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Behavioural response to boat noise weakens the strength of a trophic link in coral reefs[☆]

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ABSTRACT

In oceans, the noise generated by human activities has reached phenomenal proportions, with considerable harmful effects on marine life. Measuring this impact to achieve a sustainable balance for highly vulnerable marine ecosystems, such as coral reefs, is a critical environmental policy objective. Here, we demonstrate that anthropogenic noise alters the interactions of a coral reef fish with its environment and how this behavioural response to noise impairs foraging. *In situ* observations on the Moorea reef revealed that the damselfish *Dascyllus emamo* reacts to boat passage by moving closer to its coral bommie, considerably reducing the volume of water available to search for prey. Using boat noise playback experiments in microcosms, we studied *D. emamo*'s behaviour and modeled its functional response (FR), which is the relationship between resource use and resource density, when feeding on juvenile shrimps. Similar to field observations, noise reduced *D. emamo*'s spatial occupancy, accompanied by a lower FR, indicating a reduction in predation independent of prey density. Overall, noise-induced behavioural changes are likely to influence predator-prey interaction dynamics and ultimately the fitness of both protagonists. While there is an urgent need to assess the effect of anthropogenic noise on coral reefs, the ecological framework of the FR approach combined with behavioural metrics provides an essential tool for evaluating the cascading effects of noise on nested ecological interactions at the community level.

1. Introduction

Over the past few decades, the world's oceans have been progressively exposed to human-made noise, a major environmental pollutant with considerable impact on the marine environment (Hildebrand, 2009; Ferrier-Pagès et al., 2021). The expansion of human activities, including constant maritime traffic (Ross, 2005), the use of sonar (Bernaldo de Quirós et al., 2019), drilling, and construction (Kuşku

et al., 2018), is altering underwater soundscapes. Coral reefs are among the most ecologically complex and diverse marine ecosystems, providing vital supplies and benefits to humans (Spurgeon, 1992). These ecosystems are vulnerable to human-generated noise pollution, including recreational activities such as fishing, water sports, and boating (Dinh et al., 2018; Gonson et al., 2016). Addressing noise pollution and its impacts is becoming a priority in the sustainable management of these threatened habitats (Duarte et al., 2021;

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Ferrier-Pagès et al., 2021).

Individual responses to noise in terms of behaviour and physiology have received considerable attention. They include for instance elevated androgen and glucocorticoid secretion (Mills et al., 2020), elevated ventilation rates (Nedelec et al., 2016), elevated heart rate (Fakan and McCormick, 2019), altered mobility and attention shifts (Purser and Radford, 2011), increased hiding (Mills et al., 2020; Nedelec et al., 2016), responsiveness to threat (McCormick et al., 2018a, 2018b; 2019). In addition, motorboat noise disturbs interspecific interactions such as when bluestreak cleaner wrasses (*Labroides dimidiatus*) are less cooperative during exposure to boat noise, whilst clients do not retaliate as expected (i.e., by chasing) in response to increased cheating by cleanerfish (Nedelec et al., 2017). Sublethal and sometimes subtle changes in individual behaviour may have consequences at the level of populations, communities, and ecosystems, especially when species playing key ecological roles are impacted (e.g., high-level predatory fishes; Di Franco et al., 2020; Sarà et al., 2007). Boat noise playback, as well as direct disturbance by boats, were found to trigger stress responses in the Ambon damselfish *Pomacentrus ambionensis*, with an elevated metabolic rate and reduced responsiveness to predation simulations. As a result, *P. ambionensis* undergoes higher predation from the dusky dotyback *Pseudochromis fuscus*, one of its natural predators (Simpson et al., 2016), suggesting a strengthened trophic link. Theoretical work has shown that changes in the strength of trophic interactions and in the distribution of weak and strong links can influence community stability (estimated by species persistence over time, McCann et al., 1998; Rooney and McCann, 2012). However, case studies on noise-induced alterations in trophic links remain few and are not designed to formally assess interaction strength (Chan et al., 2010; Wale et al., 2013; McCormick et al., 2018a, 2018b; 2019; Harding et al., 2020).

