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Climate driven changes in the spawning of roach (*Rutilus rutilus* (L.)) and bream (*Abramis brama* (L.)) in the Estonian part of the Narva River basin

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Increasing water temperature in spring in Estonian inland waters has affected differently the spawning of roach and bream. Within forty years (1951–1990), the spawning of bream shifted, on average, to a ten days earlier period but the range of spawning temperature remained unchanged, while there was no shift in the spawning time for roach, which started to spawn at about three degrees higher water temperature than earlier. The difference between spawning times of roach and bream decreased from an average 22 to 13 days and the difference in average temperatures at the onset of spawning by about 3 °C. Besides water temperature, the timing of spawning was also related to the water level in spring: in years with higher water levels in March or April both fish species started to spawn earlier. The effect of water level changes on spawning was more pronounced in shallower Võrtsjärv than in Lake Peipsi.

Introduction

Recent climate warming caused mostly by increased anthropogenic emission of greenhouse gases (IPCC 2001) is associated in the northern hemisphere with the continuing positive phase of the North Atlantic Oscillation, most pronounced during the winter period (Hurrell 1995). In shallow lakes the winter NAO affects the duration of ice-cover and the water temperature shortly after the breakup of ice (Gerten and Adrian 2001).

Climate investigations in Estonia have shown that the air temperature has increased by 0.3–0.5 °C in 1966–1998 compared with the earlier 90-year period, and the largest increase (> 1 °C) has taken place in March (Jaagus 1999). The sum of effective temperatures (agrometeorological term meaning daily mean temperatures that exceed 5 °C) until 1 June has nearly doubled (from 66 °C to 107 °C). The duration of the snow cover decreased on average by 33 days in 1962–1997 (Tooming and Kadaja 1999). As a general trend, the beginning of climatic spring and summer has shifted to an earlier time. In 1946–1998, the beginning of the breakup of ice in Lake Peipsi has been recorded 31 days earlier (from 19 April to 19 March), in Lämmijärv 41 days (20 April–10 March) and in Võrtsjärv 17 days earlier (17 April–31 March). In rivers in the Narva River basin the corresponding change is on average 26 days (Järvet 2001). However, the time when the water temperature permanently exceeds 4 °C level has changed much less (Järvet *op. cit.*). In Lake Peipsi and Lämmijärv there is no significant change at all, in Võrtsjärv it has changed by 8 days (from 21 April to 13 April) and in rivers by 4 days on average.

Organisms able to survive in a given climate must respond effectively to the variation of weather. Phenological records can thus provide an integrative index of weather through the seasons, a quality that is becoming increasingly valuable in gauging trends indicative of changing climate (Lechowicz 2001). Spring period with the most pronounced climatic change is the spawning time for many fish species. Changes in the timing of fish recruitment may cause a mismatch with zooplankton development and lead to cascading effects in the food chain affecting the whole ecosystem (Blenckner 2001, Edwards and Richardson 2004). The scarcity of reliable long-term spawning records is probably the reason why there are considerably fewer publications on fish phenology as compared with studies on birds, butterflies or terrestrial plants (McCarty 2001). In this respect, Estonia is in a favourable situation because long-term data on fish spawning (Ristkok 1961, 1969a, 1969b, 1971, 1973, 1980, 1984, 1988, 1993) are available. Only few analyses based on this database have been published up to now (Ristkok 1974, Palm 2001a, 2001b).

We chose for analyses the phenological spawning data on the two most common cyprinid fish species in Estonian inland waters, roach (*Rutilus rutilus* (L.)) and bream (*Abramis brama* (L.)). The choice was primarily based on good representation of these species in the database and secondly on the differences in the phenology: roach spawns in early spring and bream in late spring/early summer.

Roach and bream have both a wide geographical distribution area and their populations are adapted to different thermal conditions (Kucharczyk *et al.* 1997). That is probably one reason why spawning temperatures found for these species in the literature vary in a wide range. Based on a literature review, Alabaster and Lloyd (1980) show that roach spawns most typically at temperatures between 8 and 19.4 °C with extremes reaching to 5 and 22 °C. For bream the typical range is 12–20 °C, while the extremes may reach 8 and 24 °C. For single locations the temperature ranges are often much narrower. So, for example, the upstream migration of roach started in a small river in Norway at water temperatures of 6–10 °C (Vøllestad and L'Abée-Lund 1987) and in the Malše River (Czech Republic) at 13–14 °C (Hladík and Kubečka 2003). Jafri (1989) demonstrated a specific narrow range of temperature for the roach, which spawned spontaneously in the laboratory when the water temperature reached 18–20 °C.

