Assessing and mitigating impacts of motorboat noise on nesting damselfish☆

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ABSTRACT

Motorboats are a pervasive, growing source of anthropogenic noise in marine environments, with known impacts on fish physiology and behaviour. However, empirical evidence for the disruption of parental care remains scarce and stems predominantly from playback studies. Additionally, there is a paucity of experimental studies examining noise-mitigation strategies. We conducted two field experiments to investigate the effects of noise from real motorboats on the parental-care behaviours of a common coral-reef fish, the Ambon damselfish *Pomacentrus amboinensis*, which exhibits male-only egg care. When exposed to motorboat noise, we found that males exhibited vigilance behaviour 34% more often and spent 17% more time remaining vigilant, compared to an ambient-sound control. We then investigated nest defence in the presence of an introduced conspecific male intruder, incorporating a third noise treatment of altered motorboat-driving practice that was designed to mitigate noise exposure via speed and distance limitations. The males spent 22% less time interacting with the intruder and 154% more time sheltering during normal motorboat exposure compared to the ambient-sound control, with nest-defence levels in the mitigation treatment equivalent to those in ambient conditions. Our results reveal detrimental impacts of real motorboat noise on some aspects of parental care in fish, and successfully demonstrate the positive effects of an affordable, easily implemented mitigation strategy. We strongly advocate the integration of mitigation strategies into future experiments in this field, and the application of evidence-based policy in our increasingly noisy world.
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1. Introduction

Ocean soundscapes throughout the world are increasingly altered by human-generated noise. This noise comes from a variety of sources including energy production, resource extraction, construction, and transportation (Hildebrand, 2009; Slabbekoorn et al., 2010). Consequently, policymakers, such as the International Maritime Organization (IMO, 2014), and legislation, such as the European Commission Marine Strategy Framework Directive (Tasker et al., 2010) and the US National Environment Policy Act,

have classified anthropogenic noise as a globally pervasive pollutant, calling for scientific assessment and informed mitigation solutions (Hawkins et al., 2015; Buxton et al., 2017). There has been an increase in evidence demonstrating the negative impacts of noise on a wide range of aquatic taxa, including effects on spatial distribution, communication, foraging, homeostasis, and con- and hetero-specific interactions (see reviews: Shannon et al., 2016; Cox et al., 2018; Kunc and Schmidt, 2019; Popper and Hawkins, 2019). However, investigation of the impacts of noise on reproductive behaviour is needed, as successful reproduction is essential for population resilience and viability (Weilgart, 2018; de Jong et al., 2020).

Parental care is a key aspect of reproductive behaviour in many fish species (Blumer, 1982), but there are relatively few studies investigating how this may be impacted by noise pollution. Parental care in fish comprises a suite of behaviours, including nest

maintenance, egg oxygenation, and defence against competitors and predators (Zoran and Ward, 1983; Haley and Müller, 2002; Hale and St Mary, 2007), which directly influence offspring survival and therefore fitness (Sabat, 1994). Bruintjes and Radford (2013) found that captive male daffodil cichlids *Neolamprologus pulcher* reduced nest-digging rate and delayed initiating this behaviour during exposure to motorboat-noise playback, with a concurrent reduction in anti-predator behaviour when there were no eggs in the nest. Similarly, but at natural nests, Picciulin et al. (2010) found a negative effect of boat-noise playback on the time spent by Mediterranean chromis *Chromis chromis* cleaning and egg tending. More recently, Nedelec et al. (2017) showed that spiny chromis *Acanthochromis polyacanthus* parents experiencing 12 days of motorboat-noise playback at natural nests increased their nest-defence behaviours, but suffered higher juvenile mortality compared to control parents experiencing ambient-sound playback. Although two of these experiments were conducted *in situ*, all used playback of recordings as a noise treatment, which does not fully replicate sound exposures that would be experienced when exposed to real noise sources (Slabbekoorn, 2015).

Here, we aim to address this knowledge gap with two *in situ* experiments that examine the effects of an ecologically relevant noise source on parental care in a wild fish population, using motorboats as a direct sound source. Nearly half of the Earth's growing population of 7.6 billion people live within 60 miles of the shore, and as humans continue to cluster around coasts, use of inshore waters will continue to increase (McCormick et al., 2018; Wright et al., 2018). For example, 11.9 million recreational vessels were registered in the USA in 2017 (NMMA, 2017) and 0.5 million recreational motorboats are expected to be using the Great Barrier Reef by 2040 (GBRMPA, 2014). Motorboats are therefore an extensive and increasing source of anthropogenic noise, and evidence is emerging regarding impacts of motorboat noise on fish endocrine and stress responses (Mills et al., 2020), development (Jain-Schlaepfer et al., 2018; Fakan and McCormick, 2019), anti-predator behaviour (Ferrari et al., 2018), reproduction (Nedelec et al., 2017), and survival (Simpson et al., 2016; McCormick et al., 2018).

