Spawning activity of European grayling (*Thymallus thymallus*)
driven by interdaily water temperature variations: Case study
Gr. Mühl River/Austria

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Funding information
National Foundation of Research, Technology and Development of Austria; Federal Ministry of Economy, Family and Youth

Abstract
Interdaily water temperature variations were studied at a known spawning site of European grayling (*Thymallus thymallus*) in the Große Mühl River, Austria. Spawning activity was visually observed from a bridge where spawners were counted and their activity/behaviour documented twice a day. The spawning of grayling was documented for a temperature range of 7.8–11.5°C. Analysis of the collected data showed that spawning activity increases significantly when water temperatures rise during a day. In addition, the results showed a significant response in the relative water temperature increase, which was +3.5°C on average; however, the absolute temperature between periods of non-activity and spawning activity exhibited no significant differences.

KEYWORDS
grayling, habitat suitabilities, spawning habitat, water temperature variation

1 | INTRODUCTION

European grayling (*Thymallus thymallus*) is an endangered salmonid fish species that exhibits a massive decrease in abundance and biomass throughout many European countries (Gum, Gross, Rottmann, Schroeder, & Kuehn, 2003; Kirchhofer, Zaugg, & Pedrol, 1990; Persat, 1996; Sušnik, Berrebi, Dovç, Hansen, & Snoj, 2004; Ublein, Jagsch, Honsig-Erlenburg, & Weiss, 2001). Among the primary reasons for the sharp decline in numerous grayling populations is habitat loss due to various anthropogenic interventions (e.g., water regulation and hydropower use). Furthermore, increased predation pressure by wintering cormorants must be emphasized (e.g., Jepsen et al., 2018; Meraner, Unfer, & Gandolfi, 2013; Weiss, Kopun, & Bajec, 2013) as well as overfishing (Näslund et al., 2005) and potentially climate change (Wedekind & Kueng, 2010; Wedekind et al., 2013). For grayling, as for other salmonids, spawning habitats, in particular, are crucial and critical habitats that can act as bottlenecks, specifically in granite mountain streams where suitable spawning gravel is also naturally restricted (e.g., Hauer, Unfer, Habersack, Pulg, & Schnell, 2013; Pulg, Barlaup, Sternecker, Trepl, & Unfer, 2013).

The abiotic characteristics at the spawning sites were examined in various scientific studies. These studies are related to spawning migration (Ovidio et al., 2004; Ovidio, Parkinson, Sonny, & Philippart, 2004; Parkinson, Philippart, & Baras, 1999), habitat selection (Mallet, Lamouroux, Sagnes, & Persat, 2000; Nykänen & Huusko, 2002; Sempeski & Gaudin, 1995), habitat modelling of
potential spawning side locations (Fukuda, De Baets, Waegeman, Verwaeren, & Mouton, 2013; Mouton et al., 2008) and potential impacts of global warming (Wedekind & Kueng, 2010). Single studies deal with the pronounced polygamous spawning behaviour of grayling (Fabricius & Gustafson, 1955). The role of temperature in spawning biology has been mentioned in various papers (e.g., Haddeland, Junge, Serbezov, & Vøllestad, 2015; Poncin, 1996) to generally characterize observed spawning activity (e.g., mean daily temperature). Temperature variability and related spawning activity were addressed only in single papers (e.g., Gönczi, 1989; Lahnsteiner & Kletzl, 2012) and interdaily quantification of temperature variations are missing.

Thus, the aim of the present study was to examine interdaily water temperature fluctuations and related spawning activity based on a case study. The study was conducted at a well-known spawning site of grayling in Große (Gr.) Mühl River in Austria (Hauer, Unfer, Tritthart, & Habersack, 2011). Observations were made in April 2020 twice a day during a three-week period. To enable a comparison of the habitat used to literature-known parameters (e.g., flow velocity and water depth), a corresponding measuring campaign was carried out 1 week after the spawning activity ended.

