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SHORT COMMUNICATION

Latency of mechanically stimulated escape responses in the Pacific spiny dogfish, *Squalus suckleyi*

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ABSTRACT

Fast escape responses to a predator threat are fundamental to the survival of mobile marine organisms. However, elasmobranchs are often underrepresented in such studies. Here, we measured the escape latency (time interval between the stimulus and first visible reaction) of mechanically induced escape responses in the Pacific spiny dogfish, *Squalus suckleyi*, and in two teleosts from the same region, the great sculpin, *Myoxocephalus polyacanthocephalus*, and the pile perch, *Rhacochilus vacca*. We found that the dogfish had a longer minimum latency (66.7 ms) compared with that for the great sculpin (20.8 ms) and pile perch (16.7 ms). Furthermore, the dogfish had a longer latency than that of 48 different teleosts identified from 35 different studies. We suggest such long latencies in dogfish may be due to the absence of Mauthner cells, the giant neurons that control fast escape responses in fishes.

KEY WORDS: Predator avoidance, Survival, Elasmobranch, Reaction time, Escape kinematics, Mauthner cells

INTRODUCTION

The ability of fishes to perform escape responses plays a vital role in avoiding predation and has been investigated to a great extent (Eaton et al., 1977; Eaton and Emberley, 1991; Hale, 2000; Domenici et al., 2004; Walker et al., 2005; Fuiman et al., 2006; Domenici, 2010; Marras et al., 2011; Ramasamy et al., 2015; McCormick et al., 2018). Many behavioral and kinematic variables have been studied, such as turning speed and angle, acceleration, the trajectory of escape, and escape latency (Webb, 1982; Eaton and Emberley, 1991; Domenici and Blake, 1997; Domenici, 2001; Walker et al., 2005; Fuiman et al., 2006; Domenici, 2010; McCormick et al., 2018). These escape variables have an ecological relevance in predator avoidance and hence survival. Escape latency, defined as the time interval between the onset of the threatening stimuli and the first visible reaction of the fish (Domenici and Hale, 2019), has been shown to predict survival with high accuracy (Katzir and Camhi, 1993; McCormick et al., 2018). A recent study by McCormick et al. (2018) investigated 13 performance variables of the white-tailed damselfish, *Pomacentrus chrysurus*, and found that latency was the best predictor of survival.

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The initiation of the escape response in teleost fishes is typically controlled by the Mauthner cells (Eaton et al., 2001), which are a pair of large reticulospinal interneurons located in the hindbrain that receive sensory inputs from visual, auditory and mechanosensory cells (Eaton et al., 1977; Korn and Faber, 2005). Action potentials from Mauthner cells are very short (∼1 ms) (Hale, 2000; Eaton et al., 2001) and lead to contralateral muscle contractions that result in a body bend away from the stimulus, which takes the general form of a C, i.e. a C-start escape response (Yasargil and Diamond, 1968; Zottoli, 1977; Hale, 2002). The C-start is typically followed by a return flip of the tail, accelerating the fish forward and away from the predator (Domenici and Blake, 1997). Although escape responses can be generated with or without Mauthner cell activity (Liu and Fetcho, 1999; Kohashi and Oda, 2008; Bhattacharyya et al., 2017), short-latency fast escape responses are typically initiated by Mauthner cells while non-Mauthner cell escape responses have longer latencies (Hale, 2000; Zottoli and Faber, 2000; Greenwood et al., 2010; Bhattacharyya et al., 2017; Hecker et al., 2020). Furthermore, ablation (Eaton et al., 1982; DiDomenico et al., 1988; Liu and Fetcho, 1999; Zottoli et al., 1999; Issa et al., 2011) or evolutionary loss of Mauthner cells (Greenwood et al., 2010) is known to result in longer latencies. In addition, recent work based on cell ablation showed that Mauthner axons are fundamental for rapid escapes and that the absence of Mauthner cells increases the vulnerability to natural predators (Hecker et al., 2020).

