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Spawning site selection and redd gravel characteristics of sea trout *Salmo trutta* in the lowland streams of Lithuania

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Key words: salmonids, reproductive ecology, microhabitat, fines, sedimentation.

Abstract

To date, no characterization of spawning habitats on scientific basis was made for the eastern Baltic salmonid populations. The aim of the present study was to characterize spawning habitat preferences and redd gravel structure of sea trout in lowland streams of western Lithuania. The redd position at the habitat-unit scale, microhabitat hydrological characteristics and the redd gravel structure have been analyzed. The spawning site selection by sea trout was related to the in-stream characteristics, but not to the riparian features. Redds were positioned mainly in the transitional pool-riffle zones, associated with close proximity to potential cover for spawners. At the microhabitat scale, sites with relatively consistent hydrological parameters (mode of water depth 0.25-0.40 m, flow velocity 0.4-0.7 m s^{-1} and Froude number 0.2-0.4) were selected from a wide range of available sites. Egg incubation conditions, in terms of the redd gravel structure in the spring, were of intermediate quality, while varied widely within particular reaches. According to the results of the present study, it is apparent that sea trout have particular preferences for spawning sites, which should be considered in emerging river-restoration projects.

INTRODUCTION

Reproductive ecology is a critical aspect of salmonid fish life history. All salmonids lay their eggs in the streambed gravel nests called redds, where they incubate for a very long period (from two to eight months) and, therefore, are vulnerable to changes in incubation conditions, which are rather unstable in the fluvial ecosystems. Thus, the spawning success largely depends on the spawning site selection and the redd quality during the incubation period (Chapman 1988, Fleming 1998, Armstrong et al. 2003). The knowledge about the natural spawning habitats has a fundamental and practical significance and is of crucial importance for salmonid stock management and river restoration projects (Madsen 1995, Rubin et al. 2004).

The global concern regarding the declining efficiency of spawning of salmonids has produced a voluminous body of information on the reproductive ecology of salmonids (Chapman 1988, Crisp and Carling 1989, Bjornn and Reiser 1991, Kondolf and Wolman 1993, Elliott 1994, Fleming 1998, Armstrong et al. 2003, Esteve 2005, Louhi et al. 2008). One of the most studied species in this subject is the brown trout *Salmo trutta* L., which is very polyphyletic, with two most common forms amongst others: stream-dwelling brown trout (*S. trutta fario*) and anadromous sea trout (*S. trutta trutta*) (Elliott 1994). The spawning habitat requirements of the sea trout and its relationship to those of the brown trout have received little attention. Most studies were done

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on resident brown trout populations (Ottaway et al. 1981, Shirvell and Dungey 1983, Witzel and McCrimmon 1983, Grost et al. 1990, Beard and Carline 1991, Zimmer and Power 2006); meanwhile the anadromous sea trout spawning habitats were far less studied (Crisp and Carling 1989, Soulsby et al. 2001, Rubin et al. 2004).

Many natural brown and sea trout, as well as some Baltic salmon *Salmo salar* L. populations occur in the Lithuanian rivers (Kesminas et al. 2000). Since 1998, a national monitoring program on salmonid population status in rivers has been implemented and in some most important rivers, spawning intensity of anadromous salmonids has been monitored routinely. However, no characterization of salmonids spawning habitats on scientific basis has been made to date. The aim of the present study was to characterize spawning site preferences and redd gravel characteristics of sea trout *S. trutta* in the Minija River basin. This is the first published information on anadromous salmonids' preferences and the quality of spawning habitats in the rivers of the eastern Baltic region. Many rivers of this area are important for salmonid reproduction, significantly contributing to the sea trout and salmon stocks in the Baltic.

STUDY AREA

The study was carried out in the spawning seasons of 2003 and 2004 in the upstream reaches of the Minija River and in its four tributaries in western Lithuania (55°42' - 56°01' N, 21°35' - 22°10' E; Fig. 1; Table 1). The Minija River belongs to the Nemunas River basin and is 201.8 km long, and drains the catchment area of 2942 km^2. The mean annual discharge at the river mouth is 38.7 m^3 s^{-1} (Gailiušis et al. 2001).

The rivers of Lithuania are considered as lowland rivers, characterized by low average channel slopes, which in the study reaches range from 0.14 to 0.38% (Table 1). The study reaches were situated in the upper part of the Minija catchment, which lies in the steeper Samogitian Highland and the West Samogitian Plateau with an altitudinal range of 23-200 m. The following tributaries were surveyed: Sausdravas (the length 25.5 km, the catchment area 96.2 km^2, the mean annual discharge at the river mouth 1.13 m^3 s^{-1}), Mišupė (25.7 km, 49.2 km^2, 0.71 m^3 s^{-1}), Blendžiava (29.2 km, 85.6 km^2, 1.06 m^3 s^{-1}) and Veiviržas (67.9 km, 668 km^2, 9.06 m^3 s^{-1}) (Jablonskis and Lasinskas 1962, Gailiušis et al. 2001).

