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CAN TURBULENCE STATISTICS REFLECT THE MESO-HABITAT CHOICE OF JUVENILE SALMONIDS?

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Variables commonly used to describe the physical habitat of Atlantic salmon *Salmo salar* L. parr are average velocity, water depth, and substrate. A variety of micro- and meso-habitat models have been developed using these variables to assess habitat quality. However, Atlantic salmon parr live in highly turbulent streams and rivers, in which intense fluctuations of water velocity occur. Laboratory experiments have shown that turbulence affects the behavior and energetics of fish. Nevertheless, habitat use in relation to the strong temporal variability of velocity in natural environments has rarely been studied. In this study, Atlantic salmon parr habitat was examined in relation to turbulence in the Patapédia River, Québec, Canada. We analyzed meso-habitat use in relation to several dynamic hydraulic variables. Our results revealed that in a natural turbulent condition, parr displayed high individual variability in habitat use in relation to turbulence. Such heterogeneous use of habitat suggests that individuals are not constrained to a single habitat type but that they have a tendency to use areas with lower turbulence.

INTRODUCTION

Distribution of Atlantic salmon parr *Salmo salar* L. in rivers and streams is strongly affected by the abiotic habitat [1]. Examinations of habitat suitability generally consider standard abiotic variables such as water depth, substrate, and mean and focal point velocity measured at the position of individual fish [2]. Parr are considered to choose focal positions that maximize access to food resources while minimizing energy expenditures [3]. The focal positions are situated close to the substrate [4] and are likely to be more turbulent than locations distant from substrate [5]. Recent laboratory studies revealed that turbulence may affect the abundance [6], energetics [7, 8], behavior [4], and distribution of stream-dwelling salmonids [9]. Juvenile salmonids seem to select focal positions characterized by lower turbulence intensities at equal average velocity [5, 9, 10].

Recent studies have demonstrated correlations between habitat features and turbulence [11]. These correlations may, however, change as a function of spatial scale. For instance, downstream from boulders and pebble clusters, which are used by fish as cover, turbulence intensity increases, and areas of strong vertical motion may be present on a micro-habitat scale [12]. On a meso-habitat or reach scale, turbulent flow patterns are dominated by large-scale flow structures occupying the entire water column, and these are controlled principally by the morphology of the river channel rather than by individual roughness elements [13]. These large-scale flow structures may be responsible for half of the turbulent kinetic energy and up to three quarters of the Reynolds shear stress [14].

In the past, it was believed that Atlantic salmon parr use only restricted habitats, but several radiotelemetry studies have recently demonstrated that juvenile Atlantic salmon parr may use much wider home ranges that can extend over an entire river reach [15]. Juvenile salmonids seem to take advantage of low turbulence areas on a micro-habitat scale [5, 6, 9], but does turbulence also affect the meso-habitat choice of juvenile salmonids on reach scale? In this study, we analyze the effects of turbulence on Atlantic salmon parr, regardless of the influence of the "standard" habitat variables of average velocity, water depth, and substrate. Turbulence variables only exhibit weak relationships with the standard habitat variables [11]. Since the effects of turbulence on fish are still unclear, our analysis included several hydrodynamic variables, such as standard deviation of the streamwise velocity, turbulent kinetic energy, Froude number, and shear stress, to identify the ones most relevant to the fish studied. Individual Atlantic salmon parr were tagged with radio transmitters, which allowed us to document the frequent repositioning (~ every 20 min). We then analyzed spatial variations in the distribution of parr in relation to turbulence. The objective of this study was to document and quantify the meso-habitat use of Atlantic salmon parr in relation to dynamic hydraulic variables. We tested on reach scale if Atlantic salmon parr preferentially use habitats characterized by lower turbulence.

