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Impacts on Fast-Start Performance: How Do Group Size and Habitat Degradation Alter the Escape Behavior of a Schooling Coral Reef Fish?

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Thesis of Monica D. Bacchus

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

August 2022

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HALMOS COLLEGE OF ARTS AND SCIENCES

IMPACTS ON FAST-START PERFORMANCE: HOW DO GROUP SIZE AND
HABITAT DEGRADATION ALTER THE ESCAPE BEHAVIOR OF A
SCHOOLING CORAL REEF FISH?

By

Monica D. Bacchus

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science

Nova Southeastern University

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Abstract

Escaping predation is essential for species survival, but prey must effectively match their response to the perceived threat imposed by a predator. Fish evaluate their surroundings using several sensory stimuli, including olfactory, visual, auditory, and mechanical cues. A range of taxa use the fast-start response to evade predators, including fishes, sharks, and larval amphibians. While the fast-start response (rapid bursts of swimming) is extensively studied in solitary fishes, the factors that mediate the collective escape response in schools of fish have historically been investigated far less. To address this knowledge gap, the collective escape behavior and individual escape performance of schools of the tropical damselfish species *Chromis viridis*, a common gregarious and coral-associated coral reef fish species found throughout the Indo-Pacific, were investigated. The first data chapter explored the theory of optimal group size, comparing various sized groups of fish. Fish strategically adjusted their escape response in coordination with other group mates, validating the connectivity within conspecific schools. The second data chapter investigated how degrading coral health influences antipredator behavior in fish schools. Habitat degradation was revealed to have a negative effect on schooling, and the combination of a chemical alarm cue intensified this impact. While the singular effect of a chemical alarm acted as a prewarning to strengthen the fast-start.

Keywords: chemical cues, optimal group size theory, fast-start escape response, *Chromis viridis*

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Introduction

Escaping predation is essential for species survival, but prey must effectively match their response to the perceived threat imposed by a predator. Theory suggests that rapid bursts of swimming are the most energetically efficient pathways to evade predators and catch prey (Weihs, 1974). The term “fast-start” was coined to describe these rapid and ephemeral movements (Webb, 1976), defined as an anaerobically-fueled burst of locomotion starting either from rest or routine swimming (Domenici and Batty, 1994). Fast-start escape responses are elicited by the acoustic-lateralis system, which is composed of the inner ear region and lateral-line organs. Electrical impulses are sent from the acoustic-lateralis system to a distributed network of neurons in the mid- and hindbrain (known as the reticulospinal system), including a large pair of neurons called Mauthner cells (M-cells) (Brownstone and Chopek, 2018; Domenici and Hale, 2019; Eaton et al., 1991; Sillar et al., 2016). When reacting to a predator threat, M-cells process and rapidly send signals to motor neurons (Shimazaki et al., 2019), which stimulate the body to contract, bend into a C- or S-shape, and position the head away from the startling response (Sillar et al., 2016; Yasargil and Diamond, 1968). Fast-start responses are highly dependent on the responsiveness of the M-cells; without them, the fast-start response is either substantially weakened (Kohashi and Oda, 2008) or lost entirely (Hecker et al., 2020). This predator escape behavior is found in a range of vertebrate taxa, including teleost fishes, sharks, and larval amphibians (Eaton et al., 1981).

The fast-start response has been extensively studied in teleost fishes and is typically categorized through two types and three stages (Karlsen et al., 2004; Takahashi et al., 2017; Weihs, 1973). First, this response is categorized as either a C-start or an S-start type, corresponding to a single or double bend respectively, and so-named by the shape of the organism’s body during the response (Weihs, 1973). C-starts are used by prey when evading predation, and S-starts are used by both predators (during foraging) and prey (for defense) (Domenici and Blake, 1997; Karlsen et al., 2004; Neill and Cullen, 2009). In this project, I focused on fast-start responses for the purpose of defense, and hereafter, will discuss only C-starts, which can be broken down into three kinematic (i.e., the analysis of movement involving body position, velocity, and acceleration) stages: 1) the preparatory stroke, when the body bends into a C shape following extensive muscle contraction on one side of the body, 2) the propulsive

stroke, completed through a second contralateral body bend, and 3) a variable stage, including coasting or continuous propulsive swimming (Domenici and Hale, 2019; Weihs, 1973(Figure 1)).

In teleost fishes, fast-start escape performance can be analyzed by measuring multiple kinematic variables. These variables are associated with both non-locomotor and locomotor components (Domenici, 2010). Non-locomotor performance can be attributed to both the neural and sensory networks that are responsible for detecting and responding to environmental stimuli. These traits include detection of the stimulus (i.e., responsiveness), response timing (i.e., latency), distance to the threat at the time of response (i.e., stimulus distance), and directionality of the response relative to the threat (Domenici, 2010; Eaton et al., 2001). Locomotor performance is indicative of both neural control of the response and muscular power for achieving speed and acceleration (Domenici, 2010; Wakeling, 2002). Locomotor variables include maneuverability of the response (i.e., angular velocity of the body during stage 1) and reaction speed and acceleration (through stages 2 and 3) (Domenici and Batty, 1994). The respective significance of each non-locomotor and locomotor trait in successful predator evasion is thought to be context and species dependent (Domenici, 2010; Domenici and Hale, 2019).

The fast-start response is highly plastic and is known to change with a range of environmental factors, including hypoxia, temperature, carbon dioxide, turbidity, and prey availability. Hypoxia has a negative impact on responsiveness, meaning that fewer individuals respond to the threat when oxygen is limited (Lefrancois and Domenici,

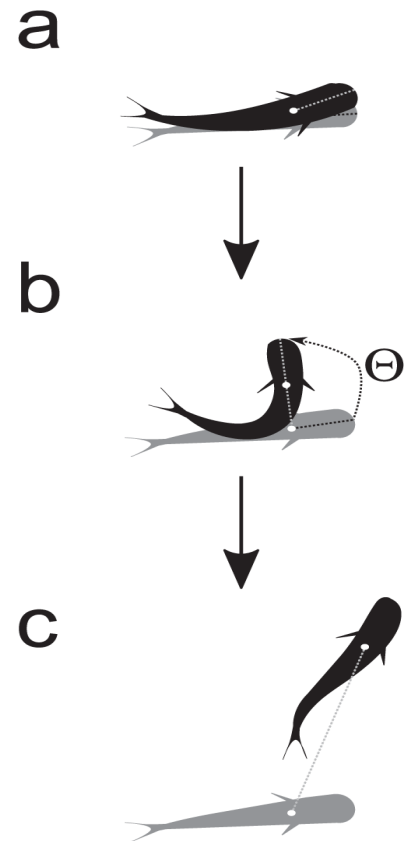


Figure 1. C-start response stages (Nadler et al., 2021). This diagram focuses on characteristics associated with the fast-start escape response (reaction timing and kinematic performance). The grey fish silhouette depicts the fish's location immediately before to stimulation in all panels a-c, and the black fish silhouette indicates the fish's position during each component of the fast-start escape reaction. A) Latency refers to the interval between the dangerous stimulus breaching the water's surface and the fish's first movement, with a lower latency indicating a faster reaction time. B) The average turning rate is calculated by dividing the angle attained during the initial unilateral bend of the reaction (i.e., Θ) by the time required to acquire that angle, with a higher turning rate suggesting more response agility through faster muscle contraction. C) Distance covered is the distance traveled in the first 42 milliseconds of the reaction, which is the average time for the study species used here (*Chromis viridis*) to perform two body bends (i.e., phases 1 and 2), and is indicative of the response's speed and acceleration.

