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**REPRODUCTIVE ECOLOGY AND SUCCESS
OF SEA TROUT *SALMO TRUTTA* L. IN A
SMALL LOWLAND STREAM OF WESTERN
LITHUANIA**

Doctoral dissertation

Biomedical sciences, ecology and environmental sciences (03B),
hydrobiology, marine biology, aquatic ecology, limnology (B260)

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KLAIPĖDOS UNIVERSITETAS
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INSTITUTAS

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**ŠLAKIŲ *SALMO TRUTTA* L. REPRODUKCIJOS
EKOLOGIJA IR EFEKTYVUMAS MAŽAME
LYGUMŲ UPELYJE VAKARŲ LIETUVOJE**

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1. INTRODUCTION

Scope of the study. Reproduction is a critical period of salmonid fish life history. All members of *Salmoninae* subfamily (trouts, salmon and charrs) lay their eggs in the streambed gravel nests, where they incubate for a long period (about half-year in temperate regions). Incubating eggs are vulnerable to changes in incubation conditions, which are rather unstable in the fluvial ecosystems, especially under increasing anthropogenic pressure (Turnpenny & Williams, 1980; Crisp, 1989; Soulsby et al., 2001). Spawning success, therefore, largely depends on the spawning site selection and nest quality during the incubation period. Substantial mortality may occur during egg-to-fry undergravel stage (Chapman, 1988; Fleming, 1998; Armstrong et al., 2003). Other, the most severe, survival bottleneck for salmonid populations is considered to be the early critical period (ECP) that starts right after fry emerge from the gravel and initiate exogenous feeding (Elliott, 1989; 1994; Armstrong & Nislow, 2006). The timing and patterns of fry emergence substantially determine the ECP survival and growth potential (Armstrong & Nislow, 2006) and in turn the strength of population recruitment and stocks of salmonid fishes (Beard & Carline, 1991; Armstrong et al., 2003). As early life stages are particularly sensitive to biotic and abiotic constraints, studying these stages in terms of survival is essential in salmonid population ecology, stocks management, conservation and restoration.

Global concern regarding declining efficiency of spawning of salmonids has produced a voluminous body of information on the reproductive ecology of salmonids (Chapman, 1988; Bjornn & Reiser, 1991; Kondolf & Wolman, 1993; Elliott, 1994; Fleming, 1996; 1998; Armstrong et al., 2003; Esteve, 2005; Louhi et al., 2008). *Salmoninae* is obviously among the best studied fish groups in the world. 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: stream-dwelling brown trout *S. trutta fario* and anadromous sea trout *S. trutta trutta* (Elliott, 1994). The spawning ecology of the sea trout and its

relationship to that of brown trout has received little attention though. There are also large geographical gaps in salmonid exploration, as the vast majority of studies were accomplished in the North America, Scandinavia, UK, France; and mainly in mountain or highland rivers. Literature search revealed an absence of information on this subject in the southeastern and eastern Baltic region and quite a few studies dealt with salmonids reproductive ecology in Poland (Radtke, 2005; 2008 and references therein).

Many rivers in the eastern Baltic region, which is considered as distinctive biogeographical region (according to Water Framework Directive), are important for salmonid reproduction and significantly contribute to the sea trout and Atlantic salmon stocks in the Baltic (Ranke et al., 1999). Many natural self-reproducing brown trout (resident and anadromous) and some Baltic salmon populations occur in Lithuanian rivers (Kesminas et al., 2000). Since 1998, national monitoring program on salmonid population status in rivers is being implemented and in some most important rivers spawning intensity of anadromous salmonids is being monitored routinely. However, no characterization of salmonids spawning habitats on scientific basis has been made to date. This study is the first attempt to fill this gap in studies of Lithuanian rivers. Coherent study on reproductive ecology of anadromous brown trout, from spawning site selection to fry emergence, was accomplished in a typical sea trout spawning stream – Blendžiava. This stream soundly represents salmonid reproductive areas in a whole Minija River basin, which is considered to be a reference river for sea trout in Lithuania. The results of this study are also applicable to other lowland type rivers of temperate regions.

Aim and objectives of the study. The aim of this work was to assess sea trout spawning sites characteristics and to estimate their effects on reproductive success in a typical lowland salmonid stream.

The main objectives of the study were:

1. to assess sea trout spawning site selection and characteristics at different spatial scales;

2. to estimate survival rate of sea trout eggs from 'eyed' stage to fry emergence in natural redds;
3. to evaluate fry emergence efficiency, timing and patterns;
4. to assess effects of redd intragravel parameters to the success of egg incubation and fry emergence;
5. to determine dispersal extent of juveniles after emergence.

Novelty of the study. This study is the first comprehensive description of salmonids reproductive ecology in the rivers of eastern Baltic region (Baltic Province ecoregion). It also provides integrated analysis of all main stages of the sea trout reproductive ecology in lowland rivers. Complex and significant effect of groundwater to different stages of reproductive process supports increasing awareness of this factor significance. Detailed sea trout fry emergence study revealed significantly later fry emergence timing than it was accepted for Lithuanian salmonids. Assessment of conditional status of salmonid fry at emergence was supported by novel approach based on the analysis of RNA:DNA ratio in emergent fry. Significant reproductive interaction in terms of sea trout redd superimposition by spring-spawning *Lampetra* lampreys was described for the first time, suggesting likely ecological effect on pre-emergent and emerging trout fry.

Scientific and practical significance of the results. Results of the study supplement our understanding of complex ecology of early life stages of salmonids and organization of ecosystems of salmonid rivers. Present findings may delineate baselines for the future researches of salmonid spawning and early life history in Lithuanian rivers. Particular attention should be taken to significance of groundwater-stream water exchange effect on incubation success, especially in rivers with considerable groundwater supply. The results of spawning conditions studies of salmonids have huge practical significance. The information about structure and functioning of natural spawning habitats is of crucial importance for river restoration

projects, which focus on channel complexity and spawning habitat restoration. Results from fry emergence studies could be useful for optimization of hydropower plants operation in the spring, to reach sustainable and ecologically sensitive river exploitation. Information about timing of particular developmental stages becomes important when facing with climate change threats, to which salmonids are particularly vulnerable. Nucleic acid ratio analysis results revealed that advanced biochemical methods could be a sound technique to investigate complex early life stages during the transition from maternal provisioning to an independent foraging in salmonids.

Defensive statements

1. Spawning site selection by sea trout in Blendžiava Stream has specific patterns at the stream-, reach- and microhabitat scale, and was related with optimal conditions for egg survival.
2. Vertical hydraulic gradient of hyporheic flow is an essential factor, which determines spawning microhabitat selection and affects intragravel physico-chemical conditions.
3. Upwelling groundwater significantly negatively affects egg incubation efficiency and fry emergence.
4. ‘Eyed‘ egg to fry survival negatively depended on the structure of spawning substrate, but survival persisted at the relatively high sedimentation extent.
5. The end of fry emergence period is critical for body condition of emergent fish.
6. Spring-spawning lampreys considerably superimpose the redds of sea trouts what may have likely ecological effect on pre-emergent and emerging stages of salmonids.
7. Initial dispersal of juveniles was associated with the native spawning site, while dispersal extent increases with decreasing availability of suitable rearing habitats for juveniles.

Scientific approval

The material of this work was presented in 7 international and 2 national conferences and seminars:

2nd and 3rd Regional Student Conferences ‘Biodiversity and Functioning of Aquatic Ecosystems in the Baltic Sea Region’, October 2006, Klaipėda; and October 2008, Juodkrantė, respectively, Lithuania;

Nordic Workshop for PhD students on *Salmo salar* and *Salmo trutta* Research (NoWPaS), March 22–25, 2007, Jyväskylä, Finland;

12th European Congress of Ichthyology, September 9–13, 2007, Cavtat (Dubrovnik), Croatia;

European Workshop for PhD Students on *Salmo salar* and *Salmo trutta* Research, February 14–17, 2008, Roskilde, Denmark;

European Workshop for Doctoral Students on *Salmo salar* and *Salmo trutta* Research, March 19–22, 2009, Southampton, England;

13th European Congress of Ichthyology, September 6–12, 2009, Klaipėda, Lithuania;

National Conferences of Young Hydroecologists, October 2005 and 2007, Anykščiai and Molėtai, respectively, Lithuania.

Two papers were published on the dissertation topic:

1. Nika, N. and Virbickas, T., 2010. Brown trout *Salmo trutta* redd superimposition by spawning *Lampetra* species in a lowland stream. *Journal of Fish Biology*, 77: 2358–2372.
2. Nika, N., Virbickas, T. and Kontautas, A., 2011. Spawning site selection and redd gravel characteristics of sea trout *Salmo trutta* in the lowland streams of Lithuania. *Oceanological and Hydrobiological Studies*, 40(1): 46–56.

Volume and structure of the thesis. The dissertation is presented in the following chapters: Introduction, Literature Review, Study Area, Material and Methods, Results, Discussion, Conclusions and References. References include 203 sources. The dissertation contains 15 tables and 36 figures. The volume of the dissertation is 136 pages.

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Definitions, specific to the stream and salmonid ecology:

Hyporheic zone – the interstitial habitat beneath a streambed surface, as a layer of the saturated sediments in which surface water and groundwater mix. It is dynamic ecotone characterised by steep chemical and biological gradients (Boulton et al., 1998).

Redd – the contiguous area of disturbed gravel containing one or several nests, composed of pit in the streambed and raised mound or tailspill of sorted gravel downstream (Crisp & Carling, 1989).

‘Eyed’ egg – developed embryo in the egg capsule, with fully pigmented eyes, which are seen through the capsule.

Alevin – free larvae hatched from the egg, dwelling under the gravel and feeding internally from a large yolk sac.

Fry – emerged from the redd gravel fish with fully absorbed yolk sac, which initiates exogenous feeding.

Emergence – swim-up of alevins or fry from the incubation substrate to the redd surface.

Parr – actively feeding juveniles with a series of dark bars on their sides (parr marks).

Specific abbreviations used in the work:

CGU – channel geomorphic unit (riffle-pool transition, riffle, run, glide and pool);

EETF – ‘eyed’ egg to fry (emergence) survival;

IB – experimental egg incubation box: incubation box;

EB – experimental egg incubation box: emergence box;

TB – experimental egg incubation box: emergence trap-box;

RDOS – relative interstitial water dissolved oxygen saturation;

ΔCND – difference in electric conductivity between interstitial water and surface stream water, indicator of groundwater;

Δtemp – difference in water temperature between interstitial water and surface stream water;

IWS – interstitial (intragravel) water sample;

VHG – vertical hydraulic gradient.

2. LITERATURE REVIEW

2.1. Reproductive ecology of salmonid fishes

Salmonid fishes *Salmoninae*, with the exception of lake trout, are typical lithophylic brood hiders, burying their eggs in the streambed gravel substratum of their breeding territories. Mature fishes in the end of summer or autumn migrate (from the sea or within river) to the upstream spawning grounds, where they seek out appropriate breeding territories. Within suitable spawning grounds they construct one or more nests in the gravel streambed, which is referred as a 'redd' (Ottaway et al., 1981; Crisp & Carling, 1989; Fleming, 1996).

The building of nests appears to serve as a means of protecting eggs and yolk-sac alevins from predation, light, flooding, desiccation during periods of low water and freezing, though it may also serve to guard against shifts in substrate caused by other females (Heard, 1991; Fleming, 1996). The redd is designed to improve intragravel conditions for developing embryos by increasing gravel porosity and forcing water currents through the nests (Chapman, 1988; Peterson & Quinn, 1996; Rubin & Glimsäter, 1996). Brown trout and sea trout usually bury their eggs in substrate at depths averaging at 5-20 cm, while average burial depth for bigger sea trout may be as big as 25 cm (Crisp & Carling, 1989; Grost et al., 1991; DeVries, 1997).

Nest construction consists of two main phases: excavation of the nest and covering of the eggs. Both phases are characterized by digging, in which females use a series of tail-beating sequences. Female turns on its side, pressing its caudal fin against the gravel, and then rapidly lifts the caudal fin, creating a water vortex that displaces gravel to downstream direction, while the current carry away fine sediment (Fleming, 1996; 1998, Esteve, 2005). As nest building progresses a female will test its shape and depth by lowering her anal fin into the pit, apparently assessing nest readiness (Esteve, 2005). When the nest is completed male joins to the female, both fish emit their gametes, and eggs are fertilized successfully because of vortexing current in the nest pit. Nest covering begins immediately

after egg deposition and fertilization, as the female attempts to rapidly protect her eggs. At this stage, digging occurs around the upstream edges of the nest, with the displaced gravel lifted onto the nest thus covering the eggs. The new nest is usually located upstream from the previous one and the last covering diggings are used to start it (Fleming, 1998; Esteve, 2005). Females of *Salmo* genus usually complete nesting within 5–6 days during which time they aggressively defend their nesting territories. Once nesting is completed, females appear not to defend their nests, descending from the spawning grounds to a nearby pool (Fleming, 1998). One female may construct several nests and this varies directly with their body size (Baglinière et al. 1990; Barlaup et al. 1994; Fleming, 1996).

Selection of nesting site is an active process during which females may dig at several different places prior to selecting a site for excavation. Even in the later stages of nest excavation, females may abandon a site if they find it to be unsatisfactory, leaving behind a ‘false’ redd containing no eggs (Crisp & Carling, 1989). The female decision as to where to spawn appears to be affected by several factors, including habitat conditions, local adaptation, traditionality, and intrasexual competition. Female breeding territories tend to be concentrated in areas having suitable habitat conditions for spawning and egg incubation (Fleming, 1998).

Spawning site characteristics such as water depth, flow velocity and substrate size are generally considered to be the most important in-stream microhabitat variables in determining spawning site selection for most salmonid fishes (Bjornn & Reiser, 1991, Geist & Dauble, 1998; Armstrong et al., 2003; Louhi et al., 2008). It was demonstrated by Crisp & Carling (1989), Kondolf & Wolman (1993) that preferred spawning habitat characteristics, basically water depth, flow velocity and substrate size, are dependent on the spawner size, bigger fish being able to spawn in faster water and on coarser substrate. According to several published studies, sea trout in different river systems and populations utilized wide range of water depths averaging at 0.16–0.75 m (Crisp & Carling, 1989, Ingendahl et al., 1995; Soulsby et al., 2001; Walker & Bayliss, 2007; Barlaup et al.,

2008; Nika et al., 2011). Flow velocities over sea trout redds, reported by these authors, ranged within 0.18–0.91 m s⁻¹, averaging at 0.18–0.65 m s⁻¹. Based on the generalized spawning habitat suitability curves established for *Salmo trutta* from many published data, the most suitable water depth and flow velocity are around 0.30 m and 0.40–0.50 m s⁻¹ respectively (Louhi et al., 2008). The generalized preferred gravel size for *Salmo trutta* is 16–64 mm (Louhi et al., 2008). In general, fish can spawn in gravels with a median diameter up to about 10% of their body length (Kondolf & Wolman, 1993).

Many additional channel geomorphic, riparian and microhabitat features, such as presence of the cover for spawners, channel slope, angle and vegetation of river banks, hyporheic temperature, dissolved oxygen and pH, substrate depth, stability, permeability and porosity, rate of bedform migration, presence of groundwater seepage and vertical hydraulic gradient were related to the spawning site selection by salmonid fishes (Bjornn & Reiser, 1991; Geist & Dauble, 1998; Knapp et al., 1998, Armstrong et al., 2003).

Survival of incubating eggs is a function of nest quality and nest persistence during the course of egg incubation (Crisp, 1993a). Many different abiotic factors responsible for decreased egg-to-fry survival were described in numerous studies, among which are water temperature (Tang et al., 1987; Stonecypher et al., 1994); pH (Donaghy & Verspoor, 1997), water quality (Lower & Moore, 2003; Finn, 2007), redd dewatering and scouring (Becker & Neitzel, 1985; Montgomery et al., 1996; DeVries, 1997). There is generally accepted that incubation efficiency of salmonids largely depends on the structure of spawning substrate (Lotspeich & Everest, 1981; Chapman, 1988; Rubin & Glimsäter, 1996; Rubin, 1998). Quality of spawning gravel (mean particle diameter, sorting and porosity) decreases with increasing excessive amount of fine sediments which fill the interstices of gravel (Chapman, 1988).

Substrate overfilled with fine sediments affects incubation efficiency in two ways: directly, when successfully hatched and reached emergence stage fry may not be able to pass through the

substrate and reach the stream bed surface, thus stay trapped and die inside the nest (Witzel & MacCrimmon, 1983b; Chapman, 1988; Rubin, 1998). However, most incubation failures were addressed to indirect effect of poor substrate structure, when impeded substrate permeability and flow rate of interstitial water through the egg pocket cause insufficient supply of oxygenated water and removal of toxic metabolic wastes. This indirect effect may cause severe mortality in different developmental stages of eggs and alevins (Chapman, 1988; Rubin, 1998; Rubin & Glimsater, 1996; Ingendahl, 2001; Greig et al., 2007).

Stage of egg development is the factor most commonly associated with changes in oxygen consumption. Two peaks in metabolism and therefore in oxygen consumption are observed during egg development. The first peak occurs early in development and has been attributed to proliferation of blastodisc (Hamor & Garside, 1977). The second peak occurs at hatching, when egg breaks free from the egg capsule and must be supported by increased oxygen uptake (Hamor & Garside, 1977; Rombough, 1988). Post-hatching, embryos become mobile, allowing them the potential to migrate from areas of low oxygen availability. Therefore, alevins may be less susceptible to mortalities resulting from oxygen deficiencies (Greig et al., 2007). After hatching, alevins remain in the gravel for several weeks absorbing their large yolk-sacs. When the yolk-sac is nearly exhausted, alevins actively move upward through the gravel and emerge into the stream as free-swimming fry.

Timing and pattern of emergence have high importance on subsequent establishing of feeding territory, further dispersal and survival (Einum & Fleming, 2000; Armstrong & Nislow, 2006). Early emergence behavior is a stress response to the confinement effects imposed by the small interstices in fine substrate (Olsson & Persson, 1986; Rubin, 1998). In such contexts, size of emergent fry decreases with subsequent potential ecological disadvantages as predation risk and limited abilities to resist the strong flow (Brännäs, 1995). Negative consequences have and delayed emergence when late emergers have to compete with territories established earlier emergent

congeners (Brännäs, 1995; Einum & Fleming, 2000; Armstrong & Nislow, 2006).

The period during emergence and the establishment of feeding territories appears to be of critical importance in the dynamics of salmonid populations. This is a time when mortality can be very high and during which the strength of the cohort may be established, termed early critical period (Elliott, 1989; 1994; Nislow et al., 2004; Armstrong & Nislow, 2006). In a study of trout the critical period extended for several months after emergence (Elliott, 1989). The dispersal of most salmon and trout from the redd can be very limited in extent (Egglishaw & Shackley, 1973).

Apart from physical factors that affect spawning efficiency of salmonids, biotic factors also have considerable effects. Such factors are cues of predators that may alter emergence timing and behavior of alevins and fry. Experimentally were found that predator cue can delay emergence (Mirza et al., 2001; Jones et al., 2003). Direct effect of predation on pre-emergent or newly emerged fry definitely is one of the most important biotic factors that can significantly reduce reproductive success. Most often documented predators preying on salmonid fry are *Cottidae* sculpins (Gaudin & Cailliere, 2000; Mirza et al., 2001) which can prey on salmonids and under the gravel (Dittman et al., 1998; Palm et al., 2010). Trout (Brännäs, 1995; Jones et al., 2003), burbot (Jones et al., 2003) or even noble crayfish *Astacus astacus* (Rubin & Svenson, 1993) also prey on emerging salmonids and may have significant effect on their reproductive success.

2.2. Estimation of spawning success

Estimation of the natural spawning success from fertilization of eggs to the emergence of fry (egg-to-fry (ETF) survival) gives information on the stream quality during the whole development period of the eggs and fry. Many different techniques have been used to estimate reproductive success of salmonids.

Laboratory experiments. This is probably mostly employed approach to relate ETF survival with variables of incubation

environment. Controlled incubation conditions allow to minimize effects of unrehearsed factors. Wide spectrum of experiments has been conducted to test survival rate depending on incubation substrate parameters (Crisp, 1993; Rubin et al., 1998; reviewed in Chapman, 1988). Rubin (1998) reported, that generally it is not possible to observe direct sediment structure effect on ETF survival in nature because, when the substrate quality is poor, most of the eggs die before emergence due to the lack of oxygen (indirect effect). In most published experimental studies these two effects are not distinguished because of the design of the relevant experiments (Chapman, 1988; Crisp, 1993; Rubin, 1998). Some laboratory studies have dealt with direct effect of substrate structure on emergence success, when oxygen concentration is maintained at particular level (Rubin, 1998).

However, it is not possible to predict precisely the natural survival of eggs and fry in the redds of salmonids on the basis of physical factors measured during laboratory studies (Rubin, 1995). Therefore, field experiments remain absolutely necessary.

Fry traps. A method of capping redds with fry-traps and collecting fry after emergence has often been used to estimate the spawning success (Phillips & Koski, 1969; Porter, 1973; Field-Dodgson, 1983; Scrivener, 1988; Ingendahl, 2001; Dumas & Marty, 2006). This method, however, has several problems including the estimation of the initial number of eggs, deposited in natural redds (Field-Dodgson, 1983; Rubin, 1995). Calculations of number of eggs in the redd could be made from the relationship between the female size and its fecundity, if the size of female which spawned on the redd is known. But such a specific fecundity-length relationship has to be computed for the particular salmonid population. Using a relationship established for another population may introduce errors because of differences between stocks (Chapman, 1988; Fleming, 1998). Even if the fecundity-size relationship has been established for the studied population, errors may appear if eggs are retained in the body cavity. Errors in estimates of the number of spawned eggs may appear if the female digs multiple redds or if another female spawns in the same location (Fleming, 1998).

Other problems limiting this method is that the presence of these traps may modify the water dynamics over the spawning ground and increase siltation within capped redd (Phillips & Koski, 1969; Hausle & Coble, 1976; Reiser et al., 1998). The emergent fry number may be underestimated due to difficulties with proper positioning of the trap; the risk of lateral fry escapement through the gravel interstices (Phillips & Koski, 1969; Garcia de Leaniz et al., 1993); or vulnerability of the trap to high flows. These latter problems, however, might be solved by specific design of trap construction (Dumas & Marty, 2006).

Despite limitations to the estimation of ETF survival, emergence traps are useful for estimation of fry emergence timing and patterns (Field-Dodgson, 1983).

Egg boxes. Incubators or egg boxes are often used to estimate egg-to-fry survival of salmonids under different environmental conditions *in situ*; and wide variety of box constructions were proposed (Harris, 1973; Hansen, 1975; Tappel & Bjornn, 1983; Rubin, 1995; Bernier-Bourgault et al., 2005; Dumas & Marty, 2006; Levasseur et al., 2006; Heywood & Walling, 2007; Pander et al., 2009). Whitlock-Vibert incubation boxes, originally used for stocking streams with trout and salmon eggs, have been used in many studies (Hansen, 1975, Tappel & Bjornn, 1983). There was argued that such incubation boxes do not imitate natural redds (Gustafson-Marjanen & Moring, 1984). Boxes of different construction were often buried in the streambed substrate, mimicking redd construction. Scrivener (1988) and Rubin (1995) used cylindrical incubation boxes, which are inserted into the substrate of natural redds with the help of special injector. Alterations to the substratum characteristics (mainly to the percentage of fine sediment) around the boxes are considered to be minimal and incubation conditions are as natural as it is possible (Rubin, 2005). The boxes may be retrieved from the redd at different incubation stages, to determine survival of particular development stage; or emergence traps could be joined to the box to collect emerging fry (Rubin, 1995; Bernier-Bourgault et al., 2005; Dumas & Marty, 2006). Such emergence traps, however, cannot allways

withstand the ice drifting during winter and high flow velocity during the spring floods. The alevins that hatched may be prevented from emerging due to sediment accumulation between the basket and emergence trap (Bernier-Bourgault et al., 2005). Other disadvantage of the boxes is that eggs in such egg boxes may be tightly clustered in larger numbers than in nature, and can become traps for fungus and sediment (Harshbarger & Porter, 1979).

Stock-recruitment models. Indirect methods to evaluate efficiency of reproduction of salmonids using data series of stocks (number of spawners, redd density) and population recruitment (eggs, fry, 0+ juveniles) to build stock-recruitment models (Knapp et al., 1998; Essington et al., 2000). Results from these models have generally supported the paradigm that salmonid populations are regulated by strong density-dependent mortality acting on the age-0+ stage soon after emergence from the gravel (Elliott, 1989; Knapp et al., 1998). The shape of the spawner-recruit relationship often provides some insight into the mechanism of density dependence. An asymptotic (Beverton-Holt) spawner-recruit relationship reflects space limitation for spawning adults or offspring, while a dome-shaped (Ricker) spawner-recruit relationship reflects resource depletion by offspring. It is often difficult to distinguish these two models from a linear (density-independent) model or to distinguish between them for several reasons. First, the requisite long time series of data over a wide range of spawning population sizes are not common. Second, the number of females, their egg production, and the number of offspring must be accurately counted. Third, the importance of density-independent mortality factors such as flooding and freezing must be minimized (Essington et al., 2000).

2.3. Characteristics of Lithuanian rivers

The territory of Lithuania lies in the zone of excessive humidity, and therefore has a dense and complex hydrographic network. The average density of rivers, including artificial channels, is 1.18 km km⁻². In general, there are 22.2 thousand rivers, streams and

ditches, which on the whole make 76.8 thousand km of total channel length. Only 17.4 % of this hydrographic network length is natural, while 60% of present network is composed of regulated stream channels and 22.6 % – of new artificial drainage ditches and canals. The highest share of hydrographic network (80% of total stream number and 51% of total length) makes waterways less than 3 km in length, vast majority of which are regulated. There are 755 middle-sized rivers and streams (10–100 km in length); and 17 rivers are longer than 100 km (Gailiušis et al., 2001).

Lithuania's territory and all its rivers belong to the Baltic Sea Basin (the southeastern Baltic). According to the Water Framework Directive, Lithuania's territory (together with Latvia and Estonia) belongs to the Baltic Province ecoregion, a distinct biogeographical region of the Europe which is characterized as relatively homogeneous area based on topography, soils, land use and natural vegetation (Illies, 1978). This area is situated in the northwestern part of East European Plain and the landscape of the territory dominates by low and rather flat surfaces. The majority of the territory (90%) lays below 160 m altitude and average altitude of the territory is 98 m (Jablonskis & Lasinskas, 1962). Similar orographic patterns of landscape are found in Latvia and Estonia, therefore the rivers of this region are considered to be lowland rivers with low channel slopes. In plain and lowland rivers of Lithuania, the average river channel slope rarely is greater than 0.1%, while the rivers in highlands and plateaus have steeper average slopes, that are always higher than 0.1%. Average slope of small streams (10–30 km) in highland areas is 0.15–0.5 %, while particular reaches within several kilometers (usually upstreams) may have 0.7–1.1 % slope (Jablonskis & Lasinskas, 1962).

The relief and main patterns of present hydrographic network in Lithuanian territory was largely shaped by the three last Scandinavian glaciations. Surface geology is composed of quaternary sediments, forming sequences of low and high landscape forms from north-west to south-east direction (Jablonskis & Lasinskas, 1962; Gailiušis et al., 2001).

The water supply of rivers in Lithuania is compound. Waters of melting snow make 30–40%, rainwaters make about 25%, and groundwaters make about 35% of the average annual runoff of the Nemunas River. In other rivers, the share of water supply sources deviate considerably from the above presented quantities: in the western Lithuania rainwaters make 53%, while groundwater – only 18%. On the contrary, the share of groundwater supply in the rivers of East Lithuania increases up to 50–60% (Jablonskis & Janukėnienė, 1978; Garunkštis, 1988). Differences in water supply also determine the nature of the annual flow regime. Most rivers of Lithuania are flooded in spring after snow melt, but in summer or winter their water levels are low, maintained mainly by the groundwater supply (Jablonskis & Janukėnienė, 1978; Gailiušis et al., 2001).

Rivers of Lithuania belong to the group of rivers with average turbidity (25–50 g m⁻³). The turbidity of lowland rivers, especially in the Southeast sandy plain is lower (less than 25 g m⁻³). Rivers which flow from highlands, carry more turbid waters (50–100 g m⁻³). The waters of Lithuanian rivers, as of all rivers flowing through forested areas, are of average mineralization (about 400–500 mg l⁻¹). Waters of the lowest mineralization (200–300 mg l⁻¹) are characteristic to the Southeast sandy plain with its lowly carbonized and deeply limy morainic subsoils. Rivers of the Middle lowland are highly mineralized (up to 800 mg l⁻¹), especially in its northern part, where highly carbonized moraine lies on limestones and dolomites (Fedosiejeva & Fetisova, 1981; Garunkštis, 1988).

