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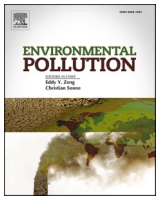

Motorboat noise playback during development limits reef fish growth and impairs predator responses with carryover effects

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ABSTRACT

Motorboat noise has been found to affect the physiology, behaviour and even survival of embryos, juveniles and adults; however, whether effects persist beyond a brief period of noise exposure or are cumulative throughout life is currently unknown. We evaluated the long-term effects of motorboat noise playback on the escape response and growth of a common reef damselfish, *Acanthochromis polyacanthus*. In a tank-based experiment, using a split-brood design, fish were exposed to playback of motorboat noise or reef sound prior to hatching (parents and embryos) and/or as juveniles for up to 78 days, and were subsequently tested for their escape response in the absence of noise and measured for growth. We found that individuals exposed to motorboat noise prior to hatching and as juveniles were less likely to respond to a simulated predator attack than those that had experienced only reef sound, and when they did respond they were more likely to swim towards the predator. We also found that individuals exposed to motorboat noise as juveniles were smaller compared to those exposed to reef sound, regardless of whether they were exposed to motorboat noise or reef sound prior to hatching. Our results demonstrate that exposure to motorboat noise during early development has the potential to affect growth and disrupt the escape response of juveniles, even when the escape response occurs in relatively quiet conditions. Limiting motorboat traffic close to reefs during the breeding season may mitigate the adverse effects of motorboat noise on reef fishes during the vulnerable early life-stages.

1. Introduction

Anthropogenic noise in marine environments is now recognised as a pollutant that can affect key indicators of ecological performance, including behaviour (e.g., communication, foraging, anti-predator responses), physiology (e.g., heart rate, growth), survival and reproduction (e.g., Simpson et al., 2016; Fakan and McCormick, 2019; Nedelec et al., 2022). One of the most prevalent sources of anthropogenic noise in marine ecosystems is small motorboats, which are predicted to increase markedly in number in coming years (GBRMPA, 2019, UNCTAD, 2020). To date, most studies evaluating the effects of motorboat noise have examined direct responses to short-term or single noise exposures (e.g., Holmes et al., 2017; McCormick et al., 2019). Few studies have examined the longer-term effects of repeated exposure (e.g., Radford et al., 2016; Neo et al., 2018; Nedelec et al., 2022), which is likely to occur in natural environments when multiple boats visit or transit an area. The impact of boat noise on fishes has been considered to be potentially "short lived", meaning that once the noise source moves away or is removed there are no remaining effects (Bruintjes et al., 2016; McCormick et al., 2019). However, some studies suggest the effects of boat noise can persist after noise exposure has stopped (e.g., Amoser and Ladich, 2003; Mills et al., 2020). Currently, it is unknown whether repeated exposure to boat noise of parents and their embryos, and/or juveniles, has detrimental effects that persist beyond the actual period of noise exposure to influence subsequent life-stages.

Most studies that have evaluated the effects of boat noise have focused on a single life-stage (e.g., Holmes et al., 2017; Mills et al., 2020, but see Fakan and McCormick, 2019). However, different life-stages are likely to be affected differently due to differences in acoustic sensitivity and energy allocation (Kenyon, 1996; Wright et al., 2011). Previous

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studies have found that boat noise can affect embryos during development. For example, in a field study, Jain-Schlaepfer et al. (2018) found that embryonic exposure to boat noise affected the heart rate of staghorn damselfish (*Amblyglyphidodon curacao*). A tank-based study by Fakan and McCormick (2019) also found that boat noise led to an increase in heart rate in spiny chromis (*Acanthochromis polyacanthus*) and the cinnamon clownfish (*Amphiprion melanopus)*. In the same study, Fakan and McCormick (2019) found that after hatching, spiny chromis juveniles previously exposed to motorboat noise were larger than individuals exposed to ambient playback. Exposure to boat noise during larval development has been found to disrupt behaviour but not affect growth of Atlantic cod (*Gadus morhua*) (Nedelec et al., 2015). Whether the detrimental effects of noise during embryonic development extend into the juvenile stage, or result in ontogenetic cumulative effects, is currently unknown.

Many studies of fish have found important intergenerational effects of stressors, where the conditions experienced by the parents influence the potential fitness of their offspring through nutritional, physiological or epigenetic effects in various taxa (e.g., Donelson et al., 2009; McGhee and Bell, 2014; Stratmann and Taborsky, 2014). This raises the question of whether offspring from parents that have been exposed to the acoustic stress of boat noise are more or less resilient to the stress of similar noise than offspring from parents that have not had that noise exposure. The strong physiological, developmental, behavioural and performance links among fish life-stages suggest that carryover and cumulative effects are fundamental in the shaping of existing populations and communities (McCormick and Gagliano, 2008, O'Connor et al., 2014). Given the adverse effects of boat noise on adult behaviour and physiology (e.g., Nedelec et al., 2017) and its direct effects on juveniles (McCormick et al., 2019), there is a need to understand the relative importance of the pre-hatching acoustic influences, potentially through parental effects during parental care, as opposed to the direct effects on juveniles. Furthermore, it is important to explore how acoustic stress during these two life-stages may combine to influence juvenile fitness. Studying these cross life-stage effects can help us understand the long-term effects of noise pollution and its population consequences (Lara and Vasconcelos, 2021), which may be underestimated in short-term or discrete exposure studies.

