

## THE IPOS FRAMEWORK: LINKING FISH SWIMMING PERFORMANCE IN ALTERED FLOWS FROM LABORATORY EXPERIMENTS TO RIVERS

R. W. JAY LACEY<sup>a\*</sup>, VINCENT S. NEARY<sup>b</sup>, JAMES C. LIAO<sup>c</sup>, EVA C. ENDERS<sup>d</sup> and HANS M. TRITICO<sup>e</sup>

<sup>a</sup> Department of Civil Engineering, Université de Sherbrooke, 2500 boul. Université, Sherbrooke, Québec, J1K 2R1, Canada

<sup>b</sup> Energy–Water–Ecosystems Engineering, Environmental Science Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6036, USA

<sup>c</sup> Whitney Laboratory for Marine Bioscience, Department of Biology, University of Florida Gainesville, 9505 Ocean Shore Blvd, St. Augustine, FL 32080, USA

<sup>d</sup> Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6, Canada

<sup>e</sup> Department of Civil/Environmental and Chemical Engineering, Youngstown State University, 1 University Plaza, Youngstown, OH 44555, USA

### ABSTRACT

The current understanding of the effects of turbulence on the swimming performance of fish is primarily derived from laboratory experiments under pressurised flow swim tunnels and open-channel flow facilities. These studies have produced valuable information on the swimming mechanics and behaviour of fish in turbulent flow. However, laboratory studies have limited representation of the flows fish experience in nature. The flow structure in rivers is imparted primarily by the highly heterogeneous nonuniform bed, and the flow is generally much more complex than in laboratory experiments. The goal of the current work is to direct future laboratory and field studies to adopt a common framework that will shape the integration of both approaches. This article outlines four characteristics of turbulent flow, which we suggest should be evaluated when generalising results from fish turbulent studies in both the laboratory and the field. The framework is based on four turbulence characteristics that are summarised under the acronym IPOS: intensity, periodicity, orientation and scale. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS: turbulence in rivers; fishes; IPOS; swimming performance; vorticity

Received 17 September 2010; Revised 12 July 2011; Accepted 26 July 2011

### INTRODUCTION

The relationships between water flow and fish have interested researchers for centuries. Numerous studies have investigated the relationships between fish habitat preference and mean longitudinal velocity,  $\bar{u}$ , both in the laboratory and in the field (*in situ*) (e.g. Heggnes and Saltveit, 1990; Jowett and Richardson, 1995). Fish species preferences for particular velocities (i.e. habitat suitability index curves) have been published and used extensively (Bovee, 1978; Hogan and Church, 1989; Lacey and Millar, 2004). Although preference curves offer general guidelines on fish habitat suitability, they do not characterise the time varying properties of flow, which exist under natural habitat conditions (e.g. turbulent flow in rivers). Although, field studies on the effects of altered flows on fish locomotion are only recently emerging, a few laboratory studies have been undertaken, focusing on the effects of altered flows (e.g. flows past bluff bodies) and turbulence on fish abundance (Smith *et al.*, 2006), physiological costs (Enders *et al.*, 2003; Liao,

2004), behaviour (Liao *et al.*, 2003a; Smith *et al.*, 2005) and stability (Tritico and Cotel, 2010).

Turbulence is characterised by the velocity and vorticity fluctuations of all three components about a statistically steady mean. The instantaneous velocity (or vorticity) at any point, for any instant in time, can be decomposed into the mean (Reynolds-averaged) velocity and velocity fluctuation (for details, see Tennekes and Lumley, 1972). In contrast, for laminar flows, there is no departure of the instantaneous velocity from the mean velocity for a statistically steady mean flow.

Fluid parcels in which the fluctuations are correlated can broadly be defined as coherent motions and are generally thought to be a result of eddies or vortices. Examples of coherent flow structures are provided through flow visualisation and particle image velocimetry (PIV) experiments of turbulent flows (e.g. Van Dyke, 1982; Falco, 1991; Adrian *et al.*, 2000). The time scales or the duration over which turbulent eddies disrupt the steady mean flow exhibits great variation from small [i.e. Kolmogorov [temporal] micro-scale =  $\sqrt{\nu/\varepsilon}$ ] to large (i.e. convective time-scale =  $L/\bar{u}_i$ ), where  $\nu$  ( $\text{m}^2/\text{s}$ ) is the kinematic viscosity,  $\varepsilon$  ( $\text{m}^2/\text{s}^3$ ) is the energy dissipation rate per unit mass,  $L$  (m) is a characteristic length scale of the channel bounding geometry (e.g. flow depth) and  $\bar{u}_i$  (m/s) is a characteristic mean velocity (e.g.

\*Correspondence to: R. W. J. Lacey, Department of Civil Engineering, Université de Sherbrooke, 2500 boul. Université, Sherbrooke, Québec, J1K 2R1, Canada.

E-mail: Jay.Lacey@USherbrooke.ca

eddy convection velocity). The smallest scale in a turbulent flow is limited by the fluid viscosity and is estimated by the Kolmogorov (spatial) microscale,  $\eta = (v^3/\varepsilon)^{1/4}$ , whereas the largest scale is characterised by  $L$ . The Reynolds number,  $Re = \bar{u}_t L / \nu$ , which is a measure of the inertial to viscous forces acting on a fluid parcel, governs the onset of turbulence and the range of eddy sizes present in the fluid (between  $\eta$  and  $L$ ; e.g. p.102, Van Dyke, 1982).

Turbulent flow structures are defined herein as intermittent coherent motions observed in the flow. A general definition used for turbulent coherent structures is of a three-dimensional (3D) region of flow over which one varying fundamental flow variable (e.g. velocity component, temperature) exhibits significant correlation with itself or another variable over a range of space and/or time (Robinson, 1991). This definition is not fully shared by all researchers, some of whom believe that vorticity is a defining characteristic of coherent structures (Hussain, 1986). A full discussion on the definition of coherent structures is beyond the scope of this article; yet, we wish to be clear on the terminology used herein. Hereafter, coherent flow structures with vorticity will be called *eddies* (e.g. Yalin and da Silva, 2001), whereas large-scale motions that occur as intermittent fronts of high- and low-speed fluid will be called *wedges* (Roy *et al.*, 2004). Large-scale motions are suggested to be composed of packets of hairpin vortices (Kim and Adrian, 1999) and have been similarly called wedge-like flow structures by Detert *et al.* (2010).

Conflicting results on the effects of turbulence on fish swimming exist in the literature. Fish abundance has been found to increase when instream obstacles are added (van Zyll de Jong *et al.*, 1997). In addition, the number of salmonids such as rainbow trout (*Oncorhynchus mykiss*) has been positively correlated with mean turbulence values measured around obstacles (Smith *et al.*, 2006). Likewise, rainbow trout are attracted to periodic flows behind a cylinder because they decrease muscle activity (Liao, 2004). Conversely, other studies have found that salmonids avoid high-turbulence locations (Smith *et al.*, 2005), and turbulence has been shown to induce higher fish swimming costs (Enders *et al.*, 2003). This absence of consensus in studies regarding flow–fish interactions may be due to differences in the characteristics of the turbulence in the respective studies. The scale of the turbulence with respect to the scale of the fish (e.g. its length, tail-beat frequency) is likely to have varied within each study. For example, a fish may show an affinity for turbulence when its body length is close to the diameter of eddies shed from an obstacle and its tail beating frequency is close to that of the eddy shedding frequency.

Many of the recent studies investigating the effects of altered flows and turbulence on fish swimming performance have been conducted in laboratory swim tunnels and open-channel flumes (e.g. Enders *et al.*, 2003; Liao *et al.*, 2003b;

Kemp *et al.*, 2005; Smith *et al.*, 2005, 2006). Reviews of literature on the effects of turbulence on fish swimming are available by Liao (2007), Tritico (2009), Castro-Santos *et al.* (2009), Webb and Cotel (2010) and Webb *et al.* (2010). Laboratory studies often represent simplified flow environments in comparison with flows occurring in natural rivers where spatial heterogeneities of the flow are much more pronounced with broad distributions of velocity fluctuations, eddy frequencies and eddy scales. The simplified bed geometries of laboratory studies are often more related to culverts than to natural stream beds. The complex flow structure in rivers is imparted primarily by the highly heterogeneous and nonuniform bed (e.g. dunes) and planform (e.g. meanders) geometry. Natural rivers are rarely straight (over a few channel widths), being highly nonuniform in horizontal plan, cross-stream section and vertical profile. In addition, in gravel-bed rivers, the topography of the bed is composed of discrete particles of various shape, size and orientation. The conglomeration of particles creates larger-scale morphological units known as bedforms, which include medium and large boulders, pebble clusters (Tritico and Hotchkiss, 2005; Lacey and Roy, 2008) and gravel bars (Church, 2006). Large-scale bedforms such as ripples and dunes are as well omnipresent in sand-bed rivers (Kostaschuk and Church, 1993; Best, 2005). Adding to the already complex morphology of rivers are large woody debris (Roper *et al.*, 1998) and aquatic vegetation (Nepf and Vivoni, 2000; Plew *et al.*, 2008). River hydrodynamics are further complicated by large flow variability, pressure gradients, wind shear and high suspended sediment concentrations. The current article focuses on observations obtained on fish in gravel-bed rivers that can be described as second- to fourth-order streams with medium to high riverbed gradients. Little is known about the effects of turbulence on fish locomotion in a wider range of natural environments, spanning from water falls to oceans, but these environments are beyond the scope of the current article. Similarly, the presented examples are biased to salmonid species because most studies in this field are conducted on salmonids. However, it is likely that future research is heading towards a wider range of species.

