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Highlights

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Influence of corrugated boundary hydrodynamics on the swimming performance and behaviour of juvenile common carp (*Cyprinus carpio*)

L.R. Newbold, P.S. Kemp *

- Carp swimming performance and behavioural response to corrugations were assessed.
- Corrugations did not improve swimming performance compared to smooth walls.
- Fish could occupy low velocity areas within large and medium corrugation troughs.
- Fish often swam in higher velocity, lower TKE flow, away from larger corrugations.
- Turbulence near the corrugated walls may have reduced fish stability.

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Influence of corrugated boundary hydrodynamics on the swimming performance and behaviour of juvenile common carp (*Cyprinus carpio*)

Q1 L.R. Newbold, P.S. Kemp *

The International Centre for Ecohydraulics Research, Faculty of Engineering and the Environment, University of Southampton, Southampton, UK

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ABSTRACT

To facilitate the upstream passage of small fish, corrugated culverts are often preferred over smooth pipes, due to the lower edge and mean cross sectional water velocities created. This benefit could be lost if greater intensities of turbulence induced by wall roughness cause instability and increase the energetic expense of fish locomotion. Common carp (*Cyprinus carpio*) swimming performance and behaviour were evaluated in a flume using four wall roughness treatments: smooth (control), small (SC), medium (MC), and large (LC) corrugations, dependent on corrugation wavelength and amplitude. Individual fish ($n = 128$, mean ± S.D. total length [TL] = 86 ± 8 mm) swam at a mid-channel velocity of 0.5 m s^{-1} for 30 min or until fatigue. Swimming performance was quantified by: (a) success (completion of 30 min trial) or failure; and (b) the time to fatigue (endurance) of those that failed. To evaluate behaviour, fish head positions were tracked manually every second. Occupancy of the area within the MC and LC troughs (concave area where velocity was lowest) was recorded and the relationships between trough occupation and (i) TL and (ii) success tested. Differences were tested for between successful and failed individuals, and among treatments, for the following dependent variables: the total distance moved, the mean distance from the flume wall occupied ($Fish_D$), and mean velocity ($Fish_U$) and turbulent kinetic energy ($Fish_{TKE}$) experienced. Treatment did not influence frequency of success (38–58% per treatment) or time to fatigue. During the MC and LC treatments, troughs were occupied for part of the trial by 56 and 55% of individuals, respectively. Trough occupation was independent of TL in both treatments, and more common for successful fish than failures in the LC treatment. For successful fish, the total distance moved did not differ among treatments. Successful $Fish_D$ varied among treatments and was higher for the LC (mean ± S.E. = 93.2 ± 22.3 mm) than the SC (33.5 ± 2.8 mm) treatment. Despite the availability of lower velocity areas, median successful $Fish_U$ was higher in the LC treatment (0.51 m s^{-1}) than in any other (median = 0.47 m s^{-1}, 0.44 m s^{-1} and 0.47 m s^{-1} in the MC, SC, and control, respectively). Treatment did not influence successful $Fish_{TKE}$ which was consistently low (median = 5.3–7.7 J m^{-3} per treatment). Although occupation of the MC and LC troughs occurred, many individuals spent little time here, and areas with lower TKE were often occupied. Under the experimental conditions created, this study does not support the assumption that low velocity areas created by wall corrugations will improve culvert passage.

1. Introduction

Culverts can create full or partial barriers to the upstream migration of riverine fish, impeding access to important spawning, rearing, or refuge habitat, and fragmenting populations (e.g. Warren and Pardew, 1998; MacDonald and Davies, 2007; Burford et al., 2009; MacPherson et al., 2012). Excessive velocities and lack of resting areas in the culvert barrel are a common cause of impediment, especially during high flow (WSDOT, 2012) and for weak swimming species (e.g. burbot, *Lota lota*, MacPherson et al., 2012; inanga, *Galaxius maculatus*, Franklin and Bartels, 2012). Designation of suitable water velocities, which are within fish swimming abilities, should be included in the culvert design to improve fish passage (Armstrong et al., 2010; Balkham et al., 2010; Barnard et al., 2013). Although velocity criteria for fish passage are usually based on the bulk cross sectional flow, utilisation of lower velocity zones at the culvert walls may allow small fish to pass upstream even when bulk flow appears to exceed their swimming capability (Ead et al., 2000; House et al., 2005). Q3

Compared to smooth culverts, corrugated pipes increase the area of low velocity near the wall (Alberta Transportation, 2010). As a result they are often recommended to facilitate the passage of

Q2 * Corresponding author. Tel.: +44 2380 595 871.
E-mail addresses: P.Kemp@soton.ac.uk, lre105@soton.ac.uk (P.S. Kemp).

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small and weak swimming fish (Clay, 1995; Barnard et al., 2013). However, few studies have quantified the effects of corrugated walls on upstream fish movement through culverts, and when they did the results were mixed (e.g. Powers et al., 1997; Johnson et al., 2012). In one study, coho salmon (*Oncorhynchus kisutch*) fry were observed to hold position close to annular and spiral corrugations in an experimental culvert, presumably utilising refuge from the higher mid channel flow (Powers et al., 1997). Yet passage efficiency for a smooth experimental culvert was greater than for corrugated barrels under several discharge conditions (Powers et al., 1997). In another study, juvenile coho salmon exited a full scale laboratory culvert via a low velocity route created along one channel wall by spiral corrugations 3.5 times more often than along the opposite wall where velocities were higher (Johnson et al., 2012; see Richmond et al., 2007 for hydraulic analysis of spiral corrugations). Despite this apparent benefit of the low velocity area, there was a negative relationship between passage efficiency and the intensity of turbulence here.