The aim of the present study was to investigate the relative influences of exposure to boat noise prior to hatching and/or during the juvenile life-stage on escape responses and growth of a juvenile reef fish. Using a split-brood design, breeding pairs of spiny chromis were maintained in ambient reef sound (hereafter reef sound) playback or motorboat noise playback treatments, and then their broods of newly hatched juveniles were split and reared either in reef sound playback or motorboat noise playback treatments. The growth and predator escape response of juveniles was then measured after 41 days. From previous research (Nedelec et al., 2017; Mills et al., 2020), we predicted that parental influences prior to hatching would limit growth in embryos in motorboat noise playback treatments, that this effect would be emphasised through juvenile development and that this would impair their subsequent performance and responsiveness to predatory challenges.

2. Materials and methods

2.1. Study species

The spiny chromis is a widely distributed damselfish species found across the Indo-Pacific, with wild adults forming pairs and breeding during the summer months (October–January) (Robertson, 1973). Parents guard clutches of embryos prior to hatching; embryonic development takes 11 days (Kavanagh, 2000). After the embryos hatch, the species has direct development (i.e., lacks a planktonic larval stage); similar to many demersal fishes, parents care for offspring (Thresher, 1984). Initially, parents care for juveniles around the nest; later, offspring use the cave in which they were hatched as shelter, staying close to their parents but gradually increasing the circumference of their range over several months, eventually dispersing into nearby waters (Thresher, 1985, author personal observations). Young may breed after 2-3 years (Thresher, 1985). For this species, the influences due to epigenetics, physiology and nutrition are inseparable from the influences of nest-tending behaviours under natural conditions. Fanning behaviour and cleaning are required to keep embryos oxygenated and healthy (Robertson, 1973; Zoran and Ward, 1983; Gross and Sargent, 1985), so if parents were removed to separate other influences on eggs, then the lack of parental care would impact the developing embryos.

Pairs of spiny chromis adults were collected using barrier nets and hand nets from shallow backreef habitat around Lizard Island (14°41′S, 145°27′E), northern Australia, during November 2016. They were then transported to indoor aquarium facilities at James Cook University, Townsville, Australia. The present study was conducted from March to July 2018 on these original pairs. All methods and research within this study were carried out in accordance with the animal ethics guidelines and regulations of James Cook University, and all protocols were approved by the James Cook University Animal Ethics Committee (approval numbers: A2408 and A2361).

2.2. Sound treatments

Sound treatments were made using archival recordings that were made at sandy-bottom locations around Lizard Island backreef in 2013. These recordings were taken from the same region as the fish in the experiment originated and represent levels of motorboat traffic that this species could realistically experience in the wild in regions of high boat traffic. Although the study was conducted several years after the sound recordings were taken, the recordings remain relevant to noise exposure conditions. Ambient reef sounds were recorded using a hydrophone during the day adjacent to healthy reefs. Boat noise was recorded from five different research station motorboats (5 m long aluminium hull with 30 horsepower 4-stroke Suzuki outboard motors). Each boat cruised at various speeds 10–100 m from the hydrophone, simulating typical boat traffic experienced around coral reefs. Recordings were taken 1 m above the seabed. Acoustic pressure was measured using a calibrated omnidirectional hydrophone (HiTech HTI-96-MIN with inbuilt preamplifier; sensitivity flat across the frequency range 0.02–30 kHz; −167 dB re 1 V μPa^{-1}; calibrated by manufacturers, High Tech Inc., Gulfport MS). Particle acceleration was measured using a calibrated triaxial accelerometer (M20-040; sensitivity following a curve over the frequency range 0–3 kHz; calibrated by manufacturers, Geospectrum Technologies, Dartmouth, Canada) and a digital recorder (Boss BR-800, 44.1 kHz sampling rate, Roland Corporation, Los Angeles, CA).

Reef sound playback and motorboat noise playbacks were created from field recordings using Audacity™ version 2.2.0 (http://www.audacityteam.org/). Five sets of each sound treatment were created by compiling reef and boat recordings from different reefs and boats, to minimise pseudoreplication. The reef playbacks were 12-h sections of ambient reef sound (played during daylight hours: 06:00–18:00). The motorboat noise playbacks were identical with the addition of a random number (minimum 3, maximum 6) of 20-min sections of motorboat noise spliced into each 12-h section of reef sound (see Fig. S1 for examples). The timing of motorboat noise sections was random within daylight hours. Silence was played during night-time hours. To control for the potential impact of the soundtrack changing from one playback track type to another in the motorboat noise treatment (e.g., if any artefacts were created in the sounds as a result of combining files), reef sound playbacks also had different reef sound sections with the same duration and timing spliced in to match the boat recordings in timing. The sound system used for playback of the treatments consisted of a battery pack (Cygnett Incharge 2500), an MP3 player (SanDisk 8 GB Clip Jam), an amplifier (18 W, Kemo Langen Germany) and an underwater loudspeaker (Lubell UW-30, University Sound, Whitehall, OH, USA,

frequency range: 0.1–10 kHz).

Acoustic pressure and particle acceleration of playbacks were recorded in one parental tank, while only acoustic pressure was measured in one juvenile tank, due to time restrictions (note that all juvenile tanks had the same dimensions; Fig. S2). Recordings were made using the same hydrophone and accelerometer as detailed above. The digital recorder used was different (Zoom F4, Zoom Corporation, Tokyo, Japan), but was calibrated in the same way (pure sine waves measured with an oscilloscope). The sound levels recorded in the field, the parent tanks and the juvenile tanks were analysed using paPAM software (Nedelec et al., 2016). Power spectral density across the frequency range 0–2 kHz (hearing range of juvenile reef fishes; Wright et al., 2010) was calculated from 30-s clips for all situations and both sound treatments using Fast-Fourier Transformation (see Fig. 1 for the acoustical representation of the field and the playback recordings).

