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Fish responses to flow velocity and turbulence in relation to size, sex and parasite load

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Riverine fish are subjected to heterogeneous flow velocities and turbulence and may use this to their advantage by selecting regions that balance energy expenditure for station holding while maximizing energy gain through feeding opportunities. This study investigated microhabitat selection by guppies *Poecilia reticulata* in terms of flow characteristics generated by hemisphere boulders in an open channel flume. Velocity and turbulence influenced the variation in swimming behaviour with respect to size, sex and parasite intensity. With increasing body length, fish swam further and more frequently between boulder regions. Larger guppies spent more time in the areas of high-velocity and low-turbulence regions beside the boulders, whereas smaller guppies frequented the low-velocity and high-turbulence regions directly behind the boulders. Male guppies selected the regions of low velocity, indicating possible reduced swimming ability owing to hydrodynamic drag imposed by their fins. With increasing *Gyrodactylus turnbulli* burden, fish spent more time in regions with moderate velocity and lowest turbulent kinetic energy which were the most spatially and temporally homogeneous in terms of velocity and turbulence. These findings highlight the importance of heterogeneous flow conditions in river channel design owing to the behavioural variability within a species in response to velocity and turbulence.

1. Introduction

Rivers differ from oceanic and estuarine habitats in that flow is primarily in the longitudinal direction and particularly subjected to disturbance events, for example flooding as a result of heavy rainfall. Natural and man-made structures, such as boulders, woody debris and bridge piers, create physical obstructions to the water flow and generate localized regions where velocity magnitudes and turbulence levels are spatially heterogeneous. Ecological theory suggests that habitat heterogeneity is positively related to fish species diversity, with flow regime strongly influencing patterns of global-scale species richness [1]. Placement of in-stream structures, such as boulders and woody debris, to improve connectivity and complexity has been increasingly employed in river rehabilitation programmes [2]. Improvement in fish species richness and abundance as a result of these restoration projects is variable, with increased densities reported for some species, but not for others, depending on species habitat requirements [3]. For example, the placement of boulders in watersheds in southwest Oregon caused an increase in the number of pools, providing more suitable habitat for coho salmon *Oncorhynchus kisutch* (Walbaum 1792) and trout *O. mykiss* (Walbaum 1792), but saw a decrease in dace *Rhinichthys* spp. (Girard 1856) and no change in abundance of young-of-year trout [3]. Thus, successful restoration projects need to be both species and site specific [2].

A stationary obstacle, for example a boulder, used in these regeneration projects or coarse river bed generates turbulence which can lead to the development of vortices. Turbulence and vortices can be either beneficial or detrimental to fish, depending on the directionality and strength of each velocity component, their temporal fluctuation, the turbulent stresses imposed and the ability of the fish to maintain stability [4]. The capability of fish to maintain position in a current relative to the substratum (station holding) [5] is an essential survival strategy to avoid being washed downstream and may limit individuals or species to specific areas of the river [6]. When station holding, stream-dwelling fish orientate themselves upstream (positive rheotaxia) in order to minimize energy expenditure, maximize food capture and intercept chemical cues [7,8] by detecting water currents with neuromasts on their lateral line [7,9]. The size of the vortices (turbulence length scale) in relation to fish length is critical when considering the effect of perturbed flow on swimming performance [10,11]. If a vortex generated from a stationary body is small relative to the body size of the fish, then the moments of force are evenly distributed across its body and balance is not affected. If the size of the vortex is equal to the size of the fish, then the rotating vortex will introduce a torque and the fish may overturn [11,12]. Lupandin [11] concluded that perch *Perca fluviatilis* (Linnaeus, 1758) swimming performance decreased when the turbulence length scale exceeded two-thirds of the fish length, but this has never been tested on other fish species.

Fish will avoid an environment where there are large fluctuations in temporal velocity (an indication of the turbulence level). In turbulent flows, water particles move irregularly causing a continuous exchange of momentum from one portion of the water to another and this momentum exchange can cause turbulent shear stress on a fish's body. This stress can have a negative effect on fish, for example individuals of *Luciobarbus bocagei* (Steindachner 1864) avoided areas of high horizontal shear stress [13]. In extreme cases, for example in hydroelectric dams, the rotating turbine can generate turbulent shear stresses which can cause fish injury or mortality [14,15] that will vary between species and size categories [16]. Additionally, turbulent shear stress, velocity shear and velocity magnitude are negatively correlated with abundance, taxa richness and community composition of macroinvertebrates [17], potential prey for fish. On the other hand, fish may use turbulence to their advantage with some species capable of capturing energy from vortices to propel themselves upstream or station hold [18]. For example, at intermediate area mean velocities of 25–50 cm s^{-1} chub *Nocomis micropogon* (Cope 1865) harnessed the energy from vortices generated by vertical cylinders to maintain position within the water column [18]. However at lower area mean velocities (less than 25 cm s^{-1}), the chub avoided swimming behind the cylinders and at higher area mean velocities (50–75 cm s^{-1}) they were displaced from their positions on the cylinder and forced to swim in the adjacent free stream [19]. Numerous studies have used experimental flumes in the laboratory to examine the critical swimming speeds and optimal longitudinal velocities ($\bar{u}$) of fish both in the laboratory and field [20–24], however, very few studies have investigated the effects of turbulence parameters (vortices, turbulent kinetic energy and turbulent shear stress) in relation to fish behaviour on a microhabitat scale [13]. Differences in behaviour within a species in response to these turbulence parameters might explain why some restoration processes using boulders have been a success while others have seen little benefit.

Biotic factors also influence fish swimming ability, for instance fin size. Wild-type zebrafish *Danio rerio* (Hamilton 1822) had significantly higher critical swimming speed than long-tailed varieties, owing to the drag effect of the larger fins [25]. Large and colourful fins in male fish are common in nature, and the evolution of this exaggerated ornamentation is driven by sexual, rather than natural selection [26]. In guppies *Poecilia reticulata* (Peters 1859), females select males with larger tails, as an indicator of reproductive fitness [27], yet males with longer tails exhibit poorer swimming performance [28], indicating a trade-off between swimming performance (natural selection) and courtship success (sexual selection). Additionally, infectious disease may impair swimming ability by causing symptoms, such as atrophy of musculature, nervous system pathology, obstruction of blood flow and physiological interference from parasite waste products [29]. Heavy infections may also reduce a host's physical agility or modify the shape and size of the fish, affecting its profile in the water, and thus generating increased hydrodynamic drag [29]. Few studies have attempted to examine the impact of infection on fish behaviour within a flow environment, with the majority of experiments being conducted in tanks of static water [30–32]. To our knowledge, no previous study has quantified how turbulence levels impact infected fish, and generally little is known about the potential implications of habitat heterogeneity on host–parasite interactions in aquatic systems. On the one hand, differences in swimming ability, different life stages or sexual segregation may cause spatial repartition of individuals within a population, thus affecting parasite transmission. On the other hand, parasite infection may cause a change in fish behaviour or reduction in swimming ability, thus affecting microhabitat use within the river system.