Turbulence can reduce fish stability (Tritico and Cotel, 2010), decrease swimming performance (Lupandin, 2005; Tritico and Cotel, 2010), and elevate the energetic costs of locomotion (Enders et al., 2005a,b). The hydraulic conditions associated with corrugations, typified by rapid fluctuations in flow (Richmond et al., 2007), may confuse or displace fish away from the wall and into the faster mid channel current, or increase the energetic cost of swimming. This may negate any benefit provided by the areas of low velocity created at the edge (Kahler and Quinn, 1998; Boubée et al., 1999; Richmond et al., 2007). Previous attempts to explore the effect of turbulence on upstream fish passage through corrugated culverts have been limited by simplistic fish passage data (e.g. Powers et al., 1997; Johnson et al., 2012) or superficial hydraulic analysis (e.g. Powers et al., 1997).

Channel roughness, in terms of corrugation wavelength and amplitude, may influence fish passage success by affecting both the intensity of turbulence and the size of eddies created (Papanicolaou and Talebbeydokhti, 2002; Nikora et al., 2003). If eddy diameter exceeds approximately two thirds of body length, fish are more likely to be destabilised and their swimming performance reduced (Lupandin, 2005; Webb, 2005; Tritico and Cotel, 2010). Furthermore, the wavelength and amplitude of corrugations determine whether individuals can occupy the concave troughs to gain refuge from higher water velocities (Powers et al., 1997; Gerstner, 1998; Gerstner and Webb, 1998; Nikora et al., 2003). Research quantifying this effect has focused on substrate ripples rather than corrugated walls; for example Atlantic cod (*Gadus morhua*) refuged within substratum ripple troughs only when the wavelength was at least two times greater than body length, due to an inability to contour their body into a smaller area (Gerstner, 1998).

Previous research on fish passage through corrugated culverts and broader relationships between turbulence, swimming ability and behaviour have tended to focus on anadromous salmonids, notably in North America (Pearson et al., 2006; Lacey et al., 2012; WSDOT, 2012). Although the effects of barriers to potamodromous migrations and mitigation options for non-salmonid species have gained greater attention in the last two decades (e.g. Lucas and Baras, 2001; Ovidio and Philippart, 2002; Godinho and Kynard, 2009; Santos et al., 2014), restoring habitat connectivity for multiple species continues to represent a considerable challenge (Bunt et al., 2012; Noonan et al., 2012). Furthermore, research regarding potamodromous migrations has largely focused on the effect of dams and weirs and suitable fish pass designs (e.g. Lucas and Batley, 1996; Lucas and Frear, 1997; Silva et al., 2012). There has been little attention given to the influence of culverts on this group. However, in areas where there is a high abundance of culverts it is likely they will have some negative impact (Fitch, 1996; Kemp and O'Hanley, 2010; Makrakis et al., 2012).

Potamodromous cyprinid species are of great economic and conservation value in many countries. For example, in China, the bighead carp (*Hypophthalmichthys nobilis*), grass carp (*Ctenopharyngodon idella*), silver carp (*Hypophthalmichthys molitrix*), black carp (*Mylopharyngodon piceus*), and common carp (*Cyprinus carpio*) are among the most commercially valuable fish species (Wu et al., 1992; Chen et al., 2004). Many Asian carp conduct large upstream migrations as adults to spawning grounds and lateral movements as juveniles to lakes and other off channel habitats (Jennings, 1988; Zhang et al., 2012). Construction of anthropogenic structures, including the disconnection of lakes from river channels, is contributing to their population declines (Fu et al., 2003; Chen et al., 2004). Although the impact of culverts on Asian carp has not been studied, lateral and longitudinal connectivity could be impacted where culvert hydraulics are poorly designed. There is little data on Asian carp swimming performance, and no research on their response to turbulence. The common carp was selected as a representative potamodromous carp species for this study as they are readily available in the UK and have a similar body morphology and comparable swimming ability to other Asian carp species (common carp, Rome et al., 1990; Tudorache et al., 2007; grass carp, Zhao and Han, 1980 silver and bighead carp, Hoover et al., 2012).

To better understand how fish utilise the hydraulic conditions created by corrugations, this study aimed to evaluate the influence of corrugated walls on the prolonged swimming performance and behaviour of juvenile common carp under four wall roughness treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugations. It was hypothesised that: (a) carp swimming performance would be higher in the corrugated treatments than the control, due to greater availability of low velocity areas; (b) performance would be positively related to corrugation dimensions, due to larger areas of low velocity and greater potential to occupy troughs when wavelength exceeded fish length; and (c) that fish would hold station in the MC and LC troughs, thus moving little and maintaining position close to the wall in lower velocity areas than under the SC and control treatments.

2. Methods

2.1. Fish collection and maintenance

Juvenile common carp were obtained from the Hampshire Carp Hatchery, Bishopstoke, UK and transported (20 min) to the International Centre for Ecohydraulics Research laboratory, University of Southampton, in oxygenated plastic bags, on 2 February 2011 (Year 1: $n = 79$, mean ± S.D. total length [TL] = 87.1 ± 7.0 mm, mass = 11.7 ± 2.7 g) and 15 February 2012 (Year 2: $n = 49$, TL = 85.4 ± 9.0 mm, mass = 11.5 ± 3.5 g). Fish were held in a 900 L aerated and filtered tank under natural photoperiod and ambient temperature in an unheated building (mean water temperature ± S.D. 2011 = 10.3 ± 0.6 °C; 2012 = 10.1 ± 0.7 °C) and fed daily. Water quality was maintained through weekly partial exchange (approximately 20% of tank volume). Trials were completed between 5 and 16 days after fish arrival.

