Wall obstacles impact escape response latency and directionality in Pacific staghorn sculpin

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Abstract

Effective escape maneuvers are critical for prey fishes, as fast-start performance has a direct impact on survival in predator-prey interactions. For fish living in structurally complex environments, physical obstacles – such as rocks for bottom-dwelling fishes – may impact fast-start behaviors and overall performance. Incorporating proxies for such obstacles in escape response studies will improve their ecological relevance and offer better insight into the predator evasion tactics employed by these fishes. In this study, we investigated the effects of wall obstacles on escape response in Pacific staghorn sculpin (*Leptocottus armatus*). We used a mechano-acoustic stimulus to trigger fast-start behaviors and used a high-speed camera to film fish with and without a wall barrier located parallel to the body. We analyzed various kinematic and performance metrics, including responsiveness, escape directionality, turning angle, and turning rate. Preliminary results confirmed a trend observed in previous studies for the escape directionality toward the stimulus to be higher when the obstacle was present. It also highlighted a greater reaction latency in obstacle trials. Additionally, further investigating the impact of fish size, obstacle experience, and stimulus positionality (left versus right) will provide a more holistic understanding of predator evasion for these bottom-dwelling fish.

Introduction

Fast starts are the main mechanisms employed by fish in predator evasion. Fast-start reactions involve the neuromuscular control system of Mauthner cells (Eaton, Lee et al. 2001), leading to accelerative burst swimming. This non-steady swimming pattern generally consists of three different stages: stage 1 and stage 2, which respectively correspond to the first and subsequent second bend of fish's body, and stage 3 in which the fish continues to swim or glide (Weihs 1973). The response starts after a period of latency which is defined as the time between stimulus onset and the first movement of the fish. Commonly, this starting movement is characterized by a C- or an S-start in stage 1, during which the fish bends its body into either a "C" or an "S" shape when reacting to a threatening stimulus (Domenici and Blake 1997). Escape response kinematics and performance have been thoroughly studied in recent years, revealing the high variability which could characterize this reaction (Domenici and Hale 2019). Indeed, multiple intrinsic and extrinsic factors can influence fish escapes (Domenici 2010). Previous studies documented differences in the escape response performance depending on inter-individual variability (Marras, Killen et al. 2011), fish size (Webb 1976, Turesson and Domenici 2007), and type of threat (e.g., when facing a different predator; Fu, Yi et al. 2021). It has also been observed that being in a school can affect both escape latency and directionality, i.e. whether a fish escapes towards the threat or away from it (Domenici and Batty 1997). Moreover, escape responses can be displayed as a simple bend of the body into a C-shape in cases of weak stimuli (Godin 1997). This C posture could help fish to camouflage with the surrounding environment, and it has been documented that this C-bend may be preparation for a more efficient response (Turesson, Satta et al. 2009).

The majority of studies investigating escape behavior only focus on species in artificial open-field environments, meaning that tanks have no obstructions during experimentation (Domenici and Blake 1991, Hale 1996, Schakmann, Becker et al. 2021). However, these experimental conditions often oversimplify the environments fish encounter in nature. Habitats are often characterized by a complex structure, especially for bottom-dwelling and intertidal marine fishes. It is known that this complexity affects predator success (providing shelters for the prey), as well as prey population equilibrium (Gotceitas and Colgan 1989). Physical obstacles typical of a structurally complex environments are likely to also impact the escape response of fish. For instance, the laterality effect (Bisazza, Rogers et al. 1998) may be one of the factors involved in avoiding an obstacle. As shown in previous studies (Dadda, Koolhaas et al. 2010), the directionality of escape relative to the stimulus might vary depending on individual lateralization; this could also be the case in the presence of an obstacle. In addition, since it has been confirmed that fish escape performance is influenced by the predator experience (Ramasamy, Allan et al. 2015), obstacle experience may also have an impact upon escape behavior. However, escape response in the presence of an obstacle - and the factors that impact it - are still poorly analyzed, except for that of larval zebrafish (Zwaka, McGinnis et al. 2022).

In this study, we investigated the potential effects of wall obstacles on escape response kinematics and performance in Pacific staghorn sculpin (*Leptocottus armatus*). *L. armatus* is a marine species that resides near shorelines in bays and estuaries along the Eastern Pacific in North America, with a native range from Alaska to Baja California. These bottom-dwelling fish reside in sandy, rocky, and muddy-bottomed environments, making this species an ideal system for studying the effects of physical obstacles in escape response.

