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Fish assemblages under climate change in Lithuanian rivers

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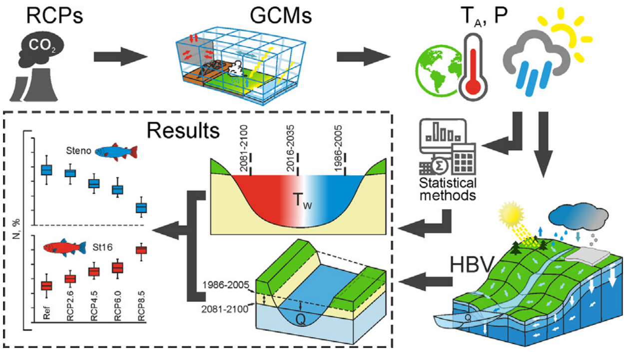
HIGHLIGHTS

- Future climate changes are likely to affect fish assemblages in rivers.
- Projections were made using hydrological modelling and statistical methods.
- River discharge is projected to decrease, while temperature is likely to increase.
- Changes of abiotic factors will cause changes in abundance of investigated fishes.
- Changes of river temperature will have most significant impact on fish abundance.

GRAPHICAL ABSTRACT



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ABSTRACT

Alterations of abiotic factors (e.g., river water temperature and discharge) will definitely affect the fundamental processes of aquatic ecosystems. The purpose of this study was to examine the impact of climate change on the structure of fish assemblages in fast-flowing rivers belonging to the catchment of the major Eastern European river, the Nemunas. Five catchments of semi-natural rivers were selected for the study. Projections of abiotic factors were developed for the near (2016–2035) and far future (2081–2100) periods, according to four RCP scenarios and three climate models using the HBV hydrological modelling tool. Fish metric projections were developed based on a multiple regression using spatial data. No significant changes in projections of abiotic and biotic variables are generally expected in the near future. In the far future period, the abiotic factors are projected to change significantly, i.e., river water temperature is going to increase by 4.0–5.1 °C, and river discharge is projected to decrease by 16.7–40.6%, according to RCP8.5. By the end of century, the relative abundance of stenothermal fish is projected to decline from 24 to 51% in the reference period to 0–20% under RCP8.5. Eurythermal fish should benefit from climate change, and their abundance is likely to increase from 16 to 38% in the reference period to 38–65% under RCP8.5. Future alterations of river water temperature will have significantly more influence on the abundance of the analysed fish assemblages than river discharge.

1. Introduction

The newest research results published by the Intergovernmental Panel on Climate Change in the Fifth Assessment Report on Climate

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Change (IPCC AR5) state that the planet's biota and ecosystem processes were strongly affected by past climate changes at rates lower than those projected during the 21st century under high warming scenarios. In the second half of this century, climate change is projected to be even more powerful stressor on freshwater ecosystems (Settele et al., 2014). The latest IPCC AR5 climate projections are based on the 5th phase of Coupled Model Intercomparison Project (CMIP5) (Taylor et al., 2011) and newly developed Representative Concentration Pathways (RCPs) (Moss et al., 2010; van Vuuren et al., 2011), which replaced the previously used emission scenarios. RCPs represent different possible values of radiative forcing (2.6, 4.5, 6.0, and 8.5 W m^2) on the Earth's atmosphere in year 2100. This way, the entire spectrum of possible changes could be evaluated. Andrews et al. (2010) and Watterson and Whetton (2011) presented one of the first global projections of air temperature and precipitation based on RCPs. RCPs have already been used in climate change projections for Lithuania (Keršytė et al., 2015; Kažys et al., 2016; Stonevičius et al., 2017).

Research in Lithuania and other Baltic countries has shown that precipitation and air temperature are the key factors responsible for runoff redistribution throughout the year (increased runoff in winter and lower flood discharges in spring) (Kriauciuniene et al., 2012; Kayhko et al., 2015; Stonevičius et al., 2017). The analysis of the water thermal regime and its projections revealed a positive trend in the water temperature of Lithuanian rivers (Jurgelėnaitė and Jakimavičius, 2014). A study by Šarauskienė et al. (2017) projected that a significant decrease of spring flood discharges and low flows of the summer period as well as a significant increases of river water temperatures are expected due to climate alterations in Lithuania at the end of the 21st century. It is certain that the projected alterations will influence shifts in the distribution of freshwater species (Ficklin et al., 2014; Settele et al., 2014; Sternberg et al., 2015).

The temperature and physical structure of rivers are considered as the main factors controlling river fish assemblages (Allan and Castillo, 2007; Logez et al., 2013). Temperature is the dominant factor at a large scale (Buisson et al., 2008; Logez et al., 2012). There are several studies in which the potential impact of an increase in temperature on fish assemblages was indirectly proved based on a spatial data analysis (Buisson and Grenouillet, 2009; Logez et al., 2013; Pletterbauer et al., 2015; Radinger et al., 2016), or directly based on a multi-year data analysis (Daufresne et al., 2003; Piffady et al., 2013). Species that live at the edges of the spreading range where the temperature is completely at the verge of the upper permissible limit are typically the most sensitive to temperature increases. Even a slight increase in water temperature may exceed the physiological tolerances of fish and force them to seek thermal refuge (Guillemette et al., 2010).

It is more difficult to predict changes in fish communities due to the redistribution or reduction of annual runoff caused by climate change. The nature of the impact depends both on the timing of the flow changes, and on the environmental needs of the fish itself. Flow variations can have effects on post-spawning factors responsible for recruitment (Humphries et al., 2002; Nislow et al., 2002; Nunn et al., 2007). High flows can increase the growth of young-of-the-year salmonids (Jones and Petreman, 2013). Similarly, a higher summer discharge has a positive influence on the juvenile abundance of benthic rheophilic species, while an increase in the mean spring flow may have a detrimental effect on juveniles of water column rheophilic cyprinidae species (Piffady et al., 2013). Since susceptibility of fish juveniles to displacement by flow declines with an increase in size, the effects of floods on stream fish communities can depend on small differences in the timing of reproduction and flooding (Harvey, 1987). In contrast, adult fishes are resilient to flooding and draughts (Franssen et al., 2006), but the fish communities' resistance and resilience to floods is associated with overall habitat complexity (Pearsons et al., 1992).

The purpose of this investigation is to explore the extent to which future climate change can influence the structure of functional guilds of fish in the main salmon rivers in the Nemunas River catchment and whether natural recruitment of Baltic salmon can be impacted as well. The current research seeks not only to project the impact of climate change and other abiotic factors on the structure of fish assemblages' structure, but also to assess the uncertainty of the obtained results.

2. Study area

Five catchments of semi-natural rivers of different sizes belonging to the catchment of the major European river, the Nemunas (Eastern Baltics) (Table 1, Fig. 1), with available multiannual data of water temperature, river hydrology and fish, were selected for the assessment. Only sites with at least good water quality and near-natural hydromorphology (no modifications of the river cross-section, river channel, bottom habitat and water flow, no impoundment, no or few alterations of the river banks and no major alteration of connectivity) were chosen for the assessment of fish response to changes in river flow and temperature in order to reduce the bias due to modifications of fish assemblage structure in relation to human activities (Pont et al., 2006). Daily data of air temperature and precipitation from 10 meteorological stations (MS) and daily discharge data from 5 water gauging stations (WGS) were used as the reference period (1986–2005) data for evaluation of changes of projections of river runoff and water temperature in the investigated rivers. The spatial distributions of WGS and MS are presented in Fig. 1.

