



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

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### ARTICLE INFO

#### Keywords:

Collective behaviour  
Ecophysiology  
Teleost fish  
Locomotion  
Energy expenditure

### ABSTRACT

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

**Summary statement:** The energy savings that sea bass experience from schooling are affected by flow speed or turbulence, moderated by group size

### 1. Introduction

Animals derive many benefits from living in groups. In addition to increased foraging efficiency and decreased predation risk, a major advantage for some animal groups is decreased costs of locomotion. In bird flocks, fish schools, and even human bicycle pelotons, individuals can position themselves to take advantage of vortices and zones of low pressure created by group mates to decrease their own energetic costs of movement (Marras et al., 2015). Fish schooling behaviour has been particularly well studied in terms of the energy savings it can afford to swimming fish (Fields, 1990; Herskin and Steffensen, 1998; Liao et al., 2003; Weihs, 1973; Zuyev and Belyayev, 1970). Specifically, trailing individuals can take advantage of the reverse von Kármán vortex street produced by fish further forwards in the school to reduce their own swimming energy costs (Fish et al., 1991; Killen et al., 2011; Liao, 2007; Liao et al., 2003). Due to the flow dynamics around fish, the economic

gains of schooling may not be limited to trailing individuals within moving groups. Remarkably, individuals in the periphery and vanguard of the school also save energy compared to swimming in isolation, albeit to a lesser extent than those that are following (Hemelrijk et al., 2015; Marras et al., 2015).

To date, studies examining the energetic costs of swimming in schools have investigated situations where two-dimensional schools (a single horizontal 'layer' of offset individuals) are swimming in a non-turbulent flow (Fish et al., 1991; Herskin and Steffensen, 1998; Killen et al., 2011; Marras et al., 2015); an idealised experimental design where only position relative to conspecifics in the school can affect energetic costs of swimming. Although truly laminar flows are difficult to establish, most studies use flumes that are designed to minimise turbulence (e.g. Fish et al., 1991; Killen et al., 2011) to a level such that turbulence is unlikely to have notable effects on swimming performance (Roche et al., 2014; Tritico and Cotel, 2010). We therefore have

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a limited understanding of how turbulence may modulate the energy-savings achieved by individual fish within schools. This is despite the fact that many fish in the wild are routinely subjected to turbulent flows (Liao, 2007), for example in river systems, coral reefs, or other marine and freshwater habitats with mixing currents or upwelling, and turbulent or unsteady flows can affect the costs of locomotion considerably (Cook and Coughlin, 2010; Enders et al., 2003; Roche et al., 2014; Taguchi and Liao, 2011). Furthermore, fish in these environments may not be able to maintain station relative to their neighbours and so it is possible that they will experience reduced benefits associated with the flow dynamics around their group mates.

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

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

## 2. Methods

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

### 2.1. Animals

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

### 2.2. Experiments

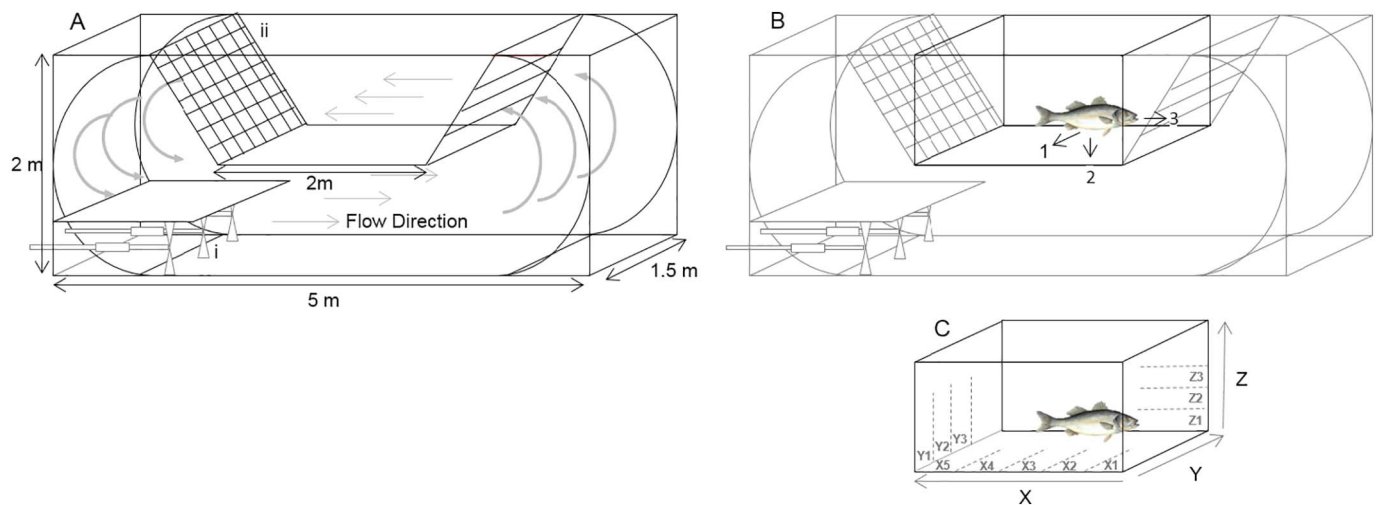
The fish were placed in the swim section of a large Brett-style flume (swim section dimensions: 200 × 150 × 70.7 cm; Fig. 1A) and left to habituate overnight at an average flow rate of 0.29 m s<sup>-1</sup>. Aerated seawater was fed into the tank at a flow rate of 0.2 L min<sup>-1</sup>, and the water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