Latency varies amongst fishes and is affected by temperature, distance to and strength of the stimuli, and foraging and schooling behavior (Webb, 1978a; Eaton and Hackett, 1984; Batty and Blaxter, 1992; Domenici and Batty, 1997; Domenici, 2010; Bohórquez-Herrera et al., 2013; Ramasamy et al., 2015). Latency tends to decrease with increasing temperature, increasing stimuli strength and decreasing distance to stimuli (Webb, 1978b; Domenici and Batty, 1997; Preuss and Faber, 2003). Furthermore, mechanical stimuli typically result in shorter latencies than visual stimuli (Eaton and Hackett, 1984; Batty, 1989). For teleosts, mean latency values generally lie within a range of 10 to 40 ms and minimum latencies within 5 to 20 ms (Eaton and Hackett, 1984; Domenici, 2010). Arguably, the minimum latency is a better representation of the physiological limitations of a fish's ability to react fast to a predator attack, i.e. the maximum performance allowed by the neural command system. The effect of the presence or absence of Mauthner cells is therefore best described by taking into account minimum latency.

While Mauthner cells have been described in many teleosts (Eaton et al., 1977; Zottoli, 1977; Eaton and Emberley, 1991; Eaton et al., 2001), these cells are absent or highly reduced in elasmobranchs, and may represent the vestige of the apparatus in an ancestral group (Bone, 1977). In particular, Mauthner cells have not been found in adult elasmobranch species, including *Mustelus vulgaris*, *Scyllium stellare*, *Scyllium canicola*, *Raja punctate*, *Torpedo ocellata* (Stefanelli, 1980), *Scyliorhinus canicula* and *Squalus achiantias*

(Bone, 1977). Escape responses are particularly understudied in elasmobranchs, probably because of their large size and difficulty in handling under experimental settings (Seamone et al., 2014). However, the majority of elasmobranchs are mesopredators, such as the Pacific spiny dogfish, *Squalus suckleyi* (Girard 1855), which are vulnerable to predation from larger sharks and marine mammals (Vaughn et al., 2007; Ford et al., 2011). Some studies have observed escape responses in spiny dogfish when startled by thrusting of a pole or by an approaching predator model (Domenici et al., 2004; Seamone et al., 2014). However, these approaches were unable to accurately determine the time between the onset of the stimuli and the reaction of the sharks (i.e. the latency). While Mauthner cells have been related to teleost escape performance and latency in particular (DiDomenico et al., 1988; Kohashi and Oda, 2008; Greenwood et al., 2010), it is unknown how the timing of the escape response of adult elasmobranchs compares with that of teleosts, given that adult elasmobranchs lack Mauthner cells (Bone, 1977; Stefanelli, 1980). To our knowledge, no studies have measured the escape latency of this species or any other elasmobranchs.

This study aimed to (1) measure the escape latency of a model elasmobranch, the Pacific spiny dogfish, *S. suckleyi*, when startled by a mechanical stimulus; (2) compare the results with the latencies of four teleost species from the same geographical area, the great sculpin, *Myoxocephalus polyacanthocephalus* (Pallas 1814), the pile perch, *Rhacochilus vacca* (Girard 1855) (both measured in this study), the shiner perch, *Cymatogaster aggregata*, and the silver-spotted sculpin, *Blepsias cirrhosus* (data for both from previous studies), all of which were assumed to possess Mauthner cells (Stefanelli, 1980); and (3) compare the findings with a literature search of published escape latencies of 45 other teleosts from a range of environmental conditions. We hypothesized that the latency of the Pacific spiny dogfish is considerably longer than that of teleosts, because of the absence of Mauthner cells.