3. Methodology

The methodology for the assessment of changes in fish assemblages' due to the future hydrological regime consists of five main stages (Fig. 2). The projections of air temperature and precipitation (Stage 1, Fig. 2) were prepared for the evaluation of the future hydrological regime in the investigated rivers. The projections of river runoff (Stage 2) and water temperature (Stage 3) were created using the HBV hydrological modelling tool and statistical methods. Fish metric projections (Stage 4) were developed based on spatial data using a multiple regression analysis. The SUSA software package was used for the sensitivity and uncertainty analysis of projections of fish metrics (Stage 5). A more detailed description of separate stages of the methodology is presented in the following chapters of this study.

3.1. Projections of air temperature and precipitation

The near future (2016–2035) and far future (2081–2100) projections of meteorological parameters (average air temperature, C°; precipitation amount, mm) were prepared according to four RCP scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5). The reference period of 1986–2005 and the projected periods were chosen according to the recommendations of the IPCC AR5 (IPCC, 2013). The projected values of monthly air temperature and precipitation were taken from the KNMI Climate Explorer (https://climexp.knmi.nl/start.cgi) database, while the daily data was obtained from the German Climate Computing Centre (DKRZ) (https://esgf-data.dkrz.de). For Lithuania, only median values of Global Circulation Models (GCMs) were analysed prior (Keršytė et al., 2015; Stonevičius et al., 2017). From the outputs of 24 GCMs, which had all four RCPs projection runs for Lithuania, GFDL-CM3 (Donner et al., 2011), NorESM1-M (Bentsen et al., 2010) and HadGEM2-ES (HadGEM2 Development Team, 2011) were chosen as the most representative GCMs for air temperature and precipitation monthly fields. These GCMs of the CMIP5 project have been already used in various studies of the Baltic Sea Region (Pushpadas et al., 2015; Karabil, 2017; Saraiva et al., 2018). Air temperature and precipitation values projected according to climate scenarios (i.e., combination of GCM and RCP) were used for the calculation of projections of investigated abiotic and biotic variables.

Table 1
Characteristics of the investigated rivers.

Hydrological characteristics	Rivers-WGS				
	Neris-Jonava	Šventoji-Ukmergė	Žeimena-Pabradė	Vilnia-Vilnius	Minija-Kartena
Catchment area, km^2	24,545	5381	2595	623	1220
Annual average discharge, m^3/s[a]	168	44.2	21.6	5.25	17.3
Water temperature of warm season, °C[a]	15.7	14.8	14.7	14.2[b]	15.1

[a] Data from 1986 to 2005.
[b] Data from 1993 to 2005.

3.2. Projections of rivers discharges

The semi-distributed conceptual HBV model developed at the Swedish Meteorological and Hydrological Institute was applied for hydrological modelling. The observed hydrometeorological and climate scenario output data were used for discharge projections of the selected rivers.

HBV is a technique of rainfall-runoff modelling used to calculate the total water balance in a catchment. The main HBV equation (Integrated Hydrological Modeling System Manual, 2005) is as follows:

$$P - E - Q = \frac{d}{dt}[SP + SM + UZ + LZ + V] \tag{1}$$

where P – precipitation, E – evaporation, Q – runoff, SP – snow pack, UZ – upper groundwater zone, LZ – lower groundwater zone, V – lake or dam volume.

Hydrometeorological information of the reference period of 1986–2005 was used for the model creation. The period of 1986–1995 was selected for model calibration, whereas the period of 1996–2005 was used for validation. The calibration process has to be performed until the correlation coefficient R is the greatest and the total deviation is the smallest. For the selected river catchments, R ranged from 0.75 to 0.88 for the calibration period and from 0.60 to 0.83 for the validation period. The created hydrological models of the selected river catchments were used for the calculation of river runoff projections in the near future (2016–2035) and the far future (2081–2100) periods while applying different climate scenarios.

3.3. Projections of river water temperature

To project the monthly water temperature (T_W) of the selected rivers, statistical relationships between river and air temperatures (T_A) measured in meteorological stations (MS) in the warm seasons (March–November) of 1986–2005 were created. Correlation coefficients were calculated between T_W of a particular river catchment and T_A of the closest meteorological stations. The meteorological station with the greatest correlation coefficient was selected for future T_W projections as the best representative of the river catchment. Linear equations of T_W projections were created for each investigated river for three different periods: (i) early spring (March–April), when T_A begins to rise faster than T_W, since water is not as inert and it is getting warmer much more slower than air; (ii) the period of May–October when changes of T_A and T_W stabilize and follow a similar pattern; (iii) November, which is considered a period of water cooling, when the relationship between T_A and T_W takes the opposite tendency to that in spring because of the already mentioned physical features of water, i.e., it needs more time to cool down than air. Most of the calculated correlation coefficients between T_A and T_W were >0.98 (0.994 in the Neris, 0.992 in the Šventoji, 0.988 in the Žeimena, 0.993 in the Vilnia, and 0.992 in the Minija); therefore, the generated equations were used to project river T_W according to RCP scenarios for the periods of 2016–2035 and 2081–2100. The performed validation of the water temperature model indicated that correlation coefficients between the observed T_W and calculated T_W ranged from 0.988 to 0.994 in different river catchments.

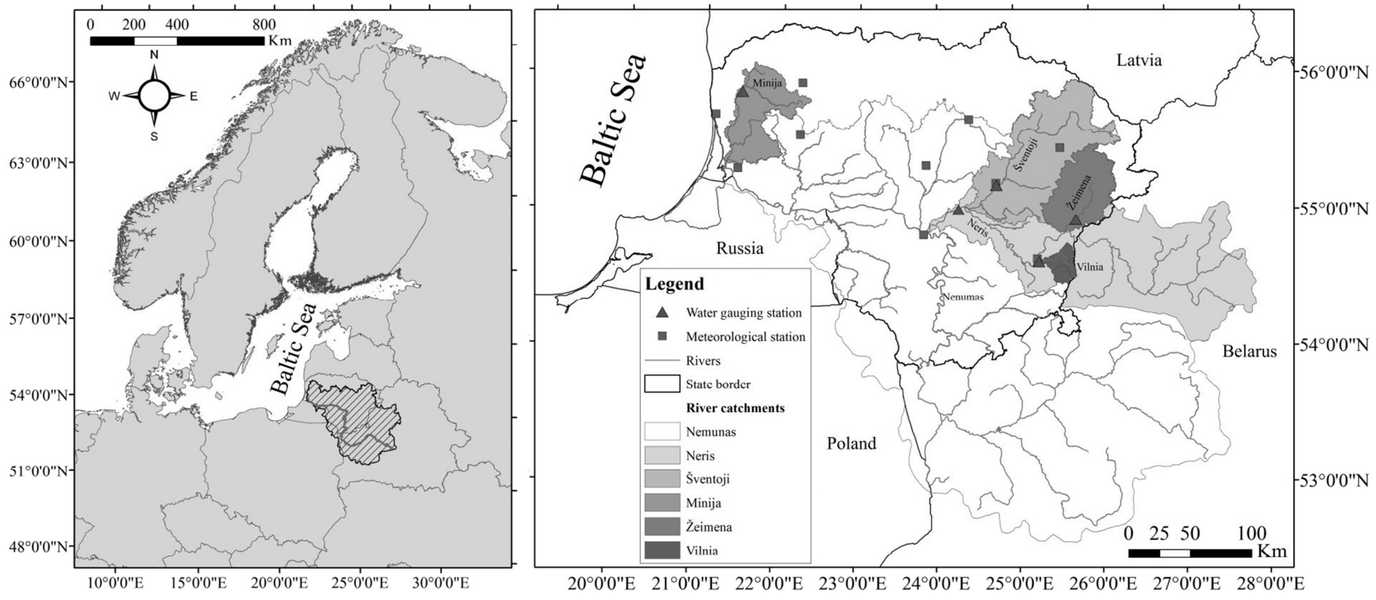

Fig. 1. Location of the investigated river basins and monitoring stations.

