

RESEARCH ARTICLE

Effects of wave-driven water flow on the fast-start escape response of juvenile coral reef damselfishes

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ABSTRACT

Fish often evade predators with a fast-start escape response. Studies typically examine this behaviour in still water despite water motion being an inherent feature of aquatic ecosystems. In shallow habitats, waves create complex flows that likely influence escape performance, particularly in small fishes with low absolute swimming speeds relative to environmental flows. I examined how wave-driven water flow affects the behaviour and kinematics of escape responses in juveniles of three coral reef damselfishes (Pomacentridae) with different body morphologies. Tropical damselfishes have similar fin and body shapes during early development, with the exception of body depth, a trait deemed important for postural control and stability. Wave-driven flow increased response latency in two of the three species tested: fish with a fusiform body responded 2.9 times slower in wave-driven flow than in still water, whereas this difference was less pronounced in fish with an intermediate body depth (1.9 times slower response) and absent in fish with a laterally compressed body. The effect of wave-driven flow on swimming performance (cumulative escape distance and turning rate) was variable and depended on the timing and trajectory of escape responses in relation to the wave phase. Given intense predation pressure on juvenile coral reef fishes during settlement, interspecific differences in how wave-driven flow affects their ability to escape predators could influence the distribution and abundance of species across spatial and temporal scales.

KEY WORDS: Body morphology, Complex flow, Swimming performance, Postural disturbance, Predator–prey interactions, Turbulence

INTRODUCTION

Avoiding and fleeing from predators is one of the most important tasks faced by animals (Ydenberg and Dill, 1986). Therefore, behaviour and locomotion are fundamental to the survival of mobile organisms during predator–prey encounters (Howland, 1974; Domenici et al., 2007; Higham, 2007). Fast-start escape responses are the primary behaviour used by fishes to evade predators (Domenici and Blake, 1997; Domenici, 2011). These rapid accelerations are particularly important for juvenile coral reef fishes (Fisher and Leis, 2010), as predation is a key factor influencing their survival (Almany, 2003; Almany and Webster, 2006; Holmes and McCormick, 2009). Predation on reef fishes is greatest during and

shortly after larvae metamorphose from a planktonic to a demersal life stage as they settle on the reef (Steele and Forrester, 2002; Almany and Webster, 2006). Owing to their small size, newly settled coral reef fishes are targeted by many generalist and piscivorous predators (Stewart and Jones, 2001; Holmes and McCormick, 2010). Estimates suggest that over 50% of juveniles, across a range of taxonomically diverse species, can be eaten within 48 h of settlement (Almany and Webster, 2006). Consequently, environmental factors that affect performance during escape responses by juveniles might have a substantial influence on the recruitment of coral reef fishes to adult populations (Rice et al., 1997; Fisher and Leis, 2010).

Many environmental parameters fluctuate dramatically in aquatic systems (Abrahams et al., 2007). Recent studies have examined the effect of temperature, dissolved oxygen, turbidity, light and pH on fish escape performance (reviewed in Domenici et al., 2007; Wilson et al., 2010). However, the importance of water motion has been largely overlooked (Higham et al., 2015; but see Anwar et al., 2016; Diamond et al., 2016). This oversight is surprising, given that water flow is a ubiquitous and highly variable physical property of aquatic ecosystems (Denny, 1988; Webb et al., 2010). In shallow marine habitats, wave-driven water motion is an important stressor for both sessile and mobile organisms (Denny, 2006; Denny and Gaylord, 2010; Webb et al., 2010). On coral reefs, for example, complex water flow from waves influences the ability of adult fishes to swim and occupy shallow, windward habitats, which leads to strong patterns of community structuring based on a species' ability to withstand ambient flow conditions (Bellwood and Wainwright, 2001; Bellwood et al., 2002).

Wave-driven water motion is characterized by unsteadiness (changes in flow velocity) and turbulence (vortices) as the water flow interacts with the reef structure (Liao, 2007; Webb et al., 2010). These complex flows can be energetically demanding (e.g. Roche et al., 2014; Maia et al., 2015; Schakmann et al., 2020) or beneficial (Taguchi and Liao, 2011; van der Hoop et al., 2018) for fishes, and can have destabilizing effects on important behaviours, including those associated with predator–prey interactions (Webb, 2002; Webb et al., 2010). Currently, the extent to which wave-driven water flow affects fish escape responses is unknown. Such biophysical interactions could be of considerable ecological importance for coral reef fishes, given the importance of predation in shaping their distribution and abundance. In addition, wave intensity and frequency are increasing in ocean basins worldwide as a result of climate change (Young et al., 2011; Rhein et al., 2013), with impacts anticipated on key processes in marine communities (Harley et al., 2006; Byrnes et al., 2011), including predator–prey interactions (Domenici and Seebacher, 2020). Basic knowledge of how waves influence the behaviour and unsteady swimming performance of fishes is essential to improve our understanding and ability to predict how environmental change will affect fish communities; for example, by altering energetic demands and the outcome of predator–prey encounters (Higham et al., 2015; Killen et al., 2016).

Here, I examined whether complex, wave-driven water flow affects behavioural and kinematic components of escape responses in post-

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Received 4 August 2020; Accepted 8 February 2021

settlement juvenile coral reef fishes in the family Pomacentridae. The damselfishes are a species-rich, morphologically diverse group, and are widely distributed throughout temperate and tropical waters around the world (Allen, 1991; Cooper et al., 2009). Many are small (<5 cm total length) and important prey items for predatory coral reef fishes (Kingsford, 1992; Beukers-Stewart and Jones, 2004). The Pomacentridae are characterized by broad differences in body depth, a trait known to influence fast-start behaviours (Domenici et al., 2007) and also linked to differences in the sustained swimming performance of juvenile coral reef fishes (Fisher et al., 2005; Fisher and Hogan, 2007). A deep, laterally compressed body is thought to improve fast-start swimming performance and postural control (Domenici and Blake, 1997; Eidietis et al., 2002; Domenici et al., 2008). Additionally, although suboptimal from a hydrodynamic/energetic perspective, owing to increased pressure and frictional drag, lateral compression has the advantage of allowing a greater expansion of the dorsal and anal fins (Webb, 2004, 2006), which also helps reduce rolling (Weihs, 2002; but see Webb, 2004).

I studied three damselfish species and examined whether effects of wave-driven water flow on escape responses varied among species with different body morphologies. I predicted greater negative effects of wave-driven flow on the response latency and escape kinematics of species with a more fusiform than laterally compressed body owing to the increased rolling stability conferred by lateral compression.

MATERIALS AND METHODS

Animals and experimental set-up

Early post-settlement juvenile fishes were collected while SCUBA diving in March 2012, using Aquic-S solution and hand nets on reefs adjacent to the Lizard Island Research Station on the Northern Great Barrier Reef, Australia (14°40'S; 145°28'E). I caught *Neopomacentrus azysron* (Bleeker 1877), *Chromis viridis* Cuvier 1830 and *Dascyllus reticulatus* (Richardson 1846) (family Pomacentridae); based on their body size, these fishes were less than 2 weeks post-settlement (Kerrigan, 1996; Fisher et al., 2005). These species co-occur on the reef but differ in their body morphology (Fig. 1). The fineness ratio (FR) is a measure of how elongate a fish is relative to its transverse sectional diameter (measured as the average of the maximum body width and maximum body depth) (Fisher and Hogan, 2007; Langerhans and Reznick, 2010): *N. azysron* has a shallow, fusiform body [standard length (SL)=12.7±0.5 mm, FR=4.23±0.12; mean±s.d.], *C. viridis* has a body of intermediate depth (SL=12.4±1.0 mm, FR=3.52±0.13), and *D. reticulatus* has a deep, laterally compressed body (SL=12.6±0.9 mm, FR=2.67±0.11). These differences are apparent in juveniles and maintained throughout adulthood. Beyond body shape, pectoral fins are also important for stability (Drucker and Lauder, 2003; Lauder and Drucker, 2004; Webb, 2004). However, pectoral fin shape is similar in juvenile damselfishes, differentiating only later in development (Fulton and Bellwood, 2002). Additionally, pectoral fins are small and transparent in juvenile reef fishes, which makes them impossible to view on whole photographs and difficult to dissect and pin (Fisher and Hogan, 2007). As such, pectoral fin shape was not considered in this study.

Captured fishes were placed in holding aquaria (40×29×18 cm; L×W×H) with seawater pumped directly from the reef. The water temperature was 29±1°C (mean±actual variation) and fishes were exposed to a natural photoperiod of 12 h for at least 3 days prior to the experiments. Fishes were fed once a day with commercial pellets (INVE NRD 2/4, Primo Aquaculture, Australia) and were not fed on the morning of the experiments. Animals were returned to their site of capture at the end of the study.

