

Chapter 5

Effects of Turbulence on Fish Swimming in Aquaculture

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Abstract The role of turbulence in aquaculture facilities is a multi-faceted, largely unexplored, and potentially important topic in understanding the energetics and behavior of rearing fishes. Here, we review some common principles of turbulent flow and discuss methods to measure and describe them. Flows that display chaotic and wide fluctuations in velocity can repel fishes, while flows that have a component of predictability can attract fishes. We reveal how fish in turbulence can save energy by using two distinct, though not mutually exclusive mechanisms; flow refuging (exploiting regions of reduced flow) and vortex capture (harnessing the energy of discrete vortices). We summarize the energetics of fish holding station in turbulent flows around a cylinder from recent work. Turbulent flows can also create instabilities that negatively affect fishes, such as reducing critical swimming speed and increasing oxygen consumption. Our aim is to discuss aspects of turbulence from key lab and field experiments which may prove productive if applied to aquaculture systems.

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5.1 Introduction

Optimizing flow conditions for fish rearing in aquaculture facilities is a challenging problem as many interrelated factors are at play. There are abiotic considerations. For example, to obtain uniform oxygen concentrations, it is important to provide enough mixing throughout the entire water column (Reig et al. 2007). In addition, waste removal may be best addressed with some level of turbulence. There are biotic factors, such as disease control and nutrition. Yet, perhaps one of the most critical and underappreciated concepts of fish rearing is swimming energetics and its relationship to turbulent flow (Jorgensen et al. 1993; Liao et al. 2003b; Przybilla et al. 2010; Taguchi and Liao 2011). It is important to note that the majority of fish species reared in aquaculture have evolved experiencing turbulent flows in their natural environment. As such, understanding how fish swim in complex flows should be a topic of considerable interest for those in the aquaculture industry, as it is for a broad scientific audience (Anderson et al. 1998; Enders et al. 2003; Fausch 1993; Heggenes 2002; Liao et al. 2003a; McLaughlin and Noakes 1998; Odeh et al. 2002a; Pavlov et al. 2000; Shuler et al. 1994; Smith et al. 2006; Triantafyllou et al. 2002). The goal of this chapter is to review basic concepts and experiments from the fields of fluid dynamics, physiology, and biomechanics in order to better understand the implications of turbulence on the rearing and behavior of fishes in aquaculture.

Turbulence is so ubiquitous and familiar that often little attention is paid to it. For our purposes here we will divide turbulence into two categories, based on a more comprehensive treatment of definitions (Liao 2007). One category is “true” turbulence which contains eddy-dominated flows (Fig. 5.1), defined by vortical flows of multiple strengths and sizes superimposed onto a mean flow velocity (Kirkbride 1993; Warhaft 2002). The other involves vortical flows with a predictable spatio-temporal component, such as a vortex street (Fig. 5.2) (Blevins 1990). Both types of turbulence have implications in the maintenance of fish in rearing facilities. Of particular interest is how vortices affect fish swimming energetics, and thus growth. In this chapter, we discuss how this depends largely on the predictability and spatial scale of vortical flows. To begin, we first outline important principles of turbulence that may apply to common aquaculture systems.

5.2 Types of Turbulence

5.2.1 Eddy-Dominated Flows

Numerous factors create velocity gradients and therefore vorticity, which in turn results in the curvature of streamlines, leading to the formation of eddies that characterize turbulent flows. Eddies can be defined as a region of finite vorticity. Vorticity is defined as the curl of the velocity vector, ω (i.e., a form of angular

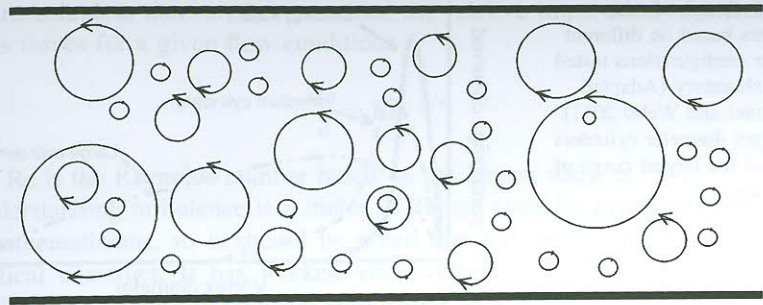


Fig. 5.1 Schematic of typical turbulent flows composed of vortices with different length and timescales