Functional response (FR) derivation, which models the relationship between *per capita* predation rate and prey density (Holling, 1959a; Solomon, 1949), is a powerful ecological approach for studying trophic links within a rigorous experimental framework. The shape and magnitude of the FR curve are strong indicators of the strength of top-down control and the stability of the trophic link. For instance, an increase in magnitude or a shift from sigmoidal type III to decelerating type II can lead to unstable boom-bust population dynamics (Murdoch and Oaten, 1975; Juliano, 2001; Gentleman and Neuheimer, 2008; Kalinkat et al., 2013). FR derivation has a long history in predation theory and has proven useful in exploring context-dependencies (i.e., how trophic links are modulated by environmental determinants) and quantifying the trophic impact of invasive species (Dick et al., 2013). In noise pollution research, FR derivation has been used only a handful of times with freshwater species (Fernandez-Declerck et al., 2023; Hanache et al., 2020; Rojas et al., 2023, 2021; Villalobos-Jiménez et al., 2017). Combining FR derivation with behavioural monitoring enables linking subtle changes in individual behaviour with alterations in trophic interaction strength. For instance, the European minnow *Phoxinus phoxinus* swims closer to its conspecifics and shows a less steep FR curve under boat noise playback (Hanache et al., 2020). The decrease in FR might result from reduced spatial occupancy and fewer opportunities to encounter prey. Conversely, the invasive round goby *Neogobius melanostomus* exhibits increased mobility and FR magnitude under boat noise (Fernandez-Declerck et al., 2023).

In the present study, we used the FR approach combined with behavioural monitoring to test the effect of boat noise on the strength of a trophic link commonly found between the Polynesian whitetail damselfish *Dascyllus emamo* and their juvenile shrimp prey within their habitat, Pocillopora sp. coral bommies. First, during predation tests in aquaria, we observed the behaviour of both predators and prey to establish a connection between changes in trophic links and individual responses to noise. Second, acknowledging that laboratory studies can sometimes induce deviations in natural behaviours (Kooijman, 2009; Maierdiali et al., 2020; Polverino et al., 2016), we conducted a field experiment to measure the proximity of wild *D. emamo* to their coral

bommie before and during the passage of real boats. We expected *D. emamo* to behave under noise similarly to how they would in the presence of a threat, showing increased use of shelter in both laboratory and natural conditions. Assuming that predator-prey encounters decrease with reduced spatial occupancy, we therefore expected that the FR would be lower in the presence of boat noise, indicating a weakening of the trophic link. The whitetail damselfish *D. emamo* (previously known as *Dascyllus aruanus* – Parmentier et al., 2022b) is a common species throughout the tropical Indo-Pacific region. It inhabits branched corals, using them as refuge when it feels threatened (Randall and Allen, 1977; Sale, 1971). Sound is an essential element in the ecology of *D. emamo*, which can both perceive and produce sounds. This fish is especially sensitive to frequencies between 100 and 2000 Hz, with their best hearing sensitivities below 400 Hz (Frédérich and Parmentier, 2016). Male damselfish produce pulsed sounds during courtship and aggressive behaviour, either to initiate fights or to chase conspecifics and heterospecifics away (Mann and Lobel, 1998; Parmentier et al., 2010, 2022b). Females produce sounds only in agonistic contests.

2. Materials and methods

2.1. Predator collection and maintenance

Every three days, from September 20 to October 20, 2022, approximately 24 *D. emamo* (total body length = 38 ± 6 mm, mean \pm SD) were collected with hand nets during snorkelling sessions on Papetoai reef ($17^{\circ}29'26.1''$ S, $149^{\circ}52'54.0''$ W, Moorea, French Polynesia), with a total number of 140 fish collected. Although the fish we sampled cannot be considered as completely naive to boat noise as some motorboats pass Papetoai reef (pers. observation), boat traffic was smaller than in the channel of Opunohu bay where we recorded the soundscape to design our playback track (see section 2.4). No distinction was made between males and females, based on the assumption that individual response to noise was not sex-specific. The fish caught during a session were placed in a cooler filled with seawater and brought back within an hour to the CRIOBE research station, where they were separated and isolated in 20-L outdoor aquaria, continuously filled with oxygenated lagoon seawater maintained at 27°C , and under a natural 12:12 light:dark cycle. Each storage aquarium contained an 8-cm PVC tube ($\varnothing = 3.5$ mm) as shelter. To avoid differences in hunger between individuals at the start of the experiment, fish were fasted for 24–48 h (applying a 24-hr fasting period to all individuals would have required additional fishing sessions, which was not feasible due to the limited availability of the boat needed to reach the snorkelling sites).