Guppies and their natural parasites *Gyrodactylus* spp. are popular host–parasite model organisms for use in ecological, genetic and behavioural studies [33,34]. This is partly owing to the fact that guppies are highly sexually dimorphic, with males being smaller in size with ornate dorsal and caudal fins. These larger caudal fins have been associated with a reduced swimming ability [28,35], and compared with females, males exhibit lower critical swimming speeds and have an affiliation for slower water velocities in the wild [28,36]. *Gyrodactylus turnbulli* (Harris 1986) is an ectoparasitic monogenean which naturally infects guppies in Trinidad and Tobago [33]. The parasite causes behavioural changes, for example by inducing erratic swimming behaviour [37], and in the later stages of infection the host fins become contracted and the fin rays fuse together [37].

The aim of this study was to assess how swimming behaviour of fish is affected by velocity and turbulence characteristics in a heterogeneous flow field generated by hemispherical boulders. Using open channel flume experiments, we explored intraspecies variation in swimming behaviour of guppies *P. reticulata* between different flow regions with respect to size, sex and parasite load. The flow regions around the boulders were characterized in terms of their spatial variation in velocity, turbulence and turbulent shear stress through relatively high-frequency measurements of velocity. The interaction of the fish within the habitat was examined in terms of the frequency of movement both in the near-field locality of the boulder and further afield between up- and downstream boulders. We hypothesized that turbulence and velocities generated by the boulders act as niche habitats for the fish to enhance station holding, and that large, female and unparasitized fish would have stronger swimming abilities, and therefore tolerate regions of higher velocity and turbulence and higher spatial variability, compared with their smaller, larger finned and parasitized counterparts.

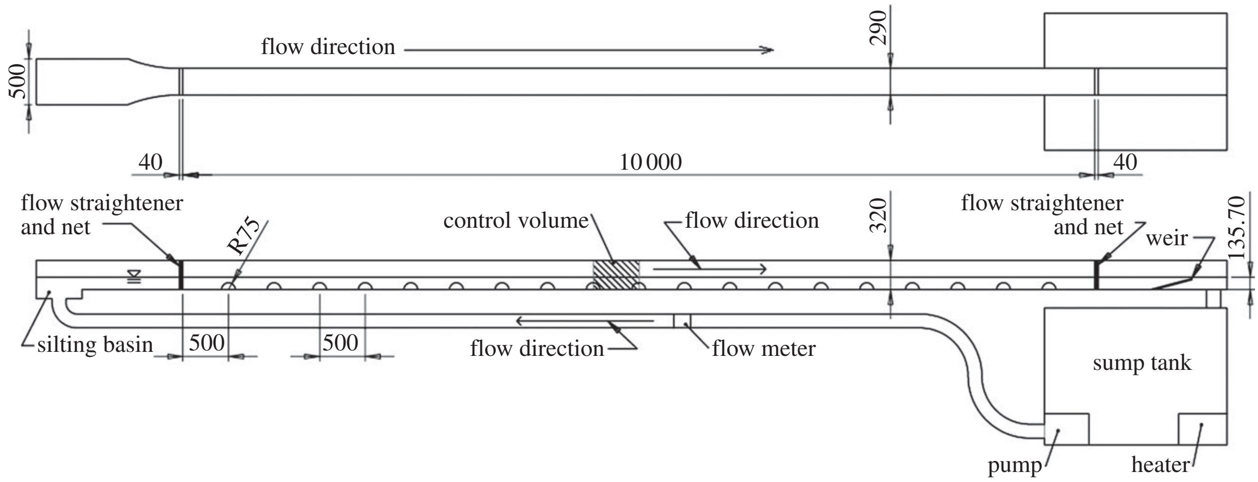

Figure 1. Plan and side view schematic showing positioning of boulders along length of open channel flume. The control volume where velocity and turbulence measurements took place is shown by the diagonal hatched area. All dimensions are in mm.

2. Material and methods

2.1. Open channel flume and velocity measurements

The study took place in a glass-walled recirculating open channel flume in the Hydro-environmental Research Centre (HRC), Cardiff University, UK. The flume was 10 m long and 0.29 m wide, and the surface water profile controlled by a downstream tailgate weir. The flume was set at a negative gradient of 1 in 1000 and concrete quasi-hemisphere boulders of diameter 150 mm and height 75 mm were positioned at 0.5 m intervals along the centreline of the flume bed (figure 1). Uniform flow conditions were established at a discharge (Q) of 0.0049 $m^3 s^{-1}$ and flow depth of 135.7 mm, which gives an average pore velocity (taking into account the boulder area) of 12.7 cm s^{-1}. The selected flow velocity is typical of natural conditions in guppy streams in Trinidad [38]. The Reynolds number of the flow was 37 062, which relates to a turbulent flow regime [39]. Chlorides were removed from the water by the addition of Haloex at 0.02 ml l^{-1}, and water was heated to 25° ± 1°C using an Electro Titanium Digital heater.

The velocity and turbulence field around the hemispheres were characterized using a Nortek Vectrino I downwards-looking acoustic Doppler velocimeter (ADV). The water was seeded using Q-Cel hollow microspheres to increase the signal to noise ratio (SNR) in order to produce sufficient sound scatter [40]. The velocity measurement grid was generated with point velocity measurements taken at 10–20 mm intervals within a representative control volume of 0.5 m length (longitudinal direction), 0.29 m width (transverse direction) and 0.06 m depth (vertical direction) located at the mid-length of the flume. The measurement grid was composed of 1112 point measurements and captured the wake immediately behind the boulder and the high-pressure region immediately upstream of the boulder. Higher densities of velocity measurements were taken in the vicinity of the boulder where velocity gradients were the steepest. All readings were taken at a sampling rate of 200 Hz for 4 min with a nominal velocity range of ±0.3 ms^{-1}, transmit length of 1.8 mm and sampling volume of 7 mm height and 6 mm diameter. The time-averaged velocity and turbulence statistics for each reading were calculated using the WinADV software [41] after filtering with a minimum correlation of 70% and minimum SNR of 20 as recommended by Rusello *et al.* [42].