While there has been recent public and political call for further mitigation of marine noise, this consideration mainly concerns impacts on marine mammals (Williams et al., 2019), despite the high abundance, prevalence, and socio-economic importance of fishes and invertebrates (Williams et al., 2015). It is conceivable that changes to guidelines for recreational motorboating can be promoted to mitigate the detrimental impacts of noise on marine ecosystems. One method which has been tested in relation to biological responses in coral reef fishes is the installation of quieter engine types onto boats (Jain-Schlaepfer et al., 2018; McCormick et al., 2018, 2019). Although this method was successful in reducing impact, it is expensive and as a result would be difficult to implement widely. There is a need for affordable mitigation options which can be integrated into policy, but can also be immediately employed by motorboat users. One such possibility is recommending the alteration of driving practice; for example, spatial management and speed restrictions could be implemented near vulnerable areas, such as coral reefs, to limit damaging noise exposure. Similar concepts are currently being promoted to protect at-risk marine mammal populations, such as the critically endangered Southern Resident killer whales *Orcinus orca* (Williams et al., 2019). In freshwater fish, MacLean et al. (2020) found that residency time in nesting smallmouth bass *Micropterus dolomieu* was adversely affected by motorboat noise playback, but only when close to the loudspeaker. However, the application of similar measures to coral reef habitats requires rigorous testing to ensure that potential benefits to wildlife are validated scientifically.

Here, we assessed the effects of motorboat noise and noise mitigation on parental care in an abundant Indo-Pacific coral-reef fish species, the Ambon damselfish *Pomacentrus amboinensis* (family Pomacentridae). This demersal-spawning species exhibits male-only parental care (McCormick, 2016) and has been shown previously to be disturbed by motorboat noise, notably in assessment of risk (McCormick et al., 2018), predator-recognition learning (Ferrari et al., 2018), anti-predator behaviours (Simpson et al., 2016), and feeding and movement (Holmes et al., 2017). Specifically, we conducted two experiments on individual male *P. amboinensis* caring for clutches of eggs. The first experiment considered the effect of noise from real motorboats on behaviours occurring inside the nest in association with the eggs, to determine whether these fish are less attentive parents in noisy conditions. The second experiment considered the impact of motorboat noise on defensive behaviours triggered by the presence of a conspecific male intruder outside the nest. Having found detrimental effects of real motorboats in our first experiment, we added a mitigation-strategy treatment (altering motorboat-driving practice adjacent to the reef edge) for our second experiment to address the paucity of experimental evidence regarding noise-mitigation methods.

2. Methods

2.1. Experimental overview

We collected data between October and December 2018 on reefs near to Lizard Island Research Station (14°4′S 145° 28′E), Great Barrier Reef, Australia. Two experiments were conducted on male *P. amboinensis* occupying artificial nests at six study sites along the reef edge. We exposed nests to the following noise treatments: ambient-sound conditions (Experiments 1 and 2), motorboats being driven nearby (Exps 1 and 2), and motorboats being driven under a mitigation regime (Exp. 2). Video cameras recorded parental-care behaviours within the nest (Exp. 1) and immediately surrounding the nest (Exp. 2) during these treatments.

2.2. Study species

On the Great Barrier Reef, male *P. amboinensis* exhibit parental care of demersal broods within a nest throughout the breeding season (October−January; McCormick and Meekan, 2007). During the parental-care period, males aggressively guard their territory from intruders and egg predators, maintain the nest, clean the broods, and oxygenate eggs by fanning with their pectoral and dorsal fins (Moyer, 1975; McCormick and Smith, 2004; McCormick and Meekan, 2007). Parental care in this species therefore involves costs in terms of time, energetic investment, and trade-offs with future reproductive opportunity (males continue to court females during this period; McCormick, 2016), but improves offspring survival at this vulnerable stage (Gross and Sargent, 1985).

2.3. Artificial nests

We placed a total of 120 artificial nests within six study sites, each consisting of 100 m stretches of continuous reef, with at least 200 m between neighbouring sites. Previous work has shown that *P. amboinensis* readily occupies artificial nests, including terracotta tiles (Kerrigan, 1997) or PVC half-pipes (Emslie and Jones, 2001). In addition to their high site-fidelity, small home ranges, and resilience to physical disturbance, this makes breeding males easy to manipulate experimentally. Our nests consisted of upturned half PVC pipes (18 cm diameter, 30 cm length) surrounded by coral rubble (approx. 0.5 m^3) (following McCormick, 1998) and placed on sandflats along reef edges at depths of 2−5 m. The distance

between each nest was determined by the natural proximity of males (minimum distance of 1 m); half-pipes were placed near relatively large individuals observed to exhibit territorial aggression, to increase the likelihood of settlement and successful courtship (McCormick and Meekan, 2007). Following placement, each nest was readily explored and subsequently adopted within minutes of placement by an individual male *P. amboinensis,* which guarded that nest for the remainder of the breeding season, as observed in earlier studies (Kerrigan, 1997; Emslie and Jones, 2001).

We monitored each of the six study sites approximately every 2−3 days in rotation, and ran experimental trials within 2 days of eggs being found at a nest, as the incubation period for a single clutch in this species is ca. 4−5 days at 28 °C (Kerrigan, 1997). Experimental trials were always conducted between 0800 and 1500 h. Trials were not conducted on days with uncharacteristically bad weather (>2 on the Beaufort scale) or heavy rainfall due to noisier ambient conditions associated with these natural phenomena (Putland et al., 2017). As spawning was asynchronous, and treatments were applied to whole sites, some individual males were exposed to our treatments before the trial in which they were recorded. However, the potential for noise-induced carry-over effects in fishes remains inconclusive (Mills et al., 2020), and given the short-term nature of the treatments (5−10 min), we do not believe that previous exposure would impact the response of an individual during a trial. Regardless, we endeavoured to minimise the likelihood of carry-over effects from motorboat-noise by staggering exposure to the same study site (no repeat exposures of the same type within 48 h). Furthermore, to reduce the potential for cross-contamination by noise to nests which were not currently being recorded, trials were not conducted in neighbouring study sites on the same day.

