



Sharks modulate their escape behavior in response to predator size, speed and approach orientation



Scott Seamone^{a,*}, Tristan Blaine^b, Timothy E. Higham^c

^a Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4R2, Canada

^b Department of Biology, University of Victoria, 3800 Finnerty Road, Victoria, BC V8P 5C2, Canada

^c Department of Biology, University of California, 900 University Avenue, Riverside, CA 92521, USA

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ABSTRACT

Escape responses are often critical for surviving predator–prey interactions. Nevertheless, little is known about how predator size, speed and approach orientation impact escape performance, especially in larger prey that are primarily viewed as predators. We used realistic shark models to examine how altering predatory behavior and morphology (size, speed and approach orientation) influences escape behavior and performance in *Squalus acanthias*, a shark that is preyed upon by apex marine predators. Predator models induced C-start escape responses, and increasing the size and speed of the models triggered a more intense response (increased escape turning rate and acceleration). In addition, increased predator size resulted in greater responsiveness from the sharks. Among the responses, predator approach orientation had the most significant impact on escapes, such that the head-on approach, as compared to the tail-on approach, induced greater reaction distances and increased escape turning rate, speed and acceleration. Thus, the anterior binocular vision in sharks renders them less effective at detecting predators approaching from behind. However, it appears that sharks compensate by performing high-intensity escapes, likely induced by the lateral line system, or by a sudden visual flash of the predator entering their field of view. Our study reveals key aspects of escape behavior in sharks, highlighting the modulation of performance in response to predator approach.

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1. Introduction

Escape responses are high-energy maneuvers that are frequently employed by fishes to evade predators during an attack. The C-start is a common escape maneuver found in an array of fish taxa where a powerful unilateral muscle contraction bends the fish into a c-shape and changes the direction of swimming (stage 1) (Domenici and Blake, 1997). This contraction is succeeded by a return flip of the tail, which accelerates the animal in the new line of movement away from the predator (Domenici and Blake, 1997). In some instances, the propulsive movement of the tail is joined by a second lateral contraction on the opposite side of the body from the initial bend (stage 2) (Domenici and Blake, 1997). Reactions are generally triggered by visual or mechano-acoustic disturbances, which stimulate Mauthner cells (M-cells) and associated neurons found inside the hindbrain in fishes (Zottoli, 1977;

Eaton et al., 1977, 1981; Nissanov et al., 1990). Escape responses have been extensively studied in the laboratory, and results show a high degree of variability due to the involvement of numerous non-locomotor (responsiveness, reaction distance and more) and locomotor variables (acceleration, speed, turning rate and others) (Domenici and Blake, 1997). A large proportion of this research has focused on describing escape behaviors induced by controlled stimuli, yet in reality, changes in ecological and predatory parameters can significantly alter these patterns (for review see Domenici, 2010). For the most part, there is a paucity of information with regard to the modulation of predatory parameters and the resulting influence on escape behavior, especially in large prey. Focusing on the context dependence of escapes is critical given that fleeing comes at a cost, and prey do not always exhibit maximum performance in the presence of a predator (Webb, 1982, 1986; Ydenberg and Dill, 1989; Dill, 1990; Domenici et al., 2004; Semeniuk and Dill, 2004).

Before an escape can occur, the prey must detect the predator. Therefore, responsiveness is an essential aspect of escape success because the lack of a reaction during a predatory attack will likely lead to prey capture. Predator–prey research involving red

* Corresponding author. Present address: Department of Biology, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada.

E-mail address: sseamone@ucalgary.ca (S. Seamone).

drum larvae (*Sciaenops ocellatus*) demonstrates the significance of responsiveness, as the ability to react accounted for the majority of the variability in escape potential (Fuiman et al., 2006). Escape responses in zebrafish (*Danio rerio*) are triggered when the rate of change of the visual angle subtended by the predator exceeds the respective threshold level of the fish (apparent looming threshold) (Dill, 1974). In addition, larval zebrafish can sense the water flow of a predator's strike by the means of a lateral line system (McHenry et al., 2009; Stewart et al., 2013). The fathead minnow (*Pimephales promelas*) responded more often when attacked by predators with a larger frontal profile (*Salmo gairdneri*, *Micropterus dolomieu* and *Ambloplites rupestris*) than predators with a smaller frontal profile (*Esox lucius* and *Esox masquinongy*), suggesting that prey are highly sensitive to the configuration of an approaching threat (Webb, 1982). Fishes are also responsive to predator speed and strength of stimuli, with *Gadus morhua* responding to a faster predator speed more often than a slower predator speed in clear waters, and *Gobius niger* only performing an escape response when exposed to the strongest level of the stimuli (Meager et al., 2006; Turesson et al., 2009). Although it is evident that responsiveness is a key component of escape, and that predatory behavior plays a role, there has been a paucity of research addressing the predatory conditions that will trigger visual versus mechano-acoustic sensory systems.

