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Effects of hydropeaking on the attached eggs of a rheophilic cyprinid species

Master thesis

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Annotation

Effects of artificial water fluctuations called hydropeaking on the detachment rates of adhesive eggs were studied using a rheophlic fish (asp *Leuciscus aspius*) as a model species. I attempted to relate egg density to abiotic conditions of the spawning ground and identify optimal conditions for the eggs. Egg densities were also studied during spawning season when hydropeaking occurred. In the experimental setup, egg detachment rates were tested with different speeds, substrate type and exposition time and critical conditions for the eggs were assessed.

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Contents

Abstract

Man-induced changes in the hydrological regime of lotic waters have a great negative impact on the riverine life. One of the most widespread changes occurs under reservoirs where hydropeaking management serves for socio-economical purposes, predominantly for creating electricity. However, the impact of the dynamic changes of water flow on the fish eggs is virtually unknown. In this study, we focus on the hydropeaking impact on the spawning ground of a rheophilic cyprinid fish, the asp *Leuciscus aspius*, selected as an example of a species that lay adhesive eggs in flowing waters. In the field part of the study, we mapped the association of the asp spawning ground to shallow depth (0.2 – 0.4 m) and fast flowing water (0.1 – 0.4 m*s^{-1}). Furthermore, we tracked the fate of the eggs on the spawning ground during their development and demonstrated their near disappearance, which may be related to several hydropeaking events that occurred on the spawning ground. Finally, we tested in the experimental setup whether the detachment rate of the eggs is related to water speed, substrate type and exposition time. The tests showed significant dependency of egg detachment rates on water speed and substrate type. The critical velocity for the eggs of model species occurs between values of 0.7 and 1 m*s^{-1}. Speed of water occurring on spawning ground during hydropeaking event is approximately fourfold higher than during off peak period, and the eggs are exposed to critical water speed, which ultimately affect their survival. Our data strongly suggest that eggs may be negatively impacted during hydropeaking and management applications are advised to protect the spawning ground.

Keywords: fish reproduction, hatching, wildlife conservation, river ecology, mortality

Introduction

Man-made reservoirs were and are still being built worldwide on the majority of rivers around the world due to their many socials benefits (Nilsson et al. 2005). Hydro power is an effective and widespread source of energy and as renewable source is generally considered environmentally friendly (Singh and Singal 2017). One of the advantages of hydropower is the ability to store kinetic energy in form of water and transform the water storage into electricity in the right time when the energy demands are high (Akinyele and Rayudu 2014). Nowadays, many rivers are under flow regulation regimes, especially in fast flowing mountain rivers such as in the European Alps (Schmutz et al. 2015). However, so called green energy has also its downsides in terms of negatively impacting the river ecosystem below hydro power plants (Bain et al. 1988; Kennedy et al. 2016; Vanzo et al. 2016; Bejarano et al. 2018a).

Various negative effects on river fauna and flora caused by artificial altering of river flow were described (Diplas and Shen 2010; Schmutz et al. 2015). In case of plant communities, the general effect of the hydropeaking is negative, although some groups of macrophytes had increased local biomass and coverage in flow regulated rivers and thrived under this regime (Bejarano et al. 2018a). Generally, the evenness of plant communities was reduced and destruction of plants by high discharge, dislocation or diversity loss of riparian plants in intensively hydropeaking rivers was described (Bejarano et al. 2018a, 2018b) In rivers where hydropeaking occurs, many of water insect groups, which lay their egg on the edge of the rivers, were unable to survive because of dewatering (Kennedy et al. 2016). Hydropeaking also causes artificial drift and potential deprivation of river benthic invertebrates (Bruno et al. 2013). Therefore, river vertebrates (predominantly fish) feeding on the invertebrates may be bottom-up limited by low densities of their invertebrate prey species (Power 1992; Dodrill et al. 2016).

Besides this indirect effect on fish fauna, hydropeaking was found to influence fish ecology also directly (Bain et al. 1988). Hydropeaking can impact vulnerable stages in fish early life history such as the eggs developing in spawning sites or freshly hatched larvae (Schmutz et al. 2015). One of the issue can be dewatering of spawning grounds (redds) when the river is off peak, which can cause high mortality of the eggs (McMichael et al. 2005; Grabowski and Isely 2007). Opposite effect on the fish early live stages may be caused by artificial increase of flow that triggers high drift downstream (Young et al. 2011). Flow fluctuations as well as temperature variations commonly connected to hydropeaking are factors causing stress, interruptions of spawning, altered hatching and migration of juvenile fish – all causing potential reduction of fish recruitment (Schmutz et al. 2015). In artificial channel with unstable current and substratum conditions, serious egg loss of spawned fish (dace, *Leuciscus leuciscus*) was described (Mills 1981).

Considering the negative effect of hydropeaking, it may be expected that particular reproductive guilds of fishes will be more vulnerable than others to effects of hydropeaking (Balon 1975). For instance, if we focus our attention on guild of rheophilic fishes (flowing water spawners) seeking open substratum for their reproduction, we can consider pelagophils less effected by hydropeaking, since their eggs are evolved to be taken by current and drift until hatch (Balon 1975; Stanley et al. 1978). Phytophilic group appears to be more vulnerable using macrophytes as their spawning ground, although partial protection from the fast laminar flow by macrophytes can be expected (Allan and Castillo 2007). Hence, likely the most vulnerable reproductive guild to rapid hydropeaking are lithophils with adhesive eggs attaching to gravel and stones, since their eggs have probably the highest probability to be washed away by increase of flow speed during hydropeaking.

As a lithophilic fish model for this study, we have chosen the asp, *Leuciscus aspius* (Linnaeus, 1758), large cyprinid predator originally inhabiting lowland rivers of Central and Eastern Europe (Kottelat and Freyhof 2007) and thriving also in many European reservoirs (Vašek et al. 2016). Asp migrate to fast flowing waters where they spawn on a stony and gravel substratum in the early spring (Šmejkal et al. 2017b). The majority of their eggs are laid at night (Šmejkal et al. 2017a, 2018), hence during the off-peak period if hydro power plants are present. Eggs are being released during the spawning in the water column and shortly after they attach to the substrate (Mills 1981) thank to modified zona radiata creating sticky structures over entire egg surface (Riehl and Patzner 1998). Juvenile fish migrate to slow flowing waters after hatching, and after reaching adulthood in their fourth to sixth year of life, they return to tributary for reproduction (Peterka et al. 2004; Říha et al. 2013; Šmejkal et al. 2017b).

There are several studies on flow regimes with hydropeaking effects river fish fauna (Schmutz et al. 2015), but detaching eggs from the substrate due to changes in the water flow regime occurring on the spawning sites was not yet been properly studied. In this study, we aim to i) identify the water current and depth in which our model lithophilic spawner preferentially lay its eggs; to ii) investigate whether the eggs are affected by the hydropeaking on the spawning ground in natural conditions and iii) to identify the detachment rates of the eggs in the on-peak conditions in the laboratory setup based on current speed, type of surface and exposition time.

