

1 **POSITION CHOICE AND SWIMMING COSTS OF JUVENILE ATLANTIC**  
2 **SALMON *SALMO SALAR* IN TURBULENT FLOW**

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15 **Abstract**

16 Swimming costs (SC) for fish have been shown to be affected by turbulence. However, this  
17 idea has not yet been implemented in habitat models, which often represent hydraulics using  
18 water velocity averaged over time and space. In this study, we analysed the habitat selection  
19 of individual juvenile Atlantic salmon *Salmo salar* (L. 1758) in relation to predicted SC in the  
20 turbulent flow of a large outdoor flume. We used a previously published SC model  
21 parameterised using mean velocity, turbulence intensity, water temperature and fish mass.  
22 Results showed that 86% of fish chose locations with significantly lower predicted SC than  
23 expected at random ( $p < 0.05$ ). Position choice was negatively related to predicted SC, mean  
24 velocity, spatial velocity gradient, and Reynolds stresses. Based on the findings, a novel  
25 habitat suitability curve is recommended for juvenile Atlantic salmon. The results are  
26 expected to contribute towards the improvement of bioenergetics modelling to increase our  
27 understanding of the impacts of environmental changes and management activities.

28

29 **Keywords:** Swimming costs; bioenergetics; turbulence; hydrodynamics; habitat; Atlantic  
30 salmon.

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33 **Introduction**

34 In recent decades two parallel trends in river research and management have led to an  
35 increasing focus on the hydrodynamics of river ecosystems (Nikora 2010; Wilkes et al. 2013)  
36 and a proliferation in the development of bioenergetics models for fish (Fausch 2014;  
37 Jørgensen et al. 2016), which include an important foraging component (e.g. Hughes & Dill  
38 1990; Hill & Grossman 1993; Booker et al. 2004). Such forage-based models seek to predict  
39 the distribution, growth, abundance or biomass of drift feeding fish by modelling the fish's  
40 net energetic intake (NEI) as a function of the gross energetic intake (GEI) acquired through  
41 prey capture and the associated swimming costs (SC):

$$(1) \quad NEI = GEI - SC$$

42 (Piccolo et al. 2014). Their appeal over traditional hydraulic habitat models, such as  
43 PHABSIM (Physical Habitat Simulation system; Milhous et al. 1984), is that they have  
44 mechanistic foundations (Lancaster & Downes 2010; Meineri et al. 2014). Traditional  
45 hydraulic habitat models rely on correlative habitat suitability curves derived from measuring  
46 simple descriptions of the fluvial environment - water velocity, water depth, and substrate  
47 where fish are present and absent - resulting in an index of habitat suitability. On the other  
48 hand, forage-based models incorporate the costs and benefits of food acquisition in an  
49 ecologically realistic way (Hayes et al., 2016).

50 In traditional hydraulic habitat models water velocity is represented by mean column  
51 velocity, whereas the SC component (equation 1) of forage-based models is typically  
52 estimated with the assumption of sustained swimming at constant speeds (Piccolo et al.

53 2014), although corrections for accelerations and turns may be made (Hayes et al., 2016). The  
54 use of mean column velocity or constant swimming speeds, however, provides a far from  
55 complete description given that fish are swimming in spatiotemporally dynamic, three-  
56 dimensional turbulent flow. Laboratory studies have revealed strong relationships between  
57 turbulent flow and SC, calling for turbulence to be considered in habitat models (Enders &  
58 Boisclair 2016). Respirometer studies by Enders et al. (2003) demonstrated that juvenile  
59 Atlantic salmon *Salmo salar* (L. 1758) may consume significantly more energy when  
60 swimming in unpredictable turbulent flow. An existing model for predicting SC based on  
61 steady swimming at mean velocity (Boisclair & Tang 1993) did not match the data of Enders  
62 et al. (2003) well, leading to the development of a new turbulent SC model (Enders et al.  
63 2005). Turbulence in this case was described as the standard deviation of the primary velocity  
64 component ( $u_{SD}$ ) but several other studies suggest that the energy efficiency of fish  
65 locomotion may be dependent on other hydrodynamic properties. In particular, the direction  
66 relative to fish body shape, the scale relative to fish body length, and the periodicity of the  
67 turbulent flow may all be important (Webb 2004; Liao 2007, Lacey et al. 2012).

68 Previous laboratory work with laterally compressed fish has shown that eddies rotating on a  
69 horizontal axis may, depending on the ratio of eddy size to fish body length, destabilize fish  
70 and result in increased energetic costs (Pavlov et al. 2000; Lupandin 2005; Tritico & Cotel  
71 2010). Silva et al. (2011 2012) found that Iberian barbel *Luciobarbus bocagei* (L. 1758)  
72 avoided areas of high Reynolds shear stress, which describes transport occurring through  
73 displacements of fluid particles without a change in momentum (accelerations and  
74 decelerations of fluid particles due to pressure and viscous forces). The mechanism appeared  
75 to be postural challenges leading to increased energetic costs at high Reynolds stresses. On  
76 the other hand, relatively predictable (highly periodic), vertically oriented eddies associated  
77 with cylinder wakes allowed rainbow trout *Onchorynchus mykiss* (Walbaum 1792) to reduce

78 SC by Kármán gaiting (Liao et al. 2003; Taguchi & Liao 2011). Further reductions in SC  
79 have been observed in rainbow trout entraining on obstacles (Cook & Coughlin 2010;  
80 Przybilla et al. 2010; Taguchi & Liao 2011). Spatial gradients in velocity have also been  
81 implicated in the position choice of juvenile Atlantic salmon and brown trout *S. trutta* (L.  
82 1758) due to their distinctive ‘sit-and-wait’ feeding behaviour (Hayes & Jowett 1994; Booker  
83 et al. 2004).

84 This study aimed to advance knowledge of how turbulence affects habitat selection in  
85 juvenile Atlantic salmon by: (i) testing the ability of a turbulent SC model (Enders et al.  
86 2005) to predict position choices in wild fish; and (ii) assessing whether this prediction may  
87 be improved upon by taking into consideration other properties of the turbulent flow,  
88 including intensity, periodicity, direction, and scale. It was hypothesised that fish would  
89 occupy positions within an artificial habitat associated with energetically favourable  
90 hydrodynamic conditions that are likely to minimise SC.

