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Effects of substrate composition and water temperature on the emergence success of lacustrine brown trout *Salmo trutta* m. *lacustris* L. fry from natural redds

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Abstract. The emergence of lake-migratory brown trout *Salmo trutta* m. *lacustris* L. fry from natural redds was observed in a small lake outlet stream. A total of 1104 emerging fry were captured in traps in nine of the 12 investigated redds during three seasons. In 2005, all the fry emerged during the daytime, but in 2007 and 2009 they emerged mostly at night. Furthermore, the timing of emergence was earlier than expected from temperature models. The fry left the redds at a water temperature range of 6.2-15.0 °C, and the emergence pattern was correlated with the moon phase. The number of fry captured was strongly affected by the percentage of fine particles < 1 mm and the 8-16 mm particle content, and was positively correlated with the geometric mean of substrate particle size (D_g) and the index of permeability: the fredle index (f_i). The estimated survival rate between egg deposition and fry emergence ranged from 0.0 to 59.8 % in individual redds. Additionally, the greatest number of fry and the highest survival rate were observed in redds that had the high water velocity and shortest duration of intragravel period.

Key words: spawning, redds, fry traps, survival, *Salmo trutta*, the Trzebiocha stream

Introduction

The emergence and dispersion of fry from gravel redds is a critical moment in the life cycle of salmonid fish. During this period, the fish complete their absorption of energy reserves contained in the yolk sac and begin active exogenous feeding. The highest mortality rate is observed shortly after emergence from the redds (Elliott 1984, Einum & Fleming 2000), while both the moment and rate of emergence determine the fate of the fry (Metcalfe & Thorpe 1992, Beer & Anderson 2001). This results from the ability of fry to avoid predatory pressure during dispersion (Brannas 1995) and to find suitable microhabitats for feeding (Mason & Chapman 1965, Elliott 1986, Chandler & Bjornn 1988).

Temperature is the main factor affecting the ontogeny of the early life stages of salmonids, including embryonic and larval development and several papers describe its influence on the brown trout *Salmo trutta* (e.g. Crisp 1988, Elliott & Hurley 1998, Ojanguren & Braña 2003). Additionally, the type of redd substrate is observed to exert a strong influence on the survival rate of eggs and larvae, as well as on the initiation and duration of emergence. Generally, survival rate decreases when the average redd substrate particle size decreases and the fraction of sand increases (Chapman 1988). This is because small particles block the interstitial spaces between gravel particles and reduce the water permeability through redds, resulting in poorer oxygenation of the eggs (Greig et al. 2007). It has been observed that emergence from redds with finer substrates occurs earlier, when the fry are in a premature state, and that the duration of the emergence period is shorter (Witzel & MacCrimmon 1983, Olsson & Persson 1988). While it is true that salmonid females clear sediment from the redd substrate prior to egg deposition (Chapman 1988, Young et al. 1989), the eggs are still exposed to sedimentation by small particles during incubation, depending on the prevailing hydrological conditions in the current (Acornley & Sear 1999, Soulsby et al. 2001, Meyer et al. 2005).

Most studies on the influence exerted by the size of gravel particles on the survival and development of salmonid embryos and fry are conducted either under laboratory conditions or in artificial redds in streams. Unfortunately, such studies cannot fully reflect the conditions that prevail in natural redds, especially those that result from specific redd architecture and egg pocket location (Chapman 1988, Peterson & Quinn 1996, Meyer et al. 2005). In addition to environmental conditions, such as temperature, substrate type, flow rate, and oxygen content, other factors (e.g. parental effect and genetic control) also affect development in early ontogeny and determine the fate of fish, both before emergence from redds (Vøllestad & Lillehammer 2000, Burt et al. 2012, Whitney et al. 2013) and during dispersion (Webb et al. 2001). Therefore, the use of eggs from artificial reproduction in artificial redds excludes the influence of these biological factors and their dependence on environmental conditions.

This insufficiencies means that extended field observations in natural spawning areas are required. So far, there have been only a few studies of fry emergence from natural redds and the impact in them of substrate composition. This may have been because of difficulties in applying the appropriate traps for capturing emerging fry in a natural streambed. The use of traps that are pushed into the substrate and enclose the entire redd can expose both the eggs and fry to the reduced water flow rates and increased sedimentation of small particles, thus increasing egg and fry mortality (Hausle & Coble 1976, Reiser et al. 1998). On the other hand, the traps can decrease natural mortality levels by limiting access to predators (Philips & Koski 1969). Additionally, the emerging fry can move horizontally through the gravel and bypass a trap, which can also result in underestimated numbers (García de Leániz et al. 1993).