Between the hours of 09:00 and 17:30 each day, three sets of experiments were carried out, whereby the fish swam against various

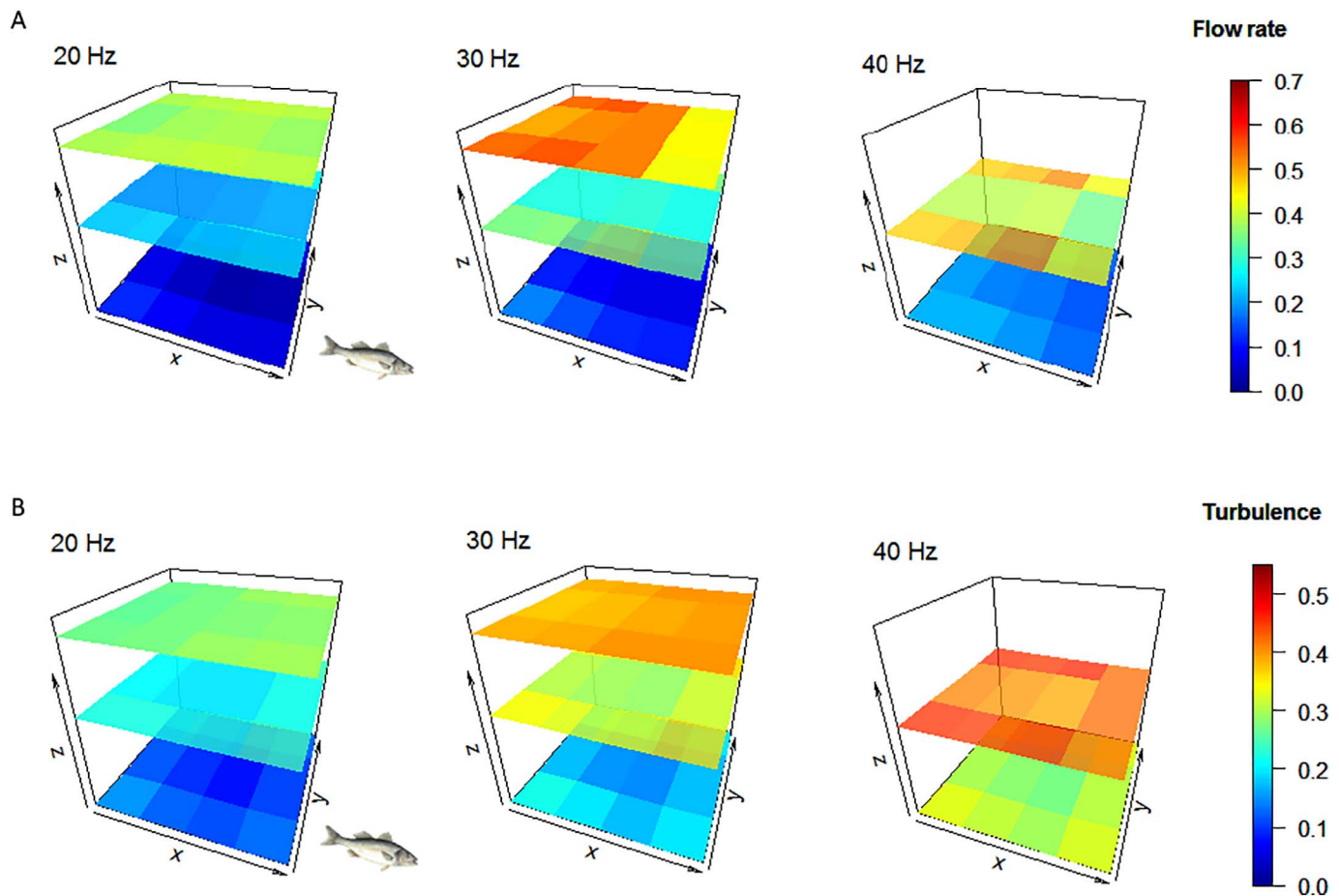
propeller-induced flows. The first experiment involved a group of 6 fish, the second a group of 3 and the third an individual ( $N = 13$  fish for group size = 3 and 6, and  $N = 12$  fish for group size = 1, where  $N$  represents the number of different fish included in each group size). The fish used in each experiment were selected to minimise the number of incidences of any given fish swimming with the same individuals (Table S1). Subsequently, all remaining fish that had not undertaken the experiments singly were subjected to the experiment for group size = 1.