Materials and methods

Study site

The study site is located in the Želivka River, the main tributary of the Želivka Reservoir (39 km long, 1602 ha), 49°578497’ N, 15°251671’ E, Czech Republic. The tributary hosts more than

2000 adult asp migrating from the reservoir in order to reproduce in the early spring (end of March to mid-April) (Šmejkal et al. 2017b). Two water power plants are placed approximately 12 km upstream, one on the Želivka River and on the Želivka tributary Trnava River. With objective to provide fast flowing water in the channel for canoe slalom trainings and races, hydropeaking occurred seven times during the asp reproductive season and egg development in 2018. This caused hydropeaking on the whole river downstream impacting also the study site (Figure 1).

Identification of spawning site and optimal velocity

Water speed was measured using FlowTracker2® (SonTrek, San Diego, USA). On approximately 150 meters of river where asp aggregates for spawning (Šmejkal et al. 2017b) we have defined 11 transects perpendicular to river flow and on each transects we measured speed of the flow 20 cm above bottom. We made at least 10 points of measurements per transect (every 1 or 2 meters). Measurements of water depth were taken simultaneously.

Assessing the effects of hydropeaking

Additionally, we used the same transects to estimate asp eggs densities on 9 April 2018. Activity of the spawning fish was known to us because of passive telemetry study on the asp presence on the spawning ground taking place simultaneously (Šmejkal et al. 2017b, 2018). In order to map the egg density, we used cameras capturing bottom surface of 0.09 m^2 every 0.5 or 1.0 meter, at least 10 points per transect. Egg densities of the whole spawning site were estimated from the transect survey. Eggs were counted using image processing software ImageJ 1.52i (ImageJ 2018). Pale spots in pictures were defined as eggs and counted if its size and shape corresponded.

Transect method was used to find out how the egg counts were affected by hydropeaking. Subsample of five transects with highest abundance of the eggs were examined repeatedly. The transects were located below the weir on its right side of the bank – between right river bank and islets. The egg density was investigated on 11, 16, 21 and 25 April 2018 between 9 am and 11 am.

On 16 and 22 April 2018 when hydropeaking occurred, turbidity measurements were made using Secchi disc (Preisendorfer 1986). We measured depth of disappearance of white parts of Secchi disc for human observer before and after hydropeaking event in the main tributary just below spawning site. Secchi disk measurements were done in main river during two days before hydropeaking and during or shortly after hydropeaking.

Experimental evaluation of critical velocity

Fish were caught on 8 April and transported to laboratory in České Budějovice in order to obtain eggs for the experiment. Asp were kept in same temperature of water as where they were caught (11 °C). Females were stimulated for ovulation by Ovopel (Unic-trade, Budapest, Hungary). All females started ovulating after 12 hours. The eggs obtained were fertilized by means of the "dry" method with semen from the batch sample obtained from 3 males (Vostradovský and Váša 1981; Targońska et al. 2008; Kupren et al. 2011). The water temperature in whole system during fertilization and for the experiment was the same.

In order to determine the influence of abiotic variables flow speed, substrate type and exposition time on the egg detachment rate, we performed experiment in which a modified Brett-type tunnel (Brett 1962, Enders and Scruton 2006) with adjustable flow ranging from 0 $m*s^{-1}$ up to 3 $m*s^{-1}$ was used for the experiment. The tunnel was made from PVC (120 * 8 * 8 cm length – width – height; Figure 2). Flow straightener was added at the begging of the tunnel to eliminate turbulences in the flow which could cause error in the measurement of flow speed. The Global Water Flow Probe was used to measure the water speed. Ten eggs were attached to 8*8 cm tiles with 3 different coarseness and 3 number of replicates for each speed and each time of exposure (excluding 2.5 $m*s^{-1}$ speed where longer time of exposure was not conducted) or in total of 18 replicates per speed including all substrate types and both times. Three types of tiles were designed to test the effect of substrate coarseness: smooth substrate with flat surface, medium with gravel of 2 – 5 mm and coarse with 70 - 120 mm gravel. Five different water speeds from 0.3 – 2.5 $m*s^{-1}$ were chosen according to spawning site water speed which were 0.16 – 0.34 $m*s-^{1}$ in normal off peaking condition (Šmejkal et al. 2017a) and discharge during hydropeaking was 3 - 6 times higher during hydropeaking according to data obtained from river authority (Povodí Vltavy) (Figure 1). Water speeds in laboratory experiment were measured using FlowProbe (Global Water, College Station, USA). The difference in detachment rates related to exposition time was tested in two-time treatments – 15 min and 60 min.

Statistical analysis

To investigate which abiotic factors are influencing asp egg density on the spawning ground, we used generalised linear models (GLM) to test explanatory abiotic variables water speed and water depth. Egg density counts used in this test were taken from measurements on 9 April closest in time to water speed and depth measurements conducted on 3 April. Density of the eggs was very low in many points of measurements, so we used Poisson family of distribution of errors. Analysis of variance was used to compare the GLM models. An interactive forward procedure based on the lowest possible Akaike information criterion (AIC) was used to select the best combination of variables (Hastie 2017).Non-parametric Spearman's rank correlation analysis was used to investigate correlation between date and egg densities measured during spawning season (Nian Shong Chok 2010).

In order to understand which factors cause asp egg detachment in laboratory, we used generalised linear models (GLM) testing the influence of individual explanatory variables on the number of detached eggs. As plenty of the measurements resulted in either all eggs detached or survived, we used quasibinomial family of distribution of errors. Water speed and time were treated as continuous variables and substrate type (surface) as a factor with three levels (smooth, medium, coarse). We used analysis of variance to compare the models and an interactive forward procedure to select the best combination of variables, based on the lowest possible AIC. R package gam was used to plot the models (Hastie 2015).

In order to recognise importance within levels of significant variables within the model, we analysed data by Kruskal-Wallis (substrate type and water speed), additional pairwise comparison using Wilcoxon rank sum test were done to see differences within the groups.

All statistical analyses were conducted in computer software R version 3.5.1 (R Development Core Team 2016). For visual presentation of the egg densities, depths and velocities on the spawning ground, we used software QGIS 3.4.2 (QGIS Development Team 2018) and GIMP 2.10.8 (GIMP Develepment Team 2018)

Results

Identification of spawning site and optimal velocity

Lowest average water speed in the spawning ground measured per transect was 0.08 m*s^{-1} and the highest was 0.38 m*s^{-1} (Figure 3). Average depth of water in the same transects ranged from 0.24 m to 1.02 maximum (Figure 4). Egg densities ranged from 0 to 1933 per m^{2}, with highest densities recorded below the weir, between the right side of the bank and the first island (Figure 5).

Egg densities measured on the study site were significantly dependent on water depth following by water speed. GLM with a single explanatory variable revealed that the egg presence is significantly influenced by water depth in a linear and even more a polynomial of degree two model and the water speed (Figure 6; Table 1). The lowest AIC for a model with a single explanatory variable was the one for depth presented as a polynomial of degree two. The strongest full model involved depth and water speed (Table 1).

Assessing the effects of hydropeaking

We recorded great loss of egg density during spawning season potentially related to hydropeaking events (Figure 1). Average egg density measured in 5 transects did not drop after first hydropeaking occurrence but increased probably due to strong spawning intensity of asp (from mean of 348 eggs per square meter on 9 April to 375 eggs per square meter on 11 April) but rapidly decreased after next hydropeaking events. On 12 April next hydropeaking occurred and egg density dropped extremely (38 eggs per square meter on 16 April). In next measurements on 21 and 25 April we counted on average 53 and 2 eggs per square meter where in between other hydropeaking took place (Figure 7). The average egg density negatively correlated with date of the sampling (rho = -0.417, p = 0.038), demonstrating rapid decrease of the egg density on the spawning ground.

