



Predation risk mediates cognitive constraints following physical exertion in schoolmaster snapper

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ABSTRACT

A large body of literature suggests that physically exhausted fish, including those that are released following fisheries interactions, experience behavioural and cognitive constraints and are at elevated risk of predation during homeostatic recovery. However, previous studies have focused on exhausted fish subsequently encountering predators, and not on fish that had been exposed to elevated predation risk prior to exhaustive exercise. Here, we exercised individual schoolmaster snapper (*Lutjanus apodus*) for 0, 1, or 4 min via hand chases following exposure to conspecific chemical alarm cues or seawater controls. The snapper were then introduced into one end of a rectangular arena supplied with mangrove prop roots as a refuge at the opposite end. Snapper exposed to the seawater control treatment demonstrated graded responses in mean times to move one body length and latency to enter the refuge, with unchased fish taking the least time and fish chased for 4 mins taking the longest. Amongst the snapper pre-exposed to alarm cues, the graded response did not occur and mean responses did not differ between chase treatments. Consistent with increased antipredator vigilance, alarm cue-exposed snapper were more likely to subsequently exit the refuge and to do so more times than fish exposed to seawater controls, independent of chase time. These observations suggest that perception of elevated predation risk may induce a conditional response offsetting the behavioural and cognitive constraints associated with physical exhaustion through an unknown physiological mechanism to prioritize immediate survival-oriented behaviours over recovery.

1. Introduction

Survival requires informed decisions about when and where to move to secure necessary resources whilst avoiding predators. Given the inherent complexity of resource heterogeneity, costs of movement, and an ever-changing landscape of fear [14, 18, 22, 27], behavioural decision making needs to be lucid to survive. Yet, at times, organisms may experience cognitive constraints that impair their ability to make optimal decisions. This topic has been reasonably well explored in fishes, where high intensity exercise to physiological exhaustion thresholds may lead to cognitive impairments [3, 5]. These cognitive impairments appear to occur independent of, or in parallel to, behavioural constraints stemming from impaired locomotor capacity.

Spanish flag snapper (*Lutjanus carponotatus*) exercised to exhaustion would approach coral refuges but took longer to enter even though doing so would require moving no more than one body length. By comparison, control fish or those exercised and held for a period to enable physiological recovery entered the refuge in seconds and remained within for the duration of recorded trials [5]. After swimming

the length of a behavioural arena, albeit more slowly than control or recovered fish, exhausted Spanish flag snapper were apparently unable to identify the refuge as a safe space [5]. A similar study using juvenile great barracuda (*Sphyrna barracuda*) conducted in an isolated mangrove swamp yielded similar findings of impaired refuging ability following physical exertion during simulated catch-and-release angling events [3]. Collectively, these results suggest that although fish exercised to exhaustion may have the physiological capacity to undertake a given behaviour, their ability to decide to do so may be constrained. Alternatively, exhaustion may alter the cost-benefit ratio associated with an otherwise adaptive behavioural response in low-risk contexts.

There is a growing literature base on the physiology of predator-prey interactions and how they are mediated by stress levels (particularly the glucocorticoid stress hormone axis: [17, 23, 24]), yet there remain few attempts to understand the ecological aspects of cognitive constraints and their mediators. Elevated predation risk has broad non-consumptive effects on the behaviours [8, 12, 29] and physiologies [1, 2, 5, 23, 24] of prey species, but how aspects of predation risk interact with cognitive constraints are unknown. For example, if a specific