According to general models (Billard *et al.* 1978), the reproductive cycle of salmonid fishes is mostly controlled by the length of the photoperiod and that of cyprinids by temperature. Contradictory statements on the effect of water temperature on the onset of spawning in cyprinid species can often be found in the literature. For example, Wilkońska and Żuromska (1967) observed earlier spawning of roach in Mazurian Lakes in years with higher annual mean temperature. An increase of water temperature by 3 °C in the Meuse River (Belgium) downstream of the Tihange Nuclear Power Plant shifted the spawning of roach three weeks earlier (Mattheeuws *et al.* 1981). Warm water in Lake Licheń (western Poland) also heated by a power plant, shifted the spawning of white bream (*Blicca bjoerkna* (L.)) and tench (*Tinca tinca* (L.)) to a much earlier date whilst the spawning time of roach changed only slightly and, as a result, spawning proceeded at higher temperatures than formerly, approximately at 16–18 °C (EIFAC 1969).

Our aim was to study whether there are significant trends in the spawning time and/or temperature ranges for roach and bream representing fishes of different temperature optima for spawning. We hypothesised that the earlier ice breakup and earlier warming of water in spring have affected the spawning of the two species.

Site description

The Narva River basin (56 225 km^2) is shared among Russia (35 369 km^2), Estonia (17 145 km^2) and Latvia (3711 km^2). We limited our study area to the Estonian part of the basin, which includes two large shallow lakes, Peipsi

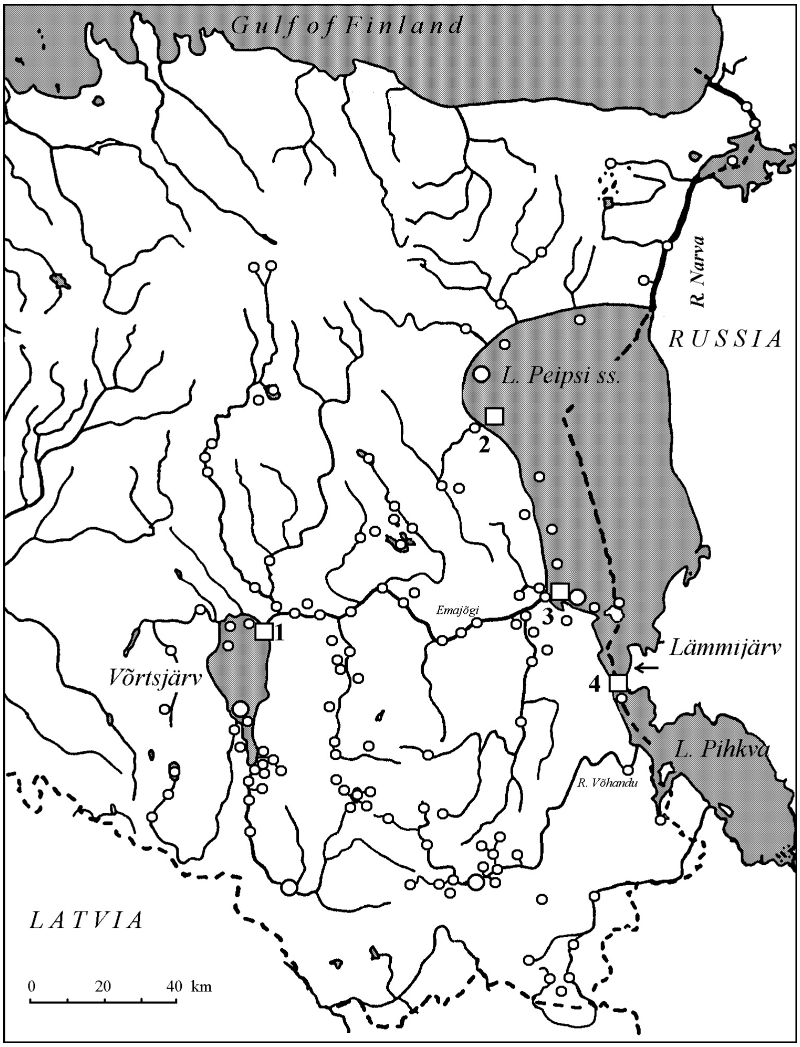

Fig. 1. Study area. Small circles = stations of fish observations; large circles = stations with 20 or more years of fish observations; squares = stations of water temperature measurement: Rannu-Jõesuu (1), Mustvee (2), Praaga (3) and Mehikoorma (4).