Water flow rate and turbulence were affected by three propellers located symmetrically across the back wall of the flume, and driven by electric motors. The resultant flow was measured throughout the flume by a Nortek Vectrino II acoustic Doppler velocimeter (Nortek AS, Vangkroken, Norway). To quantify the flow and turbulence, after the experiments the water was seeded using Q-Cel® hollow microspheres which served to increase the signal to noise ratio within the flume (Nortek, 2009). Measurements were taken at 45 locations within one vertical half of the swim section, defined by three-dimensional co-ordinates (Fig. 1B), at a sampling rate of 100 Hz for 60 s per location. The measured values were assumed to be mirrored on the other half of the (symmetrical) tank. Measurements could not be obtained towards the surface of the water due to the water churn periodically exposing the velocimeter to air; these values were assumed to be the same as those measured in their neighbouring locations in the tank along the horizontal axis (the axis which has the least spatial variability). Time-averaged velocity and turbulence were calculated using W<sub>IN</sub>ADV software (Wahl, 2011) after filtering using the methods described in Rusello et al. (2006). The propellers delivered mean flow rates of  $0.15 \pm 0.07$ ,  $0.23 \pm 0.12$  and  $0.31 \pm 0.22$  m s<sup>-1</sup> when the propeller motors turned over at 20, 30 and 40 Hz (hereafter termed the ‘propeller speeds’), respectively. These flow rates spanned the preferred swim speed of free-swimming European sea bass (0.8 body lengths/s; Sureau and Lagardère, 1991). However, at each propeller speed there was considerable spatial variation in flow rate; mean values at each measured location in the tank ranged from 0.02 to 0.42, 0.07 to 0.58, and 0.12 to 0.64 m s<sup>-1</sup> at 20, 30 and 40 Hz, respectively (Fig. 2A, Table S2). In summary, flow rates tended to be lower at the bottom (Z1) and the centre (Y2–Y3) of the flume, and fairly constant from front to back (X1 to X5) (Fig. 1C), but not always (Fig. 2A). Turbulence measured in all three dimensions was calculated as the turbulence kinetic energy (Hockley et al., 2014) - the mean kinetic energy per unit mass associated with eddies in turbulent flow, characterised by the root-mean-square of velocity fluctuations. Mean values were 0.18, 0.26 and 0.38 m<sup>2</sup> s<sup>-2</sup> at the three propeller speeds, while the ranges of the mean values across the tank were 0.08 to 0.3, 0.14 to 0.42, and 0.27 to 0.55 m<sup>2</sup> s<sup>-2</sup> (Fig. 2B, Table S3). Higher propeller speeds generated both higher mean flow rates and higher mean levels of turbulence, however within each propeller speed there was considerable spatial variation in both factors (Fig. 3).