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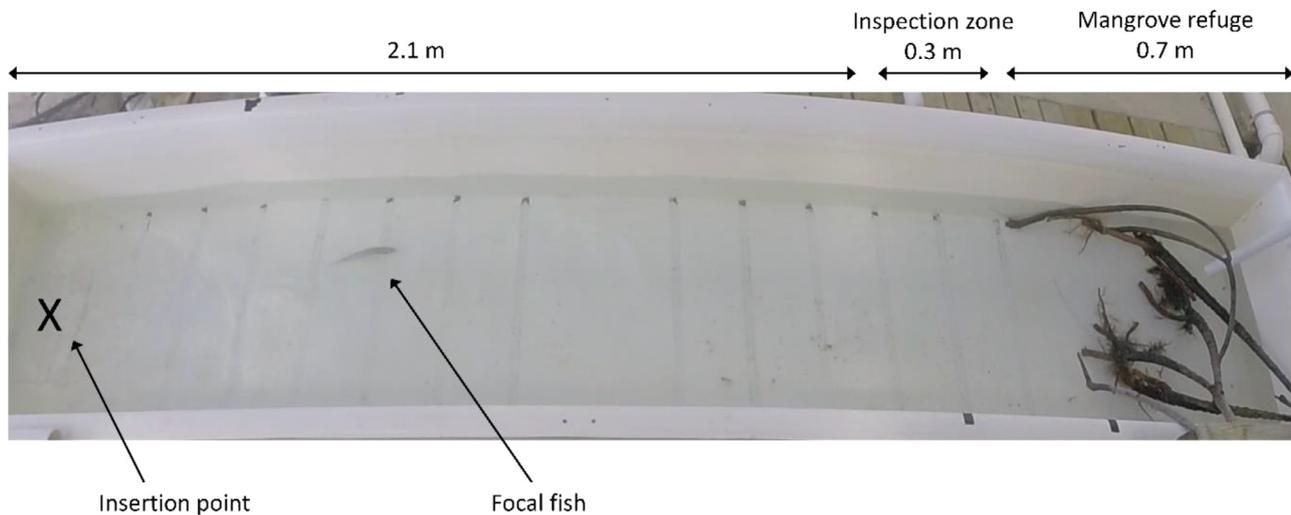


Fig. 1. Trial arena setup in a fiberglass raceway (3.1 m length \times 0.65 m width) filled with seawater to a depth of 15 cm.

predation threat is detected prior to experiencing exhaustive exercise, cognitive constraints may be less detrimental to survival if detection elicits context-appropriate decisions on risk mitigation.

Fish routinely engage in high intensity exercise as a result of interactions with anthropogenic infrastructure (e.g. dams, fishways) or activities (e.g. fisheries interactions: [4, 31, 33, 38]), and these encounters are presumably only going to become more common with human population growth and waterway development [26]. Moreover, predators are ubiquitous and predation risk has yet to be incorporated into the experimental design of existing studies on the effects of exhaustive exercise on recovery and survival [3, 5]. To address this lacuna, we exposed wild-caught juvenile schoolmaster snapper (*Lutjanus apodus*) to simulated predation risk in the form of damage-released chemical alarm cues [36, 39] or seawater controls prior to forced swimming sessions of varying durations. The snapper were then introduced into a novel arena supplied with a mangrove prop root refuge and their exploratory and refuging behaviours were recorded in standardized open-field behavioural assays to test the hypothesis that inducement of an alarm response via pre-exposure to risky cues would mediate cognitive constraints following physical exertion. Using schoolmaster snapper as a model species enabled us to contextualize our work relative to other studies on behavioural impairment [5] and the physiology of predation risk (e.g., [23, 24]) in this group of fishes.

2. Methods and materials

2.1. Fish collection and housing

We collected schoolmaster snapper ($N = 93$; standard length 6.4 – 17.6 cm; $11.9 \text{ cm} \pm 2.19 \text{ cm}$, mean \pm SD) using two identical cylindrical minnow traps (80 cm length \times 40 cm diameter) baited with commercially-obtained frozen mackerel at the mouth of Page Creek, Rock Sound, Eleuthera, The Bahamas, over the course of 2 h on the afternoon of 17 January 2017 during ebb tide. Captured snappers were transported to the wet lab facility at the nearby Cape Eleuthera Institute and held in a rectangular raceway tank (3.1 m length \times 0.65 m width \times 0.45 m depth) filled with seawater drawn from \sim 30 m offshore and supplied with red mangrove (*Rhizophora mangle*) prop roots below the water surface and branches above for cover.

