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Shift of spawning season and effects of climate warming on developmental stages of a grayling (Salmonidae)

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Abstract

River-dwelling fish, such as European graylings (*Thymallus thymallus*), are susceptible to changes in climate because they can often not avoid suboptimal temperatures, especially during early developmental stages. We analyzed data collected in a 62-year-long (1948-2009) population monitoring program. Males and females were sampled about 3 times/week during the yearly spawning season in order to follow the development of the population. The occurence of females bearing ripe eggs was used to approximate the timing of each spawning season. In the last years of the study, spawning season was more than 3 weeks earlier than in the first years. This shift was linked to increasing water temperatures as recorded over the last 39 years with a temperature logger at the spawning site. In early spring water temperatures rose more slowly than in later spring. Thus, embryos and larvae were exposed to increasingly colder water at a stage that is critical for sex determination and pathogen resistance in other salmonids. In summer, however, fry were exposed to increasingly warmer temperatures. The changes in water temperatures that we found embryos, larvae, and fry were exposed to could be contributing to the decline in abundance that has occurred over the last 30 to 40 years.

Introduction

Recent changes in climate appear to be affecting species distributions, demographic factors, coevolutionary interactions, growth of individuals, and timing of life-history events (Mawdsley et al. 2009). River-dwelling fishes are affected by climate change because they can often not avoid suboptimal temperatures (Daufresne & Boet 2007). This is especially so for cold-water fishes such as salmonids (Haugen & Vøllestad 2000).

Salmonids exhibit both resident and migrating life-history strategies, often within a single population, but all salmonids spawn in well-oxygenated and relatively cold freshwater. Salmonids are often keystone species of considerable cultural, commercial, and recreational importance, and valuable models for evolutionary and ecological research (Waples & Hendry 2008). However, there are many uncertainties about the effects climate change may have on these fishes and about their potential to adapt to such changes (Battin et al. 2007; Jensen et al. 2008). It is therefore important to evaluate existing monitoring programs and to develop hypotheses from observed changes (Mawdsley et al. 2009).

We examined a well-studied lake population of European graylings (*Thymallus thymallus*). European graylings are fast-growing, shoaling salmonids that live in cold rivers and lakes and reach a maximal length of about 60 cm. They spawn in spring in rivers where there is fine gravel and moderate current. After several weeks, offspring emerge from the gravel as fry (Penáz 1975). We examined changes in the timing of spawning and changes in temperature to which embryos, larvae, and fry have been exposed over 39 years.

Methods

The study population of graylings lives in the subalpine Lake Thun (surface area, 48 km^2; maximal depth, 218 m), Switzerland , and in the lake's outlet, the river Aare (mean flow rate 40 m^3/s in winter and 200 m^3/s in summer). The only spawning location of this population is in the river between the lake and a weir 1.3 km downstream (46°45'24''N, 7°37'57''E). In this part of the river graylings have been protected from angling and commercial fishing since 1952. The population has been monitored since 1948. In general fishing effort was low until 1962, when monitoring efforts were improved and standardized. Since then, spawning fish have been caught about 3 times/week during spawning season (average catches range from 16.7 to 450.5 graylings per day and year) . These fish were kept in holding tanks and released after collection of their gametes (by stripping). In the years 1986, 1989, 1993, 1994, and 2005, scales from in total 388 spawning individuals were collected and used to determine the age of the fish. Mean (SD) age was 5.0 years (1.2). Mean length of sampled fishes was 451.0 mm (30.1). We considered the days when the first and the last egg-bearing female with ripe eggs were caught as the start and the end of the spawning season, respectively.

Water temperature at the spawning site has been recorded at 1-minute intervals with an automatic logger since April 1970. We used mean daily temperatures that were calculated from these original measurements. Local air temperatures are only available from June 2006 on. Therefore we obtained the yearly sugar content of pinot noir grapes from a winery in the region (3 km away from the spawning site). After each harvest since 1968, sugar content was measured in degrees Oechsle. In relatively cold wine-growing regions, such as this one, an increase in grape sugar content may indicate regional increases in air temperate (Jones et al. 2005).

We used accumulated thermal units (ATUs) (i.e., the number of days since gamete fusion x the average daily temperature) to describe the temperature environment of naturally spawned embryos and fry relative to their developmental stage. Pearson's correlation coefficient *r* and corresponding *p*-values (2-tailed) were used to test for changes over time.

