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How does school size affect tail beat frequency in turbulent water?

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23 **Abstract**

24 The energy savings experienced by fish swimming in a school have so far been investigated in an
25 near-idealised experimental context including a relatively laminar water flow. The effects of
26 explicitly turbulent flows and of different group sizes are yet to be considered. Our repeated-
27 measures study is a first step in addressing both of these issues: whether schooling is more
28 energetically economical for fish when swimming in a quantified non-laminar flow and how this
29 might be moderated by group size. We measured tail beat frequency (tbf) in sea bass swimming in a
30 group of 3, 6 or singly. Video data enabled us to approximately track the movements of the fish
31 during the experiments and in turn ascertain the water flow rates and turbulence levels experienced
32 for each target individual. Although the fish exhibited reductions in tbf during group swimming,
33 which may indicate some energy savings, this saving appears to be attenuated, presumably due to
34 the water turbulence and the movement of the fish relative to each other. Surprisingly, tbf was
35 unrelated to flow rate when the fish were swimming singly or in a group of three, and decreased
36 with increasing flow rates when swimming in a group of six. However, the fish increased tbf in
37 greater turbulence at all group sizes. Our study demonstrates that under the challenging and
38 complex conditions of turbulent flow and short-term changes in school structure, group size can
39 moderate the influences of water flow on a fish's swimming kinematics, and in turn perhaps their
40 energy costs.

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45 **Summary statement**

46 The energy savings that sea bass experience from schooling are affected by flow speed or
47 turbulence, moderated by group size

48 Introduction

49 Animals derive many benefits from living in groups. In addition to increased foraging efficiency and
50 decreased predation risk, a major advantage for some animal groups is decreased costs of
51 locomotion. In bird flocks, fish schools, and even human bicycle pelotons, individuals can position
52 themselves to take advantage of vortices and zones of low pressure created by group mates to
53 decrease their own energetic costs of movement (Marras et al., 2015). Fish schooling behaviour has
54 been particularly well studied in terms of the energy savings it can afford to swimming fish (Fields,
55 1990; Herskin and Steffensen, 1998; Liao et al., 2003; Weihs, 1973; Zuyev and Belyayev, 1970).
56 Specifically, trailing individuals can take advantage of the reverse von Kármán vortex street
57 produced by fish further forwards in the school to reduce their own swimming energy costs (Fish et
58 al., 1991; Killen et al., 2011; Liao, 2007; Liao et al., 2003). Due to the flow dynamics around fish, the
59 economic gains of schooling may not be limited to trailing individuals within moving groups.
60 Remarkably, individuals in the periphery and vanguard of the school also save energy compared to
61 swimming in isolation, albeit to a lesser extent than those that are following (Hemelrijk et al., 2015;
62 Marras et al., 2015).

63 To date, studies examining the energetic costs of swimming in schools have investigated situations
64 where two-dimensional schools (a single horizontal 'layer' of offset individuals) are swimming in a
65 non-turbulent flow (Fish et al., 1991; Herskin and Steffensen, 1998; Killen et al., 2011; Marras et al.,
66 2015); an idealised experimental design where only position relative to conspecifics in the school can
67 affect energetic costs of swimming. Although truly laminar flows are difficult to establish, most
68 studies use flumes that are designed to minimise turbulence (e.g. Fish et al., 1991; Killen et al.,
69 2011) to a level such that turbulence is unlikely to have notable effects on swimming performance
70 (Roche et al., 2014; Tritico and Cotel, 2010). We therefore have a limited understanding of how
71 turbulence may modulate the energy-savings achieved by individual fish within schools. This is
72 despite the fact that many fish in the wild are routinely subjected to turbulent flows (Liao, 2007), for
73 example in river systems, coral reefs, or other marine and freshwater habitats with mixing currents
74 or upwelling, and turbulent or unsteady flows can affect the costs of locomotion considerably (Cook
75 and Coughlin, 2010; Enders et al., 2003; Roche et al., 2014; Taguchi and Liao, 2011). Furthermore,
76 fish in these environments may not be able to maintain station relative to their neighbours and so it
77 is possible that they will experience reduced benefits associated with the flow dynamics around their
78 group mates.

