

# A field test of the “graveyard hypothesis” reveals avoidance of chemical but not visual cues in Bahamian queen conch (*Aliger gigas*)

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## ABSTRACT

Queen conch (*Aliger gigas*) are large gastropod molluscs harvested for their meat, shells, and pearls and as they are generally easy to collect by hand, they are vulnerable to overfishing. In The Bahamas, fishers often clean (or “knock”) their catch and dispose of the shells away from collection sites, forming midden heaps or “graveyards”. Although queen conch are motile and found throughout shallow water habitats, live animals are rarely observed in the vicinity of middens, giving rise to a common belief that conch actively avoid graveyards, possibly by moving offshore. Here, we experimentally evaluated avoidance behaviours of queen conch to chemical (tissue homogenate) and visual (shells) cues indicative of harvesting activity using replicated aggregations of six size-selected small (< 14 cm shell length) and large (> 14 cm) conch at Eleuthera Island. Large conch were consistently more likely to move, and to move farther, than small conch, independent of treatment. Small conch, however, demonstrated greater occurrence of movement in response to chemical cues vs seawater controls, while conch of both sizes demonstrated equivocal responses to visual cues. Collectively, these observations suggest that more economically desirable large conch may be less vulnerable to capture during successive harvest events than smaller juveniles due to their greater propensity to move, and that chemical cues consistent with damage-released alarm cues may play a greater role in eliciting avoidance behaviour than the visual cues typically associated with queen conch graveyards.

**Data Availability:** Data and R code are archived and freely available at Open Science Framework (<https://osf.io/x8t7p/>); DOI: 10.17605/OSF.IO/X8T7P).

## 1. Introduction

Queen conch (*Aliger gigas*) are one of the most culturally significant species in The Bahamas, with a recent survey reporting that 90% of Bahamian respondents viewed the species as of personal importance as well as a dietary staple (Blue Earth Consultants, 2016a). Queen conch constitutes a valuable commercial fishery in The Bahamas, one of the largest remaining conch fisheries in the Caribbean. A recent study estimated that Bahamian conch exports generate \$3.7 – \$5.9 M USD annually, accounting for approximately 7% of all exported fisheries products, while the internal conch market was estimated at \$2.5 – \$7.7 M USD nationally (Blue Earth Consultants, 2016b). As a direct result of consumer demand for their flesh, shells, and pearls, in combination with

relative ease of harvest and possible resulting overfishing, queen conch are imperiled throughout much of their native range with harvest banned in the Florida Keys since 1986 (Delgado and Glazer, 2020a; b). The species has been listed under CITES Appendix II since 1992 (Theile, 2005), with different national and population-specific harvest and export limits determined based on ongoing stock assessments (Aiken et al., 1999; Acosta, 2006; Cash, 2013; Mueller and Stoner, 2013; Prada et al., 2017).

Queen conch are large, relatively long-lived gastropod molluscs that reach terminal shell length and can begin to demonstrate shell lip-flaring associated with sexual maturity at 3.5–6 years of age (Stoner et al., 2012b; Mueller and Stoner, 2013). They may survive up to 40 years (McCarthy, 2007) although the average lifespan is likely 25–30 years

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Fig. 1. Adult queen conch (*Aliger gigas*) in The Bahamas (a) foraging over sandy substrate; (b) a midden heap of knocked shells exposed during low tide; (c, d) fishers removing meat from knocked shells for human consumption. All images © Shane Gross ([shanegross.com](http://shanegross.com)), used by permission.

(Davis, 2005; Mueller and Stoner, 2013). Adults and juveniles alike are most commonly found nearshore in shallow habitat dominated by coral rubble or sandy substrates to maximum depths of 75 m, with most individuals inhabiting areas < 30 m in depth (McCarthy, 2007). Conch are often found in discrete feeding (Berry et al., 2016) or mating (Stoner et al., 2012a; Stoner et al., 2012b; Delgado and Glazer, 2020a) aggregations associated with algal cover and seagrass (notably *Thalassia* spp.) meadows (Stoner, 2004; Davis, 2005; Boman et al., 2019). As a result of these habitat preferences, queen conch are accessible to fishers using snorkeling gear and can be readily harvested by hand (Davis, 2005). Female queen conch demonstrate positive relationships between reproductive frequency and both age and size with older and larger females having greater fecundity than younger, smaller ones (Stoner et al., 2012b; Delgado and Glazer, 2020a). However, sexual maturity in queen conch is variable and site-specific (Boman et al., 2018): one study in The Bahamas showed that the minimum lip thickness for males reaching sexual maturity is 9 mm (mean 24 mm) while sexually mature females had a minimum lip thickness of 12 mm (mean 26 mm: Stoner et al., 2012b). In general, a lip thickness threshold of 15 mm has been suggested as widely applicable to standardize harvest practices to and prevent the removal of sexually immature animals throughout the Caribbean (Mueller and Stoner, 2013).

