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Environmental effects on fish escape responses: impact of flow on the escape performance of the Hawaiian stream goby, *Sicyopterus stimpsoni*

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ENVIRONMENTAL EFFECTS ON FISH ESCAPE RESPONSES: IMPACT OF
FLOW ON THE ESCAPE PERFORMANCE OF THE HAWAIIAN STREAM GOBY,
SICYOPTERUS STIMPSONI

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Biological Sciences

by
Kelly M. Diamond
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Accepted by:
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ABSTRACT

The ability of fish to escape from predators is a critical behavior for their survival. Experimental measurements of escape performance in fishes have typically been based on trials conducted in still water; however, such environmental conditions are rare in nature due to waves and currents that expose fishes to unsteady and/or directional flow. I examined the effects of water flow and predator attack direction on the escape behavior of fish, using juveniles of the amphidromous Hawaiian goby *Sicyopterus stimpsoni* as a model system. In nature, these fish must escape ambush predation by the Hawaiian sleeper, *Eleotris sandwicensis*, while exposed to rapidly flowing water. I measured the escape performance of juvenile gobies while exposing them to a range water velocities encountered in natural streams (0 cm/s, 15 cm/s, and 30 cm/s), stimulating fish with water jets from three different directions (front, side, and rear) to simulate the bow wave of an approaching predator. For trials in which stimulation elicited an escape response, there were limited effects of either flow speed or attack direction on escape trajectory, velocity, or acceleration. However, comparisons of response failure across treatments showed a strong effect of flow conditions on escape responses: whereas juvenile *S. stimpsoni* had uniformly high response rates for attacks from behind, rates of response for attacks from the front decreased dramatically as flow speed increased, up to 70% failure at 30 cm/s. Bow waves from predators attacking from the front might be masked by the flow environment, impairing their potential to be detected by the lateral line systems of prey. Thus, the likelihood of successful functional performance in fishes can depend

critically on environmental context, suggesting that changing environmental conditions might bear significantly on the outcomes of predator-prey interactions.

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INTRODUCTION

The ability of prey to detect and respond to stimuli produced by predators is a critical factor in determining the outcome of predator-prey interactions (Howland, 1974). In fishes, one of the most common responses to predatory stimuli is the fast-start escape behavior (Webb, 1976; Hale, 1999; Domenici, 2002). This behavior has been characterized as including three stages: 1) an initial tail flip forming a C or S shape directed away from the stimulus; 2) bending that proceeds down the body, adjusting escape trajectory; and 3) unpowered gliding combined with periodic lateral movements that return the fish to steady swimming (Anderson, 1988). The fast start escape response can be triggered visually using a neurological pathway involving rapid signal transmission via Mauthner cells (Eaton et al., 1977; Zottoli et al., 1999; Hale, 2002) or mechanically from stimulation of the lateral line system (Stewart et al, 2013; 2014). Extensive study of this response has shown that many different aspects of fish biology can affect fast-start escape performance, including prey morphology (Webb, 1976; Law & Blake, 1996; Domenici, 2001), developmental stage (Hale, 1996, 1999), behavior (Eaton et al., 1977; Boho´rquez-Herrera et al., 2013), physiology (Foremen and Eaton, 1993; Hale, 2002; Lefrançois & Domenici, 2006; Abrahams et al., 2007; Fu et al., 2015), and specific gravity (Stewart and McHenry, 2010).

Although previous studies have clarified several intrinsic aspects of prey fish that can affect escape success, nearly all have tested fish in still water. Since few natural habitats are predominantly comprised of still water, the potential impact of a major environmental variable on escape performance remains largely untested. For example,

Danos (2012) reared zebrafish across a gradient of fluid viscosities to model the influence of flow on locomotor development; however, this study did not apply stimuli to elicit fast start escapes, and instead only measured performance during steady turns (Danos, 2012). Exceptions to still water escape trials include studies by Roche (2014), who demonstrated that unsteady flows produced by waves can have significant effects on escape performance variables such as response latency and total distance traveled in juvenile reef fishes. Additionally, Binning et al. (2013), found that reef fishes exposed to greater directional changes in flow exhibited different fin morphologies, faster swimming speed and greater aerobic scope. However, comparing the effects of such environments on escape responses across broader ranges of fish species is difficult, due to the multi-directionality of wave-induced flows.

In contrast to unsteady reef environments, stream habitats may provide a more tractable opportunity to assess the impact of environmental conditions on escape performance in fishes. The predominantly unidirectional (downstream) flow of streams can be simulated in lab studies using standard equipment such as flow tanks, which are commonly used for the study of general swimming kinematics (e.g., Jayne and Lauder, 1995; Blake, 2006) and gaits (e.g., Liao et al., 2003), and have contributed to modeling frameworks used to link the swimming performance of fish in the laboratory to natural river conditions (Lacey et al., 2012). Such tanks were used to compare escape responses in still versus flowing water for schools of Giant danio (*Devario aequipinnatus*) in response to a looming visual stimulus (Chicoli et al., 2014). These trials found patterns in the numbers of fish within a school initiating escapes. However, they were not

designed to evaluate the performance of individuals, or to stimulate the lateral line system, which is the predominant source of sensory input for detecting and responding to aquatic predators in fish that employ fast-starts to escape (Stewart et al., 2014).