MATERIALS AND METHODS
Animals
Pacific spiny dogfish, *S. suckleyi* (n=11; total length 76.25±6.05 cm, mean±s.d.; Table 1), were caught off Pier H in Friday Harbor, San Juan Island, WA, USA, in July 2019 with hook and line. The sharks were then transported in an aerated cooler (106×48×50 cm) and kept in three separate circular flow-through seawater tanks (224×100 cm, 12.0–14.4°C, 12 h:12 h light:dark photoperiod) at Friday Harbor Laboratories, University of Washington. The sharks were fed to satiation once per day, with locally caught fish from beach seining.

Two teleost species, the great sculpin, *M. polyacanthocephalus* (n=7; total length 16.30±1.30 cm, mass 44.90±8.90 g, means±s.d.), and the pile perch, *R. vacca* (n=10; total length 15.85±1.76 cm, mass 54.17±20.30 g, means±s.d.) were used to determine escape latency in teleosts living in the same area (Table 1). Both species were caught by beach seining at Jackson Beach, San Juan Island, WA, USA, in July 2019. All fish were separated by species and kept in several flow-through seawater tanks (90×60×15 cm, 12.0–14.4°C, 12 h:12 h light:dark photoperiod) at Friday Harbor Laboratories, University of Washington. Fish were fed every other day with pieces of shrimp and fasted for 2 days before the experiment commenced. All experiments were performed under IACUC protocol number 4238-03.

Experimental setup
Experimental trials inducing escape responses in the Pacific spiny dogfish, *S. suckleyi*, were performed in a 3870 l circular flow-through experimental tank with a diameter of 3.60 m and a water height of 45 cm. A cylindrical PVC tube with a diameter of 17 cm

and a height of 1.30 m was hung 3 cm above the water surface and 10 cm from the wall of the tank. Inside the tube was a 75 cl plastic bottle, filled with sand, hung from a string and dropped from a height of 1.33 m. The stimulus was dropped from inside the tube to ensure that the sharks would not be able to detect the object falling (i.e. no visual stimulation) and the time of mechanical stimulation was considered to correspond to the frame in which the object broke the surface of the water (t_0) (Fig. 1A). The stimulus was not initiated if the shark was between the stimulus and the closest wall and as fish escape responses typically result in a bend away from the stimulus (Domenici, 2010) the sharks always had plenty of space between them and the opposite wall towards which they escaped. A GoPro (GoPro Hero5 Black) was placed 3.45 m above the water surface and 35 cm from the tank wall, next to the tube, recording the escape response at a frame rate of 240 frames s^{-1}. A mirror was attached to the side of the tank 15 cm from the tube and placed right at the water surface at a 45 deg angle. This enabled the detection of stimulus onset, i.e. when the stimulus broke the water surface (t_0).

The experimental setup for the great sculpin consisted of a flow-through tank (130×110×74 cm) and smaller flow-through tank (130×60×40 cm) for the pile perch with a water height of 21 cm for both. The test area for the pile perches was smaller to allow fish to remain within the camera's field of view. A cylindrical PVC tube with a diameter of 10 cm and a height of 54 cm was placed 6 cm off center from the long axis, with its lower edge 2 cm above the water. A 50 ml conical test tube, filled with sand, was hung on a string with an electromagnet, and dropped from a height of 56 cm inside the tube, to avoid visual stimulation while the stimulus fell from above the water. An Olympus Tough TG-870 camera was mounted 77 cm above the water, recording at a frame rate of 240 frames s^{-1}. A mirror was mounted on the side of the tank at a 45 deg angle so the camera could detect the moment when the object broke the water surface (t_0).

Protocol
Preliminary trials showed that sharks that had been fasted were more likely to actively swim around the tank in contrast to fed sharks that tended to rest at the bottom. As mostly only the active hungry sharks would repeatedly swim close to the mechanical stimuli, the sharks were starved for 5 days before the experiment commenced (Bangley and Rulifson, 2014). Furthermore, preliminary trials also showed that calm sharks typically swam slowly around the tank close to the edge. Once startled, however, they would immediately increase their swimming speed and frequently cross the center section of the test tank. Following each startle trial, it took 5–15 min for the sharks to calm down and resume their calm pre-stimulus swimming behavior.

