

The feeding behaviour of juvenile Atlantic salmon in relation to turbulent flow

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(Received 12 September 2003, Accepted 8 October 2004)

The feeding behaviour of juvenile Atlantic salmon *Salmo salar* in the Sainte-Marguerite River, Quebec, Canada, varied with the characteristics of turbulent flow. Simulations indicated that juveniles would decrease their swimming costs during attacks by 19.8% in low and by 31.1% in high turbulent conditions by initiating movements in low-speed flow events. The real swimming costs did not differ from the swimming costs estimated for a situation where fish initiate their movements at randomly selected flow velocities. The juvenile Atlantic salmon did not seem to prefer low-speed flow events when initiating their movements. The proportion of time used for movements by fish decreased with an increase in the mean and the s.d. of the flow velocity.

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Key words: feeding motion; fish behaviour; juvenile Atlantic salmon; *Salmo salar*; turbulent flow.

INTRODUCTION

Bioenergetics models may be used to assess fish habitat quality by assigning values of net energy gain which fishes are expected to obtain while using specific habitats (Fausch, 1984; Vehanen *et al.*, 2000). Fish growth is expected to occur only in habitats with positive values of net energy gain where food energy intake surpasses energy expenditure. Therefore, it has been hypothesized that stream salmonids select microhabitats characterized by the presence of low flow velocities to minimize the energy spent on swimming and by the proximity of swift flow velocities providing invertebrate drift (Everest & Chapman, 1972; Fausch & White, 1986). Hence, the balance between the benefits and the costs of habitat utilization allows not only the prediction of fish growth under specific environmental conditions but also their spatial distribution (Fausch, 1984; Guensch *et al.*, 2001).

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Swimming costs are estimated by combining observations of fish behaviour under given flow conditions with models that adequately represent the cost of performing specific behaviours. The estimation of the costs of habitat utilization in rivers, however, is impeded by the lack of knowledge about the cost of swimming in turbulent flows (Enders *et al.*, 2003) and about the effects of flow turbulence on fish behaviour (McLaughlin & Noakes, 1998). Generally, the cost of performing a specific movement is estimated by the product of fish swimming speed, the cost of swimming at that speed and the time spent on swimming (Guensch *et al.*, 2001). The effective swimming speed is taken as the sum of fish apparent movement (relative to the river bed) and the average flow velocity at the location of the fish (Hinch & Rand, 2000). In gravel-bed rivers, however, stream-dwelling fishes live in highly turbulent flows. The structure of turbulence in gravel-bed rivers is dominated by a temporal succession of large-scale flow structures which extend over the entire water column. Large-scale flow structures consist of quasi periodic successions of high- and low-speed flow events of a duration ranging from 0.5 to 5 s. Measurements of these turbulent flow structures suggest that the flow velocity can change from three- to eight-fold relative to average flow velocity within 1 to 5 s (Roy *et al.*, 2004). Detection and use by fishes of low-speed flow events could greatly minimize their costs of habitat utilization. If fishes take advantage of low-speed flow events, the use of the average flow velocity at the location of the fishes to estimate their effective swimming speed can cause an overestimation of the costs of habitat utilization. Such a behavioural adaptation can be expected because it has been shown that fishes can perceive changes in flow velocities with the use of one class of lateral line receptors, the neuromasts, which detect pressure changes (Northcutt, 1997). This behavioural adaptation, however, may only be expected if the food distribution is similar between high- and low-speed flow events. Unfortunately, no data on the drift distribution on this fine temporal scale is currently available.