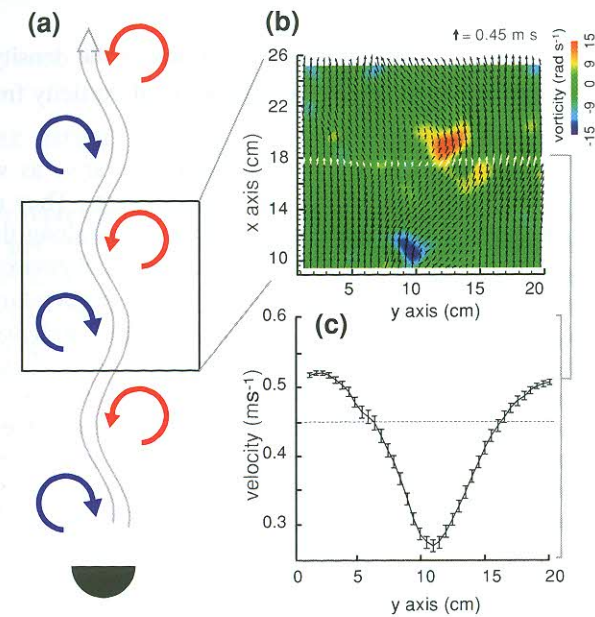
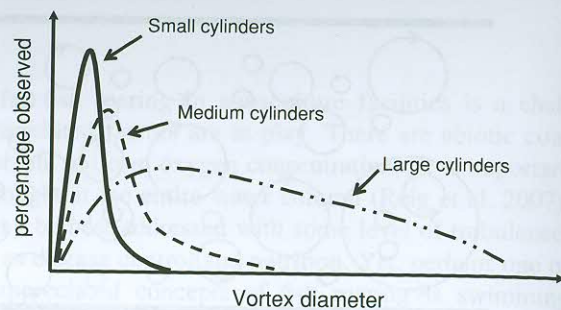


Fig. 5.2 **a** Schematic of a von Kármán vortex street behind a D-section cylinder, where blue represents clockwise flow and red represents counterclockwise flow. Wavy gray lines represent the velocity deficit in the midline of the cylinder wake where the average flow is slower than the free stream. **b** Color-coded vorticity (as in **a**) and velocity vector plot from experimental digital particle image velocimetry (DPIV) data. The length and orientation of the velocity vectors represent the magnitude and direction of the flow. One row of vectors is highlighted in white to demonstrate the velocity deficit in the midline of the wake. **c** When flow velocity (shown with standard error bars) for one row of vectors is averaged over time, the velocity deficit reveals itself to be about half of the velocity of the uniform flow (0.45 m s^{-1} , dashed line). Note that the flow is faster on the outside edge of the wake due to the direction of vortex circulation

Fig. 5.3 Range of eddy diameters based on different cylinder configurations tested in the laboratory (Adapted from Cotel and Webb 2011). The larger diameter cylinders produced the largest range of eddy sizes



velocity) and is generated through different physical processes. The vorticity equation provides the source terms for generating vorticity in aquaculture systems:

$$\frac{D\vec{\omega}}{Dt} = \nu \nabla^2 \omega + \frac{\nabla \rho \times \nabla \rho}{\rho^2} + \vec{\omega} \cdot \nabla \vec{U} \quad (5.1)$$

where ν is the kinematic viscosity, p the pressure, and ρ the density. $\nu \nabla^2 \omega$ represents the diffusion of vorticity, $\frac{\nabla \rho \times \nabla \rho}{\rho^2}$ the generation of vorticity from baroclinic torques, and $\vec{\omega} \cdot \nabla \vec{U}$ the stretching term.

The most significant and common physical processes arise as wakes behind objects in the flow and shear layers due to velocity gradients. They are due to (1) viscous dissipation due to the presence of boundary layers along the slopes and bottom of ponds or raceways; (2) baroclinic torque in marine environments (such as sea cages for saltwater species) where gravity acting on temperature and salinity gradients can create significant flows; (3) local stretching of vorticity in turbulent flows produces very intense vortices called “filaments of vorticity”. Over time and further downstream from a source of vorticity, the eddy composition of a flow develops increasingly finer scaled turbulence, until the smallest eddy size, λ_o , reaches the Kolmogorov scale (Kolmogorov 1941). The most common eddies found in these flows are of intermediate size, and are a product of the larger, initial vortices. The dynamics of these intermediate-sized eddies are not controlled by viscous dissipation. Nevertheless, eddies at the Kolmogorov scale are eventually damped by viscosity and their energy dissipated as heat. The full range of eddy sizes, in flow defined as fully developed, occurs when an inviscid core from which an eddy calves has disappeared and the viscous effects have spread throughout the fluid. The largest eddy size in fully developed flow is determined by the physical constraints of the system, such as the gyre filling the North Pacific Ocean delineated by the American and Asian continents, or raceway width and depth in aquaculture applications. The eddy composition of fully developed flow can be described as a frequency distribution of eddy sizes, with many small-sized eddies and few large-size eddies. Figure 5.3 illustrates how physical obstructions in the flow such as cylinder arrays manipulate the range of eddy sizes observed in turbulent flows for the same value of Reynolds numbers (Cotel and Webb 2011). The ratio of the largest to smallest eddy sizes is a function of Reynolds number, which

is a dimensionless number that quantifies the relative importance of inertial and viscous forces for a given flow condition:

$$\frac{\lambda_o}{\delta} = Re^{-3/4} \quad (5.2)$$

where Re is the Reynolds number based on the largest eddy, δ .

Understanding turbulence is a major challenge even for engineers, physicists, and mathematicians, so it should be noted that the inertial subrange idea is a theoretical construct. It has worked very well in engineering applications by providing a framework to compare eddy characteristics and to quantify turbulent flows. Therefore, this approach to turbulence is by no means a closed subject. Nevertheless, it is proving useful to classify turbulent situations to which fish react (Webb et al. 2009; Tritico and Cotel 2010). By analogy, the influential classic work in the 1960s and 1970s also used the theoretical construct of vortex sheets to develop ideas on fish swimming (Lighthill 1975; Newman and Wu 1975; Wu 1977).