2006). Temperature also alters the escape response due to its impact on fish physiology (Collar et al., 2020; Lyon et al., 2008). M-cell excitability increases with rising temperature, which can result in greater responsiveness as well as reduced accuracy in escape trajectory away from a simulated threat (Szabo et al., 2008). These changes can result in either wasted energy responding to benign stimuli or greater mortality if the escape trajectory directs the fish prey straight into a predator's mouth. Elevated CO₂ levels can also negatively impact on both prey escape (Allan et al., 2013; Näslund et al., 2015), by increasing risky behavior and reducing a fish's ability to recognize a threat (Cattano et al., 2019). These fish were observed to spend more time outside coral shelters and responding to food stimulus more often, making them increasingly vulnerable to predation events (Cattano et al., 2019). Increased turbidity particularly impacts visually mediated escape behavior. In juvenile Atlantic cod (*Gadus morhua*), reduced visual acuity due to higher turbidity resulted in lower escape success due to decreased responsiveness and poorly timed escapes (Meager et al., 2006). These results are likely due to visual impairment, giving the fish less time to react to a rapidly incoming predator and providing the fish inadequate information about the threat that results in decreased locomotor performance (Meager et al., 2006). A reduction in predator vigilance related to foraging can also alter the fast-start response, with longer reaction latencies during and immediately following foraging as well as reduced responsiveness following prey consumption (Bohórquez-Herrera et al., 2013). These results indicate that the fast-start response varies within an individual based on their perception of the threat and a multitude of external factors.

Many fishes partake in social (i.e., shoaling behavior) primarily to dilute their individual risk of predation and to share the costs associated with predator vigilance (Hall et al., 1986). One hypothesis, known as the 'many eyes hypothesis', states that through the vigilance of other group members, individuals can reduce their own investment in vigilance (Roberts, 1996). An individual's risk of predation depends on a predator's detection of the group, the attack rate of the predator, and the likelihood of the individual escaping the attack (Roberts, 1996). While prey in larger shoals are less at risk per capita than those in smaller shoals, these larger shoals are at higher risk of predator detection as they are more conspicuous (Krause and Godin, 1995). When a predator is detected, shoals collectively modify their response based on available sensory information, in a process known as threat sensitivity (Brown et al., 2006; Marras et al., 2012; Rieucou et al., 2014). The efficiency of information transfer about threats among members of a

shoal increases with shoal density due to greater internal organization (Rieucau et al., 2014). However, certain individuals in the shoal may play a more prominent role in the survival of the group as a whole, with certain individuals consistently leading the group's escape while others typically follow (Marras and Domenici, 2013). While larger group sizes increase the capacity for predator vigilance, there is a tradeoff between defensive benefits of a larger group size and greater competition for limited resources, such as food and habitat (Gil et al., 2017), which theoretically results in an optimal group size that balances these costs against potential benefits (Brown, 1982).

Many shoaling fishes use chemical cues to signal alarm to members of their group. Epidermal, damage-released chemical alarm cues (CAC) are released when the prey's skin is damaged by a predator, serving as a pre-warning to nearby fishes (Chivers and Smith, 1998; Wisenden and Millard, 2001). Chemical cues are advantageous in an aquatic medium due to the ease with which they are transmitted (Hara, 1975). Individuals warned by these signals may gain a survival benefit, as they are primed to execute a rapid escape response (Wisenden et al., 1999). These chemical cues may be especially important when visual senses are limited, such as in high-turbidity conditions or at night (Smith, 1992). These responses are species specific, suggesting that these chemical cues are highly specialized within taxa (McCormick and Allan, 2017a; McCormick and Lönnstedt, 2016).

To maximize the ability to communicate and coordinate with members of the group, social fishes may engage in a specialized form of shoaling behavior known as schooling (Figure 2), in which they execute a highly polarized alignment that allows for rapid communication related to movement via the lateral line system (Pitcher, 1986). When startled by a predator, this polarized alignment enhances the group's ability to mount a coordinated response away from the predator (Domenici and Batty, 1994; Domenici and Batty, 1997). The speed of the collective response is maximized by schooling with familiar conspecifics, which reinforces the ability of individuals in the school to develop their specialized leader and follower niches that enhance the ability to escape the predator (Chivers et al., 1995; Griffiths et al., 2004; Nadler et al., 2021).

Living and traveling in a group maximizes foraging opportunities and minimizes predation (Krause and Ruxton, 2002; Ward et al., 2011). Fish exist in social groups (i.e., shoals and schools) and vary their coordination (i.e., polarized alignment) and cohesion (i.e., distance to the nearest neighbor) depending on the context, decreasing their coordination and cohesion in

response to available food and increasing these traits during times of threat (Bode et al., 2010). Individuals must theoretically weigh the tradeoffs between dilution of predation risk and competition for resources when determining their optimal group size (Brown, 1982). However, limited empirical evidence is available to help us understand these processes.

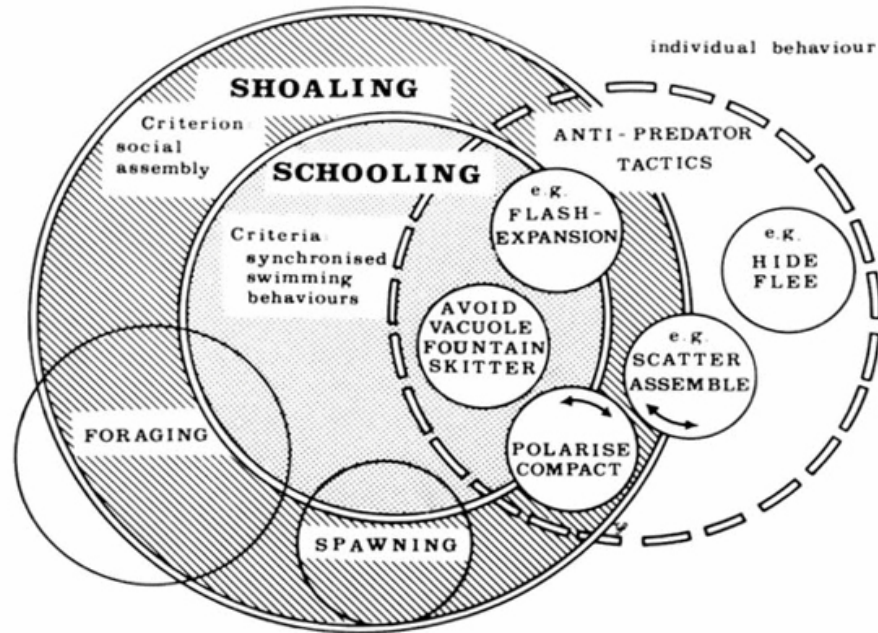


Figure 2. Shoaling versus schooling behavior (Pitcher, 1986). 'Shoals' are any social aggregations of three or more fish, while "schools" are a special type of fish shoal that swims in unison in a polarized alignment. Shoals and schools are primarily thought to socialize for the purpose of avoiding predators and finding food.

Coral reefs provide an essential habitat and nutrient structure to numerous fish species and in turn, reef fish play a crucial role in the community dynamics of coral reefs (Wilson et al., 2006). Social behavior, such as shoaling and schooling, are common strategies among coral reef fishes (Connell and Gillanders, 1997; Fishelson et al., 1974). Shoaling behavior is especially important in coral reef environments with high predation pressure (Hixon and Beets, 1993). Social coral reef fishes must adopt strategies to avoid predation in high predation coral reef environments. Some species are site-attached and rely on living coral structure for protection against predators (Jones et al., 2004) while others live higher up in the water column and use athletic abilities to escape from predators (Clifton, 1991; Wolf, 1987). Many site-specific species associate with certain coral species or morphologies at critical stages of their development

(Munday, 2004). The presence of different coral species influences the structure of fish communities present in that area (Holbrook et al., 2002). Smaller site-attached species, such as some damselfish, may prefer smaller school sizes since their growth rates decrease with group size (Booth, 1995; Booth, 2004). Alternatively, species that live higher in the water column and are less associated with the reef structure commonly aggregate in larger schools to maximize their foraging abilities; as larger group sizes allow these fishes increased group vigilance thus allowing individuals more time to feed since one member of the group may forage while others look for predators (Clifton, 1991; Wolf, 1987). Coral reef fishes must use a variety of strategies to succeed in their dynamic coral reef community.