2.2. Velocity and turbulence definitions

A number of terms are used to describe the velocity and turbulence field both temporally and spatially (see table 1 for definitions). The time-averaged point velocities in the longitudinal, transverse and vertical directions are denoted as $\bar{u}, \bar{v}$ and $\bar{w}$, respectively. The instantaneous turbulent fluctuation of the longitudinal velocity from the time mean velocity is

$$u'(t) = u(t) - \bar{u}. \tag{2.1}$$

The turbulence strength is defined as

$$u_{\mathrm{RMS}} = \sqrt{\overline{u'(t)^2}}, \tag{2.2}$$

where 'RMS' is the root-mean-square. Similar definitions apply to the transverse and vertical velocities, $v(t)$ and $w(t)$. The turbulent kinetic energy (k) which is a measure of the total turbulent energy production, and hence a bulk measure of the turbulence intensity was calculated as

$$k = 0.5(u_{\mathrm{RMS}}^2 + v_{\mathrm{RMS}}^2 + w_{\mathrm{RMS}}^2). \tag{2.3}$$

The normalized turbulent kinetic energy is defined by $\sqrt{k}.u^{-1}$ and is used in this study to normalize the turbulence intensity from the velocity magnitude. The turbulent shear stress (Reynolds stress) in each plane was calculated as

$$\tau_{uv} = |\rho\overline{u'v'}|; \quad \tau_{uw} = |\rho\overline{u'w'}| \quad \text{and} \quad \tau_{vw} = |\rho\overline{v'w'}|, \tag{2.4}$$

where ρ is the density of water and $u'v'$, $u'w'$ and $v'w'$ are the covariance of the instantaneous velocity fluctuations. The volume-averaged velocity and turbulence parameters for each flow region are denoted using the square brackets, i.e. $\langle\bar{u}\rangle$, $\langle\bar{v}\rangle$, $\langle\bar{w}\rangle$, $\langle\bar{k}\rangle$ and $\langle\sqrt{k}\,\bar{u}^{-1}\rangle$, etc. The ratio of volume-averaged longitudinal, transverse and vertical turbulent length scale to fish standard length of an individual fish is given by $\langle l_u\rangle/\mathrm{SL}, \langle l_v\rangle/\mathrm{SL}$ and $\langle l_w\rangle/\mathrm{SL}$, respectively. The turbulent length scale was calculated using the autocorrelation function [48] where the longitudinal turbulent length scale l_u is given by

$$l_u = \bar{u}\int_0^T R(t)\,\mathrm{d}t, \tag{2.5}$$

where T is the sampling time and R is the autocorrelation function defined as

$$R(t) = \frac{\overline{u'(t).u'(t+s)}}{\overline{u'(t)^2}}, \tag{2.6}$$

where s is the time lag in seconds. The transverse and vertical turbulent length scales (l_v and l_w) were calculated in a similar manner.

Table 1. Glossary of terms.

term	definition	reference
area mean velocity, $\bar{u}$	mean velocity of a cross-sectional area of the channel defined as the volume rate of discharge, Q, divided by the cross section area, A	[39]
control volume	a three-dimensional region selected for the purposes of fluid analysis to which specific fundamental physical laws can be applied	
discharge, Q	total volume of fluid flowing in unit time past a cross-section of a channel. Also known as flow rate	[39]
mean parasite intensity	mean number of individuals of a particular parasite species per infected host in a sample	[43]
parasite intensity	number of individuals of a particular parasite species in the infected host	[43]
prevalence	number of individuals of a host species infected with a particular parasite divided by number of hosts examined. Usually expressed as a percentage	[43]
rheotaxis	behaviour in which animals detect and orientate themselves to the flow of water. With positive rheotaxia fish orientate themselves by positioning themselves with their head pointing upstream	[44]
sham infection	method by which the fish are anaesthetized and manipulated so to simulate the infection process, without the transfer of parasites	
standard length	measurement from the most anterior tip of the body (tip of snout) to the mid-lateral posterior edge of the hypural plate or posterior end of the vertebral column	[45]
station holding	the ability of a fish to maintain position in a current relative to the substratum	[5]
turbulence length scale	turbulence length scale is a physical property which represents the size of the largest dominant eddies in turbulent flows	[46]
turbulent flow	turbulence is defined as the three-dimensional time-dependent motion characterized by rapid fluctuations superimposed on the mean velocity. Defined by the Reynolds number, which is the ratio of the inertial forces to the viscous forces. In open channels, turbulent flow occurs when the Reynolds number based on the hydraulic radius is greater than 2000	[39,47]
turbulent shear stress (Reynolds stress)	turbulent shear stress is caused by the irregular movement of fluid particles and their continuous exchange of momentum from one portion of fluid to another	[46]
velocity shear	fluid particles in a turbulent flow experience different velocities depending on their spatial positions within a cross-section. These different particle velocities generate velocity shear	

2.3. Region characterization

From the depth-averaged velocity field, each boulder control volume was divided into four regions (figure 2). The areas where the flow accelerates around the sides of the boulder are referred to as the high-velocity regions (region H), and the regions downstream where the flow decelerates and recovers are referred to as the 'moderate-velocity regions' (region M). A recirculation zone lies directly in the wake of the boulder (region R), and a region of low velocity in the boulder wake forms the velocity-deficit region (region L). A summary of the volume-averaged data are given in table 2.

2.4. Study system

Guppies *Poecilia reticulata* imported from the lower Aripo River, Northern Trinidad in 2003, were maintained in aquarium facilities at the School of Biosciences, Cardiff University, UK. At the time and place of sampling, the lower Aripo River had width 481 cm, depth 17 cm and surface flow rate approximately 8.5 cm s^{-1} (measured by the mean time for a plastic float to travel 100 cm), and is known to be a high-predation site [49]. Holding tanks each had an air supply and filter, and fish were maintained under a 12 L : 12 D regime at 22° ± 1°C, fed on a diet of fish flakes (Aquarian) and bloodworm. A total of 60 female (mean ± s.d. standard length 21.3 ± 3.5 mm) and 51 male guppies

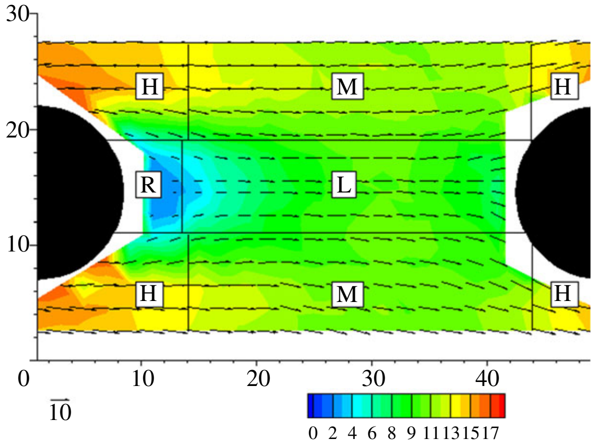

Figure 2. Flow regions around boulders defined by depth- and time-averaged longitudinal velocity $\bar{u}$. (H) High-velocity region where there is an acceleration of flow between the side walls and the boulder, (M) moderate-velocity region where the flow from region H decelerates, (R) the recirculation zone, and (L) the velocity-deficit zone in the wake of the boulder (solid black areas). The white areas around the boulders are the limits of the ADV probe so measurements were not taken in these areas. Velocity units are in cm s^{-1} and length units are in cm.