5.2.2 Vortex Streets

Periodic flows represent a special case of eddy-dominated flows. Periodic flows have distinct and repeatable features more clearly identified than most turbulent flows, e.g., the Kármán vortex street (Fig. 5.2). These types of flow occur in the wake of stationary objects placed in uniform flow, due to separation and viscous effects. Eddies are shed from the object at a given frequency related to the value of the Strouhal number for that particular situation. The Strouhal number,

$$St = fd/U \quad (5.3)$$

is a useful dimensionless number describing oscillating flow phenomena where f is the eddy shedding frequency, d is the size of the object, and U is the flow velocity. The Reynolds number for these flows is in the turbulent regime but on the lower end of the spectrum so that the eddy size is constrained to a smaller range, making it possibly easier for fish to recognize, predict, and anticipate eddy trajectories superimposed on the background flow.

5.3 Quantifying Turbulence

The most common tool to measure flow in the field and laboratory is the acoustic doppler velocimeter (ADV). An ADV uses sound bouncing off particles to measure fluctuations in the magnitude and direction of water velocity in a very small volume—essentially one point—as a function of time. The sampling frequency

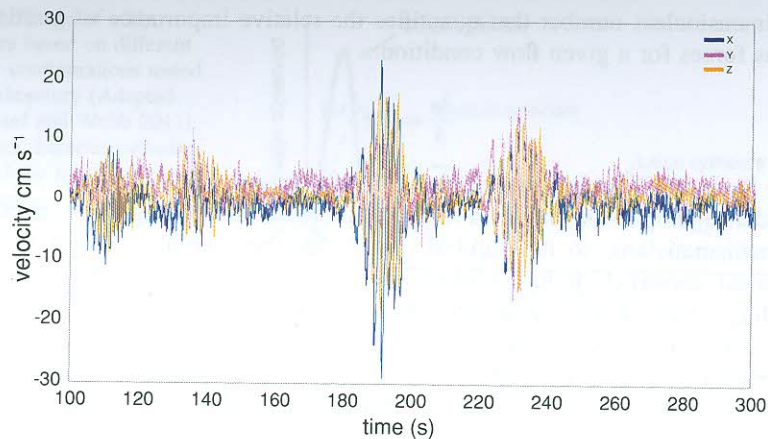


Fig. 5.4 Example of Acoustic Doppler Velocimetry time series data. Velocities in x, y, and z direction as a function of time for a turbulent wake

typically varies from a few Hz to several hundred Hz depending on manufacturer and instrument. ADV data consist of temporal signals of velocity in three directions, u , v , and w in x , y , and z direction, respectively. Various statistical descriptions relating to flow are calculated from the instantaneous u , v , and w values. Engineers most commonly use the root mean square (rms) velocity, u_{rms} , as a measure of mean flow, recognizing potential effects of velocity variation, and hence of turbulence. The turbulent velocity fluctuation, u' , is calculated from the mean square deviation in resultant velocity from the mean, numerically the statistic variance. The instantaneous resultant velocity, u_{inst} , is calculated from the three components of velocity u , v , and w as a function of time (Fig. 5.4). Average velocities \bar{u} , \bar{v} , \bar{w} are calculated from a time series of measurements over a long period, commonly two or more minutes.

5.3.1 Turbulence Intensity

A commonly used non-dimensional parameter relating mean speed and variance is the *Turbulence Intensity*, TI, (Odeh et al. 2002a; Pavlov et al. 2000; Sanford 1997) where:

$$TI = u' / (\bar{u}^2 + \bar{v}^2 + \bar{w}^2)^{1/2} \quad (5.4)$$

TI takes into account a speed-dependent aspect of stability. The velocity variance challenges stability while the momentum of a fish contributes to damping disturbances. As current speed increases through very low values, fish first orient to the flow (rheotaxis), therefore lowering drag and helping with station holding (Webb 1989). Threshold current speeds at which roach, *Rutilus rutilus*, first oriented to the flow were generally lower when turbulence intensities increased

(Pavlov et al. 2000). As current speed increases, many species of fish holding station on the bottom eventually slip and need to transition from a station holding behavior to free swimming (Arnold and Weihs 1978). Maximum and prolonged swimming speed also decreased as TI increased for many species such as perch, roach and gudgeon. Similarly, maximum burst speeds were reduced with increasing TI for roach. The effects of TI were larger for fishes from quieter-water habitats (Pavlov et al. 2000).

5.3.2 Turbulent Kinetic Energy

Another parameter commonly used to quantify turbulent flows is the turbulent kinetic energy (TKE) which measures the increase in kinetic energy due to turbulent fluctuations in the flow, where σ_u , σ_v , σ_w are the standard deviations of the instantaneous velocity in the x , y , and z directions, respectively:

$$TKE = 0.5(\sigma_u^2 + \sigma_v^2 + \sigma_w^2) \quad (5.5)$$

TKE is a good predictor of juvenile rainbow trout densities in flumes (Smith et al. 2006). The relationship between the energy in the flow and fish swimming kinematics is a challenging topic as the energy in the flow is coupled to the energy expended by the fish. No simple relationship is apparent. Of the two metrics, TKE proved the best predictor of fish density, with highest numbers at intermediate TKE in the case of trout swimming in a flume with various hydraulic regimes and geometric features (Smith and Brannon 2005). Observations in a natural trout stream showed that brown trout, *Salmo trutta*, occupy habitats with intermediate levels of turbulence (Cotel et al. 2006). These situations also have dome-shaped relationships between turbulence levels chosen versus current speed, consistent with the behavior of individual fishes in flumes.