79 Although free-living, conspecific fish schools contain varying numbers of fish (Johansen et al., 2010),
80 no study thus far has investigated the effects of school size on swimming energy costs in turbulent
81 flow. An increased understanding of how group size further modulates energy savings would provide
82 additional information on the adaptive value of group membership as well as optimal group size. For
83 example, maintenance of position by a fish within a group may also be affected by factors such as
84 spatial competition (Herskin and Steffensen, 1998), with the number of fish within a school affecting
85 the ability of individuals to occupy their preferred position relative to group mates. It is also possible
86 that emergent group-level behaviours may play a greater role at larger group sizes, with global
87 properties such as overall school size and shape influencing the degree of energy-savings
88 experienced by individual fish (Rieucau et al., 2015). Turbulent water may moderate the effect of
89 group size on swimming energetics because such an environment may make it more difficult for fish
90 to maintain optimal positioning within a school.

91 The sea bass *Dicentrarchus labrax* is a gregarious benthopelagic species that is primarily marine but
92 can also inhabit brackish waters. Here we report on the first flume-based experiments using a non-
93 laminar flow where that flow is quantified and the three-dimensional position of the fish within the
94 flume measured such that the local flow rate and turbulence experienced by each individual is
95 known. With these data we examine how group size and water turbulence affect the tail beat
96 frequency of sea bass at various flow rates, which provides some insights into differences in energy
97 expenditure in these various conditions.

98

99 **Methods**

100 All experiments were regulated by the UK Animals (Scientific Procedures) Act 1986 and carried out
101 under the authority of UK Home Office project licence PPL 80/2434, having been approved by the
102 Cefas ethical review process. Data presented in this study are available on Dryad.

103 *Animals*

104 European sea bass (N = 18) were obtained from the Sea Life Centre at Great Yarmouth, Norfolk, UK
105 and held at the Cefas Laboratory, Lowestoft, in a tank supplied with aerated seawater at ambient
106 temperatures (12.5-16.5 °C). They were fed a mixture of sand eel and sprat. The lengths of the fish
107 used in the experiments ranged from 49 to 61 cm, with masses from 1490 to 3240 g. Each fish was
108 given a unique t-bar tag for identification purposes.

109 *Experiments*

110 The fish were placed in the swim section of a large Brett-style flume (swim section dimensions: 200 x
111 150 x 70.7 cm; Figure 1A) and left to habituate overnight at an average flow rate of 0.29 m s⁻¹.
112 Aerated seawater was fed into the tank at a flow rate of 0.2 L min⁻¹, and the water temperature in
113 the tank ranged between 12.5-16.5 °C.

114 Between the hours of 09:00 and 17:30 each day, three sets of experiments were carried out,
115 whereby the fish swam against various propeller-induced flows. The first experiment involved a
116 group of 6 fish, the second a group of 3 and the third an individual (N = 13 fish for group size=3 and
117 6, and N = 12 fish for group size=1, where N represents the number of different fish included in each
118 group size). The fish used in each experiment were selected to minimise the number of incidences of
119 any given fish swimming with the same individuals (Table S1). Subsequently, all remaining fish that
120 had not undertaken the experiments singly were subjected to the experiment for group size=1.

121 Water flow rate and turbulence were affected by three propellers located symmetrically across the
122 back wall of the flume, and driven by electric motors. The resultant flow was measured throughout
123 the flume by a Nortek Vectrino II acoustic Doppler velocimeter (Nortek AS, Vangskroken, Norway). To
124 quantify the flow and turbulence, after the experiments the water was seeded using Q-Cel[®] hollow
125 microspheres which served to increase the signal to noise ratio within the flume (Nortek, 2009).
126 Measurements were taken at 45 locations within one vertical half of the swim section, defined by
127 three-dimensional co-ordinates (Figure 1B), at a sampling rate of 100 Hz for 60 s per location. The
128 measured values were assumed to be mirrored on the other half of the (symmetrical) tank.
129 Measurements could not be obtained towards the surface of the water due to the water churn