The Minija River with its main tributaries is considered to be a sea trout reference river in Lithuania (Kesminas et al. 2000), characterized by one of the highest mean basin densities of the *Salmo trutta* population in Lithuania during the last decade (5.14 – 31.50 ind. 100 m^{-2}). Baltic salmon are absent from this basin and no data exist on natural reproduction up to date (CORPI 2009). Study reaches were selected as the known primary sea trout spawning grounds (Kontautas and Rauckis 1994, CORPI 2009).

MATERIALS AND METHODS

Conditions and timing of the observations

Due to low water transparency during the autumnal flood, the direct observations of salmonids spawning are seldom feasible in the rivers of the western part of Lithuania. In both autumnal spawning seasons of 2003 and 2004, measurements of redd dimensions, water depth and velocity were taken within two weeks after the completion of spawning redds, when the water transparency allowed visual inspection of the streambed. The exact locations of individual redds were marked with permanent markers on the stream bank and more detailed characterization of redd and its environment was accomplished in the subsequent springs (April 2004 and 2005), when the water levels were close to these of the autumnal observations.

Spawning habitat and redd characterization

The redd location was identified in the surrounding algal or sediment-covered substratum as a patch of clean gravel with a mound (or tailspill) of gravel at the downstream direction from a depression in the streambed. The redd tailspill length and the width were recorded parallel and perpendicular to the flow direction respectively. The redd shape was recorded and the redd size was calculated mostly as an elliptical area using two measured axes.

The spawning site selection at the habitat-unit scale was evaluated as the longitudinal position of a redd within a particular riffle or a run-habitat section in terms of the distance from a riffle (front) crest. The crest or break of the riffle is considered here as a point in the transitional pool-riffle zone, up to which the water depth considerably decreases, creating a negative streambed slope in relation to the overall channel slope, and the downstream section from the riffle break has a substantially positive channel slope,

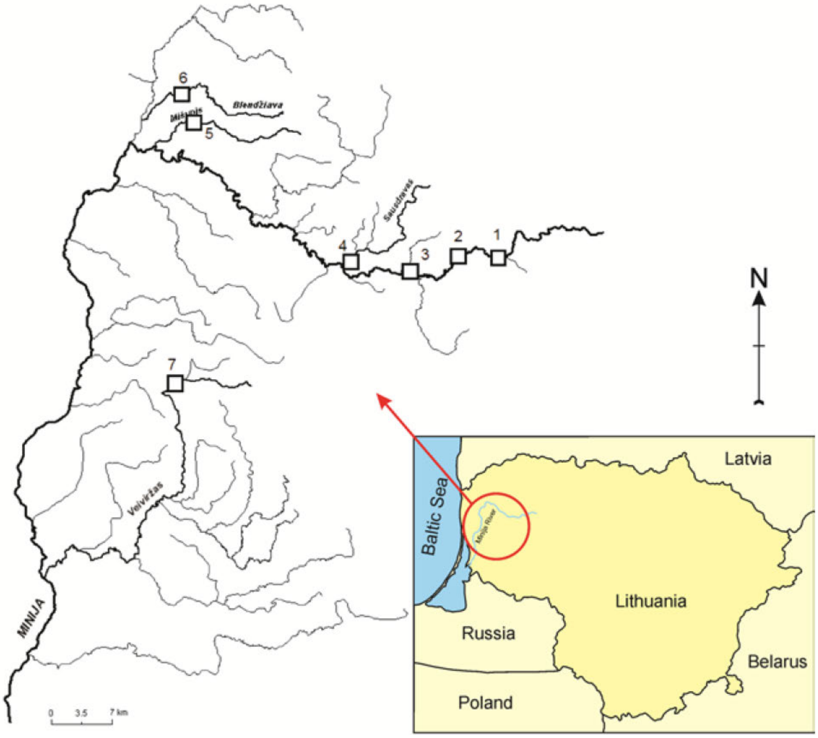

Fig. 1. The map of the Minija Basin with the study sites: 1) Minija-1; 2) Minija-2; 3) Minija-3; 4) Sausdravas; 5) Mišupė; 6) Blendžiava; 7) Veiviržas.

Table 1

Characteristics of the study reaches and the number of redds studied. Average annual discharge, average channel slope and the altitudinal data at the study sites come from Jablonskis and Lasinskas 1962.