We used a mechano-acoustic stimulus to trigger fast start behaviors in sculpin and filmed escape responses using a high-speed camera. From the recorded videos, we determined fish responsiveness, the latency of the reaction, and escape directionality (i.e., away from the stimulus or towards it), and we determined whether the fish performed a single or double bend maneuver while escaping. By considering the angle of positioning between the fish and the stimulus and the fish and the obstacle, we also measured fish turning angle for both escape stages 1 and 2 and turning rate during stage 1. We compared all the observed variables between control and obstacle trials, as well as between trial types depending on the obstacle experience (i.e., whether the obstacle exposure came before or after control trials). Our analyses also considered whether the stimulus location was on the left or the right flank of the fish, to account for potential laterality effects.

Materials and Methods

Test species and fish maintenance

All Pacific staghorn sculpin were collected at Jackson Beach (San Juan Island, 48°31'12.0" N, 123°00'26.8" W) by multiple beach seining collections, spanning July 2023 through August 2023. Upon collection, individuals were promptly transported to the University of Washington Friday Harbor Laboratories (48°32'46.0" N, 123°00'41.8" W) where they were kept in 120 x 60 x 15 cm (*length* x *width* x *depth*) flow-through holding tanks continuously supplied with unfiltered seawater. Salinity and temperature in the tanks fluctuated according to ambient ocean temperature outside Friday Harbor Laboratories, with the average temperature being 12.8 ± 0.65℃. Individuals were allowed a minimum of 24 hours of acclimation with no feeding before being used in trials.

Experimental equipment and procedure

A 122 x 110 x 60 cm (*l* x *w* x *d*) arena with rounded corners and a water depth of 22 cm housed an individual sculpin during experimentation. The individual was constantly monitored via a Trust TYRO full HD webcam attached to wooden planks above the arena, which showed the real-time video on a computer screen (HP Elitebook 8570p). We used the same wooden plank setting to also attach a high-speed camera (Sony Cybershot RX100 VII) above the tank, allowing for high-framerate video capture of each individual.

For this study, we dropped a 350 g 21.5 x 7 cm (*height* x *diameter*) cylindrical stimulus in the arena; this stimulus was hanging inside a 110 x 7 cm (*h* x *d*) PVC tube to ensure a purely mechano-acoustic trigger. The cylindrical PVC tube was suspended two centimeters above the water surface and aligned with a 26 x 10 cm (*l* x *w*) mirror to allow the high-speed camera to film the moment the stimulus hit the water for latency calculations (see below).

To test for fish obstacle experience, we used a 78 x 35.5 (*l* x *h*) white flat barrier as an obstacle. The obstacle was placed in the arena only during obstacle trials (i.e., for 50% of the time, being removed during control trials) and was vertically positioned beside the fish to obstruct the swimming direction away from the stimulus. To estimate distances in the recorded videos, a 10 x 10 cm (*l* x *w*) square was placed at the bottom of the tank (Fig.1).