The experimental protocol was designed to trigger a maximum of five successful escape responses in each individual with a 30 min re-acclimation period between each response (i.e. double the time it took them to resume calm swimming behavior). Before escape response trials commenced, each individual of the Pacific spiny dogfish was acclimated to the experimental tank for 1 h, until they exhibited calm swimming behavior. The first stimulus was then initiated. If the shark did not react to a stimulus, a second attempt was performed within 60 s. This procedure was followed by a waiting period of 30 min to let the sharks resume calm swimming behavior before the next stimulus onset. Trials were continuously run until five escape responses had been collected for each individual. If an individual showed no response in three consecutive trials, the experiment was terminated after the third trial. As a result, the experiments yielded the following combinations of individual sharks (S) and their responses (R): 3S with 5R, 3S with 4R, 2S with 3R, 1S with 2R, 2S with 1R (i.e. a total of 11 individuals with 37 trials).

Table 1. Descriptive data and escape latency from the present study and available literature

Species	Stimuli	Latency (ms; mean±s.d. or range)	Min. latency (ms)	n	Body length (cm; mean±s.d. or range)	Temperature (°C)	Reference
Clupea harengus	Mechano-acoustic	38.9±36.3	15	117	18–23	12.5	Domenici and Batty (1997)
Cymatogaster aggregata	Mechano-acoustic	119±10.4	12	46	8.9±0.9	13	Dadda et al. (2010)
Squalus suckleyi	Mechano-acoustic	97.8±18.2	66.7	11	76.3±6.1	13.3	Present study
Myoxocephalus polyacantho-cephalus	Mechano-acoustic	44.6±5.4	20.8	7	16.3±1.3	13.3	Present study
Rhacochilus vacca	Mechano-acoustic	60.8±23.4	16.7	10	15.9±1.8	13.3	Present study
Blepsias cirrhosus	Mechano-acoustic	24.7±18.5	12	11	13.1±0.8	14	Bohórquez-Herrera et al. (2013)
Rhodeus ocellatus	Mechano-acoustic	19.2±5.8	–	10	3.4±0.1	15	Penghan et al. (2016)
Engraulis japonicus	Mechano-acoustic	6.3±4.0	–	20	9.9±0.9	15	Nasuchon et al. (2016)
Parabramis pekinensis	Electric shock	17*	–	8	7.0±0.6	15	Peng et al. (2014)
Carassius auratus	Mechano-acoustic	14.3±0.7	–	6	11.5±0.2	15	Szabo et al. (2008)
Etheostoma caeruleum	Electrical shock	20–44*	20	–	6.2±0.7	15	Webb (1980)
Cottus bairdii	Electrical shock	30–43*	30	–	7.5±0.8	15	Webb (1980)
Salmo gairdneri	Electrical shock	2–18*	2	–	19.5±0.7	15	Webb (1980)
Esox lucius	Electrical shock	6–14*	6	–	21.7±1.2	15	Webb (1980)
Perca flavescens	Electrical shock	16–32*	16	–	15.5±0.6	15	Webb (1980)
Lepomis macrochirus	Electrical shock	20–35*	20	–	15.3±1.3	15	Webb (1980)
Notropis cornutus	Electrical shock	13–27*	13	–	10.7±1.8	15	Webb (1980)
Pimephales promelas	Electrical shock	20–25*	20	–	5.6±0.9	15	Webb (1980)
Carassius carassius	Mechano-acoustic	13.4±6.3	–	81	–	16	Domenici et al. (2008)

Studies were only included if the experiments were done on single individuals that were either juvenile or adult and kept at temperatures between 12.5 and 16°C. Unreported values are indicated by a dash. Asterisks indicate values that were found by extrapolating graphs. n, number of fish.

