SYMPOSIUM

Turbulence, Temperature, and Turbidity: The Ecomechanics of Predator–Prey Interactions in Fishes

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Synopsis Successful feeding and escape behaviors in fishes emerge from precise integration of locomotion and feeding movements. Fishes inhabit a wide range of habitats, including still ponds, turbulent rivers, and wave-pounded shorelines, and these habitats vary in several physical variables that can strongly impact both predator and prey. Temperature, the conditions of ambient flow, and light regimes all have the potential to affect predator–prey encounters, yet the integration of these factors into our understanding of fish biomechanics is presently limited. We explore existing knowledge of kinematics, muscle function, hydrodynamics, and evolutionary morphology in order to generate a framework for understanding the ecomechanics of predator–prey encounters in fishes. We expect that, in the absence of behavioral compensation, a decrease in temperature below the optimum value will reduce the muscle power available both to predator and prey, thus compromising locomotor performance, suction-feeding mechanics of predators, and the escape responses of prey. Ambient flow, particularly turbulent flow, will also challenge predator and prey, perhaps resulting in faster attacks by predators to minimize mechanical instability, and a reduced responsiveness of prey to predator-generated flow. Reductions in visibility, caused by depth, turbidity, or diel fluctuations in light, will decrease distances at which either predator or prey detect each other, and generally place a greater emphasis on the role of mechanoreception both for predator and prey. We expect attack distances to be shortened when visibility is low. Ultimately, the variation in abiotic features of a fish's environment will affect locomotion and feeding performance of predators, and the ability of the prey to escape. The nature of these effects and how they impact predator–prey encounters stands as a major challenge for future students of the biomechanics of fish during feeding. Just as fishes show adaptations for capturing specific types of prey, we anticipate they are also adapted to the physical features of their preferred habitat and show a myriad of behavioral mechanisms for dealing with abiotic factors during predator–prey encounters.

Introduction

Capturing prey and escaping from predators are two fundamental aspects of an animal's survival, thus representing key aspects of fitness. Both rely on sensory feedback, motor control, musculoskeletal function, and integration among higher-level complex systems, such as locomotion, vision, and feeding. For example, a predator must employ its locomotor system to approach the prey, assuming the prey is not within striking distance upon detection (Higham 2007b). The prey must detect the predator and decide whether to initiate an escape response, move to a hiding place, or simply monitor the movements

of the predator. If the predator attacks, the goal of the prey is to successfully evade the strike. All of these complexities are amplified by ever-changing environmental conditions (Fig. 1), although the intricacies are poorly understood. Because the capture of aquatic prey and evasion of predators are intimately dependent on abiotic and biotic factors, an ecomechanical approach, which combines biomechanics and ecology (Denny and Helmuth 2009), is extremely valuable. Ecomechanics strives to utilize physics to understand and make predictions for how species or individuals might respond to change (Denny and Gaylord 2010). Predator–prey
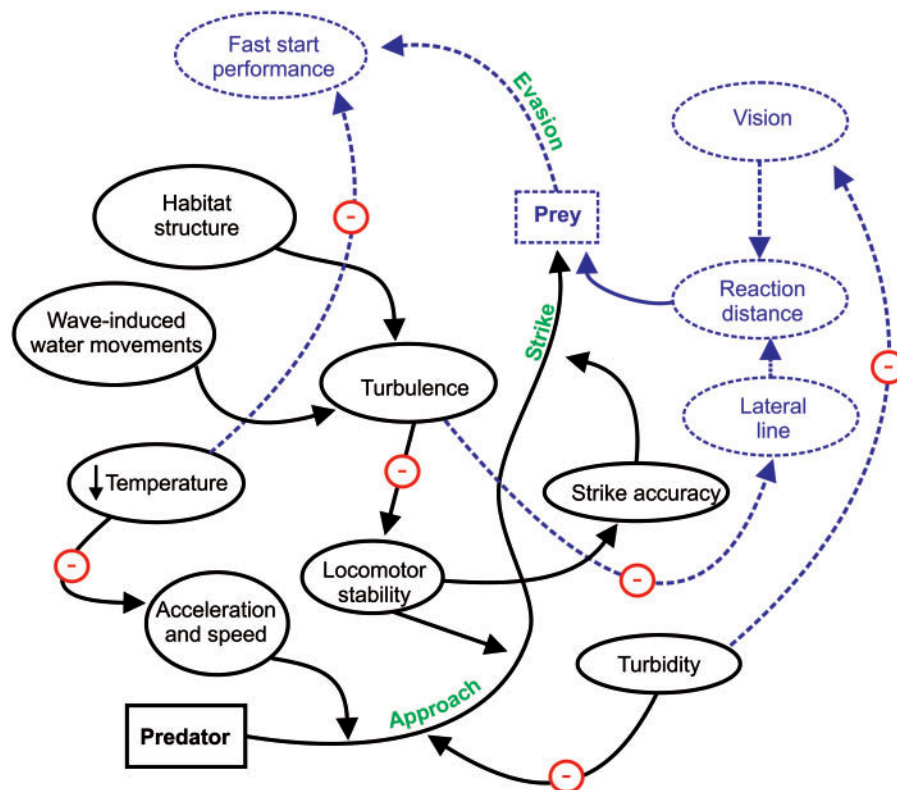
Fig. 1 A schematic of some of the factors that can impact the capture of prey and the evasion of predators in fishes. The solid ellipses refer to the predator, and dashed ellipses refer to the prey. Environmental factors, including turbulence, turbidity, and temperature, will generally have negative impacts (negative signs) on both the predator and prey during an encounter, but the magnitude of these impacts will depend on the situation, species, and whether the fish is a predator or a prey. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

encounters in fishes are ideal for examining the relationships between ecology and biomechanics, given that fishes occupy a wide range of habitats, exhibit immense morphological diversity, and utilize multiple complex systems both for capturing prey and for evading predators (Helfman et al. 2009).

Aquatic environments impart a number of physical constraints on the motion of animals, and these constraints change in response to temperature, turbidity, flow regime, and many other factors (Fig. 2). The goal of this article is to explore the potential insights that may be gained into predator–prey dynamics through the effects of these abiotic factors. We review the effects of temperature on feeding and locomotion in predatory fishes and the fishes that are their prey, the effects of the complex ambient flow regimes such as when high flows encounter fixed physical structures, and the effects of reduced levels of light caused by turbidity, deep water, and diel variation in light. We develop a framework for quantifying predator–prey encounters among fishes in nature, something that is rarely done in experimental biology. Finally, we discuss the pathway toward more

ecologically-relevant laboratory studies of predator–prey encounters among fishes.