Escape performance in flowing stream habitats could be especially critical to species of fishes that exhibit life histories with migratory phases. One example of such a species is the amphidromous Hawaiian goby, *Sicyopterus stimpsoni*. After being swept downstream to the ocean upon hatching, larval *S. stimpsoni* develop in marine habitats before returning to freshwater streams and undergoing metamorphosis (McDowall, 2003; Watanabe et al., 2014). Juvenile *S. stimpsoni* then swim upstream, against flow, attracted by organic matter that may indicate suitable habitat for growth into reproductive adulthood (Fitzsimmons et al., 1997; Julius, 2007; Leonard et al., 2012). These gobies are well known for their ability to climb waterfalls to reach adult upstream habitats (Schoenfuss and Blob, 2003; Blob et al., 2007; Moody et al., 2015). However, before reaching these predator-free environments, juvenile *S. stimpsoni* must escape attacks from a non-climbing, ambush predator, the Hawaiian sleeper *Eleotris sandwicensis* (Blob et al., 2010; Maie et al. 2014). *S. stimpsoni* thus provides a system in which the examination of escape responses in flow has particular ecological relevance.

In *S. stimpsoni*, escape responses directed upstream would carry fish in the same direction as their migration, but would be against strong currents that would increase drag and potentially make fish susceptible to capture. Conversely, downstream escapes could have improved performance if aided by stream flow, but would carry an energetic cost for fish to retrace migratory travel. However, the original direction of the attack stimulus

might be an overriding factor in the direction of escape. Because fish typically attempt to move in a direction that is generally opposite to a predator's attack (Domenici et al. 1997), escape direction might be expected to be opposite of an attack stimulus direction, regardless of flow.

Fast-start escape responses are triggered by the physical perception of stimuli (Eaton et al., 1984; Domenici, 2002; Stewart et al., 2014); however, flowing water might mask perception of water pressure waves by the lateral line system (Stewart et al., 2013), reducing escape performance as flow speeds increase. Such effects may be especially pronounced in stimuli aligned with flow (i.e., coming from upstream), as opposed to the side or rear of a fish headed upstream. Studies of the Black Goby showed that fish react to lower perceived threats with less body bending, but respond with full fast-start escapes to stronger threats (Turresson et al., 2009). If higher flow speeds dampen the ability of an individual to detect a stimulus, then larger angles of escape might be expected in still water compared to flowing water.

Escape performance might also correlate with morphological characteristics of juvenile gobies that could aid progress upstream. In previous studies of the fast start escape response, the fineness ratio has been used as an indicator of overall body shape (Webb and Weihs, 1986). Fish with larger fineness ratios have more streamlined body shape, whereas fish with smaller fineness ratios have deeper bodies better for producing thrust in the second stage of the fast start escape response. Juvenile *S. stimpsoni* exhibit a morphological trade-off, in which tall-bodied fish (lower fineness ratios) that are better at escaping predation, via higher thrust production, exhibit a lower ability to climb

waterfalls, in which streamlined bodies (higher fineness ratios) help to reduce drag from oncoming water (Blob et al., 2010). Similar trade-offs between body shape and performance have been noted across species of fishes that emphasize cruising versus acceleration (Webb, 1984), and found in salmon and trout raised under fast and slow flow conditions (Pakkasmaa and Piironen, 2001). Based on these studies, in flowing water, fish with a more streamlined morphology (higher fineness ratios) might be expected to escape upstream (into oncoming flow) more often than those that are less streamlined (lower fineness ratios).

The fast-start escape behavior was, historically, viewed as a fixed action pattern (Eaton & DiDomencio, 1986; Anderson, 1988, Domenici & Blake 1991). Although many aspects of fast-starts in fishes, including their speed and acceleration, have typically been found independent of external factors (Binning et al., 2014; Fu et al., 2015), recent studies have indicated that the fixed action view of fast-starts is too simple (Tytell & Lauder, 2008; Marras et al., 2011; Stewart et al., 2013). It is possible that flow could affect escape velocity and acceleration, depending on the direction of attack in relation to ambient flow conditions. For example, if a fish were oriented upstream and was attacked from the front (i.e., the same direction as stream flow), it might turn in the same direction as flow during its escape; thus, surrounding flow conditions might increase the velocity and acceleration of the escape. Alternatively, if fish oriented upstream were attacked from the back, escaping away from a predator might require heading into flow, potentially increasing drag and decrease the velocity and acceleration of the escape. Such

impacts on fast-start performance might become more pronounced as flow speed increased.

In contrast to escape velocity and acceleration, other aspects of fast-start performance have been shown to vary in relation to the conditions under which fish are attacked. For example, larval zebrafish show similar escape speeds when attacked while still or while swimming; however, the probability of responding to an attack decreases significantly among swimming fish (Feitl et al., 2010). If environmental factors such as flow mask the perception of predator-induced pressure waves by the lateral line system, this could increase the percentage of fish that fail to perform an escape response, with fewer fish predicted to respond at higher flow speeds, particularly when attacked from the same direction as flow.

To test for potential impacts of environmental flow on fast-start performance in fishes, I collected high-speed video of fast-start escapes in response to multiple stimulus directions and across a gradient of flow speeds, using juvenile *S. stimpsoni* as a model system. With these data, I tested the following specific predictions: 1) escape direction is correlated with attack stimulus direction, regardless of flow speed, 2) escape angle is related to flow speed, with larger escape angles occurring in still water than in faster flow, 3) escape direction is correlated with fish morphology, with more streamlined fish tending to escape upstream more often than less streamlined fish, 4) flow speed and attack direction are correlated with the peak velocity and acceleration at which fast-start escape behaviors occur, with fish attacked from the front having higher peak accelerations and peak velocities than fish attacked from the side or back directions due

to aid from ambient flow, particularly as flow speed increases, and 5) the proportion of fish that attempt to escape from attack stimuli will decrease as flow speeds increase, or as fish are attacked in the same direction as flow. More generally, these analyses provide perspective on the importance of considering environmental context during the use of lab studies for understanding functional performance in nature.