Salmonid emergence plays a key role in population dynamics, because the emergence success strongly affects the recruitment and the strength of the cohort during its whole lifespan (Elliott 1984, Lobon-Cervia 2007). Moreover, knowledge about the environmental conditions in which salmonids spawning occurs and their impact on fish abundance is vitally important for the management and protection of these species. The reproductive biology of brown trout is relatively well understood (Jonsson & Jonsson 2011), however, little is known about fry emergence from natural redds. The present paper describes the emergence period of the lacustrine brown trout fry from natural redds in a small lake outlet stream. The objective of this study was to determine the time and duration of fry emergence, and to estimate the number and survival rate of fry until their emergence in relation to basic environmental factors.

Material and Methods

Study area

The study was performed on the Trzebiocha stream, a small tributary of the upper River Wda (the Vistula River basin, Baltic Sea) that flows through Lake Wdzydze in the Kashubian Lakeland (Northern Poland). Both the Wda and Trzebiocha rivers are used by adult brown trout from Lake Wdzydze for spawning. The middle section of the Trzebiocha stream above Lake Sudomie is referred to as the Pilica stream. About 2.5 km before the mouth of the Trzebiocha there is a weir for supplying with water to the hatchery (Fig. 1). At the spawning grounds in the Pilica, the average width of the stream is 4.0-6.0 m, while the depth is 0.2-0.5 m. In the lower Trzebiocha the stream depth is similar as in the Pilica, however, the riverbed width ranges within 7.0-9.0 m. The slope in the lower Trzebiocha and the Pilica is 1.4 ‰ and 0.9 ‰, respectively.

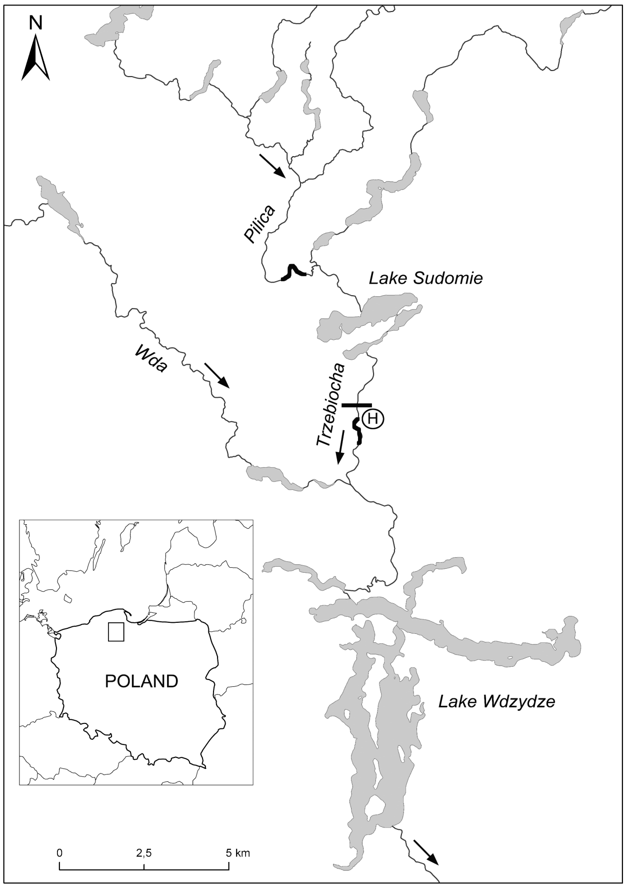

Fig. 1. Locality of investigated redds in the Trzebiocha stream; black thickened stretches – spawning areas in the middle (Pilica) and lower section; (H) – hatchery; black thick line which is transversal to the lower Trzebiocha represents weir near the hatchery.

Table 1. Redd characteristics and results of cap-trap catches in two sections of the Trzebiocha stream (D_g – geometric mean diameter of particles, S_o – sorting index, f_i – freddle index).

Section and redd symbol	Lower section							Middle section (Pilica)				
	T1/05	T2/05	T3/05	T1/07	T1/09	T2/09	T3/09	P1/05	P2/05	P3/05	P4/05	P5/05
Tailspill length (cm)	84	70	110	70	120	110	135	60	100	120	40	40
Tailspill width (cm)	62	65	90	60	110	110	120	80	100	95	60	60
Tailspill height (cm)	4	2	6	9	8	13	13	4	6	8	5	6
Pit depth (cm)	11	11	5	4	29	17	16	16	21	12	2	2
Water velocity (m s^{-1})	0.82	0.91	0.61	0.95	0.85	0.90	0.85	0.59	0.64	0.83	0.67	0.66
D_g (mm)	13.6	8.8	10.0	17.4	19.2	19.4	12.8	7.8	10.1	4.1	3.0	5.1
S_o	2.1	3.6	3.8	2.1	2.0	1.9	2.6	3.6	2.5	3.7	4.0	3.9
f_i	6.4	2.5	2.6	8.2	9.7	10.3	4.8	2.2	4.0	1.1	0.7	1.3
Content of sand (%)	11.4	16.9	13.5	7.2	4.5	3.9	11.0	20.1	12.0	25.4	36.5	23.7
Spawning observed	Yes	Yes	Yes	Yes	No	Yes	No	No	No	No	No	Yes
Number of captured fry	9	1	41	217	49	158	606	22	0	0	0	1
Estimated survival (%)	1.8	0.3	3.0	59.8	2.3	8.5	20.5	4.9	0	0	0	0.6