Juvenile Atlantic salmon *Salmo salar* L. were selected for this study because their natural habitat encompasses gravel-bed rivers characterized by highly turbulent flows. The behaviour of juvenile Atlantic salmon comprises so-called 'sit-and-wait' phases during which the fish swim just above the substratum, often at the downstream edge of a rock, used as a protection against the turbulent flow. The rock preferentially used by a territorial juvenile Atlantic salmon is referred to as its 'home-rock'. The sit-and-wait behaviour represents the largest part of the time budget of fish (>80%; Puckett & Dill, 1985). The juvenile Atlantic salmon intermittently perform 'attacks' that consists of upward movements from the river bed to the water column. These attacks are undertaken to capture drifting invertebrates (Kalleberg, 1958). The fish forage in a wide range of flow velocities (Wankowski, 1979) and experience, during these movements, rapid changes in the structure of flow. Thus, the juvenile Atlantic salmon live under conditions where it may be energetically advantageous to use low-speed flow events. As the fish may be sensitive to variations in the benefits and the costs of feeding in running water, they may modify their foraging behaviour accordingly.

The aim of this study was to observe and to analyse the *in situ* behaviour of juvenile Atlantic salmon in relation to the turbulent flow environment. This was achieved by testing three specific hypotheses: (1) the fish have a potential

energetic advantage of using low-speed flow events; (2) the occurrence of fish movements is related to low-speed flow events characterized by a low flow velocity; (3) the proportion of time used by fish to perform movements is related to the mean and s.d. of flow velocity.

MATERIALS AND METHODS

The hypotheses were tested by simultaneously filming the behaviour of stream-dwelling fish and recording the structures of the flow they experienced under natural conditions. This was performed for eight individual fish under a range of flow conditions. Each series of observations consisted of the recording of fish behaviour and of flow characteristics during 30 min.

SAMPLING SITE

Observations of fish behaviour and flow characteristics were made in the Sainte-Marguerite River, Quebec, Canada. The sampling site was a 500 m² riffle located c. 4 km from the junction of the Sainte-Marguerite River and the Saguenay River (48°15' N; 69°55' W). The river section at the sampling site had a width of 50 m at the bankfull condition. The mean \pm s.e. water depth at the home-rocks where fish were observed was 33 \pm 2.3 cm. The substratum of the river bed at the sampling site ranged from pebble to boulder, the median diameter axis (D_{50}) of substratum components being 60 mm. The water temperature was 19° C during the observations in 1999 and 22° C in 2000. All observations were made between 1000 and 1700 hours under sunny conditions (<20% cloudiness).

SAMPLING PROCEDURE

The behaviour of juvenile Atlantic salmon was recorded using a submersible stereocinematographic video system (Boisclair, 1992). The underwater cameras were installed where a snorkeller observed fish displaying intermittent feeding behaviour. The cameras were installed at 0.5 to 1 m from the location of the fish. This range of distance allowed the cameras to be sufficiently close to the fish to precisely record their movements and sufficiently far from the fish to film their complete trajectory during their most extensive movements. Fish were filmed for 30 min. The exact time of recording (h, min, s and ms) was assigned to each frame filmed by a time and day camera titler (TDCT, Panasonic WJ-410) for the later synchronization of the behaviour records with the corresponding flow velocity time series. Velocity measurements were carried out simultaneously to the recording by positioning the current meters at distances ranging from 4 to 9 cm to the fish. To ensure the synchronization of the behaviour records with the corresponding flow velocity time series, the current meters were turned on as the time code of the TDCT was initialized.

Observations were made during two periods (11 to 12 September 1999 and 26 to 28 July 2000) further defined as sampling periods I and II, respectively. Two different types of current meters were used for the two sampling periods. During sampling period I, three bi-directional Marsh-McBirney Electromagnetic current meters (ECMs) were deployed to measure the flow velocity in the vicinity of the fish [Fig. 1(a)]. The three ECMs were mounted vertically to detect the advection of high- and low-speed flow events (Buffin-Bélanger *et al.*, 2000). The ECM sensor head is 1.3 cm in diameter and allows sampling of velocity at a 20 Hz frequency. The diameter of the sampling volume is three times that of the sensor head (sampling volume = 31.1 cm³). The ECMs were set 8 cm apart on a vertical wadding rod. The lowest ECM was situated 4 cm above the fish's sit-and-wait position. Hence, the lowest ECM was able to record the focal point velocity of the fish as suggested by DeGraaf & Bain (1986) and Morantz *et al.* (1987). The setup did not disturb the fish. The juvenile Atlantic salmon stayed on their home-rock during the installation of the cameras and current meters or came back to their home-rocks within a