2.2. Alarm cue preparation

Damage-released chemical alarm cues were extracted from two donor fish (standard length $11.9 \text{ cm} \pm 2.19 \text{ cm}$, mean \pm SD) euthanized via cervical dislocation. Skin filets were removed from lateral

surfaces, measured, mechanically homogenized, and diluted in filtered (25 μm) and UV-sterilized seawater to a final volume of 1.05 l at a concentration of $1 \text{ cm}^2 \text{ skin} \cdot \text{ml}^{-1}$. Alarm cues were frozen in 40 ml aliquots at $-20 \text{ }^\circ\text{C}$ until use.

2.3. Trial arena and experimental protocol

Individual fish were removed haphazardly from the holding tank via dipnet and placed into a seawater-filled rectangular chase arena (0.6 m length \times 0.3 m width, filled to a depth of 20 cm). The fish were allowed to acclimate for 5 min, at which time they were exposed to injections of chemical stimuli into the chase arena. Injections consisted of 20 ml of either chemical alarm cues or seawater as a control delivered through a 1.2 m length of standard aquarium airline tubing, followed immediately by 60 ml injections of seawater to flush the tubing and ensure delivery of the full stimulus volume to the arena. The fish were then subjected to one of three physical exercise treatments: simulated chases with a hand for 1 min, 4 min, or an unchased control, yielding a total of 6 treatment combinations. Chases consisted of hand movements in the water following the fish at uniform speeds, with tail pinches and upside-down turns of the fish used to force swimming past their initial quit points (as per [20]). Control (unchased) fish were left in the chase arena for 5 min post-stimulus injection; the 4 min chases were started at 1 min post-injection, and the 1 min chases were started at 4 min post-injection. Following the 10 min periods in the chase arena, fish were dip-netted directly into 3 l buckets filled with 750 ml of seawater, and then released into the trial arena.

The arena consisted of a raceway tank identical to the holding tank, filled with seawater to a depth of 15 cm. At one end of the tank, we placed several mangrove prop branches in an area 0.7 m in length to provide a familiar refuge. We designated 0.3 m sections immediately in front of the refuges as inspection zones. Fish were released at the opposite end of the arena, away from the refuges, centered 0.1 m from the wall (Fig. 1). Each open-field assay lasted 5 min, during which we used two digital stopwatches to record: (1) time (s) for the focal fish to move one body length; (2) time (s) spent in the inspection zone; (3) latency (s) to enter the refuge; (4) latency (s) to exit the refuge, if applicable; (5) time (s) spent out of the refuge; as well as (6) whether or not the fish left the refuge, and (7) the number of times the fish exited the refuge, if applicable. From these measures, we could calculate (8) the overall proportions of time spent in the refuge. Following each trial, test fish were measured and released into a nearby tidal mangrove pond and we observed no mortalities or injuries prior to release.

2.4. Statistical analyses

All trials in which the focal fish did not move at least one body length within the 5 min observation period ($N = 11$) were discarded from the final dataset used to compare the measures listed above; however, we retained these data to calculate the odds of these null results in relation to the treatment combinations. Two trials were extended past 5 min (309 s and 375 s, respectively), as the focal fish had both moved at least one body length before the cutoff and were moving slowly towards the refuge at the 5 min point. We repeated each discarded trial to achieve a total of $N = 78$ trials ($N = 13$ for each of the 6 treatment combinations).

All data were analyzed as generalized linear models. Continuous data that did not meet the assumptions of normality (Shapiro-Wilk test; $P > 0.05$) were rank-transformed [35] and analyzed against Gaussian distributions with F -tests; binary data (whether or not a fish moved at all, or whether or not a fish exited the refuge after having entered) were analyzed against the binomial distribution using Wald's χ^2 and subsequent odds ratio testing; and count data (number of times a fish exited the refuge) were analyzed against the Poisson distribution using a likelihood-ratio χ^2 test. In all generalized linear models, we included stimulus, chase time, and their interaction as fixed-effects factors, and fish size (standard length, cm) and water temperature ($^{\circ}\text{C}$) as linear covariates. Post-hoc comparisons were performed when any behavioural response varied significantly with one or more fixed factor using Nemenyi's test with χ^2 -correction for tied ranks for the transformed continuous data, and Tukey's HSD test for the binomial and count data. All tests were conducted using R version 3.4.1 [30] and the 'car' [13] and 'PMCMR' [28] packages. Figures were generated using 'gplots' [40].