Site	Study years (n. of redds studied)	Channel width (m)	Depth (m)	Average discharge ($m^3 s^{-1}$)	Altitude (m)	Average slope (%)
Minija 1	2003 (6)–2004 (4)	5.5	0.2–1.0	0.94	137	0.38
Minija 2	2004 (5)	7.5	0.3–1.3	1.05	115	0.38
Minija 3	2003 (3)–2004 (5)	12.5	0.3–1.7	2.87	97	0.16
Sausdravas	2003 (7) –2004 (7)	8.5	0.15–0.7	1.13	82	0.34
Mišupė	2003 (9)–2004 (5)	5	0.15–0.8	0.55	55	0.34
Blendžiava	2003 (3)–2004 (10)	7	0.15–1.2	0.81	50	0.36
Veiviržas	2003 (10)	6	0.3–0.8	0.83	70	0.14

which creates fast turbulent current. The distance from the riffle front was considered as the distance below the crest, and any position upstream from the riffle crest was considered as the distance of 0 m. The distance from the closest cover, suitable for spawners, was measured and the type of cover was identified. The potential cover in this study was treated as a relatively deep place (>0.5 m) with some flow obstructions or overhead cover, enabling fish to hide from flow and sight during the rest. Environmental characteristics were assessed visually within the upstream and downstream sections from the redd position in the length of one stream width. The structure of the streambed was evaluated by dividing the coverage of each of the following fractions: boulder, cobble, gravel, sand and silt. Characteristics of both banks along the evaluation segment were determined: the type of bank (eroding or stable bank, entrenched with tree roots or grass), inclination of the banks (<30°, 30-60° and 60-90°) and the coverage of the banks by vegetation (trees and shrubs). The distance of a redd from the nearest bank was recorded. The avoidance or preference for particular bank character was tested, expressed in terms of the proximity of a redd to a stream bank with particular features..

To characterize spawning site selection at the microhabitat scale, the depth and the water velocity were measured beside thea redd. The same measurements were done at 2-3 random sites near a redd, covered with gravel of the same or similar to redd structure. The depth of a redd-site was measured in front of redd tailspill and at several sites beside a redd edge over the undisturbed substratum, which represents pre-spawning conditions experienced by spawners. Water velocity (m s^{-1}) was measured at the same sites with the Flow Probe FP101 water velocity meter (Global Water Instrumentation Inc., U.S.A.) at about 60% of the water depth and both, the water depth and velocity are presented as an average. Using the depth and velocity data, the Froude number was calculated as:

$$\frac{v}{(dg)^{0.5}}$$

where *v* represents water velocity, *d* water depth and *g* gravitational acceleration (9.81 m s^{-2}). The Froude number was suggested as an index for the characterization of salmonid spawning habitat hydrological conditions, because it provides means to account for interdependence of depth and water velocity, and is dimensionless and comparable between different species (Moir et al. 2002).

Redd gravel analysis

In spring 2004, the redd gravel size was measured as the intermediate axis of the dominating size random gravel particles from a redd. In spring 2005, after the incubation period ended, redd gravel samples were collected for the complete gravel structure analysis. The samples were collected with a modified shovel, which had welded walls to reduce loss of fine material during lifting a sample from the water. On average the samples were taken from 15 cm depth, which representatively reflects the depth at which *Salmo trutta* usually buries its eggs (11-20 cm according to Crisp and Carling 1989). Depending on the size of a redd, two to three samples were taken and pooled together as one redd sample, weighing on average 7 kg of dry weight. After air drying, the whole sample was mechanically sieved through the series of standard sieves (64, 32, 16, 8, 4, 2 and 1 mm) and the retained sediment from each sieve was weighed. The weight of each size fraction was expressed in relative frequency (%) and a cumulative distribution curve was constructed. Five percentiles of the particle diameter were drawn from the cumulative curve: 16^{th}, 25^{th}, 50^{th}, 75^{th} and 84^{th}, which were used in further calculations of standard indices for gravel quality (Bunte and Abt 2001). There were calculated the median diameter D_{50}, as the 50^{th} percentile of the cumulative distribution, and the mean geometric diameter d_g, as:

$$d_g = (D_{16} \times D_{84})^{0.5}$$

which describe the central measure of gravel particles' distribution (Chapman 1988, Kondolf and Wolman 1993, Bunte and Abt 2001). Other standard spawning gravel quality descriptors were determined: the sorting coefficient S_o, as:

$$S_o = (\frac{D_{75}}{D_{25}})^{0.5}$$

presenting the size distribution of sediment particles in a sample (Lotspeich and Everest 1981, Chapman, 1988); the Fredle index F_i, as:

$$F_i = \frac{d_g}{S_o}$$

that characterizes the quality of redd gravels for salmonid reproduction. F_i is a measure of both pore size and relative permeability, both of which increase as the index value increases (Lotspeich and Everest 1981). The sample content (%) of fine sediments, less than 2 mm in diameter (<2 mm fines), was used in the analysis.

Statistical analysis

The spawning site selection preferences at the microhabitat scale were determined by comparing the average values of the water depth, the flow velocity and the Froude number of redd-sites with those, measured at random near a redd. The two samples Student *t* test has been applied after testing for the data normality and homogeneity of the variances. Kruskal-Wallis non-parametric ANOVA was used for comparisons of redd hydrological characteristics, redd dimensions and gravel structure descriptors in different sampling reaches. If a statistically significant difference was found, individual pairs were compared using the Mann-Whitney *U* test to differentiate significantly different pairs. Linear Pearson and Spearman rank correlation analyses were applied to examine relationships between redd characteristics and environmental parameters. The significance level for all tests was P<0.05.