MATERIALS AND METHODS

Study site

The study was conducted in the Patapédia River, located in the Restigouche watershed, at the border between Québec and New Brunswick, Canada (47°53'54"N; 67°27'54"W; Figure 1). The Patapédia River is a gravel-bed river characterized by riffle-pool sequences. Substrate sizes ranged from gravel to boulder. In the ~ 80 m long study reach, which was used by the studied individuals, mean river width was 30 m and maximum pool depth was 3 m. During the observation periods (21 August to 2 September 2003 and 18-29 August 2004), water temperature ranged from 7.6 to 16.3°C and 10.1 to 13.9°C and water level ranged from 1.38 to 1.43 m and 1.36 to 1.61 m, respectively.

Fish collection and surgical tagging procedure

Eight Atlantic salmon parr were captured in the river reach by electrofishing (Smith-Root backpack, model 12-B) in 2003 (n = 4) and 2004 (n = 4). Due to the mass of the radio transmitter (ATS Inc., model F1410, 40 MHz, trailing whip antenna, 1.0 g in air), parr larger than 28 g were chosen to ensure that ‘tag to body mass’ ratio was always less than 3.5% (Table 1). Studies analyzing the impact of radio transmitters on fish swimming performance have shown that the surgical implantation of radio transmitters into juvenile salmonids representing up to 12% of fish body mass did not affect their swimming performance [16, 17]. Fish were immediately anaesthetized in a solution of 2-phenoxy-ethanol of 0.2 ml·l^{-1}. Subsequently, fish were laid with their ventral side uppermost, on a molded tissue soaked with anesthesia. A midventral incision was made and a radio transmitter was inserted. The transmitter antenna was threaded through the body wall approximately 5 mm posterior and dorsal to the incision [17], and the incision was closed with two independent sutures (Vycril, 5/0, 3/8 c). After surgery, fish were allowed a short recovery (~ 5 min) in a holding tank before they were released close to their capture site. This short recovery period was chosen to reduce potential effects of postoperative care. For the first 24 h after surgery, fish were not tracked to exclude potential tagging effects.

Table 1. Fork length and body mass of Atlantic salmon parr selected for the radiotelemetry study. The ‘tag ratio’ represents the ‘tag to fish body mass’ ratio in percentage.

Fish ID	Fork length (cm)	Body mass (g)	Tag ratio (%)	Tagging date
1	135	30.4	3.3	21/08/2003
2	137	28.2	3.5	21/08/2003
3	131	28.2	3.5	21/08/2003
4	139	29.6	3.4	21/08/2003
5	143	36.2	2.8	18/08/2004
6	131	28.4	3.5	18/08/2004
7	135	29.3	3.4	22/08/2004
8	128	29.5	3.4	22/08/2004

Radio tracking

From 23-29 August 2003 and 20-26 August 2004, we tracked the fish every 20 min during two periods (0300-0800 and 1700-2200 EST). Fish were tracked with a radio receiver (ATS Inc., FieldMaster^{TM}) and directional loop antenna (ATS Inc.) using a triangulation method. Geo-referenced landmarks were positioned 10 m apart along the river bench of the study reach and equipped with a fixed north oriented graduated circle (see [15} for details). Parr were tracked from three different spatially referenced landmarks. Using the variation of power in the radio signal, the observer detected minimum signal strength, which corresponds to fish direction, and then determined the corresponding azimuth. These data were transmitted by radio to calculate and map fish positions via triangulation. Methodological testing with artificially placed transmitters demonstrated that the accuracy of the locations was within 2 m^2 in 90% of the trials.

Physical habitat assessment

After the 7-d tracking surveys, we conducted topographical surveys of the riverbed using a tacheometric station (Leica Geosystems AG, TC-805L). Velocity was measured using two acoustic Doppler velocimeters (ADV, Sontek), which allowed simultaneous measurement of the three-dimensional velocity components (streamwise u, lateral v, and vertical w) at a frequency of 25 Hz. A total of approximately 600 velocity time series were measured in each year within the 80-m long reach in which fish were observed. The velocity time series of at least 1 min [18] were taken 10 cm above the riverbed to avoid excessive bottom echo noise arising from the pulse signals rebounding off the heterogeneous gravel bed [19] along a 2-m by 2-m grid within the river reach.

