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Boat noise alters behaviour of two coral reef macroinvertebrates, *Lambis lambis* and *Tridacna maxima*

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ABSTRACT

Boat noise has been shown to distract and cause harm to many marine organisms. Most of the study effort has focused on fish & marine mammals, even though invertebrates represent over 92 % of all marine life. The few studies conducted on invertebrates have demonstrated clear negative effects of anthropogenic noise pollution. The small giant clam *Tridacna maxima* and the spider conch *Lambis lambis* are two invertebrate species which play key roles in coral reef ecosystems, and are little studied for the effects of noise disturbance. *T. maxima* functions as prey for many fish species, contributes up to 9 % of the reef's calcium carbonate budget, and plays a role in nutrient cycling. The herbivorous strombid *L. lambis* can occur in large numbers on reef flats and is prey for other snails and several elasmobranchs. Using two case study reefs, we show that both boat noise and biotic sounds are prominent sound sources in Red Sea reef habitats. In-situ controlled exposure experiments were conducted on two shallow central Red Sea reefs, where Daily Diary smart tags were used to measure the reactions of *T. maxima* and *L. lambis* during underwater playback of boat noise and ambient reef sound. Both macroinvertebrates exhibited behavioral changes during the boat noise treatment. Our results suggest that *L. lambis* and *T. maxima* individuals may spend energy averting the invisible "threat" of boat noise, rather than feeding or staying open for symbiotic algae to perform photosynthesis, in the case of *T. maxima*. As boat noise is prevalent on Red Sea reefs, invertebrates may be affected on a large scale in the Red Sea.

1. Introduction

Sound propagates faster and farther underwater than in air, and farther than other sensory cues (such as light or chemical cues) (Urick, 1983). As a result, marine fauna has evolved sensitivity to sound over a wide range of frequencies. With sound as a highly effective form of sensory communication under water, the reliance of organisms on sound for survival in the ocean increases their vulnerability to human activity, especially given the sustained increased levels of human noise, which may interfere with their capacity to use sound as a sensorial cue effectively (Wenz, 1962).

Soundscapes, defined as "*ambient sound in terms of its spatial, temporal, and frequency attributes, and the types of sources contributing to the sound field*" (Pijanowski et al., 2011), are changing rapidly throughout the ocean. Anthropogenic sound sources have increased dramatically in number and level (Howe et al., 2019) altering the sound levels of vocalising animals, while anthropogenic climate change is altering the contribution of geophysical sources, such as sea ice and storms, to marine soundscapes (Nystuen and Miksis-Olds, 2010; Boyd et al., 2021; Shajahan et al., 2025). As a result of these processes, the soundscape of the "anthropocene ocean" is fundamentally different from that of pre-industrial times and continues to change rapidly with expanding human impacts and altered climates (Duarte et al., 2021). In contrast to the long-standing recognition of the effects of anthropogenic

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Abbreviations: CEE, controlled exposure experiment; DD, Daily Diary animal tag; SPL, Sound Pressure Level; VeDBA, vectorial dynamic body acceleration.

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sound in terrestrial systems (Pijanowski et al., 2011), impacts on ocean soundscapes have received relatively limited attention. This neglect percolates in reviews of cumulative stressors (Halpern et al., 2008; Boyd, 2011) and drivers of global change in the ocean (Duarte, 2014; Levin and Breitburg, 2015), as well as in scientific assessments (Ingeman et al., 2019) and policy frameworks (UNCBD, UNCLOS, UN SDGs) aimed at improving ocean conservation and sustainability. Anthropogenic noise is a pervasive form of marine pollution, yet uniquely manageable: while its impacts may linger, its presence as a pollutant ceases immediately when the source stops. Given the rapid pace of change in ocean soundscapes, there is an urgent need to understand and mitigate human impacts on ocean soundscapes as a necessary foundation for a healthy ocean.

Coral reefs are particularly important targets for studies assessing the impact of noise, as they are biodiversity hotspots and are often visited by a variety of vessels, such as fishing boats, and boats used for tourism and recreational activities. Accordingly, the impact of noise resulting from boat engines on fish behavior in reef ecosystems has received some attention (Holles et al., 2013; McCormick et al., 2018; Nedelec et al., 2022), yet the impacts of noise on reef invertebrates, and indeed invertebrates altogether, remain understudied (Murchy et al., 2019; Solé et al., 2023; Przeslawski et al., 2018; Hubert et al., 2022; Davies et al., 2024). This includes not only small, cryptic species, but also large keystone species such as the Spider Conch *Lambis lambis*, and the Small Giant Clam *Tridacna maxima*. Both are present in the Red Sea, and their hearing capacities are poorly understood. Among reef invertebrates, snapping shrimps have received the greatest attention, because of their prevalent contribution to coral reef soundscapes (Lillis et al., 2017; Lillis and Mooney, 2018). Yet, coral reefs contain a large number of invertebrates, central to ecosystem functioning, which have received no or limited attention in assessments of the impacts of anthropogenic noise. A meta-analysis of shipping noise on invertebrates found negative effects, especially in Gastropoda (Murchy et al., 2019). For Bivalvia, this analysis consisted of two studies (Jolivet et al., 2016; Charifi et al., 2017). The first showed oysters transiently closing their valves at low frequencies similar to those emitted by boat engines (energy, 0.02 ms-2 at 122 dBrms re 1 μPa, maximum sensitivity from 10 to 200 Hz) (Charifi et al., 2017). In the second study, larval settlement was triggered in blue mussels under boat sounds (Jolivet et al., 2016), potentially causing larvae to settle in environments that are unfavorable to subsequent survival. A recent study tested for the reaction of *Tridacna maxima* to boat noise in Mo'orea, French Polynesia (Doyle et al., 2020), finding that *T. maxima* stayed open for longer when exposed to both flow and boat noise, but found no change with the addition of just one of these sensory inputs.

The tropical small giant clam *Tridacna maxima*, has the widest range of all Tridacnidae (giant clam) species, extending from East Africa to the Central Pacific (Van Wynsberge et al., 2016) and is common in the Red Sea (Vine, 1986; Rossbach et al., 2019). The first population estimate of the Saudi Arabian coast was conducted in 2020, finding 0.17 (±0.37) individuals per square meter (or approximately 1 *Tridacna* clam per 5.88m^2) (Rossbach et al., 2021). For the overall mean calcium carbon budget of Red Sea coral reef communities, Tridacninae have an estimated average contribution of 0.7 %, with a potential to contribute up to 9 % to reef carbonate accretion (Rossbach et al., 2021). They can perceive light/shadow through eye-spots located along the margin of the siphon, inside the mantle tissue (Wilkens, 1986; Land, 2003; Dehaudt et al., 2019), which allows recognition of predators, and triggers mantle retraction and closure (Fig. 1.A). The usual manner a species of Tridacnidae is predated upon is small nips off the mantle from piscivorous fish such as Scaridae and Labridae (Land, 2003).

A recent study on *T. maxima* showed individuals also protectively closed when exposed to UV-B, suggesting the ability to gauge environmental factors is integral for self-preservation (Rossbach et al., 2019). As well as relying on symbiotic algae, *T. maxima* are also sessile filter feeders, and must remain open to do so (Wilkens, 1986). Although bivalves have not been found to produce noise for communication, the sound produced by movement is quantifiable (Júnior et al., 2019). *T. maxima* has recently been tested in terms of reaction to low frequency boat noise, as an individual stimulus, as well as in combination with water flow (Doyle et al., 2020). Doyle et al. (2020) found that the clams responded to the sound, flow, and the combination of both by increasing frequency of mantle retractions, and simultaneous water jetting from the exhalant siphon (an anti-predator response), suggesting boats as a significant stressor. Mantle retractions are the precursor to full shell closure (Fig. 1.A). The delay, or latency, to close the shell fully, or reemerge the mantle did not change with the effect of sound alone. However, when exposed to both stimuli simultaneously, the latency increased,