Table 2. Volume-averaged velocity and turbulence parameters for the four velocity regions depicted in figure 2. Ranges of the minimum and maximum time-averaged velocity for the longitudinal, transverse and vertical velocity components together with the turbulence intensities (u', v' and w'), turbulent kinetic energy (k) the relative turbulence intensity ($\sqrt{k}\bar{u}^{-1}$), turbulent shear stresses (τ_{uv}, τ_{uw} and τ_{vw}) and turbulent length scale (L_u, L_v, L_w) within each flow volume are given. Negative velocities for $\bar{u}$, $\bar{v}$ and $\bar{w}$ refer to upstream, towards the left-hand side flume wall (looking in the downstream direction) and downwards movement, respectively. The standard deviation (σ) for each volume-averaged parameter is given in brackets.

parameter		moderate-velocity region	high-velocity region	velocity-deficit region	recirculation region
$\langle \bar{u} \rangle$ (σ)	(cm s^{-1})	11.67 (1.28)	14.05 (2.26)	9.15 (3.18)	6.46 (6.97)
range $\bar{u}$		8.87 – 15.07	2.85 – 17.36	0.62 – 17.42	−2.56 – 17.90
$\langle u' \rangle$ (σ)		2.91 (0.60)	2.74 (0.88)	3.49 (0.60)	4.04 (0.89)
range u'		1.98 – 4.79	1.88 – 5.78	2.39 – 5.30	2.38 – 5.89
$\langle \bar{v} \rangle$ (σ)	(cm s^{-1})	−0.52 (1.90)	−0.26 (2.22)	−0.47 (1.29)	−0.38 (1.25)
range $\bar{v}$		−5.90 – 5.34	−7.07 – 7.78	−4.36 – 5.98	−3.13 – 2.93
$\langle v' \rangle$ (σ)		2.98 (1.64)	2.96 (1.23)	3.90 (1.15)	4.11 (1.16)
range v'		1.80 – 18.63	1.85 – 12.38	2.06 – 6.41	1.92 – 6.08
$\langle \bar{w} \rangle$ (σ)	(cm s^{-1})	0.12 (0.46)	−0.25 (0.82)	−0.50 (0.94)	−1.18 (1.07)
range $\bar{w}$		−1.63 – 1.51	−2.18 – 1.32	−2.95 – 3.26	−3.29 – 0.38
$\langle w' \rangle$ (σ)		1.31 (0.26)	1.39 (0.33)	2.06 (0.56)	2.48 (0.58)
range w'		0.92 – 2.34	0.57 – 2.78	0.82 – 3.46	0.82 – 3.52
$\langle k \rangle$ (σ)	(cm^2 s^{-2})	3.56 (6.09)	5.07 (13.73)	10.83 (17.60)	25.28 (27.92)
range k		0.01 – 36.54	0.00 – 71.88	0.02 – 99.16	0.02 – 89.28
$\langle \sqrt{k}\bar{u}^{-1} \rangle$ (σ)	n.a.	0.13 (0.12)	0.12 (0.23)	0.42 (0.61)	0.74 (5.04)
range $\sqrt{k}\bar{u}^{-1}$		0.01 – 0.63	0.00 – 1.64	0.02 – 5.71	−12.68 – 27.50
$\langle \tau_{uv} \rangle$ (σ)	(Nm^{-2})	0.17 (0.18)	0.14 (0.25)	0.29 (0.31)	0.36 (0.38)
range τ_{uv}		0.00 – 0.83	0.00 – 1.14	0.00 – 1.30	0.00 – 1.22
$\langle \tau_{uw} \rangle$ (σ)	(Nm^{-2})	0.09 (0.05)	0.09 (0.10)	0.16 (0.10)	0.33 (0.34)
range τ_{uw}		0.00 – 0.36	0.00 – 0.62	0.00 – 0.62	0.01 – 1.33
$\langle \tau_{vw} \rangle$ (σ)	(Nm^{-2})	0.02 (0.02)	0.03 (0.03)	0.04 (0.04)	0.08 (0.08)
range τ_{vw}		0.00 – 0.18	0.00 – 0.18	0.00 – 0.31	0.00 – 0.51
$\langle l_u \rangle$ (σ)	(cm)	10.46 (0.79)	12.23 (1.80)	8.56 (2.51)	6.36 (4.95)
range l_u		8.09 – 12.83	3.36 – 15.06	0.80 – 14.32	0.28 – 14.89
$\langle l_v \rangle$ (σ)	(cm)	0.59 (0.08)	0.35 (1.01)	0.42 (0.75)	0.33 (0.74)
range l_v		0.008 – 4.82	0.01 – 6.30	0.01 – 3.97	0.03 – 3.02
$\langle l_w \rangle$ (σ)	(cm)	0.08 (0.28)	0.28 (0.46)	0.51 (0.55)	1.09 (0.81)
range l_w		0.01 – 2.08	0.01 – 1.93	0.01 – 2.70	0.01 – 2.77

(mean ± s.d. standard length 16.2 ± 1.3 mm) were used in the behavioural experiments. The standard length (L_s) to fork length, and L_s to dorsal fin length ratios were 25 and 36% larger in males than females, respectively (t-test, $t = -8.29$ and -8.45, d.f. = 50 and 38, both $p < 0.001$), from a subsample of 60 individuals.

An isogenic strain of the ectoparasitic worm *G. turnbulli* (Gt3) was used to infect 30 females and 27 males with four worms per individual following standard procedures, e.g. [32]. The remaining 30 female and 24 male guppies were sham-infected under anaesthetic without exposure to parasites. All fish were housed in individual 1 l pots and the infections developed for 8 days. Infection was confirmed by restraining each individual in a small amount of water in a crystallizing dish under stereo-microscope. All uninfected fish were sham-screened. After 8 days postinfection, the mean intensity of *G. turnbulli* was 24.8 (s.e. 2.76) worms. No individuals showed any symptoms of infection, such as fin clamping or notable reduced mobility.

2.5. Experimental trials

The open channel flume behavioural experiments took place on 1–27 February 2012 between 8.00 and 19.00. Each fish was given a 30 min acclimatization period and then observed for 10 min, recording position in relation to the boulders (figure 2), starting with the position of the fish at the end of the acclimatization period. Frequency of movement was recorded as the number of times the fish moved from one boulder region to another, and the distance moved up- and downstream was recorded as the number of movements to a different boulder control volume (figure 1) in each direction. If the fish entered an area within 0.5 m length of the up- or downstream ends of the flume, the timer was paused until the fish returned to the main working section, as these flow areas may be subjected to disturbance from the flow straightening material at the upstream end of the flume and the weir at the downstream end. If the fish moved into the top 70 mm elevation of the flow depth, data were discarded as