Preliminary trials in the two teleosts (great sculpin and pile perch) showed that they resumed pre-startle behavior within 2 min of each startle, defined as resting at the bottom of the tank for the great sculpin and slowly swimming around the tank with no burst swimming and with no frequent stops for the pile perch. Thus, a waiting period of 5 min between each escape response trial was implemented (i.e. double the time it took them to resume calm pre-stimulus behavior). Similar to the shark trials, the teleosts were allowed to acclimate to the test tank for 1 h before escape response trials started, and trials were run continuously until five escape responses per individual were induced, unless an individual showed no response in three consecutive trials. As a result, the trials yielded the following combinations of individual sculpin (Sc) and their responses (R): 4Sc with 5R, 2Sc with 4R, 1Sc with 3R (i.e. a total of 7 individuals with 31 trials). Pile perch (P) and their responses (R) were 6P with 5R, 2P with 4R, 1P with 3R and 1P with 2R (i.e. a total of 10 individuals with 43 trials).

Literature search

A literature search on Google Scholar was performed using a combination the following keywords: fish, teleost, latency, latencies, fast-start, escape response, escape kinematics, Mauthner cells. Studies that had reported the latency ranges, averages and/or minimums of adult or juvenile teleosts were included and resulted in 33 articles reporting latencies of 45 teleost (see Table S1 for the full list from the literature search).

Measurements and statistical analysis

The latency of the escape responses of all three species was measured as the time interval between the mechanical stimulus, i.e. the object, breaking the surface of the water (t_0), and the first detectable movement of the test subject initiating an escape response (t_1).

To test for differences in latency between the three species, the Pacific spiny dogfish, the great sculpin and the pile perch, both the
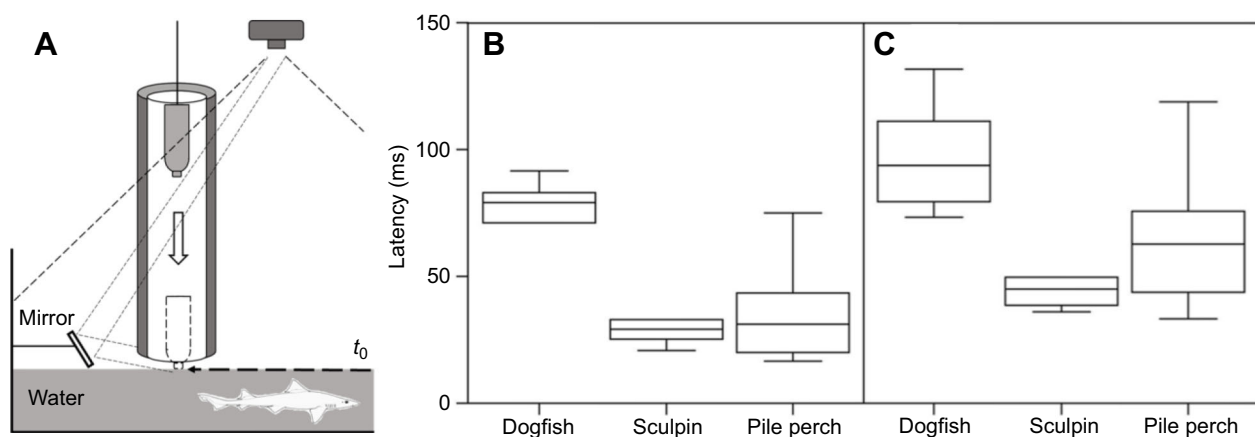
Fig. 1. Illustration and results of mechanically stimulated escape responses. (A) Illustrative drawing showing the cylindrical tube with the lower edge placed just above the water surface, and a bottle inside that acts as a mechanical stimulus for the shark once it breaks the water surface. The position and field of view of the camera at the top and the position of the mirror allow the camera to detect the moment of stimulation onset, i.e. when the bottle breaks the surface of the water (t_0). Drawing is not to scale. (B) Minimum and (C) average latency of the Pacific spiny dogfish (n=11), the great sculpin (n=7) and the pile perch (n=10). Minimum and average latency were significantly different between dogfish and the two teleosts, but not between the two teleosts (P<0.001).