Results

Since 1962, yearly sampling effort did not change significantly ($r = 0.14$, $p = 0.33$; mean number of days at which spawners were caught 8.8 (SD 0.5), but the abundance of the spawning population of grayling declined (males and females: $r = -0.42$, $p = 0.003$; Fig. 1a). The average yearly water temperatures at the spawning site increased over the last 39 years (Fig. 1b). Sugar content of grapes in the region also increased (Fig. 1b), which suggests that the increased water temperature was caused by a regional change in climate.The average (SD) length of the spawning season was 24.7 days (7.4) and did not increase significantly over time ($r = 0.20$, $p = 0.18$) (Fig. 1c). By the late 2000s the spawning season was on average 3-4 weeks earlier than in the early 1960s (Fig. 1c). This shift in the timing of spawning was paralleled by the regional climate change (Fig. 1b,c; Fig. 2a).

At the beginning of the spawning season the water temperature was approximately 6 °C every year. This temperature did not differ significantly from year to year (Fig. 1d), but it was reached increasingly earlier over time (Fig. 2a). Spawning typically starts after a distinct temperature rise (Fig. 2b).

The change in the timing of spawning has changed the temperatures under which embryos, larvae, and fry develop (Fig. 2c). Significant temperature reductions over time occurred during embryogenesis, hatching, metamorphosis from larva to fry, and emergence from gravel (i.e., the first 500 ATUs) (Table 1, Fig. 2c). In the summer months, temperatures increased significantly from 1971-2009 (Fig. 2a, c). These temperature changes correlated with a decrease in the number of egg-bearing females (Table 1).

Discussion

We believe the significant increases in river temperatures we found are linked to a regional change in climate (as suggested by the increased sugar content of grapes in the region). These temperature increases have also occurred in other Swiss waters (Hari et al. 2006). The timing of spawning of our study population shifted to 3-4 weeks earlier in the year. In the grayling population we examined, spawning typically began after a distinct temperature increase at around 6 °C. This phenomenon suggests spawning is temperature induced, as has been suggested for other populations of graylings (Barson et al. 2009). The regional climate change the data show seems to be associated with the changes we found in the timing of grayling reproduction.

Effects of climate change on other salmonids have been studied (e.g., anadromous Pacific salmon for which freshwater temperature imposes strong selection). Summer temperature, for example, is often negatively correlated with juvenile survival (Brannon et al. 2004), and temperature-linked shifts in migration timing are predicted to affect the timing of other life-history transitions such as, for example, spawning, emergence from gravel, and downstream migration (Crozier et al. 2008a). Life-cycle models predict that these changes increase the probability of quasiextinction (Crozier et al. 2008b). Evolutionary responses to climate change are difficult to predict because too little is known about the strength of various selection pressures, heritability of important traits, interaction between genetics and ecology, and relative roles of plasticity and genetics (Gienapp et al. 2008).Crozier et al. (2008a) argue, however, that the timing of salmonid emergence may typically be under stabilizing selection: the ideal emergence time may be when food (i.e. zooplankton in the case of graylings) becomes available. Emerging too early increases the probability of starvation, whereas the period for growth is reduced if a cohort emerges late in the season (Einum & Fleming 2000). An evolutionary response to climate changes may therefore include an adjustment of the spawning date or a change of the temperature-specific embryo developmental rate. The heritability of the latter trait is typically low (Hebert et al. 1998; Kinnison et al. 1998), whereas significant heritability of spawning date has been found repeatedly (Quinn et al. 2002; Hendry & Day 2005; Carlson & Seamons 2008). It remains to be tested whether the observed shift in the spawning of graylings is adaptive.