2.2. Prey collection and maintenance

Benthic crustaceans form part of *D. emamo*'s diet, along with zooplankton and algae (Frédérich et al., 2009). Different shrimp species were collected at two sites located in a wide sandy strip of the back reef in the northern lagoon of Moorea (Taahiamanu beach, $17^{\circ}29'26.7''$ S $149^{\circ}51'11.7''$ W). At each site, six coral colonies of *Pocillopora* sp. were securely attached to breeze blocks and placed in a circle at 2-m depth. To enable efficient shrimp recruitment, artificial lighting was placed in the centre of the circle, exposing the colonies at night to a 360° illumination ranging from 6.4 lux to 20 lux. Clove oil was used to remove potential shrimp predators from the coral colonies. Shrimps (between 300 and 800 on average) were collected every three days, on the same day as fish collection. Colonies were sampled and rinsed to dislodge all animals. Shrimps were sorted with a graduated pipette in the laboratory, and juveniles of four species were selected: the anemone shrimp *Periclimenes inornatus*, the snapping shrimp *Alpheus lottini*, the shrimp *Cuapetes elegans*, and the rock shrimp *Harpiliopsis beaupresii*. They were randomly assigned to one of two 3-L plastic tanks, which were supplied with live coral and algae, and continuously filled with sea water. They were fed with a stone covered in algae.

2.3. Experimental setup and design

Four large aquaria (24 × 70 × 45 cm, 70-L) were placed on two layers of acoustic foam to limit vibration coming vibrations transmitted from the ground and vibrational structures (Berendt et al., 1976; Davidson et al., 2007) and filled with a 4-cm layer of washed sand from Moorea lagoon to attenuate sound reverberation inside the aquaria (Buckingham, 2000). To avoid any visual disturbance from outside the aquarium, an opaque black film was placed over three of the walls. Above the four aquaria, a diffuse, constant light source was switched on. A UW30 underwater loudspeaker (Electro-Voice, Lincoln, NE, USA) was positioned on one side of each aquarium, submerged to mid-depth and away from the wall to prevent vibration transmission (Fig. 1). The underwater loudspeakers were connected to a stereo amplifier (MFA1200-BT, LTC), itself connected to a TASCAM DR-05 digital audio recorder. Just prior to fish introduction (see next paragraph), the aquaria were filled with sea water pumped directly from the bay at 27 °C. Based on preliminary settings, and because we had to turn off the air conditioning during the predation tests to avoid extra noise, we regulated the room temperature at 22 °C to prevent the aquaria water from overheating over time. The predation tests were carried out in a smaller unit (13 × 22 × 14 cm, 3.5-L, predation tank hereafter) placed inside each aquarium to reduce the volume of water available for hunting (i.e., performing the predation tests in the large aquarium would require too many prey to derive the FR) while isolating the prey from the sand where they would be lost. It contained a PVC tube (the same size as those in the outdoor storage aquarium) to provide shelter for the fish and was positioned on the opposite side of the loudspeaker (Fig. 1). The loudspeaker was suspended to prevent vibrations being transmitted to the aquaria walls. A camera (X'Trem Ultra HD, Storex) was placed beside each large tank, in front of the predation tank.

At the start of each trial, one fish was placed inside the predation tank. Fish size did not differ between acoustic treatments (control or boat) or between prey densities (ANOVA, gaussian family, p-value = 0.89 and 0.39 respectively). According to our previous tests, an individual needs less than an hour to return to their normal behaviour (swimming fluidly at a constant speed, no excessive ventilation, unchanged coat color). Therefore, after a 1-h acclimatization period with no sound being broadcasted, an ambient reef sound (= control sound) was played for 1 h (Fig. 2). Then, one of the two treatments (control or