It has also been suggested that measurements of flow gradients are more important than absolute measurements of flow variation. Spatial gradients would be associated with larger asymmetries than point effects when integrated along a linear dimension of a fish, and would be expected to amplify destabilizing forces. Thus, du/ds is thought to affect the location preferred by salmonids (Fausch and White 1986; Hayes and Jowett 1994), where u is the local velocity in a given direction and s the spatial coordinate in the same direction. $dTKE/ds$ has been shown to affect salmonid density at a stream-reach level (Crowder and Diplas 2002).

5.4 Turbulence in Raceways: Flow Speed

Some of the chief hydraulic concerns in the design of raceways have been adequate water supply through a system of pipes, pumps, fittings, etc., and creating an average velocity high enough throughout the facility to keep issues of poor water

quality under control (Burrows and Chenoweth 1970). In open water farms, a maximum speed of 5 cm/s is preferred to ensure adequate food availability (Pillay and Kutty 2005). Moderate speed in raceways is correlated with more homogeneity in growth and size distributions of salmonids (Jorgensen et al. 1993). The growth rate for fish swimming in flows with velocity of the order of 1.0–1.5 BL/s (body length per second) is significantly higher than for fishes swimming at higher speeds or fishes reared in standing water.

5.4.1 Oxygen Level

Oxygen levels need to be kept at adequate levels. In raceways, the bottom of the water column can become an area of low oxygen concentration leading to an unhealthy environment for sedentary, benthic species. Reig et al. (2007) showed that effluent concentrations do not provide accurate measurements of the conditions fish are subjected to, and in fact provide consistently higher oxygen concentration measurements than those typically encountered by fish. Finer spatial measurements of where fish are located are essential in accurately assessing their environment. Simple changes to tank design can prove to be significant, such as the addition of more inlets and outlets to increase circulation and mixing throughout raceways and tanks (Timmons et al. 1998).

5.4.2 Waste

Wastes need to be evacuated from tanks, ponds, or raceways without increasing stress levels in fishes. CO₂ and NH₃ have negative effects on the growth. For example, CO₂ levels higher than 30 mg/L are detrimental to growth rate of salmonids (Fivelstad et al. 1998). Ammonia production is also a parameter to consider for water quality and its impact on growth rate. In addition, bacterial counts have to be kept low to reduce mortality rates. Because of the design of some of these systems, wastes from overfeeding and metabolites accumulate in slow velocity regions or corners. For circular tanks, mechanical cleaning devices (McRobbie and Shinn 2011) have been put in place at the bottom to sweep wastes toward a central column where they get aspirated by a low-pressure system. Note that fish have been observed in the presence of such a device and when compared to a controlled experiment no additional stress was reported. Other systems have been designed to eliminate the wastes from a center drain (Timmons et al. 1998). By maintaining appropriate levels of turbulence, pressure differences at specific locations in rearing tanks can help in the removal of wastes.

5.4.3 Disease

Flowing water has been found to be an effective treatment in keeping Ichthyophthiriasis, or ich, under control (Bodensteiner et al. 2000). Ich is a common disease found in aquaculture systems causing significant mortality. Chemical treatments have been tried over the years but care needs to be taken as the treated fish will enter the food chain and could ultimately affect human health. Bodensteiner et al. (2000) found that increased water velocity and more importantly turnover rate greatly reduced fish mortality. This provides a non-toxic solution to itch that is also economically viable as water depth can be used as the tuning parameter in order to achieve the appropriate range of velocity and turnover rate.

Previous work has linked turbulent flows to the survival rate of bacteria such as *E. coli* (Cotel and Semrau 2003) or zebra mussel larvae (Rehmann et al. 2003). A key factor is the high strain rate produced at small length scales in strongly turbulent flows. For example, in the experiments performed by Cotel and Semrau (2003), the Reynolds number ranged from 3,000 to 56,000, the measured near-field concentration of *E. coli* was reduced by at least 40 %. A similar dynamics was observed for zebra mussels in turbulent flows; specifically when the mussel shell size was of the order of 90 % of the small eddy size, a higher mortality rate was measured. Typical Reynolds numbers in raceways will be of the order of 10⁶, assuming an average speed of 10 cm/s and a channel width of 1 m. This in turn implies a Kolmogorov scale (defined earlier) of the order of a few microns, which is typically the size of bacteria, and a very large strain rate at that size. The strain rate will be large enough to affect growth and even survival rates for a wide range of bacteria. It is worth noting that the large strain rate is felt at the small scale and not at the fish scale; therefore, the parameters can be optimized so that no negative effects are imposed on swimming fish. In addition, by placing nozzles and jets in strategic locations along raceways or in circular tanks, one might be able to achieve multiple goals at once.