In summer, the average monthly water temperature changes correspondingly to the air temperature, but usually is 1–2°C lower. In winter the water temperature is about 0°C. The water temperature of many brooks, streams and medium-sized rivers, even in summer, rarely exceeds 20°C (Garunkštis, 1988), thus they are suitable to live for stenothermic *Salmonidae* fish.

Distribution of salmonid rivers in Lithuania has particular pattern, defined by local orographic, geomorphic, climatic and anthropogenic conditions in the river catchments. Main Baltic salmon populations are found in the rivers of eastern Lithuania. Main sea trout

rivers, with abundant populations are common in the western Lithuania. Meanwhile in the middle Lithuania's rivers (Mūša, Nemunėlis, Nevėžis, Šešupė) salmonids are absent (Kesminas et al., 2000), due to unfavourable hydrologic and hydro-chemical conditions.

3. STUDY AREA

The study was carried out in a small lowland stream Blendžiava situated in western Lithuania, Kretinga District (Fig. 1). This is a 29.2 km length, third-order stream that discharges into the downstream of Salantas River, which further enters the Minija River at its middle section. Blendžiava is a typical lowland stream which starts at an altitude of 135 m and reaches its mouth at an altitude of 26 m and has an average channel slope of 0.33% (Jablonskis & Lasinskas, 1962; Gailiušis et al., 2001). Under mean flow conditions mean channel wetted width of Blendžiava Stream is 6–8 m and the dominant depth is 0.2–0.5 m (based under sampling sites measurements). The channel is dominated by plane-bed sections (run, glide and pool type channels), while the general structure of the stream follows pool and riffle type channel sequencing, characteristic for lowland streams.

Blendžiava drains a catchment of 85.6 km², which is situated in the area of West Samogitian plateau (upstream) and West Samogitian plain. Most of the catchment's area is located in a flat moraine plain which is overlain by a variety of glacial moraines, mainly sandy and clay loam rich in boulders. The very downstream part of Blendžiava (1.2 km section) falls into Erla-Salantas-Minija old valley formed by streams of melting glacier, which is covered with glaciofluvial and alluvial sediments (Jablonskis et al., 1991; Gailiušis et al., 2001). Therefore streambed structure of this section of Blendžiava Stream is considerably dominated by gravel substrates. The dominant soil types in a catchment area are turfy podzols and gleyic loams and sands. Land use in a catchment's area is dominated by grasslands and arable land with relatively few forests, while stream

itself flows in relatively deep and well-expressed valley with overgrown slopes and stream banks. Riparian vegetation is dominated by grey alders *Alnus incana*, maples *Acer platanoides* and bird cherries *Prunus padus*.

No direct hydrologic measurements are made routinely in the stream. The discharge at the mouth of the stream during the study period (2007–2009) was calculated from the daily discharge data of Minija River at Kartena hydrology station using the runoff model of $12.9 \text{ l s}^{-1} \text{ km}^2$ (Gailiušis et al., 2001) (Fig. 2). As the distance between the Blendžiava and the Minija River at Kartena is only 8 km and both rivers' basins fall within the same runoff rate distribution isolines ($11\text{--}13 \text{ l s}^{-1} \text{ km}^2$), the runoff calculation for Blendžiava could be made with reasonable accuracy. The mean annual discharge at the mouth is $1.06 \text{ m}^3 \text{ s}^{-1}$ (Jablonskis & Lasinskas, 1962).

The water supply of rivers in the study area is of *R-us* type. The average annual water runoff of the Minija River at Kartena is composed of 53% of rainwaters (*R*), 25% of underground water (*u*) and 22% of snowmelt water (*s*) (Jablonskis & Janukėnienė, 1978). Seasonal distribution of Blendžiava runoff is complex and rather unpredictable as for other streams of western hydrological region of Lithuania. Annual precipitation in this area is amongst the highest in Lithuania (700–900 mm). Climate of this region is transitional with dominating maritime character, with the maximum precipitation in the end of summer and autumn. The runoff is usually peaking in the spring after snow melting and during winters with regular thaws, what cause frequent winter floods. Often winter floods are higher than spring flood due to frequent thaws and therefore low snow accumulation. First half of summer usually is relatively dry, therefore water level in rivers is the lowest in June–July (Jablonskis & Janukėnienė, 1978; Gailiušis et al., 2001) (Fig. 2).

Five milldams were installed in the stream in the past century. Nowadays the only one left dam is located 18 km from the mouth, in Šateikiai town, and creates impassable barrier for migrating fish. The other lower ones fell apart, however some have accessible ruins left which still can be the obstruction for migration under low water level.

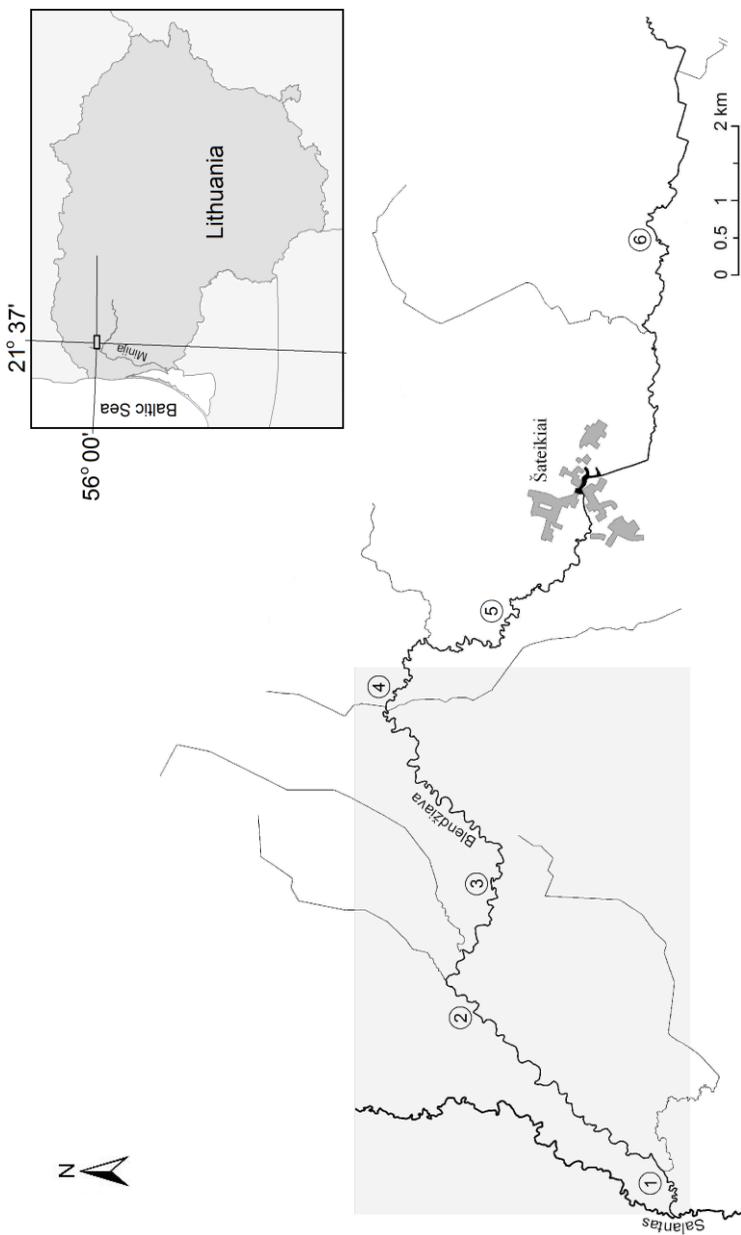


Fig. 1. The catchment of Blendžiava Stream and studied part of the stream (marked as shaded area). Circled numbers indicate electrofishing sites for *S. trutta* population density estimation (Table 1).

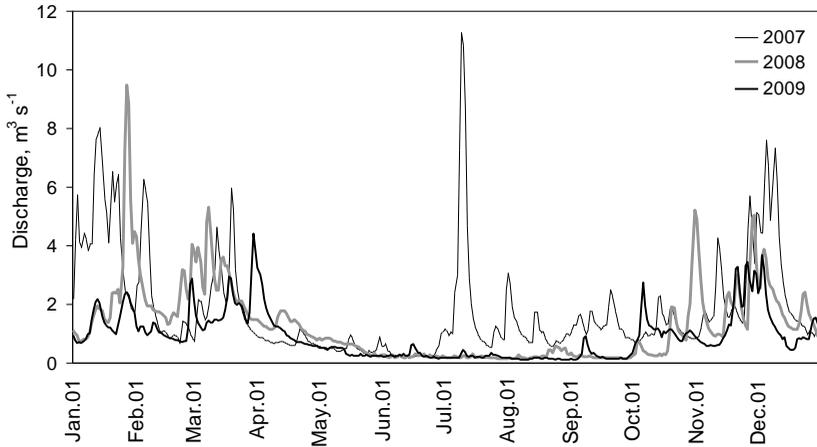


Fig. 2. Discharge ($\text{m}^3 \text{s}^{-1}$) of Blendžiava Stream at the mouth in 2007–2009, calculated from the daily discharge data of Minija River at Kartena hydrological station, according to area runoff model of $12.9 \text{ l s}^{-1} \text{ km}^2$ (Gailiusis et al., 2001).

Table 1. *Salmo trutta* population density, biomass and share of 0+ age juveniles in Blendžiava Stream, estimated by electrofishing in different years (Kontautas et al., 2010; Nika unpubl. data). The locations of electrofishing sites are shown in Fig. 1.

Site number and name	Year	Density, ind. 100 m^{-2}	Biomass, $\text{kg } 100 \text{ m}^{-2}$	0+ age group, %
1. Kūlsodis	2007; 2010	8.1; 5.7	0.163; 0.298	66; 17
2. Skaudaliai	2007; 2010	4.2; 3.6	0.452; 0.071	33; 66
3. Gaivališkė	1998-2010 (n=13)	32.0 ± 18.9 (10.0-84.8)	0.551 ± 0.231 (0.293-1.007)	66 ± 19 (37-86)
4. Reketė	2007; 2010	23.0; 13.1	0.274; 0.376	81; 59
5. below Šateikiai	2008; 2010	152.1; 18.2	1.253; 0.338	80; 65
6. Kadaičiai	2010	3.6	0.210	0
Average \pm SD*		30.0 ± 32.7	0.483 ± 0.287	62 ± 20

*Average is given for sea trout population at sites 1-5. Upstream reach at Kadaičiai (site 6) has only resident brown trout population.

Below the Šateikiai dam Blendžiava is a state ichthyological reserve established for protection of salmonid population and their spawning grounds. This is a typical salmonid stream of western Lithuania, being an important sea trout spawning area. According to a long-term monitoring data in the midstream part (for years 1998-2010) *Salmo trutta* population density ranges from 10.0 to 84.8 ind. 100 m⁻² (average \pm SD: 32.0 \pm 18.9 ind. 100 m⁻²) and is one of the highest in Lithuanian rivers (Kesminas et al., 2000; Kontautas et al., 2010). Population of *S. trutta* is dominated by anadromous sea trout juveniles (Table 1) with relatively not abundant older brown trout (age \geq 2+). Other species of the stream fish community are: river lamprey *Lampetra fluviatilis* (L.), brook lamprey *Lampetra planeri* (Bloch), Eurasian minnow *Phoxinus phoxinus* (L.), stone loach *Barbatula barbatula* (L.), bullhead *Cottus gobio* L., dace *Leuciscus leuciscus* (L.), gudgeon *Gobio gobio* (L.), riffle minnow *Alburnoides bipunctatus* (Bloch), three-spined stickleback *Gasterosteus aculeatus* L. and nine-spined stickleback *Pungitius pungitius* (L.).

4. MATERIAL AND METHODS

The study was carried out in two spawning seasons: 2007/2008 and 2008/2009. The spawning site selection by sea trout females and characteristics of spawning sites at different spatial scales were determined. Spawning intensity distribution among different stream sections was considered as the macro-scale spawning site selection. Association of spawning redds with different geomorphic channel units considered as reach-scale spawning site selection; and characteristics of spawning redds represent spawning conditions at the microhabitat scale.

To test how the spawning site selection influence reproductive success, *in situ* experiment on survival of sea trout eggs, study on fry emergence from natural redds and on dispersal of juveniles after emergence were accomplished (Table 2). Additionally, the study on reproductive interaction between sympatric lampreys and salmonids were accomplished in both study seasons.

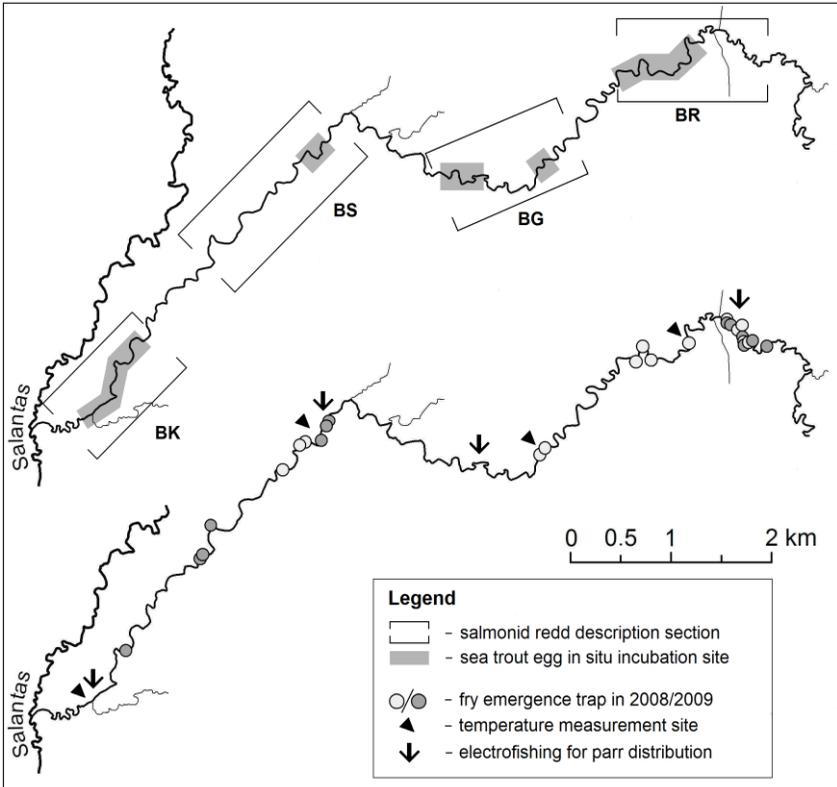


Fig. 3. Distribution of study sites in 2008 and 2009. Four principal stream sections named according to nearby village: BK – Blendžiava at Kūlsodis; BS – at Skaudaliai; BG – at Gaivališkė; and BR – at Reketė (see the text below for geomorphological and hydrological differences of these sections).

All study parts were conducted in four principal stream sections: BR, BG, BS and BK (Fig. 3). These sections well represented different environmental conditions found in the stream. BR section is characterized by upstream flow conditions and stable channel with well-expressed riffle-pool structuring. BG section is pool and run dominated (riffles not common), with sandy bottom and

significant groundwater supply (as during winter this section do not freeze over). BS section – wide boulder, cobble and sand dominated channel with relatively few suitable spawning gravel grounds. BK section has well-expressed pool-riffle channel structuring, with relatively high channel slope and flow velocity. The streambed dominates by gravel substratum, however these gravel grounds are highly mobile during floods, as well as unstable eroding banks.

Table 2. Sampling efforts in four principal study sections in 2008 and 2009: R – redds characterized; S – experimental redds for sea trout egg survival; E – fry emergence traps on natural redds; J – juvenile dispersal study sections.

Study section/study object		2008	2009
	BK/R	8	4
	BK/S	7	3
	BK/E	-	1
	BK/J	-	1
<hr/>			
	BS/R	3	9
	BS/S	-	3
	BS/E	3	6
	BS/J	-	1
<hr/>			
	BG/R	11	20
	BG/S	8	8
	BG/E	2	-
	BG/J	-	1
<hr/>			
	BR/R	19	54
	BR/S	8	9
	BR/E	9	7
	BR/J	-	1
<hr/>			
Total:	R	128	41
	S	46	23
	E	28	14
	J	4	-
			4

4.1. Characterization of spawning sites of *Salmo trutta*

Field surveys for characterization of *Salmo trutta* spawning habitats and redd distribution mapping were carried out in the autumn

after the spawning and in the spring of both study seasons. Counts of salmonids redds were performed after the spawning from November to January, within the designated redd description sections (in 2008) or along the entire 15 km length section (from the mouth to the most upstream study point) (in 2009). The density of spawning redds within particular section was calculated and most preferred spawning sections designated. The redd density was estimated as a number of redds per one kilometer of the stream (no. km^{-1}) at the end of spawning period. The redds less than 0.25 m^2 , which were attributed to resident brown trout or false nests, were not counted.

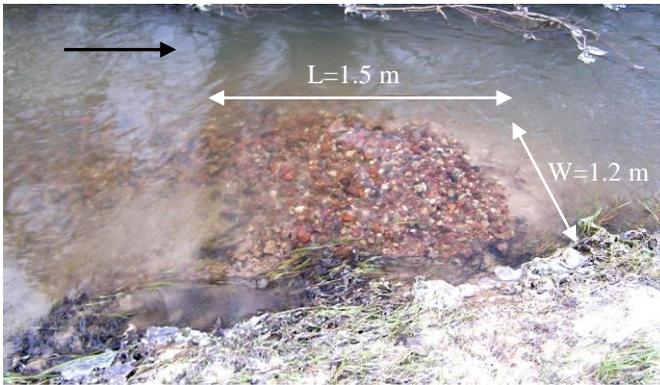


Fig. 4. View of a typical salmonid (sea trout) redd in a small stream. Redd tailspill length (L) and width (W) measurements are shown in respect to flow direction (indicated by black arrow).

Counts of the redds were performed from the stream bank or by wading. Redd locations were identified as a patch of clean gravel in comparison to the surrounding algal or sediment covered substrate, with the mound (or tailspill) of gravel at the downstream direction from a depression in the streambed (Fig. 4). Redd was divided into pit bottom (PB), tailspill front (TSF), tailspill crest (TSC) and tailspill end (TSE) (Fig. 35). The redd positions were recorded with a GPS device and, additionally, the tailspill front and the end were marked with permanent markers on the stream bank. Redd tailspill length and

width (± 0.1 m) were measured along and perpendicular to the flow direction respectively. The redd shape (ellipse, round or irregular) was recorded and the redd size was calculated using two measured axes.

Further explicit characterization of randomly selected redds and their environment was accomplished in the subsequent spring and summer, during and after fry emergence period.

4.1.1. Geomorphic channel units used for spawning and spawning habitat characterization

The spawning site selection at the reach-scale was considered as an association of the spawning redd with one of the stream channel geomorphic units (CGU) classified according to McCain et al. (1990): riffle, run, glide, pool or pool-riffle transitional zone.

Riffle consists of a shallow reach with swiftly flowing, turbulent water with some partially exposed substrate, cross-sectional depths typically being less than 0.3 m, and substrate dominated by boulder, cobble and gravel.

Run is considered as swiftly flowing reaches with little surface agitation and no major flow obstructions, with depth less than 0.3–0.5 m, and gravel, cobble and boulders substrates.

Glide is relatively wide, shallow (<0.5 m) pool, flowing smoothly and gently, with low water velocities and little or no surface turbulence; substrate usually consists of cobble, gravel and sand.

Pool consists of slow flowing area with cross-sectional depths of >0.5 m and with fine substrate dominated by gravel to silt.

Transitional zone, at which water depth was considerably decreased and flow velocity increased and characterized by negative streambed slope in relation to the overall channel slope was assigned to *pool-riffle transition* unit. This is usually short channel sections transitioning from a deeper (pool, glide) to a shallower area (riffle or run), mainly extending to the riffle crest where flow breaks. The downstream section from the riffle break, where a substantial positive slope creates a fast current was considered as a riffle. Among other habitat geomorphic features, the channel slope was important for

distinguishing between riffles, runs and glides. Runs and glides had no noticeable bed inversions and usually *c.* 0 % water surface slope.

Some features of spawning habitat within particular geomorphic unit were recorded. The distance from spawning redd to the closest potential cover, suitable for spawners, was measured and the type of cover was identified. Potential cover in this study was treated as the relatively deep place (>0.5 m) with some flow obstructions or overhead cover, enabling fish to hide from flow and visual sight. Structure of the streambed was assessed visually, within upstream and downstream sections from the redd position in a distance equal to one stream width at that site, and described as a share of the following fractions according to Wentworth sediment size classification scale: boulder (>250 mm), cobble (64-250 mm), gravel (2-64 mm), sand (<2 mm) and silt (<0.063 mm) (Bunte & Abt, 2001).

4.1.2. Redd intragravel hydraulic and interstitial water parameters

The redd intragravel hydraulic conditions in this study were attributed to substrate permeability (hydraulic conductivity, cm hr^{-1}), which is a measure of the ability of a porous medium to pass water; and vertical hydraulic gradient (VHG), which characterizes hyporheic water exchange patterns.

The permeability was measured with modified Terhune Mark V standpipe at the substrate depths of ~15 cm. The standpipe was constructed and the permeability measurements were done according to Barnard & McBain (1994) (Fig. 5). Standpipe was constructed from a 1.2 m length of 3.8 cm inner diameter stainless steel pipe. The top end of the pipe served as a driving head to absorb the impact of a sledge hammer used to drive the pipe into the substrate. The lower end, just above the steel driving point, is perforated with forty eight 3.2 mm diameter perforations in sixteen evenly spaced rows, connected by grooves to help prevent blockage of the holes by small particles (Fig. 5).

When the standpipe is driven into a streambed, interstitial water enters the pipe through the holes and permits the determination of inflow rate. A suction system maintained a 2.5 cm pressure head (below the water level outside) creating a pressure gradient that drives interstitial water to flow through the substrate and into the standpipe at a rate equal to inflow. In maintaining this pressure head, the 12V battery powered diaphragm vacuum pump (model 107CDC20, Thomas) evacuated water from the standpipe. This water was stored in a 1000 ml graduated cylinder so that the volume per unit time (ml s^{-1}) can be measured.

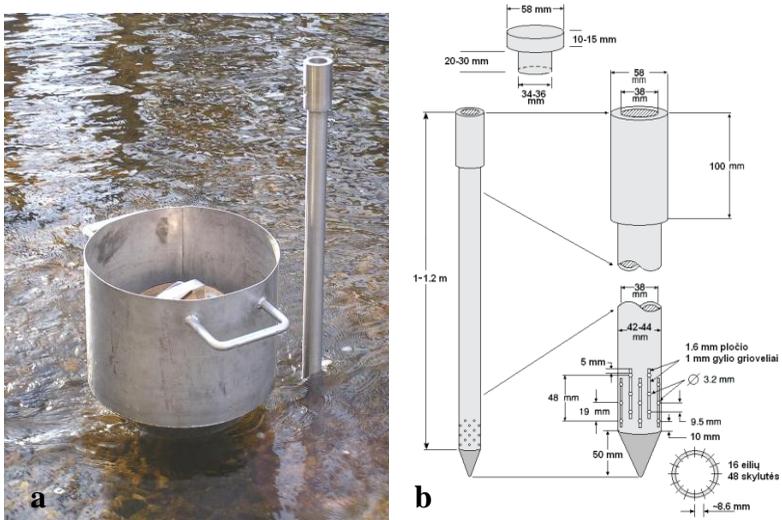


Fig. 5. a) McNeil bulk-core substrate sampler (on the left) and modified Terhune Mark V standpipe, constructed by 'Garant' (Klaipėda); b) scheme of the standpipe, used in this study (redrawn from Barnard & McBain (1994)).

Three or more pump tests were conducted at each standpipe location and the mean inflow rate for each sample site was calculated. The inflow rate (ml s^{-1}) was calculated from the measured volume and time and then used to interpolate the sample permeability (cm hr^{-1}) from the calibration curve given by Barnard & McBain, (1994).

Because permeability is a function of temperature, all the values were standardized to a temperature of 10 °C, using water viscosity correction factor (Barnard & McBain, 1994).

At each standpipe measuring occasion, physico-chemical characteristics of interstitial water sample (IWS) were measured simultaneously. Dissolved oxygen concentration (DO, mg l⁻¹), temperature (temp, °C), electric conductivity (CND, μS cm⁻¹) and pH were measured in the standpipe by lowering the electronic probes of oximeter (WTW Oxi 330i), conductivity meter (WTW Cond 330i) and pH meter (WTW pH 315i).

After permeability and interstitial water hydrochemistry measurements were determined, vertical hydraulic gradient (VHG) for the same site was evaluated as:

$$VHG = h_1 - h_2 / L;$$

where h_1 – water pressure head inside the standpipe, h_2 – stream water head, L – the depth from streambed surface to uppermost perforations of the pipe inside the gravel (Baxter et al., 1993). VHG is a dimensionless index, with negative values indicating the downwelling of surface water into the streambed, and positive values indicating upwelling sites where hyporheic water outflows to the bed surface (Baxter et al., 2003).

The origin of interstitial water (surface or groundwater) was determined according to differences between surface and standpipe interstitial water (IWS) physico-chemical parameters. Significant deviation from the surface water DO, CND and temperature values indicated the presence of groundwater. Therefore, ΔCND and $\Delta temp$, as $CND_{interstitial} - CND_{surface}$ and $temp_{interstitial} - temp_{surface}$, were calculated and used in analysis. Measurements of dissolved oxygen taken inside and outside the standpipe were used to calculate the ‘relative DO saturation’ (RDOS, %) of interstitial water to surface water:

$$RDOS = DO_{interstitial} * 100 / DO_{surface}$$

4.1.3. Analysis of redd substrate samples

Redd substrate was sampled after the undergravel life stage of salmonids and emergence have been completed, to represent cumulative conditions of egg incubation. Redd substrate samples were taken with McNeil bulk-core sampler (McNeil & Anhell, 1964) (Fig. 5) from a depth of 18 ± 2 cm, which well represents an average burial depth for sea trout eggs (deVries, 1997). The maximum depth of sampler insertion into streambed was 20-22 cm, while minimum depth of sample limited by coarse cobble or stone laying below the upper redd substrate layer was 10 cm. Depending on the size of the redd two to three samples were taken and pooled together as one redd sample, weighing on average 13 kg of dry weight. After air drying, the whole sample was mechanically sieved through the series of standard square-meshed sieves: 64, 32, 16, 8, 5, 2, 1, 0.5, 0.25, 0.125 and 0.063 mm. Sieving was accomplished with automatic sieve shaker (AS 300 Control, Retsch), a piece of sample sieved for 15 min. The weight of sediments retained on each particular sieve was measured after sieving. Weight of each size fraction was expressed in percentage parts and cumulative particle size distribution was calculated. The quartiles (25th, 50th, 75th) of particle diameter were calculated from cumulative distribution and used for calculations of standard substrate quality indices (Bunte & Abt, 2001).

Median substrate particle diameter D_{50} , as a 50th percentile of cumulative particle size distribution and mean geometric diameter d_g , which describe central measure of substrate particles distribution, were calculated (Chapman 1988, Kondolf & Wolman 1993, Bunte & Abt 2001). The d_g was calculated according to Lotspeich and Everest (1981) as:

$$d_g = (d_1^{w_1} * d_2^{w_2} * \dots * d_n^{w_n});$$

where d_g – geometric mean particle size; d – midpoint diameter of particles retained by a given sieve and w – decimal fraction by weight of particles retained by a given sieve.

Other standard spawning substrate quality descriptors were determined: particles sorting coefficient S_o , showing size distribution of sediment particles in a sample (Lotspeich & Everest 1981, Chapman, 1988) and calculated as:

$$S_o = (D_{75}/D_{25})^{0.5};$$

Perfectly sorted substrate (with only one grain size) will have an S_o of 1. Sorting coefficient greater than 1 implies that pores between large grains are filled with smaller grains that impede permeability; hence S_o is inversely proportional to permeability (Lotspeich & Everest 1981). These authors proposed to use the Fredle index F_i describing quality of redd substrate for salmonid reproduction, which use two above presented parameters. F_i is a measure of both pore size and relative permeability, both of which increase as the index number becomes larger (Lotspeich & Everest 1981):

$$F_i = d_g/S_o;$$

Content (%) of fine sediments less than 2 mm in diameter (<2 mm fines) and silt (<0.063 mm) in a sample were used in the analysis, as variables critically affecting salmonid egg survival (Chapman, 1988; O'Connor & Endrew, 1998; Lapointe et al., 2004).