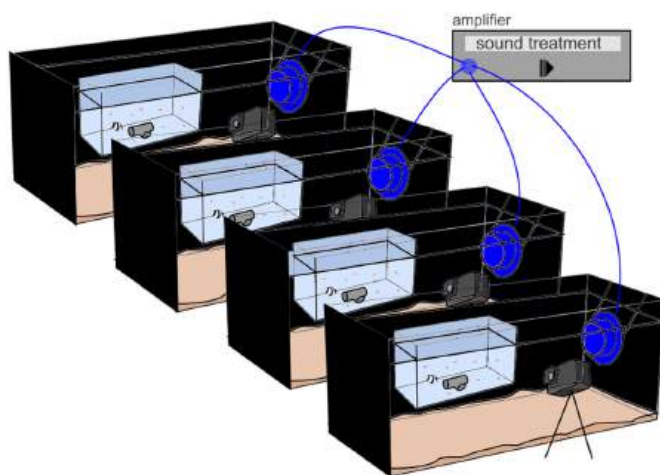


Fig. 1. Schematic drawing of the experimental setup shows four large aquaria (24 × 70 × 45 cm), each equipped with an underwater loudspeaker (dark blue) connected to an amplifier (grey). Within each aquarium is a predation tank (13 × 22 × 14 cm) housing a single whitetail damselfish *Dascyllus emamo* with its shrimp prey and a PVC tube. A camera (black) was positioned in front of each aquarium to record behaviour. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

boat, see 2.4) began, lasting 45 min. As soon as playback started, shrimps were introduced all at once using a 50-ml Falcon tube, and evenly distributed in the small tank. We tested seven prey densities: $N_0 = 2, 4, 8, 16, 32, 64,$ and 128 shrimps, with ten replicates ($n = 10$) per density and per treatment (a total of 5080 shrimps and 140 fish over 140 trials). When calibrating the playback tracks, we noticed that the sound played back in an aquarium was detectable in the aquarium next to it. For this reason, in a same run of four predation tests, the four aquaria received the same acoustic treatment but with different prey densities. To balance the effect of the experimental setting, we alternated the acoustic treatments every two series of trials. Trials were repeated in 3-day cycles. At the end of the trial, the fish was carefully removed with a hand net, measured for total length, and then returned to a community aquarium before being released back on the Papetoai reef, but not too close to our fishing site to avoid collecting the same individual twice. The remaining live juvenile shrimps were collected using a hand net (0.5-mm mesh) and counted while removing the water from the aquarium (which ensured that all shrimps were removed). As no deaths or cannibalism were observed among the shrimps, prey mortality was attributed solely to fish predation. The predation tanks were rinsed and the water changed between two consecutive series trials to remove any chemicals released.

2.4. Playback tracks

We used two different acoustic treatments: 1) playbacks of the natural ambient soundscape of *D. emamo* at its coral bommie, which served as the control treatment (reef sound), and 2) playbacks of the natural ambient soundscape supplemented with a series of boat passages (boat treatment). Both treatments were prepared using a two-day continuous recording made at a depth of 2 m near the channel of Opunohu bay (17°29'19"0.5 S 149°51'26.8" W). The recording was made using an autonomous SNAP acoustic recorder (Loggerhead Instruments; Sarasota, FL, USA; <https://www.loggerhead.com/snap>) equipped with a HTI-96-Min hydrophone (sensitivity of 169.9 dB re 1 V for a sound pressure of 1 μPa; flat frequency response from 2 Hz to 30 kHz) at a sampling frequency of 44.1 kHz. From this recording, the average boat abundance over 45 min was determined and a library of the boat sounds detected over the entire recording was created.

We used the Audacity Software 3.2.3 to create the playback tracks. The frequency range over which damselfish are able to detect sounds lies between 100 and 2000 Hz, with their best hearing sensitivities at low frequencies (<400 Hz) (Parmentier et al., 2009). Consequently, both tracks were filtered above 2000 Hz. A 1-h audio snippet of the reef soundscape captured over two days (from 7 a.m. to 5 p.m.) and containing only naturally occurring biological sounds was used as control treatment.