Importantly, lip thickness as an indicator of sexual maturity may not be widely used within the fishing community in The Bahamas, with harvest regulations specifying only that “[N]o person shall take, have in his (*sic*) possession or sell any conch the shell of which does not possess a well, fully-formed flared lip” (Statute Law of The Bahamas, 1977). A recent update to the legislation (The Bahamas Fisheries Resources (Statute Law of The Bahamas, 2020) did, however, reduce bag limits for conch. Based on this equivocal language, sexually immature conch could potentially be legally harvested, with an earlier study estimating that as much as 38% of the legal harvest consists of immature animals (Acosta, 2006; Cash, 2013). In addition, there is no closed fishing season for queen conch in The Bahamas. Because of these confounding factors, the species may not be afforded legislative protection sufficient to sustain

the fishery (Theile, 2005) and signs of overharvesting including decreases in population density (Cash, 2013) and shell sizes of both adults and juveniles (Tewfik et al., 2019) have been documented (Stoner et al., 2019).

In common practice, Bahamian fishers typically remove the animal from its shell by breaking (also called “knocking” or “cracking”) the shell at the attachment point of the adductor muscle. The fleshy meat is detached from the unpalatable tissue, and then both shell and offal are discarded into the water near the shoreline or where fishers moor their boats, in piles or middens (Fig. 1). While the mass of each animal increases with shell length (from ~100 g per 14 cm shell to ~500 g per 27 cm shell), edible soft tissue mass is independent of lip thickness and total shell length (Stoner et al., 2012b). Knocked shells close to 14 cm in length are frequently observed in Bahamian conch graveyards; from an economic perspective, a sexually immature conch may yield as much edible and salable meat as a similarly-sized, sexually mature conch, or even a much larger, older animal (Stoner et al., 2012b). There is a widespread belief amongst fishers in The Bahamas known as the “graveyard hypothesis”: namely, that queen conch move away from or avoid midden heaps (or graveyards) of discarded conch shells. The graveyard theory is cited by some fishers as the reason inshore conch populations are declining, ostensibly due to offshore emigration instead of overharvesting. A stakeholder analysis including fishers, buyers, processors, vendors, restaurateurs, and the general public showed that 21% of respondents referenced the graveyard theory as a reason why the Bahamian conch population is in decline (Blue Earth Consultants, 2016b).

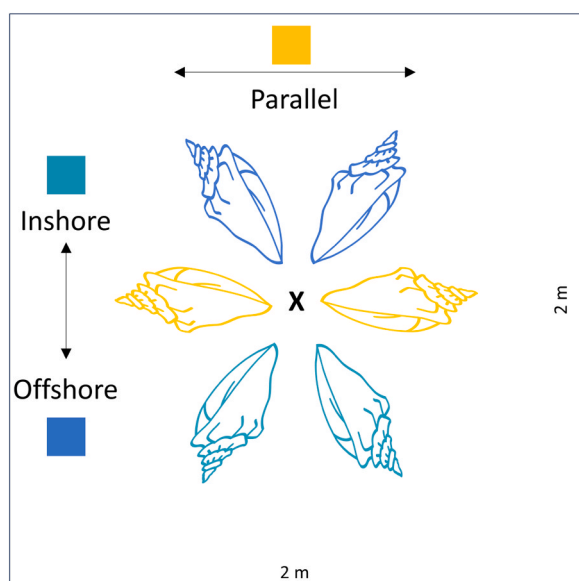
Here, we experimentally evaluate claims of conspecific avoidance of conch graveyards simulated by both chemical (tissue homogenate consistent with damage-released alarm cues) and visual cues (knocked shells varying in age simulating midden heaps) indicative of harvest via knocking. As shells of dead conch occur commonly away from midden heaps, we hypothesize that queen conch do not avoid middens based on visual cues, and instead we predict that they will demonstrate avoidance behaviours in response to chemical cues, with larger and more motile

**Table 1**

Summary of size class distributions of queen conch (*Aliger gigas*) in replicate groups of six individuals (i.e. per trial) exposed to chemical (Experiment 1) or visual (Experiment 2) cues of harvesting activity.