Hydropeaking caused considerable decrease in water clarity. On 16 April we measured 175 cm Secchi depth at 11:50 am and only 60 cm at 1:20 pm at the same day. Similarly, on 22 April at 11:00 am the Secchi disc measured clarity was 135 cm and the same day at 7:00 am we measured only 60 cm again. This shows on average almost 63 % decrease of water clarity or increase of turbidity caused by hydropeaking.

Experimental evaluation of critical velocity

Water speed was the most significant abiotic variable causing egg detachment from tiles in the laboratory tests, but also substrate type had significant influence (Table 2, Figure 8). GLM with a single explanatory variable water speed revealed that the egg detachment is significantly influenced by water speed both in a linear and a polynomial of degree two model, and the substrate type (Table 3). The lowest AIC was in the case of polynomial of degree two water speed (Figure 9). Exposition time was not significant. The best full model was egg detachment explained by polynomial degree of two of speed and substrate type (detach ~ poly (speed, 2) + substrate).

Abiotic variable water speed had significantly different impact on the egg detachment rate (Kruskal-Wallis test: $\chi2$ (df = 4) = 35.046, $p < 0.001$), differences within speed level groups are presented in Table 4 by pairwise comparisons using Wilcoxon rank sum test. Critical change occurs between 0.3 and 0.7 m*s^{-1}. Types of substrate also provide different impact on the egg detachment rates (Kruskal-Wallis test: $\chi2$ (df = 2) = 12.429, $p = 0.002$), differences within types of substrates are presented in Table 5 by pairwise comparisons using Wilcoxon rank sum test.

Discussion

Our results demonstrate that extremely fast water speed occurring during hydropeaking may have potentially fatal impact on fish eggs laid in rivers exposed to artificial alterations of the water current. We found out that egg density is mostly dependent on water depth but also on water speed. During spawning season several hydropeaking events took place some of them exceeding normal discharge four times, almost equivalent water speed increase is expected (Vanzo et al. 2016). Water speed exceeding 1 m*s^{-1} on the spawning ground can have possibly fatal impact on attached asp eggs (in this speed 61.7 % eggs detached in total in our laboratory experiment).

Our field results showed high dependency on water depth but not so significant on water speed. This could be potentially influenced by the fact that water speed measurements were taken only near river bottom to investigate speed impacting attached eggs. Water speed more distant from bottom can be in this parts (where egg densities were high) faster and could possibly be more explanatory as speed chosen by spawners releasing their eggs in current and egg randomly attach to substrate (Mills 1981; Rosenfeld et al. 2011). Shallow fast running waters are usually more saturated with oxygen (Allan and Castillo 2007) so the demand for high oxygen level for asp eggs is expected.

In the experimental part of the study, we proved that speed has an impact on the asp egg detachment rates and water speed equal or higher than 0.7 m*s^{-1} detached on the average more than 66 % of the eggs. Different detachment rates for different types of tiles were also recorded, so we may expect that river substrate occurring on the spawning ground also has importance in the egg survival. Data demonstrate that in the particular species under study, critical change in water speed occurs between 0.3 and 0.7 m*s^{-1} and higher speeds do not increase the detachment rates substantially (Figure 7, 8) - especially in case of the smooth substrate, which is the most common in the river environment (Thomson et al. 2001; Allan and Castillo 2007). This implies that there is a threshold of critical water speed for the eggs somewhere between 0,3 to 0.7 m*s^{-1} dependent on the type of substrate. The studies dealing with hydropeaking are rarely focused on fate of the eggs, and focus instead on the adult fishes (Scruton et al. 2008; Young et al. 2011; Schmutz et al. 2015). The studies dealing with fish eggs focused on the off-peak periods, where eggs may suffer from dewatering (McMichael et al. 2005; Casas-Mulet et al. 2015).

The lab experiment in small artificial tunnel was not so complex as a real hydropeaking in a river for several reasons. The tiles used for the experiment were made with three different coarseness, but river bottom of the study site is much more diverse and therefore, the experiment simplifies the factors affecting egg survival. The river substrate consists of flat stones of various sizes, gravel, sandy parts, woody debris and scarce macrophytes (Vannote et al. 1980). In the experimental channel eggs were exposed to laminar current of constant speed but in the river the flow is more turbulent and variable in its speed and direction as water run over stones and bumps. Additionally, the eggs in nature are spawned above the river bottom and then are attached to the substrate to random places (e.g. can be attached on exposed surface or even behind stone where could be protected from the direct river flow; Mills 1981, Šmejkal et al. 2017a). On the other hand, we registered high increase of turbidity during hydropeaking meaning that much more of small particles are being scattered in the water and this could also potentially contribute to higher egg detachment rates due to higher erosion ability (Finger et al. 2006; Diplas and Shen 2010; Wang et al. 2013; Vanzo et al. 2016). High speed inducted from navigation operations can cause resuspension of sediments and dislocation of eggs with substrate and cause their destruction (Wolter and Arlinghaus 2003). Similar effects could be expected during some extreme hydropeaking evens. In the laboratory experiment, we only considered few factors in particular exposure time, coarseness of substrate and water speed. Future studies may investigate also pressure connected to water depth and shear stress (Rosenfeld et al. 2011), which may help our understanding of the processes influencing the egg detachment rates.

Studying the impact on fish may not be so often conducted due to methodological difficulties when assessing the damage done on the eggs, which we also found to be difficult in the river conditions especially due to increased turbidity, which disabled camera observation just after hydropeaking. It was impossible to visually monitor spawning ground during the hydropeaking and several hours after due to high turbidity (Anselmetti et al. 2007; Wang et al. 2013), which enabled monitoring only the day after hydropeaking occurrence. We took pictures of the bottom when water clarity was high, so we could recognise eggs with high certainty. The turbidity issue makes it impossible to estimate the real damage done by hydropeaking by visual methods, and spawning ground would be damaged by benthic sampling techniques. Egg densities and their decrease during spawning season and hydropeaking events may show us washing away majority of eggs. However, there is a lack of decrease after first hydropeaking, probably possible to explain by observation of very high number of females on the spawning ground in the nigh following the peak (M. Šmejkal, personal communication). Observed eggs may have been replaced by the eggs produced by new spawners.

The visualization of the egg densities on the spawning ground relies on the precision of the camera monitoring. In some pictures eggs could lay on top of each other in clutches or behind stone and then should not be visible in picture. However, we believe that the counting is precise enough to make good estimate of the egg densities on the spawning ground. Observed disappearance of the asp eggs during the spawning season could be described as a consequence of hydropeaking or explained by predation or combination of both (Paradis et al. 1996; Vanzo et al. 2016; Šmejkal et al. 2017a), but cannot be possibly explained by hatching of eggs because incubation takes longer time (Targońska et al. 2008). According to experiments of Kujawa et al. (1997) lowest time of hatching is 7 days in 17 °C water temperature. In our study site, water temperature increases gradually from 6 °C to approximately 12 °C, which implies hatching after approximately 20 days. All in all, according to our study, the management of the spawning ground is likely not optimal because of disappearance of the vast majority of the eggs.