Twenty-three boat passages with durations between 25-sec to 60-sec and intensities ranging from 120 to 133 dB re 1 μPa reflecting variations in boat type, speed and distances from the recorder, were selected from the original two-day recording and randomly added to the 45-min playback of the reef soundscape. Boat sounds were amplified to levels from 1 to 20 dB re 1 μPa louder than the one of the reef soundscape (mean relative sound pressure was 84.5 dB re 1 μPa for the control treatment and 92.8 dB re 1 μPa for the boat treatment – Fig. 3). To monitor the quality of the acoustic stimuli inside the predation tanks, the original audio tracks were played in the experimental tank through the loudspeakers and were recorded with a TASCAM-DR05 recorder (TEAC Corporation, Tokyo, Japan) connected to a HTI-96-Min hydrophone (sensitivity of 170.1 dB re 1 V for a sound pressure of 1 μPa) placed in the predation tank. The acoustic parameters of the playback tracks (frequency and intensity) were adjusted with Audacity (version 3.2.3) to deal with the reverberations and echoes caused by the aquaria and make the signals as close as possible to the original recordings. The final playbacks were rechecked with a TASCAM-DR05 recorder to ensure that they matched the loudness of the original two-day recording.

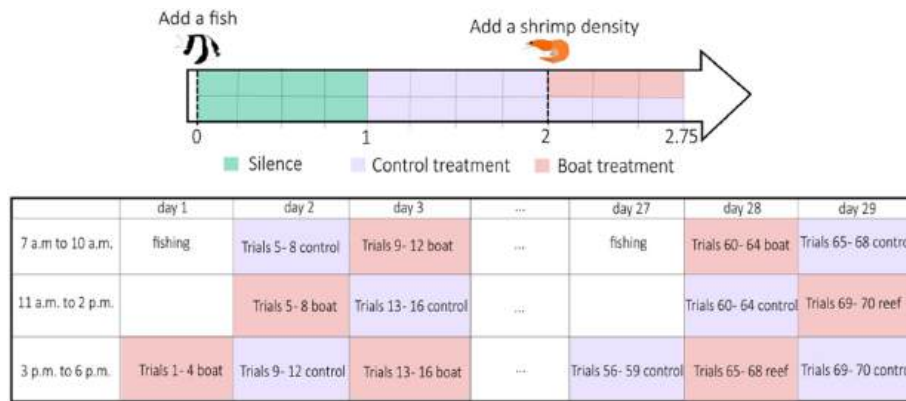


Fig. 2. Trial timeline. From 0 to 1 h: acclimatization in silence (green); from 1 to 2 h: acclimatization in ambient reef sound (control, violet), and from 2 to 2.75 h: predation under a playback of ambient reef sound alone (control, violet) or supplemented with motorboat noise (red). The procedure was repeated in 3-day cycles for a total of 6 cycles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

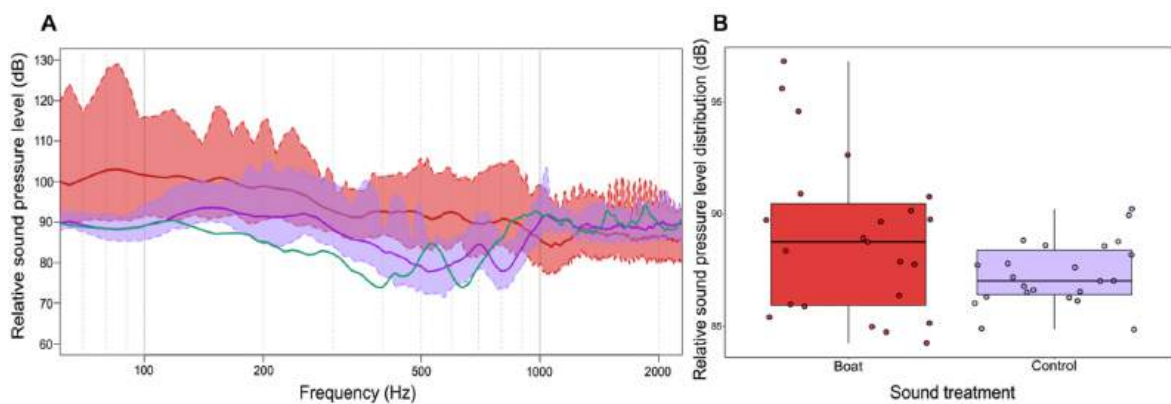


Fig. 3. A. Frequency spectra of the control treatment (purple) used as a control and the boat treatment (red) recorded in the predation tank, compared with the natural reef soundscape recorded in the sea (green). Shaded areas represent the range (max – min over 24 tracks) of relative sound pressure levels (dB re 1 μ Pa). B. Boxplot of the relative sound pressure level of the 23 boat playbacks (red) and 23 random parts of the reef playback (purple) recorded in the experimental tank over the 45 min. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.5. Behavioural responses