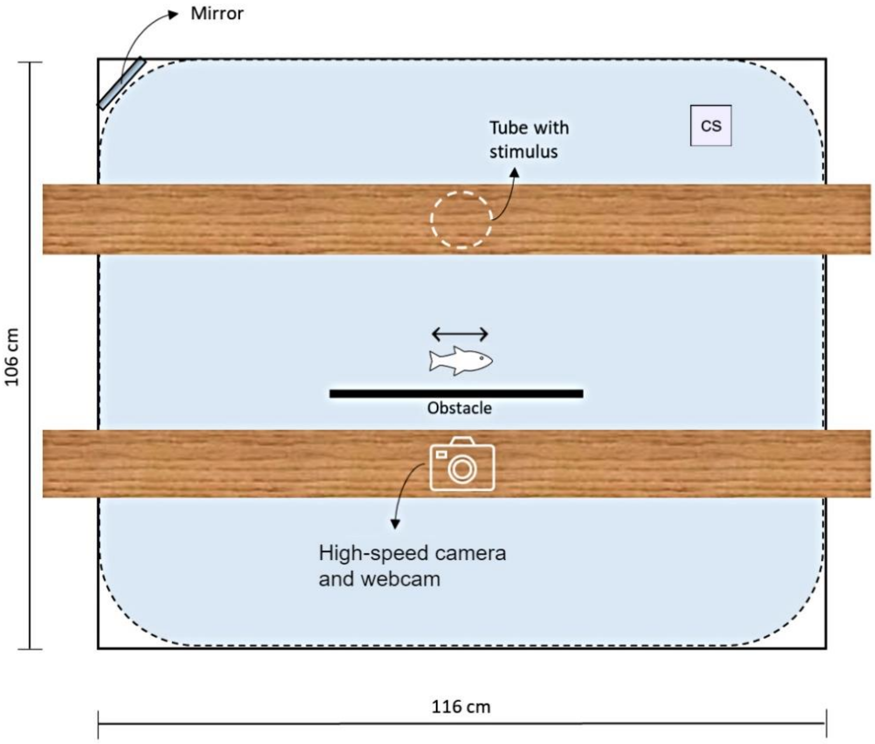

Fig. 1 Experimental tank setup, observed from above, for the analysis of escape response in Pacific staghorn sculpin (*Leptocottus armatus*) in presence or absence of an obstacle. The two wooden beams illustrated above the tank were suspended to hang two cameras (high-speed camera and webcam) and the PVC tube for releasing a mechano-acoustic stimulus. Escape responses were filmed through the high-speed camera using remote control. The exact moment in which the stimulus hit the water surface was observed through a mirror aligned with the bottom of the tube. To calibrate distances in the collected videos a calibration square (CS) of 10 by 10 cm was placed on the bottom of the tank.
The fish was placed in the center of the tank after a coaxing session so that it was positioned parallel to both the stimulus and the obstacle (if present, as shown in the illustration). The positioning of the fish was oriented either by having the stimulus along the right or left side of the fish (as in the case reported here).

We carried out both a control and an obstacle trial for each individual. Prior to starting an experiment, we used a haphazard (random) method to decide whether the fish would experience the control (C) or obstacle setting (O) as the first trial of the sequence (hereafter respectively defined as sequence $C_1 – O_2$ and sequence $O_1 – C_2$). Trials were initiated by moving a fish to the middle of the arena. Each individual was left undisturbed for 10 minutes to acclimate after being handled. At the end of this acclimation period the fish was gently coaxed (using small fishing nets to reduce water splashes) for a maximum of 5 minutes to be positioned parallel to the stimulus tube and the obstacle if present (the coaxing stopped as soon as the fish was in an acceptable position). Each fish had at least 1.5 body lengths (BL) of distance between itself and the stimulus and was about 0.25 BL from the obstacle (if present). Once the fish was in the correct position, we waited an additional minute to let the fish acclimate before dropping the stimulus. The side in which each fish faced the stimulus was decided during the coaxing session of the first trial: whenever the fish was in the correct position (i.e. alongside the stimulus on the left or right flank), we coaxed the fish toward the same side for the second trial.

Each high-speed video was recorded using a remote control (phone application: Imaging Edge Mobile) on the camera by capturing the 6-seconds immediately following the impact of the stimulus on the water. As soon as the first trial was filmed, the obstacle was then immediately either removed or placed in the arena to run the second trial. After 1 minute of acclimation, the fish was coaxed again following the same criteria. At the end of each double trial, the length of each fish was measured using a ruler, and the water in the arena was replaced using a pump (Active Aqua 1110 gph model AAPW1000) to remove olfactory cues.

All the described timing criteria were followed whenever the fish maintained their position in the tank after a coaxing session of a maximum of 5 minutes before releasing the stimulus. For those cases in which the fish moved after the coaxing or were coaxed for more than 5 minutes, we waited 5 additional acclimation minutes before repeating the coaxing session. Fish were considered over-stressed and discarded from the experiment whenever it was impossible to set their positioning in the tank after the second acclimation and coaxing procedure.

Video processing

The trial videos were recorded with the high-speed camera at 500 frames-per-second and then processed using the Kinovea software (Charmant 2004) on 1920 x 1080 resolution screens.

We first categorized each video depending on the side in which the fish was stimulated, responsiveness (i.e. response, C-bend response, no response), and the escape direction (i.e., away from or towards the stimulus). We defined in Kinovea the exact timing of each of the reaction stages of the fish. Precisely, by counting the frame number, we determined several key frames: the moment when the stimulus touched the water surface (frame 0), the starting moment of the escape reaction (i.e., the latency of reaction after frame 0; frame A), and the ending moment of both stages 1 and 2 of the escape response (frame B and C, respectively).