Coral bleaching is the process of losing the zooxanthellae algae endosymbionts that the coral host depends on due to a variety of environmental stressors (Brown, 1997). Corals may survive the bleaching event by regaining zooxanthellae or bleaching events can lead to coral mortality (Nakamura et al., 2003). Mass bleaching events lead to habitat degradation when coral reefs are rapidly overtaken by turf algae (Hutchings, 1986; Nakamura et al., 2003). Habitat degradation is particularly impactful on smaller-bodied fishes that depend more on the living coral structure for defense (Wilson et al., 2010). Multiple laboratory and field experiments examine how habitat degradation that results from coral bleaching affects the anti-predator response in coral reef fishes. One experiment demonstrated that degradation severely impacts individual risk assessment and settlement choices in juvenile damselfish (Lönnerstedt et al., 2012; McCormick et al., 2010). Dead coral also alters the behavior of fishes, making them more risk oriented and less responsive to predator attacks (Lönnerstedt et al., 2014; McCormick and Allan, 2017a; McCormick and Lönnerstedt, 2016). Chemicals from degraded coral reef habitats may mask detection of CAC from conspecifics in some fishes, preventing its pre-warning of ambient risk (Lönnerstedt et al., 2012; McCormick and Lönnerstedt, 2016). These sensory effects may impact specialist species that rely on live coral more than generalist species that are able to thrive in a wide variety of environmental conditions or can make use of a variety of different resources (McCormick and Allan, 2017a). To date, experiments studying habitat degradation and CAC disruption impacts have focused on responses in individuals, leaving a knowledge gap about its impact on the fast-start response in schooling fish.

For many schooling coral reef fishes, live coral is important for foraging, finding suitable habitat, developing risk assessment, and avoiding predation (Holyoak and Heath, 2016).

Evidence suggests that the presence of the sensory cues from healthy coral enhances their antipredator behavior. However, detection of conspecific CAC can be altered by the presence of degraded coral, such that the cue is either inappropriately identified or not recognized at all (Lönnstedt et al., 2012). Hence, the loss of live coral is likely to negatively impact escape behavior in coral reef fishes. While previous work has provided evidence for the detrimental effect of coral degradation on the antipredator behavior of solitary fishes, there is a knowledge gap in the literature on how this behavior is altered in fish schools following habitat degradation. As projected future climate change is likely to have devastating impacts the health of sensitive coral reef ecosystems (Hughes et al., 2007), studies are needed to understand how fitness enhancing processes are impacted by these changes in species that rely on the coral reef structure to survive.

In my first data chapter, I used video-recordings of behavioral studies in the tropical damselfish species *Chromis viridis* to compare the fast-start performance of fish schools composed of four, eight, and 16 fish. I hypothesized that schools of fish with a smaller number of individuals will exhibit increased school cohesion and coordination due to a perceived higher threat level, as well as faster a faster latency time due to less distraction from a larger group. However, larger group sizes will exhibit a faster average turning rate and distance covered, due to greater socially transmitted information from school-mates.

In my second data chapter, I again used video-recordings of the species *C. viridis* to assess differences in fast-start responses (using the individual and school traits defined above) among the following treatments: 1) Healthy coral + no CAC; 2) Healthy coral + CAC; 3) Degraded coral + no CAC; and 4) Degraded coral + CAC. I hypothesized that schools of fish exposed to cues of degraded coral will exhibit slower kinematic performance as well as reduced school cohesion and coordination following the pre-warning of a CAC than groups exposed to cues of healthy coral.

Chapters one and two were the first studies to examine in combination how group size, habitat quality, and chemical cues affect fast-start performance in schooling fish. In fish schools, individuals depend on social cues to survive predator attacks. While many studies have investigated fast-start performance in solitary fishes, this study will greatly increase our understanding of the factors that modulate escape behavior for animals that live in a social context.

Chapter 1: Effect of group size on the fast-start response in schools of *Chromis viridis*

Materials and Methods

Experimental work was conducted prior to my MS thesis in November to December 2014. The primary focus of my MS thesis was the analysis of this video dataset. The following research was performed with approval from the James Cook University Animal Ethics Committee (approved protocol number A2103), the Great Barrier Reef Marine Park Authority (Permit G13/25909.1), and Queensland Government General Fisheries (Permit 170251).

a. Study species, collection, and husbandry

The tropical damselfish species *Chromis viridis* (n=336 fish) was used in this experiment at the Lizard Island Research Station (LIRS) in the northern Great Barrier Reef, Australia (14°40' 08"S; 145°27'34"E). Using monofilament barrier netting, schools of *C. viridis* were captured from reefs in the lagoon close to LIRS. After collections, schools were maintained in a flow-through aquarium system in groups of four, eight, and 16 individuals each (n=36 schools; n=12 per treatment). Due to the possibility that differences in body size within and among schools could affect performance at both the individual and school level, body size variation in terms of standard length was minimized both within schools (0.5 cm range from smallest to largest individual in a group) and among schools (mean standard error: 3.32 ± 0.01 cm; range: 2.86-3.70 cm) (Morley and Buckel, 2014). Fish were fed freshly hatched *Artemia* spp. and INVE Aquaculture pellets twice daily ad libitum.

b. Escape response experimental procedure: School size and fast-start performance

Experiments were conducted in a laminar flow swim chamber that replicated the natural flow of a coral reef (working section: 50 cm long by 40 cm wide by 9 cm high) (Johansen, 2014; Nadler et al., 2018; Nadler et al., 2021). Between each trial, the swim chamber was drained and refilled.

Using a standardized and reproducible threat protocol approach, escape responses were induced (Nadler et al., 2021; Terzibasi et al., 2008). A tapered test tube covered with black

electrical tape (measuring 2.5 cm diameter \times 12 cm length, 37.0 g), served as the stimulus and was kept 137 cm above the arena by an electromagnet. The stimulus was discharged through a white PVC pipe (to prevent visual detection of the stimulus prior to reaching the water surface) once >50% of the school had gathered in the center of the arena (i.e., more than two body lengths from any arena wall). A piece of fishing line kept this stimulus from making contact with the actual experimental arena. Ripples in the water's surface were minimized by the tapered shape of the stimulus and the fishing line. A high-speed video camera was used to film the fast-start responses of individuals and school swimming behavior using a mirror that was angled 45° beneath the swim chamber (240 fps; Casio Exilim HS EX-ZR1000).

c. Behavioral analysis

Individual fast-start escape performance was evaluated using reaction timing and kinematics (Figure 1), including latency (the interval between the aerial mechanical stimulus first breaking the water's surface and the fish's initial head movement), average turning rate (AVT, the maximum turning angle, Θ , achieved by the fish during stage 1 divided by the time it took to achieve that angle, which serves as a proxy for the response's agility through speed of muscle contraction), and distance covered (DC; distance moved in the first 42 ms of the reaction, which is the average time for this species to achieve stages 1 and 2; used as a proxy for swimming speed and acceleration). Since all of the features mentioned above are influenced by the stimulus distance, the distance between the center of mass of each fish and the stimulus was also measured and included as a covariate in all analyses (Domenici and Hale, 2019).

Throughout the response, the school's cohesion and coordination were measured through school density (mean two-dimensional area per individual as a measure of horizontal spread of the school, calculated by dividing the school area by the number of fish in the group), nearest neighbor distance (NND; the distance between each fish's center of mass and their most proximal neighbor's center of mass in the school), and alignment. Alignment is the angle made by each individual in the group with respect to the water's flow (0°). Using the Oriana 4 program, circular statistics were used to find the mean (i.e., the circular vector) once all school members' angles had been determined. The length of the mean circular vector, r , which ranges from 0 (random angles) to 1 (all angles coordinated), was used to determine variation in alignment in the school as a measure of school coordination (Bachelet, 1981). These characteristics were