	Small	Large	N	Total trials
Experiment 1:	2	4	1	46
Chemical Cues	3	3	45	
Experiment 2:	0	6	1	81
Visual Cues	1	5	5	
	2	4	13	
	3	3	20	
	4	2	35	
	5	1	5	
	6	0	2	

\* N refers to the number of trials with each number of Small (< 14 cm) and Large (> 14 cm) conch (six conch total per trial/group).



**Fig. 2.** Initial placement of six queen conch (*Aliger gigas*) around the central cue introduction site (X) in replicate 2 m × 2 m quadrats. Colours on the scales indicate the possible directions of movement (inshore, offshore, parallel to shore) and colours of the conch indicate where they would be expected to move without a directional change.

mature conch demonstrating greater responses than smaller conch.

## 2. Materials and methods

### 2.1. Animal collection and housing

Free-ranging, solitary queen conch ( $N = 762$ ) were collected by hand during repeated snorkeling sessions ( $N \approx 30 - 50$  per session) along the beachfront (50 – 200 m offshore, depth 0.5 – 2 m) at the Cape Eleuthera Institute, Eleuthera, The Bahamas (24° 49' 51.6" N, 76° 19' 40.8" E), from February – June 2016. The conch were divided by size into small or large size classes based on shell lengths (SL) where small conch were < 14 cm SL (range 7.8 – 13.5 cm;  $10.9 \pm 1.2$  cm, mean  $\pm$  SD) and large conch were all > 14 cm SL (range 14.2 – 22.6 cm;  $17.6 \pm 2.3$  cm, mean  $\pm$  SD), following the size threshold proposed by Mueller and Stoner, 2013) and had some degree of lip-flaring (lip thickness range 5.5 – 15 mm;  $7.4 \pm 3.8$  mm, mean  $\pm$  SD, based on measurements from a subset of  $N = 86$  conch in the large size group in Experiment 2). Conch were haphazardly collected such that the two size classes were nearly equally represented in both the whole sample ( $N = 355$  large;  $N = 407$  small) and between Experiments 1 and 2 (Table 1). Animals were held offshore in hollow

concrete reef balls (~1.5 m circumference) from time of capture until they were assayed (1 – 3 days) and then released into an adjacent bay.

### 2.2. Experimental protocol

We marked out a series of 2 × 2 m quadrats located 40 – 100 m offshore throughout the ~3600 m<sup>2</sup> capture area, and four quadrats separated by at least 20 m were used in each experimental block of concurrent trials. The quadrats were chosen based on substrate characteristics (flat, sandy, limited structure and macrophytes) and the absence of other conch within the field of view of the experimenters before each trial. Each quadrat was measured out with a field tape and marked at each corner with small orange flags (triangular, ~10 cm per side) attached to aluminum rods (~45 cm length, ~3 mm diameter) that were placed and removed immediately before and after each trial. Groups of 6 conch were placed in circular clusters with their shell vents pointed inwards within 1 SL of each other at the center of their quadrats (Fig. 2). Conch groups were exposed to either chemical (Experiment 1) or visual (Experiment 2) cues of harvested conspecifics and then left undisturbed for 60 min. After the 60 min had elapsed a snorkeler located each individual and recorded: i) whether or not it had moved; ii) distance displaced (in cm) from the center point of the quadrat to the final position for each individual in Experiment 1; iii) the direction of movement (inshore, offshore or parallel to the shore); and iv) its size class.

### 2.3. Experiment 1: responses to chemical cues

We obtained the carcasses of 10 freshly harvested conch consisting of all the unpalatable soft tissues that are normally discarded after cleaning from local fishers (Blue Earth Consultants, 2016a). This tissue was mechanically homogenized into microfiltered and UV-sterilized seawater, diluted to a final concentration of 1 g tissue per 10 ml of seawater and frozen in 120 ml aliquots until use. Chemical alarm cues extracted from vertebrates (e.g., fishes, larval amphibians) are typically diluted to concentrations of 1 cm<sup>2</sup> of skin per 10 ml of water (Brown and Godin, 1997; Brown et al., 2009; Elvidge et al., 2013), and while a standardized protocol and concentration has not been described in molluscs, the concentration used here is likely to be more potent as 1 cm<sup>2</sup> of fish skin constitutes less tissue than 1 g of conch carcass.