MATERIALS AND METHODS

Juvenile *Sicyopterus stimpsoni* ($N=208$) were collected in March 2014 and March 2015 from Hakalau Stream on the Island of Hawai'i. As with most streams on Hawai'i, Hakalau Stream exhibits high variation in flow environment due to frequent flooding events (Blob et al., 2010). It also shows a high abundance of predators in a small area immediately below a low water bridge that creates a waterfall close to the mouth of the stream. Fish were caught with dip nets near the entry of the stream to the ocean and transported by car, in buckets of stream water, to the field station of the Division of Aquatic Resources for the State of Hawai'i in the city of Hilo. Fish were housed in aerated stream water, and all trials were conducted between 24 and 48 hours of capture.

Fast-start trials were conducted in a custom built, variable speed flow tank with continuous speed control and a 127.0 cm x 10.2 cm x 12.7 cm working area, fitted with a flow-through experimental chamber that restricted trials to a smaller filming area (22.9 cm x 10.2 cm x 12.7 cm) without the risk of fish encountering walls (juvenile *S. stimpsoni* average <25 mm in length: Schoenfuss and Blob, 2003). Trials were filmed with high-speed video (Fastec Highspec 2G, 1000 Hz), using a mirror angled at 45° to the

clear bottom of the tank. *S. stimpsoni* are strongly positively rheotactic, and preferentially attach to substrates using a ventral sucker formed from their pelvic fins (Schoenfuss and Blob, 2003; Maie et al., 2007, 2012). Therefore, prior to all trials, fish were allowed to attach to the bottom of the tank and orient in the same, head-upstream direction.

Escape responses were stimulated by applying a rapid pulse of water via transparent airline tubing connected to a syringe, modeling the water displacement imposed by the bow wave of a predatory strike (Stewart et al., 2013; Maie et al., 2014). To keep the application of the stimulus as consistent as possible across trials, the syringe was filled to the same volume (5 mL) and depressed by the operator with maximum force for each trial. Each trial was conducted on a new fish. Thus, the order of trial categories (see below) was not randomized, but rather each block of trials under a set of conditions was completed before beginning a new block under different conditions, helping to ensure maximal consistency of trial conditions within a block. If the application of a stimulus failed to elicit an escape response from a fish, the trial was considered valid and contributed to the evaluation of the proportion of fish that responded under each treatment; however, further performance variables were not calculated for these trials (i.e., average values for treatments do not include zeros for trials with failed responses).

Trials were conducted at three flow speeds (still water, 15 cm/sec and 30 cm/sec), spanning a common range of flow speeds encountered by *S. stimpsoni* in nature (Kinzie, 1988; Fitzsimons et al., 1997; pers. obs., 2014). Speeds were determined by calibrations of the digital motor control of the flow tank with a FlowMate 200 portable flow meter

(Marsh-McBirney Inc.). Water depth in the tank and the depth at which flow speed measurements were taken were kept consistent across all trials (12.7 cm and 2.5 cm, respectively). Water was prevented from excessive heating above ambient stream conditions ($<25^{\circ}\text{C}$) by placing ice water around the return tube of the flow tank. Attack stimuli were applied from one of three different directions relative to the starting orientation of the fish: front (0° - 60° ; $\bar{x} = 20.9^{\circ} \pm 14.9^{\circ}$), side (61° - 120° ; $\bar{x} = 89.9^{\circ} \pm 16.4^{\circ}$), and back (121° - 180° ; $\bar{x} = 164.5^{\circ} \pm 12.5^{\circ}$). This combination of flow speeds and stimulus directions produced nine treatment categories (Figure 1).

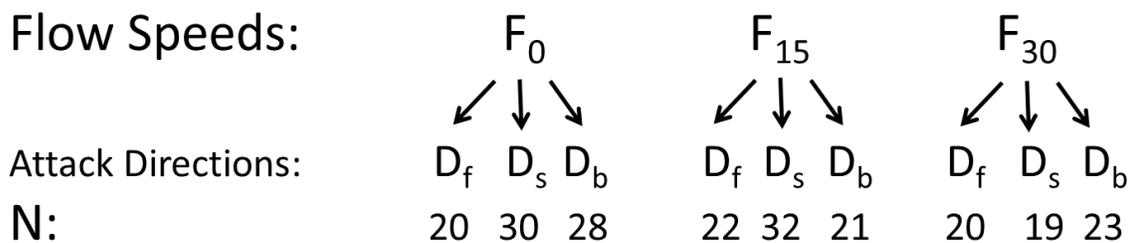


Figure 1. Experimental design of sampled flow speeds and attack directions for fast-start trials in *S. stimpsoni*. Flow speeds in the first row are indicated by F_0 (still water), F_{15} (15 cm/sec) and F_{30} (30 cm/sec). Three attack directions were tested for each flow speed, listed in the second row and indicated by D_f (attacked from the front), D_s (attacked from the side), and D_b (attacked from the back). The final row (N) indicates the number of fish used for each category of measurements. Differences in sample size between categories were due to failures of the camera recording system that invalidated some trials, or reassignment of fish to different categories after angles of attack were calculated.

Angles of attack and escape were measured from each trial as circular variables (Domenici and Blake, 1993), using points tracked from video frames via DLT Data Viewer (Hedrick, 2008). The angle of attack was calculated from the first video frame of each trial, and defined as the angle between two vectors, the first from the center of mass to the anterior most point of the fish, and the second from the center of mass to the

stimulus point (Domenici and Blake, 1991; Stewart et al., 2013). Based on data from 10 representative fish, center of mass was calculated following methods of Webb (1978) and Xiong and Lauder (2014) as approximately 44% of body length, starting at the rostrum. The angle of escape was calculated for each video frame as the difference between the orientation of the center of mass-to-rostrum vector for that frame, and the orientation of that vector in the first analyzed frame (i.e., the starting orientation of the fish). Comparisons of angle of escape across trials were based on the value measured at 30 ms after the escape response commenced (Walker et al., 2005). This time increment was chosen because it is within the average time taken by predatory *E. sandwicensis* to perform successful strikes on juvenile goby prey (Maie et al., 2014). Instantaneous angular velocity and acceleration were also calculated for each escape response from the tracked points, using a double differentiation of a quintic spline function fit to the position of the center of mass through time, which was smoothed using a replicate validation method developed by Dr. Jeffery A. Walker.