2.4. Experimental noise production

To introduce motorboat noise experimentally to study sites, motorboats (5 m long aluminium hull with 4-stroke 30-horsepower Suzuki DF30A outboard engine) were driven at varying speeds and distances, depending on treatment type. A total of five motorboats of similar size, hull type, and engine type were used in rotation throughout the study to minimise pseudoreplication. The motorboats were always driven by the same individual (K.P.M) to standardise driving style between trials.

Each experimental trial was conducted under one of three noise conditions: ambient sound (no motorboat), motorboat noise, or mitigated-motorboat noise (hereafter referred to as ambient, motorboat, and mitigation, respectively). All ambient trials which experienced unplanned boat passes within 500 m of the focal study site were discarded, however this was rare (<5 occurrences) as this location experiences minimal traffic (<5 boats a day). The motorboat treatment consisted of full-speed passes by a single motorboat parallel to the reef and 10−20 m from the reef edge. For the mitigation treatment, the motorboat was excluded from an 'acoustic buffer zone' within 20 m of the reef edge, and was driven parallel to the reef through two zones: 20−120 m from the reef where speed was reduced to quarter throttle, and >120 m from the reef where the motorboat was driven at full speed. Although each nest would experience a fluctuating level of noise during the treatments, they would have received the same cumulative sound exposure level at the end of the treatment (i.e. each nest experienced the same number of boat passes at one speed and distance from the reef).

2.5. Acoustic recordings and analysis

The acoustic properties of the ambient, motorboat, and mitigation treatments were recorded at each of the six study sites, in sea states between 0 and 2 on the Beaufort scale, and in the absence of rain. Sound pressure was recorded using an omnidirectional hydrophone with inbuilt digital recorder (SoundTrap 300 STD; Ocean Instruments NZ, Auckland, New Zealand). Particle-acceleration recordings were made using a triaxial accelerometer (M20-040; sensitivity following a curve over the frequency range 0−3 kHz; calibrated by manufacturers; Geospectrum Technologies, Dartmouth, Canada) connected to a digital 8-track recorder (F8 field recorder, sampling rate 48 kHz; Zoom Corporation, Tokyo, Japan). Recordings were made at the approximated midway point of each study site over sandy-bottom areas along the reef edge, at 1.5−2.5 m depth. At each of the six sites, we recorded ambient conditions once and motorboat and mitigation treatments three times. By recording noise from three of the five motorboats used in the experiments, we included potential acoustic variation between motorboats in our acoustic analysis.

We analysed the recordings in *MATLAB R2017b* using *PAMGuide* (sound pressure; Merchant et al., 2015) and *paPAM 0.9* (particle acceleration; Nedelec et al., 2016a), analysing across a frequency range of 1−2000 Hz; the likely hearing range relevant to pomacentrid fishes (Kenyon, 1996; Wright et al., 2011). Power spectral densities (PSD) (Fig. 1a and b), root-mean-square levels (SPL_{rms} and SAL_{rms}), and cumulative sound exposure levels (SEL_{cum} and AEL_{cum}) (Table 1) were calculated in both the sound-pressure and particle-acceleration domains using a Hamming filter with a window length of 1024 and 50% overlap over batch-processed 1-min subsamples of the recordings (n = 6 ambient recordings; n = 18 motorboat recordings; n = 18 mitigation recordings). These subsamples were selected to represent closely the acoustic conditions of each treatment for analysis. For motorboat-treatment recordings, our subsamples included three full motorboat passes, typically at the middle of recordings to avoid acceleration and deceleration portions. Lastly, we subsampled mitigation-treatment recordings to include one full slow-driving approach and departure, towards and away from the recording equipment (usually lasting about 30 s), along with 1−2 full-speed passes farther than 120 m away from the reef.

2.6. Experiment 1: egg tending

To investigate the impact of motorboat-noise exposure on egg tending, data were collected on four within-nest behaviours of male *P. amboinensis*: nest visitation, egg fanning, nest maintenance, and vigilance (Table 2). We approximated the duration of a dorsal fanning event as 0.5 s (from a mean of 30 events) in order to give combined counts and durations for dorsal fanning and pectoral fanning together.

We recorded behaviours at each nest under each of two treatments (ambient and motorboat). Both treatments of a single nest occurred on the same day and multiple nests at the same site were treated simultaneously; the first trial was completed between 0800 and 1000 h and the second between 1300 and 1500 h. We randomly assigned which treatment would occur first each day at each study site and counterbalanced treatment order on subsequent days to avoid ordering bias at each. Within-nest behaviours were filmed using weighted GoPro Hero 5 cameras set approximately 10 cm from the entrance to the nest by a snorkeler who then left the area. In both treatments, the first 5 min was not analysed to allow the fish to resume normal behaviour following disturbance (Nedelec et al., 2016b), after which 10 min was recorded to determine baseline level of behaviour in ambient-sound conditions. Following this, fish were given a 10-min exposure period under either the motorboat or ambient treatment, as described above. We collected videos for both treatments at 38 nests over 11 non-consecutive days.
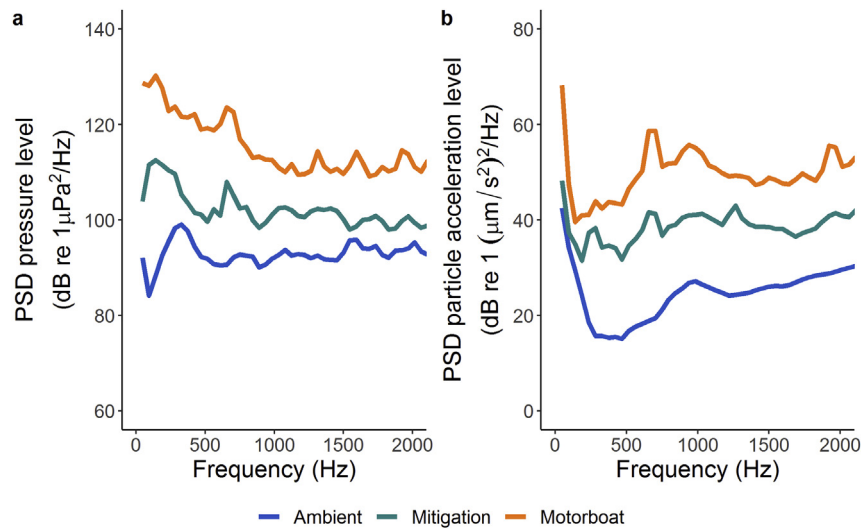
Fig. 1. Mean power spectral densities (PSD) of ambient, motorboat, and mitigation treatments in both (a) sound pressure and (b) triaxial particle acceleration, giving an average sound profile for each treatment (fft length = 1024, Hamming evaluation window, 50% window overlap, 1–2000 Hz).