Observations of spawning and fry catches

The redds for catching the fry were selected during the spawning season in the autumn. The spawning grounds in the lower Trzebiocha were monitored regularly every 1-3 days and in the Pilica every week. Only single redds were selected, i.e. those with a clearly outlined pit and tailspill, each of which had been created by an individual female (based on observations of spawning and the shape of the redds). Three redds were chosen in the Trzebiocha and five in the Pilica in the 2004-2005 season. Adult trout were observed spawning at all the redds in the Trzebiocha and at one in the Pilica (Table 1). In the 2006-2007 season, one redd in the Trzebiocha where spawning was observed was selected. Among the three redds chosen in the 2008-2009 season, spawning was observed at only one. After spawning, the basic size parameters of the redds were recorded (Table 1).

In the lower Trzebiocha at five of seven redds the spawned females and the spawning acts were observed. At the other two redds, it was possible to establish the moment of spawning based on the redd creation time with an accuracy of 1-2 days. These observations were used to determine the start of eggs incubation period. As the Pilica stream was monitored rarely, it was impossible to state precisely the time of spawning there. Therefore, this stretch was excluded from the determination of duration of eggs and larvae intragravel period.

A total of 12 natural redds were selected for catching the emerging trout fry using cap traps installed on the redd tailspills (Radtke 2008a). Each trap has been designed that surrounds the redd at the surface of the streambed, which does not obstruct the water flow through the substrate surrounding the eggs. This results in undisturbed conditions inside the redd; the trap however has a lower catchability. This type of trap permits the timing and course of fry emergence to be determined and, by including the catchability of the gear, it also allows fry numbers to be estimated. The size of the traps was individually tailored to each tailspill. The diameter of the metal frame ranged from 0.6 to 1.2 m, and the diameter of the PVC tube (the container for fry) was either 10 or 20 cm. The traps were set in early spring prior to fry emergence, the approximate timing of which was determined based on a temperature models (Crisp 1988, Elliott & Hurley1998). In the lower reaches of Trzebiocha, the traps were monitored twice a day at approximately 07:00 and 19:00 hours. Because of the large distance between segments, the traps in the Pilica were monitored once a day in the evenings. The captured fry were counted and then released below the redds. The time (date) when half of the total number of fry were caught at each redd was defined as 50 % emergence. Since the trout from Lake Wdzydze are threatened and not abundant (c.a. 100 females), these fry were released as soon as they were removed from a trap without taking any measurements; the average state of the yolk sac was the only parameter that was noted, i.e. full yolk sac, no yolk sac, and intermediate form. The term "fry" was applied to emerging fry with yolk sacs (alevins) and to those with reabsorbed yolk sacs. To estimate the survival rate between eggs deposition and fry emergence, the potential number of deposited eggs in redds was determined based on the fecundity of female trout from Lake Wdzydze, as 2000 eggs per 1 kg of female body weight, after length-weight transformation (Sakowicz 1961). The female length was established as 55 % of the mean diameter of redd tailspill (Radtke 2008b), and the mean traps catchability was determined of 37 % (Radtke 2008a).

Because of difficulties of valuation of the fertilisation rate and eggs loss in natural redds, these parameters were not considered, however Elliott (1995) found, that the eggs loss are minor.

Redd substrate, thermal conditions and statistical analysis

Samples of substrate were collected from the head sections of the tailspills immediately after fry emergence in spring. The shovel sampling method was adopted as easy to use and well representative of gravel texture (Grost et al. 1991a). These method was modified by placing the samples into densely-woven material bags stretched over metal frames, measuring 50 × 25 cm and submerged directly downstream from the sampling site. After drying, the samples (mean weight 7.4 kg) were sieved through ten different mesh sizes. The procedure of sieve method and description of substrate was followed by Lotspeich & Everest (1981). The basic parameters of the substrate were determined as follows: weight contribution (%) of individual fractions i.e. < 1 mm, 1-2 mm, 2-4 mm, 4-8 mm, 8-16 mm, 16-32 mm, 32-63 mm, geometric mean of particle size (D_g), the sorting index refers to substrate particle differentiation (S_o), and the fredle index refers to water permeability through the gravel, $f_i = D_g/S_o$.