After escape response trials, fish were euthanized using a 0.25 g/L tricaine methanesulfonate (MS-222) solution, photographed for morphological measurements, and preserved in formalin. Preserved specimens were curated in the collections of Clemson University's Campbell Museum of Natural History. Measurements were collected from photographs using ImageJ software (NIH, Bethesda, MD, 2014), and included standard length and maximum height. Fineness ratio was then calculated as the standard length of the fish (total length excluding caudal fin) divided by the maximum height of the fish (Webb and Weihs, 1986). This measurement of overall body shape was

considered a reflection of relative streamlining, and was compared with escape performance to test for correlations between body shape and escape angle.

All statistics were performed in JMP v 11.0.0 (SAS Institute Inc.). For escape angle, peak acceleration, and peak velocity, I ran an analysis of covariance (ANCOVA) comparing each variable across flow speeds and angles of attack and the interaction between these two variables, using fineness ratio as a covariate. Only fish that responded with a fast-start escape response were used in these analyses. If the ANCOVA produced a significant result, least square mean differences were calculated with a Tukey's Honest Significant Difference (HSD) for flow speed and attack direction, and linear regression were used to evaluate patterns in fineness ratios. I also calculated effect sizes (ω^2) for flow speed and attack direction for each of these variables following the recommendations of Olejnick and Algina (2003). Finally, to compare the proportion of fish responding to attacks under different conditions, I performed a log linear analysis by constructing two 3x3 contingency tables to compare the number of fish that escaped and that failed to escape across all flow treatments and attack directions. I then used a post-hoc Fisher's Exact Test to distinguish significant differences among the nine treatments. Additionally, I used logistic regression to test whether there were differences in overall body shape (fineness ratio) between fish that responded to stimuli and fish that failed to perform an escape response

RESULTS

Escape Angle

Average escape angles ranged from 29.52° to 69.10° among the treatments, averaging 33.19° at 30 ms after first movement in response to the stimulus (Figure 2, Table 2). ANCOVA identified a significant difference in escape angle among flow speed and attack direction treatments and interactions when fineness ratio was used as a covariate ($F_{6,133}=2.64$, $p=0.019$, $\omega^2=0.073$). Effect tests from the ANCOVA show that only attack angle influences the escape angle ($p=0.004$) with no significant effect of flow speed, fineness ratio, or the interaction between attack angle and fineness ratio. Escape angles for fish attacked from the front averaged over 50° for all three flow treatments, whereas escape angles for fish attacked from other directions typically averaged less than 40° (Figure 2, Table 2). However, Tukey's HSD indicated a significant difference ($p=0.047$) only between fish attacked from the front at moderate flow speed (treatment cf_15) and fish that were attacked from the side at high flow speeds (treatment cs_30), with cs_30 fish showing the lowest average escape angles of any group (29.52 ± 8.84) and cf_15 fish averaging escape angles 37° greater (Table 2).

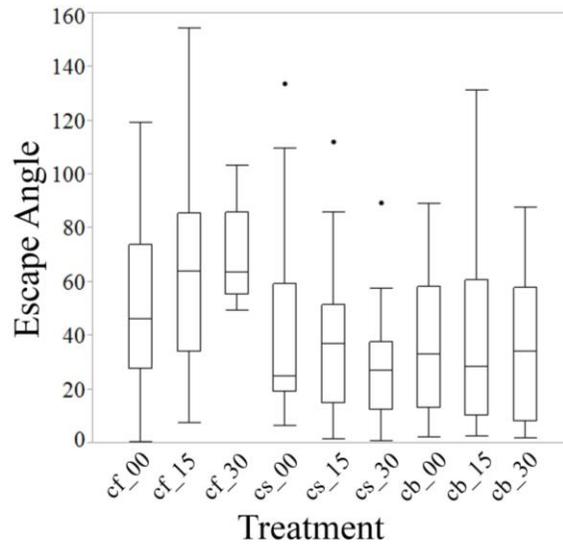


Figure 2. Box plots of escape angle for each of the nine treatments. Attack directions are coded cf for front, cs for side, and cb for back. Flow speeds are coded 00 for still water, 15 for 15 cm/sec and 30 for 30 cm/sec. The boxes represent the first and third quartiles for each treatment. Horizontal lines within the boxes represents the median sample values. Lines outside of the boxes extend to the outermost data point falling within the interquartile range of the given treatment. Black dots above boxes represent outliers.

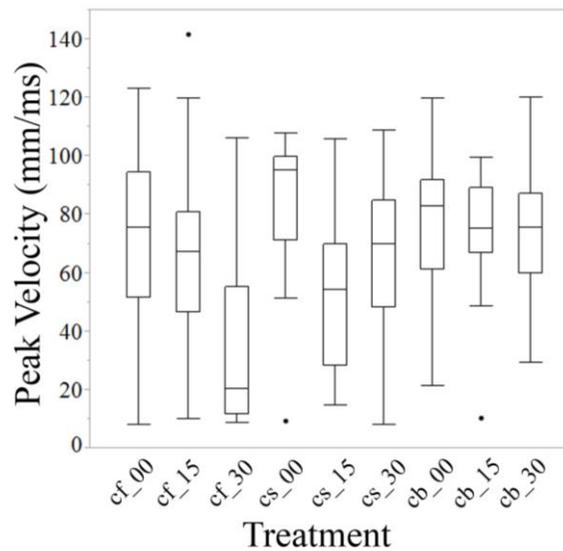


Figure 3. Box plot of peak velocity for each of the nine treatments. Attack directions are coded cf for front, cs for side, and cb for back. Flow speeds are coded 00 for still water, 15 for 15 cm/sec and 30 for 30 cm/sec. Format for plots follows that shown in Figure 2.