Data and statistical analyses

The velocity time series were visually inspected to detect any anomaly in the signal. Velocity time series were then processed in WinADV (http://www.usbr.gov/wrrl/twahl/winadv) by filtering times series from data points with correlations of less than 70% and signal-to-noise ratios of less than 20 as suggested by the manufacturer and [20]

We used the following four variables to describe the turbulent condition: standard deviation of the streamwise velocity, turbulent kinetic energy, Froude number, and shear stress.

Standard deviation of the streamwise velocity (u_{SD}, $cm \cdot s^{-1}$, hereafter referred to as velocity fluctuation) was estimated as follows:

$$u_{SD} = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(u_i - \overline{u})^2} \quad (1)$$

where u_1, u_2,…, u_n are instantaneous streamwise velocities and $\overline{u}$ is mean streamwise velocity of a given velocity time series in $cm \cdot s^{-1}$.

The turbulent kinetic energy (TKE, $cm^2 \cdot s^{-2}$, hereafter referred to as kinetic energy) is a measure based on the sum of the variances of the velocity fluctuations of all three velocity components:

$$TKE = 0.5\,(u_{SD}^2 + v_{SD}^2 + w_{SD}^2) \quad (2)$$

where u_{SD}, v_{SD}, and w_{SD} are, respectively, the standard deviations of the streamwise (longitudinal), lateral, and vertical velocity components in $cm \cdot s^{-1}$.

The Froude number Fr is a dimensionless variable comparing the inertial forces to gravitational forces in the flow using the ratio of the mean streamwise velocity (measured at 0.6 times the water depth) to the water depth. In the present study, we calculated the bed Froude number (Fr_0, hereafter referred to as Froude number) using the ratio of the mean streamwise velocity close to the bed to the water depth.

(3) $$Fr_0 = \frac{\overline{u}}{\sqrt{g \cdot d}}$$

where $\overline{u}$ is the mean streamwise velocity measured 10 cm above the riverbed in cm·s^{-1}, g is the acceleration due to gravity in cm·s^{-2}, and d is the water depth in cm. Water depth and velocity are known to be important predictors of fish habitat quality [2]. Due to its dimensionless nature and significance in characterising flow hydraulics, the Froude number has been proposed as a single descriptor for hydraulic habitat modelling being more versatile than the use of water depth and velocity independently [21]. Furthermore, the Froude number is widely used in open-channel hydraulics as a powerful descriptor of the flow state and regime in streams.

Shear stress (τ, g·cm^{-1}·s^{-2}) is a common variable used to characterize sediment transport and deposition [22]. It is possible to estimate bed shear stress (τ_0) from the Reynolds stress as:

(4) $$\tau_0 = -\rho\overline{u'w'}$$

where ρ is water density in g·cm^{-3} and $\overline{u'w'}$ in cm^2·s^{-2} is the covariance between the streamwise and vertical velocity components. Positions of stream-dwelling salmonids are often associated with shear stress that occurs when water flows around pebbles and boulders [9]. With their streamlined body shape, salmonids are evolutionarily well adapted to severe velocities, velocity fluctuation, and may use shear stress and turbulence to their advantage while swimming head-on into the flow [7]. However, if flow is coming from behind or at extremely high levels (e.g., in hydroelectric turbines), shear stresses can lead to sublethal physiological effects on fish equilibrium, lift and tear off scales, pry open the operculum, rupture or dislodge eyes, and damage gills [23].

Maps of these four turbulence variables were created using linear interpolation in *Vertical Mapper 3.0*. Positions of parr were overlaid on these maps to examine the habitat use of individual fish in relation to habitat availability. Values of each hydraulic variable at the fish positions were extracted to compare the frequency distribution of habitat use and availability. We tested for differences between use and availability for each hydraulic variable using Mann-Whitney tests. Significance was set at the $p \leq 0.05$ level for all statistical tests, and Bonferroni adjustments were used for multiple comparisons.