Table 1
Root-mean-square and cumulative sound exposure levels in both sound pressure (SPL_{rms} and SEL_{cum}) and triaxial particle acceleration (SAL_{rms} and AEL_{cum}) for each treatment.

Treatment	SPL_{rms} (dB re 1 μPa)	SEL_{cum} (dB re 1 μPa² s)	SAL_{rms} (dB re (1 μm/s²)	AEL_{cum} (dB re (1 μm/s²)² s)
Ambient	106.8	132.3	73.5	91.3
Mitigation	120.1	150.4	84.0	102.3
Motorboat	131.6	161.9	96.5	114.1

2.7. Experiment 2: nest defence

To investigate the impact of motorboat-noise exposure and a noise-mitigation strategy on nest defence, data were collected on five defensive behaviours of male *P. amboinensis*: time in shelter, time interacting with an intruder, displaying, striking, and chasing (Table 3).

Each nest received three treatments (ambient, motorboat, and mitigation). We ran trials across three consecutive days at each nest, administering one treatment at that nest per day in a Latin-square block design to counterbalance for order effects, after which no repeat trials were recorded for that nest. Multiple nests were treated simultaneously at the same site, and three sites were treated per day, between 1000 and 1200 h. For the experimental trials, we introduced one conspecific male 'intruder' (mean standard length 6.5 ± 0.1 cm) outside each nest. Conspecific intruders were collected from neighbouring locations outside of the study areas by divers using hand nets. To reduce the number of captured fish, intruders were used at multiple sites throughout the day and released after the last trial to their original collection locations. We transported these fish in a large container that provided physical and visual isolation, as well as shade from the sun, replacing the holding water between sites with fresh seawater to remove waste and provide oxygenation during transport. Care was taken to avoid previously used collection areas on subsequent days, so that intruders were naïve to the experiment each day. The intruder for each trial was presented in an 8-L plastic bag, which we secured in place with a steel rod within 0.5 m of the guarded nest (McCormick and Meekan, 2007). Aggressive behaviours towards a presented intruder began instantly, necessitating an experimental design with no acclimation period (cf. Exp. 1) and required the noise treatment to start 5 min prior to intruder presentation. Trials lasted for 10 min and defensive behaviours were recorded with one weighted GoPro Hero 5 camera per nest, which we placed approximately 0.5 m away from the nest entrance and angled so that the nest entrance and intruder bag were fully in frame. A total of 69 videos were collected at 23 guarded nests. However, five nests were excluded from subsequent analysis due to loss of broods by either predation or hatching, resulting in an incomplete set of trials for those nests in the matched experimental design and a final sample size of 18.

2.8. Video analysis

All videos collected in the field were cropped using *ffmpeg 4.1.3* (ffmpeg.org). For the egg-tending experiment (Exp. 1), videos were cut to baseline and exposure periods (10 min each). Two nests were removed from analysis due to unusable camera angles, and two more were removed due to filming of non-focal species occupying the nests. For the nest-defence experiment (Exp. 2), videos were cut to 5-min clips starting approximately 30 s after the snorkeler was last visible in the camera frame.

All videos were saved with coded file names and were watched with no sound so that we (K.E.C for Exp. 1; K.P.M for Exp. 2) were blind to the noise treatment during observation. We scored behaviours from the videos using the behavioural observation software *BORIS 7.6.1* (Friard and Gamba, 2016).

2.9. Statistical analysis

For Experiment 1, we calculated rates (for counts) and time-budget proportions (for durations) by dividing the data by the total time that the fish spent in the nest in that 10-min period. The change in behaviour from the baseline period (ambient-sound condition) to the exposure period (motorboat or ambient) was calculated for each behavioural variable. We analysed the

Table 2
Ethogram for the recorded egg-tending behaviours exhibited by male *P. amboinensis* within the nest (Experiment 1).

Behaviour	Description	Variables
Nest visitation	When the male was underneath the artificial nest	Count, duration, intervals
Egg fanning	Combined scores of: (1) pectoral fanning, when the male faced the brood, fanning with its pectoral fins and often pecking at the clutch with its mouth; and (2) dorsal fanning, when the male wriggled the length of its body along the eggs with the dorsal fin in contact with the clutch	Count, duration
Nest maintenance	When the male exhibited tidying of the nest, including removing objects (e.g. shells), mouth-pecking away from the brood, and digging in the substrate	Count
Vigilance	When the male was stationary in the nest entrance, looking out	Count, duration

baseline−exposure change in the ambient treatment against the baseline−exposure change in the motorboat treatment as paired data for each fish (n = 34 individuals) using paired t-tests and paired Wilcoxon signed-ranks tests, depending on whether the data met the assumptions for parametric testing. Where a significant difference between treatments was found, one-sample t-tests or one-sample Wilcoxon signed-ranks tests were used to determine whether the behavioural measure in the exposure period (motorboat or ambient) was significantly different from the baseline within each treatment. Three pairs of data were identified as outliers (using Interquartile Range) and omitted from the analysis of the mean interval between nest visits. Holm-Bonferroni corrections for multiple measures were used for nest visitation (three measures), fanning (two measures), and vigilance (two measures).

