

# Assessing possible effects of fish-culture systems on fish swimming: the role of stability in turbulent flows

Paul W. Webb · Aline J. Cotel

Received: 10 July 2010 / Accepted: 9 November 2010 / Published online: 15 May 2011  
© Springer Science+Business Media B.V. 2011

**Abstract** Fish are cultured in ponds, recirculating systems, raceways, and cages. Turbulence is associated with one or more of mechanisms to facilitate food accessibility, maintain adequate levels of oxygen, remove carbon dioxide, urinary and fecal wastes, as well as from locomotion of fishes themselves. Turbulence has been shown to have positive and negative effects on fish swimming, feeding, and energetics, usually with negative impacts at very low and at high levels, and least effects and sometimes positive effects at intermediate levels. Differences in responses of fishes with varying levels of turbulence are related to the size of eddies relative to the size of a fish (larvae, juveniles, and adults). Impacts on locomotor functions are associated with eddy diameters of the order of  $0.5\text{--}1L$ , where  $L$  is the total length of a fish. Negative locomotor impacts of turbulence are associated with eddies challenging stability, while positive effects promote drafting and station holding with reduced locomotor motions. Deployment of control surfaces increases with the level of turbulence up to a threshold

where control is overwhelmed. The design of culture facilities is expected to affect levels of turbulence and may be engineered to provide optimal levels facilitating high growth.

**Keywords** Swimming · Turbulence · Eddies · Aquaculture · Stability

## Introduction

Fish are cultivated in a range of systems; ponds, recirculating tanks, raceways, and cages in river or tidal streams. All fish-culture systems must provide certain physical requirements (Huet and Timmerans 1994; Tucker 1998; Lekang 2007; Timmons and Ebling 2007) to distribute adequate oxygen throughout the water column and remove carbon dioxide, urinary, and fecal wastes. Food should be provided at rates and with a distribution that achieves the highest possible growth and survival rates.

A general principal for maximizing growth for a given ration is to minimize metabolic energy losses (Brett 1979). The largest component of metabolic losses is from locomotion (Brett 1995), so that practices that minimize swimming costs should be beneficial. Although energy from food is not limiting for aquaculture, the gross conversion of food energy to new tissues is small (Brett 1979, 1995). As such, even small changes in energy use have the potential for large proportional increases in growth.

---

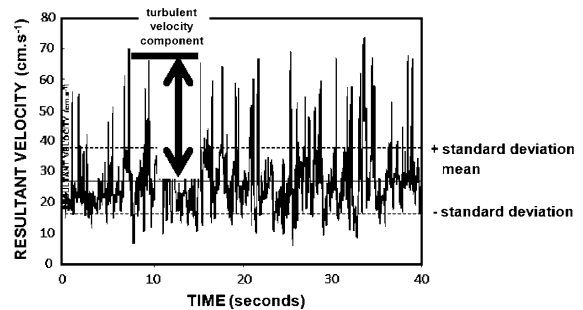
P. W. Webb (✉)  
School of Natural Resources and Environment  
and Dept of Ecology and Evolutionary Biology,  
University of Michigan, Ann Arbor, MI 48109, USA  
e-mail: pwebb@umich.edu

A. J. Cotel  
Department of Civil and Environmental Engineering,  
University of Michigan, Ann Arbor, MI 48109, USA  
e-mail: acotel@umich.edu

Fish-culture facilities commonly use flows to satisfy the physical requirements. Flows commonly bring oxygen into the system, dilute or remove wastes, and distribute food through the system. Flows may involve water recirculation and treatment, and/or through-flows from external sources. The highest flows are usually associated with culture of high-value end-products, such as salmonids. Pond culture differs from other installations as flow is typically low or negligible. Wastes are biologically recycled as part of an ecologically balanced system to enhance production of food production, while hypoxia-tolerant species, notably carp, may be chosen (Huet and Timmermans 1994; Tucker 1998). Fishes in pond culture create flows during feeding and swimming that are well known to disturb substrate and that may affect other fishes.

Three categories of swimming costs may be recognized as potentially affecting energy uses of fishes in culture systems. First, fishes in currents created by tidal flows, rivers and streams, and raceways must swim to hold position, with energy costs associated with translocation (McKenzie and Claireaux 2010). Second, routine swimming involves maneuvers. In low-flow situations, maneuvers involves variable trajectories while milling (Nursall 1973). In all situations, fishes maneuver to catch food and in intraspecific interactions and such maneuvers may be especially prevalent in high-density culture situations. Maneuvers can increase the cost of swimming over tenfold (Puckett and Dill 1984, 1985; Webb 1991; Boisclair and Tang 1993; Krohn and Boisclair 1994; Boisclair 2001; Enders et al. 2003). Lastly, flows create turbulence, seen in temporal and spatial variations in the direction and magnitude of velocity (Fig. 1). Indeed, because turbulent flows are characterized by variations in velocity around some mean value for the overall flow, the difference between the mean velocity and fluctuations is defined as the turbulent velocity component of the flow. The turbulent velocity components create perturbations that may cause displacements of body posture and/or swimming trajectory necessitating locomotor stabilizing correction responses. Controlling stability is mechanically similar to maneuvering, and the few measurements that have been made show increases in metabolic rate of over twofold (Webb 1994b, 2006).