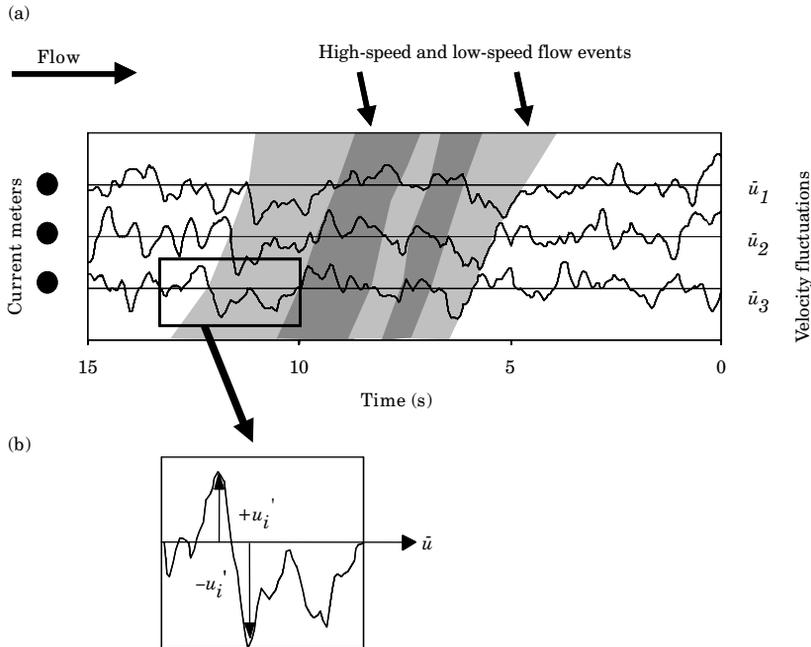


FIG. 1. Electromagnetic current meter (ECM) velocity time series: (a) velocity time series at three heights over the gravel-river bed measured synchronously with three ECMs (□, low-speed flow events stretching out over the entire water column; ▨, high-speed flow events) and (b) illustration of the fluctuating proportion u'_i and the average proportion \bar{u} of the velocity signal.

few minutes. The fish subsequently showed the same frequency of movements as before the installation of the instruments (χ^2 , $n=228$, $P=0.81$ and $n=128$, $P=0.48$, respectively). Using this setup, the movements of two fish (hereafter referred to as fish 1 and fish 2) were recorded for 30 min each. During sampling period II, a Sontek Field Acoustic Doppler Velocimeter (ADV) was used. The ADV has the advantage of having a smaller sampling volume (0.25 cm^3) located 5 cm away from the probe. Therefore, the focal point velocity of the fish was measured more precisely at a frequency of 25 Hz. With the ADV, however, only the focal point velocity was measured. Using this setup, a second series of observations was carried out and six films of 30 min were obtained from six different fish (hereafter referred to as fish 3 to fish 8) with synchronous flow velocity measurements.

CHARACTERISTICS OF TURBULENT FLOW

For each time series of flow velocity, four flow characteristics were described that differed in terms of the temporal scales used for their calculations. Two global scale characteristics (mean flow velocity, \bar{u} and s.d. of flow velocity, u_{SD}) were calculated using the velocity time series. The two fine scale characteristics were defined using events occurring at a temporal scale ranging from 1 to 4 s: the number of flow events in the time series and the duration of flow events. Time intervals during which flow velocity measures were continuously faster than \bar{u} over a time period >1 s were defined as high-speed flow events (Lu & Willmarth, 1973). Uninterrupted time intervals during which flow velocity values were slower than \bar{u} over a time period >1 s were defined as low-speed flow events [Fig. 1(b)]. The time intervals in between high- and low-speed flow events were defined as medium-speed flow events. Because fish may behave different while staying in low, medium or fast flows this specific data set (pairs of feeding motion and flow event) was classified for the further analyses into three subsets: low (fish 1 to 3,

$n = 3$, \bar{u} ranged from 25.1 to 27.8 cm s⁻¹), medium (fish 4 and 5, $n = 2$, \bar{u} ranged from 32.0 to 34.6 cm s⁻¹) and high (fish 6 to 8, $n = 3$, \bar{u} ranged from 46.1 to 49.2 cm s⁻¹) flow velocity conditions using \bar{u} (Table I).