Integration of locomotion and feeding in fishes

The majority of fishes capture their prey by suction (Lauder 1982; Ferry-Graham and Lauder 2001; Wainwright et al. 2007, 2015), which occurs when the buccal (mouth) cavity is rapidly expanded, thereby generating a negative pressure inside the mouth relative to the surrounding fluid, and driving nearby water and prey into the fish's mouth (Lauder 1980; Muller et al. 1982; Day et al. 2005, 2007, 2015; Higham et al. 2006a, 2006b). Although suction feeding is powerful and produces very high velocities and forces, it only impacts water within a single gape-diameter from the mouth (Alexander 1967; Day et al. 2005) due to the exponential decay of suction with distance (Day et al. 2005, 2007; Holzman et al. 2008). Therefore, locomotor movements are almost always employed during successful attempts at feeding (Rand and Lauder 1981; Webb 1984; Wainwright
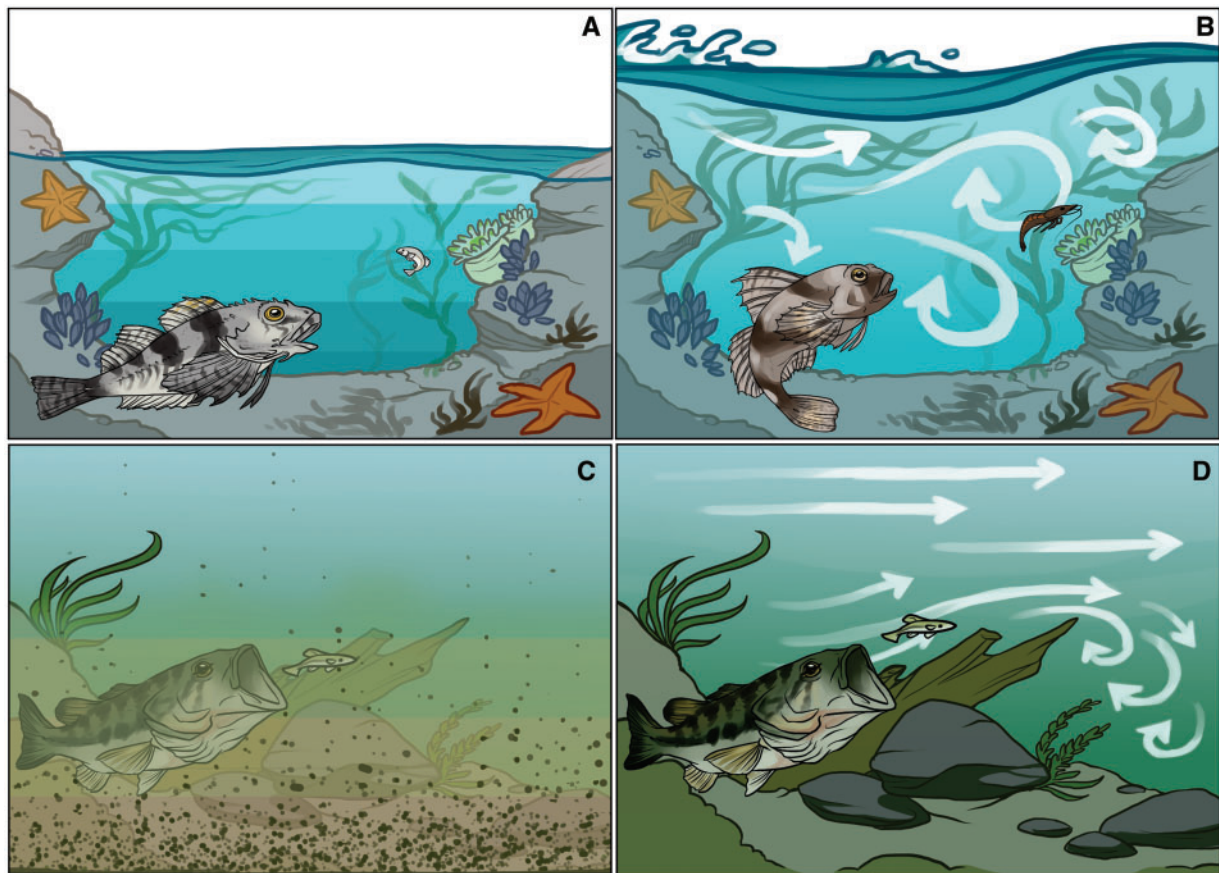
Fig. 2 Variables commonly encountered in natural environments (tide pool: **A** and **B**; river: **C** and **D**), including temperature gradients (A and C, different shades of color), turbulence (B and D), and turbidity (C). The tide-pool habitat varies over time as the tide recedes (A) and advances (B), whereas a riverine habitat exhibits more constant flow.

et al. 2001; Higham et al. 2005a, 2005b, 2007; Higham 2007a, 2007b; Rice and Hale 2010; Kane and Higham 2011). Environmental conditions, including temperature, ambient flow, and level of ambient light, will impact these locomotor movements toward the prey, as well as the ability to detect and capture the prey (Domenici et al. 2007). The nature of integration of locomotion and feeding also varies among species, and among different types of prey (Rice and Hale 2010; Kane and Higham 2015), suggesting that environmental conditions will differentially impact the locomotor and feeding systems of fishes, which may then alter the integration between these systems.

The accuracy of a strike is essential for successful feeding by fishes (Drost 1987; Coughlin 1991; Higham et al. 2006a; Higham 2007b; McLaughlin et al. 2000; Nauwelaerts et al. 2008; Kane and Higham 2014), and depends on many factors. A recent study examined the three-dimensional kinematics of three species of centrarchid fishes and related accuracy to success. They found that accuracy

explained 52.7% of successful captures, and predators were 30 times more likely to successfully capture prey with one standard deviation increase in accuracy (Kane and Higham 2014). Any variable that destabilizes locomotor movements, decreases the accuracy of a strike, or limits the ability to detect hydrodynamic disturbances has the potential to make successful capture of prey more difficult (Fig. 1). We explore these variables, and their potential impacts, below.

