



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

Lewis G. Halsey<sup>a,\*</sup>, Serena Wright<sup>b</sup>, Anita Racz<sup>c</sup>, Julian D. Metcalfe<sup>b</sup>, Shaun S. Killen<sup>c</sup>

<sup>a</sup> Department of Life Sciences, University of Roehampton, Holybourne Avenue, London SW15 4JD, UK

<sup>b</sup> Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft NR33 0HT, UK

<sup>c</sup> Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, UK



### 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

\* Corresponding author.

E-mail address: [l.halsey@roehampton.ac.uk](mailto:l.halsey@roehampton.ac.uk) (L.G. Halsey).

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 (Rieucou 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 ± 0.07, 0.23 ± 0.12 and 0.31 ± 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 error 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

Download English Version:

<https://daneshyari.com/en/article/8318266>

Download Persian Version:

<https://daneshyari.com/article/8318266>

[Daneshyari.com](https://daneshyari.com)