Given the differences between laboratory and field environments, the generalisation of laboratory fish studies to natural environments may be tenuous. The current review outlines four characteristics of turbulent flow, which we suggest should be evaluated when generalising results from studies of fish locomotion in turbulent flow. The four turbulence characteristics are summarised under the acronym IPOS: intensity, periodicity, orientation and scale. Within this framework, turbulence characteristics in natural flows are compared with those found in the laboratory. From this comparison, the potential similarities and differences in fish swimming behaviour are discussed, including the limitations

of laboratory experiments for predicting swimming performance in the field.

In Castro-Santos *et al.* (2009), the authors proposed seven fish passage research questions. One of those questions was ‘How does turbulence structure influence swimming performance?’ Their brief review does an excellent job of defining the problem and listing commonly measured and proposed turbulence metrics. Because of the brevity of the section and the fact that the primary intent was to define their research problem, discussions of the parameters or physical mechanisms for eddy–fish interaction are not expounded. In the current article, we broaden the discussion of turbulent eddy–fish interactions by describing the physical parameters in detail, by grouping similar parameters into a coherent framework and by using this framework to indicate directions for future research and application.

### IPOS

Turbulent flow structure is often described using a multitude of metrics, which include turbulence intensity (i.e. the square root of the normal Reynolds stresses), turbulent kinetic energy (TKE), relative turbulence intensity, Reynolds shear stresses, vorticity, eddy length scale, eddy diameter, circulation, turbulent energy dissipation rate, axis of eddy orientation, direction of dominant fluctuation and energy. Such a range of variables makes direct comparison across studies and extrapolation from the laboratory to the field difficult. To discuss trends and simplify interpretation, we have grouped the different variables into one of four overarching characteristics important to understanding the interaction between fish and turbulence: intensity and Reynolds stress, predictability or periodicity, orientation and scale (IPOS; Figure 1). The authors propose the IPOS acronym as a helpful mnemonic for categorising and discussing the interaction between fish and turbulence.

#### Intensity, Reynolds stress and vorticity

The turbulence intensity,  $\overline{u_i' u_i'}$ , is a vector quantity with each component derived from the three normal Reynolds stress terms in the Reynolds-averaged Navier–Stokes equation formulated in compact tensor notation with repeated indices  $i$  and  $j = 1, 2, 3$  indicating summation:

$$\rho \frac{\partial \overline{u_i u_j}}{\partial x_j} = \rho g_i - \bar{f}_i + \frac{\partial}{\partial x_j} \left[ -p \delta_{ij} + \mu \left( \frac{\partial \overline{u_i}}{\partial x_j} + \frac{\partial \overline{u_j}}{\partial x_i} \right) - \rho \overline{u_i' u_j'} \right] \quad (1)$$

Each instantaneous velocity component  $u_i = u_1, u_2, u_3 = u, v, w$  is decomposed into its time-mean and turbulent fluctuation,  $u_i = \bar{u}_i + u_i'$  along its respective axis  $x_i = x_1, x_2, x_3 = x, y, z$ .

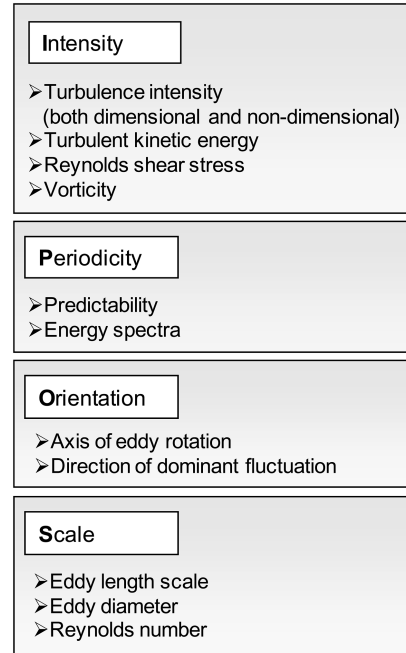


Figure 1. IPOS. A method for organising and discussing the various turbulence parameters reported in the literature.

The instantaneous velocities  $u, v, w$  are defined herein as the longitudinal, lateral and vertical velocity component, respectively.

The Reynolds-averaged Navier–Stokes equation is a statement of Newton’s second law that balances the rate change of momentum of a fluid element per unit volume by the forces per unit volume acting on the fluid element ( $\text{N/m}^3$ ). Forces on the right-hand side of the equation are, respectively, the gravitational body force, the mean drag force, the isotropic hydrostatic pressure force, the viscous stresses, which are negligible outside the viscous sublayer, and the Reynolds stresses caused by turbulence. The Reynolds stress tensor is symmetric and includes six terms, three along the diagonal that are normal stresses and three nondiagonal terms that are shear stresses.

$$\begin{bmatrix} \rho \overline{u' u'} & \rho \overline{u' v'} & \rho \overline{u' w'} \\ & \rho \overline{v' v'} & \rho \overline{v' w'} \\ & & \rho \overline{w' w'} \end{bmatrix} \quad (2)$$

The square root of the normal stresses divided by the density,  $\sqrt{\overline{u' u'}}$ ,  $\sqrt{\overline{v' v'}}$  and  $\sqrt{\overline{w' w'}}$ , are denoted alternatively in the literature as turbulence intensities, RMS,  $u_{\text{RMS}}$ ,  $v_{\text{RMS}}$  and  $w_{\text{RMS}}$ , or standard deviations of each velocity component,  $\sigma_i = \sigma_u, \sigma_v, \sigma_w$ .

Historically, the longitudinal turbulence intensity,  $\sigma_u$ , has been adopted as a measure of the amount of turbulence. This is likely a result of the limitation of one-component instruments for measuring turbulence, like hot-wire anemometers

that were used in the past (e.g. McQuivey, 1973). A second measure of turbulence at a point is the TKE, which includes all turbulence intensity components,  $TKE = 0.5 (\sigma_u^2 + \sigma_v^2 + \sigma_w^2)$ . Turbulence intensities are commonly normalised by the shear velocity,  $u_* = \sqrt{\tau_o/\rho} = \sqrt{gHS}$ , or the local longitudinal mean velocity,  $\bar{u}$  (termed relative turbulence intensity). Shear velocity, which is the velocity scale associated with the bed shear stress, can be estimated by several different methods such as from the logarithmic velocity profile or the linear Reynolds shear stress distribution (for a comparison of six different methods, see Biron *et al.*, 2004).

Nezu and Nakagawa (1993) derived semiempirical equations to describe relative turbulence intensity in the intermediate flow region, indicating a decrease in relative turbulence intensity with increasing distance from the bed:

$$\sigma_u/u_* = 2.30 \exp(-z/H) \quad (3)$$

$$\sigma_v/u_* = 1.63 \exp(-z/H) \quad (4)$$

$$\sigma_w/u_* = 1.27 \exp(-z/H) \quad (5)$$

$$TKE/u_*^2 = 4.78 \exp(-2z/H) \quad (6)$$

Equations (3)–(6) are only applicable in the intermediate region  $0.1 < z/H < 0.6$  of a fully developed turbulent boundary layer and should not be used for disrupted or developing boundary layers such as those induced by flow separation (McLean *et al.*, 1994) and/or in perturbed flows. Scaling by  $u_*$  in the wake of bluff bodies is incorrect because the flow structure is no longer influenced by the bed shear stress and the turbulent energy generation is not equal to dissipation. These equations, however, have been shown to give good predictions of measured relative turbulence intensity profiles over unobstructed smooth and rough bed open channels irrespective of Reynolds and Froude numbers (Nezu and Nakagawa, 1993). A recent comparison by Neary and Sale (2010), which includes additional high Reynolds number river turbulence measurements, supports this observation. The measurements of mean velocity and relative turbulence intensity for rivers with large Reynolds numbers compared with laboratory flumes are rare because of the difficulty of deploying hot-wire anemometers and acoustic Doppler velocimeters (ADV) in deep flows with fast currents. The data compiled and evaluated by Neary and Sale (2010) represents, to the authors knowledge, all known turbulence measurements reported to date for rivers over one meter depth, including those by Nikora and Smart (1997) and Holmes and Garcia (2008). Results are shown in Figures 2 and 3. Flow depths in this data set vary from approximately

$H = 0.5$  m to 35 m for the Mississippi River, with mean velocities ( $\bar{u}$ ) ranging from 0.5 to 3.8 m/s. Considering the challenge of accurate measurements of turbulence in large rivers as well as the difficulty in estimating the shear velocity, the comparison between measured and predicted profiles shown in Figure 2 indicates that Nezu and Nakagawa's models 3 to 5 perform fairly well in large rivers. The turbulence intensity along with velocity profiles has also been included in Figure 3.

The normalisation (or scaling) of turbulence statistics is performed to evaluate and compare values between studies under varying flow and boundary conditions (e.g. experiments with differing bed roughness) and to develop universal expressions. However, for studies investigating fish–flow interactions, it is important to consider the magnitude (i.e. dimensional values) of the turbulence experienced by fish. If studies are to be generalised to natural flows, the maximum values of turbulence should be comparable. For example, maximum turbulence levels (e.g. maximum TKE values) obtained in laboratory experiments may not be sufficient to evoke a particular behavioural response, especially for larger fish. Moreover, normalising turbulence by  $u_*$  or  $\bar{u}$  tends to obscure the magnitude of the turbulence experienced as illustrated by comparing longitudinal intensity, nondimensionalised shear velocity (Figure 2) with its the dimensionalised value Figure 3. Normalising by the shear velocity masks the effect of the longitudinal velocity and could have a marked effect on the experimental observations and conclusions. For example, the normalised turbulence intensity measured in two separate experimental setups may be quite similar, whereas the turbulence magnitudes could be of different orders. In the first studies on fish performance in turbulence, Pavlov *et al.* (2000) normalised their turbulence statistics using mean velocity ( $\sigma_u/\bar{u}$ ), making it difficult to extract the actual hydraulic conditions fish were experiencing during the experiments.