RESULTS

The results on spawning site selection at the habitat-unit scale are presented as combined results for all sampling reaches in both study seasons. The spawning redd-sites of the sea trout were distributed mainly in the riffle and run type habitats (97%). The streambed structure in the exploited spawning habitats was composed of boulder, on average (±SD) from 5.2 ±6.1% (mode 0; range 0-30); of cobble 18.5 ±17.0% (mode 5; 0-80); of gravel 46.8 ±20.7% (mode 50; 5-90); of sand 26.2 ±15.5% (mode 20; 0-65) and of silt 3.3 ±3.2% (mode 0; 0-10). Within the riffle type habitats, most of the redds were built in the first-half of the riffle unit (Fig. 2a). The most intensively used parts for nest building were the sections upstream from the riffle crest (42% of 0 m from the riffle front) (Fig. 2b). These sections are characterized by the decreasing depth that accelerates the flow and creates the substantial negative streambed slope in the downstream direction.

were built up to one meter from any of the banks (and 80% up to 2 m). In terms of avoidance or preference for particular bank character, as the redd's proximity to a stream bank with particular features, the latter had no statistical significance (Mann-Whitney *U* and Kruskal-Wallis tests, P>0.05).

75% of all redds were associated with the presence of potential cover relatively close (up to 6 m) to a redd-site (Fig. 3). The dominating, very close cover (up to 2 m) was located mainly upstream of a redd, while with the increasing distance from a redd-site, the cover had no clear location patterns. The potential cover was composed mostly of large pieces of woody debris or its aggregations (68%). The remaining cover types were undercut banks, lateral scour pools or deep channel pools (26%), and large single boulders or groups of boulders (6%).

No statistically significant difference was found between the hydrological characteristics measured after spawning over the redd-sites in 2003 and 2004 (Student *t* test, P>0.05), and these were pooled for further analysis. When selecting spawning sites at the microhabitat scale (within few meters), females used water depths in the vicinity of a redd-site, which on average were not significantly different from the available ones (Table 2). From a wide range of available depths (0.12 – 0.75 m) over the suitable

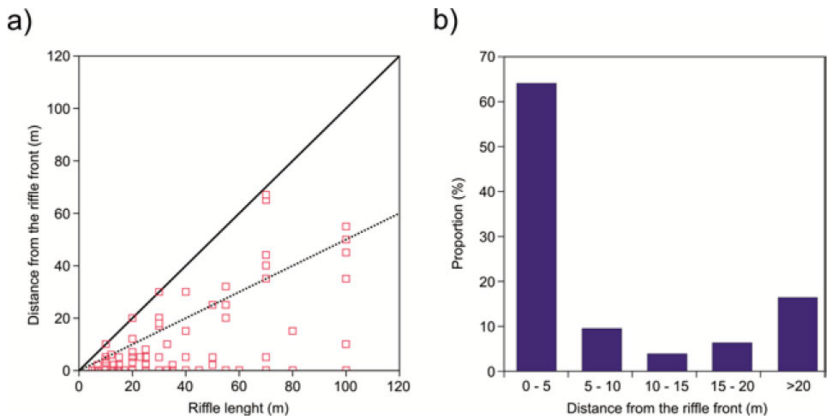

Fig. 2. (a) – Longitudinal position of *Salmo trutta* redds within a particular riffle-run section, where the solid line denotes the end of the section, and the dotted line: half of the section length; (b) – frequency distribution of the distance below the rifle front (crest).

The width of the channel at redd-sites varied from 1 (the side channel) to 15 m. The frequency distribution of a stream bank type (stable or eroding), the steepness and the vegetation cover beside a redd, gave no clear evidence of the spawning site selection preference for any riparian features. 59% of the redds

gravel, females used relatively constant water depths, of not less than 0.15 m, with the mode being 0.30 – 0.35 m. Some outliers of the used depth (0.57 – 0.63 m) were recorded in the Minija 3 study reach, where redd microhabitats were on average deeper than in the remaining study reaches (Kruskal-Wallis test,

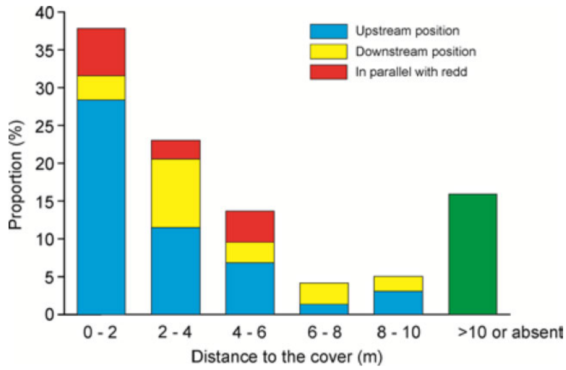

Fig. 3. The association of *Salmo trutta* spawning redds with a potential cover for spawners.