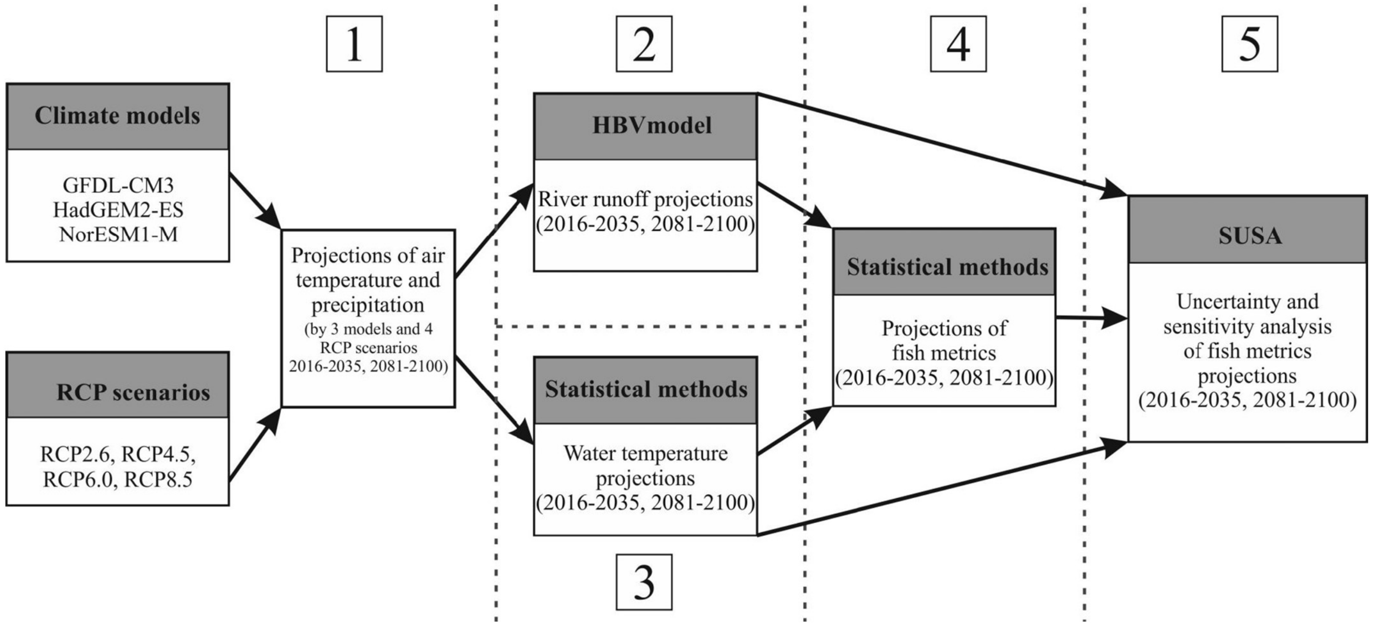

Fig. 2. The principal scheme of the study.

3.4. Projections of fish metrics

The monitoring data of fish in the selected semi-natural rivers from the period of 2003–2014 were used for the analysis of the dependence of fish metrics on abiotic factors (Q and T_W).

Fish were sampled during low-flow periods, either by wading or by boat, depending on river depth. To make the data consistent between samples collected in different years and using different strategies, only the catch from single-pass electric fishing was used. A single pass is sufficient to estimate the relative abundance of fish in streams (Bertrand et al., 2006). In total, the database included 44 fishing occasions at 20 river sites (3–6 sites per sub-basin), in which a total of 32 fish species were caught. The descriptive statistics of fish abundance and environmental characteristics of the river sites are showcased in Table 2.

The rivers are dominated by cyprinid fish species. The share of salmonid species (Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*) in the fast-flowing stretches amounts on average up to 4.4% in the Neris, 7–7.5% in the Minija and Šventoji, and 22.4–43.5% in the Žeimena and Vilnia rivers. Under undisturbed conditions, salmonids, along with the other fish species that are sensitive to human-induced disturbance, as well as to an increase in water temperature (common bullhead *Cottus gobio*, grayling *Thymallus thymallus*, schneider *Alburnoides bipunctatus*) (Grenouillet and Schmidt-Kloiber, 2006; Froese and Pauly, 2018), make up 27–45% of all fish in the assemblage, depending on the catchment size. In smaller tributaries with a predominance of groundwater supply, salmonids (mostly brown trout) make up approximately 40% of all fish, or 60% along with other intolerant fish species (Virbickas and Kesminas, 2007; WFD, 2011).

Table 2
Descriptive statistics of fish abundance, species diversity and environmental characteristics of the studied river sites.

	Mean	Median	25%	75%	Min-Max
Number of species	11	10	9	12	8–17
Fish abundance (ind. 100 m^{-2})	450	373	138	534	55–1178
Catchment area (km^2)	4486	2419	320	4300	200–24,892
Discharge (m^3/s)	31.5	18.0	3.6	35.3	1.1–184.1
Average temperature in March–November (°C)	12.1	12.2	11.4	12.6	9.9–14.0
Average temperature in June–August (°C)	19.6	19.6	17.7	21.5	15.5–24.6

The metrics of fish species (absolute and relative abundance) and functional guilds (absolute and relative abundance and number of species) were calculated for the selected river sites. Functional guilds selected for the study covered various aspects of the strategy of fish reproduction (absolute and relative fecundity, egg diameter, spawning time, spawning substrate, incubation period and female maturity age), thermal preference, feeding and overall tolerance. Fish species were assigned to functional guilds based on the ecological classification of European fish (Grenouillet and Schmidt-Kloiber, 2006), while the guild of summer spawning fish was sub-divided into two groups: those spawning at lower than and higher than 16 °C. This division was based on the published data on the reproduction of fish in the region (Virbickas, 2000; Plikšs and Aleksejevs, 1998). In total, 74 fish metrics or their combinations were calculated.

Prior to the analysis, the normality of variables was tested with the Shapiro-Wilk's test. When necessary, the variables were log-transformed. Pearson's correlations were calculated between the fish metrics and the monthly T_W and Q, T_W and Q of the summer dry period (June–July, July–August or June–August) and the average annual values in March–November. Only the metrics with a correlation coefficient ≥ 0.45 (at $P < 0.05$) with either T_W or Q were analysed. A correlation matrix was calculated to select non-redundant ($R < 0.8$) metrics. The multiple regression equations for the reference (1986–2005), near future (2016–2035) and far future (2081–2100) periods were compiled to describe the dependence of the selected fish metrics on T_W and Q in the investigated rivers. The models were tested by comparing the measured values of the fish metrics with the values simulated for the same year in 5 independent river sites (one site per sub-basin), in which fish were sampled 3 times, every three years during 2003–2014. Because of the small sample size, the Mann-Whitney *U* test was used to test the significance of differences.

3.5. Uncertainty and sensitivity analysis of projections of fish metrics

The main sources of uncertainty in projections of fish metrics are annual water discharge (Q) and average water temperature in warm season (T_W) (Poff et al., 2002; Logez et al., 2013). The uncertainty and sensitivity analysis of fish metrics projections was performed using the GRS method (Hofer, 1999; Krzykacz et al., 1994). This method is based on a probabilistic quantification of the uncertainty of the investigated parameters (Q and T_W in this investigation).

The first step of this method is the identification of potentially relevant uncertainties of abiotic factors (Q and T_W) used in the calculation of fish metrics in the selected rivers. The projections of metrics are presented for five rivers and two different twenty-year future periods (2016–2035, 2081–2100) according to 4 RCP scenarios; therefore minimum, mean and maximum values of Q and T_W were determined for each case (40 in total). Since the projected values of fish metrics were going to be compared with the data of the reference period, the ranges of Q and T_W variation in each river were estimated additionally during the period of 1986–2005.