Several recent laboratory studies performed on fish in altered flows have presented dimensional TKE, providing good comparisons with *in situ* turbulence values measured behind obstacles in gravel-bed rivers. Smith *et al.* (2005) investigated the hydraulic characteristics associated with the focal position of juvenile rainbow trout behind obstacles in a laboratory flume. At a low flow, the intensity of the turbulence (measured by TKE) did not seem to influence the holding position of the juvenile rainbow trout. At a higher flow, although the statistical significance was low, there was a tendency for fish to prefer locations of lower TKE. The study by Smith *et al.* (2005) suggests that a minimum turbulence intensity threshold is required to trigger a particular behavioural response. The maximum magnitude of TKE in the Smith *et al.* (2005) experiments (for the high flow) was  $0.016 \text{ m}^2/\text{s}^2$ . This TKE value is almost 10 times lower than *in situ* TKE values observed by Tritico and Hotchkiss

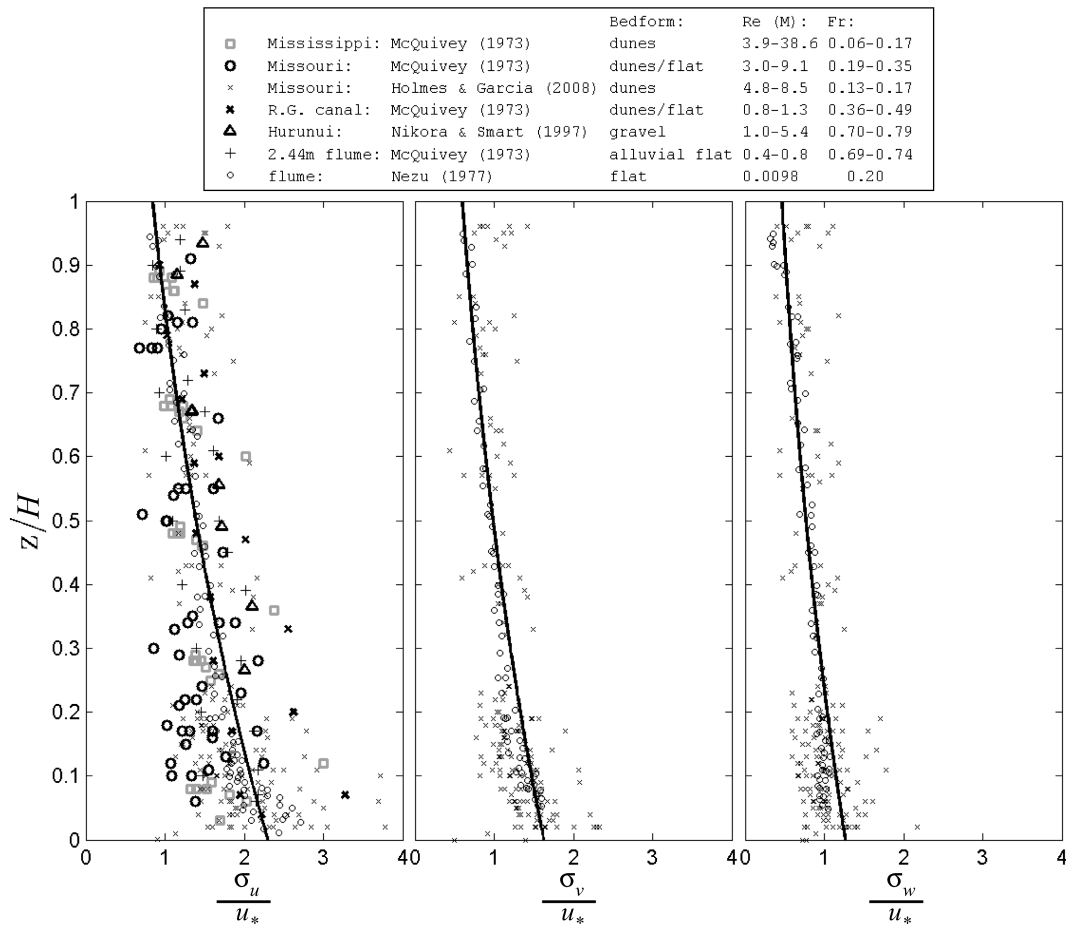


Figure 2. Comparison of field and laboratory relative turbulent intensities with semiempirical curves (Equations (1)–(3)) (borrowed with permission from Neary and Sale, 2010).

(2005) behind a surface protruding boulder in a gravel-bed river (where  $TKE > 0.08 \text{ m}^2/\text{s}^2$  was reported). Similarly, Lacey and Roy (2008) observed  $TKE > 0.06 \text{ m}^2/\text{s}^2$  behind a submerged pebble cluster in a gravel-bed river. The TKE values obtained from these two separate field studies were measured at channel flow depths much less than bankfull. Consequently, they represent a conservative estimate on turbulence levels in the wake of obstacles. Thus, turbulence levels in the natural rivers are likely to far exceed those in the Smith *et al.* (2005) experiments.

Nikora *et al.* (2003) present a laboratory flume study comparing the time to fatigue of inanga (*Galaxias maculatus*) under varying turbulent flow conditions. Turbulence was generated using corrugated plastic sheets placed on the side walls of the flume. The results showed that the turbulence did not affect the time to fatigue of the fish tested. Nikora *et al.* (2003) suggested that the small length scale of the generated turbulence was likely a leading factor in the lack of correlation between the time to fatigue and the intensity of the turbulence. The maximum

magnitude of TKE observed in their experiments was less than  $TKE = 0.008 \text{ m}^2/\text{s}^2$ , which may not have been sufficient to illicit a response in the fish. Under natural conditions, the fish may experience much higher values of TKE (as discussed earlier).

Reynolds shear stresses (i.e.  $-\rho\overline{u'v'}$ ,  $-\rho\overline{v'w'}$  and  $-\rho\overline{u'w'}$ ) represent the turbulent flux of momentum within the fluid, which is related to force by Newton's second law. Given their physical importance, Reynolds shear stresses should affect fish swimming performance and holding position. The comparison of Re shear stresses between laboratory fish experiments and *in situ* conditions is difficult because Re shear stresses in fish experiments are seldom reported. An exception is the laboratory flume study of Smith *et al.* (2005) who do report Re shear stresses. Maximum values of  $-\rho\overline{u'v'}$  and  $-\rho\overline{u'w'}$  were 4.9 and 2.1  $\text{N}/\text{m}^2$ , respectively (from Smith *et al.*, 2005, with corrections by D.L. Smith 2010, personal communication). These Re shear stresses are approximately 10 times less than those reported by *in situ* studies investigating flow in the wake of cobbles and boulders (Tritico

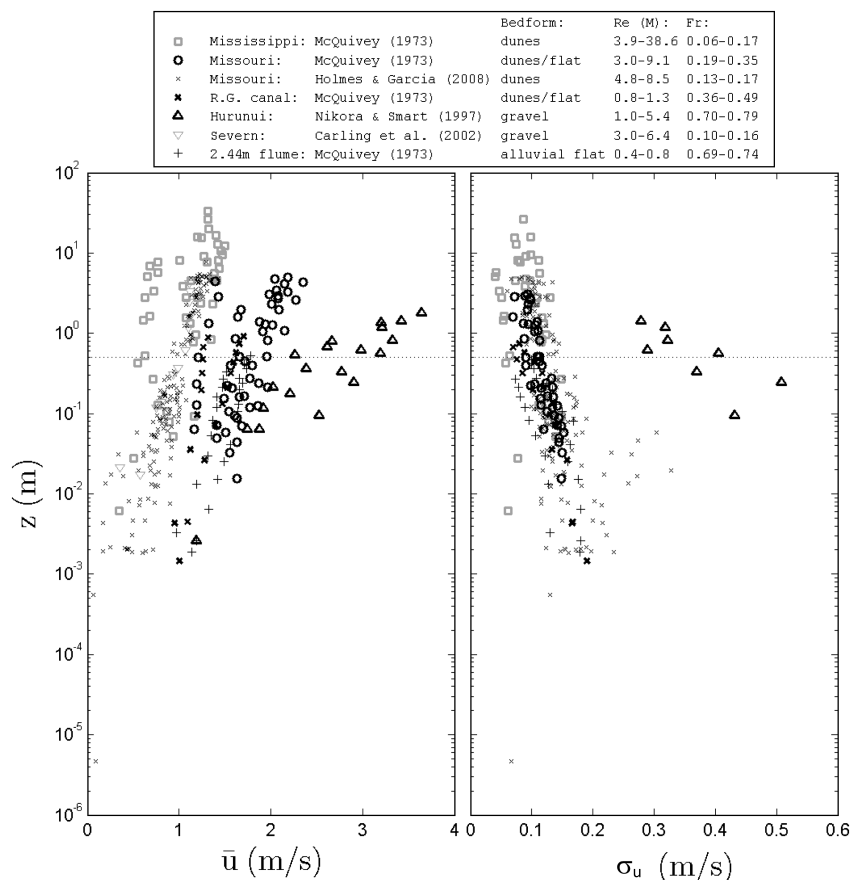


Figure 3. (A) Mean longitudinal velocity profiles. (B) Longitudinal turbulence intensity profiles. The dashed horizontal line indicates  $z = 0.5$  m (borrowed with permission from Neary and Sale, 2010).

and Hotchkiss, 2005; Lacey and Roy, 2008). Smith *et al.* (2005) observed negative correlations between juvenile rainbow trout focal positions and  $-\rho\overline{u'w'}$  and no significant correlations between focal positions and  $-\rho\overline{u'v'}$ . This indicates a distinction between the two (lateral and vertical) momentum fluxes and suggests that higher values of  $-\rho\overline{u'v'}$  can be tolerated by fish. This point is likely related to the orientation of eddies shedding from the obstacles in the Smith *et al.* (2005) experiments (the implication of eddy orientation is discussed further in the Orientation section). The lack of correlation between lateral momentum flux and fish focal position is unexpected and could be because the maximum values of  $-\rho\overline{u'v'}$  achieved in the experiments of Smith *et al.* (2005) were not beyond a specific threshold required to illicit a behavioural response in the fish.