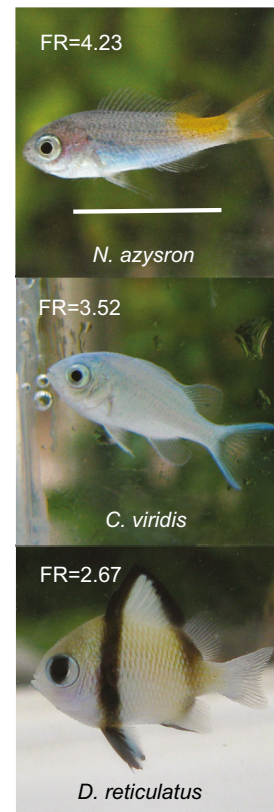


Fig. 1. Experimental species: *Neopomacentrus azysron*, *Chromis viridis* and *Dascyllus reticulatus*. Indo-Pacific damselfishes (Pomacentridae) with different body plans: *N. azysron* (fusiform body), *C. viridis* (intermediate body depth) and *D. reticulatus* (laterally compressed body). FR, fineness ratio. Scale bar: 10 mm.

Experiments were conducted in two rectangular acrylic tanks (70×60×35 cm; L×W×H) (Fig. 2). Water depth was maintained at 12 cm. Owing to their small size and to facilitate filming, individual fish were placed in a fine nylon mesh enclosure (large net breeder, Aqua One, Australia; 26.5×15×15.5 cm; 1 mm stretched mesh) at the centre of the experimental tanks. Four programmable pumps (Vortech MP10wES, EcoTech Marine, USA) were positioned at the back of each tank and wirelessly synchronized to generate complex flow approximating the orbital flow created by waves (see 'Flow visualization' section). Under still water conditions (water velocity <0.2 cm s⁻¹), the pumps remained on, but the propellers were removed to control for any effects of noise and/or vibrations from the pumps. A mirror was inclined at 45 deg below the aquarium to film escape responses and avoid image distortion from surface water movements (see Domenici and Blake, 1991). Floodlighting was provided by three 150 W spotlights, 70 cm above the water level. The experimental tank was continuously supplied with recirculating seawater, which kept the water temperature constant (29.0±0.7°C, mean±actual variation).

Animal collections and experiments were approved by the Great Barrier Reef Marine Park Authority (permit G11/34462.1) and the Australian National University (ANU) Animal Experimentation Ethics Committee (protocol A2011_21), and conformed to the relevant regulatory standards.

Experimental protocol

Prior to each fast-start trial, a test fish was transferred to the mesh enclosure in an experimental tank and left undisturbed for 30 min. Escape responses were induced by mechano-acoustic stimulation

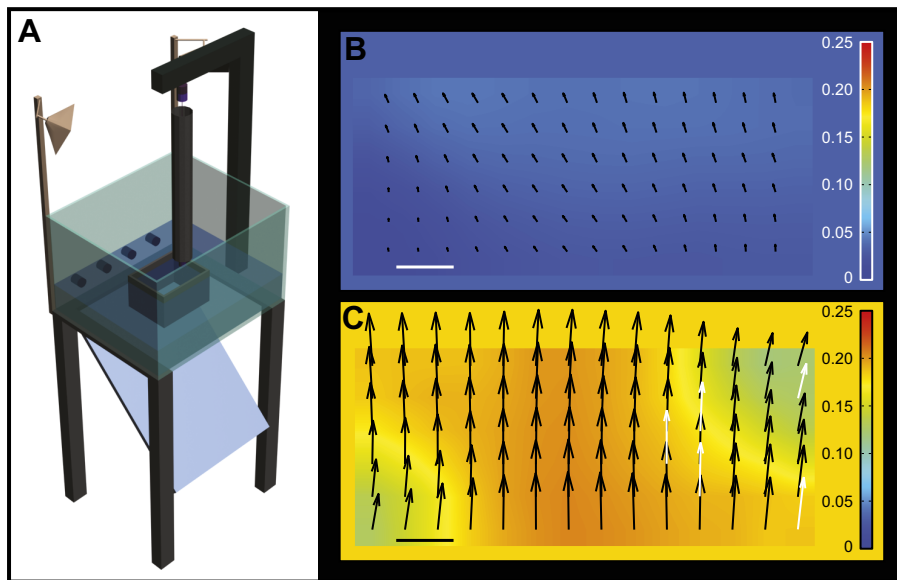


Fig. 2. Experimental setup for evaluating the escape responses of three species of Pomacentridae and particle image velocimetry (PIV). (A) Four programmable pumps (Vortech MP10wES, EcoTech Marine, USA) on the back wall of the experimental tank created wave-driven flow that travelled back and forth in the aquarium at a frequency of 0.85 ± 0.01 Hz (mean \pm s.d.). Juvenile fish were placed in a mesh enclosure at the centre of the tank and startled with a remotely operated mechano-acoustic stimulus. (B,C) PIV analysis showing flow velocity (black arrows) in the mesh enclosure in wave-driven flow conditions during flow direction change (B) and at the wave crest (C). The colour map represents the magnitude of flow velocity in m s^{-1} . White vectors are values interpolated by the software owing to spurious or missing data points. Scale bars: 0.20 m s^{-1} . For frame sequences of velocity vector and vorticity fields, see Movie 2.

(Dadda et al., 2010; Marras et al., 2011) (Movie 1). A 50 ml cylindrical container filled with lead weights was released by an electromagnet 45 cm above the water surface. The stimulus fell inside the mesh enclosure containing the test fish, 1 cm from the mesh wall (Fig. 2). To avoid visual stimulation prior to contact with the water, the stimulus fell inside a PVC tube (11 cm diameter) positioned 1 cm above the water surface (Lefrançois et al., 2005). The stimulus was attached by a string to the stand holding the electromagnet to prevent it from hitting the bottom of the tank. The exact time of stimulus contact with the water surface could be observed in the mirror below the tank (see Marras et al., 2011). Fish moved around freely in the mesh enclosure and were stimulated when in mid-water, at the centre of the mesh enclosure, to avoid wall effects. The camera's field of view excluded sections of the mesh enclosure within 1 cm from the walls. The distance of the fish's body (centre of mass) and angle relative to the stimulus were controlled for in the statistical analyses.

Escape responses were recorded at 420 Hz by a camera (Casio Exilim EX-FH100, Casio Computer Co., Tokyo, Japan) mounted on a tripod in front of the aquarium, facing the mirror. Typically, fast-start trials are conducted in shallow water to limit vertical displacement and facilitate kinematic measurements of fish movements in two dimensions (e.g. Langerhans, 2009). Here, a minimum water depth was necessary to create wave-driven flow. I used a second camera (Casio Exilim EX-FH100) to film through the aquarium front wall. If the fish moved a vertical distance greater than its body depth, the trial was excluded from the analyses. This distance was chosen to minimize measurement errors of displacement in the horizontal plane. Few trials (<2%) were excluded for this reason.

Fourteen fish were tested per species in each of the two flow conditions in a full factorial design. Individual fish were tested at least three times with a rest period of 30 min between trials (see Jornod and Roche, 2015). More than three trials were run (with a maximum of five) when fish made sudden movements before the stimulus hit the water surface, covered a vertical distance greater than their body depth, or exited the camera's field of view at the onset of stage 3 of the escape response (see 'Measurements of escape performance' section). For 12 of the 84 fish tested, only two trials could be obtained for analysis. Immediately following experiments, individual fish were sedated by submersion in a cool

(5°C) water bath for 3 s and then photographed on wetted, plasticized gridded paper. Photographs were analysed in ImageJ v.1.45 to measure size and FR. FR is calculated by dividing body length by the average of the maximum body width and maximum body depth (Bainbridge, 1960). I used SL as body length because an accurate measure of total length could not be obtained from photographs for 13 *N. azysron*. SL was measured from the tip of the snout to the narrowest point of the caudal peduncle. I used a value of 1.9 mm for the maximum body depth of all fishes because the body width of the juvenile damselfishes I examined was similar (1.8–2.0 mm) and difficult to measure accurately without handling and harming these small animals.