Here, the challenges associated with turbulence and controlling stability are considered. The study of



**Fig. 1** Variations in resultant velocity measured at the focal point occupied by a brown trout, *Salmo trutta*, in a sand-bed stream using acoustic Doppler velocimetry. The turbulent velocity component of the flow is the difference between the mean velocity and a velocity

interactions of turbulence with fishes is in its infancy so that the discussion of impacts of turbulence on fishes in culture practices is speculative. Nevertheless, much research has reported negative effects of turbulence, notably on reducing swimming speeds and increasing metabolic costs (Pavlov et al. 2000; Webb et al. 2010). However, a few studies show that fishes can use some turbulence as a booster, reducing energy costs and/or affecting ground speed, reducing times to traverse a stretch of river (Webb and Cotel 2010). Positive or negative impacts of turbulence on fishes could affect productivity. Thus, designs affecting turbulence in fish-culture installations might influence productivity in fish-culture operations.

### The nature of turbulent flows

Flow measurements in fish habitat are usually values averaged over several seconds made at one point using mechanical or electromagnetic flow meters (Murphy and Willis 1996). Measuring velocity variations in turbulent flow requires more frequent sampling, most commonly by means of acoustic Doppler velocimetry (ADV), using sound to measure velocities  $u_x$ ,  $u_y$ , and  $u_z$  simultaneously in  $x$ ,  $y$ , and  $z$  directions at rates of 40 Hz (Nikora and Goring 1998; Webb et al. 2010). From these data, the resultant velocity,  $u_{res}$ , may be determined as:

$$\bar{u}_{res} = \sqrt{u_x^2 + u_y^2 + u_z^2}$$

The velocity fluctuations in  $u_x$ ,  $u_y$ , and  $u_z$  can be described statistically by the mean values,  $\bar{u}_x$ ,  $\bar{u}_y$ , and

$\bar{u}_z$ , and standard deviations,  $\sigma_x$ ,  $\sigma_y$ , and  $\sigma_z$ , respectively, as well as  $\bar{u}_{res}$  and  $\sigma_{res}$  for the resultant velocity. A measure of the level of turbulence, the turbulent Intensity, *TI*, is often used based on these statistical measures (Nikora and Goring 1998; Smith et al. 2006; Webb et al. 2010):

$$TI = \sigma_{res} / \bar{u}_{res}$$

The differences in the actual velocities recorded and the average velocity are the turbulent velocity components (Fig. 1) of the flow,  $u_x - \bar{u}_x$ ,  $u_y - \bar{u}_y$ ,  $u_z - \bar{u}_z$  and  $u_{res} - \bar{u}_{res}$ . By virtue of motion, any body, as well as the particles of water in a flow, carry momentum and energy. The energy associated with turbulent velocity components of a flow affects transport of materials and mixing, and also helps drive perturbations of objects embedded in the flow, such as a fish. Another common statistical measure of turbulence (Smith and Brannon. 2005) captures the energy associated with turbulence as the turbulent kinetic energy, *TKE*, given by:

$$TKE = 0.5(\sigma_x^2 + \sigma_y^2 + \sigma_z^2)$$

The dimensions of *TKE* are actually length<sup>2</sup>·time<sup>-2</sup>, so that the measure is correctly kinetic energy per unit mass or for water with a density close to unity, per unit volume.

Velocity–time traces such as that illustrated in Fig. 1 are found throughout turbulent flow. When such traces are analyzed, patterns are found that repeat over time, with velocity variations of similar magnitude at recurring intervals. Similarly, measurements made simultaneously at various points also show repeating patterns with velocities of similar magnitude. Thus, turbulence is not a truly random phenomenon. Instead, there is structure in turbulent flow that is predictable on a coarse scale. These structures are often called vortices, or orbits in wave driven environments, and eddies.

### Orbits and eddies

Circular water motions created by waves will affect fish-culture systems exposed to wind and boat wakes for open-water locations such as in embayments or run-of-the-river installations. Waves induce water particles to trace orbital circular or elliptical paths in the water column as a wave passes. These

wave-induced eddies may be called orbits (Webb et al. 2010). Orbits have their largest diameter at the surface, which declines with water depth, so that orbits essentially vanish at a depth equal to half the wavelength of the wave. In shallow water, circular orbital motion becomes elliptical, with the long axis parallel to the bottom (Denny 1988; Webb et al. 2010).