Sub-maximal escape performance in fishes is common, and prey will often exhibit a combination of reaction distance and escape speed to reach safety (Webb, 1982, 1986; Helfman, 1989; Ydenberg and Dill, 1989; Dill, 1990; Helfman and Winkelman, 1997; Domenici et al., 2004; Semeniuk and Dill, 2004). Reaction distance has been proposed to be directly related to predator size and speed (looming rate), and inversely related to the apparent looming threshold (ALT) of the prey (Dill, 1974). Therefore, reaction distance of visually stimulated prey should increase with size and speed of an approaching predator because ALT is relatively constant for a given species (Dill, 1974). At the same time, the so-called 'matador strategy' suggests that minimizing reaction distance as much as possible (relative to the predator's size and approach speed), and then leading the predator off target by a slight maneuver, would be an advantage because it would limit the time for the predator to adjust to the reaction (Blaxter and Fuiman, 1990). When the fathead minnow (*Pimephales promelas*) responded to the smaller frontal profile of the tiger musky (*Esox lucius* and *Esox masquinongy*) the reaction distances were shorter, while escape speeds and turning rates were higher, than when they escaped from the larger frontal profile of trout, bass and rock bass (*Salmo gairdneri*, *Micropterus dolomieu* and *Ambloplites rupestris*) (Webb, 1982). Cowtail stingray (*Pastinachus sephen*) also exhibited a negative relationship between intensity of response and reaction distance (Semeniuk and Dill, 2004). However, when a predator model stimulated *Gadus morhua*, there was no significant relationship between predator speed and reaction distance; rather, an increase in predator speed led to an increase in head turning rate and distance covered over a fixed time interval (Meager et al., 2006). Higher intensity responses were also induced more often by a flash of light from an electronic flash-gun compared to a looming image, demonstrating that a sudden visual cue may startle fish (Batty, 1989). Escaping at faster speeds can enhance the likelihood of a successful escape, with increases in speed potentially increasing survival by 2–3 times (Walker et al., 2005). Although recent work has illuminated many variables related to successful escape, it is still unclear why prey will increase reaction distance vs. locomotor performance (escape speed, acceleration and head turning rate) during a predatory attack. Therefore, examining the link between predator size and speed, in addition to predatory approach, with relation to prey behavior will provide valuable insight into the modulation of escape behavior in aquatic animals.

Sharks generally occupy higher trophic levels in aquatic food webs, and it is therefore not surprising that predator–prey interactions in sharks are often examined with them as the predators rather than the prey. Nevertheless, many shark species are mesopredators that are vulnerable to predation by larger animals. For example, *Squalus acanthias* is a secondary consumer that is preyed upon by large sharks and marine mammals (Ebert, 1994, 1991; Vaughn et al., 2007), and they readily perform C-start escape responses (Domenici et al., 2004). Relative to other marine fishes, *S. acanthias* is highly maneuverable with low escape acceleration and maximum speed (Domenici et al., 2004). Given that *S. acanthias* can modulate C-start escape performance, with turning rates ranging from 434 to 1023 deg s⁻¹, it appears these sharks can assess the level of potential threat and respond accordingly (Domenici et al., 2004). However, predatory conditions that induce maximum escape performance are currently not well understood, especially for sharks. This is likely due to the challenges associated with observing shark predator–prey interactions in the wild or in the laboratory.

We used realistic shark models to determine how the spiny dogfish shark (*S. acanthias*) reacts to predators of different size, speed and approach orientation (head-on vs. tail-on). Sets of eyes that are aligned slightly forward on the side of the head provide sharks with a large binocular field of view (McComb et al., 2009). In *S. acanthias*, this misalignment, in addition to the shape of the pectoral girdle, produces a posterior blind spot that extends 35–40° along the horizontal (Harris, 1965). Therefore, sharks will likely have minimal capabilities of visually detecting a predator approaching from behind. However, sharks, like teleost fish, possess a lateral line that contributes to navigation and prey capture by the detection of weak water disturbances (Denton and Gray, 1983; Boord and Northcutt, 1988; Kalmijn, 1989; Gardiner and Atema, 2014). We predict head-on attacks will be perceived visually, resulting in greater reaction distance, but lower locomotor performance (escape speed, acceleration and head turning rate), when compared to tail-on attacks. The latter will likely involve the lateral line system, or a sudden visual cue, and therefore, result in a reduced reaction distance, but increased locomotor performance. Furthermore, an increase in predator model size is expected to raise the level of escape responsiveness, whereas increased predator model speed and size are expected to elevate locomotor performance of the sharks.