Vorticity, being twice the angular velocity, describes how fast a region of fluid is spinning. The faster an eddy spins, the more likely it is to spin an object that it interacts with. Experiments by Tritico and Cotel (2010) demonstrated that eddies with low vorticity had no measurable effect on the stability of fish, whereas eddies with high vorticity resulted in rapid body rotations. The occurrence of these

rapid body rotations (termed spills) increased with increasing vorticity. Vorticity, like turbulence intensity and TKE, is a measure of the strength of fluid motion and does not account for the scale (or volume of water) that the motion occurs over. Tritico *et al.* (2007) reported *in situ* instantaneous vorticity measurements using PIV in the Huron River, Michigan, up to  $9 \text{ s}^{-1}$ . Vorticity data for laboratory experiments and computer models is much more complete (Meynart and Lourenco, 1984; Adrian, 1986; Meneveau and Katz, 2000; Raffel *et al.*, 2007). The vorticity measurements of boundary layer vorticity in the laboratory often exceed  $40 \text{ s}^{-1}$  (White *et al.*, 2004), and the maximum vorticity reproducible in the laboratory is primarily governed by the maximum flume velocity. This indicates that as long as velocities in the laboratory are similar to the field conditions, vorticity magnitudes should be comparable.

The previous discussion indicates that turbulence intensity, TKE and Reynolds shear stress are likely to increase *in situ*, whereas the vorticity measurements of submerged eddies in rivers have not been fully investigated. Following laboratory results, this increase in turbulence should promote increases in energy expenditures (Enders *et al.*, 2003)

devoted to hydrostatic and kinetic stability, thrust, propulsion and control of swimming trajectory (Webb, 2002). The exploitation (e.g. vortex capture) and the avoidance responses of fishes may differ substantially because of the increased turbulence fluctuations, and care should therefore be taken when generalising laboratory results in rivers.

#### Periodicity (predictability)

Liao *et al.* (2003a) reported reduced energy use in the presence of turbulence, whereas Enders *et al.* (2003) and Tritico and Cotel (2010) reported increased energy use in the presence of turbulence. This apparent conflict of results in the literature may be due to differences in the periodicity of the flows that the fish were exposed to. In the Liao *et al.* (2003a) laboratory experiments, rainbow trout were swimming downstream from a single vertical D-section cylinder used to promote steady vortex shedding. The flow upstream from the cylinder was very nearly rectilinear, and the effect of the cylinder was to produce a metronomic vortex shedding (Figure 4a). In this flow field, the fish were observed to adjust their gait to synchronise and take advantage of the alternating eddies in the flow. This predictable vortex shedding pattern is in contrast to the randomly generated pulsed flows of Enders *et al.* (2003) and the chaotic wakes produced downstream from the cylinder arrays of Tritico and Cotel (2010). It is likely that the lack of a single dominant frequency in these flows impeded rather than enhanced swimming performance. Although fish have been shown to adjust their gait in periodic flows, the swimming pattern of fish in nonperiodic flows is difficult to predict (Figure 4b).

The period of a sinusoidal signal (or waveform) is defined as the time over which the signal completes one cycle. For

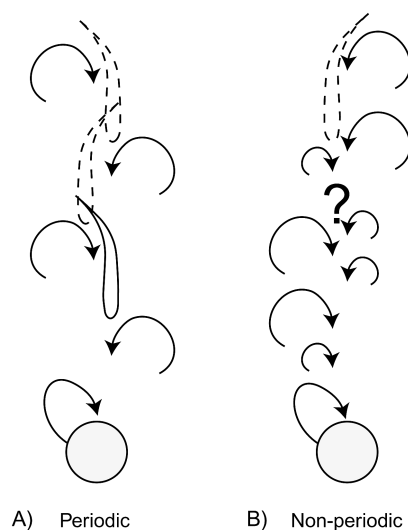


Figure 4. Schematic (plan view) of fish behaviour downstream of A) periodic and B) nonperiodic eddies shed from an upstream obstacle.

a waveform, the period is the inverse of the frequency ( $T = 1/f$ ). Velocity time series, measured in the wake of bluff bodies (such as cylinders) at low particle Reynolds numbers ( $Re_D = 40-150$ ), display a distinct 'stable' periodic laminar shedding regime (Williamson, 1996);  $Re_D$  is the particle Reynolds number  $Re_D = \bar{u}D/\nu$ , where  $D$  is the body diameter. As  $Re_D$  increases ( $Re_D = 300-10^4+$ ), the velocity fluctuations show distinct irregularities (Williamson, 1996). This is supported by Blevins (1990), who suggested that vortex shedding from a stationary cylinder at higher  $Re_D$  does not occur at a single distinct frequency but rather wanders over a narrow band of frequencies with a range of amplitudes. Reasons for the irregularities in the shedding frequency may be due to the instabilities induced in the wake, which are magnified in higher  $Re_D$  flows and/or the interactions between initial shear layer vortices as they advect downstream. These interactions include merging and pairing (as well as fluid entrainment) and the amalgamation of vortices gives rise to secondary structures, which advect downstream (Fuchs *et al.*, 1980; Hasan, 1992; Williamson, 1996).

Spectral analysis through Fourier transforms is commonly used to analyse turbulent flows, and its application can be found in standard turbulence texts (e.g. McComb, 1990). The spectral analysis of velocity time series can give accurate estimations of shedding frequency, provided the instantaneous velocities are sinusoidal, are measured within the shear layer and the signal is not disrupted by surrounding flow patterns (as in the laboratory experiments of Achenbach, 1974). Although spectral analysis is a useful technique for identifying structure in a time series, the technique can only identify a structure that is periodic or linear (Rubin and McDonald, 1995). If eddies are shed over a range of frequencies or if the structures evolve through deformations or interactions with each other, the spectral signal will give a much broader lower amplitude peak over a range of frequencies. Rubin and McDonald (1995) have shown how nonperiodicity is introduced downstream of bluff bodies when placed in proximity to (or against) a bounding wall (instead of being centred in the flow). The authors performed a series of experiments investigating the effect of wall boundaries on object shedding frequencies. In small-scale flume experiments, Rubin and McDonald (1995) were able to demonstrate that for an object with a wake showing evident periodicity (while centred in the flow), when the object was placed against a plate (or the wall boundaries) the wake became nonperiodic. Rubin and McDonald (1995) as well performed larger-scale experiments with a lateral obstruction in a wide flume (4 m wide) and showed that the power spectrum displayed a relatively broad peak for signals obtained very close to the separation point. Velocity time series obtained from locations further away from the separation point (at the reattachment point of the boundary layer) displayed no significant peak at all. The

study by Rhoads and Sukhodolov (2004) illustrated the difficulty of obtaining a clear shedding frequency in a river environment at high Reynolds numbers  $Re$ . Spectra were estimated from ADV measurements within a confluence shear layer ( $Re \approx 10^5$ ). Tracer visualisation identified shedding structures with vertical axis vorticity, yet no distinct peak could be observed in the power spectra over an anticipated range of  $f=0.1$  Hz to 1.0 Hz.

An alternative approach to spectral analysis involves the decomposition of the velocity signal using wavelet transforms instead of Fourier transforms (detailed explanation is given by Torrence and Compo, 1998). The appropriateness of wavelet analysis for turbulence studies was shown two decades ago (e.g. Farge, 1992), but it remains an uncommon technique compared with standard Fourier transforms. Wavelet analysis is most appropriate for identifying intermittent processes where the scales of variability evolve temporally and spatially as a function of time (or space) (Hardy *et al.*, 2009). Unlike Fourier transforms, wavelet analysis produces scale-dependent power values for a set of locations in time over a range of frequencies. As such, shedding structures in the wake of obstacles, which are intermittent and evolving in time and space, should be much better characterised using wavelet transforms. Recent studies have used wavelet analysis to identify shedding structures both in laboratory and in field studies (Rinoshika and Zhou, 2005; Hardy *et al.*, 2009).

The characteristics of the upstream velocity field are as well important when comparing and transferring the results from controlled laboratory flume studies to natural rivers. Becker *et al.* (2002) investigated the flow structure in the wake of a bed mounted cube under both a uniform velocity distribution and one due to a simulated boundary layer. Although the authors were able to observe a peak in the velocity spectra under the uniform velocity condition, the wake became nonperiodic when the boundary layer was simulated. This result, although little explored in the literature, has significant ramifications for the comparison of laboratory and field studies as many laboratory flumes, which are used to investigate flow structures with or without fish, are often of insufficient length to allow for the full development of a turbulent boundary layer (which is omnipresent in natural rivers). Studies have found that over smooth boundaries, the longitudinal distance required for the development of a turbulent boundary layer, which extends to the free surface, is greater than 50 times the flow depth (Kirkgoz and Ardiclioglu, 1999).

Although the predictability of the shedding eddies likely affects fish swimming performance, the affinity of fish for shedding eddies must as well depend on the shedding frequency. Periodic shedding frequencies from bluff bodies can be predicted in theory using the nondimensional Strouhal number  $St=fD/\bar{u}$ , where  $f$  is the frequency of vortex shedding.  $St$  is a function of  $Re_D$ , and controlled

laboratory experiments have shown that  $St$  is typically between  $St=0.13$  and  $0.21$  over a large range of  $Re_D$  ( $6000 < Re_D < 3 \times 10^5$ ) (Achenbach, 1974). Moreover, a mean value of  $St=0.2$  is suggested by Tritton (1988) for various shaped bluff bodies. Although the Strouhal number is commonly applied to predict shedding frequencies in bluff-body laboratory experiments (e.g. Acarlar and Smith, 1987; Nakamura, 1996), accurate predictions of shedding frequency using  $St$  in natural flows have been mixed. The study by Tritton and Hotchkiss (2005) found 10 times difference between predicted and observed shedding frequencies ( $St=0.2$ ), whereas the predicted shedding frequency in a study by Lacey and Roy (2007) compared favorably ( $St=0.18$ ). Venditti and Bauer (2005) presented a summary table of  $St$  estimated from laboratory and field studies in the lee of bedforms where values ranged from  $St=0.1$  to  $0.25$ . Given the differences in  $St$  obtained in various field studies, it is not clear whether a universal  $St$  can be applied to natural flows. Yet, under most situations, it seems to offer an order of magnitude estimate of the mean shedding frequency.