Queen conch groups were placed into four quadrats in each block of trial replicates. Immediately before starting each 60 min trial, we injected 120 ml of either seawater as a control (Control;  $N = 22$ ) or conspecific chemical alarm cues (AC;  $N = 24$ ) via plastic syringes, with each treatment applied twice per replicate block. Cues were injected directly towards the conchs' siphons (i.e. 20 ml each) from distances of 1–2 cm to simulate acute cue detections.

### 2.4. Experiment 2: responses to visual cues

Queen conch groups (as in Experiment 1) were placed into four quadrats with one of four visual treatments placed at the center point of each quadrat: i) nothing as a negative control (Control;  $N = 21$ ); ii) a rock ('Rock': diameter  $16.7 \pm 4.9$  cm, mean  $\pm$  SD;  $N = 23$ ) as a positive visual control; iii) an old knocked conch shell ('OS': SL  $18.5 \pm 2.4$  cm, mean  $\pm$  SD;  $N = 20$ ); or iv) a freshly knocked conch shell ('FS': SL  $19.3 \pm 4.5$  cm, mean  $\pm$  SD;  $N = 17$ ) with each treatment represented once per replicate block of trials. The old conch shells (OS) had likely been harvested > 1 year earlier and were collected in the same area as the experimental conch were captured. The freshly knocked shells (FS) were obtained by snorkeling at an active midden heap at a nearby boat dock used by fishers to clean their catch and discard the shells into the water, likely ~1 week before they were collected for this experiment. Freshly knocked shells may also have contained traces of chemical cues as in Experiment 1.



**Table 2**

Summary of likelihood-ratio  $\chi^2$  tests of generalized linear models of binary queen conch (*Aliger gigas*) behavioural responses (Move: moved from initial position during 60 min trials) between treatments (either visual or chemical), size class (small: < 14 cm shell length; large: > 14 cm shell length), and with their interaction term against binomial error distributions with experimental replicate as a random term.

Cue Type	Response	Model term	Wald $\chi^2$	df	P
Chemical (Experiment 1)	Move	Treatment	7.99	1,44	0.043
		Size	35.9	1228	< 0.0001
		Treatment×Size	1.23	1228	0.27
Visual (Experiment 2)	Move	Treatment	3.65	3,77	0.31
		Size	47.53	1401	< 0.0001
		Treatment×Size	2.36	3401	0.51