CHARACTERISTICS OF FISH BEHAVIOUR

Each video-recording was visually analysed to detect and describe all movements undertaken by juvenile Atlantic salmon. For each movement, the time at which the fish initiated the movement and that at which fish returned to its initial location were noted (± 0.03 ms). Each movement was then divided into two phases: (1) the phase of attack (forward movement) and (2) the phase of return (return movement to the initial

TABLE I. Water depth, current meter used, mean flow velocity (\bar{u}), s.d. of the flow velocity (u_{SD}), number, mean and s.d. of the duration of high- (HSFE) and low-speed flow events (LSFE), in the focal point for eight juvenile Atlantic salmon in the Sainte-Marguerite River during observations. The univariate statistics summarizes the number of movements per amplitude and the total number of movements per 30 min of observation and the proportion of time used for movements compiled for each individual fish

	Fish number							
	1	2	3	4	5	6	7	8
Depth (cm)	26	28	40	30	45	35	28	32
Current meter	ECM	ECM	ADV	ADV	ADV	ADV	ADV	ADV
Flow characteristics								
Global scale								
\bar{u} (cm·s ⁻¹)	27.8	26.8	25.1	32.0	34.6	46.1	49.2	49.2
u_{SD} (cm·s ⁻¹)	4.3	7.7	4.3	10.3	8.2	10.7	13.4	10.7
Fine scale								
HSFE								
n	120	210	90	114	138	102	60	102
Mean (s)	1.2	1.5	1.4	1.5	1.6	1.3	1.3	1.4
s.d. (s)	0.1	0.4	0.4	0.3	0.7	0.3	0.2	0.3
LSFE								
n	150	216	84	150	156	78	66	132
Mean (s)	1.5	1.8	1.4	1.3	1.7	1.3	1.2	1.4
s.d. (s)	0.3	0.5	0.3	0.3	0.5	0.3	0.2	0.3
Characteristics of fish behaviour								
Number of movements								
A1	50	40	76	69	55	25	42	48
A2	34	13	86	71	53	22	37	38
A3	32	11	26	23	14	4	4	6
Total	116	64	188	162	123	50	83	92
Proportion of time used for movements (%)	13.4	8.1	23.7	18.9	16.4	5.5	11.1	9.1

ADV, Sontek Field Acoustic Doppler Velocimeter; ECM, Marsh-McBirney Electromagnetic current meter; A1, movements towards the river bed that did not extend >4 cm from the original fish position; A2, movements towards the mid-water which extended up to 20 cm; A3, movements reaching the water surface (movements >20 cm).

location). The exact time of the beginning and the end of each phase was noted. Each movement was also classified according to its amplitude (further referred to as amplitude class): amplitude A1 described movements towards the river bed that did not extend >4cm from the original fish position, amplitude A2 described movements towards the mid-water which extended up to 20cm and amplitude A3 described movements reaching the water surface (movements of >20cm). Consequently, in this study, fish behaviour was defined by the number and the duration of movements per amplitude class and the proportion of time used for these movements over the entire 30 min of sampling (Table I).