What we know about the evasion of predators

Even with predators employing suction, prey fishes are remarkably effective at evading capture. Startled prey may evade predators by initiating a rapid maneuver called the fast-start escape response, or simply "fast-start". To execute this maneuver, a fish rapidly curls its body in to a C-shape (stage 1) before unfurling the body in the opposite direction (stage 2) and rapidly swimming away from the predator (stage 3) (Eaton et al. 1977). All stages of the fast-start

displace the prey from its original location (Tytell and Lauder 2008), resulting in nearly instant evasive motion. Laboratory experiments have shown the fast-start to be very effective against predatory fishes. For example, zebrafish larvae evaded 70% of attacks from adult zebrafish (Stewart et al. 2013), fathead minnows evaded over 70% of attacks both from smallmouth bass and from rock bass (Webb 1982), and bluegill sunfish escaped 97% of attacks by largemouth bass (Webb 1986).

In order for the fast-start to be effective, the prey must first detect the predator's strike. Several sensory modalities may trigger a fast-start, such as vision (Dill 1974), hearing (Zottoli 1977; Fuiman et al. 1999), and mechanoreception (Blaxter and Fuiman 1989; Liu and Fetcho 1999). Of particular importance to prey is the lateral line system, which is sensitive to flow and can detect the subtle water disturbances ahead of approaching predators (Fig. 3) (Stewart et al. 2013) and trigger a fast-start with a response latency of only 4 ms (Liu and Fetcho 1999). Vision can also be important to prey by allowing fishes to search for predators from a distance, when conditions permit (Cronin 2005). Irrespective of the triggering stimulus, the escape of a prey fish ultimately depends on its ability to detect the predator, respond quickly (Fuiman et al. 2006) from the appropriate distance (Scharf et al. 2003; Stewart et al. 2013), and accelerate rapidly (Webb 1976; Domenici and Blake 1997) in the correct direction (Domenici et al. 2011). However, nearly all previous studies on the evasion of predators by fish have occurred in a tank containing clear and still water, making it unclear how biotic and abiotic environmental conditions affect the detection of predators and the performance of fast-starts.

The role of abiotic factors in predator–prey encounters

Temperature

Muscles power the expansion of the buccal cavity during the capture of prey, the swimming movements of the predator toward the prey, and the escape movements of the prey away from the predator. Muscle power is equal to force multiplied by shortening velocity, and the latter typically decreases as temperature drops (Ranatunga 1982; Josephson 1993). This decrease is, in part, due to slower release of Ca^{2+}, slower diffusion of Ca^{2+} to the actin and myosin, and slower reuptake of Ca^{2+} by the sarcoplasmic reticulum (Brill and Dizon 1979). This ultimately results in slower cross-bridge cycling. Based on this basic principle, we expect that the output of

power both of locomotion and of feeding will become greater with increasing temperatures up to the optimal temperature and decrease rapidly as temperatures are elevated above the optimal value (Donley et al. 2007). For both the suction-feeding strike and an escape response, peak power will occur at the species' optimal temperature and fall off at temperatures above and below that value.

The effects of temperature on locomotion may have more influence on a prey's success in escaping than on a predator's ability to feed. Even subtle decreases in locomotor performance greatly hinder a prey fish's ability to survive an attack. For example, guppies with an increase in fast-start performance of only a single standard deviation were reported to have a three-fold increase in their chances of evading a predator's attack (Walker et al. 2005). Even if temperature only slightly affects locomotor performance, such changes may drastically influence the ability of prey to escape. It should also be noted that, in most cases, the predatory fish is the one that initiates a predator–prey encounter (Weihs and Webb 1984). This requires the evasive prey to react after the predator has a head-start, often once the predator has already achieved a high speed (Seamone et al. 2014; Stewart et al. 2013). Because the prey's escape critically depends on its timely detection of the predator, followed by rapid acceleration (Webb 1976), even subtle effects of decreased temperature on swimming performance may further compromise the already disadvantaged prey (Fig. 1).

There are several lines of evidence that suggest locomotor movements are hindered by decreasing temperatures, although it is important to note that, after a period of acclimation, fishes have some ability to compensate for acute decreases in temperature, within a certain range (reviewed by Domenici and Blake 1997). During fast-starts at 15°C, the short-horned sculpin (*Myoxocephalus scorpius*) exhibits greater velocity (stage 2), greater maximum velocity, greater tail-beat amplitude, and greater strike distance when acclimated at 15°C compared with 5°C (Beddow et al. 1995). Although it appears that changes in temperature can impact velocity and acceleration of locomotor movements, the impact of temperature may also play an important role in the latency of escape, and therefore in the vulnerability of the prey (Domenici and Blake 1997).

The impact of temperature on locomotion is just one piece of the puzzle. The impacts of temperature on feeding are less understood, but they generally align with studies on locomotion. For bluegill (*Lepomis macrochirus*) capturing prey in water of different temperatures (18°C, 24°C, and 30°C), the time
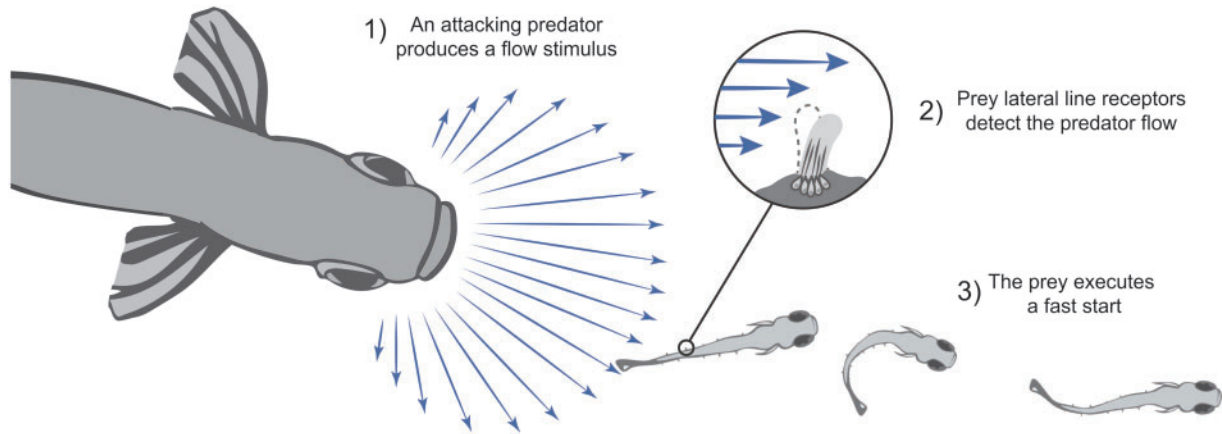
Fig. 3 Prey fish use the lateral-line system to detect approaching predators in still water. Predatory fish disturb the water ahead of themselves while swimming. When approaching prey, this disturbance provides a mechanical stimulus to the prey's lateral line, which may trigger a fast-start in an attempt to escape. Previous work in still water has shown that the sensing of flow is crucial for evading predators, but it is unclear how different environmental conditions, such as turbulent water, may affect the ability of prey to detect flows generated by the predator. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