Fish position was defined in XY coordinates within the video for the established key frames 0, A, and B, by calibrating the XY system to real world measurements using the 10 x 10 cm reference square. The calibration was double-checked in every video by measuring the fish length through a Kinovea measurement tool and comparing this digital length to the observed (ruler) length collected during trials. Each individual was then digitized at two points in every key frame: at the tip of the head (i.e., the most anterior point of the snout) and at the center of mass (precisely, the center of mass was set at 35% of total fish length using Kinovea measurements). In addition, we digitized the XY positions of both the stimulus and the obstacle (if present) to calculate their distance from the fish's center of mass. The stimulus was digitized by accounting for the center of the PVC tube, whereas the obstacle was digitized at the bottom of the barrier, parallel to fish's center of mass to obtain the minimum distance between them (i.e. setting the same X-coordinate for the obstacle and fish center of mass).

All the data collected in Kinovea were imported into R (R Core Team 2023) using a custom function through the R-studio interface to calculate the distances and angles needed for the statistical analyses. Knowing the collected XY positions in every video, we calculated the distance between both the fish and the stimulus, the fish and the obstacle, and the total shifting distance of each individual during the escape response. We also measured the angle at frame 0 between the fish and the center of the stimulus, as well as the angle between the fish and the obstacle barrier. Through the same function, we also measured the turning angle at the end of both stages 1 and 2 and calculated turning rate during stage 1 in degrees-per-second.

Statistical analysis

All the preliminary analyses were performed in R to have an overview of fish escape directionality, latency, and turning rate. We analyzed a preliminary subset of data by selecting 20 individuals (2 videos per fish for n = 40 videos total), in which half of the fish were stimulated on the right side (10 individuals, n = 20 right videos total) and the other half were stimulated on the left side (10 individuals, n = 20 left videos total). All fish selected were confirmed to have an escape response; this preliminary data set does not include any fish that did not respond to our stimulus.

We performed chi-squared (χ^2) tests of independence to determine whether the proportions of responses "away" and "toward" the stimulus differed among trial types. Each chi-squared test was performed with the Yates continuity correction (χ^2 Yates) to account for the small sample size of each comparison ($n \leq 40$ videos). We conducted the following comparisons:

- All control (C) versus all obstacle (O) trials (regardless of obstacle experience or stimulus directionality) to compare overall escape response
- C_1 versus C_2 trials and O_1 versus O_2 trials to assess potential effects of obstacle experience
- Right side C versus left side C trials and right side O trials versus left side O trials to assess potential laterality differences

We also used paired samples Wilcoxon (W) tests to evaluate differences in escape response performance (i.e. analyzing escape latency and turning rate) depending on the trial type, given the presence of outliers in the preliminary data overview. Both fish latency and turning rate were analyzed by comparing the C_1 – O_2 and O_1 – C_2 trials.

Results

A total of 75 Pacific staghorn sculpin were caught for this study with estimated sizes ranging from 9.4 cm to 22.65 cm (mean body length = 14.97 cm, SD = 2.67). The analysis was conducted on 73 individuals and 2 individuals were discarded due to fish over-stress or defects in the video collection. Each individual included in the analysis was observed during two consecutive trials, totaling 35 individuals who received the stimulus from the right side and 38 from the left side. We recorded a complete double trial for 59 out of 73 fish, whereas 14 individuals reacted in only one trial, and 3 individuals never reacted to the stimulus.

The reported preliminary results are related to the observation of 10 individuals stimulated on the right side and 10 individuals stimulated on the left side. All 20 individuals were randomly selected among the fish who reacted in both trials, resulting in a subset of 11 fish that were tested with the C_1 – O_2 sequence and 9 fish with the O_1 – C_2 sequence. The fish were placed between 1.57 and 5.94 BL from the stimulus and the obstacle was between 0.13 and 0.48 BL of distance from the fish's center of mass.

When comparing the overall relative proportions of away and toward responses, we observed a strong tendency in having a majority of responses directed away from the stimulus in control trials (χ^2 Yates = 3.609, df = 1, p = 0.05747). More precisely, over 60% of the reactions were directed away from the stimulus in control cases (Fig. 2). On the other hand, when facing the obstacle, around the 70% of the fish escaped towards the stimulus (Fig. 2).