Flow in fish-culture systems, however, is more likely to be dominated by eddies (Webb et al. 2010). In fish habitat and culture systems, eddies arise where there are velocity gradients. Fluids resist shear and other deformations, a physical property quantified by viscosity. Viscous effects create areas of shear stress that result in the trajectories of water particles—streamlines—bending, and eventually rolling up forming eddies. Hence, eddies arise as a result of viscous effects in shear flows. The curvature, or curl, in velocity vectors is called vorticity,  $\omega$ , i.e., a form of angular velocity. Thus, eddies are areas of the flow where the streamlines curve, leading to circular motions, such as a whirlpool and indeed, eddies are in fact best defined as regions of finite vorticity.

Shear flows in which eddies occur are generated in various ways. Gravitational forces act on water falling into fish containers and on food items falling into the water, resulting in cascades that create eddies. However, most turbulence derives from velocity gradients. Some velocity gradients are created directly when there are changes in cross-sectional area in raceways and recirculating systems or where submerged jets are used to create flow. Velocity gradients leading to eddy formation also occur as a result of flow interacting with the sides and bottom of culture systems and with surfaces of objects protruding into the flow, such as netting, struts, supporting structures, etc. (Panton 1984). A no slip condition applies at boundaries, where the velocity is zero. Due to viscosity, the velocity in the flow adjacent to a boundary increases from zero to that of the free-stream—where the flow is unaffected by the boundary or surface—over a region called the boundary layer. Here, velocity gradients and shear forces are large, leading to the creation of vorticity (Saffman 1992).

Eddies vary in size, and frequency of occurrence. Small eddies are common and large eddies rare (Denny 1988; Tritico and Cotel 2010). The upper limit of eddy diameter is set by the physical size of a system, with

some eddies growing to span the system as the flow moves downstream. Eddies also calve smaller eddies. The smallest eddies applicable to fishes in culture systems and natural habitats are so small that they are dissipated by viscosity, their energy appearing as heat. These smallest eddies are defined as the Kolmogorov scale eddies (Kolmogorov 1941). The flow velocity variations measured at a point in turbulent flow (Fig. 1) reflects the passage of eddies of many different sizes, and the repeating flow magnitudes in time and space reflect the passage of many eddies of varying size and vorticity. The difference between the mean velocity and the actual velocity due to turbulence is the turbulent velocity component in the flow.

### Effects of turbulence on fishes

Various interactions have been described between fishes and turbulent flows. Such interactions can be illustrated for swimming speed, an exemplary and widely used measure of performance. Changes in swimming speed can be used to quantify impacts for a wide range of environmental conditions on fishes (Brett 1995; Beamish 1978; McKenzie and Claireaux 2010) including turbulence (Pavlov et al. 2000; Odeh et al. 2002; Lupandin 2005; Tritico and Cotel 2010).

Swimming behavior is comprised of multiple gaits that are recruited in succession as swimming speed increases (Alexander 1989; Webb 1994a, b; Drucker 1996). Gaits range from hovering in still or slow water, through station holding to avoid swimming by interacting with the bottom, to high-speed sprints and transient, high-acceleration fast-starts; swimming performance should be compared for fishes when swimming in the same gait.

The lowest-speed gait is hovering when water-current speed is zero. Other fishes may mill rather than hover in still water (Nursall 1973), swimming around along various trajectories. These behaviors might be anticipated in culture systems in ponds and in bays, locations where wind-driven waves can create orbits that may pose challenges to stability. Observations in natural habitat show that orbits with diameters of the order of fish total length cause displacements of fishes that can exceed stability control capabilities (Cotel and Webb 2004).

As current speed increases, fish first exhibit rheotaxis, orienting head-upstream into the flow

(Arnold and Weihs 1978; Webb 1989; Pavlov et al. 2000; Blake 2010). Fishes swimming in the water column orient themselves to swim directly into the current, and benthic fishes on the bottom turn to face upstream. Threshold speeds at which rheotaxis occurs are lower at higher TI (Pavlov et al. 2000). Benthic fishes holding station on the bottom to avoid swimming and its attendant energy costs can remain oriented into the flow as current speeds increases above that triggering rheotaxis until a limit is reached at which the fish begins to slip downstream. Above this slip speed, benthic fishes begin swimming above the bottom. Slip speeds also decrease at higher TI (Pavlov et al. 2000).

The lowest speeds at which fishes swim continuously are aerobic cruising speeds, speeds that can essentially be sustained indefinitely. Fishes use a wide range of motor systems for cruising, involving median and paired fins (MPF swimming) and/or body and caudal fin motions (BCF swimming) (Webb and Gerstner 2000). Most studies show that maximum cruising speeds decrease as TI increases (Odeh et al. 2002; Pavlov et al. 2000; Lupandin 2005; Tritico and Cotel 2010). Higher sprint speeds using anaerobic metabolic pathways are maintained for only a few seconds before fish fatigue. These sprint speeds also decrease with increasing TI (Pavlov et al. 2000). Finally, acceleration performance in startle responses can be reduced by higher levels of turbulence for hybrid striped bass, *Morone saxatilis*, and Atlantic salmon parr, *Salmo salar* (Odeh et al. 2002).