2 STUDY REACH

The Gr. Mühl River is an orographically left-sided tributary of the Danube in the western granite and gneiss highlands in Upper Austria (Figure 1). Due to the geomorphological characteristics, spawning substrates and spawning sites for salmonids are limited. Only 20% of the riverbed provides a suitable substrate for spawning (Hauer et al., 2013). The study site is located 538 m a.s.l, 41 km downstream.
of the source with a river width of 20–30 m. In detail, the spawning areas are situated at the upstream end of the head of impoundment of a small hydropower plant (N48°38′25.82″/E13°57′29.33″) (Figure 1). This place is well known for spawning of both brown trout (Salmo trutta) and European grayling. Directly upstream is a bridge that was used for fish spotting during the spawning period.

3 | METHODS

To fulfil the objectives of the present study, three different steps were performed: (i) water temperature measurements, (ii) counting spawning fish and documenting the activity of the fish twice a day and (iii) measuring the abiotic parameters water depth (m), depth-averaged and near-riverbed flow velocity (m s⁻¹) at the studied spawning site.

Water temperature was measured on an hourly basis with a continuous iButton Thermochron® logger (resolution of water temperature measurements = 0.06°C). The logger was placed 620 m upstream of the spawning site (N48°38′45″/E13°57′28″). Data were transmitted every week in a compatible database format. A metal hull enabled secure placement at the bank as well as undisturbed transmission of water temperature changes to the logger. No tributaries discharge into the Gr. Mühl River between the temperature-logging site and the observed spawning ground (620 m downstream). Thus, the recorded data were suitable for the determination of the open flow water temperature.

Counting of grayling at the spawning site was performed twice a day, every day during a period of 3 weeks. One time slot was in the morning from 10:00 a.m.–12:00 a.m.; --the second time slot in the afternoon from 2:00 p.m.–4:00 p.m. The observation period ranged from April 4, 2020–April 26, 2020. Statistical testing for comparing the number of fish in the two groups (morning/afternoon) was performed by using a paired t-test for two independent samples. In Table 1, the exact time when the spawning site was monitored is presented. At least 10–30 min were spent on-site to count spawners and document spawning activity. As an observation point, a bridge was used, which is directly located upstream of the

**Table 1** Numbers (morning/afternoon) of European grayling (Thymallus thymallus) at the studied spawning site in relation to interdaily water temperature fluctuations; in addition to the time periods of observation, the water temperature during the morning and afternoon observations as well as the minimum and maximum water temperatures during the monitoring days are listed

