

# Response latencies to postural disturbances in three species of teleostean fishes

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## Summary

Flow in aquatic systems is characterized by unsteadiness that creates destabilizing perturbations. Appropriate correction responses depend on response latency. The time between a disturbance induced by either removal of a flow refuge or striking various parts of the body with a narrow water jet was measured for three species, chosen as examples of modes in teleostean body/fin organization that are expected to affect stability. Creek chub *Semotilus atromaculatus* is representative of fusiform-bodied soft-rayed teleosts, smallmouth bass *Micropterus dolomieu* of fusiform-bodied spiny-rayed forms and bluegill *Lepomis macrochirus* of deep-bodied spiny-rayed forms. Observations were made at 23°C. Loss of refuge resulted in a surge that fish corrected by starting to swim within 129±29 ms (mean ± 2 S.E.M.) for chub, which was significantly shorter than minimal times of approximately 200 ms for bluegill and bass. Slips and heaves induced by water jets initially resulted in extension of the median and paired fins that would damp growth of

the disturbance, but otherwise these disturbances were ignored. Yaws and pitches were more likely to cause fish to swim away from the stimulus, making corrections as they did so. There were no differences in latencies for slip, heave, yaw and pitch disturbances within each species, but latencies varied among species. For these disturbances, responses averaged 123±19 ms for chub, again significantly smaller than those of 201±24 ms for bass and 208±52 ms for bluegill. Values for the two centrarchids were not significantly different ( $P>0.08$ ). The response latency for rolling disturbances did not differ among species but was significantly smaller than that for other disturbances, with an overall latency of 70±15 ms. The greater responsiveness to hydrostatic rolling instability is attributed to functions requiring an upright posture and differences among species in habitat preferences.

Key words: teleost fish, body/fin organization, posture, response latency, stability.

## Introduction

Flow in aquatic systems is characterized by turbulence from gravity and wind-driven currents interacting with the water–air, water–water and water–solid surfaces, and with structures projecting into those currents (Denny, 1988; Vogel, 1994; Webb, 2002, 2004; Bellwood and Wainwright, 2001; Fulton et al., 2001; Fulton and Bellwood, 2002). Consequently, destabilizing perturbations with a range of amplitudes and periods are expected to be characteristic of most fish habitats (Webb, 2002). Turbulence may reduce swimming performance (Pavlov et al., 1982, 1983, 2000; Shtaf et al., 1983; Pavlov and Tyurukov, 1988) as stability control is expected to increase locomotor energy costs (Webb, 2004). Thus, fishes would be expected to correct disturbances promptly.

An important factor affecting the ability to make appropriate corrections for disturbances is response latency, the interval between the occurrence of a perturbation and the start of a response to the resulting disturbance. Among fishes, the ability to successfully power corrections using body and fin motions depends on the latency being relatively small compared to the perturbation period. Otherwise a correction may add to a disturbance, with results graphically described as ‘pilot

induced error’ (Anderson and Eberhardt, 2001; Webb, 2002). There are no measurements of this critical aspect of stability. Therefore, I measured response latencies to flow-induced disturbances for three species of bony fishes.

Fishes are extremely diverse. Within this diversity are various body/fin organization modes and these are believed to affect motor and stabilizing capabilities (Harris, 1937a, 1953; Moy-Thomas and Miles, 1971; Rosen, 1982; Lauder and Liem, 1983; Webb, 1998, 2004; Eidi et al., 2002; Drucker and Lauder, 2003). Studies on locomotion typically use species representative of modes, such as various dogfishes typical of less derived selachians (e.g. Harris, 1937b, 1938; Wilga and Lauder, 1999, 2000, 2001), salmonids as models for less derived teleosts (e.g. Bainbridge, 1958; Brett, 1964; Liao et al., 2003), and centrarchids indicative of more derived teleosts (e.g. Gibb et al., 1994; Jayne et al., 1996; Drucker and Lauder, 2001a,b). In this study, three species were chosen to represent teleost modal forms of (1) soft-rayed fishes, (2) fusiform spiny-rayed fishes and (3) deep-bodied spiny-rayed fishes (Rosen, 1982). The modal body/fin organization of soft-rayed fishes is a fusiform body with antero-ventral pectoral fins and postero-

ventral pelvic fins, for which the cyprinid, creek chub (*Semotilus atromaculatus* Mitchell), was chosen. This body/fin organization facilitates swimming in body-caudal fin gaits (Webb, 1994), and the main propulsors also provide median-fin control surfaces not only posterior to but also distant from the center of mass. This promotes unconscious control or self-correcting stability (Aleyev, 1977; Weihs, 2002; Webb, 1998). Then a change in orientation of a control surface due to a disturbance generates a force that opposes and corrects the disturbance, as with the feathers of an arrow.