Dascyllus emamo's behaviour was recorded, and the videos were analysed using a customized Python program (version 3.11.5, *conda* package version 23.7.4) to automatically track the fish for 45 min. Its position was recorded every 0.2 s, taking the second black band on the coat as the reference point, and five parameters were measured: two measures of hiding: the total time spent in the shelter (*pvc_time_sec*, in sec, time during which the fish is not visible) and the average distance to the shelter (*dist_pvc*, in cm, between the second black band to the middle of the PVC tube), one measure of activity: the total distance moved (*dist_cm*, in cm) and two measures of speed: the average (*mean_speed*, in cm/sec) and maximum (*max_speed*, in cm/s) speeds. Because we used one camera *per* aquarium, the measurements were made in two dimensions only: length and height. Although this might have had a slight impact on our results, all the fish were processed consistently, and it is very unlikely that boat noise affected the movements in the plane not captured by our camera more than those in the other planes. The low resolution of the camera made it impossible to record the behaviour of the juvenile shrimps. However, in a preliminary experiment, we observed juvenile shrimps under control and playback conditions in the absence of fish predators, to ensure that cannibalism did not occur and that their behaviour was not altered by the experimental context. All the shrimps were still alive, and their mobility was unchanged after 45 min of both playbacks.

2.6. In-situ experiment

We tested the behavioural response of *D. emamo* to boat passages directly on Papetoai reef. We chose a total of 10 coral bommies (*Pocillopora* sp.) emerging from sand and naturally colonized by *D. emamo* only. A stand-alone camera (X'Trem Ultra HD, Storex) was positioned in front of each coral bommie, filming from the sandy bottom to the surface of the water column for 20 min. We allowed the fish to acclimatise for 10 min (Nanninga et al., 2017) after placing the camera. We then filmed a 10-min experiment for each bommie, consisting of a 5-min recording before the boat passage (control with only reef background noise) and a 5-min recording during the boat passage at a distance of 1–5 m, a distance chosen as it was navigable without hitting corals in water less than 2 m deep. The noise levels during this phase corresponded to the highest values recorded in the laboratory experiments, with signal-to-noise ratio not exceeding 20 dB. We counted the number of fish outside the bommie every minute from a still frame of the video, both during the control and boat passage phases. The experiment was conducted during the day, within the same time frame as the tank trials.

2.7. Statistical analyses

We performed statistics using the R software (version 4.1.2, R Core Team, 2022) and the Rstudio add-on (version 2022.07.1) with a significance level of $\alpha = 0.05$.

We carried out Generalized Linear Models (GLM) with Gaussian regression to confirm the absence of a difference in fish size between the acoustic treatments and prey densities.

Functional Response (FR) analysis was based on the workflow implemented in the *FRAIR* R package (Pritchard et al., 2017). To discriminate between the decelerating type-II FR and the sigmoidal type-III FR, we performed logistic regressions explaining the proportion of prey consumed as a function of the prey density initially provided. Using the *frair_test* function, we found a significant negative first-order term for both acoustic treatments, suggesting type-II FRs (control noise: estimate coefficient = -0.017 , $z = -16.74$, p -value <0.001 ; boat noise: estimate coefficient = -0.008 , $z = -7.17$, p -value <0.001). Because consumed prey were not replaced in our experiments, we used the Rogers' random predator equation, which is a modified type-II FR that accounts for prey depletion during the course of the predation test (Rogers, 1972). The number of prey eaten (N_e) follows the relationship:

$$N_e = N_0(1 - \exp(-a(N_e h - T))),$$

where N_0 is the initial prey density, a is the attack rate, h is the handling time, and T is the total experimental time. The attack rate, also called space clearance rate, quantifies predator's feeding efficiency when there is little prey (low prey densities) and is proportional to the initial slope of the FR curve (the higher the attack rate, the steeper the initial slope). The handling time corresponds to the time interval between two consecutive captures which, under saturation (i.e., with a quasi-infinite number of prey), should ideally be restricted to prey handling time (but see Li et al., 2018). It defines the magnitude of the FR curve (the smaller the handling time, the higher the asymptote) and its inverse quantifies the maximum feeding rate ($1/h$: the feeding rate calculated under predator saturation, at high prey densities).