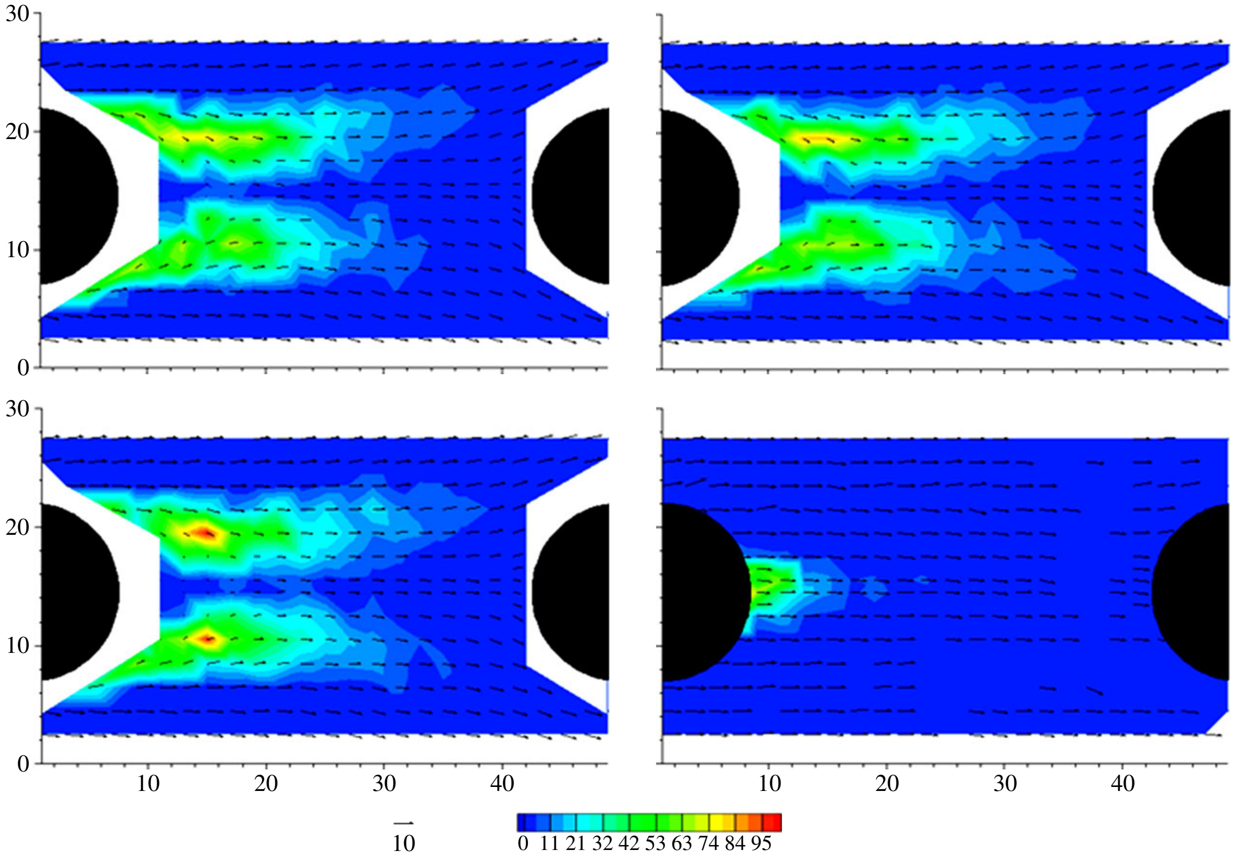

Figure 3. Turbulent kinetic energy (*k*) plots of flow at normalized elevations (*z*/H) (*a*) 0.05, (*b*) 0.09, (*c*) 0.12, and (*d*) 0.85 around boulders in an open channel flume. Flow elevation (*z*) is normalized by the boulder height (H). Units are given in cm s^{-1}.

velocity measurements could not be taken in this region owing to the measurement limitations of the downward-looking ADV. This resulted in a mean observation period of 4 min 36 s per fish. Parasite infection, host size or sex did not affect the time spent in the top 70 mm of the flow depth (generalized linear model (GLM), $p > 0.05$). Individual fish were tested only once, so the total sample size was 30 infected and 30 uninfected females and 27 infected and 24 uninfected males.

2.6. Statistical analysis

All analyses were conducted using R v. 2.1.0 statistical software [50].

The total time individual fish spent in each flow region was totalled and the different volumes of each region was corrected by dividing time by the region volume (to give units of s cm^{-3}) producing a comparative value for time budget allocation in each different-sized region. Times were converted to percentage of total time occupying each velocity region and arcsine transformed for statistical analysis.

Differences in the time spent in each region for the pooled data were analysed using a linear mixed model (GLMM) with Gaussian distribution using the lmer function in the lme4 package [51] followed by Tukey's honestly significant difference (HSD) multiple comparisons using the ghlt function from the multcomp package [52]. Because individual fish spent time in multiple regions, the term 'Fish ID' was included in the GLMM as a random effect to account for autocorrelation.

The effects of host standard length, sex, parasite prevalence and intensity on the distance moved up- and downstream, and the frequency of movement between boulder regions were analysed using a GLM with negative binomial error distribution and square root link function. The host effects on per cent time spent in each flow region were analysed using a GLM with inverse-Gaussian error distributions and either identity or $1\ \mu^{-2}$ link functions. Fish sex and standard length were included in the models as an interaction term to account for size differences of male and female guppies, and parasite intensity and standard length were included as an interaction term to account for any differences in parasite infection between different-sized fish. GLMs were refined using Akaike information criterion (AIC) values to select the best-finishing model.

3. Results

3.1. Microhabitat hydrodynamics

An open channel flume was used to quantify guppy swimming behaviour according to fish size, sex and parasite load in relation to microhabitat variation around hemispherical boulders placed at 0.5 m intervals. Flow was ejected over the boulder crest and there was a strong downwards movement in the lee of the boulder where the vertical velocity reached as high as 3.29 cm s^{-1}, which is 26% of the longitudinal average pore velocity of 12.7 cm s^{-1} (table 2). While it was difficult to precisely interpret the type of coherent flow structure, it was clear that this recirculating region had the highest kinetic energy (figure 3), the highest relative turbulence intensity and the strongest shear stresses in the horizontal, longitudinal and vertical planes (table 2). In the recirculating region, the flow was highly three-dimensional and the magnitude of the shear stresses in both horizontal and vertical planes was fairly equal. Although the longitudinal velocity was the lowest in this region, the spatial and temporal variability of the longitudinal velocity was the greatest. Furthermore, this region had the greatest turbulent shear stresses in all planes and the highest mean vertical turbulent length scale l_w which ranged between 0.01 and 2.77 cm, and therefore exceeded the size of the fish in some instances.