Table 2

Mean ±SD hydrological characteristics of redd-sites of *Salmo trutta* in the Minija basin during the spawning seasons of 2003 and 2004. Ranges of measured values are presented in parentheses.

Site	Water depth (m)	Flow velocity (m s^{-1})	F_r
Minija 1 (n = 10)	0.35 ±0.08 (0.25–0.50)	0.64 ±0.15 (0.37–0.91)	0.35 ±0.08 (0.20–0.47)
Minija 2 (n = 5)	0.34 ±0.07 (0.25–0.40)	0.65 ±0.12 (0.52–0.82)	0.35 ±0.05 (0.29–0.42)
Minija 3 (n = 8)	0.45 ±0.10 (0.35–0.63)*	0.60 ±0.15 (0.35–0.84)	0.29 ±0.08 (0.15–0.42)
Sausdravas (n = 13)	0.32 ±0.05 (0.26–0.42)	0.54 ±0.13 (0.40–0.86)	0.31 ±0.09 (0.21–0.54)
Mišupė (n = 13)	0.33 ±0.06 (0.22–0.42)	0.52 ±0.10 (0.35–0.74)	0.29 ±0.07 (0.17–0.41)
Blendžiava (n = 13)	0.32 ±0.07 (0.18–0.39)	0.57 ±0.10 (0.43–0.80)	0.33 ±0.07 (0.22–0.47)
Veiviržas (n = 10)	0.37 ±0.06 (0.30–0.45)	0.59 ±0.14 (0.45–0.84)	0.31 ±0.07 (0.20–0.43)
Total used (n = 72)	0.35 ±0.08	0.57 ±0.13	0.32 ± 0.07
Adjacent available (n = 162)	0.37 ±0.15	0.62 ±0.24	0.33 ± 0.11
Student *t* test, *P*	> 0.05	> 0.05	> 0.05

* A statistically significant difference from all other study reaches (Kruskal-Wallis test, $P < 0.05$).

P<0.05). Between other study reaches, there were no statistically significant differences in the exploited depths (Mann-Whitney *U* test, P>0.05), despite the morphological and size differences between them (Table 1). The mean flow velocity and Fr number over redd-sites were not significantly different between all reaches (Kruskal-Wallis test, P>0.05). The general average, exploited flow velocity (0.57 ±0.13 m s^{-1}) was lower as compared to the available one at the adjacent sites (0.62 ±0.21 m s^{-1}; the range 0.18 – 1.20 m s^{-1}), though the difference was not statistically significant (Student *t* test, P>0.05). The minimum water flow at which females were found digging their redds was 0.35 m s^{-1}, and generally fast flowing microhabitats were used (mode 0.5 – 0.6 m s^{-1}). The F_r number, which describes hydrological features of a microhabitat, integrating both the water depth and velocity, was used proportionally to its availability (0.12-0.73) (Fig. 4). The most occupied microhabitats were those with the F_r number of 0.2 – 0.4, and avoided sites - with F_r <0.15 (deep, slowly flowing sites) and >0.55 (shallow and very fast flowing sites).

The shape of redd tailspill was mostly elliptical or round, with less common irregular forms (8%). The later ones were significantly bigger (4.30 ±3.41 m^2, n = 6) than redds of other shapes (1.57 ±1.03 m^2, n = 70) (Mann-Whitney *U* test, P<0.05). The general (n = 76) average (±SD) redd tailspill length was 1.65 ±0.62 m (the range 0.8 – 4.0); the width 1.28 ±0.63 m (the range 0.6 – 4.0) and the tailspill area 1.79 ±1.52 m^2 (the range 0.47 – 9.42). The redd size did not correlate (Pearson and Spearman rank correlation r<0.2 or P>0.05) with any of the redd position parameters, bank characteristics, microhabitat hydrological characteristics and with redd gravel parameters.

Sea trout females from a wide range of available substrata have used mostly the coarse gravel (within 16 – 32 mm), while the redd background gravel matrix ranged from very coarse (46 mm, in Sausdravas) to medium-sized gravel (14 mm, in Blendžiava). The detailed redd gravel analysis performed in spring 2005, shortly after fry emergence, represents the cumulative incubation conditions for eggs rather than the actual preference