Flow visualization

I used particle image velocimetry (PIV) to characterize the flow conditions in the wave-driven flow treatment (Fig. 3). Flow velocity and vorticity were estimated by filming neutrally buoyant particles (Fluorescent Green Polyethylene Microspheres 1.025 g cm^{-3} , 63–75 μm , Cospheric, Santa Barbara, CA, USA) at 30 Hz in high

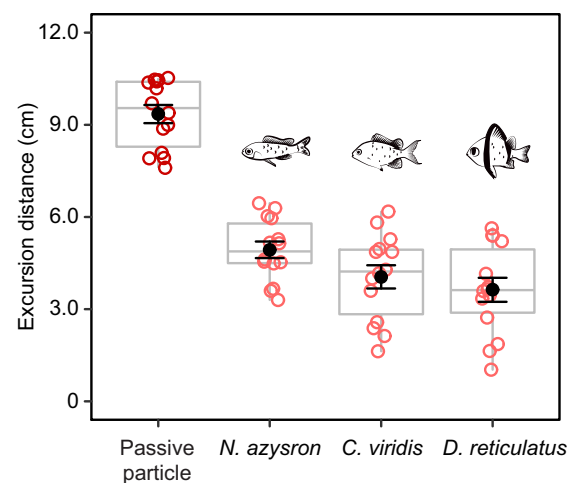


Fig. 3. Excursion distance of a passive particle and three species of Pomacentridae in wave-driven flow. Red circles are individual data points ($N=14$ for each group); black dots are means; error bars are 1 s.e.m. Box plots show the median and interquartile range (IQR); whiskers are 1.5 times the IQR.

definition with a Casio Exilim EX-FH100 camera. Microspheres were illuminated using a NOVALaser X100 laser pointer (NOVALasers, Toronto, Canada; power output 100 mW at 532 nm) fitted with a collimating lens to create a light sheet 2 mm thick (Ryerson and Schwenk, 2012). The light sheet intersected the mesh enclosure in mid-water, 6 cm above the tank bottom. No fish was present at the time of recording. Image sequences were pre-processed in the video editor Avidemux v.2.5.4 (<http://avidemux.sourceforge.net>) to maximize the contrast between the particles and the black background, and then imported into PIVlab v.1.32 (<https://pivlab.blogspot.com.com.au/>). PIVlab estimates the probable shift of particles by cross-correlation between the same interrogation areas in image pairs. Vector maps and velocity or vorticity fields were generated using a 256×256 pixel interrogation area and a 128 pixel step (i.e. the vertical and horizontal distance between the centre of the interrogation areas). The wave frequency was 0.85 ± 0.01 Hz, and the absolute flow velocity in the experimental arena ranged between 0.5 ± 0.4 and 17.5 ± 2.5 cm s⁻¹ (means±s.d.) (Fig. S1, Movie 2). Wave height was consistent and ranged between 6.2 and 7.1 cm.

Measurements of escape performance

Fast-start escape responses typically consist of a unilateral contraction of the axial musculature (stage 1), which bends the body into a ‘C’ shape, and a subsequent contralateral contraction, resulting in a half tail beat (stage 2) (Domenici and Blake, 1997; Eaton et al., 2001). Escape sequences were analysed using the software ImageJ v1.45 and the plugin MtrackJ (<https://imagejscience.org/meijering/software/mtrackj/>). All kinematic measurements are in the environmental frame of reference (i.e. movement relative to the ground) as flow visualizations were carried out without fish in the experimental arena. The two-dimensional *x*–*y* coordinates of the fish’s centre of mass (CoM) were plotted every 2.4 ms, starting 12 ms before and ending 48 ms after the onset of the stimulus (25 frames in total). The CoM was estimated on four fish per species using frozen specimens; a needle was inserted along the body midline until the point of balance was identified (Domenici et al., 2004). As fish were too small to mark their CoM directly on the body, the CoM was visually determined at a fixed distance from the tip of the snout during video analysis. Measurement error on displacement data from visually estimating the CoM was assessed by digitizing videos from five fish, two times each (Langerhans, 2009). This error was <4% for all videos tested. Seven escape performance variables were measured following Lefrançois and Domenici (2006): responsiveness (the percentage of fish that performed an escape response when stimulated); response latency (the time between the moment when the stimulus contacted the water and the first head movement of the fish); cumulative distance travelled (D_{esc}); maximum escape speed (U_{max}); maximum acceleration (A_{max}); stage 1 turning angle (the angle between the

straight line joining the tip of the head and the CoM at the onset and end of stage 1); and stage 1 turning rate (stage 1 turning angle divided by stage 1 duration). Distance–time variables (D_{esc} , U_{max} , A_{max}) were evaluated within a fixed time period of 24 ms from the first head movement, corresponding to the mean duration of stages 1 and 2 for all three species. Measuring distance–time variables within a fixed time period avoids performance biases related to differences in the duration of escape responses (Domenici, 2011). A five-point quadratic polynomial regression (Lanczos, 1956) was used to obtain smoothed values of speed and acceleration, the first and second derivatives of distance (Walker, 1998; Lefrançois and Domenici, 2006).

Statistical analysis

I compared body size (SL) among the three damselfish species with a general linear model (LM) containing three predictors: species, water flow condition and their interaction. I used a simple LM (one-way ANOVA) to examine differences in the excursion distance of a passive particle and the three fish species in wave-driven water flow. Model assumptions were assessed graphically with diagnostic plots.

I used three general linear mixed-effects models (LMMs) to examine how species and water flow condition (still versus wave-driven) affected three measures of escape performance: response latency (ms), D_{esc} (mm) and turning rate (deg ms⁻¹). Standard length, body angle relative to the stimulus (the angle between the straight line connecting the snout to the CoM of the fish and the tangent to the perimeter of the stimulus) and distance to the stimulus were scaled (i.e. divided by their s.d.) and included as covariates in each model; an interaction term was included between species and flow condition. The identity of fish was specified as a random factor to account for repeated measurements on individuals. Response latency was log-transformed to normalize model residuals. Differences in U_{max} and A_{max} were not tested to reduce the number of statistical tests (and hence the probability of spurious results), and because U_{max} and A_{max} are less reliable measures of distance–time performance than D_{esc} (Domenici and Blake, 1997). Values of U_{max} and A_{max} for each species and flow treatment are indicated in Table 1. I used the function ‘lmer’ (<https://cran.r-project.org/web/packages/lme4/index.html>) to specify each model as response.variable~scale(SL)+scale(sin(angle.stim))+scale(dist.stim)+species*flow+(1|individual). I calculated the adjusted repeatability (R_{adj}) of response latency, D_{esc} and turning rate in still water with the function ‘rptR’ (<https://cran.r-project.org/web/packages/rptR/index.html>), specifying species, standard length, body angle relative to the stimulus and distance to the stimulus as fixed predictors.

For fishes in wave-driven flow, I examined how the timing of escape responses in relation to the wave phase affected D_{esc} using an LMM specified as $D_{\text{esc}} \sim \text{scale}(\sin(\text{angle.stim})) + \text{scale}(\text{dist.stim}) + \text{scale}(\text{SL}) + \text{species} * \text{wave.phase} + (1|\text{individual})$. The factor ‘wave

Table 1. Descriptive statistics: escape responses of three species of Pomacentridae in still water and wave-driven flow

Variable	<i>N. azysron</i>		<i>C. viridis</i>		<i>D. reticulatus</i>	
	Still	Wave-driven	Still	Wave-driven	Still	Wave-driven
Latency (ms)	9.9±5.4	28.3±28.0	10.1±4.7	19.6±8.6	14.7±8.0	17.1±7.8
D_{esc} (mm)	14.9±3.7	15.9±4.20	11.6±2.6	11.6±3.4	13.9±2.5	14.5±2.4
U_{max} (cm s ⁻¹)	88.1±22.2	92.5±28.0	74.7±16.8	76.7±24.0	83.4±14.6	92.0±18.2
A_{max} (m s ⁻²)	67.8±17.1	65.9±22.8	47.8±10.7	52.6±22.9	55.4±10.6	61.6±16.8
Turning rate (deg ms ⁻¹)	11.8±2.8	11.2±3.14	9.3±2.4	9.6±2.5	9.9±2.4	11.1±2.8

Measures of escape performance (means±s.d.) for three species of damselfish (Pomacentridae) with different body morphologies: response latency (latency), escape distance (D_{esc}), maximum swimming speed (U_{max}), maximum acceleration (A_{max}) and turning rate.