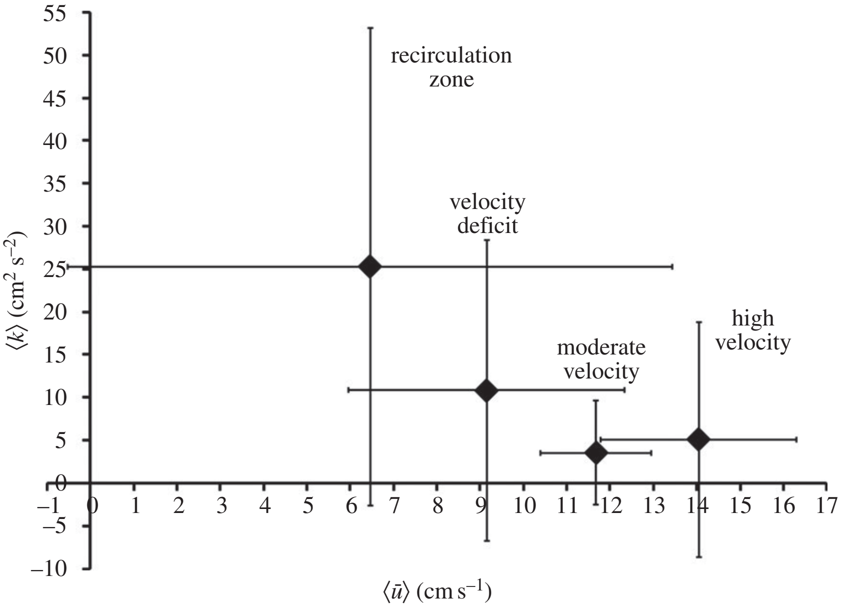

Figure 4. Volume-averaged turbulent kinetic energy (*k*) in relation to volume- and time-averaged longitudinal velocity for each velocity region. Horizontal and vertical error bars show the standard deviation of the volume-averaged value for each velocity region.

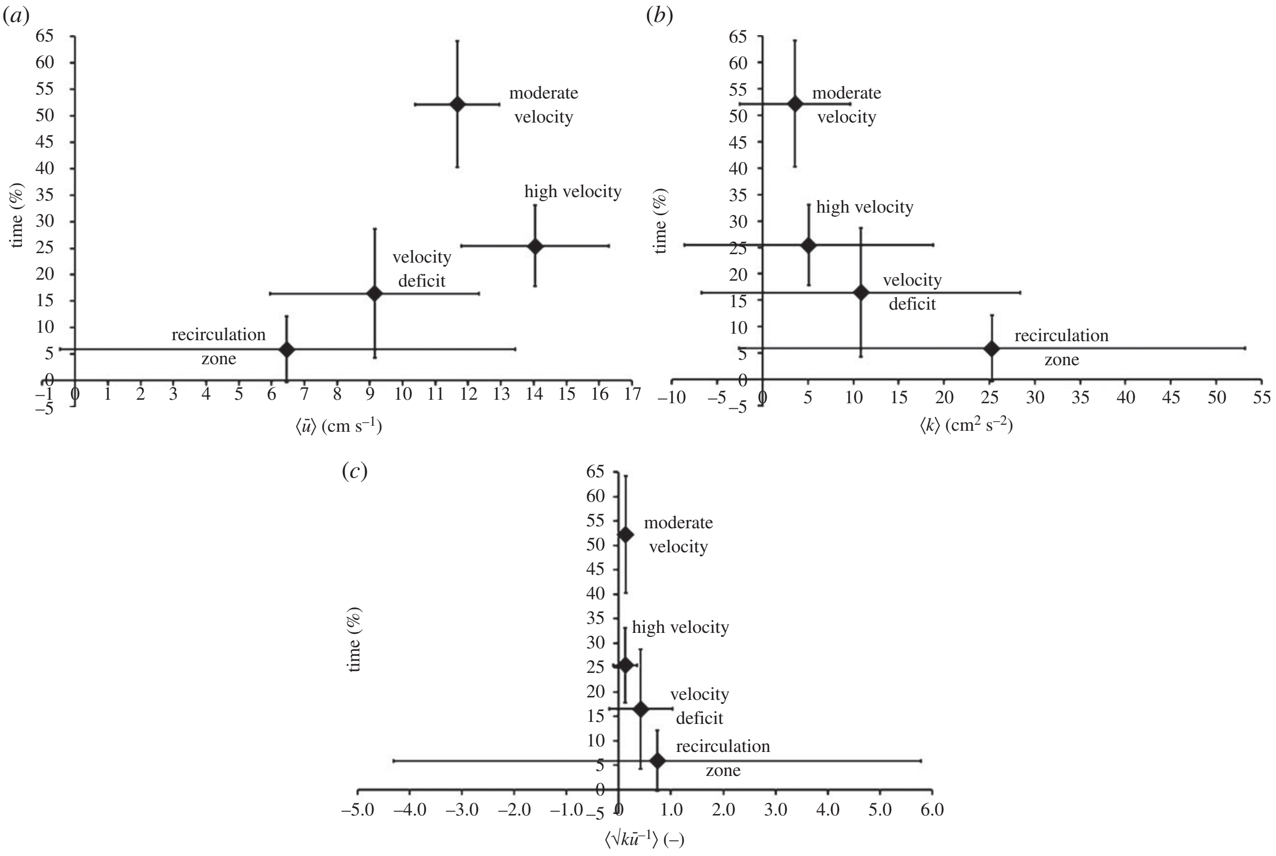

Figure 5. Time spent by guppies in the four velocity regions around a hemisphere boulder in relation to volume-averaged (*a*) longitudinal velocity ($\langle \bar{u} \rangle$) (*b*) turbulent kinetic energy ($\langle k \rangle$) and (*c*) relative turbulence intensity ($\langle \sqrt{k\bar{u}^{-1}} \rangle$). The horizontal and vertical bars shown in (*a,b*) denote the standard deviation of the time spent in each region and the spatial variation of the longitudinal velocity and turbulent kinetic energy, respectively.

The proximity of the flume wall to the boulder sides created a region of accelerated flow around the boulders (H in figure 2). The high-velocity region had the highest longitudinal velocity, highest turbulent length scale in the horizontal plane, but the lowest turbulent kinetic energy and shear stresses, relatively low turbulence intensities and low standard deviations of relative turbulence intensity (figures 4 and 5; table 2). This indicates that while the velocity was at its highest, the temporal variability of the velocity and turbulence at a given point within this region was relatively low. The narrowing of the channel at this point resulted in enhanced shear layer development between the flow at the walls and in the wake of the boulder, which probably enhanced rotational strength of the vortices in the recirculation region (figure 3).

The moderate-velocity region had moderate longitudinal velocities (figures 4 and 5*a*), the lowest turbulent kinetic energy (figures 4 and 5*b*), low relative turbulence intensities (figure 5*c*), low turbulent shear stresses in all planes and the lowest spatial variation for each parameter as indicated by the standard deviations in figures 4 and 5. These low values indicate that this region was the most spatially and temporally homogeneous region within the boulder control volume, and therefore the most predictable and stable region (see comparison, table 2). This region had the highest turbulent length scale in the horizontal plane L_v, but with the lowest standard deviation, again suggesting a relatively stable region.

A summary of the volume- and time-averaged parameters of each velocity region (figure 2) around the boulders is presented in table 2. For each velocity region, volume-averaged parameters and the standard deviation with respect to the time allocation of the fish in these regions are shown in figures 4 and 5. For all regions, the turbulent length scale exceeded the size of the fish in the longitudinal plane (L_u).