Population of asp in Želivka Reservoir is being strengthened by stocking artificially spawned juvenile asp for several decades (Vostradovský and Váša 1981). During two season study which took place on Želivka reservoir in 2017 and 2018, stocked 0+ asp were marked and in control electrofishing, which was designed to estimate proportion of stocked individuals in the recruitment, almost none of the captured asp came from natural recruitment (Blabolil et al. 2018). This study therefore suggests very low success natural spawning. While the main cause may be the hydropeaking, the other important factor can be high concentration of migrating fish from reservoir to the tribute which occurs during spring period (Hladík and Kubečka 2003, 2004). Migrating fish are forced to stop by weir situated just above the spawning ground and their concentration may be increased on the spawning ground. This may lead to enhanced predation pressure on the asp eggs in comparison with freely flowing river without artificial barriers (Šmejkal et al. 2017a, 2018). On the other hand, this situation is common in many fragmented rivers and potentially affects also other rheophilous fish species.

The hydropeaking and restriction of cyprinid migration has been affecting the population for several decades (Křížek and Vostradovský 2002) and so their negative impact on asp population combined with long-term artificial stocking may occur. Generally, there is a strong evidence of lowering of the fitness of natural fish by stocking the captive bred individuals (Araki and Schmid 2010; Milot et al. 2013; Christie et al. 2014). Genetic adaptation caused by unintentional domestication selection can occur in single generation and be harmful for natural fish population (Christie et al. 2012). In our case adhesive ability of the eggs may not be favoured in environment of captive breeding, where asp eggs are treated with solutions of different types for example with milk or clay to remove adhesiveness and facilitate their successful development (Targońska et al. 2008; Kupren et al. 2011).

Problem of hydropeaking destructive effect on the fish eggs can probably occur in many other riverine systems where water flow is man-regulated. Potentially, fish with shorter hatching time may be less vulnerable due to lower exposure to hydropeaking than fish requiring several months to hatch (Gillooly et al. 2002; Targońska et al. 2008). The probability of egg loss is somehow higher in species with long development time, since one fatal hydropeaking may destroy all-year population recruitment (Crisp 1988). Developmental time of our model species is somewhere in the centre on this scale with approximate development time of 20 days (Kujawa et al. 1997). Potential management restrictions on the water regime are easier to achieve in species with short development time, if the spawning period is well defined.

Thanks to the long-term telemetry study, we have knowledge on the arrivals and departures of asp on the spawning ground, and it is possible to approximate the development time of the eggs (Šmejkal et al. 2017b, 2018). This information can be used to determine exact time when hydropeaking should be limited or at least decreased in its scale. Many species of fish at early life stage smaller then 40mm of total length are unable to withstand water flow speed of 0,6 – 1 m*s^{-1} for more than a few seconds (Wolter and Arlinghaus 2003), meaning that even hatched juvenile asp could be drifted by hydropeaking and possible harm to newly hatched recruits may be expected (Peterka et al. 2004; Wolter et al. 2004; Lagarde et al. 2017). Current speed can be lowered to suitable speeds for juvenile fish in some parts of river by creating small local bays (Wolter et al. 2004) and this application of potential purpose built structures in river (e.g. bays) could possibly lower hydropeaking impact on juvenile fish and some eggs. However, based on the mapping of the spawning ground, asp favours the highly exposed sites to flow for laying the eggs, and therefore only minority of the eggs would be protected by this measure.

Management applications and conclusions

As suggested in some of previous studies, lowering an amplitude of peaks can improve the situations for the spawning sites (García et al. 2011; Schmutz et al. 2015; Bejarano et al. 2018a). We recorded no difference between the two treatments of exposure time, so this finding potentially suggests that hydropeaking should be preferably done with smaller flow rate but could last longer time when certain amount of water is needed to be discharged. The flow speed in spawning site should be lower than 0.7 m*s^{-1}. We conclude that hydropeaking may have considerable impact on the egg survival on the spawning ground and should be eliminated at least in rivers where rare rheophilic fish species with adhesive eggs are reproducing. The demand for production of environmentally friendly electricity is high. Small scale hydropower plants in regime “run-of-river”, meaning that they have no dam or water storage, are less productive than large hydropower plants but new innovations in its technologies are being developed (Paish 2002). Considering environmental risks of hydropeaking, hydropower plants in regime “run-of-river” should be preferred environmental friendly solution in the future.

Authors’ contributions

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DB, MŠ and JK participated in the field work. MŠ, JK and DB designed the study. DB and MŠ contributed to the statistical analysis. DB and MŠ graphically presented data. DB wrote the first draft.

Competing interest

The authors declare no competing interests.

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Tables

Table 1: Generalized linear models of asp *Leuciscus aspius* egg density influenced by abiotic factors measured on the spawning ground (water speed, depth). The most significant single explanatory model of egg density is polynomial of degree two depth (*poly(depth,2)*) and strongest full model is with water speed added (in bold).

model	**Df**	**Resid. Dev.**	**P**	**AIC**
NULL (egg density ~ +1)	272	106855		106857
egg density ~ water speed	1, 27	105015	<0.001	105019
egg density ~ depth	1, 27	79143	<0.001	79147
egg density ~ poly (depth, 2)	2, 27	64156	<0.001	64162
egg density ~ depth + water speed	1, 27	77556	<0.001	77562
egg density ~ poly (depth,2) + water speed	**1, 27**	**64136**	**<0.001**	**64144**

Table 2: Presentation of data from lab experiment conducted in the flow tunnel: percentage of detached eggs of asp *Leuciscus aspius* and first quartile (Q_1), median (M) and third quartile (Q_3) presented for abiotic variables: substrate type (coarseness), exposition time (min) and flow speed (m*s^{-1}).

flow speed	coarseness									exposition time					
	smooth			medium			coarse			15			60		
	Q_1	M	Q_3	Q_1	M	Q_3	Q_1	M	Q_3	Q_1	M	Q_3	Q_1	M	Q_3
0.3	5	20	27.5	0	0	37.5	2.5	15	27.5	0	0	10	20	30	50
0.7	65	85	97.5	30	30	37.5	32.5	45	65	30	50	90	40	50	60
1	77.5	100	100	42.5	55	60	30	45	75	50	80	100	30	60	70
1.7	100	100	100	60	60	67.5	62.5	70	85	70	90	100	60	60	70
2.5	100	100	100	40	50	55	95	100	100	60	100	100			
total	55	100	100	30	50	60	30	50	75	30	60	100	30	50	62.5

Table 3: Generalized linear models of asp *Leuciscus aspius* eggs detachment in flow tunnel (*detach*) related to explanatory variables. Strongest model with single explanatory is polynomial of degree two water speed (*poly(speed,2)*) and the strongest full model of egg detachment is explanation of water speed (polynomial of degree two) and substrate type as factor (*subs factor*) (in bold).

model	**Df**	**Resid. Dev**	**P**	**AIC**
NULL (detach ~ +1)	80	45.763		46.481
detach ~ speed	1, 79	32.516	<0.001	33.952
detach ~ poly(speed,2)	2, 78	29.976	<0.001	31.864
detach ~ subs factor	2, 78	40.094	0.001	42.632
detach ~ time	1, 79	45.308	0.313	47.094
detach ~ poly (speed, 2) + subs factor	**2, 76**	**22.908**	**<0.001**	**25.659**
detach ~ poly (speed,2)+time	1, 77	29.913	0.6571	32.467
detach ~ poly (speed,2)+subs factor + time	1, 75	22.838	0.6152	26.184