Redd substrate sedimentation experiment was done in sandy bottom dominated BG study section in 2007/2008. The design of sedimentation traps was based on Heywood & Walling (2007). Sedimentation trap with sieved well sorted gravel (with particles >16 mm) was inserted in the periphery of 5 redds. The depth of the sedimentation trap was 20 cm, the top was flush with the redd surface. Traps were installed in December 2007 (in the beginning of 'eyed' egg period) and left for subsequent incubation period till the spring. Infiltrated fine material was sieved and expressed as sedimentation extent kg m^{-2} and kg dm^{-3} during the tested period. However, 2 traps were lost soon after installation (they were pull out and thrown away), and only three sedimentation traps were analyzed.

4.2. *In situ* experiments on survival of sea trout eggs

To determine how characteristics of spawning sites affect egg incubation efficiency, *in situ* incubation experiments were conducted in natural redds of sea trout (Fig. 3). The ‘eyed’ eggs were incubated in experimental incubation boxes and the survival rate from ‘eyed’ egg to fry (emergence) (EETF) was estimated.

Sea trout eggs of ‘eyed’ stage for experiments were obtained from the hatcheries of former Lithuanian State Pisciculture and Fishery Research Center (LVŽŽTC): Rusnė fish hatchery in January 2008; and Žeimena salmonid fish hatchery in January 2009. The eggs were obtained from wild fishes, collected in Jūra River (Nemunas Basin) at Tauragė Town. Fertilized eggs were kept in the hatcheries till the ‘eyed’ stage was reached.

4.2.1. Design of experimental equipment

The design of experimental boxes was slightly modified from the model of Rubin (1995); and two types of boxes were constructed: incubation (IB) and emergence boxes (EB) (Fig. 6a). The cylindrical incubation boxes (diameter: 8 cm; height: 10 cm; volume: 500 cm³) were made of a PVC mesh (mesh size 2x2 mm). PVC hoops were tightened with clamps on the top and bottom parts of the box and supported its structure. The box was sealed with flexible mesh (1 mm) in the bottom. The top sealing was fastened in the field after eggs were placed in the box. On the upper clamp long string was connected to mark box position. The whole box surface area was screened, what allowed free pass of interstitial water and sediment accumulation. The emergence boxes EB were similar to the incubation boxes but had a special nozzle, shifting from 8 to 5 cm diameter tube, on the anterior end (Fig. 6a). Four windows were opened on the funneling sides of the additional tube, which were screened with 1 mm sized mesh. The height of emergence box increased to 17 cm. For trapping emergent fry, emergence trap-boxes (TB) (diameter: 8 cm; height: 6 cm) (Fig. 6b) were constructed to fit tightly to anterior end of emergence box.

Trap-box has perforated lateral wall and the top was sealed with flexible, 1 mm sized mesh. The trap-box inside, at the entry, has transparent funnel to prevent backward movements of fry into gravel. After passing through this funnel, the fry arrived in the trap-box's upper chamber. TB was connected to EB when suppositional time of experimental eggs was approaching.

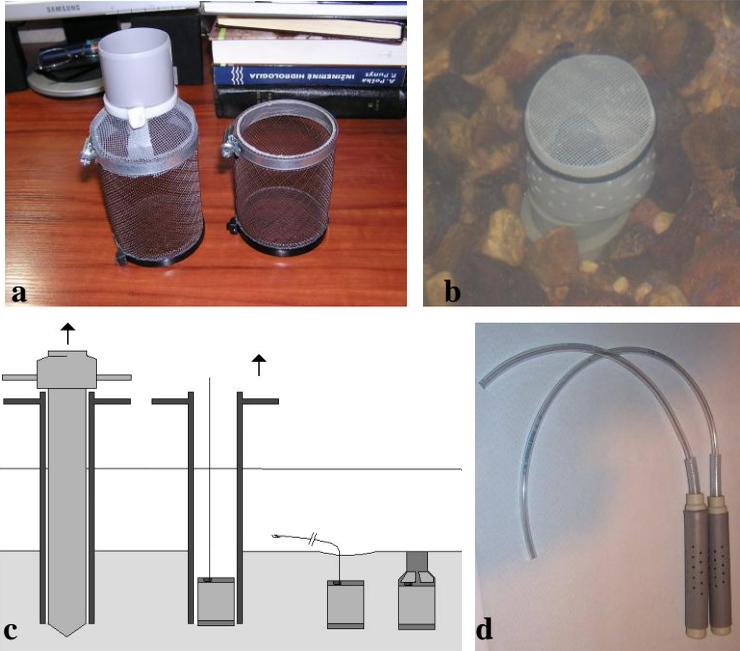


Fig. 6. a) Experimental egg incubation boxes: EB (on the left) and IB (on the right); b) emergence trap-box TB in use, connected to the upper tube of EB; c) insertion of experimental boxes into streambed by the injector, constructed according to (Scrivener, 1988 and Rubin, 1995). Depth position of IB and EB boxes are shown on right side of the figure. d) Interstitial water samplers.

A special injector based on the model proposed by Scrivener (1988) was constructed to insert the experimental boxes into the streambed. It was composed of a metal pipe (10 cm inner diameter) inside which a solid metal tube could be placed. The gravel boxes

were planted in the streambed by driving the injector into the substratum, removing the interior injector tube, placing a box in the pipe and removing the pipe (Fig. 6c). Thereby, alterations to the substratum characteristics (mainly to the percentage of fine sediment) around the boxes were minimal (Rubin, 1995).

4.2.2. Experimental set-up

Egg incubation experiments were arranged for EETH ('eyed' egg to hatching) and EETF ('eyed' egg to fry (emergence)) survival evaluation. In both 2008 and 2009 January 23 natural sea trout redds were equipped with 2 different experimental egg incubation boxes: IB and EB. The boxes were installed in front of redd tailspill at its periphery, to place experimental eggs to conditions as close as possible to natural ones, but the same time to avoid significant damage to the natural egg pockets in the redd. Interstitial water samplers were inserted in front of each box at the depth corresponding to the depth of boxes; and occasional IW samples were taken in 2009. Boxes were filled with the gravel from particular redd, to represent specific local conditions. Gravel of 2-32 mm size was used. Layer of gravel was added and layer of eggs was sunk into box, where they distributed between crevices of gravel. 100 eggs per box were filled (at density of 20 eggs 100 cm⁻³). Filled with gravel and eggs boxes were kept in bucket with stream water, till the boxes were inserted into redd.

Emergence TB was connected to EB in the March, before expected onset of emergence. Experimental boxes were retrieved in April-May, after emergence had finished. Before extraction of the boxes, gravel permeability, VHG and interstitial water parameters were measured. The boxes were retrieved when McNeil sampler was placed onto box positions, upper layer of gravel sample were removed and when box was partly dug out, it was lifted quickly and carefully from the water. The gravel sample was taken from the depth of 18 cm. Content of the box was evaluated directly in the field and the eggs and fry were separated into following categories: dead eggs, dead alevins, dead fry and live fry.

4.3. Study of fry emergence from natural redds

Brown trout fry emergence timing and patterns (frequency distribution and morphological features of emergent fry) from the natural redds were determined in 2008 and 2009 by trapping emerging fry from natural redds capped with individual fry traps. Fry traps, described by Porter (1973) and Dumas & Marty (2006) with some modifications (Fig. 7), have been used for this purpose.

In both study years 14 lens-shaped traps of various size (from 0.8 to 2.5 m²) were used, covering the whole redd surface area, except four traps (see below). The mesh size of the net of the trap was 2-3 mm, while the fry collection pocket has mesh size of 1-2 mm. The traps were maintained by a wide metal wire frame, tightly anchored to the bottom by metal stakes and bordered by a 20 cm wide skirt buried in the peripheral substratum to prevent lateral fry escapement under the gravel (Garcia de Leaniz et al., 1993). At the downstream end trap has long arm to the emergent fry collecting pocket. Entry to the pocket has transparent funnel, which prevented backward movements of fry. Several coarse gravel particles were placed into fry collection pocket to create simple shelter for fry. Caught fry were emptied through the pocket's end, which has drawstring, enabling easy and fast inspection of the trap.

Caught fry were counted and released adjacent to the native redd, while some (depending on the daily catch: from 1 to 10 random individuals) were taken to the laboratory for morphological analysis. Fry were killed overdosing anesthetic MS222 and batch sample of fry were put into vial containing preservation solution of formalin (100 ml), acetic acid (50 ml), distilled water (850 ml) and NaCl (10 g) and freeze (-20°C) for later laboratory analysis (Syrjänen et al., 2008).

Redds were capped about two weeks before expected onset of emergence (March 29-31 in 2008 and April 10-15 in 2009) and inspected daily till no new fry appeared for about a week.

The expected onset of emergence was determined according to the sum of accumulated degree-days during the incubation period (Crisp, 1988), and was considered to be at 500-550 degree-days in this

study. Water temperature was not observed routinely for this period, and only approximate accumulation of degree-days was calculated based on the occasional stream water temperature measurements. The traps were installed at about 400 degree-days in both years.

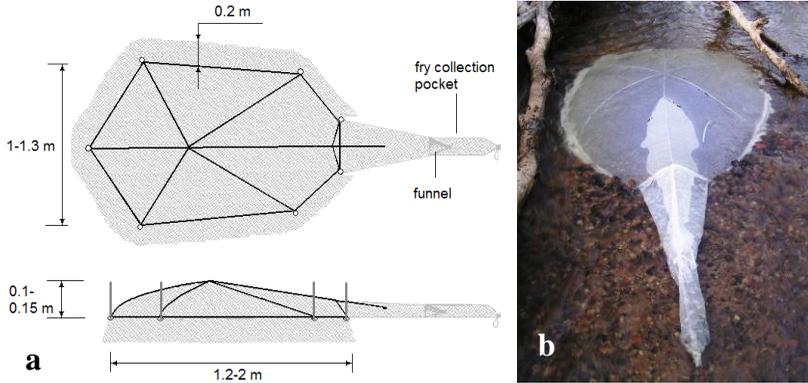


Fig. 7. a) The layout of presently used fry emergence trap; b) the trap in use. The flexible tube of interstitial water sampler is seen outside the trap net.

The general emergence period was estimated according to the pooled catches from all redds, while data from redds with total catch of more than 20 fry individuals were used for timing and distribution patterns statistical analysis. Cumulative emergence distribution was used for calculation of several principal emergence stages: start, 5%, median, 95% and the end. The cumulative emergence dates were determined for general emergence (pooled data) and for individual redds. For statistical analysis Julian dates (day of the year) were used.

Since several traps (BR/E08-1, BR/E08-9, BS/E08-1 and BR/E09-1) covered redd only partly (60-80% of the total redd area), the caught fry number was corrected for uncovered redd area and disturbed area by trap skirt insertion. The corrected fry number redd⁻¹ was as follows: from 403 to 672 fry for BR/E08-1; 191 to 382 fry for BR/E08-9; 679 to 800 for BS/E08-1 and 170 to 227 for BR/E09-1. Other trap catches were considered as total fry number emerged from particular redd.

Emergence timing and patterns were related to the environmental parameters. Before traps were installed, one or two (depending on the redd size) interstitial water samplers were inserted into redd at its periphery at the depth of about 7-12 cm; and interstitial water parameters were tracked during the emergence study period. Samplers were made of 32 mm inner diameter PVC tube, perforated with a number of 3.2 mm diameter holes. Perforated area occupied 5 cm sampler's width, so the interstitial water was collected approximately from the 5 cm substrate layer. The upper end extended to transparent flexible tube, through which water samples were drawn. Samplers were inserted vertically into substrate with an installer of a similar construction to the egg incubation box injector, though of smaller size (1.2 m length and of 40 mm inner diameter). Interstitial water samples (IWS) were drawn with a 100 ml syringe connected to the sampling tube. Several test suction were made to remove surface water and sediments. Physicochemical water parameters were measured immediately in the opened syringe with electronic probes.

Flexible tube was left outside the trap net and water samples periodically were taken. Dissolved oxygen, temperature, electric conductivity and pH of water samples were measured in the field. At the end of emergence period in 2009, additional water samples were taken to the laboratory to determine concentrations of $\text{NO}_2\text{-N}$, $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ (mg l^{-1}). Water temperature measurements were made daily and maximum reached temperature (with min-max thermometers) were recorded in four sites (marked as black pointers in the map, Fig. 3). In the results water temperature is given as an average value from all 4 sites. After traps were removed, redd substrate permeability, VHG and interstitial water parameters were measured and substrate samples were taken.

Several trap disturbance incidents happened during the study years, while they were back installed and operated further with, losing of one day's data. As this had happened before fry emergence started or in the end of emergence period when relatively few fry emerged, the lost catches were considered as being not significant for data series.

4.3.1. Morphological analysis of emergent fry

Before analysis fry samples were carefully defrost in cool water, individually held in deionized water for 10-15 min and after blotting with paper towel morphological measurements were made. Total body length (L_T , mm) and wet weight (WW_T , mg) were measured. Each individual was dissected, remaining yolk-sac were separated, wet weighted and expressed as the relative amount to the total wet weight ($WW_{Y\%}$, %). The relation between wet weight and length, known as a Fulton's condition factor K was calculated:

$$K = WW_T * 100 / L_T^3$$

Nourishment status was determined individually indicating presence or absence of food items in digestive system (stomach or gut). The dry weight of body (DW_B , mg) and yolk sac remains ($DW_{Y\%}$, %) were determined after drying at 60 °C for 48 hours. All weighing were done with 0.1 mg accuracy and length measurements were made with electronic calipers to the nearest 0.01 mm.

It is known that preserving larval fish in solutions, containing formalin, results in their shrinkage and weight increase or reduction (Karjalainen, 1992; Ando & Miyakoshi, 2004). Thirty test individuals of sea trout fry from *in situ* incubation boxes were taken to the laboratory and L_T and WW_T were measured of fresh animals. Test individuals were placed into marked vials containing preserving solution, as used in the field, and after several hours incubation at room temperature, samples were placed in the freezer (-20°C). Additional full morphological analysis of preserved test fry was made together with other fry samples. Correction factors for L_T and WW_T were calculated and values for preserved fry samples were corrected to those of fresh fry.

4.3.2. Analysis of muscle RNA:DNA ratio in emergent fry

In the present study RNA:DNA ratios were determined for newly emergent trout fry as their conditional status at the emergence.

There was tested the hypothesis, that most fry from a given redd emerge at optimal time, when fry still have remains of yolk sac and feed from internal resources. When emergence comes to an end, yolk sac is fully exhausted and late emergers are exposed to starving until they emerge and start exogenous feeding. The main objective was to compare RNA:DNA ratios of two emergence groups: mainstream emergers (up to 95% of cumulative emergence) and the last emergers (>95 %).

Newly emerged fry of *S. trutta* were collected in spring 2009 from 8 natural redds. Sample of up to 7 individuals were taken for analysis from particular redd at the peak emergence, at late emergence (80-95% emerged) and some very last emergers (>95% emerged) also were collected. To preserve from RNA degradation in the field, individual fry was placed into marked 2 ml sterile, RNase and DNase Free and non-pyrogenic cryogenic tube, which immediately was placed into the liquid nitrogen (-160 °C). From liquid nitrogen sample tubes were transferred and stored in a deep freezer (-80 °C) for 6.5 months. RNA:DNA analysis was conducted in the laboratory of Department of System Ecology, Stockholm University, where samples were transported on dry ice (-78 °C).

Nucleic acids were quantified fluorometrically using methods described in Gorokhova (2005) and Höök et al. (2008). One-dye method was applied to quantify both RNA and DNA in the same sample replicate, staining with non-specific nucleic acid dye RiboGreen, followed by RNase digestion. RiboGreen binds to both nucleic acids and first fluorescence reading (F1) was assigned to both RNA and DNA. After RNase treatment, second fluorescence reading (F2) was assigned to DNA; and the RNA was calculated as a difference between initial and remaining sample fluorescence (F1-F2). From this difference, RNA concentrations in the samples were calculated based on the standard curve against known RNA concentrations. Respectively, DNA concentrations in the sample were calculated from F2 fluorescence readings, based on the DNA standard curve.

Working reagents included: nucleic acid dye RiboGreen (Molecular Probes); RNA standards (16S and 23S from *Escherichia coli*); DNA standards (calf thymus, Sigma); DNase-free RNase working solution (Q-biogene); N-lauroysarcosine (Sigma); TE buffer (Q-biogene). Four concentrations of RNA and DNA standards each (RNA concentrations of 0.01-1.31 $\mu\text{g ml}^{-1}$ and DNA concentrations of 0.016-0.511 $\mu\text{g ml}^{-1}$) were used to build standard curves. Negative controls were also prepared and analyzed with all samples. The fluorescence was quantified using a FLUOstar Optima microplate reader (BMG Labtechnologies, filters: 485 nm for excitation and 520 nm for emission) and black solid flat-bottom microplates (Greiner Bio-One GmbH).

Both RNA and DNA concentration were quantified for individual trout fry, dissecting a small piece of dorsal muscle immediately after fish was taken from -80 °C freezer. Subsampled muscle from individual trout fry were immediately placed in Eppendorf tube containing 1 ml extraction buffer (1% sarcosyl in TE buffer). Piece of muscle were homogenized by twisting moves using RNase-free Kontec pestles. Samples were subjected to a repeated (x3) sequence of ultrasound (30 s) and ice bath (1 min). Subsequently, samples were allowed to shake for 1.5 h at room temperature. 5 μl well⁻¹ of sample extract and negative controls were diluted with 65 μg TE buffer. Three replicates of each individual fry sample were analyzed. To each well (samples, NA standards, blanks and controls) 70 μl of RiboGreen dye was added and after 5 min of incubation at room temperature, plates were scanned with 0.2 s well measurement time and 10 measurements per well. All measurements were done at constant 37 °C temperature. Second fluorescence reading of all wells was conducted after digestion with RNase (5 μl well⁻¹; incubation at 37 °C for 45 min).

Mean standard curve slope ratio (mDNA/mRNA), determined according to Caldarone et al. (2006), was 1.11, and was considered as reference, to which all standard curves of measuring occasions were standardized, by calculating standardization factor SF (Caldarone et al., 2006).

4.4. Evaluation of dispersal of juveniles after emergence

The distribution and density of *S. trutta* parr (0+) one month after the end of emergence period was observed. In 2009 June 22-23 electric fishing was pursued and juveniles of age 0+ were caught in four 200-700 m length sections (Fig. 3). The fishing was carried out with backpack electric fishing gear (IG200/2B, Hans-Grassl GmbH) with pulse current (50-80 Hz; 400-500 V; 20 A). Single upstream fishing run per section was conducted and only 0+ age fishes were taken.

The study reach was divided into 10-20 m length subsections and the number of fishes was estimated within these subsections. The positions of redds and boundaries of subsections were recorded with GPS device and the distances between the redd and the parr dispersal were calculated from the map. The dispersal distance from the closest redds is given in 20 m intervals scale.

Fish density in the study section was calculated according to Zippin (1956), using catchability coefficient of 1.4. The total and standard length (L_T and L_S , cm) and the mean weight (g) of juveniles were measured.

4.5. Characterization of sea trout redd superimposition by spawning lampreys

It was noticed in previous years that in rivers of western Lithuania, spring-spawning river lamprey *Lampetra fluviatilis* L. and brook lamprey *L. planeri* (Bloch) use the same spawning habitats as sea trout in the autumn. In spring 2008 and 2009 the study was conducted in BK and BR sections to test potential of the river lamprey and brook lamprey to superimpose the redds of salmonids under sympatric conditions. Spawning sites of lampreys were characterized simultaneously with *S. trutta* redds to test, how the redd site features correspond to the requirements of lamprey spawners for nesting sites. Concomitantly with trout fry emergence evaluation, the timing of the spawning of both lamprey species was evaluated, to test the

hypothesis, that these reproductive processes overlap, suggesting a potential effect of redd superimposition on pre-emergent or emerging salmonid fry.

The exact position of any particular salmonids redd, marked in previous autumn-winter (GPS and bank markers), was known during lamprey spawning in the following spring. The exact nesting position on the redd and approximate superimposed area (%) of redd tailspill was recorded. The superimposition rate was evaluated as percentage of superimposed redds by any *Lampetra* species.

All nest and microhabitat related measurements were conducted simultaneously for the three species in the spring 2008, during the course or shortly after lampreys spawning. Lamprey nest locations were identified as patches of clean gravel with specific lamprey nest structures. Distinguishing between the nests of *L. fluviatilis* and *L. planeri* was based either on the presence of spawners in the nest or/and on the size and structure of the nest (Fig. 8).

The total nest length and width (along and perpendicular to the flow) were measured and the nest area calculated. The diameter and depth of individual lamprey nest pits were measured to characterize their scouring abilities. The depth of a particular pit was measured as a difference between the water depth at the deepest point of the pit and over an adjacent undisturbed area.

The spawning site selection at the reach-scale was evaluated similarly as for *S. trutta* (see section 4.1.1). At the microhabitat scale, spawning site characteristics of depth, flow velocity, sediment size and streambed slope were measured. The water depth was measured as close as possible to the *Lampetra* spp. nest edge over undisturbed substratum, representing pre-spawning conditions, at several sites and given as an average. Water depth over *S. trutta* redd was measured at several sites in the tailspill front (TSF) of the redd (Fig. 35). Flow velocity was measured at the same sites with a Flow Probe FP101 flow velocity meter (Global Water Instrumentation Inc., U.S.A.) at about 60 % of water depth and is presented as an average. Using depth and velocity data, the Froude number was calculated as $v/(dg)^{0.5}$, where v represents flow 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 hydraulic conditions, which are characterized by Fr number around 0.3 (Moir *et al.*, 2002). The microhabitat slope (%) along a 2–4 m segment beside the nest was measured and calculated as the difference in streambed relative elevation between the downstream and upstream points of the measured segment, divided by the length of the segment. The difference in relative streambed elevation was measured as a difference in water depth within the segment if the water surface hydraulic gradient was negligible; otherwise, if the hydraulic gradient was noticeable, measurements of the streambed relative height difference were done with a laser level and measuring rod. The slope (%) of redd tailspill was measured from the deepest point in the pit to the tailspill crest of the redd. For some river lamprey nests the VHG was measured.

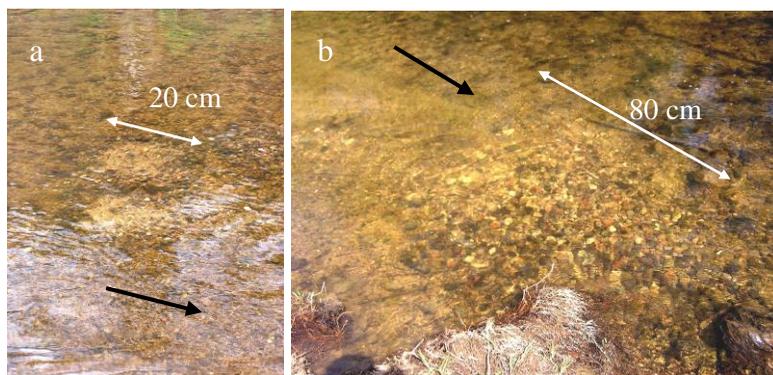


Fig. 8. View of a typical spawning nest structures of: a) brook lamprey which usually consists of shallow and small (≤ 30 cm in diameter) depression in the streambed; and b) river lamprey nest with a flat disturbed gravel area composed of one or several pits (usually > 30 cm in diameter) and relatively big tailspill of sorted gravel downstream, resembling salmonid redd structure. Nest length measurement and flow direction (black arrows) are shown.

Spawning timing of lampreys was evaluated by inspecting spawning study sections for a new or an extended nest every two-three days from the banks or by wading. The spawning period was considered starting with the appearance of the first digging marks on suitable spawning grounds. The peak of spawning was defined as the time when most new nests appeared and the nests' area was mostly expanded (c. 60–80%), while the end of spawning was considered as the date from which no *Lampetra* spawners were seen on the nests and no further nest progression was observed.

The final nest density, nest dimensions and extent of salmonid redd superimposition was corrected according to the last inspection of study sections made after the spawning of lampreys had finished.

4.6. Statistical data analysis

The characteristics of spawning habitats, substrate structure and interstitial water were compared principally between four studied sections and four different CGU types (pool-riffle transition, riffle, run, and combined pool and glide type units). Pool and glide units are morphologically similar, and as there were few redds in each of these units, they were combined in the analysis. Pool and glide units were treated separately only in reach-scale spawning site selection analysis.

To test the relationship between redd hydraulic parameters (permeability and VHG) and IWS parameters, all data sets (every single measurement site of the redd) were used; while to compare these characteristics between different study years, study sections and CGU types, average estimate of the redd was used.

Fry emergence distribution for individual redds was determined from the daily catches, only in redds with total catch more than 20 fry individuals. For emergence distribution asymmetry and peakedness description, standardized skewness and kurtosis measures were calculated. The average morphological and conditional descriptors of emergent fry were compared between five designated cumulative emergence stages: <5%, 5–25%, 25–75%, 75–95% and >95%.

The data before the analysis were tested for normality (Kolmogorov-Smirnov test) and homogeneity of the variances (Levene and Cochran's C tests). If needed, logarithmic or square root transformations were applied to meet the parametric test assumptions. For some data no suitable transformation was found to remove the violations of parametric test assumptions and non-parametric test was used.

Standard statistical methods were used in the study (one-way and two-way ANOVA, non-parametric Kruskal-Wallis ANOVA, two-tailed t-test and nonparametric Mann-Whitney U test, Pearson correlation analysis, linear regression and multiple regression analysis). Multiple regression analysis followed by stepwise backward selection procedure was applied separately for ETF survival in 2008 and 2009 to determine significant factors for egg survival.

Multivariate principal component analysis (PCA) and redundancy analysis (RDA) were used in the study. PCA was applied to redd's hydraulic and interstitial water physicochemical characteristics data; and to the data of emergent fry morphological and conditional parameters. RDA technique was used to relate various emergence characteristics (emergence distribution, timing and emergent fry morphological characteristics) to the environmental variables of the redd. Data from 2008 and 2009 were pooled, year and section were added to the analysis as the nominal variables.

The mean value with the standard deviation (\pm SD) is used to represent the estimated parameters and their variability. The significance level for all tests was $P < 0.05$. The power of the test was considered in interpretation of insignificant results. The desired power of the test was 0.8 at alpha 0.05. Less than desired power indicates less likelihood to detect a difference when one actually exists; the negative results should be interpreted cautiously.

The statistical analyses were performed using Statgraphics Plus for Windows (Statistical Graphics Corp.), SigmaPlot for Windows 11.0 (Systat) and Brodgar (Highland Statistics Ltd.) softwares.

5. RESULTS

5.1. *Salmo trutta* spawning site selection and characteristics

5.1.1. Stream-scale distribution of spawning sites

According to the results of redd counts in 2007/2008 and 2008/2009 spawning seasons (further 2008 and 2009), the highest number of sea trout spawning redds was recorded in the upper Blendžiava Stream part, particularly in BR section (Fig. 9). Similar patterns of spawning redds spatial distribution was observed in both years. In 2009, additionally, redd count was conducted further upstream from the BR section, where redd density was estimated to be 5–6.5 redd km⁻¹, therefore the BR section likely supports the highest spawning potential of salmonids in the stream.

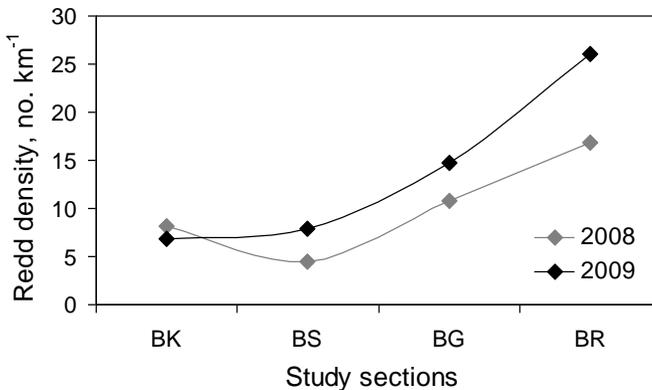


Fig. 9. Sea trout redd density in different study sections in 2008 and 2009.