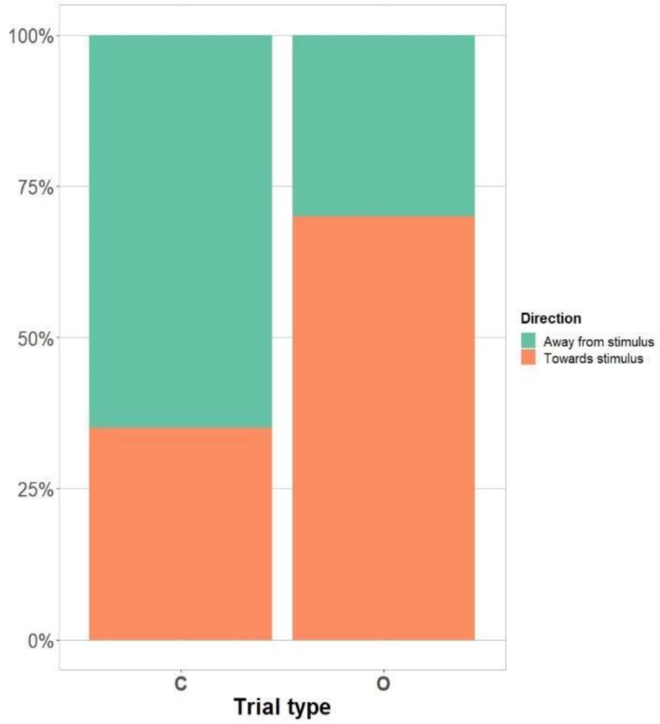

Fig. 2 Relative proportions of escape response directions tested for 20 Pacific staghorn sculpin in two different conditions: control trial type (C) or in presence of an obstacle during the trial (O). Escape responses were tested in an experimental tank setting and classified depending on first fish bend, classified on whether it was directed away (teal) from the stimulus or towards (orange) the stimulus.

For both control (C_1 versus C_2) and obstacle (O_1 versus O_2) trials, there were no significant differences in directionality proportions depending on trial order. Despite a higher percentage of responses directed towards the stimulus after the obstacle experience (i.e. in trails C_2), there were no significant differences by comparing both C_1 with C_2 trials (χ^2 Yates = 0.10878, df = 1, p = 0.7415 for control cases; Fig. 3a) and O_1 with O_2 trials ($\chi^2 = 0$, df = 1, p = 1 for obstacle cases; Fig. 3b).

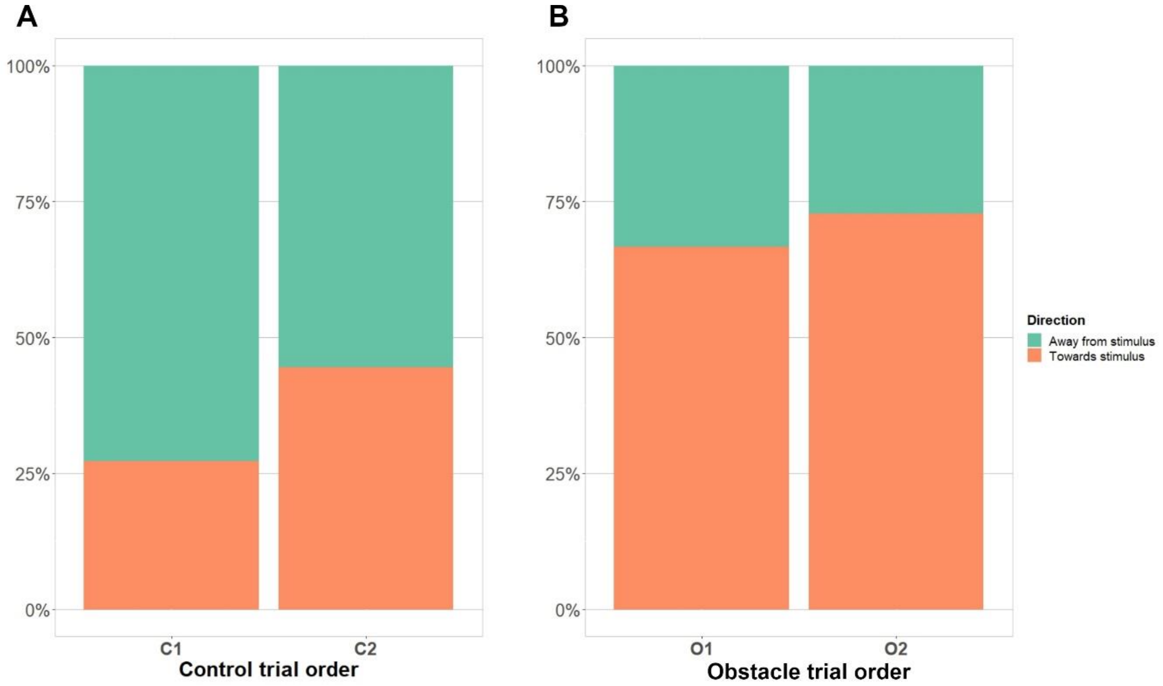

Fig. 3 Relative proportions of escape response directions tested for 20 Pacific staghorn sculpin in two different conditions (i.e. during control trials, C, or in presence of an obstacle, O) and alternating the trials by having the control experiment as the first or second trial. Each fish was tested twice, with the obstacle faced either in the first trial (O_1 – C_2 sequence) or in the second trial (C_1 – O_2 sequence). Reported here are the proportions of responses directed away (teal) from the stimulus or towards (orange) the stimulus with comparisons for both control cases (A) and obstacle cases (B) depending on their order.