ENERGY BENEFITS OF THE USE OF LOW-SPEED FLOW EVENTS

The first hypothesis tested is that juvenile Atlantic salmon obtain significant energy benefits by using low-speed flow events during feeding movements. It is theoretically conceivable that fish displaying an intermittent feeding behaviour (suite of sit-and-wait and attacks) under harsh flow conditions that fluctuate at temporal scales similar to those used to perform their movements may benefit by using low-speed flow events. No data, however, are available to support such a hypothesis. The hypothesis was tested by comparing the energy expenditures associated with fish movements as they occur under field situations (with regards to the number of movements, the amplitude of movements and the temporal arrangement of the movements relative to the fluctuations of flow velocities) to the energy expenditures that may occur under two hypothetical situations. In the first case, the fish would initiate its movements, only and always, at the beginning of a low-speed flow event. In the second hypothetical case, fish would perform its movements at randomly chosen times. Expected energy expenditures for movements as they occur under field situations and for both hypothetical situations were simulated using the data for fish 1 and 2 because velocity data at three points over the water column were available for these fish. Three simulations based on observations made with fish 1 and 2 were performed: one for which fish initiated their movements as observed under field conditions, one for which a hypothetical fish initiated its movements only in low-speed flow events and one for which a hypothetical fish initiated its movements at randomly chosen times and flow velocities. For every simulation, the number of movements and their amplitudes were identical to the number of movements and their amplitudes observed under field conditions. Flow conditions were kept constant for any given fish. Only the temporal arrangement of the movements relative to flow conditions was modified among the simulations to correspond to the desired situation.

The energy expenditures simulated according to the three situations were estimated only for the attack phase of the fish. The calculations focussed on the swimming costs of the attack phase because it is during this phase that fish have to swim against the flow in the water column whereas, during the return phase, juvenile Atlantic salmon could profit from the re-circulating zones created by the river-bed heterogeneity to return to the initial position (McLaughlin & Noakes, 1998). Furthermore, in the simulations, only movements of amplitudes A2 and A3 were considered because it was postulated that the motions of amplitude A1 are too short and too small for fish to profit from a low-speed flow event. Swimming costs were estimated using the distance and the duration of fish movements and the average flow velocity during the attack phase. The distance of the fish movement was estimated from the stereocinematographic recordings. First, the apparent swimming speed of the fish (V_1 ; cm s^{-1}) was calculated by dividing the distance fish swam during the attack phase by the duration of the attack phase. Then, the effective swimming speed of the fish (V_3 ; cm s^{-1}) was calculated as the vectorial sum of the apparent swimming speed of the fish (V_1) and the average flow velocity during the attack phase (V_2 ; cm s^{-1}): $V_3 = \sqrt{(V_1^2 + V_2^2)}$.

The oxygen consumed for every motion was estimated using the duration of the motion t_a , the effective swimming speed V_3 and the multispecies respirometric model of Boisclair & Tang (1993). This model was selected because when swimming under turbulent flows

fish perform swift changes in speed and direction. The fish total length (L_T) was estimated from the stereocinematographic recordings and converted to fish mass with a length-mass relationship of juvenile Atlantic salmon in the Sainte-Marguerite River (E.C. Enders & D. Boisclair, unpubl. data). Swimming costs ($\text{mg O}_2 \text{h}^{-1}$) over 30 min periods were estimated as the sum of the costs of the individual movements (attacks of amplitudes A2 and A3). The same approach was used to estimate swimming costs according to the three situations.

STATISTICAL ANALYSES

The first hypothesis that fish swimming costs under turbulent conditions are affected by the temporal arrangement of fish movements and flow velocities was examined using a *t*-test. In particular, the hypothesis was tested that swimming costs estimated using combinations of fish movements and flow velocities observed in the field are statistically different from swimming costs estimated for a hypothetical fish which would perform movements only during low-speed flow events. Similarly, the hypothesis was tested that swimming costs estimated using combinations of fish movements and flow velocities observed in the field are statistically different from swimming costs estimated for a hypothetical fish which would perform movements at randomly chosen flow velocities.

The hypothesis was tested that the occurrence of movements of any given amplitude is related to low-, medium- and high-speed flow events. This was achieved by constructing a contingency table based on the frequency of motions of amplitudes A1, A2 and A3 under three classes of flow velocity conditions (low: fish 1 to 3, medium: fish 4 and 5 and high flow velocity condition: fish 6 to 8). The Freeman–Tukey deviate statistics was applied with a significance level of $P < 0.05$ (Legendre & Legendre, 1998).