Table 2. Inferential statistics: escape responses of three species of Pomacentridae in still water and wave-driven flow

Variable	Predictor	χ^2	d.f.	<i>P</i>	R_m^2	R_c^2
Latency	Sin(angle)	2.65	1	0.103	0.277	0.499
	Distance	1.09	1	0.297		
	Body size	0.43	1	0.513		
	Species	6.12	2	0.047		
	Flow	32.83	1	<0.001		
	Species×flow	8.93	2	0.012		
D_{esc}	Sin(angle)	2.34	1	0.126	0.233	0.665
	Distance	0.26	1	0.611		
	Body size	3.82	1	0.051		
	Species	7.76	2	0.021		
	Flow	1.20	1	0.273		
	Species×flow	0.71	2	0.700		
Turning rate	Sin(angle)	0.12	1	0.726	0.108	0.203
	Distance	0.08	1	0.778		
	Body size	0.002	1	0.989		
	Species	14.99	2	<0.001		
	Flow	0.83	1	0.362		
	Species×flow	4.15	2	0.129		

Effects of body angle, distance to stimulus, body size, species and water flow condition on three measures of escape performance. Escape performance was measured as response latency, escape distance (D_{esc}) and turning rate in three species of damselfish (Pomacentridae) with different body morphologies. R_m^2 , marginal *R*-squared; R_c^2 , conditional *R*-squared. Statistically significant *P*-values are indicated in bold.

phase' was used to distinguish whether fish escaped against the wave path (315–45 deg), perpendicular to the wave path (46–134 deg or 226–314 deg), during a wave trough (water flow speed <5 cm s⁻¹, escape in any direction) or in the direction of the wave path (135–225 deg). The direction of the escape response relative to the wave path was measured as the angle between the straight line connecting the fish's CoM at the start of stage 1 and the end of stage 2, and the straight line parallel to the wave path.

The assumptions of mixed-effects models were checked with residual diagnostics using DHARMA (<https://CRAN.R-project.org/package=DHARMA>). Analyses were done in R v3.6.3 (<http://www.R-project.org/>).

RESULTS

Individuals of all three species in both flow conditions were similar in size (LM: $F_{2,78}=0.30$, $P=0.742$, $\eta^2=0.007$) (Fig. S2). All three species moved less (i.e. had a shorter excursion distance) than a passive particle in the wave-driven flow treatment (LM: $F_{3,52}=60.64$, $P<0.001$, $\eta^2=0.778$). Excursion distance was similar for all three species, with the exception of *D. reticulatus* (laterally

compressed body), which was displaced 26% less than *N. azysron* (fusiform body) (Fig. 1, Table S1).

Responsiveness was high in all three species, with fishes responding to the stimulus in 100% of cases in still water and 94% of cases in wave-driven flow. However, fish were slower to respond to the stimulus in wave-driven flow than in still water for two of three species (Tables 1 and 2). *Neopomacentrus azysron* (fusiform body) and *C. viridis* (intermediate body depth) were 2.86 and 1.94 times slower, respectively, at responding to the stimulus in wave-driven flow than in still water. Response latency for *D. reticulatus* (laterally compressed body) was similar in both flow treatments (Tables 1 and 3, Fig. 4A,B). In still water, response latency [$R_{adj}=0.49$ (0.35–0.61)] and D_{esc} [$R_{adj}=0.47$ (0.27–0.65)] were moderately repeatable across all three species, whereas turning rate was not [$R_{adj}=0.17$ (0.00–0.40)] (Fig. S3).

On average, wave-driven flow did not affect escape kinematics: differences in D_{esc} and turning rate between flow treatments were less than 7% and 12.5%, respectively, for all three species (Tables 1 and 2, Fig. 4C–F). *Neopomacentrus azysron* (fusiform body) and *D. reticulatus* (laterally compressed body) escaped farther than *C. viridis* (intermediate body depth) irrespective of flow conditions (Tables 1 and 3). *Neopomacentrus azysron* exhibited an overall higher turning rate than *C. viridis*, but not *D. reticulatus*. *Chromis viridis* and *D. reticulatus* had similar turning rates (Tables 1 and 3).

When considering the timing of a fish's escape response in relation to the wave phase, all species covered a greater D_{esc} and had a faster turning rate when escaping with the water flow rather than perpendicular to or against the water flow (LMM: flow $\chi^2_{(3)}=35.7$, $P<0.001$; interaction flow*species, $P=0.174$) (Fig. 6).

Results were qualitatively similar whether I considered all trials per individuals or only an individual's best performance across trials (Table S2), as is sometimes done in studies of fast-start swimming performance.

DISCUSSION

Several biotic and abiotic factors are known to influence the fast-start escape response of fishes, including fin and body morphology, muscle composition, temperature, hypoxia, turbidity and pollutants, among others (Domenici, 2010a; Wilson et al., 2010). Here, I document differences in escape response among species and water flow conditions.

Interspecific differences in escape performance

There is a dearth of information on the fast-start escape performance of early-stage coral reef fishes (but see Allan et al., 2014; McCormick and Allan, 2017; Allan et al., 2020). Studies over the past two decades have shown that pre- and post-settlement coral reef

Table 3. Group comparisons of escape performance of three species of Pomacentridae

Variable	Comparison	<i>t</i>	d.f.	<i>P</i>	Effect size (95% CI)
Latency	<i>N. azysron</i> : still vs wave-driven	-5.73	76.8	<0.001	-1.96 (-2.71, -1.22)
	<i>C. viridis</i> : still vs wave-driven	-4.42	76.0	<0.001	-1.51 (-2.22, -0.79)
	<i>D. reticulatus</i> : still vs wave-driven	-1.55	79.7	0.125	-0.54 (-1.23, 0.16)
D_{esc}	<i>N. azysron</i> vs <i>C. viridis</i>	4.68	83.3	<0.001	1.64 (0.90, 2.38)
	<i>N. azysron</i> vs <i>D. reticulatus</i>	1.56	80.1	0.270	0.53 (-0.15, 1.22)
	<i>C. viridis</i> vs <i>D. reticulatus</i>	-3.17	83.1	0.006	-1.11 (-1.82, -0.39)
Turning rate	<i>N. azysron</i> vs <i>C. viridis</i>	4.10	85.7	<0.001	0.81 (0.40, 1.22)
	<i>N. azysron</i> vs <i>D. reticulatus</i>	2.10	80.3	0.097	0.40 (0.02, 0.78)
	<i>C. viridis</i> vs <i>D. reticulatus</i>	-2.11	84.5	0.095	-0.41 (-0.81, -0.02)

Post hoc comparisons and effect sizes for response latency, escape distance (D_{esc}) and turning rate in three species of damselfish (Pomacentridae) with different body morphologies. Because wave-driven water flow had no overall effect on D_{esc} and turning rate (see Table 2), interspecific comparisons are presented for these two variables. Statistically significant *P*-values are indicated in bold.