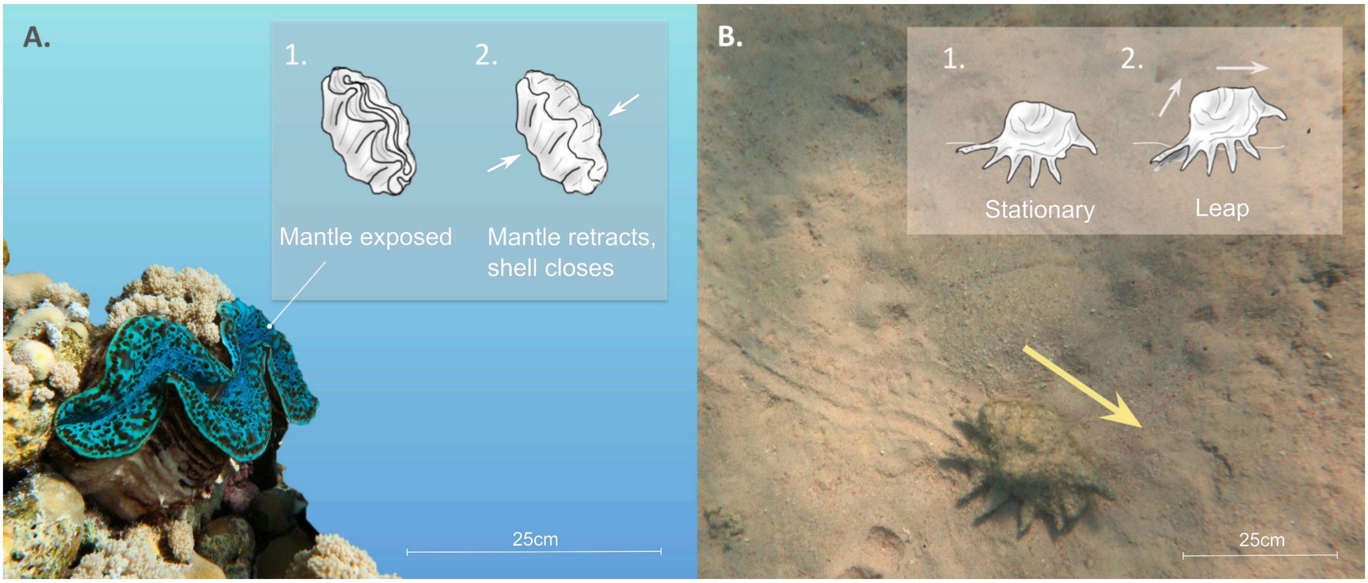

Fig. 1. A. Shows the opened state of *T. maxima* with exposed mantle (1) vs (2) closed state, with mantle retracted and arrows showing direction of shell closure (Photo: S. Rossbach). B. Sequence of locomotion of L. *lambis* (inset) showing change of movement from (1) stationary to (2) pushing up and forward using the modified operculum. Image shows direction of travel (yellow arrow) and tracks left behind in the sand – note the circular marks left by the operculum (Photo: J. Hubert). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

T. maxima staying open for a longer period of time (Doyle et al., 2020). This infers the clams were potentially distracted, perceiving the sound and flow in an additive way, suggesting that they are especially vulnerable to unavoidable marine noise pollution.

The Spider Conch *Lambis lambis* is a large strombid mollusc (Family: Strombidae), growing up to 29 cm in length, with coarse transverse ridges and seven spider-like protrusions of varying length from the base of the shell (Berg, 1974; MolluscaBase, 2020). It inhabits reef flats and mangroves, and is widely distributed in tropical and subtropical zones from the Red Sea to the South Pacific (Vine, 1986). Strombidae feed using a long flexible tube called a siphon, extending from its anterior side, which draws water over the osphradium in the mantle cavity, an organ which assists respiration, and also detects scents, distinguishing between food, predators and mates (Heller, 2015). Their flexible eye stalks are frequently subject to attack by fish, though they are able to regrow them (Heller, 2015). Its main predators are other predatory snails, such as the dart-shooting cone snail, eagle rays, and nurse sharks (Berg, 1974). Unlike most other molluscs, *L. lambis*, characteristic of the family Strombidae, do not glide slowly along the substrate, but rather use their muscular foot and modified, pointed operculum to propel forward in leaps (Fig. 1.B). The current population of *L. lambis* in the Red Sea is unknown, although being a shallow-water dweller, and prized in the Red Sea area for its flesh and shell, it is likely in risk of over-fishing. No studies are currently available assessing the hearing capacity of *L. lambis*, or its reaction to sound.

The Red Sea has one of the most extensive coral reef systems in the world, flanking a narrow, deep central channel, which represents the main shipping lane across the Red Sea. With a passage of 17,000 vessels per year between the northern connection to the Mediterranean (the Suez Canal) and the southern opening to the Gulf of Aden, noise levels can be estimated to increase similarly to other parts of the world where shipping is present (Alahmadi et al., 2019). Currently only one modelling study has been undertaken in the Red Sea, estimating shipping noise, showing a basin-wide prominence of noise pollution, concentrated around the coasts and ports (Larayedh et al., 2024).

Through this study, we contribute to the understanding of the unstudied soundscapes of Red Sea coral reefs and the responses of two associated keystone invertebrate species to anthrophony represented by boat noise by (a) characterising the soundscape of two reefs in the Central Red Sea, and (b) determining whether the rate and degree of animal movement directly respond to the disturbance of boat noise, the prevalent source of noise in this ecosystem. Responses were recorded using animal-attached movement tags, during Controlled Exposure Experiments (CEEs) playing back pre-recorded undisturbed, ambient reef soundscapes (i.e. ambient treatment), and pre-recorded small boat movements (i.e. boat treatment).

We postulated that boat noise would affect the movement patterns of the target species, expecting different movement rates to the ambient soundscape treatment. Firstly, for *T. maxima*, the only previous study available suggests that there should be less opening and closing movement during the boat treatment, versus the ambient treatment. For *L. lambis*, due to expected escape locomotion behaviour, the conch should move less and slower during the ambient treatment than in the boat treatment. Secondly, the degree of movement, measured using the Vector of Dynamic Body Acceleration (VeDBA) in *L. lambis* is expected to be significantly higher under boat treatment compared to the ambient treatment, as the boat sound may be perceived as a threat and prompt greater acceleration in each movement.

2. Materials & methods

2.1. Ethics statement

All experiments were conducted within the Institutional Animal Care and Use Committee (IACUC) and Institutional Biosafety and Bioethics Committee (IBEC) regulations as stipulated by KAUST Research Compliance office (2020).

2.2. Experimental design

2.2.1. Natural soundscape

To understand ambient conditions, continuous recordings from a SoundTrap ST300 hydrophone (Ocean Instruments, NZ) was retrieved from two reef locations on and near the planned experiment sites: the outer reef on the offshore location Qita al Kirsch (22°25'39.0”N, 38°59'38.2”E) and the inshore, shallow patch reef Abu Shosha (22°18'13.74"N, 39°2'51.79"E) in December 2019 (08-11/12/19) and August 2019 (07-10/08/19) respectively. Subsequent long-term averaged spectrograms (LTSA) were created using the program CHORUS (Curtin University) (Gavrilov and Parsons, 2014) & PAMGuide (Merchant et al., 2015) in MATLAB. The software Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2024) was also used to aurally confirm the biological or anthropogenic nature of certain sound signatures.

2.2.2. Exposure experiment

2.2.2.1. Study sites. Controlled Exposure Experiments (CEEs) are defined as “a field procedure in which controlled doses of an acoustic stimulus are applied to focal animals for the purposes of assessing their behavioral and/or physiological responses” (Tyack et al., 2003). CEEs were conducted on the sheltered side of Abu Shosha (22°18'13.74"N, 39°2'51.79"E) (30/1/2020–13/2/2020) and Tahla North (22°16'44.97"N, 22°15'24.77"N) (19/2/2020–5/3/2020) (Fig. 2.A). Both reefs are located in the central Red Sea, off the coast of Thuwal, Saudi Arabia. Reefs were selected for proximity to the coastline, for ease of access, and presence of both *T. maxima* and L. *lambis*. Suitable areas were located along the back-reef where *T. maxima* clams were accessible by snorkeling, and within ~3–5 m of a sandy sea-floor. *L. lambis* were collected from the nearby reef crest, with one individual tagged per trial. *L. lambis* were collected two at a time and placed into a plastic holding box filled with ~10 cm of water on-board the research boat. This allowed for exposure of just the top-most part of the shell for efficient tagging, which took ~5 mins, after which they were placed back in the water simultaneously to the speakers.