2.3. Experimental design

Spiny chromis adult pairs (n = 28) were each placed within 200 L plastic tanks (60 × 45 cm) and maintained at 28.5°C, with a light cycle that matched natural summer conditions (12 h:12 h light:dark). Each tank contained half a terracotta pot as a shelter and a spawning site. An underwater loudspeaker was suspended at the side of the tank in the middle of the water column, so that the sides of the loudspeaker were approx. 1 cm from the side of the tank (to avoid touching the side of the tank but allow maximum swimming space for the fish), facing the shelter (Fig. S2A). Pairs were fed twice daily with O.range NRD G12 fish hatchery diet. Each pair was randomly assigned to reef sound playback (n = 14) or motorboat noise playback (n = 14). Two tanks in the motorboat noise treatment experienced equipment malfunction and were excluded from the analysis, while one pair from the reef sound

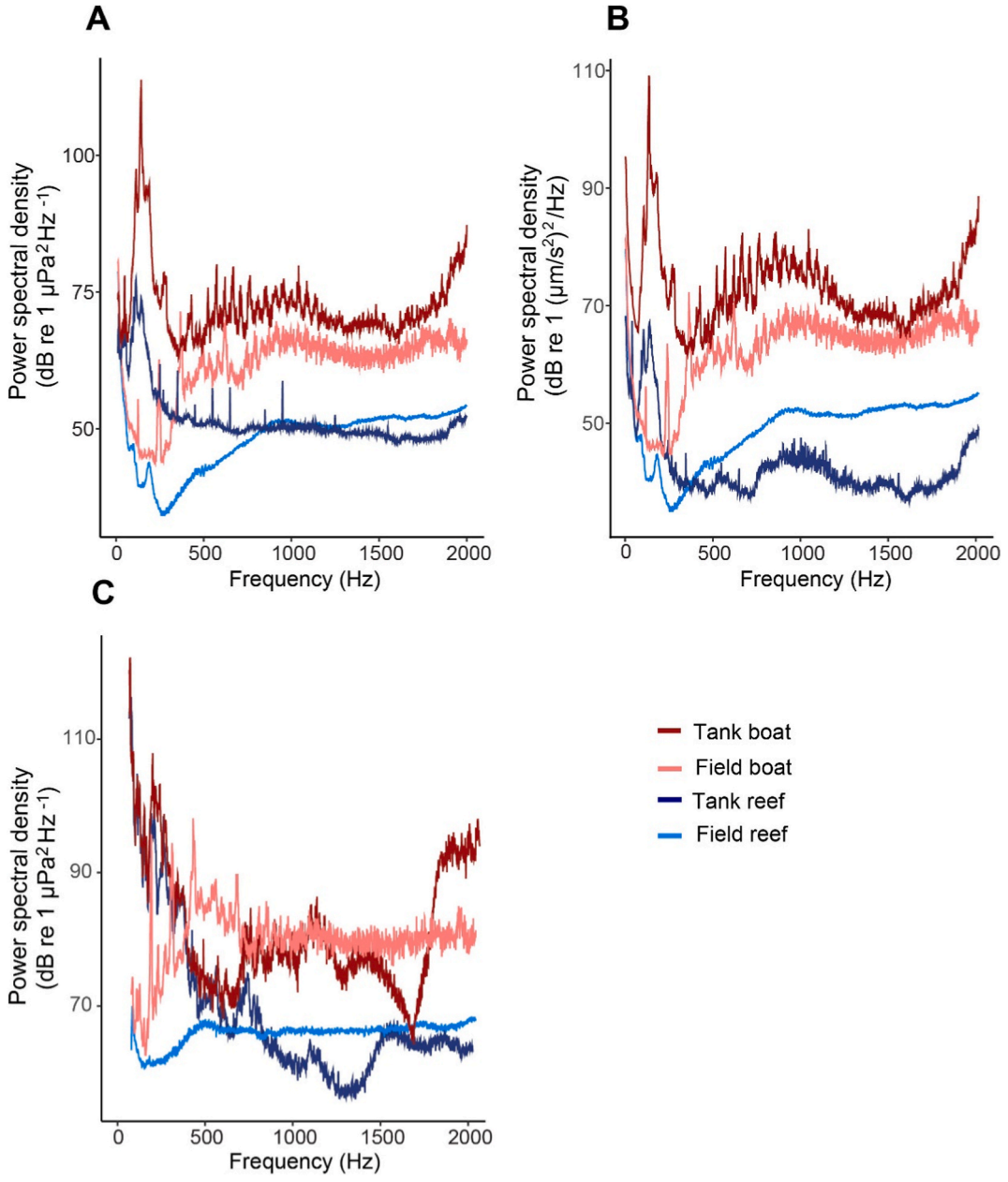

Fig. 1. Acoustical representation of the field and the playback recordings within tanks (27 locations in a 3 × 3 × 3 grid within adult tank, 1-min sample of motorboat playback and ambient reef sound playback for each case). (A) Power spectral density for sound-pressure levels and **(B)** triaxial particle-acceleration levels in parent tanks compared to field recordings. **(C)** Power spectral density sound-pressure levels in the juvenile tanks (inside the buckets that housed the juveniles) compared to field recordings (Particle-acceleration levels in the juvenile tanks were not measured due to small size of the tanks).

playback and three pairs from the motorboat noise playback did not produce a clutch. This resulted in a total of 13 breeding pairs from the reef sound playback (mean standard length: 10.7 ± 0.1 cm) and nine breeding pairs of the motorboat noise playback (10.8 ± 0.1 cm). There was no significant difference between the number of clutches produced per treatment (see Gatenby, 2018).