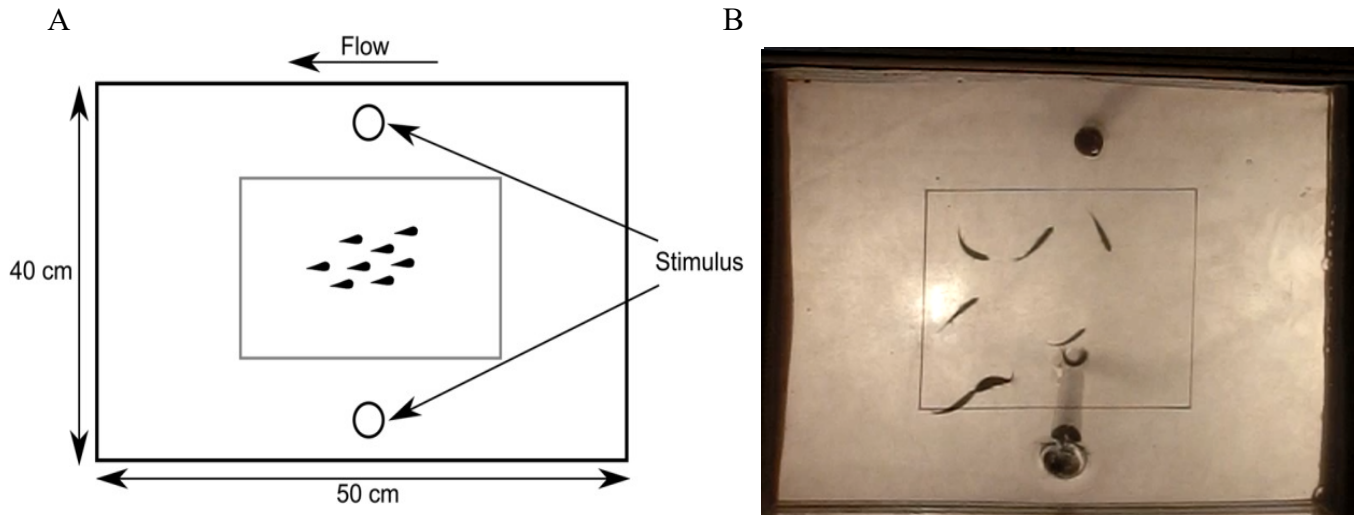


Figure 3. Laminar flow swim chamber (Nadler et al., 2018), including (A) a diagram of the device and (B) screenshot of the school's response following the stimulus. This custom-made laminar flow swim chamber (50 cm length×40 cm width×9 cm height) was used for all trials, which mimicked the conditions on a the fish's home reef on a calm weather day with a slow uniform flow of approximately 1 body length s^{-1} (3.2 cm s^{-1} (Johansen, 2014).

examined at intervals following the stimulus, including 0 ms (representing the school's cohesiveness and coordination right before the stimulus), 30 ms (representing the typical time for this species to complete stage 1), and 100 ms (the average time for individuals to complete both stages 1 and 2).

The videos were examined frame by frame using the application Potplayer (v. 1.7.21566) to find crucial points in the individual's and school's response to the stimulus. Screenshots of these timepoints were collected and analyzed in ImageJ (v. 1.53n 7), including the time of stimulus (the frame once the stimulus initially breaks the surface of the water), reactivity (yes or no), latency (time from the stimulus initially breaking the surface of the water to the fish's first movement), school density (measured in number of fish per cm^2), NND, stimulus distance, AVT, and DC. Due to the limits that proximity to wall of the experimental arena can have on kinematic performance, the kinematic attributes (AVT and DC) were only assessed if the fish was at least 3 cm away from any wall of the experimental arena.

d. Statistical analyses

R Programming Language v. 1.3.1093 was used for all statistical analyses (R Development Core Team, 2022). Non-responders ($n=3$; those fish that did not respond within two seconds of

the stimulus) were assigned the maximum measured latency in this study (1003.8 ms). The fish that were <3cm from the wall were not included in analyses of AVT and DC. The differences among treatment groups were evaluated using linear mixed-effects models (LMM) in the "lme4" package, with the explanatory variables (Group size and Time) as fixed effects and Video as a random effect. Group size (4,8, and 16) and time post-stimulus (0, 30, 100 ms) were fixed variables in analyses of school traits (NND, school density, alignment), while video identifier was a random effect (such that each datapoint was nested within the video from which it originated to account for the repeated measures design). Group size was analyzed as a fixed effect, stimulus distance was analyzed as a covariate, and video identifier was analyzed as a random effect so that each individual was nested within its school of origin.

Visual inspection of the quantile-quantile plots and residuals plots, as well as Shapiro-Wilk and Bartlett tests, were used to verify that the assumptions of normality and homogeneity of variance were met. To meet these assumptions, density, NND, latency, and DC were boxcox transformed using the package "car." Best-fit models were identified using the AIC model selection.

Results

a. Individual fast-start escape performance

All measures of performance were maximized at the lowest group size, including those related to reaction timing and kinematics. Latency (Figure 4A) in groups of 4 was 39% lower than groups of 8 and 47% lower than groups of 16, indicating a faster reaction time with smaller group size ($F_{1,34} = 5.03$, $p = 0.03$). A 7.4% higher AVT (Figure 4B) was found in groups of 4 compared to groups of 8 and a 25% higher AVT in groups of 4 compared to groups of 16 as well ($F_{1,34} = 7.50$, $p = 0.01$). This faster reaction timing and AVT also resulted in a higher DC ($F_{1,33} = 6.71$, $p = 0.01$; Figure 4C), with fish in the smallest groups traveling 30% further in the first 42 ms of their response than the largest group size.

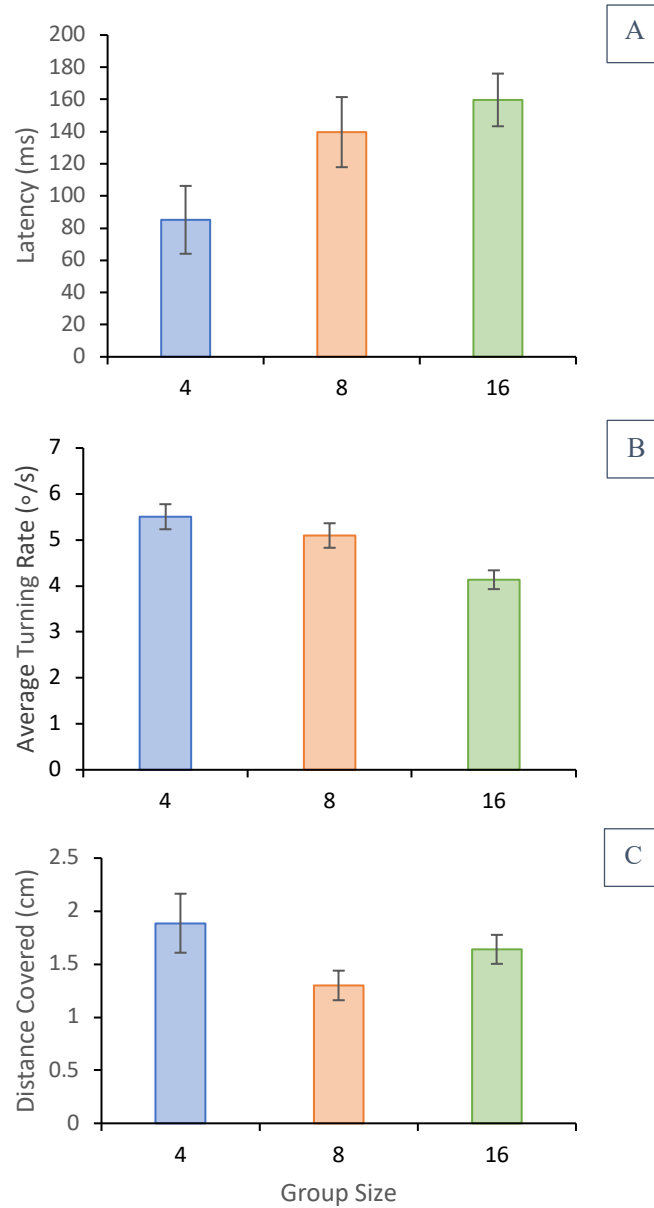


Figure 4. The effect of group size (four, eight, and 16 individuals) on the fast-start escape response of schools of *Chromis viridis*, including (A) latency, (B) average turning rate, and (C) distance covered. Bars represent mean \pm s.e.

b. School traits

All school traits changed significantly through time after the stimulus, including alignment ($F_{1,71} = 10.80$, $p = 0.002$; Figure 5A), density ($F_{1,71} = 10.36$, $p = 0.0002$; Figure 5B), and NND ($F_{1,34} = 5.00$, $p = 0.007$; Figure 5C). Both density ($F_{1,34} = 29.21$, $p < 0.0001$) and NND ($F_{1,33} = 20.78$, $p < 0.0001$) also changed significantly with group size, with density (as fish took up more two-dimensional area in larger groups) and NND decreasing (indicating fish were closer to their

nearest neighbors at larger group sizes). Alignment showed a similar but non-statistically significant trend ($F_{1,34} = 2.91$, $p = 0.09$), in which alignment decreased with increasing group size.