130 periodically exposing the velocimeter to air; these values were assumed to be the same as those
131 measured in their neighbouring locations in the tank along the horizontal axis (the axis which has the
132 least spatial variability). Time-averaged velocity and turbulence were calculated using W_{INADV}
133 software (Wahl, 2011) after filtering using the methods described in Rusello et al. (2006). The
134 propellers delivered mean flow rates of 0.15 ± 0.07 , 0.23 ± 0.12 and 0.31 ± 0.22 $m\ s^{-1}$ when the propeller
135 motors turned over at 20, 30 and 40 Hz (hereafter termed the 'propeller speeds'), respectively.
136 These flow rates spanned the preferred swim speed of free-swimming European sea bass (0.8 body
137 lengths / s; Sureau and Lagardère, 1991). However, at each propeller speed there was considerable
138 spatial variation in flow rate; mean values at each measured location in the tank ranged from 0.02 to
139 0.42, 0.07 to 0.58, and 0.12 to 0.64 $m\ s^{-1}$ at 20, 30 and 40 Hz, respectively (Figure 2A, Table S2). In
140 summary, flow rates tended to be lower at the bottom (Z1) and the centre (Y2-Y3) of the flume, and
141 fairly constant from front to back (X1 to X5) (Figure 1C), but not always (Figure 2A). Turbulence
142 measured in all three dimensions was calculated as the turbulence kinetic energy (Hockley et al.,
143 2014) - the mean kinetic energy per unit mass associated with eddies in turbulent flow,
144 characterised by the root-mean-square of velocity fluctuations. Mean values were 0.18, 0.26 and
145 $0.38\ m^2\ s^{-2}$ at the three propeller speeds, while the ranges of the mean values across the tank were
146 0.08 to 0.3, 0.14 to 0.42, and 0.27 to $0.55\ m^2\ s^{-2}$ (Figure 2B, Table S3). Higher propeller speeds
147 generated both higher mean flow rates and higher mean levels of turbulence, however within each
148 propeller speed there was considerable spatial variation in both factors (Figure 3).

149 No correction was made for solid blocking in the flume as the fractional error was $< 1\%$ (Bell and
150 Terhune, 1970). Each flow rate condition lasted 20 min, after which the propeller speed was
151 gradually changed to the next one over the following minute. Two video cameras (Hercules Deluxe
152 Optical Glass) were attached to the tank (in front and to the side, respectively) enabling the position
153 of the fish within the tank in three dimensions to be recorded along with their tail beat frequency
154 (tbf), at 30 frames per section (> 15 times the highest tbf recorded). Tbf is often used as a proxy of
155 rate of energy expenditure (e.g. Steinhausen et al., 2005), and has been correlated with rate of
156 oxygen consumption in sea bass, though only while swimming in a laminar flow (Herskin and
157 Steffensen, 1998). We were not able to measure tail beat amplitude, which can sometimes
158 moderate the relationship between tbf and rate of energy expenditure, e.g. tuna (Blank et al., 2007).
159 However, tbf typically relates to swimming speed linearly (e.g. Bainbridge, 1958), and hence
160 positively to rate of oxygen consumption. Fish were kept in a holding tank ($8.8\ m^3$) when they were
161 not in the flume, with swimming conditions arranged such that fish were not moved unnecessarily.
162 At the end of the experiments the fish were killed using a UK Home Office Licence schedule 1
163 procedure.

164 *Data manipulation*

165 Within each experimental condition, denoted by group size and flow rate, all the fish present were
166 observed, independently over four different 30-s periods. These periods were chosen within
167 consecutive three-minute intervals starting 4 minutes into the condition (and therefore also
168 excluding the final four minutes of the condition). The 30-s periods were based on when the fish
169 could be most clearly observed on the video footage. These sequences included horizontal or
170 vertical movement of the fish within the flume, but sequences were not analysed if the fish
171 performed turning motions that caused them to be perpendicular to the overall direction of the
172 flow, or moved location repeatedly. The mean tbf (Hz) of the fish was calculated for each period

173 (one tail beat was defined as one complete oscillation of the tail). Furthermore, a simple index of the
174 amount that the fish moved position within the tank during that period was calculated. The location
175 of the fish was recorded at the beginning and end of each period in terms of whether it was central,
176 off centre, or towards a side of the tank, in each of the three dimensions separately (Figure 1C). Thus
177 in each dimension (i.e. side to side, top to bottom and front to back) the fish was recorded at one of
178 five locations at the start and end of the recording period. In turn, in each dimension individually,
179 the net amount the fish moved between the start and end of the recording period was recorded,
180 where 0 = maintained station and 5 = moved from one side to the other. These values were then
181 summed for the three dimensions to calculate a 'movement count'.

182 To estimate the environment experienced by each fish in terms of flow rate and turbulence during
183 each 30-s period of observation, their approximate mean position was calculated as the average of
184 their three-dimensional start and end positions. This mean location was used to estimate the mean
185 flow and turbulence experienced by the fish during that 30-s period based on the Doppler
186 velocimeter measurements.