2. Materials and methods

2.1. Animal collection and housing

Seven male dogfish sharks (mean standard length 55.57 cm ± 1.02; mean ± S.E.M.) were caught using hook and line, as well as bottom trawls in Barkley Sound, British Columbia. The sharks were then transported in opaque containers by boat to the Bamfield Marine Sciences Centre (BMSC) where they were housed in a holding tank (11 m in diameter, 2.4 m deep, with a volume of approximately 912,000 l) with flow-through seawater at 9 °C. The sharks acclimated for one week prior to experiments. During this period, the sharks were not fed. After the acclimation period, sharks were fed frozen fish every evening, but individuals were not fed for 12 h before their respective days of experimentation.

2.2. Predator models

Three predator models were constructed using wood, plastic, styrofoam and cloth. Due to the electrosensory abilities of elasmobranchs, no metal was used in the models to avoid any confounding variables. The models were 167.6 cm, 106.7 cm and 45.7 cm standard length, with maximum body diameters of 38.1 cm,

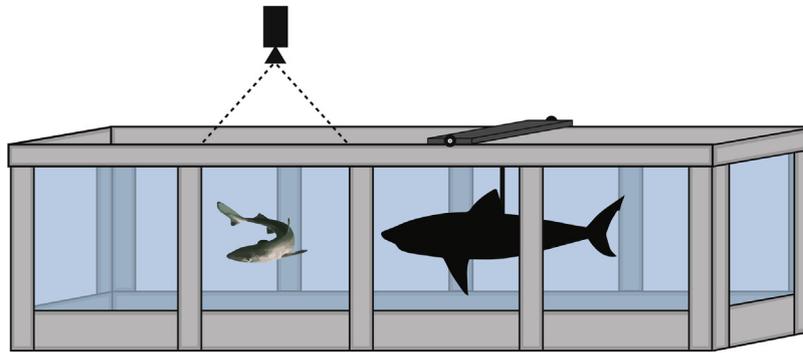


Fig. 1. A schematic of the experimental procedure. The flume was 12 m long, 2 m wide, and contained approximately 45,000 l of non-flowing water. Predator shark models (standard length \times body diameter: 167.6 cm \times 38.1 cm, 106.7 cm \times 22.9 cm, 45.7 cm \times 7.6 cm) were pushed from one direction (head-on or tail-on) towards a shark. High-speed video recorded a dorsal view of each event.

22.9 cm and 7.6 cm, respectively. In order to accurately replicate a potential threat, the shapes of the models were designed to simulate the dimensions of a stereotypical predatory shark. Each model had a fusiform shape, with a caudal fin, a dorsal fin, and pectoral fins. The models were black to eliminate the impact of color (Fig. 1). A wooden pole located behind the dorsal fin on the model was used to attach the submerged models to a movable beam that crossed the width of the top of the flume. Each model was pushed down the length of the flume towards the shark, with the model being approximately the same depth in the water as the shark. The beam, without a model, was also pushed down the flume in separate trials while the shark was swimming to act as a control.

2.3. Data collection

An individual shark was transferred to the BMSC flume (12 m in length, 2 m in width, with a volume of approximately 45,000 l of non-flowing water) and was given 12 h to acclimate (Fig. 1). The walls of the flume were opaque to avoid any visual distraction. The following day the shark was tested randomly with each model, approaching at three general speed categories, with the beam pushed by hand at walking, jogging and sprinting speed. This resulted in speeds of 24–260 cm s⁻¹ from both the head-on and tail-on direction. Although we recognize the natural variation in speed associated with this design, our goal was to maximize the variation for each model and shark. In addition, the exact speed of the model was quantified as it moved through the field of view. A single trial consisted of one model, moving at one speed, from one direction. Each shark underwent a total of 18 trials. The direction of the trial was defined by the shark (depending on whether it was positioned with its head towards the predator model or not), not the model. Sharks were given a 30-min rest period between each trial and the next one. Each response to the models was recorded using a high-speed video camera (300 fps; Casio Exilim EX-F1; Casio Computer Co., Tokyo, Japan). The camera was mounted above the flume, providing a dorsal view of the simulated predator–prey interaction. The approximate field of view was 278.5 cm (lengthwise), and no additional lighting was provided. The distance between the shark and the model at the onset of the interaction was approximately 9 m.