Water temperature was measured only in the lower reach of the Trzebiocha, downstream from the weir near the hatchery (Fig. 1). Temperatures were recorded twice a day (at approximately 07:00 and 16:00 hours), and the arithmetic means of these temperatures were used to calculate the mean temperatures and the sum of the temperatures (degree-days) during the incubation and emergence periods (Fig. 2). Additionally, the phase of the moon during emergence was registered.

The relationship between the number of emergent fry and the substrate parameters was determined using a non-parametric Spearman's rank correlation

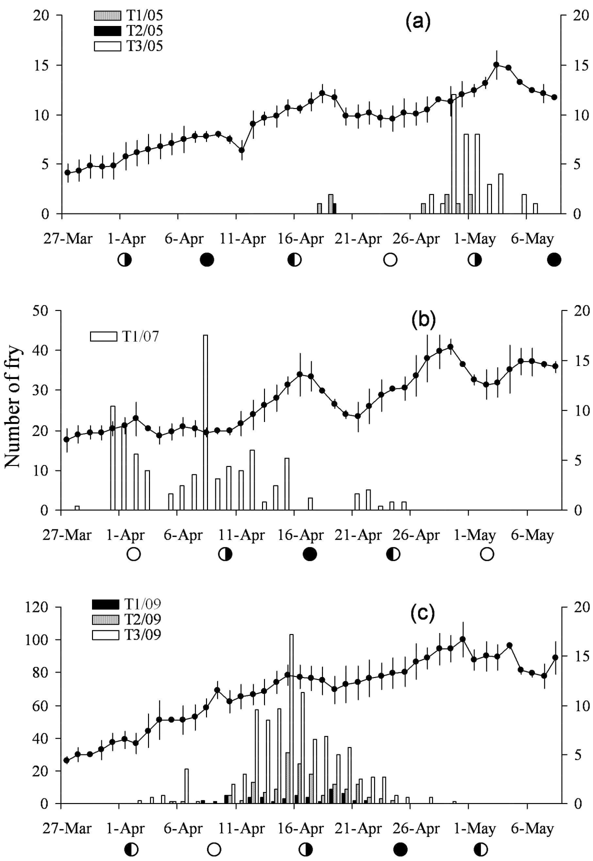

Fig. 3. Course of fry emergence from the redds in the lower Trzebiocha; bars – number of fry, plots – water temperature, vertical lines – temperature range; below the OX axis the moon phases are presented (○ – full moon, ● – new moon); (a) – year 2005, (b) – year 2007, (c) – year 2009; note – the OY axis is on a different scale.

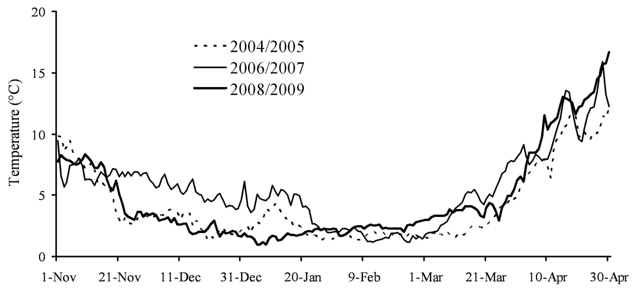

Fig. 2. Course of water temperature in the lower Trzebiocha during the development of trout embryo and larvae in the seasons analysed.

Table 2. Expected and observed duration from spawning to 50 % emergence, mean water temperature at incubation to emergence (T_{ITE}), temperature at emergence (T_{AE}), and percent of emergent fry at daytime in the lower Trzebiocha redds.

Redd symbol	T_{ITE} (°C)	T_{AE} (range) (°C)	50 % emergence				Percent of emergents at daytime
			Observed		Expected (days)		
			days	D°	after Crisp 1988	after Elliott & Hurley 1998	
T1/05	3.7	11.7 (10.5-12.4)	166	613	217	194	100.0
T2/05	3.9	11.6	176	683	209	187	-
T3/05	3.7	12.3 (10.5-15.0)	148	545	217	194	100.0
T1/07	4.4	8.8 (7.7-13.8)	141	623	189	170	11.5
T1/09	3.8	11.8 (9.5-12.8)	161	606	213	191	4.1
T2/09	4.0	12.2 (7.9-13.3)	170	680	204	183	8.9
T3/09	3.3	11.9 (6.2-15.9)	136	452	237	211	8.1

coefficient (r_s). A non-parametric Mann-Whitney U-test was used to compare the differences between substrate parameters in the redds that were studied.