Model fitting was done with the *frair_fit* function which uses optimization by Maximum Likelihood Estimation (MLE) and provides ML estimators corresponding to the two FR parameters a and h (see Pritchard et al., 2017 for further detail).

Since both FRs were of the same categorical type (II), it was possible to perform a pairwise FR comparison between the two noise conditions based on the estimates of a and h using the delta (or difference) method implemented by the *frair_compare* function. This tests whether Da and Dh (the differences in attack rate and handling time) differ significantly from zero (Juliano, 2001; Pritchard et al., 2017). In addition to the delta method, we generated multiple estimates of curves and parameters (a and h) through nonparametric bootstrapping with the *frair_boot* function ($n = 2000$) and reported bias corrected and accelerated 95% confidence intervals (because a and h are bias, skew and bounded). We then plotted empirical approximations of the 95% CIs on the entire FR curves with the *drawpoly* function and visually inspected how they overlapped, using the absence of overlap as the equivalent of a null hypothesis (Pritchard et al., 2017).

We used a PERmutation Multivariate Analysis Of VAriance (PERMANOVA) to test the effects of boat noise, prey density and their interaction on the multivariate behaviour of *D. emamo* including the five behavioural responses measured (i.e., average and maximum speeds, total swimming distance, total time spent in the hiding place and average distance to the hiding place), the majority of which being not normally distributed (Shapiro test: $w = 0.87, 0.79, 0.82, 0.98$ and 0.93 , respectively, p -values <0.05 except for maximum speed with p -value = 0.23). The PERMANOVA was applied to a Bray-Curtis dissimilarity matrix (Anderson, 2017) using the *adonis2* function of the *vegan* R package with 9999 permutations. Due to the multidimensional nature of the response variable, it may be that non-significance in the PERMANOVA is actually masking differences in specific dimensions. This can be tested by carrying out univariate analyses after the PERMANOVA (see Saccenti et al., 2014; Khomich et al., 2021). We therefore used GLM to explain the variation in each of the five behaviours as a function of the noise condition, prey density and their interaction. The mean and

maximum speeds, total swimming distance and average distance to the shelter were approximated by a Gaussian distribution after log-transformation while the total time spent in the shelter was approximated by a negative binomial distribution.

Data relating to the *in-situ* behavioural response of *D. emamo* to boat passages were not normally distributed (Shapiro test: $w = 0.89$, p -value <0.05). We therefore compared the number of fish outside the coral bommie before and during boat passages using a paired Wilcoxon test.

3. Results

3.1. Functional response

Regardless of the acoustic treatment, the *per-capita* predation rate increased with prey density at a decelerating rate up to an upper asymptote leading to a type-II functional response (FR, Fig. 4). According to the delta method, boat noise significantly reduced the attack rate ($Da = 1.01$, p -value $<10^{-3}$) and tended to increase the handling time ($Dh = 0.008$, p -value <0.055) compared to the control treatment (control treatment: $a = 1.48$, $h = 0.022$; boat treatment: $a = 0.47$, $h = 0.031$). This resulted in a less steep and lower FR under boat noise. The 95% CI of the FR curves did not overlap, except at the highest prey density (Fig. 4).

3.2. Fish behaviour

The multivariate behaviour of *D. emamo* was not significantly affected by the acoustic treatment, prey density or their interaction (PERMANOVA; acoustic treatment: $r^2 = 0.008$, p -value = 0.49 ; prey density: $r^2 = 0.02$, p -value = 0.97 ; interaction between acoustic treatment and prey density: $r^2 = 0.02$, p -value = 0.97). Among the five behavioural responses examined, the only notable difference was that the average distance to the shelter tended to be smaller under boat noise compared to the reef soundscape (GLM: $\chi^2 = 3.42$, p -value = 0.06 ; all p -values >0.20 for the four other behaviours, Fig. 5).