The previous examples highlight four important issues related to the predictability of eddies shed from bluff bodies and the transferability of results from the laboratory to the field:

- (1) With increasing particle Reynolds numbers, the strict periodicity of the shedding eddies decreases.  $Re_D$  in rivers can be orders of magnitude larger than those on which laboratory experiments are based. At higher  $Re_D$ , the velocity signal becomes nonperiodic a short distance away from the obstacle (e.g. at the point of reattachment) because of the interactions between the shedding vortices and the entrainment of surrounding fluid.
- (2) Bluff bodies placed against a wall (such as a cylinder lying flat) may display a nonperiodic signal compared with when the cylinder is centred in the flow.
- (3) The upstream velocity distribution can have a significant effect on the periodicity or nonperiodicity of the wake and the turbulence structure.
- (4) Spectral analysis using wavelet transforms is likely more appropriate for characterising the properties of wake shedding eddies.

Rivers are complex environments where eddies across many scales are shed from (i) individual particles making up the riverbed, (ii) larger bedforms and (iii) macroscale channel morphology (see Nikora, 2008). It is likely that these background eddies would interact with the structures in the wake of individual objects enhancing nonperiodicity within the shear layer.

#### Orientation

In the same way that the relative orientation of the mean flow will affect the drag and swimming performance of a



fish, the orientation of the unsteady eddies affects the ability of a fish to hold position. Eddies with sufficiently high vorticity can disorient fish causing it to pitch, roll or yaw and lose position. Longitudinal intermittent fronts of high- and low-speed fluid (wedges) on the other hand will cause the fish to surge upstream or downstream (Enders *et al.*, 2003), whereas other wedge orientations are expected to induce vertical or transverse wobbling (Cotel and Webb, 2004). Because of the differences in cross-sectional body shape in each of the orthogonal planes, it is expected that velocity fluctuations that act in a plane with low surface area will result in lower resultant forces. For most stream-dwelling fishes, the smallest projected area, and therefore the least anticipated effect of turbulence, will occur in the longitudinal (surge) direction. Laterally compressed fishes will experience the largest resultant forces in the transverse direction and fusiform shaped fishes will experience relatively equal forces in the transverse and vertical directions (Webb 2002). Body shape and flexibility, along with fin distribution, are not radially symmetric (Webb *et al.*, 1996; Schrank *et al.*, 1999). Tritico and Cotel (2010) found that creek chub (*Semotilus atromaculatus*) experiencing vertically oriented eddies were influenced less often and recovered more quickly than fish swimming in large horizontally oriented eddies (Figure 5). In fact, fish that lost postural alignment in a turbulent flow field dominated by horizontal eddies often rolled onto their side to use the caudal fin as a control surface for quick reorientation to the flow. We predict that rainbow trout cannot Kármán gait (Liao *et al.*, 2003a) behind horizontal cylinder because of the small caudal fin surface area in the frontal plane and the reduced ventral–dorsal flexibility (Figure 5).

Eddies and wedges in rivers tend to be complex 3D structures, and at any given instream location, a wide range of eddy orientations likely exists. This complexity will likely shroud the effects of orientation in future field results, except for regions clearly dominated by a simple geometric obstruction such as a those directly downstream from a protruding boulder (Tritico and Hotchkiss, 2005).

### Scale

As previously discussed, turbulent coherent structures in rivers range from the Kolmogorov microscale (on the order of 0.1 mm) to many times the river depth (Roy *et al.*, 2004; Nikora, 2010). Although fish residing in rivers experience thousands of eddies and wedges per day, it is likely that only a fraction will have the specific characteristics (e.g. orientation, scale) to affect the fish's ability to hold position in the water column (Pavlov *et al.*, 2000; Cada and Odeh, 2001; Nikora *et al.*, 2003; Lupandin, 2005; Liao, 2007; Tritico and Cotel, 2010).

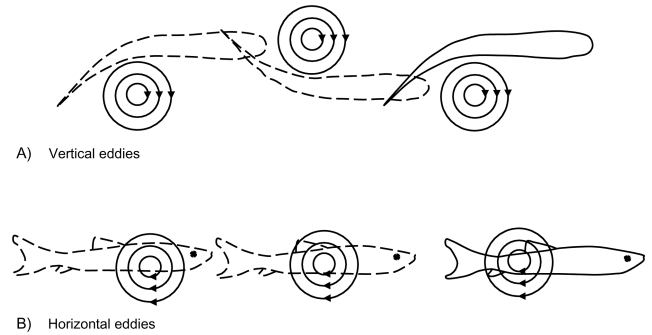


Figure 5. Schematic showing the effect of eddy orientation on fish swimming behaviour. A) Plan view—vertically oriented eddies enabling Kármán gait in fish. B) Side view—horizontal eddies where the eddy axis of rotation is perpendicular to the dominant bending morphology of the fish; therefore, Kármán gait is not expected.

The most commonly calculated turbulent length scale in rivers is the correlation length or integral length scale ( $L_u$ ) (Lupandin, 2005; Lacey and Roy, 2007). This scale, also often called the *eddy length scale*, is a measure of the spatial extent over which a region of fluid is correlated and is therefore a better indicator of the scale of wedges in a river. The most commonly reported metric for eddies in the laboratory is the eddy diameter (Drucker and Lauder, 1999; Tritico and Cotel, 2010), which is a measure of the spatial extent of the rotating fluid. When the scale of eddies is small compared with the fish scale (fish length,  $L_f$ ), they lack the momentum required to affect the fish (Tritico, 2009; Figure 6a).

A wedge with a convection velocity,  $u_e$ , will have a momentum proportionate to  $\rho L_u^3 u_e$ , where  $\rho$  is the water density. A fish encountering this wedge will have a momentum proportionate to  $\rho L_f^3 u_f$ , where  $u_f$  is the fish velocity. The ratio of the wedge momentum to the fish momentum is therefore

$$\frac{\text{Wedge momentum}}{\text{Fish momentum}} \sim \left(\frac{L_u}{L_f}\right)^3 \cdot \frac{u_e}{u_f} \quad (5)$$

The first term in this momentum ratio ( $L_u/L_f$ ) is the relative scale of the wedge to that of the fish. For example, a wedge with a relative length scale one fourth the fish length will have momentum on the order of 1/64th the fish's momentum and is not likely to affect the swimming performance of the affected fish (Figure 6a). This analysis also holds for eddies. For instance, Cada and Odeh (2001) hypothesised that eddies with small diameters relative to the fish length will not provide sufficient torque to destabilise a fish. Tritico and Cotel (2010) demonstrated that when the largest eddies in a turbulent flow reach approximately three fourth of the fish length, creek chub had difficulty maintaining posture in the flow and their critical swimming

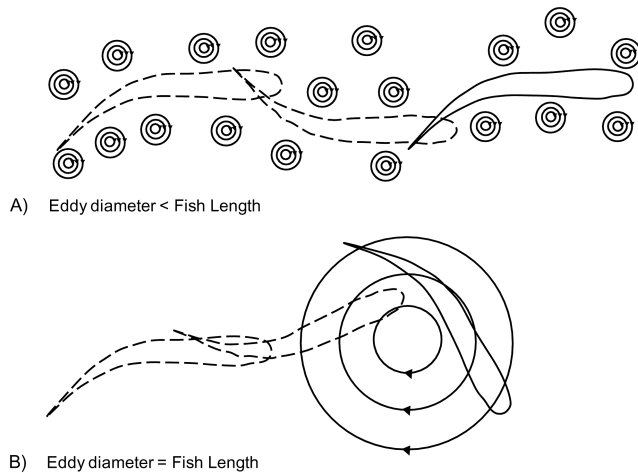


Figure 6. Schematic (plan view) illustrating the effect of eddy scale on fish behaviour. A) Smaller scale eddies showing a minimal effect. B) Larger-scale eddy shown to influence the swimming pattern of the fish.

speed was reduced by 20% (Figure 6b). Pavlov *et al.* (2000) and Lupandin (2005) showed that when wedges reach two third of the fish length, swimming performance begins to decrease.

Liao *et al.* (2003a) showed empirically that in a flow field composed of large eddies with a predictable pattern fish dramatically changed their swimming kinematics and reduced their muscle activity compared with station holding in the water column of a uniform flow. In particular, the propagating wave of axial red muscle activity was replaced by a novel pattern of anterior muscle activity (Liao, 2004). Altering vortex shedding frequencies and spacing revealed that the major predictor for fish exploiting Kármán street vortices in the laboratory is that the ratio of fish length to cylinder diameter approach 1:2. These findings underscore the importance of scale in dictating the potential of eddies to affect swimming performance either positively or negatively.

Before the investigations discussed earlier, most laboratory work on position holding in the water column was conducted in swim tunnels with upstream flow straightening grids (Brett, 1963; Webb *et al.*, 1984). These grids were designed to provide quasi-rectilinear flow and produced eddies that were on the order of the grid size, which is often less than a centimeter. Therefore, although most of laboratory swimming capacity tests are applicable to environments where the maximum length scale is on the order of a centimeter, they do not accurately represent most fluvial environments. The largest wedges in a river tend to scale with the river depth (Roy *et al.*, 2004). The largest flumes used to analyse the swimming performance of fish have depths on the order of a couple meters. Consequently, even these flumes are unable to reproduce wedge scales associated with most major rivers.