## 91 **Material and methods**

### 92 *Experimental Setup*

93 Experiments were conducted in a 2 m long section of an outdoor flume at the International  
94 Centre for Ecohydraulics Research (ICER), University of Southampton. **The flume is 2 m**  
95 **wide and 60 m long with a trapezoidal cross-section and a concrete bed. The test section was**  
96 **covered with a heavy canvass tent.** Test conditions were created using artificial habitat  
97 features consisting of 24 small (50 mm in diameter) and 16 large (100 mm in diameter)  
98 transparent plastic hemispheres that were fixed to the bottom of the stream channel (Figure  
99 1). Transparent habitat features were used to reduce the likelihood of fish responding to  
100 visual cues. **We further reduced this likelihood by performing trials in darkness (<0.001 lux).**

101 Discharge ( $0.056 \text{ m}^3 \text{ s}^{-1}$ ) and flow depth (16.5 cm) were constant throughout the experiments.  
102 The flow depth was set to be within the natural range of depths reported to be used by  
103 juvenile Atlantic salmon (Symons and Heland 1978; Kennedy and Strange 1982; Morantz et  
104 al. 1987; Heggenes 1990). During the experiments, water temperature was maintained at 15  
105 °C ( $\pm 0.1 \text{ }^\circ\text{C}$ ). Instantaneous water velocities at set locations around the hemispheres (Figure  
106 1) were measured with a 3-D acoustic Doppler velocimeter (ADV) (model Vectrino II,  
107 Nortek International, Rud, Norway) at a frequency of 25 Hz for 90 s, providing a highly  
108 resolved characterisation of the turbulent flow. This frequency and record length has been  
109 shown to be optimal in gravel-bed rivers (Buffin-Bélangier and Roy 2005). Velocities were  
110 measured at 20-24 mm above the bottom of the flume, to approximate the focal point velocity  
111 of juvenile salmonids (Heggenes & Saltveit 1990; Riehle & Griffith 1993).

112 [Figure 1 near here]

### 113 *Experimental procedure*

114 A total of 46 juvenile (0+) Atlantic salmon ( $96.30 \pm 0.51 \text{ mm TL}$ ) were electrofished (50 Hz  
115 pulsed DC) from the River Frome, Dorset, UK on 6 September 2012 and transported (tanks  
116 with aerated river water at a temperature of  $12 \text{ }^\circ\text{C}$ ) to the ICER experimental facility. Fish  
117 were maintained in a holding tank (1000 L; filtered, oxygenated, dechlorinated mains water)  
118 and acclimated for a minimum of 7 d to ambient temperatures ( $14.6 \pm 1.4 \text{ }^\circ\text{C}$ ) and natural  
119 photoperiod before the trials began. Efficient aeration and filtration systems were used and  
120 water quality was monitored and maintained within the range considered suitable for fish  
121 husbandry. Water was regularly replenished. During this time, fish were fed with defrosted  
122 chironomid larvae but not fed for 24 h prior to experimental trials. Each trial began by adding  
123 an individual fish to the flume at a random position in the test section. After 30 min to  
124 acclimatise to the flow and explore the habitat, the position of each fish was recorded for 10

125 min using an infra-red camera (Sony 1000TVL, 720P, IR-CUT). All trials were conducted at  
126 night to avoid any confounding diurnal effects. Fish were not fed during the trials. At the end  
127 of each trial, the fish was removed from the test section and held separately from other fish  
128 for 24 h to monitor its health. Trials were conducted between dusk and dawn on 13, 14 and  
129 15 September 2012.

### 130 *Data processing*

131 ADV data were post-processed using a phase-space filter (>95% good pass criterion), with  
132 inconsistent data points replaced using a third-order polynomial fitted to the data either side  
133 of the spike (Parsheh et al. 2010). The data were rotated into the resultant vector in three  
134 dimensions, so that:

$$(2) \quad \bar{v} = \bar{w} = 0$$

135 where  $v'$ , and  $w'$  are instantaneous velocities in the vertical and spanwise directions  
136 respectively, and overbars denote ensemble averages. The rotated data were used to calculate  
137 the following hydraulic variables: mean velocity ( $U$ ), turbulence intensity ( $u_{SD}$ ) and Reynolds  
138 stresses on the streamwise-vertical ( $\tau_{uv}$ ), and streamwise-lateral ( $\tau_{uw}$ ) planes:

$$(3) \quad \tau_{uv} = \rho \overline{u'v'}, \tau_{uw} = \rho \overline{u'w'}$$

139 where  $\rho$  is the water density ( $1000 \text{ kg m}^{-3}$ ) and  $u'$  is the instantaneous velocity in the  
140 streamwise component.

141 Average eddy length ( $L_u$ ) was calculated using a second-order autoregressive model:

$$(4) \quad L_u = u_t U$$

$$u_t = a_1 u_{t-1} + a_2 u_{t-2} + e_t$$

142 where  $a_1$  and  $a_2$  are coefficients of the velocity at a given time lag and  $e_t$  is a random  
 143 component (Clifford and French 1993a). All the hydraulic variables were interpolated to a 25  
 144 mm mesh grid using an Ordinary Kriging method (Oliver 1990) in ArcGIS 10 (ESRI 2011).  
 145 The 25 mm mesh size was chosen as a scale consistent with the fish size, the scale of the  
 146 hemispheres and the resolution of the ADV measurements.

147 SC was predicted for each cell according to the equation for the turbulent SC model ( $SC_{pred}$ )  
 148 (Enders et al. 2005):

$$(5) \quad \log SC_{pred} = 0.23 \log T + 0.64 \log M + 2.43 \log U + 0.67 \log u_{SD} - 4.06$$

149 where  $T$  is water temperature and  $M$  is the fish body mass.  $SC_{pred}$  was calculated for the  
 150 average mass of fish used in this study (9 g) at a temperature of 15 °C. Spatial velocity  
 151 gradient ( $V_{grad}$ ) was also calculated for each cell as the standard deviation of  $U$  in all  
 152 neighbouring cells within a 200 mm radius (approximately two body lengths, the foraging  
 153 radius of **juvenile salmonids**; Fausch 1984).