Afterwards, the definition of uncertainty ranges (minimum and maximum values) was determined and a specification of probability distributions (in this case, a uniform distribution) over these ranges was made. Using the Monte Carlo method, random samples of size n for Q and T_W from their probability distributions were generated. According to these parameter sets, fish metrics were calculated using equations (relationship between fish metrics and abiotic factors Q and T_W). After that, the calculation of quantitative uncertainty statements (two-sided statistical tolerance limits such as upper and lower limit values with 95% probability content and 95% confidence) was performed. Finally, the calculation of quantitative sensitivity measures (Spearman's correlation coefficient) was carried out in order to identify the uncertain parameters that contribute most to the uncertainty of the results.

Based on proven statistical procedures, the major advantage of the GRS method is that the number of calculations is independent from the number of uncertain parameters to be considered. For a 95% probability and a confidence level of 95%, 93 calculations need to be made. However, a total number of 100 calculations is typical for the application of an uncertainty analysis.

Sensitivity measures by using regression or correlation techniques from the sets of abiotic factors (Q and T_W) and from the corresponding calculation results of fish metrics allow the ranking of uncertain parameters in relation to their contribution to the output uncertainty. Spearman's correlation coefficient is used to assess how well the relationship between the two variables can be described using a monotonic function (Myers and Well, 2003). The X_i and Y_i are converted to ranks x_i and y_i, and Spearman's correlation coefficient (ρ) is calculated as follows:

$$\rho=\frac{\sum_i(x_i-\overline{x})(y_i-\overline{y})^2}{\sqrt{\sum_i(x_i-\overline{x})^2\sum_i(y_i-\overline{y})^2}} \tag{2}$$

The SUSA (Software System for Uncertainty and Sensitivity Analyses) software developed by GRS (Gesellschaft für Anlagen- und Reaktorsicherheit) has provided a choice of statistical tools to be applied during the uncertainty and sensitivity analysis (Kloos and Hofer, 2002). The generation of a random sample of size n for model parameters (by the Monte Carlo method) and the calculation of quantitative sensitivity measures (Spearman's correlation coefficient) are performed using this software.

4. Results

4.1. Changes in projections of abiotic factors ***for the selected rivers***

The uncertainties of river water discharge and temperature projections are highly dependent on air temperature (T_A) and precipitation (P) patterns. The changes of meteorological parameters in near and far future periods were evaluated by comparing projections of T_A and P according to 4 RCP scenarios (averaged by GFDL-CM3, HadGEM2-ES and NorESM1-M) with the reference period (Fig. 3). In the study area, the increase of air temperature varies from 1.5 °C (RCP 2.6) to 1.9 °C (RCP 8.5) in the near future (2016–2035) period and from 2.2 °C (RCP 2.6) to 5.7 °C (RCP 8.5) in the far future (2081–2100) period. The changes in projections of annual precipitation could have both negative and positive tendencies compared with the reference period. The change of annual precipitation amount will vary from −0.6 to +7.3% depending on RCP scenario and future period.

Projections of discharge (Q, m^3/s) and water temperature (T_W, °C), as well as the observed values in the reference period, are presented in Fig. 4. No clear tendencies of changes in discharge of the investigated rivers were identified in the projections of the near future. According to separate RCP scenarios, Q may either increase by 0.8–5.7% or decrease by 0.4–16.5% compared with the reference period (Fig. 4). According to all RCP scenarios, Q is projected to decrease in most of the investigated rivers, ranging from 4.0% (in the Žeimena) to 13.9% (in the Neris). Only in the Minija should it slightly increase to 1.8%. In the near future, the smallest rise of T_W of the warm period is projected under RCP6.0 (0.4–0.7 °C), while the greatest rise is projected in case of the high warming RCP8.5 scenario (0.8–1.1 °C). On average, T_W should increase from 0.6 °C (in the Žeimena) to 0.9 °C (in the Neris) compared with the reference period.

The performed projection revealed that the largest shifts of Q and T_W values of the investigated rivers are expected in the far future period. At the end of the century, river discharge is likely to decline from 1.0 to 13.8% according to RCP2.6 and from 16.7 to 40.6% in case of the most extreme RCP8.5 scenario relative to the reference period. During the same period, T_W is going to increase from 0.8 to 1.3 °C under RCP2.6 and from 4.0 to 5.1 °C under the RCP8.5 scenario (Fig. 4). The average decrease of Q is projected to be from 5.6% in the Minija River to 24.6% in the Neris River, while T_W is expected to increase from 2.2 °C in the Žeimena River to 2.9 °C in the Neris River.

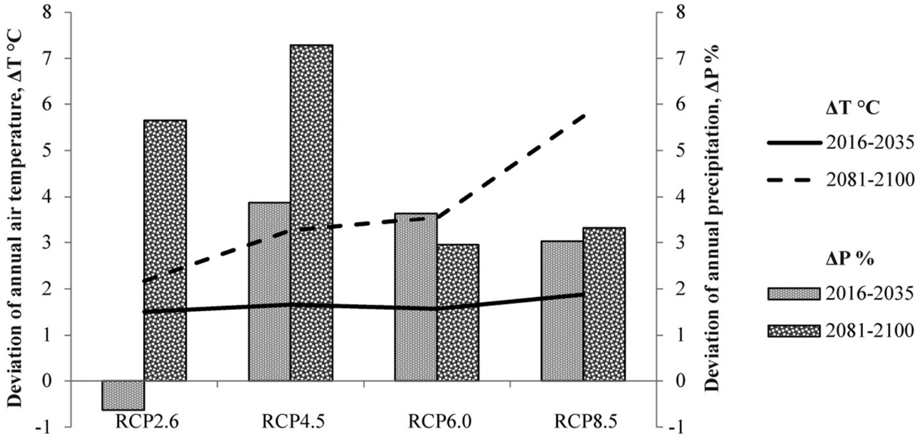

Fig. 3. Deviations of annual air temperature and precipitation from the reference period values (average values of MS in study area).