Observations of 2 min critical swimming speeds, of creek chub, *Semotilus atromaculatus*, show that the axis of rotation of eddies affects swimming performance (Tritico and Cotel 2010). In that study, the critical swimming speed was measured as the maximum speed attained in an increasing velocity with speed increments of  $\approx 0.3$  body length  $\cdot s^{-1}$  at 2 s intervals. Critical speeds were decreased more when swimming in flow dominated by horizontal eddies compared to flows comprised of vertical eddies. Chub have a somewhat compressed body, and it is likely that vertical eddies would have greater impacts than horizontal eddies on fishes with compressed body forms (Webb and Cotel 2010). It is likely that the effect of the axis of rotation of eddies on fishes will depend on their body form. Vertical eddies are likely to have less impact than horizontal eddies on fishes with compressed body cross-sections, and vice versa

for fishes with depressed body cross-sections (Webb and Cotel 2010). Thus, culture systems may need to consider eddy orientation in designing installations for the culture of different species. In addition, for both cruising and sprint speeds, fishes from lotic (no, or low current habitats such as ponds) habitats are more strongly affected by TI than those from lentic (flowing water habitats such as streams) habitats, which should be taken into consideration in determining the design of fish-culture systems for different species.

Not all studies on swimming performance have shown negative effects of turbulence. Ogilvy and DuBois (1981) found elevated turbulence had no effect on cruising speeds of bluefish, *Pomatomus saltatrix*, and Nikora et al. (2003) found similar results for sprints by inanga, *Galaxias maculatus*. Odeh et al. (2002) found startle responses of juvenile rainbow trout, *Oncorhynchus mykiss*, were unaffected by turbulence levels that did affect this behavior in hybrid striped bass and Atlantic salmon parr (Odeh et al. 2002).

It is also generally assumed that eddies could improve swimming abilities, usually by giving a boost in the direction in which a fish is traveling (Liao et al. 2003a, b; Liao 2008). For example, eddies are thought to improve performance during migration (Hinch and Rand 1998, 2000; Enders et al. 2003; Standen et al. 2004) and in schools (Weihs 1973; Partridge and Pitcher 1980; Herskin and Steffensen 1998; Svendsen et al. 2003). In flume experiments, Standen et al. (2004) found swimming speeds of sockeye salmon, *Oncorhynchus nerka*, migrating through a turbulent river were 1.4 to 76 times higher than expected from tail-beat frequencies of fishes swimming in rectilinear steady flow. These results suggest fishes can extract energy from turbulent flows, but more studies are needed.

Benefits can also be realized by fishes interacting with structures that are sources of eddies to avoid swimming and attendant energy costs. They may entrain in the flow close to and immediately downstream of bluff bodies such as cylindrical shapes, and in the upstream bow-wave (Sutterlin and Waddy 1975; Webb 1998; Przybilla et al. 2010). Eddies are shed regularly in predictable ways by bluff bodies, with rows of alternating staggered eddies forming a Kármán vortex street. Fishes can orient themselves in such vortex streets and “slalom” between the eddies,

a behavior called the Kármán gait. In doing so, minimal muscle is used (Liao et al. 2003b; Liao 2004, 2008). As noted above, although energy from food is not limiting for aquaculture, changes in energy use have the potential for increasing growth. Thus, the ability of fishes to use eddies to avoid swimming and decrease energy costs might provide options for culture systems to facilitate growth or for fishes to attain larger sizes at harvest.

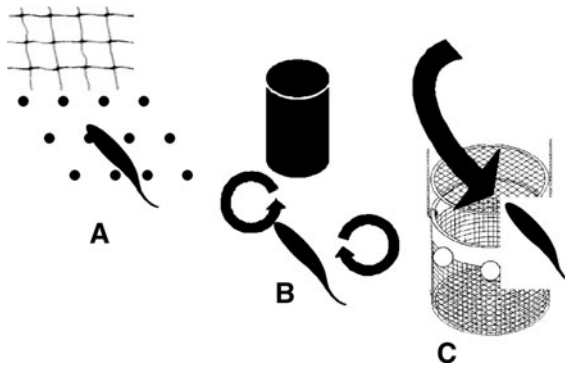
Most of the results described above are from experimental studies in which turbulent flows were imposed on fishes. The results, however, reflect habitat choices in the field when fish have choices among different naturally occurring turbulent situations. Fishes tend to avoid high TI conditions when swimming at low and at high speeds, and at intermediate speeds choose habitats with some intermediate level of turbulence (Webb 1998, 2002, 2006; Pavlov et al. 2000; Smith and Brannon 2005; Smith et al. 2006; Tritico 2009). At low speeds, a fish's momentum is presumed to be low compared to that of eddies so that disturbances readily occur. Because speed is low, trimming forces are small, and powered control is essential. However, generating swimming forces at low swimming speed is energetically expensive (Blake 1979). Thus, the metabolic costs to control stability at low speeds are expected to be high. In contrast, at high speeds, fish momentum is large, facilitating damping disturbances. Translocation costs are also high, leaving little scope for responding to stability challenges. In addition, eddy vorticity, momentum, and energy are also high at high speeds, and fishes can be overwhelmed before a response can be initiated. At intermediate speeds, turbulence is presumed within the control capabilities of fishes, without high costs, while food and oxygen are delivered at high rates (MacKenzie and Kiørboe 1995; Pavlov et al. 2000; Boisclair 2001; Galbraith et al. 2004). Thus, as with organismic responses to physical factors, response curves to turbulence tend to be u-shaped, with a minimum, or optimal value that if achieved in an aquaculture system could promote productivity.