2.4. Data analysis

Video sequences were imported and cropped using MPEG streamclip (Squared 5 srl, Rome, Italy). Known landmarks along the length of the flume enabled us to calibrate the distance, and therefore calculate meaningful distance–time variables. For each trial, the X and Y coordinates of the center of mass (CoM) were determined for each frame by digitizing the sequences in ImageJ

(Rasband, 1997–2014). The CoM on each shark was measured as 33% of the total body length of the shark (Domenici et al., 2004). In addition, the angle between a pseudo x -axis, and the line connecting the CoM and the tip of the snout was quantified. These data points were smoothed using a quintic spline in R software (R Development Core Team, 2008) and then imported into Microsoft Excel in order to calculate maximum speed, acceleration and turning rate. Speed and accelerations were calculated for each frame of the video by fitting a quintic spline to the digitized points and then taking the first and second derivatives of the spline function, respectively (Walker, 1998). Responsiveness and reaction distance were also calculated. A response was defined as a change in the snout angle or speed of swimming by 5% as the model passed the shark. Reaction distance was calculated as the distance between the CoM of the shark and the snout of the model at the onset of the response. Only the initial unilateral contraction (stage 1) was analyzed to maintain consistency because the contralateral contraction (stage 2) was not always present. A total of 14 trials (6, 4 and 4, for the large, medium and small models, respectively) were dropped from analyses, as they did not satisfy our requirements.

2.5. Statistics

All statistical analyses were carried out in SYSTAT v. 13 (Systat Software Inc., Chicago, IL, USA). To determine the role of predator speed, predator approach orientation (head-on or tail-on) and predator size, we performed 4-factor analyses of variance (ANOVAs) using these factors as independent variables. Predator speed, although a continuous variable, was separated into 3 categories for analyses given that it was generated using three categorical human behaviors (walk, jog and sprint). The average model speeds resulting from the walk, jog, and sprint categories were 47.8 cm s⁻¹, 132.6 cm s⁻¹, and 191.4 cm s⁻¹, respectively. Individual variation was accounted for by including it as a random factor. Afterwards, modified F -tests were used to determine significance (Zar, 1996). In these cases, the F -value was calculated by dividing the mean square of the main factor by the mean square of the individual \times main factor interaction term, as outlined in Zar (1996). This is also robust to unequal sample sizes, which preclude a repeated-measures ANOVA. If there was no significant impact of individual, it was removed from the analyses. Dependent variables included reaction distance, maximum head turning rate (HTR), maximum speed, and maximum acceleration (Table 1). A p -value of 0.05 was the threshold for significance.

3. Results

From 112 trials analyzed, there were 51 responses. The largest model prompted the greatest responsiveness of 75.0% (27 total

Table 1
Results from 4-way ANOVAs. Independent variables are in columns and dependent variables are in rows. HTR, head turning rate; NS, not significant.

	Predator orientation	Predator speed	Predator size	Individual
Reaction distance (cm)	<0.001	NS	NS	NS
Maximum HTR (deg s ⁻¹)	<0.001	0.008	NS	NS
Maximum speed (cm s ⁻¹)	<0.001	NS	NS	NS
Maximum acceleration (cm s ⁻²)	<0.001	NS	0.02	NS

responses: 15 head-on and 12 tail-on). The rates of responsiveness from the medium and small models were 60.5% (23 total: 12 head-on and 11 tail-on) and 2.6% (1 total: 1 head-on and 0 tail-on), respectively. An increase in predator model speed and size induced a significant increase in the maximum head turning rate (Table 1; ANOVA; $p=0.008$) and maximum escape acceleration (Table 1; ANOVA; $p=0.02$), respectively (Fig. 2). Model speed did not impact any other prey variable (Table 1). Additionally, model size had no other impacts on prey escape behavior or performance (Table 1). When compared to a head-on approach, tail-on approaches elicited significantly shorter reaction distances (Table 1; $p<0.001$), but also greater maximum head turning rates (Table 1; $p<0.001$), speed (Table 1; $p<0.001$) and acceleration (Table 1; $p<0.001$).