Results

The course of fry emergence

In spring 2005, fry emerged from all three redds in the lower Trzebiocha and in two of the five redds in the Pilica (Table 1). In the lower reaches of the stream, emergence began between April 17 and April 19 when the mean daily temperature reached 12.1 °C (Fig. 3). The temperature afterwards dropped rapidly, and the emergence was not observed. The main emergence period in 2005 was from April 27 to May 6, when the highest mean daily water temperature was 15.0 °C. In the lower Trzebiocha, where the traps were monitored twice daily, all of the fry individuals emerged during the daytime (Table 2).

In 2007, fry emergence was observed in a single, small redd in the lower Trzebiocha about three weeks earlier than in 2005 (Fig. 3). The fry appeared from March 28 to April 25 at a mean daily temperature range of 7.7-13.8 °C. In contrast to the redds observed in 2005, however, most of the fry (88.5 %) emerged at night (Table 2). Similarly to the observations made in 2005, after a decrease in water temperature no emergence was observed. The first emerging individuals had unresorbed yolk sac, but the fry that emerged last had no yolk sac.

In 2009, fry emerged simultaneously in the three observed redds from the beginning to the end of April, with the culmination in the middle of the month (Fig. 3). The first individuals emerged at a temperature of 6.2 °C, while the peak emergence occurred at 13.1 °C. The last individuals were observed at a temperature of 15.9 °C. These increases in temperature were fairly constant, and the emergence events were almost unimodal (Fig. 3). All of the emerging fry at redd T1/09 had a fully resorbed yolk sac; however, in the initial phase of emergence, the fry from the other redds had an unresorbed yolk sac, which decreased in size as the emergence continued. Similarly to 2007, the majority of fry emerged at night in 2009 (Table 2). In the lower Trzebiocha stream, the observed time between spawning (fertilization) and fry emergence (50 % emergents) was shorter than expected from the predictions of the models and ranged from 136 to 176 days, or from 452 to 683 degree days, respectively (Table 2). There were distinct differences in the time of the day when fry emerged in different seasons. In 2005 all of the fry emerged during the daytime while, in the other years, the majority of fry emerged at night. In all of the years of observations, emergence began between the first quarter and the full moon, while the emergence peak occurred between the full moon and the third quarter (Fig. 3).

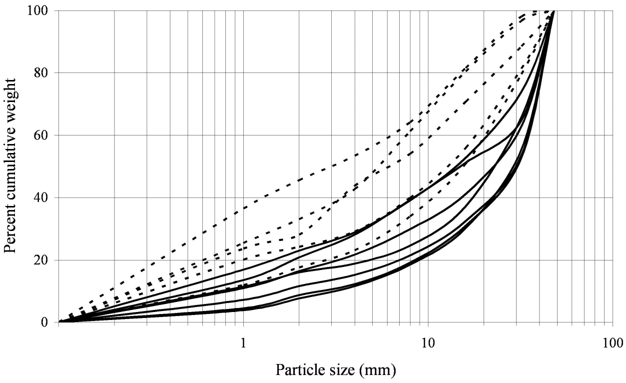

Fig. 4. Cumulative size distribution curves of gravels from investigated redds; solid lines – lower Trzebiocha, broken lines – Pilica.

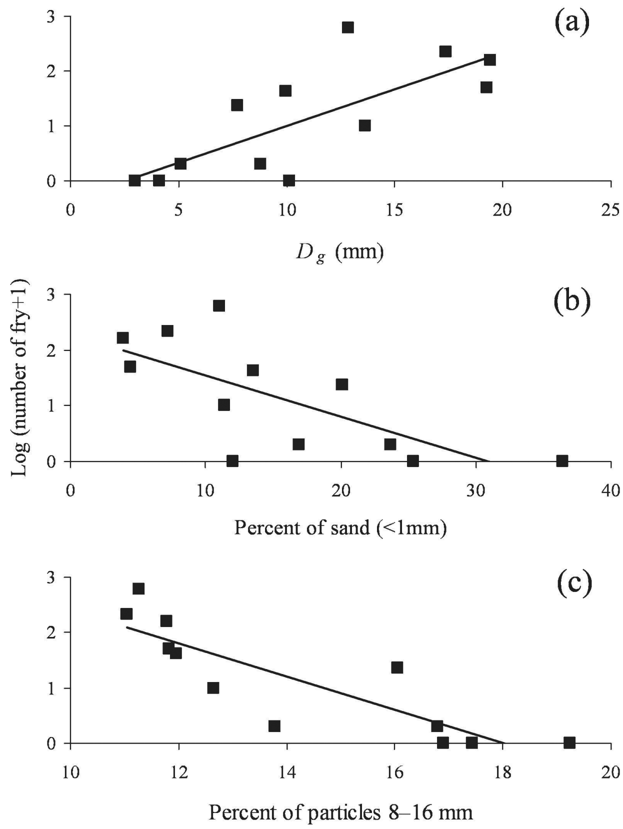

Fig. 5. Relationships between the number of captured fry (log n + 1 transformed) and substrate parameters in 12 observed redds; (a) – between the number of fry and the geometric mean of particles (D_g), $y = 0.1343x - 0.3356$, $P = 0.0046$, $r^2 = 0.569$; (b) – between the number of fry and the sand content, $y = -0.074x + 2.2818$, $P = 0.0110$, $r^2 = 0.492$; (c) – between the number of fry and content of an 8-16 mm fraction, $y = -0.3003x + 5.4062$, $P = 0.0004$, $r^2 = 0.732$; note – the OX axis is on a different scale.