Spiny-rayed fishes have radiated about a fusiform body with antero-lateral pectoral fins and antero-ventral pelvic fins (Rosen, 1982; Lauder and Liem, 1983). The centrarchid, smallmouth bass (*Micropterus dolomieu* Lacépède), was chosen as in many other studies (e.g. Gibb et al., 1994; Jayne et al., 1996; Drucker and Lauder, 2001a,b). The bass body/fin organization extends the swimming range with gaits based on the median and paired fins (Webb, 1994), and appears to be associated with greater fin mobility used to actively generate control forces (Webb, 1998). Many spiny-rayed fishes have deep bodies, providing for larger median fins. These further expand capabilities in median and paired fin gaits (Webb and Gerstner, 2000; Webb, 2004), and also could improve powered control of stability. A common model species for this mode of body/fin organization is the bluegill (*Lepomis macrochirus* Rafinesque) (Gibb et al., 1994; Jayne et al., 1996; Drucker and Lauder, 2001a,b), which was chosen here. The three species were also chosen because they are sympatric warm-water fishes. As a result, fishes could be tested at a common temperature within the normal range for all three species. Finally, the size ranges of the three species overlap.

Chub were expected to be more reliant on unconscious control and least reliant on active detection and correction of disturbances. As a result, short response latencies may be less critical. Bass were expected to depend more on powered control when a shorter latency in responding to disturbances would be expected. The greatest dependence on powered control by bluegill was expected to result in the shortest latencies. Overall, fishes were expected to respond and correct for all types of flow-induced disturbances, with latencies ranking as: chub>bass>bluegill. In practice, these results were not found and differences among species reflected the nature of habitats typically occupied.

## Materials and methods

### Fish

Creek chub *Semotilus atromaculatus* Mitchell, smallmouth bass *Micropterus dolomieu* Lacépède and bluegill *Lepomis macrochirus* Rafinesque were obtained from the Saline River, Michigan by seining. Fish were held in 110 l tanks for at least one week at 19–21°C and then acclimated to 23°C by increasing the temperature approximately 1°C per day. Fish were held for a further week at this temperature before use. Tanks were continuously aerated and supplied with fresh

water. The fish were fed Tetramin® flake food to excess once per day.

### Responses to loss of a flow refuge

Experiments were performed in an enclosed recirculating flume based on the design described by Vogel and LaBarbera (1978). Fish swam in an observation section, 15 cm square and 60 cm long, preceded by a 45 cm upstream entry section. There was a 10 cm long collimator made with 1.25 cm×1.25 cm×1.25 cm grid at the upstream end of the observation section. The downstream end of the observation section was delineated with a wire grid that could be electrified if necessary to encourage fish to swim. The observation section had bottom and side panels with 5 cm wide black and white stripes to facilitate station holding.

A single 19 mm wide vertical strut extended from the top to the bottom of the observation section, 20 cm from the upstream collimator. The strut passed through the top of the observation section to a block linked to a weight. Remote removal of a brake caused the weight to rotate the strut from an orientation normal to the flow through 90° to lie parallel to the flow within 10 ms. This exposed a fish to the full speed of the flow, causing a sudden displacement downstream, a surging disturbance.

The sudden change in strut orientation occurred near the head in the visual field of the fish. As a result, a response presumed to be due to the hydrodynamic disturbance might be a response to a visual component of the stimulus triggering an escape behavior. Therefore, observations were made both in the dark (<2 lux red light) to eliminate the visual component of the stimulus and under normal laboratory illumination (45 lux white light).