2.2. Experimental setup and protocols

Experimental trials were conducted in a large, open channel, rectangular, re-circulatory flume (21.40 m long, 1.37 m wide, 0.60 m deep), powered by three electrically driven centrifugal pumps (maximum discharge = 0.47 $m^3 s^{-1}$). Wire mesh screens (12 mm square) were placed 1.3 m apart to create a rectangular test section half way along the flume channel (Fig. 1). The test section width was reduced to 1.16 m by inserting temporary vertical walls of varying roughness, to create smooth (control), small (SC), medium

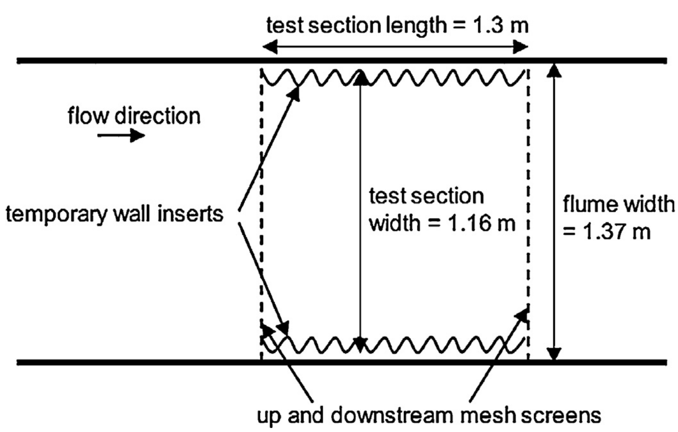

Fig. 1. Plan view of a test section in a recirculatory flume (21.40 m long, 1.37 m wide and 0.60 m deep) used to evaluate the swimming performance and behaviour of juvenile common carp (*Cyprinus carpio*) under 4 wall roughness treatments.

(MC) and large (LC) corrugation treatments (Table 1). Corrugation wavelengths were selected to be less than, approximately equal to, and greater than fish length. The area of velocity less than mid-channel flow was positively correlated to corrugation dimensions (Fig. 2a) and was typified by relatively high turbulent kinetic energy (TKE) in the MC and LC treatments (Fig. 2b).

Fish were placed in perforated containers within the flume for at least 30 min prior to the start of trials to acclimate to water temperature (mean ± S.D. 2011 = 10.1 ± 0.6 °C; 2012 = 11.4 ± 0.5 °C). Individuals were transferred to the test section and swam for 10 min at 0.2 m s^{-1}, followed by a further 10 min at 0.3 m s^{-1}, before being exposed to the test mid-channel velocity (0.5 m s^{-1}). Discharge and depth remained constant at 0.18 $m^3 s^{-1}$ and 0.26 m, respectively, regardless of treatment. Although some short culverts may be traversed in a single high speed burst (Johnson et al., 2012), fish, particularly smaller weaker swimming individuals, may spend several minutes ascending a barrel (e.g. up to 47 min Peterson et al., 2013). Therefore, the test velocity was selected to evaluate prolonged swimming performance (maintainable for >20 s but <200 min; swimming speed categories defined in Beamish, 1978). Trials were ended after 30 min, unless fatigue (>3 s impingement on the downstream screen) occurred first. TL (mm) and mass (grams) of the test fish were recorded. A black plastic screen along the flume length prevented visual disturbance by the observer and fish behaviour was recorded using an overhead camera (2 m above the flume floor). Successful fish were more likely to exhibit steady swimming for extended periods than those that failed. Therefore, to explore fish behaviour in response to the hydrodynamic conditions, a sufficient number of successful fish per treatment were required. As a result of variable success rate between treatments, the total number of fish tested per treatment was unequal (Table 1).

Table 1
The dimensions of corrugated walls placed in a 1.3 m long test section of a flume to create four roughness treatments, and the number of juvenile common carp (*Cyprinus carpio*) tested under each.

Treatment	Wavelength (mm)	Amplitude (mm)	*n*
Smooth (control)	N/A	N/A	37
Small corrugations (SC)	40	10	26
Medium corrugations (MC)	76	20	34
Large corrugations (LC)	150	50	31

2.3. Hydraulic conditions

Water velocity was measured at 60% depth along transects perpendicular to the flow using two downward and one sideways facing Acoustic Doppler Velocimeters (ADV; Nortek AS, Oslo, Norway), separated by 120 mm to prevent interference. The sideways looking ADV was used to record data close to the corrugated walls and was mounted 50 mm lower than the downwards facing probes to ensure data was collected from an equivalent depth. Velocity was recorded at a frequency of 50 Hz for 60 s, using a 3.1 mm sample depth. Dependent on the hydraulic complexity of treatments, between 12 and 32 transects were completed. The distance between transect sample points increased from 0.02 m close to the walls to 0.20 m in the flume centre (see Fig. 2a for sample locations). Raw data was filtered to remove erroneous spikes using a velocity correlation approach that accounted for all three dimensions of flow (described in Cea et al., 2007). At each point the mean velocity vector (*U*) was subsequently calculated as: $U = \sqrt{\bar{u}2 + \bar{v}^2 + \bar{w}^2}$ where $\bar{u}$,$\bar{v}$, and $\bar{w}$ are the mean longitudinal, lateral, and vertical velocity components (m s^{-1}), respectively.