### Scaling of eddies to fishes

There is clearly a range of possible interactions between fishes and eddies. It is essential to know the

conditions under which responses are positive or negative to avoid the former and perhaps exploit the latter. The key to understanding fish-eddy interactions is recognizing that fish interact with the structural elements of turbulent flow. These vary in size, and thus responses depend on the size of an eddy relative to the size of a fish (Fig. 2). Cotel (personal communication) has shown that a limit to the ability of fishes to respond to eddies and maintain stability is reached in eddies with diameter, momentum, and energy of the same order as that of the fish. Pavlov et al. (2000) considered that the large range of negative effects of turbulence on fish swimming was associated with mean eddy diameters of about  $0.66L$ , illustrated by Fig. 2b. Similarly, Tritico and Cotel (2010) found small reductions in swimming speed over a wide range of eddy sizes. Large decreases in performance occurred as stability failure was approached in flows containing eddies with  $\lambda/L$  from about 0.75–0.9 where  $\lambda$  is the characteristic eddy diameter and  $L$  is the typical total length of a fish.

Positive effects of swimming in a Kármán Vortex Street have been shown to occur when  $\lambda/L$  is of the order of 0.3–0.5. Eddy-assisted migration has been described for oceanic gyres (Webb et al. 2010), with



**Fig. 2** Variations in eddy size relative to fish size. **a** Structures such as restraining nets in fish-culture systems will shed small eddies, with  $\lambda \ll L$  for a portion of the eddy field shed by all the net filaments being illustrated. Such eddies are too small to affect fishes. **b** Larger structures such as supports for eddies will shed larger eddies, including some with  $\lambda = 0.5\text{--}1L$ , relative sizes that challenge and can overwhelm control systems. **c** Natural flows create large eddies and gyres limited in size by the physical boundaries of rivers, bays, etc., when  $\lambda \gg L$ . Eddies of this scale are viewed by a fish as a rectilinear flow, and will not induce stability problems. Flows at this scale will create eddies of smaller sizes when they interact with structures, as in **a** and **b**

$\lambda \gg L$ , when the dimensions of an eddy become large enough that a fish may treat the angular velocity as a rectilinear flow. Presumably, fish can get a boost from eddies over the range  $L > \lambda \gg L$ . In aquaculture situations, large eddies impinging on a facility would be seen by fishes as an additional rectilinear current component (Fig. 2c).

For smaller eddies, down to the Kolmogorov scale, with  $\lambda/L \ll 1$ , there is little if any measurable effect of such fine-scale turbulence on swimming. Such eddies would be shed by small-diameter structures in fish-culture installations, such as netting (Fig. 2a), and would be expected to have no measurable effects on fishes.

The mechanisms whereby eddies affect fish have not been explicitly explored, in part because simultaneous recording of fish and flow is difficult. Observations of control failure, when fishes “spill”, that is they lose control over posture and/or swimming trajectory, usually with curving and/or twisting the body and being displaced downstream (Tritico and Cotel 2010), suggest that failure is associated with positive feedback. Thus, a spill occurs when a displacement is amplified sufficiently during the delay between stimulus and response such that recovery is not possible (Webb and Cotel 2010). Then, fishes may intentionally amplify a displacement to swim downstream, thereby gaining time and increasing their momentum to turn back into the flow, or use large amplitude body and caudal fin motions to head back upstream.

### Controlling stability

Turbulence challenges stability of posture and swimming trajectory and fish respond to counteract disturbances (Puckett and Dill 1985; McLaughlin and Noakes 1998; Webb 2002, 2006; Tritico 2009). Hydrostatic and hydrodynamic forces affect stability control. Fishes are not generally hydrostatically stable. As a result, hydrodynamic forces are most important in controlling stability (Eidietis et al. 2002; Webb 2002).

Hydrodynamic forces are generated when water flows over a surface of the body and any or all appendages (Aleyev 1977; Webb 2002, 2006). Trimming forces are generated from flow over a control surface as a result of the motion of the fish to which

the surface is attached. Powered forces are generated when the flow is created by the motion of a control surface independent of the overall motion of the fish. In practice, it is likely that the net force on a control surface arises from both trimming and powered sources. For example, an extended pectoral fin will generate trimming forces while added motion can generate powered forces to supplement, or be supplemented by the trimming component.