The preliminary analyses showed a potential effect of laterality on escape response, as we found significant differences in escape directionality proportions in obstacle trials. Specifically, fish directionality was not affected by the side from which they received the stimulus during control trials (χ^2 Yates = 0, df = 1, p = 1 for control cases; Fig. 4a). However, in presence of an obstacle, when the stimulus was received on the right side of the fish, all observed responses were directed towards the stimulus (χ^2 Yates = 5.9524, df = 1, p = 0.0147 for obstacle cases; Fig. 4b).

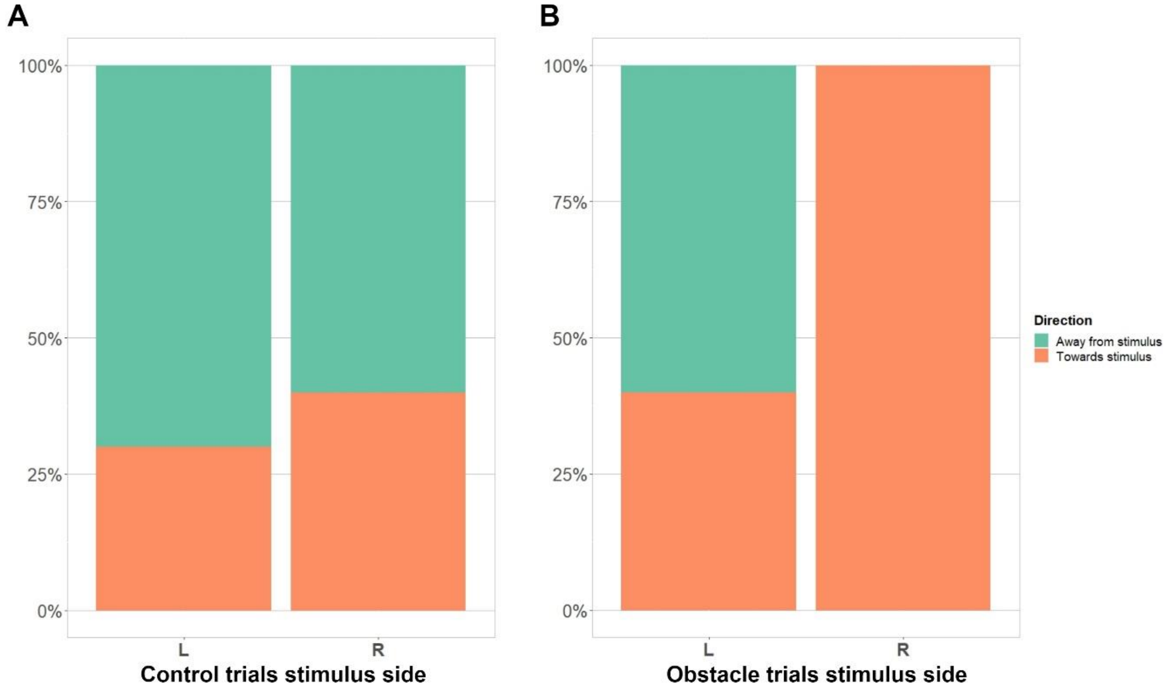

Fig. 4 Relative proportions of escape response directions tested for 20 Pacific staghorn sculpin in an experimental tank setting, by having a control situation (A) or in presence of an obstacle beside the fish (B). Fish were positioned between and parallel to the stimulus and the obstacle, by having the stimulus at least 2.5 body lengths (BL) apart and being at approximately 0.25 BL from the obstacle. Proportions of responses directed away (teal) from or towards (orange) the stimulus are reported by considering whether the fish was stimulated along the left (L) or the right (R) side. Directionality proportions were similar during control trials (A) regardless of the side of the stimulus, whereas in presence of an obstacle (B), when the fish was stimulated on the right side, the resulting reaction direction was greatly lateralized.