to maximum gape, time to maximum depression of the lower jaw, and time to closing of the mouth, among other variables, increases with decreasing temperature (Wintzer and Motta 2004). Mouth-opening movements of largemouth bass are also slower at lower temperatures (DeVries and Wainwright 2006). Despite this, the impact of temperature in both species was less than expected, suggesting that the fish were increasing the number of motor units recruited for opening the mouth at lower temperatures, in order to ameliorate the negative impacts on muscle contractility. This illustrates the potential for behavioral compensation for some inevitable physical constraints. It is difficult to know whether an animal is performing maximally at any given time, which means there might be room for compensation as environmental variables change. Finally, the negative impacts of temperature changes can be circumvented by the use of elastic recoil mechanisms during feeding (Anderson and Deban 2010; Higham and Irschick 2013), which has been observed in multiple species of fishes (Van Wassenbergh et al. 2008, 2009).

Few situations rival the diel fluctuations in temperature that occur in tide pools, where water temperature can increase dramatically over short periods of time during the day, as the pool is isolated at low tide (Fig. 2). For example, tide pools in southern California can exhibit temperatures that exceed those of the surface water of the subtidal zones by 10°C (Davis 2001). When the tide pool is engulfed by the rising tide, there will be a period of time when the fishes from the tide pool will have an elevated temperature relative to those outside the pool

(Fig. 2). This potential for different body temperatures might amplify differences in the ability to capture prey or evade predators, given that increases in temperature, to a point, typically result in increases in power output. Thus, there might be a short period of more frequent attempts by fishes within the tide pools to capture prey.

When temperature decreases, water viscosity increases, causing greater resistance to movement. The combined effects of temperature on muscle contractility and on the viscosity of water make it somewhat challenging to assess which is causing a decrease in whole-organism performance. However, adding substances such as dextran allows viscosity to be manipulated independently of temperature. Adult goldfish (*Carassius auratus*) were exposed to water temperatures of 5°C, 20°C, and 20°C with dextran added (to mimic the viscosity at 5°C), but escape performance was only impacted by temperature (Johnson et al. 1998). This same study examined the impact of viscosity on a smaller fish (guppy, *Poecilia reticulata*), and found that high viscosity negatively impacted escape performance, suggesting that smaller fishes are more vulnerable to the mechanical changes that occur as temperature, and therefore viscosity, change. This is likely due to the fact that, at small sizes, viscous forces, due to low Reynolds number, are dominant and would resist the motion of the fish. A more recent study examined the impact of viscosity on the escape responses of zebrafish, *Danio rerio* (Danos and Lauder 2012). Increasing viscosity significantly decreased displacement of the center of mass during stage 1 of the escape, maximum velocity of the center of mass,

and maximum angular velocity and acceleration during stage 1 (Danos and Lauder 2012). Overall, it appears that changes in viscosity associated with physiological responses to temperature might have a dramatic impact on the ability of fishes to capture prey, as well as on the ability of prey to escape.

Ambient flows

Few fishes live in completely still water (Liao 2007). Rivers, streams, coral reefs, and shoreline habitats are all characterized by movement of water (Fig. 2), and these flows have been shown to strongly affect the distribution of species (Fulton et al. 2005). Although probably rare, the flow in a habitat may be laminar, meaning that the instantaneous velocities of all points throughout a fluid are comparable (Lacey et al. 2012). At higher Reynolds numbers, or with wave or flow-induced movements of the water, the flow may become turbulent (Webb et al. 2010). Given the ubiquity of such motion, it is quite surprising how little is known about its impacts on predator–prey encounters in fishes. The spatial and temporal dynamics of the flow an animal experiences will depend heavily on the environment. Some environments, such as a river, are characterized by continuous (not necessarily laminar) flow. Thus, predator–prey encounters often will occur in moving fluid. The general impacts that steady or altered flows have on fishes has been characterized to some degree (see Liao 2007 for review), but many details remain poorly understood.

Turbulence is the unpredictable and chaotic flows of multiple strengths and sizes within an overall flow of water (Liao 2007), resulting in temporal and spatial variability in velocities. Put another way, turbulence involves fluctuations of velocity and vorticity within the fluid about a steady mean value (Lacey et al. 2012). This complex stirring and mixing of the fluid results from fine-scale eddies and vortices (Denny and Gaylord 2010) that can be produced by wind, boats, habitat structure, density gradients of thermoclines and haloclines, and many other factors (Webb et al. 2010). In natural systems, flowing water often involves turbulent flows (Monismith 2007), and few places exemplify this more than rocky marine intertidal zones, which are punctuated by oceanic waves that crash on the shore (Gaylord 2007). Turbulence in relation to biological events, such as external fertilization among benthic invertebrates and locomotion among fishes, are well documented (Liao 2007; Denny and Gaylord 2010), but turbulence in relation to predator–prey encounters among fishes is poorly understood. Before examining how predators and prey might deal with turbulent flows in their natural habitat, it is important to establish how turbulence might impact them. Although it might be intuitive to think that turbulence will only hinder locomotor movements, ample evidence suggests that some fishes can reduce locomotor costs by exploiting predictable areas of turbulence, such as that generated by water moving past physical structures or generated by other fishes (Liao 2007; Liao et al. 2003).