The spatial distribution of available potential reproductive areas (sections with suitable hydrologic conditions and spawning

grounds) was somewhat different from the distribution of used spawning sites. The highest amount of potential spawning areas was observed in the downstream BK section (~30% of the investigated section length; particularly 2 km upstream from the mouth); and the least in BS (5–8%) and BG (< 5%) sections. Roughly 10–15% of the BR section has conditions suitable for salmonids spawning.

5.1.2. Reach-scale spawning site selection and characteristics of spawning habitats

Reach-scale spawning site selection here is considered as an association of spawning redds with particular stream channel geomorphic unit (CGU). Investigated spawning redds of sea trout were mainly distributed in the riffle and run type channel units (pooled relative number for both years: 88%), with mostly preferred transitional pool-riffle zones (57% in 2008 and 44% in 2009) (Fig. 10). Such zones, characterized by decreasing depth that accelerates flow and creates substantial negative streambed slope to the downstream direction, were the least common channel unit type along the surveyed stream sections.

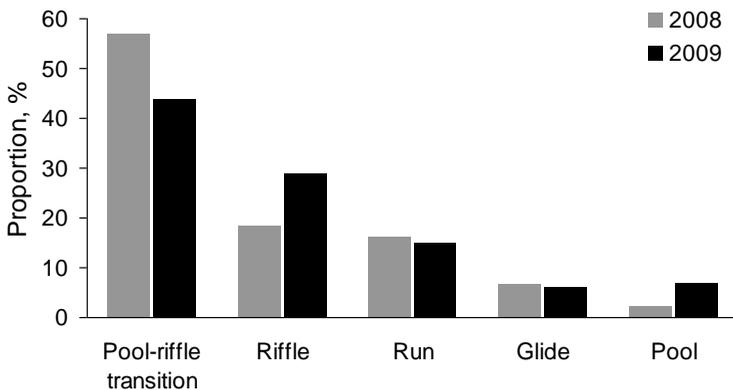


Fig. 10. Distribution of spawning redds in different stream channel geomorphic units in Blendžiava Stream in 2008 ($n=41$) and 2009 ($n=87$).

The dominant channel types in Blendžiava Stream were the plane-bed runs and glides and the pool type channels; while sea trout females showed clear avoidance of glide and pool type CGU's (Fig. 10) (6% of redds in glide channels and 5% in pool channels according to pooled data of both years).

Wetted width of the channel at the redd-sites was 5–10 m. The general structure of the streambed in used spawning habitats in 2009 (n=87) was composed from: 5.4±7.6% (range 0–40%) of boulder; 18.3±20.7% (range 0–75%) of cobble; 48.4±23.1% (10–95%) of gravel; 24.8±20.1% (0–75%) of sand and 3.0±3.7% (0–10%) of silt.

Table 3. The average (\pm SD) amounts (%) of different streambed sediment fractions of the spawning habitats in different channel geomorphic units (glide and pool CGU's are pooled) in 2009. The non-matching letters indicate significantly different groups after comparison of $\log(x+1)$ transformed data with Tukey's HSD test ($P < 0.05$)

Sediment fractions	Pool-riffle transition	Riffle	Run	Glide-pool
n	38	25	13	11
Boulder	4.8±5.8 ^a	5.5±8.3 ^a	2.0±2.8 ^a	7.1±7.3 ^a
Cobble	20.1±22.3 ^{ab}	22.8±21.5 ^a	4.1±4.5 ^b	15.3±18.6 ^{ab}
Gravel	48.2±23.3 ^a	55.8±25.4 ^a	51.2±20.6 ^a	37.3±20.0 ^a
Sand	23.9±18.7 ^{ab}	15.3±15.4 ^a	37.7±21.2 ^b	33.6±22.1 ^b
Silt	2.5±3.2 ^b	0.6±1.7 ^a	5.3±3.7 ^c	7.2±3.5 ^c

Statistically significant differences were observed between $\log(x+1)$ transformed amount of cobble, sand and silt in spawning habitat bed structure from different CGU types (glide and pool CGU's pooled) (one-way ANOVA; $F=4.31$ for cobble, 5.41 for sand and 14.28 for silt; d.f. = 3; $P < 0.01$); while $\log(x+1)$ transformed amount of gravel and boulder fractions didn't differed between different CGU types ($P > 0.05$). The highest portion of the streambed around the redds was covered with gravel substratum (4–64 mm) in all types of channel units (Table 3). As a rule of thumb, area of gravel required for

particular redd construction usually was $>2 \text{ m}^2$ and never less than 1 m^2 . The low amount of cobble was observed in the run units, but as in glide-pool CGU's, considerable amount of sand and significantly higher portion of silt was found than in the other units (Table 3).

Important in-stream structure of spawning habitats was the presence of cover potentially suitable for spawners to hide during the spawning course. The distance to the redd and relative longitudinal position (upstream or downstream) of potential cover were determined in 2009 for some redds ($n=74$) (Fig. 11), however their actual use by spawners is not known. 73% of all redds were associated with the presence of potential cover relatively close (up to 6 m, what is approximately the distance of one wetted width) to the redd-site. No statistically significant difference was detected comparing the distance between the potential cover and redd found in different CGU's types (Kruskal-Wallis ANOVA, $d.f.=3$, $P >0.05$), while the distance was shorter in the glide-pool channel units ($3\pm 1 \text{ m}$), than in other CGU types ($5\pm 3 \text{ m}$ in pool-riffle transition; $6\pm 3 \text{ m}$ in riffle; and $5\pm 2 \text{ m}$ in run).

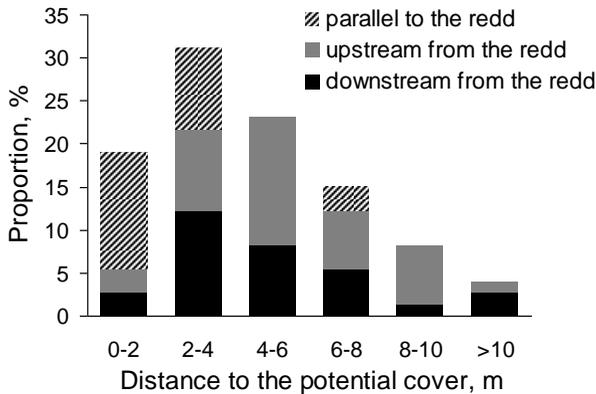


Fig. 11. The distribution of the distance and longitudinal position of potential cover for spawners, associated with the sea trout spawning sites, assessed in 2009 ($n=74$).

The potential cover was mostly the pieces of large woody debris or its aggregations (46%). Other cover types were deep channel pools (28%) and undercut banks or lateral scour pools (26%), usually with additional cover of large woody debris and boulders.

Coverage of stream banks by vegetation (trees and shrubs) at the spawning sites was 20-100%, with most dominant 80-100% coverage. Stream bank features of spawning habitats were not assessed routinely as there was no clear evidence on the spawning site selection for any riparian features in earlier studies (Nika et al., 2011).

5.1.3. Characteristics of spawning redds (microhabitat scale)

Comparing the results of the two consecutive years' redd counts revealed a consistent and strictly defined micro-scale spawning site selection patterns in subsequent years. 37% of all redd-sites recorded in 2008 were reused in 2009 with striking ± 2 m accuracy.

The structure of sea trout redds in Blendžiava was typical for salmonid fishes, structured into pit upstream and conspicuous tailspill below. The topography of the redd is characterized by the negative downstream slope from the pit to the crest of tailspill (-5 to -33% within 1-2.5 m section). In spring the average slope was $-11.6 \pm 4.8\%$ in 2008 (n=41) and $-13.9 \pm 5.0\%$ in 2009 (n=59). The considerable persistence of redd topography and size was observed during the incubation period under typical hydrological regime. Repeatedly measured redd size in 2009 spring did not differ significantly from 2008 autumn-winter measurements (paired t-test on log-transformed data; d.f.=67; $P > 0.05$).

The redd tailspill was mostly elliptical or round in shape (85%), while occurrence of irregular forms was considerably lower (15%). The redds of irregular shape were significantly larger (5.0 ± 2.6 m², n=19) than redds of elliptical and round (pooled) shapes (1.9 ± 1.0 m², n=109) (Mann-Whitney *U* test, $P < 0.0001$). The overall (n=128) mean redd tailspill length was 1.8 ± 0.7 m (range 0.6-5.6 m); the width 1.6 ± 0.8 m (range 0.7-6.0 m) and the tailspill area 2.33 ± 1.77 m² (range 0.50-9.62 m²), with dominating 1-2 m² redds (Fig. 12a).

The largest redds were found in BR study section in both years (Fig. 12a and b), while there was no statistically significant difference neither between study sections, nor study years applying two-way ANOVA test on the redd size after log-transformation ($F=1.23$; $d.f.=1$; $P > 0.05$ for study year; $F=2.05$, $d.f.=2$; $P > 0.05$ for studied sections (BK and BS sections were pooled); and $F=0.05$; $d.f.=2$; $P > 0.05$ for interaction effect). The power of the performed test (power=0.22, 0.07 and 0.05 for main effects and interactions respectively) was far below the desired power of 0.80.

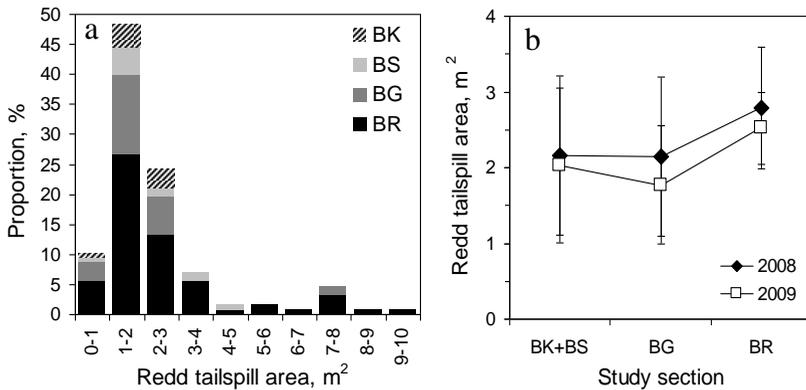


Fig. 12. The distribution of redd tailspill size in Blendžiava Stream ($n=128$) (a); and the mean ($\pm 95\%$ confidence interval) redd tailspil area in different study sections (BK and BS sections data are pooled) in the two years.

One-way ANOVA revealed no statistical difference in log-transformed redd size between different CGU types ($F=1.52$; $d.f.=3$; $P > 0.05$). However the smallest redds were observed in a pooled glide-pool channel units (1.59 ± 0.55 m², $n=15$), while in the run, riffle and transitional pool-riffle channel units the size of the redds were reasonably larger (2.76 ± 2.20 m², $n=20$; 2.40 ± 2.05 m², $n=32$; and 2.34 ± 1.62 m², $n=61$ respectively). The significant difference might be missed to detect because of low power of the test (power=0.15).

5.1.3.1. Redd substrate structure and permeability

Description of spawning substrate in different study sections is based on the data collected in spring 2008 from 37 redds (overall 51 sample) (Table 4). Some trend of redd substratum worsening from upstream (BR) to downstream (BK) could be spotted, in terms of increasing amount of <2 mm fines and, in turns, decreasing values of substrate particle diameter d_g and D_{50} , and Fredle index F_i (Table 4). However, no statistically significant differences were found for all redd substrate characteristics when comparing redds between different study sections (BR, BG, and pooled BS and BK) (one-way ANOVA, d.f.=2, $P > 0.05$ for all comparisons); and between different channel geomorphic units (excluding glide-pool unit, as from this CGU only one redd was sampled for substrate analysis) (one-way ANOVA, d.f.=2, $P > 0.05$ for all comparisons).

At the end of embryo incubation period, the central measures of particle size distribution d_g and D_{50} were conditionally low, in some redds reaching only 3.9 and 6.5 mm respectively. The mean sea trout embryo incubation conditions in terms of redd substratum Fredle index F_i was from low to moderate. The particle sorting was very poor ($S_o > 3$), indicating spaces in the matrix gravel being filled with finer sediments. The amount of fine sediment (<2 mm) was critically high, in all study sections averaging above 15 % of sample weight.

Sedimentation experiment (3 sediment traps in redds of BG section) revealed high extent of fine sediment accumulation in a redd area during the incomplete egg incubation period. Sediment traps (volume 3540 cm³) containing >16 mm gravel were completely filled with sand (median grain size being 0.29-0.41 mm) during 5 months period. Traps accumulated from 695 to 1393 g of fine sediments (<2 mm) per trap; i.e. from 19.4 to 30.4 % of the initial trap substratum weight. Sedimentation extent to the streambed of well sorted gravel during 5 months amounted in 38.6-77.4 kg m⁻² or 0.201-0.394 kg dm³.

Table 4. Mean (\pm SD) redd substrate characteristics in different study sections (BK, BS, BG and BR), determined from spring 2008 samples. Range of measured values is given in parentheses.

	BK	BS	BG	BR	Total
n	7	3	10	17	37
d_g , mm	7.8 \pm 2.2	9.4 \pm 1.6	10.2 \pm 4.0	11.0 \pm 3.9	10.0 \pm 3.6 (3.9-19.2)
D_{50} , mm	12.1 \pm 2.8	14.1 \pm 3.0	15.6 \pm 6.4	16.1 \pm 5.5	15.0 \pm 5.3 (6.5-29.5)
S_o	3.2 \pm 0.7	3.1 \pm 0.8	3.0 \pm 0.7	2.8 \pm 0.6	3.0 \pm 0.7 (1.9-4.4)
F_i	2.7 \pm 1.1	3.1 \pm 1.1	3.7 \pm 2.1	4.3 \pm 2.2	3.7 \pm 2.0 (0.9-9.0)
Content of fines, %:					
<2mm	22.8 \pm 5.9	20.0 \pm 4.9	19.9 \pm 6.7	17.6 \pm 6.6	19.4 \pm 6.4 (7.9-31.8)
<0.063mm	0.25 \pm 0.22	0.12 \pm 0.09	0.27 \pm 0.26	0.21 \pm 0.17	0.23 \pm 0.20 (0.05-0.87)

Table 5. Pearson correlations between log-transformed substrate structure characteristics (D_{50} , d_g , S_o , F_i , content of <2 mm and <0.063 mm fines), substrate permeability (Perm) and relative DO saturation of interstitial water (RDOS) ($n=51$). Statistically not significant values ($P>0.05$) are bolded.

	d_g	D_{50}	S_o	F_i	<2 mm fines	<0.063 mm fines
D_{50}	0.936					
S_o	-0.783	-0.656				
F_i	0.972	0.881	-0.908			
<2 mm fines	-0.931	-0.827	0.891	-0.966		
<0.063 mm fines	-0.655	-0.593	0.629	-0.680	0.643	
Perm	0.738	0.649	-0.726	0.773	-0.767	-0.465
RDOS	0.412	0.343	-0.366	0.416	-0.414	0.015

All log-transformed spawning substrate structure indices were highly correlated ($P < 0.001$), and the quality of redd substrate, in terms of mean geometric diameter d_g and Fredle index F_i , were strongly negatively affected by the content of < 2 mm fines (Table 5).

The intragravel egg incubation conditions directly depend on the substrate structure through its control on the hydraulic permeability. Strong correlation ($P < 0.001$) between log-transformed substratum quality indices (F_i index and content of < 2 mm fines) and permeability was determined for the redd substrate samples of 2008 (Table 5), therefore the substrate permeability could be used as a crude proxy for its structure. Substratum structure of 2009 sampled redds could be predicted from the measurements of permeability by linear relationship between log-transformed permeability and content of < 2 mm fines (Fig. 13).

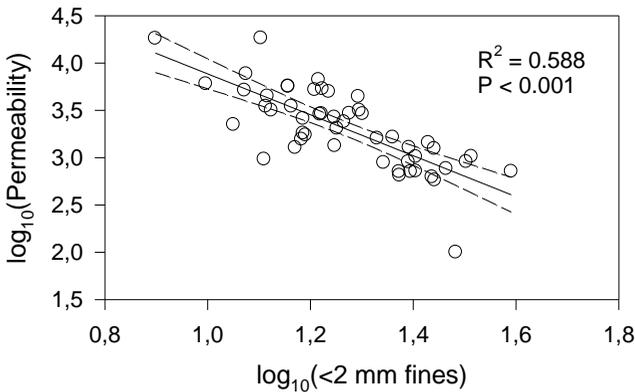


Fig. 13. The negative relationship between log-transformed permeability and content of < 2 mm fines in the redd substrate ($n=51$): $\log_{10}(\text{Permeability}) = 6,048 - (2,162 * \log_{10}(< 2 \text{ mm fines}))$.

Hydraulic permeability of substrate at the depth of 14 ± 2 cm varied from very low (100 cm hr^{-1}) to extremely permeable gravel mixture (47035 cm hr^{-1}) among redd sites. The average permeability of redds was $3143 \pm 2942 \text{ cm hr}^{-1}$ ($100\text{-}19206 \text{ cm hr}^{-1}$, $n=120$) and has

highly positively skewed distribution. Applying two-way ANOVA test on log-transformed average redd permeability, no statistically significant differences between the two years and between stream sections were found ($F=0.06$; $d.f.=1$; $P > 0.05$ for study year factor; $F=1.21$, $d.f.=2$; $P > 0.05$ for stream sections factor (BK and BS sections were pooled); and $F=0.59$; $d.f.=2$; $P > 0.05$ for factor interaction effect)). Log-transformed redd substrate permeability did not differ between four channel geomorphic units either (one-way ANOVA, $F=1.54$, $d.f.=3$, $P > 0.05$).

Highly variable permeability was found within redd tailspill area, indicating highly heterogeneous intragravel incubation environment at the very small scales. The difference in permeability between the measurements sites at the distance < 50 cm could be as high as 10-20 times.

5.1.3.2. Vertical hydraulic gradient and interstitial water characteristics within redds

Simultaneously to permeability measurements, vertical hydraulic gradient (VHG) was determined at the same redd sites. The average VHG of redds was -0.0137 ± 0.0173 (ranging from -0.0673 to 0.0254 , $n=120$) with dominant downwelling conditions (negative VHG) in 85 % of studied sea trout redds (Fig. 14a).

Average VHG of the redd did not differ neither between the study years, nor the study sections (redds from BK and BS sections were pooled in analysis) applying two-way ANOVA test ($P > 0.05$ for main effects and interaction effect of the factors), indicating no macro-scale vertical hydraulic gradient distribution patterns among sea trout redds.

Meantime, high micro-scale spatial variability of VHG magnitude and character (+ or -) was observed within individual redds. Usually the downwelling flow dominated and was stronger in the front of the redd tailspill, while in the end of the tailspill upwelling conditions might be observed.

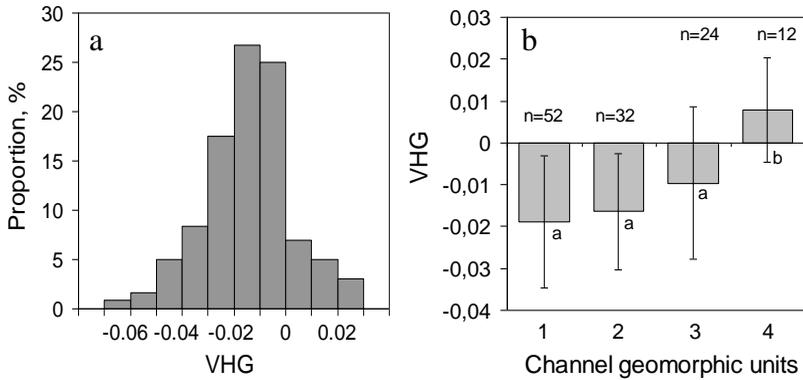


Fig. 14. Frequency distribution of redd's average vertical hydraulic gradient (VHG) ($n=120$) (a); and mean ($\pm SD$) VHG of redds in different channel geomorphic units (CGU): 1-pool-riffle transition; 2-riffle; 3-run; 4-glide and pool (pooled) (b). Different letters in (b) denote statistically significant difference at $P < 0.05$ (Tukey's HSD post hoc test).

Vertical hydraulic gradient was clearly related to the channel morphology and streambed profile. VHG of redds in various stream channel geomorphic units (CGU) differed in magnitude and character (+ or -) significantly (one-way ANOVA, $F=10.49$, $d.f.=3$, $P<0.001$; power of the test=0.998) (Fig 14b). The strongest downwelling was recorded in the preferred by sea trout pool-riffle transition areas (92% of redds with downwelling) and riffles below (94% of redds with downwelling), while in the glide-pool units upwelling conditions dominated (only 25 % of redds with downwelling).

The magnitude of water exchange within streambed in terms of VHG value was in general weak. The water pressure head difference between the streambed and the stream (h_1-h_2) at the streambed depth of 12 ± 2 cm was on average 0.13 ± 0.23 cm (from -1.4 to 1.0 cm). The measurements coincided with the low (lowest) water level in the stream (April-May in 2008 and May-August in 2009; Fig. 2), while the temporal variability of VHG is unknown.

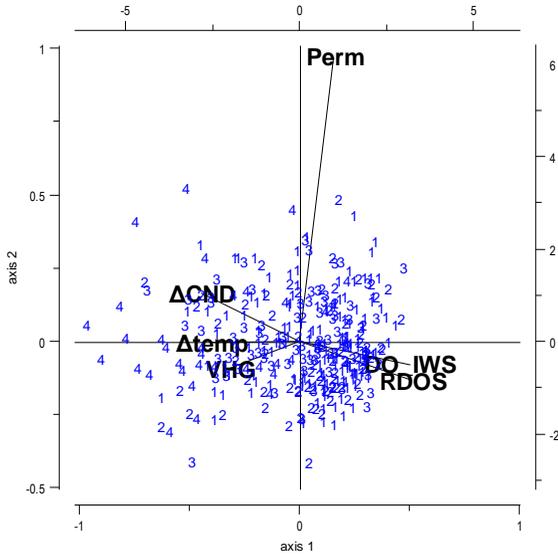


Fig. 15. PCA correlation biplot for the redd substrate hydraulic parameters: log-transformed substrate permeability (*Perm*), vertical hydraulic gradient (*VH*); and interstitial water physicochemical characteristics: dissolved oxygen concentration (*DO_IWS*), log-transformed relative to surface water dissolved oxygen saturation (*RDOS*), log($x+1$) transformed electric conductivity and temperature difference from the surface water (Δ *CND* and Δ *temp*). Number of sampling site refers to the redds in different channel geomorphic units: 1-pool-riffle transition, 2-riffle, 3-run, and 4-glide-pool.

Dissolved oxygen (DO) concentration, essential intragravel parameter for incubating salmonids, in the redd's interstitial water ranged from 0.4 to 13.8 mg l⁻¹. DO saturation in the stream water during the sampling periods of the two years was always normoxic (77-126 %), and concentrations ranged between 7.0-14.3 (10.1±1.5) mg l⁻¹, with consistent temporal decrease trend (from April to August). Despite the downwelling conditions dominated, DO concentrations in IWS weakly correlated with the surface water DO ($r=0.463$, $P < 0.001$, $n=1064$). Therefore, relative to surface water dissolved oxygen saturation (*RDOS*) was used in the analysis, to be comparable for

prolonged sampling periods of the two years. Overall variation of RDOS was 4.7-104.9% and, according to IWS DO concentrations and RDOS linear regression model ($R^2=0.73$, $P < 0.001$, $n=1061$), $>70\%$ value represents suitable oxygen regime for salmonids ($>7 \text{ mg l}^{-1}$).

Oxygen and other determined physicochemical characteristics of interstitial water samples (IWS) were related to the hyporheic water exchange patterns, as was revealed by ordination of redd substrate hydraulic and IW physicochemical characteristics using principal component analysis (Fig. 15). First two axes explained 68% of the data variability (52% and 16%). First axis approximated variation in IWS dissolved oxygen concentration (DO_{IWS}) and RDOS, differences of IWS electric conductivity and temperature to the surface water (ΔCND and Δtemp); and vertical hydraulic gradient. Highly correlated DO_{IWS} and RDOS were negatively related to the upwelling (positive VHJ) hyporheic water which was usually characterized by increased electric conductivity (ΔCND) and decreased temperature in comparison to surface water (Fig. 15; Table 6). The second PC axis approximated variation in substrate permeability, which did not correlate with any other variable used in PCA ($P > 0.05$) (Fig. 16c).

Highly significant differences were found in IWS physicochemical characteristics between downwelling and upwelling sites (Mann-Whitney U test, d.f.=317, $P < 0.001$ for all parameters) (Table 6).

Table 6. The comparison of physicochemical parameters of interstitial water samples (dissolved oxygen concentration (DO), mg l^{-1} ; relative DO saturation of interstitial to surface water (RDOS), %; intrerstitial to surface water difference in electric conductivity (ΔCND) and temperature (Δtemp)) from the downwelling and upwelling (0 and positive VHJ) sites. Data from all individual measuring occasions included ($n=318$).

VHG	DO	RDOS	ΔCND	Δtemp
Downwelling (-)	8.0±1.7	84.4±15.4	5.7±13.8	0.2 ±0.2
Upwelling (0 and +)	6.1±2.1	67.9±21.8	15.5±23.2	0.6±1.0

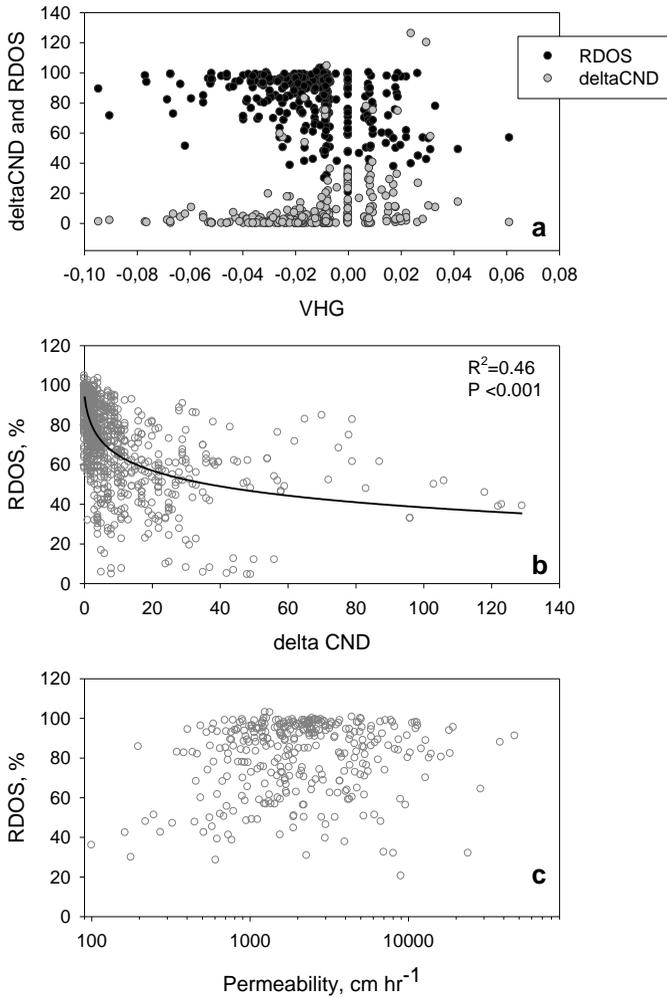


Fig. 16. Relationship between *relative dissolved oxygen saturation in interstitial water (RDOS)* and *vertical hydraulic gradient (VHG)* (a); *groundwater index ΔCND* (b); and *substrate permeability* (c).

The downwelled surface water in the redd was indicated by RDOS values close to 100 % and ΔCND close to zero, while departure from these values indicates groundwater supply (Fig. 16a). Both positive and negative ΔCND values indicated presence of groundwater in the redd, as were associated with reduced RDOS; therefore in the analysis negative ΔCND values were converted into positive ones). In the stream water CND ranged from $362 \mu\text{S cm}^{-1}$ in the first half of April to $509 \mu\text{S cm}^{-1}$ in the end of August, averaging at $451 \pm 27 \mu\text{S cm}^{-1}$.

The groundwater effect was associated with lower IWS pH in comparison to surface water. Additionally, analysis of the nitrogen $\text{NO}_3+\text{NO}_2\text{-N}$ and $\text{NH}_4\text{-N}$ in some IW samples gives indication that interstitial water supplied by hypoxic groundwater might be associated with increased ammonia and decreased nitrite-nitrate concentrations (Fig. 17).