154 Fish focal position was **recorded manually** using tracking software (Kinovea 0.8.15) every 5  
 155 s, giving 121 observations per fish referenced to the same grid cell system as the hydraulic  
 156 data. These results were used to calculate a selection index ( $SI$ ) of the fish for each cell. This  
 157 index was calculated based on the number of times a fish was observed in that cell (cell  
 158 occupancy,  $CO_{cell}$ ):

$$(6) \quad CO_{cell} = \sum_{i=1}^n fish_{i,cell}$$



$$SI = \frac{CO_{cell}}{CO_{max}}$$

159 where  $fish_{i,cell}$  is the occupancy count for each fish in each cell and  $CO_{max}$  is the maximum  
 160 cell occupancy or, in other words, the  $CO_{cell}$  associated with the most popular cell.

### 161 **Statistical analyses**

162 A permutation test was used to test the null hypothesis that fish chose cells at random,  
 163 independently of  $SC_{pred}$ . The null distributions of  $SC_{pred}$  were constructed from 10,000  
 164 bootstrap samples of 121 random cells (with replacement). For each fish, the probability ( $p$ )  
 165 that the fish chose cells at random was calculated as:

$$(7) \quad p = \frac{\sum_{i=1}^n (SC_{null} \geq SC_{fish})}{k} - 1$$

166 where  $k=10,000$  permutations,  $SC_{null}$  is the mean  $SC_{pred}$  associated with each bootstrap sample  
 167 and  $SC_{fish}$  is the mean  $SC_{pred}$  of cells used by each fish.

168 Generalised linear models were used to predict  $SI$  using two sets of explanatory variables: (i)  
 169  $SC_{pred}$ ; and (ii) a linear combination of hydrodynamic variables ( $U$ ,  $u_{SD}$ ,  $\tau_{uv}$ ,  $\tau_{uw}$ ,  $L_u$ , and  $V_{grad}$   
 170 were considered), which we term the ‘hydrodynamic habitat model’. Habitat selection was  
 171 found to follow a Poisson distribution. Nevertheless, due to the high number of zeros as result  
 172 of the fact that fish could not occupy all cells (even where the habitat was suitable), a zero-  
 173 inflated negative binomial (ZINB) model was applied in order to deal with overdispersion:

174

$$(8) \quad g(\mu_i) = \beta_0 + X^T \beta, \quad g(\pi_i) = \beta_0 + X^T \beta$$

175 where  $g$  is a link function,  $\beta_0$  is the intercept,  $X^T$  is a vector of  $m$  predictor variables, and  $\beta$  is a  
176 vector of  $m$  regression coefficients. Thus, we modelled the probability of finding false zeros  
177 (*i.e.*, locations in which fish were not observed but nevertheless represented suitable habitat;  
178 see Zuur et al. 2009) separately to the count ( $SI$ ) data. A log link was used for the count  
179 model ( $\mu$ ), whilst the binomial model ( $\pi$ ) was facilitated by a logit link function.

180 The Akaike information criterion (AIC), an inverse measure of goodness-of-fit, was used to  
181 compare results for the  $SC_{pred}$  and hydrodynamic habitat models. AIC was also used for  
182 model selection along with likelihood ratio tests for nested models. All statistical procedures  
183 were carried out using R3.2.4 (R Core Team 2015).

## 184 **Results**

### 185 *Flow conditions in the test section*

186 Resultant mean velocities and turbulence intensities ranged from 0.16 to 20 cm s<sup>-1</sup> and 0.38 to  
187 8.13 cm s<sup>-1</sup>, respectively (Figure 2a-b). A wide range of length scales (0.26 <  $L_u$  < 34.98 cm)  
188 were distributed throughout the test arena (Figure 2c). Regions of highest turbulence intensity  
189 (Figure 2b), Reynolds shear stresses (Figure 2d-e), and flow divergence and convergence  
190 (Figure 2f) were associated with bed protrusions, conditions typically associated with flow  
191 around pebble clusters (Buffin-Bélanger and Roy 1998; Lawless & Robert 2001). Velocity  
192 spectra showed peaks in the region 0.01-0.2 Hz and typically became flattened downstream  
193 of hemispheres (Figure 3). The conditions on each side of the test section were noticeably  
194 different, with the right side generally exhibiting higher velocities, greater turbulence  
195 intensities, and larger scales.  $SC_{pred}$  was distributed between 0.01 and 3.89 mg O<sub>2</sub> h<sup>-1</sup> (0.19-  
196 75.39 J h<sup>-1</sup> assuming no anaerobic component; Heath, 1995). Following the general hydraulic

197 patterns observed,  $SC_{pred}$  was higher on the right side of the test section and in the vicinity of  
198 bed obstacles (Figure 4).

199 [Figure 2 near here]

200 [Figure 3 near here]

201 [Figure 4 near here]

## 202 ***Habitat selection***

203 Fish moved around the test section to varying degrees. Some fish remained in the same or  
204 adjoining cells for the duration of observations, whereas others used a wider range of  $SC_{pred}$ .  
205 Figure 5a shows two fish trajectories that exemplify this range of behaviours. Thus,  
206 individual fish were classified as ‘station-holding’ (remaining in the same or adjoining cells  
207 for the duration of observations) or ‘searching’ (Table 1). Fish most often selected cells close  
208 to hemispheres (both large and small hemispheres) and the edges of the test section (Figure  
209 5b). Figure 6 shows the frequency distribution of mean  $SC_{pred}$  under the null model (random  
210 cell selection). The permutation tests revealed that 86% of fish chose cells with significantly  
211 lower mean  $SC_{pred}$  than expected at random ( $p < 0.05$ ), including all fish that exhibited station-  
212 holding behaviour for the duration of observations (Table 1). Results of ZINB modelling  
213 showed that  $SC_{pred}$  was negatively related to habitat selection (Figure 7). Observed  $SI$  was  
214 clustered around low  $SC_{pred}$ . The probability of finding a false zero (*i.e.* where the habitat is  
215 suitable but no fish were observed) was consistently low (Figure 7). Count ( $SI$ ) model  
216 coefficients were highly significant (Table 2).