3.2. Fish movement and position in relation to microhabitat hydrodynamics

Results of all statistical models relating fish behaviour to host factors and parasite infection are provided in the electronic supplementary material.

Fish moved both up- and downstream continuously throughout the 10-min observation period, and spent only short periods station holding within different areas of the flume. With increasing standard length, guppies moved more frequently between boulder velocity regions (GLM, adjusted $R^2 = 0.964$, $Z_{1,109} = 3.40$, $p < 0.001$) and swam a greater distance in both the up- and downstream directions (GLM, adjusted $R^2 = 0.923$ and 0.934, $Z_{1,109} = 3.443$ and 3.33, $p < 0.001$). There was no effect of host sex, parasitism (prevalence or intensity) or the interaction terms on the frequency of movement or distance moved.

In terms of flow microhabitat use around the boulders, guppies spent significantly more time in the region of moderate velocity magnitude compared with the high, velocity-deficit and recirculation zones (Tukey's HSD multiple comparisons following GLMM $F = 5.508$, 0.771 and 7.468, respectively, all $p < 0.001$). This region may therefore represent the best trade-off between reduced longitudinal velocity and stable turbulence levels. There was a significant interaction between parasite intensity and fish standard length (GLM, adjusted $R^2 = 0.126$, $t_{3,107} = -2.496$, $p = 0.014$), with an increase in time spent in the moderate-velocity region with increasing parasite intensity but this relationship was stronger for smaller fish (figure 6). There was no difference in the time spent in the moderate-velocity region between male and female guppies.

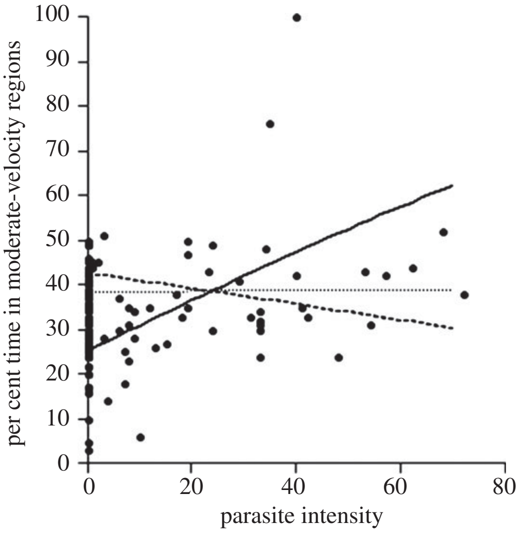

Figure 6. Interaction between parasite intensity and host standard length significantly affecting the percentage of time spent by guppies in the moderate-velocity regions around boulders. Filled circles show actual data, lines show predictions from the GLMs at standard length 13 mm (solid line), 25 mm (dotted line) and 29 mm (dashed line).

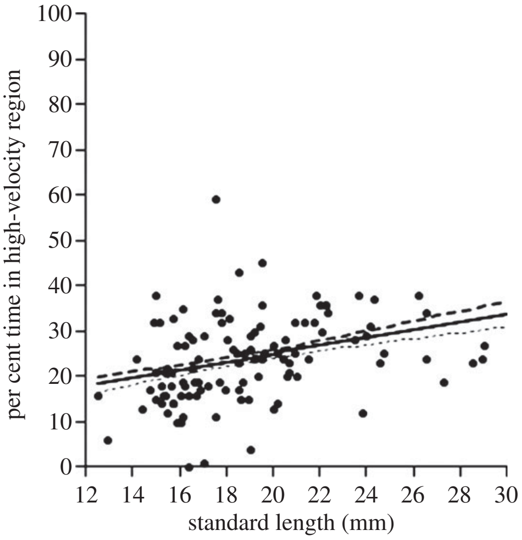

Figure 7. Host factors significantly affecting the percent time spent by guppies in the high-velocity regions around boulders. Black lines represent the predicted relationship from the GLMs, and dotted grey lines indicate standard errors of the models.

The second most frequented region was the high-velocity region (H in figure 2), although the time spent in this region was not significantly higher than that in the velocity deficit or recirculation zone. This region had the lowest shear stresses in all planes and was also a predictable environment for the fish to swim owing to the low temporal variation in velocity. Time spent in the high-velocity region was significantly related to fish standard length (GLM, adjusted $R^2 = 0.102$, $t_{2,108} = 3.634$, $p < 0.001$), with larger guppies spending increasingly more time in the high-velocity region (figure 7). Host sex, parasite infection (prevalence or intensity) and the interaction terms had no effect on the time spent in the area of high velocity.

The velocity-deficit region (L in figure 2) had intermediate values of longitudinal velocity, turbulent kinetic energy and relative turbulence intensity. Male guppies spent significantly more time in the velocity-deficit region (mean 25.3%, s.d. 15.0) compared with females (mean 18.9%, s.d. 12.8), regardless of standard length (GLM, adjusted $R^2 = 0.032$, $t_{2,108} = -2.253$, $p = 0.026$). Parasite infection (prevalence or intensity) and the interaction terms had no effect on the time spent in the velocity-deficit region.

Fish spent the least amount of time in the recirculation zone (R in figure 2) where the relative turbulence intensity, turbulent shear stresses and ratio of vertical turbulent length scale to fish standard length were at their greatest (table 2). Time spent in the recirculation zone was negatively associated with fish standard length, with smaller fish spending more time in this region than their larger counterparts (GLM, adjusted $R^2 = 0.039$, $t_{2,108} = 2.906$, $p = 0.004$; figure 8). Fish sex and

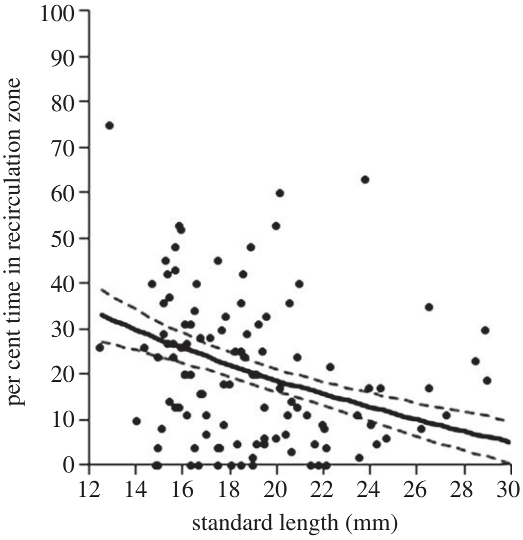

Figure 8. Host factors significantly affecting the percent time spent by guppies in the recirculation zones around boulders. Black lines represent the predicted relationship from the GLMs, and dotted grey lines indicate standard errors of the models.

parasite infection (prevalence or intensity) had no effect on the time spent in the recirculation region.