2.2.2.2. Controlled exposure experiments (CEEs). One *L. lambis* was placed in the location along the reef selected for the trial, below one *T. maxima* (Fig. 2.B). The maximum amount of trials achievable per day was four. Each session, two trials were run simultaneously on the same reef, approximately 50 m apart. Per session, one trial used boat playback, and the other used ambient noise playback. This distance was confirmed to be sufficient to ensure playbacks were not audible in the respective trial, using the program Raven Pro (1.6.5) to inspect data. Soundtrap ST300 hydrophones (Ocean Instruments, set to record continuously at 96 kHz, individually factory calibrated) were placed ~50 cm away from the *T. maxima*, the same distance from the speakers as the animal. UW30 (Lubell) underwater speakers, paired with an amplifier (M033N, Kemo) were used for the playbacks. The speakers were swum from the boat and suspended 1 m off the seafloor with weights and a subsurface buoy. A large amount of slack was left in the rope, connecting the speakers to a buoy with the power source to minimize sound interference from waves (Fig. 2.B).

Overall, each experiment lasted 2 h. In the boat treatment, the playback track consisted of one 1 h track of ambient playback, called the ambient pre-treatment period (to ensure acclimation/settling of individuals after tagging), followed by one 1 h track of a concatenated boat playback track. Boat tracks were randomized to ensure the same boat track was not played twice in succession near the same location (Figs. 2.C, 3.A). The ambient control treatment likewise was one 1 h ambient pre-treatment playback for acclimation, and an additional 1 h

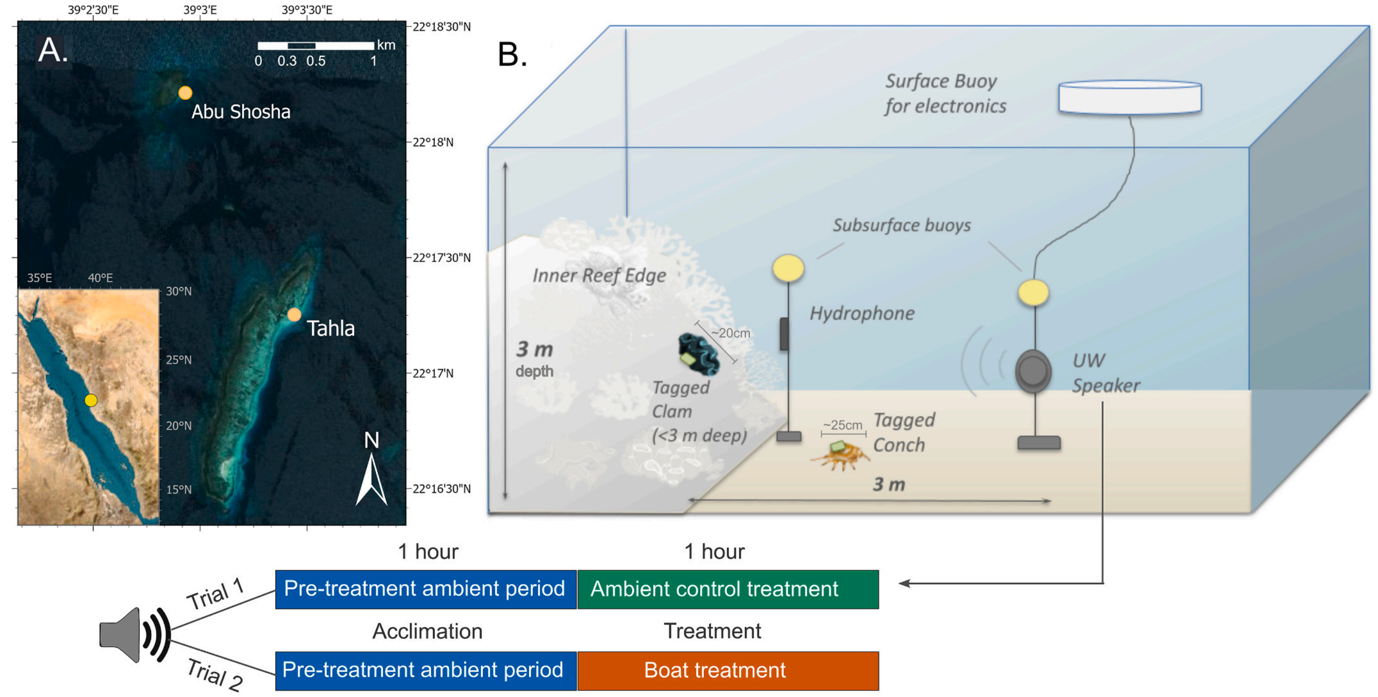

Fig. 2. A. Reef locations of trials in Saudi Arabia, showing relative location in the Red Sea (inset). B. Experimental set-up of Controlled Exposure Experiments (CEEs), showing *L. lambis* conch and *T. maxima* clam with Daily Diary tags. Treatment design of CEE playback tracks.

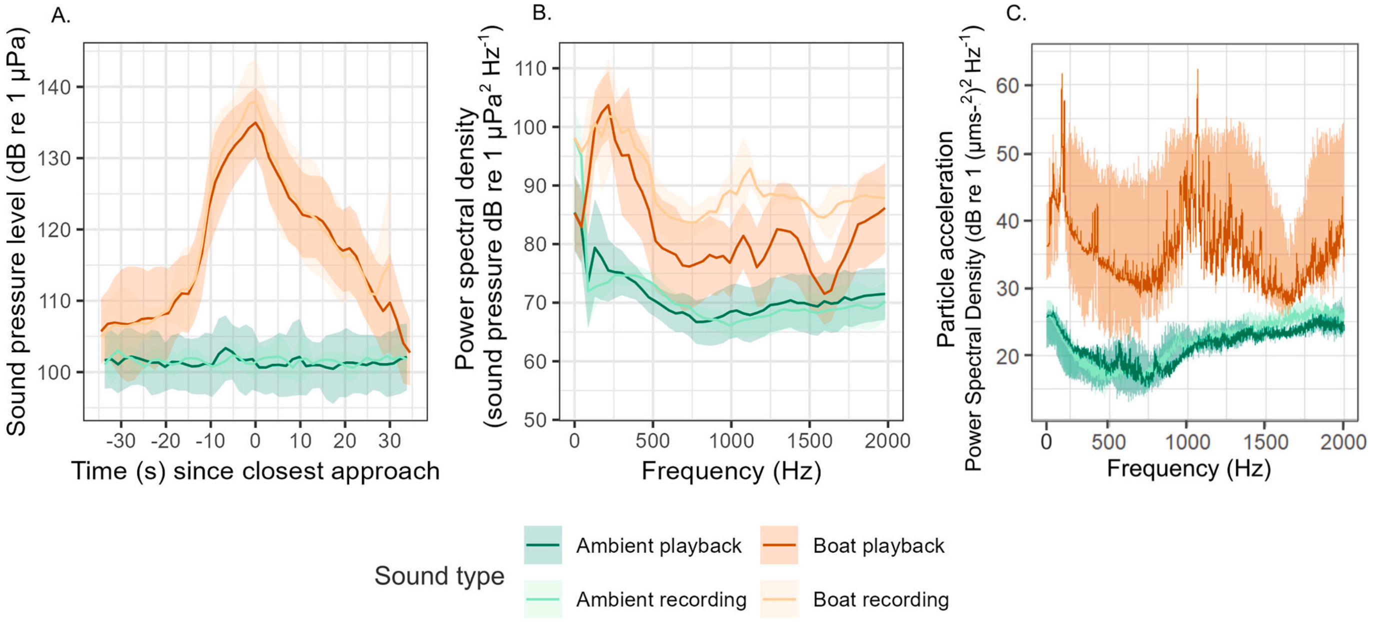

Fig. 3. A. Median sound pressure levels (SPL) and B. power spectral density (PSD) over the 1:15 min underwater recordings vs. the measured playback during the trials (using UW30 underwater speakers, and ST300 hydrophone). C. Spectral content of control and boat noise recordings, as well as the ambient conditions in the field (obtained by M20-040 Geospectrum accelerometer). Median power spectral densities (n = 3) of both playback treatments are shown, as well as the control ambient conditions in the field. 5th and 95th percentiles are shown in light colors. (FFT length = 44.1 kHz, Hamming evaluation window, 50 % overlap.)

of ambient playback, both using mixed ambient recordings from the trial reef and a nearby reef (Figs. 2.C, 3.A). Once a trial session was completed, tags were removed and returned to the boat, along with the speakers. The set-up was then moved to the next location for the second trial session of the day, approximately 20 m from the previous. While independence between the first and second session sites in the same day were not explicitly measured, interfering factors were controlled as much as possible. The distance between sessions was limited by the length of the reef/availability of clams. To account for this in the most plausible way, the opposing playback treatment was played in the adjacent site during the second trial session of the day, to control for repetition between the groups.