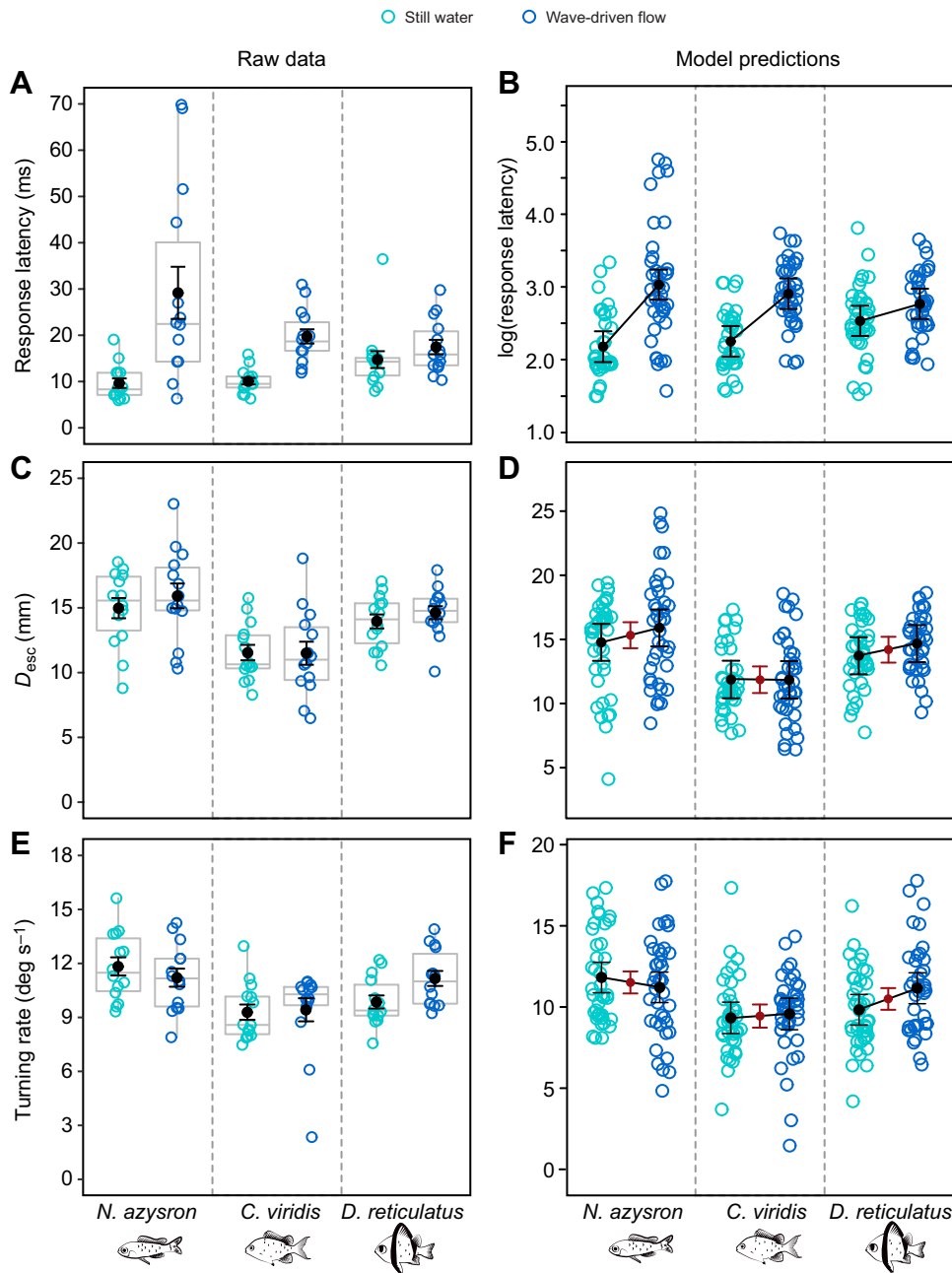


Fig. 4. Response latency, escape distance (D_{esc}) and turning rate for three species of Pomacentridae in still water and wave-driven flow. (A,C,E) Raw data: circles are the mean for each individual ($N=14$ individuals per species); black dots are group means; error bars are 1 s.e.m. Box plots show the median and IQR; whiskers are 1.5 times the IQR. (B,D,F) Marginal effects plots showing partial residuals (circles) and estimated marginal means for each group (black dots); red dots are estimated marginal means for each species ($N=28$ individuals) when there was no effect of flow condition; error bars are 95% confidence intervals. Estimated marginal means and partial residuals account for the fixed and random effects included in the statistical model.

fish larvae can achieve high sustained swimming speeds of 30–50 body lengths s^{-1} , indicating that these larvae are not passive organisms adrift in the plankton (e.g. Stobutzki and Bellwood, 1994; Leis and Carson-Ewart, 1997; Fisher et al., 2005; Nilsson et al., 2007). The three species tested here achieved high maximum fast-start swimming speeds, occasionally exceeding 100 cm s^{-1} (85 SL s^{-1} ; Table 1). In relative terms, these values are almost twice the maximum burst speeds reached by temperate species at similar sizes, including salmonids (fig. 11.5 in Fisher and Leis, 2010). Fast-start escape responses influence the ability of juvenile coral reef fishes to avoid predation and are therefore directly relevant to their ecology (Fisher and Leis, 2010). The impressive locomotor performance of small pomacentrids is perhaps not surprising, given that wild and laboratory measures place them among the fastest-swimming coral reef fish larvae (Leis and Carson-Ewart, 1997; Nilsson et al., 2007).

Escape distance (D_{esc}) differed consistently among species in still water and wave-driven flow: *N. azysron* (fusiform body) and *D. reticulatus* (laterally compressed body) exhibited similar performances and escaped farther in a fixed amount of time than *C. viridis* (intermediate body depth), irrespective of flow conditions (Tables 1 and 2, Fig. 4D). Evidence suggests that differences in fast-start swimming performance result from different, and sometimes opposing, morphological features (Domenici, 2003; Walker, 2004; Langerhans and Reznick, 2010). On one hand, traits such as a shallow, elongated body, a small head and large dorsal and anal fins (such as in pike, *Esox lucius*) are associated with high burst swimming speeds (Webb, 1984; Domenici, 2003; Langerhans et al., 2004). On the other hand, a deep, laterally compressed body has also been shown to enhance burst swimming performance by allowing a lateral profile that increases the mass of water accelerated by body movements (Weihs, 1973; Domenici and Blake, 1991). For

example, the deep body of crucian carp (*Carassius carassius*) induced in the presence of predators led to higher burst swimming performance (escape distance, speed, acceleration and turning rate) than that of shallow body morphs found in predator-free habitats (Domenici et al., 2008). These two contrasting profiles roughly correspond to those of the two pomacentrids that escaped the farthest and were at the opposite ends of the body plan spectrum I examined. Turning rate, a measure of agility, mirrored the pattern observed for D_{esc} , although differences in performance between *D. reticulatus* and *C. viridis* were less pronounced for turning rate (11.1%) than escape distance (19.3%) (Table 3, Fig. 4D,F). This result was unexpected, as lateral compression has previously been reported to improve agility (Domenici et al., 2008).

Response latency to the threatening stimulus in still water was distinctly higher for *D. reticulatus* than for the other two species (47% difference; Table 1, Fig. 4A). The deep, laterally compressed body of *D. reticulatus* is a trait frequently associated with reduced vulnerability to gape-limited predators (e.g. Pseudochromidae, Labridae), which are abundant on coral reefs (Rice et al., 1997; Holmes and McCormick, 2010; Domenici, 2011). It is possible that selection pressure for rapid responses in juvenile *D. reticulatus* is less than in the other two species, which have shallower, more fusiform body plans, making the latter vulnerable to a greater range of piscivorous predators.

Effects of wave-driven flow on escape performance

Reef fishes routinely experience a range of flow velocities and vorticity in the wild, depending on weather conditions, reef exposure to waves, microhabitat and depth below the surface. For example, Johansen (2014) recorded flow velocities ranging between 0 and 82 cm s⁻¹ on reefs of different depths and wave exposure at Lizard Island, where test fishes were collected. The wave-driven flow treatment in the current study was representative of water flow speeds routinely experienced by fishes under winds of 15 knots and intermediate wave heights on semi-exposed reefs at Lizard Island (D.G.R., unpublished data; Fulton and Bellwood, 2005). The maximum flow velocity was 66% of the critical swimming speed (26.3 cm s⁻¹) achieved by congeneric juvenile pomacentrids after settlement on the reef (Stobutzki and Bellwood, 1994).

Responsiveness to the stimulus was high for all three species in both flow conditions, and similar to values reported in another juvenile damselfish exposed to the same type of stimulus used here (>97% responsiveness; Allan et al., 2014). This indicates that wave-driven flow of the magnitude examined in the present study (Fig. S1) did not impede the ability of the test fishes to sense the stimulus. Fishes detect approaching predators by sensing water flow through the lateral line (Stewart et al., 2013), and it has been suggested that environmental flows might impede perception (Higham et al., 2015; Diamond et al., 2016). However, fishes also rely on other senses to perceive threats, such as hearing, vision and smell. It is likely that the mechanosensory, auditory and visual nature of the stimulus and its large size relative to the test fishes produced a signal strong enough to elicit a response even when dampened by wave-driven flow (see Domenici, 2010a). Supporting this interpretation is the indication that a fish's distance (range: 3.0–14.8 cm) and body angle (range: 14.4–179.6 deg) relative to the stimulus had little influence on behavioural and kinematic measures of escape performance (Table 2).

On average, escape kinematics (D_{esc} , turning rate) were similar in still water and wave-driven flow within species (Table 1, Fig. 4C–F). This pattern is a consequence of the large variation in escape performance by fishes in wave-driven flow, which was driven by

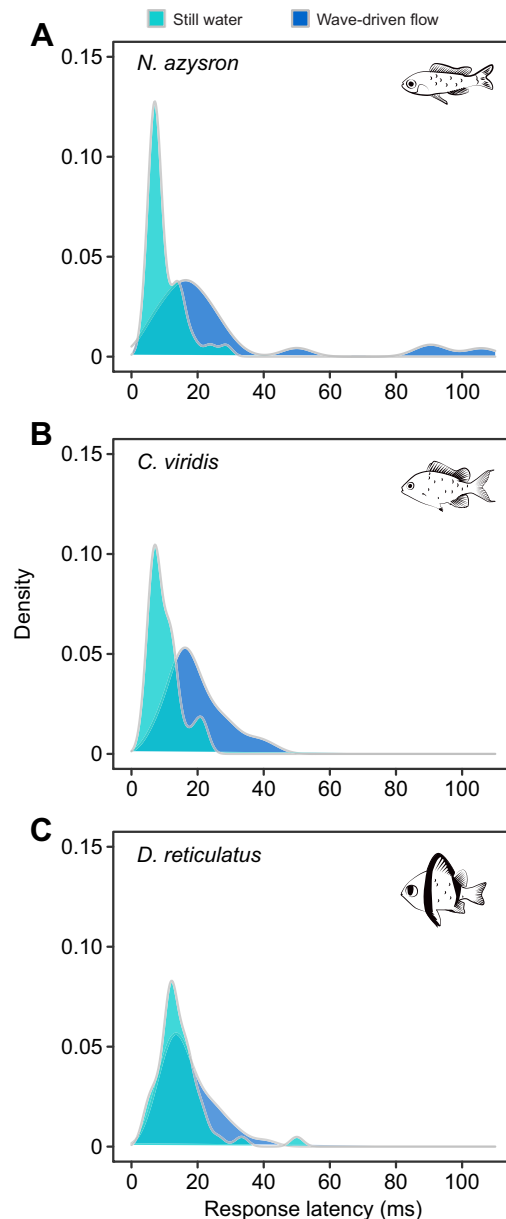


Fig. 5. Response latency of three species of Pomacentridae in still water and wave-driven flow. (A–C) Kernel density plots showing the distribution of response latency (ms) for *N. azysron* (A), *C. viridis* (B) and *D. reticulatus* (C) in still water and wave-driven flow.