RESULTS

Dynamic hydraulic habitat

We observed a wide range of turbulent conditions available to Atlantic salmon parr. Velocity fluctuation (u_{SD}) ranged from 0.0-30.9 cm·s^{-1} in 2003 to 4.6-25.4 cm·s^{-1} in 2004. Observed values of kinetic energy (*TKE*) varied between 0.0-954.6 cm^2·s^{-2} in 2003 and 22.6-765.9 cm^2·s^{-2} in 2004. Froude number (Fr_0) ranged from 0.0-0.6 in 2003 and 0.1-0.4 in 2004, respectively. Finally, in 2003 a 1,105-fold and in 2004 a 17,000-fold difference in shear stress (τ_0) were observed within the river reach.

Habitat use of Atlantic salmon parr in relation to habitat availability

The comparison of habitat availability in the river reach vs. habitat use by parr revealed that individual parr used a broad range of turbulence conditions in a relatively short period rather than stay in a restricted range of turbulence. Particularly in 2003, significant differences were observed between available and used habitat for all fish and all hydraulic habitat variables (Mann-Whitney U tests, all $p \leq 0.002$). However, habitat selection was inconsistent between individual fish. For example, parr 1 and parr 2 were observed in habitats with lower values for all hydraulic variables than in those with the most frequently occurring values. In contrast, parr 3 and 4 selected habitats with higher values for the hydraulic variables, which corresponded to more turbulent conditions (Figure 2a-d). During 2004, significant differences between available and used habitat were observed for only one parr with regard to velocity fluctuation. Parr 7 was observed in habitats characterized by lower velocity fluctuation than the average value available (Mann-Whitney test, $p < 0.002$; Figure 2a). No significant differences between available and used habitat were observed for kinetic energy (Mann-Whitney tests, all $p > 0.002$; Figure 2b). However, all four fish (parr 5-8) selected habitats with lower Froude number, and two (parr 6 and 8) selected habitats with lower shear stress than the average available (Mann-Whitney tests, $p < 0.002$; Figure 2c and 2d).

DISCUSSION

We analyzed habitat use of individual parr in relation to hydraulic variables that capture aspects of turbulence. This approach is based on recent studies that have shown that behavior and swimming costs of fish are affected by the intensity of turbulence [5, 7-9]. In our study, all four dynamic hydraulic variables used to describe turbulence revealed relevant habitat choices by parr. Fish preferentially used areas characterized by low to medium turbulence. Although most fish were observed over the entire range of habitat available, with few exceptions, they preferred lower Froude number and shear stress. Parr may choose areas of reduced turbulence to decrease their energy cost, as the energetic cost of swimming may increase with increasing turbulence intensity [8].

Habitat models for juvenile stream-dwelling salmonids have been developed on both a micro- and a meso-habitat scale [24, 25]. In gravel-bed rivers, the presence of roughness elements such as protuberant boulders affects turbulence only at a local scale and over short distances [12]. Recently, it has been shown that on a micro-habitat scale, juvenile salmonids select focal position characterized by lower turbulence intensities at equal average velocity [5, 9, 10]. Turbulent velocity patterns on the reach scale are dominated by large-scale flow structures occupying the entire water column, and these are controlled principally by the morphology of the river channel rather than by individual roughness elements [13].

Figure 1. Location of the study site in the Patapédia River, Québec, Canada (47°53’54”N; 67°27’54”W).

The present study indicates that on a reach scale or meso-habitat scale, a broad range of turbulence variables were used by individual parr indicating that individuals are not restricted to a single habitat type. It is likely that juveniles react on a smaller distances of cm to body lengths to flow heterogeneity. This scale was, however, unidentifiable at the resolution available for both fish positioning and the velocity measurements in this study.