For Experiment 2, we calculated the proportion of time spent sheltering by dividing the time of observed behaviours by the total time spent on screen. To investigate the remaining responses independently of changes to the sheltering proportion, variables were calculated to include only time spent out of shelter and swimming in open water. Therefore, we calculated the proportion of time spent interacting with the conspecific intruder (duration) and all behavioural rates (counts of displaying, striking, and chasing) by dividing the data by the total time that the focal male spent on screen and out of shelter. We analysed the differences between the three treatments (ambient, motorboat, and mitigation) for each fish (n = 18 individuals) using one-way repeated measures ANOVA tests with the *ez 4.4-0* package (Fazio et al., 2012) or Friedman tests using the *rstatix 0.4.0* package (Kassambara, 2019), depending on whether the data met assumptions for parametric testing. Holm-Bonferroni corrections were used for the analyses of strikes and displays, as these behaviours often occurred simultaneously and displays were measured in two ways. *Post hoc* comparisons were conducted using either pairwise t-tests or pairwise Wilcoxon signed-rank tests, both with Holm-Bonferroni corrections.

All analyses were completed in R V3.5.2 (R Core Team, 2018). Statistical significance was assumed where $p < 0.05$. We derived statistical effect sizes for significant results using the *rstatix* package: Cohen's d for t-tests, Wilcoxon's effect size r for Wilcoxon tests, and Kendall's W for Friedman tests. Furthermore, we calculated absolute effect sizes for significant results as percentage difference (to the nearest whole percent) of the mean (parametric tests) or median (non-parametric tests) value, from the baseline to the exposure period in Experiment 1, and from the ambient to the motorboat treatment or from the motorboat to the mitigation treatment in Experiment 2. All other values presented in the Results are means ± standard error of the means.

3. Results

3.1. Experiment 1: egg tending

Male *P. amboinensis* spent 159 ± 14 s (mean ± SE) in the nest in the 10-min baseline period, visiting the nest for 9 ± 1 s at a time every 30 ± 3 s. There were no significant differences between the treatments in the baseline−exposure change in: the total time spent inside the nest, hereafter *nest time* (paired t-test: $t_{33} = 0.483$, $p = 0.633$), the mean duration of nest visits (Wilcoxon test: $V_{33} = 386$, $p = 0.282$), or the mean interval between visits ($V_{30} = 334$, $p = 0.282$).

Egg fanning occurred at a baseline rate of 17.5 ± 1.4 events per min of nest time, taking up 38.4 ± 1.7% of total nest time. There was no significant difference between treatments in the baseline−exposure change in fanning rate (paired t-test: $t_{33} = -0.37$, $p = 0.711$). The change in the proportion of nest time spent on fanning was close to, but did not meet, the threshold of α (0.05) for statistical significance (Wilcoxon test $V_{33} = 421$, $p = 0.069$). Upon further evaluation of this trend, we found there was a significant decrease from the baseline in the motorboat treatment ($V_{33} = 180$, $p = 0.044$, $r = 0.35$), where males spent on average a 19% lower proportion of time fanning when exposed to motorboat noise, but no significant change from the baseline in the ambient treatment ($V_{33} = 360$, $p = 0.293$).

Males undertook nest-maintenance at a baseline rate of 0.4 ± 0.1 events per min of nest time. There was no significant difference between the treatments in the change in nest-maintenance rate (Wilcoxon test: $V_{33} = 175$, $p = 0.484$).

Males exhibited vigilance at a baseline rate of 3.3 ± 0.3 events per min of nest time, taking up 8.5 ± 0.7% of total nest time. Treatment significantly affected the baseline−exposure change in vigilance rate by the males (paired t-test: $t_{33} = -3.20$, $p = 0.006$, $d = 0.55$; Fig. 2a), which significantly increased by 34% from the baseline in the motorboat treatment (one-sample t-test: $t_{33} = 3.11$, $p = 0.004$, $d = 0.53$) and did not significantly differ from the baseline in the ambient treatment ($t_{33} = -1.86$, $p = 0.072$). There was also a significant effect of treatment on the change in proportion of nest time spent on vigilance (Wilcoxon test: $V_{33} = 182$, $p = 0.048$, $r = 0.34$; Fig. 2b). There was a significant increase of 17% from the baseline in the motorboat treatment ($V_{33} = 371$, $p = 0.046$, $r = 0.34$), compared to no significant change from the baseline in the ambient treatment ($V_{33} = 234$, $p = 0.581$).

3.2. Experiment 2: nest defence

Male *P. amboinensis* spent 290 ± 3 s within the camera frame, or 97.1 ± 0.8% of the total 5-min time window. There was no significant difference in the total time spent in frame between the three treatments (ambient, motorboat, and mitigation) (one-way repeated measures ANOVA: $F_{2,34} = 0.31$, $p = 0.73$).

Table 3
Ethogram for the recorded nest-defence behaviours exhibited by male *P. amboinensis* when presented with a conspecific intruder (Experiment 2).