The TKE was selected to quantify the intensity of turbulence within treatments because it is a dimensional number directly comparable to other laboratory and field studies (Lacey et al., 2012). The TKE was calculated at each sample point as: TKE (J m^{-3}) = $0.5.\rho.(\sigma_u^2 + \sigma_v^2 + \sigma_w^2)$, where ρ is the density of water and σ is the standard deviation of velocity. The U and TKE were plotted in ArcView GIS (v. 9.3, ESRI, Redlands, USA) and interpolated using kriging (cell size = 0.5 cm, search radius = 12 point; Fig. 2a and b).

2.4. Swimming performance

Swimming performance was quantified as: (a) the ability to complete the 30 min fixed velocity trial (categorised as success or failure), and (b) the time to fatigue (endurance) for those that failed.

As there was no association between year and success (Pearson's chi-square test: $\chi^2 = 0.43$, d.f. = 1, $P = 0.51$) all data were combined for further analysis. Water temperature and endurance data were log transformed prior to parametric statistical analysis. Association between success and treatment was tested using a Pearson's chi-square test. The effects of TL and water temperature on success were evaluated using two-way factorial ANOVAs with treatment and success included as independent variables. To evaluate the effect of treatment on endurance a Kaplan Meier survival analysis was used (Kaplan and Meier, 1958). The 'survival time' was recorded as the endurance of individual fish, and the probability of fatigue occurring at a given time period was calculated. Those fish that swam for the total 30 min trial were included as censored individuals because their true fatigue time was unavailable. The log-rank test was used to determine whether a significant difference in the probability of fatigue occurring at any time point existed among treatments (Bewick et al., 2004; Bland and Altman, 2004).

2.5. Fish behaviour

Fish head position was tracked every second using Logger Pro Q6 (v. 3.8.2, Vernier Software & Technology, Oregon, USA) and plotted in ArcView GIS. The digitisation error (±8 mm) due to manual tracking was quantified by digitising a single fish head location, where flow was most turbulent, 100 times.

For each head location the distance to the closest corrugation trough (i.e. the point furthest from the flume centre) was calculated. This allowed recording of two elements of trough