## 2.5. Statistical analyses

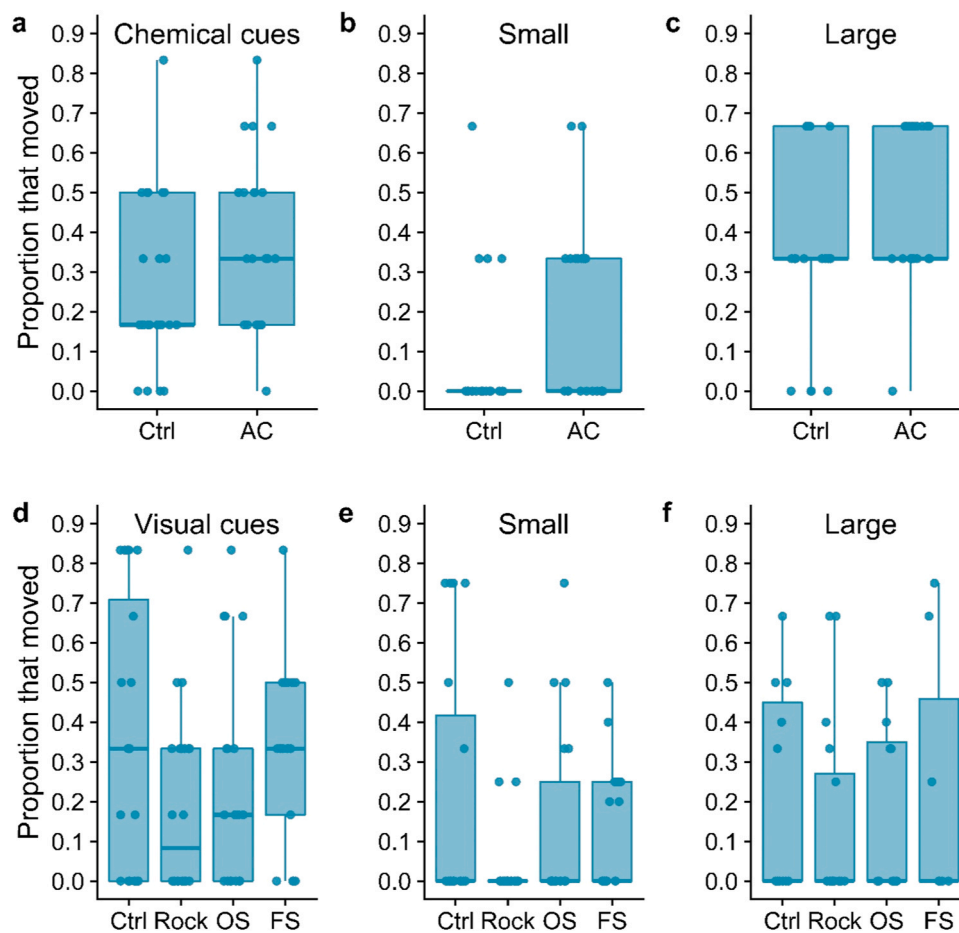
Whether or not an individual conch moved (binary response) was examined with treatment and size class as categorical factors and experimental replicate (with  $N = 6$  conch per replicate) as a random factor against binomial error distributions in generalized linear models (GLMMs) using the 'lme4' package (Bates et al., 2015) with Type 3 Sums of Squares and likelihood-ratio  $\chi^2$  tests in the 'car' (Fox and Weisberg, 2011) package. GLMMs from Experiment 2 (visual cues) were further examined for pairwise differences between treatments with Holm-corrected Tukey post-hoc tests using the 'multcomp' package (Hothorn et al., 2008). Distances displaced by the conch that moved in

Experiment 1 (chemical cues) were analyzed in a linear mixed-effect model (LME) with treatment and size class as categorical factors and replicate as a random error term using 'lme4' and 'lmerTest' (Kuznetsova et al., 2017). Direction of movement from the initial epicenter was assessed by treating the area covered by the conch at the end of each trial as a circle, with one hemisphere defined as Inshore, the opposite hemisphere as Offshore, and Parallel consisting of final locations falling along the division between hemispheres. Directions were tested for deviations from equal frequencies (i.e. the assumption that undirected movement should be equally likely to occur in the three general directions; Fig. 2) using  $\chi^2$  contingency tests. All analyses and figures were generated using R v3.5.2 (R Core Team, 2019) and the 'ggplot2' (Wickham, 2016), 'cowplot' (Wilke, 2019), and 'wesanderson' (Ram and Wickham, 2018) packages.

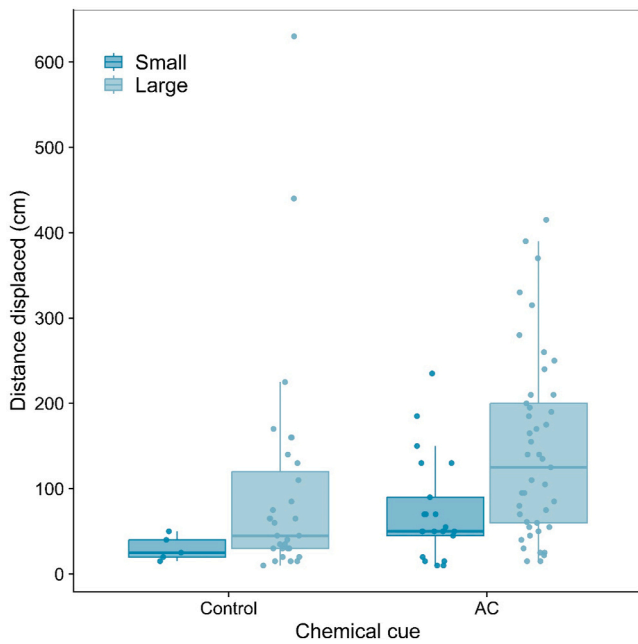
## 3. Results

### 3.1. Experiment 1: responses to chemical cues

Out of 276 total conch, 106 moved (38.4%) independent of treatment. However, movement was recorded in 30.3% of animals in the control treatment (40/132) and 45.8% in the alarm cue treatment, with this pattern persisting when the animals were divided by size class (small: 11.9% control, 29.2% alarm cue; large: 49.2% control, 62.5% alarm cue). Queen conch were significantly more likely to move during the trials with alarm cues than during control trials (Table 2; Fig. 3a) with size-based differences where significantly more large conch moved than small conch in both treatments (Fig. 3b, c). The interaction term