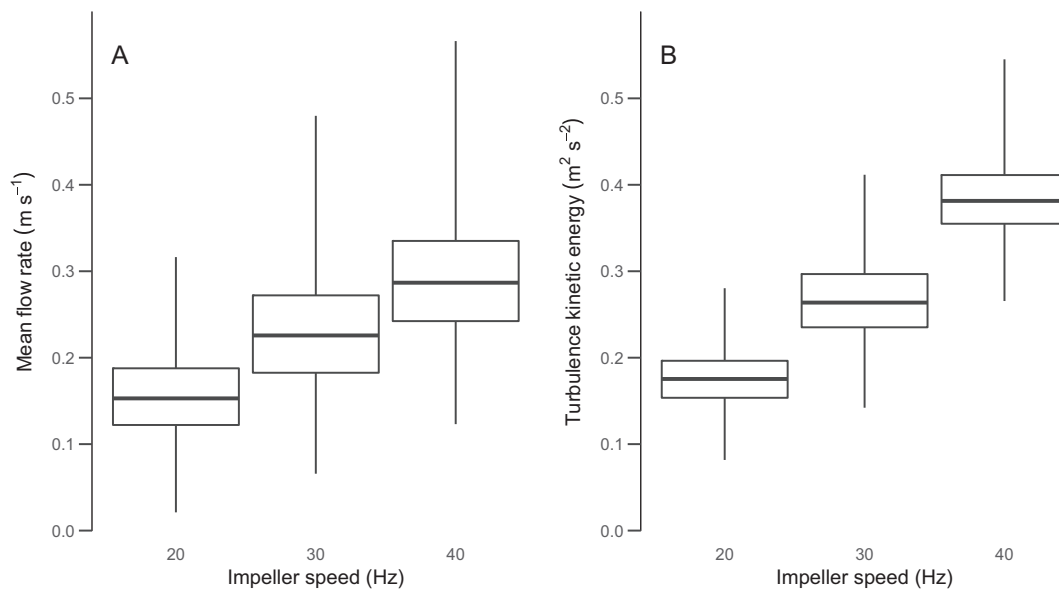
No correction was made for solid blocking in the flume as the fractional flow was < 1% (Bell and Terhune, 1970). Each flow rate condition lasted 20 min, after which the propeller speed was gradually changed to the next one over the following minute. Two video cameras (Hercules Deluxe Optical Glass) were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



**Fig. 1.** Schematic illustrating the Brett-style flume and the coordinate systems associated with certain measurements taken within it. A: The main flow 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 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, 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 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 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 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 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 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).



**Fig. 2.** Contour plots of (A) mean measured flow rate ( $\text{m s}^{-1}$ ) and (B) mean turbulence kinetic energy ( $\text{m}^2 \text{s}^{-2}$ ) in a Brett-style flume, at the three propeller 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 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 measured due to turbulence at the water surface. As shown in Fig. 1C, the Z3 layer does not include the uppermost water layer because turbulence 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 during the experiments; flow and turbulence measurements were taken after the experiments.



**Fig. 3.** Flow characteristics within a Brett-style flume at three propeller speeds (excluding the layer Z3; see Fig. 1). A: mean flow rate; B: turbulence 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 values within  $1.5 \times$  inter-quartile range (lower and upper whiskers). While there is a clear correlation between mean flow rate and turbulence kinetic 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 experiment.

moved unnecessarily. At the end of the experiments the fish were killed using a UK Home Office Licence schedule 1 procedure.

### 2.3. Data manipulation

Within each experimental condition, denoted by group size and flow rate, all the fish present were observed, independently over four different 30-s periods. These periods were chosen within consecutive three-minute intervals starting 4 min into the condition (and therefore also excluding the final 4 min of the condition). The 30-s periods were based on when the fish could be most clearly observed on the video footage. These sequences included horizontal or vertical movement of the fish within the flume, but sequences were not analysed if the fish performed turning motions that caused them to be perpendicular to the overall direction of the flow, or moved location repeatedly. The mean tbf (Hz) of the fish was calculated for each period (one tail beat was defined as one complete oscillation of the tail). Furthermore, a simple index of the amount that the fish moved position within the tank during that period was calculated. The location of the fish was recorded at the beginning and end of each period in terms of whether it was central, off centre, or towards a side of the tank, in each of the three dimensions separately (Fig. 1C). Thus in each dimension (i.e. side to side, top to bottom and front to back) the fish was recorded at one of five locations at the start and end of the recording period. In turn, in each dimension individually, the net amount the fish moved between the start and end of the recording period was recorded, where 0 = maintained station and 5 = moved from one side to the other. These values were then summed for the three dimensions to calculate a 'movement count'.