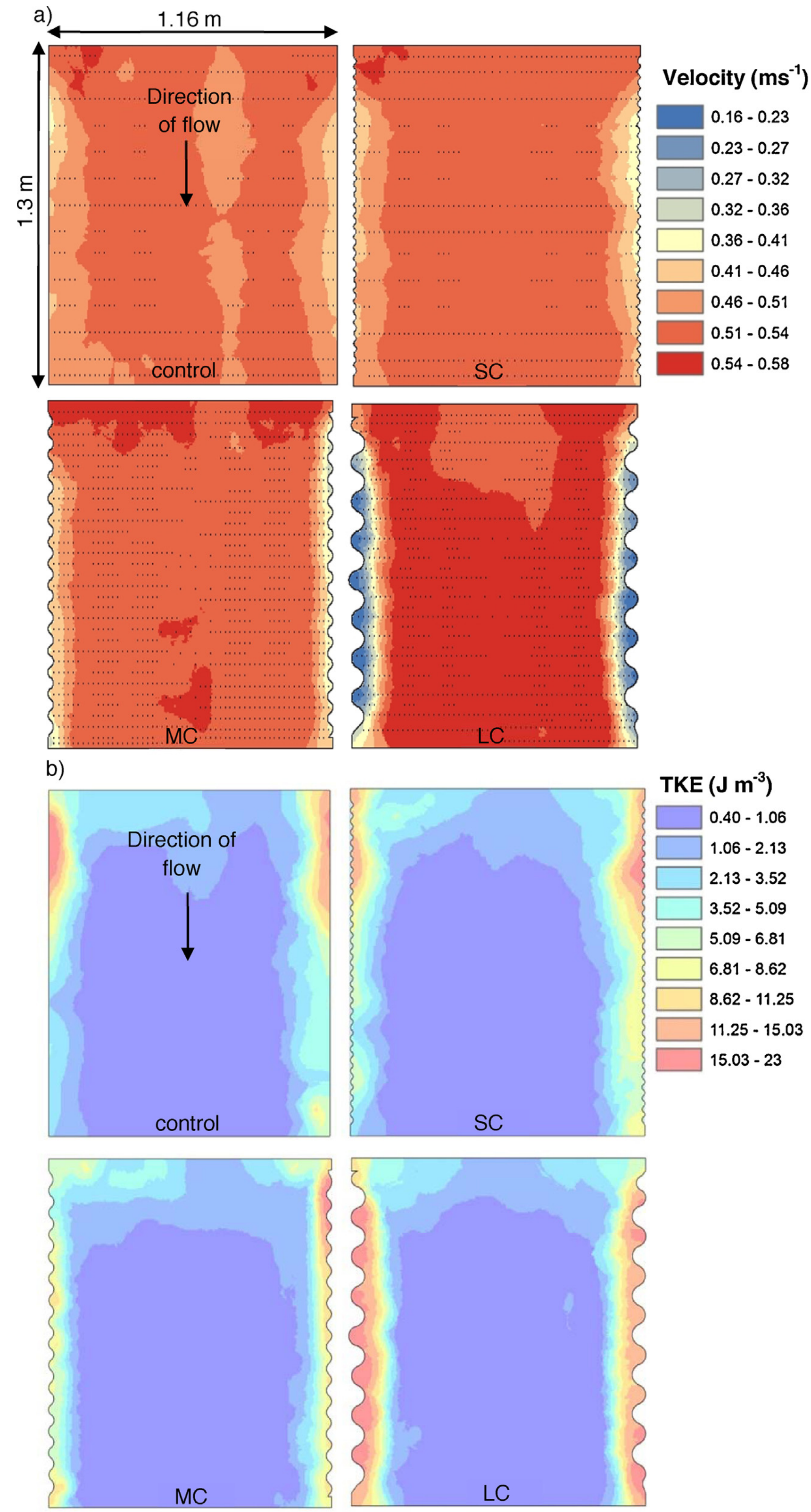

Fig. 2. (a) The mean velocity vector (U), and (b) Turbulent kinetic energy (TKE) profiles for four treatments used to test the effect of wall corrugations on the swimming performance and behaviour of juvenile common carp: smooth (control), small (SC), medium (MC) and large (LC) corrugations. The test section was created in a 21.4 m long flume at the International Centre for Ecohydraulics Research laboratory, Southampton, UK. Point velocity data were collected using three Acoustic Doppler Velocimeters at each point shown in Fig. 2a.

occupancy behaviour during the MC and LC treatments: swimming within the corrugation troughs for more than five consecutive seconds (trough occupation); and the percentage of time spent within the troughs. Fish did not occupy the troughs under the SC treatment because wavelength was too small (40 mm). Using the head co-ordinates, the total distance moved during a trial was calculated. The 60% depth U and TKE at each head location were extrapolated from the hydraulic data layer and used to estimate the hydraulic conditions experienced by fish. Fish behaviour and the hydraulic conditions experienced were summarised as mean distance from the wall occupied ($Fish_D$), mean velocity ($Fish_U$), and mean TKE ($Fish_{TKE}$).

As assumptions of normality were violated for TL and $Fish_D$, data were log transformed prior to parametric analysis. A chi-square was used to test whether there was a difference in the frequency of trough occupation by fish between the MC and LC treatments, and the relationship between success and trough occupation for both treatments. TL was compared (*t*-test) between individuals that occupied troughs in the MC and LC troughs and those that did not.

To evaluate the difference in $Fish_D$, $Fish_U$ and $Fish_{TKE}$ between successful and failed fish within each treatment, an independent *t*-test or Mann–Whitney test was used depending on whether data met assumptions of normality.

Due to the tendency for unsuccessful fish that exhibited unsteady swimming to fatigue quickly, further analysis on the hydrodynamic conditions experienced was conducted only for successful individuals. Further, one successful fish in the control and two in each corrugation treatment were excluded from this analysis because they held position in the centre of the upstream screen for the majority of the 30 min trial (identified as: mean distance from wall >20 cm, S.D. < 10 cm). One-way ANOVA and Gabriel's post hoc tests for unequal sample sizes were used to investigate the relationships between treatment and the total distance moved and $Fish_D$ for successful fish. Due to failure to meet assumptions of normality and an inability to successfully transform the data, the effect of treatment on the $Fish_U$ and $Fish_{TKE}$ was evaluated using Kruskal–Wallace and post hoc Bonferroni corrected Mann–Whitney tests. All statistical analysis was conducted using IBM SPSS Statistics v. 19 (IBM Corp., Armonk, NY, USA). A *P* value of less than 0.5 was reported as significant for all analysis.

3. Results

3.1. Swimming performance

Between 38% (MC) and 58% (SC) of fish successfully completed the 30 min fixed velocity trial under the four treatments tested (Fig. 3). There was no relationship between treatment and frequency of success ($\chi^2 = 2.75$, d.f. = 3, $P = 0.43$). Successful fish had a greater TL (mean = 88 mm) than those that failed (mean = 85 mm) ($F_{1,119} = 5.50$, $P = 0.02$). There was no difference in TL among treatments ($F_{3,119} = 0.86$, $P = 0.47$), nor an interaction between treatment and success ($F_{3,119} = 0.43$, $P = 0.73$). Water temperature did not differ between successful and unsuccessful fish ($F_{1,120} = 0.73$, $P = 0.40$) or among treatments ($F_{3,120} = 0.65$, $P = 0.59$). There was no effect of treatment on the rate of fatigue (Log rank $\chi^2 = 2.68$, $P = 0.44$; Fig. 3).

3.2. Fish behaviour

Fish did not occupy the SC troughs because the wavelength was too short. Troughs were occupied for more than five consecutive seconds by 56% and 55% of fish in the MC and LC treatments, respectively. There was no difference in trough occupation between the MC and LC treatments ($\chi^2 = 0.007$, $P = 0.93$). For the MC treatment there was no difference in the occurrence of trough occupation between fish that were successful (69%) or failed (48%) to swim for 30 min ($\chi^2 = 1.52$, $P = 0.22$). For the LC treatment more successful fish occupied troughs (87%) than failures (25%) ($\chi^2 = 11.89$, $P = 0.001$). There was no influence of TL on trough occupation (MC: $t_{32} = 0.60$, $P = 0.56$, LC: $t_{29} = -0.15$, $P = 0.87$). The proportion of time spent occupying troughs was highly variable among individuals (MC = 2–79%; LC = 9–95%).