Cada and Odeh (2001) theorised that there is another length scale threshold above which the effect of eddies and/or wedges decreases. It is hypothesised that these large eddies act like secondary currents temporarily adjusting the orientation of the mean flow but not requiring active stabilisation or substantial acceleration/deceleration. This upper threshold has not yet been explored.

The importance of scale is therefore to determine whether an eddy and/or wedge have the ability to affect the fish's swimming performance. The magnitude of this effect, and whether it is beneficial or detrimental to the fish, will depend on the intensity, predictability and orientation of the eddy and/or wedge.

## PROSPECTUS AND CONCLUSIONS

The morphological and hydrodynamic complexity of natural rivers provides challenges and opportunities for fish, including the avoidance and utilisation of turbulence associated with vortical flows. Swimming mechanics and fish physiology have mainly been observed for laboratory flume studies in which vortices are experimentally generated, for example, around a cylinder (for a review, see Liao, 2007), but field studies quantifying behavioural responses to turbulence are quickly emerging (Enders *et al.*, 2005; Cotel *et al.*, 2006; Enders *et al.*, 2009).

Turbulence intensity, periodicity, orientation and scale may differ markedly between laboratory and natural channels, and these parameters need to be considered when conducting fish-hydraulics experiments. The relative turbulence intensities (scaled with  $u^*$ ) of larger rivers with Reynolds numbers much higher than laboratory flumes are shown to compare favorably with semiempirical curves originating from laboratory studies in open channels. The field measurements in rivers presented in Figures 2 and 3, however, are limited to reaches where more complex 3D effects (e.g. secondary currents) and vortex shedding from bluff bodies (e.g. boulders) are not present and so do not represent the full range of turbulence conditions found in fish habitats. Turbulence intensities, TKE and Reynolds shear stresses that have not been made dimensionless in rivers are generally larger than those of laboratory flumes and therefore care should be taken in flume experiments to ensure certain minimum thresholds of turbulence are achieved to evoke a swimming behaviour in experimental fish.

Determining the effect of a particular turbulence variable on fish swimming performance or habitat use in the field is challenging because swimming mechanics and habitat choices may be associated with multiple, correlated variables. For example, food availability is correlated with local water velocity, which is, in turn, often correlated with TKE. Consequently, it is

difficult to separate the effects of individual variables on fish behaviour in the field.

In contrast, the power of laboratory studies is to be able to isolate and identify mechanisms by which fish interact with turbulent eddies and wedges. The experimental control and level of technology required for this analysis is currently out of reach for studies conducted in the field. However, current laboratory studies do not encompass the full hydrodynamic complexity of natural flow environments. How do we maintain the strengths of laboratory experiments and field observations while beginning the process of integrating the two approaches?

Steps can be taken to introduce more complexity into the experimental setup in the laboratory, without relinquishing the ability to control variables and decipher mechanisms and limitations of fish swimming physiology and behaviour under turbulent conditions. Likewise, field studies can benefit from more rigorous approaches to analysing organismal behaviour and focus on the key variables of biologically relevant flows. Below, we provide recommendations for laboratory and field studies to bridge the gap in the context of the IPOS framework.

#### Laboratory experiments

- (1) Future fish experiments in laboratories should measure and report turbulence metrics that have not been made dimensionless so that comparisons can be made with rivers and streams. Such metrics include Reynolds shear stresses, TKE and vorticity. When designing the experimental setup of laboratory studies which are to represent natural conditions, researchers should strive to use roughness elements to simulate the topography of natural riverbeds. Ideally (although generally difficult to achieve), experiments should be performed in flumes that are long enough to allow for the full development of a turbulent boundary layer (channel length  $L \geq 50 \times H$ ) and are wide enough to avoid effects from secondary currents (channel width  $W \geq 5 \times H$ ). We recognise that these dimensions are impractical for single-use laboratories, but multiuse facilities can provide this much needed resource. The use of wide flumes will diminish wall effects that confine wake development and vortex shedding downstream of the bluff body. More studies are needed in which the physiological and behavioural responses of fishes (kinematics, positional preference to vortex-shedding structures, muscle activity, oxygen consumption and lateral line ablation experiments) are determined over a range of turbulence levels.
- (2) Further research is needed on the effect of nonperiodic turbulence signatures on fish swimming performance (i.e. move away from vortex streets shed from isolated, simple, geometric bluff bodies) that more closely emulate the diversity of natural turbulence arising from physical habitat complexity. Wavelet analysis promises to be a more appropriate technique to investigate the nonperiodic turbulence signatures.
- (3) Controlling the orientation of vortices in laboratory experiments will allow the determination of the axes of stability for fish. Insight can also be gained from comparative experiments with fishes with differing body morphology. In addition, this information is crucial to understand how species in a natural ecosystem partition spatial habitat resources.
- (4) Altering the diameter (and frequency) of eddies will test the range of beneficial to detrimental turbulence conditions. This is especially important for larger adult fish and requires the facilities of a large flume capable of high velocity flow.
- (5) Developing sensors that mimic the size, shape and flexibility of the fish and its lateral line would allow us to more accurately determine what flow parameters fish can detect.

#### Field studies

- (1) One of the main challenges of analysing the effect of turbulence on fish in a natural environment is the difficulty to obtain precise fish positions and the corresponding measurements of the turbulence. More effort is needed to measure the appropriate turbulent flow variables and scales.
- (2) The field measurements of turbulence are presently limited to ADVs or profiling ADVs that provide a measurement at a point or a profile of approximately 3 cm at sufficient sampling frequencies (25–200 Hz) to resolve the production and most of the inertial subrange of the spectral energy distribution. Such instruments, in contrast to PIV, make it very difficult to measure complex vortex shedding from instream structures such as boulders. They also cannot adequately characterise the flow field around a fish over small and large spatial scales. (However, they could, if accurately positioned, provide sufficient sampling frequency to resolve short time scales associated with burst swimming and tail beating frequencies of fish). These limitations of field sampling may be alleviated in the future using multiple synchronised ADV clusters and/or profiling ADVs and *in situ* PIV systems (e.g. Bertuccioli *et al.*, 1999; Tritico *et al.*, 2007; Katija and Dabiri, 2008), which are in development. A theoretical deployment of an *in situ* PIV system is presented in Figure 7 and illustrates how wedges could be quantified *in situ*. Further difficulties arise with the deployment of current velocimetry techniques such as ADVs in large rivers at large depths and

fast currents (e.g. DeMoyer and Vermeyen, 2007). The vortex-induced vibration of the mount and probe stem can introduce significant measurement errors in fast currents.

- (3) More importantly, and much more difficult, is the need to measure relevant and quantifiable aspects of fish behaviour so that they can be compared across studies. At the simplest level, this would be quantitative observational data on fish spatial position related to their preference. There are now inexpensive commercial high-speed cameras that can be used to collect high-resolution images to quantify swimming kinematics, which can be compared with a large laboratory data set. More informative would be to measure muscle activity in natural flows to understand the energetic demands of different turbulent flow environments. The most direct assessment of fish swimming costs is to measure its oxygen consumption, but this can only be accomplished in sealed respirometers of relative small water volume.
- (4) Finally, we suggest that future research should focus on a wider range of species with different perceptions of turbulence, body morphologies and consequently swimming capacities (Webb and Cotel, 2010).

As more tools for physiological analysis develop for the field, our goal to understand fish behaviour in turbulent flow conditions will advance considerably. In the interim, and while laboratory work continues, bringing laboratory and field experiments together under a common language is a vital first step.

#### *Are we measuring the right thing?*

More than a decade ago, the guidelines of fish passage suggested that fish avoid high turbulence areas and that energy

dissipation factor (EDF) should be kept low (Bell, 1990). Turbulence when considered was either calculated using EDF or was measured using turbulence intensity metrics. We now know that the intensity of turbulence is only one part of the interaction between fish and eddies and studies linking EDF to fish passage remain absent from the literature. Instead, this article proposes a suite of metrics that must be considered: intensity, scale, orientation and periodicity of eddies. These four additional parameters promise to shed new light on the interaction between fish passage success and turbulence. It is, however, unlikely that practitioners will increase the number of parameters they measure and design for by four without demonstrations of clear benefits to fish passage. To determine whether the consideration of four new design criteria will significantly improve passage efficiency, new research in fishways will be needed. Experiments that evaluate classic fishways for passage efficiency under standard conditions and conditions where turbulence parameters have been accounted for would begin to address the magnitude of effect turbulence has on passage efficiency.

In an effort to reduce the number of parameters to be measured, there have been various calls for combining intensity and scale metrics (e.g. spatially averaged turbulent intensity: Evans *et al.*, 1999; circulation: Crowder and Diplas, 2000; angular momentum: Tritico, 2009; and angular impulse: Castro-Santos *et al.*, 2009). Reducing the number of required measurement/design parameters will reduce complexity and make it more likely that turbulence will be considered in future designs or retrofits. Future research is warranted to determine which of the parameters is most important to fish passage and whether a single metric is appropriate under all scenarios.

#### ACKNOWLEDGEMENTS

The authors are grateful to Dr. Ted Castro-Santos and an anonymous reviewer for providing thorough and thoughtful reviews, which significantly improved this manuscript.