Table 4: Pairwise comparison using Wilcoxon rank sum test for percentage of detached asp *Leuciscus aspius* eggs by water speed groups (P values). Significant P values are given in bold.

flow speed ($m*s^{-1}$)	0.3	0.7	1	1.7
0.7	**<0.001**	-	-	-
1	**<0.001**	0.4505	-	-
1.7	**<0.001**	**0.0190**	0.245	-
2.5	**<0.001**	**0.0383**	0.207	0.555

Table 5: Pairwise comparison using Wilcoxon rank sum test for percentage of detached asp *Leuciscus aspius* eggs by tile coarseness (P values). Significant P values are given in bold.

tiles coarseness	smooth	medium
medium	**0.002**	-
coarse	**0.021**	0.240

Figures

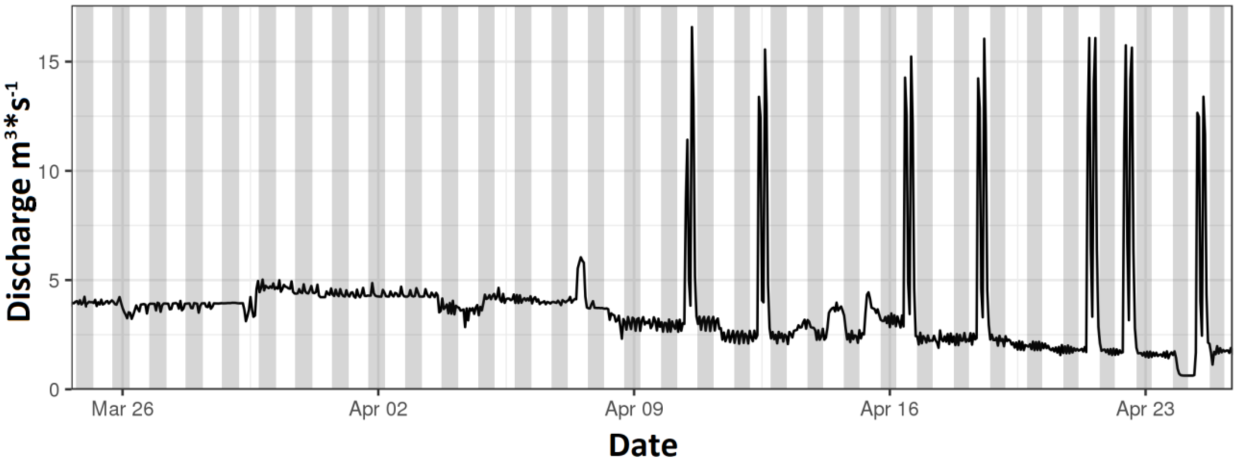

Figure 1: Water flow changes on the spawning ground caused by hydropeaking of water power plant Trnávka for canoe slalom purposes. White panels represent day and grey panels represent night. The water power plant is situated approximately 12 km upstream from the spawning ground. The hydropeaking in given day consist of two separate peaks, which affect the spawning ground for approximately for an hour starting around 12 am and 4 pm.

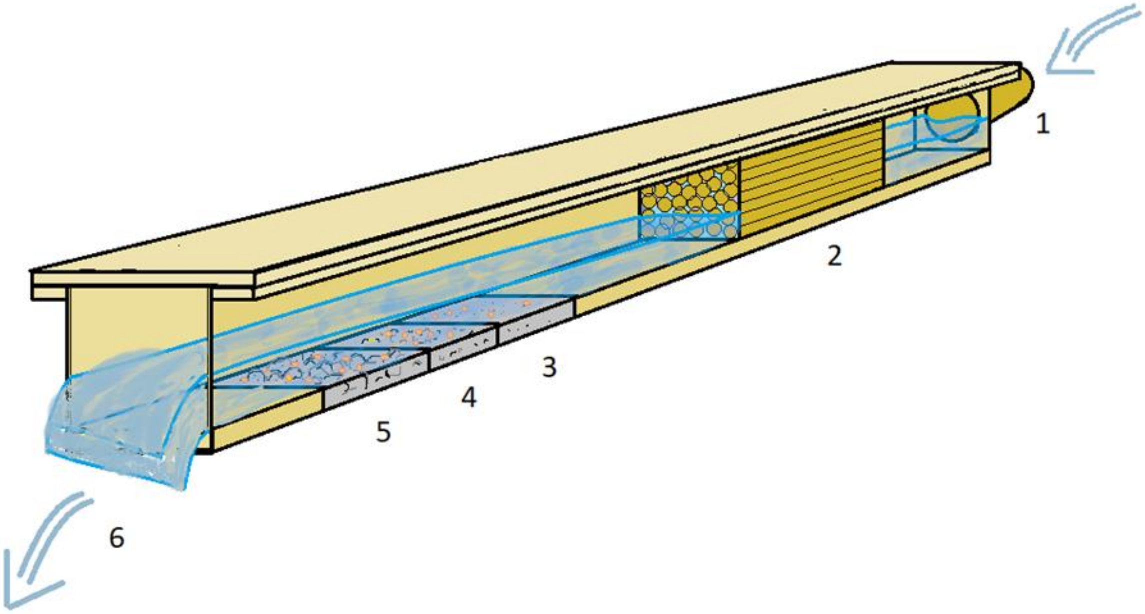

Figure 2: Flow tunnel graphical visualization. Description: 1 – water input from water pump with adjustable speed, 2 – flow straightener, 3 – tile with smooth substrate, 4 – tile with medium substrate, 5 – tile with coarse substrate, 6 – water output returning water to circulation.

