



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



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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

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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<sup>-1</sup>, 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,

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