A single fish was selected at random and placed in the flume. The flume temperature was the same as the acclimation temperature. The fish remained in the flume for at least 12 h at a current speed of approximately 0.5 L s<sup>-1</sup> (where L = total body length) and with the strut normal to the flow. After this acclimation period, speed was increased at 10 min intervals by increments of approximately 0.5–0.75 L s<sup>-1</sup>. When a fish entrained on the strut, the strut was rotated parallel to the flow. The fish began to be displaced downstream by the current as soon as the strut began to rotate. Fish responded by starting to swim upstream. Once the fish returned to steady swimming, the strut was reset normal to the flow, and the procedure repeated. The tests were run until the fish was fatigued, which was defined as an inability to swim off the downstream screen.

Fish were videotaped at 250 frames s<sup>-1</sup> from above via a 45° mirror. Videotape was analyzed frame by frame to record the behavior of each fish. Response latency was defined as the time from the beginning of the rotation of the strut to a change in the use of median and/or paired fins leading to the onset of swimming. These motions were clearly distinct from those during entrainment.

At the end of each experiment, the fish was killed with an overdose of 3-aminobenzoic acid ethyl ester (MS 222). Total body length L and maximum body depth were measured to the nearest 1 mm and body mass to the nearest 0.01 g (Table 1).

Table 1. Morphometric characteristics of the fishes used in experiments to determine response latency to postural disturbances

	Type of disturbance					
	Caused by rotation of strut used for station holding			Caused by water jet while taking food		
	Body length (cm)	Mass (g)	Body depth (cm)	Body length (cm)	Mass (g)	Body depth (cm)
Creek chub	13.4±1.8 (9)	22.88±5.65	2.4±0.4	12.1±1.7 (10)	17.47±5.89	2.4±0.4
Smallmouth bass	11.9±1.2 (9)	17.35±2.60	2.6±0.3	12.2±1.3 (12)	21.47±2.96	2.9±0.3
Bluegill	11.9±1.2 (9)	24.96±3.31	4.4±0.7	11.0±1.2 (9)	20.54±3.89	4.8±0.7

Values are means ± 2 S.E.M., with sample sizes shown in parentheses.

### Responses to water jets

Experiments were performed in a 50 cm×50 cm still-water tank filled to a depth of 30 cm. The temperature was the same as the acclimation temperature. Fish were trained to take food from a fixed location, as described by Alexander (1969). While taking food, a narrow water jet remotely triggered *via* a solenoid valve was directed at different parts of the body from a distance of 10–20 mm. The jet caused various types of disturbance: (1) a lateral jet close to the center of mass caused a slip (lateral translation), (2) a jet from above at the longitudinal location of the center of mass caused a heave (a ventrally directed translation), (3) a lateral jet ≈25% of the body length anterior to the center of mass primarily caused a yaw (a rotation about the dorso-ventral axis), (4) a jet from above ≈25% of the body length anterior to the center of mass primarily caused a pitch (a rotation about the lateral axis) and (5) a lateral jet at ≈30% of the body depth above the center of mass caused a roll (rotational disturbance about the long axis).

The water jet was gravity-driven from a constant head tank attached *via* 1.25 cm diameter tubing to a 2.5 cm long, narrow (0.35 cm diameter) aluminum tube. The water in the tubing was tinted with food coloring to be visible on videotape. The maximum force generated by the jet was measured using rigid flat disks of various diameters attached to a force transducer. Maximum force was measured for various driving heads for discs of 10, 15 and 20 mm diameter at distances of 5–30 mm from the orifice. The minimum height of the constant head tank for which the water jet first caused a fish response was found to be approximately 65 cm, generating a force of approximately 0.05 N. Experiments were performed with supra-threshold water heights generating forces of 0.09–0.1 N.

Fish responses were recorded on videotape (250 frame s<sup>-1</sup>), and subsequently analyzed frame by frame to observe behavior patterns and response latencies. Response latency was defined as the time from the beginning of a displacement to the first deployment of median and/or paired fins. These clearly differed from normal fin motions of fishes at the feeding station. Each fish was used once for each of the disturbances, and sample sizes are included in Table 1.

At the end of an experiment each fish was killed with an overdose of 3-aminobenzoic acid ethyl ester. Total body length and maximum body depth were measured to the nearest 1 mm and body mass was measured to the nearest 0.01 g (Table 1).