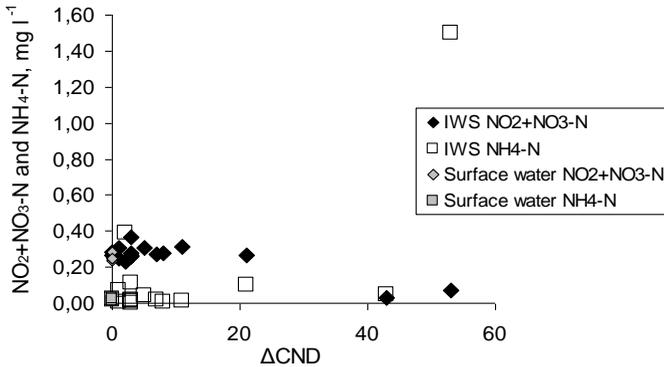


Fig. 17. Nitrite-nitrate and ammonia nitrogen concentrations in interstitial water samples (IWS) from some study redds in 2009 versus ΔCND . Nutrient concentrations in stream water were determined, as a control ($\Delta\text{CND}=0$).

Multiple linear regression analysis on RDOS as response variable versus substrate permeability, VHG and ΔCND as explanatory variables ($R^2=0.299$, $P < 0.001$, $n=318$), revealed that variation in interstitial water dissolved oxygen saturation is related to ΔCND and VHG ($P < 0.001$ for both parameters), but not to

permeability ($P > 0.05$) (Fig.16b and c). Based on 51 substrate sample, RDOS was weakly related to the substrate structure characteristics (Table 5). RDOS negatively correlated with the content (%) of < 2 mm fines in the substrate samples, but was not related to the silt (< 0.063 mm) content ($P > 0.05$).

5.2. Survival of experimental sea trout eggs in natural redds

In total 46 natural redds were examined for sea trout egg survival in 2008 and 2009 using incubation boxes (Table 2). The experimental ‘eyed’ sea trout eggs were inserted into the redds in January and experimental set-up was arranged to determine embryo survival at two developmental stages: ‘eyed’ egg-to-hatching and ‘eyed’ egg-to-fry emergence survival. However, in 2008 incubation boxes (IB) for ‘eyed’ egg-to-hatching survival estimation were failed to retrieve at the expected hatching time (last decade of February) due to low transparency and increased water level. The IB boxes were recovered later, at the end of April to first half of May, at the time of fry emergence. As most of the live alevins and fry in the boxes were concentrated in the upper layer of gravel in the box, they were considered as ready to emerge. The top of the IB boxes were at about 3-6 cm under the gravel surface, therefore the survival rate in IB boxes was considered to be very close to the actual survival to fry emergence. At the same time, determination of ‘eyed’ egg-to-fry survival in emergence boxes (EB) was biased due to unexpected early premature emergence before trap-boxes (TB) installation (the anterior end of EB were not sealed during box insertion). The expected onset of emergence from EB boxes was in the mid-April, and the trap-boxes were installed in the end of March. Additionally, several TB or its sealings were lost during the operation (removed due to lamprey superimposition, strong flow, or anglers).

Therefore the survived ‘eyed’ eggs to ready-to-emerge fry in IB boxes retrieved at the time of fry emergence, only were used in further analysis and referred as ‘eyed’ egg-to-fry (EETF-2008)

survival. Live or recently died alevins and fry were counted in the boxes, and average estimated EETF-2008 survival of experimental redds was $35.5 \pm 30.4\%$, ranging from 0 to 88% in individual redds ($n=23$).

In 2009 the ‘eyed’ egg to fry emergence survival (EETF-2009) was determined from the number of live or dead emerged fry in the trap-boxes. Mean number of fry in TB was $33.8 \pm 29.6\%$ (from 0 to 91%, $n=23$ redds).

Because of the different developmental stages of embryos at the time of insertion and retrieval of the boxes in 2008 and 2009, the evaluation approach differs and the survival results from the two years are not directly comparable.

The highest mean EETF-2008 and EETF-2009 survival was recorded in redds of BR section (Fig. 18), while statistically significant difference between the mean survival in different study sections (for 2009 analysis BK and BS sections were combined) was not detected applying one-way ANOVA for the two years separately ($F=0.82$, $d.f.=3$, $P > 0.05$ for EETF-2008 survival; and $F=0.64$, $d.f.=2$, $P > 0.05$ for EETF-2009).

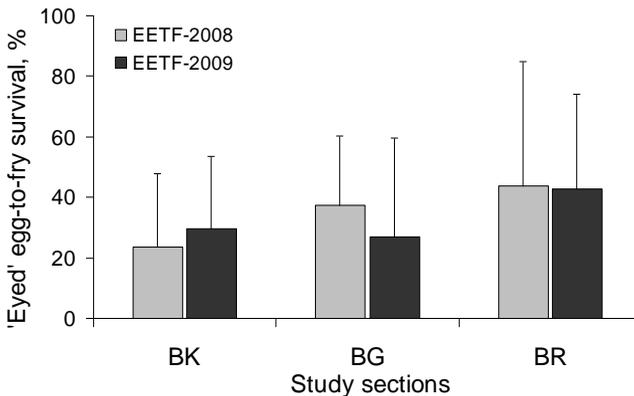


Fig. 18. Survival ($\pm SD$) of ‘eyed’ eggs to fry (EETF-2008 and EETF-2009) in different study sections. EETF-2009 survival in BK section was estimated from pooled BS ($n=3$) and BK ($n=4$) experimental redds.

The experiments were not designed to test egg survival in redds of different channel geomorphic units, therefore the sample size is very unbalanced. However, EETF-2008 and EETF-2009 was considerably lower in glide-pool type channels than in others CGU (Fig. 19).

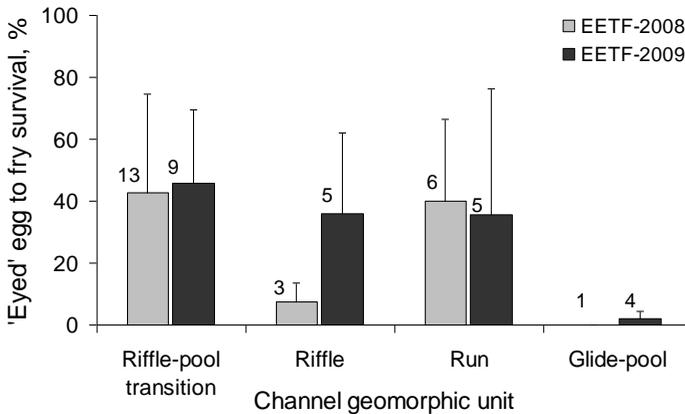


Fig. 19. Survival (\pm SD) of ‘eyed’ eggs to fry (EETF-2008 and EETF-2009) in different channel geomorphic units (CGU). Numbers above bars indicate sample size. EETF-2008 survival in glide-pool CGU was 0.

To define environmental redd parameters responsible for ‘eyed’ egg to fry survival, multiple linear regression was applied separately for EETF-2008 and $\log(x+1)$ transformed EETF-2009 survival (Table 7). Substrate permeability, content of <2 mm fines, vertical hydraulic gradient, dissolved oxygen saturation (RDOS) and groundwater presence (Δ CND) explained 60% of variance in EETF-2008 survival ($P < 0.001$). After stepwise backward selection of model’s variables, <2 mm fines was found to be the only variable significantly contributing to EETF-2008 survival ($R^2=0.50$, $P < 0.001$) (Fig. 20a). High amounts of fine sediments (<2 mm) found in 2008 redd substrate samples at the end of intragravel period negatively affected survival, however it was still significant at very high sediment amounts (Fig. 20a). Average EETF survival could be

expected to be approx. 50% at 15% of <2 mm fines content. Critical (lethal) level of sediments for EETF survival was >25%.

Table 7. Results of multiple regression analysis between ‘eyed’ egg to fry (EETF-2008 and $\log(x+1)$ transformed EETF-2009) survival and explanatory redd variables.

Explanatory variable	b	t	P	Beta
EETF-2008, $R^2=0.599$, $F=12.05$, $P<0.001$, $n=25$				
Permeability	0.001	0,863	0,399	0,173
RDOS	0.294	0,608	0,550	0,134
Δ CND	-1.335	-1,142	0,268	-0,215
VHG	382.445	1,647	0,116	0,304
Content of <2mm fines	-2.966	-2,473	0,023	-0,619
$\log((EETF-2009)+1)$, $R^2=0.728$, $F=5.67$, $P<0.05$, $n=23$				
Permeability	0.000	0.713	0.485	0.090
RDOS	0.031	5.364	<0.001	1.013
Δ CND	0.008	0.954	0.353	0.181
VHG	3.215	0.543	0.594	0.091

The multiple regression analysis of $\log((EETF-2009)+1)$ survival versus substrate permeability, vertical hydraulic gradient, RDOS and Δ CND indicated that these redd environmental characteristics explained 73% of variation in log-transformed ‘eyed’ egg to fry emergence survival ($P < 0.05$). After stepwise backward selection procedure, RDOS was the only variable in model significantly contributing to $\log((EETF-2009)+1)$ survival ($R^2=0.698$, $P < 0.001$).

Log-transformed EETF-2009 survival was not related to the substrate quality, in terms of its permeability ($P > 0.05$), which did not correlate with RDOS in 2009 experimental redds ($n=23$, $P > 0.05$). Meantime RDOS was strongly negatively correlated with the presence of groundwater (Δ CND) ($r=-0.73$, $P < 0.001$, $n=23$). In turn, Δ CND was partly responsible for decrease in $\log((EETF-2009)+1)$ survival ($r=-0.513$, $p<0.05$), when at the clear groundwater presence sites (>15 Δ CND) survival to emergence in experimental boxes were only 0-4% (Fig. 20c).

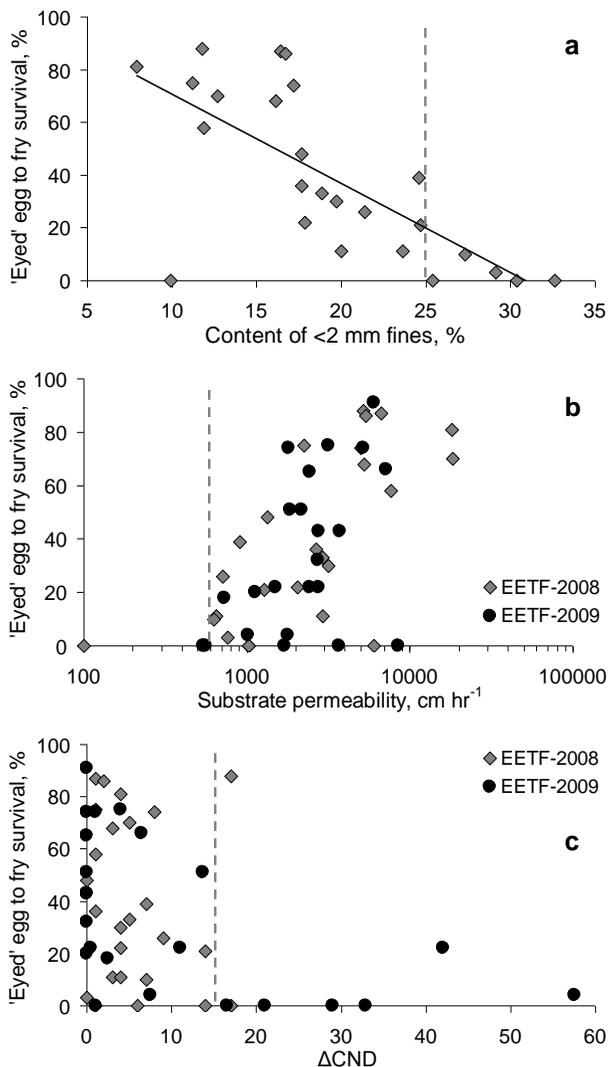


Fig. 20. 'Eyed' egg to fry survival in relation to content of <2 mm fines (data of 2008) (a); to substrate permeability (b); and ΔCND (c) in 2008 and 2009. Dashed lines indicate critical (lethal) limit of redd environmental parameters to egg survival.

5.3. Fry emergence from natural redds

Salmo trutta fry emergence from 28 natural redds in spring 2008 and 2009 was generally successful. Emergence was evident from all 14 trapped redds in 2008 and from 12 in 2009. The redds BK/E-1 and BS/E-4 were excluded from further emergence analysis due to the wrong trap installation time (too late) for one redd and misidentified exact redd tailspill position for the second.

In total, 4124 fry in 2008 (from 3 to 1429 fry redd⁻¹) and 3006 fry in 2009 (from 1 to 933 fry redd⁻¹) were caught from trapped redds (Fig. 21), estimated average of the total number of emergent fry from redd (in several redds total fry number is corrected for untrapped area (see in section 4.3. for details)) being 336±427 and 255±287 respectively. No statistically significant difference (Mann-Whitney U test, d.f.= 25, P >0.05) between the two year average fry numbers was found. The average number of fry per redd did not differ between the stream sections (BR and pooled BS and BG; Mann-Whitney U test, d.f.=25, P >0.05) and emerging fry number was highly variable in relatively close redds. Pooled results reveal that in Blendžiava Stream one average redd (c. 2 m²) yields 299±71 (±SE) emergent fry.

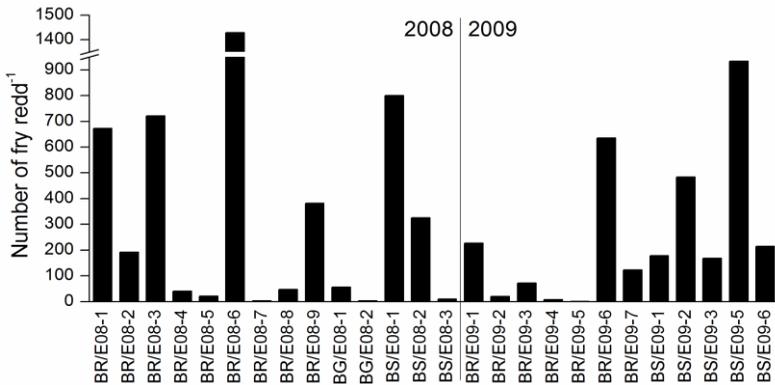


Fig. 21. Estimated number of emergent fry from all studied redds in 2008 and 2009. Redd number indicates its downstream position within particular section denoted as BR, BG and BS.

5.3.1. Emergence timing and distribution patterns

In 2008, traps were installed onto redds about a week before expected onset of emergence. Most of the traps were situated in the BR study section and two groups of two-three traps were situated in BG and BS sections (Fig. 3). From 25 March till the 14 April newly emerged trout fry were occasionally sought in different reaches of the stream from the mouth to the most upstream study point by inspecting typical fry hiding places in vicinity of redds with a dip-net or checking under upper gravel layer of the redds. Within this control section until 11 April 2008, no fry were caught in nursery habitats; however fry were present in the redds, close to gravel surface. So, although trapped redds were positioned mainly in the upper sections, it is considered that the fry emergence period, established from fry traps catches, is applicable to the whole stream section.

In 2009, the traps were installed about one-two weeks before expected onset of fry emergence. However in BG section on 26 April some fry were seen and one sampled was of 31 mm L_T and of 239 mg WW_T . Later on (8 May) in this section were caught some actively swimming fry of 27-32 mm L_T and of 138-252 mg WW_T . Therefore it is likely that in some redds or particular stream sections, emergence started slightly earlier.

In 2008, fry emergence in Blendžiava Stream started on 4 April and finished on 25 May, with an overall duration of 52 days, while the duration of emergence from individual redds was on average 29 ± 8 days (16-41 days). Despite a very long general emergence period, 90 % of fry emerged in the course of three weeks from 18 April (5 % emerged) till 8 May (95 % emerged) (Fig. 22b).

In 2009, fry emergence period was similar to that of previous year (Fig. 22), but the start and the median emergence from the individual redds was significantly later in 2009 than in 2008 (Mann-Whitney U test, $P < 0.05$) (Table 8). Total emergence duration in 2009 was 32 days (20 ± 6 days for individual redds), and lasted significantly shorter if compared to 2008 (Mann-Whitney U test, $P < 0.05$). Despite the start and median of emergence from individual redds was

significantly earlier in 2008, the termination of emergence were observed at the same time in both years (Table 8).

No significant differences were found for the start, median, end and duration of emergence when comparing redds from different study sections: BR and pooled BS and BG (Mann-Whitney U test, d.f.=20, $P > 0.05$).

Table 8. Mean (\pm SD) dates of emergence from individual redds and of general emergence period (pooled data) for 2008 and 2009: the initiation (Start) and the end of emergence, and the 5 %, 50% (Median) and 95% percentiles of cumulative emergence distribution. P-value is given for comparison of mean dates between the two years with Mann-Whitney U test.

	Start	5 %	Median	95 %	End
2008					
General	Apr.04	Apr.18	Apr.29	May.08	May.25
Mean \pm SD (n=11)	Apr.16 \pm 9 (Apr.04- May.01)	Apr.25 \pm 7 (Apr.05- May.02)	Apr.30 \pm 5 (Apr.18- May.07)	May.07 \pm 6 (Apr.26- May.18)	May.14 \pm 7 (May.04- 25)
2009					
General	Apr.25	Apr.29	May.06	May.12	May.26
Mean \pm SD (n=10)	Apr.28 \pm 3 (Apr.25- May.03)	Apr.30 \pm 3 (Apr.27- May.04)	May.05 \pm 7 (Apr.29- May.09)	May.10 \pm 4 (May.01- 17)	May.17 \pm 5 (May.07- 26)
	P <0.05	P <0.05	P <0.05	P >0.05	P >0.05

Emergence frequency distribution in both years followed near normal distribution; however in 2008 the initial emergence phase (to reach 5 % cumulative distribution) took 15 days (8 ± 5 days on average for a redd), whereas in 2009 emergence started rapidly with cumulative 5% stage reached within first 5 days (3 ± 2 days on average for a redd). After emergence in 2008 started, short-term increase in water level was observed after rain what coincided with emergence suspension (Fig. Fig. 22a and b). The distribution in 2008 was slightly skewed to the left (-0.25 skewness) and had conspicuous peak period (1.24 kurtosis) (Fig. 22b) if compared to normal distribution with no sharp peaks in 2009 (0.22 kurtosis; 0.30 skewness).

Considering emergence distribution patterns in different investigated redds they were very variable, both right or left skewed. However left skewness of emergence was considerably less expressed (-0.40 ± 0.37) with only one observed highly negatively skewed emergence (-1.23) (Fig. 23d). Meantime specific characteristic seems to be highly peaked emergence, as 76 % of all redds had highly positive kurtosis (2.03 ± 1.50 ; up to 4.33). Usually there are one or several peak-days, when emerge 12-38 % of fry day⁻¹ (Fig. 23).

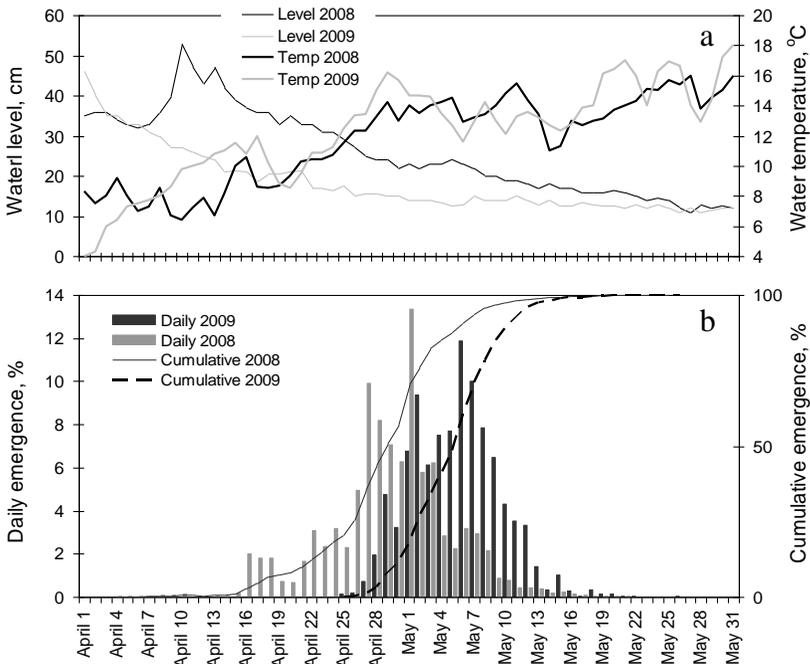


Fig. 22. Relative water level at the BR study section and maximum daily water temperature as an average from temperature measurements sites during fry emergence study (a); and generalized fry emergence relative (daily) and cumulative distribution in 2008 and in 2009 (b).

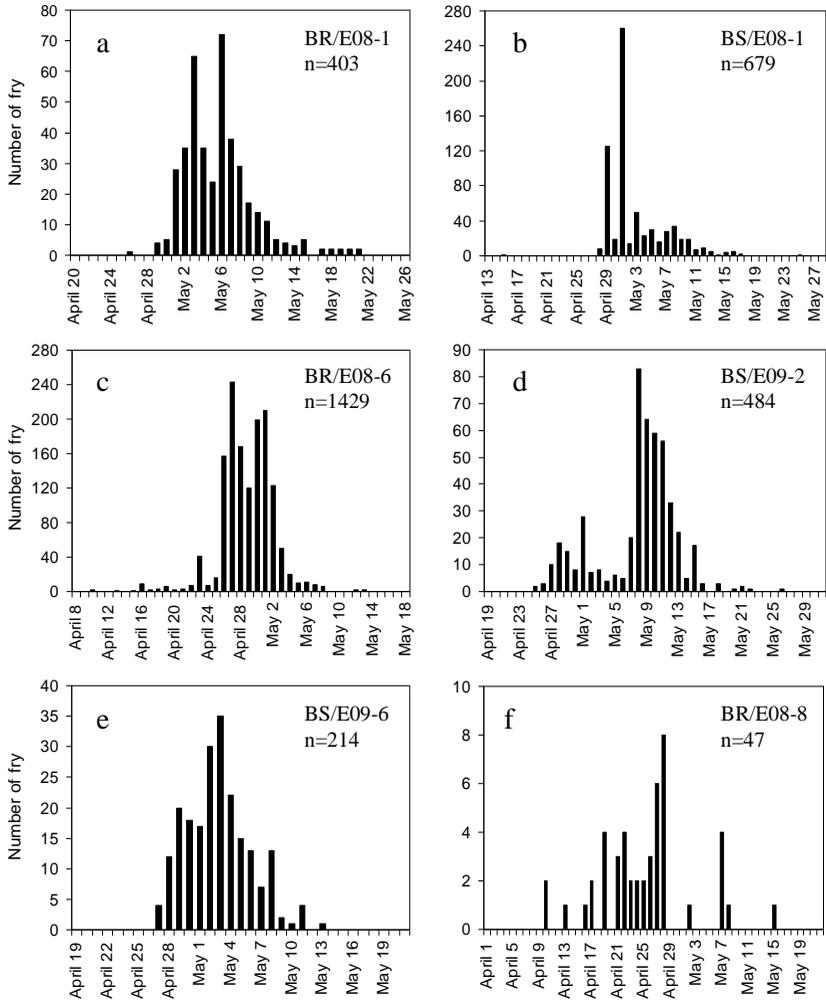


Fig. 23. Examples of fry emergence distribution patterns: positively skewed emergence distribution with intensive beginning and several high peaks (a) and (b); negatively skewed distribution with long not intensive initial phase (c) and (d); untypical bimodal distribution (d); normally shaped intensive emergence (e); and not intensive and not efficient fry emergence (f).

5.3.2. Morphology, conditional and nutritional status of emergent fry

The storage of test fry samples in preserving formalin solution fractionally but statistically significantly reduced both L_T and WW_T by 1.3 ± 0.3 mm (4.9 ± 1.2 %) and 6.9 ± 3.6 mg (6.9 ± 3.8 %) respectively (paired t-test, $t=19.3$, $d.f.=29$, $P < 0.05$). Therefore all the 2008 and 2009 fry samples (stored for 11-14 months), were corrected to the calculated correction factor of 1.052 for L_T and 1.076 for WW_T .

The average size of newly emergent fry during the whole emergence period (both years, all redds, $n=1068$) was 26.9 ± 1.5 mm for L_T (ranging from 20.3 to 30.9 mm), 116.4 ± 17.4 mg for WW_T (ranging from 60.1 to 171.8 mg) and 19.7 ± 3.0 mg for DW_T (ranging from 8.7 to 28.6 mg).

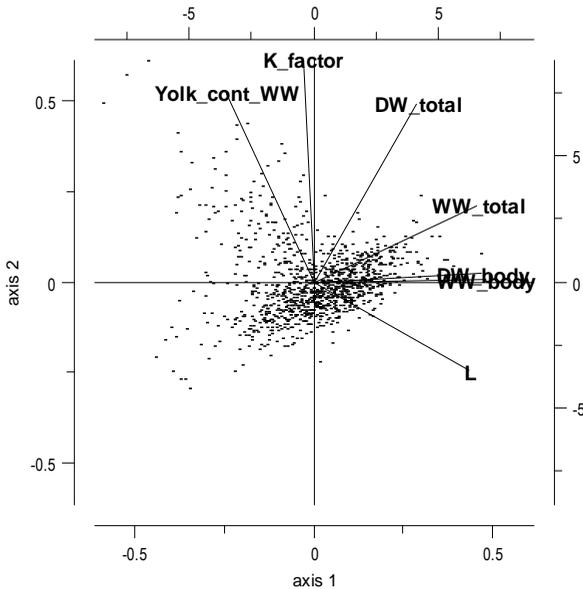


Fig. 24. PCA biplot for the morphological and conditional characteristics of emergent fry: total length (L), total and body wet weight (WW_{total} and WW_{body}), total and body dry weight (DW_{total} and DW_{body}), yolk content of WW_T ($Yolk_cont_WW$) and Fulton's condition factor K .

Principal component analysis on the emergent fry morphological and conditional characteristics revealed specific inter-relationship patterns between these characteristics (Fig. 24). First two axes explained 87.1% of the morphological data variability (57.3% and 29.8% for the first and second axes respectively).

Relatively high variation of total dry weight DW_T in relation to total wet weight WW_T ($r=0.675$, $P<0.001$, $n=1051$) may indicate the variation of water content in preserved tissues during measurements, or the effect of dense yolk sac tissues. High correlation between fry body (without yolk-sac) wet WW_B and dry weight DW_B ($r=0.863$, $P<0.001$, $n=1051$) likely supports the second statement. High variation of WW_T at a given total length L_T of fry was observed (Fig. 25). Relationship between fry body length L_T and wet weight WW_T indicates a negative allometric fish growth pattern (as regression slope is <3), what may indicate poor conditional status during transitional stage from yolk to independently feeding fry.

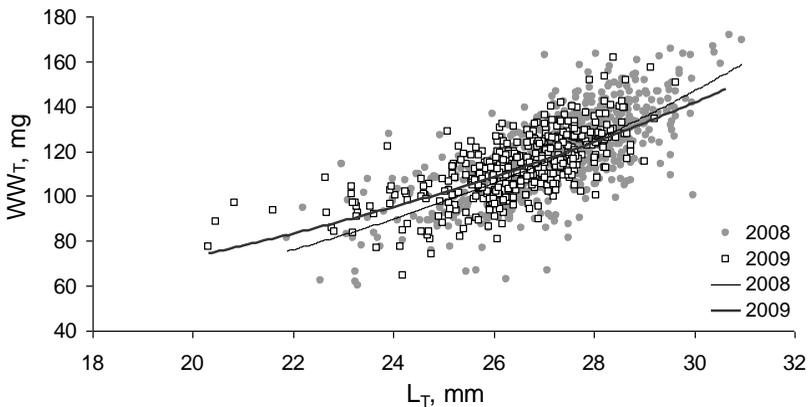


Fig. 25. Length-weight relationship ($WW_T=aL_T^b$) of emergent fry in 2008 ($n=646$) and 2009 ($n=422$). Regression characteristics: $a=0.0811$ and $b=2.2048$ for 2008 data ($R^2=0.512$) and $a=0.3145$ and $b=1.7952$ for 2009 ($R^2=0.480$).

Mean Fulton's body condition factor K for sea trout fry was low: 0.61 ± 0.08 (range: 0.34–1.07). Although Fulton's body condition factor K is the function of length and weight, the strongest correlation of K was found with the content (%) of yolk-sac wet weight $WW_{Y\%}$ ($r=0.612$, $P < 0.05$, $n=848$). Most of fry started to emerge when their yolk sac reserves were nearly or fully absorbed. The average yolk content ($WW_{Y\%}$) of newly emerged fry constituted $3.8 \pm 6.7\%$ of WW_T and $7.4 \pm 12.2\%$ of DW_T ($DW_{Y\%}$). Yolk content was the most variable parameter of emergent fry, which is presented by second principal component (Fig. 25). Yolk content depends on the body length at emergence ($r=-0.645$, $P < 0.001$, $n=844$), the largest fry emerging with less or no yolk reserves left (Fig. 26).