Median and paired fins are deployed for stabilization at low speeds during BCF (body-caudal fin) swimming in low turbulence rectilinear flows (Webb 2006). This reflects the difficulties of stability control at low speeds. McLaughlin and Noakes observed young-of-the-year brook trout, *Salvelinus fontinalis* deployed their pectoral fins when swimming in turbulent flows. As swimming speed increases, the median and paired fins are progressively furled (McLaughlin and Noakes 1998; Webb 2004). Tritico (2009) found that pectoral fins of creek chub were deployed for longer periods of time as the level of turbulence increased, reaching 100% deployment at turbulence levels where spills occurred. Tail-beat frequencies of salmonids swimming in the field where turbulence is the norm are often irregular compared to those when swimming in a flume (Puckett and Dill 1985; McLaughlin and Noakes 1998).

Deployment of control surfaces would be expected to increase energy costs of swimming. Metabolic rates of Atlantic salmon, *Salmo salar*, increased by 30% as TI increased from 0.28 to 0.36 when swimming at approximately  $18 \text{ cm}\cdot\text{s}^{-1}$ . When swimming at approximately  $23 \text{ cm}\cdot\text{s}^{-1}$  there was a 1.6-fold increase in metabolic rate as TI increased from 0.21 to 0.30 (Enders et al. 2003). Control is mechanically very similar to maneuvering, which can increase energy expenditure by over tenfold (Blake 1979; Weatherley et al. 1982; Puckett and Dill 1984, 1985; Webb 1991; Boisclair and Tang 1993; Krohn and Boisclair 1994; Boisclair 2001; Enders et al. 2003).

### Lessons for fish-culture systems

In general, there appears to be u-shaped response curves relating fish responses to the level of turbulence, as is common for many environmental factors (Diana 2004; Smith and Smith 2008). Consequently,

there will be some level of turbulence comprised of eddies with  $\lambda/L$  that is optimal in terms of minimizing impacts on swimming performance and energy costs. In addition, it is well known that moderate exercise increases production in aquaculture systems (Davison and Goldspink 1977; Jørgensen and Jobling 1993). Because turbulence can reduce swimming performance, it is possible that induction of eddies could impose a mechanically equivalent exercise regime, but at lower overall flow speeds through a system.

Thus, fish-culture facilities might be designed to create turbulence in an appropriate range to maximize growth. For installations using nets in bays and run-of-the-river situations, the structural supports might be manipulated to shed eddies with appropriate characteristics. Gravity-fed intakes and inserts in the flow of recirculating systems could also be used to generate turbulence at levels that might be utilizable by fishes to reduce energy losses and increase production.

In practice, there are several factors that probably militate against manipulating eddy composition into a range that would be beneficial. First, the optimal values of  $\lambda/L$  may change little during ontogeny, but the size of beneficial eddies would be expected to change as fish grow. It seems likely that it would not be practical to build a system with the capacity to vary eddy sizes, but a culture system with multiple fish sizes might be an option to tap the range of eddies expected in typical fish-culture systems. Second, eddies that are favorable for minimizing locomotor costs in culture systems would be those providing opportunities for entraining, bow-wave riding and using the Kármán gait. This would require a substantial investment in physical structures that does not seem practical. In addition, such structures in flows dissipate energy. As a result, the scope for such a design would be limited through the flow of nets and recirculating systems. If nets and their supports were involved in facilities in streams or embayments, added drag could make systems vulnerable to damage during peak-flow events and storms. In-stream objects in recirculating systems would require larger pumps.

It seems most likely that manipulation of eddies would be most beneficial in simply seeking to create an isotropic flow of vortices with sizes where  $\lambda/L \ll 1$ . This would approach microturbulence as perceived by the fishes, and would provide high oxygen

diffusion through the system and similar removal of wastes without creating turbulence intensities necessitating stabilizing responses and associated energy costs.