217 [Table 1 near here]

218 [Table 2 near here]

219 [Figure 5 near here]

220 [Figure 6 near here]

221 [Figure 7 near here]

## 222 ***Hydrodynamic habitat model***

223 Due to intercorrelation between  $U$ ,  $u_{SD}$  and  $L_u$ , ( $0.78 < r < 0.95$ ), only  $U$ ,  $\tau_{uv}$ ,  $\tau_{uw}$  and  $V_{grad}$  were  
224 entered as explanatory variables for the hydrodynamic habitat model. In the case of  $\tau_{uw}$ , the  
225 magnitude of turbulence-related disturbances on this horizontal plane, rather than the  
226 direction, is of most interest. Thus, absolute values were used ( $|\tau_{uw}|$ ).

227 Reynolds stresses were the weakest contributing variables to the model and, therefore, we  
228 examined the effect of dropping both of these variables simultaneously. The solution that  
229 dropped both  $\tau_{uv}$  and  $|\tau_{uw}|$  from the count model was optimum as this was the most  
230 parsimonious model with the lowest AIC (Table 3). All coefficients for both the count and  
231 binomial components of this optimum model were significant (Table 4). Predicted  $SI$  was  
232 negatively related to  $U$  and  $V_{grad}$ , whilst the probability of finding false zeros, where the  
233 habitat was suitable but no fish were observed, was also negatively related to Reynolds  
234 stresses (Figure 8). The AIC of the hydrodynamic habitat model was lower than for the  $SC_{pred}$   
235 model ( $6925.55 < 6967.16$ ).

236 [Table 3 near here]

237 [Table 4 near here]

238 [Figure 8 near here]

## 239 **Discussion**

240 This study advances understanding of the role of swimming energetics and turbulent flow in  
241 the habitat selection of juvenile Atlantic salmon in a realistic hydrodynamic environment.  
242 Mean velocities and turbulence intensities were within the range used to construct the SC  
243 model of Enders et al. (2005). Furthermore, all hydrodynamic variables were within an order  
244 of magnitude of those reported in gravel-bed rivers (Lacey et al. 2007; Smith & Brannon  
245 2007; Roy et al. 2010). Our findings suggest that turbulence and swimming energetics do  
246 affect position choice. The results of permutation tests and ZINB modelling using a turbulent  
247 SC model (Enders et al. 2005) supported the hypothesis that the fish would select locations  
248 that minimised SC.

249 A hydrodynamic habitat model that included  $U$ ,  $V_{grad}$ , and Reynolds stresses performed better  
250 than the  $SC_{pred}$  model, as evidenced by a lower AIC despite the model being less  
251 parsimonious. Whilst a negative relationship between  $U$  and  $SI$  was expected on an energetic  
252 basis, it was unexpected that  $V_{grad}$  would also be negatively related to  $SI$  given that the  
253 feeding behaviour of juvenile salmonids makes them better suited to focal positions with low  
254 velocity that are situated close to zones of high velocity (Hayes & Jowett 1994; Booker et al.  
255 2004). One explanation for this could be that the fish were not active due to low light levels.  
256 Fraser and Metcalfe (1997) found that juvenile Atlantic salmon were relatively inactive at  
257 illumination levels lower than those equivalent to dawn and dusk. However, observations of  
258 high nocturnal activity in summer (Gries et al. 1997) and lower rates of nocturnal hiding at  
259 temperatures above 9 °C (Valdimarsson et al. 1997) suggest that this species and life-stage  
260 will seek habitats suitable for feeding in darkness at the temperatures tested in this study,  
261 although we cannot rule out the possibility that fish were not searching for feeding stations  
262 because they were not fed during trials. Another possibility is that velocity gradients in the  
263 test section were not great enough to elicit a response from the fish. Mean velocity in gravel-  
264 bed rivers can range from near zero to  $>50 \text{ cm s}^{-1}$  over small multiples of fish body length

265 (Roy et al. 2004; Buffin-Bélanger et al. 2006). The mean velocity range of  $0 < U < 20 \text{ cm s}^{-1}$   
266 within our test section is typical of the smallest range expected in natural settings (Buffin-  
267 Bélanger et al. 2006).

268 Negative values of  $\tau_{uv}$  were associated with suitable habitat, whereas high positive values  
269 were not. This suggests that the fish exhibited a preference for locations at which there was a  
270 net flux of turbulent momentum towards the bed, presumably because this aided station-  
271 holding. Areas of high  $|\tau_{uv}|$  were not preferentially occupied by the fish. The likely reason  
272 that Reynolds stresses were not included in the optimum count (*SI*) model is that maximal  
273 values were two orders of magnitude lower than reported in some previous laboratory  
274 experiments showing clear avoidance of high Reynolds stress zones (Silva et al. 2011; 2012).  
275 However, other studies found that similar Reynolds stresses to observed here elicited  
276 responses in terms of avoidance (Hockley et al. 2014) and swimming speed (Alexandre et al.  
277 2013).

278 Locations downstream of hemispheres suitable for entraining ( $< c_D$  downstream of  
279 hemisphere, where  $c_D$  is hemisphere diameter) and Kármán gaiting ( $3 < c_D < 5$  downstream;  
280 Liao 2006) had relatively high *SI*. It remains uncertain whether the chaotic flow in the test  
281 section, with velocity spectra lacking pronounced peaks and relatively high Reynolds  
282 numbers compared with previous work (Enders et al. 2003; Liao et al. 2003, Liao 2006;  
283 Taguchi & Liao 2011), would be suitable for Kármán gaiting. It is also difficult to evaluate  
284 role of eddy length relative to body length (*bl*) as  $L_u$  was highly correlated with  $U$ . Relative  
285 eddy lengths in the test section included the range  $0.6 < L_u/bl < 0.66$  thought to cause instability  
286 in cyprinid fish (Pavlov et al. 2000; Lupandin 2005; Tritico & Cotel 2010), but these values  
287 were associated with regions of high *SI*. It is possible that the flow was too chaotic (Enders &

288 Boisclair 2016) or eddy momentum was too low (Tritico & Cotel 2010) to elicit an avoidance  
289 response. Alternatively, juvenile Atlantic salmon may not be susceptible to such instabilities.