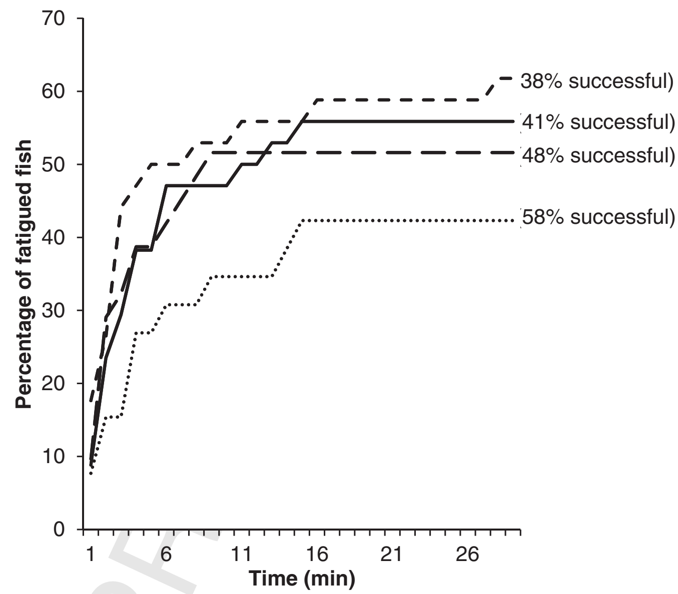

Fig. 3. The percentage of common carp that fatigued at 1 min intervals during 30 min endurance tests conducted under smooth (solid line), small (dotted line), medium (short dashed line) and large (long dashed line) corrugated wall treatments. Mid channel test velocity was 0.5 m s^{-1}. The percentage of successful fish is shown in parenthesis for each treatment.

$Fish_D$ was lower for successful fish than for those that failed under all treatments ($P < 0.05$) except the MC ($t_{32} = 1.88$, $P = 0.07$). $Fish_U$ was lower for successes than for failures under the control ($U = 80.5$, $P = 0.03$) and SC ($U = 16$, $P = 0.001$), but not MC ($U = 105$, $P = 0.27$) or LC ($U = 76$, $P = 0.08$) treatments. The $Fish_{TKE}$ for successful individuals was lower than for failures in the control, SC and LC treatments ($P < 0.05$), but equal in the MC treatment ($U = 100$, $P = 0.20$). Fish that fatigued within 30 min often exhibited unsteady swimming behaviour, typified by rapid bursts of erratic movement around the flume. In contrast, the successful individuals tended to settle in one area of the flume for prolonged periods.

Excluding the seven fish that held position in the centre of the upstream screen, there was no difference in the total distance successful individuals swam among treatments ($F_{3,50} = 2.50$, $P = 0.07$). $Fish_D$ differed among treatments ($F_{3,50} = 3.83$, $P = 0.02$), with that for the LC (mean ± S.E. = 93.2 ± 22.3 mm) being greater than for SC (33.5 ± 2.8 mm). $Fish_D$ for the control and MC treatment were intermediate (control = 75.3 ± 99.7 mm; MC = 55.6 ± 24.9 mm).

$Fish_U$ for successful individuals was influenced by treatment (Fig 4a; Kruskal–Wallis $\chi^2 = 11.01$, $P = 0.01$), being highest under the LC (median = 0.50 m s^{-1}) and lowest under the SC treatment (0.44 m s^{-1}). Post hoc tests indicated differences in $Fish_U$ between the control (median = 0.47 m s^{-1}) and SC (0.44 m s^{-1}), and between the MC (0.47 m s^{-1}) and SC treatments ($P < 0.008$). In the LC treatment, $Fish_U$ varied considerably among individuals due to variation in trough occupancy (Fig. 5d). $Fish_{TKE}$ for successful individuals was not influenced by treatment (Fig. 4b; Kruskal–Wallis $\chi^2 = 5.52$, $P = 0.14$) and was consistently low, with

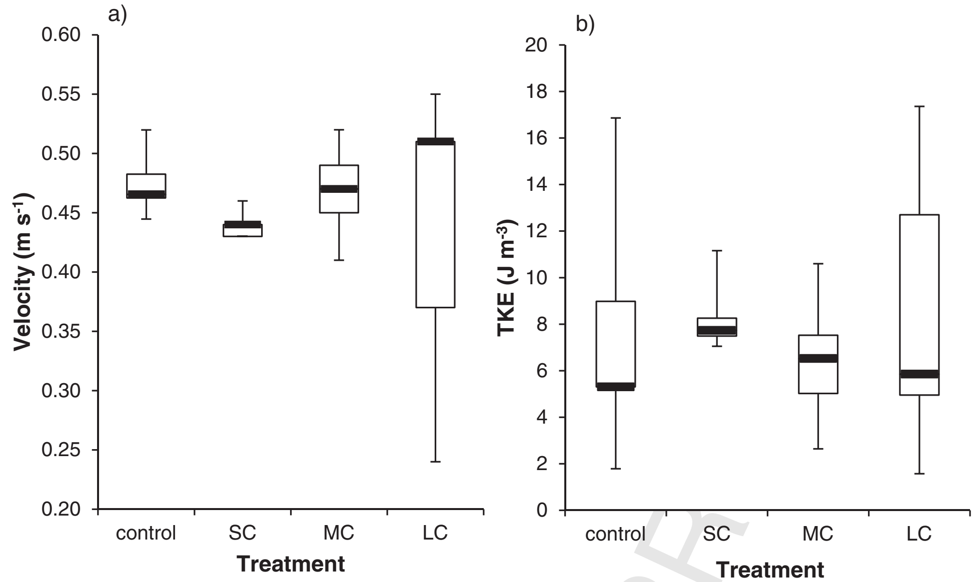

Fig. 4. The median, interquartile range and minimum/maximum whiskers of the: (a) mean trial velocity ($Fish_U$); and (b) mean trial TKE ($Fish_{TKE}$) experienced by common carp swimming for 30 min in a $0.5\ m\ s^{-1}$ fixed velocity trial under four treatments: smooth (control), small (SC), medium (MC) and large (LC) corrugated walls.

the treatment median ranging between $5.3\ J\ m^{-3}$ (control) and $7.7\ J\ m^{-3}$ (SC).