## References

- Alexander RMcN (1989) Optimization and gaits in the locomotion of vertebrates. *Physiol Rev* 69:1199–1227
- Aleyev YG (1977) Nekton. Junk, The Hague
- Arnold GP, Weihs D (1978) The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa*). *J Exp Biol* 75:147–169
- Beamish FWH (1978) Swimming capacity. In: Hoar WS, Randall DJ (eds) *Fish Physiology, Locomotion*, vol VII. Academic Press, New York, pp 101–187
- Blake RW (1979) The energetics of hovering in the mandarin fish (*Synchropus picturatus*). *J Exp Biol* 82:25–33
- Blake RW (2010) Biomechanics of rheotactic behaviour in fishes. In: Domenici P, Kapoor BG (eds) *Fish locomotion: an eco-ethological perspective*. Science Publishers, Enfield, pp 40–61
- Boisclair D (2001) Fish habitat models: From conceptual framework to functional tools. *Can J Fish Aquat Sci* 58:1–9
- Boisclair D, Tang M (1993) Empirical analysis of the swimming pattern on the net energetic cost of swimming in fishes. *J Fish Biol* 42:169–183
- Brett JR (1979) Environmental factors and growth. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish physiology, bioenergetics and growth*. Academic Press, New York, pp 599–675
- Brett JR (1995) Energetics. In: Brett JR, Clark C (eds) *Physiological-Ecology of Pacific Salmon*, Gov. Canada. Dept-Fish. Oceans, Ottawa, pp 3–68
- 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
- Davison W, Goldspink G (1977) The effect of prolonged exercise on the lateral musculature of the brown trout *Salmo trutta*. *J Exp Biol* 70:1–12
- Denny M (1988) *Biology and the mechanics of the wave-swept environment*. Princeton University Press, Princeton
- Diana JS (2004) *Biology and ecology of fishes*. Biological Sciences Press, Cooper Publishing Group, Traverse City
- Drucker EG (1996) The use of gait transition speed in comparative studies of fish locomotion. *Amer Zool* 36:555–566
- Eidietis L, Forrester TL, Webb PW (2002) Relative abilities to correct rolling disturbances of three morphologically different fish. *Can J Zool* 80:2156–2163
- Enders EC, Boisclair D, Roy AG (2003) The effect of turbulence on the cost of swimming for juvenile Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 60:1149–1160
- Galbraith PS, Browman HI, Racca RG, Skiftesvik AB, Saint-Pierre J (2004) Effect of turbulence on the energetics of foraging in Atlantic cod *Gadus morhua* larvae. *Mar Ecol Prog Ser* 201:241–257
- Herskin J, Steffensen JF (1998) Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. *J Fish Biol* 53:366–376
- Hinch SG, Rand PS (1998) Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Can J Fish Aquat Sci* 55:1821–1831
- Hinch SG, Rand PS (2000) Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Can J Fish Aquat Sci* 57:2470–2478
- Huet M, Timmermans J (1994) *Textbook of fish culture: breeding and cultivation of fish*. Blackwell Science, Cambridge, MA
- Jørgensen EH, Jobling M (1993) The effect of exercise on growth, food utilisation and osmoregulatory capacity of juvenile Atlantic salmon (*Salmo salar*). *Aquaculture* 116:233–246
- Kolmogorov AN (1941) Local structure of turbulence in an incompressible viscous fluid at very high Reynolds numbers. *Dokl. Akad. Nauk SSSR* 30, 299, reprinted in *Usp. Fiz. Nauk* 93, 476–481 (1967), transl. in *Soviet Physics Uspekhi* 10: 734–736 (1968)
- Krohn MM, Boisclair D (1994) Use of a stereo-video system to estimate the energy expenditure of free-swimming fish. *Can J Fish Aquat Sci* 51:1119–1127
- Lekang O-I (2007) *Aquaculture engineering*. Wiley, New Jersey
- Liao JC (2004) Neuromuscular control of trout swimming in a vortex street: implications for energy economy during the Kármán gait. *J Exp Biol* 207:3495–3506
- Liao JC (2008) A review of fish swimming mechanics and behavior in perturbed flows. *Phil Trans R Soc B* 362: 1973–1993
- Liao JC, Beal DN, Lauder GV, Triantafyllou M (2003a) The Kármán gait: Novel body kinematics of rainbow trout swimming in a vortex street. *J Exp Biol* 206:1059–1073
- Liao JC, Beal DN, Lauder GV, Triantafyllou MS (2003b) Fish exploiting vortices decrease muscle activity. *Science* 302:1566–1569
- Lupandin AI (2005) Effect of flow turbulence on swimming speed of fish. *Biol Bull* 32:461–466
- MacKenzie BR, Kiørboe T (1995) Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent environments. *Limnol Oceanogr* 40:1278–1289
- McKenzie DJ, Claireaux G (2010) The effect of environmental factors on the physiology of aerobic exercise. In: Domenici P, Kapoor BG (eds) *Fish locomotion: an eco-ethological perspective*. Science Publishers, Enfield, pp 296–332
- McLaughlin RL, Noakes DL (1998) Going against the flow: an examination of the propulsive movements made by young brook trout in streams. *Can J Fish Aquat Sci* 55:853–860
- Murphy B, Willis DW (1996) *Fisheries techniques*. American Fisheries Society, Bethesda
- Nikora VI, Goring DG (1998) ADV turbulence measurements: can we improve their interpretation? *J Hydraul Engin* 124:630–634