290 There are several factors that could have confounded our quantification of habitat selection in  
291 relation to the turbulent flow. Firstly, the fish were assumed to be responding to hydraulics  
292 but, although trials were performed in darkness and the artificial habitat features  
293 (hemispheres) were transparent, the possibility that fish used their lateral line system to select  
294 locations based on proximity to physical structures (*e.g.*, hemispheres or netting) cannot be  
295 ruled out. Secondly, the data analysis methods used ignored the possibility of strong spatial  
296 intercorrelation in the response of individual fish. If it is assumed, as the results suggest, that  
297 the fish chose energetically favourable locations then a third related factor is the possibility  
298 that they chose local, rather than global, energetic minima (*i.e.*, that they are only selecting  
299 the ‘best’ habitat from a small area). The use of random starting co-ordinates and the time  
300 allowed for acclimation and habitat exploration was an attempt to mitigate this. Furthermore,  
301 many fish were observed to be rapidly moving from one side or end of the test arena to the  
302 other, indicating that they were able to ‘sample’ the available habitat.

### 303 *Implications for research and management*

304 By integrating hydrodynamics and bioenergetics this work integrates two parallel trends in  
305 river research and management (Nikora 2010; Jørgensen et al. 2016). Bioenergetics models  
306 have been suggested as an advance on the simplistic, empirical approach taken by traditional  
307 hydraulic habitat models such as PHABSIM, yet their application has been limited because of  
308 their complexity and resource-intensiveness (Dunbar et al. 2012). The application of reliable  
309 habitat models is critical to evaluating the impacts of river barriers (Urabe et al. 2014), low  
310 flows (Rosenfeld & Ptolemy 2012), habitat degradation (Hafs et al. 2014), and stream

311 restoration (Railsback et al. 2013), all of which involve modifications of the turbulent  
312 flow.

313 Our findings show how the hydraulic component of habitat models may be improved. We  
314 recommend the SC model of Enders et al. (2005) for inclusion as a parameter as it is a  
315 compromise between parsimony and causality, although we realise that many habitat  
316 modelling applications will lack the resources to collect sufficiently detailed data on the  
317 turbulent flow. Future research should investigate the accuracy of predictions made using this  
318 model in field settings that are likely to include a wider range of hydraulic conditions than  
319 studied here. A similar approach could be applicable to other species but relationships  
320 between flow and SC are likely to be species-specific. Turbulence may also be implicated in  
321 the energetic intake component of forage-based models for drift-feeding fish, in terms of the  
322 spatiotemporal variability in prey concentration and capture rates (Piccolo et al. 2014). This  
323 also warrants future research.

## 324 **Conclusions**

325 A recent accumulation of evidence has confirmed strong and complex relationships between  
326 turbulent flow and fish swimming energetics (*e.g.*, Enders et al. 2005; Tritico & Cotel 2010;  
327 Taguchi & Liao 2011; Lacey et al. 2012; Enders & Boisclair 2016) but these relationships  
328 have not yet been incorporated into models that predict position choice and habitat quality for  
329 fish. We establish, for the first time, a link between turbulent flow, swimming costs, and  
330 habitat selection in juvenile Atlantic salmon. The resulting habitat suitability curve based on  
331 the energetic costs of swimming in turbulent flow is in a format that can readily be  
332 implemented in habitat models.

333



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343 **References**

- 344 Alexandre CM, Quintella BR, Silva AT, Mateus CS, Romão F, Branco P, Ferreira MT, Almeida PR.  
345 2013. Use of electromyogram telemetry to assess the behavior of the Iberian barbel  
346 (*Luciobarbus bocagei* Steindachner, 1864) in a pool-type fishway. Ecol. Eng. 51:191-202.
- 347 Boisclair C, Tang M. 1993. Empirical analysis of the influence of swimming pattern on the net  
348 energetic cost of swimming in fishes. J. Fish Biol. 42:169-183.
- 349 Booker DJ, Dunbar MJ, Ibbotson A. 2004. Predicting juvenile salmonid drift-feeding habitat  
350 quality using a three-dimensional hydraulic-bioenergetic model. Ecol. Model. 177:157-177.
- 351 Buffin-Bélanger T, Roy AG. 1998. Effects of a pebble cluster on the turbulent structure of a  
352 depth-limited flow in a gravel-bed river. Geomorphology 25:249–267.
- 353 Buffin-Bélanger T, Roy AG. 2005. 1 min in the life of a river: selecting the optimal record length  
354 for the measurement of turbulence in fluvial boundary layers. Geomorphology 68:77–94.
- 355 Buffin-Bélanger T, Rice S, Reid I, Lancaster J. 2006. Spatial heterogeneity of near-bed hydraulics  
356 above a patch of river gravel. Water Resour. Res. 42. DOI: 10.1029/2005WR004070.
- 357 Clifford NJ, French JR. 1993. Turbulence: Perspectives on flow and sediment transport.  
358 Chichester: Wiley. Chapter 1, Monitoring and modelling turbulent flow: Historical and  
359 contemporary perspectives; p. 1-34.
- 360 Cook CL, Coughlin DJ. 2010. Rainbow trout *Oncorhynchus mykiss* consume less energy when  
361 swimming near obstructions. J. Fish Biol. 77:1716–1723.
- 362 Dunbar MJ, Alfredsen K, Harby A. 2012. Hydraulic-habitat modelling for setting environmental  
363 flow needs for salmonids. Fish. Manag. Ecol. 19:500-517.

364 Enders EC, Boisclair D. 2016. Effects of environmental fluctuations on fish metabolism: Atlantic  
365 salmon *Salmo salar* as a case study. J. Fish Biol. 88:344-258.

366 Enders EC, Boisclair D, Roy AG. 2003. The effect of turbulence on the cost of swimming for  
367 juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 60:1149-1160.

368 Enders EC, Boisclair D, Roy AG. 2005. A model of total swimming costs in turbulent flow for  
369 juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 62:1079-1089.