Lastly, while acoustic influence of shipping traffic is common in the Red Sea, it does not influence these shallow reef sites at Abu Shosha and Tahala, as the shipping lane is located further offshore in deeper water. In total 40 CEEs were conducted (ambient control treatment: 17, boat treatment: 23) involving 40 tagged individuals of both *T. maxima* and *L. lambis*. Final sample size for results from working tags was n = 22 for *T. maxima*, and n = 14 for *L. lambis*.

2.2.2.3. Playback tracks. Recordings of three different local boats (with engines of 200 kW or more) were taken using a Soundtrap ST300 hydrophone (Ocean Instruments, NZ) set at a sampling rate of 96 kHz, with a high pre-amp gain to increase sensitivity of measurements, at the experimental reef Abu Shosha. The hydrophone was placed at 6 m depth, and the boats each passed within 10 m over the hydrophone at a continuous speed, approaching from about 100 m away. These boats were chosen as typical representations of watercraft the local *T. maxima* and *L. lambis* in the area would be exposed to. A minimum of three separate boat recordings for separate playback tracks (within the boat treatment) were important to ensure the resulting reaction was not due to a certain individual boat sound, but boat noise in general (i.e., pseudoreplication). Tracks were edited and assembled with the audio editing program Audacity. Three one-hour ambient playback tracks were made (A1, A2 & A3) using five 1:15 (m:ss) ambient recordings from the experiment reef Abu Shosha, as well as three one-hour tracks with boat passes using three 1:15 (m:ss) recordings from the three separate boats (B1, B2, B3). These were concatenated and looped using a 2 s linear crossfade. Each boat track alternated between boat passes and ambient clips, to minimize any "jolting" effect in the playback, resulting in 25 total boat passes during one playback session. All tracks were band passed with 150–2000 Hz filters, anticipating speaker limitations and expected hearing of the study species based on other mollusk sensitivities (Charifi et al., 2017). Ambient and boat tracks were normalized to the same sound levels, to ensure the original sound levels were not hidden confounding factors, rather than the sound signatures themselves. Before CEEs commenced, the sound field of playbacks was analyzed with measurements from a calibrated triaxial accelerator and hydrophone sensor (M20-040; sensitivity 0–3 kHz; Geospectrum Technologies, Dartmouth, Canada), to measure perceived pressure received by the organisms. The RMS SPL is the level of the root-mean-square sound pressure level, expressed in dB 1 μPa in water. For sound pressure, the RMS SPL (100–1600 Hz) of the boat playbacks was *∼130* dB re 1 μPa at the point of closest approach, and * ∼ 100* dB re 1 μPa of the ambient playbacks (Fig. 3.A, B; SPL over time & PSD). A customized R script (R Core Team, 2025) was used to analyze 1.15 min recordings of the playbacks to define characteristics (Campbell, 2020). It was found that the trial playbacks mimicked the same SPL and Power spectral density (PSD) signatures, at slightly lower levels, as expected due to attenuation of sound from the speakers (Fig. 3.A & B). PSD expresses the variability in sound levels by frequency.

Most marine life, including invertebrates primarily perceive sound using particle motion rather than SPL (Popper and Hawkins, 2018; Nedelec et al., 2016). In addition to SPL, monoaxial particle acceleration was measured using a calibrated triaxial accelerometer (M20-040; sensitivity 0–3 kHz; Geospectrum Technologies, Dartmouth, Canada) connected to a digital field recorder (Zoom F8 field 33 recorder, sampling rate 48 kHz, Zoom Corporation, Tokyo, Japan), according to Nedelec et al. (2016). All recording levels were calibrated using a 1 kHz pure sine wave signal of known voltage recorded in-line with an oscilloscope. For analysis, 20 s of motorboat passes from the three different boats used in the experiments were appended together into a single recording, 20 s from each of three different ambient recordings were similarly appended into a single recording. The recordings were analyzed with the paPAM acoustics analysis package using MATLAB v 2016a (Nedelec et al., 2016) (Fig. 3.B).

2.2.2.4. Movement monitoring. As both species are diurnally active, all experiments were held during the day (between 7:00–16:00). Firstly, animals were tagged with Daily Diary (DD) animal movement tags (Figs. 2.B, S1). A total of 40 individuals of both species (*T. maxima* and *L. lambis* respectively) were tagged and 40 trials in total were conducted. The DD tag (Wildbyte Technologies) is a small, electronic "smart" tag (size in waterproof box: 3 cm × 3 cm × 4 cm), powered by a 3.6 V lithium battery, and records multiple parameters of animal movement at infra-second rates, including triaxial acceleration (Wilson et al., 2008; Walker et al., 2015). Its small size allows it to be attached directly to the animal, in this case the shell of *T. maxima* and *L. lambis*, with minimal hindrance of natural movement. Tags were placed in waterproof latex balloon casings and attached on the animals with epoxy putty, under water in the case of *T. maxima* and on the boat for *L. lambis*. In both species, it was found that it was most effective to gently scrub off algae to create a surface for the epoxy to adhere to. Putty was chosen for ease of removal from the animal, causing only an imperceptible effect on the shell and causing minimal stress (Wilson and McMahon, 2006). After the experiments, tags were removed, and *L. lambis* were returned close to their location of origin. To understand the direction and type of movements performed by *L. lambis*, photos were taken before and after using a GoPro (Hero 4). These photos were then classified into categories of sex (male, female, unknown), by assessment of the shell protrusions (Walls, 1980). Movement direction was also assessed, relative to the starting position (forward, backwards, stationary), to the main reef structure (forward, backwards, stationary), and whether or not individuals found shelter (reached shelter, stopped next to it, stayed in the open).

2.2.2.5. Analysis of movement. The vector of dynamic body acceleration (VeDBA) is calculated from the tri-axial acceleration (in the x, y and z directions corresponding to the surge, heave and sway of the animal) recorded by the tag (calibrated pre-deployment) and can be used as a suitable proxy for movement-based power and therefore energy expenditure. When a tag is immobile, the vectorial sum will always equal 1 g, the Earth's gravitational field. VeDBA will show differences with respect to this resting value when the animal moves. Values higher or lower than g are given with movement, as the recorded acceleration will be superimposed on those values given by the Earth's gravitational field (Wilson et al., 2020). This allows detection of different movement states even in slow moving animals. The VeDBA values were calculated within the associated DD software Daily Diary Multiple Trace (DDMT), using the equation: VeDBA = (DAx2 + DAy2 + DAz2)0.5, where "A" is acceleration, "D" denotes the dynamic acceleration calculated given subtraction of the smoothed acceleration data from the raw, and the x, y, z represent the orthogonal axes (Wilson et al., 2020). The recorded information from the DD tag also allows specific movements to be discerned, by using tri-axial magnetometry from a solid-state compass. In the case of the bivalve *T. maxima*, the tag was placed on one side of the clam, to detect changes in opening of the valves. To assess frequency of movements, *T. maxima*'s closing movement was used for further study rather than opening movements, because the gradual nature of the clam's opening movement made it difficult to determine when this was occurring from the DD tag data alone. The closing movement was determined visually in the DD movement monitoring software program (DDMT Trace, 2018) after collection. For *L. lambis*, it was placed on the proximal flat portion of the shell, before the flared outer-lip, to detect movement via their typical 'leaps'.