Turbulence and stability

During predator–prey encounters, the chaotic nature of turbulent flows will likely depress the predictability of the prey's location or, from the perspective of the prey, the location from which the predator approaches. Swimming fishes often experience external perturbations (Webb 2002; Weihs 2002), and this probability increases in turbulent flow. This means that the swimming trajectory must be stabilized by hydrostatic or hydrodynamic damping and correcting forces (Webb 2002). Median and paired fins permit self-correction and controlled trimming. With specific body shapes, fins can damp and self-control yawing, pitching, heaving, and slip disturbances. Paired fins also have the capability of damping and self-correcting rolling disturbances (Webb 2002). Regardless of the mechanism, the fish must exhibit appropriate latencies of response, not exceeding or approaching half the period of the disturbance, in order to avoid amplifying the disturbance (Webb 2006). One study examined the ability of three fish species to respond to slip, heave, yaw, pitch, and roll disturbances induced by a narrow jet of water (Webb 2004). Fishes generally are faster at responding to roll disturbances (average = 70 ms) than to slip, heave, yaw, or pitch disturbances (130–200 ms) (Webb 2004). It was suggested that rolling disturbances might be more important to correct, due to the fact that fishes are hydrostatically unstable in a roll because their center of mass is almost always above the center of buoyancy (Webb 2002). Given the relatively short duration (and therefore high speeds) of many predator–prey encounters, it is predicted that most fishes would use their fins and body to self-correct (Webb 2006).

The amplitude of the eddies that make up turbulent flows is likely a major determinant of the resulting instability (Lacey et al. 2012). Intermediate eddies that are comparable in size to a fish are very likely to cause changes in posture (Webb 2006). Rotational disturbances seem to induce greater control problems than translational disturbances. However, any

perturbation that may decrease accuracy during predator–prey encounters is likely very important (Fig. 4). In addition to a decrease in successful captures due to changes in the accuracy of strikes, rotational motions may be detected by the visual system of the prey, resulting in an earlier escape response.

Although not always the case, dealing with turbulent flow can be costly. A recent study found that bluegill become destabilized by streamwise vortices, which induce unsteady behaviors, such as accelerations, to accommodate (Maia et al. 2015). Associated with this is an increase in oxygen consumption, which means there is an energetic cost to swimming in flow in this case. In contrast to streams and rivers, intertidal habitats may experience transient periods of increased flow. If the conditions of flow, especially turbulence, have a negative impact on feeding or escape performance, which they often do (e.g., Gilbert and Buskey 2005), it is reasonable to predict that predators or prey will become less active during times when the velocity of flow is high (Green 1971). This ability to select appropriate habitat conditions is common across all animals and habitats. However, detailed ecological data are required to determine when and how predator–prey encounters occur.

For visual predators, turbulent water may alter the position of the prey in unpredictable ways. Despite all efforts on the part of the predator, this can decrease the accuracy of a strike. For fishes that feed at night or in low-light, turbulent or rapidly flowing water may disrupt other sensory systems, such as the lateral line system, necessary for the capture of prey. Hydrodynamic disturbances generated by the prey may go undetected, resulting in a failed attempt to capture.

Turbulent flows found in nature are inherently complex, making it difficult for researchers to measure or replicate "natural" turbulence for laboratory experiments. In addition to being unpredictable, the fundamental characteristics of turbulent flows, i.e., the turbulence's intensity, periodicity, orientation, and scale (IPOS framework, Lacey et al. 2012), differ among environments. Quantification of these specific parameters in a fish's habitat is a first step toward predicting the potential impact of turbulence on predator–prey behavior (Fig. 5A, B). This requires detailed field measurements of flow, which could involve cantilever-style drag-sphere flow probes with strain gauges (Johansen 2014; Gaylord 1999), particle imagine velocimetry (PIV) (Lacey et al. 2012), acoustic Doppler velocimeters (Garcia et al. 2005), or injection of dye (Fig. 5B). Once the natural conditions of flow are quantified (e.g., dispersion rate, Fig. 5B), realistic turbulence may be created in the

laboratory to investigate the effects of flow regime on predator–prey encounters (Fig. 5C). Unfortunately, creating realistic turbulence is not trivial, and will require sophisticated flow tanks exhibiting actuators and obstacles to produce the appropriate turbulent flow (Fig. 5C). The degree of turbulence can then be quantified using PIV to measure the dispersion rate (Fig. 5C, D).

Prey strategies in turbulence

Rapidly flowing or turbulent water may severely compromise the ability of a prey fish to detect a predator (Fig. 1). It is known that prey fishes will utilize their lateral line system, which is sensitive to flow, to detect suction being generated by an approaching predator (McHenry et al. 2009) as well as the disturbances caused by the body of the incoming predator (Fig. 3; Stewart et al. 2013, 2014), especially when the predator approaches from behind (Seamone et al. 2014). The lateral line system consists of a series of mechanoreceptors, called neuromasts, that project into the surrounding fluid and detect movements of water near the body (Fig. 3; Dijkgraaf 1962). The lateral line is crucial for prey fishes to survive predatory attacks. For example, pharmacologically disabling the lateral line system in zebrafish larvae caused a 93% decrease in the likelihood of evading a predator's suction strike (Stewart et al. 2013). Considering this reliance on sensing flow, turbulence in the environment may hinder the detection of predators by saturating the prey's neuromasts or by masking predator-generated flows. Turbulence hinders the ability of some flow-sensitive invertebrates to detect the flow of predatory fishes (Gilbert and Buskey 2005). For fishes that are prey, it has been shown that prey are less responsive, both to an artificial flow (Feitl et al. 2010) and to an actual predator (Stewart et al. 2013), when swimming. This suggests that the turbulent, self-generated flows produced while swimming may interfere with lateral-line function, underscoring the potential impact of turbulence on sensing flow. Nonetheless, such effects would be detrimental to survival of the prey, given that unresponsive prey almost never escape (Stewart et al. 2013; Kane and Higham 2014).