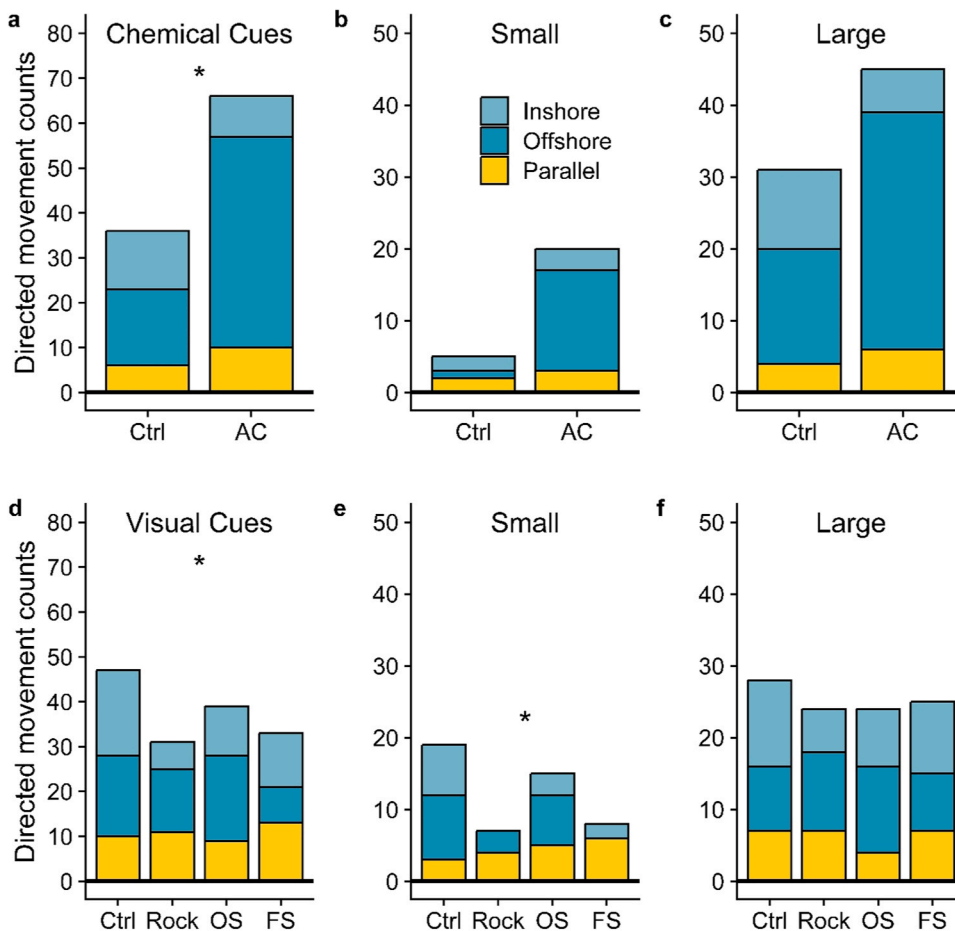


**Fig. 3.** Proportion of queen conch (*Aliger gigas*) that moved from their initial position during 60 min trial replicates when exposed to chemical (Control: seawater; AC: chemical alarm cues; a-c) or visual (Control: nothing; Rock: rock; OS: old conch shell; FS: fresh conch shell; d-f) cues indicating recent harvesting activity. Data presented are for all sizes (a,d) and small (< 14 cm shell length; b,e) and large (> 14 cm shell length; c,f) size classes.



**Fig. 4.** Distance displaced (cm) over 60 min by individual small (shell length SL < 14 cm) and large (SL > 14 cm) queen conch (*Aliger gigas*) exposed to seawater (Control) or chemical alarm cues (AC). Statistically significant differences were found between treatments and size classes as main effects (both  $P < 0.05$ ) but not their interaction term ( $P > 0.05$ ).

between chemical treatment and size class was non-significant.