(3555 km^2, mean depth 7.1 m) and Võrtsjärv (270 km^2, mean depth 2.8 m), and several smaller lakes together with the connecting river network (Fig. 1). Peipsi consists of three parts: the largest northern part Peipsi *sensu stricto* and the southern part Pihkva are connected by a narrow part called Lämmijärv. The largest rivers in this area are the Emajõgi (catchment area 9745 km^2) flowing from Võrtsjärv to Peipsi and the Võhandu (1420 km^2) entering Lämmijärv from the southwest.

The area studied is located in the temperate zone. The North-Atlantic cyclone belt, locally modified by the Baltic Sea, dominates the climate. It is characterised by rather warm summers and moderately mild winters. According to the climatic regionalisation of Estonia, the Narva River basin area is located in the East-Estonian climatic subregion. Continental climate features, well expressed in winter, are characteristic of the area. Thus, the west–east gradient is greater in the main climatological elements than the north–south one. The topography, particularly uplands in the southeastern part of Estonia, play an important role in the distribution of precipitation and in the duration of the snow cover.

Due to size differences the large lakes in the area have several discrepancies in their thermal regime and ice conditions (Table 1). The duration of the ice cover (defined as the period during which there is no free water visible from the observation station) was the longest, on average 134 days, in Võrtsjärv and at the Mustvee station in Peipsi. At the Praaga station the ice duration was the shortest and reflected mostly the regime of the Emajõgi. Ice melted almost at the same time at Praaga and Mehikoorma stations while at Mustvee it happened a week later. In large lakes the melting period from the appearance of the first open water stretch until the total disappearance of ice lasts usually 2–3 weeks and is characterised by different ice phenomena like shore ice and drifting ice. Based on the analysis of 15-year data from 1951–1965, Ristkok (1974) pointed out that the breakup of ice in Estonian rivers started on average on 8 April, 11 days earlier than in lakes and ended on 12 April, 13 days earlier than in lakes.

There are also differences in the spring and summer warming of lakes. The warming is faster in shallow Võrtsjärv, Pihkva and Lämmijärv while the deeper and larger Peipsi *s.s.* warms up slower and remains cooler during the summer (Jaani 2001).

In the very shallow Võrtsjärv the annual mean amplitude of water level fluctuations (1.4 m) is equal to half of the mean depth of the lake, and the absolute range of water level fluctuations (3.2 m) even exceeds the mean depth. Changing water level affects strongly the functioning of all levels of the ecosystem in this lake. The corresponding values for the water level variability in Peipsi are similar (1.2 and 3.0 m) but as the lake is deeper, their direct influence is not so obvious.

Material and methods

As the main data source we used the ichthyophenological database by Ristkok (1961, 1969a, 1969b, 1971, 1973, 1980, 1984, 1988, 1993). In his work Ristkok adopted several principles used in phyto- and zoophenological observations in Finland (Reuter 1952a, 1952b). According to the published guidelines (Ristkok 1957) observers, mostly amateur fishermen, who regularly visited some sites at waterbodies were asked to keep records of dates (number of day in a year starting from 1 January) when they observed certain ichthyological phenomena at that site. These phenomena included the appearance of fishes at the spawning grounds (start of the spawning migration), the onset and end of spawning, disappearance from the spawning grounds, and appearance of young-of-the-year fishes. For multiple spawners and for fishes which spawn in sequential groups, also the time ranges for the second and third spawning runs were asked in the questionnaire. If the exact onset or end of spawning or migration could not be fixed due to the occasional character of observations, there was an option to register just the time when these phenomena were observed. There were no detailed recommendations in the guidelines how to make the observations (just by eye or using some fishing gear). Perhaps both ways were used for data collection. While collecting the data, Ristkok checked suspicious data by contacting the observers and asking about the circumstances in which the observations took place. The unreliable observations were not included in the database (Ristkok 1974).