370 ESRI. 2011. ArcGIS Desktop: Release 10. Redlands, California: Environmental Systems Research  
371 Institute.

372 Fausch KD. 1984. Profitable stream positions for salmonids: relating specific growth rate to net  
373 energy gain. Can. J. Zool. 62:441-451.

374 Fausch KD. 2014. A historical perspective on drift foraging models for stream salmonids.  
375 Environ. Biol. Fish. 97:453-464

376 Fraser NHC, Metcalfe NB. 1997. The costs of becoming nocturnal: feeding efficiency in relation  
377 to light intensity in juvenile Atlantic salmon. Funct. Ecol. 11:385-391.

378 Gries G, Whalen KG, Juanes F, Parrish DL. 1997. Nocturnal activity of juvenile Atlantic salmon  
379 (*Salmo salar*) in late summer: evidence of diel activity partitioning. Can. J. Fish. Aquat. Sci.  
380 54:1408-1413.

381 Hafs AW, Harrison LR, Utz RM, Dunne T. 2014. Quantifying the role of woody debris in providing  
382 bioenergetically favourable habitat for juvenile salmon. Ecol. Model. 285:30-38.

383 Hayes JW, Jowett IG. 1994. Microhabitat models of large drift-feeding brown trout in three New  
384 Zealand Rivers. N. Am. J. Fish. Manage. 14:710-725.

385 Hayes JW, Goodwin E, Shearer KA, Hay J, Kelly L. 2016. Can Weighted Useable Area Predict Flow  
386 Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model  
387 Incorporating Drift-Flow Processes. *Trans. Am. Fish. Soc.* 145:589-609.

388 Heath AG. 1995. *Water Pollution and Fish Physiology*. CRC Press, Boca Raton.

389 Heggenes J. 1990. Habitat utilisation and preferences in juvenile Atlantic salmon (*Salmo salar*)  
390 in streams. *Regul. River.* 5:341-354.

391 Heggenes J, Saltveit SJ. 1990. Seasonal and spatial microhabitat selection and segregation in  
392 young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *J.*  
393 *Fish Biol.* 36:707-720.

394 Hill J, Grossman GD. 1993. An energetic model of microhabitat use for rainbow trout and  
395 rosyside dace. *Ecology.* 74:685-698.

396 Hockley FA, Wilson CAME, Brew A, Cable J. 2014. Fish responses to flow velocity and turbulence  
397 in relation to size, sex and parasite load. *J. R. Soc. Interface.* 11. DOI: 10.1098/rsif.2013.0814.

398 Hughes NF, Dill LM. 1990. Position choice by drift-feeding salmonids: model and test for arctic  
399 grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. *Can. J. Fish. Aquat.*  
400 *Sci.* 47: 2039-2048.

401 Jørgensen C, Enberg K, Mangel M. 2016. Modelling and interpreting fish bioenergetics: a role for  
402 behaviour, life-history traits and survival trade-offs. *J. Fish Biol.* 88:389-402.

403 Kennedy GJA, Strange CD. 1982. The distribution of salmonids in upland streams in relation to  
404 depth and gradient. *J. Fish Biol.* 20:579-591.

405 Lacey RWJ, Legendre P, Roy AG. 2007. Spatial-scale partitioning of in situ turbulent flow data  
406 over a pebble cluster in a gravel-bed river. *Water Resour. Res.* 43:W03416.

407 Lacey RWJ, Neary VS, Liao JC, Enders EC, Tritico HM. 2012. The IPOS framework: linking fish  
408 swimming performance in altered flows from laboratory experiments to rivers. *River Res. Appl.*  
409 28:429–443.

410 Lancaster J, Downes BJ. 2010. Linking the hydraulic world of individual organisms to ecological  
411 processes: putting ecology into ecohydraulics. *River Res. Appl.* 26:385-403.

412 Lawless M, Robert A. 2001. Three-dimensional flow structure around small-scale bedforms in a  
413 simulated gravel-bed environment. *Earth Surf. Process. Landf.* 26:507–522.

414 Liao JC. 2006. The role of lateral line and vision on body kinematics and hydrodynamics  
415 preference of rainbow trout in turbulent flow. *J. Exp. Biol.* 209:4077-4090.

416 Liao JC. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Phil. Trans.*  
417 *R. Soc. B.* 362:1973-1993.

418 Liao JC, Beal DN, Lauder GV, Triantafyllou MS. 2003. Fish exploiting vortices decrease muscle  
419 activity. *Science.* 302:1566-1569.

420 Lupandin AI. 2005. Effect of flow turbulence on swimming speed of fish. *Biol. Bull.* 32:461-466.

421 Meineri E, Deville AS, Grémillet D, Gauthier-Clerc M, Béchet, A. 2015. Combining correlative and  
422 mechanistic habitat suitability models to improve ecological compensation. *Biol. Rev.* 90:314-  
423 329.

424 Morantz DL, Sweeney RK, Shirvell CS, Longard DA. 1987. Selection of microhabitat in summer  
425 by juvenile Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 44:120–129.

426 Milhous RT, Wegner DL, Waddle T. 1984. Users guide to the Physical Habitat Simulation System  
427 (PHABSIM), Instream Incremental Flow Information Paper 11. US Fish and Wildlife Service:  
428 FWS/OBS-81/13 (revised).

429 Nikora V. 2010. Hydrodynamics of aquatic ecosystems: an interface between ecology,  
430 biomechanics and environmental fluid mechanics. *River Res. Appl.* 26:367-384.

431 Oliver MA. 1990. Kriging: A method of interpolation for Geographical Information Systems. *Int. J.*  
432 *Geogr. Inf. Sci.* 4:313-332.

433 Parsheh M, Sotiropoulos F, Porté-Agel F. 2010 Estimation of power spectra of acoustic Doppler  
434 velocimetry data contaminated with intermittent spikes. *J. Hydraul. Eng.* 136:368–378.

435 Pavlov DS, Lupandin AI, Skorobogatov MA. 2000. The effects of flow turbulence on the  
436 behaviour and distribution of fish. *J. Ichthyol.* 40:232-S261.