average latency and the minimum latency were used. The average latency was taken as an average of all successful trials for each individual. The minimum latency was defined as the shortest latency an individual achieved across all its successful trials. Hence, only one data point (for both minimum and average latency) was used per individual in the statistical analysis and the number of fish (n) was 11, 7 and 10 for the dogfish, great sculpin and pile perch, respectively. Both datasets were tested for normality with a Kolmogorov–Smirnov and Lillifors test and for homogeneity with a Bartlett chi-squared test. A one-way ANOVA was then run followed by a Tukey HSD for multiple comparisons. Lastly, a linear regression analysis was performed on the distance between the stimulus and the shark (using the point on the shark that was closest to the stimulus) and the latency of the first escape response of each individual to test whether distance to the stimulus had an effect on latency.

Latency was measured using the video-analysis program Kinovea (version 0.8.15), statistical analysis was performed in Statistica (version 13.3.704) and graphic illustrations were made in Graphpad Prism 8 (version 8.2.1. 2019).

RESULTS AND DISCUSSION

The latency of escape responses (based on $n=37$ trials) of the Pacific spiny dogfish showed a clear peak in the frequency distribution, with 56.8% being between 70 and 80 ms (Fig. 2). The shortest latency was recorded at 66.67 ms and the mean latency was 97.75± 18.17 ms (mean±s.d., $n=11$; Table 1). We found no effect of the distance between the shark and the stimulus on the latency to response for this species ($F_{1,9}=0.9183$, $P=0.36$; $R^2=0.0927$).

Among the teleosts, the mean latency was 44.15±5.39 ms (mean± s.d., $n=7$) for the great sculpin and 64.33±23.42 ms (mean±s.d., $n=10$) for the pile perch (Table 1). A one-way ANOVA found significant differences for both the minimum ($F_{2,25}=46.2$, $P<0.0001$) and average latency ($F_{2,25}=17.8$, $P<0.0001$). Specifically, 90.3% of latencies for the great sculpin and 67.4% for the pile perch were

shorter than the shortest dogfish latency (66.7 ms). A *post hoc* test (Tukey HSD) showed that both the great sculpin ($P<0.001$) and the pile perch ($P<0.001$) had significantly shorter minimum and average latencies than the Pacific spiny dogfish whereas neither differed between the two teleost ($P=0.624$ and $P=0.106$, respectively) (Fig. 1B,C). Both the great sculpin and pile perch exhibited a clear peak in frequency at 30 ms (Fig. 2) and a minimum latency more than 3 times shorter than that of the Pacific spiny dogfish (Table 1). The shiner perch from Dadda et al. (2010) had a peak between 20 and 30 ms and the silver-spotted sculpin from Bohórquez-Herrera et al. (2013) had a peak at 10 ms (Fig. 2). Both had about 5.5 times lower minimum latency than that of the Pacific spiny dogfish (Table 1). The Pacific spiny dogfish also had between 2.2 and 33.3 times longer minimum latency than the 18 different teleosts species tested at similar temperatures (12.5–16°C) (Table 1). While statistics cannot be run because of the lack of raw data from many previous studies, the relative difference appears considerable. Similarly, the Pacific spiny dogfish had between 2.2 and 33.3 times longer minimum latency than the 48 different teleosts identified across 35 different studies with various environmental and experimental conditions (see Table S1).