#### NOTATION

$D$	= cylinder (or bluff-body) diameter, m
$Fr$	= Froude number, $Fr = \bar{u}/\sqrt{gH}$
$f$	= shedding frequency, $s^{-1}$
$\bar{f}$	= body force per unit volume of fluid, N/m <sup>3</sup>
$g$	= gravitational acceleration constant, m/s <sup>2</sup>
$H$	= local water depth, m
$k_s$	= characteristic roughness length scale, m
$L_u$	= integral length scale, m
$L_f$	= fish length, m

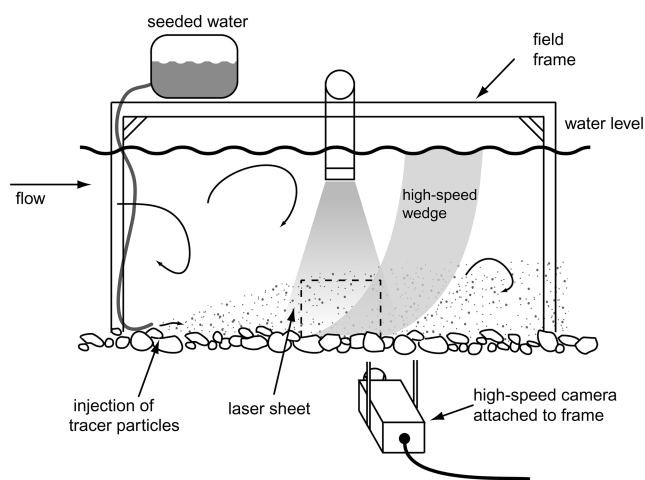


Figure 7. Schematic of *in situ* PIV.

$p$  = isotropic hydrostatic pressure force,  $\text{N/m}^2$   
 $\text{Re}$  = Reynolds number,  $\text{Re} = \bar{u}_i L / \nu$   
 $\text{St}$  = Strouhal number,  $\text{St} = fD / \bar{u}$   
 $S$  = bed slope  
 $T$  = wave period, s  
 $u_*$  = shear velocity,  $\sqrt{\tau_o / \rho}$ , m/s  
 $u, v$  and  $w$  = instantaneous longitudinal, lateral and vertical velocities, respectively, m/s  
 $\bar{u}, \bar{v}, \bar{w}$  = time-averaged velocities, m/s  
 $u', v', w'$  = instantaneous fluctuating velocities, m/s  
 $\sqrt{u'u'}, \sqrt{v'v'}, \sqrt{w'w'}$  =  $\sigma_i$  = standard deviation of velocities, m/s  
 $u_e$  = convection velocity, m/s  
 $u_f$  = fish velocity, m/s  
 $W$  = local channel width, m  
 $x, y$  and  $z$  = longitudinal, lateral and vertical coordinate distance, respectively, m  
 $\varepsilon$  = energy dissipation rate per unit mass,  $\text{m}^2/\text{s}^3$   
 $\kappa$  = Von Kármán constant  
 $\rho$  = fluid density,  $\text{kg/m}^3$   
 $\delta_{ij}$  = Kronecker delta function equal to one when  $i=j$  and zero when  $i \neq j$   
 $\tau_o$  = bed shear stress,  $\text{N/m}^2$   
 $\mu$  = dynamic viscosity,  $\text{N s/m}$   
 $\nu$  = kinematic viscosity,  $\text{m}^2/\text{s}$

## REFERENCES

- Acarlar MS, Smith CR. 1987. A study of hairpin vortices in a laminar boundary layer. Part 1/Hairpin vortices generated by hemisphere protuberance. *Journal of Fluid Mechanics* **175**: 1–41.
- Achenbach E. 1974. Vortex shedding from spheres. *Journal of Fluid Mechanics* **62**: 209–221.
- Adrian RJ. 1986. Multi-point optical measurements of simultaneous vectors in unsteady flow – a review. *International Journal of Heat and Fluid Flow* **7**(2): 127–145.
- Adrian RJ, Meinhart CD, Tomkins CD. 2000. Vortex organization in the outer region of the turbulent boundary layer. *Journal of Fluid Mechanics* **422**: 1–54.
- Becker S, Lienhart H, Durst F. 2002. Flow around three-dimensional obstacles in boundary layers. *Journal of Wind Engineering and Industrial Aerodynamics* **90**: 265–279.
- Bell MC. 1990. Fisheries handbook of engineering requirements and biological criteria, 3rd ed. U.S. Army Corps of Engineers, North Pacific Division: Portland, Oregon.
- Bertuccioli L, Roth GI, Katz J, Osborn TR. 1999. A submersible particle image velocimetry system for turbulence measurements in the bottom boundary layer. *Journal of Atmospheric and Oceanic Technology* **16**: 1635–1646.
- Best J. 2005. The fluid dynamics of river dunes: A review and some future research directions. *Journal of Geophysical Research* **110**(F04S02). doi: 10.1029/2004JF000218
- Biron PM, Robson C, Lapointe MF, Gaskin SJ. 2004. Comparing different methods of bed shear stress estimates in simple and complex flow fields. *Earth Surface Processes Landforms* **29**(11): 1403–1415.
- Blevins RD. 1990. Flow Induced Vibration, 2nd edition. Krieger Publishing Company: Malabar, Florida.
- Bovee KD. 1978. Probability of Use Criteria for the Family Salmonidae. U.S.D.I., Fish and Wildlife Service, Office of Biological Services. Instream Flow Information Paper No. 4: Fort Collins, Colorado.
- Brett JR. 1963. Energy required for swimming by young sockeye salmon with a comparison of drag force on a dead fish. *Transactions of the Royal Society of Canada* **1**: 441.
- Cada GF, Odeh M. 2001. Turbulence at hydroelectric power plants and its potential effects on fish. *Report to Bonneville Power Administration Contract No. 2000AI26531, Project No. 200005700*: 1–37.
- Castro-Santos T, Cotel AJ, Webb PW. 2009. Fishway evaluations for better bioengineering—an integrative approach. In Challenges for diadromous fishes in a dynamic global environment, Haro AJ, Smith KL, Rulifson RA, et al. (eds). American Fisheries Society, Symposium, 69. American Fisheries Society: Bethesda, MD; 557–575.
- Church M. 2006. Bed material transport and the morphology of alluvial river channels. *Annual Review of Earth and Planetary Science* **34**: 325–354.
- Cotel AJ, Webb PW. 2004. Why won't fish wobble? *Proceedings of the 17th ASCE Engineering Mechanics Conference, June 13–16, 2004*, University of Delaware.
- Cotel AJ, Webb PW, Tritico H. 2006. Do brown trout choose locations with reduced turbulence? *Transactions of the American Fisheries Society* **135**, 610–619.
- Crowder DW, Diplas P. 2000. Evaluating spatially explicit metrics of stream energy gradients using hydrodynamic model simulations. *Canadian Journal of Fisheries and Aquatic Science* **57**(7): 1497–1507.
- Demoyer C, Vermeyen T. 2007. Measuring point velocities and near bed turbulence parameters with an acoustic Doppler velocimeter in environmental river studies. In *Proceedings of the Hydraulic Measurements and Experimental Methods (HMEM) Conference, Lake Placid, September 10–12, New York, USA*, EWRI & IAHR.
- Detert M, Nikora V, Jirka GH. 2010. Synoptic velocity and pressure fields at the water-sediment interface of streambeds. *Journal of Fluid Mechanics* **660**: 55–86.
- Drucker EG, Lauder GV. 1999. Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *Journal of Experimental Biology* **202**: 2393–2412.
- Enders EC, Boisclair D, Roy AG. 2003. The Effect of Turbulence on the Cost of Swimming for Juvenile Atlantic Salmon. *Canadian Journal of Fisheries and Aquatic Science* **60**: 1149–1160.
- Enders EC, Buffin-Bélanger T, Boisclair D, Roy AG. 2005. The feeding behaviour of juvenile Atlantic salmon in relation to turbulent flow. *Journal of Fish Biology* **66**: 242–253.
- Enders EC, Roy ML, Ovidio M, Hallot EJ, Boyer C, Petit F., Roy AG. 2009. Habitat choice by Atlantic salmon parr in relation to turbulence at a reach scale. *North American Journal of Fisheries Management* **30**: 1819–1830.
- Evans, JG, Falih HA, Haskins RW, Nestler JM. 1999. Multiple sensor fish surrogate interface system for acoustic and hydraulic data collection and analysis. Patent 5,995,451. November 30, 1999.
- Falco RE. 1991. A coherent structure model of the turbulent boundary layer and its ability to predict Reynolds number dependence. *Philosophical Transactions of the Royal Society of London A* **336**: 103–129.
- Farge M. 1992. Wavelet transforms and their applications to turbulence. *Annual Review of Fluid Mechanics* **24**: 395–457.
- Fuchs HV, Mercker E, Michel U. 1980. Mode expansion of coherent structures in the wake of a circular disk. In *Turbulent Shear Flows 2*, Bradbury LJS, Durst F, Launder BE, Schmidt FW, Whitelaw JH (eds). Springer-Verlag: New York, 282–296.
- Hasan MAZ. 1992. The flow over a backward-facing step under controlled perturbation – laminar separation. *Journal of Fluid Mechanics* **238**: 73–96.

