreasing over the time. This result shows that the prevalence of the environmental factors in the temporal organization of the community is changed by the prevalence of the competition (Tokeshi 1986; Reinhardt et al. 2013). This trend is monotonic during the study period, but weakly correlated with the trend of the average annual air temperature. This suggested that the nature of this trend is due to the regular oscillatory components of the annual course of temperature, which may be modeled by the dbMEM-variables. The complex nature of the temperature action on the spawning phenology is also emphasized by the fact that between the date of the spawning start and the water temperature at this date there is a correlation. This indicates that the water temperature is a limiting factor for fish spawning, but not a trigger, starting the spawning activity. If the water temperature is below the critical value, spawning can not occur, but achievement of the water such a temperature does not start spawn automatically. Climate induced phenology shifts could have positive or negative consequences for the populations involved (Forrest & Miller-Rushing 2010). Obviously, the dynamics of the environment properties in the previous spawning period determines the possible moment of its occurrence. The changes in spawning phenology have consequences for the structure and functioning of the community as a whole (Turner et al. 2010). The increase of temporal spawning overlap of the different fish species helps to reduce predation on a population of the species, but simultaneously decreases the trophic resources because it need to share with other species. The decrease of temporal spawning overlap may have the opposite effect.

During the period of studies it was found that the spawn of the early spawning species began to start earlier and the late spawning species began to start later. This fact also indicates that the increase of the average annual temperature is not the key cause of such changes. The same results were obtained in the study of climate driven changes in the spawning of roach and bream in the Estonia (Noges & Jarvet 2005). As response on the long-term trend of the water temperature increasing it was found that the date of the bream spawning shifted to early period but the range of spawning temperature remained unchanged but in contrast there was no shift in the spawning time for roach but spawn start was at higher water temperature. In our investigation the much more intense change in the timing of the spawning start than spawning end led to temporal trend of the niche overlapping decrease.

We have used MEM-approach for modeling the temporal dynamics of the annual temperature variation. We proceeded from the assumption that phenology is a manifestation of the life cycle adaptation to repeated patterns of the environment variations. The approach has shown that there is a wide variety of the regular oscillator patterns of the temperature dynamics that have an impact on fish spawning phenology. These patterns have different frequency characteristics and reflect the oscillator variation in the annual temperature course of the varying periodicity. The amplitude of oscillation decreases with increasing frequency of the corresponding process, but the biological role does not depend on the amplitude monotonically. The most important are broad-scale and fine-scale oscillatory processes. The seasonal temperature and broad-scale component of the temperature variation can be identified as the "ultimate" factors. The fine-scale of the temperature variation may be viewed as "proximate causes", directly acting as spawning triggers.