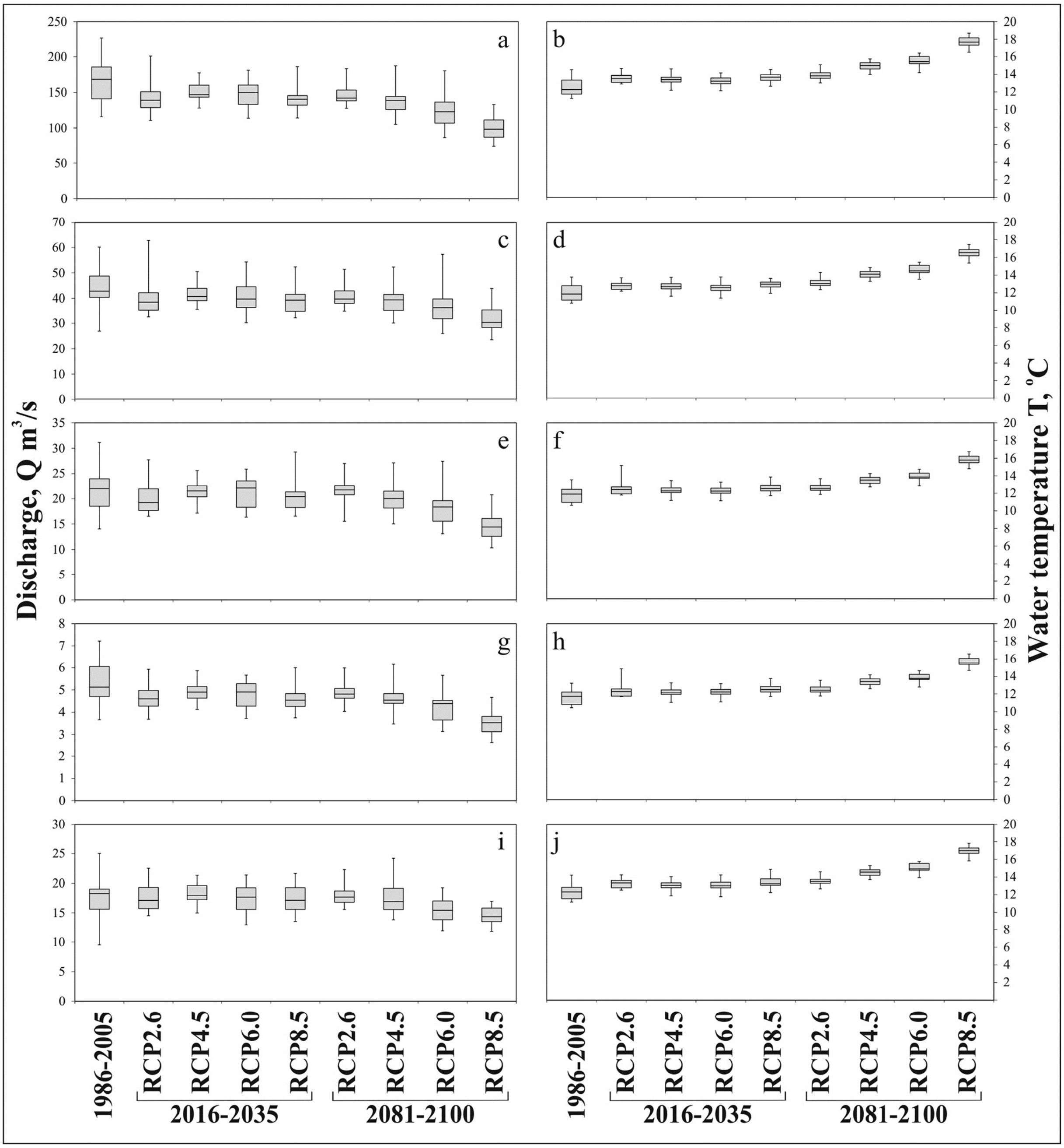

Fig. 4. Comparison of the observed discharge and water temperature values (1986–2005) with the projected values in the near (2016–2035) and far (2081–2100) future periods: a, b – the Neris, c, d – the Šventoji, e, f – the Žeimena, g, h – the Vilnia, i, j – the Minija rivers.

4.2. Fish metrics projections in the 21st century according to RCP scenarios

The abundances of only 3 species were significantly correlated with T_W either positively (bleak *Alburnus alburnus* and chub *Squalius cephalus*), or negatively (*S. trutta*), but the determination coefficients were small ($r^2 = 0.12–0.16$; $p < 0.05$) and did not meet the metrics selection criteria. Thirteen functional guild metrics showed significant correlations ($r^2 > 0.2$; $p < 0.05$) with either T_W or/and Q: those representing abundance or/and diversity of omnivorous, intolerant and stenothermal species; species with an egg incubation time less than or equal to 7 days and those with an egg incubation time >14 days; species with relative fecundity less than or equal to 57; and species that spawn in winter and those that spawn in summer at a T_W higher than 16 °C. Two of them, the relative and absolute abundance of omnivorous species, were rejected as highly redundant with the metric of the relative and absolute abundance of species that spawn in summer at a T_W >16 °C (thereafter St16). Another three metrics, representing the relative abundance of species with egg incubation time of less than or equal 7 days, those with relative fecundity less than or equal 57, and species, that spawn in winter, were rejected as highly redundant with the metric of the relative abundance of species with an egg incubation time >14 days (thereafter Ip14). The metric, representing the number of intolerant species, was rejected as highly redundant with the metric of the number of stenothermal species (thereafter Steno). After the redundancy test, only seven metrics were retained, representing the relative and absolute abundances of Ip14 species, the relative and absolute abundances and number of St16 species and the relative abundance and number of Steno species (Table 3). All these metrics correlated most significantly with the average annual March–November temperature. Correlations of metrics with an average value of T_W at various intervals of the summer dry period or individual summer months are also significant, but the coefficients of the determination were lower. Two metrics, the relative abundances of Steno species and St16 species, were significantly correlated both with the average annual water temperature and with the average annual flow. The Steno guild covers all Ip14 species, except one, common dace *Leuciscus leuciscus*. Therefore, only the relative abundances of Steno species and St16 species were finally chosen for the calculation of projections of changes in fish functional guild structure due to changes in T_W and Q. The regression equations describing the dependence of fish metrics on the abiotic factors mentioned above are as follows:

$$\mathrm{St16} = 5.8 \times T_W + 10.7 \times \mathrm{LogQ} - 58.1; \tag{3}$$

$$\mathrm{Steno} = -8.2 \times T_W - 12.6 \times \mathrm{LogQ} + 155.5 \tag{4}$$

where: St16 – the relative abundance of fish that spawn above 16 degrees, Steno – the relative abundance of stenothermal fish, T_W – the average river water temperature of the warm season, °C, Q – the average annual discharge, m^3/s.

Values of St16 and Steno, simulated based on actual T_W and Q, did not significantly differ from those measured in the river sites where fish were sampled every 3 years in the period 2003–2014 (Man-Whitney U test; Steno: $p = 0.68$; St16: $p = 0.07$; $n = 15(30)$).

Based on the simulated values of fish metrics, significant changes should not occur in the near future (2016–2035). Differences in fish metrics among the projections of RCP scenarios are slight, and no clear tendencies can be identified (Fig. 5). Well-defined changes of fish metrics in the selected rivers are projected to occur in the far future period (2081–2100). The least changes will happen in the case of the RCP2.6 scenario, when the relative abundance of fish metrics is likely to be similar to the average of all RCPs projected for 2016–2035. Major shifts in the investigated fish variables are projected under the RCP8.5 scenario: in the Šventoji and Minija Rivers, stenothermal fish will get very close to extinction (Steno N will decrease to 2%) by the end of the century, whereas in the Neris River they will become extinct. According to RCP8.5, the relative abundance of St16 will rise and reach values from 38 to 65% (in the reference period they were 16–38%; Fig. 5).

Table 3
Results of a multiple regression analysis of T_W and Q and a regression analysis of T_W on fish metrics (N% – relative abundance; LogN – logarithm of absolute abundance; Sp – number of species).

Fish metric	Variable	Q	T_W	R^2	*F*	SE of estimate
Steno N%	*B*	−12.569	−8.233	0.319	12.892[**]	27.076
	SE B	5.168	3.543			
	β	−0.327[*]	−0.312[*]			
St16 N%	*B*	10.741	5.751	0.463	19.418[**]	15.488
	SE B	2.781	2.095			
	β	0.495[**]	0.314[**]			
Steno Sp	*B*		−0.869	0.276	16.002[**]	1.461
	SE B		0.217			
	β		−0.525[**]			
St16 Sp	*B*		0.806	0.226	13.461[**]	1.32
	SE B		0.22			
	β		0.476[**]			
St16 LogN	*B*		0.361	0.277	15.291[**]	0.521
	SE B		0.092			
	β		0.526[**]			
Inc14 LogN	*B*		−12.222	0.318	19.901[**]	0.688
	SE B		2.74			
	β		−0.564[**]			
Inc14 N%	*B*		−0.487	0.321	19.875[**]	17.822
	SE B		0.109			
	β		−0.567[**]			

[*] $p < 0.05$.
[**] $p < 0.01$.

4.3. Uncertainty and sensitivity analysis of fish metrics projections according to RCP scenarios

The uncertainty analysis of the projected changes of abiotic factors (Q and T_W) and their impact on fish productivity was performed using the SUSA software package. The dependencies of St16 and Steno fish metrics on Q and T_W were described by Eqs. (3)–(4).