Variability in the hydraulic conditions experienced (i.e. range of $Fish_U$ and $Fish_{TKE}$ among successful fish was lower in the SC than the MC and LC treatments (Fig. 5). Successful fish in the LC treatment could experience the highest hydrodynamic heterogeneity (Fig. 2), dependent on time spent in the troughs, close to the peaks, or further away from the wall (Fig. 5d). Occupation of these

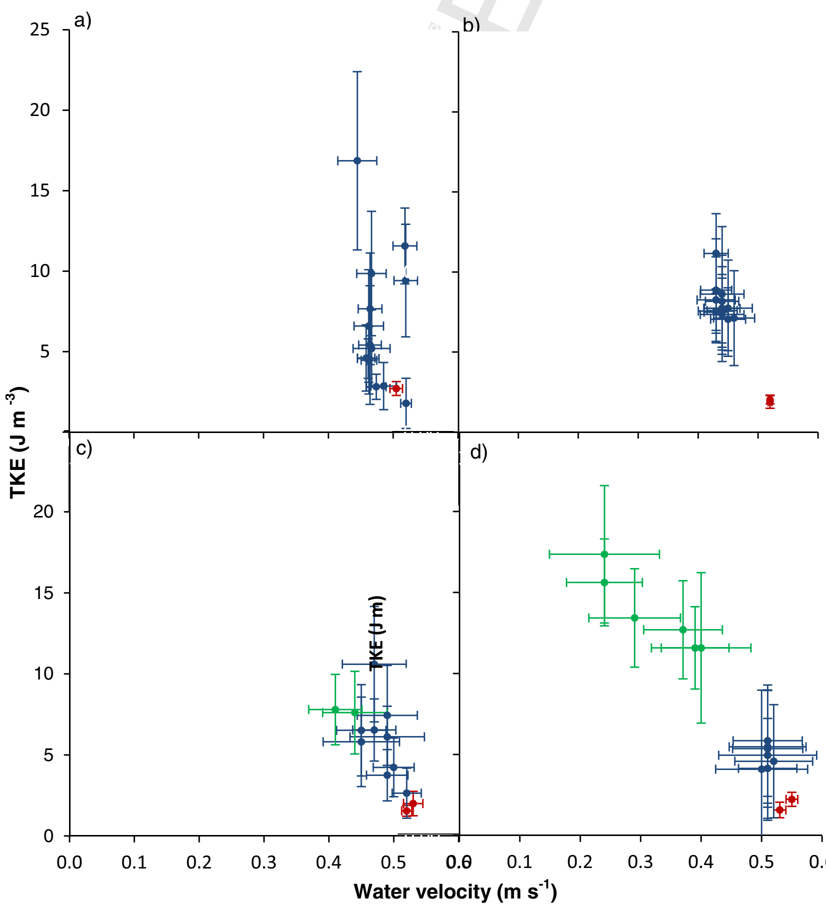

Fig. 5. Individual common carp $Fish_U$ and $Fish_{TKE}$ (points) and the standard deviation (error bars) of velocity and TKE experienced by fish that successfully swam for 30 min at $0.5\ m\ s^{-1}$ under: (a) smooth (control); (b) small (SC); (c) medium (MC); and (d) large corrugation (LC) treatments. Under MC and LC treatments fish either occupied corrugation troughs for more than (grey dots) or less than 50% (black triangles) of the trial. Under SC and control treatments trough occupation was not possible and all individuals are denoted as black triangles.

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broad locations was also apparent for fish swimming in the MC treatment (Fig 5c). In the control the range in $Fish_U$ was low, but the $Fish_{TKE}$ range was greater than the SC and MC treatments, presumably due to the high values present at the front of the test section (Fig. 2b).

4. Discussion

Corrugated culverts are often assumed to improve upstream fish passage due to the large areas of low velocity created at the walls when compared with smooth pipes (Ead et al., 2000; Barnard et al., 2013). The low velocity areas within the corrugation troughs can be utilised by small fish to rest during passage (Powers et al., 1997). Furthermore, when mid-channel velocities exceed swimming ability, fish may ascend along the area of lower velocity close to the corrugations (Clark et al., 2014). Yet contrary to the hypothesis, the swimming performance of juvenile common carp in this study was not enhanced under the different corrugation treatments tested compared to smooth walls, and some fish avoided the corrugated walls when holding station. Under the conditions presented for juvenile common carp, this study did not support the suggestion that corrugations provide the hydrodynamic conditions necessary to enhance swimming performance, and as a consequence upstream passage efficiency.

The juvenile carp frequently occupied both the medium and large corrugation troughs where velocities were between 0.1 and 0.45 $m\,s^{-1}$, compared to 0.50 $m\,s^{-1}$ in mid-channel. Although swimming at a lower velocity should improve endurance (Bainbridge, 1960; Katopodis and Gervais, 2012), neither frequency of success, nor endurance of those that failed, was influenced by treatment. In a similar experimental study, Powers et al. (1997) described the utilisation by coho salmon of areas close to a corrugated culvert wall where velocities were consistently below the limits of swimming capability. Despite this, occupying the low velocity region did not fully compensate for negative effects of higher flow as passage success was negatively related to the mean cross-section channel velocity (Powers et al., 1997). Although velocity is lower within corrugation troughs, TKE is higher here than elsewhere and may affect swimming performance and passage efficiency.