For the present study, we used the spawning data on roach and bream in the Estonian part of the Narva River basin. For better comparison and in order to diminish the already high variability in the data, we included only the data for the first and most massive spawning group.

Table 1. Long-term average characteristics of the ice regime on large lakes in Estonia. Ice cover is defined as the period during which there is no free water visible from the observation station, spring ice phenomena last from the first open water stretch until the total disappearance of ice.

Lake, site	No. in Fig. 1	Period	Average ice cover duration (days)	Average end of ice cover	Average end of ice phenomena
Võrtsjärv	1	1924–1998	134 ± 20	10 April	23 April
Peipsi					
Mustvee	2	1922–2001	134 ± 29	6 April	26 April
Praaga	3	1922–2001	109 ± 28	31 March	16 April
Mehikoorma	4	1948–2001	117 ± 27	1 April	15 April

Observations made at 148 sites (Fig. 1) during 40 years (1951–1990) were included in the analysis. Series from most of the observation sites were short and fragmentary, and only from five sites they covered a period of 20 years or more (a maximum of 32 years). Altogether 751 records for roach (409 dates for the beginning and 342 for the end of spawning) and 595 records for bream (325 for the start, 270 for the end) were analysed. Number of records per year ranged from 4 to 25 (average 8) for roach and from 4 to 23 (average 10) for bream. The records were divided between lakes and rivers as 541:210 for roach and as 480:115 for bream.

For analysis the study area was divided into three subbasins: Peipsi, Võrtsjärv and the Emajõgi subbasin consisting of the main water body together with rivers and lakes directly connected to it. Observations made in the outflowing Narva River and in the Narva reservoir (190 km^2, only one site) were also assigned to the Peipsi subbasin.

To analyse the data we created two worksheets. The first worksheet contained all single observations on the onset and end of the first spawning for all stations within the area. In the second worksheet we calculated annual median values of these variables over observation sites in the three subbasins mentioned above. There were generally no big differences between median and mean values but we chose the formers as being less sensitive to single extremes.

We complemented the worksheet containing single observations with daily water temperature measurements at four stations within the area (Fig. 1). Temperature was measured at the depth of 0.5 m from the surface. We applied the water temperature measured in Võrtsjärv for all stations located within the lake and its watershed, temperature measured at the downstream end of the Emajõgi was applied for this particular river and its tributaries, temperature measured in Lämmijärv was coupled with spawning records in lakes Pihkva and Lämmijärv (including tributaries), and temperatures at Mustvee were applied to spawning records from Peipsi *s.s.* and rivers connected to it (except the Emajõgi). We fully recognise that the temperatures measured at the four sites were not equally representative for the whole network of spawning sites and hence the absolute values (e.g. those shown in Table 2) should not be compared with temperature ranges from spawning sites reported by other authors. However, we presumed a general coherence of temperature changes at different spawning sites allowing us to judge upon relative interannual and long-term changes in spawning temperatures. Data on water temperatures as well as monthly mean water level data for Võrtsjärv used in the analysis were obtained from the Estonian Institute of Meteorology and Hydrology.

We complemented the second worksheet containing annual median values of spawning times with sums of daily water temperatures for the

Table 2. Median values (upper and lower quartiles in parenthesis) of spawning time and temperature of roach and bream within the Narva River basin in 1951–1990. Median values set in boldface differ significantly (Mann-Whitney test: $p < 0.05$) between lakes and rivers.

	Roach			Bream		
Waterbody type	All	Lakes	Rivers	All	Lakes	Rivers
Onset of spawning (day number)	123 (116–131)	125 (118–132)	1 (114–127)	140 (133–148)	**142** (134–148)	**136** (129–142)
End of spawning (day number)	130 (122–136)	**132** (125–137)	**124** (118–132)	145 (137–152)	146 (139–154)	140 (132–144)
Duration of spawning (day)	5 (3–8)	**5** (3–9)	**3** (2–5)	3 (2–6)	**3** (2–6)	**2** (1–3)
Water temperature* at start of spawning (°C)	8.4 (6.1–11.4)	**8.7** (6.1–11.4)	**7.8** (5.2–10.3)	13.2 (11.2–15.4)	13.3 (11.4–15.6)	12.9 (10.8–14.9)