187 *Data analyses*

188 The effect on tbf of flow rate, turbulence, group size and their interactions was investigated with
189 general linear mixed models (LMMs) using type III sums of squares. Group size was either 1, 3 or 6
190 and was set as a categorical factor, while flow rate and turbulence were input as continuous
191 covariates. A unique identifier for each fish was included as a random factor to account for the
192 presence of multiple data points per fish, per condition. These random effects employed a variance
193 components variance-covariance structure, which returned lower information criteria scores than
194 alternative structures. Model estimates were calculated using maximum likelihood. To investigate
195 the effects of speed and turbulence on tbf while controlling for the other independent variable, the
196 models took the form $tbf \sim \text{flow rate} + \text{turbulence} + \text{individual}[\text{random}]$, each model defined by a
197 different group size. To then investigate the effect of group size on tbf and how this factor interacts
198 with flow rate and turbulence, a further model included group size, the interaction between group
199 size and flow rate, and the interaction between group size and turbulence.

200 To investigate the effects of propeller speed on the changing of location of the fish within the flume
201 (movement count), a generalised linear mixed model (GLMM) was generated, recognising a Poisson
202 distribution in the count data by a log link function. The linear predictor was flow rate, turbulence
203 and group size, with individual as a random factor.

204 LMMs and GLMMs were built, and associated analysis was undertaken, in R v. 3.3. Visual inspection
205 of histograms of the residual plots from LMMs did not reveal any strong deviations from
206 homoscedasticity or normality in each model. There was no over-dispersion in the GLMM. Within
207 the text, descriptive statistics are presented alongside \pm one standard error (SE), while estimate
208 values from models are presented along with their associated 95% confidence interval (CI). In the
209 bar graph presented, the errors bars shown depict estimates \pm one standard error suitable for
210 repeated measures designs. These focus on within subject variance (Loftus and Masson, 1994) and
211 are calculated from the mean square values output from repeated measures two-way ANOVA of the
212 mean values, a calculation which assumes sphericity.

213 Interpretation of these analyses was based predominantly on sample effect sizes and their precision,
214 visualised with graphs incorporating error bars where appropriate (Lavine, 2014; Loftus, 1993). This
215 interpretation was secondarily supported by null hypothesis significance testing to provide some
216 indication of the strength of evidence for observed patterns. In the present article the p value is
217 treated as a continuous variable providing a very approximate level of evidence against the null
218 hypothesis (Fisher, 1959), rather than referring to arbitrary cut-offs, which are problematic and
219 limiting in several ways (Boos and Stefanski, 2011; Halsey et al., 2015).

220

221 **Results**

222 For fish swimming singly, where the linear predictor was flow rate and turbulence, there was no
223 evidence that flow rate was a predictor of tbf ($F_{1,130} = 0.44$, $p = 0.51$; Figure 4A) whereas turbulence
224 clearly was ($F_{1,130} = 27.98$, $p = 0.00$; Figure 4D). A $0.1 \text{ m}^2 / \text{s}^2$ increase in turbulence resulted in an
225 increase in tbf of 0.13 [CI: 0.08 to 0.18] Hz. A similar pattern was apparent for fish swimming in a
226 group of three individuals (flow rate: $F_{1,180} = 1.06$, $p = 0.30$, Figure 4B; turbulence: $F_{1,180} = 6.10$, $p =$
227 0.01 , Figure 4E), though the estimated effect of turbulence on tbf was smaller (0.05 [CI: 0.01 to 0.1]
228 Hz per $0.1 \text{ m}^2 / \text{s}^2$ increase in turbulence). For fish swimming in a larger group of six individuals,
229 however, both flow rate ($F_{1,288} = 18.02$, $p = 0.00$, Figure 4C) and turbulence ($F_{1,288} = 44.73$, $p = 0.00$,
230 Figure 4F) were clear predictors. An increase in flow rate of 0.1 m/s is related to a decrease in tbf of -
231 0.04 [CI: -0.06 to -0.02] Hz, whereas an increase in turbulence of $0.1 \text{ m}^2 / \text{s}^2$ is related to an increase
232 in tbf of 0.09 [CI: 0.06 to 0.1] Hz.

233 For the next LME, where the linear predictor was group size as well as flow rate and turbulence,
234 along with first order interactions, group size was not an important predictor ($F_{2,598} = 1.79$, $p = 0.17$).
235 However, along with evidence that both flow rate ($F_{1,598} = 3.15$, $p = 0.08$) and turbulence ($F_{1,598} =$
236 65.97 , $p = 0.00$) were predictors of tbf, both the interaction between group size and flow rate ($F_{1,598}$
237 $= 5.79$, $p = 0.00$) and between group size and turbulence ($F_{1,598} = 3.19$, $p = 0.04$) were predictive
238 elements of the model. Table 1 presents the fixed effect estimates and associated CIs for this model.