4. Discussion

This is the first study to examine realistic predator–prey interactions under controlled conditions with sharks as prey (Fig. 1). It is well understood that large sharks and marine mammals prey upon smaller sharks, and we demonstrated how predator size, speed and approach orientation impacted the behavior and performance of escapes in sharks. We found that the size of the predator model dictated the responsiveness of the sharks. Therefore, sharks respond to a predator based on the frontal profile (body diameter) in a similar manner to teleost fishes (Webb, 1982). When only considering the responses, the orientation of the approach appears to be the most influential factor dictating escape performance (Table 1). Thus, we

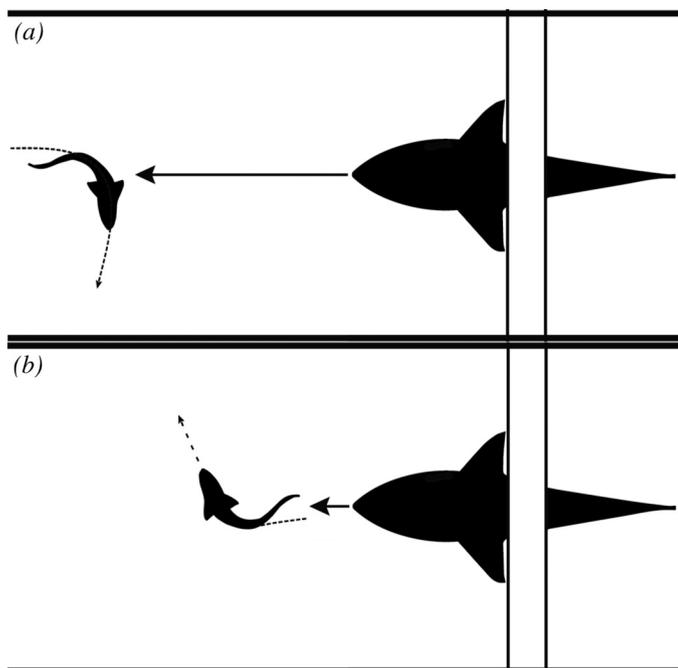


Fig. 2. A dorsal view schematic of the large model approaching a spiny dogfish shark from a (a) head-on and (b) tail-on direction. The length of the arrow extending from the model indicates a larger reaction distance. The curve of the dashed line indicates a change of direction of the shark from its initial orientation. Greater spacing between dashes indicates increased acceleration.

suggest sharks modulate escape performance in response to the behavior of the predator. This is possibly controlled and triggered by the use of different sensory systems for detecting predators, including vision for detecting predators in front of the shark and most likely the lateral line system for detecting predators behind the shark.

Much like in bony fishes, these results demonstrate that the looming rate of a predator is important for determining the escape behavior of sharks (Dill, 1974). Our results reveal an increase in locomotor performance rather than reaction distance, as previously observed in bony fishes (Dill, 1974; Meager et al., 2006). It should be noted, however, that, although the flume that we used was very large, natural predator–prey interactions likely occur over even larger areas. Thus, reaction distance might be impacted under more natural conditions. Apex sharks and marine mammals are generally large animals that can chase prey over great distances due to the ability to sustain high speeds of swimming for extended periods of time. However, their ability to maneuver should decrease with size and speed, and therefore, the ‘matador strategy’ could be an advantage for small sharks (Blaxter and Fuiman, 1990). In other words, small sharks likely focus energy towards outmaneuvering predators, with sharp turns and short bursts of acceleration rather than reacting at a greater distance and attempting to swim away at a high sustained speed.

4.1. Approach orientation

Approach orientation, and thus the ability to visually detect an approaching predator from a distance, appears to be the most influential factor on the escape behavior in *S. acanthias* (Table 1). It essentially separates escape behavior into avoidance (head-on attacks) and startle reactions (tail-on attacks) (Fig. 3). In addition to being a more economical behavior during head-on attacks, avoidance may simply be the optimal strategy given that a startle reaction may be ineffective when the predator and prey are separated by a considerable distance. Another possibility is that the looming rate of the predator model during head-on approach was simply not great enough to trigger the threshold of a reaction stimulated by M-cells. During a tail-on approach, the predator was oriented towards the posterior blind spot of the shark, making visual detection of the predator models very unlikely (Harris, 1965). Moreover, the mean reaction distance ($71.9\text{ cm} \pm 36.2\text{ cm}$) induced by a tail-on approach was within the detectable field of the lateral line system in sharks, while head-on approach likely provoked responses outside the mechanosensory range ($264.24\text{ cm} \pm 111.79\text{ cm}$) (Denton and Gray, 1983; Boord and Northcutt, 1988; Kalmijn, 1989; Gardiner and Atema, 2014). Therefore, it is expected that the bow wave of the predator models during a tail-on approach likely stimulated the lateral line and caused *S. acanthias* to perform a startle response (i.e. greater locomotor performance) similar to the escape results observed by Domenici et al. (2004). Nevertheless, it is still possible that in some instances it was the sudden flash of the predator model entering the visual field of the sharks that stimulated a startle response of higher intensity as seen by Batty (1989). Future studies that incorporate the mouth opening of the predator, which might reduce the bow wave, would provide more insight into whether tail-on