### Results

#### Responses to loss of a current refuge

During the acclimation period, fishes explored the observation section before choosing a location at which they spent most of their time. As swimming speed increased during the increasing velocity test, fishes entrained on the strut. Chub entrained at current speeds between 43 and 69 cm s<sup>-1</sup>, while bass and bluegill tended to entrain at speeds from 15 to 50 cm s<sup>-1</sup>. Successful entrainment was more variable than described by Webb (1998), in that fish often entrained at some speeds, but not others, but without there being an obvious pattern. When entrained, the fish's head was close to the strut, sometimes touching it. The body was typically either parallel to the bottom, or the body was tilted with the tail higher in the water column than the head. While entrained, the fish showed no regular swimming motions. However, the various fins, especially the paired fins and to a lesser extent the caudal fin, made irregular, small amplitude motions (Webb, 1998).

Fishes were immediately displaced downstream when the strut was rotated parallel to the flow. Most fish began swimming to return upstream. Occasionally, a fish showed a startle response, turning downstream and then heading back upstream usually before contacting the grid.

Response latencies for fishes in normal white light and low intensity red light did not differ for the three species studied (two-tailed *t*-tests,  $P>0.4$ ). Therefore, these data were combined for each species. Response latencies were independent of the water speed for chub, averaging 129±29 ms (mean ± 2 S.E.M.;  $N=59$ ). However, latency declined with speed for bass and bluegill (Fig. 1) from approximately 700 ms at entrainment speeds of 10 to 20 cm s<sup>-1</sup> to approximately 200 ms at speeds between 35 and 50 cm s<sup>-1</sup>. Because of the experimental design, it could not be determined if the decrease in latency with speed involves an adaptive response to the increasing rate of disturbance at higher speeds and/or learning. The mean response latency for chub was significantly smaller than the minimum values for bluegill ( $N=25$ ) and bass ( $N=26$ ) [repeated-measures analysis of variance (ANOVA) followed by Tukey's multiple comparison tests,  $P<0.01$ ], but values for bass and bluegill were similar ( $P>0.9$ ). The average speed at which a response was initiated for chub and the minimum values for bluegill and bass were independent of species (ANOVA,  $P>0.06$ ) averaging 5.7±1.8 cm s<sup>-1</sup>.

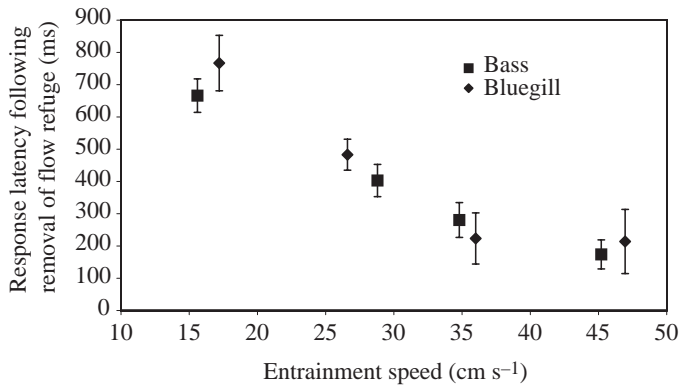


Fig. 1. The relationship between response latency following removal of the strut flow refuge and the current speed at which fish entrained for bass (solid squares) and bluegill (solid diamonds). Values are means  $\pm$  2 S.E.M.

#### Responses to water jets

The force generated by the water jet increased with the driving gravitational head (Fig. 2). The jet was coherent enough that force was essentially unaffected by either the disc diameter or the distance from the orifice to the body for the range of distances used in the experiments (ANOVA,  $P>0.9$ ).

All fish were displaced by the water jet. At the beginning of a response to a translational disturbance, the average displacement speed was similar for slips and heaves, and independent of species (ANOVA,  $P>0.14$ ), averaging  $7.6\pm 3.0$  cm s<sup>-1</sup>. Rotation rates at the start of a response were also independent of species ( $P>0.11$ ), averaging  $21\pm 9$  deg. s<sup>-1</sup> for yaw and pitch, consistently higher, but not significantly so ( $P>0.1$ ) than that of  $16\pm 7$  deg s<sup>-1</sup> for rolls.