Tanks were checked daily for the presence of a new clutch. All pairs were exposed to their acoustic treatment for a minimum of 4 days before the first egg clutch; maximum exposure before laying was 26 days (Fig. 2). Embryos were kept with the parents throughout the 10-day embryonic phase (with day laid counted as day 0), meaning that they were exposed to the same acoustic treatment. As a result, parental and embryological effects cannot be isolated with the current design. Nevertheless, this is the natural situation in the current species, where embryos are guarded, oxygenated and maintained by the parents (Robertson, 1973).

On the day of hatching, juveniles from a brood were separated evenly into two separate 5 L buckets (21 × 19 cm), located within a 400L plastic cylindrical tank (inside circumference 100 x water depth 40 cm; Fig. S2B). Each bucket had an individual inflow and mesh-covered holes at the top in the side to allow water to drain into the main tank, from where water drained out of a standpipe. The number of individuals placed into each treatment varied according to the survival within each brood (see Table S1 for final numbers). A loudspeaker was placed in the centre bottom of the tank, facing upwards to ensure a symmetrical sound field within the tank. The buckets were sitting on terracotta pots around the outside of the tank, forming a circle around the loudspeaker. This set-up maximised the depth for the sound field while keeping juveniles in suitably sized subdivisions (Fig. S2B). Juvenile tanks were exposed either to reef sound playback or motorboat noise playback resulting in four treatments (pre-hatching – juvenile treatment): RR = Reef–Reef, RB = Reef–Boat, BB = Boat–Boat and BR = Boat–Reef (see Fig. 2). Juveniles were initially fed twice a day with *Artemia spp*. Nauplii; after three weeks, individuals were fed twice a day with O.range WEAN-S fish hatchery diet. Individuals were exposed to their respective treatment for 41 days, after which they were tested for their escape response and measured for length.

2.4. Escape-response protocol

The testing arena consisted of a circular experimental arena (diameter 20 cm) contained within a large opaque-sided plastic tank (38 cm × 58 cm x 4 cm water height) with a transparent bottom to allow responses to be recorded from below the tank. Water temperature was 27.5°C. The tank containing the experimental arena was covered with an opaque white lid, to minimise laboratory disturbances. It was illuminated for the entire duration that the fish were in the tank with a strip of LED lights around the tank, placed above the water surface (Fig. S3).

Individuals were deprived of food for 24 h prior to the start of the trials to standardise for satiation. Additionally, individuals were isolated from playback noise for approximately 14 h (overnight and the morning of the test) and isolated from conspecifics for 2 h (on the morning of the test) before the trial to allow them to acclimatise to being alone (Fig. 2). For each trial, a single fish was introduced to the testing arena via a water-filled sample jar (an attempt to minimise stress associated with the movement from the tank to the arena). After a 10-min acclimation period, a tapered weight was released into the tank from above the water surface. This was accomplished by turning off an electromagnet to which the weight was attached via a metal disc (15 mm in diameter); the stimulus was released through a white PVC tube (diameter 48.5 mm) suspended above the experimental tank, with the bottom edge at 10 mm above the water level, to provide a sudden stimulation. Responses to the stimulus were recorded on video at 480 frames per second with a camera (CASIO EX-ZR1000). Water in the experimental arena was stirred between trials to homogenize potential olfactory cues and it was changed completely every four trials. Analysis of escape response variables was restricted to the first two kinematic stages of the escape response (the first two axial bends, i.e., stages 1 and 2 defined based on Domenici and