Fig. 6 presents the distribution functions of relative abundance of St16 and Steno in the reference (1986–2005), near future (2016–2035, RCP2.6–1–RCP8.5–1) and far future (2081–2100, RCP2.6–2–RCP8.5–2) periods. According to the average of three climate models and four RCP scenarios, significant changes of St16 and Steno metrics are expected as a response to projected alterations of abiotic factors in the future. In the investigated rivers, St16 and Steno metrics of the reference period were distributed in a wider range than those projected in the future (Fig. 6). The implication is that the investigated metrics in the reference period have greater uncertainty, while the metrics projected according to the climate scenarios outputs have smaller uncertainty (i.e., the curve of the abundance distribution is steeper). The standard deviations of the projected relative abundance of St16 and Steno are different for separate future periods: in the near future period, standard deviation (the average of all five rivers: $\sigma = 2.5$) and the uncertainty of St16 and Steno metrics are greater, whereas in the distant future, both the standard deviation of the distribution ($\sigma = 2.2$) and uncertainty of the investigated metrics are smaller.

No significant changes of the uncertainty range in respect to a particular RCP were detected when comparing the data of the reference and near future periods. Meanwhile, the projection results for the far future have a markedly greater uncertainty compared with the reference data (Fig. 7). Depending on the scenario used to project relative abundance, the uncertainty range (i.e., interval in which the projected metrics vary) may rise from 1.5% (Steno in the Neris River) to 19.4% (Steno in the Vilnia River) compared with the reference period values.

The Spearman's correlation coefficients presented in Tables 4 and 5 illustrate the impact of abiotic factors (Q and T_W) on fish metrics in the selected rivers. The results show a positive impact of Q and T_W on eurythermal St16 and a negative impact on stenothermal Steno fish. Future alterations of river T_W will have a significantly greater influence on the relative abundance of the analysed functional guilds of fish than river discharge. The analysis of the response of relative abundance to abiotic factors reveals that this response is more dependent on the projected period than on a particular RCP. The impact of Q (an average of 4 RCPs) on the relative abundance of fish in the selected rivers is projected to be greater in the far future period, whereas the impact of T_W is expected to be more evident in the near future period.

5. Discussion

The present study was designed to assess the response of fish assemblages in Lithuanian rivers to temperature and hydrological regime changes as well as the response's uncertainty. The assessment was performed for two twenty-year future periods (2016–2035 and 2081–2100) according to changes in the climate system predicted by different scenarios. Projections for the 21st century of both RCP2.6 and RCP8.5 (two most diverse pathways) show that in Lithuanian territory, the air temperature is going to increase, while annual precipitation will have both negative and positive tendencies. These findings are in agreement with the obtained results of previous studies (Keršytė et al., 2015; Stonevičius et al., 2017).

As a consequence of changed climate indices, river water temperature and river discharge will undoubtedly experience alterations in the future as well. However, the projected climate changes are not very significant and alterations of investigated abiotic factors do not have evident trends in the near future period (2016–2035). In the far future (2081–2100), an increase of river water temperature and a decrease of river discharge are expected to manifest themselves

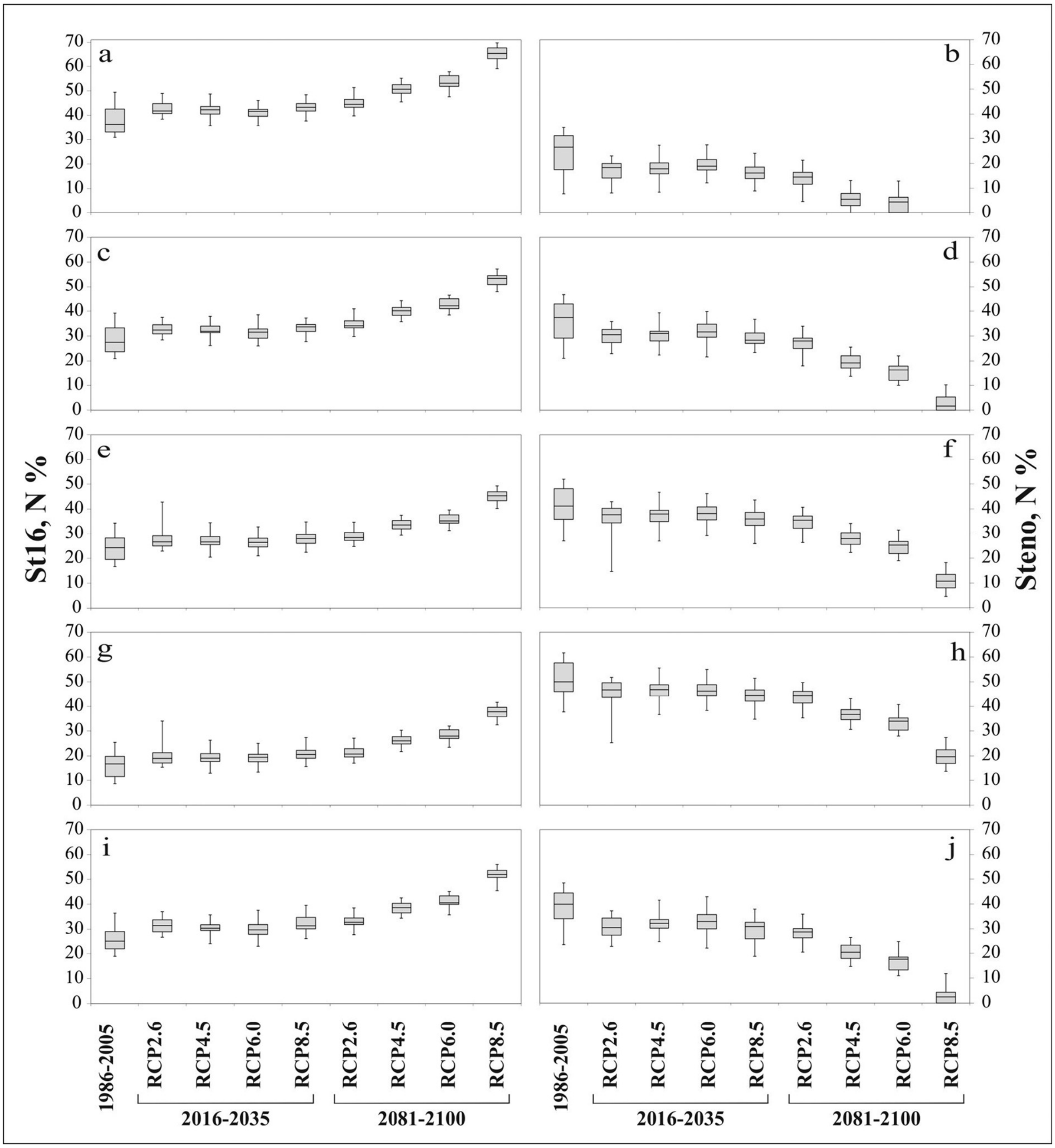

Fig. 5. Changes of St16 (N %) and Steno (N %) metrics in the reference period (1986–2005), and in the near (2016–2035) and far (2081–2100) future periods according to four RCP scenarios: a, b – the Neris, c, d – the Šventoji, e, f – the Žeimena, g, h – the Vilnia, i, j – the Minija rivers.

considerably. A projected strong relationship between hydrological and climatic factors, especially in the distant future period, has been reported in several studies (Ficklin et al., 2014; Gebre and Ludwig, 2015; Šarauskienė et al., 2017).