Response patterns to disturbances were similar for all three species. Fish first responded to both translational and rotational disturbances by extending the median and caudal fins and usually the paired fins. Fishes usually made no further substantial motor responses to translational disturbances. Thus after the initial fin extension, fishes essentially ignored

translational disturbances. Similarly, fish sometimes ignored yawing and pitching disturbances. Usually they swam away from the feeding site, correcting posture as they did so with various median (including caudal), and paired fin motions. Rolling disturbances were never ignored. Fish from all three species actively corrected rolls. Some fish corrected the roll while swimming away from the stimulus area, but most used asymmetrical beats of median and paired fins to return the body to an upright posture.

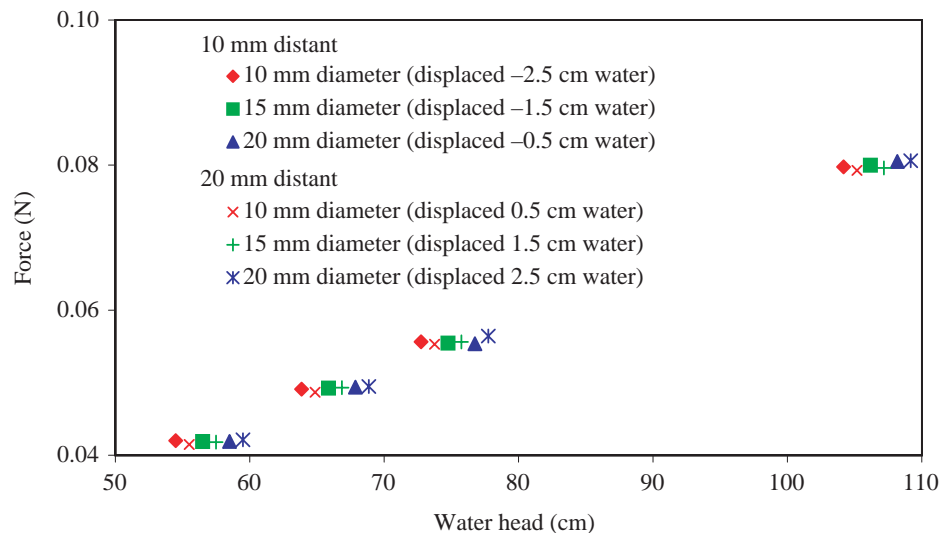
There were no differences in response latencies for translational, pitching and yawing disturbances (ANOVA,  $P>0.05$ ) for each species (Fig. 3). Therefore, these data were combined. The resultant response latencies varied,  $123\pm 19$  ms for chub being significantly smaller than those of  $201\pm 24$  ms for bass and  $208\pm 52$  ms for bluegill (ANOVA followed by Tukey's multiple comparison tests,  $P<0.05$ ). Values for the two centrarchids were not significantly different ( $P>0.08$ ).

The response latency for rolling disturbances for each of the three species studied was significantly smaller than that for other disturbances ( $P<0.05$ ), but there were no significant differences among species ( $P<0.04$ ). The overall average response latency was  $70\pm 15$  ms.

#### Discussion

The purpose of these experiments was to determine how fishes respond to disturbances induced by flow perturbations and latencies between the start of that perturbation and the fish response. Two different disturbances were induced, with fish starting from zero speed in an environmental frame of reference in both situations. First, a downstream surge was induced by the removal of a flow refuge. Second, slip, heave, yaw, pitch and roll disturbances were induced by a narrow water jet. The initial expectation was that fish would correct all disturbances with propulsive motions of median and paired fins, as observed for the surges and rolls, and latencies would vary among species with chub having the longer response times. In practice, responses were more variable, depended on

Fig. 2. The mean maximum force of water jets impinging on circular discs of various diameters from a distance of 10 or 20 mm as a function of the driving water head. Variation was small and not distinguishable within the dimensions of the symbols. The water heads for the various discs have been displaced along the x-axis as shown in the key, in order to lend some clarity to the otherwise overlapping data.