3. Results

In general, fish chased for 1 min demonstrated some sluggishness but were still maintaining equilibrium and were actively swimming to avoid the experimenters' hands, while fish chased for 4 min were not maintaining equilibrium or actively avoiding the chase stimulus. Of the 11 trials in which the fish did not move at all in the trial arena, 7 occurred following 1 min chases (2 paired with alarm cue, 5 with seawater controls), 3 following 4 min chases (2 paired with alarm cue, 1 with seawater), and 1 following the double control treatment (seawater paired with no chase). Odds of failure to move > 1 body length associated with each treatment are listed in Table 1. No response measure was influenced by fish body size (all $P > 0.05$) or water temperature ($P > 0.05$), which ranged from 23° to 24°C during the experiment.

Times taken to move one body length after being placed in the trial arena varied significantly with chase time ($F_{2,70} = 14.25$, $P < 0.0001$), but not with chemical cue ($F_{1,70} = 0.3$, $P = 0.59$; Fig. 2a). The 4 min chases resulted in significantly longer times than the controls (Nemenyi's post hoc with corrections for tied ranks, $P < 0.0001$), but not the 1 min chases ($P = 0.075$). The 1 min chases also did not differ from the unchased controls in their times to move one body length ($P = 0.065$; Fig. 2b). Time spent in the inspection zone in front of the mangrove refuge varied significantly with chase time ($F_{2,70} = 4.45$, $P = 0.015$) but not with chemical cue ($F_{1,70} = 0.33$, $P = 0.57$; Fig. 2c). Snapper chased for 4 min spent significantly longer in the inspection zone than

Table 1

Odds of individual schoolmaster snapper (*Lutjanus apodus*) failing to move at least one body length during the 5 min trials. Odds of 1 indicate 50–50% chances of an event occurring.

Treatment combination			Alarm cues		
Seawater control			Unchased	1 min chase	4 min chase
Unchased	1 min chase	4 min chase			
0.077	0.38	0.077	0.000000086	0.15	0.15

those chased for 1 min ($P = 0.047$) but not the unchased controls ($P = 0.053$), while the 1 min chases did not differ from the controls ($P = 0.999$; Fig. 2d). Latency to enter the refuge area varied with chase time ($F_{2,70} = 14.25$, $P < 0.0001$) but not chemical cue ($F_{1,70} = 0.05$, $P = 0.83$; Fig. 2e), with 4 min chases resulting in significantly greater latencies than both the 1 min chases ($P = 0.0134$) and the unchased controls ($P < 0.0001$) while the 1 min chases did not differ from the controls ($P = 0.11$; Fig. 2f).

Proportion of time spent in the refuge varied significantly with chemical stimulus ($F_{1,70} = 5.49$, $P = 0.022$), chase time ($F_{2,70} = 3.99$, $P = 0.023$), and their interaction ($F_{2,70} = 3.2$, $P = 0.047$). Snapper exposed to the seawater control spent greater mean proportions of time refuging than those exposed to chemical alarm cues (Fig. 3a). For chase time, the sole pairwise significant difference was between 4 min and the unchased controls ($P = 0.036$), with longer chase times resulting in significantly lower proportions of time spent refuging. There were no differences between the 1 min chases and the controls ($P = 0.648$) or the 4 min chases ($P = 0.258$; Fig. 3b). Snapper exposed to alarm cues and chased for 1 min demonstrated greater proportions of time refuging than seawater-exposed control fish chased for 1 min, but this pattern was reversed following 4 min chases as the seawater-exposed fish in this treatment took longer to enter the refuge initially.