2.3. Statistical analysis

R (v 3.6.2) (R Core Team, 2025) was used for analysis. The Kruskal-Wallis non-parametric test was used to examine whether *L. lambis* movement intensity was affected by the boat noise playbacks, followed by Wilcoxon rank-sum test. Hedge's G Posthoc test was further used for VeDBA results for *L. lambis*, examining any significant differences between treatments. Treatments were compared with a negative binomial generalized linear model (GLM), and differences further investigated using pairwise contrasts.

3. Results

3.1. *Red Sea patch reef soundscapes*

Sound Pressure Level (SPL) calculated using PAMGuide (from 40 Hz – 48 kHz) showed strong diurnal fluctuation of broadband levels on both Abu Shosha and Qita al Qirsch (Fig. 4), dominated mainly by invertebrate activity (snapping shrimp, of the family *Alpheidae*) as verified visually and aurally, using the software Raven (1.6.5) as well as comparison to literature examples (Lillis and Mooney, 2018). The sonic activity of simultaneous shrimp "snaps" increased the sound pressure levels (SPL) before dawn and after sunset, as well as an increase in lower frequency bands attributed to fish, mainly during the day. The presence of a typical dawn and dusk chorus of fish (Fig. 4) in the low frequency band (100 Hz–1000 Hz) was present on both recordings. However, this natural pattern in SPL levels was disrupted on the offshore patch reef Qita al Qirsch, where sound signatures of vessels were present even during the night (in total ~ 10 h during 24 h), presumably in the form of shipping (Fig. 4.B).

Further inspection of the sound characteristics revealed the sound masking properties of the boat engines, across all frequencies, but especially in the lower frequencies (1–10 kHz), important for communication in marine life (Nedelec et al., 2016). It is clear that much of the low frequency band of fish vocalizations, as well as part of the high frequency shrimp band can be masked by the sound of a boat engine (Fig. 4.B).

3.2. *Movement frequency for T. maxima & L. lambis*

Heteroscedasticity was tested using Levene's test, which confirmed significant variance differences between treatments for *T. maxima* (F(2, 855) = 21.54, P < 0.001) and *L. lambis* (F(2, 543) = 3.71, P = 0.025). Due to overdispersion in the data, (*T. maxima* dispersion = 1.72, *L. lambis* dispersion = 6.65; based on Pearson residuals), a negative binomial GLM was used.

For *T. maxima*, results showed significantly lower movement counts during both the ambient control (β = −1.97, P < 0.001) and boat treatment (β = −0.83, P < 0.001) compared to the ambient pre-treatment period, in a trend corresponding with *L. lambis*. Post-hoc pairwise comparisons revealed that *T. maxima* exhibited significantly more movement during the boat playback than during the ambient control treatment (P < 0.001) (Fig. 5.A).

For *L. lambis*, the model revealed a significant effect of treatment phase on movement counts (P < 0.05). Post-hoc pairwise comparisons indicated that movement was significantly reduced during the ambient control treatment compared to the ambient pre-treatment period (P < 0.05). No significant differences were observed between the boat treatment and either the ambient pre-treatment period (P > 0.05). However, estimated rate ratios revealed moderate to large effect sizes: Although movement during the boat treatment was not statistically distinguishable from either ambient phase, it was approximately 29 % higher than during the ambient control, suggesting a potential arousal in response to boat noise. *L. lambis* made more movements in the ambient control than the boat treatment until the 30 min mark, whereby the latter increased (Fig. 5.B). While movement was suppressed during the first half hour of the boat treatment, it proceeded to ramp up in the second half hour. *L. lambis* appeared to habituate and proceeded to make more movements, leading to cumulative differences in movement towards the end of the experiment.

3.3. *Vector of dynamic body acceleration (VeDBA) values for L. lambis*

The mean VeDBA was highest in the ambient control treatment at 0.034 g (SE ± 0.06), followed by the ambient pre-treatment period, at

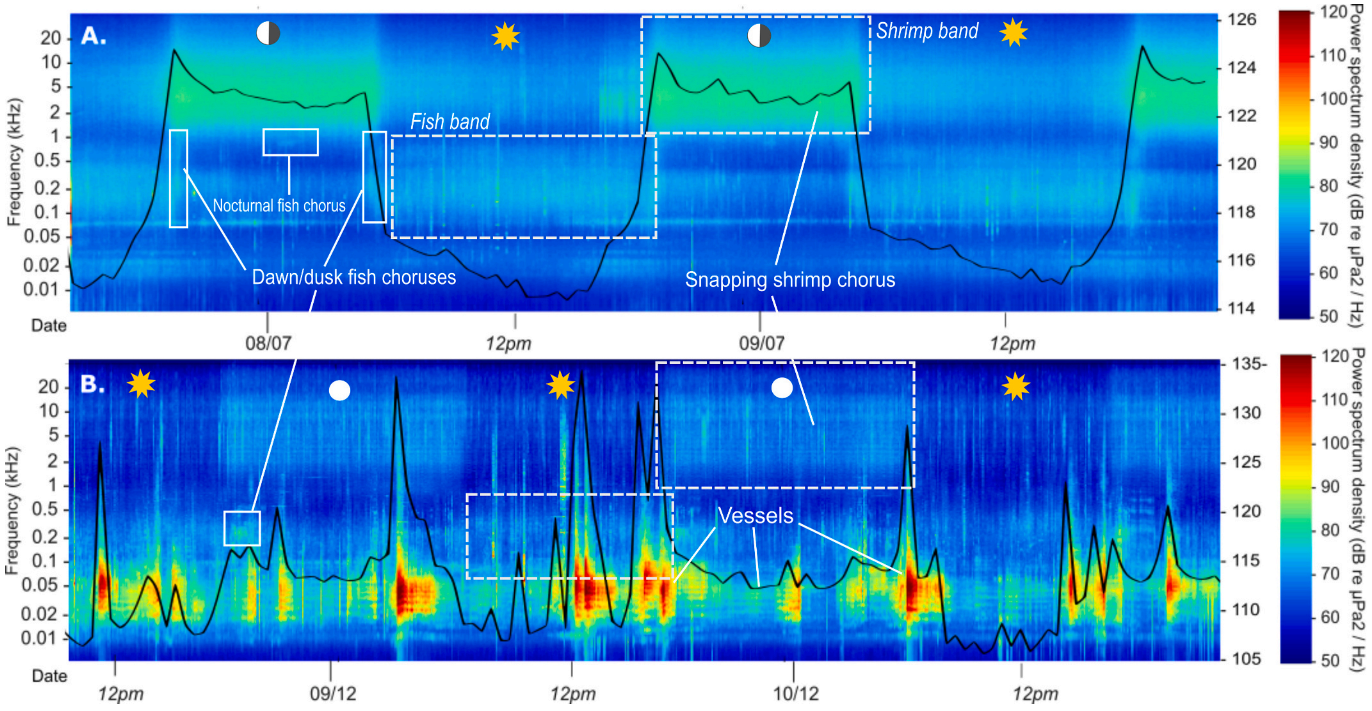

Fig. 4. Long-term spectral averages (LTSA), overlaid with broadband sound pressure level in black (SPL dB re 1 μPa, calculated from 40 Hz–48 kHz) of two Red Sea reef locations: A. Abu Shosha (07–10/07/19) inshore shallow reef consequently chosen as the first experiment location B. Qita al Qirsch (08–11/12/19) offshore reef, with the hydrophone located on a steep wall (also known as Shark Reef). Both LTSAs were made using the packages CHORUS (averaging time of 0.08333, minimum level 50 dB, and a maximum level 120 dB) and PAMGuide in MATLAB (Merchant et al., 2015; Gavrilov and Parsons, 2014). Lower frequency bands dominated by fish and higher bands by shrimp are denoted by white dotted line. Examples of dawn/dusk and nocturnal fish chorus are also labeled, denoted by a white square outline. Examples of vessel noise (seen as red spikes in SPL) caused by shipping and other recreational/fishing vessels are also labeled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