| Date       | Nb.fish morning | Nb.fish afternoon | Time morning (h:min) | Time afternoon (h:min) | Temp. morning (°C) | Temp. afternoon (°C) | Min. daily temperature and time (°C/h:min) | Max. daily temperature and time (°C/h:min) |
|------------|-----------------|-------------------|----------------------|------------------------|---------------------|----------------------|--------------------------------------------|--------------------------------------------|
| 04.04.2020 | 3               | n.s.              | 11:45–12:00          | n.s.                   | 5.3                 | n.s.                 | n.s.                                       | 7.5 (17:00)                                |
| 05.04.2020 | 2               | 14                | 10:44–11:05          | 15:00–15:30            | 5.6                 | 7.8                  | 4.8 (8:00)                                  | 8.3 (18:00)                                |
| 06.04.2020 | 3               | 10                | 11:15–11:30          | 15:15–15:35            | 6.6                 | 8.9                  | 5.8 (8:00)                                  | 9.3 (18:00)                                |
| 07.04.2020 | 1               | 8                 | 11:40–11:55          | 16:00–16:15            | 7.8                 | 9.7                  | 6.4 (8:00)                                  | 9.9 (17:00)                                |
| 08.04.2020 | 4               | 11                | 11:25–11:40          | 15:45–16:00            | 7.8                 | 10.2                 | 7.0 (9:00)                                  | 10.3 (17:00)                               |
| 09.04.2020 | 3               | 12                | 11:15–11:30          | 15:00–15:15            | 7.6                 | 9.8                  | 6.8 (8:00)                                  | 10.4 (18:00)                               |
| 10.04.2020 | 3               | 9                 | 11:15–11:35          | 15:30–15:45            | 9.0                 | 10.9                 | 8.2 (5:00)                                  | 10.9 (16:00)                               |
| 11.04.2020 | 2               | 6                 | 11:17–11:35          | 15:00–15:15            | 8.7                 | 10.5                 | 7.9 (8:00)                                  | 10.8 (16:00)                               |
| 12.04.2020 | 1               | 8                 | 11:00–11:20          | 15:50–16:10            | 8.5                 | 11.2                 | 7.5 (8:00)                                  | 11.3 (17:00)                               |
| 13.04.2020 | 1               | 7                 | 11:15–11:35          | 14:30–15:00            | 8.7                 | 10.9                 | 8.2 (8:00)                                  | 11.0 (16:00)                               |
| 14.04.2020 | 1               | 2                 | 11:15–11:30          | 14:30–14:45            | 7.5                 | 8.2                  | 7.1 (9:00)                                  | 8.3 (16:00)                                |
| 15.04.2020 | 1               | 4                 | 11:45–12:00          | 14:30–14:40            | 6.0                 | 7.8                  | 4.6 (8:00)                                  | 8.5 (18:00)                                |
| 16.04.2020 | 1               | 7                 | 11:30–11:40          | 14:30–15:00            | 7.1                 | 9.3                  | 6.0 (8:00)                                  | 10.6 (18:00)                               |
| 17.04.2020 | 4               | 7                 | 11:50–12:00          | 15:30–15:45            | 9.3                 | 11.5                 | 7.5 (8:00)                                  | 11.8 (18:00)                               |
| 18.04.2020 | 2               | 5                 | 11:40–11:55          | 14:00–14:20            | 9.5                 | 11.3                 | 9.0 (8:00)                                  | 11.3 (17:00)                               |
| 19.04.2020 | 1               | 1                 | 11:30–11:45          | 15:30–15:45            | 9.3                 | 10.0                 | 9.1 (8:00)                                  | 10.4 (18:00)                               |
| 20.04.2020 | 0               | 0                 | 11:50–12:00          | 15:00–15:30            | 8.0                 | 9.8                  | 7.5 (9:00)                                  | 10.4 (18:00)                               |
| 21.04.2020 | 0               | 0                 | 11:50–12:00          | 15:50–16:05            | 8.4                 | 10.4                 | 7.1 (8:00)                                  | 10.7 (17:00)                               |
| 22.04.2020 | 1               | 1                 | 11:30–11:40          | 16:00–16:10            | 8.2                 | 11.0                 | 7.3 (8:00)                                  | 11.4 (17:00)                               |
| 23.04.2020 | 0               | 1                 | 11:30–11:40          | 16:00–16:10            | 8.9                 | 11.7                 | 8.0 (8:00)                                  | 12.0 (18:00)                               |
| 24.04.2020 | 0               | 1                 | 10:30–10:40          | 15:55–16:10            | 8.3                 | 11.2                 | 8.1 (8:00)                                  | 11.5 (18:00)                               |
| 25.04.2020 | 0               | 1                 | 10:30–10:40          | 15:30–15:40            | 8.6                 | 11.5                 | 8.2 (8:00)                                  | 12.1 (17:00)                               |
| 26.04.2020 | 1               | 1                 | 11:50–12:00          | 14:30–14:40            | 9.7                 | 10.9                 | 8.4 (8:00)                                  | 12.0 (18:00)                               |

Note: No. = number of observed grayling; n.s. = not sampled.
spawning site (compare to Figure 1). From the bridge, fish could be spotted without disturbing their activity. In addition to counting on-site and matching the related time of observation, pictures and videos of spawning activity were taken (see Supplementing Material). Spawning activity was scored when (i) mutual chasing of males or courting of females by males occurred or (ii) actual spawning was observed. To characterize the physical spawning habitat of European grayling at this specific spot of the Gr. Mühl River, three different parameters were sampled 1 week after the last spawning activity was documented. Both water depth and flow velocity were taken in a random sampling approach (15 points sampled on 38 m²) to characterize the spawning site (comparable to Simonson et al., 1994). Water depth was measured using a depth stick with an accuracy of 1 cm. Flow velocities were measured in a two-step approach by using the 1-D SEBA-FlowSens® for (i) depth-averaged flow velocity in 40% of the documented water depth and (ii) near-bottom flow velocity, as important parameters for the hydraulic characterization of salmonid spawning sites (compare to Hauer et al., 2011). The near-bottom flow velocity was measured approximately 3 cm above the river substrate.