Predators' strategies in turbulence

Predators can avoid attacking prey when turbulent conditions persist, or they can attempt to overcome the challenge. To capture a prey fish in turbulent conditions, the predatory fish has multiple options (Fig. 4). The most likely alteration in predatory behavior is an increase in swimming speed during
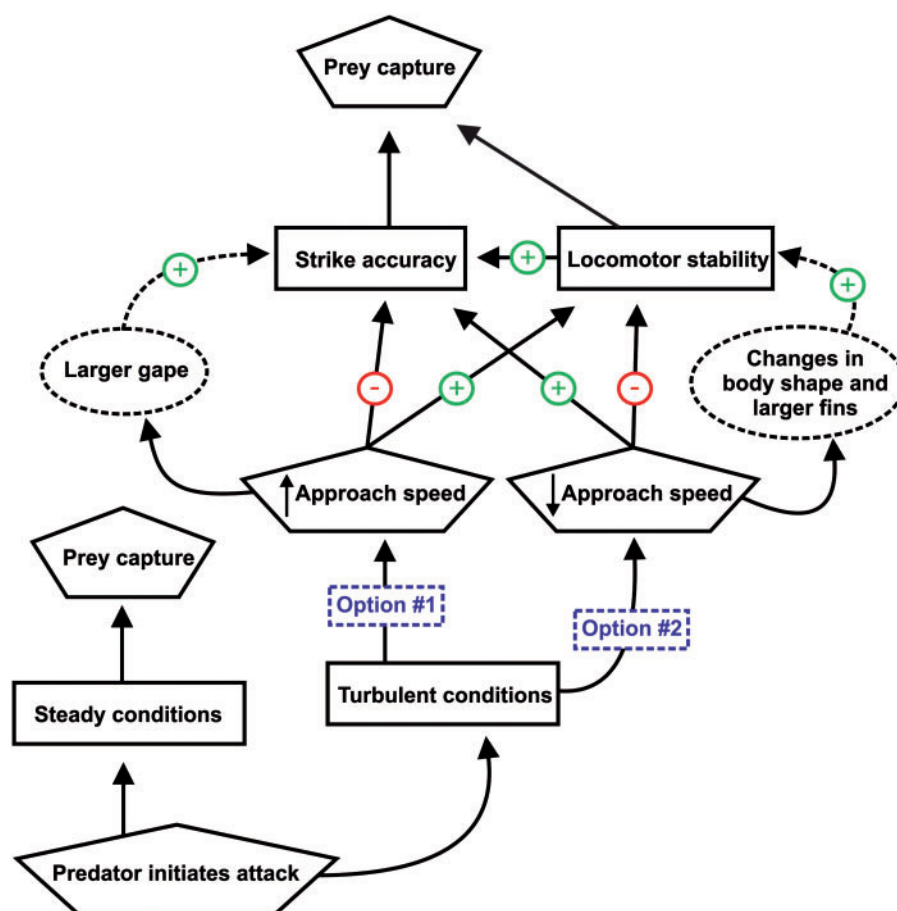
Fig. 4 The potential strategies for a predator attacking a prey in turbulent conditions. The pentagons are behaviors, the ellipses are morphological traits, and the rectangles are attributes of the water or predator. Option no. 1 involves an increase in the speed of approach, which will increase stability, but decrease the accuracy of the strike due to the limited amount of time for the predator to react to changes in the prey's position. However, this decrease may be balanced by the increase in stability, which might allow the predator to maintain its trajectory more effectively. If the predator adopts a strategy in which locomotor speed decreases (option no. 2), accuracy may increase, but locomotor stability will decrease. The predicted trade-offs have not been quantified. Morphological changes that might facilitate each strategy are indicated. Faster speeds among predatory fishes are typically associated with larger gapes, so fish living in fast-flowing environments that adopt option no. 1 are expected to have larger mouths. Finally, selection may favor changes in body shape and increases in the area of the fins for fishes that live in environments that might more frequently cause instabilities. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

strikes. Faster locomotion, involving greater momentum and energy, will be better able to damp and correct displacements caused by turbulent flow (Webb and Cotel 2010). Although the increase in speed might alleviate the impact on stability, it may come at a cost (Fig. 4). Faster predators will have less time to react to small changes in the prey's position, which may have strong consequences on the accuracy of the strike (Higham et al. 2006a, 2007; Higham 2007a, 2007b). If this is the case, faster speeds during attack may generally be less accurate, and may exhibit a decrease in the success of the attack. This could have negative energetic consequences, since more attempts would be necessary to obtain an adequate amount tof food.

Effects of disturbances to flow on the diversity of fishes

The pervasive impact of flow on predator–prey encounters has likely contributed to the evolution of morphological traits among fishes. Those predators living in faster flows not only will benefit from larger fins for stabilization, but also from a more streamlined body for swimming faster. If the predator adopts a strategy in which locomotor speeds are elevated during the capture of prey, relative to the speeds of predators living in slowly flowing water, then accuracy will decrease. Thus, larger mouths may be expected in order to compensate for the increased speed and decreased accuracy (Higham 2007b; Higham et al. 2007).
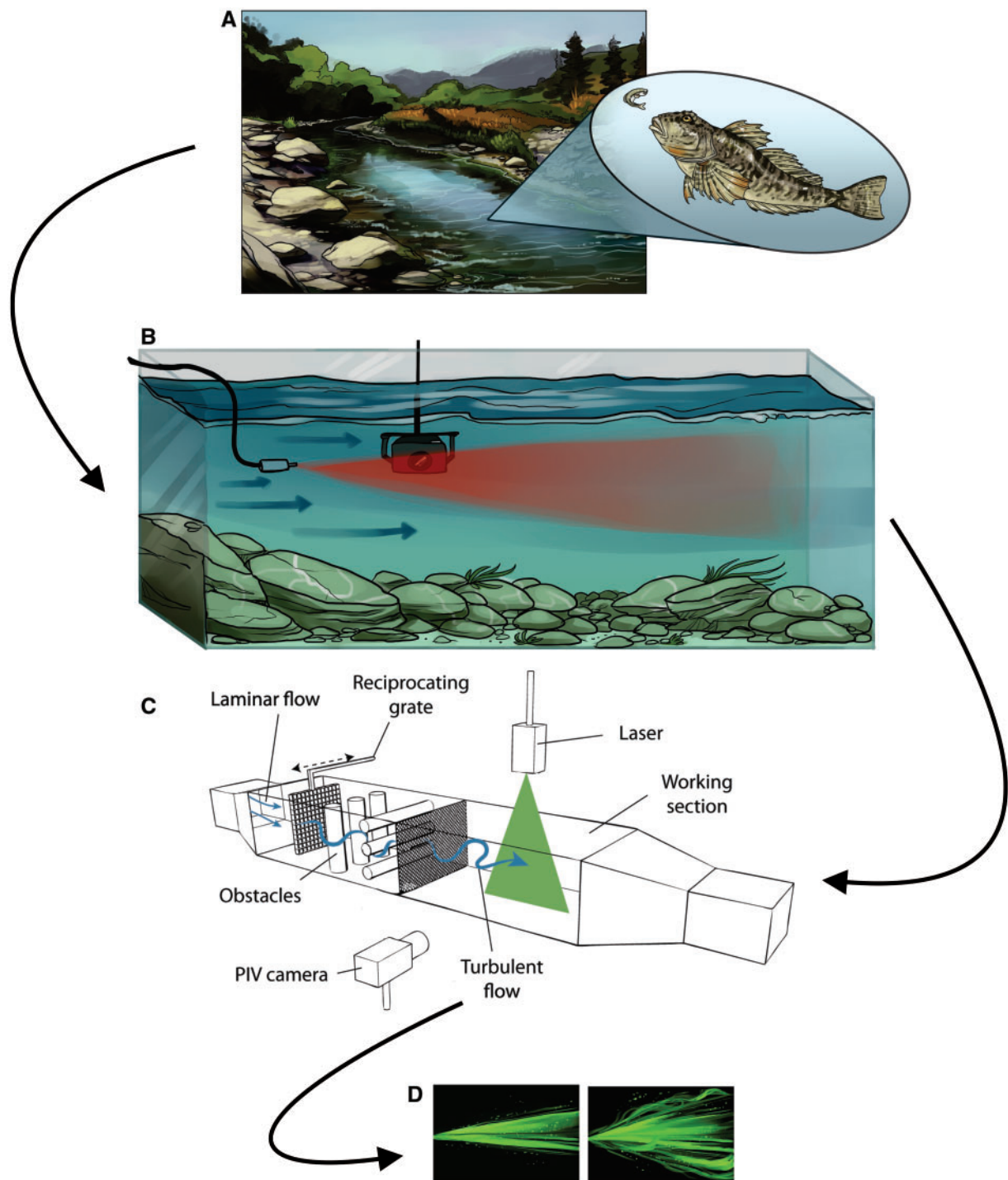
Fig. 5 Methods for understanding ambient flows, spanning environmental measurements to visualizing fluid movements in the laboratory. Once a fish is located in a flowing environment (**A**), a dye can be injected into the stream and the dispersion can be recorded using a camera (**B**). Using obstacles and/or a reciprocating grate, a turbulent flow can be created in the laboratory, and visualized using particle image velocimetry (PIV) (**C**). Again, the dispersion rate can be quantified (**D**). (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