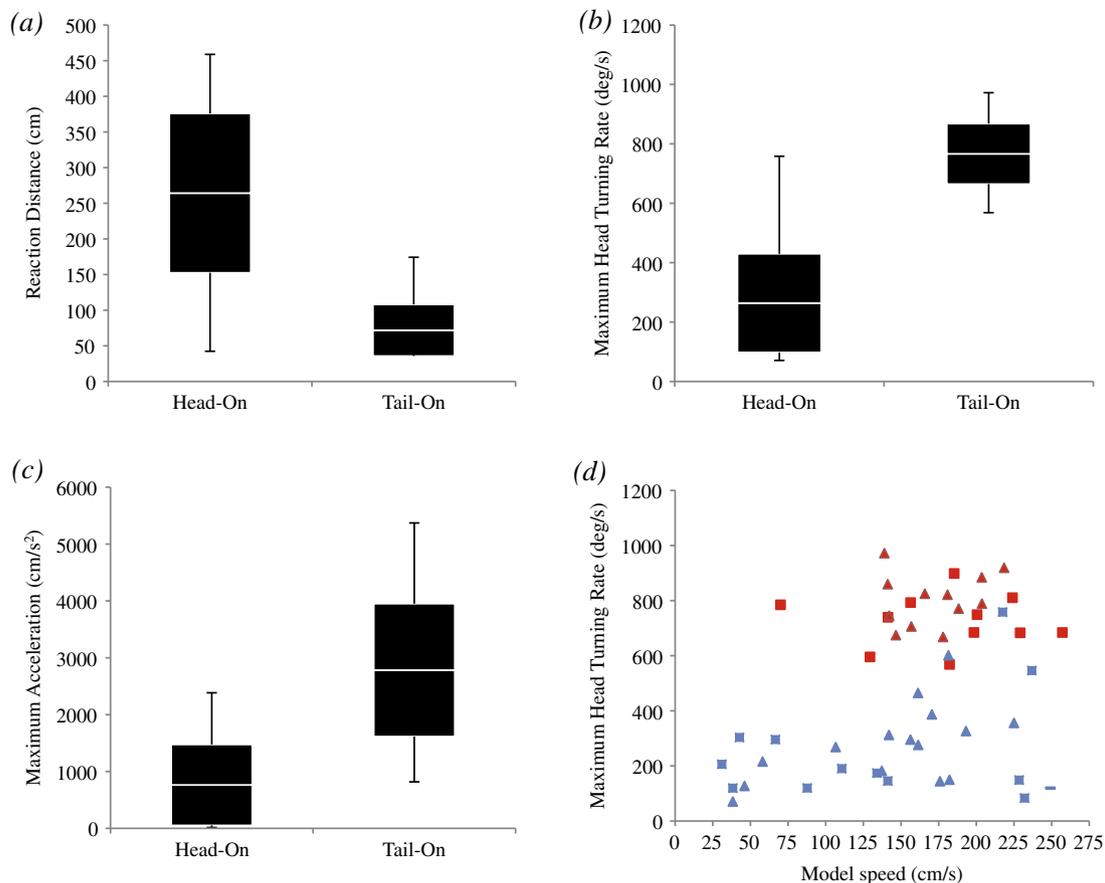


Fig. 3. The effects of approach orientation on (a) reaction distance, (b) maximum head turning rate (HTR) and (c) maximum acceleration. Black boxes represent one standard deviation and the vertical lines extend to the maximum and minimum values. Relative to head-on, tail-on attacks resulted in lower reaction distance ($p < 0.001$), greater maximum HTR ($p < 0.001$) and greater maximum acceleration ($p < 0.001$). Also shown is (d) the influence of model speed on maximum HTR ($p = 0.008$). Blue represents a head-on approach, while red represents a tail-on approach for the large (triangles), medium (squares) and small (dashed) models. Model speeds ranged between 24 and 260 cm s^{-1} .

stimulation was induced by lateral line, or by a sudden visual flash.

Most sharks are thought to be incredibly adept visual predators. They have exceptional binocular vision and can see in front of them during the pursuit of prey (Harris, 1965; McComb et al., 2009), but our results provide the first evidence that sharks are not necessarily good at detecting predators that approach from behind. Our ecologically relevant experiment indicates that the optimal attack strategy for large predators approaching a shark is likely from the caudal direction, consequently putting the predator in a position to immobilize its prey by striking the caudal fin. However, sharks can modulate their escape performance depending on the reaction distance, and in result are not completely defenseless against a tail-on approach. Overall, our results support the idea that selection has favored a visual system focused on prey capture rather than predator detection. Given that predation on sharks is likely infrequent, this makes biological sense. Future work relating escape behavior to the diversity of the visual system in sharks may illuminate the link between ecology, sensory biology, and biomechanics.