Peak Velocity and Acceleration

In contrast to escape angles, no significant differences emerged among flow speed, attack direction, or fineness ratio for peak velocity ($F_{6,134}=0.44$, $p=0.892$, $\omega^2=-0.025$) within the first 30 ms of the escape response (Table 2, Figure 3). However, ANCOVA identified a significant difference in peak acceleration within the first 30ms of the escape response across flow speed and attack direction treatments when fineness ratio was used as a covariate ($F_{6,134}=2.71$, $p=0.016$, $\omega^2=-0.030$). Effect tests indicated that peak acceleration was influenced by both attack angle ($p=0.010$) and fineness ratio ($p=0.002$). While average peak accelerations were higher in treatments with fish attacked from the front vs the back (Table 2, figure 4), I found no significant difference among these treatments using Tukey's HSD test. When I regressed fineness ratio on peak acceleration for each of the nine treatment groups, the only significant result I found was for the cf_15 treatment ($p=0.027$), with more streamlined fish (fish with larger fineness ratios) having higher peak accelerations (Table 1, Figure 5).

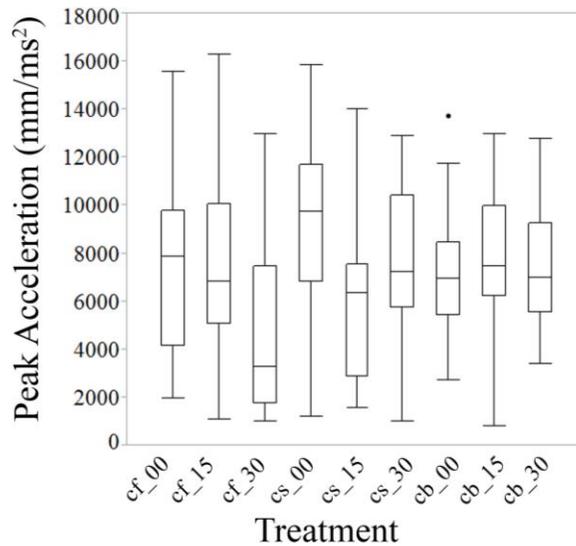


Figure 4. Box plot of peak acceleration for each of the nine treatments. Attack directions are coded cf for front, cs for side, and cb for back. Flow speeds are coded 00 for still water, 15 for 15 cm/sec and 30 for 30 cm/sec. Format for plots follows that shown in Figure 2.

Table 1. Results of linear regression of fineness ratio on peak acceleration for juvenile *S. stimpsoni* for each of the nine treatments. Attack directions are coded cf for front, cs for side, and cb for back. Flow speeds are coded 00 for still water, 15 for 15 cm/sec and 30 for 30 cm/sec. Bold numbers indicate a significant relationship between acceleration and body shape within the specified treatment.

Treatment	N	R²	F	P
cf_00	16	0.215	3.839	0.073
cf_15	17	0.286	6.017	0.027
cf_30	6	0.002	0.007	0.940
cs_00	13	0.010	0.112	0.745
cs_15	16	0.017	0.246	0.627
cs_30	11	0.053	0.502	0.497
cb_00	22	0.014	0.278	0.604
cb_15	16	0.057	0.847	0.373
cb_30	23	0.017	0.367	0.551

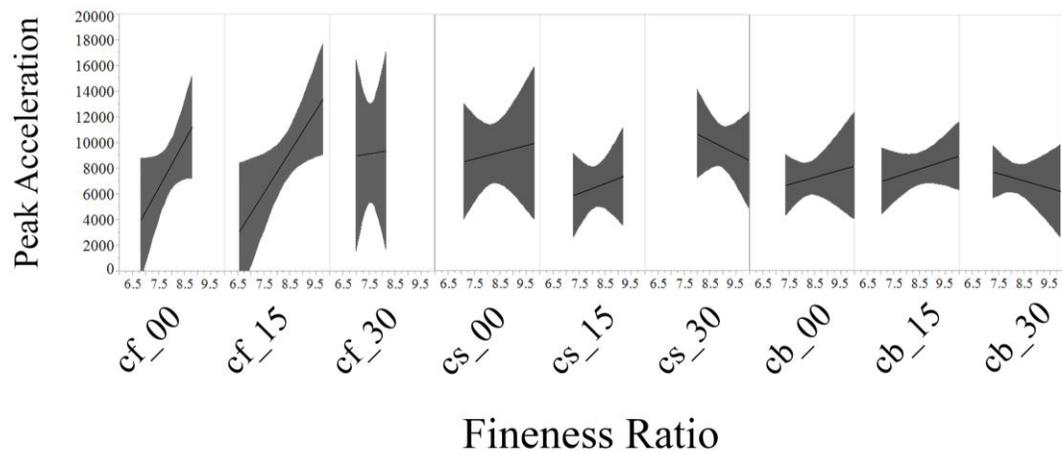


Figure 5. Peak acceleration of juvenile *S. stimpsoni* regressed on fineness ratio for each of the nine treatments. Black line represents line of best fit and shaded region represents the standard error. Attack directions are coded cf for front, cs for side, and cb for back. Flow speeds are coded 00 for still water, 15 for 15 cm/sec and 30 for 30 cm/sec. Only cf_15 shows a significant trend (Table 1).