239 The movement count data indicated that the fish did not typically maintain station in the flume
240 during the experiments (Figure 5). There was no evidence of an effect of group size (with group
241 size=1 as the base; group size=3: $z = 1.13$, $p = 0.26$, group size=6: $z = 1.43$, $p = 0.15$) or turbulence ($z =$
242 -0.56 , $p = 0.57$) on movement count. There was some evidence of an effect of speed ($z = -1.86$, $p =$
243 0.06), however the effect size was small: an increase in speed of 1 m/s is related to an estimated
244 decrease in movement count of 0.4 .

245

246 **Discussion**

247 Several previous publications have documented energy savings in fish when swimming in a school in
248 a relatively laminar flow (Herskin and Steffensen, 1998; Killen et al., 2011; Marras et al., 2015). The
249 present results indicate that for sea bass swimming in the more complex scenario of turbulent water
250 and not maintaining station, group size influences how both the flow rate and the turbulence of the
251 water influence their tail beat frequency (tbf), with turbulence effects outweighing the effects of
252 speed.

253 Tbf of fish swimming in a group (totalling either 3 or 6 fish) was around 7.5% lower than when they
254 were swimming singly (Figure 4), which implies a modest reduction in energy costs (Herskin and
255 Steffensen, 1998). However, this interpretation must be made caveated with the recognition that
256 fish may sometimes be able to exploit turbulence such that little axial muscle activity is required to
257 maintain station (Liao, 2004), resulting in a different relationship between tbf and rate of oxygen
258 consumption in turbulent versus laminar flows.

259 Tentatively applying the calibration equation for single sea bass in a laminar flow by Herskin and
260 Steffensen (1998), the aforementioned 7.5% change in tbf represents a similar percentage change in
261 rate of oxygen consumption. This estimated reduction in energy costs due to swimming in a group is
262 considerably less than that reported elsewhere (Fish et al., 1991; Herskin and Steffensen, 1998;
263 Marras et al., 2015; though see Svendsen et al., 2003). For example, group-swimming grey mullet
264 *Liza aurata* experienced approximately a 20% decrease in tbf and an estimated 15% decrease in rate
265 of oxygen consumption (Marras et al., 2015). The experimental context of water turbulence and
266 positional changes by the fish in the present study afford a reasonable explanation for the reduced
267 effect size found. Turbulence likely increases the temporal variability in energy demands (Lorke and
268 Probst, 2010; Roche et al., 2014), and may also reduce the energy saving achieved from the flow
269 dynamics associated with being close to other fish. Positional changes within a group of swimming
270 fish are perhaps associated with social and competitive interactions between individuals (Herskin
271 and Steffensen, 1998; Olst and Hunter, 1970), and probably increase energy costs due to additional
272 accelerating and decelerating (Kramer and McLaughlin, 2001; Zamparo et al., 2014). The percentage
273 saving in energy expenditure due to group swimming tentatively estimated in the present study was
274 similar to that found for striped surfperch *Embiotoca lateralis* by Johansen et al. (2010), who
275 reported that the fish exhibited a constantly changing swimming position within the flume when in a
276 group but not when swimming alone.

277 The predominant influence of group size acted through its effects on the relationships between tbf
278 and both flow rate and turbulence. Not only was tbf unrelated to flow rate when the fish were
279 swimming singly or in a small group, but tbf decreased with increasing flow rate when the fish were
280 in a larger group of six individuals. The lack of a correlation between tbf and flow rate for sea bass
281 swimming singly is not surprising given that the flow rates they experienced ranged from around 0.2
282 to 1 body lengths / s, which while recognised to be their preferred swimming speeds (Sureau and
283 Lagardère, 1991), are also at the lower end of their swim speed range. The grey mullet studied by
284 Marras et al. (2015) showed no change in tail beat frequency between 1 and 2 body lengths / s. In
285 both cases, the fish were apparently swimming within a range of flow rates that did not require
286 systematic adjustment of their tbf in response to changes of swim speed. When swimming within
287 the larger group size, there is presumably more scope for interactions between individuals and for
288 energy savings from the flow dynamics of swimming in a group. The decreases in tbf by the sea bass
289 in a group of six when swimming in higher flows may therefore be explained by reduced interactions
290 with other fish and/or the fish positioning themselves relative to their conspecifics more accurately
291 in order to obtain energy savings to counteract the increased swimming effort. However, these
292 interpretations are caveated by the possibility that at these low speeds the fish modulated the
293 power output from their tail by adjusting tail beat amplitude instead of tbf; tail beat amplitude was
294 not a variable we were able to reliably quantify from the video footage.