Behaviour	Description	Variables
Time in shelter	When the male sought refuge either in the artificial nest or nearby coral/rubble	Duration
Time interacting with an intruder	When the male was within one body length of the intruder's plastic bag	Duration
Displaying	When the male extended its dorsal and anal fins or fanned its caudal fin at the intruder	Count, duration
Striking	When the male lunged at the bag, delivering a bite	Count
Chasing	When the male rapidly swam toward the intruder	Count

Sheltering occurred at a rate of 1.9 ± 0.3 events per min of time within the camera frame, taking up $16.3 \pm 2.8\%$ of total frame time. Males differed in the proportion of time spent sheltering during the three treatments (Friedman test: $X^2_2 = 6.79$, $p = 0.03$, $W = 0.19$; Fig. 3a). They spent a 154% higher proportion of time sheltering during motorboat-noise exposure than during the ambient treatment (Wilcoxon test: $V_{17} = 30$, $p = 0.03$, $r = 0.57$). Furthermore, the males spent an 80% lower proportion of time sheltering in the mitigation treatment compared to the motorboat treatment ($V_{17} = 158$, $p < 0.001$, $r = 0.74$). There was no significant difference between ambient and mitigation treatments ($V_{17} = 113$, $p = 0.09$).

Males interacted with the presented conspecific intruder at a rate of 6.5 ± 0.5 events per min of time swimming in open water, taking up $58 \pm 2.9\%$ of the total time unsheltered. Male *P. amboinensis* differed significantly in the proportion of time spent interacting with the intruding conspecific males during the three noise treatments (Friedman test: $\chi^2_2 = 10.11$, $p = 0.006$, $W = 0.28$; Fig. 3b). Males spent a 22% lower proportion of time interacting with the intruder during motorboat-noise exposure than in the ambient treatment (Wilcoxon test: $V_{17} = 139$, $p = 0.04$, $r = 0.55$). Additionally, they spent a 35% greater proportion of time interacting in the mitigation treatment compared to the motorboat treatment ($V_{17} = 18$, $p = 0.006$, $r = 0.69$). There was no significant difference between ambient and mitigation treatments ($V_{17} = 65$, $p = 0.39$).

Displays occurred at a rate of 6.1 ± 0.5 per min, for $20.7 \pm 2.2\%$ of total time spent swimming in open water. Males did not significantly differ between treatments in either display rates (one-way repeated-measures ANOVA: $F_{2,34} = 1.30$, $p = 0.573$) or the

proportion of time spent displaying (Friedman test: $\chi^2_2 = 7$, $p = 0.091$). Strikes occurred at a rate of 11.1 ± 1.2 per min. There was no significant difference in strike rate during the three noise treatments (one-way repeated-measures ANOVA: $F_{2,34} = 0.54$, $p = 0.588$). Lastly, charges occurred at a rate of 0.93 ± 0.2 per min with no significant difference in charge rate between the three noise treatments ($F_{2,34} = 0.66$, $p = 0.52$).

4. Discussion

We found that motorboat noise affected some behaviours of the tropical damselfish *Pomacentrus amboinensis* both inside and outside the nest during the breeding season; a critical life-history phase. While inside the nest, egg-tending males exposed to motorboat noise significantly increased the proportion of time spent on vigilance and tended to decrease the proportion of time spent fanning eggs, compared to their behaviour in ambient conditions. Outside the nest, males exposed to motorboat noise spent proportionally more time seeking refuge and devoted proportionally less time to interacting with a conspecific intruder compared to those in ambient conditions. Employing a change in motorboat driving practice effectively lowered noise-exposure levels to nesting males, and mitigated these effects on defensive behaviours.