It is evident from both the minimum and average latency that the Pacific spiny dogfish reacts slower to a predatory stimulus than all other examined teleosts, probably because of the absence of Mauthner cells (Bone, 1977). Previous studies of fishes with and without these interneurons have shown longer latencies in species lacking them (DiDomenico et al., 1988; Nissanov et al., 1990; Greenwood et al., 2010). For instance, Greenwood et al. (2010) found *Tetraodon nigroviridis*, which possesses Mauthner cells, to have less than half the response latency than that of *Diodon holocanthus* (11.2±1.3 and 27.3±1.2 ms, respectively), which lack Mauthner cells. Because Mauthner cell are absent in most adult stages of elasmobranchs (Bone, 1977; Stefanelli, 1980), long escape latencies may be a common feature of this taxon.
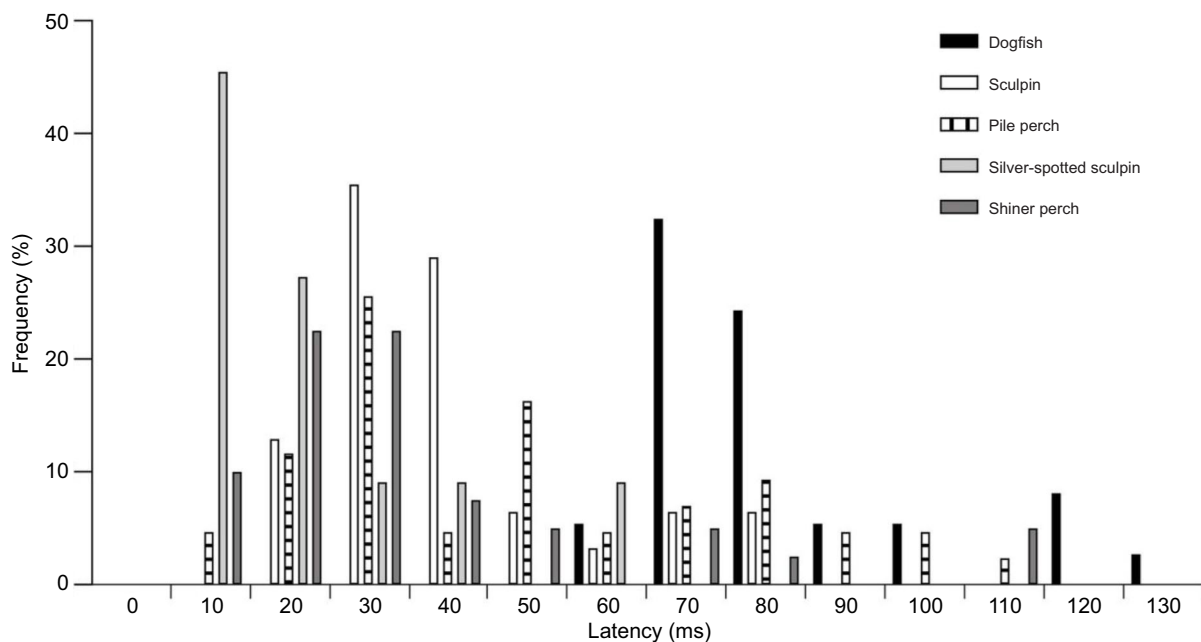
Fig. 2. Frequency distribution of latency to react to mechanical stimuli for four species of teleost and one elasmobranch, all from San Juan Island, WA, USA. Data for the Pacific spiny dogfish (black; $n=37$ trials) and two teleost species, the great sculpin (white; $n=31$ trials) and the pile perch (striped; $n=43$ trials), were from this study, while those for the silver-spotted sculpin (light grey; $n=11$ fish with one trial) were from Bohórquez-Herrera et al. (2013) and those for the shiner perch (dark gray; $n=46$ fish with one trial) were from Dadda et al. (2010). Each latency bin contains values in the interval up to the next bin, i.e. bin 10 contains all values ≥10 ms and ≤20 ms.