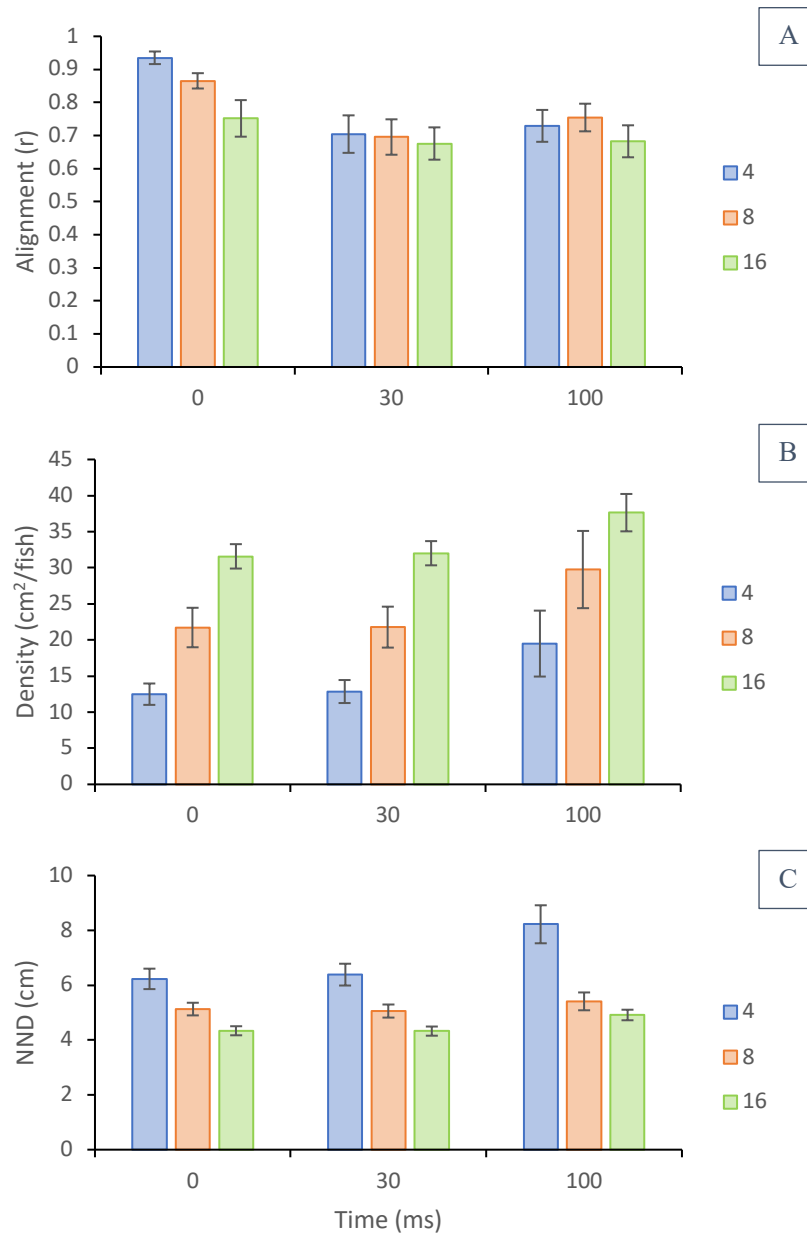


Figure 5. The effect of group size (four, eight, and 16 individuals) on the cohesion and coordination of schools of *Chromis viridis* following a simulated predator attack, including (A) alignment (as measurement through length of mean circular vector, r), (B) school density (cm²/fish), (C) and nearest neighbor distance (cm). Bars represent the mean \pm s.e.

Chapter 2: Role of habitat degradation and chemical alarm cues on the escape behavior of a schooling coral reef fish

Materials and Methods

Experimental work was conducted prior to my MS thesis in December 2017. The primary focus of my MS thesis was the analysis of this video dataset. The live-animal component of this research project was conducted following guidelines and regulations from the James Cook University Animal Ethics Committee (approved protocol number A2408), the Great Barrier Reef Marine Park Authority (Permit G13/5909.1), and Queensland Government General Fisheries (Permit 170251).

a. Study species, collection, and husbandry

This experiment was conducted at the Lizard Island Research Station (LIRS) in the northern Great Barrier Reef, Australia (14°40' 08"S; 145°27'34"E) using the gregarious tropical damselfish species *C. viridis* (n=176 fish). Schools of *C. viridis* were collected from reefs in the lagoon adjacent to LIRS using a monofilament barrier net. Once collected, schools were maintained in groups composed of eight individuals (n=22 schools) in a flow-through aquaria system at a density of 1 fish per 2.5 L (20 L aquaria). Body size variation in terms of standard length was minimized within schools (<0.5 cm range from smallest to largest individual in a group) and among schools (mean \pm standard error: 3.7 ± 0.02 cm; range: 3.0-4.1 cm), as variation in body size within and among schools could alter individual and school-level performance (Morley and Buckel, 2014). Schools were randomly assigned to either the degraded or the healthy coral cue treatment (n=11 schools per treatment). Each 30 L header sump contained three pieces of *Pocillopora* spp. coral (either healthy coral or coral rubble) with a diameter of ~15 cm. These sumps had continuous seawater flow, which fed into the fish holding tanks. Fish were held in this treatment for a minimum of three days prior to beginning experimentation and fed to satiation twice daily with INVE Aquaculture pellets and newly hatched *Artemia* spp.

b. Escape response experimental procedure: Coral health versus chemical alarm cue

Experimental trials were completed in a laminar flow swim chamber (working section: 50 cm length \times 40 cm width \times 9 cm height; Figure 3), which mimicked the natural flow of a coral reef on a calm weather day (Johansen, 2014; Nadler et al., 2018; Nadler et al., 2021). The swim chamber was filled prior to each trial using a 500 L sump containing 10 pieces of coral (either healthy coral or coral rubble) with a diameter of \sim 15 cm. This sump was filled at least three hours prior to each experimental trial, after which it was maintained as a closed system with aeration to allow the coral cue to permeate. In both the fish holding and experimental sumps, healthy coral was changed out every 2-4 days to ensure that it remained healthy, while degraded coral rubble was changed out weekly. The swim chamber was drained and refilled with water from the respective coral health treatment between each trial.

Experimental schools of fish were acclimated to the swim chamber for four hours. Following this acclimation period, all schools were exposed to one of two cues prior to experiencing a simulated predator threat: 1) a sham seawater treatment (SW), or 2) a chemical alarm cue (CAC) treatment. The CAC was made from two conspecific fish (*C. viridis*) per CAC exposure. Each fish was given 5 cuts through the skin to release CAC on each side of the body (thus 10 cuts per fish, 20 cuts total) using a standard scalpel blade. These cuts were washed with 50mL of seawater to saturate the CAC in solution. Within 10 mins of preparation, this CAC was injected with a syringe into the experimental arena, and the tubing was flushed with 50 mL of seawater to flush the tubing. For the control seawater trials (SW), 50 mL of seawater was injected into the experimental aquaria, followed by an additional 50 mL of seawater to flush the tubing.