- Hardy RJ, Best JL, Lane SN, Carbonneau PE. 2009. Coherent Flow Structures in a Depth-Limited Flow Over a Gravel Surface: the Role of Near-Bed Turbulence and Influence of Reynolds Number. *Journal of Geophysical Research-Earth Surface* **114**.
- Heggenes J, Saltveit SJ. 1990. Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., in a Norwegian river. *Journal of Fish Biology* **36**(5): 707–720.
- Hogan DL, Church M. 1989. Hydraulic geometry in small, coastal streams - progress toward quantification of salmonid habitat. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 844–852.
- Holmes RR, Garcia MH. 2008. Flow over bedforms in a large sand-bed river: A field investigation. *Journal of Hydraulic Research* **46**(3): 322–333.
- Hussain AKMF. 1986. Coherent structures and turbulence. *Journal of Fluid Mechanics* **173**: 303–356.
- Jowett IG, Richardson J. 1995. Habitat preferences of common, riverine New Zealand native fishes and implications for flow management. *New Zealand Journal of Marine and Freshwater Research* **29**: 13–23.
- Katija K, Dabiri J. 2008. In situ field measurements of aquatic animal-fluid interactions using a self contained underwater velocimetry apparatus (SCUVA). *Limnology and Oceanography: Methods* **6**: 162–171.
- Kim KC, Adrian RJ. 1999. Very large-scale motion in the outer layer. *Physics of Fluids* **11**: 417–422.
- Kirkgoz MS, Ardiclioglu M. 1999. Velocity profiles of developing and developed open channel flow. *Journal of Hydraulic Engineering* **123**(12): 1099–1105.
- Kemp PS, Armstrong JD, Gilvear DJ. 2005. Behavioural responses of juvenile Atlantic salmon (*Salmo salar*) to presence of boulders. *River Research and Applications* **21**: 1053–1060.
- Kostaschuk RA, Church MA. 1993. Macroturbulence generated by dunes: Fraser River, Canada. *Sedimentary Geology* **85**: 25–37.
- Lacey RWJ, Millar RG. 2004. Reach scale hydraulic assessment of instream salmonid habitat restoration. *Journal of the American Water Resources Association* **40**(6): 1631–1644.
- Lacey RWJ, Roy AG. 2007. A comparative study of the turbulent flow field with and without a pebble cluster in a gravel bed river. *Water Resources Research* **43**, W05502.
- Lacey RWJ, Roy AG. 2008. Fine-scale characterization of the turbulent shear layer of an instream pebble cluster. *Journal of Hydraulic Engineering* **134**(7): 925–936.
- Liao JC, Beal DN, Lauder GV, Triantafyllou MS. 2003a. Fish exploiting vortices decrease muscle activity. *Science* **302**: 1566–1569.
- Liao JC, Beal DN, Lauder GV, Triantafyllou, MS. 2003b. The Kármán gait: novel body kinematics of rainbow trout swimming in a vortex street. *Journal of Experimental Biology* **206**: 1059–1073.
- Liao JC. 2004. Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Karman gait. *Journal of Experimental Biology* **207**(20): 3495–3506.
- Liao JC. 2007. A review of fish swimming mechanics and behavior in altered flows. *Philosophical Transactions of the Royal Society B* **362**(1487): 1973–1993.
- Lupandin AI. 2005. Effect of Flow Turbulence on Swimming Speed of Fish. *Biology Bulletin* **32**(5): 558–565.
- McComb WD. 1990. *The Physics of Fluid Turbulence*. Oxford University Press: New York, New York.
- McLean SR, Nelson JM, Wolfe SR. 1994. Turbulence structure over 2-dimensional bed forms - implications for sediment transport. *Journal of Geophysical Research-Oceans* **99**: 12729–12747.
- McQuivey RS. 1973. Summary of turbulence data from rivers, conveyance channels and laboratory flumes. *U.S. Geological Survey, Prof. Paper 802-B*.
- Meneveau C, Katz J. 2000. Scale-invariance and turbulence models for large-eddy simulation. *Annual Review of Fluid Mechanics* **32**: 1–32.
- Meynart R, Lourenco, LM. 1984. Laser speckle velocimetry in fluid dynamics applications. In *Flow visualization and digital image processing. Lecture Series 1984–03*. von Karman Inst. for Fluid Dynamics: Rhode Saint Genese, Belgium.
- Nakamura Y. 1996. Vortex shedding from bluff bodies and a universal Strouhal number. *Journal of Fluids and Structures* **10**: 159–171.
- Neary VS, Sale DC. 2010. Flow characteristics of river resources for hydrokinetic energy conversion. *Conference Proceedings, HydroVision International, July 27–30, 2010, Charlotte, NC*.
- Nepf HM, Vivoni ER. 2000. Flow structure in depth-limited, vegetated flow. *Journal of Geophysical Research* **105**(C12): 28547–28557.
- Nezu I, Nakagawa H. 1993. *Turbulence in Open-channel Flows*. A.A: Balkema, Rotterdam.
- Nikora VI, Smart GM. 1997. Turbulence characteristics of New Zealand gravel-bed rivers. *Journal of Hydraulic Engineering* **123**: 764–773.
- Nikora VI, Aberlee J, Biggs BJF, Jowett IG, Sykes JRE. 2003. Effects of Fish Size, Time to Fatigue, and Turbulence on Swimming Performance: A Case Study of *Galaxias maculatus*. *Journal of Fish Biology* **63**: 1365–1382.
- Nikora V. 2008. Hydrodynamics of gravel-bed rivers: scale issues. In *Gravel-Bed Rivers VI: From Process Understanding to River Restoration*, Habersack H, Piégay H, Rinaldi M (eds). Elsevier B.V.: Amsterdam, The Netherlands; 61–81.
- Nikora V. 2010. Hydromechanics of aquatic ecosystems: An interface between ecology, biomechanics and environmental fluid mechanics. *River Research and Applications*. **26**(4): 367–384. doi: 10.1002/rra.1291
- Pavlov DS, Lupandin AI, Skorobogatov MA. 2000. The effects of flow turbulence on the behaviour and distribution of fish. *Journal of Ichthyology* **40**(S2): S232–S261.
- Plew DR, Cooper GC, Callaghan FM. 2008. Turbulence-induced forces in a freshwater macrophyte canopy. *Water Resources Research* **44**, W02414. doi:10.1029/2007WR006064
- Raffel M, Willert C, Werely S, Kompenhans J. 2007. *Particle image velocimetry, a practical guide*, 2nd edition. Springer Scientific: Berlin.
- Rhoads BL, Sukhodolov AN. 2004. Spatial and temporal structure of shear layer turbulence at a stream confluence. *Water Resources Research* **40**, W06304. doi: 10.1029/2003WR002811
- Rinoshika A, Zhou Y. 2005. Orthogonal wavelet multi-resolution analysis of a turbulent cylinder wake. *Journal of Fluid Mechanics* **524**: 229–248.
- Robinson SK. 1991. Coherent Motions in the Turbulent Boundary-Layer. *Annual Review of Fluid Mechanics* **23**: 601–639.
- Roper BB, Konhoff D, Heller D, Wieman K. 1998. Durability of Pacific Northwest in stream structures following floods of a five-year or greater return interval. *North American Journal of Fisheries Management* **18**: 686–693.
- Roy AG, Buffin-Bélanger T, Lamarre H, Kirkbride A. 2004. Size, shape, and dynamics of large scale turbulent flow structures in a gravel bed river. *Journal of Fluid Mechanics* **500**: 1–27.
- Rubin DM, McDonald RR. 1995. Nonperiodic eddy pulsations. *Water Resources Research* **31**: 1595–1605.
- Schrank AJ, Webb PW, Mayberry S. 1999. How do body and paired-fin positions affect the ability of three teleost fishes to maneuver around bends? *Canadian Journal of Zoology* **77**: 203–210.
- Smith DL, Brannon EL, Odeh M. 2005. Response of juvenile rainbow trout to turbulence produced by prismatic shapes. *Transactions of the American Fisheries Society* **134**: 741–753.
- Smith DL, Brannon EL, Shafii B, Odeh M. 2006. Use of the average and fluctuating velocity components for estimation of volitional rainbow trout density. *Transactions of the American Fisheries Society* **135**: 431–441.
- Tennekes H, Lumley JL. 1972. *A First Course in Turbulence*. MIT Press: Cambridge, Mass.
- Torrence C, Compo GP. 1998. A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society* **79**: 61–78.

- Tritico HM. 2009. The effects of turbulence on habitat selection and swimming kinematics of fishes. *Ph.D. dissertation*, University of Michigan, 166.
- Tritico HM, Hotchkiss RH. 2005. Unobstructed and obstructed turbulent flow in gravel bed rivers. *Journal of Hydraulic Engineering* **131**: 635–645.
- Tritico HM, Cotel AJ, Clarke JN. 2007. Development, testing and demonstration of a portable submersible miniature particle imaging velocimetry device. *Measurement Science and Technology* **18**: 2555–2562.
- Tritico HM, Cotel AJ. 2010. The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *The Journal of Experimental Biology* **213**: 2284–2293.
- Tritton DJ. 1988. *Physical Fluid Dynamics*, 2nd edition. Oxford University Press: New York.
- Van Dyke M. 1982. *An Album of Fluid Motion*. Parabolic Press: Stanford, CA.
- van Zyll de Jong MC, Cowx IG, Scruton DA. 1997. An evaluation of instream habitat restoration techniques on salmonid populations in a Newfoundland stream. *Regulated Rivers-Research & Management* **13**(6): 603–614.
- Venditti JG, Bauer BO. 2005. Turbulent flow over a dune: Green River, Colorado. *Earth Surface Processes Landforms* **30**(3): 289–304.
- Webb PW. 2002. Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology* **42**: 94–101.
- Webb PW, Kostecki PT, Stevens ED. 1984. The effect of size and swimming speed on locomotor kinematics of rainbow trout. *Journal of Experimental Biology* **109**: 77–95.
- Webb PW, LaLiberte GD, Schrank AJ. 1996. Does body and fin form affect the maneuverability of fish traversing vertical and horizontal slits? *Environmental Biology of Fishes* **46**: 7–14.
- Webb PW, Cotel AJ. 2010. Turbulence: Does vorticity affect the structure and shape of body and fin propulsors. *Integrative and Comparative Biology* **50**: 1155–1166.
- Webb PW, Cotel AJ, Meadows LA. 2010. Waves and eddies: effects on fish behavior and habitat distribution. In *Fish Locomotion: An Ecological Perspective*, Domenici P, Kapoor BG (eds). Science Publishers: Enfield, New Hampshire, 1–39.
- White CM, Somandepalli VSR, Mungal MG. 2004. The turbulence structure of drag-reduced boundary layer flow. *Experiments in Fluids* **36**: 62–69.
- Williamson CHK. 1996. Vortex dynamics in the cylinder wake. *Annual Review of Fluid Mechanics* **28**: 477–539.
- Yalin MS, da Silva AMF. 2001. *Fluvial Processes*. IAHR monograph: Delft, The Netherlands.