In Experiment 1, we found a 34% increase in the rate of vigilance events, which corresponded with a 17% increase in the proportion of nest time spent on vigilance during the motorboat-noise exposure. Therefore, male *P. amboinensis* may be investing more time in vigilance, potentially at the expense of other parental-care behaviours when exposed to noise; a trade-off which has previously been
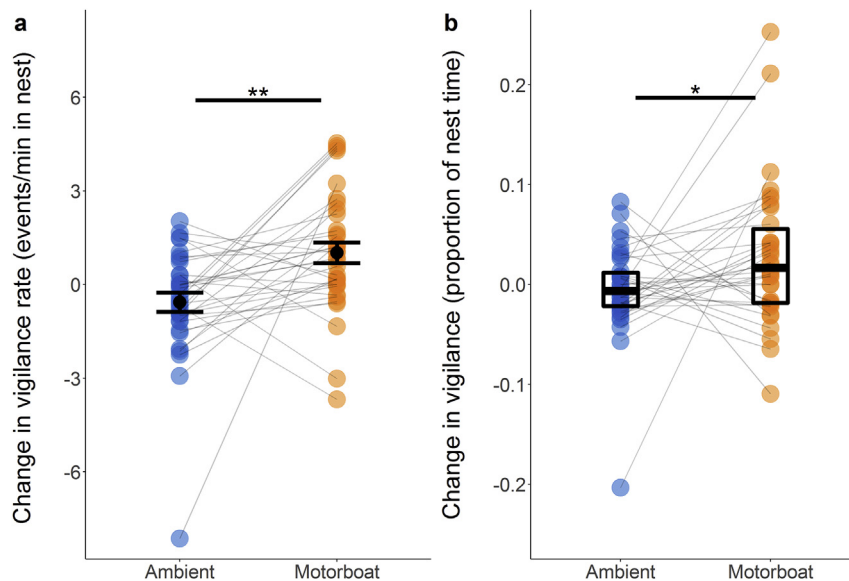
Fig. 2. Treatment responses in (a) vigilance rate and (b) proportion of nest time spent on vigilance by male *P. amboinensis* in the two treatments. Black points in (a) show mean treatment responses $\pm$ SEM error bars; boxes in (b) show median and interquartile range; coloured points show treatment responses; grey lines indicate paired data from individuals across the two treatments. *$p < 0.05$, **$p < 0.01$. n = 34 individuals for both response measures.
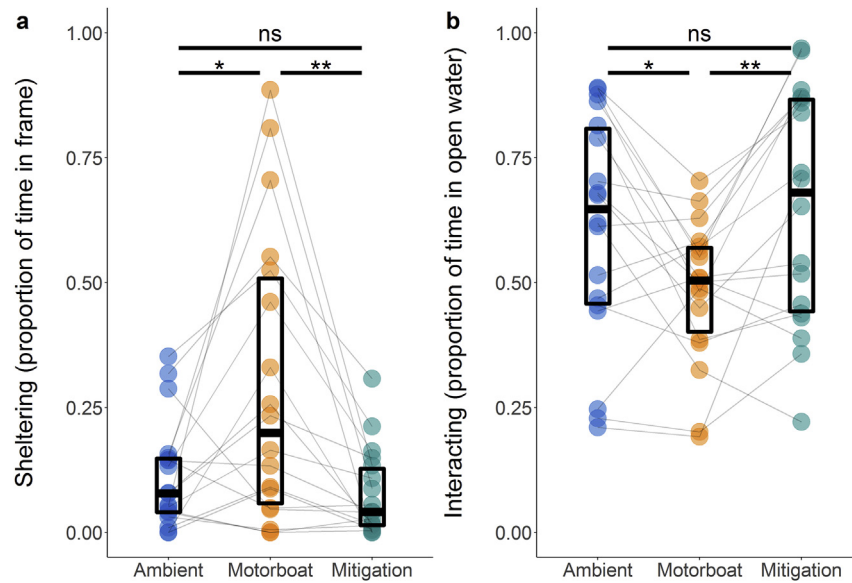
Fig. 3. Treatment responses of male *P. amboinensis* in (a) proportion of frame time spent sheltering and (b) proportion of open-water time spent interacting with the intruder. Boxes show median and interquartile range; coloured points show treatment responses; grey lines indicate paired data from individuals across the three treatments. Post-hoc pairwise comparisons are designated by annotated lines; 'ns' = non-significant, * = $p < 0.05$, ** = $p < 0.01$. n = 18 individuals for all response measures.

considered in ambient conditions (Lissåker and Kvarnemo, 2006). Empirical studies examining the interplay of sensory modalities (e.g. vision, olfaction, and hearing; Hartman and Abrahams, 2000; Manassa et al., 2013) have suggested that a reduction in the efficacy of hearing may lead to sensory compensation, with complementary information obtained from other senses such as vision and olfaction (Nedelec et al., 2017; McCormick et al., 2018). Thus, by increasing vigilance, males may be attempting to compensate for the potential masking of acoustic information regarding possible threats in the nest vicinity during motorboat disturbance (Holles et al., 2013; Radford et al., 2014). While vigilant, males may also be seeking to identify the source of the noise, may perceive the noise as a threat, or may be responding to a noise-induced change in community composition; vigilance can improve the latency of response to threats, such as egg predators or conspecific competitors (Krause and Godin, 1996).

We also observed a trend of a 19% lower proportion of time spent on fanning the clutch during motorboat exposure. Frequent fanning of the clutch with the pectoral, caudal, and dorsal fins ventilates the eggs, which increases oxygen consumption and promotes development and survival (Zoran and Ward, 1983; Green et al., 2006). Additionally, fanning is often accompanied by mouth-pecking at the clutch for the removal of damaged, diseased or dead eggs (Blumer, 1982). Embryonic development has been shown to be compromised by noise exposure in the spiny chromis *Acanthochromis polyacanthus* (Fakan and McCormick, 2019) and the sea hare *Stylocheilus striatus* (Nedelec et al., 2014), although the hatching success of captive daffodil cichlids *Neolamprologus pulcher* was unaffected by noise playback (Bruintjes and Radford, 2014). Further evidence would be required to determine the potential impacts on development that could result from a reduction in egg fanning during noise exposure.

In Experiment 2, nest-guarding males spent a 22% lower proportion of time interacting with a conspecific intruder during the motorboat treatment compared to the ambient treatment. For demersal-spawning fishes, vulnerability to egg predation during development can have substantial consequences for overall embryo mortality (Emslie and Jones, 2001). Furthermore, cannibalism by non-parental conspecifics has been observed in *P. amboinensis* and

other species when there is intense competition for limited nest space and/or mates (Gross and MacMillan, 1981; Nakazono et al., 1989; Emslie and Jones, 2001; Pereira et al., 2017). Therefore, the observed decrease in interaction with a conspecific intruder could result in a higher risk of egg predation and non-parental cannibalism, ultimately impacting embryo mortality and reproductive success for the noise-exposed resident male.