4. Discussion

In this study, we identified intraspecific variation in fish swimming behaviour under different flow conditions in terms of longitudinal velocity and turbulence within a heterogeneous habitat and for the first time demonstrated that microhabitat use can be affected by parasite infection. With increasing standard length, fish were more active and spent more time in areas of high velocity and low velocity. Males spent more time in the region of low velocity and moderate turbulence, indicating a trade-off between velocity reduction and turbulence level increase. When infected, smaller fish appear to opt for the most stable flow conditions. Although we are unable to determine whether spatial repartition of the fish is owing to active habitat selection or is a constraint owing to energy depletion or insufficient physical ability to station hold, we discuss possible reasons for the spatial position of individuals.

Guppies spent most time swimming in the moderate- and high-velocity regions which were the least spatially and temporally variable providing a more stable and predictable environment. The least amount of time was spent in the recirculation region characterized by low velocity, high turbulence and high shear stress, where the spatial variability of the parameters was also the highest. This reiterates the conclusions by Silva *et al.* [13] who demonstrated a significant negative correlation between horizontal shear stress and transit time by *L. bocagei* in an experimental fishway. Thus, shear stress could be an important turbulence property to consider when observing fish behaviour. Additionally, the mean turbulent length scale in the vertical plane (l_w) was greater than two-thirds of the standard length for 28% of the fish in the recirculation region. As Lupandin [11] proposed this threshold as being important in affecting fish swimming ability, this could be an additional reason as to why this region was avoided by the fish in this study.

The time spent in the high-velocity region increased with increasing standard length, indicating that larger fish were better able to tolerate the relatively higher flow velocities associated with this area compared with the highly three-dimensional flow field experienced in the recirculation zone immediately downstream of the boulder wake. Fish standard length was also associated with time spent in the recirculation zone which had low velocity, high turbulent and high shear stress, with smaller guppies spending more time in this region than their larger counterparts. The size effect of guppies on swimming behaviour is in line with previous studies that have shown that smaller fish occupy slow-moving water, and move to faster moving water as they become larger [22]. It has also been demonstrated that large juvenile rainbow trout select channels with high-velocities and low-turbulence over the low-velocity, high-turbulence channels [53]. However, small juveniles had no preference for either channel until the area mean velocity reached 28 cm s^{-1} where they selected the low-velocity and highly turbulent channel [53]. As discussed by Plaut [54], as fish grow their swimming ability improves, as there is a positive correlation between critical swimming speed and body size. The higher energy requirement of larger fish means that they will be more able to move out into areas with higher velocity magnitude, where the chances of food capture are higher [8].

The size of guppies also correlated with the amount of movement in the open channel. Large guppies displayed more frequent movement, between the velocity regions and swam further distances both up- and downstream. This increased movement may be owing to the enhanced swimming ability of bigger fish to tolerate changes in velocity magnitude and turbulence intensity as they move around the open channel flume. Fish constantly explore their surroundings to forage and seek shelter and this has previously been found to be associated with body size, for example Kramer & Chapman [55] found a positive relationship between home-range size and body size in several coral reef fishes. In guppies, there is a significant positive relationship between fork length and the amount of movement between natural pools separated by riffles in a Trinidadian stream [56], which could be owing to a higher energy requirement of larger fish, interaction between fish size and reproductive strategy or benefits of dispersal for colonization by larger individuals [56].

After taking into account standard length of the fish, male guppies were found to occupy the region of velocity deficit more frequently than females. Guppies are sexually dimorphic, with males being smaller in size, more colourful and have longer dorsal and caudal fins. Although longer fins serve as a secondary sex characteristics in guppies [27,57], for a given velocity a fish with larger fins experience increased drag compared with smaller finned counterparts [25]. Indeed several studies have attributed reduced guppy swimming performance and predator escape response [28] to the larger fin size [28,35]. In a study where the surface area of three shapes of caudal fins of guppies did not differ, there was no observed difference in swimming ability [24]. Therefore, it appears that the longer tails in guppies are a trade-off between sexual selection and natural selection. Differences in microhabitat selection between sexes have also been observed in wild guppies, for example with regard to shallow water usage [58]. In the wild, male guppies are found more commonly in shallower habitats [36] and slower moving water

[28], with females occurring in deeper water [36]. This leads us to question whether the longer tail fins in male guppies also cause a reduction in tolerance to turbulence and shear stresses in the wild.

Even after a relatively short infection period, *G. turnbulli* caused behavioural changes in guppies, with increasing time spent in the regions of moderate velocity magnitude with increasing parasite intensity, but this relationship was only apparent in small fish. The moderate-velocity regions had the lowest turbulent kinetic energy, relative turbulence intensity, turbulent shear stresses and the lowest spatial variability of these measures, making these regions the most stable and predictable. A small infected fish may seek these stable areas in order to offset energetic costs associated with the parasite infection. Although the influence on habitat structure on the transmission of parasites is not a new concept (see review by Sousa & Grosholz, [59]), few studies have focused on the aquatic environment (e.g. [60]). Extreme flow events during spate conditions are important in affecting guppy swimming ability when parasitized [61] and previous studies have reported fin clamping associated with late stages of gyrodactylid infection [37], which would inevitably result in decreased swimming performance. By affecting the swimming behaviour, and therefore foraging ability of their hosts, parasites may exert strong selection pressures by population control. Host–parasite interactions may be affected by habitat heterogeneity in several ways: (i) the habitat may cause spatial segregation of the hosts, thus affecting parasite transmission opportunities; (ii) the habitat may cause spatial segregation of the parasites, whether free living or via intermediate hosts or vectors or (iii) the parasites themselves may affect host behaviour, and thus affecting spatial positioning and further transmission opportunities for the parasite.

In summary, we demonstrate that fish of the same species but of varying size, sex and parasite intensity have different requirements in terms of microhabitat use around boulders in relation to velocity magnitude, turbulence and turbulent shear stress. Smaller and male fish (characterized by having larger fins than females) spent more time in the region of low-velocity magnitudes, whereas larger fish more frequently swam in the region of increased velocity magnitude. Small guppies infected with an increasing number of *G. turnbulli* worms spent more time in the moderate-velocity, low-turbulence and low turbulent shear stress regions, where the spatial and temporal variability of the velocity field was the lowest. This demonstrates the importance of flow heterogeneity within a river system for fish species populations, to provide shelter for weaker or smaller individuals or those at different life stages. In the natural environment, guppies are further restricted in microhabitats not only owing to velocity and turbulence tolerances, but also due to exclusion by predators and competitive exclusion from larger or more dominant individuals. Headwater stream habitats are devoid of predators and guppies are found to be more widely distributed compared with the downstream populations where they are restricted to shallower, slow-moving waters owing to the presence of predators in deeper water [62]. Although boulder placement is commonly employed to encourage habitat diversity in river restoration schemes, the success in improving fish populations has been variable [2,3]. Relatively few studies have bridged the gap between field observations and the use of static flow tanks (e.g. [2,19] and this study), particularly with regard to intraspecific variation in fish behaviour.

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