The latency of sculpins reaction also seemed to be affected by the presence of the obstacle. In trials C_1 – O_2, the latency time increased significantly from 31.45 ms to 61.63 ms on average, respectively (W = 1, p = 0.012; Fig. 5a). However, the obstacle experience in cases O_1 – C_2 does not lead to significant differences in the latency (W = 20, p = 0.83), with mean values of 37.11 ms and 38 ms, respectively (Fig. 5b).

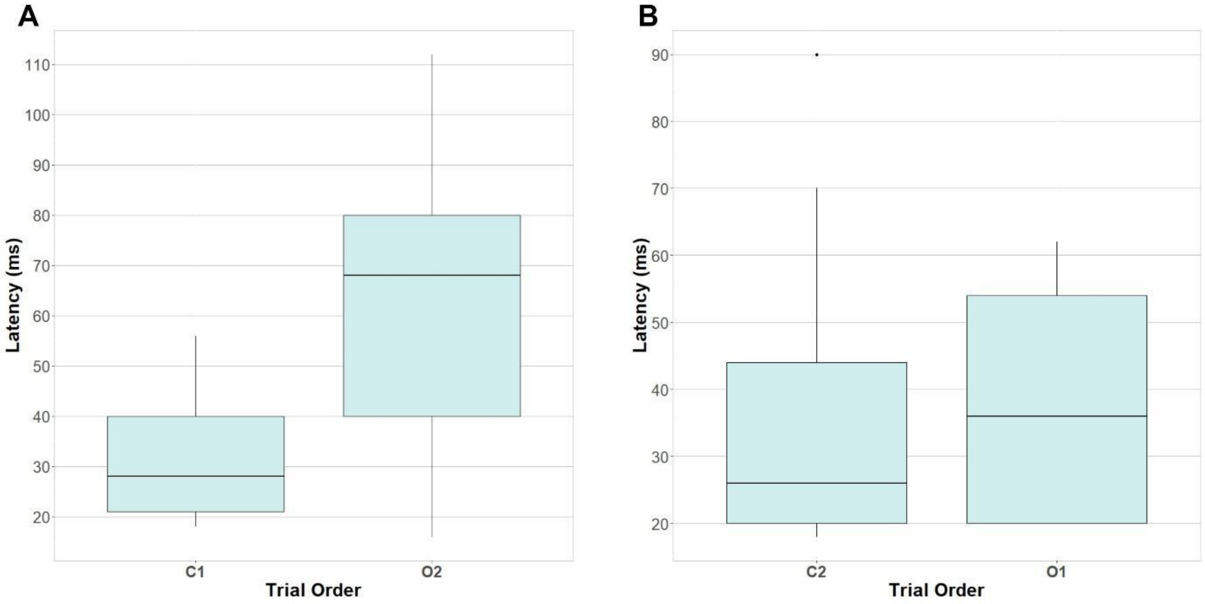

Fig. 5 Latency of reaction reported in milliseconds for 20 Pacific staghorn sculpin tested in experimental tank conditions with two different types of trial sequences. Each fish was tested twice by having a control trial first and then facing an obstacle (C_1 – O_2, panel A), or vice versa (O_1 – C_2, panel B).

Finally, preliminary analyses showed no significant differences in escape response performance (turning rate) due to the experience of the obstacle (Fig. 6). For trials with sequence $C_1 – O_2$, the average turning rate was 1712.67 degrees/s and 1587.88 degrees/s, respectively (W = 39, p = 0.6377). Whereas in cases $O_1 – C_2$ the average turning rate was 1632.44 degrees/s, respectively and 1660.75 degrees/s (W = 19, p = 0.7344).