The proportion of time males spent under shelter, including the artificial nest as well as natural shelters such as coral covers, was 154% higher during exposure to motorboat noise compared to ambient-sound conditions in Experiment 2. Similar increases in sheltering have been found for the red-mouthed goby *Gobius cruentatus* (Picciulin and Sebastianutto, 2010) and European bass *Dicentrarchus labrax* (Spiga et al., 2017). However, no changes in nest visitation were found in Experiment 1. The difference in outcomes of our two experiments may be due to an increase in sheltering outside of the nest only in Experiment 2, or simply a contextual response to the presence of an intruder (Figueira and Lyman, 2007; Bruintjes and Radford, 2013). Sheltering outside of the nest would reduce the time available for egg tending (Picciulin and Sebastianutto, 2010), potentially compounding the trend of decreased fanning found in the egg-tending experiment, and an increase in sheltering outside the nest would also reduce the time available to invest in defensive behaviours against egg predators or territory competitors (Lissåker and Kvarnemo, 2006). This could increase the likelihood of territory takeover by a conspecific male, which would not only result in the loss of the current clutch but also the loss of the nest site, potentially affecting future reproductive opportunity (Magnhagen and Vestergaard, 1991; Smith and Wootton, 1995). However, given our findings from Experiment 1, it is possible that sheltered males are also remaining vigilant outside of the nest, for surveillance and maintenance of the territory, without direct interaction with an intruder.

The impacts of motorboat noise on *P. amboinensis* behaviour found in our two experiments could have arisen via three major mechanisms. First, noise can result in physiological stress (Simpson et al., 2014; Celi et al., 2016; Vazzana et al., 2017; Mills et al., 2020), which could alter decision-making processes or reduce cognitive performance, potentially resulting in negative reproductive

outcomes (e.g. males resorting to filial cannibalism as a cost-effective way to gain energy; McCormick, 2016). Second, noise may be a source of distraction that causes natural behaviours (e.g. defence from intruder or parental care) to be performed with reduced efficiency and/or causes important environmental and social cues and signals to be ignored (Chan et al., 2010; Purser and Radford, 2011). Finally, if artificial noise in an environment occurs at similar frequencies to biologically important sounds, for example from egg-predators or conspecific intruders, masking can occur, inhibiting the ability of receivers to perceive vital acoustic information effectively (Vasconcelos et al., 2007; Holles et al., 2013; Pine et al., 2016).

The nest-defence behaviours of *P. amboinensis* in the mitigation treatment were not significantly different from the ambient treatment, including those behaviours affected by motorboat noise, demonstrating the value of our mitigation regime and corroborating similar results in freshwater fish (MacLean et al., 2020). Adherence to a noise-conscientious motoring protocol considerably lowered root-mean-square levels and frequency power spectra in both acoustic domains (RMS levels of motorboat noise were ca. 4 times higher than mitigation noise) to more closely match ambient-sound conditions, as shown in the acoustic analyses (Fig. 1a and b; Table 1). Three recent studies conducted on the Great Barrier Reef (Jain-Schlaepfer et al., 2018; McCormick et al., 2018, 2019) successfully mitigated biological responses to motorboat noise in embryonic and juvenile reef fish using 4-stroke engines instead of 2-stroke engines (the former are comparatively quieter). Due to the high cost of switching engines, and potential reluctance from motorboat owners to invest to limit their noise output, alteration of driving practice may be a more viable alternative to mitigate biological effects of traffic noise in many places. Our mitigation treatment combined changes to the motorboat speed and distance of the driving path from the reef into a zone-based strategy, which we believe would be easy to implement, however the relative importance of these separate factors in reducing behavioural impacts warrants further study. Vitally, our strategy reduced overall noise-exposure levels at the nests. Currently, there is enough evidence that anthropogenic noise harms marine life to prompt action and management (Shannon et al., 2016; Kunc and Schmidt, 2019), and we strongly advocate the use of simple, accessible noise-mitigation measures that principally focus on reducing noise-exposure levels, such as presented here, to reduce the detrimental impacts of noise on wildlife.

5. Conclusion

Our results provide *in situ* experimental evidence that nesting behaviours of wild *P. amboinensis* can be detrimentally affected when exposed to motorboat noise, and therefore have the potential to impact offspring indirectly via impairment of the behaviours of the nest carer. These findings have implications for coral-reef communities globally due to the widespread use of small motorboats for tourism, recreation, and the exploitation of marine resources in these habitats. However, our study also demonstrates that, by altering motoring practice to reduce noise, policymakers, managers, and users can make noise-conscientious decisions to help lessen the harmful impacts of motorboat noise on marine life.

Ethics statement

This work was approved by the University of Exeter Animal Ethics Committee (Application, 2013/247), the University of Bristol Animal Welfare Ethical Review Board (University Investigator Number UB/16/057) and James Cook University Animal Ethics Committee (Application A2361), and was completed in strict accordance with the guidelines of the Australian Code of Practice for the Care and Use of Animals for Scientific Purposes (8th Edition, 2013). Permits were granted by the Great Barrier Reef Marine Park Authority and Queensland Parks and Wildlife Service (Permit G17/39752.1) and the Queensland Department of Agriculture Fisheries and Forestry (Permit 170251).

Contributions

Kieran P. McCloskey: conceptualisation, methodology, data collection, project administration, data analysis & interpretation, writing - original draft, writing - review & editing, visualisation, graphical abstract, funding acquisition; Katherine E. Chapman: conceptualisation, methodology, data collection, project administration, data analysis & interpretation, writing - original draft, writing - review & editing, visualisation; Lucille Chapuis: conceptualisation, methodology, field supervision, data collection, project administration, writing - review & editing, funding acquisition; Mark I. McCormick: conceptualisation, methodology, resources, writing - review & editing, funding acquisition; Andrew N. Radford: conceptualisation, methodology, supervision, data interpretation, writing - review & editing, funding acquisition; Stephen D. Simpson: conceptualisation, methodology, supervision, data interpretation, writing - review & editing, funding acquisition.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.115376.

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