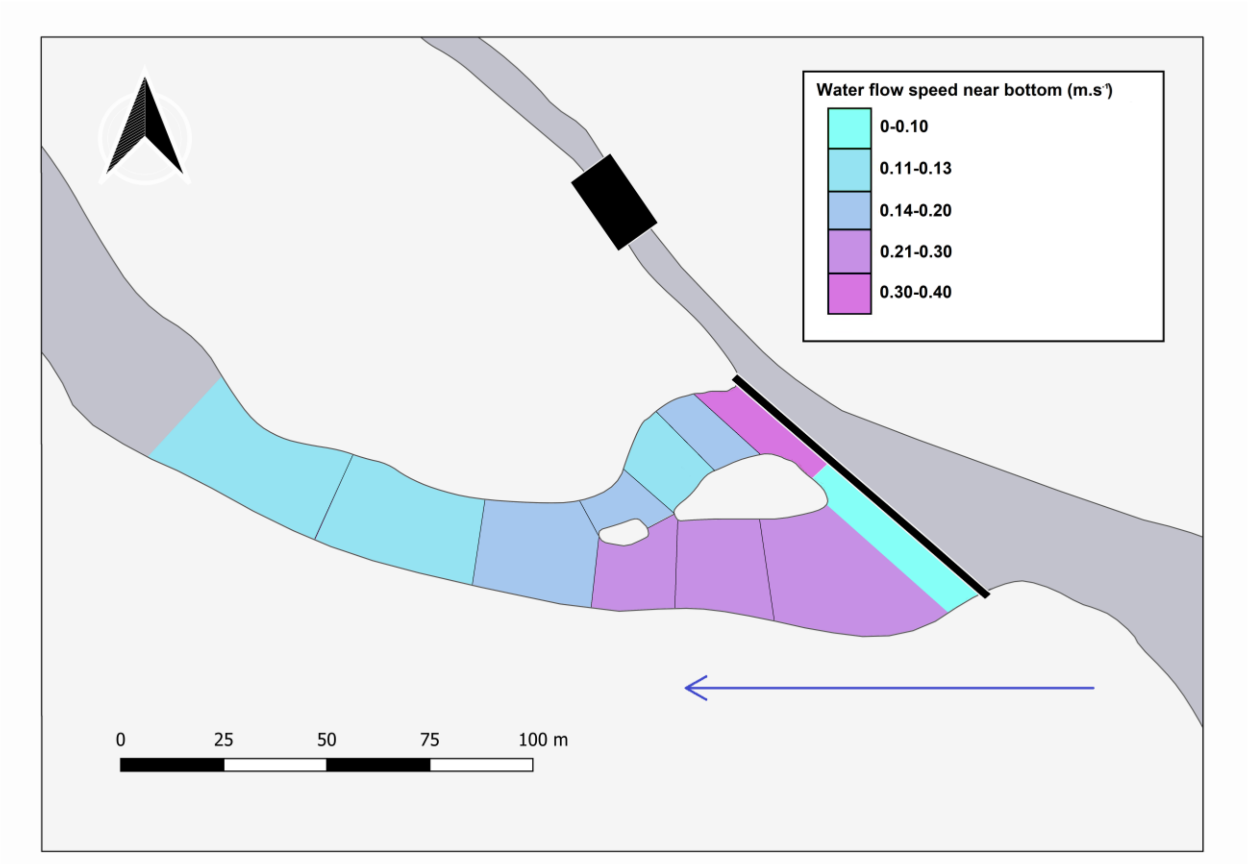

Figure 3: Map illustrates average water flow speed measured 20 cm above bottom. It was measured in off-peak situation recorded on 3 April between 1 pm and 4 pm. The highest flow speed is recorded just below weir near right river bank. The arrow shows the direction of the flow, main flow is going through measured area (in colour), the black rectangle in the top centre represents old watermill on millrace, where nearly no water runs through. The grey area represents the parts of river that was not investigated based on previous definition of the spawning ground (Šmejkal et al. 2017b).

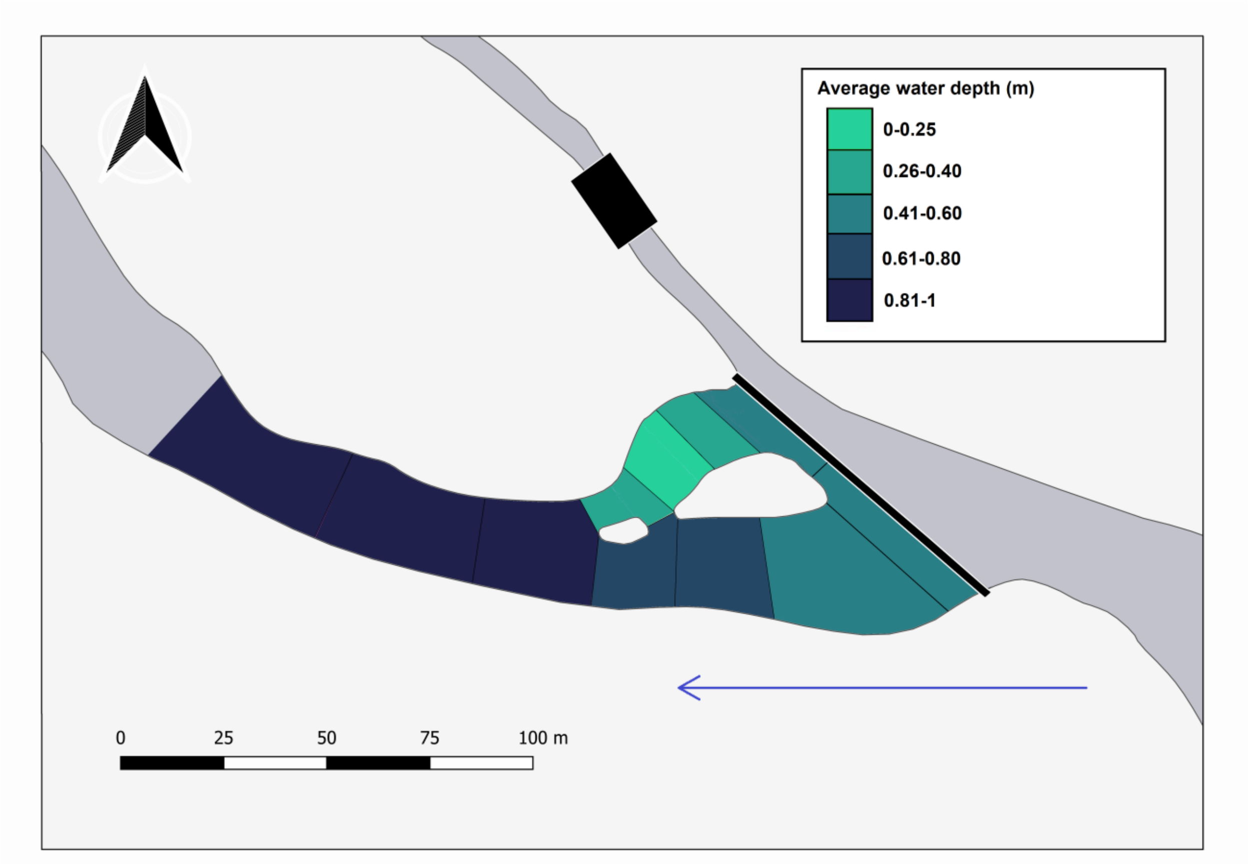

Figure 4: The schematic representation of the depths measured on the spawning ground during the off-peak period on 3 April between 1 pm and 4 pm. Lowest average water level was observed just below weir and between bigger islet and right river bank which is the same location where the highest density of egg was. See legend of Figure 3 for the detailed description of the scheme.