4.2. Conclusions and future research directions

Our experiment accounted for several variables (predator size, speed and approach orientation), but there are many other variables that should be addressed in future research. One factor that we did not account for is the mouth opening during the strike. It is likely that the bow wave is somewhat decreased during a dynamic feeding event because water will flow into the opening

mouth, counteracting the water being pushed forward (Higham et al., 2005). Thus, future experiments utilizing a model with an opening mouth (and water moving into it) would be more realistic. Furthermore, future research should investigate whether sharks have three-dimensional defense capabilities to match the three-dimensional environment in which they live. Our predator models were involved in simulated attacks along a single plane that included the long axis of the sharks. However, predators could potentially also attack from below (Martin et al., 2005), which would add another level of complexity that can be examined in future studies.

Studying predator–prey interactions in large animals is challenging (Morice et al., 2013). Two approaches are possible, one of which was employed in our study. The alternative is to tag and track large animals in the wild, which is challenging and rarely done (Watanabe and Takahashi, 2013). Recently, however, autonomous underwater vehicles have been used to track tagged leopard sharks, which is a very promising technique for future research (Clark et al., 2013). Our laboratory setup included an extremely large tank, thus facilitating this type of experiment. Nevertheless, tracking sharks with high-resolution accelerometers, or obtaining high-speed video of them in the wild, would provide further insight into the dynamics of predator–prey interactions in large animals.