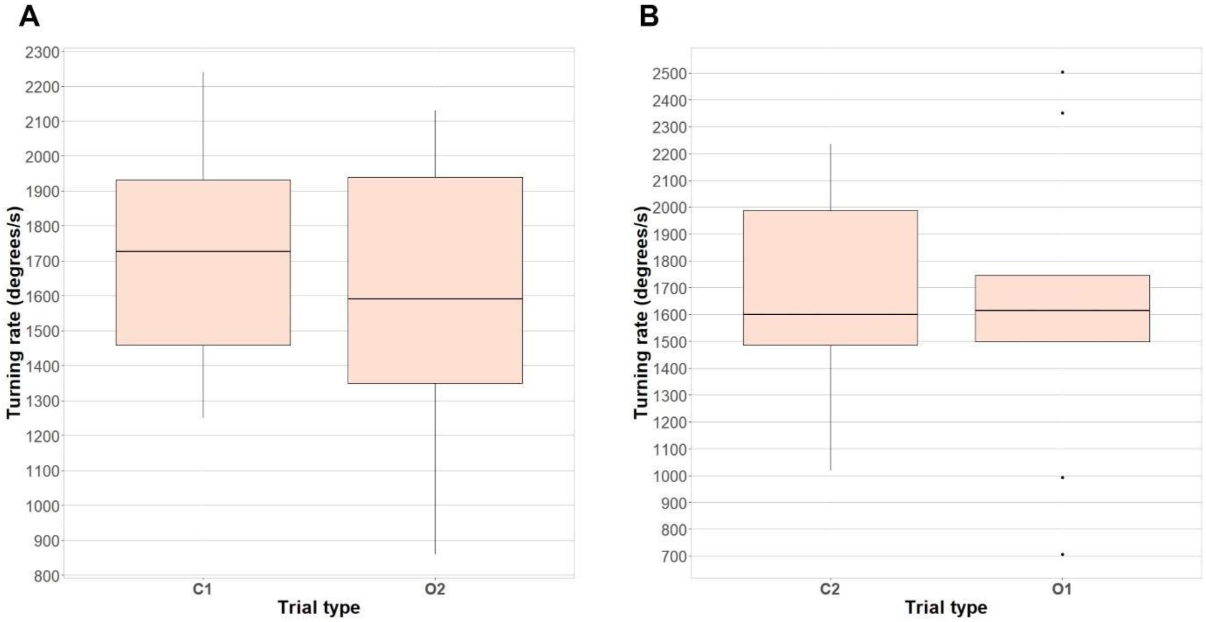

Fig. 6 Turning rate during escape response measured in degrees-per-second (degrees/s) for 20 Pacific staghorn sculpin tested in experimental tank conditions with two different types of trial sequences. Each fish was tested twice by having a control trial first and then facing an obstacle ($C_1 – O_2$, panel A), or vice versa ($O_1 – C_2$, panel B).

Discussion

Obstacles have a strong tendency to affect the directionality and latency of escape response in Pacific staghorn sculpin. However, there was no obstacle experience effect, nor an effect of obstacles on stage 1 turning rate. From our study, fish also seemed affected by lateralization when an obstacle obstructed one side of their surrounding space, particularly when the fish was stimulated on the right flank.

The initial directionality trend resulting from this study confirmed that fish aim to avoid obstacles while escaping (Zwaka, McGinnis et al. 2022), in this case by swimming toward the stimulus. Together with the observed increase in latency time, this presents a scenario in which a fish facing an obstacle on one side takes a longer time before reaction, possibly because the classic escape route (i.e., away from the stimulus) is not available. The higher latency time of sculpins could also be a consequence of their adaptation to living on the ocean floor, particularly in intertidal habitats. By commonly being surrounded by multiple obstacles (e.g. rocks and sessile invertebrates), and also being mimetic, these fish may not respond at all to a threatening stimulus (i.e. freezing) or assume the C-shape pose (Godin 1997), thus hiding in the environmental background.

Our results displayed an effect of lateralization on escape directionality in the presence of an obstacle. It has been demonstrated in various taxa that the cerebral hemispheres - and therefore their contralateral visual fields - are specialized to process different kind of stimuli (Ocklenburg and Gunturkun 2012, Salva, Regolin et al. 2012): while the right-brain-left-eye system better reacts to unpredictable events, the left-brain-right-eye system controls familiar behaviors. It is possible that by having the stimulus along the right flank (i.e., with the left visual field obstructed by the obstacle) the fish experiences an unfavorable situation which predisposes it to swim away from the obstacle, thus toward the stimulus.

Finally, turning rate was not found to be influenced by obstacle presence nor obstacle experience. This aligns with what is already known about this species, as a previous study reported that escape response cannot be modulated once initiated in Pacific staghorn sculpin (Kimura, Pfalzgraff et al. 2022).

Hence, the presence of obstacles - typical of sea bottom and other structurally complex habitats - seem likely to lead to deviations and modulations in the escape response of sculpins, possibly presenting additional difficulty for these fish when avoiding potential threats.

Conclusion

This study presents preliminary evidence which sets the basis for future research regarding escape directionality in *L. armatus* when facing obstacles and other conditions more similar to their natural environments. Further analyses and results may present a more comprehensive overview of the factors which influence this type of escape response, e.g. by evaluating if other determinants (such as fish size) also influence this behavior. These data may bring new insights applicable to multiple species of bottom-dwelling fish.

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