Statistically significant differences were found between the average body length L_T , total wet weight WW_T and yolk content $WW_{Y\%}$ of fry from the two years (Table 9). Larger and with less remaining yolk-sac fry emerged in 2008. However in practice, L_T and WW_T difference between the years is very tenuous (2.5% and 4.6% for L_T and WW_T respectively). High significance of the results, revealed by two-sample t-test, likely is related to the large sample size resulting in high test power (power at $\alpha=0.05$ was 0.998-1.000).

Table 9. Mean (\pm SD) morphological and conditional measures of emergent fry in 2008 and 2009. Statistical significance of the difference between years was tested with two-sample t-test, which P-value is given.

	L_T, mm	WW_T, mg	DW_T, mg	$WW_{Y\%}$, %	K
2008	27.2	118.6	19.7	3.1	0.60
	± 1.4	± 18.8	± 3.1	± 5.4	± 0.08
2009	26.5	113.1	19.6	4.5	0.61
	± 1.4	± 14.3	± 2.8	± 7.7	± 0.08
t	8.27	5.17	0.32	-3.16	-1.48
d.f.	1066	1066	1059	844	1066
P-value	<0.001	<0.001	>0.05	<0.001	>0.05

Temporal changes of morphological, conditional and nutritional traits of emergent fry were observed during the course of

2008 and 2009 emergence, and the patterns of these changes, are shown in Fig.26. Highly significant differences were found in morphological and conditional parameters between five cumulative emergence stages (Kruskal-Wallis ANOVA test, d.f.=4, $P < 0.0001$ for all parameters) (Table 10).

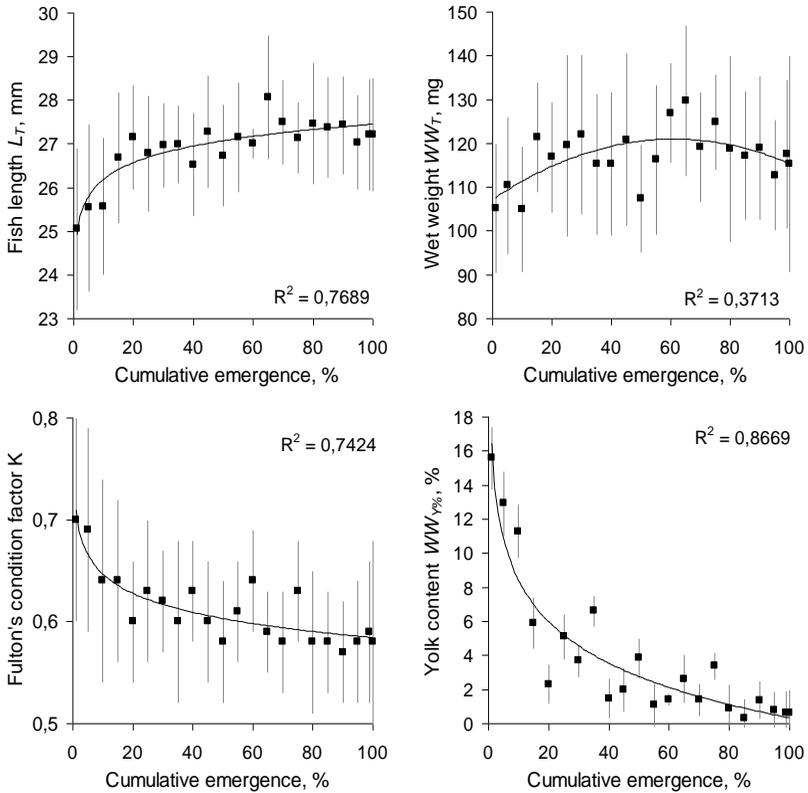


Fig. 26. The changes of emergent fry body length, total wet weight, condition factor K and yolk content in the course of emergence. Mean (\pm SD as whiskers) values are plotted at the 5% intervals (with additional 1 and 99% stages) of cumulative emergence distribution.

The first 5% of emergers have relatively high amount of yolk, which decreases as emergence progresses (Fig. 26; Table 10). During the peak emergence (25-75% of cumulative emergence) fry still have yolk reserves (mainly internal), however it is nearly exhausted. The yolk-sac below 5 % of WW_T seems to be the trigger for emergence (Fig. 28a). The last emergers (>75% cumulative emergence) had less than 1% of yolk reserves left and this was reflected by decreased body weight, and in turn, in conditional status of fry individuals. The late emerging fry with the greatest body length have the worst body condition status (Fig. 26 and 27). Freely swimming, actively feeding fry have considerably higher condition factor K , comparing to that, of largest emerging fry (Fig. 27). At the late emergence stages (>75% cumulative emergence), when yolk reserves are depleted, fry are vulnerable to starving condition if emergence is impeded.

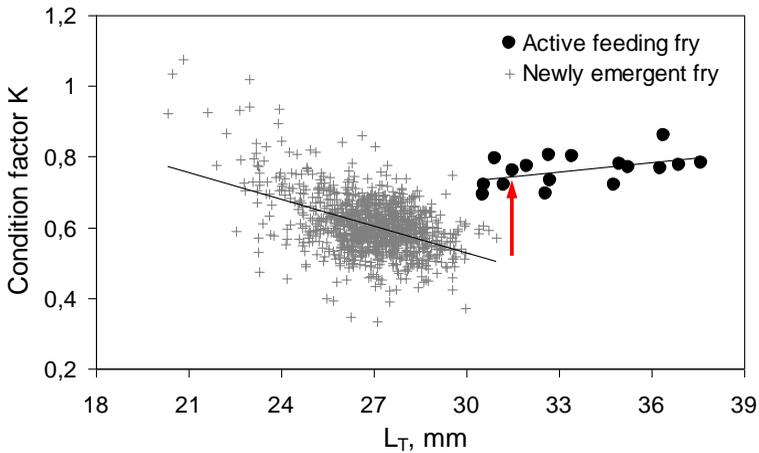


Fig. 27. Relation of Fulton's condition factor K to fry body length L_T . Additional black circles correspond to morphological data of actively feeding fry after emergence (occasional catches). Arrow indicates the shift of body condition factor, in fry with overlapping body length, after feeding initiation. The relationship between K and L_T changes into positive for actively feeding fry.

Table 10. Mean (\pm SD) morphological and conditional parameters between five defined cumulative emergence stages. Different letters indicate significantly different groups (Dunn's multiple comparisons test, $P < 0.05$)

Stage	L_T	WW_T	DW_T	$WW_Y(\%)$	K
<5%	25.3 \pm 1.9 ^a	108.0 \pm 15.4 ^a	21.1 \pm 3.1 ^a	14.0 \pm 9.9 ^a	0.69 \pm 0.10 ^a
5-25%	26.6 \pm 1.5 ^b	115.3 \pm 17.4 ^b	20.4 \pm 2.8 ^{ab}	6.1 \pm 7.5 ^b	0.62 \pm 0.08 ^b
25-75%	27.2 \pm 1.2 ^c	119.0 \pm 16.6 ^c	20.2 \pm 2.7 ^b	3.0 \pm 4.5 ^c	0.60 \pm 0.06 ^c
75-95%	27.4 \pm 1.2 ^c	117.3 \pm 16.0 ^{bc}	18.9 \pm 2.5 ^c	0.8 \pm 1.9 ^d	0.58 \pm 0.06 ^d
>95%	27.2 \pm 1.3 ^c	115.9 \pm 19.8 ^b	18.1 \pm 3.3 ^d	0.6 \pm 1.7 ^d	0.58 \pm 0.08 ^d

Nutritional status of emergent fry followed temporal patterns during emergence (Fig 28b). The most of newly emergent fry did not initiate exogenous feeding in the first day, as 82.5% of sampled fry had no food in their digestive tract. 9.6% of fry had traces of food in their stomach or gut, and only 7.9 % were found with full stomach. Two latter nutrition classes of fry indicate not-active occasional feeding and active feeding, respectively. Fry emerging in the beginning were not fed; still relying on yolk-sac reserves, while the last emergers, having no yolk left, initiates feeding sooner and more actively.

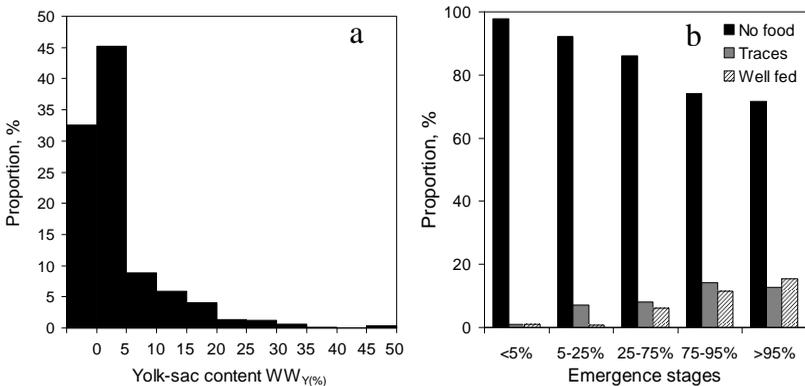


Fig. 28. a) Frequency distribution of yolk-sac content in newly emerged fry ($n=848$) (a); and nutritional status for different emergence stages (b).

5.3.3. Conditional status of emergent fry assessed by RNA:DNA ratio

For biochemical analysis, 158 freshly emerged fry were collected in spring 2009 from 9 natural redds trapped with fry emergence traps (11-23 fry samples redd⁻¹). The mean value of RNA:DNA ratio was 1.31 ± 0.33 (range of individual ratio: 0.68–2.54). The tested hypothesis, that in the end of emergence fry with depleted yolk reserves have reduced RNA to DNA ratio, indicating starving effect, was supported by the results. The general temporal decrease in average RNA:DNA ratio was observed during the sampled period (Fig. 29). This was evident in all redds except BS/E6.

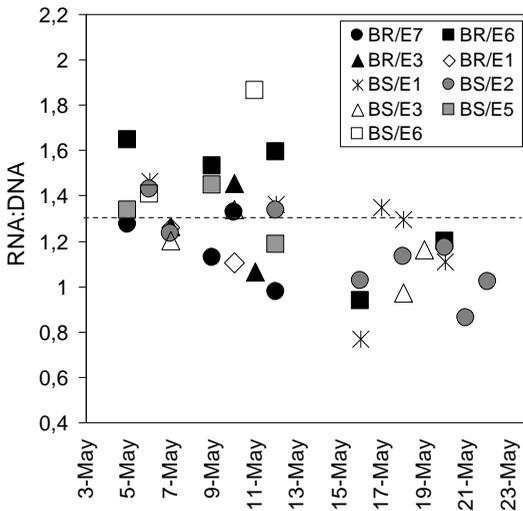


Fig. 29. Temporal changes of RNA:DNA ratio (average for separate sampling occasion or values of single individuals sampled in the end of emergence). The dashed line indicates an overall mean of ratio.

When linked to the cumulative emergence stage, average RNA:DNA ratio of sampling occasion remains fairly constant following the general average trend until 90-95 % cumulative emergence is reached (Fig. 30a). In the very last emergence stages the variation of RNA:DNA ratios increases, while conspicuous decreasing trend could be drawn.

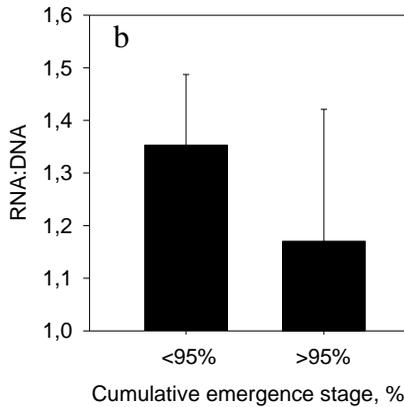
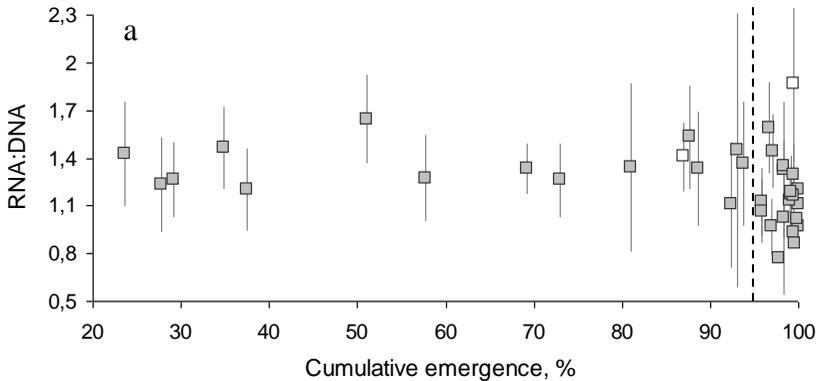


Fig. 30. Variation of RNA:DNA ratio in the course of fry emergence (a). Squares represent mean ($\pm SD$) of sampling occasion or value of single sampled individual from all 9 redds (two white squares represent data points of BS/E6 redd, and the dashed line indicates 95% stage); and mean ($\pm SD$) RNA:DNA ratio of fry from the two cumulative emergence groups (b).

Sampled fry were assigned to two principal emergence groups: mainstream emergers (emerging till 95% of cumulative distribution) and the last emergers (>95% of cumulative emergence). Average RNA:DNA ratio of the last emergers was statistically significantly lower, than of the mainstream emergers (two-sample t-test; $t=2.64$; $d.f.=35$; $P < 0.05$) (Fig 30b). Significant difference was found when comparing average fry RNA:DNA ratio between the two principal emergence groups from individual redds (Wilcoxon signed

rank test, d.f.=7, $P < 0.05$), but only when data from BS/E6 redd was excluded from analysis.

Decrease in body condition status for the last emerging fry was soundly represented by biochemical body index RNA:DNA, what was not detected by traditional morphological and conditional measures.

5.3.4. Factors influencing fry emergence success and patterns

The size of the redd is rough estimate for the female's size and amount of eggs placed in the redd, however presently estimated emergent fry number moderately related to the redd size ($R^2 = 0.317$, $P < 0.05$) (Fig. 31). This relation in many cases is modified and weakened by environmental parameters, which determine the egg-to-fry survival (sections 5.2). Exclusion of < 50 fry redd⁻¹ data points (ineffective emergence) increase the share of explained fry number variance by the redd size ($R^2 = 0.511$).

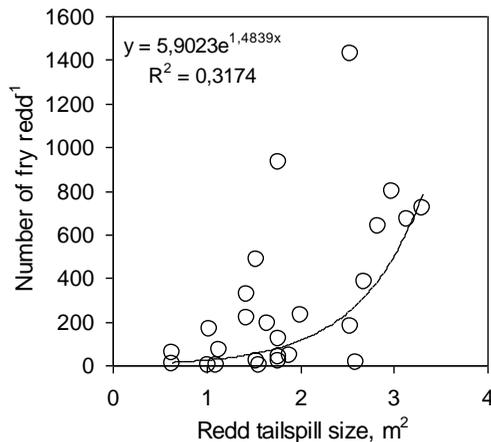


Fig. 31. Relation of estimated number of fry to the size of redd tailspill ($n=26$).

Multiple regression analysis was used to examine whether the efficiency of emergence, in terms of emergent fry number per redd, was related to the substrate permeability (as its structure index), to the vertical hydraulic gradient VHG and to average interstitial water parameters (RDOS and Δ CND), measured during the course of emergence.

Table 11. Results of multiple regression analysis between log-transformed number of fry redd⁻¹ and explanatory redd variables ($R^2=0.571$, $F=6.99$, $P < 0.001$ $n=26$). Statistically significant factors are bolded.

Explanatory variable	b	t	P	Beta
log(Permeability)	1.563	3.893	<0.001	0.586
RDOS	0.001	0.147	0.884	0.025
Δ CND	-0.021	-2.171	0.042	-0.390
VHG	-9.318	-1.176	0.253	-0.182

The number of emergent fry varied greatly between redds, therefore log-transformation was applied, and 57% of log-transformed fry number redd⁻¹ variation (not accounting for the redd size) was explained by VHG, RDOS, CND and log-transformed permeability (Table 11). Stepwise backward selection revealed that log-transformed permeability and presence of groundwater were the two most important factors explaining 54% of fry number variation, while relative DO saturation and VHG was not relevant to emergence efficiency ($P > 0.05$). The presence of groundwater (increased Δ CND) affects through temporal or extended supply of hypoxic water to incubating eggs ($r=-0.522$, $P < 0.01$, $n=26$). Additionally the groundwater may be related with increased ammonia concentrations, which is toxic for incubating embryos (Fig. 17).

The redundancy (RDA) analysis showed that redd substrate permeability, relative dissolved oxygen saturation, groundwater supply and year with section as nominal variables explained 50% of variation in different emergence parameters, and 86% of this (72% and 14% first and second axis respectively) were represented by first

two axes. The forward selection and permutation tests results (Table 12) indicated that all variables, except ΔCND , were significant ($P < 0.05$).

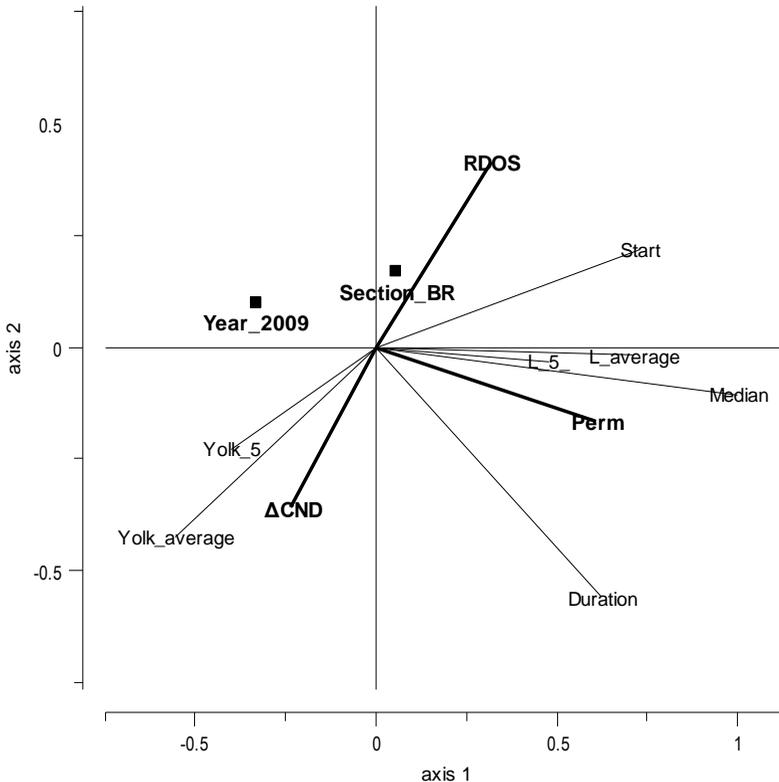


Fig. 32 . RDA biplot for fry emergence characteristics (length of emergence period (duration), relative start and median of emergence, average and of first 5% emergers length and yolk sac amount (L_average, L_5, Yolk_average and Yolk_5) with redd substrate permeability (Perm), interstitial water average RDOS and ΔCND during the emergence period as explanatory variables. Study section and sampling year used as nominal explanatory variables.

Table 12. *Conditional effects of redd intragravel variables for the fry emergence patterns data. The total sum of all canonical eigenvalues is 0.50 and the total inertia is 1. The second column shows the increase in explained variation due to adding an extra explanatory variable. The third column shows an eigenvalue as % using only one explanatory variable.*

Variable	Conditional effects	Eigenvalue as %	F-statistic	P-value
Year 2009	0.25	49.46	6.988	0.001
RDOS	0.10	16.34	2.942	0.029
Section	0.08	12.43	2.605	0.036
Permeability	0.07	29.70	2.498	0.042
Δ CND	0.01	9.31	0.342	0.900

Δ CND was highly negatively correlated with RDOS and these two explanatory variables correlated with the start of emergence. Fry tended to emerge earlier when oxygen regime in the redd is unfavourable, having more yolk-sac reserves left. On the contrary, when oxygen amount in the interstitial water is considerable, fry stay longer in the redd, absorb the yolk and emerge at the optimal time. Start of emergence also correlates with the body length (both, with emergence period average and of first 5% emergers). Redd substrate permeability (log-transformed) determines the length of emergent fry, which decreases with decreasing permeability. Permeability correlated with the date of median emergence and with the length of emergence period.

Study year factor explained the highest portion of emergence parameters. In 2009, emergent fry were smaller, with higher amount of yolk-sac left and the duration of emergence was shorter.

5.4. Dispersal of juveniles after emergence

Most of the fry were observed in a very close vicinity to the native redd (up to 10 m) to both upstream and downstream directions in a first week after they emerged. Strong initial association with the native redd could be illustrated by the fact that some large resident fry

(29.9-36.9 mm L_T ; 205-367 mg WW_T) were recovered from the redd area after removal of the emergence traps.

During the first two months juveniles disperse up to 200 m from the redd and probably further, however the highest number of juveniles was still caught in native riffle or run habitat area (Table 13). The further from the spawning habitat, the less parr were found and such distribution pattern was characteristic to all sections (Table 13). The increased share of caught juveniles above 100 m from the redds is the cumulative number of fishes caught between 100-200 m section below the redds. The distribution of 0+ parr was related to the distribution of suitable juvenile rearing habitats. As study sections BR and BK are characterized by relatively high amount of riffle sections, suitable habitats for juveniles are located closer and require shorter dispersal distance. In the BG and BS sections spawning takes place in sparsely distributed short riffle-type habitats what governs more distant fry dispersal to acquire suitable feeding habitat.

Table 13. The distribution (%) of juveniles' catches within assigned subsections from the identified redds.

Study section	Distance from the redd, m					
	<20	20-40	40-60	60-80	80-100	>100
BR	47	17	17	8	0	11
BG	39	30	12	3	11	5
BS	31	22	18	2	2	25
BK	50	11	12	9	3	15

After emergence fry start to grow intensively, increasing their body weight at about 10-12 times in one month. Slightly but significantly larger parr individuals were observed in BK than in rest sections, when comparing fish L_T , L_S and WW (one-way ANOVA, $F=6.28$, 8.10 and 6.67 , $d.f.=3$, $P < 0.05$ for all size measurements respectively, followed by Tukey's HSD *post hoc* test, $P < 0.05$) (Table 14). The average fish body Fulton's condition factor K did not differ between study sections (one-way ANOVA, $F=0.44$, $d.f.=3$, $P > 0.05$) and was on average 0.962 ± 0.144 ($0.609-1.438$, $n=138$).

Similar 0+ age fish size distribution patterns were observed in 23 July 2007, when the smallest parr were caught at BR section (7.1 ± 0.7 cm L_T and 3.7 ± 1.0 g WW), while in the two lower reaches BG and BK parr were significantly larger (7.6 ± 0.5 cm = 7.7 ± 0.5 cm of L_T ; and 4.3 ± 1.0 g < 5.1 ± 0.5 g of WW, in BG and BK respectively) (one-way ANOVA followed by Tukey's HSD post hoc comparisons, $P < 0.05$).



Fig. 33. The maximum observed size difference between newly emerged and approx. three weeks emerged fry in BR section.

Table 14. The total length, standard length and wet weight of 0+ age parr (mean \pm SD) and estimated section's density of 0+ age fishes in different Blendžiava sections one month after general emergence termination (22-23 June 2009). Different letters denote statistically significant difference for fish size measurements between 4 stream sections (Tukey's HSD test, $P < 0.05$).

Study section	n	L_T , cm	L_S , cm	WW, g	Density, ind. 100 m ²
BR	35	5.0 ± 0.6^a	4.2 ± 0.6^a	1.2 ± 0.5^a	8.4
BG	40	5.2 ± 0.6^a	4.4 ± 0.6^a	1.4 ± 0.4^a	7.7
BS	30	5.0 ± 0.6^a	4.4 ± 0.5^a	1.2 ± 0.3^a	6.2
BK	33	5.5 ± 0.4^b	4.8 ± 0.4^b	1.7 ± 0.5^b	4.9

Different fish size may indicate different length of growth period due unevenly distributed fry emergence timing. The last emerging fry may be smaller in 25-35 % for L_T and even 70-85 % for WW_T from individuals, which emerged about three weeks earlier (Fig. 33).

5.5. *Salmo trutta* redd superimposition by lampreys

In 2008, the spawning of river lamprey *L. fluviatilis* was most abundant (71.2 nest km⁻¹) in the downstream BK study section and about 15 times lower in the upstream BR section (Fig. 34). The nest density of river lamprey in BS and BG sections was low and usually below 10 nest km⁻¹. The spawning of river lamprey was concentrated in the first 3 km of the stream channel from the mouth. The main spawning grounds of brook lamprey *L. planeri* were in the upper stream part, where the density of nests was the highest. In 2009, the spawning intensity of both *Lampetra* spp. was considerably lower than in 2008. In the BR section, no spawning activities of river lamprey were recorded (Fig. 34).

In 2008, river lamprey partially, or in a few cases, almost fully superimposed 83% of sea trout redds in BK section. In the BR section, sea trout redds were superimposed only by brook lamprey, and the superimposition rate was 48 %. Sparsely distributed river lamprey nests (4.1 nest km⁻¹) did not overlap with the *S. trutta* redds. With low *Lampetra* spawning intensity in 2009, the superimposition frequency constituted 12–14 % in both study sections (Fig. 34).

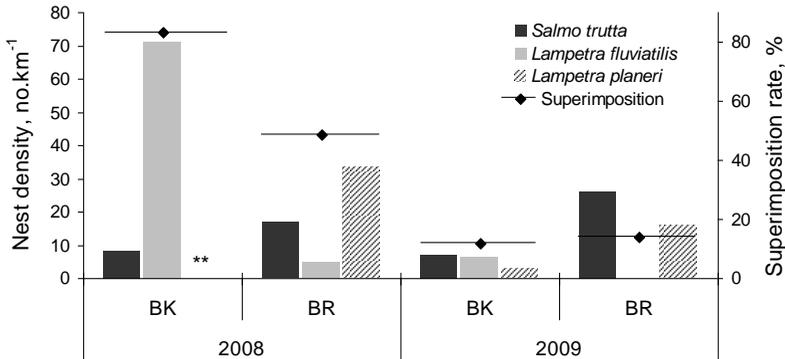


Fig. 34. Densities of spawning nests of sea trout, river lamprey and brook lamprey in BK and BR study sections in 2008 and 2009. Superimposition rate of all redds in a given section by both *Lampetra* species is shown. ** – density of *L. planeri* nests was not evaluated.

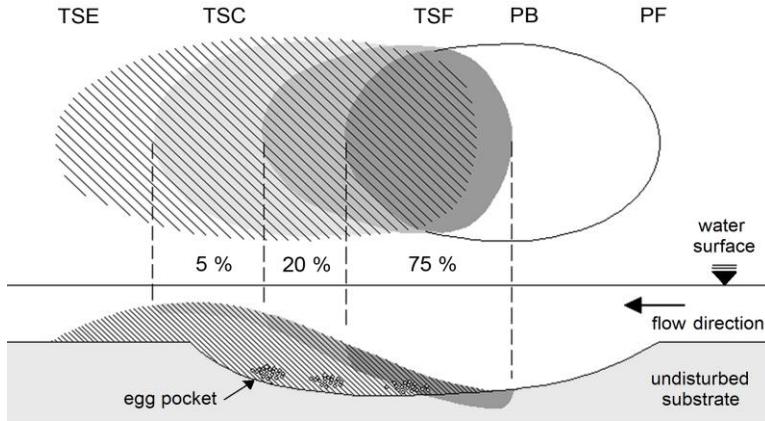


Fig. 35. The layout of the typical sea trout redd structure in plane (top) and cross-sectional (below) view with its partitioning to the tailspill end (TSE), tailspill crest (TSC), tailspill front (TSF), pit bottom (PB) and pit front (PF) and with the most likely egg pocket sites shown (according to Chapman (1988) and Grost et al. (1991)). High probability spawning places of the brook lamprey are shown as a dark grey area with decreasing occurrence likelihood in the light grey area. These areas are defined by relative distribution (%) of *L. planeri* nest positions on sea trout redds recorded in Blendžiava Stream, in 2008 and 2009 ($n = 24$).