Redd parameters

The size parameters differed among all of the observed redds (Table 1). The gravel size distribution curves clearly indicated that substrate composition also

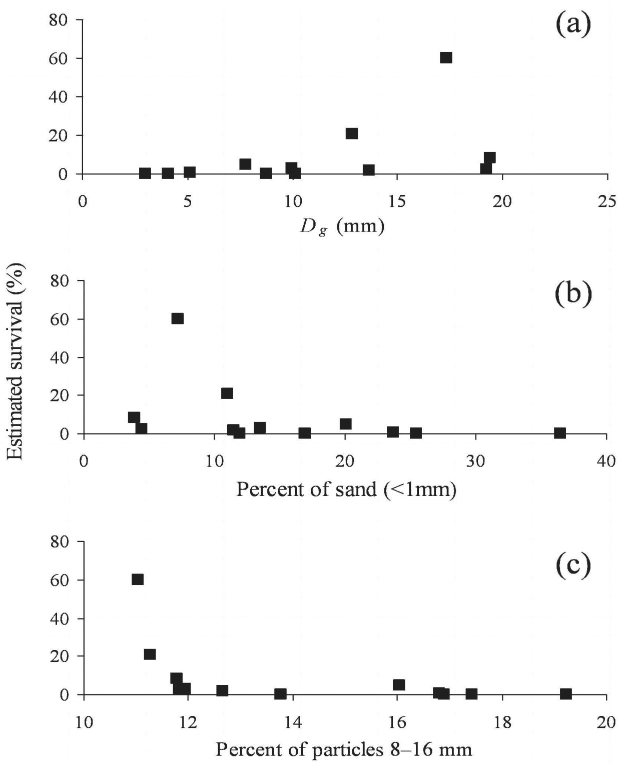

Fig. 6. Relationships between estimated egg-to-fry survival and the redds substrate parameters; (a) – between survival rate and the geometric mean of particles (D_g), (b) – between survival and the sand content, (c) – between survival rate and content of an 8-16 mm fraction; note – the OX axis is on a different scale.

Table 3. Spearman's rank correlation coefficient (r_s) between the number of captured fry and the redd substrate parameters; D_g – geometric mean diameter of particles, f_i – freddle index, S_o – sorting index.

Substrate parameter	r_s	*P*-value
D_g (mm)	0.73	< 0.01
S_o (mm)	–0.57	NS
fi	0.73	< 0.01
Grain fraction (mm)		
< 1	–0.78	< 0.01
1-2	–0.61	< 0.05
2-4	–0.60	< 0.05
4-8	–0.59	< 0.05
8-16	–0.96	< 0.001
16-32	0.16	NS
32-64	0.85	< 0.001

NS – non significant; n = 12.

differed at the studied redds, and the most uniform distribution of particular fractions occurred in the lower Trzebiocha (Fig. 4). The geometric mean of the particle size (D_g) in the lower segment was twice the mean particle size in the middle sections (Pilica). The sand fraction in the Pilica redds was more than twice as high as for the lower Trzebiocha; these differences were statistically significant (Mann-Whitney U-test, $P < 0.05$, n = 12). In the Pilica the sorting index (S_o) was higher and the freddle index (f_i) was lower than in lower Trzebiocha, and this differences were also significant ($P < 0.05$, n = 12).

The number of fry, estimated survival and impact of redd parameters

Emerging fry were noted at nine of the 12 observed redds. A total of 1104 fry were caught, and the number of fry at individual redds ranged from one to 606 individuals (Table 1). Considering trap catchability, the estimated total number of fry emerged was approximately three to 1638 individuals per redd. The number of fry caught in the lower Trzebiocha was distinctly greater than in the middle section (Pilica). The estimated survival rate between egg deposition and emergent fry was highly variable and ranged from 0.3 to 59.8 % in the redds where fry were observed (Table 1). In the lower Trzebiocha, the greatest number of fry and the highest survival rate was noted to occur in two redds (T1/07 and T3/09), in which the duration of the intragravel period, i.e. between egg deposition and emergence, was the shortest (Tables 1, 2).