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

### 2.4. Data analyses

The effect on tbf of flow rate, turbulence, group size and their interactions was investigated with general linear mixed models (LMMs)

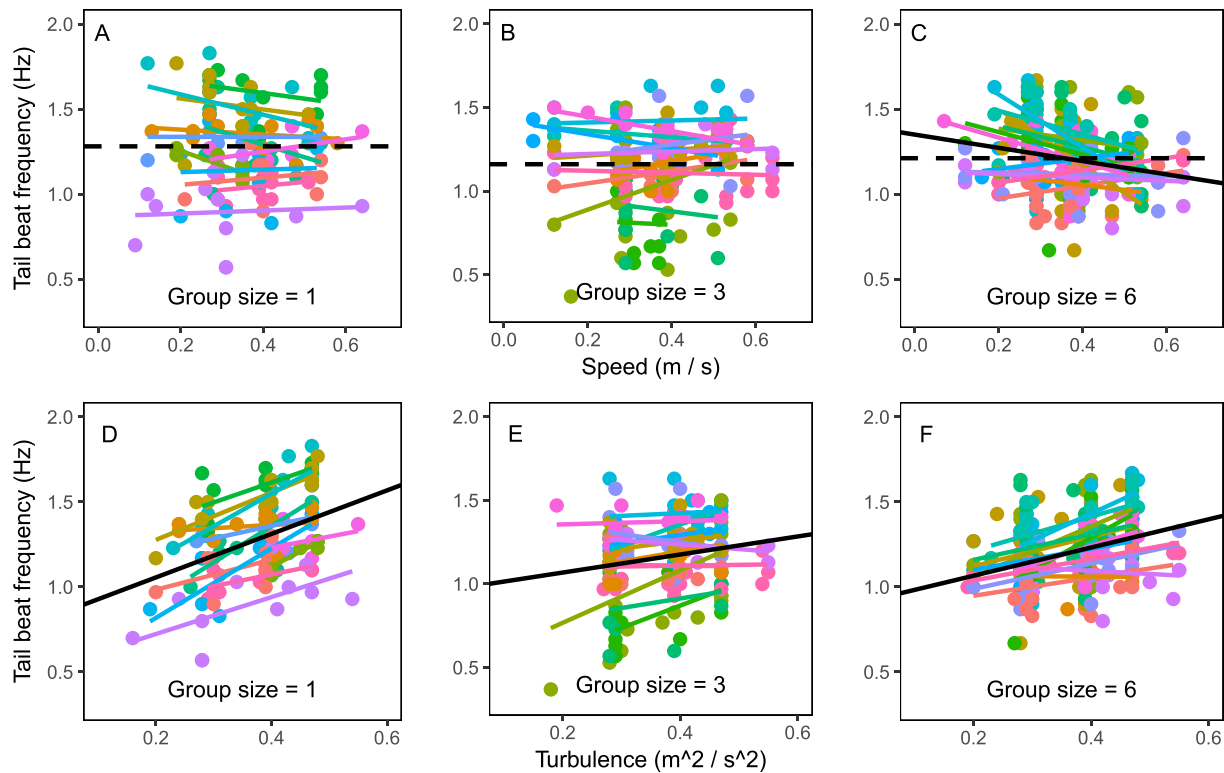
using type III sums of squares. Group size was either 1, 3 or 6 and was set as a categorical factor, while flow rate and turbulence were input as continuous covariates. A unique identifier for each fish was included as a random factor to account for the presence of multiple data points per fish, per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

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

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

Interpretation of these analyses was based predominantly on sample effect sizes and their precision, visualised with graphs incorporating error bars where appropriate (Lavine, 2014; Loftus, 1993). This interpretation was secondarily supported by null hypothesis significance testing to provide some indication of the strength of evidence for observed patterns. In the present article the  $p$  value is treated as a





**Fig. 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;  $N = 13$ ), regressed against flow rate and turbulence independently. Colours denote individual fish. Full black lines represent the overall best fit line for all the data, accounting for the repeated measurements of each individual fish, and are presented where there is statistical evidence that the independent variable is an 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 affected by correlations between flow rate and turbulence, since models including both of these dependent variables did not change the group sizes where 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 statistical output. Note that the x and y axes do not start at 0. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

continuous variable providing a very approximate level of evidence against the null hypothesis (Fisher, 1959), rather than referring to arbitrary cut-offs, which are problematic and limiting in several ways (Boos and Stefanski, 2011; Halsey et al., 2015).