Fish size has been related to differences in performance variables in escape responses (Domenici, 2001). Size could also cause longer latencies because of the increased length of axons of the Mauthner cells with increased body size and the possible lack of compensation in larger fish (Funch et al., 1981). However, results from Turesson and Domenici (2007) showed that no relationship could be found between total body length and minimum latency of gray mullets ranging from 6.1 to 28.5 cm. The size range used in this study was larger (76.25±6.05 cm for the Pacific spiny dogfish and 15.85± 1.76 cm for the pile perch, means±s.d.) (Table 1). Therefore, we cannot exclude that size may have played a role in the long latencies of the Pacific spiny dogfish, although it is unlikely to have caused such a large difference in latency given that a 22 cm range did not generate any effect (Turesson and Domenici, 2007).

Increasing distance from the fish to where the object breaks the surface of the water (the stimulus) has been shown to increase the latency and slow turning rate during an escape response (Domenici and Batty, 1994; Domenici and Batty, 1997). Here, we found no relationship between the distance to the stimulus and the latency of the Pacific spiny dogfish, possibly because we used a smaller range of stimulus distances (1.1–15.9 cm used here as opposed to 25–55 cm in Domenici and Batty, 1997). Because of the difference in water height between the experimental tank for the teleost and sharks (21 and 45 cm, respectively), we cannot exclude that stimulus distance was consistently longer for the sharks than for the teleost, causing the sharks to have higher latencies. However, we kept the stimulus distance short which is likely to be the reason why we found no relationship between stimulus distance and latency, in line with Domenici and Batty (1997), who found that almost 100% of the escape responses were of short latency for herring below a stimulus distance of 35 cm. In addition, other previous work on teleosts used a longer stimulus range (e.g. 8.3–24.8 cm in Bohórquez-Herrera et al., 2013, and 11.8–37.6 cm in Dadda et al., 2010) than we used (1.1–15.9 cm), yet the latencies found in such previous work were much shorter than those found for the dogfish. Therefore, it is unlikely that an increase in vertical distance of only a few centimeters was the cause of the longer latencies of the Pacific spiny dogfish.

The disadvantage the Pacific spiny dogfish might suffer in terms of predator avoidance by having longer response latencies (Katzir and Camhi, 1993; McCormick et al., 2018; Hecker et al., 2020) could be counteracted by other types of performance in a predator–prey situation. Domenici et al. (2004), for example, found that the Pacific spiny dogfish had a small relative turning radius (in body lengths) compared with most other teleosts, which is probably due to its morphology exhibiting comparatively high maneuverability and flexibility (Webb, 1978a, 1984; Domenici et al., 2004). A tight turning radius can be important during predator–prey interactions (Howland, 1974; Webb, 1976), as prey usually have a much tighter turning radius than their predators, which can be used to their advantage (Weihs and Webb, 1984; Domenici, 2001). Webb (1976) suggested that it is a relevant trait for survival and a key variable when evaluating performance in a predator–prey interaction. Hence, the dogfish species might be able to make up for the longer latency by turning at the same rate as teleosts but with a smaller radius (Domenici et al., 2004), thereby regaining some advantage in maneuverability both as predator and as prey.

Our study shows that the shortest latency of escape responses that the Pacific spiny dogfish was able to achieve was at least 3 times longer than that of teleosts from the same environment. Taken together with results from previous studies, our findings support the hypothesis that the absence of Mauthner cells in the Pacific spiny

dogfish and other elasmobranchs may be associated with longer latencies when escaping from a threat.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Methodology: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Validation: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Formal analysis: M. Schakmann, V.B., J.J., J.S., P.D.; Investigation: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Resources: J.J., J.S., P.D.; Data curation: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Writing - original draft: M. Schakmann; Writing - review & editing: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Visualization: M. Schakmann, V.B., M. Sogaard, J.J., J.S., P.D.; Supervision: J.J., J.S., P.D.; Project administration: V.B., J.J., J.S., P.D.; Funding acquisition: M. Schakmann, V.B., M. Sogaard.

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Table S1. Descriptive data and escape latency from the present study and available literature. Studies were only included if the experiments were done on single individuals that were either juvenile or adult. – indicates unreported values and * indicates values that were found by extrapolating graphs as the values were not reported.

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