Table 2. Summary statistics of escape angle, fineness ratio, peak velocity, peak acceleration, and percent failure for each of the nine treatments. N is the number of fish tested for each treatment. For evaluations of “percent failure,” fish that did respond, but moved out of the frame before 30ms elapsed, were considered as successes in the total sample. “Group” represents the significance category based on least square means calculated for Tukeys HSD test, where treatments with different letters represent significantly different groupings and treatments with the same letter are not significantly different.

Treatment	Escape Angle		Fineness Ratio		Velocity		Acceleration		Percent Failure		
	N	Mean±SE	N	Mean±SE	N	Mean±SE	N	Mean±SE	N	Percent	
cf_00	16	53.57±7.97	16	7.89±0.15	16	74.92±6.23	16	8041.29±781.44	A	20	10
cf_15	17	66.83±7.73	17	8.34±0.15	17	77.31±6.05	17	8899.09±758.12	A	22	23
cf_30	5	69.10±14.26	6	7.54±0.25	6	68.84±10.17	6	9202.88±1276.09	A	20	70
cs_00	13	43.26±8.84	14	8.22±0.16	13	83.42±6.91	13	9168.76±866.93	A	22	23
cs_15	16	38.41±7.97	16	8.13±0.15	16	60.51±6.23	16	6595.27±781.44	A	32	47
cs_30	13	29.52±8.84	11	8.93±0.18	13	73.80±6.91	13	9121.57±866.93	A	19	21
cb_00	23	36.12±6.65	23	8.24±0.13	22	77.52±5.31	22	7225.88±666.42	A	28	4
cb_15	16	36.71±7.97	16	8.49±0.15	16	77.59±6.23	16	8008.38±781.44	A	20	5
cb_30	23	36.88±6.65	23	8.16±0.13	23	73.77±5.20	23	7255.49±651.77	A	23	0
Grand Mean	142	33.19±2.79	142	8.24±0.06	142	74.52±2.09	142	7974.94±265.70		206	23

Proportion of Fish Responding to Stimulus

Results from the log linear analysis show that flow speed ($G^2=8.52$, $p=0.014$), attack direction ($G^2=31.18$, $p<0.001$), and the interaction between flow speed and attack direction ($G^2=60.36$, $p<0.001$) all had a significant effect on the probability of a fish to respond to an attack stimulus. When fish were attacked from the front, the proportion of fish that failed to escape was significantly greater for the high flow (30 cm/sec) treatment compared to both no flow and mid flow (15 cm/sec) treatments (Table 3, Figure 6). Moreover, trials from the front appeared to show a dramatic increase in response failure as flow speed increased, moving from 10% failure in still water to 23% failure at 15 cm/s to 70% failure at 30 cm/s (Figure 5). In contrast, for fish attacked from the back, the percentage of fish responding was consistently high (95% or higher) regardless of flow speed (Table 3, Figure 6). In high flow, the percentage of fish failing to respond consistently increased as attacks shifted from the back, to the side, to the front (Table 4, Figure 6). Such consistent directional patterns did not emerge at lower flow speeds. Logistic regression indicated that there was no difference in fineness ratio between nonresponsive and responsive individuals ($F_{1, 202}=0.003$, $p=0.954$).

Table 3. Fisher's Exact Tests comparing frequency of escape responses for juvenile *S. stimpsoni* between different flow speeds within each attack direction. No flow represents 0 cm/sec, mid flow 15 cm/sec, and high flow 30 cm/sec. Values reported are p values for these tests with bold values representing significant differences between indicated flow categories.

Attack Direction	No Flow vs Mid Flow	No Flow vs High Flow	Mid Flow vs High Flow
Front	0.414	<0.001	0.005
Side	0.091	1.000	1.000
Back	1.000	1.000	0.465

Table 4. Fisher's Exact Tests comparing frequency of escape responses for juvenile *S. stimpsoni* between different attack directions within each flow speed. No flow represents 0 cm/sec, mid flow 15 cm/sec, and high flow 30 cm/sec. Values reported are p values for these tests with bold values representing significant differences between indicated directions.

	Front vs Side	Front vs Back	Side vs Back
No Flow	0.414	0.563	0.075
Mid Flow	0.091	0.187	0.002
High Flow	0.004	<0.001	0.035