Turbulent flow is energetically costly because fish must constantly stabilise their posture and correct position (Enders et al., 2005a,b; Tritico and Cotel, 2010). This can reduce overall swimming performance (Pavlov et al., 2000; Lupandin, 2005; Tritico and Cotel, 2010) and influence microhabitat selection (Smith et al., 2005; Cotel et al., 2006). In this study, the equal swimming performance among treatments and a lack of a clear preference for low velocity zones close to the corrugated walls may have reflected a response to the higher levels of turbulence encountered here (Powers et al., 1997; Kahler and Quinn, 1998; Johnson et al., 2012). The TKE associated with corrugations was comparable to those used in previous experiments of fish swimming performance and energetic costs (e.g. Nikora et al., 2003; Enders et al., 2005a,b). The total swimming cost for juvenile Atlantic salmon (*Salmo salar*) (mass = 4.3–17.6 g) was on average 25% higher when the TKE was 14.4 compared to 6.9 $J\,m^{-3}$ ($\bar{u} = 0.23\ m\,s^{-1}$; Enders et al., 2005a,b). In the large corrugation treatment the TKE close to the wall was between 11 and 23 $J\,m^{-3}$, suggesting the cost of swimming in this area may have been elevated due to turbulent flow. It is possible that a trade-off between the energetic costs of swimming in the turbulent zones close to the corrugated walls and the higher velocity areas further away caused the observed individual variation in swimming locations and time spent occupying troughs in the MC and LC treatments.

The different hydraulic conditions experienced and lower trough occupation for failures may have reduced their probability of success. However, several fish failed to complete the trial despite exhibiting trough occupancy, particularly in the MC treatment, and $Fish_U$ was not significantly lower for successful individuals under MC and LC treatments than for failures. Unsuccessful fish tended to exhibit unsteady and erratic swimming characterised by bursts of activity in areas where velocities were higher. A stress response to the test conditions (Swanson et al., 1998) or weak swimming ability may have induced this swimming behaviour among unsuccessful fish. Therefore, it cannot be determined whether experiencing unfavourable hydraulic conditions caused early fatigue, or whether erratic behaviour caused the occupation of such conditions.

The dimensions of corrugations are positively related to the size of eddies created (Nikora et al., 2003). When eddy diameter is substantially smaller than fish length, destabilisation is less likely because forces are evenly distributed along the body (Pavlov et al., 2000; Lupandin, 2005; Tritico and Cotel, 2010). Swimming performance is reduced when eddy dimensions exceed a critical threshold, found to be greater than two thirds of body length for Perch (*Perca fluviatilis*) (Lupandin, 2005), while creek chub (*Semotilus atromaculatus*) experience body rotation and downstream displacement at eddy diameters approximately three quarters of fish length (Tritico and Cotel, 2010). The small corrugated walls in this study would have produced eddies with a smaller diameter, that exerted a lower impact on fish stability, than either of the larger corrugations. Indeed, when compared to the large corrugations, successful fish under the small corrugation treatment were found closer to the flume walls, and while not statistically significant, occupied lower water velocities, and overall the probability of success and fatigue rate was lower. Further study with different combinations of corrugation wavelength and amplitude will provide more detailed information on fish response to turbulence, to facilitate optimisation of culvert design.

In addition to the response to hydrodynamic conditions encountered, position maintenance is influenced by a structure's physical dimensions relative to fish body size. The wavelength and amplitude of corrugations and natural substrate ripples determine whether fish can occupy troughs (Gerstner, 1998; Gerstner and Webb, 1998; Nikora et al., 2003; Webb, 2006). Here, some individuals were observed to hold station within the medium and large corrugation troughs, where wavelength was similar to the mean and 1.7 times the mean TL, respectively. The bodies of most fish occupying lotic freshwater habitats are more flexible in the lateral than vertical direction due to their muscle structure (Webb, 1984). This may explain why carp could contour their bodies to allow flow refuging in wall corrugations with a wavelength similar to their body length, whereas Atlantic cod required the substratum ripple wavelength to be greater than twice their body length before exhibiting flow refuging behaviour (Gerstner, 1998; Webb, 2006).

5. Conclusion

This study provides insight into fine scale fish swimming behaviour in response to the hydraulic conditions created by corrugated walls under experimental conditions. Behaviour varied among treatments and individual fish, potentially illustrating a trade-off between the energetic benefits of swimming within low velocity zones and the costs of increased turbulence associated with corrugated walls. Compared to a smooth channel, turbulence induced by corrugations appeared to limit the benefit of the larger areas of low velocity and many fish instead occupied higher velocity areas away from the wall. Further investigation over a

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range of flows will be useful as the response to turbulence depends on velocity magnitude (Gerstner, 1998; Smith et al., 2005; Cotel et al., 2006). Furthermore, fully developed flow occurs approximately two to three diameters downstream of corrugated culvert inlets (Ead et al., 2000; Richmond et al., 2007), and corrugated walls extending upstream of the test area would create conditions more realistic of long culvert barrels. Following fine scale laboratory analysis, in situ validation of culvert passage should be conducted with naturally migrating fish through pipe culverts of varying barrel roughness. The results of the current study indicate that corrugations may not always benefit swimming performance compared to smooth channels, or provide suitable refuge areas for juvenile cyprinids during culvert ascent. Furthermore it is clear that behaviour is an important consideration in assessing and designing less environmentally damaging river infrastructure.

Q7 **Uncited references**

Belford and Gould (1989), Tritico and Hotchkiss (2005) and Zhong and Power (1996).

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