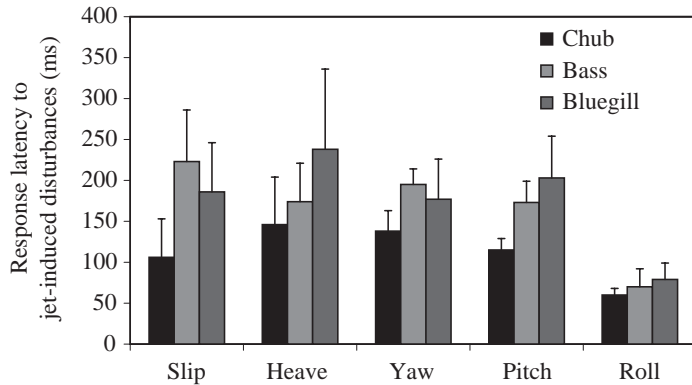


Fig. 3. Response latencies to postural slip, heave, yaw, pitch and roll disturbances induced by narrow water jets for three species of fishes. Vertical bars represent 2 S.E.M.

the nature of the disturbance, and chub typically had shorter latencies than the two centrarchids.

The initial response to all the jet-induced disturbances was extension of the median (including the caudal) fins and the paired fins. Such fin extension would increase resistance to translational and rotational motions, and hence damp further growth of a disturbance. In contrast, fin extension in the flume would increase drag, increasing the rate at which a fish was accelerated to the current speed, and hence increasing the rate of displacement downstream. Therefore, fin extension in the flume would amplify the downstream surging disturbance. Fin extension, however, did not occur following strut rotation in the flume. Thus fishes responded in appropriate ways to minimize amplification of the disturbance in the two dynamically different treatments of current in the flume and in still water.

Corrections to the jet-induced disturbances after the initial fin extension varied with the nature of the disturbance. Translational disturbances were usually not corrected. Rotational yaw and pitch disturbances were occasionally corrected. Rolls were always corrected. Rolls were also distinct in that response latencies were smaller, averaging 70 ms, compared to latencies of the order of 130–200 ms for other disturbances.

These response patterns suggest that the various types of disturbances differ in their importance. The long latency and absence of a motor correction to slip and heave disturbances suggests these do not pose functional problems for fishes. Yawing and pitching disturbances, while having the same latency as translational disturbances, were sometimes corrected, and hence presumably present some challenge. Surges and rolls were always corrected and hence presumably present important challenges to a fish. In the flume, failure to correct a surge would result in a fish becoming impinged on the downstream grid. A similar correction should be expected in natural habitats because failure to correct a current-induced surge would result in a fish being displaced from preferred habitats, typically those with favorable flow and/or food supply (Fausch, 1984; Allan, 1995).

The importance of rolling stability probably relates to

functions associated with the normal upright posture (Eidietis et al., 2002; Webb, 2002). Fishes are hydrostatically unstable in roll (or at best neutrally stable) because the center of mass is typically above the center of buoyancy (Aleyev, 1977; Webb and Weihs, 1994; Webb, 2002). Therefore fishes must work continuously to control posture (Alexander, 1990; Eidietis et al., 2002; Webb, 2002) and control systems to detect and correct rolling disturbances are essential. In contrast, fish are essentially hydrostatically stable in all planes and pitch and yaw.

Control of posture is also important for camouflage (Cott, 1940; Muntz, 1990). Fish are typically light when viewed from below and dark from above, so that rolling would make fish more visible. Translations and yawing rotations would not affect the orientation of cryptic coloration. Fishes naturally pitch (tilt) when swimming at low speeds (He and Wardle, 1986; Webb, 1993; Wilga and Lauder, 1999, 2000, 2001), which has the potential to affect camouflage. Pitch angles may be as large as 10–15°, but these are presumably insufficient to substantially affect camouflage.

Eidietis et al. (2002) also suggested that rolling could have negative impacts on sensory systems. Vision, in particular, may be affected. The underwater light environment is complex, with light intensity and wavelength differing along all lines of sight (Muntz, 1973, 1990; Lanchester and Mark, 1975; Lythgoe, 1979; Land, 1999). The distribution of rods and cones sensitive to different wavelengths often varies over the retina. This is associated with differences in light characteristics falling on different retinal areas when the body is upright. Translational and yawing disturbances would not affect general patterns of incident light. Pitching could cause light from various environmental origins to fall on different parts of the retina, but given the occurrence of tilting in normal behavior, this is presumably small at normal pitch angles. In contrast, rolling would quickly alter light patterns within the eye. Degradation of sensory signals as a result of rolling might also be anticipated for other distance senses, such as the lateralis system.