**Fig. 5.** Observed frequencies (counts) of directed movements (inshore, offshore, parallel to shore) over 60 mins by queen conch (*Aliger gigas*) exposed to chemical (Ctrl: seawater; AC: chemical alarm cues; a-c) or visual cues (OS: old shell; FS: fresh shell; d-f) indicating recent harvest activity. Data are presented for all sizes (a,d) and by small (< 14 cm shell length; b,e) and large (> 14 cm shell length; c,f) size classes. Asterisks (\*) indicate significant deviations ( $P < 0.05$ ) from predicted equal counts in  $\chi^2$  contingency tests. Final positions of the conch from the epicenter were evaluated by considering a circle, with one hemisphere defined as Inshore, the opposite hemisphere as Offshore, and Parallel consisting of final locations falling along the dividing line between hemispheres such that equal proportions of conch in each replicate were expected to travel in each direction.

Distances displaced during the 60 min trials differed significantly between treatments (LME:  $F_{1,44.003} = 4.91$ ,  $P = 0.032$ ) and size classes ( $F_{1228.38} = 47.95$ ,  $P < 0.001$ ), but not their interaction term ( $P > 0.05$ ). Within each chemical treatment, alarm cue exposure was associated with greater distances travelled compared to seawater controls (Fig. 4). In general, large conch displaced farther than small conch independent of chemical treatment with the greatest distances travelled by large conch exposed to alarm cues, and the shortest distances by small conch in the control treatment (Fig. 4).

Overall (combined size classes), chemical cue exposure resulted in significant deviation from predicted (uniform) directions of movement ( $\chi^2 = 7.626$ ,  $P = 0.022$ ), with greater frequency of offshore-directed movements in alarm cue trials compared to control trials (Fig. 5a). Although statistically non-significant, the same pattern of greater frequencies of offshore-directed movements were demonstrated by both the small ( $\chi^2 = 3.681$ ,  $P = 0.159$ ; Fig. 5b) and large ( $\chi^2 = 5.372$ ,  $P = 0.068$ ; Fig. 5c) size classes.

### 3.2. Experiment 2: responses to visual cues

Out of 486 conch, 153 demonstrated movement during the trials (31.5%), with more large conch moving than small conch (47.2% vs 18.7%, respectively). Whether or not an individual queen conch moved during a 60 min trial was significantly influenced by both visual treatment and size, but not their interaction term (Table 2). There were no significant pairwise differences in movement independent of size (Fig. 3d), and there were also no significant pairwise differences within the two size classes (Fig. 3e,f; Tukey test, all  $P > 0.05$ ). Direction of movement was not influenced by visual treatment independent of size (likelihood ratio  $\chi^2 = 9.176$ ,  $P = 0.164$ ; Fig. 5d). However, there were

significant differences between treatments in small conch ( $\chi^2 = 13.056$ ,  $P = 0.042$ ; Fig. 5e) with offshore oriented movements more common than inshore movements in both size classes, although this was statistically non-significant for large conch ( $\chi^2 = 3.919$ ,  $P = 0.688$ ; Fig. 5f).

#### 4. Discussion

Queen conch responses in this study provided equivocal support to the graveyard avoidance hypothesis. Chemical cues putatively associated with recent harvest activity and discarding of soft tissues (Experiment 1) elicited avoidance behaviours in large conch that were more likely to move, to move farther, and to move offshore instead of inshore or parallel to the shore, than small conch. However, these movement differences were independent of chemical cue type, although large conch did demonstrate significantly greater responses to alarm cues than to seawater controls. Conversely, queen conch responses to visual harvest cues intended to simulate actual midden heaps (Experiment 2) did not support the graveyard avoidance hypothesis. These conch again demonstrated size-based differences in their movement patterns, with large conch more likely to move than small conch. Harvested (knocked or cracked) conch shells, whether they were fresh or old and weathered, did not elicit different movement responses relative to control trials. Exposure to a shell-sized rock as a positive visual control resulted in significantly lower occurrence of movement than the negative (no visual cue) control trials, with this stimulus-response pattern also expressed qualitatively within the individual size classes. Collectively, the visual cues were associated with decreased movement compared to the negative visual control treatment, possibly indicative of a non-specific startle response elicited by proximity to any unexpected object following the initial handling and placement. Visual cues overall did not drive movement in any particular direction and large conch in particular were equivocal in their directional movement patterns over our 1 hr trial periods.