variation in the timing of the stimulus (and hence the escape response) relative to the wave phase (Table S3, Fig. 6). Irrespective of body morphology, fish escaping with the flow achieved a greater D_{esc} and faster turning rate than fish escaping perpendicular to or against the flow as well as during a wave trough (Fig. 6). Because maximum muscle power output is unaffected by flow conditions, these patterns support the prediction that differences in fast-start swimming performance between flow conditions should equal differences in water flow velocity. Indeed, maximum flow speeds were ~20% of the maximum escape speeds achieved by fishes (Table 1, Fig. S1), and fish escaping in the direction of the water flow achieved a D_{esc} that was, on average, 20.3% greater than that achieved in still water (Table S3). These results both concur and contrast with those of studies on fish escape responses in steady flow: Anwar et al. (2016) found a preference for downstream escapes by bluegill sunfish

(*Lepomis macrochirus*), resulting in a greater escape distance and speed than escapes in still water or upstream flow (flow speeds: 9.4 cm s^{-1} and 23.1 cm s^{-1}); conversely, Diamond et al. (2016) found no evidence that flow speed influenced peak escape velocity in the Hawaiian stream goby (*Sicyopterus stimpsoni*) (flow speeds: 15 cm s^{-1} and 30 cm s^{-1}).

Speed (D_{esc}) and agility (turning rate) are important locomotor determinants of escape responses (Walker et al., 2005); however, escape success also largely depends on behavioural components, namely the responsiveness and response latency of prey to an attacking predator (Domenici, 2010b; Domenici and Hale, 2019). For example, Fuiman et al. (2006) observed that the responsiveness of red drum larvae (*Sciaenops ocellatus*) to a stimulus was the main predictor of survival during a predator–prey encounter and explained 86% of the variation in survivorship. Similarly, zebrafish (*Danio rerio*) larvae are over three times more likely to evade predation if they initiate their escape before instead of after adult conspecifics open their mouth to prey on them (Stewart et al., 2013). I found that wave-driven water flow increased the response latency of some species but not all (Fig. 5). *Neopomacentrus azysron* (fusiform body) and *C. viridis* (intermediate body depth) were 2.86 and 1.94 times slower, respectively, in responding to the stimulus in wave-driven flow than in still water. By contrast, the response latency of *D. reticulatus* (laterally compressed body) was unaffected (Table 1, Fig. 4B).

Slower responses to the stimulus in wave-driven flow could be caused by two main factors: first, the destabilizing effect of water motion and the added challenge of maintaining an upright posture

and adequate orientation relative to the flow; and second, the challenges of perceiving a threat owing to added noise in complex flow versus still water. All else being equal, a more laterally compressed body should improve resistance to rolling disturbances (Eidietis et al., 2002; Weihs, 2002). A deep body plan should also improve mechanoreception by allowing the placement of the lateral line away from moving body parts (i.e. pectoral fins), a trait that has been posited to decrease self-generated noise and increase the signal-to-noise ratio (Dijkgraaf, 1963; Coombs and Braun, 2003). These two considerations might explain why the longer response latency in wave-driven flow was inversely related to body depth in the three species I examined. Notably, *D. reticulatus* tended to orient more directly into the flow and was less displaced by water motion (i.e. had a shorter excursion distance) than the fusiform-shaped *N. azysron* (Fig. 7), although no such difference was apparent with *C. viridis*, which has an intermediate body depth (Fig. 3, Table S1). Given that reactivity to potential threats (i.e. responsiveness, response latency) is a key determinant of escape success, even moderate flow, such as the one tested here, might increase predation risk for juvenile fishes that are more vulnerable to postural disturbances.

Fast starts in fishes are typically controlled by the Mauthner cells, a pair of large reticulospinal neurons that receive various sensory inputs, such as visual and mechano-acoustic signals (Eaton et al., 2001). High-speed neural transmission and processing via these cells allows for rapid responses to imminent threats within 5–20 ms. Interestingly, *N. azysron* (fusiform body) exhibited much greater variation in escape latency in wave-driven flow than the other two

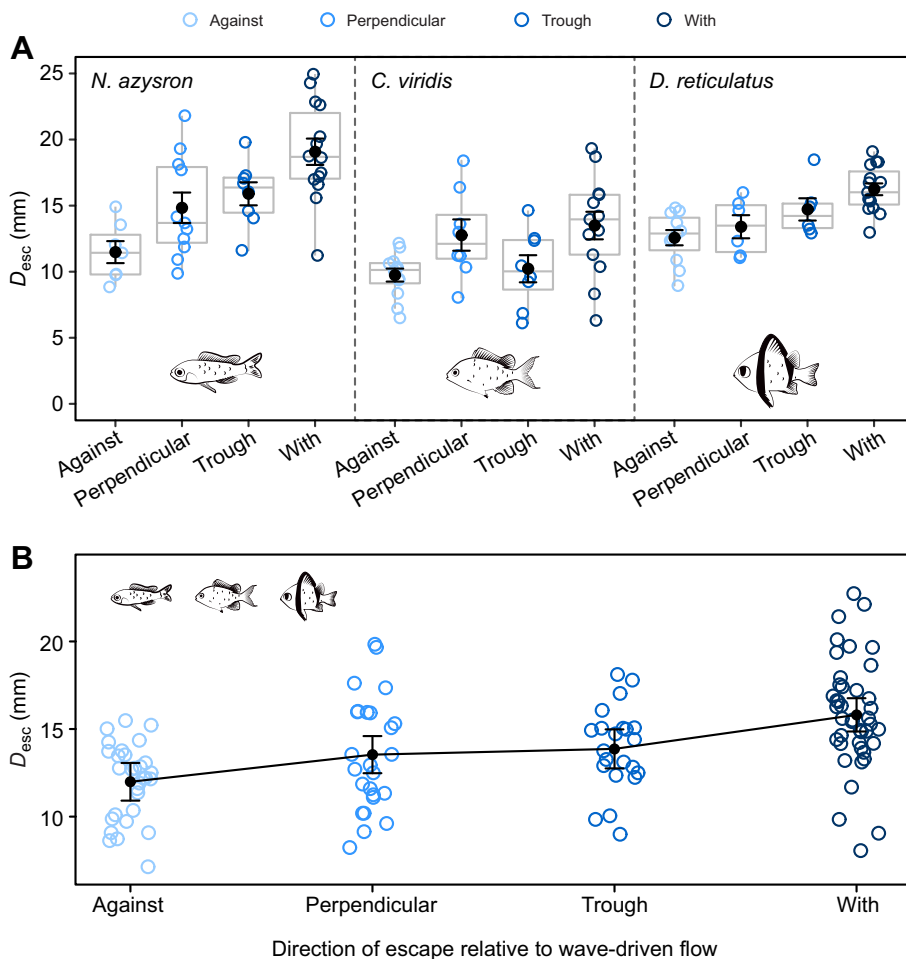


Fig. 6. Escape distance (D_{esc}) in a fixed time interval (24 ms) for three species of Pomacentridae in wave-driven flow conditions. Fish escaped against the wave path (against), perpendicular to the wave path (perpendicular), during a wave trough (flow speed $<5 \text{ cm s}^{-1}$; trough) or in the direction of the wave path (with). (A) Raw data for each of the three species (sample sizes in Table S3); black dots are group means; error bars are 1 s.e.m. Box plots show the median and IQR; whiskers are 1.5 times the IQR. (B) Marginal effects plots showing partial residuals (circles) and estimated marginal means (black dots) across all three species; error bars are 95% confidence intervals.

species tested (Fig. 5B). The strong positive skew in the distribution of its response latency (Fig. 5A) suggests that some escape responses in wave-driven flow were not Mauthner cell mediated. Other pathways, through different reticulospinal cells, can control escape responses but have longer latencies (Domenici, 2010a; Domenici and Hale, 2019). Slower responses are generally associated with lower performance (e.g. slower turning rates), and are observed both in healthy fish and in fish with an ablated Mauthner system (Domenici, 2011; Hecker et al., 2020). In wave-driven flow, postural disturbances from waves and associated stability control issues seemingly led to some non-Mauthner cell escapes, with longer latencies (>40 ms), in at least one species.