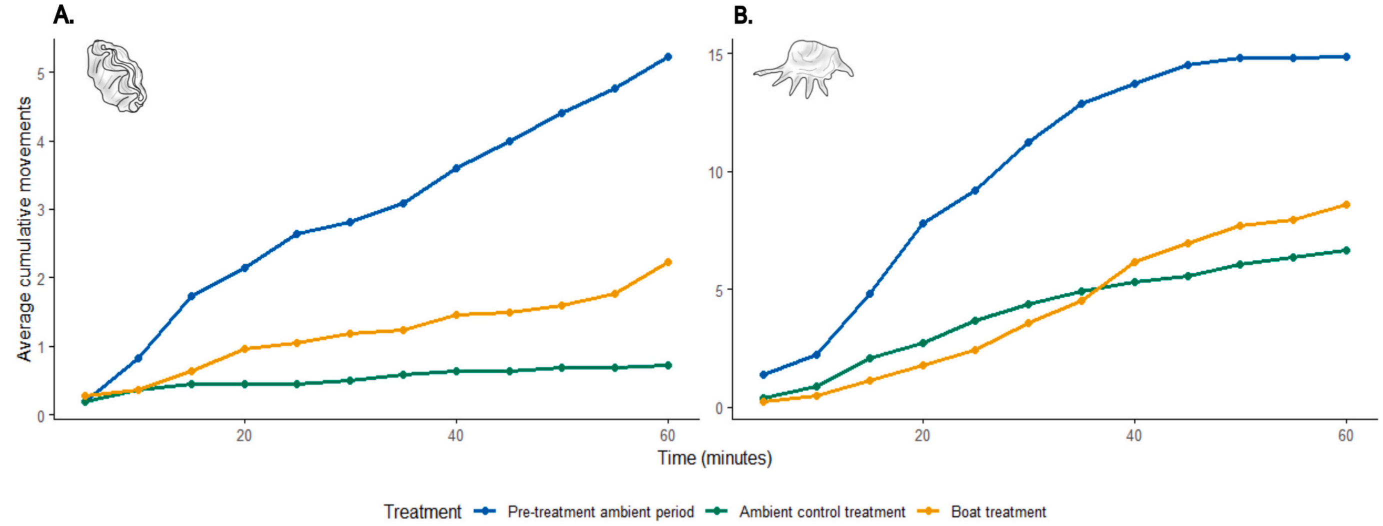

Fig. 5. Average cumulative movements of (A) *T. maxima* and (B) *L. lambis*, plotted over time (in minutes) on the x-axis. The y-axis represents the cumulative mean movement count of all individuals in that time bin. For *T. maxima*, cumulative movements were substantially higher during the ambient pre-treatment period compared to both the boat and ambient control treatments. A generalized linear model (GLM) with a negative binomial distribution indicated significantly lower movement counts during both the ambient control ($\beta = -1.97$, $P < 0.001$) and boat treatment periods ($\beta = -0.83$, $P < 0.001$) compared to the ambient pre-treatment. For *L. lambis*, the GLM also showed a significant overall effect of treatment ($P < 0.05$), with post-hoc comparisons revealing reduced movement during the ambient control period compared to the ambient pre-treatment ($P < 0.05$), but no significant differences between the boat treatment and either ambient phase.

0.147 g (SE ± 0.025), then the boat treatment at 0.058 g (SE ± 0.002) (Fig. 6). Statistical analysis revealed significant differences among treatments (Kruskal–Wallis test, $\chi^2 = 8.19$, df = 2, $P < 0.01$). Wilcoxon's post-hoc test then showed a significant difference between the ambient control and boat treatments ($P < 0.01$), as well between the ambient pre-treatment period and the ambient control ($P < 0.01$). The ambient pre-treatment period and boat treatments showed no significance ($P = 0.07$). Additional analysis using Hedge's G test showed the largest impact was between the ambient control and boat treatment (g=0.64, medium effect) showing that boat noise significantly reduced the movement of *L. lambis*. A small but noticeable effect was present between the ambient pre-treatment period and ambient control treatment (g = -0.47) (Tables S3 & S4). Due to non-independence of repeated measures, however, results should be interpreted cautiously. While further statistical comparisons of mean VeDBA across treatments did not yield significant differences, moderate effect sizes between pre-treatment and boat playback suggest potential biological relevance.

3.4. Movement direction of *L. lambis*

Still photographs taken with a GoPro (HERO 4) before and after experiments of *L. lambis* were visually analysed for directionality relative to the starting position and shelter (Fig. 7, Table S1). As conches are visual creatures, it was thought they may direct themselves towards the largest shelter available, the main reef. Due to corrupted files, only 23 photos were available, but were spread evenly between treatments with

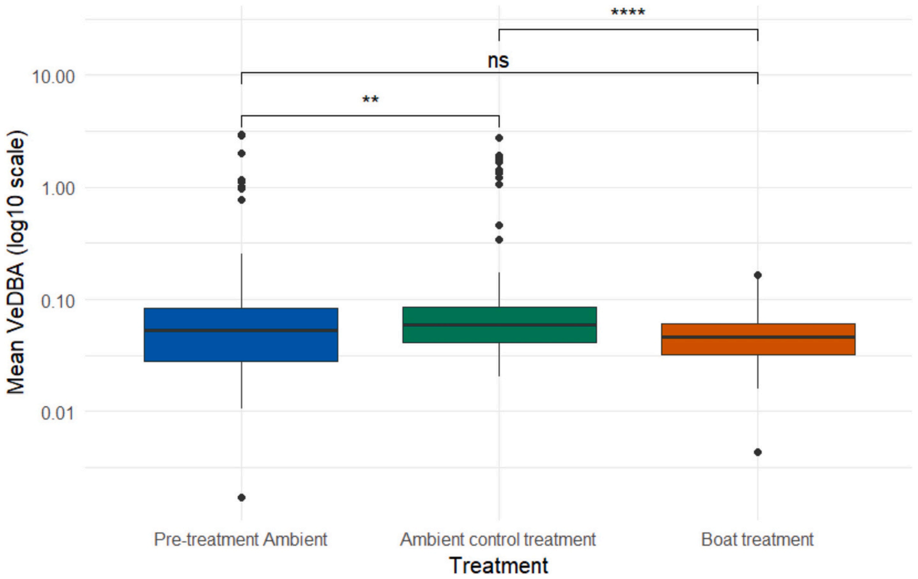

Fig. 6. Mean vector of dynamic body acceleration (VeDBA) (g) of individual movements per treatment as measured by the Daily Diary tag on *L. lambis*, over 1 h for the ambient pre-treatment playback (mean = 0.147 g, median = 0.072 g, SE ± 0.025 g), ambient control treatment (mean = 0.337 g, median = 0.064 g, SE ± 0.066 g) and boat treatment (mean = 0.058 g, median = 0.056 g, SE ± 0.002).