The extent to which two lamprey species were able to superimpose sea trout redds was significantly lower for brook lamprey (Mann-Whitney U test, $P < 0.001$). Mean superimposed area of the sea trout redd tailspill by river lamprey constituted $34 \pm 29\%$ (5–90%, $n=11$). Four of superimposed redds (36%) by river lamprey had disturbed more than half of tailspill area. Brook lamprey was able to reuse only $3.3 \pm 1.8\%$ (1.0–6.5%, $n=17$) of trout redd area. The nest sites of brook lamprey were well-directed to the upstream edge of the sea trout redd tailspill. Most of the nests were situated in the tailspill front and the pit bottom area (Fig. 35). Similar patterns of superimposition were observed for river lamprey, with 64 % of the superimposed redds reused in the tailspill front and pit bottom area.

5.5.1. Temporal overlap in fry emergence of sea trout and spawning of lampreys

The timing of both *Lampetra* species spawning significantly overlapped with the emergence period of sea trout fry in both years, coinciding the overall periods and the peaks of these reproductive processes (Fig. 36).

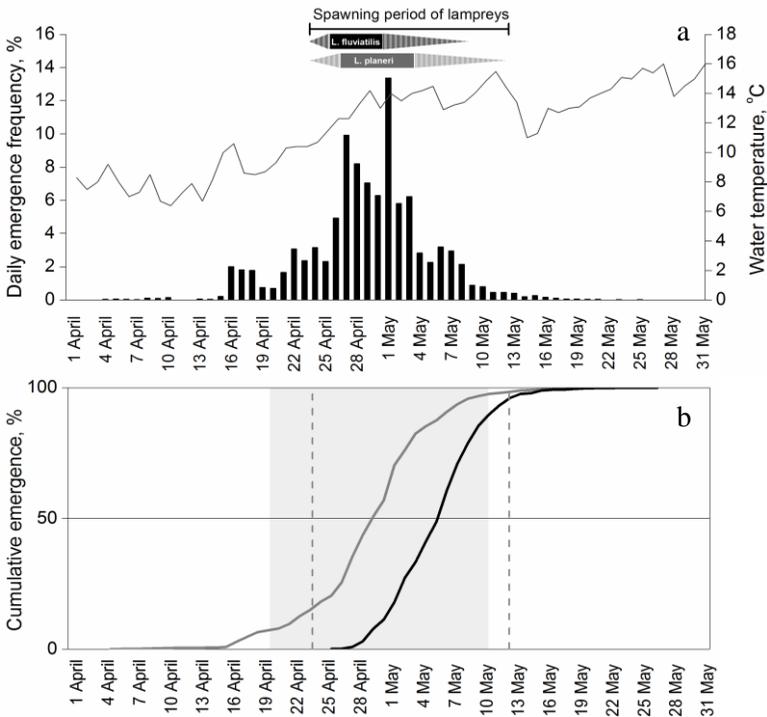


Fig. 36. Sea trout fry emergence distribution in 2008 and periods of river lamprey and brook lamprey spawning with shown relative intensity of nest construction: intensive nest construction (■ ■), and not intensive initial phase and ending phase of spawning (descending ||||) respectively (a); and overlap of sea trout emergence period determined in 2008 (—) and in 2009 (---) with overall duration of *Lampetra* spp. spawning in 2008 (---) and in 2009 (■) (b).

The spawning period of lamprey species was very similar in both years (Fig. 36b). The onset of spawning of both *Lampetra* species in 2008 was observed on 23–24 April, but the spawning of *L. fluviatilis* was shorter and more concentrated (Fig. 36a). The spawning of the *L. fluviatilis* in the BK section peaked in 26–30 April 2008 with most of the nests being constructed and the termination of spawning was observed on 6 May 2008. In the BR section, *L. fluviatilis* spawned slightly later: nest construction started on 30 April 2008 and finished on 8 May 2008. In 2009, *L. fluviatilis* in the BK study section spawned from 28 April till 10 May 2009 and *L. planeri* in both study sections spawned from 20 April till 3 May 2009 (Fig. 36b).

5.5.2. Overlap in spawning site preferences by sea trout and lampreys

In total 65 spawning nests of *L. fluviatilis* (in the BK and BR study sections), 50 spawning nests of *L. planeri* (in the BR section only) and 41 *S. trutta* redd (in all study sites) were sampled for spawning site characterization in spring 2008. The distribution of spawning sites between the geomorphic stream channel units revealed similar patterns in the spawning site selection at the reach-scale of all three species. 86 % of the brook lamprey and 91 % of the river lamprey were associated with riffle and run type channel. The transitional pool-riffle type zones were most intensively used for nest building (43–44 % of both *Lampetra* species), particularly straight upstream to the riffle break point.

There was no statistically significant difference between the spawning habitat hydraulic characteristics such as flow velocity (log-transformed) and the Froude number found beside the nests of sea trout, river and brook lampreys (one-way ANOVA, $F=2.83$ and 1.60 , $d.f.=2$, $P > 0.05$, respectively) (Table 15). The water depths at which *Lampetra* dug their nests were the same for both species, while the depths in the sea trout redd were slightly, but significantly greater than that of the both *Lampetra* spp. (one-way ANOVA, $F=12.69$, $P < 0.0001$; followed by Tukey's HSD *post hoc* test, $P < 0.05$).

Table 15. Mean±SD values of spawning microhabitat and spawning nest characteristics of river lamprey, brook lamprey and sea trout, measured in spring 2008 during or just after lamprey spawning. Range of measured values is given in parentheses.

Microhabitat descriptors	<i>Lampetra fluviatilis</i>	<i>Lampetra planeri</i>	<i>Salmo trutta</i>
Dominant substrate	coarse-very coarse gravel (16–64 mm)	medium-coarse gravel (8–32 mm)	coarse-very coarse gravel (16–64 mm)
Depth (m)	0.23 ± 0.06 (0.11–0.40)*	0.21 ± 0.06 (0.08–0.33)	0.27 ± 0.07 (0.15–0.42)
Flow velocity (m s ⁻¹)	0.51 ± 0.17 (0.18–0.91)	0.44 ± 0.13 (0.15–0.75)	0.50 ± 0.13 (0.25–0.86)
Froude number	0.34 ± 0.12 (0.09–0.57)	0.32 ± 0.11 (0.09–0.79)	0.31 ± 0.08 (0.16–0.57)
Slope (%)	-3.8 ± 3.8 (-13.5–4.7)	-7.9 ± 4.3 (-17.5–-1.5)	-11.6 ± 4.8 (-30.0–-5.0)**
VHG	-0.035 ± 0.035 (-0.126–0.027)	ND	-0.029 ± 0.021 (-0.066–0.026)***
Nest characteristics****			
Nest area (m ²)	1.33 ± 1.44 (0.10–6.91)	0.07 ± 0.06 (0.01–0.24)	2.47 ± 1.52 (1.02–7.85)
Nest length (cm)	129.4 ± 80.4 (40.0–400.0)	29.4 ± 16.7 (10.0–80.0)	186.0 ± 56.0 (120.0–350.0)
Nest width (cm)	105.0 ± 85.6 (25.0–400.0)	28.2 ± 13.3 (10.0–60.0)	171.0 ± 99.0 (100.0–600.0)
Pit diameter (cm)	37.1 ± 9.4 (15.0–65.0)	24.8 ± 9.0 (10.0–42.5)	ND
Pit depth (cm)	6.5 ± 2.3 (2.0–12.0)	3.9 ± 2.0 (1.0–9.0)	ND

ND not determined; *one outlier of 0.7 m was removed from the analysis; ** *S. trutta* microhabitat slope here is the slope generated by redd structure itself, measured from the deepest redd pit point to the tailspill crest; ***VHG is given for the front part of redd; *****S. trutta* nest area, length and width here is given as redd tailspill measurements, without pit included.

Brook lamprey built their nests exclusively (100 %) on the gravel grounds with negative slope. A negative microhabitat streambed slope associated with the spawning sites of river lamprey was found in 79 % cases, while the rest of the spawning sites were characterized by a positive slope or plain streambed (≥ 0 %). The mean microhabitat slope of brook lamprey was significantly steeper than that of river lamprey. Consequently, the slope generated by the structure of a sea trout redd was significantly steeper than that found in the *Lampetra* spp. spawning microhabitats (one-way ANOVA, $F=46.0$, $d.f.=2$, $P < 0.0001$; followed by Tukey's HSD test, $P < 0.05$).

For some river lamprey spawning sites, the vertical hydraulic gradient was determined in gravel at a depth of 13 ± 2 cm. There was no significant difference between VHG in the *L. fluviatilis* spawning site and in front of *S. trutta* redd tailspill (Student t-test, $t=0.80$, $d.f.=54$, $P > 0.05$). As for sea trout, downwelling conditions dominated within the river lamprey spawning sites (88 %).

The structure of a completed river lamprey nest resembled the structure of a salmonid redd by having a flat gravel tailspill and pit upstream. The solid tailspill of the completed *L. fluviatilis* nest may reach 4 m in width and 3.2 m in length. Some nests did not aggregate into the solid nest but were composed of many separate nests that were partly joined. The maximum length and width of such a cluster of nests were measured and it was considered as one spawning redd. The nest of *L. planeri* was usually structured as a small single separate pit without tailspill (only 18 % had tailspill). The size of separate pits is given as its diameter, which was significantly bigger for *L. fluviatilis* compared to *L. planeri* nest pits (Student t-test, $t=7.94$, $d.f.=154$, $P < 0.0001$) (Table 15). Pit depth also differed between the two species (Student t test, $t=7.25$, $d.f.=194$, $P < 0.0001$).

All other *L. fluviatilis*, *L. planeri* and *S. trutta* nest size measurements (nest area, length and width) were significantly different between the three species with the smallest nests of *L. planeri* and the largest of *S. trutta* (non-parametric Kruskal-Wallis ANOVA, $d.f.=2$, $P < 0.0001$, followed by Dunn's multiple comparison test, $P < 0.05$ for all nest size measurements).

6. DISCUSSION

6.1. Influence of spawning site selection on sea trout reproductive success

The survival of salmonids embryos, which develop throughout winter and spring, depends on the location of the redd (Crisp, 1993a; Fleming, 1998; Bardonnnet & Bagliniere, 2000). Female breeding behaviour in salmonid species, appears to be shaped, to a large extent, by natural selection for offspring survival (Fleming, 1998) and breeding territories tend to be concentrated in areas having suitable habitat requirements for spawning and egg incubation.

Sea trout showed distinct distribution patterns of spawning intensity along the stream gradient. The availability and distribution of suitable spawning gravel is of fundamental importance in determining the reproductive potential and may limit salmonid populations in many streams (Crisp, 1993a; Kondolf & Wolman, 1993). The highest density of spawning redds in both study years were found in the upper part of the stream, particularly in BR study section. Meanwhile the downstream section with the highest availability of suitable spawning grounds was characterized by low spawning intensity. Streambed structure of the downstream BK study section was considerably dominated by the gravel substratum, which, however, was highly mobile, often being scoured or refilled in considerable extents. During several years of observation high instability and erosion of the channel and stream banks during floods was noticed in BK section. In 2009 this section has about 10-15 % of newly formed channel comparing to its length in 2006. The disturbances of the streambed (October-March) coincided with the intragravel development period of salmonids. Displacement by high stream flows that scour the streambed is considered one of the major factors affecting salmonid survival during undergravel period (Peterson & Quinn, 1996, Montgomery et al., 1996; DeVries, 1997). In December 2006, preliminary egg incubation experiment was conducted in this downstream section and 12 natural or artificially build redds in typical sea trout spawning sites were

equipped with egg incubation boxes. Five (42 %) experimental redds were lost (severely scoured or refilled with new layer of gravel) due to bankfull flood soon after the start of the experiment. Extremely high spring flood in March 2010 completely scoured or considerably affected all redds recorded in the BK section. On the contrary, high stability and consistent structuring of the stream channel was characteristic to the upstream BR section, suggesting lower disturbance extent of redds by high water events. Consequently, differences in potential of reproductive success (egg-to-fry and post-emergence survival) between the downstream and upstream reaches may exist. Low spawning intensity in the BK and high – in BR section indicates avoidance of the downstream section by sea trout females.

Sea trout (Shearer, 1955) as all other anadromous salmonids (Heggberget et al., 1988b; Dittman & Quinn, 1996) show high fidelity to their natal river, where they had resided as juveniles. There is also circumstantial evidence of local homing on a fine scale to specific locations within river (Heggberget et al., 1988b; Youngson et al., 1994). Such local homing may be a means for parents to identify suitable rearing environments for their progeny, because they themselves had grown successfully as juveniles at the same locality (Fleming, 1996). In a long-term perspective, coupling the local homing effect and the difference in cohorts' strength between the stream sections due to stream-scale processes, more fishes will eventually return to spawn in the more suitable upper reaches.

Comparing the substrate quality of used spawning grounds and experimental eggs survival between the studied sections, no significant evidences were found for the superior reproductive conditions in any of the study sections ($P < 0.05$). However, the quality of spawning substrate and experimental eggs survival rate were somewhat higher in BR section, comparing to the downstream BK section. Lack of significance for the results of some tests is related to unbalanced within-group sample size, what led to a very low power of the tests (< 0.10). These results, therefore, should be interpreted cautiously (Underwood, 1999).

The highest proportion of large redds was found in BR section, indicating biological quality of spawners. Large females may dig larger redds (Crisp & Carling, 1989; Fleming, 1998); and it was shown that body size explained over 80% of the variance in female breeding success in wild salmon (Fleming et al., 1996). The size of sea trout spawners is not known for Bledžiava, while generally for Minija River basin, sea trout spawners in years 1990-1991 reached 66-71 cm mean total length (Kontautas & Rauckis, 1994).

Determined incubation conditions, egg survival and fry emergence were highly variable between relatively close redds or even within redd area and was affected by the spawning microhabitat selection by females, rather than by stream-scale processes.

In present study traditional factors for the spawning site selection such as water depth, flow velocity or substrate at the time of spawning were not determined. These parameters have been evaluated in previous study of sea trout spawning site selection in Minija Basin rivers, including Blendžiava Stream (Nika et al., 2011). Water depth and flow velocity at sea trout redds were in high agreement with those, determined for other populations (Crisp & Carling, 1989; Soulsby et al., 2001; Walker & Bayliss, 2007; Barlaup et al., 2008). Sea trout females in Minija basin used relatively narrow range of water depths and velocities. It is likely that modal depth of 0.25-0.40 m and flow velocity of 0.4-0.7 m s⁻¹ were optimal for Minija's Basin sea trout. Strong avoidance of shallow places (less than 0.15 m) for spawning was unlike to most other brown trout populations studied (reviewed in Louhi et al., 2008). Rivers of western hydrological region of Lithuania are characterized by complex hydrology, when after autumn-winter floods, water level in rivers considerably decreases in the second-half of winter (Gailiūšis et al., 2001). Selection of relatively deep spawning grounds may be an adaptation to strongly fluctuating water level, to avoid dewatering or freezing of shallow redds later in the winter. Deep spawning sites (0.5-1 m) used for sea trout and Atlantic salmon spawning in Norwegian rivers (Barlaup et al., 2008) may be related to the heavy freezing in winter and thick ice cover.

Important in-stream feature for salmonid spawning site attraction and suitability, though not affecting incubation efficiency, is the presence of cover for spawners (Witzel & MacCrimmon, 1983; Armstrong et al., 2003; Rubin et al., 2004; Zimmer & Power, 2006; Kuzishchin et al., 2009; Nika et al., 2011). As spawning takes up to several days, during this time both the male and female spawners hide and rest periodically in deep water (Armstrong et al., 2003; Esteve, 2005). Close stay to the redd-site may represent the need to effectively defend the redd from other conspecific pairs (Esteve, 2005) or the energy saving strategy during exhausting spawning. If suitable for resting deep water is not available close to gravel grounds, these may not be used by spawning salmon no matter how good the gravel may be (Armstrong et al., 2003). 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).

Presently evaluated vertical hydraulic gradient (VHG) of hyporheic flow was proven to be one of the essential factors in determining spawning microhabitat selection. The downwelling of surface water into the streambed was principal feature of preferred spawning pool-riffle transitional zones (Fig. 14). These habitats are known to play a significant role in the spawning site selection for most salmonids (Bjornn & Reiser, 1991; Louhi et al., 2008; Barlaup et al., 2008; Kuzishchin et al., 2009). When female digs the nest, at intervals she probes the pit by lowering her anal fin into its bottom (Esteve, 2005). Apparently this is done to assess the flow of water through the gravel below the pit (Crisp, 1993a). Therefore the vertical hydraulic gradient is essential factor determining suitability of nest site and incubation conditions. The spawning of lithophilic brood hidiers in downwelling 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 & Reiser, 1991; Greig et al., 2007). On the contrary, sea trout avoided pool type channel units, which

additionally to such adverse conditions as low flow velocity and accumulation of sediments, were characterized by upwelling long-residence hypoxic groundwater.

Dissolved oxygen (DO) concentration in interstitial water is essential factor determining success of salmonid egg development and survival (Chapman, 1988; Rombough, 1988; Crisp, 1993; Rubin & Glimsäter, 1996; Greig et al., 2007). Many studies reported critical oxygen levels negatively or lethally affecting salmonid eggs and alevins. Rombough (1988) estimated metabolic rates and critical DO concentrations for rainbow trout at intervals between fertilization and complete yolk exhaustion at different temperatures. He found that critical oxygen concentrations increased continuously during embryonic development from $<1 \text{ mg l}^{-1}$ shortly after fertilization to $7.5 - 9.7 \text{ mg l}^{-1}$, depending on the temperature, just before hatch. Levels sharply dropped by $2 - 3 \text{ mg l}^{-1}$ at hatch and then declined gradually to reach stable levels of $2.3 - 4.8 \text{ mg l}^{-1}$ depending on the temperature. Critical level increased at all stages with increasing temperature as a direct reflection of increased metabolic demands (Rombough, 1988). Scrivener (1988) reports lethal *in situ* DO level for chum salmon of 4.6 mg l^{-1} . In tributaries of the River Rhine sea trout fry emerged from natural redds only where mean DO concentration was $>6.9 \text{ mg l}^{-1}$ (Ingendahl, 2001). Egg survival of Atlantic salmon was not detected at $\text{DO} < 5 \text{ mg l}^{-1}$ in the stream of southern England (Heywood & Walling, 2007), or $<7 \text{ mg l}^{-1}$ in two south-west France streams (Dumas et al., 2007). Survival of sea trout and Atlantic salmon eggs from fertilization to hatching was zero at DO level of 7.6 mg l^{-1} in a near-pristine upland stream in Scotland (Malcolm et al., 2003). Even higher lethal limit of 10 mg l^{-1} was determined for sea trout in Gotland by using artificial incubation boxes (Rubin & Glimsäter, 1996).

In the present study, sea trout 'eyed' egg to fry survival was not observed at $<6 \text{ mg l}^{-1}$ DO concentrations. The same critical level was observed for fry emergence redds, where at DO below 6 mg l^{-1} emerged less than 50 fry redd^{-1} . This is highly compatible with general critical-lethal DO level for *Salmo* salmonids determined elsewhere.

Oxygen concentrations within redd depends on the supply rate (Heywood & Walling, 2007), which is related to the substrate permeability and intragravel flow velocity. Oxygen demand within riverbed depends on decomposing accumulated organic matter (Greig et al., 2007). Presently dissolved oxygen saturation was not related to the silt content in substrate samples, despite the quantities were relatively high.

Groundwater seepage was the main factor affecting oxygen concentrations within redd, especially in 2009, when more redds with groundwater presence were characterized. Both higher and lower ΔCND values of interstitial water were related to the reduced DO concentrations. Relative DO saturation might be predicted to be 60% (average DO concentration of 6 mg l^{-1}) at or above ΔCND of $15 \mu\text{S cm}^{-1}$. Hypoxic groundwater in redds of salmonids were reported by other authors (Sowden & Power, 1985; Malcolm et al., 2003; 2004).

In some redds ammonia, nitrite and nitrate concentrations were determined and results revealed that groundwater might be associated with increased ammonia concentrations. It is widely known that nitrogen compounds are highly toxic to incubating embryos (Finn, 2007). The sources of ammonia usually are the sewage and agricultural leakage (Finn, 2007; EPA, 2009), infiltrating to the groundwater aquifers and discharging to the stream. Modelled annual loads of $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ with the groundwater in the Blendžiava are not high (EPA, 2009). From the other hand, the origin of increased ammonia concentrations (unoxidized to the NO_3 because of nearly anoxic conditions) in redd interstitial water samples could be the wastes of decomposing eggs and alevins (Massa et al., 2000) which died because of low hypoxic groundwater.

The upwelling groundwater definitely caused adverse incubation conditions and significantly reduced survival of experimental 'eyed' eggs and natural eggs in emergence study redds. Despite this, 12% of investigated redds were found in the pool type channel units, with dominating upwelling groundwater. Intensive use of groundwater upwelling sites was reported in different salmonid species as: brown trout (Hansen, 1975; Brabrand et al., 2002), rainbow

trout (Sowden & Power, 1985), charrs *Salvelinus* (Witzel & MacCrimmon, 1983; Curry et al., 1995; Essington et al., 1998; Baxter & McPhail, 1999), Pacific salmon (Lorenz & Eiler, 1989; Geist & Dauble, 1998; Geist et al., 2002) and Atlantic salmon (Grant et al., 2006). Preference for groundwater sites is generally related to a stable and possibly more favourable temperature regime for embryo development than that of running waters (Sowden & Power, 1985; Geist et al., 2002). Groundwater temperature generally is higher than temperatures of surface water during winter (Hansen, 1975; Geist et al., 2002; Brabrand et al., 2002). However this, together with low groundwater DO level, may increase the consumption of oxygen.

Measurements in Blendžiava were made during late spring and summer, when groundwater share increases in runoff under low water level (Gailiušis et al., 2001). Unfortunately, temporal variation of vertical hydraulic gradient and upwelling of groundwater was not determined in current study; but it was demonstrated elsewhere, that VHG and groundwater seepage vary temporally with changing stream discharge (Curry et al., 1994; Geist & Dauble, 1998; Malcolm et al., 2004). When stream water level is high the upwelling is not pronounced and hyporheic groundwater is diluted. In western Lithuania sea trout spawn in October-December under increased water level, when rainwater predominates in the runoff and the groundwater is probably considerably diluted with well-oxygenated surface water (Curry et al., 1994). Later in winter, water level in rivers of western Lithuania drops considerably (in January-February) and may be as low as in the summer (Gailiušis et al., 2001). Therefore the groundwater supply to hyporheic zone may be similar to the measured during summer. Sea trout females may fail to select spawning site at higher water level, when groundwater sites are selected in favour of more advantageous temperature within substrate.

Recognition of the importance of groundwater and knowledge of its role in ecology is growing (Brunke & Gonser, 1997; Geist et al., 2002; Malcolm et al., 2004). It is obvious, that the effect of groundwater is complex, species-specific and often difficult to evaluate. Measurements of only standard microhabitat variables may

not sufficiently explain spawning site selection patterns and success of reproduction. Therefore it should be considered in future researches of salmonid reproductive ecology.

Relative DO saturation weakly correlated with substrate permeability. Rubin & Glimsäter (1996) report that substrate permeability $<2000 \text{ cm hr}^{-1}$ was critical for sea trout egg-to-fry survival in Gotland streams. Barnard & McBain (1994) related permeability to anadromous rainbow trout egg-to-fry survival and found that permeability of 100 cm hr^{-1} lead to 50 % survival. Presently measured permeability was found to be lethal for experimental eggs at $500\text{--}600 \text{ cm hr}^{-1}$. It was the primary factor explaining natural egg to fry survival in emergence study redds.

One of the early premises of this work was to evaluate survival of sea trout eggs in a lowland stream with considerable sedimentation extent. Preliminary experiment has been conducted in a BS section, with high sand amount and likely high spawning gravel sedimentation. Based on preliminary experiment results, redd substrate sedimentation was high. Gravel in the traps was completely filled with $<2 \text{ mm}$ fines. However, this experimental gravel of $>16 \text{ mm}$ particle diameter was well sorted, what is not the case in natural redds. Additionally, fine sediments may form a seal on the top gravel layer, preventing deeper intrusion of fines (Meyer et al., 2005).

Many attempts, both laboratory and *in situ*, have been made to quantify the relationship between gravel composition and the survival of the intragravel stages (Hausle & Coble, 1976; Turnpenny & Williams, 1980; Witzel & MacCrimmon, 1983b; Chapman, 1988; Rubin & Glimsäter 1996; O'Connor & Andrew, 1998; Rubin, 1998; Dumas & Marty, 2006; Julien & Bergeron, 2006). It is generally considered that amount of $<2 \text{ mm}$ fines at or above 15% is critical for salmonids survival (Chapman, 1988; O'Connor & Andrew, 1998; Louhi et al., 2008). Presently determined 'eyed' egg to fry survival was still significant at 15 % of $<2 \text{ mm}$ fines and lethal limit was higher than determined by most others authors.

Direct entrapment effect of emergent fry was likely significant for natural emergence success as the permeability was the most

important factor. Crisp (1993b) experimentally found that alevins of brown trout and Atlantic salmon are able to pass successfully through up to 8 cm thick layer of sand on the gravel. Rubín (1998) experimentally found that fry can emerge in substrate with the geometric mean particle diameter $d_g > 15$ mm and < 6 mm. This pattern can be explained by the fact that two main physical factors determine fry emergence success through the substratum directly: the interstitial space between particles and the particle weight. In substrata of $d_g \geq 15.0$ mm the interstitial spaces between particles were large enough to let the fry pass through. In substratum ≤ 6 mm emergence was again possible, even easier, as emerging fry may displace particles (Rubín, 1998). However natural substrate is usually poorly sorted, and emergence will negatively depend on the substrate sorting (Ingendahl, 2001).

In general, two independently acting factors were proven to be responsible for incubation success in Blendžiava Stream. In some redds with strong groundwater effect survival was 0%, even if permeability was considerable (> 2000 cm hr^{-1}). The worst case scenario of incubation conditions in Blendžiava is the low permeability coupled with upwelling of groundwater. The effect of the two factors is synergetic, when at low substrate permeability hypoxic groundwater has longer residence time within egg pockets.

One of the tasks of present work was to estimate the reproductive success of sea trout in a lowland stream. This was based on the measurements of natural emergence efficiency and survival rate of experimental 'eyed' sea trout eggs in natural redds. Estimated mean survival from 'eyed' egg to fry in experimental boxes reached 34-36%. However, it is not possible to use this estimate to judge about natural survival rates in the stream. Several restrictions are valid for present results. Firstly, in the experiment not complete incubation from egg fertilization was determined. Survival rate from fertilized to the 'eyed' sea trout eggs was found to be generally high, when incubated in similar experimental boxes (Rubín & Glimsäter 1996), while it may vary significantly depending on the incubation conditions (Chapman, 1988; Julien & Bergeron, 2006). Secondly, as argued by Chapman

(1988), incubation in boxes does not represent precisely natural incubation conditions. The third restriction is that experimental eggs were collected from wild broodstock from other, Jūra River, basin; and this may introduce some biases. There was estimated significant genetic differentiation of Lithuanian sea trout population between rivers systems and within the same river system (Samuilovienė et al., 2009), what indicates that populations are likely structured into distinct breeding units. Maternal effect can be important contributor to the phenotypic variation in offspring early life stages appearance, which may be environmentally mediated, but may also have a genetic basis (Donaghy & Verspoor, 1997; Einum & Fleming, 2000). The only conclusion from the results of incubation experiments is that the natural incubation success in the stream definitely will be not higher than the estimated survival rate (<30%).

Meantime, valuable result of present work is the mean natural outcome from the redd, which was *c.* 300 emergent fry individuals. This seems satisfactory number for lowland stream with considerable sedimentation extent. There are not much comparable results from natural emergence evaluation studies. Ingendahl (2001) estimated 477 fry redd⁻¹ (0-1723) from natural sea trout redds in tributaries of river Rhine, with survival rate *c.* 11%. Dumas & Darolles (1999) determined 502 fry redd⁻¹ for Atlantic salmon in Pyrenean rivers, with estimated survival rate of *c.* 13%.