Whether or not a fish exited the refuge after having entered it was significantly influenced by chemical stimulus (Wald's $\chi^2_1 = 9.14$, $P = 0.0025$) but not chase time ($\chi^2_1 = 5.39$, $P = 0.068$), nor their interaction. Snapper exposed to chemical alarm cues were more likely to leave the refuge than those exposed to seawater controls (Fig. 4a), and within the alarm cue group, the proportion leaving the refuge decreased with an increase in chase time. No snapper exposed to seawater controls and chased for 4 mins left the refuge (Fig. 4a,b). Latency to exit the refuge (log-transformed) was also influenced by chemical stimulus ($F_{1,12} = 6.17$, $P = 0.029$), but not chase time ($F_{2,12} = 3.25$, $P = 0.075$), or their interaction. Snapper exposed to alarm cues took less time on average to exit the refuge than those exposed to seawater controls (Fig. 4b). The number of exits from the refuge was significantly influenced by both chemical stimulus (likelihood-ratio $\chi^2_1 = 36.59$, $P < 0.0001$) and chase time ($\chi^2_2 = 33.62$, $P < 0.0001$), but not their interaction. Snapper exposed to chemical alarm cues exited the refuge on average more times than those exposed to seawater controls, with the number of exits in the alarm cue group decreasing in proportion to chase time (Fig. 4c). Between the chase time treatments, 4 min chases resulted in significantly fewer exits from the refuge than the unchased controls ($P = 0.022$), and the number of exits decreased with increasing chase times (Fig. 4d). Odds of exiting the refuge for each treatment combination are listed in Table 2.

4. Discussion

Engaging in appropriate threat-sensitive behavioural responses to predation risk requires both physiological and cognitive capacities to do so. Schoolmaster snapper pre-exposed to seawater controls in this study demonstrated behaviours consistent with induced conditional constraints on threat responses. Following sessions of forced exercise we observed a graded response pattern where fish exposed to 1 min chase sessions had responses intermediate to the 4 min chases and the unchased control group. These behavioural constraints manifested in positive relationships between exercise time and times to move one body length and to enter the refuge, resulting in more-exercised fish spending progressively lower proportions of time refuging during behavioural assays similar to the impaired refuging behaviours previously reported in Spanish flag snapper [5]. Conversely, schoolmaster snapper pre-exposed to seawater controls and chased for 4 min never exited the refuge whereas some fish (~10–60%; Fig. 4a) in every other treatment group did, suggesting that exhaustively exercised snapper were allocating time and energy to physiological recovery over exploratory behaviours [41]. Pre-exposure to chemical alarm cues appeared to mediate the