Following this cue, escape responses were induced using a standard and repeatable threat protocol procedure (Domenici et al., 2008; Nadler et al., 2021). This stimulus was composed of a tapered test tube wrapped in black electrical tape (2.5 cm diameter \times 12 cm length, 37.0 g) that was maintained 137 cm above the arena using an electromagnet during the acclimation period and cue administration. Once $>50\%$ of the school was in the center of the arena (i.e., > 2 body lengths from any wall of the arena), the stimulus was released through a white PVC pipe (to prevent visual detection of the cue prior to reaching the water surface). The object's tapered shape helped to minimize ripples in the water's surface after it contacted the water, and a piece of fishing line prevented this stimulus from contacting the experimental arena itself. Using a mirror placed at a 45° beneath the swim chamber, individual fast-start responses and school

swimming behavior was recorded with a high-speed video camera (240 fps; Casio Exilim HS EX-ZR1000). Each school was tested twice, once with the seawater sham and once with the chemical alarm cue treatment. The order of these treatments was randomized among schools.

c. Behavioral analyses

Individual fast-start escape performance was assessed through reaction timing and kinematics, including latency, AVT, and DC (using the same definitions as described in chapter 1; Figure 1). The distance from each fish's center of mass to the stimulus was also measured (i.e., stimulus distance) and was included as a covariate in all analyses, as all traits listed above are affected by the stimulus distance (Domenici and Hale, 2019). School traits are characterized by overall cohesion and organization, which includes school density, NND, and alignment (using the same definitions provided in chapter 1). These traits were analyzed at 0, 30, and 100 ms after the stimulus.

Videos were analyzed frame-by-frame using the program Potplayer (v. 1.7.21566) and screenshots of these timepoints were analyzed using ImageJ (v. 1.53n 7), including stimulus time, fish reactivity, latency, school density NND, stimulus distance, AVT, and DC (as defined in chapter 1). Note that the kinematic traits (AVT and DC) were only measured if the fish was at least 3 cm (~1 body length) away from any wall of the experimental arena, due to the constraints that the wall can have on kinematic performance. The raw data was blinded with coded video names to prevent any unconscious bias by the observer (Tuytens et al., 2014).

d. Statistical analyses

All statistical analysis was performed in R Programming Language v. 1.3.1093 (R Development Core Team, 2022). Non-responders (n=4) were assigned the highest measured latency (961.8 ms). Those fish < 3 cm from the wall were not used in the analyses of AVT and DC. In one school, one fish jumped out of the testing arena mid-experiment and thus was removed from data analysis. The differences between treatment groups were assessed using the "lme4" package's linear mixed-effects models (LMM), with the explanatory variables (Health, Cue, and Time) as fixed effects and School as a random effect. Analyses of school traits (NND, school density, alignment) included coral health (healthy, degraded), cue (seawater, chemical alarm cue), and time post-stimulus (0, 30, 100 ms) as fixed effects and school identifier as

random effect (such that each datapoint was nested within the school from which it originated to account for the repeated measures design). Analyses of individual fast-start performance included coral health and cue as fixed effects, stimulus distance as a covariate, and school identifier as a random effect such that each individual was nested within its school of origin. The assumptions of normality and homogeneity of variance were checked qualitatively using visual inspection of the quantile-quantile and residuals plots and quantitatively through Shapiro-Wilk and Bartlett tests. Alignment, NND, and latency were boxcox transformed using package “car” to meet these assumptions. Best fit models were selected using AIC model selection.

Results

a. Individual fast-start escape performance

There was no effect of coral health or cue on either latency (Figure 6A; $p > 0.05$) or DC (Figure 6B; $p > 0.05$). However, for AVT, while coral health had no effect, CAC treatment prior to the stimulus led to a 14.43% higher AVT when compared to sham treatment with SW (Figure 6; $F_{1,286} = 14.616$, $p = 0.0002$).

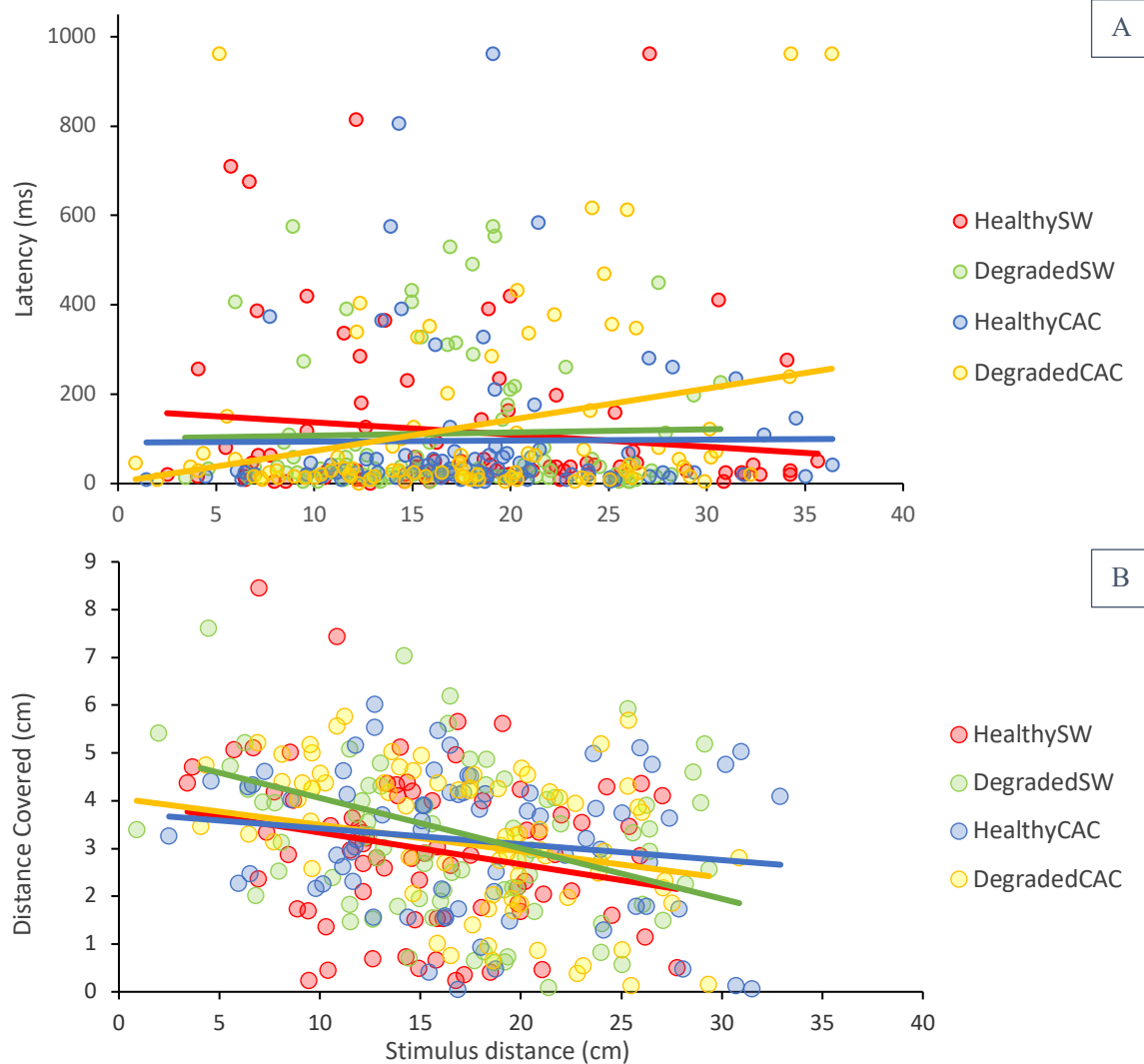


Figure 6. Individual latency (A) and distance covered (B) in schools of *Chromis viridis* in different coral health (healthy versus degraded) and cue (seawater sham – SW versus chemical alarm cue – CAC) treatments. According to linear mixed-effects model analyses, there was no significant link between coral health or cue with either of these variables.

b. School traits

All fish regardless of coral health and cue treatments exhibited similar trends through time, becoming less coordinated and cohesive following the stimulus. However, schools from the degraded coral treatment that were exposed to CAC were less coordinated before stimulus than other treatments and had the lowest coordination at 30ms compared to others (Figure 7). Time had a significant effect on both density ($F_{1,101}=25.7306$, $p < 0.001$, Figure 8A) and alignment ($F_{1,101} = 9.34$, $p = 0.003$, Figure 8B), with both decreasing after the stimulus (from 100ms

for density and 30ms for alignment). Alignment also had a significant three-way interaction among time, health, and cue ($F_{2, 101} = 3.63$, $p = 0.030$), as CAC drove lower alignment at 0 ms in both healthy and degraded reef and the degraded reef schools recovered to pre-stimulus alignment by 100ms under CAC conditions (Figure 8B). While NND did not change through time, it had a non-statistically significant trend ($F_{2,1026} = 2.60$, $p = 0.08$) for an interaction between coral health and chemical alarm cue (Figure 9).