4 | RESULTS

The results of the water temperature monitoring in combination with the results of the visual observations from April 2020 are presented in Figure 2. When comparing morning and afternoon data, it can be seen that the number of fish present at the spawning site in the afternoon was significantly higher ($p < .05$). All grayling observed at the spawning site during the afternoon observations showed spawning behaviours except on 14 April and 15 April and after 17 April. April, where all fish were inactive (Figure 2). Over the monitoring period, the water temperature showed a mean of 8.1°C with a SD of 1.1°C. However, evident interdaily fluctuations in water temperature were documented with increases from +2.7°C (April 10, 2020) to +4.6°C (April 16, 2020). The lowest water temperatures within a day were recorded mostly at 08:00, and the highest temperatures were recorded between 16:00 and 18:00 (compare to Table 1). The average daily increase was +3.5°C (SD = 0.6°C) for the dates of spawning activity ($n = 11$). Spawning activity was documented only in the afternoon (2 p.m.–4 p.m.) with an average afternoon water temperature of 10.2°C (SD = 1.2°C) starting from 7.8°C (April 5, 2020) to 11.5°C maximum on April 17, 2020. Interestingly, no absolute threshold in water temperature concerning spawning activity was documented. Spawning activity was mapped at 7.8°C at the beginning of the spawning season (April 5, 2020). However, no spawning activity was observed during the morning hours (09:00–12:00) on any day of the study period. A clear behavioural temperature response was given at a recorded drop in water temperature, which occurred due to a short-term cold period over 2 days (14th and 15th April), where the spawning activity immediately stopped (Figure 2). However, after these 2 days and a new increase in water temperature, spawning activity resumed immediately, with active spawning on April 16 (water temperature: 10.3°C). Spawning activity completely ended after 18 April, when the morning minimum water temperature already reached 9°C (Figure 2). From the 18th of April on, single grayling males were still present at the spawning site, but no further spawning activity was observed (Figure 2).

**FIGURE 2** Time dependent development of the water temperature (black line) and the number and/or activity of graylings in the defined spawning habitat; grey solid line = discharges on an hourly basis at gauging station Furthmühle (48°36′14″/14°01′08″)
The physical habitat characterization showed that grayling spawned in an area where the mean water depth was 0.32 m (SD = 0.06 m), the mean depth-averaged flow velocity was 0.28 m s\(^{-1}\) (SD = 0.05 m s\(^{-1}\)), and the mean near-bottom velocity was 0.20 m s\(^{-1}\) (SD = 0.04 m s\(^{-1}\)). The results are presented in Figure 3, underlining the low variability of all investigated parameters within the sampled site (compare to Figure 1c).

5 | DISCUSSION

The measured water temperature during spawning activity was 10.2°C on average (SD = 1.2°C). These values were above the values of Görnczi (1989), who documented spawning of grayling within the range of 5–7°C for the Inalsälven and 5.6–9.6°C for the Ammeran (both rivers located in Sweden). Similar ranges of mean temperatures were published by Lahnsteiner and Kletzl (2012), who reported temperatures between 5.5 and 7.2°C for five alpine grayling populations in Austria. This synchrony of the Austrian and Swedish population is surprising, since the populations studied by Görnczi (1989) live much farther north. Lahnsteiner and Kletzl (2012) also compared the timing of the spawning period of four populations with the number of days since December 21. This period varies between 98 and 111 days for the four riverine populations (Lahnsteiner & Kletzl, 2012). The spawning period at Große Mühl begins on 05 April after 106 days (375 days) and thus lies centrally within the determined range (Lahnsteiner & Kletzl, 2012). This fact could indicate that day length is more central to the initial triggering of the spawning time than water temperature, as the Große Mühl population spawned during the same period as the populations studied by Lahnsteiner and Kletzl (2012), but at significantly higher water temperatures. On the other hand, the diurnal temperature cycle seems to drive spawning activity within the spawning period.