295 Water turbulence had a more consistent influence on tbf, with the fish responding by increasing tbf
296 in greater turbulence at all group sizes. Indeed, turbulence appears to have had more of an influence
297 on swimming kinematics, and perhaps therefore energy expenditure, than did swimming speed, at
298 the range presented in the current study. Water turbulence is likely not only to force the fish to work
299 against the buffeting effects of the non-laminar flow, but may also cause the fish greater difficulty in
300 controlling their position relative to their neighbours, in turn being less able to maintain an optimal
301 spatial position.

302 Our study demonstrates that the energy advantages of swimming in a group may be attenuated
303 under the challenging and complex conditions of turbulent flow and short-term changes in fish
304 position within schools. It also shows that group size may moderate the influences of water flow rate
305 and turbulence on a fish's energy costs as it moves through its environment (i.e. group size affects its
306 energy landscape; Shepard et al., 2013). More detailed information on the spatio-temporal
307 variability of naturally encountered flows along with the prevalence of solitary and group swimming
308 is required to support better predictions of the energy costs for wild fish populations.

309

310 **Acknowledgements**

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312 **Competing interests**

313 The authors have no competing interests.

314

315 **Author contributions**

316 SSK, LGH and SW devised the study; SW, SSK and FH collected the data; AR prepared the data and LH
317 statistically analysed them; LGH, SW and SSK wrote the manuscript.

318

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Table 1. Estimates of fixed effects from a linear mixed effects model describing tail beat frequency (Hz) from group size, flow rate (m / s) and turbulence (m² / s²).

Parameter	Estimate	Std. Error	95% Confidence Interval	
			Lower Bound	Upper Bound
Intercept	1.05	0.07	0.91	1.18
Group size = 1	-0.21	0.12	-0.45	0.02
Group size = 3	-0.15	0.11	-0.36	0.08
Flow rate (m / s)	-0.45	0.12	-0.67	-0.21
Turbulence (m ² / s ²)	0.88	0.15	0.59	1.17
Group size = 1 * flow rate	0.33	0.20	-0.06	0.71
Group size = 3 * flow rate	0.58	0.17	0.24	0.92
Group size = 1 * turbulence	0.43	0.27	-0.11	0.94
Group size = 3 * turbulence	-0.34	0.25	-0.83	0.15

325 Estimate values for group sizes of 1 and 3, and their interactions with flow rate and with turbulence,
 326 are relative to group size = 6 and its equivalent interactions, respectively.

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331 Figure 1. Schematic illustrating the Brett-style flume and the coordinate systems associated with certain measurements taken within it. A: The main flow
332 direction within the flume generated by the propellers (i). Sea bass were held in the swim section of the flume (ii); B: The coding of the movement
333 observations made of the fish during the experimental periods. The fish's net movement, i.e. its change in position between the start and end of the period,
334 was recorded in each of the three dimensions: (1) side to side; (2) top to bottom and (3) front to back. In each of these dimensions, the fish was recorded as
335 being in one of five locations spanning that dimension; C: The co-ordinate system used to denote three-dimensional locations within the swim section of
336 the flume. The flow (mean flow rates and turbulence) within this area were calculated at 45 locations represented by the locations X1:X5, Y1:Y3 (the flow
337 was measured from the centre to the side of the tank along the y-denoted dimension and was assumed to be mirrored on the other half of the symmetrical
338 tank) and Z1:Z3 (due to turbulence at the water surface it was not possible to obtain flow readings in the upper water levels at all propeller speeds; Z3 is
339 deeper than Z1 or Z2 because Z3 incorporates the Z4 layer in conditions where Z4 was not compromised by the waves at the water surface.

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343 Figure 2. Contour plots of (A) mean measured flow rate (m s^{-1}) and (B) mean turbulence kinetic energy ($\text{m}^2 \text{s}^{-2}$) in a Brett-style flume, at the three propeller
344 speeds of 20, 30 and 40 Hz. The raw data are presented in Tables S2 and S3 for flow rate and turbulence, respectively. The middle layer, Z2, is partially
345 transparent to aid viewing the lower layer, Z1. The upper layer measured, Z3, is not shown at 40 Hz propeller speed because few locations could be
346 measured due to turbulence at the water surface. As shown in Figure 1C, the Z3 layer does not include the uppermost water layer because turbulence
347 levels meant that measurements near the water surface could not be taken. A fish is included in the figures to indicate the orientation of the sea bass
348 during the experiments; flow and turbulence measurements were taken after the experiments.