- Nikora VI, Aberle J, Biggs BJF, Jowett IG, Sykes JRE (2003) Effects of size, time-to-fatigue and turbulence on swimming performance : a case study of *Galaxias maculatus*. J Fish Biol 63:1365–1382
- Nursall JR (1973) Some behavioral interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). J Fish Res Board Can 30:1161–1178
- Odeh M, Norika JF, Haro A, Maynard A, Castro-Santos T, Cada GF (2002) Evaluation of the effects of turbulence on the behavior of migratory fish. Final Report 2002, Report to Bonneville Power Administration, Contract No, 00000022, Project No. 200005700, pp 1–55
- Ogilvy CS, DuBois AB (1981) The Hydrodynamics of swimming bluefish (*Pomatomus saltatrix*) in different intensities of turbulence: variation with changes in buoyancy. J Exp Biol 92:67–85
- Panton RL (1984) Incompressible flow. Wiley, New Jersey
- Partridge BL, Pitcher TJ (1980) Evidence against a hydrodynamic function for fish schools. Nature (London) 279: 418–419
- Pavlov DS, Lupandin AI, Skorobogatov MA (2000) The effects of flow turbulence on the behavior and distribution of fish. J Ichthyol 40(Suppl 2):S232–S261
- Przybylla A, Kunze S, Rudert A, Bleckmann H, Brücker C. (2010) Entraining: a swimming mode of fish to save energy in unsteady flow. J Exp Biol (*In press*)
- Puckett KJ, Dill LM (1984) Cost of sustained and burst swimming of juvenile coho salmon (*Oncorhynchus kisutch*). Can J Fish Aquat Sci 41:1546–1551
- Puckett KJ, Dill LM (1985) The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). Behaviour 92:97–111
- Saffman PG (1992) Vortex dynamics. Cambridge University Press, Cambridge
- Smith DL, Brannon EL (2005) Response of juvenile trout to turbulence produced by prismatic shapes. Trans Amer Fish Soc 134:741–753
- Smith TM, Smith RL (2008) Elements of ecology. Pearson Benjamin Cummings, San Francisco
- Smith DL, Brannon EL, Shafii B, Odeh M (2006) Use of the average and fluctuating velocity components for estimation of volitional rainbow trout density. Trans Amer Fish Soc 135:431–441
- Standen EM, Hinch SG, Rand PS (2004) Influence of river speed on path selection by migrating adult sockeye salmon (*Oncorhynchus mykiss*). Can J Fish Aquat Sci 61:905–912
- Sutterlin AM, Waddy S (1975) Possible role of the posterior lateral line in obstacle entrainment by brook trout (*Salvelinus fontinalis*). J Fish Res Board Can 32:2441–2446
- Svendsen JC, Skov J, Bildsoe MJ, Steffensen F (2003) Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions. J Fish Biol 62:834–846
- Timmons MB, Ebling JM (2007) Recirculating aquaculture. Cayuga Aqua Ventures, Piedrahíta
- Tritico H (2009) The effects of turbulence on habitat selection and swimming kinematics of fishes. PhD Dissertation. University of Michigan, Ann Arbor
- Tritico HM, Cotel AJ (2010) The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). J Exp Biol (*In press*)
- Tucker CS (1998) Marine fish culture. Kluwer Academic Publishers Group, Dordrecht
- Weatherley AH, Rogers SC, Pinock DG, Patch JR (1982) Oxygen consumption of active rainbow trout, *Salmo gairdneri* Richardson, derived from electromyograms obtained by radiotelemetry. J Fish Biol 20:479–489
- Webb PW (1989) Station holding by three species of benthic fishes. J Exp Biol 145:303–320
- Webb PW (1991) Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss*. Can J Fish Aquat Sci 48:583–590
- Webb PW (1994a) Exercise performance of fish. In: Jones JH (ed) Advances in veterinary science and comparative medicine. Academic Press, Orlando, pp 1–49
- Webb PW (1994b) The biology of fish swimming. In: Bone Q, Maddock L, Rayner JMV (eds) Mechanics and physiology of animal swimming. Cambridge University Press, Cambridge, pp 45–62
- Webb PW (1998) Entrainment by river chub, *Nocomis micropogon*, and smallmouth bass, *Micropterus dolomieu*, on cylinders. J Exp Biol 201:2403–2412
- Webb PW (2002) Control of posture, depth, and swimming trajectories of fishes. Integ Comp Biol 42:94–101
- Webb PW (2004) Maneuverability—general issues. IEEE J Ocean Engin 29:547–555
- Webb PW (2006) Stability and maneuverability. In: Shadwick RE, Lauder GV (eds) Fish physiology. Elsevier Press, San Diego, pp 281–332
- Webb PW, Cotel AJ (2010) Turbulence: Does vorticity affect the structure and shape of body and fin propulsors? Integ Comp Biol. doi:10.1093/icb/icq020
- Webb PW, Gerstner CL (2000) Swimming behaviour: predictions from biomechanical principles. In: Domenici P, Blake RW (eds) Biomechanics in animal behaviour. Bios Scientific Publishers Ltd, Oxford, pp 59–77
- Webb PW, Cotel AJ, Meadows LA (2010) Waves and eddies: effects on fish behaviour and habitat distribution. In: Domenici P, Kapoor BG (eds) Fish locomotion: an eco-ethological perspective. Science Publishers, Enfield, pp 1–39
- Weih D (1973) Hydromechanics of fish schooling. Nature (London) 241:290–291