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References

- Batty, R.S., 1989. Escape responses of herring larvae to visual stimuli. *J. Mar. Biol. Assoc. U.K.* 69, 647–654.
- Blaxter, J.H.S., Fuiman, L.A., 1990. The role of the sensory systems of herring larvae in evading predatory fishes. *J. Mar. Biol. Assoc. U.K.* 70, 413–427.
- Boord, R.L., Northcutt, R.G., 1988. Medullary and mesencephalic pathways and connections of lateral line neurons of the spiny dogfish *Squalus acanthias*. *Brain Behav. Evol.* 32, 76–88.
- Clark, C.M., Shinzaki, D., Gage, C., Farris, M., Lowe, C.G., Moline, M., 2013. Tracking and following a tagged leopard shark with an autonomous underwater vehicle. *J. Field Robot.* 30, 309–322, <http://dx.doi.org/10.1002/rob>.
- Denton, E.J., Gray, J., 1983. Mechanical factors in the excitation of clupeid lateral lines. *Proc. R. Soc. Lond. Ser. B* 218, 1–26.
- Dill, L.M., 1974. The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. *Anim. Behav.* 22, 711–722.
- Dill, L.M., 1990. Distance-to-cover and the escape decisions of an African cichlid fish, *Melunochromis chipokkze*. *Environ. Biol. Fishes* 27, 147–152.
- Domenici, P., 2010. Context-dependent variability in the components of fish escape response: integrating locomotor performance and behavior. *J. Exp. Zool.* 313A, 59–79.
- Domenici, P., Blake, R.W., 1997. The kinematics and performance of fish fast-start swimming. *J. Exp. Biol.* 200, 1165–1178.
- Domenici, P., Standen, E., Levine, R., 2004. Escape manoeuvres in the spiny dogfish (*Squalus acanthias*). *J. Exp. Biol.* 207, 2339–2349.
- Eaton, R.C., Bombardieri, R.A., Meyer, D.L., 1977. The Mauthner-initiated startle response in teleost fish. *J. Exp. Biol.* 66, 65–81.
- Eaton, R.C., Lavender, W.A., Wieland, C.M., 1981. Identification of Mauthner-initiated response patterns in goldfish: evidence from simultaneous cinematography and electrophysiology. *J. Comp. Physiol.* 144, 521–531.
- Ebert, D.A., 1991. Diet of the seven gill shark *Notorynchus cepedianus* in the temperate coastal waters of southern Africa. *S. Afr. J. Mar. Sci.* 11, 565–572.
- Ebert, D.A., 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. *S. Afr. J. Mar. Sci.* 14, 213–218.
- Fuiman, L.A., Rose, K.A., Cowan, J.H., Smith, E.P., 2006. Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. *Anim. Behav.* 71, 1389–1399.
- Gardiner, J.M., Atema, J., 2014. Flow sensing in sharks: lateral line contributions to navigation and prey capture. In: Bleckmann, H., Mogdans, J., Coombs, S.L. (Eds.), *Flow Sensing in Air and Water*. Springer, Berlin, pp. 127–146.
- Harris, J.A., 1965. Eye movements of the dogfish *Squalus acanthias* L. *J. Exp. Biol.* 43, 107–130.
- Higham, T.E., Day, S.W., Wainwright, P.C., 2005. Sucking while swimming: evaluating the effects of ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. *J. Exp. Biol.* 208, 2653–2660.
- Helfman, G.S., 1989. Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. *Behav. Ecol. Sociobiol.* 24, 47–58.
- Helfman, G.S., Winkelman, D.L., 1997. Threat-sensitivity in bicolor damselfish: effects of sociality and body size. *Ethology* 103, 369–383.
- Kalmijn, A.J., 1989. Functional evolution of lateral line and inner ear sensory systems. In: Coombs, S., Görner, P., Münz, H. (Eds.), *The Mechanosensory Lateral Line*. Springer, New York, pp. 187–215.
- Martin, A., Hammerschlag, N., Collier, R.S., Fallows, C., 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *J. Mar. Biol. Assoc. U.K.* 85, 1121–1135.
- McComb, D.M., Tricas, T.C., Kajiura, S.M., 2009. Enhanced visual fields in hammerhead sharks. *J. Exp. Biol.* 212, 4010–4018.
- McHenry, M.J., Feitl, K.E., Strother, J.A., Van Trump, W.J., 2009. Larval zebrafish rapidly sense the water flow of a predator's strike. *Biol. Lett.* 5, 477–479.
- Meager, J.J., Domenici, P., Shingles, A., Utne-Palm, A.C., 2006. Escape responses in juvenile Atlantic cod *Gadus morhua* L.: the effects of turbidity and predator speed. *J. Exp. Biol.* 209, 4174–4184.
- Morice, S., Princebourde, S., Darboux, F., Kaiser, W., Casas, J., 2013. Predator–prey pursuit–evasion games in structurally complex environments. *Integr. Comp. Biol.* 53, 767–779.
- Nissanov, J., Eaton, R.C., DiDomenico, R., 1990. The motor output of the Mauthner cell, a reticulospinal command neuron. *Brain Res.* 517, 88–98.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org>
- Rasband, W.S., 1997–2014. ImageJ. U.S. National Institutes of Health, Bethesda, MD, <http://imagej.nih.gov/ij/>
- Semeniuk, C.A.D., Dill, L.M., 2004. Cost/benefit analysis of group and solitary resting in the cowtail stingray, *Pastinachus sephen*. *Behav. Ecol.* 16, 417–426.
- Stewart, W.J., Cardenas, G.S., McHenry, M.J., 2013. Zebrafish larvae evade predators by sensing water flow. *J. Exp. Biol.* 216, 388–398.
- Turesson, H., Satta, A., Domenici, P., 2009. Preparing for escape: anti-predator posture and fast-start performance in gobies. *J. Exp. Biol.* 212, 2925–2933.
- Vaughn, R.L., Shelton, D.E., Watson, A., Timm, L.L., 2007. Dusky dolphin (*Lagenorhynchus obscurus*) feeding tactics and multispecies associations. *N.Z. J. Mar. Freshw. Res.* 41, 391–400.
- Walker, J.A., 1998. Estimating velocities and accelerations of animal locomotion: a stimulation experiment comparing numerical differentiation algorithms. *J. Exp. Biol.* 995, 981–995.
- Walker, J.A., Ghalambor, C.K., Griset, O.L., McKenney, D., Reznick, D.N., 2005. Do faster starts increase the probability of evading predators? *Funct. Ecol.* 19, 808–815.
- Watanabe, Y.Y., Takahashi, A., 2013. Linking animal-borne video to accelerometers reveals prey capture variability. *Proc. Natl. Acad. Sci. U.S.A.* 110, 2199–2204.
- Webb, P.W., 1982. Avoidance responses of fathead minnow to strikes by four teleost predators. *J. Comp. Physiol.* 147, 371–378.
- Webb, P.W., 1986. Effects of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* 43, 763–771.
- Ydenberg, R.C., Dill, L.M., 1989. The economics of fleeing from predators. *Adv. Study Behav.* 16, 229–249.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, NJ.
- Zottoli, S.J., 1977. Correlation of the startle reflex and Mauthner cell auditory responses in unrestrained goldfish. *J. Exp. Biol.* 66, 243–254.