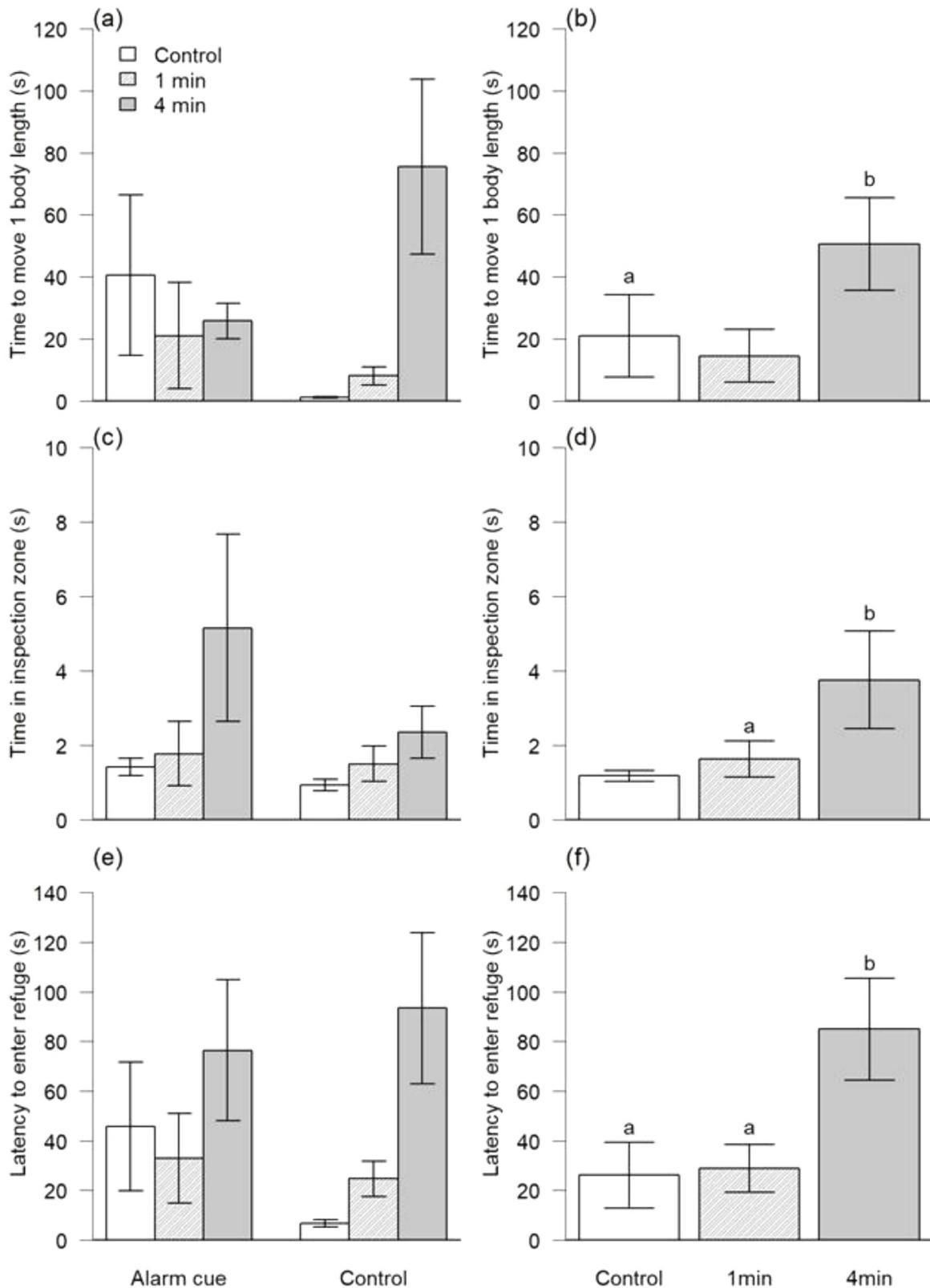


Fig. 2. Mean (\pm SE) (a,b) time to move one body length (s), (c,d) time spent in the inspection zone (s), and (e,f) latency to enter the refuge (s) by schoolmaster snapper (*Lutjanus apodus*) exposed to conspecific chemical alarm cues or seawater controls prior to unchased controls treatments, 1 min or 4 min forced chases (left column). Letters denote significant pairwise differences ($P < 0.05$) between chase times (right column) from Nemenyi's post hoc test.

constraints of physical exercise and allowed fish to maintain appropriate behaviours. Alarm cue-exposed snapper in all exercise treatments demonstrated similar, non-graded behaviours consistent with maintained cognitive functioning and behaviour.

Non-lethal stressors such as exhaustive exercise may contribute to subsequent indirect mortality via predation through behavioural impairments [4, 6, 9, 33] including slower swim speeds and locomotory impairment [7], decreased shoal cohesion [42], shorter flight initiation