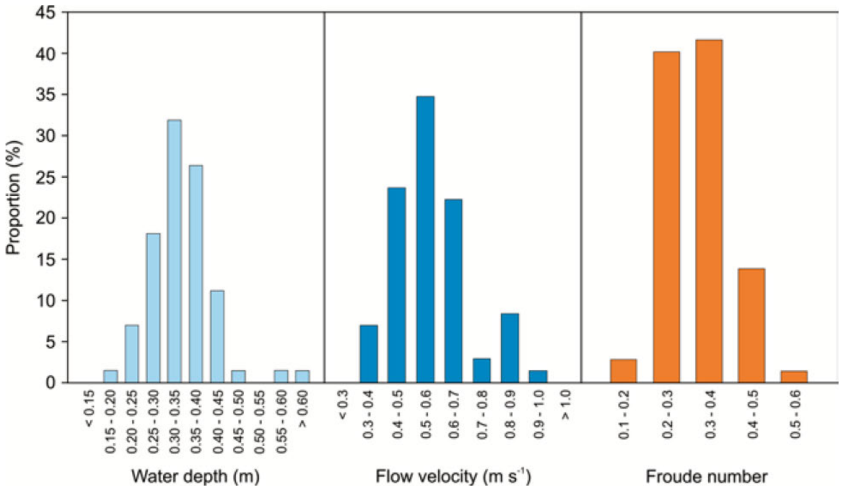

Fig. 4. Hydrological characteristics of spawning microhabitats exploited by *Salmo rutta* in the Minija basin (n = 72).

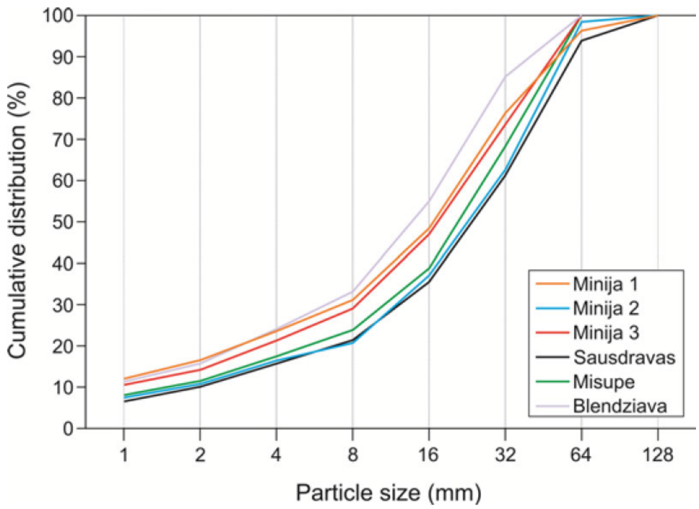

Fig. 5. Mean cumulative size distribution of redd gravels in different Minija study reaches in spring 2005.

for spawning gravel. Different sized substratum particles (from fine sediments to cobble) in redd gravels in different Minija reaches and its tributaries were mostly normally distributed (Fig. 5). Descriptive characteristics of spawning gravel in different study reaches are presented in Table 3. All calculated indices depend on the content of <2 mm fines (fines vs. d_g, D_{50} and F_i, r = -0.77 – -0.90; and fines vs. S_o, r = 0.70, P<0.001) (Fig. 6). Comparing the redd gravel structure from different reaches, the least content of fines was found in Sausdravas, Minija 2 and Mišupė, and the highest amount of fines: in Blendžiava, Minija 1 and Minija 3 reaches, though these differences are not statistically significant (Kruskal-Wallis non-parametric ANOVA, P>0.05). The highest median and mean geometric diameters, and in turn the best incubation conditions (F_i) were found respectively in reverse order (Table 3). The differences between sorting coefficients from different redd-sites were statistically insignificant (Kruskal-Wallis test, P>0.05), and in all cases they were on average small (>2). Within a particular study reach, redd gravel parameters varied widely even in relatively close redds, from very bad to good ones. As an example, in the study section of Blendžiava, the sediment content ranged from 6.3 to 26.4%, or F_i from 1.15 to 10.12, indicating small scale differences in sedimentation patterns.

Table 3

Mean ± SD characteristics (ranges of measured values in parentheses) of *Salmo trutta* redd gravel, sampled in spring 2005. Different letters indicate significantly different pairs (Mann-Whitney *U* test, $P < 0.05$).

	<2 mm fines (%)	D_{50} (mm)	d_g (mm)	S_o	F_i
Minija 1 (n = 4)	16.6 ±3.1	18.0 ±5.5	8.5 ±2.8^b	2.55 ±0.59	3.54 ±1.87^b
	(12.0 – 18.5)	(9.8 – 21.0)	(5.0 – 11.8)	(1.87 – 3.04)	(2.23 – 6.31)
Minija 2 (n = 5)	11.5 ±4.3	23.0 ±2.5^a	13.2 ±3.3	2.10 ±0.31	6.56 ±2.51
	(5.5 – 16.3)	(19.5 – 26.0)	(8.8 – 17.6)	(1.74 – 2.56)	(3.44 – 10.11)
Minija 3 (n = 5)	14.3 ±3.8	18.5 ±5.7	10.0 ±3.5^b	2.28 ±0.42	4.61 ±2.23^b
	(9.0 – 18.8)	(9.5 – 24.5)	(5.3 – 14.9)	(1.84 – 2.98)	(2.39 – 8.10)
Sausdravas (n = 7)	10.2 ±4.0	24.9 ±7.1^a	16.2 ±6.6^a	2.08 ±0.24	8.13 ±4.01^a
	(5.2 – 14.4)	(16.5 – 36.0)	(9.3 – 25.0)	(1.73 – 2.31)	(4.12 – 13.93)
Mišupė (n = 5)	11.6 ±3.3	21.2 ±4.1^a	12.1 ±3.0	2.03 ±0.30	6.22 ±2.23
	(7.3 – 15.6)	(17.0 – 25.5)	(9.2 – 15.3)	(1.70 – 2.51)	(3.67 – 8.94)
Blendžiava (n =9)	16.3 ±7.1	14.5 ±5.8^b	8.2 ±4.5^b	2.35 ±0.39	3.80 ±2.82^b
	(6.3 – 26.4)	(7.0 – 25.0)	(3.3 – 16.8)	(1.66 – 2.88)	(1.15 – 10.12)
Total (n = 35)	13.5 ±5.2	19.7 ±6.4	11.3 ±5.1	2.23 ±0.39	5.49 ±3.15