*Temperature measured at four stations located in lakes

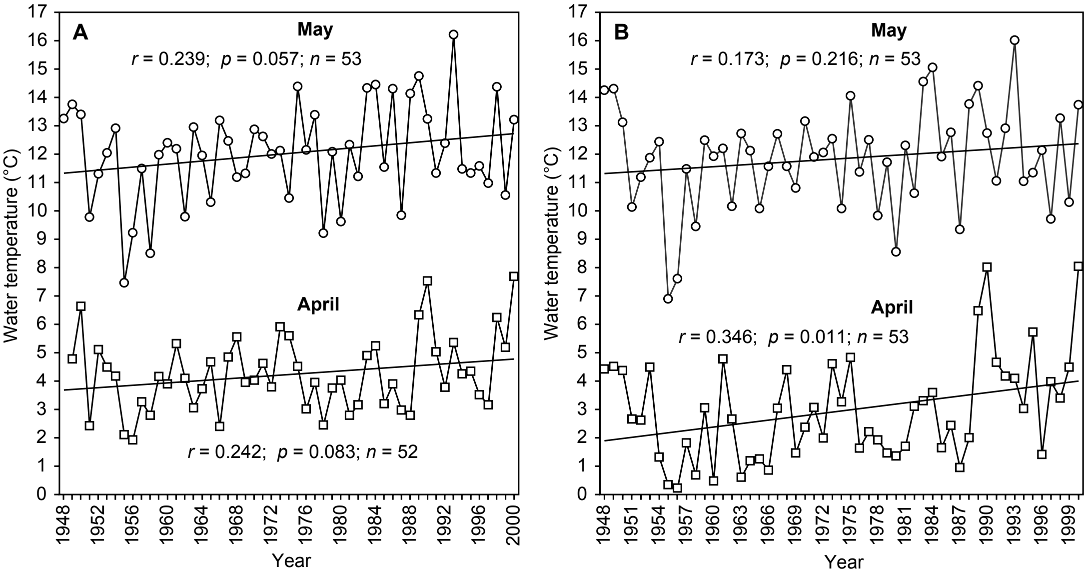

Fig. 2. Long-term changes in monthly mean water temperature in April and May in Võrtsjärv (**A**) and Peipsi at Mehikoorma (**B**). Straight lines show the linear trends.

second half of April and for the first half of May as well as with monthly average water levels for March, April, and May measured in lakes Peipsi and Võrtsjärv.

We used multiple regression (Statistica 6.0, StatSoft Inc.) to analyse relationships between spawning time and physical variables, and Mann-Whitney *U*-test to estimate the significance of differences in median values of fish spawning times in lakes and rivers. The distributions of all variables (spawning time, temperature, water level) did not differ from normal distribution (Chi-square test) and, hence, no transformations of data were needed prior to the analysis.

Results

Changes in physical environment

Analysing the long-term water temperature data from the large lakes for April and May 1948–2000, we found a statistically significant ($p < 0.05$) increasing trend for Peipsi in April and a nearly significant trend for Võrtsjärv in May (Fig. 2). According to these trends, the average water temperature for these months increased by 1.0–1.5 °C during the last half century.

Changes in spawning

Roach started to spawn on average around 30 April (day no. 120) in rivers and around 5 May in lakes within the Narva River basin (Table 2). One half of all measurements fell into a range of 16 days between 26 April and 11 May. Spawning started in lakes when the median water temperature measured at four stations in large lakes reached 8.7 °C. During roach spawning in rivers, the lake temperature was almost one degree lower. The spawning in lakes lasted significantly longer and ended later in comparison with rivers.

There was no significant trend in spawning dates for roach (Fig. 3), but the increase of water temperature corresponding to the time of spawning was highly significant (Fig. 4; $p = 0.001$, $n = 409$). This trend proved to be significant also in all single subbasins: Võrtsjärv ($n = 99$, $p = 0.006$), Peipsi ($n = 177$, $p = 0.048$) and the Emajõgi subbasin ($n = 133$, $p = 0.018$). According to linear trendlines, the water temperature at which roach started to spawn increased by 3–3.5 °C within the period of 1951–1990.