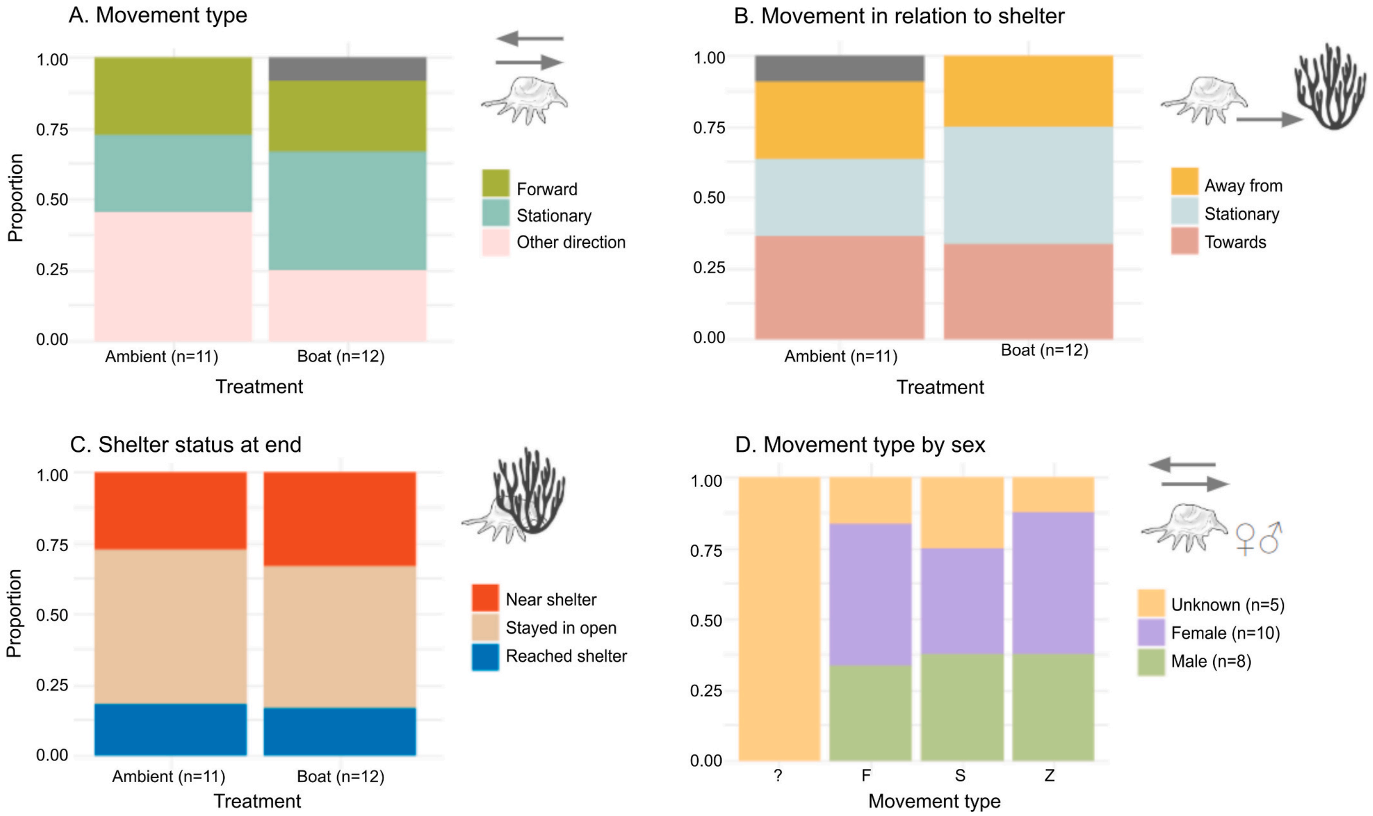

Fig. 7. Visual assessment of *L. lambis* activity during CEEs, noting A. movement type, B. movement direction in relation to shelter, C. whether or not individuals reached shelter at the end of the experiment, and D. movement type by sex showing F (forward), S (stationary), Z (other) and ? (where neither sex nor movement was known, n = 1). The grey in (A) and (B) represent missing data from one instance where no video was available.

n = 11 in the ambient treatment, and n = 12 in the boat treatment. Movement type was split into three categories: forward, stationary and other (including backwards and diagonal movement). Out of all individuals, a higher proportion of individuals stayed stationary in the boat treatment than the ambient treatment, (0.417 vs 0.273 respectively). A similar proportion moved forward in the boat vs ambient treatment (0.25 vs 0.273), while the ambient treatment saw a higher proportion of individuals move in the "other" category compared with the boat treatment (0.455 vs 0.25). In relation to shelter, similar proportions in both ambient and boat treatments moved towards (0.333 vs 0.364) and away from it (0.273, 0.25) (Fig. 7.B). End status, or the location where the conch was seen at the end of the experiment, saw a similar proportion of conch reaching shelter in ambient (0.182) and boat (0.167) treatments, while a higher proportion reached within a radial distance of 20 cm away from shelter (ambient = 0.273, boat = 0.333). The highest proportion of individuals in both groups respectively remained in the open (ambient = 0.545, boat = 0.5) (Fig. 7.C). While it was postulated *L. lambis* may move forward regardless of position to shelter, no significant difference was found (fishers test, $p > 0.05$). Finally, of the 23 individuals, 10 were female, 8 were male and 5 did not have shell protrusions adequate for assessment (Table S1). Sex was found non-significant to movement type ($\chi^2(6) = 4.26$, $P > 0.05$).

4. Discussion

A high prevalence of boat noise in a case study (Fig. 4.B), lead to the current study on the potential impacts of this noise. Two large invertebrate species (*T. maxima* and *L. lambis*) were found to change their behavior during exposure to boat noise.

4.1. Soundscapes of Red Sea reef ecosystems

This study provides the first acoustic fingerprint of a mid-shelf patch reef, and an inshore shallow reef, in the Saudi Arabian central Red Sea. Marine soundscapes are a relatively new area of study and to date no Red Sea reefs have been characterised. Our data showed boat noise was prevalent on the mid-shelf reef (Qita al Qirsch) showing incidences of vessel noise during the day as well as nighttime, the latter assumed to be the influence of shipping rather than recreational vessels. The small, but deep mid-shore reef presents similar attributes to those reported for other tropical reefs studied. A pronounced dawn and dusk chorus is also present (Cato, 1978) that consists of a combination of a ramping up of nocturnal invertebrate activity, and the tendency for fish to increase low frequency communication before coming to rest (or feeding, if nocturnally active) during the night. The frequency bands where fish calls are typically identified is between 50 and 1000 Hz (Amorim, 2006; Popper and Hawkins, 2019), while the higher frequency bands around 2-15 kHz are dominated by the invertebrate snapping shrimp (Au and Banks, 1998; Lillis and Mooney, 2018; Lillis et al., 2017) (Fig. 4.A, B). Snapping shrimp make broadband impulsive sounds, with bubbles erupting at their claw-tips, creating the well-known crackling of a reef soundscape (Au and Banks, 1998). The dusk chorus increased ambient broadband day-time SPL levels from 105 dB (re 1 μPa) by approximately 8 dB (re 1 μPa) at dusk, which ramped down again after dawn at Qita al Qirsch, and by over 10 dB (re 1 μPa) on the shallow, inshore reef Abu Shosha, from 114 dB to 125 dB (re 1 μPa). As a comparison, a soundscape study on the U.S. Virgin Islands, at three reefs, measured between 5 and 14 m, analyzed SPL values between the frequency range 2–20 kHz, with the lowest SPL values between 108 and 112 dB (re 1 μPa) and at peak levels between 111 and 115 dB (re 1 μPa) (Kaplan and Mooney, 2015).

The study of underwater soundscapes is a rapidly growing pursuit, as underwater sound is gaining recognition as one of the most integral parts for communication & navigation of marine organisms (Pijanowski et al., 2011), though earlier studies began around 40 years ago (Cato, 1978). Reproducible standard methods for recording are also being developed to estimate biodiversity, or health of reefs using hydrophones to produce continuous recordings (Elise et al., 2022; Staaterman et al., 2017; Lin et al., 2021). These periodic recordings can give key insights into the health of a reef habitat, whereby higher quality reefs are significantly louder, and have a higher load of acoustic events (transient sounds, such as snapping shrimp) (Gordon et al., 2018), and provide an option for monitoring reef health that is easier than most modalities, and can be deployed over large scales and time periods (Dimoff et al., 2021). The presence of a typical reef sound signature is important, as sound will propagate over longer distances, notably attracting larvae for settlement on the reef (Gordon et al., 2018; Vermeij et al., 2010). It is clear that habitat degradation causes a sharp decline in the acoustic strength and propagation of this signature, reducing the probability of repopulation by settlement of larvae (Butler, 2016). The effect can potentially be reversed, with a novel conservation method found to be successful in attracting larval and juvenile species of fish with playing back healthy sounds on the reef (Simpson et al., 2005; Gordon et al., 2019). The application of this might benefit inshore reefs of lower quality in the Red Sea.

Concern has already been raised about the vulnerability of inshore reefs, such as the study reefs Abu Shosha and Tahla, with some key indicators marking susceptibility to stressors. For example, inshore reefs of the study area (Thuwal) have a high coverage of turf algae and abundance of a symbiotic algae-farming herbivore, the damselfish *Stegastes nigricans*, and higher rates of coral mortality and disease has been associated with the presence of this duo (Khalil et al., 2017). Inshore reefs can also be less resilient to coral bleaching events, with less exposure to cooler currents during heatwaves (Fifer et al., 2021; Nakamura and Van Woesik, 2001; Page et al., 2021). There is a unique opportunity to conduct long-term studies of these vulnerable reef ecosystems, which are in close proximity to a major shipping zone, and investigate multiple stressors to marine life.