Ovidio, Parkinson, et al. (2004); Ovidio, Paquer, et al. (2004) showed that spawning migrations were temperature related and spawning occurred at mean daily temperatures from 7 to 11°C for a stream in the Belgian Ardenne, which are in agreement with the recorded data of the present study. Görnczi (1989) also highlighted that spawning of European grayling occurred between 12 a.m. and 3 p.m., but did not perform detailed analyses of this, as the temperature was only a minor parameter in their study. Also, Vivier (1958) roughly confirms that spawning activity increases in the afternoon. Thus, their findings are in line with the observations of the present study, as spawning activity was solely documented in the afternoon. In any case, no spawning activity was detected even in the morning (10:00 a.m.–12:00 p.m.) on April 9, April 13, or April 16 (see Figure 3b), although the water temperature was already approximately 8°C on these days, even in the morning. Instead, it seems that the relative temperature increase, potentially in combination with the length of day (light), might trigger spawning activity (Figure 2). As maximum daytime temperatures are always reached slightly later (16:00–18:00) than the peak spawning activity (14:00–16:00), we hypothesize that brighter light conditions earlier in the afternoon, in addition to temperature, could also influence the timing of spawning behaviour. The observation that spawning occurs only during the warmest hours of a day is, to our knowledge, the first evidence of this behaviour in a wild grayling population.

Our study thus confirms the study of Fabricius and Gustafson (1955), who studied the spawning behaviour of a Swedish lake population in a flow-through aquarium tank. In their experiment, grayling spawned primarily between 12 noon and 08:00 p.m., with a maximum between 04:00 p.m. and 06:00 p.m. leading to the conclusion that rising temperature during the day seems to stimulate spawning behaviour activities (Fabricius & Gustafson, 1955). During a cold-weathers phase between April 14 and 15, the spawning activities completely stopped. However, during these days, more fish were
present at the site in the afternoon but remained inactive, although the afternoon temperature on the 15th was as high as that on the fifth, when fish were active (Table 1). Spawning activities ended after April 17, and only a few male graying events were observed in the spawning area until the 26th. It remains unclear whether all female graying in the area had already spawned by this time or whether this was related to the further increase in water temperature.

Comparing the physical parameters of the spawning site (n = 3) with the study of Sempeski and Gaudin (1995), it turned out that the water depth used was similar (range of 0.1–0.4 m). The mean flow velocity of the Gr. Mühl River sites, however, was obviously lower (mean = 0.28 m s⁻¹) compared to 0.49 m s⁻¹ (mean) in the study of Sempeski and Gaudin (1995). The same holds true for habitat suitability descriptions of Nykänen and Huusko (2002), who found a similar depth range, but even higher flow mean velocity (50–60 cm s⁻¹).

These comparable lower flow velocities at the study site might be related to the downstream backwater of a small hydropower facility. For such anthropogenic influences on spawning sites, it turned out that the near-bottom flow velocity seems to be the most decisive parameter for the selected spawners (compare to Hauer et al., 2011). These numbers of near bed flow velocities are in the range of documented numbers for spawning site free-flowing sections (e.g., Hauer et al., 2011).

6 | CONCLUSIONS

The present study showed the coupling of the spawning activity of European graying to a relative increase in daily water temperature after snowmelt. Spawning activity over a three-week period occurred solely in the afternoon. The documented water temperatures were slightly above documented numbers from other European countries. In relation to this deviation in activity, the number of fish at the spawning site in the morning and the number of fish in the afternoon were also significantly different. The physical characteristics of the spawning site were partly similar to those of free-flowing sections, such as the water depth and the near-bed flow velocity. The mean-flow velocity was lower than that in other international studies.

ACKNOWLEDGEMENTS

The financial support by the Federal Ministry of Economy, Family and Youth and the National Foundation of Research, Technology and Development of Austria is gratefully acknowledged.

DATA AVAILABILITY STATEMENT

The raw data of the measured water temperature as well as the observation numbers are available from the authors.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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**How to cite this article:** Hauer, C., & Unfer, G. (2021). Spawning activity of European grayling (*Thymallus thymallus*) driven by interdaily water temperature variations: Case study Gr. Mühl River/Austria. *River Research and Applications*, 37(6), 900–906. https://doi.org/10.1002/rra.3816