Bream started to spawn 16–17 days later than roach, the median dates being 16 May for rivers and 22 May for lakes. One half of all measurements fell into a range of 16 days between 13

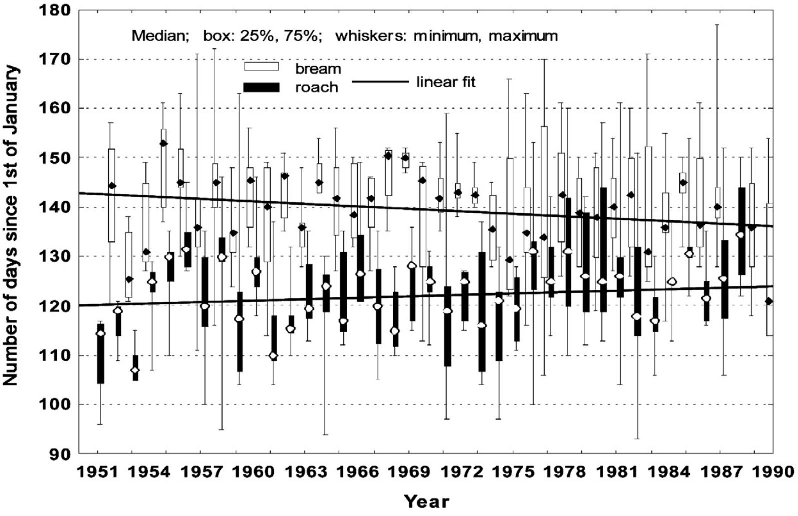

Fig. 3. Timing of the onset of spawning of roach and bream in waterbodies within the Estonian part of the Narva River basin in the period 1951–1990. Linear fittings are added to the series for visual purposes although the trends are not significant.

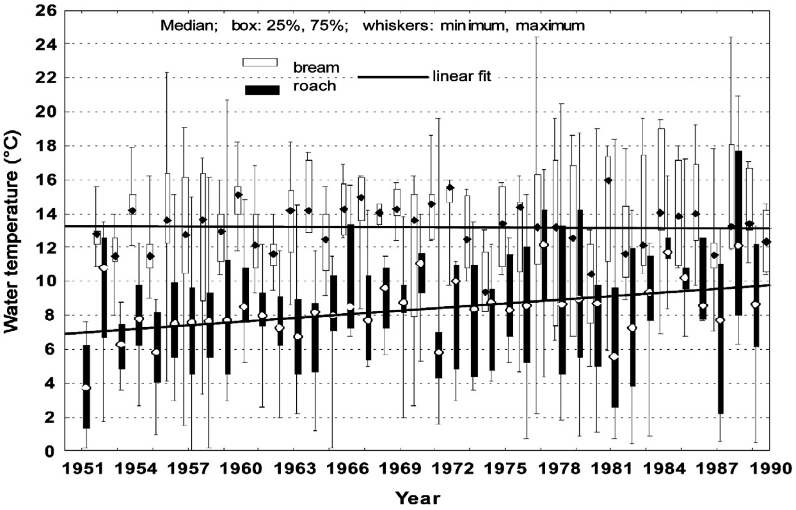

Fig. 4. Water temperature in Peipsi and Võrtsjärv at the onset of spawning of roach and bream in waterbodies within the Estonian part of the Narva River basin in the period 1951–1990. Linear fittings are added to the series for visual purposes although there is no trend in the series for bream. For roach the trend is highly significant (p = 0.001, n = 409).

and 28 May. As for the roach, the spawning of bream also lasted significantly longer in lakes than in rivers (Table 2). The median water temperature measured in large lakes at the beginning of spawning of bream in rivers respective in lakes (correspondingly, 12.9 and 13.3 °C) was not significantly different.

We found significant decreasing trends in spawning dates for bream in the Võrtsjärv subbasin ($p = 0.014$, $n = 118$ for the beginning date, and $p = 0.003$, $n = 103$ for the ending date). In this area, the onset of spawning of bream became on average 10 days earlier and the end of spawning 12 days earlier during the analysed 40-year period. For all data the decreasing trend (Fig. 3) remained insignificant. Despite a substantial interannual variability, the long-term median spawning temperature of bream remained unchanged (Fig. 4) and we found no trends in any of the subbasins.

In 1951–1990, the difference between spawning times of roach and bream decreased from an average of 22 days to 13 days ($p = 0.023$; $n = 39$) and the difference in spawning temperatures decreased from 5.8 to 3.5 °C ($p = 0.037$; $n = 39$).

In both fish species strong negative correlations occurred between temperature sums in the second half of April or in the first half of May and annual average spawning dates. Temperature in these periods explained 23%–34% of the interannual differences in the spawning onset of roach and 13%–18% of that of bream (Table 3).

