

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 (τ_{uv}), and streamwise-lateral (τ_{uw}) planes:

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

139 where ρ is the water density (1000 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} , τ_{uv} , τ_{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, β_0 is the intercept, X^T is a vector of m predictor variables, and β 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 (μ), whilst the binomial model (π) 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⁻¹ and 0.38 to
187 8.13 cm s⁻¹, 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 O₂ h⁻¹ (0.19-
196 75.39 J h⁻¹ 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 , τ_{uv} , τ_{uw} and V_{grad} were
224 entered as explanatory variables for the hydrodynamic habitat model. In the case of τ_{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 τ_{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 τ_{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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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 ₂ h ⁻¹)	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.

Term	Estimate	SE	z value	p
	$g(\mu)$			
(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.

Dropped term	df	AIC	LR test
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, $p = 0.00444$)
τ_{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, $p = 1.84 \times 10^{-4}$)
τ_{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, $p = 2.26 \times 10^{-10}$)
τ_{uv} and $I\tau_{uw}I$ from count model	9	6925.55	$X^2 = 3.0203$ (df = 2, $p = 0.221$)
τ_{uv} and $I\tau_{uw}I$ from binomial model	9	6964.11	$X^2 = 41.584$ (df = 2, $p = 9.34 \times 10^{-10}$)
τ_{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.

Term	Estimate	SE	z value	p
<i>g</i> (μ)				
(Intercept)	1.31874	0.18825	7.005	2.47 x 10 ⁻¹²
<i>U</i>	-0.14748	0.02827	-5.217	1.82 x 10 ⁻⁷
<i>V_{grad}</i>	-0.29105	0.09463	-3.076	0.0021
log (theta)	-2.62764	0.099	-26.543	< 2 x 10 ⁻¹⁶
<i>g</i> (π)				
(Intercept)	0.47686	0.27764	1.718	0.08588
<i>U</i>	0.16404	0.05232	3.135	0.00172
<i>V_{grad}</i>	-0.60384	0.17324	-3.485	4.91 x 10 ⁻⁴
τ_{uv}	-0.05798	0.01423	-4.074	4.62 x 10 ⁻⁵
$\mathbf{I}\tau_{uv}\mathbf{I}$	-0.09924	0.03010	-3.297	9.77 x 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 (μ_i / μ_{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 (τ_{uv}) and horizontal
513 (τ_{uw} , absolute) planes. Count model results standardised (μ_i / μ_{max}) and all model predictions smoothed
514 using a loess smoother (span = 0.5) to visualise results. Symbols denote observed SI for each cell.