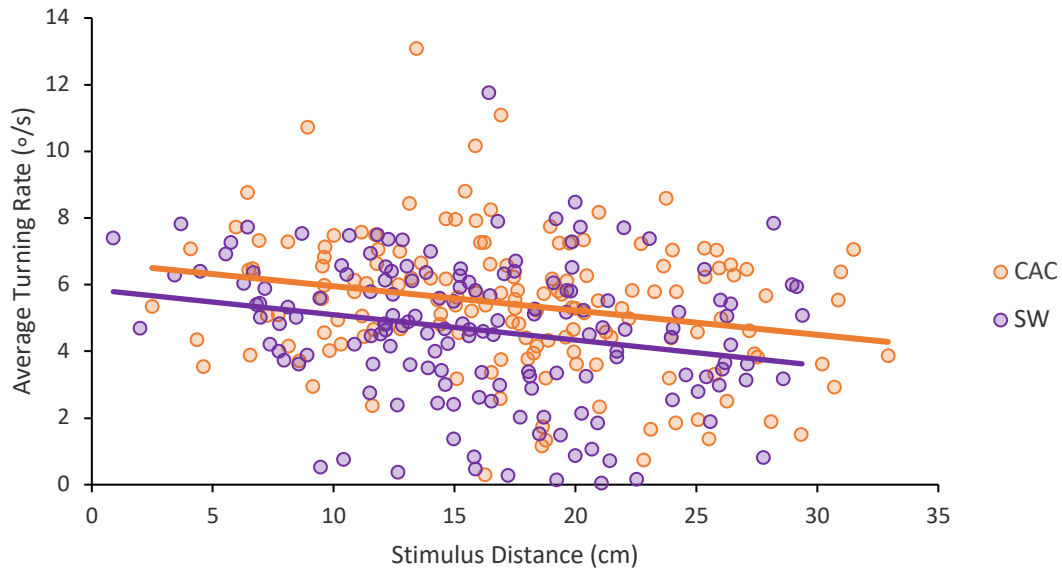


Figure 7. Average turning rate (AVT) in schools of *Chromis viridis* in different cue (seawater sham– SW versus chemical alarm cue– CAC) treatments. Linear mixed-effects model analysis indicates that CAC generates a significantly higher AVT than a seawater sham ($F_{1,286} = 14.616$, $p=0.0002$).

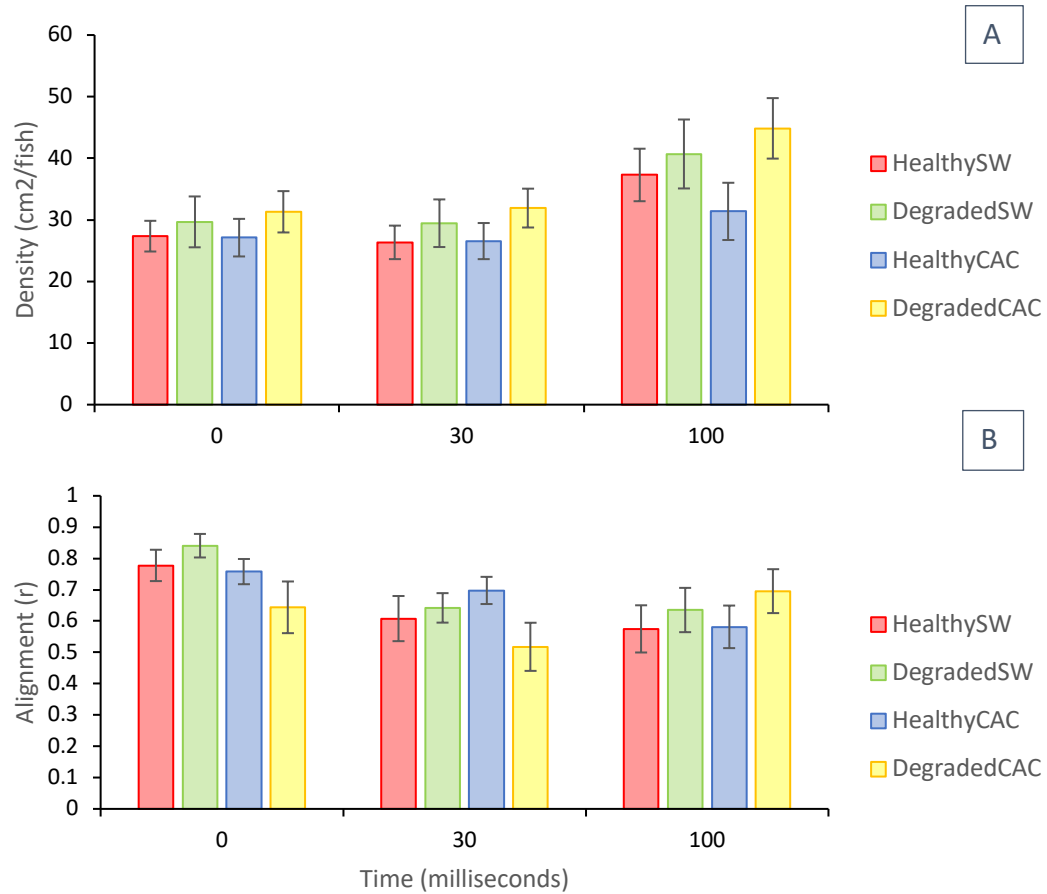


Figure 8. School density (A) and alignment (B) in schools of *Chromis viridis* in different coral health (healthy versus degraded) and cue (seawater sham – SW versus chemical alarm cue – CAC) treatments at 0, 30, and 100 ms following a simulated predator attack. Bars represent mean \pm s.e.

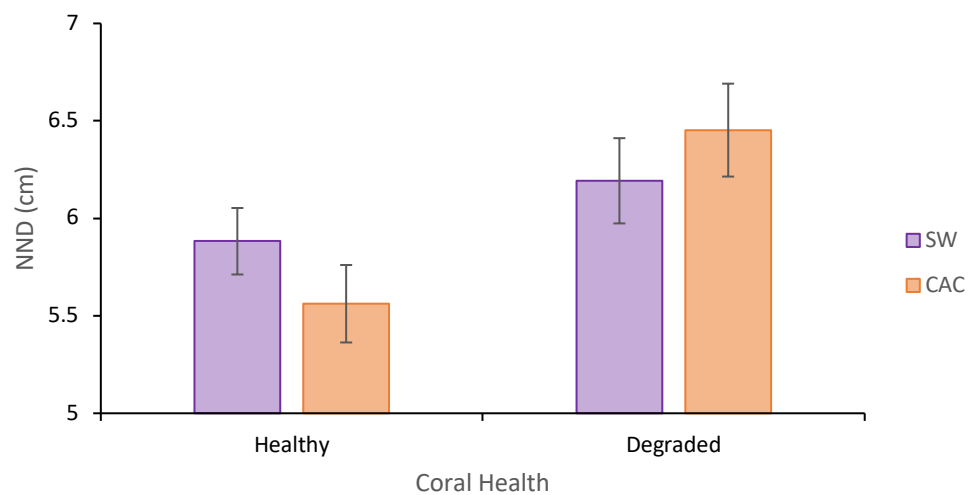


Figure 9. Nearest neighbor distance (NND) in schools of *Chromis viridis* in different cue (seawater sham – SW versus chemical alarm cue – CAC) treatments. Bars represent the mean \pm s.e.

Discussion

The fast-start response varies within an individual based on their perception of the threat and a multitude of factors. In a social group, the combination of pairwise interactions among individuals dictates the collective behavior that emerges (Jolles et al., 2020). When the sensory abilities of all individuals are combined, the likelihood that members in a school will detect a threat increases (Krebs, 1991; Lazarus, 1979). Fish create schools that vary in cohesion, coordination, and group size depending on cues such as those related to food or threats (Hoare et al., 2004).