### 3. Results

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

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

**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 ( $\text{m}^2/\text{s}^2$ ).

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 ( $\text{m}^2/\text{s}^2$ )	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

estimates and associated CIs for this model.

The movement count data indicated that the fish did not typically maintain station in the flume during the experiments (Fig. 5). There was no evidence of an effect of group size (with group 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 ( $z = -0.56$ ,  $p = 0.57$ ) on movement count. There was some evidence of an effect of speed ( $z = -1.86$ ,  $p = 0.06$ ), however the effect size was small: an increase in speed of  $1 \text{ m s}^{-1}$  is related to an estimated decrease in movement count of 0.4.

### 4. Discussion

Several previous publications have documented energy savings in

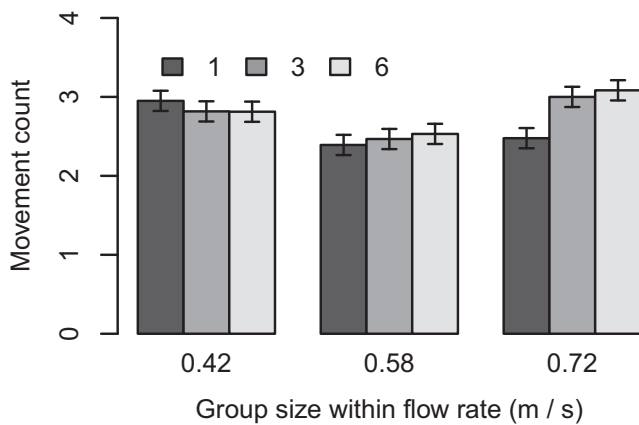


Fig. 5. Mean movement count (see the [Methods](#) section for details) of sea bass swimming in turbulent flow at three flow rates, either singly ( $N = 12$ ) or in a group of 3 or 6 (both  $N = 13$ ) as denoted by the legend. Errors bars represent  $\pm$  one within-subject standard error of the mean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

fish when swimming in a school in a relatively laminar flow ([Herskin and Steffensen, 1998](#); [Killen et al., 2011](#); [Marras et al., 2015](#)). The present results indicate that for sea bass swimming in the more complex scenario of turbulent water and not maintaining station, group size influences how both the flow rate and the turbulence of the water influence their tail beat frequency (tbf), with turbulence effects outweighing the effects of speed.

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

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

The predominant influence of group size acted through its effects on the relationships between tbf and both flow rate and turbulence. Not only was tbf unrelated to flow rate when the fish were swimming singly or in a small group, but tbf decreased with increasing flow rate when the fish were in a larger group of six individuals. The lack of a

correlation between tbf and flow rate for sea bass swimming singly is not surprising given that the flow rates they experienced ranged from around 0.2 to 1 body lengths/s, which while recognised to be their preferred swimming speeds ([Sureau and Lagardère, 1991](#)), are also at the **lower** end of their swim speed range. The grey mullet studied by [Marras et al. \(2015\)](#) showed no change in tail beat frequency between 1 and 2 body lengths/s. In both cases, the fish were apparently swimming within a range of flow rates that did not require systematic adjustment of their tbf in response to changes of swim speed. When swimming within the larger group size, there is presumably more scope for interactions between individuals and for energy savings from the flow dynamics of swimming in a group. The decreases in tbf by the sea bass in a group of six when swimming in higher flows may therefore be explained by reduced interactions with other fish and/or the fish positioning themselves relative to their conspecifics more accurately in order to obtain energy savings to counteract the increased swimming effort. However, these interpretations are caveated by the possibility that at these low speeds the fish modulated the power output from their tail by adjusting tail beat amplitude instead of tbf; tail beat amplitude was not a variable we were able to reliably quantify from the video footage.

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

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

## Acknowledgements

## Competing interests

The authors have no competing interests.

## Author contributions

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

## Funding

SSK was supported by NERC Advanced Fellowship NE/J019100/1 and European Research Council Starting Grant 640004. S.W. was funded by a postgraduate scholarship from the Fisheries Society of the British Isles. Experiments were supported by a seed corn grant from the Centre for Environment Fisheries and Aquaculture (DP268).

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

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cbpa.2018.01.015>.

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