Many ecological characteristics of a river are linked to temperature (Durance & Ormerod 2007). Thus, the optimal time for emergence of grayling fry could have shifted in accordance with temperature shifts in the study area. However, a temperature-induced onset of spawning may not fully compensate for the effects of climate change on embryos and fry during ontogeny. Although spawning was earlier, the temperature of the water rose more slowly over time. Thus, embryos and larvae were exposed to increasingly colder temperatures around the time of hatching. This is a potentially critical period at which salmonids are exposed to microbial pathogens (Wedekind et al. 2010) and exhibit behavioral (Wedekind 2002) and immunological reactions (von Siebenthal et al. 2009) to infections that may be temperature dependent. Additionally, sex determination occurs during embryonic and larval development in some other salmonids (Baroiller et al. 2009). The sex determination of graylings has, to our knowledge, not been studied in much detail. However, salmonids typically have genetic sex determination with male heterogamety. Their sex can be reversed by temperature changes at early developmental stages; colder temperatures usually induce masculinization (Davidson et al. 2009). Individuals that have undergone sex reversals are viable and fertile and could potentially influence population dynamics, negatively or positively (Stelkens & Wedekind 2010). Indeed, the percentage of males at our study site has increased over the last decades, and the apparent lack of an evolutionary response to the observed change in sex-ratio is linked to a relatively low genetically effective population size (C.W. & G. Evanno, unpublished data).

Juveniles are found year-round in the river Aare (Guthruf 1996). The changed temperature regime may therefore affect juvenile metabolism, nutritional needs, growth, and survival during the summer months, by which time the water temperature may have increased to stressful levels (Farrell 2009).

The long-term effects of these ecological changes are unclear, but the abundance of the population has been declining during the last decades despite considerable protection from harvest since the 1950s (as a consequence, the population is fully protected from any harvest at all possible whereabouts since January 2008). If increased temperatures drive decreases in abundance, some conservation actions that have been discussed, such as increased shading of water bodies, installation of heat exchangers, or temperature treatment of eggs and larvae in hatcheries, may help solving the problem. However, there is a possibility that temperature manipulations lead to the disappearance of sex-determining genetic factors (Kanaiwa & Harada 2002; Cotton & Wedekind 2009). Moreover, conservation actions that do not affect water temperature may give populations more time to adapt to environmental changes (Haugen & Vøllestad 2001).

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Table 1 Results of a forward stepwise regression analysis of the effect of the average temperatures experienced by naturally spawned embryo and fry grayling on the number of egg-bearing females that were recorded 5 years later.[a]

	r^2	Parameter estimate (SE)	*F*	*p*
Intercept[b]		253.9 (449.3)	0.3	0.58
1500-2000 ATU[b]	0.163	-48.4 (17.1)	8.0	0.01
0-500 ATU[b]	0.261	90.7 (44.7)	4.1	0.05
1000-1500 ATU	0.270	0	0.3	0.56
500-1000 ATU	0.271	0	0.1	0.78

[a] Developmental stages are separated into consecutive periods of 500 accumulated thermal units (ATUs). The parameter estimates, *F*, and *p* refer to the final model ($F_{2,31} = 5.5$, $p < 0.01$).

[b] Included in the final model.

Figure legends

Figure 1 Changes over time in (a) number of egg-bearing female graylings caught at the spawning site (shaded area, years of lower fishing effort; change since 1962: $r = -0.63$, $p < 0.0001$), (b) average yearly water temperatures (circles and solid line, $r = 0.70$, $p < 0.0001$) and average sugar content in degrees Oechsle (°Oe) of grapes growing in the area (stars and dashed line, $r = 0.61$, $p < 0.0001$), (c) day the first egg-bearing females were caught at the spawning site (open circles, $r = -0.80$, $p < 0.0001$) and day the last egg-bearing females were caught (solid circle, $r = -0.70$, $p < 0.0001$) (shaded area, spawning time ; grey line, connects "peak" days up to which half the spawners of a spawning season had been sampled [$r = -0.92$, $p < 0.0001$]; ordinal date = number of days since Jan 1st), and (d) average water temperature on the day the first egg-bearing females were caught at the spawning site ($r = -0.16$, $p = 0.33$). All lines give the regressions.

Figure 2 (a) Daily water temperatures at the spawning site averaged from 1971 to 1980 (thin grey line), 1981 to 1990 (thick grey line), 1991-2000 (thin black line), and 2001-2009 (thick black line). The rectangles indicate the average start, duration, and end of the spawning seasons for each decade. (b) Average (SE) daily temperature change before the start of a spawning season. (c) Average water temperature at the grayling spawning site versus offspring development in accumulated thermal units (ATUs) (days since fertilization x average daily temperature). Developmental processes in the first 300 ATUs include embryogenesis and hatching from eggs. The subsequent developmental interval (300-500 ATUs) include mostly larval stages. Metamorphosis to fry is expected to happen within this period or shortly thereafter. Average temperature to which the various developmental stages are exposed when spawning was at the beginning of the spawning season (circles), at midseason (12 days later, squares), and at the end of the spawning season (24 days later, triangles). Corresponding averages for the 1970s, 1980s, 1900s and the years from 2001 to 2009 (from left to right) are connected with lines.