The hypothesis was tested that the proportion of time used by fish to perform movements is related to the mean flow velocity \bar{u} and the s.d. of the flow velocity u_{SD} . This was done using linear regression analysis with data from fish 3 to 8. The data from fish 1 and 2 were not included because these fish spent relatively less time for movements than fish 3 to 8 which might be due to different environmental conditions during the two sampling periods.

RESULTS

ENERGY BENEFITS OF THE USE OF LOW-SPEED FLOW EVENTS

Swimming costs estimated for the attack phase of fish movements as they occur in the field ranged from $0.34 \text{ mg O}_2 \text{h}^{-1}$ (fish 2) to $0.62 \text{ mg O}_2 \text{h}^{-1}$ (fish 1). Under the first hypothetical situation tested, fish 1 observed in a less turbulent flow would decrease its swimming costs during attacks by 19.8% (to $0.49 \text{ mg O}_2 \text{h}^{-1}$) by initiating all its motions in low-speed flow events. Adoption of this situation to the fish 2 living in a more turbulent flow would decrease its swimming costs by 31.1% (to $0.23 \text{ mg O}_2 \text{h}^{-1}$). For both levels of turbulence, the swimming costs estimated with the situation that fish use only low-speed flow events were statistically smaller than the swimming costs of the attacks as they occur in the field (*t*-test, $n = 65$, $P < 0.001$ and $n = 24$, $P = 0.001$, respectively). The costs of attacks obtained under the situation that fish initiate their motions at flow velocities selected at random (0.61 and $0.35 \text{ mg O}_2 \text{h}^{-1}$ for fish 1 and 2, respectively) were not significantly different from the costs estimated

for attacks as they occur in the field (t -test, $n=65$, $P<0.78$ and $n=24$, $P=0.84$, respectively).

RELATIONSHIP BETWEEN FISH MOVEMENTS AND FLOW CHARACTERISTICS

The occurrence of movements of amplitudes A1, A2 and A3 was not related to the occurrence of low-, medium- or high-speed flow events for fish living in areas characterized by low flow velocity (Table II; contingency table analysis, $n=368$, $P>0.05$). The occurrence of movements of different amplitudes was related to the occurrence of specific flow events in medium (contingency table analysis, $n=285$, $P<0.05$) and high flow velocity conditions (contingency table analysis, $n=225$, $P<0.05$). *A posteriori* test indicated that fish performed significantly fewer movements of amplitude A3 in medium (Freeman–Tukey deviate = 3.89, $P<0.05$) and high flow velocity conditions (Freeman–Tukey deviate = 3.20, $P<0.05$) than expected by chance.

During sampling period II, the proportion of time used for movements by fish 3 to 8 decreased with increasing mean flow velocity and the s.d. of the flow velocity (Fig. 2). A linear relationship was found between the proportion of time used for movements and the mean flow velocity (linear regression analyses, $n=6$, $r^2=0.71$, $P=0.02$). The juvenile Atlantic salmon did not significantly adjust the proportion of time used for movements to the s.d. of flow velocity (linear regression analyses, $n=6$, $r^2=0.48$, $P=0.08$).

TABLE II. Observed frequency distribution of the movements classified by their amplitude (see Table I) and the occurrence in a specific flow event in low flow velocity ($n=3$, \bar{u} ranged from 25.1 to 27.8 cm s⁻¹), medium flow velocity ($n=2$, \bar{u} ranged from 32.0 to 34.6 cm s⁻¹) and high flow velocity ($n=3$, \bar{u} ranged from 46.1 to 49.2 cm s⁻¹) conditions and expected frequency distribution of the movements with the contingency table analysis in parentheses

Flow	Amplitude	Frequency of movements (%) at a specific flow event		
		High	Medium	Low
Low flow velocity	A1	7.3 (7.5)	29.2 (29.4)	9.1 (8.7)
	A2	6.5 (5.8)	23.0 (22.8)	5.9 (6.7)
	A3	2.6 (3.1)	12.3 (12.3)	4.1 (3.6)
Medium flow velocity	A1	11.6 (10.3)	23.2 (25.3)	11.6 (11.0)
	A2	9.6 (9.4)	23.2 (23.0)	9.6 (10.0)
	A3	0.9 (2.4)*	7.9 (6.0)	2.3 (2.6)
High flow velocity	A1	6.1 (4.5)	31.6 (33.7)	8.8 (8.4)
	A2	3.5 (4.3)	32.9 (32.0)	7.8 (8.0)
	A3	0.0 (0.9)*	7.7 (6.7)	1.5 (1.7)

*, significantly different ($P<0.05$) from the expected frequency based on Freeman–Tukey deviate statistics.