Our results identify size-based differences in short-term movement patterns influenced by external stimuli with larger conch moving more than smaller conch, around a suggested size threshold that may be indicative of early sexual maturation (15 cm shell length: Mueller and Stoner, 2013). Further, conch demonstrated avoidance responses to areas chemically labelled as “risky” during trials featuring injections of chemical cues from conch tissue homogenate, although only small (juvenile) conch demonstrated a significant difference in response to chemical cues or seawater controls due to the greater propensity of large conch to move during control trials. However, we observed no clear patterns of response to visual cues (shells) indicating recent or historical localized mortality via harvesting of conspecifics. In general, large conch here demonstrated significantly greater motility than small conch and this may reflect the greater ability and propensity of larger animals to disperse, including from harvest and knocking sites. Larger and more motile animals may have more success at subsequently locating suitable refuge habitat compared to smaller conch, who are generally constrained to nursery habitat presenting ideal growth conditions (Stoner, 2004; Boman et al., 2019). These observations are consistent with other reports of size-based differences in daily queen conch movement (Doerr and Hill, 2013), including experiments that found similar small-scale movement patterns between small and large queen conch using tri-axial accelerometers (Brownscombe et al., 2015; Dujon et al., 2019) and visual surveys that identified seasonal movements between habitats in large conch (Stoner and Sandt, 1992) but not small conch (Stoner and Davis, 1994).

At the population level, larger and more motile conch that may be less vulnerable to harvest by avoiding areas subject to fishing pressure likely also have higher fecundity and have already achieved some degree of reproductive success (Acosta, 2006; Stoner et al., 2012b). In contrast, smaller, pre- or early-reproductive conch may be less motile and more vulnerable to overharvesting while still yielding sufficient meat to make their harvesting efficient and profitable for fishers.

Collectively, avoiding the introduction of damage-released chemical cues from soft tissues or forming new middens of freshly knocked shells where they may be detected by aggregated queen conch may be a simple means of avoiding disruption of aggregations. In the context of the graveyard avoidance hypothesis and its belief amongst some Bahamian fishers (Blue Earth Consultants, 2016b), large middens of old shells may create and constitute undesirable habitats that queen conch avoid, instead of directly providing cues that elicit avoidance responses of the middens themselves.

From a fisheries management perspective, two imperative points are highlighted from our results. First, prohibiting harvest of pre- or early-reproductive conch may benefit harvested populations not only through increasing genetic contributions of smaller individuals to future cohorts, but also by reducing pressure through repeated fishing in nursery areas supporting greater numbers of economically and genetically valuable juveniles (Stoner et al., 2012b; Cash, 2013; Stoner et al., 2019). Second, as queen conch form aggregations to support essential life history processes in permissive habitats (i.e. growth and reproduction: Stoner and Davis, 1994; Stoner, 2004; Berry et al., 2016; Delgado and Glazer, 2020a), identifying areas where aggregations occur (Stoner, 2004; Stoner et al., 2012a; Dujon et al., 2019) and designating harvest-prohibited or protected status (i.e., no-take reserves or marine protected areas) should be a continued priority. Notably, the establishment of protected areas has already been shown to have beneficial effects on conch population status in the Caribbean (Béné and Tewfik, 2003; Acosta, 2006; Kough et al., 2017). In addition, a best-practice recommendation consistent with existing harvest patterns of limiting knocking and disposal of shells in midden heaps to areas consisting of unsuitable queen conch habitat may help dissociate the graveyard avoidance hypothesis from local perceptions of population decline drivers.

#### Compliance With Ethical Standards

All work was conducted in accordance with Bahamian law and under approval from Carleton University’s Animal Care and Use Committee with funding from NSERC (Canada). We declare no conflict of interest.

#### CRediT authorship contribution statement

**Chris K. Elvidge:** Conceptualization, Methodology. **Candice Brittain:** Conceptualization, Methodology. **Petra Szekeres:** Conceptualization. **Claire Thomas:** Conceptualization, Methodology. **Steven J. Cooke:** Conceptualization, Editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data and code are archived online at OSF.io and the URL and DOI have been included in the manuscript.

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