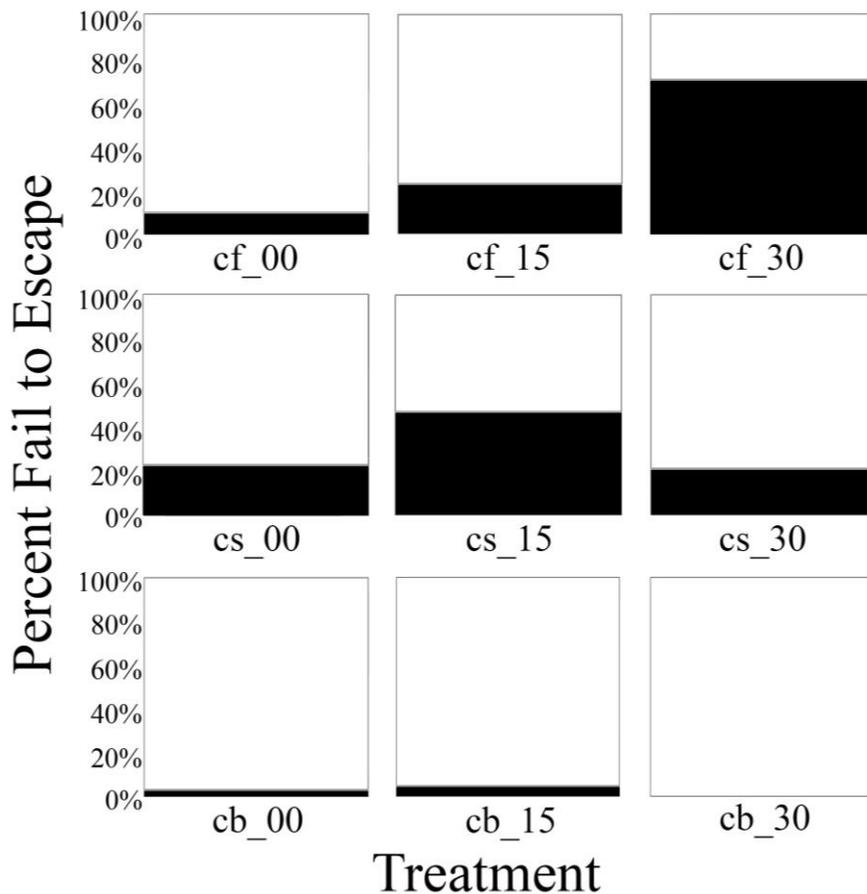


Figure 6. Bar plots representing the percentage of fish that failed to escape for each treatment. Each row represents a different attack direction, coded cf for front (top row), cs for side (middle row), and cb for back (bottom row). Each column represents a different flow speed, coded 00 for still water (left column), 15 for 15 cm/sec (middle column), and 30 for 30 cm/sec (right column).

DISCUSSION

Previous consideration of how flow conditions might affect the escape responses of fishes has been limited. The results of my experiments show that flowing water can have a range of effects on escape responses, though these effects did not always follow predicted patterns, and may depend substantially on the direction of attack.

The average escape angle of juvenile *S. stimpsoni* showed limited, but significant, differences across treatments. In general, fish attacked from the front tended to show higher escape angles than fish attacked from other directions (Figure 2); however, post hoc tests identified only one significant difference between treatments (fish attacked from the front, in mid flow, showed escape angles averaging 37° greater than fish attacked from the side in high flow: Table 2). I had initially predicted that still water trials might show greater escape angles than trials in flow, potentially due to hydrodynamic drag imposed by flow that might impede movement by escaping fishes. However, still water trials do not show consistently greater escape angles than trials in flow. Thus, the impact of flow-induced drag on escape performance may be minimal over the flow speeds evaluated. Instead, it is possible that passive drift imposed by flow might contribute to escape angles of fish attacked from the front in flow, which showed the highest escape angles of any treatment.

The limited relationship between escape angle and attack direction, particularly between attacks from the side versus the back, is striking, because it indicates that *S. stimpsoni* rotate a similar amount in their escapes, regardless of the direction from which a predator attacks. Because fish were all oriented upstream at the start of trials, this

indicates that fish actually rotate toward an attack from behind during the initial phase of an escape. Such responses within the average duration of a predatory strike could be disadvantageous, even if modulated in later stages of the escape. However, these results are at least partly consistent with analyses in which larval zebrafish were found to move away from an attack most successfully when positioned lateral and ventral relative to the predator (Stewart et al., 2014). They are also consistent with behavioral evidence suggesting that the underlying neural command of fast-starts is ballistic, and does not use additional sensory information from stimuli once movement begins (Eaton and Emberly, 1991). This response thus overrides the strong directional rheotaxis exhibited by juvenile *S. stimpsoni* during upstream migrations (Smith & Smith, 1998).

Environmental factors such as flow speed (Pakkasmaa & Piironen, 2001), and predation pressure (Law & Blake 1996; Domenici et al., 2008) can influence prey morphology in species that exhibit phenotypic plasticity, and can also exert strong selection on body shape in fishes (Blob et al., 2010). For *S. stimpsoni* in particular, I predicted that more streamlined fish might tend to escape in a more upstream direction that could potentially be more advantageous for their ultimate migratory trajectory. However, results from this study showed no association between body shape and escape angle.

The peak velocity of *S. stimpsoni* showed no significant associations with flow speed, refuting my prediction. Many studies have found limited responses of fast-start velocity and acceleration to changing conditions. For example, in larval zebrafish, the act of swimming was found to diminish the probability, but not the speed, of response to a

flow stimulus (Feitl et al., 2010). Similarly, pale chub from high predation populations were found to have higher escape performance, but this was achieved through shorter response latency rather than improved fast-start speed or acceleration (Fu et al., 2015). Because the movement of water from my jet stimulus was not visible, it was not possible to evaluate response latency in this study, but further trials (e.g., with jets of dyed water) could be performed to test for such responses.

In contrast to peak velocity, peak acceleration was influenced by attack direction and fineness ratio. For attacks from the front at intermediate flow speeds, more streamlined fish exhibited higher peak accelerations than taller-bodied fish. These results support the potential for ambient flow conditions to affect fast-start escape response, as fish attacked from the front would be aided by ambient flow during movement away from a predator, whereas fish attacked from the side or back would incur higher drag, induced by the same flow conditions, during movement away from a predator. Although these patterns were limited to a single treatment, the fact that more streamlined fish had higher peak accelerations supports a role for ambient flow in contributing to performance. Streamlined fish would typically be viewed as less proficient in thrust production for escape than taller fish (e.g., Walker, 1997); thus elevated accelerations by streamlined fish could indicate the use of ambient flow conditions to aid in escape response.