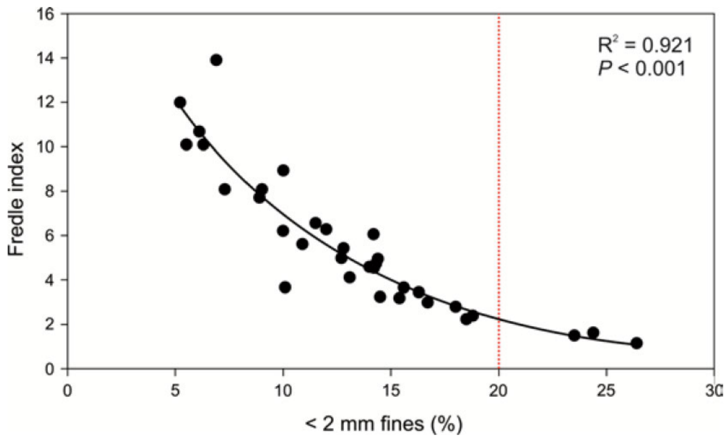

Fig. 6. The relationship between the content of sediments in the redd gravel (n = 35) and the Fredle index based on the gravel structure of the samples. The dotted line indicates the critical level of sediments for incubating salmonid embryos (O'Connor and Andrew 1998, Louhi et al. 2008).

Discussion

According to the present study findings, it is apparent that sea trout in boreal lowland rivers have particular preferences for spawning site selection. The results indicate that spawning site selection has been directly controlled only by in-stream, rather than by bank-related variables. No significance of any tested bank-related parameters on the distribution patterns of redds was detected. Some other studies indicated that bank characteristics had a significant effect on salmonid spawning site selection (Knapp et al. 1998, Kuzishchin et al. 2009).

Spawning site characteristics, such as water depth, flow velocity and substratum size are generally considered to be the most important in-stream microhabitat variables in determining the spawning site selection for most salmonid fishes (Bjornn and Reiser 1991, Louhi et al. 2008). It was demonstrated by Crisp and Carling (1989), Kondolf and Wolman (1993) that preferences for these variables depend on the spawner size - bigger fish are able to spawn in faster water and on a coarser substratum. At maturation, resident brown and sea trout reach significantly different size, fitness and fecundity (Campbell 1977, Fleming 1998), thus it is likely that different spawning site preferences should exist between them.

Presently, the measured water depth and velocity at sea trout redd-sites are in high agreement with those determined for *Salmo trutta* spawning sites in other river systems and populations (Shirvel and Dungey 1983, Witzel and MacCrimmon 1983, Raleigh et al. 1986, Crisp and Carling 1989, Grost et al. 1990, Beard and Carline 1991, Soulsby et al. 2001, Zimmer and Power 2006). Based on the generalized spawning habitat suitability curves established for brown trout, the most suitable water depth and velocity are around 0.30 m and 0.40 – 0.50 m s^{-1} respectively (Raleigh et al. 1986, Louhi et al. 2008). Sea trout females in the Minija basin used a relatively narrow range of water depth and velocity. It is likely that the depth of 0.25 – 0.40 m and flow velocity of 0.4 – 0.7 m s^{-1} are optimal for the presently studied sea trout. However, the measured depth and flow velocity are somewhat higher than those of most other published brown trout populations, and are more close to suitability criteria established for Atlantic salmon (Louhi et al. 2008) or other large anadromous salmonids (Bjornn and Reiser 1991) than for resident brown trout. Strong avoidance of shallow places (less than 0.15 m deep) for spawning was unlikely for most of the other studied brown trout populations. This could be attributed to spawner's size-related preferences (Crisp and Carling 1989). The average total length of the sea trout, arriving in the Minija basin in order to spawn, reaches 66 – 71 cm (Kontautas and Rauckis 1994), while most studies were done on resident brown trout, whose spawners are usually <50 cm long . The rivers of the western hydrological region of Lithuania are characterized by complex hydrology; after autumn-winter floods, the water level in rivers considerably drops in the second half of the winter due to poor supply by groundwater, (Gailiušis et al. 2001). Selection of relatively deep spawning grounds during the autumnal flood may be an adaptation to a strongly fluctuating water level, to avoid dewatering or freezing of shallow redds later in the winter.