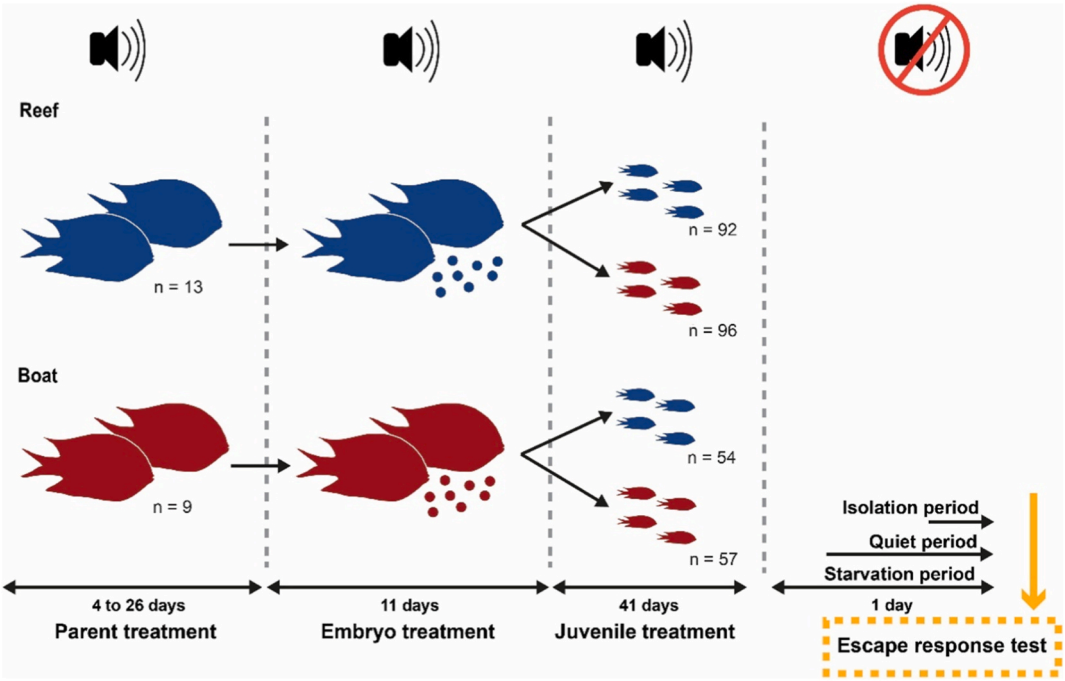

Fig. 2. Breeding and rearing design to examine the long-term effects of motorboat noise exposure on spiny chromis. Breeding pairs and embryos were exposed to either reef sound playback (blue, *n = 13 pairs*) or motorboat noise playback (red, *n = 9 pairs*). Offspring from each brood were divided randomly between juvenile reef sound (blue) and motorboat noise (red) treatments. Abbreviations: RR = Reef–Reef (*n = 92 offspring*), RB = Reef–Boat (*n = 96 offspring*), BR = Boat–Reef (*n = 54 offspring*) and BB = Boat–Boat (*n = 57 offspring*). Samples sizes correspond to the final number of individuals tested. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Blake, 1997), which is the period considered crucial for avoiding predator ambush attacks (Domenici and Blake, 1997).

Escape-response videos were analysed using ImageJ software (https://imagej.nih.gov/ij/), blind to the acoustic treatment. Distances in videos were calibrated using the diameter of the PVC tube as a reference. The distance to the stimulus at the onset of the response was recorded as a potential covariate. Variables were measured based on the centre of mass of the fish when straight (based on Webb, 1976).

Escape response variables were defined as follows:

Non-locomotor variables:

1. Responsiveness: whether individuals responded with a sudden acceleration to the stimulus (i.e., binary response: 1 = startled, 0 = not startled; Fuiman et al., 2006).
2. Directionality: whether the first detectable movement of the head during a response was orientated away or towards the stimulus (Domenici, 2010).
3. Response latency (s): the time interval between the stimulus onset (the moment the stimulus contacted the surface of the water) and the first detectable movement of the fish (Domenici, 2010).

Locomotor variables (defined based on Domenici and Blake, 1997):

4. Response distance (m): the total distance covered by the fish during the escape response.
5. Mean escape speed (m/s): the distance covered within the first two tail flips (24 ms). The first two tail flips are considered the crucial time to avoid predator attacks.
6. Maximum escape speed (m/s): the maximum speed reached at any time during the escape response.

After the trials, individuals were humanely euthanized according to ethical procedures permitted by James Cook University. A photograph of each individual was taken using a Casio EX-ZR1000 camera next to a ruler as scale. Length measurements were made blind to the acoustic treatment using ImageJ version 152.d (https://imagej.nih.gov/ij/).

2.5. Statistical analyses

Mixed-effects logistic regressions were used to analyse the effect of pre-hatching treatment, juvenile treatment, their interaction, days of parental exposure and standard length on juvenile responsiveness and directionality, while controlling for the random effects of clutch and juvenile tank. Linear mixed-effects models fitted by maximum likelihood were used to test for the effect of pre-hatching treatment, juvenile treatment, their interaction and days of parental exposure on response latency, response distance, mean escape speed and maximum escape speed, as well as standard length, while controlling for the random effects of clutch and juvenile tank. For all models, the minimal model was obtained by sequential removal of fixed effects and their interactions when found to be non-significant. Significance was tested by likelihood ratio model comparisons of the maximal model with the nested model where an effect in question was dropped. Chi-squared statistic and p-values for fixed effects in the minimal model were obtained by likelihood ratio test comparing the minimal model with a model excluding the fixed effect of relevance. Distance and speed were square-root transformed to meet normality assumptions. Model assumptions were assessed using residual plots, all of which were satisfactory. Post-hoc pairwise comparisons were performed using the Tukey method. The assumptions of normality and homogeneity of variance were examined graphically and found to be satisfied for maximum speed and latency. Statistical modelling was performed in the software R version 4 using the lme4 package (Bates et al., 2015).

3. Results

Playback tank recordings differed from field recordings due to near-field effects and interference caused by reflections and reverberations within the tank walls. However, acoustic analysis showed a clear difference between the motorboat noise treatment and the reef sound treatment in both the parent and juvenile tanks. The sound-pressure and particle-acceleration levels of the reef sound treatment were lower than the motorboat noise treatment levels. Sound-pressure and particle-acceleration levels in the tanks were greater than values in the field recordings, especially in low frequencies (<300 Hz) for both acoustic treatments. The juvenile-tank playbacks had a higher level of spectral distortion than field recordings, resulting in almost 40 dB greater sound-pressure levels in frequencies under 500 Hz (Fig. 1).

Spiny chromis juvenile length was significantly affected by juvenile treatment (LME: $\chi = 4.47$, $p = 0.034$; clutch: variance = 0.006, s.d. = 0.08; juvenile tank: variance = 0.008, s.d. = 0.09) and days of parental exposure ($\chi^2 = 5.09$, $p = 0.024$). Juveniles exposed to motorboat noise playback after hatching were 7% shorter compared to individuals exposed to reef sound playback (Tukey, $t = 2.18$, $p = 0.042$; Fig. 3). Additionally, as days of parental exposure increased individuals were smaller (Fig. S4). However, there was no significant effect of pre-hatching treatment ($\chi^2 = 2.57$, $p = 0.108$) or an interaction between pre-hatching and juvenile treatment ($\chi^2 = 0.12$, $p = 0.728$) on juvenile length.