Spiny-rayed fishes (Acanthomorpha) with actively controlled appendages, and more ideally situated paired fins (relative to the center of mass) (Drucker and Lauder 2002), will result in enhanced passive and active stabilizing potential when disturbed during the capture of prey. Using digital particle image velocimetry, Drucker and Lauder (2002) showed that bluegill sunfish are effective at executing braking maneuvers without inducing any pitching moments around the center of mass. This is

in contrast to rainbow trout, which exhibit pronounced pitching of the body during braking due to their ventrally positioned pectoral fins. Overall, spiny-rayed fishes have paired fins that exhibit reaction forces that go through the fish's center of mass, thereby minimizing destabilizing torques (Harris 1938). This should enhance the ability to deal with perturbations during the capture of prey.

We predict that larger predators will be less impacted by turbulent flow during the capture of prey. Eddies of small amplitude, relative to the size of the fish, likely cancel out over the body, whereas eddies of intermediate size can cause control problems (Webb 2006). We also predict that body size may be under selective pressures in relation to the typical disturbance in a given habitat. Given that predators are almost always larger than prey, the advantage appears to fall toward the predator.

Indirect effects of flow on predator–prey encounters

Not all of the impacts of turbulence on predator–prey encounters will be direct. Many factors will play dominant roles in shaping an animal's morphology, for example. The conditions of flow have been implicated numerous times, with fishes living in faster flows typically exhibiting more slender bodies, and a higher aspect-ratio of their caudal fins (see Langerhans and Reznick [2010] for review). Many of these differences in morphology are between closely related species or between populations within a species. This appears to occur both for predator and for prey, and so the impact on predator–prey encounters is likely complex.

For benthic fishes in the marine intertidal zone or in rapidly flowing streams, such as sculpins (Fig. 2A, B) or darters, flow regime can lead to extreme morphological traits both for the body and the fins (Kerfoot and Schaefer 2006; Carlson and Lauder 2010, 2011; Kane and Higham 2012). Although these are often directly related to station holding, including the ability to grip the substrate and generate negative lift (Kane and Higham 2012), their impacts on stability and, more generally, predator–prey encounters, are poorly understood (Kane and Higham 2011). Despite the demands of turbulent and high-flow environments, living in this type of environment can also provide benefits. For example, the strong gradient in velocity in rivers (Fig. 2D) can lead to an increase in foraging opportunities (Pavlov et al. 2000; Liao 2007). As mentioned above, prey fishes that are found in turbulent areas may also be more susceptible to predation.

Turbidity and diel activity patterns

Visual predators use ambient light to see their prey. Two key aspects of an animal's habitat will influence the amount of light reaching the fish. First, the penetration of light is a function of depth, such that deeper fishes will receive less light. Extreme situations involving limited light include deep-sea fish, cave-dwelling fishes, and nocturnal fishes, in which light can be completely absent. This often results in alternative specializations, such as an emphasis on other sensory systems like the lateral line (Pohlmann et al. 2004). A second mechanism of decreased penetration of light is turbidity (Fig. 2C), which is often caused by near-shore sedimentation. Turbidity has a drastic impact on the ability to see prey in the water column (Fig. 2C). It has been proposed that turbidity will be more detrimental to predators attacking from greater distances since turbidity will differentially impact vision from far away compared with up close. To test this, a study examined the differential impact of turbidity on feeding success by piscivorous and planktivorous fishes (Robertis et al. 2003). As expected, piscivorous fishes were more sensitive, since they often detect prey visually from greater distances. However, the methods for creating turbidity differed for the piscivores and planktivores, potentially impacting the results. This idea should be tested on a much larger sample of species from a variety of habitats, phylogenetic history, behavior, and morphology.

A more recent analysis of turbidity on capture success in coral reef fishes found that relatively low levels of turbidity (4 nephelometric turbidity units) caused a reduction in average success of capture by up to 56% (Johansen and Jones 2013). However, this impact was greater in the mid-shelf to outer-shelf species, which were less likely to encounter higher levels of turbidity. This suggests that species exposed to high turbidity have evolutionary adaptations that maintain successful capture despite the reduction in visual capacity. Interestingly, this study also observed a greater reduction in success for all species capturing mobile prey, with success being up to 14 times lower (Johansen and Jones 2013). These results suggest that major changes in fishes' distribution and diversity may coincide with future human-mediated changes in turbidity.