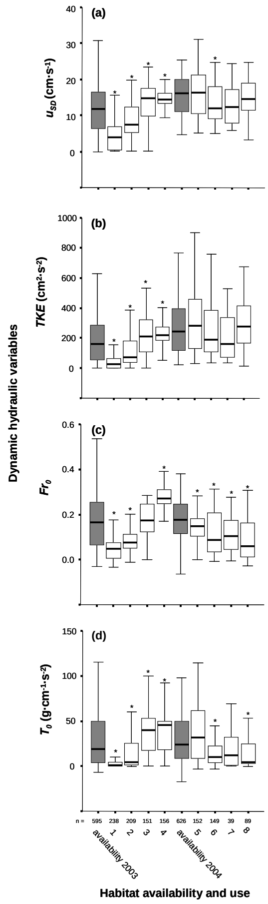

Figure 2. Box-Whisker plots of habitat availability in 2003 and 2004 (shaded symbols) and habitat utilization (open symbols) by eight Atlantic salmon parr (1-8) for (a) velocity fluctuation u_{SD}, (b) kinetic energy *TKE*, (c) Froude number Fr_0, and (d) shear stress τ_0. Significant differences between available and used habitat are indicated (*). Horizontal lines forming the bottom, middle, and top of each box represent the 25th, 50th, and 75th percentiles of each set of observations, respectively. The vertical lines at the bottom and top of each box extend to the values of the 5th and 95th percentiles, respectively.

Therefore, we can only speculate that Atlantic salmon parr may be using mirco-habitat refuges (e.g., behind protuberant boulders) characterized by reduced turbulence. Furthermore, the variability observed in habitat use among individuals with respect to turbulence may be due to other habitat variables, which may override habitat selection based on turbulence [26]. Alternatively, there may be a strong preference for specific turbulence characteristics, but an individual may be forced by competition to use alternative habitat characterized by flow conditions other than those preferred [27]. Whereas Atlantic salmon parr seem to react and respond to turbulence on a smaller micro-habitat scale, the application of dynamic hydraulic variables on reach scale seem not lead to a useful tool for fisheries and habitat managers.

There are intrinsic trade-offs in any study design, and in this study the principal trade-off was the additional data derived from intensive radio tracking, which was offset by the use of only a few fish. With a larger sample size, the cost would have been less frequent observations. However, the intensive radio tracking revealed that parr may be far more mobile than previously assumed [15]. Close tracking also indicated high variability among individuals in terms of both range size and habitat use. Sub-sampling of the mobility data obtained from Atlantic salmon parr demonstrated a significant loss in precision and accuracy of estimates on mobility patterns and home ranges [15]. Frequent observations were therefore necessary to fully describe parr utilization of space. Consequently, the intense survey of a small number of fish successfully contributes to the overall picture of Atlantic salmon parr habitat use. However, given the high variation seen among individual parr with regard to habitat use, a larger sample size will be needed to generalize about observed traits for the population, particular as only larger parr were studied due to the size of the radiotelemetry transmitter.

Future research should aim to analyze parr reaction and distribution in relation to variables that account for the spatial aspects of turbulence such as vorticity and eddy length on a micro-habitat scale. These variables have been shown to affect fish under laboratory settings [7]. However, determining the effect of a particular variable on fish habitat use is challenging, as fish habitat choices may be associated with multiple, correlated variables. For example, food availability is correlated with water velocity, which is in turn often correlated with turbulent kinetic energy [5]. Consequently, it is difficult to separate the effects of individual variables on fish behavior. Velocity represents a trade-off between food availability and energy costs related to holding in a desired position [28]. Thus, if parr select habitat to optimize the balance between energy gains and costs, they would choose areas of moderate velocity and relatively low turbulence that are close to faster velocities [29], which may explain the broad range of habitat use for individual Atlantic salmon parr documented in the present study. Furthermore, turbulence may affect the feeding behavior of parr. Parr seem to adjust to temporal variations in habitat conditions such as food availability on a reach scale [30]. The proportion of time used for feeding decreases with the mean and standard deviation of velocity [4]. However, on a local scale, parr may demonstrate only minor adjustments to habitat conditions with individual variation in habitat use primarily affected by dominance status [27].

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