It is known that some sites are used for redds constantly, year by year with striking accuracy (few meters scale) (Nika unpubl. data), what indicates that these microhabitats probably have some specific traits to be attractive as spawning places (Fleming 1998). This is usually the downwelling flow, an essential trait for pool-riffle transitional zones, which is known to play a significant role in the redd site selection for most salmonids (Crisp and Carling 1989, Bjornn and Reiser 1991, Kuzishchin et al. 2009). The spawning of salmonid fishes in such areas is an adaptation to improve egg incubation conditions as downwelling surface water efficiently provides incubating eggs with well oxygenated water and removes metabolic wastes (Chapman 1988, Bjornn and Reiser 1991). The strategy of redd placement in front of the riffle type habitat may have an additional aspect of evolutionary adaptation, other than improvement of water flow through eggs. It is well documented that newly emergent salmonid fry disperse mostly downstream from a native redd, due to limited abilities to resist the flow (Ottaway and Clarke 1981, Daufresne et al. 2005). Dispersing away from a redd, the fry begin to compete for resources and those who are unable to establish a feeding territory will have the ecological disadvantages, such as the increased predation risk or dislodgement to less suitable areas. The survival after the fry emergence during the early critical period is strongly density-dependent and is an important population bottleneck (Elliott 1994, Madsen 1995). Therefore, the redd placement in front of the riffle may increase the reproductive success through improved survival of progeny after the fry emergence, by widening the dispersal area downstream from a redd. This approach of spawning site selection is somewhat compatible with the present study results, when most of the redds were distributed in the first-half of the riffle section, and the redd's position was usually "within the safe distance" from the end of this riffle section.

The presence of cover for spawners is an important in-stream feature of salmonid spawning site attraction and suitability (Witzel and MacCrimmon 1983, Armstrong et al. 2003, Rubin et al. 2004, Zimmer and Power 2006, Kuzishchin et al. 2009). As redd digging takes up to several days, during this time both male and female spawners hide and rest periodically in deep water (Armstrong et al. 2003, Esteve 2005). Potential covers in the currently studied streams were positioned mostly upstream from a redd, in its close vicinity. This is related to spawning site selection multi-functionality: when mostly exploited sections for the redd placement were in very front of the riffle, the most suitable and nearest cover in such a case are a channel pool or a lateral scour pool upstream of the riffle front, often with aggregates of drifted woody debris at the pool's tail. Other authors presented similar results for the use of covers by salmonids during the spawning course (Witzel and MacCrimmon 1983, Kuzishchin et al. 2009). Staying very close to a redd-site may represent the need to effective defense of a redd from other conspecific pairs (Esteve 2005) or the energy saving strategy during the exhausting spawning. If suitable for resting, the deep water is not available close to gravel grounds, which may not be used by spawning salmon, no matter how good the gravel is (Armstrong et al. 2003). According to present observation, 16% of redds had no suitable cover within 10 m downstream or upstream. A more distant cover position may represent a trade-off between the spawning success in a proper spawning microhabitat and the energy expenditures, though the cover use behaviour during the spawning season was rarely reported and is still poorly understood. The significance of in-stream morphological and structural complexity for salmonid spawning habitat must be considered in every river channel management and restoration projects, as an effective tool for restoration of spawning habitats and salmonid populations (Madsen 1995, Rubin et al. 2004).

The analysis of spring-collected redd gravel samples characterize the gravel structure as an egg incubation environment, rather than preferences for redd construction material. Considering that the content of sediments less than 2 mm in diameter, amounting to 20%, has a significant negative effect (usually lethal) on the egg-to-fry survival (O'Connor and Andrew 1998, Louhi et al. 2008); in the present study, the trout egg incubation conditions were within the acceptable limits. The average sediment amount did not differ between all study reaches, though high variation of redd sedimentation was determined within particular reaches. Obviously, besides the overall stream sediment load, the local-scale redd sedimentation patterns affect the redd quality; and the redd-site selection will determine the persistence and the quality of a redd during the incubation period. One of the worst gravel qualities was found in the Blendžiava study reach, where average d_g and F_i were among the lowest recorded ones; 33% of the redds contained >20% of fine sediments, and high sedimentation occurs in this study reach (Nika unpubl. data). Meanwhile, according to the long-term monitoring data from the same reach, the density of *S. trutta* population is 33.38 ±19.03 ind. 100 m^{-2}, and this is one of the highest in Lithuanian rivers (CORPI 2009). Good embryo survival in some of the redds with good substratum quality may buffer the effects of the high sedimentation level and maintain a dense population. On the other hand, the effect of high amount of sediments on sea trout embryos is unknown for the studied lowland rivers, and the effect may differ from that determined by other studies.

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