The strongest indication that flow conditions can affect the escape responses of fish emerged through comparisons of response failure across treatments. Whereas juvenile *S. stimpsoni* had uniformly high response rates for attacks from behind, rates of response for attacks from the front decreased dramatically as flow speed increased,

shifting from 10% failure in still water to 70% failure at 30 cm/s (Figure 3, Table 2). The common failure of fish to respond to flow pulses from the front in high flow may be because these pulses are masked by the flow environment, impairing their potential to be detected by the lateral line. The strength of a stimulus relative to strength of alternative environmental cues has been shown to influence the type and number of escape responses in animals, including fish (Batty & Blaxter, 1992; Abrahams, 1997; Domenici, 2010; Roche, 2014). Moreover, fish with compromised lateral line systems typically fail to perform fast-start escapes in response to stimuli, even when the visual system remains intact (Stewart et al., 2014). A flow pulse in a direction opposite from surrounding flow is likely to provide a stronger stimulus to the lateral line than a pulse moving in the same direction as a surrounding flow field. Further, Eaton et al. (1984) found that even in fish with intact Mauthner cell pathways, non-Mauthner cell circuits functionally substitute for this system when fish were attacked from behind. Such mechanisms may help fish respond effectively to threats from directions in which vision is likely most limited.

Considering the common failure of juvenile *S. stimpsoni* to respond to frontal attacks in high flow, it seems likely that positively rheotactic fish, like this species, may be most vulnerable to attacks from the front during upstream migrations. Field observations of attack directions by *E. sandwicensis* on migrating gobies could test whether predators typically attack from directions or flow speeds that advantageously mask their approach in stream environments. In this context, it is noteworthy that on the island of Hawai'i, adult *S. stimpsoni* commonly select microhabitats with low flow speeds (Kinzie, 1988), but adult *S. lagocephalus* studied in Australian wetlands select higher

flow speeds in their natural habitats (Donaldson et al., 2013). Such patterns of microhabitat selection could expose these closely related species to differing susceptibility to predation.

Migratory fishes that depend on flow stimuli, such as *S. stimpsoni*, have been used to detect early changes in stream ecosystems in response to anthropogenic activities (Schoenfuss & Blob, 2007; Donaldson et al., 2013). Many streams can be subject to rapid changes in flow conditions (e.g., flash flooding), but little is known about how changes in flow conditions affect stream communities (Fitzsimmons et al., 1997; Julius, 2007). Results of this study show that the likelihood of successful functional performance can depend critically on environmental context. Understanding the escape performance of fish in flow environments should help improve understanding of predator-prey interactions in nature, and how these might be affected by the prospect of changing environmental conditions.

FUTURE DIRECTIONS

Repeatability of Response

While the effects of the fast-start escape performance on fitness are expected to be strong (fish that do not respond get eaten), and variation in the response of fish to stimuli have been demonstrated by the current study, the heritability of the behavioral response to stimuli in *S. stimpsoni* has yet to be assessed (Arnold, 1983). If this behavior is heritable, it should be repeatable, with individual fish responding or not responding to multiple stimuli. The production of, or failure to produce, an escape response could be

viewed as two alternative strategies: 1) by not responding, fish might increase their energy reserves available for climbing waterfalls or 2) by responding, fish might increase their probability of reaching a waterfall by escaping predation. These strategies may have different success depending on which type of stream a juvenile goby enters. For fish on the island of Hawai'i, it may be more advantageous to save energy reserves for climbing as the first waterfall is near stream mouth. However, on waterfalls on Kaua'i are much further inland, potentially making response to predator strikes a superior strategy that would increase chances of reaching the first waterfall and, hence, adult habitat. To test this prediction, I will test individual fish from both Hawai'i and Kaua'i multiple ($N \geq 5$) times under consistent conditions with at least one hour of rest between trials. I will conduct trials with the same variable speed flow tank described in the present study to determine if fish that respond to stimuli always respond, and fish that fail to respond never respond to stimuli. For these trials I will further constrain the testing arena to a minimum size that will not affect the turning ability of the fish, but will also limit the swimming area available to the test subject. By analyzing this dataset I will be able to test whether the fast-start escape responses of juvenile *S. stimpsoni* are repeatable. However, if I find there is high variation in individual escape responses, it would suggest that alternative trade-offs exist between escape performance and other ecologically important variables (Marras et al., 2011).

Eleotrid Attack Patterns

Although the trials described above provide information on *S. stimpsoni* performance in response to stimuli from different directions, field data to indicate

whether attacking *E. sandwicensis* show preferences in their attack direction are lacking for strikes in flowing water. Attacking downstream might allow water displacement towards prey to be masked by stream flow; however, it would also allow prey better visual perception of predators (which would be striking towards their heads).

Alternatively, attacks from behind prey might limit visual perception, but stand out with regard to pressure sensation. Using GoPro cameras (GoPro, USA) mounted in Hakalau Stream, I was able to film predatory attacks by *E. sandwicensis* during March, 2015.

From these videos, I will calculate the angle of attack in relation to the goby body and flow direction. I predict that *E. sandwicensis* will attack most often from the front or side directions and at higher flow speeds to minimize the potential for pressure wave detection by prey.

Adult Escape Behavior

Blob et al. (2007) found that climbing ability in the three Hawaiian climbing goby species diminished after attaining adult morphology due to increased body size relative to the size of the pelvic sucker. As adults no longer need to climb to escape from predation or find suitable habitat, this limitation does not seem to put these fish at a fitness disadvantage. However, because adults also do not face predation from *E. sandwicensis*, differences in predator escape performance may also exist between goby species or life stages. In zebrafish, it has been proposed that there is a point during development at which the scaling of fast-start kinematic variables with length changes dramatically (Hale 1999). Hawaiian stream gobies would be an appropriate system to test this hypothesis due to the presence and absence of predators at different life stages in these species.

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