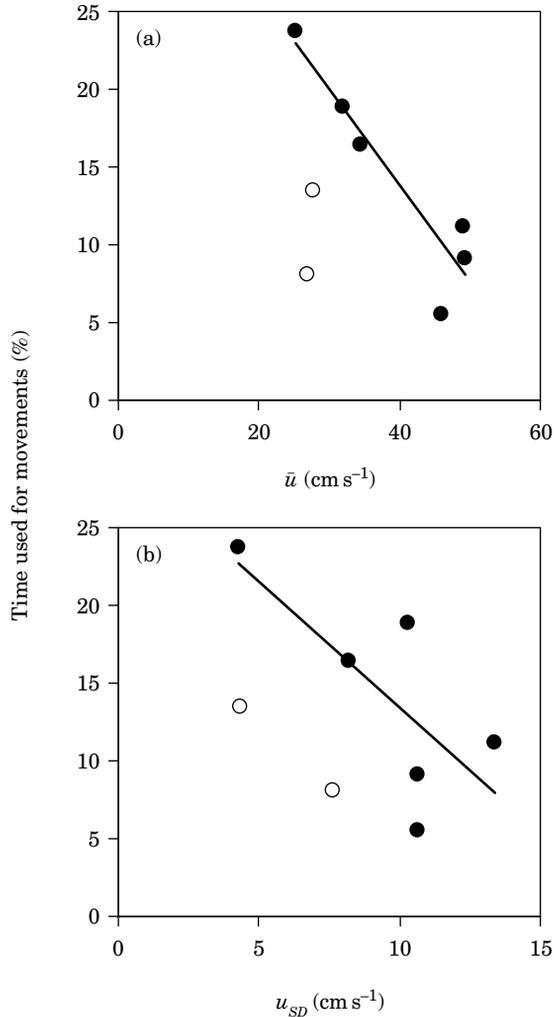


FIG. 2. Proportion of time used by the fish for movements in relation to (a) mean flow velocity (\bar{u}) and (b) s.d. of flow velocity (u_{SD}). Measurements were for sampling periods I (○) and II (●). The curves (only the data of sampling period II were considered) were fitted by: (a) $y = -0.62x + 38.37$ and (b) $y = -1.63x + 29.73$.

DISCUSSION

The simulations of the three hypothetical situations indicated that fish may benefit from an energy advantage by using low-speed flow events. Fish 1 in less turbulent flow would decrease its swimming costs by 19.8% by undertaking all its movements in low-speed flow events. Fish 2 by staying in more turbulent flow would even decrease the swimming costs by 31.1%. According to optimal foraging theory (Krebs, 1978), juvenile Atlantic salmon should be sensitive to variations in swimming costs when taking foraging decisions.

McLaughlin & Noakes (1998) analysed the behaviour of young-of-the-year brook charr *Salvelinus fontinalis* (Mitchell) in their natural habitat and stated

that swimming movements may be influenced by the temporal and spatial heterogeneity of the flow. They showed that young-of-the-year brook charr use spatial flow velocity refuges to reduce their swimming costs. These authors could not analyse the relationship between short-term fluctuations and behaviour as the velocity measurements were taken as averages over 60 s. They suggested that fish might react to temporal heterogeneity of the flow. In the present study, the flow velocity was measured at high temporal resolutions of 20 and 25 Hz, respectively. Therefore, the relationship between the initiation of the movements and a fine scale characteristic such as the occurrence of turbulent flow events could be analysed. In the present study, however, juvenile Atlantic salmon did not appear to use low-speed flow events when initiating a movement. The statistical analysis based on a contingency table showed that the amplitude of movement and its occurrence in a specific flow event were independent for fish in low flow velocity conditions. In contrast, for fish swimming in medium and high flow velocity conditions the amplitude of a movement and its occurrence in a specific flow event were related. The analysis also indicated that fish performed significantly less high amplitude movements in high-speed flow events than expected by the contingency tables analysis in medium and high flow velocity conditions. The biological significance of these results is difficult to assess since the frequency of high amplitude movements differed by only 1.5% (0.9% observed *v.* 2.4% predicted) at medium flow velocity conditions and 0.9% (0.0 observed *v.* 0.9% predicted) at high flow velocity conditions. These very small differences appear not to be biologically meaningful.