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354 Figure 3. Flow characteristics within a Brett-style flume at three propeller speeds (excluding the layer Z3; see Figure 1). A: mean flow rate; B: turbulence
355 kinetic energy. The box plots show the means (central solid line), the second and third quartiles (the top and bottom of the box) and the lowest and highest
356 values within 1.5 x inter-quartile range (lower and upper whiskers). While there is a clear correlation between mean flow rate and turbulence kinetic
357 energy, there is considerable spatial variability in both at all three propeller speeds, underlining the need to track the position of the target fish during each
358 experiment.

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362 Figure 4. A: Mean tail beat frequency of sea bass swimming singly (A and D; N=12) or in groups of 3 (B and E; N=13) or 6 individuals (C and F; N=13),
363 regressed against flow rate and turbulence independently. Colours denote individual fish. Full black lines represent the overall best fit line for all the data,
364 accounting for the repeated measurements of each individual fish, and are presented where there is statistical evidence that the independent variable is an
365 important predictor (C: $y = -0.39x + 1.35$; D: $y = 1.28x + 0.80$; E: $y = 0.54x + 0.96$; F: $y = 0.83x + 0.90$). For all group sizes these findings are not qualitatively
366 affected by correlations between flow rate and turbulence, since models including both of these dependent variables did not change the group sizes where
367 those variables were important predictors. The horizontal, dashed lines in A, B and C indicate mean tbf across individuals. See main text for the associated
368 statistical output. Note that the x and y axes do not start at 0.

369

370

371 Figure 5. Mean movement count (see the Methods section for details) of sea bass swimming in
372 turbulent flow at three flow rates, either singly (N=12) or in a group of 3 or 6 (both N=13) as denoted
373 by the legend. Errors bars represent \pm one within-subject standard error of the mean (see Loftus and
374 Masson, 1994).

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467

468 **Supplementary material**

469 Table S1. Individual fish used in sets of experiments involving a group size of 6, then 3 and then 1 (here labelled A to E), where each individual fish is
 470 represented by an ID from 1 to 13. Subsequently, certain individual bass were also swum in the days after these experiments to ensure that all fish were
 471 swum in group size = 1.

Group Size	Sets of experiments				
	A	B	C	D	E
6	1	7	13	8	2
	2	13	9	10	3
	3	9	3	1	12
	4	10	4	12	8
	5	11	11	6	5
	6	12	5	7	9
3	4	7	13	8	2
	5	13	4	10	3
	6	9	11	1	12
1	1	7	13	10	12

472

473 Table S2. The mean and standard deviation of measured flow rate (m s^{-1}) in the Brett-style flume, in the direction against which the fish were swimming, at
 474 the three propeller speeds of 20, 30 and 40 Hz. Table cells correspond to 3-dimensional grid locations (Figure 1B). The greyed-out area denotes the
 475 locations where the turbulence levels were sufficiently high that the flow probe was not always underwater and thus a consistent reading could not be
 476 taken; estimate values are presented for those locations occupied by the fish and which were thus included in the statistical analyses (see main text for
 477 further details).