The success of a school ultimately depends on individual actions and social communication. In my first chapter, I found that the reaction timing and kinematics of fast-start escape responses improved in smaller groups versus larger groups, potentially indicating that fish in small groups rely more on individual performance than larger groups that gain protection through dilution of their individual risk of predation (Foster and Treherne, 1981; Treherne and Foster, 1980). My second chapter demonstrated that despite shifting coral health, *C. viridis* maintain social communication, and that stronger escape responses may be elicited through exposure to CAC. The CAC may act as a dependable warning sign of a hazard nearby, priming the escape reaction (McCormick and Allan, 2017b). In some species, degraded coral can mask fishes' ability to detect CAC (Chivers et al., 2019), but *C. viridis* are robust to that sensory disruption. Taken together, these studies provide greater insight into the plasticity of schooling behavior, and how their response to predators shifts under different contexts.

Group size and the fast-start response in schooling fish

The underlying principle of the "many eyes" concept is information transmission, which is the ability of school members to perceive danger without requiring each individual to independently confirm the level of the hazard (Bertram, 1978; Lazarus, 1979; Magurran, 1990). Fish adjust their own behavior based on information gained from those that have observed a predator (Magurran and Higham, 1988). Larger groups benefit from knowledge sharing, resulting in higher 'collective intelligence', but may confront additional coordination issues (Papageorgiou and Farine, 2020). The oddity effect suggests that coordination is crucial for evading predators, since moving together as a single unit is an effective form of camouflage

(Pitcher and Magurran, 1983; Smith and Warburton, 1992). My first chapter found that when the mechanical stimulus reached the water (prior to the moment most school members had reacted), coordination in the form of alignment decreased with increasing school size, potentially because fish in smaller groups may be more reliant on their own sensory abilities while larger groups can benefit from a higher 'collective intelligence'.

Fish in larger groups are typically bolder in the presence of predator exploration (Pitcher and Magurran). The group's greater collective vigilance may allow for individuals to concentrate on other tasks like foraging and exploration (Pitcher and Magurran, 1983; Smith and Warburton, 1992), reducing the need for individual investment in vigilance (Roberts, 1996). Here, all measures of performance were maximized at the lowest group size. The fish reacted faster and moved further in smaller group sizes. In this case, the fish in larger groups may have been distracted by other tasks that delayed their reaction timing (Bohórquez-Herrera et al., 2013). Further, fish in larger schools may need to reduce their speed to prevent collisions with their school-mates (Katz et al., 2011). The longer latency, shorter distance covered responses seen in larger schools may be an attempt to coordinate with each other in the limited space allocated in the experimental. Despite the potential disadvantages of a slower reaction time, greater latencies may be essential in larger schools to prioritize movement coordination (Domenici and Batty, 1997).

Animal groupings are extremely plastic and are known to change depending on various external factors (Guayasamin et al., 2016). A school's inherent attraction and repulsion forces are required for maintaining the school's formation such that the distance between individuals is appropriate for sensory detection of neighbors' movements (Inada and Kawachi, 2002). Individuals will likely have a greater awareness of the behavior of closer neighbors than more distant school-mates as the strength of sensory cues reduces exponentially with distance (Inada and Kawachi, 2002). Thus, the nearest neighbor's behavior may exert the strongest external influence on an individual's response. The results of this study showed that each fish was found to take up more space in larger groups, but their closest neighbor is closer, correlated with a significantly lower NND and density in larger groups. Individuals may be joining smaller subgroups or pairs when in larger overall group sizes. As group size increases, temporary subgroups may increase the complexity of group form and internal organization (Hemelrijk and Hildenbrandt, 2012).

Modulating effects of habitat degradation and chemical alarm cue on the fast-start response of a gregarious coral reef fish

Individual risk assessment and settlement decisions in young damselfish may be adversely impacted by coral degradation (Holmes and McCormick, 2010; Lönnstedt et al., 2012). Dead coral can also modify fish behavior, making fish more risk averse and less vulnerable to predator attacks (Lönnstedt et al., 2014; McCormick and Allan, 2017a; McCormick and Lönnstedt, 2016). The present study found that there was no effect of coral health on fast-start performance. These results differ from previous work that used solitary fishes, which suggests that information sharing through redundant multi-sensory channels may generate resilience despite changing coral health (Lönnstedt et al., 2014; McCormick and Allan, 2017a; McCormick and Lönnstedt, 2016).

According to studies on risk assessment, prey should try to maximize their reaction to risk by using information from all sensory systems that may be relevant to the prospective threat (Ferrari et al., 2010). In the present study, average turning rate was 14.43% higher following a CAC than SW sham cue, which is in line with previous studies that found that individuals exposed to this threat cue displayed a stronger escape response (Ramasamy et al., 2015). The capacity to detect this pre-warning cue in degraded reef ecosystems varies by species, with a recent study showing that while one species (*Pomacentrus amboinensis*) could not detect CAC under habitat degradation, a closely related congener (*P. coelestis*) remained unaffected (McCormick and Allan, 2017b). Similarly, McCormick and Allan (2017a) discovered that when the Ambon damselfish *P. amboinensis* was exposed to CAC, its escape ability improved, but only in healthy coral water sources. The apparent priming effect of the warning odor was cancelled by water that had flowed through deteriorated coral. In my second chapter, I found that alignment was less coordinated following CAC when combined with degraded habitat. Degraded coral can affect the ability to perceive conspecific CAC, causing the cue to either be incorrectly detected or not recognized at all (Lönnstedt et al., 2012). Highly polarized alignment enables quick movement-related communication via the lateral line system (Pitcher, 1986). The less aligned a school is, the less communication is available. Here, the combination of degraded coral and CAC may reduce coordination and communication within the fish school. This research reveals the plasticity and variability in the escape responses.

Limitations of these studies

While laboratory studies are useful for controlling variation among treatment, natural conditions are rarely fully replicated in a laboratory setting, and therefore, the behavior of the study organisms is usually altered (Campbell et al., 2009). For the escape response, laboratory research is the most feasible option, as maintaining control within a behavioral experiment is one of the most critical aspects as to minimize the effect of external factors not being studied (Domenici and Hale, 2019). Field studies are crucial to validate results found in a lab and should be implemented in future studies to validate the functional consequences of behavioral changes on prey survival of predator attacks (McCormick et al., 2018). Here, the fish's response may also have been limited by the size of the experimental arena. Freely formed group sizes are highly context dependent, with fish establishing shoals of varying sizes in response to food or alarm cues (Hoare et al., 2004). Allowing fish in future studies to freely form various school sizes may further validate the results found in the present study.

Conclusions

This study highlights the plasticity of school structure and escape performance under predation in various simulated conditions, and the success of a school ultimately depends on the actions and communication made by individuals. While increasing group size often increases resource competition while decreasing predation risk and some foraging costs (Alexander, 1974), there is uncertainty about how shifting coral reef structural complexity with habitat degradation will impact intraspecific relationships in schooling fish (Gonzalez-Rivero et al., 2017). The results of these studies demonstrated that fish in larger groups reacted slower due to possible knowledge sharing. The lowest group sizes had the highest performance to coordinate movement among many individuals. In larger groups, fish were found to form smaller sub groupings with their neighbor. Habitat degradation was found to have no effect on fast-start escape response. The addition of a CAC elicited a stronger escape response, but in combination with degradation, it negated the previous finding. Projected future climate change is likely to have devastating impacts the health of sensitive coral reef ecosystems (Hughes et al., 2017; Hughes et al., 2018). Currently, there is uncertainty around how climate change will impact interspecific relationships.

Future studies should consider focusing on expanding findings related to climate change in the field. There are various studies of predator-prey interactions in laboratory settings. Although it is difficult to control for variables in the field, this data can be used to validate laboratory work. Studies should also continue to research the effect of stressors in combination. Escape response has been shown to be altered by several stressors, and these effects may be amplified when combined (Mager et al., 2018). To get a fuller knowledge of these relationships, additional study is required. To better comprehend these interactions, additional study is required. Overall, this is the first study to examine how group size, habitat quality, and chemical cues affect fast-start performance in schooling fish. The following study has greatly widened our understanding of the factors that modulate escape behavior for animals that live in a social context.

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