Figure 1

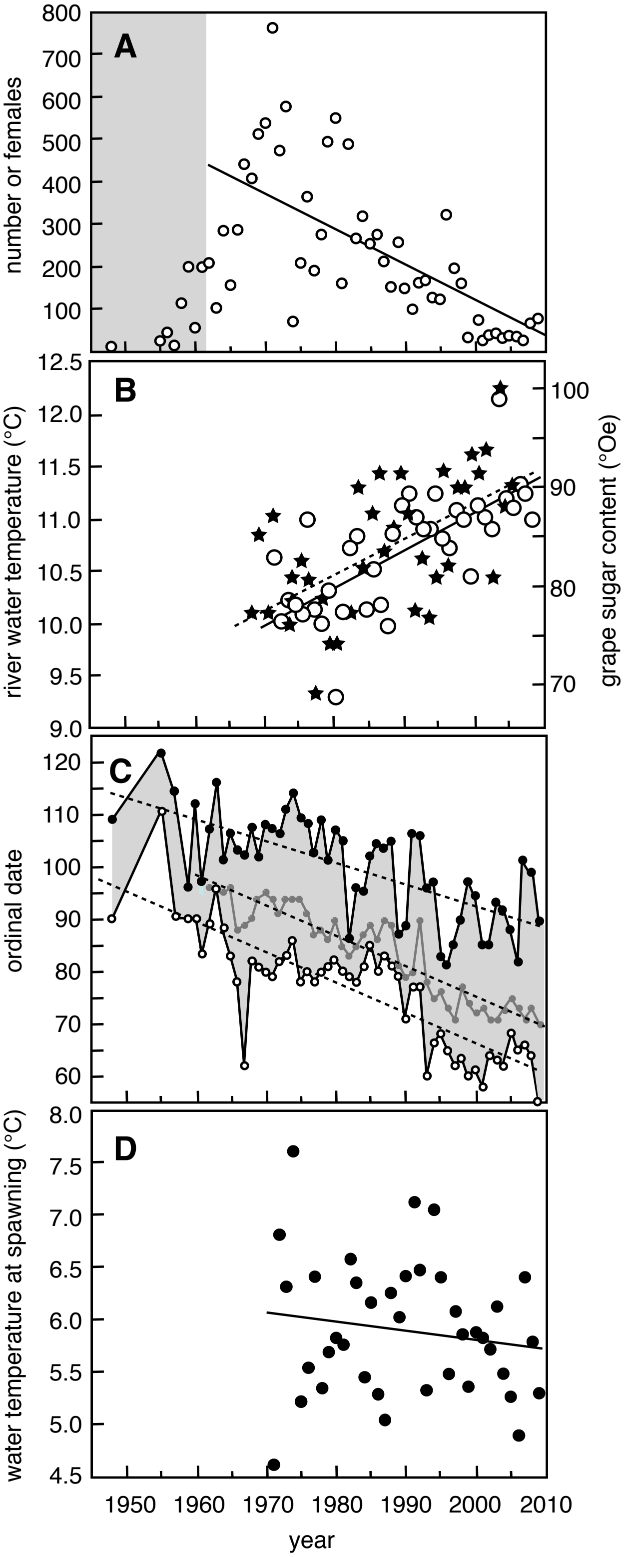
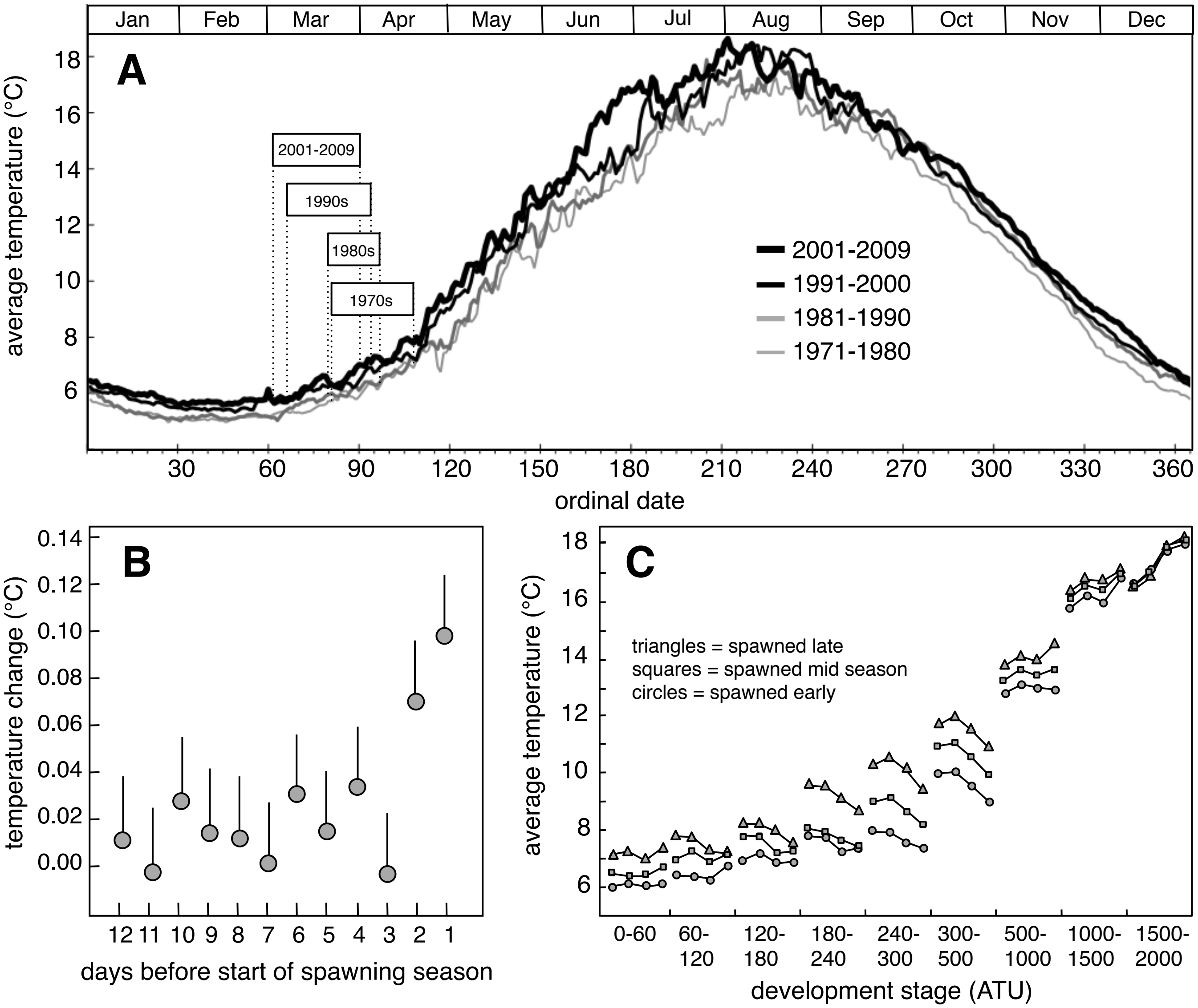

A
number or females
800
700
600
500
400
300
200
100
B
river water temperature (°C)
12.5
12.0
11.5
11.0
10.5
10.0
9.5
9.0
grape sugar content (°Oe)
100
90
80
70
C
ordinal date
120
110
100
90
80
70
60
D
water temperature at spawning (°C)
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
1950
1960
1970
1980
1990
2000
2010
year

Figure 2:


Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
A
average temperature (°C)
18
16
14
12
10
8
6
2001-2009
1990s
1980s
1970s
2001-2009
1991-2000
1981-1990
1971-1980
30
60
90
120
150
180
210
240
270
300
330
360
ordinal date
B
temperature change (°C)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
12
11
10
9
8
7
6
5
4
3
2
1
days before start of spawning season
C
average temperature (°C)
18
16
14
12
10
8
6
triangles = spawned late
squares = spawned mid season
circles = spawned early
0-60
60-120
120-180
180-240
240-300
300-500
500-1000
1000-1500
1500-2000
development stage (ATU)