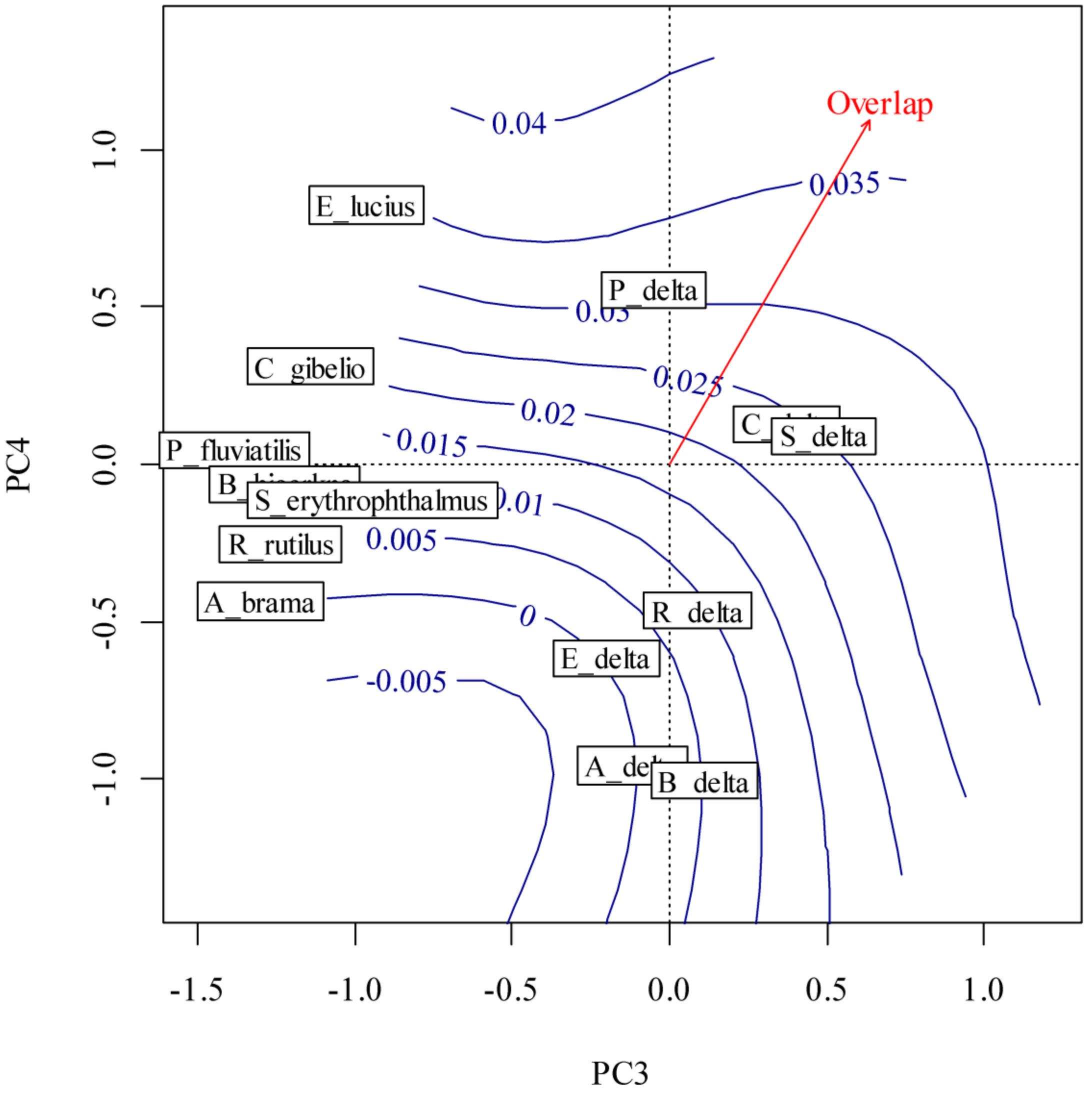

Figure 15. The variation of the Pianka mean niche overlap index deviation from random alternative within principal components 3 and 4. Spawning start: B_bjoerkna – *Blicca bjoerkna*, C_gibelio – *Carassius gibelio*, S_erythrophthalmus – *Scardinius erythrophthalmus*, A_brama – *Abramis brama*, P_fluviatilis – *Perca fluviatilis*, R_rutilus – *Rutilus rutilus*, E_lucius – *Esox lucius*; regression residuals of the spawning end dependence from the start: B_delta – *Blicca bjoerkna*, C_delta – *Carassius gibelio*, S_delta – *Scardinius erythrophthalmus*, A_delta – *Abramis brama*, P_delta – *Perca fluviatilis*, R_delta – *Rutilus rutilus*, E_delta – *Esox lucius.*

Conclusion

The increasing of the average temperature from 1998 to 2018 was documented in the study area. The annual course of the temperature takes a sinusoidal waveform and the residuals of the corresponding polynomial trend are specific for each year. The residuals may be decomposed on the broad-, medium-, and fine-scale oscillatory components. There were temporal overlaps between spawning of the different species. The decreasing trend of the Pianka mean niche overlap indexes was observed during the study period. The changes of the niche overlapping are caused by both the exogenous and the endogenous factors. The evaluation of the role of the exogenous factors reveals that there is no statistically significant correlation between the average annual air temperature and the level of the niche overlap but the degree of niche overlapping depends on broad-, medium-, and fine-scale patterns of the temperature variation. The endogenous factors are the result of the competition between fish species, leading to a variation of the niche overlap. A role of the endogenous factors for structuring fish communities demonstrates increasing as the response on the global trend of the climate warming.

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