5.5 Effects of Turbulence on Fish

Any time force is applied to a fluid, either when water moves past a stationary object or when a fish undulates its body through water, vortices are generated. Since most aquaculture fish are suspended in the water column, they are subjected to these three-dimensional forces. Biologists have long observed that fishes living in current-swept habitats will associate with structures such as boulders and woody debris to take advantage of velocity refuges (Bustard and Narver 1975; deGraaf and Bain 1986; Hartman 1965; Shirvell and Dungey 1983). In nature turbulent flows are a valuable and limited resource and are often associated with resting positions and foraging opportunities. Yet we still know very little about the interactions between structure shape and size, species, body size, and flow speed. Progress has been made in the last several years in understanding the mechanisms of how fish relate to turbulence, mostly through careful laboratory studies.

5.5.1 Saving Energy

Noted ichthyologist Charles Breder was perhaps the first to articulate the potential benefits of swimming in turbulent flows (Breder 1965). He suggested that fish swimming among vortices may be “taking advantage of the lessened flow downstream of the side of the vortex which is moving countercurrent.” Since then numerous field and laboratory studies have shown that fish can exploit turbulence to enhance their swimming performance (Breder 1965; Coutant and Whitney 2000; Fausch 1993; Gerstner 1998; Herskin and Steffensen 1998; Hinch and Rand 2000; Liao et al. 2003a, b; McMahon and Gordon 1989; Montgomery et al. 2003; Shuler et al. 1994; Smith and Brannon 2005; Streitlien and Triantafyllou 1996; Sutterlin and Waddy 1975; Webb 1998; Weihs 1973).

5.5.1.1 Station Holding

Fish can take advantage of regions of reduced flow velocity behind bluff bodies. In this case, the average velocity in the turbulent wake is reduced relative to its steady-state condition prior to interaction with the bluff body. When fish seek refuge from the main current, they can be described as “flow refuging” (i.e., the ability to exploit regions of reduced flow velocity) (Webb 1998). This behavior usually occurs near the interface between a fluid and a solid, and can present an opportunity for station holding, which is the ability to maintain position in a current relative to the Earth’s frame of reference without actively swimming (Gerstner 1998). This is the most commonly implicated mechanism of flow exploitation in the fisheries literature (Heggenes 2002; McMahon and Gordon 1989; Puckett and Dill 1984; Shuler et al. 1994).

Bow wake and entraining When a cylinder is placed in a laboratory flume, a high pressure region (i.e., stagnation point where fluid velocity is zero) is established at the upstream side of the cylinder. A stable low pressure suction region is established (i.e., attached eddy) at the downstream side of the cylinder (Vogel 1994; Zdravkovich 1997), both of which fish can exploit. For example, compared to fish swimming in uniform flow (Fig. 5.5a), fish holding station in the reduced flow region of the bow wake (Fig. 5.5b) exhibit very little body undulation (Liao et al. 2003a). Similarly, when fish entrain near the low-pressure suction region of the cylinder (Fig. 5.5c) they make no regular axial swimming motions and yet can still balance thrust and drag forces to hold station relative to the Earth’s frame of reference. When fish entrain they position their heads close to, but not touching, the cylinder and their fins are continuously in motion without any discernable pattern (Przybilla et al. 2010; Webb 1998). Presumably, fish are taking advantage of the attached eddy and making fine scale corrections with their fins. Although no axial muscle activity measurements have been made, the drastically reduced body motions while in the bow wake or entraining strongly suggest that these positions are energetically favorable. At times, swimming in the bow wake or entraining

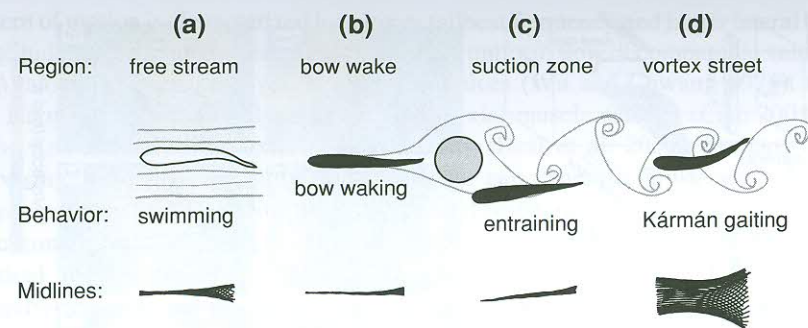


Fig. 5.5 Several distinct regions that fish hold station around a cylinder in flow, along with superimposed body midlines for one tailbeat cycle below. **a** A fish swimming in uniform flow is shown for comparison. **b** Fish can swim in the high pressure bow wake region in front of the cylinder. **c** Fish can entrain in the suction region just downstream of the cylinder. **d** Fish can Kármán gait in the vortex street located further downstream (>2 cylinder diameters) and behind the cylinder. In all cases, fish are holding station in a current relative to an external reference point

(Fig. 5.5b, c) are preferred over swimming in uniform flow or in the vortex street behind a cylinder (Fig. 5.5a, d) (Liao et al. 2003a; Webb 1998). Video analyses reveal that fish often spend the entire duration of the experiment in the bow wake or entraining, and if displaced they respond by swimming through the cylinder wake to resume position (Liao 2006; Liao et al. 2003a).