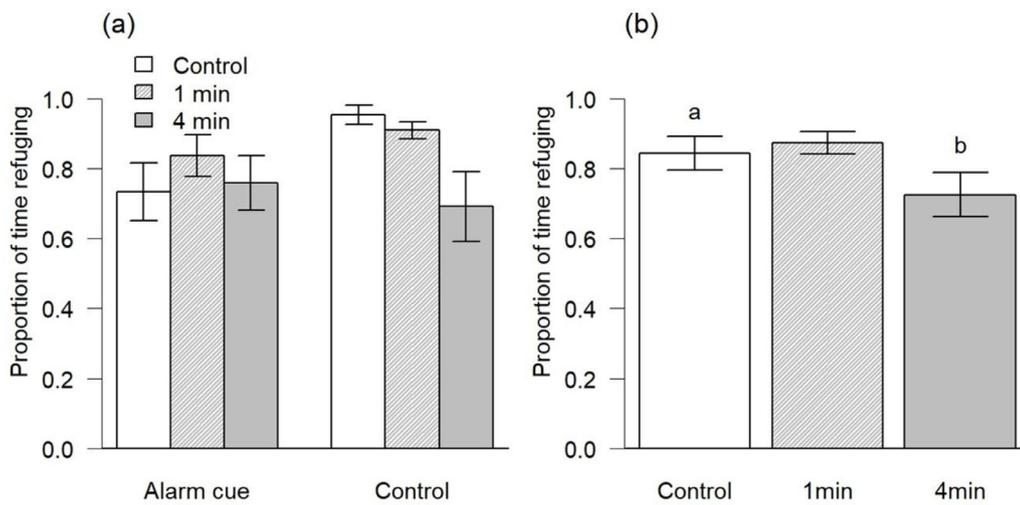


Fig. 3. Mean (\pm SE) proportions of time refuging by schoolmaster snapper (*Lutjanus apodus*) exposed to (a) conspecific chemical alarm cues or seawater controls prior to forced chase treatments, and (b) between grouped forced chase treatments. Letters denote significant pairwise differences ($P < 0.05$) between chase times from Nemenyi's post hoc test.

distances from potential predators [33], and decreased refuging [3, 5] during recovery. Notably, schoolmaster snapper pre-exposed to alarm cues in the present study did not demonstrate these graded responses to increasing levels of exhaustion, instead displaying behaviours consistent with unconstrained risk-averse antipredator strategies prioritizing survival over recovery. The relative importance of predation to post-release mortality of fish subject to catch-and-release angling and other fisheries-related interactions remains difficult to quantify [31], although bonefish (*Albula vulpes*) were found to be most vulnerable to predation within the first 30 mins following release [6] with the duration of vulnerability proportional to handling stress and level of

Table 2

Odds of individual schoolmaster snapper (*Lutjanus apodus*) exiting the refuge area after entering it for each of 6 treatment combinations. Odds of 1 indicate 50–50% chances of an event occurring.

Treatment combination			Alarm cues		
Seawater control			Unchased	1 min chase	4 min chase
Unchased	1 min chase	4 min chase			
0.182	0.083	0.0000000086	1.6	0.857	0.182