4.2. *Tridacna maxima movement in response to boat noise*

During the first hour after tagging, *T. maxima* showed an increased frequency of closing movements, suggesting a predator response (Land, 2003) induced by handling (Fig. 5.A). During the boat treatment clams produced more closing movements than in the ambient control ($P < 0.001$). This differential response may be an indicator that boat noise on its own is a stressor to the clam, inspiring more protective movements, though no visual threat is immediately present.

Only one other study has exposed *T. maxima*, or any Tridacnidae, to controlled noise (Doyle et al., 2020). *T. maxima* were filmed, and exposed to boat noise and an aquatic pump (to simulate water flow from a boat engine). During the presence of the speaker and aquatic pump (before playback or applied flow) the clams exhibited more mantle twitches (the precursor to closure) than without, similar to the increase of full closures in our results. Doyle et al. (2020) then proceeded to rub along the mantle of the clam with a pencil eraser to stimulate closing, and measure latency to close under the separate treatments, with the clams becoming slower to close fully, only under both sound and flow combined, and indicating the distracting potential of sound disturbance. This behavior has been shown in other marine organisms such as the Caribbean hermit crab, which allowed an object to approach more closely under playback of noise, as well as flashing lights, than an object with just noise (Chan et al., 2010).

Our results suggest that noise may have the potential to disrupt the energy balance of the clam, closing more frequently and retracting its mantle under boat noise, reducing time for both filter feeding and photosynthesizing, as photosynthesis by symbiotic algae provides much of the energy balance of this species (Norton et al., 1993). It would be interesting to further test this hypothesis in a similar manner to both Doyle et al. (2020) and Chan et al. (2010), adding another stimulator such as an object to produce a visual cue, or lights.

4.3. *Lambis lambis movement in response to boat noise*

The calculation of the Vector of Dynamic Body Acceleration (VeDBA) gave a key insight into energy expenditure, and therefore potential stress levels of *L. lambis*. Previous research has shown *L. lambis* will increase the intensity of up/forward movement (shown in Fig. 1.B) in “escape locomotion” when posed with a threat such as the predatory cone snail, shark or octopus (Berg, 1974; Heller, 2015). The combination of the information from movement frequency, and VeDBA as given by the DD tag, provided evidence for a change in the behavior under boat noise. Movement count during the boat treatment was 29 % higher than during the ambient control treatment (rate ratio = 1.29). While this difference was not statistically significant, the moderate effect size may reflect a biologically meaningful response to anthropogenic noise.

Visual, tactile and chemical sensory modalities are used most commonly by *L. lambis* in detection of food, predators and mates (Heller, 2015). While acoustic pressure does not affect these modalities directly (Walsh et al., 2017), acoustic interference has been shown to influence behaviors in macroinvertebrates in an indirect way (Roberts and Laidre, 2019). Usually, movements of *L. lambis* are leisurely when travelling for foraging and sifting the substrate for algae and detritus, but increase in pace and intensity of movement when evading a threat (escape locomotion) (Berg, 1974). The VeDBA measured in the first hour of ambient pre-treatment playback, was lower than during the ambient control treatment (Fig. 6, 0.147 g, SE ± 0.025, $P < 0.05$), despite the fact that more movements were made during this time period (Fig. 5.B). A higher “escape locomotion” was an expected escape reaction after tagging and release, however it took an hour of acclimation to initiate. In comparison, individuals in the boat treatment indicated lower intensity of body movement, in conjunction with the reduced movement count in the first 30 min.

Mean VeDBA was highest during the ambient treatment (0.337 ± SE 0.066), followed by the ambient pre-treatment (0.147 ± SE 0.025) and lastly the boat treatment (0.058 ± SE 0.002) (Fig. 6). Although this difference seems very slight, for a slow-moving, small organism such as the conch it is more relevant than one which is large and fast-paced (Wilson et al., 2020). Overall Dynamic Body Acceleration (ODBA) has previously been described, for the Caribbean queen conch (*Strombus gigas*), another member of the *Strombidae* family with similar behavioral patterns to *L. lambis* (Dujon et al., 2019). ODBA is highly comparable with VeDBA, measuring the Overall Dynamic Body Acceleration, simply based on the absolute dynamic acceleration values, from the three acceleration axes summed together (Wilson and McMahon, 2006). They found an ODBA of 0.05 g as a mean over a full cycle of movement, and maximum values often <0.1 g.

4.4. *Start and end position of L. lambis*

The visual nature of the invertebrates was indicative of the behavior noted, where during the ambient control treatment, with no threat perceived, they continued to move. There is potential that the conches tested at the Tahla reef site may have been moving more during the boat treatment, as they were more accustomed to a low frequency signature of waves crashing directly above them, on the reef flat near the outer edge of the reef open to the ocean, therefore none remained stationary. The origin of sound direction is probably not perceived by invertebrates (Solé et al., 2023; Coffin et al., 2004) but the low frequency sound may have created confusion.

Most of the individual *L. lambis* were collected from under or next to shelter created by the main reef structure, therefore visually locating and seeking shelter was assumed to be a potential natural response. However, from the individuals analyzed from the GoPro recordings (n = 23), around half remained out in the open in both treatments (Fig. 7.A, B). It is possible that during the day *L. lambis* is less cautious of predation by larger creatures such as elasmobranchs (typically crepuscular/nocturnal predators), therefore the results may be different at dusk or night, when activity patterns may differ. It is also possible that this part of the Red Sea is not as heavily populated by these predators, due to overfishing (Spaet and Berumen, 2015; Shellem et al., 2021). *L. lambis* may also bury itself in the sand, however this behaviour was not noted. Differences in movement type between the sexes differed only marginally and was found non-significant (Fig. 7.D), which was also the case in a study monitoring movement and home range of L. *lambis* (Konzewitsch and Evans, 2020).

5. Conclusions

Both the Spider Conch *L. lambis*, and the Giant Clam *T. maxima* changed their behaviour under conditions altered by playback of small outboard motor boat noise, on a small Red Sea near-shore reef. Reef ecosystems are particularly vulnerable to sound pollution, relying on sound cues for navigation by fish and coral larvae to populate an area (Gordon et al., 2018; Vermeij et al., 2010). This replenishment will become increasingly critical as the incidence of coral bleaching, and coral die-offs become more common with climate change, as well as over-fishing continuing on local reefs (Khalil et al., 2013), degrading healthy soundscapes and therefore navigation cues. As inshore reefs, Abu Shosha and Tahla are already susceptible to pressure from bleaching (Fifer et al., 2021). Our study shows that further investigation is warranted on the impacts of boat noise on invertebrates, including any physiological changes such as stress, metabolic rate or energy expenditure.

Although this study does not focus on large vessel noise such as shipping, the implied effects on offshore reefs are presumably similar, if not more pronounced due to the extended exposure times, potential higher sound pressure levels, and high frequency of vessel presence. Anthropogenic noise in the ocean continues to rise worldwide. Open ocean ambient noise levels have increased approximately 3.3 dB per decade between 1950 and 2007, in conjunction with global economic trends, and are predicted to continue to increase (Frisk, 2012). Shipping (Larayedh et al., 2024) has been shown to contribute substantially to the entire Red Sea coastal soundscape. A shipping lane with such a volume of ships per year as the Suez Canal Red Sea connection to Europe and Asia (Alahmadi et al., 2019) must be characterized further with insitu measurements in order to understand the effects this will continue to have on marine life and coastal reef ecosystem drivers already under pressures from climate change and pollution, and allow for mitigation measures to effectively be put into place.

This study on behavioral changes of invertebrates in response to boat noise adds to a growing body of evidence showing that boat noise is a threat that must be regulated to meet goals of halting biodiversity losses by 2030.

CRediT authorship contribution statement

M.N. Havlik: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **N.R. Geraldi:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Conceptualization. **L.W. Hopkins:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. Hubert:** Writing – review & editing, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L. Chapuis:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **L.P. Gaffney:** Writing – review & editing, Methodology, Investigation. **R.P. Wilson:** Writing – review & editing, Supervision, Software, Resources, Conceptualization. **S.D. Simpson:** Writing – review & editing, Supervision, Resources, Conceptualization. **F.J. Juanes:** Writing – review & editing, Supervision, Methodology, Conceptualization. **C.M. Duarte:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.118650.

Data availability

Data will be made available on request.

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