Water temperature and discharge had a significant effect on two opposite fish guilds with different thermal preferences and overall tolerance to quality of habitat. This is very similar to European fish assemblage functional structure distribution along two main opposing suites of coevolved traits, described by Logez et al. (2013). The effect of temperature on the structure of the functional guilds was more significant than the influence of the flow, indicating that water temperature is the dominant factor not only on a large spatial scale (Buisson et al., 2008; Logez et al., 2012) but also on small scale, even in plains where the variability of physical characteristics of rivers of comparable size is usually lower in comparison with hilly areas. Logez et al. (2013) found that the structure of fish assemblages on a European scale largely depends on the average air temperature in July. At a local level, the differences in air temperature may be too small to cause greater differences in water temperature. The latter may also depend on shading from riparian vegetation (Moore et al., 2005; Woltemade and Hawkins, 2016) and influence of groundwater influx (Gaffield et al., 2005; Loinaz et al., 2013). Perhaps because of this, on a small spatial scale, fish metrics correlated better with the average water temperature in March–November than with the water temperature in individual summer months (June or July).

The water temperature in the studied rivers in July (the warmest month) ranged from 18.6 to 23.1 °C. It was completely on the verge or even slightly above the upper thresholds for feeding of juvenile *S. salar* (21–22 °C) (Elliot, 1991), coincides with the critical feeding temperature for *S. trutta* (19.4–23.0 °C; Elliott et al., 1995; Forseth et al., 2009)

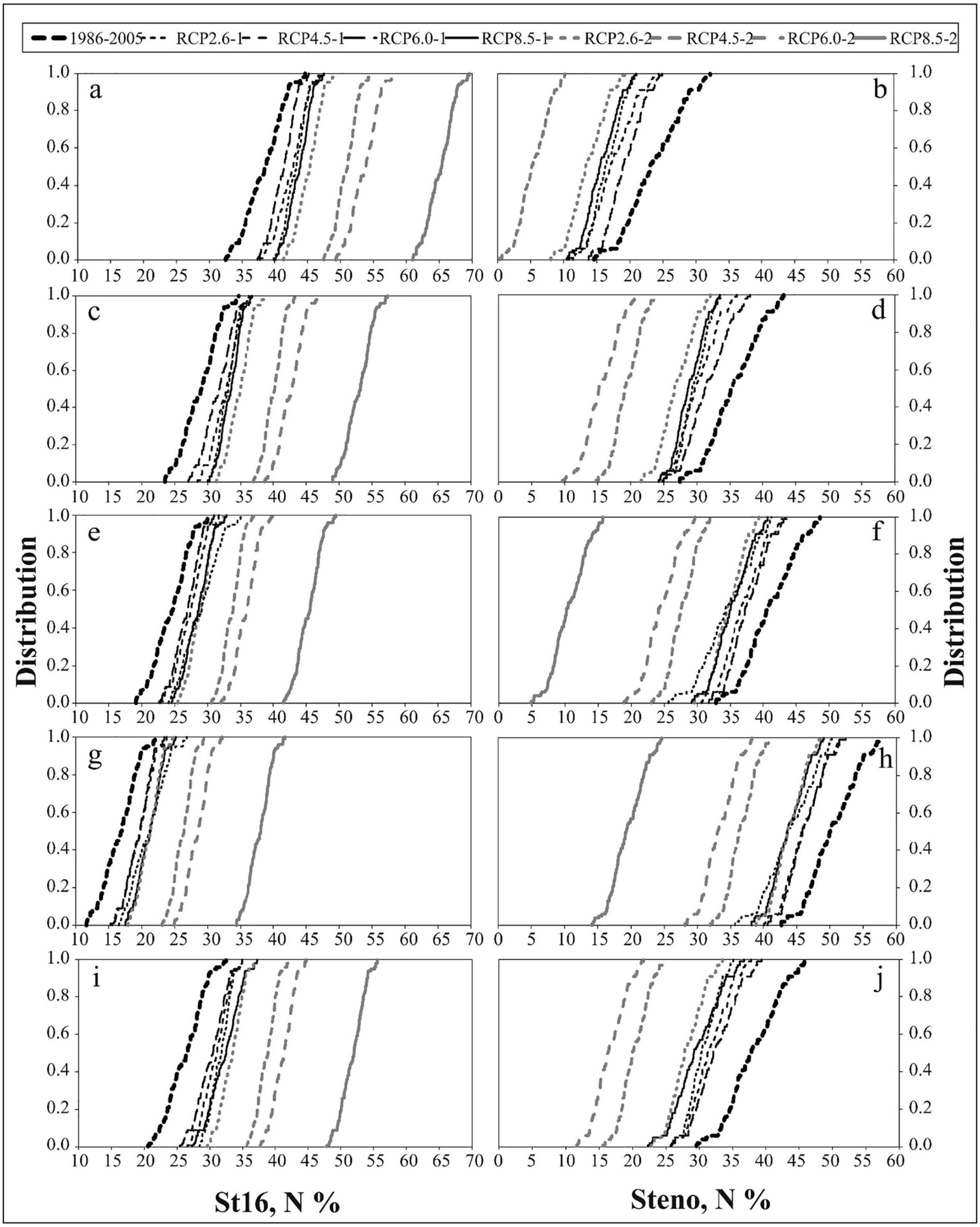

Fig. 6. Distribution functions of St16 and Steno according to 100 sets: a, b – the Neris, c, d – the Šven-toji, e, f – the Žeimena, g, h – the Vilnia, i, j – the Minija. 1986–2005 – the reference period, RCP2.6–1–RCP8.5–1 – the projections for 2016–2035; RCP2.6–2–RCP8.5–2 – the projections for 2081–2100.

and corresponds to or exceeds the optimum temperature for some other native species (e.g., *C. gobio*, *T. thymallus*, *A. bipunctatus*, Eurasian minnow *Phoxinus phoxinus*) (Froese and Pauly, 2018). The simulation results showed that the increase in the water temperature in the rivers was followed by a decrease in the discharge. Studies of large rivers indicate that flow reduction increases water temperatures even more (Sinokrot and Gulliver, 2000; Meier et al., 2003) while increased discharge maintains cooler temperatures (Bartholow, 1991). Considering all of this, the conditions in rivers can become even more unfavourable for stenothermal fish. In addition, the studied medium-sized and large rivers cover all the main spawning grounds of *S. salar* in the Nemunas River catchment, and an increase in T_W can have a particularly strong negative effect on the survival of juvenile salmon. In search of thermal refuge, cold-water fish can migrate to areas upstream (Buisson and Grenouillet, 2009), but there they have to compete with local fish for food and habitat. The most likely increase of competition is between

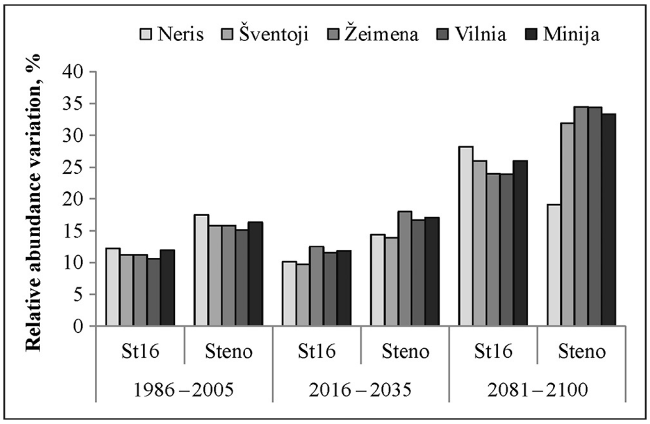

Fig. 7. The range of relative abundance variation (%) of the investigated fish metrics (St16 and Steno) in the investigated rivers for different periods.

salmon and brown trout, which usually live and spawn in smaller rivers. Although these two species are ecologically compatible, *S. salar* dominates over *S. trutta* in the areas where they coexist (Gibson and Cunjak, 1986), and an increase in the density of *S. salar* may lead to a decrease in the density of *S. trutta* (Hesthagen et al., 2017). Therefore, an increase in temperature (which directly affects *S. salar*) can also indirectly affect the abundance of *S. trutta* in smaller rivers of the Nemunas River catchment that are more resistant to rising air temperature.