Response latencies also proved variable among disturbance types and among species. In general, response latencies were large compared with those of about 12 ms for the initiation of fast starts following artificial stimulation (Eaton and Hackett, 1984; Casagrand et al., 1999; Eaton et al., 2001; Webb and Zhang, 1994). This behavior, however, is initiated as a reflex response to potentially life-threatening situations (Eaton et al., 2001). Other behaviors require more complex assessment of both stimuli and an appropriate response. For example, response latencies of predators responding to prey maneuvers are about 100 ms (Webb, 1984). Postural response latencies are of the same order as these, although rolling response latencies were substantially shorter and others were longer (Fig. 3).

The small response latencies for rolling disturbances, the convergence of these latencies among the three species tested, and the immediate correction of rolling disturbances all support the idea that rolling disturbances present special challenges for fishes, necessitating prompt correction.

In addition to the expectation that fishes would respond to

all disturbances, it was anticipated that latencies would vary among species. The body/fin organization of less derived soft-rayed fishes and behavior in wakes suggest these fish are more reliant on self-correction (Breder, 1926; Harris, 1937a, 1953; Aleyev, 1977; Webb, 2004; Liao et al., 2003). As a result, response latency might be diminished in importance. In contrast, the median and paired fins play a larger role in swimming of more derived fishes, which also seem to make greater use of powered control, actively generating forces to correct a disturbance (Webb, 1998). In practice, fishes are usually in dynamic equilibrium, with corrective forces balanced among many control surfaces in orthogonal planes distributed around the center of mass (Lauder and Drucker, 2003; Webb, 2003, 2004). As such, short latencies would promote stability for all three species. However, similar response latencies were found only for rolling disturbances, which, it is argued above, present the greatest challenges to overall functionality for all species.

Latencies for other disturbances tended to be shorter for chub, rather than longer as anticipated. Given that fishes appear to be in dynamic equilibrium, it seems more likely that habitat features underlie response differences among species (Webb, 2004). Thus creek chub, as the name indicates, are stream fishes and, like other soft-rayed species, are common in more turbulent riffles and races (Schlosser, 1982; P. W. Webb and A. G. Fairchild, manuscript submitted for publication). Salmonids, also are soft-rayed species, well known for occupying turbulent streams. In lakes, cyprinids are abundant in shallow littoral zones, even during storm conditions (P. W. Webb, unpublished observations). Bluegill and ecomorphologically similar species are more common in lakes and ponds (Scott and Crossman, 1973) where flow is greatly reduced. In these habitats, percomorphs tend to move offshore and avoid storm-induced turbulent situations (Helfman, 1986). Bass are found in both lotic and lentic habitats, but in slow moving water in streams (Probst et al., 1984).

Thus fishes appear to respond to disturbances in two general ways. First, they may correct the disturbances, and when fishes are in dynamic equilibrium, active modulation of trimming forces and creation of powered forces will be essential. Nevertheless, the large response latencies suggest that such control may be limited to low frequency perturbations. Recent studies of fish interacting with Kármán wakes downstream of a D-shaped strut have shown that fish not only respond to but also exploit low frequency disturbances ( $\leq 4$  Hz; Liao et al., 2003). In contrast, long response latencies may require reliance on self-correction for many naturally occurring disturbances. Body shape can provide self-correction (Bartol, 2002, 2003). Fin deployment, especially of fins posterior to the center of mass, also provide some measure of self-correction (Breder, 1926; Alexander, 1967; Gosline, 1971; Aleyev, 1977; Weihs, 1989, 1993; Webb, 2004). Self-correction may be most important at high speeds when control surface anterior to the center of mass may be furled (Webb, 2004).

Second, fish may avoid unsteady flows. Turbulence generators exploit this in fish barriers (Fletcher, 1990, 1992;

Cada, 2001). In streams, low current speeds are expected to be associated with lower turbulence intensities and low currents are often selected by fishes (Fausch, 1984; P. W. Webb and A. G. Fairchild, manuscript submitted for publication). During migration, salmonids seek low speeds where flow is likely to be more steady (Hinch and Rand, 1998; Hinch et al., 2002). Many reef fishes shelter or vacate the immediate reef vicinity on flood tides, and tend to be active towards ebb tides (Potts, 1970; Hobson, 1974). Finally, fishes with lower stabilizing abilities chose hydrodynamically quieter habitats.

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