The level of ambient light affects when, and how, predatory fishes feed. Many predatory fishes feed in the low light of dawn and dusk (Cerri 1983), while others are completely nocturnal (Hobson 1965), and some species stop feeding altogether in darkness (Stewart et al. 2013). The preference of predators

to feed in low light can be attributed to several factors, including the compromised visual system of prey (Pitcher and Turner 1986), the reduced frequency of anti-predator behaviors (e.g., schooling) as light decreases (Cerri 1983), and the fact that predatory fishes are less conspicuous to their own predators (Cerri 1983). Other species, such as largemouth bass, completely change their predatory strategy in darkness, switching from high-speed ram attacks in the light to low-speed approaches and strong suction in the dark (New and Kang 2000; Gardiner and Motta 2012). Predators feeding in the dark locate prey using olfaction and the sensing of flow, and diurnal predators usually employ vision (Gardiner and Motta 2012). Considering the diverse effects of light level on predatory behavior, the influence of changing ambient light will likely be complex, and species-specific. We predict that piscivorous fishes, which often rely on vision for capturing prey (e.g., Nyberg 1971) will alter their strategy in low light by reducing their locomotor speed, thereby increasing suction performance, and reducing their attack distances.

Differential impacts of environmental conditions on predators and prey

Predator–prey encounters are typically more of a surprise to the prey, which means that the prey has less time to achieve a maximum velocity (i.e., higher accelerations). This increased demand on the locomotor system of prey suggests that changes in temperature, and hence the speed of muscle contraction, will have a greater impact on prey than on predators. This is primarily due to the physiological impacts on the contractile speed of muscles. Smaller fishes appear to be differentially impacted by viscosity, suggesting again that they will be impacted to a greater extent. In addition, smaller fishes are more likely to be entrained in a turbulent vortex of a given size (Webb et al. 2010), suggesting that smaller fishes will suffer more in the event of unsteady flow.

Given that predators and prey will often use different sensory systems during a predator–prey encounter, there are likely considerable differences in how they are impacted. Some of this requires additional studies to understand the mechanisms of these systems in relation to capturing prey or evading predators, but the ultimate goal should be to incorporate and integrate this information into an ecomechanical model. Coupling information on vision, hearing, and lateral-line function in relation to the movements of predator and prey will provide critical insight into their co-evolution.

It has long been recognized that many predatory fishes are crepuscular, feeding at twilight when the visual capabilities of the prey may be compromised (Munz and McFarland 1973; Hobson 1979; Helfman 1981, 1986). The challenge is that this period of time is a transition between photopic (high light) and scotopic (very low light) vision. Successful predation during this period of transition is achieved by having rhodopsins with sensitivities that match the background light available during the evening and morning twilight, as well as having moderate numbers of very large cones (Munz and McFarland 1973). This differential impact of light intensity is, in part, due to the fact that predators can select when they attempt to capture prey, whereas prey can only respond.

Quantifying predator–prey encounters in nature

Compared with terrestrial systems, little is known about the dynamic encounters between predators and prey in natural aquatic habitats. This is, in part, due to the limitations associated with underwater filming and accessibility. In addition, predator–prey encounters are inherently unsteady, with both the predator and prey exhibiting high accelerations and velocities. Coupling this with the complex conditions that fishes typically experience in nature makes it quite a challenge to successfully and repeatedly examine these events. Regardless, there are a number of important reasons for why we should aim to understand the dynamics of natural predator–prey encounters. First, laboratory situations naturally are limited by space. A rare study examining 3-D strikes in nature found that the attack covered almost 5 m (Hughes and Kelly 1996), which is much farther than almost all filming arenas in laboratory studies. Many encounters likely occur over distances greater than that available in a laboratory, and this might lead to biases in the characterization of the nature of these encounters.

There are multiple techniques that will be important for advancing our understanding of natural predator–prey encounters. First, triaxial accelerometers and triaxial gyroscopes allow quantification of movement during natural behaviors of fishes in nature (Noda et al. 2013). This has been employed to a much greater extent in terrestrial (Wilson et al. 2013) and aerial (Hedrick et al. 2004) systems, and each has its own challenges. In contrast to terrestrial systems, the mass of the device will be less constraining in an aquatic environment, but may create hydrodynamic disturbances. Additionally, these devices

must be able to work under water and under a range of pressures and temperatures.

Large tanks potentially would be suitable for quantifying realistic predator–prey encounters. As a general guide, the shortest horizontal dimension of the experimental tank should be at least four times longer than the predator's body. Achieving this may be relatively easy for smaller species, but not for larger ones like sharks or adult marine piscivores. For example, a recent study examined the escape responses of dogfish sharks as they were approached by a model of a predator (Seamone et al. 2014). This was conducted in an extremely large flume (12 m in length), which permitted approach distances of several meters. Although this may provide the space necessary for studying larger animals, the fact that the setting is artificial still has some confounding factors.

Creating realistic flows in the laboratory is a challenge. Visualization of fluid (e.g., PIV), in concert with high-speed video, is one way to quantify complex and turbulent flows (Westerweel et al. 2013), but this is not easy either to measure in the field or to simulate different turbulent flows in the laboratory (Fig. 5). The latter is impossible without a thorough understanding of flow patterns in nature where the animals are likely going to be active. To do this in a stream or river, one could measure the rate of dispersion of dye in the field using cameras and a dye injector (Fig. 5A, B). This could be replicated in the laboratory using a series of obstacles or oscillating grids, and quantified using PIV (Fig. 5C, D).

Conclusions

Incorporating realistic environmental variables into our understanding of the biomechanics of predator–prey encounters will enable us to make predictions about responses to future changes in the environment. All of the ecological variables outlined above may be impacted by climatic change and other anthropogenic alterations to the environment. Increases in water levels will increase wave action and flow. Increases in temperature will be accompanied by changes in pH, and a variety of human-driven processes will increase the turbidity of aquatic environments, all of which are likely to have major consequences for fish assemblages. As outlined in previous work (Denny and Gaylord 2010), ecomechanics has the potential to predict how animals can respond to environmental change. Inter-population studies across a range of conditions will perhaps enable us to understand how plastic fishes

can be, and how they might rapidly evolve in response to changing conditions (e.g., Barrett et al. 2011). Regardless, we must understand how variables such as flow, turbidity, and temperature impact the biomechanics of predator–prey encounters before we can understand how fishes will respond to changing conditions.

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