Water temperature also had a significant effect on the abundance of Inc14 species. All Ip14 species that live in the Nemunas River catchment are also stenothermal, with the exception of *L. leuciscus*. Daufresne et al. (2003) found that, due to the increase in water temperature, *L. leuciscus* was progressively replaced by more thermophilic fish species in the Upper Rhône River (France). Similarly, Ruiz-Navarro et al. (2016) showed that the predicted climate space for *L. leuciscus* in the rivers of Great Britain expanded under low-emission scenarios but substantially contracted under high emission scenarios, suggesting the presence of some climate-distribution thresholds. Thus, *L. leuciscus*, although it is considered eurythermal, is less tolerant to an increase in temperature than other eurythermal species. This may be due an evolutionary adaptation to spawning at low temperatures and prolonged incubation of eggs, which is typical of many stenothermic fish and, conversely, is not characteristic of any of the St16 species that spawn at a higher temperature.

The functional guild metrics correlated with T_W and Q much better than the abundances of individual species. Even the abundances of salmonid species showed only a weak, although significant, correlation with T_W. This may be due to the natural variability of species abundance among rivers of the same type. Even small differences in morphological characteristics can determine different abundances of species, exploiting habitat in a similar way. The ratio of sympatric salmonid species may vary in similar habitats of different streams, and depending on the stream, significant differences in preferences for certain environmental variables can be present or absent (Gibson and Cunjak, 1986). Other fish species can also affect the abundance and distribution of salmonids as well as non-salmonids (Degerman and Sers, 1993, 1994; Näslund et al., 1998), especially in rivers inhabited by a larger number of species. The importance of abundance information increases in the spatial analysis of small streams and species-poor fish types, whereas in larger rivers with a greater diversity of species, functional metrics are more informative (Schmutz et al., 2000; Hughes et al., 2004). Perhaps due to this reason, in most studies covering a larger number of rivers and wider geographical area, the impact of climate change was analysed in the context of the distribution range and presences/absence of species (Santiago et al., 2016, 2017; Buisson and Grenouillet, 2009; Ruiz-Navarro et al., 2016), the relative abundance of functional guilds (Logez et al., 2013) or changes in the values of structural indices (Pletterbauer et al., 2015). Patterns of the changes in the abundance of individual fish species due to climatic factors were described by Daufresne et al. (2003). However, unlike other studies, the latter study was conducted using long-term data from stationary sites located in a short segment of the same river, which minimized the effect of differences in morphological structure and species composition. Similarly, the analysis of long-term monitoring data of salmonids (2000–2016) from one site in the least-altered Lithuanian large river Žeimena showed that the absolute abundance of juvenile *S. salar* significantly correlates with the average water temperature in July ($R = 0.55$; $p < 0.05$). However, after grouping the data with those from other sites and other rivers, the correlation becomes insignificant (unpublished data). The use of functional guild metrics, apparently, softens the influence of the natural variability of the abundance of individual species.

Table 4
The impact of water temperature (T_W) and discharge (Q) on St16 expressed by Spearman correlation coefficients.

Period	Neris		Šventoji		Žeimena		Vilnia		Minija	
	Q	T_W	Q	T_W	Q	T_W	Q	T_W	Q	T_W
1986–2005	0.18	0.98	0.22	0.97	0.23	0.97	0.21	0.98	0.26	0.97
2016–2035	0.21	0.98	0.24	0.97	0.18	0.98	0.17	0.98	0.17	0.98
2081–2100	0.24	0.97	0.27	0.96	0.30	0.95	0.26	0.95	0.21	0.97

The uncertainty of the accomplished fish projections depends on the uncertainty of future hydrological parameters. Since the projections of Lithuanian river runoff show that the accuracy of hydrological projections is more dependent on the emission scenarios than on global climate models (Kriaučiūnienė et al., 2013), in this study, it was chosen to concentrate on the contribution of new RCP scenarios to the uncertainty of the results. The uncertainty analysis helped to assess the fish response to changes of abiotic factors (water temperature and river discharge) projected by RCP scenarios that encompass a wide range of future changes (from the least to the most significant or even of vital importance).

Calculation of Spearman's correlation coefficients (ρ) allowed the identification of the parameters that contribute most to the uncertainty of results. A greater absolute value of ρ means that the parameter had a greater impact on the calculation results. The Spearman coefficients calculated for abiotic factors revealed that both analysed fish metrics (St16 and Steno) mostly depended on warm season water temperature. For all investigated rivers, the impact of T_W on eurythermal fishes (St16) expressed by ρ ranged from 0.95 to 0.98, while the impact on stenothermal fishes (Steno) ranged from −0.97 to −0.99. The impact of water discharge on fish projections is not as significant. The predicted changes in the discharge are not so significant that they themselves cause changes in the number of fish species or the share in different environmental guilds. The guild structures of fish assemblies in >1000 km^2 catchment size rivers of the Nemunas River Basin are very similar. The slope of the riverbed has a much greater influence on the structure and composition of fish assemblages and is used to differentiate between Lithuanian rivers with a catchment size of >1000 km^2 (WFD, 2011).

The accuracy of projections of fish metrics mostly depended on the correct definition of projections of warm season water temperature. A significant impact of increased water temperature is also highlighted in the report written by Poff et al. (2002), where this impact is considered to be altering fundamental ecological processes and the geographic distribution of aquatic species. Uncertainties arising in projections of climate change impact on biota are emphasized by other studies as well (Pereira et al., 2010; Bellard et al., 2012).

Rivers of different European biogeographical regions feature different structures and compositions of aquatic communities. However, the results of the study can be extrapolated to the rivers of other countries of the eastern and south-eastern Baltics, which have a very similar structure of fish communities as in the rivers belonging to the Nemunas River catchment.

Table 5
The impact of water temperature (T_W) and discharge (Q) on Steno expressed by Spearman correlation coefficients.

Period	Neris		Šventoji		Žeimena		Vilnia		Minija	
	Q	T_W	Q	T_W	Q	T_W	Q	T_W	Q	T_W
1986–2005	−0.15	−0.99	−0.18	−0.98	−0.19	−0.98	−0.17	−0.98	−0.21	−0.98
2016–2035	−0.17	−0.98	−0.20	−0.98	−0.15	−0.99	−0.14	−0.99	−0.14	−0.99
2081–2100	−0.20	−0.98	−0.22	−0.97	−0.25	−0.97	−0.21	−0.97	−0.17	−0.98

6. Conclusions

1. In the near future period (2016–2035), no clear tendencies in projections of the investigated (both abiotic and biotic) variable changes were identified in the analysed rivers of the Nemunas River catchment.
2. In the far future period (2081–2100), the abiotic factors are projected to change significantly. River water temperature is going to increase from 0.8 to 1.3 °C (RCP2.6) to 4.0–5.1 °C (RCP8.5), whereas river discharge should decrease from 1.0 to 13.8% (RCP2.6) to 16.7–40.6% (RCP8.5).
3. In the far future period, the abundance of Steno and St16 fish is likely to change considerably. The relative abundance of Steno fish is projected to decline from 24 to 51% in the reference period to 14–44% under RCP2.6 and to 0–20% (i.e., in some rivers it may become extinct) under RCP8.5. Meanwhile, St16 fish should survive and adapt to the warmer water and their abundance is likely to rise from 16 to 38% in the reference period to 21–45% under RCP2.6 and to 38–65% under RCP8.5.
4. The response of Steno and St16 abundance to abiotic factors reveals a greater dependence on the projected period (near or far future) than on a particular RCP. Future alterations of river T_W will have significantly more influence on the abundance of the analysed functional guilds of fish than the river discharge.

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