Responsiveness of spiny chromis juveniles to the startle stimulus was significantly affected by the interaction between pre-hatching treatment and juvenile treatment (GLMER: $\chi^2 = 9.35$, $p = 0.002$; clutch: variance = 1.11, s.d. = 1.05; juvenile tank: variance = 0.72, s.d. = 0.85; pre-hatching treatment: $\chi^2 = 0.11$, $p = 0.738$; juvenile treatment: $\chi^2 = 1.08$, $p = 0.298$; days of parental exposure: $\chi^2 = 0.08$, $p = 0.769$). The significant interaction was driven by a difference in responsiveness between juveniles that had pre-hatching experience with boat noise and then went on to experience either motorboat noise or reef sound playback, and those that experienced reef sound playback as juveniles (Fig. 4A). A significantly lower proportion of juveniles in the boat–boat treatment responded to the stimulus (68%) compared to individuals in the boat–reef treatment (83%; Tukey, z = 2.81, $p = 0.025$). However, there were no differences in the proportion of individuals that responded to the stimulus between the reef–reef and reef–boat treatments (Tukey, z = 0.72, $p = 0.88$; z = 1.45, $p = 0.462$ respectively; Fig. 4A).

Direction of the escape response was significantly affected by the

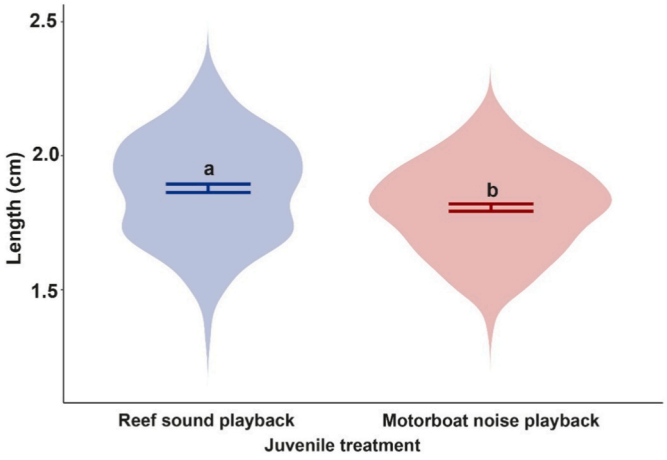

Fig. 3. Standard length (mean ± s.e.) of spiny chromis juveniles exposed to reef sound playback (blue) and motorboat noise playback (red) after hatching. Bars with different letters differed significantly according to the Tukey's HSD post-hoc means comparisons. Shading shows data distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

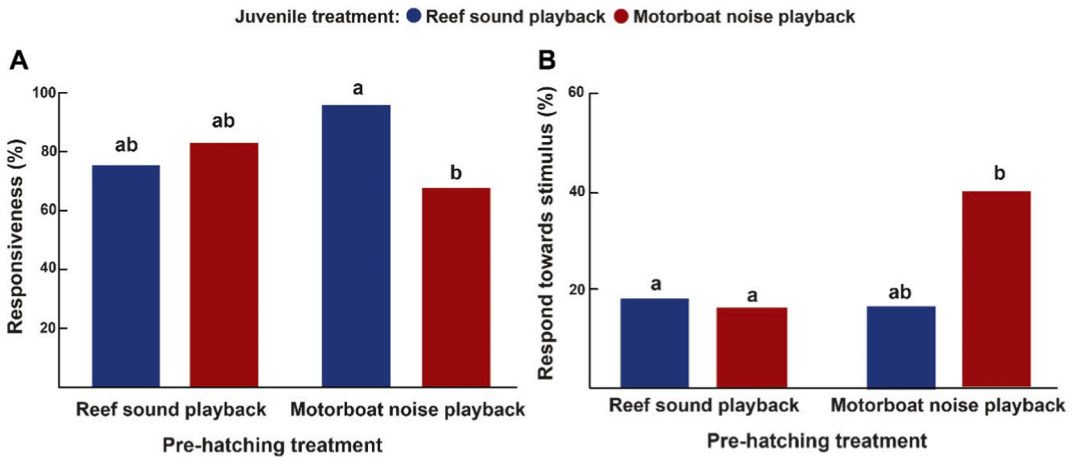

Fig. 4. Non-locomotor escape response variables of spiny chromis individuals across acoustic treatments. (A) Proportion of individuals that responded to the simulated predator attack, and **(B)** proportion of individuals that swam towards the stimulus when startled. Bars with the same letter did not differ significantly according to the Tukey's HSD post-hoc means comparisons.

interaction of pre-hatching treatment and juvenile treatment (GLMER: interaction: $\chi^2 = 4.52$, $p = 0.033$; clutch: variance = $4e^{-14}$, s.d. = $2e^{-07}$; juvenile tank: variance = 0, s.d. = 0; pre-hatching treatment: $\chi^2 = 4.08$, $p = 0.043$; juvenile treatment $\chi^2 = 1.43$, $p = 0.231$; days of parental exposure: $\chi^2 = 4.97$, $p = 0.025$). Individuals that experienced pre-hatching motorboat noise and then experienced motorboat noise playback had a significantly higher proportion of juveniles swimming towards the startle stimulus compared to individuals in all the other treatments. A significantly higher proportion of juveniles from the boat–boat treatment swam towards the stimulus (40%) compared to individuals in the reef–boat treatment (16.4%; Tukey, z = 3.01, $p = 0.013$) and the reef–reef treatment (18%; z = 2.56, $p = 0.051$), but not compared to the boat–reef treatment (17%; z = 2.44, $p = 0.069$; Fig. 4B).