437 Piccolo JJ, Frank BM, Hayes JW. 2014. Food and space revisited: The role of drift-feeding theory  
438 in predicting the distribution, growth, and abundance of stream salmonids. *Environ. Biol. Fishes.*  
439 97:475-488.

440 Przybilla A, Kunze S, Rudert A, Bleckmann H, Brücker C. 2010. Entraining in trout: a behavioural  
441 and hydrodynamic analysis. *J. Exp. Biol.* 213, 2976–2986.

442 R Core Team. 2015. R: A language and environment for statistical computing. Vienna, Austria: R  
443 Foundation for Statistical Computing. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

444 Railsback SF, Gard M, Harvey BC, White JL, Zimmerman JK. 2013. Contrast of degraded and  
445 restored stream habitat using an individual-based salmon model. *N. Am. J. Fish. Manage.* 33:384-  
446 99.

447 Riehle MD, Griffith JS. 1993. Changes in habitat use and feeding chronology of juvenile rainbow  
448 trout (*Oncorhynchus mykiss*) in fall and the onset of winter in Silver Creek, Idaho. *Can. J. Fish.*  
449 *Aquat. Sci.* 50:2119-2128.

450 Rosenfeld JS, Ptolemy R. 2012. Modelling available habitat versus available energy flux: do  
451 PHABSIM applications that neglect prey abundance underestimate optimal flows for juvenile  
452 salmonids? *Can. J. Fish. Aquat. Sci.* 69:1920-34.

453 Roy AG, Buffin-Bélanger T, Lamarre H, Kirkbride AD. 2004. Size, shape and dynamics of large-  
454 scale turbulent flow structures in a gravel-bed river. *J. Fluid Mech.* 500:1-27.

455 Roy ML, Roy AG, Legendre P. 2010. The relations between 'standard' fluvial habitat variables  
456 and turbulent flow at multiple scales in morphological units of a gravel-bed river. *River Res.*  
457 *Appl.* 26:439-455.

458 Silva AT, Santos JM, Ferreira MT, Pinheiro AN, Katopodis C. 2011. Effects of water velocity and  
459 turbulence on the behaviour of Iberian barbel (*Luciobarbus bocagei*, Steindachner 1864) in an  
460 experimental pool-type fishway. *River Res. Appl.* 27:360–373.

461 Silva AT, Katopodis C, Santos JM, Ferreira MT, Pinheiro AN. 2012. Cyprinid swimming behaviour  
462 in response to turbulent flow. *Ecol. Eng.* 44:314-328.

463 Smith DL, Brannon EL. 2007. Influence of cover on mean column hydraulic characteristics in  
464 small pool riffle morphology streams. *River Res. Appl.* 23:125-139.

465 Symons PEK, Heland M. 1978. Stream habitats and behavioural interactions of underyearling  
466 and yearling Atlantic salmon (*Salmo salar*). *J. Fish. Res. Board Can.* 35, 175–183.

467 Taguchi M, Liao JC. 2011. Rainbow trout consume less oxygen in turbulence: the energetics of  
468 swimming behaviors at different speeds. *J. Exp. Biol.* 214:428–1436.

469 Tritico HM, Cotel AJ. 2010 The effects of turbulent eddies on the stability and critical swimming  
470 speed of creek chub (*Semotilus atromaculatus*). *J. Exp. Biol.* 213:2284-2293.

- 471 Urabe H, Nakajima M, Torao M, Aoyama T. 2014. Application of a bioenergetics model to  
472 estimate the influence of habitat degradation by check dams and potential recovery of masu  
473 salmon populations. *Environ. Biol. Fishes.* 97:587-598.
- 474 Valdimarsson SK, Metcalfe NB, Thorpe JE, Huntingford FA. 1997. Seasonal changes in sheltering:  
475 effect of light and temperature on diel activity in juvenile salmon. *Anim. Behav.* 54:1405-1412.
- 476 Webb PW. 2004. Response latencies to postural differences in three species of teleostean fishes.  
477 *J. Exp. Biol.* 207:955-961.
- 478 Wilkes MA, Maddock I, Visser F, Acreman M. 2013. *Ecohydraulics: An integrated approach.*  
479 Chichester:Wiley. Chapter 1, Incorporating hydrodynamics into ecohydraulics: The role of  
480 turbulence in the swimming and habitat selection of river-dwelling salmonids; p. 9-30.
- 481 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed effects models and extensions*  
482 *in ecology with R.* New York: Springer.



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Table 1 – Summary of predicted swimming costs for each fish, including the mean predicted SC expected at random ('Null'), and the probability ( $p$ ) that each fish chose cells at random.

Fish	Mean $SC_{pred}$ (mg O <sub>2</sub> h <sup>-1</sup> )	Behaviour	$p$
(Null)	0.5	NA	NA
1	0.08	Station-holding	0
2	0.19	Searching	0
3	0.48	Searching	0.37
4	0.29	Searching	0
5	0.03	Searching	0
6	0.23	Searching	0
7	0.09	Station-holding	0
8	0.03	Searching	0
9	0.64	Searching	0.99
10	0.71	Searching	0.99
11	0.02	Searching	0
12	0.14	Searching	0
13	0.03	Searching	0
14	0.05	Searching	0
15	0.32	Searching	0
16	0.1	Searching	0
17	0.28	Searching	0
18	0.002	Station-holding	0
19	0.58	Searching	0.95
20	0.03	Station-holding	0
21	0.02	Station-holding	0
22	0.39	Searching	0.008
23	0.039	Searching	0
24	0.05	Searching	0
25	0.06	Searching	0
26	0.33	Searching	0
27	0.33	Searching	0
29	0.41	Station-holding	0.04
30	0.11	Searching	0
31	0.46	Searching	0.24
32	1.38	Searching	1
33	0.3	Searching	0
35	0.02	Station-holding	0
36	0.36	Station-holding	0.0006
37	0.06	Station-holding	0
38	0.21	Station-holding	0
39	0.03	Station-holding	0
41	0.01	Station-holding	0
43	0.05	Station-holding	0
44	0.25	Station-holding	0
45	0.13	Station-holding	0
46	0.29	Station-holding	0

Table 2 – Results of ZINB modelling for the swimming costs model.