The number of fry caught was positively related to the geometric mean of particle size (D_g), and negatively related to the percent of sand and the percent of particles 8-16 mm (Fig. 5). Estimated egg-to-fry survival was not significantly related to D_g, but an increase in survival was observed when $D_g > 10$ mm (Fig. 6). The relationships between survival and percent of sand and percent of 8-16 particles were also not significant, however, the survival rates were highest when the contribution of sand and 8-16 fraction were less then about 12 % respectively. The correlation between the number of fry and the geometric mean of the particle size (D_g) was significant and the same correlation was noted for the fredle index (f_i) (Table 3). The negative correlation between the contribution of sand and the number of fry was also significant. In addition, a correlation was observed between the number of fry and the contribution of other particles, and the strongest negative correlation was noted for the 8-16 mm fraction (Table 3). Additionally, most of the fry were caught at few redds in the Trzebiocha when water velocity over the redds was at least 0.85 m s^{-1} (Table 1). The only redd size parameter that was linked significantly to the number of fry was tailspill height ($r_s = 0.58$, $P < 0.05$, n = 12).

Discussion

Time of fry emergence

Previous studies indicate that the fry of trout *Salmo trutta*, similar to salmon *Salmo salar*, emerge mainly at night (Elliott 1986, Bardonnet et al. 1993, García de Leániz et al. 2000). This nocturnal activity is caused by the negative reactions of fry to light (Fraser et al. 1994, Rubin 1998), and can be interpreted as an anti-predatory tactic (Gustafson-Marianen & Dowse 1983). It has been observed, however, that the emergence period is shorter at higher temperatures and that most fry in these conditions emerge from the redds during the day (Brannas 1987). Based on an analysis of the environmental parameters, it is difficult to explain why the trout in the Trzebiocha emerged during the daytime in spring 2005, but a similar phenomenon was observed in artificial redds located in the same stream during the same period (Radtke 2010). Only the lowest range of temperature during the 2005 emergence was higher than in the other years, exceeding 10 °C.

In the Trzebiocha redds, the phase of the moon may have an impact on the moment the fry choose to leave the redds, as is demonstrated by the mutual relationship between emergence and the moon phase observed in all three years of the study. Considering the low intensity of moonlight in comparison to daylight, the lunar phase appears not to be a controlling factor for emergence, but its effect cannot be excluded in nature (Fraser et al. 1994). Because of the differences in the daily emergence patterns in particular years in the Trzebiocha, it is difficult to explain this concurrence with the impact of light, including moonlight; however, the relationship between the moon phase and fry activity was fairly clear.

In the initial phase of emergence, the newly-emerged fry have a full yolk sac, while the last emerging individuals have no yolk remaining (García de Leániz et al. 2000, Skoglund & Barlaup 2006). Such situation occurred in the most of observed redds, but in redd T1/09 all of the fry individuals had a fully reabsorbed yolk sac. It can suggest, that this delayed emergence was a result of water temperatures that were too low when fry reached the developmental stage, which permits them to leave the redd.

Estimation of survival and substrate influence

Significant correlations between the number of fry and the substrate parameters were observed in the current study; however, fry survival appears to be a better biological indicator. Unfortunately, it is difficult to estimate egg-to-fry survival in natural salmonid redds, because of difficulties in precisely determining the number of deposited eggs (Young et al. 1990, Rubin 1995). If the size of the spawning female is known, the number of eggs can be estimated from the size-fecundity relationship (Blanchfield & Ridgway 2005, Meyer et al. 2005). When these data are not available, it is possible to estimate female size from redd measurements (van den Berghe & Gross 1984, Crisp & Carling 1989). In the present study, however, the mean trap catchability was used to establish egg-to-fry survival at different redds. These difficulties caused the data to be less precise and they therefore should be treated cautiously as estimates. However, since each trap was bespoke fitted to the size of each tailspill, the results obtained from individual redds are comparable.

The estimated survival rate between deposition of eggs and fry emergence was highly variable in the Trzebiocha, which is mainly attributed to differences in the substrate quality. In two tributaries of the River Rhine, the survival rate was also highly differentiated; the mean was about 10 % in 11 observed sea trout *Salmo trutta* redds (Ingendahl 2001). Additionally, there was a significant relationship between the number of fry and the oxygen level and the sorting coefficient (S_o). The mean survival rate of Atlantic salmon *Salmo salar* measured until emergence for 10 samples from two natural redds in the River Nivelle was above 12 % (Dumas & Darolles 1999). Besides, significant relationships between the survival and substrate parameters at this samples were obtained. A distinctly differentiated, but higher survival rate was observed in seven Chinook salmon *Oncorhynchus tshawytscha* redds where cap traps were deployed, and the mean was 29.2 % (McMichael et al. 2005).