Response latency, mean speed, maximum speed and response distance of spiny chromis juveniles were not significantly affected by pre-hatching treatment, juvenile treatment, their interaction or length (see extended data Table S2 and Fig. S5).

4. Discussion

We found that long-term exposure to motorboat noise playback can affect growth and escape response of a juvenile fish. Individuals exposed to motorboat noise playback as juveniles were smaller than those exposed to reef sound playback, independent of their pre-hatching acoustic treatment. Moreover, pre-hatching and juvenile exposure to motorboat noise playbacks for up to 78 days caused lasting effects on behavioural traits related to survival. Juveniles exposed to motorboat noise playback both prior to hatching and as juveniles were less likely than those who experienced reef sound playback to respond to a simulated predator attack and when they did respond they were more likely to swim towards the simulated predator strike. Individuals exposed to motorboat noise playback either before hatching or as juveniles, but not during both time periods, showed no lasting effects on either aspect of their escape response, suggesting that carryover effects on escape response were the cumulative result of exposure prior to hatching and as juveniles. Potentially, exposure during the embryonic phase may have increased individual sensitivity to that particular noise during the juvenile phase. These findings of cumulative effects are particularly pertinent to the study species as they brood their young (Kavanagh, 2000), and therefore a combination of parental, embryonic and juvenile exposure to motorboat noise is likely to occur in high traffic areas. It is in these areas that we would predict lower juvenile survival (Nedelec et al., 2022). Additionally, our results suggest that long-term effects of motorboat noise can vary depending on the life-stage and the duration of noise exposure.

Individuals exposed to motorboat noise playback as juveniles were smaller compared to juveniles exposed to reef sound playback. Previous studies have found inconsistent effects of noise on growth. For example, Nedelec et al. (2015) found that after two days of exposure to ship noise Atlantic cod larvae were smaller than to those exposed to reef sound; however, after 16 days there was no significant difference in larval length between treatments. Davidson et al. (2009) found that the noise from aquaculture systems affected growth of rainbow trout (*Oncorhynchus mykiss*), but only in the first month of exposure, with growth converging after five months of exposure. In a laboratory study, Nedelec et al. (2022) found that after 21 and 42 days post hatching spiny chromis juveniles in a limited-boating treatment were longer than those in a busy-boating treatment. In our study, after 41 days of juvenile exposure individuals exposed to motorboat noise playback were smaller. Stress is a potential underlying mechanism explaining the effects on growth. Stress causes changes in energy allocation such that resources that may have been invested in growth (Wendelaar Bonga, 1997) are allocated to cope with the stressor (i.e., motorboat noise). Size is a critical trait in behavioural interactions in vertebrates (Werner and Gilliam, 1984), particularly fishes (McCormick, 2016), with bigger individuals being dominant and having better access to food (Coates, 1980), and with these advantages being accentuated through time to affect fitness (Walker et al., 2007; McCormick et al., 2010, McCormick et al., 2018). Moreover, modified growth has been found to be a key parameter that can carryover between life-history stages, particularly in fishes (Gagliano et al., 2007). Together, this research suggests that the effects of repeated motorboat noise on juveniles can detrimentally affect growth trajectories, which may be accentuated through time to cause higher mortality through the correlations between low growth, small size-at-age, social status and vulnerability to predation (McCormick and Gagliano, 2008; McCormick, 2016).

Long-term exposure to motorboat noise playback resulted in carryover effects on non-locomotor traits of the escape response, where both exposure prior to hatching and during the juvenile stage combined to have detrimental effects on responsiveness and directionality (Walker et al., 2005; Fuiman et al., 2006). An unresponsive fish or a fish that startles towards the predator is less likely to survive a predator attack (Metcalfe et al., 1987; Domenici, 2010). There are three non-exclusive potential explanations for the detrimental effects of ongoing exposure to motorboat noise playback from parents through to juveniles: an effect on parental condition that leads to negative effects on the offspring; a direct effect on embryos; and/or a direct effect on juveniles.

The role of parents in preparing offspring for the conditions within

their natal environment is well known (Uller, 2008). In the current study, parents were exposed to motorboat noise playback for between 4 and 26 days before eggs were laid, and we found a significant effect of days of parental exposure on direction of the escape response. It is possible that individuals experienced a negative influence from parents exposed to motorboat noise playback, which could have increased their susceptibility to motorboat noise as juveniles. Previous studies have found that motorboat noise can lead to elevated stress, affecting energetic and physiological condition of adult fishes (Bracciali et al., 2012; McCloskey et al., 2020), which can lead directly to lower condition offspring (e.g., McCormick, 1998, 2006). For example, Donelson et al. (2008) found that spiny chromis offspring from parents with a good body condition tend to be bigger at hatching, have bigger yolk sacks and have higher survival. Motorboat noise playback may also have disrupted parental behaviour (e.g., Nedelec et al., 2017), and parental care can be important for offspring development and survival (Sabat, 1994, Sargent et al., 1987). For example, McGhee and Bell (2014) found that three-spined stickleback (*Gasterosteus aculeatus*) juveniles deprived of parental care had higher anxiety, which resulted in juveniles being attacked and captured by a predator faster compared to individuals that received parental care. In a related study, parents exposed to motorboat noise reduced the time spent fanning their eggs (Nedelec et al., 2022), which would reduce oxygen circulation around the eggs and hamper offspring development (Green and McCormick, 2005; Green et al., 2006). A reduction in the time fanning may also have led to a disruption of sensory and neural development (e.g., the lateral line, Lefrançois et al., 2005; Mirjany and Faber, 2011; Mirjany et al., 2011), which could explain the effects we found on direction of the escape response. Although parental condition and behaviour can influence offspring through indirect genetic effects or transgenerational effects (McGhee and Bell, 2014), our experimental design does not allow us to separate parental from embryological effects and future studies are required to isolate them.