Other examples of station holding By systematically subjecting cod (*Gadus morhua*) to substratum ripples of different natural heights and spacings in a laboratory flume, Gerstner (1998) was able to identify a specific flow range that elicited station holding behavior. Fish would be displaced if flow velocity exceeded the upper limit of this range, and avoid substratum ripples when velocity was slower than the lower limit of this range. Similarly, Webb (1998) found that fishes only preferred to swim behind horizontally oriented cylinders approximating submerged tree branches at intermediate flow speeds. During periods of fast flow fish were displaced from the cylinder and during slow flow they avoided cylinders altogether. A preference to exploit a specific range of turbulence reveals that fish can be quite sensitive to turbulent cues. Indeed, Smith (2003) found that for juvenile rainbow trout (*Oncorhynchus mykiss*) swimming at a constant average flow velocity, differences in turbulence level can provide sufficient information to discriminate between habitats.

5.5.1.2 Kármán Gaiting

The second mechanism of energy reduction while swimming involves recapturing the energy of discrete, environmentally generated vortices. Vorticity control is a relatively new paradigm in fish locomotion (Anderson 1996; Streitlien and Triantafyllou 1996; Triantafyllou et al. 2002, 2000). Harnessing the energy inherent in turbulent environments can be substantial; it has been experimentally and theoretically demonstrated

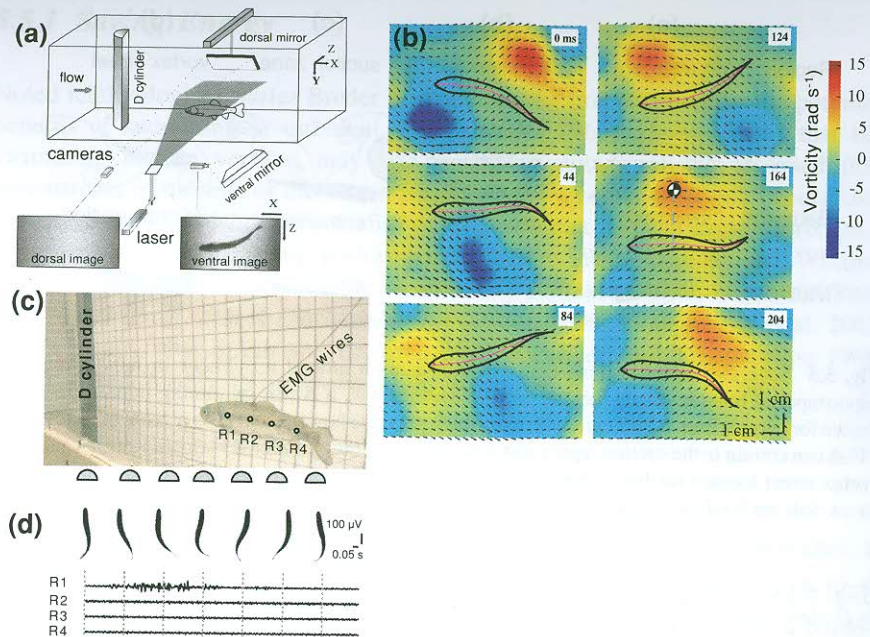


Fig. 5.6 Fish use less muscle when exploiting vortices shed behind a cylinder. **a** Experimental setup to simultaneously visualize vortices shed from a D-section cylinder using DPIV and the body kinematics of station holding trout. **b** DPIV time series showing the interaction of a trout with cylinder vortices. Time series of the midline (purple) and silhouette (black) of the body superimposed onto a color-coded vorticity and velocity vector (black arrow) plots of the cylinder wake. Red and blue represent clockwise and counterclockwise vorticity, respectively. **c** Rostro-caudal array of red axial muscle recordings (R1-4) for a trout Kármán gaiting behind a cylinder placed in a 3.5 L s^{-1} flow, where L is the body length. **d** Typically, over the course of one tailbeat cycle the fish only activates its anterior-most red muscles (R1)

that thrust can be generated entirely passively by a foil when placed in an oscillating flow (Anderson 1996; Beal 2003; Bose and Lien 1990; Wu and Chwang 1975). The ability to extract energy from vortices can thus greatly enhance propulsive efficiency (Anderson 1996; Golpalkrishnan et al. 1994; Streitlien and Triantafyllou 1996). This is largely because as the lateral component of the flow heaves a foil from side to side, the foil's chord maintains a favorable angle of attack with respect to the incident flow and facilitates both lift and thrust production (Bose and Lien 1990; Wu and Chwang 1975). This depends critically on an appropriate ratio of vortex diameter to fish length as well as low levels of background turbulence (Liao et al. 2003a, b; Triantafyllou et al. 2002). When fish hold station in a vortex street behind a cylinder for several swimming cycles they can exploit the energy of vortices (Fig. 5.6), a behavior called “Kármán gaiting” (Liao et al. 2003a). Trout reveal varying abilities to synchronize their body motions to altered shedding frequencies of cylinder vortices. The wake wavelength (i.e., the downstream spacing between successive vortices) is consistently shorter than body wavelength, and may have an effect on head angle and body curvature. This unique

pattern of motion is characterized by a lower tailbeat frequency and larger lateral body amplitudes and curvatures than for swimming in uniform flow of comparable velocity.