6.2. Fry emergence ecology

Detailed two years emergence study gave much information about sea trout emergence timing and patterns in a temperate region lowland stream. Significantly different beginning of emergence was observed for the investigated redds between the two years. Timing of salmonid fry emergence is the evolutionary adaptation to emerge at the optimal time into the most suitable conditions (Einum & Fleming, 2000; Armstrong & Nislow, 2003) and is determined, to a large extent, by the time of spawning in late autumn when the eggs are fertilized and the water temperature within redd during incubation

(Crisp, 1988; Donaghy & Verspoor, 1997; Beer & Anderson, 2001; Armstrong & Nislow, 2006). The spawning in both years took place at very similar time: in mid-November in 2008 and in the beginning of November in 2009; and in both years emergence started at about 500 accumulated degree-days. The length of incubation period was related to different meteorological situation in the two years. In 2008, the winter was unusually warm, the stream has ice cover only for approx. one week, while in 2009 winter was considerably colder with periodic ice cover for about a month (thus water temperature of ~ 0 °C). Elliott et al. (2000) found that sea trout fry emergence in a small stream of U.K. correlated significantly with general climatic patterns (North Atlantic Oscillation). Median emergence date in this stream over the 30 years ranged between April and May, and is similar to presently determined for Blendžiava Stream.

There was considered that *Salmo trutta* fry emergence in Lithuanian rivers occurs in March-April (Sukackas, 1956; Gaigalas et al., 1992; Virbickas, 2000). However, until now there were no observations made on salmonid fry emergence and the exact timing and patterns of swim-up from the redds were unknown. Present results revealed that timing of emergence, adapted from other temperate region salmonid populations, was not accurate, even considering earlier started emergence in 2008.

The dynamic of emergent fry body condition was determined during the whole emergence period. Early emergent fry were the smallest and with highest amount of yolk-sac. The size of early emergent fry decreases with subsequent potential ecological disadvantages as predation risk and limited abilities to resist the strong flow (Brännäs, 1995; Einum & Fleming, 2000; Armstrong & Nislow, 2006). Although early-emerging offspring may incur heavy predation initially, they may subsequently outcompete later emerging conspecifics and incur reduced predation because of their greater size resulting from early growth (Brännäs, 1995; Armstrong & Nislow, 2006). Thus, a trade-off exists between early and late emerging, and this trade-off is likely affected by female phenotype (Fleming, 1996).

Most of fry from individual redd emerged synchronously during the peak emergence (25-75%) which usually lasted several days in a whole long emergence period. Peak emergers were characterized by the optimal body condition with the greatest length and body weight, while still having some yolk reserves left. The average yolk amount of emergent fry was 3.1% and 4.5% in 2008 and 2009 respectively. The remaining yolk of <5 % may be reasonably consider as the trigger for the individual emergence initiation. Remainings of yolk may buffer the critical transitioning process from internal to external feeding (Armstrong & Nislow, 2006).

The late emergers (>75% of cumulative emergence) were characterized by depleted yolk sac and low body condition factor. There was no significant difference in body length, yolk amount and body condition factor between the two late emergence stages (75-95% and >95%), while there was evident decreasing fish wet and dry weight. When the yolk is depleted, fish starts to lose mass, primarily due to the use of protein from muscle as an energy source. It has been reported that white muscle is the amino acid and energy store for other tissues during starvation periods (Houlihan et al., 1986). Worsening body condition in the end of emergence period was reflected by decreased condition factor K and by the negative allometric growth, according to length-weight relationship of emergent fry (Fig. 25). Regression coefficients b of length-weight relationship were less than 3 for both years, and this indicates that fish with increasing length becomes thinner, its body elongates (Froese, 2006). This is related to the decreasing yolk-sac, but also to the decreasing weight of white muscles, indicating starvation (Kamler, 2008). Therefore the end of emergence period is critical for late emerging fish, and obstruction for emergence, such as poor substrate quality, becomes even more important.

Delay of emergence was demonstrated to be related to the cues of predators (Mirza et al., 2001; Jones et al., 2003), high amount of sand in the redd (Hausle & Coble, 1976). Other possible explanation may be a slower development of some fry within redd due to micro-scale variation in incubation conditions. When water

temperature increases sharply after spring flood, the development and yolk absorption increases as well, what leads to a less efficient utilization of yolk and smaller body size (Ojanguren et al., 1999; Kamler, 2008). Migration through the substrate to the surface requires a lot of energy from fry, which in case of starving late emergers will be gained by metabolizing muscle proteins. To recover fry need initiate external feeding soon after emergence, while this is critical process and not all emergent fry successfully initiate feeding (Skoglund & Barlaup, 2006).

Little is known about the feeding ecology of salmonid fish between hatching and emergence when dwelling within redd substrate (Williams, 1980; Armstrong & Nislow, 2006; Skoglund & Barlaup, 2006). Alevins of salmonid fishes rely on yolk-sac reserves during the intragravel developmental period and usually do not feed externally, till emerge to substrate surface. Skoglund & Barlaup (2006) found that 29% of pre-emergent brown trout fry, having less than 10% of yolk-sac left, had initiated feeding in river of western Norway. In present study, 26-28% after emergence caught fry of later emergence stages (>75% cumulative emergence) had food in their digestive system. This food is considered to be consumed within less than 12 hours after emergence. Salmonid fry emerge generally at night (Bardonet et al., 1993; Riley & Moore, 2000), while the traps were usually emptied in the first-half of the day.

Late emergers, additionally to low body condition, have many ecological disadvantages as the severe competition for the resources with early emergent and feeding territories established congeners (Brännäs, 1995; Bujold et al., 2004; Armstrong & Nislow, 2006). As shown in Fig. 33, the size differences between last emergers and early emergers may be dramatically large; and late emergers have few possibilities in direct competition with large rivals.

6.3. Initial dispersal of juveniles in the stream

Dispersal of fry in the stream after emergence is complex behaviour, controlled by different factors, which are poorly

understood (Webb et al., 2001). This was reported to be specific rheotactic behaviour of salmonids, to migrate downstream to the rearing areas seeking out suitable rearing territories (Nagata et al., 1994; Bradford & Taylor, 1997). Dispersal (mainly downstream) were often addressed to compulsory drifting downstream due to displacement by high water velocities (Ottaway & Forrest, 1983; Daufrensne et al., 2005) or forced by intense intra-cohort competition for the resources (Elliott, 1994; Johnsson et al., 1999; Bujold et al., 2004; Skoglund & Barlaup, 2006).

Preliminary study conducted in Blendžiava Stream to evaluate dispersal of juveniles during first two months after emergence, revealed that dispersal extent was generally low, restricted to the native spawning habitat.

Emergence and dispersal often coincides with spring freshets when newly emergent fry, being weak swimmers, may be displaced downstream by strong currents (Ottaway & Forrest, 1983; Bradford & Taylor, 1997; Daufresne et al., 2005). In Blendžiava Stream emergence occurred at the low water level periods (Fig. 22a), when flow velocities were generally low. The newly emergent fry were seen freely swimming in the vicinity both upstream and downstream to the redds. Later in summer 2009, water level was also very low (Fig. 2), therefore it is not likely that initial sea trout dispersal was affected by high flow velocities.

After emergence from the native redd salmonid fry enter critical period for survival, called early critical period (ECP) (Elliott, 1989; Armstrong & Nislow, 2006). This phenomenon has been studied in the population of sea trout in a stream in the English Lake District (Elliott, 1989; 1994). Competition during this period is intense and failure to obtain territories is likely to reduce survival considerably, since 1-2 % of the fry may survive the first month after emergence. There was a clear period of exceptionally high mortality up to *c.* 65 days after emergence (Elliott, 1994). Density-dependent processes regulate juveniles' survival, growth and dispersal during this stage. To avoid competition for essential resources (shelter, food) juveniles disperse in the stream to acquire unoccupied feeding territory

(Armstrong & Nislow, 2006). It was proven, that drifting downstream Atlantic salmon fry was of lower body length, weight and condition factor comparing to the resident individuals (Bujold et al., 2004), what indicates that downstream drifting smaller individuals loose the competition for the territories (Johnsson et al., 1999; Bujold et al., 2004; Skoglund & Barlaup, 2006).

Beall et al. (1994) found that most of Atlantic salmon fry migrated up to 400 m downstream during early dispersal following emergence, while after two months fry were found dispersed up to 2400 m downstream and 750 m upstream, with most population established within 900 m. Garcia de Leaniz et al. (2000) reported 2.5 m day⁻¹ rate of initial dispersal for Atlantic salmon fry. Meantime, Egglshaw & Shackley (1973), Gustafson-Greenwood & Moring (1990) observed very limited dispersal extent for Atlantic salmon fry, exhibiting strong residence over redds. In one month after emergence fry established territories within 5 m upstream, downstream and laterally from the redd (Gustafson-Greenwood & Moring, 1990).

Dispersal in the stream is related to increased predation risk (Madsen, 1995, Bujold et al., 2004), therefore this behaviour may be not preferable by young fishes. In the Blendžiava Stream juveniles have relatively few potential predators. The two potential predators on young sea trout are older trout (>0+) and bullhead, while their densities are low in the stream (Nika unpubl. data).

Presently, the maximum recorded dispersal distance within the investigated sections was about 200 m (maximum observed section length without redds); and probably is greater. However most fry resided close to the redd-sites, as 50-70 % of electrofished fishes were distributed in riffle and run type habitats with redds.

The only reasonable factor, to control sea trout dispersal, likely was availability of suitable habitats (Heggenes & Borgstrøm, 1991). Salmonid 0+ age parr occupy shallow stream-margin habitats, behind boulders, cobble and other shelter (Madsen, 1995; Gustafson-Greenwood & Moring, 1990; Armstrong et al., 2003; Bardonnet et al., 2006). Juveniles in our stream used the same habitats, mostly shallow moderately flowing riffle margins with different shelter; and avoided

deeper slowly flowing areas. When the redd was placed in relatively long riffle or run section with plenty of suitable shelter for fry, they exhibit stronger residence to the native sites. When redd was placed in short riffle type sections surrounded by deeper areas (as in BS study section), less fry resided in a native redd-site and dispersed more widely.

From this point of view, the placement of the redd by female may affect initial dispersal and survival potential. Strategy of redd placement in the front of the riffle type habitat may have an additional aspect of evolutionary adaptation, other than improvement of downwelling water flow conditions through the eggs. Dispersing away from the redd, fry begin to compete for resources and those, who are unable to establish a feeding territory, will have the ecological disadvantages, as the increased predation risk or dislodgement to less suitable areas. Therefore, redd placement in front of the riffle may increase reproductive success through likely improved survival of progeny after fry emergence, by widening suitable dispersal area downstream from the redd. Spawning activity therefore imposes spatial structuring on the initial distribution of progeny in the stream.

Rough calculations of post-emergence survival have been conducted. The estimated 0+ age juvenile density was related to the probable number of emergent fry in the study section. The probable fry number was calculated from actual emergent fry number per redd or using the average estimated number (300) for not investigated redds in the section. The approximate average post-emergence survival was 11% in the first two months. This number is considerably higher than that given by Elliott (1994), probably indicating underused carrying capacity of the stream and, in turn, weaker intra-cohort competition. Meanwhile the estimated post-emergence survival was different between sections, the highest being in BK section (*c.* 20%) and the lowest in BR section (*c.* 6%), giving suspicions about density-dependent effects. Statistically significantly larger parr individuals were found in BK section than in the rest ones. This supports the assumption of density-dependence processes, as at the lower population density, growth of individuals was demonstrated to be

better (Parra et al., 2010). From the other hand, different fish size might be related to the different growth potential due to habitat quality, food quantity and quality or to different length of growth period due unevenly distributed fry emergence timing.

Preliminary study revealed that period after emergence is important for sea trout, during which significant mortality may occur and regulate the population recruitment.

6.4. RNA:DNA ratio as an index of conditional status of early life stages of salmonids

The nucleic acid RNA:DNA ratio has proven to be a reliable estimator of recent growth and condition of larval and juvenile fish (Caldarone et al., 2006) and other organisms (Gorokhova, 2005). The ratio is based on the assumption that the quantity of DNA in somatic cells is normally stable, even during starvation, but the quantity of RNA, primarily associated with ribosomes, is closely related to the rate of protein synthesis. Thus RNA:DNA ratio is an indicator of protein-synthesizing potential of a cell (Bergeron, 1997; Buckley et al., 1999; Caldarone et al., 2006). Well-fed, active, growing individual should have a relatively high RNA to DNA ratio compared to a starving, inactive individual. The ratio has been shown to respond to changes in feeding conditions and growth after periods as short as 1-3 days in a variety of fish species (Buckley et al., 1999). The ratio has been used as an indicator of physiological status, growth and nutritional condition for various fish, mainly marine species (Bergeron, 1997; Buckley et al., 1999; Fonseca & Cabral, 2007).

This technique has been relatively rarely used for salmonid fishes and generally older individuals (smolt or adult stages) were investigated (Grant, 1996; Suresh & Sheehan, 1998; Arndt, 2000; Sveier et al., 2000). In present study RNA:DNA ratio has been used to assess fry conditional status at emergence. The tested hypothesis was that depletion of yolk-sac reserves in late emerging fry probably leads to a starving incident, what should be reflected in decreased RNA:DNA ratio comparing to earlier emerging individuals with some

yolk reserves left. Statistically significant results supported study hypothesis, as the last 5% emerging fry has lower RNA:DNA ratio than earlier emerging fry. Buckley et al. (1999) notes, that RNA:DNA levels are typically stable through the yolk-sac stage of larvae and decrease for a period of days after yolk absorption.

The fluorometric assay of nucleic acid is very sensitive to procedural details and choice of standards (Buckley et al., 1999). Several important factors should be accounted analyzing nucleic acids. Consistent subsampling of the specific tissue should be made for the results to be comparable. The piece of unthawed muscle was subsampled consistently from the dorsal muscles. Olivar et al. (2009) and Grant (1996) noted that muscle were the most suitable tissue to detect starved and fed conditions, because fasted fishes may obtain energy by mobilising proteins from muscle. White muscle is the amino acid and energy store for other tissues during starvation periods (Houlihan et al., 1986).

Larval and juvenile fishes usually have ratios >2 under optimal nutritional status (Bergeron, 1997; Buckley et al., 1999; Fonseca & Cabral, 2007), while enormous variation exist between species and study conditions, as example from 0.68 for bluegill under severe hypoxia (Aday et al., 2000) up to 20 for red drum under normal feeding conditions (Rooker et al., 1997). Presently determined RNA:DNA ratio for sea trout fry was on average 1.3 ± 0.3 and ranged around 1. Determined ratios for other salmonids were at similar level: 0.64-1.19 for Atlantic salmon mature parr (Arndt, 2000); 1.85-1.99 for rainbow trout parr and 1.1-1.3 for 19-days age alevin (100 mg weight) (Valente et al., 1998).

However, presently recorded RNA and DNA concentrations were very similar. It is unclear, do these low RNA concentrations indicate low protein synthesis pace, or indicate net degradation of RNA. Some unrehearsed violations of the analysis protocol, underestimated or degraded (during storing or transportation) RNA or overestimated DNA concentration might cause biases. However, as the samples were collected, stored and transported at the same time and under the same conditions, and consistent analysis protocol,

standards and chemicals were applied, the estimated RNA:DNA ratios could be used to test for between-group differences.

Preliminary results of the RNA:DNA analysis revealed that this advanced biochemical index was suitable to detect worsening of conditional status of last emerging fry, when standard morphological measurements did not indicate that. Using body condition measurements as total length and weight for determination of conditional status of salmonid emergent fry may not always be sufficient way to detect changes in somatic body condition. Biochemical methods are sensitive to short-term changes in body physiological processes and reflect the nutritional, conditional status of hours, days to weeks (Buckley et al., 1999; Belchier et al., 2004).

RNA:DNA has been used to detect effects of hypoxia for juvenile bluegill (Aday et al., 2000) or common carp (Zhou et al., 2001). Significant decrease in RNA:DNA ratio was detected under severe hypoxia treatment (1-2 mg l⁻¹) in both studies. As the development of salmonid embryos within redd substrate depends on yolk-sac feeding, they are all relatively of the same nutritional status at particular developmental stage. The temperature, oxygen concentration and metabolic wastes are the main factors affecting development rate, yolk consumption, metabolism, muscle development of embryos and alevins (Hamor & Garside, 1979; Chapman, 1988; Rombough, 1988; Matschak et al., 1997; Ojanguren et al., 1999; Finn, 2007). Therefore the RNA:DNA ratio method could be useful tool for assessing sublethal effects of hypoxia and metabolic wastes in salmonid alevins.

6.5. Could the lamprey affect pre-emergent salmonids?

Superimposition of redds by conspecific females is a common interaction in anadromous Pacific salmon (Heard, 1991; Fukushima et al., 1998; Essington et al., 2000), but can also be substantial in other salmonids, as brown trout *Salmo trutta* (Beard & Carline, 1991; Essington et al., 1998; Rubin et al., 2004). Interspecific reproductive interaction in terms of redd superimposition was intensively studied in

stream-resident salmonids (Hayes, 1987; Sorensen et al., 1995; Scott & Irvine, 2000; Taniguchi et al., 2000; Nomoto et al., 2010; Weeber et al., 2010), meantime, little is known about reproductive interaction between salmonids and other fish species.

Salmonids and lampreys (*Petromyzontidae*), phylogenetically remote fish groups, have many remarkable similarities in their reproductive ecology (Savvaitova et al., 2007). Like salmonids, lampreys are typical brood hiders, laying their eggs in streambed gravel nests (Kelly & King, 2001; Maitland, 2003). Because of the similar spawning habitat requirements and sympatry, spatial overlap of spawning sites between the two fish groups is likely, though such a phenomenon has rarely been reported. Gritsenko (1968) demonstrated that anadromous Arctic lamprey *Lethenteron camtschaticum* in Sakhalin enters the same rivers and lays eggs in the same spawning grounds as Pacific salmon. Indirect reproductive interaction between the sea lamprey *Petromyzon marinus* and Atlantic salmon has been reported in the Shannon River in Ireland. In May, spawning sea lamprey digs the same gravels as salmon and essentially cleans and prepares it for salmon to spawn later in the year (Meskell, 2000).

Presently, considerable superimposition of sea trout redds by *L. fluviatilis* and *L. planeri* was observed in a small lowland stream under sympatric conditions. The striking overlap in spawning habitat preferences between the three species (Table 15) is the main explanation for the high occurrence of phenomenon. Water depth, flow velocity and sediment size are generally considered to be the most important in-stream microhabitat variables in determining the spawning site selection of stream fishes (Manion & Hanson, 1980; Grabowski & Isely, 2007; Louhi et al., 2008), and these variables measured in spring 2008 are overlap significantly for sea trout, river and brook lamprey. Microhabitat variables of anadromous sea trout redds were more compatible with anadromous river lamprey microhabitat preferences than with those of stream-resident brook lamprey, yet these differences were not significant. Stone (2006) observed that spawning microhabitat criteria for anadromous Pacific lamprey *Lampetra tridentata* overlap with those for anadromous

Pacific salmon *Oncorhynchus*, and spawning microhabitat of Western brook lamprey *Lampetra richardsoni* overlap with those of the resident trouts. Similar preferences for spawning site depth, flow velocity and sediment size by different species of salmonids and lampreys could be defined on a much larger scale (Hardisty, 1944; Manion & Hanson, 1980; Morman et al., 1980; Bjornn & Reiser, 1991; Taniguchi et al., 2000; Takayama, 2002; Mundahl & Sagan, 2005; Jang & Lucas, 2006; Louhi et al., 2008; Nomoto et al., 2010). As correlations between reproductive traits of salmonids and lampreys are likely in more larger scales, the phenomenon of salmonid redd superimposition by lamprey spawners probably is not unique to the studied stream, but can be widespread throughout the sympatric occurrence range of both fish groups, or at least within the range of the presently studied species.

The essential factor in determining the spawning site selection for *Lampetra* spp. seems to be the streambed profile. All nests of brook lamprey and majority of those of river lamprey were placed at sites where the streambed locally rises in the downstream direction, creating a negative bed slope profile. Such a negative slope is an essential trait for pool-riffle transitional zones which were the most preferred spawning habitats for the three species. The nests of *Lampetra*, found in sections with positive or no overall gradient were still mostly associated with negative streambed forms at the microhabitat scale. Such a significant negative micro-scale bed profile is created by the redd structure of salmonids. Therefore, salmonid redds create suitable microhabitat conditions for lampreys to spawn, which put the redds under a higher susceptibility to be superimposed.

The superimposition rate in a particular reach was the function of spawning intensity (nest density and used area) of both sea trout and *Lampetra* spp. The highest superimposition potential is characteristic for anadromous lampreys such as river lamprey, which spawn in numerous groups and form expanded clusters of big nests (Jang & Lucas, 2006; present study). The extent of a redd superimposition by *L. planeri* is considerably lower due to their relatively small nest size, recorded in the present study (on average 3

% of the sea trout redd tailspill area). Despite such limited overdigging abilities, *L. planeri* placed their nests exclusively in front of the redd tailspill where the most likely egg pocket sites are located (Chapman, 1988; Grost et al., 1991). Vertical scouring potential of *L. planeri* in terms of nest pit depth was also low. The scouring depth of nesting *Lampetra* spp., however, is deeper than the established depth of nest pits, as in the preparation of the nest and laying eggs, lampreys lower vigorously vibrating tail several centimetres into the substratum and stir up the sand and gravel to move loose stones, gravel and fine material (Manion & Hansen, 1980, Kelly & King, 2001). Considering the measured mean depth of nest pit for *Lampetra* spp. (even considering greater disturbance depth), studied lamprey species would not be likely to significantly scour the egg pocket positions of anadromous *S. trutta* (DeVries, 1997). Significantly different depths of egg deposition by salmonids can prevent the negative effect of redd superimposition on reproductive success (Weeber et al., 2010).

In the present study, the spawning of both *Lampetra* species considerably coincided with the emergence of sea trout fry in both years. When emergence approaches, fry move upwards through the gravel and concentrate close to the gravel surface before the emergence (Heard, 1991; Skoglund & Barlaup, 2006; present study). Such pre-emergent fry positions are susceptible to the scouring, even by relatively shallow digging brook lamprey. Only few studies dealt with similar temporal overlap of reproductive processes. Taniguchi et al. (2000) reports the superimposition of autumn-spawning native charrs *Salvelinus* redds by introduced spring-spawning rainbow trout *Oncorhynchus mykiss* in Japanese streams, suggesting potentially negative effect of redd disturbance on alevins of *Salvelinus*.

Closely related sympatric fish species must have evolved mechanisms such as spatial and temporal segregation of spawning processes that limit negative reproductive interaction (Heggberget et al., 1988a; Grabowski & Isely, 2007; Savvaitova et al., 2007). The spawning of sympatric sea trout and *Lampetra* spp. was not spatially segregated; also, the incomplete temporal segregation between reproductive processes was evident over the two years studied.

Considerable temporal overlap of lampreys spawning with the emerging stages of sea trout resulted in vertical overlap between pre-emergent fry positions and nests of both *Lampetra* species, which suggests the likely effect of superimposition on pre-emergent and emerging stages of salmonids. The absence of spatial and lack of temporal segregation of reproductive processes, however, may indicate an absence or lack of negative outcomes of this interaction between the two studied sympatric fish groups. On the other hand, this interaction may be beneficial for salmonids. Further more specific research is needed to evaluate ecological implications that may result from this newly described aspect of reproductive interaction.

Several possible outcomes of redd superimposition by spawning lampreys are likely, which would differ in character (positive or negative) depending on the time of superimposition in regard to the developmental stage of salmonids.

The likely negative impact is the disturbance of incubating eggs, alevins or fry directly or by the disturbance of surrounding gravel when lampreys dig the nest and spawn. Vigorous stirring of gravel potentially can injure pre-emergent fry or alevins, though the sensitivity of pre-emergent fry stages to such mechanical effect is unknown. Meantime, the physical disturbance is particularly harmful for salmonid eggs between fertilization and the start of the 'eyed' stage (Crisp, 1990) and any significant movement during this stage can kill the embryos. Such negative impact is more likely to occur for spring spawning salmonids of Northern Hemisphere. Savvaitova et al. (2007) indicated a very similar spawning time of Arctic lamprey *L. camtschaticum* and anadromous rainbow trout in Kamchatka rivers. Trout spawn earlier, from the second half of May until the first-third of June while the spawning of lamprey overlaps that of the trout, but generally occurs two weeks later. Similar requirements for spawning sites were indicated for both species (Savvaitova et al., 2007), therefore spatial overlap in spawning sites and redd superimposition is likely. Negative interspecific reproductive interaction was observed in a stream of central Washington between the sympatric rainbow trout and bridgelip sucker *Catostomus columbianus*, when spawning of

these two species overlapped spatially and temporally (Murdoch et al., 2005). Superimposed rainbow trout redds by bridgelip sucker had lower egg survival to fry emergence comparing to the protected from superimposition redds.

Other likely negative effect may be the shift in fry emergence timing and patterns, when spawning activity of lampreys may cause the premature emergence or the dislodgement of alevin or fry from the substrate. Spawning lampreys can easily uncover and dislodge pre-emergent fry or may cause responsive emergence as a result of the surrounding gravel disturbance.

Described reproductive interaction also may have positive effect, when timing of lamprey spawning coincides with the emergence of fry, as in the present study. Superimposition of emerging salmonids positions may facilitate the emergence of fry from substrate clogged with excessive fine sediments, which entrap emerging fry and reduce the overall emergence success (Chapman, 1988; Bjornn & Reiser, 1991; Armstrong et al., 2003). Other indirect positive effect was evident in present study, when area of loose, free from sand sorted gravel which is formed as a result of nest construction by *L. fluviatilis* served as a shelter for newly emergent salmonid fry. Many of them were found in a redistributed unembedded gravel of some superimposed redds. Described spatial and temporal overlap may also affect reproductive success of lampreys, as emerged and actively feeding salmonid fry residing in the nest area or close to it may prey on later emerging and downstream drifting tiny *Lampetra* spp. larvae.

The described phenomenon of superimposition and its likely ecological consequences under certain conditions may significantly contribute to the reproduction success of salmonids at the scale of particular superimposed redd or at the scale of highly used particular stream section. Understanding the causes and consequences of interspecific reproductive interactions becomes more important for management and conservational purposes. Modifications to river systems, naturally or through artificially expanding ranges of closely related species or increases in their population size, may increase the likelihood and ecological significance of the phenomenon.

7. CONCLUSIONS

1. Sea trout preferred to spawn in riffle-type geomorphic channel units, with the most intensively used transitional pool-riffle zones (44–57 %), where downwelling of surface water into the streambed dominated. Fishes avoided pool-type channel units (9–13 %), where upwelling of groundwater dominated. The vertical hydraulic gradient was significant factor determining spawning microhabitat selection.
2. Egg incubation conditions were negatively affected by the upwelling of long-residence hypoxic groundwater. Relative dissolved oxygen saturation negatively correlated with the groundwater presence (increased ΔCND) in interstitial water ($P < 0.001$).
3. Estimated mean ‘eyed’ egg to fry survival in experimental boxes was 35.5 ± 30.4 % in 2008 and 33.8 ± 29.6 % in 2009, while the success of natural egg incubation will be lower (<30%). Mean ($\pm\text{SE}$) estimated natural yield of average redd (c. 2 m^2) in Blendžiava Stream is 299 ± 71 emergent fry.
4. Specific fry emergence patterns were observed: first 5% smallest premature fry with high amount of yolk-sac; peak emergers (25–75%) having optimal body parameters (large body size, largest weight and still some reserves of yolk); and the late (>75%) emergers with depleted yolk reserves, decreasing body weight and the lowest body conditional status. The very last emergers (>95%) experience starving conditions, as revealed by RNA:DNA ratio analysis.

5. Two groups of independently acting factors were responsible for success of egg incubation and fry emergence. The first group includes redd substrate structure and permeability, which affected 'eyed' egg to fry survival, and emergence efficiency and patterns. The second group includes physico-chemical parameters of interstitial water, related to the presence of hypoxic groundwater. Hypoxic intragravel conditions reduced egg to fry survival and modified emergence timing, causing premature emergence.
6. Dispersal rate of juveniles during the first two months after emergence was in general low, most caught 0+ age juveniles dwelling close to the redd-sites (up to 40 m). The dispersal distance increased with decreasing availability of suitable juveniles rearing habitats close to the spawning sites.
7. Considerable spatial and temporal overlap of reproductive processes between spring-spawning *Lampetra* lampreys and autumn-spawning salmonids was observed under sympatric conditions. High superimposition rate of sea trout redds by both river lamprey (up to 83%) and brook lamprey (up to 48%) was found, when the spawning intensity of *Lampetra* spp. was high. The occurrence of this phenomenon was the result of the considerable overlap in the spawning habitat preferences for the three species. Closely overlapped timing of lampreys spawning with the emergence of sea trout fry suggests a probable ecological effect of superimposition on sea trout in the pre-emergent and emerging stages.

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