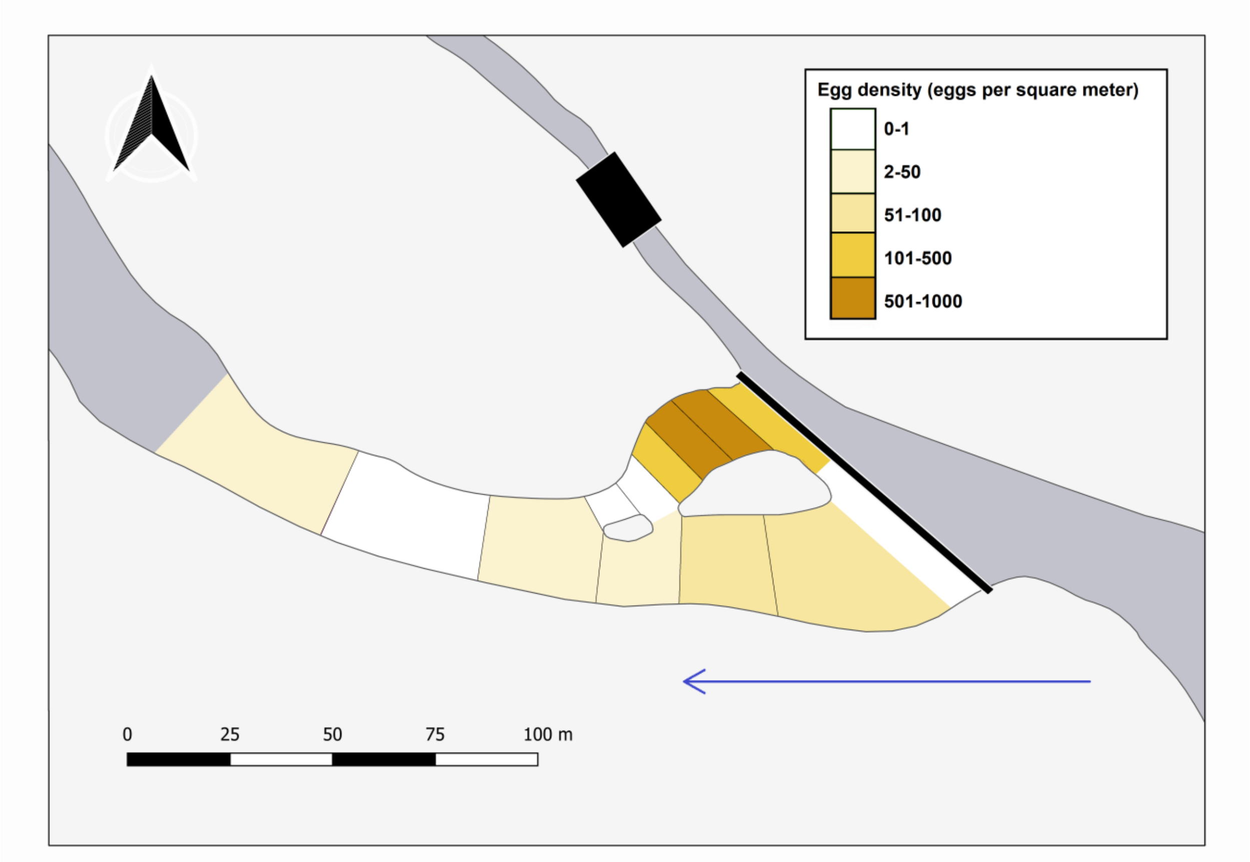

Figure 5: The schematic representation of the average density of asp egg recorded on 9 April. Eggs were counted from captured pictures of bottom of 0.09 m2 and then average egg densities per m^2 of transect were counted and colour scaled to areas shown on the map. See legend of Figure 3 for the detailed description of the scheme.

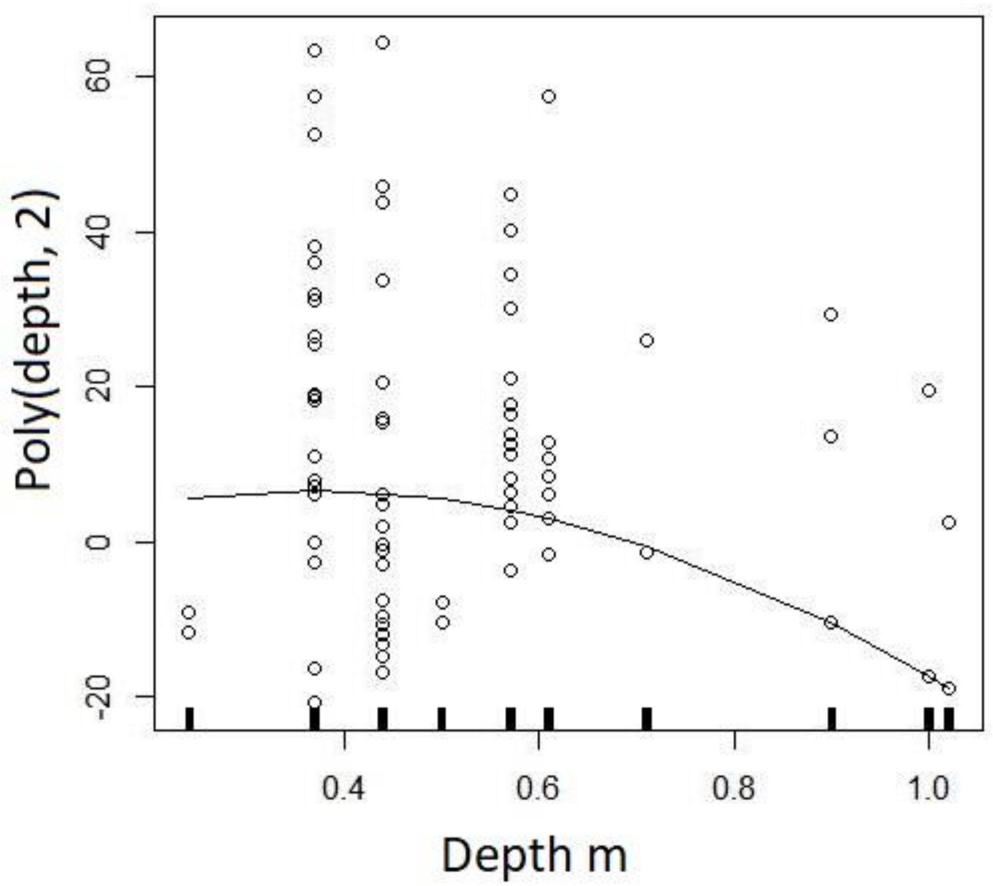

Figure 6: Polynomial of degree two regression of water depth and egg density (logit transformed) on the spawning site showing decreasing density in water deeper than 0.6 m.

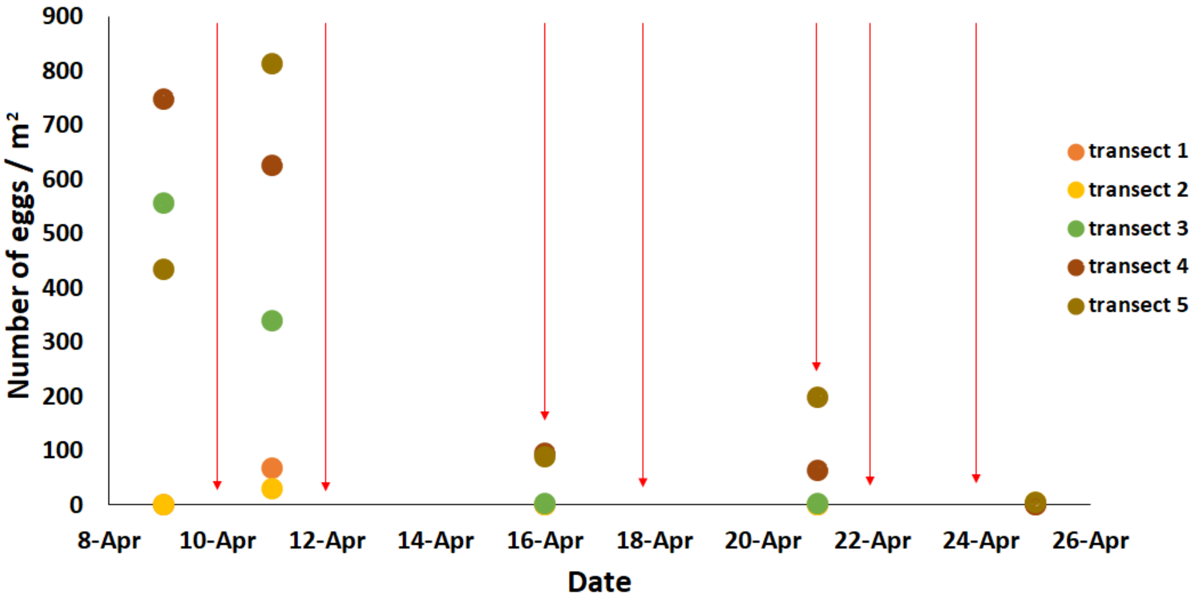

Figure 7: Representation of egg density in transects located on the spawning ground and their loss during season when hydropeaking events (presented as red arrows) were occurring.