		Z1					Z2					Z3				
		X1	X2	X3	X4	X5	X1	X2	X3	X4	X5	X1	X2	X3	X4	X5
20	Y1	0.09±0.08	0.09±0.06	0.11±0.07	0.15±0.08	0.16±0.08	0.31±0.09	0.32±0.08	0.31±0.07	0.25±0.08	0.28±0.08	0.40±0.07	0.42±0.06	0.41±0.06	0.40±0.06	0.40±0.06
	Y2	0.05±0.08	0.03±0.06	0.03±0.05	0.07±0.06	0.10±0.07	0.23±0.09	0.21±0.09	0.20±0.08	0.19±0.09	0.20±0.09	0.37±0.07	0.39±0.06	0.39±0.06	0.37±0.07	0.36±0.08
	Y3	0.03±0.07	0.02±0.05	0.03±0.05	0.06±0.06	0.07±0.06	0.20±0.09	0.20±0.09	0.19±0.08	0.19±0.09	0.20±0.09	0.35±0.07	0.38±0.07	0.38±0.07	0.36±0.07	0.35±0.08
30	Y1	0.14±0.13	0.14±0.09	0.18±0.11	0.23±0.12	0.24±0.12	0.35±0.23	0.48±0.10	0.47±0.11	0.39±0.12	0.43±0.12	0.41±0.33	0.47±0.33	0.58±0.16	0.58±0.08	0.58±0.09
	Y2	0.07±0.11	0.08±0.08	0.08±0.08	0.10±0.09	0.14±0.09	0.25±0.22	0.31±0.11	0.29±0.12	0.28±0.13	0.29±0.13	0.35±0.32	0.51±0.16	0.54±0.10	0.52±0.11	0.49±0.12
	Y3	0.07±0.12	0.07±0.08	0.08±0.08	0.09±0.09	0.11±0.09	0.26±0.20	0.29±0.12	0.29±0.12	0.28±0.13	0.29±0.13	0.37±0.30	0.53±0.10	0.53±0.10	0.50±0.11	0.48±0.12
40	Y1	0.16±0.29	0.19±0.25	0.24±0.26	0.25±0.31	0.20±0.33	0.40±0.27	0.64±0.14	0.64±0.15	0.54±0.17	0.57±0.18	0.07±0.48	0.12±0.48	0.12	0.12	
	Y2	0.13±0.27	0.18±0.22	0.18±0.21	0.19±0.22	0.22±0.23	0.28±0.27	0.42±0.15	0.39±0.15	0.38±0.17	0.39±0.18	0.19±0.50	0.27±0.50	0.27	0.27	
	Y3	0.12±0.26	0.17±0.22	0.16±0.22	0.19±0.22	0.20±0.22	0.29±0.26	0.39±0.16	0.39±0.16	0.41±0.16	0.40±0.17	0.23±0.49	0.29±0.49	0.29	0.29	

478

479 NB the range of Y spans only 1 to 3 because the flow was measured from the centre to the side of the tank along the y-denoted dimension and was
 480 assumed to mirror the other half of the tank; the range of Z spans only 1 to 3 because due to turbulence at the water surface it was not possible to obtain
 481 flow readings in the upper water levels at all propeller speeds.

482

483 Table S3. The mean turbulence kinetic energy ($\text{m}^2 \text{s}^{-2}$) in the Brett-style flume (incorporating all three dimensions of flow: $k = 0.5(u_{RMS}^2 + v_{RMS}^2 +$
 484 $w_{RMS}^2)$, where u , v and w represent the time-averaged point velocities in the longitudinal, transverse and vertical directions, respectively), at the three
 485 propeller speeds of 20, 30 and 40 Hz. The greyed-out area denotes the locations where the turbulence levels were sufficiently high that the flow probe was
 486 not always underwater and thus a consistent reading could not be taken; estimate values are presented for those locations occupied by the fish and which
 487 were thus included in the statistical analyses (see main text for further details).

		Z1					Z2					Z3				
		X1	X2	X3	X4	X5	X1	X2	X3	X4	X5	X1	X2	X3	X4	X5
20	Y1	0.16	0.14	0.14	0.18	0.18	0.28	0.27	0.26	0.24	0.26	0.30	0.31	0.29	0.27	0.28
	Y2	0.14	0.09	0.08	0.11	0.14	0.24	0.20	0.19	0.20	0.21	0.29	0.29	0.28	0.27	0.26
	Y3	0.12	0.08	0.08	0.11	0.12	0.23	0.20	0.19	0.21	0.21	0.28	0.28	0.28	0.27	0.26
30	Y1	0.24	0.19	0.22	0.26	0.26	0.40	0.41	0.39	0.36	0.40	0.41	0.42	0.40	0.40	0.39
	Y2	0.20	0.15	0.14	0.17	0.19	0.35	0.29	0.28	0.30	0.31	0.40	0.39	0.39	0.38	0.37
	Y3	0.20	0.15	0.14	0.17	0.17	0.34	0.30	0.30	0.31	0.31	0.40	0.39	0.39	0.37	0.37
40	Y1	0.36	0.31	0.33	0.37	0.35	0.50	0.54	0.55	0.49	0.54	0.45	0.43	0.43	0.43	
	Y2	0.34	0.28	0.27	0.29	0.31	0.46	0.39	0.38	0.40	0.41	0.48	0.47	0.47	0.47	
	Y3	0.33	0.28	0.28	0.30	0.30	0.45	0.40	0.40	0.42	0.42	0.48	0.47	0.47	0.47	

488

489 NB the range of Y spans only 1 to 3 because recordings were taken from the centre to the side of the tank along the y-denoted dimension and were
 490 assumed to mirror the other half of the tank; the range of Z spans only 1 to 3 because due to turbulence at the water surface it was not possible to obtain
 491 readings in the upper water levels at all propeller speeds.

492