Conclusion

Hydrodynamic stability is advantageous for fishes moving in high-energy coral reef environments characterized by turbulence and rapid changes in flow velocity (Bartol et al., 2003). I found variable effects of wave-driven water flow on the escape response of juvenile damselfishes with different body morphologies, increasing the response latency of species with a more fusiform body profile. Juvenile reef fishes are highly sensitive to environmental variables (Leis and McCormick, 2002), and negative effects on their settlement and survival patterns can have important consequences for adult populations (Munday et al., 2008). Wave intensity and frequency is increasing across ocean basins worldwide as winds and severe weather events become more frequent with climate change (Webster et al., 2005; Rhein et al., 2013). Strong winds and waves coinciding with juvenile recruitment pulses could affect not only larval dispersal (e.g. Burgess et al., 2007), but also predator-prey interactions and the survivorship of post-settlement juveniles. Many damselfishes recruit seasonally (Russell et al., 1977; Williams, 1983) and are initially limited by habitat as they settle on the reef (Sale, 1978). Once the recruitment pulse is over, post-settlement mortality becomes important because juveniles that are predated on can no longer be replaced even if habitat becomes available. Given the present findings, future studies should examine whether relationships exist between wave intensity, predation rates and recruitment patterns in the wild, as well as differences in the effect of wave-driven flow on predators and prey owing to size differences (see Abrahams et al., 2007; Domenici et al., 2019).

Acknowledgements

I thank A. Muir, J. Rucksa, S. Green, T. Wilson, P. McKinlay, R. Phillips and D. Barwick from the ANU Research School of Biology workshop for their help designing and building the experimental setup. A. Roche and C. Rowan also contributed valuable input to its design. 3D CAD models of the experimental setup were kindly made by H. F. Zhu. S. A. Binning, C. Juan, C. Layton, S. Heathwole, P. Vespa, L. Binning, J. R. Binning, C. Rowan, A. Roche and staff at the Lizard Island Research Station contributed valuable assistance in the field. M. D. Jennions, S. A. Binning, P. Domenici and two anonymous reviewers provided helpful comments on the manuscript. Sections of this paper are reproduced from the PhD thesis of the author (Roche, 2013).

Competing interests

The author declares no competing or financial interests.

Funding

This study was funded by grants from the Australian National University, the Centre of Excellence for Coral Reef Studies, Australian Research Council, the Natural Sciences and Engineering Research Council of Canada, the Ian Potter Foundation (Lizard Island, a facility of the Australian Museum), the Society for Integrative and Comparative Biology, the Ecological Society of Australia and Total Diving Montréal.

Data availability

The data and analysis script for this study are publicly accessible from the figshare digital repository (<https://doi.org/10.6084/m9.figshare.12735446>) and were made available to the editors and reviewers at the time of submission.

Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.234351.supplemental>

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Table S1. Group comparisons of excursion distance in wave-driven flow. Group (post-hoc) comparisons and effect sizes (analogous to Cohen's *d*) of excursion distance for a passive particle and three damselfish species (Pomacentridae) in wave-driven flow.

comparison	t	df	<i>P</i>	effect size (95% CI)
<i>Passive particle – N. azysron</i>	9.25	52	<0.001	3.50 (2.47, 4.52)
<i>Passive particle – C. viridis</i>	11.10	52	<0.001	4.19 (3.07, 5.31)
<i>Passive particle – D. reticulatus</i>	11.98	52	<0.001	4.53 (3.36, 5.70)
<i>N. azysron – C. viridis</i>	1.85	52	0.264	0.70 (-0.07, 1.47)
<i>N. azysron – D. reticulatus</i>	2.73	52	0.042	1.03 (0.25, 1.82)
<i>C. viridis – D. reticulatus</i>	0.882	52	0.814	0.33 (-0.43, 1.09)

Table S2. Descriptive statistics: best values of escape performance in still water and wave-driven flow. Best values of escape performance (mean \pm s.d.) across trials for three damselfish species (Pomacentridae) with different body morphologies: response latency (latency), escape distance (D_{esc}), maximum swimming speed (U_{max}), maximum acceleration (A_{max}), and turning rate (T_{rate}).

Variable	<i>N. azysron</i>		<i>C. viridis</i>		<i>D. reticulatus</i>	
	still	wave-driven	still	wave-driven	still	wave-driven
Latency (ms)	7.0 \pm 2.4	16.2 \pm 11.1	7.1 \pm 1.9	13.4 \pm 4.6	10.7 \pm 5.5	12.1 \pm 5.5
D_{esc} (mm)	16.9 \pm 2.9	18.1 \pm 4.32	12.4 \pm 2.5	12.6 \pm 3.3	15.4 \pm 1.9	16.1 \pm 2.2
U_{max} (cm s ⁻¹)	101.0 \pm 18.8	110.0 \pm 23.8	80.8 \pm 14.2	86.7 \pm 29.2	91.5 \pm 11.3	101.0 \pm 17.5
A_{max} (m s ⁻²)	77.3 \pm 13.5	80.2 \pm 18.6	54.4 \pm 11.0	65.3 \pm 27.6	62.2 \pm 7.8	74.2 \pm 14.5
T_{rate} ($^{\circ}$ ms ⁻¹)	13.9 \pm 2.5	14.0 \pm 2.2	10.8 \pm 2.4	10.8 \pm 2.9	11.9 \pm 1.9	13.5 \pm 2.4

Table S3. Mean escape distance (D_{esc} , mm) for each species in still water and at different moments of the wave phase in wave-driven flow. Numbers in square brackets are [one standard deviation, sample size]. Note that the sample sizes include repeated measurements on individuals in still water conditions.

	<i>N. azysron</i>	<i>C. viridis</i>	<i>D. reticulatus</i>
against wave	11.48 [2.20, 7]	9.74 [1.70, 12]	12.57 [1.92, 11]
perpendicular	14.83 [3.82, 11]	12.77 [3.35, 8]	13.40 [2.14, 6]
wave trough	15.89 [2.46, 8]	10.22 [2.90, 8]	14.71 [2.06, 6]
with wave	19.08 [3.73, 14]	13.49 [3.76, 13]	16.24 [1.73, 15]
still water	14.90 [3.72, 41]	11.58 [2.59, 39]	13.93 [2.45, 41]
ratio with/still	1.28	1.17	1.17

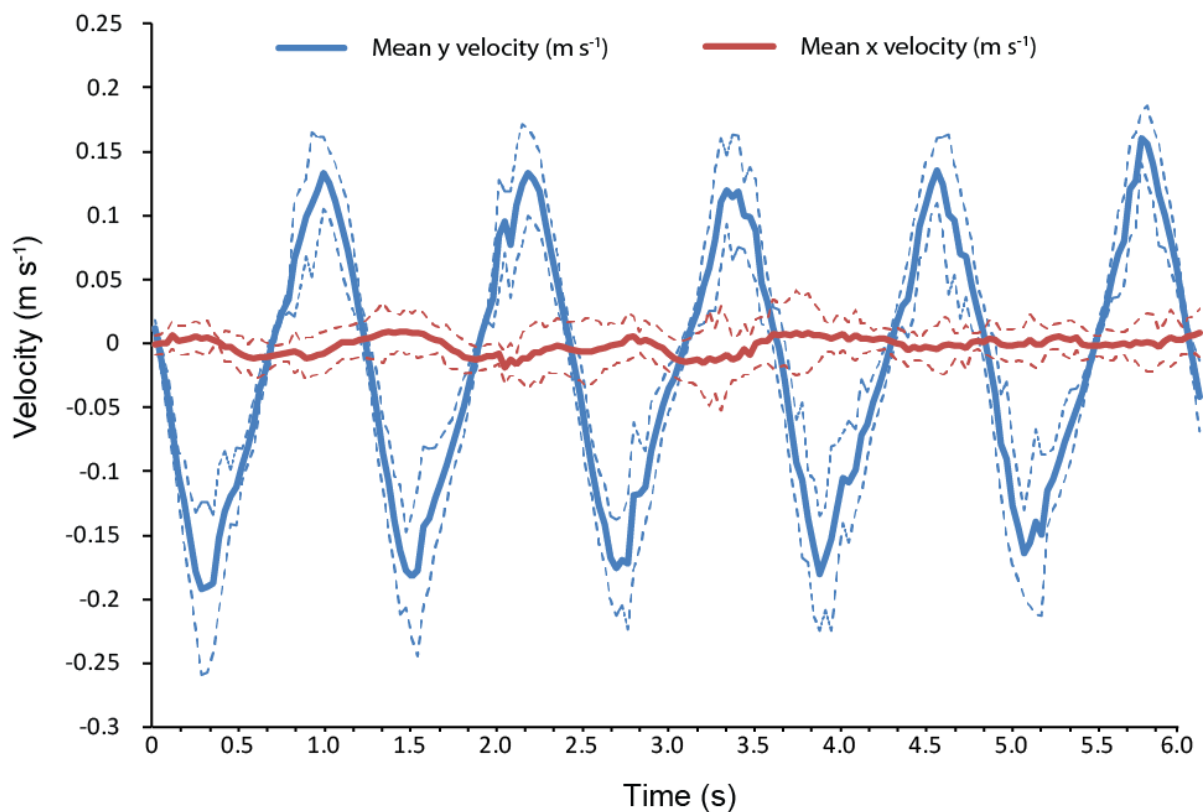


Fig. S1. Velocity of wave-driven flow through time. Example flow profile showing X and Y components of mean flow velocity in the experimental arena over six seconds. The mean flow velocity at each point in time was computed by averaging all vectors per frame in the software PIVlab v.1.32. Dotted lines represent one standard deviation from the mean.