The height of the water level in spring was another factor related to the onset of spawning. In years with higher water levels in March and April both fish species tended to spawn earlier, while high water level in May associated significantly with later spawning (Table 3). Monthly average water levels from March to May in various combinations explained 16%–19% of the variability in spawning onset of the two fish species within the Peipsi subbasin and 23%–35% of those in the Võrtsjärv subbasin. Including both the water temperature and water level into multiple regression analysis increased the explained variability (R^2) of the onset of fish spawning to 38%–44% in the Võrtsjärv subbasin, but did not improve the model for the Peipsi subbasin (water level data were rejected by the stepwise procedure).

Discussion

There are several reasons to have doubts regarding the scientific exactness of phenological databases collected by non-professionals. The first problem is related to the discontinuity: both the observers and the observation sites changed during these 40 years. Undoubtedly, this discontinuity introduced additional variability to the database, but we do not know any reason which could systematically bias the data. Missing the right onset of spawning could cause another error that biases the data towards later onset of spawning and shorter spawning duration. Data for sites where either the onset or the end of spawning was missing in a particular year were still included in the database but could not be used to calculate the spawning duration.

In cases when the fish spawned in several groups (bream), the first spawning run could be missed and some of the later spawning runs described as the first one. However, in this case we would expect a bigger variability in the onset of spawning of bream as compared with that of roach. In fact, the variability was exactly equal in both species showing that this kind of error did not probably play an important role.

Additional variability was introduced to the database by combining the spawning observations with the daily temperature measurements. During spring warming, temperature differences between different parts of lakes are considerable, reaching e.g. in Peipsi 8–10 °C (Jaani 2001). Relating of spawning records from the whole

Table 3. Results of multiple regression analysis between the onset day of spawning of roach and bream in the Peipsi and Võrtsjärv subbasins as dependent variables and water temperature (T) and water level (L) as independent variables. Averaging periods in subindices: A2 = second half of April; M1 = first half of May; III, IV, and V = March, April, and May, respectively. For the Peipsi subbasin L and T measured at the Mustvee station were used. The magnitude of standardized regression coefficients (β) allows to compare the relative contribution of each independent variable in the prediction of the dependent variable.

	Võrtsjärv				Peipsi			
Species	Variable	β	Adjusted R^2	p	Variable	β	Adjusted R^2	p
Roach	T_{A2}	–0.59	0.335	< 0.001	T_{A2}	–0.5	0.23	0.001
	L_{IV} L_{V}	–0.94 0.73	0.346	< 0.001	L_{IV} L_{V}	–0.73 0.59	0.164	0.014
	T_{A2} L_{IV}	–0.58 0.37	0.442	< 0.001				
Bream	T_{M1}	–0.39	0.126	0.015	T_{A2}	–0.45	0.183	0.004
	L_{III}	–0.50	0.231	0.001				
	T_{M1} L_{III}	–0.40 0.52	0.378	< 0.001	L_{III} L_{V}	–0.68 0.62	0.192	0.008

river basin to temperatures measured at some single points in lakes markedly blurs the relationship, which therefore cannot be used for specifying the absolute temperature preferences of fish species. Hence, we used the temperature data only to follow the relative changes in spawning conditions. The fact that we found similar effects of the climate change on fish spawning for all three subbasins separately encouraged us to consider these regularities real and not an artefact caused by the noisy character of the input data.

Roach is a single spawner and spawning in several groups was observed in rare cases. Earlier investigations (Haberman *et al.* 1973) have shown that the spawning of roach in shallow Võrtsjärv may start already in mid-April. Male roaches reach their sexual maturity at (2)3–4(5) years age when they are 8–11 cm long. Female first time spawners are older, (3)4–5(6) years, and bigger (10–13 cm). Eggs for next spring start to develop already in July and gonads of the male fishes in August. In Lake Peipsi roach starts to spawn at the end of April at water temperature of 8–10 °C, and mass spawning takes place at 10–13 °C (Pihu and Kangur 2001). Spawning ends during the second half of May. Our analysis revealed a rather short spawning duration of roach (median 5 days) at a particular spawning ground, but obviously due to large spatial variability of conditions in the whole basin, the spawning period is extended to several weeks.