Pre-hatching exposure to motorboat noise playback may have had a direct effect on embryo development. Fish embryos within benthic clutches have been found to be affected by anthropogenic noise (Simpson et al., 2005). Developing in a stressful environment may disrupt the development or damage sensory organs such as the lateral line. In a laboratory experiment, Uribe et al. (2018) found that white noise caused damage to the lateral line hair cells of zebrafish (*Danio rerio*) after 80 min of exposure. In our study, embryos were exposed to motorboat noise playback for 11 days suggesting that their lateral line hair cells may have been damaged; the lateral line provides inputs to the Mauthner cells which trigger the escape response in fish (Mirjany et al., 2011; Medan and Preuss, 2014). Another possible explanation is that, as a consequence of developing in a stressful environment, offspring reduced the energy they allocate for neural, muscular or morphological development (McCormick, 2009; Besson et al., 2020). Fakan and McCormick (2019) found that spiny chromis embryos exposed to motorboat noise had a higher heart rate and smaller yolk sacks compared to individuals developed in reef noise conditions. Besson et al. (2020) found that stress caused by elevated temperature and pesticides interfered with the development of olfactory, visual and mechanosensory structures, and resulted in higher predation.

Motorboat noise playback may have also affected juveniles directly. Juveniles exposed to motorboat noise playback displayed reduced responsiveness and poor directionality choices. Effects on responsiveness and directionality could also be explained by stress and effects of noise on sensory development. Responsiveness is determined by the strength of the threat and the environmental context (Domenici, 2010; Domenici and Hale, 2019). While we controlled for the strength of the threat of the simulated predatory attack (i.e., the stimulus was the same across trials), exposure to motorboat noise playback during juvenile development could have resulted in a stressful environment disrupting decision-making (i.e., economic model theory, Ydenberg and Dill, 1986). Moreover, directionality is determined by behavioural and neurophysiological mechanisms. Whether the lateral line continues developing after the eggs hatch is unknown, but a previous study found that olfactory and skeletal ossification development of spiny chromis continued after hatching (Kavanagh and Alford, 2003), suggesting that exposure to motorboat noise could disrupt the development of other sensory organs.

Tank-based studies allow for long-term exposure experiments and the recording of behavioural responses in detail, while controlling for environmental variables such as noise and light. Recent studies have found that individuals display similar behavioural responses when conducting field and tank-based experiments simultaneously (e.g., Simpson et al., 2016, Pieniazek et al., 2020). However, tank-based experiments have acoustic disadvantages (as discussed by Rogers et al., 2016; Slabbekoorn, 2016). In the present study, acoustic treatments were distorted due to near-field effects, reverberations and loudspeaker effects. These distortions were more significant for the reef sound treatment, where sound pressure (SPL re 1 μPa) was increased by 20 to 40 dB in frequencies under 500 Hz. Qualitatively, our findings are in line with similar work that has been carried out in the field with playbacks and with real motorboats (e.g. Nedelec et al., 2017, 2022). However, the playback of motorboat noise was above the level of the original motorboat noise recording at these low frequencies, meaning that our results must be taken with caution with regard to the specific sound levels that cause these effects.

The effects of motorboat noise are generally assumed to be transient and only manifested during the period when fish are exposed to noise. However, we found that a history of exposure to the playback of motorboat noise disrupted the ability of juveniles to react to a simulated predator attack, even when the escape response of juveniles occurred in the absence of noise. These carryover effects lasted for at least 14 h demonstrating that impacts of noise do not diminish in the absence of noise, at least over this timeframe. Moreover, we found juveniles exposed to motorboat noise playback were smaller than those exposed to reef sound playback. The observed effects on anti-predator responses and growth have the potential to be fatal. Long-term effects of motorboat noise on escape response can have future implications for population and community dynamics, by increasing the vulnerability of juveniles to predation and reducing the numbers of individuals that survive to the next life-stage. It would be beneficial for further work to explore the duration of these carryover effects to explore whether they are permanent or transient. Noise pollution represents a recently recognised stressor in marine environments (Williams et al., 2015; Duarte et al., 2021), but compared to other stressors such as ocean warming, its mitigation and management is easier. Our results suggest that fishes inhabiting busy motorboat areas are more likely to be affected due to long-term exposure and suggests that protection from motorboat noise during the breeding and recruitment season (October–December) could reduce the impact of motorboat noise on reef fish populations.

CRediT authorship contribution statement

L. Velasquez Jimenez: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **M.I. McCormick:** Writing – review & editing, Supervision, Resources, Formal analysis, Conceptualization. **P.M. Gatenby:** Investigation. **A.N. Radford:** Writing – review & editing, Funding acquisition, Conceptualization. **S.D. Simpson:** Writing – review & editing, Funding acquisition, Conceptualization. **S.L. Nedelec:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization.

Declaration of competing interests

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Sophie L Nedelec reports equipment, drugs, or supplies was provided by Geospectrum Technologies. If there are other authors, they 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.envpol.2026.128975.

Data availability

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