<b>Term</b>	<b>Estimate</b>	<b>SE</b>	<b>z value</b>	<b>p</b>
	$g(\mu)$			
(Intercept)	0.1009	0.1521	0.664	0.507
CR	-0.8979	0.1129	-7949	< 0.001
log (theta)	-3.1132	0.1287	-24.186	< 0.001
	$g(\pi)$			
(Intercept)	-1.829	1.127	-1.622	0.105
CR	-1.214	0.817	-1.486	0.137
			Log-lik = -3504 on 5 df	
			AIC = 6967.16	

Table 3 – Summary of ZINB model selection for the bespoke hydrodynamic habitat model.

<b>Dropped term</b>	<b>df</b>	<b>AIC</b>	<b>LR test</b>
None	11	6926.53	
$U$ from count model	10	6938.33	$X^2 = 13.8$ (df = 1, $p = 2.03 \times 10^{-9}$ )
$V_{grad}$ from count model	10	6932.62	$X^2 = 8.0965$ (df = 1, $p = 0.00444$ )
$\tau_{uv}$ from count model	10	6925.05	$X^2 = 0.5291$ (df = 1, $p = 0.467$ )
$I\tau_{uw}I$ from count model	10	6927.45	$X^2 = 2.92$ (df = 1, $p = 0.0875$ )
$U$ from binomial model	10	6936.66	$X^2 = 12.128$ (df = 1, $p = 4.97 \times 10^{-4}$ )
$V_{grad}$ from binomial model	10	6938.52	$X^2 = 13.989$ (df = 1, $p = 1.84 \times 10^{-4}$ )
$\tau_{uv}$ from binomial model	10	6945.09	$X^2 = 20.567$ (df = 1, $p = 5.76 \times 10^{-7}$ )
$I\tau_{uw}I$ from binomial model	10	6964.76	$X^2 = 40.231$ (df = 1, $p = 2.26 \times 10^{-10}$ )
$\tau_{uv}$ and $I\tau_{uw}I$ from count model	9	6925.55	$X^2 = 3.0203$ (df = 2, $p = 0.221$ )
$\tau_{uv}$ and $I\tau_{uw}I$ from binomial model	9	6964.11	$X^2 = 41.584$ (df = 2, $p = 9.34 \times 10^{-10}$ )
$\tau_{uv}$ and $I\tau_{uw}I$ from both models	7	6963.14	$X^2 = 44.614$ (df = 4, $p = 4.78 \times 10^{-9}$ )

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Table 4 – Results of ZINB modelling for the optimal bespoke hydrodynamic model.

<b>Term</b>	<b>Estimate</b>	<b>SE</b>	<b>z value</b>	<b>p</b>
<i>g</i> ( $\mu$ )				
(Intercept)	1.31874	0.18825	7.005	$2.47 \times 10^{-12}$
<i>U</i>	-0.14748	0.02827	-5.217	$1.82 \times 10^{-7}$
<i>V<sub>grad</sub></i>	-0.29105	0.09463	-3.076	0.0021
log (theta)	-2.62764	0.099	-26.543	$< 2 \times 10^{-16}$
<i>g</i> ( $\pi$ )				
(Intercept)	0.47686	0.27764	1.718	0.08588
<i>U</i>	0.16404	0.05232	3.135	0.00172
<i>V<sub>grad</sub></i>	-0.60384	0.17324	-3.485	$4.91 \times 10^{-4}$
$\tau_{uv}$	-0.05798	0.01423	-4.074	$4.62 \times 10^{-5}$
$\mathbf{I}\tau_{uw}\mathbf{I}$	-0.09924	0.03010	-3.297	$9.77 \times 10^{-4}$
				Log-lik = -3454 on 9 df
				AIC = 6925.55

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492 Figure 1 – Map of test section and sample locations for acoustic Doppler velocimeter (ADV)  
493 measurements.

494 Figure 2 – Maps of (a) mean velocity, (b) turbulence intensity, (c) average eddy length, (d, e)  
495 Reynolds shear stresses, and (f) resultant velocity vectors illustrating the sampling locations in the test  
496 area of the experimental stream channel.

497 Figure 3 – Example velocity spectra over a large hemisphere (a-d) and a small (e-h) hemispheres  
498 located at  $x=125$ ,  $z=185$ , and  $x=135$ ,  $z=17.5$  respectively, where  $x$  and  $z$  are streamwise and spanwise  
499 coordinates within the test arena (cm). Spectra shown for locations upstream ( $z-5$  cm) and  
500 downstream (e.g.,  $z+5$  cm) of hemispheres.

501 Figure 4 – Map of predicted swimming costs.

502 Figure 5 – Maps illustrating (a) typical station-holding (fish 9) and searching (fish 38) behaviours and  
503 (b) the habitat selection index, a measure of cell occupancy by  $n=46$  fish with  $t=121$  observations per  
504 fish (see equation 6).

505 Figure 6 – Null distribution of predicted swimming costs based on 10,000 bootstrap samples of 121  
506 random cells from the artificial habitat.

507 Figure 7 – (a) Count (selection index,  $SI$ ) and (b) binomial (probability of false zero,  $p$ ) results for the  
508 predicted swimming costs ( $SC_{pred}$ ) model. Count model predictions standardised ( $\mu_i / \mu_{max}$ ) to visualise  
509 results. Symbols denote observed  $SI$  for each cell.

510 Figure 8 – (a-b) Count (selection index,  $SI$ ) and (c-f) binomial (probability of false zero,  $p$ ) results for  
511 the optimal bespoke hydrodynamic habitat model, including parameters mean resultant velocity ( $U$ ),  
512 spatial velocity gradient ( $V_{grad}$ ) and Reynolds stresses in the streamwise vertical ( $\tau_{uv}$ ) and horizontal  
513 ( $\tau_{uw}$ , absolute) planes. Count model results standardised ( $\mu_i / \mu_{max}$ ) and all model predictions smoothed  
514 using a loess smoother (span = 0.5) to visualise results. Symbols denote observed  $SI$  for each cell.