Analogous to a passive foil exploiting vortices (Wu and Chwang 1975), trout can Kármán gait temporarily with very little axial muscle activity (Liao 2004) or, if the fins are active, no axial muscle activity (Beal et al. 2006). Perhaps more surprising, dead trout towed behind a cylinder can generate thrust passively and move upstream on a slack line when the natural resonance of their body allows for synchronization with vortices (Beal et al. 2006; Liao 2004). An analogy to the nautical mechanism of “tacking” was proposed to explain the Kármán gait, whereby the alternating camber and angle of a flexible body generates thrust passively (Liao et al. 2003a). This reveals that given proper musculoskeletal compliance and body position in the vortex street, at times no axial muscle activity is needed to maintain station or even move upstream in turbulent flows. When muscle recordings and flow visualization techniques are employed in the laboratory, it is clear that trout holding station behind a cylinder are not just seeking refuge in reduced flow or using a propagating wave of muscle activity, but using the energy of the vortices (Liao et al. 2003a, b).

Previous results therefore indicate that the relative size of eddies and fish is critical for vortex exploitation. Destabilizing disturbances in eddy-dominated flow are related to the relative size of eddies compared to the size of a fish (Cotel and Webb 2011). Thus, eddies very much larger than fish size (e.g., large gyres, such as the North Pacific Gyre) are certainly important in dispersal and migration, but it is likely that fish respond to them in the same way as they would to uniform flow. At the opposite end of the spectrum, eddies that are an order or magnitude smaller than the body length will have a minimal impact on swimming. In an aquaculture setting, they may however contribute to the health of the system of other ways by maintaining high dissolved oxygen levels. Studies indicate that the ratio of cylinder diameter to body length needs to fall between 1:12 and 1:2 for fish to be attracted to the wake (Liao et al. 2003a; Montgomery et al. 2003; Sutterlin and Waddy 1975; Webb 1998).

5.5.1.3 Oxygen Consumption in Turbulence

Kármán gait kinematics differ from bow waking or entraining; the latter shows no correlation to the expected vortex shedding frequencies when cylinder size and flow speed are varied (Liao et al. 2003a; Przybilla et al. 2010; Webb 1998). As flow velocity increases from rest past a cylinder, swimming costs should be low as the vortex street develops and fish begin to Kármán gait. When trout are unable to utilize vortices in a vortex street, such as when encountering extreme wake wavelengths or high levels of background turbulence, axial muscle activity is predicted to increase as propulsive movements are introduced. Above a certain vortex shedding frequency, swimming costs may be expected to rise as the fish becomes unstable and ultimately abandons the cylinder wake.