In the present study, the most productive redds were those at which content of sand fraction (< 1 mm) did not exceed of 12 % and the geometric mean of particle sizes (D_g) was higher by about 10 mm. The highest egg-to-fry survival for sea trout *Salmo trutta* with experimental boxes used in streams was recorded with a geometric mean particle size exceeding 15 mm (Rubin & Glimsäter 1996). The highest numbers of fry and survival in redds with a coarser substrate confirms the major role of water permeability in the redds, which determines the oxygenation of eggs and fry (Greig et al. 2007). However, in the Trzebiocha stream, the 8-16 mm fraction was found to have a strong negative impact on fry survival, which was surprising and difficult to interpret. Nonetheless, the varied contribution of these particles is a good reflection of the quality of all substrates in the redds, and this is apparent in the cumulative size distribution curves for the redd gravel (Fig. 4). The most uniform distribution of all fractions in the natural redds found in the lower Trzebiocha might explain the occurrence of the highest survival rate there.

The differentiation in the natural redd substrate and the small interstitial spaces between gravel particles could have made it difficult for the fry to squeeze through and could have delayed their emergence when compared to conditions in the homogeneous substrate of artificial redds, which are often used to estimate intragravel survival. On the other hand, homogenous and coarse substrate in artificial spawning grounds could provide fine infiltration inside the redds, which can choke larvae and cause premature emergence or higher mortality. Egg pockets are located in the centre of natural salmonid redds and are surrounded by the largest substrate particles (Chapman 1988, Grost et al. 1991b, Peterson & Quinn 1996). The outer cover, however, is built of a smaller fraction, which could protect the eggs from the intrusion of fine sediment and from penetration by external predators (Meyer et al. 2005).

Influence of temperature and other factors

Observations in the Trzebiocha stream supports a fundamental role of temperature at emergence of salmonids. Temperature affected the duration time of intragravel period, and also timing and duration of emergence. In observed redds, the temperature increase initiated the fry to left the redds, but decrease of temperature prevents the fry from emergence (Fig. 3). In the Trzebiocha redds, the timing of emergence was earlier than expected from temperature models. This could be due to differences in the environmental conditions in natural redds in the Trzebiocha as compared to laboratory conditions. Also, differences related to the genetic background can not be exclude (Burt et al. 2012, Whitney et al. 2013). In some cases, the diversity between surface water temperature in stream and in the center of the redds may occur. Although water temperatures are generally more stable in the deeper gravel layers, the temperature might be higher inside the substrate during the initial phase of egg development (winter), but such differences are equalized in the spring during fry development (Acornley 1999). No temperature differences were noted between the water surface and 20 cm beneath the gravel in sea trout redds (Ingendahl 2001).

Climate-related factors apparently have an impact on water temperature dynamics in spawning streams, and consequently on the timing of emergence from redds (Elliott & Elliott 2010). This is becoming increasingly important since climate warming is inducing changes in the thermal regimes of streams, and these changes can cause shifts in the individual reproductive cycles of fish, including the period of fry emergence from redds (Hari et al. 2006, Jonsson & Jonsson 2009). The spawning period of the brown trout occurs over a long period according to the geographical locality (Gortazar et al. 2007). In the case of trout from Lake Wdzydze, spawning extends from mid October to early January (Sakowicz 1961, Radtke 2008b). Nevertheless, the emergence from redds takes place from late March to early May, and fry survival depends on the timing of egg deposition and the prevailing thermal and oxygen conditions during incubation. In streams with a high rate of transport and sedimentation of fine particles, lower temperatures over an extended incubation period and the resulting exposure to disadvantageous conditions can contribute to decreased survival. Higher temperatures, however, will shorten the exposure time, which will in turn contribute to higher fry survival. This situation was observed in the Trzebiocha; most fry were observed in two redds where the period between egg deposition and fry emergence was the shortest. The earlier emergence and the higher survival noted in 2007 in comparison to other years can be explained by the warmer winter of 2006-2007 (Table 2).

Among the biological factors that influence embryos and larvae development and reproductive success, the impact of females is evident mainly in the size and number of eggs (van den Berghe & Gross 1989, Einum & Fleming 1999, Jonsson & Jonsson 1999). In addition, larger females choose spawning sites with a faster water flow (Crisp & Carling 1989) and coarser substrate (Kondolf & Wolman 1993). This results in greater water permeability through the redd, providing better oxygenation and, in effect, higher larval and fry survival. This indicates that it is of major importance for a female to choose an appropriate spawning site. When a population is not abundant, as is the case for the trout from Lake Wdzydze, this might have significant biological implications, since one of the side-effects of highly differentiated fry survival is that the core stock only comprises offspring from a few females.

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