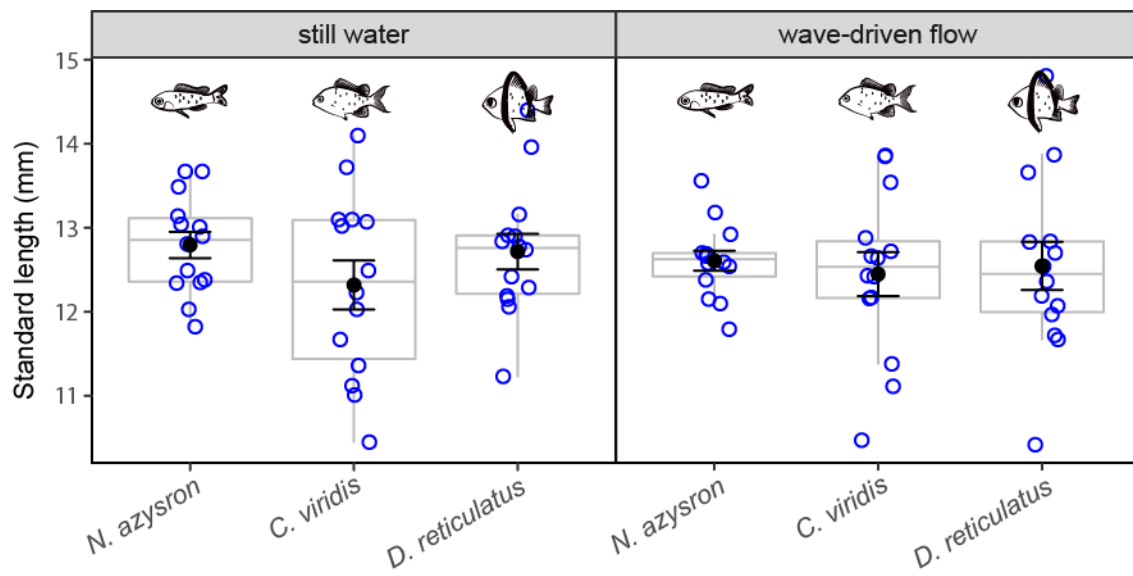


Fig. S2. Body size of test fishes. Standard length (mm) of individuals in three species of damselfish (Pomacentridae) tested in still water and wave-driven flow (n = 14 per group). Blue circles are individuals; black dots are means; error bars are s.e.m. Box plots show the median and interquartile range (IQR); whiskers are 1.5 times the IQR.

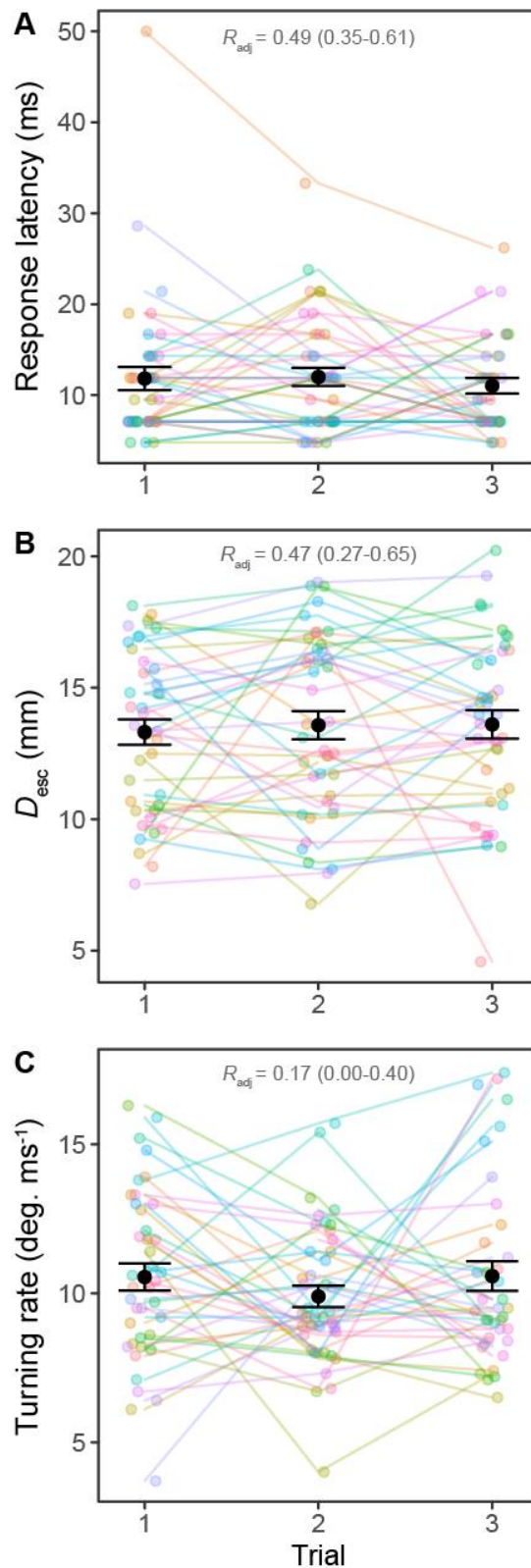
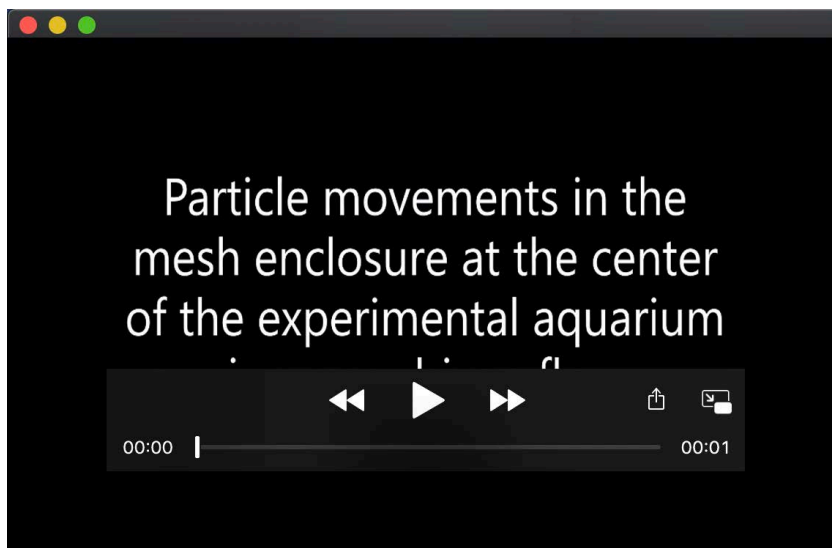


Fig. S3. Reaction norms of escape performance metrics. (A) Response latency, (B) D_{esc} , and (C) turning rate across three repeated trials per individual for three fish species in still water: *Neopomacentrus azysron* (n=14), *Chromis viridis* (n=14), and *Dascyllus reticulatus* (n=14). Mean values and their 95% confidence intervals are indicated by black dots and error bars. Adjusted repeatability (R_{adj}) and its 95% CI are indicated for each species. Data points are jittered along the X axis for presentation purposes.



Movie 1. Examples of escape responses for *Chromis viridis*, *Dascyllus reticulatus*, and *Neopomacentrus azysron* in still water and wave-driven flow conditions (ventral view; recorded at 420 Hz; played at 30 Hz).



Movie 2. Particle movements and frame sequences of velocity vector fields and vorticity fields in the fine mesh enclosure at the center of the experimental aquarium in wave-driven flow (see Fig. 2). Recorded at 30 Hz; played at 30 Hz.