According to Haberman *et al.* (1973) male breams reach sexual maturity in Võrtsjärv at the age of (6)7–9(10) years being 25–32 cm long. Female breams are (6)7–10(11) years old and 26–36 cm long at the time of their first spawning. Spawning starts at water temperature of 13–14 °C and reaches its peak at 16–19 °C. Bream is a single spawner in the sense that in one individual all eggs mature synchronously. However, local fishermen distinguish between different spawning groups of bream in this lake (Mikelsaar 1984 *cit.* Haberman 1964). On the basis of other phenological phenomena these groups are called "särjelatik" (roach–bream), which spawns in the beginning of May together with roach, "toomelatik" (bird-cherry bream) — the most numerous group which spawns at the time of bird cherry (*Prunus padus* L.) flowering in the end of May or beginning of June, and "kesalatik" (fallow bream) which spawns around midsummer. Also in Peipsi breams lay their eggs usually in 2–3 groups during the spawning period. Bigger individuals of both sexes are commonly earlier spawners than the smaller ones (Pihu and Kangur 2001). In both lakes the spawning grounds of bream are rather limited and located mostly in southern parts of the lakes, which forces bream to undertake long spawning migrations. Being located at different distances, fish reach the spawning grounds at different times. In rivers bream reached the spawning grounds located in the lower course always earlier than those in the upper course (Ristkok 1974). As a rule, the number of spawning groups is smaller in rivers than in lakes (Tuvikene *et al.* 2003). When fish are ready to spawn, several warm days always function as a trigger of massive spawning but windy days or an abrupt decrease in temperature may stop the spawning. According to A. Järvalt (pers. comm.), different migration distances together with the variability in weather are probably the most important factors causing the subsequent spawning groups of bream in Võrtsjärv and Peipsi.

Our data show that the increase in temperature caused by a climate change induced earlier spawning in bream but not in roach, which started to spawn at higher temperature but at the same date as earlier (Figs. 3 and 4). In general, the differences in spawning time and in preferred temperature ranges of these species became smaller. A similar levelling of the spawning differences can be seen in a geographical gradient from north to south. So, for example, in Římov Reservoir (Czech Republic) the cyprinids roach, bleak (*Alburnus alburnus* L.), chub (*Leuciscus cephalus* L.), and bream migrate upstream and spawn nearly synchronously (Hladík and Kubečka 2003). The timing of these migrations depends both on water temperature and weather, but the authors could not find any simple temperature value triggering the migration.

At the moment, we can only speculate about the causes of the different reactions found in roach and bream. Both species had a rather similar temperature dependence of spawning. Roach has a short gonadal quiescent period and new vitellogenesis starts already in late summer (Rinchard and Kestemont 1996) and the gonads grow in autumn and winter. The spawning of roach takes place at low temperatures very soon after the breakup of ice. In order to start the physiological processes leading to spawning in time, roach needs an early signal other than temperature. Presumably the length of the photoperiod may play an important role in triggering the spawning physiology. A special investigation carried out to study the effects of photoperiod and temperature manipulation on the reproduction in roach (Jafri 1989) showed that a combination of long photoperiod and warm water conditions was necessary for successful spawning. Importance of the length of the photoperiod for roach, a variable that is not affected by climate change, could explain the rather constant spawning time despite changed thermal conditions. In years when there is a fast temperature increase, the response in roach may be delayed resulting in a higher temperature at spawning. In bream the higher spawning temperature itself may guarantee a more adequate reaction of the species to changing temperature and a smaller need to use light as an early "warning signal".

There could be several mechanisms behind the strong correlation found between the water level and the spawning time of the fishes. Firstly, as the spring flood is a seasonal phenomenon, its timing is correlated with other variables with a pronounced seasonality. The flood peak is higher in years when there is a fast melting of snow and large amounts of meltwater enter the lake. Fast changes in water chemistry can probably also affect the timing of spawning. Another explanation for lower temperature measured in lakes at the spawning time in years of high water level could be the more extensive flooding. Shallow water covering large flood plains in wet years is heated up much faster than the water in lakes where the temperature was measured. Flooded areas are the favourite spawning grounds both for roach and bream (Vetemaa *et al*. 2003, Tuvikene *et al*. 2003). In years with low water level lakes and rivers stay in their beds and the temperature difference between the spawning sites and the sites of temperature measurements is smaller.

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