The fact that juvenile Atlantic salmon initiate their movements independently of hydrodynamic conditions is surprising since the simulations of three hypothetical situations indicated that fish may benefit from an energy advantage by using low-speed flow events. Nonetheless, the linear regression analyses indicated that the behaviour of juvenile Atlantic salmon seem to be affected by flow characteristics. Fish subjected to two-fold faster and 2.4-fold more turbulent flow allocated a 4.3-times smaller proportion of the time budget to movements than fish in slower and less turbulent flow. These observations demonstrated that, in a natural situation under turbulent flow, salmonids decrease the amplitude of their movements to intercept drifting prey particles and therefore the time spent on foraging as flow velocity increases. As such these field observations support the laboratory studies of Godin & Rangeley (1989) and O'Brien & Showalter (1993).

One reason that may explain why juvenile Atlantic salmon may not initiate their movements only during low-speed flow events may be that other criteria co-determine this decision. For instance, fish may not decide to initiate a movement in a low-speed flow event when no drifting food particles are available during that specific time period. Hence, fish movements may not only be related to the occurrence of a specific flow event but more likely to a combination of the occurrence of potential food particles and flow velocity. Drift particle density has been shown to be positively related to flow velocity (Elliott, 1967). On a smaller temporal scale, however, drift might not be equally distributed. There are three contradictory hypotheses regarding drift distribution in relation to short-term flow events: (1) low-speed flow events, consisting

mainly of the ejection of slow moving flow erupting from the river bed towards the water surface, which may cause uplifts into the water column of particles deposited at the bed. Therefore, low-speed flow events may contain a higher amount of suspended particles per unit of time (Lapointe, 1992); (2) high-speed flow events may be argued to contain more food particles because there is a larger water volume passing by in a given time interval resulting in a higher food particle concentration per time; (3) particles may accumulate at the limit between high- and low-speed flow events, a process similar to the accumulation of particles between the front of two water masses (Ott, 1988). In this study, however, drifting prey particles could not be tracked either visually or on the video recordings. Further studies of simultaneous measurements of drift, flow velocity and feeding behaviour at a high temporal and spatial resolution are needed to test these hypotheses.

Nevertheless, the present study contributes to approaches to study fish behaviour under turbulent flows. Although fish seem not to prefer low-speed flow events when initiating their movements, the proportion of the time budget used for activity was affected by the flow. More importantly, observations performed during this study indicated that fish subjected to similar mean flow velocities but different s.d. of flow velocities may have a different behaviour. The data do not allow the ultimate cause of the observed differences (energy of swimming against a turbulent flow or the quantity of the drift within the flow) to be assessed but these results suggest that both the mean and s.d. of flow velocity should be quantified when studying fish behaviour under turbulent flows.

We thank É. Pelletier for her help in the field, P. Biron for lending us the ADV and the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA) for logistic support. We would like to thank two anonymous referees for their valuable and constructive comments on the earlier version of this manuscript. Funding for this research was provided by an individual grant from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Fonds pour les Chercheurs et l'Aide à la Recherche (FCAR-Équipe) to D. Boisclair. E.C. Enders was supported by scholarships from the Fondation Joseph-Arthur Paulhus, the Faculté des Études Supérieures (Université de Montréal) and the Groupe de Recherche Interuniversitaire en Limnologie (GRIL, FCAR-Centre). This is a contribution to the CIRSA programme.

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