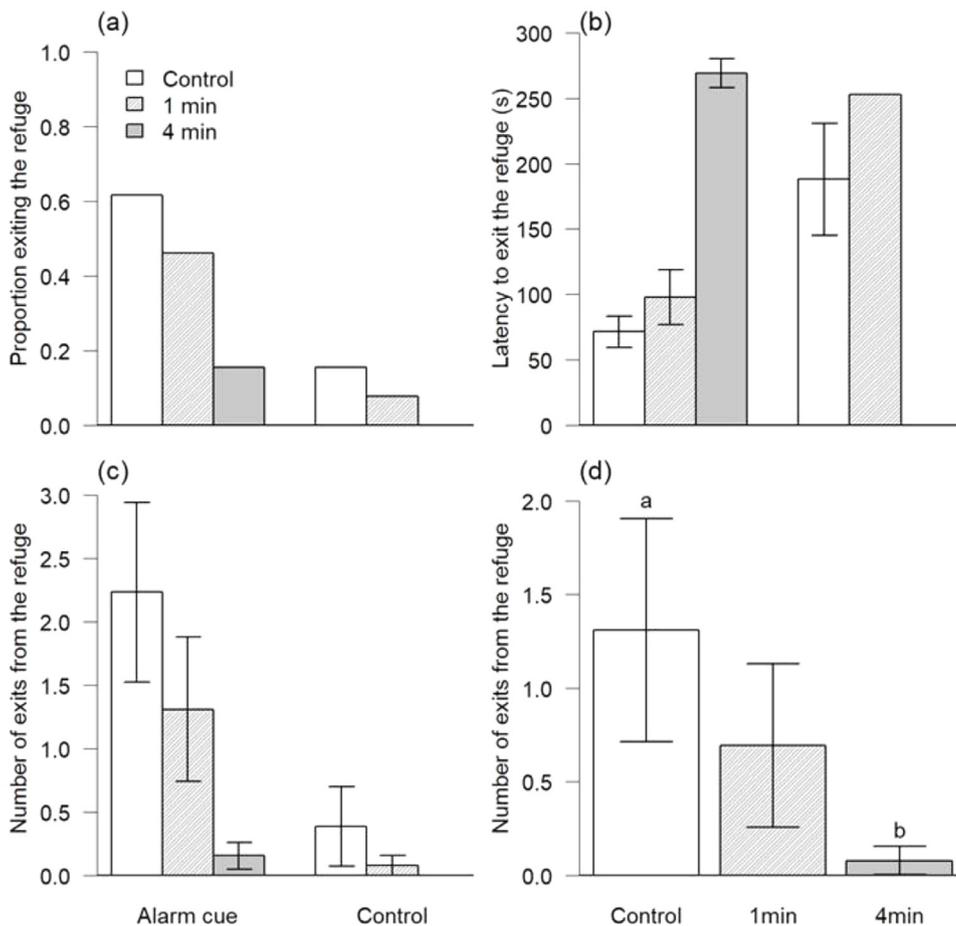


Fig. 4. (a) Proportion of schoolmaster snapper (*Lutjanus apodus*) that exited the mangrove refuge, and their mean (\pm SE) (b) latency (s) to exit the refuge after entering, and number of exits from the refuge (c) in response to both treatment factors and (d) as a function of chase time. Letters denote significant pairwise differences from Nemenyi's post hoc test.

exhaustion [38].

Exercise and exhaustion have physiological effects including acid-base and ionic changes in fish blood [41], with the severity of these effects and ability to recover influenced by individual variability and physical condition [16, 20], as well as relative level of exhaustion. For example, nesting male smallmouth bass (*Micropterus dolomieu*) allowed to fight for 2 min during angling sessions had lower blood pH, higher blood CO₂, higher muscle lactate, decreased energy reserves, and longer latencies to return to their nests than fish with fight times limited to 20 s [21]. Non-lethal stressors, including fisheries-induced exhaustive exercise, also generally increase blood corticosteroid titres [25, 32], and these hormones can in turn be detected by nearby conspecifics as disturbance cues [15] and potential predators as foraging cues [4, 10, 17]. Schoolmaster snapper implanted with cortisol to mimic a state of elevated stress did not experience greater predation rates than control fish in tethering experiments [23, 24], suggesting that increased mortality via predation following exhaustive exercise is due primarily to constrained behavioural responses, with a negligible role played by chemical predator attraction (sensu [11]). Similar to exercise, exposure to chemical alarm cues has been shown to elicit both behavioural [36, 37] and physiological [34] responses in fishes.

The effects of multiple stressors on fish impairments are largely unpredictable and vary between species and contexts. Brown trout (*Salmo trutta*) exposed to cold shock or cold shock paired with a forced swim remained comatose at 10 min post-swim while fish exposed only to a forced swim had resumed baseline activity levels, with no differences in immediate physiological stress (cortisol) responses between treatments. By 24 h post-swim all fish survived and had returned to baseline stress levels [19], highlighting the importance of short-term constraints (minutes) on survival behaviours. The schoolmaster snapper in this study demonstrated constrained behavioural responses following exhaustive exercise consistent with physiological constraints on behaviours, but not when pre-exposed to an additional non-lethal stressor in the form of chemical alarm cues. The conditional response to alarm cues may have mediated the effects of exhaustive exercise by pre-initiating the corticosteroid glucose-mobilizing response and increasing energy availability to enable fight-or-flight reactions or by increasing acid-metabolizing activity [41], suggesting that multiple stressors in the context of predation risk may not elicit complementary or additive effects on the behavioural and physiological responses of fish.

Detection of elevated predation risk may offset the constraining effects of exhaustive exercise on cognitive function and allow fish to maintain appropriate refuging behaviours. This phenomenon may occur through an unknown physiological mechanism mediating energy allocations to immediate survival-related behaviours versus physiological recovery. Future study of the interaction of threat perception and fright responses with other non-lethal stressors should combine physiological measures with additional stressor levels (i.e. longer periods of forced exercise) and different qualities of refugia to quantify functional limits on the short-term trade-offs between survival behaviours and recovery.

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