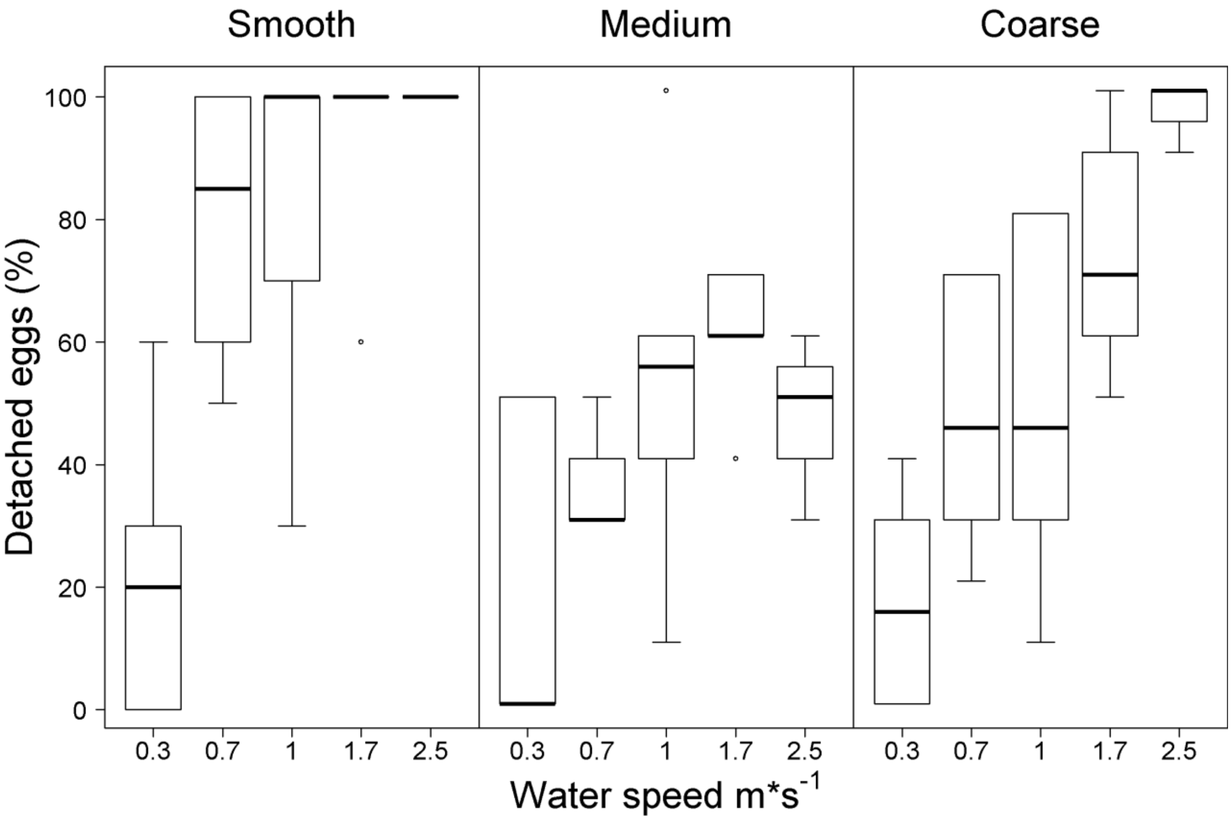

Figure 8: Percentage of detached eggs in the experiment under influence of significant abiotic variables water speed and substrate type. The boxes represent the boundaries of the upper and lower quartiles, the thick lines represent medians, the whiskers represent 95% confidence intervals and the dots outlying observations. Number of observations per treatment was 6 (3 in 2.5 m*s^{-1}).

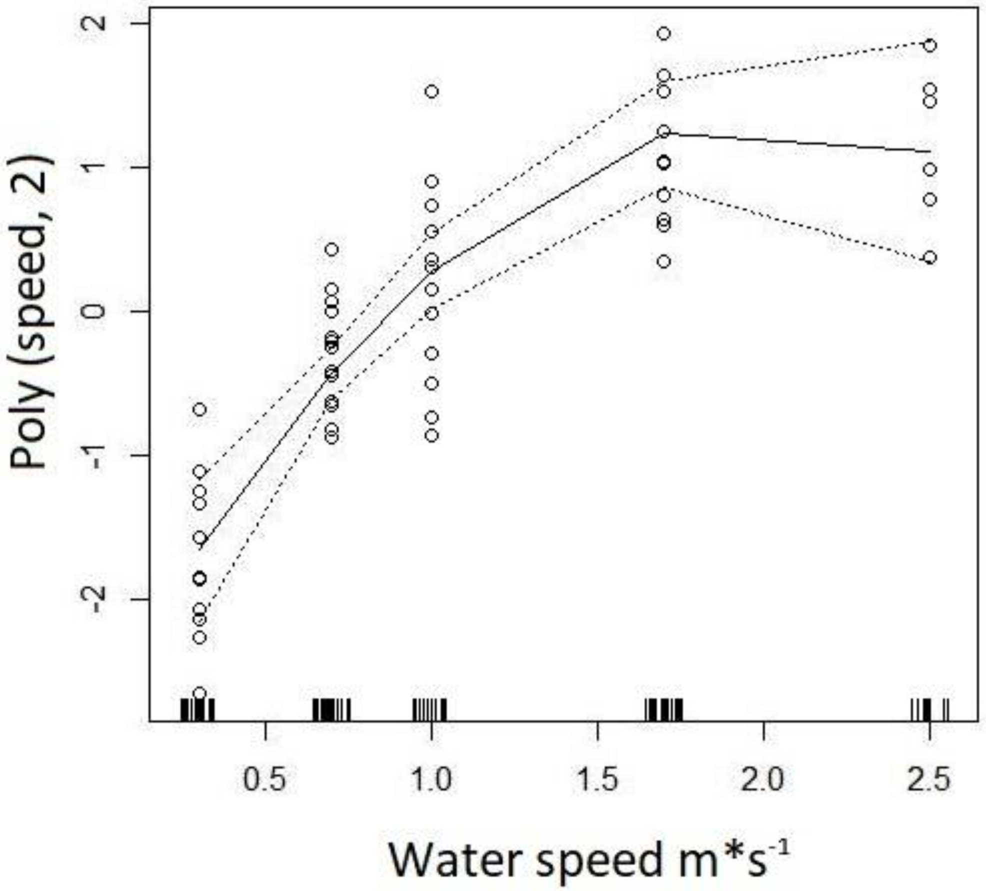

Figure 9: Detachment of asp egg (logit transformed) in laboratory experiment presented as polynomial degree of two regression dependent on water speed, demonstrating that detachment rate maximum is reached in 1.7 m*s^{-1}.