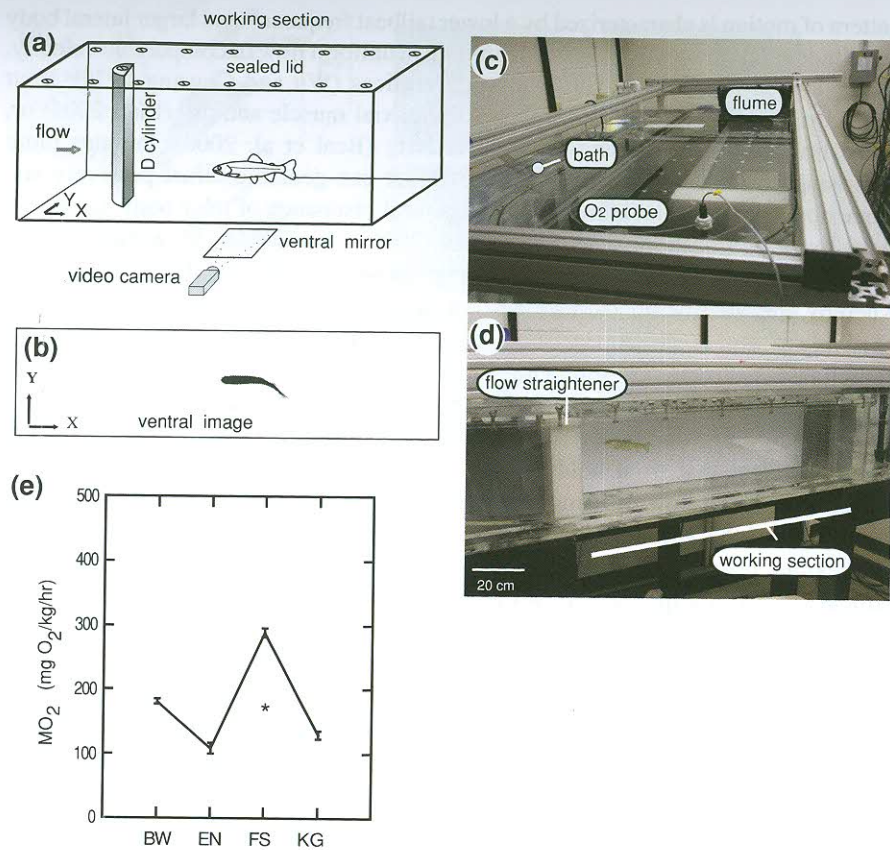


Fig. 5.7 Fish swimming in turbulent flow may use less energy than fish swimming in the free stream. **a** Schematic of experimental setup. Fish are sealed in a flume respirometer in which a cylinder can be mounted. **b** A video camera pointed at a 45° front-surface mirror verified the position of the fish during the experiment. **c** Image of the flume respirometer illustrating the position of the oxygen probe (black arrowhead) and the drilled ports for cylinder placement (white arrowheads). The flume is submerged in an ambient water bath (white dot) that is maintained at 100 % oxygen saturation, which serves as a source to flush the flume between experimental trials. **d** Lateral view of the working section of the flume. **e** Statistical comparison of the rate of oxygen consumption (MO₂) values between Kármán gaiting (KG) and other behaviors at 3.5 L s⁻¹, where L represents body length. Compared to other behaviors at this speed, KG requires significantly less oxygen than swimming in the free stream (FS, 47 %) and bow waking (BW, 73 %), but requires more oxygen than entraining (EN, 116 %). KG fish use 21 % less oxygen compared to fish swimming in the free stream at half the flow speed (i.e., 1.8 L s⁻¹, asterisk), which is the average flow speed found behind the cylinder. This supports the original hypothesis that KG fish save energy by exploiting vortices in addition to receiving the benefit of the velocity deficit behind a cylinder (Liao et al. 2003a). Values are reported as the mean ± the standard error

Measuring the consumption of oxygen (MO₂) during swimming most directly reveals the energetics of fish locomotion. Station holding rainbow trout have substantially different oxygen requirements based on which hydrodynamic

microhabitats they choose to occupy around a cylinder. Certain swimming behaviors are more energetically costly than others, both across behaviors at one flow velocity as well as across speeds for a single behavior (Fig. 5.7). For example, at intermediate swimming speeds entraining shows the lowest MO₂, followed by Kármán gaiting, bow waking, and then free stream (i.e., uniform flow) swimming (Taguchi and Liao 2011). As flow speed increases the costs associated with cylinder positions change in complex ways. At times, MO₂ actually decreases as flow velocity increases. Entraining demands the least oxygen at low and intermediate speeds, while bow waking requires the least oxygen at high speeds. Consequently, a behavior at one speed may have a similar cost to another behavior at another speed. The effect of body and fin shape most likely determines the complex patterns of oxygen consumption for fish negotiating turbulence. It is worth noting that the most energetically favorable position to hold station around a cylinder may not result in the best farmed product. Indeed, the active use of the axial body and multiple fins as control surfaces to negotiate turbulence and provide stability may produce animals with a better muscle texture.

5.5.2 The Cost of Turbulence

While the benefit of understanding how fish can benefit from turbulence is an attractive topic in designing aquaculture facilities, there is also a need to understand how turbulence can be detrimental to fish swimming. Though this topic is not treated in detail here, there have been studies showing that fishes swimming in turbulent flows can increase their cost of locomotion due to the stability requirements in negotiating complex, three-dimensional flows (Enders et al. 2003; Hinch and Rand 1998; Pavlov et al. 1982, 2000; Webb 1998). In one study, juvenile Atlantic salmon (*Salmo salar*) swimming at a constant average flow velocity increased their oxygen consumption when exposed to turbulence, which was generated as wide fluctuations of flow velocity around a mean flow value (Enders et al. 2003). This increase in cost was especially dramatic for trials conducted at higher mean flow velocities. Fishes also exhibit increased respiratory rates and a decreased ability to perform escape behaviors after experimental turbulence trials (Odeh et al. 2002b). Vortices of intermediate size (>0.5 body lengths) are associated with negative effects such as reduced swimming performance, and can cause displacements triggering stability failure (Pavlov et al. 2000; Trítico and Cotel 2010; Webb et al. 2009).

5.6 Conclusion

This chapter summarizes a growing body of work on fish swimming in turbulence which can be applied to aquaculture practice. Since turbulence can improve oxygen mixing and thus water quality for sedentary benthic species, adding strategic inlets

and outlets to increase circulation while providing station holding regions behind geometric objects may improve the yield and market quality of certain species. Likewise, raceways may be designed to generate fish-friendly flows that would double to prevent wastes and bacteria from accumulating in slow velocity regions or corners. Flowing water provides a non-toxic, effective treatment in keeping certain diseases such as *Ichthyophthiriasis* under control (Bodensteiner et al. 2000).

We demonstrate that the effects of turbulence on fishes can be beneficial or detrimental, depending on the specific features of the flow environment. For studies involving cylinder wakes, a systematic exploration of the lower and upper limit of vortex size at which fish can no longer entrain or Kármán gait is needed. Similarly, the behavior of fish in the wake behind different orientations and aggregations of geometric objects may prove beneficial in energy savings. There is an extensive body of work in the hydrodynamics literature that establish the conditions that generate specific flow phenomena (Gerrard 1966; Grass et al. 1991; Zdravkovich 1997), and this information can be used to initiate novel turbulence designs in raceways. The applications of understanding how fish associate with turbulence are especially timely and important given the state of fisheries worldwide. The design of the next generation of aquaculture facilities would benefit by considering both the abiotic and behavior implications of turbulence..

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