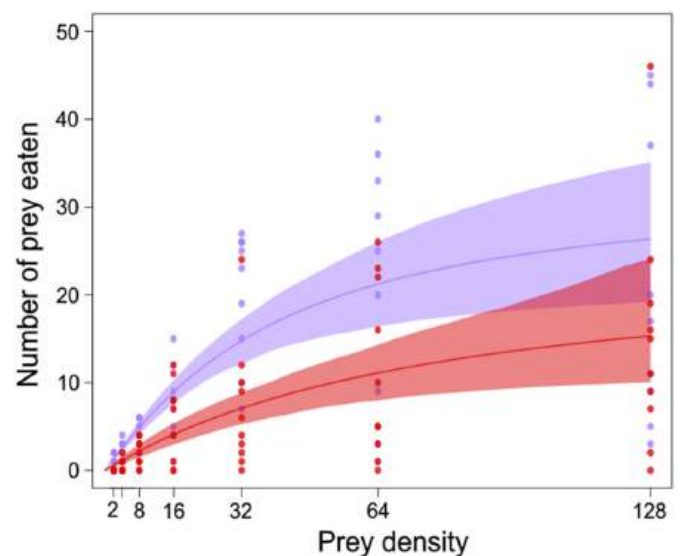


Fig. 4. Number of prey eaten as a function of prey density (functional response, FR) for the whitetail damselfish *Dascyllus emamo* feeding on juvenile shrimps under two acoustic playback treatments: reef sound (control, purple) and reef sound supplemented with boat noise (red). Dots are direct observations from individual fish (10 replicates *per* trial) and curves are the fits of the best FR model. Shaded areas represent the bootstrapped 95% confidence intervals ($n = 2000$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

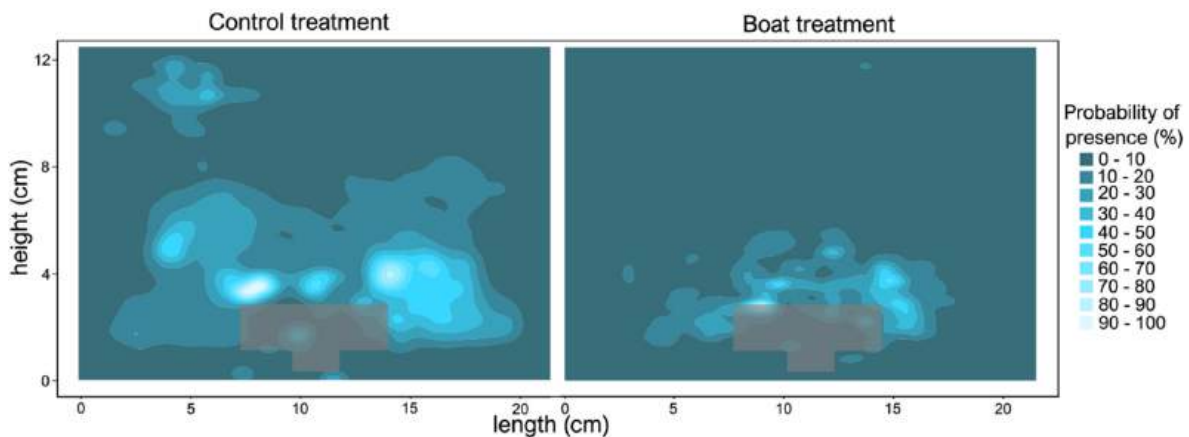


Fig. 5. Average 2D density plot illustrating the spatial distribution of a single damselfish individual (*Dascyllus emamo*) while feeding on juvenile shrimps in the predatory tank equipped with a shelter (grey shape) and under two acoustic treatments: reef sound as control (left) and reef sound supplemented with boat noise (right). The color gradient shows the probability level of presence (%) ranging from high (light blue) to low (dark blue), averaged over the ten replicates of the seven prey densities for each acoustic treatment (see text for further details). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. In situ response to boat passages

Fish responded to the passage of a boat by hiding inside their coral bommie. On average, 4.5 ± 3.03 fish were outside their colony in the absence of boat compared with 1 ± 3.14 when a boat passed (Wilcoxon paired test, $V = 103.5$, p -value < 0.005 – Fig. 6).

4. Discussion

Using the functional response (FR) derivation approach in conjunction with behavioural monitoring, we demonstrated how a fish's response to boat noise can weaken the strength of a trophic interaction between a predator and its prey. Whether in the field or in aquaria, the noise associated with the passage of a boat provokes hiding behaviour in the damselfish *Dascyllus emamo* and, consequently, a sharp decrease in the slope and magnitude of the FR curve in aquaria. Our experiment shows that boat noise influences *D. emamo*'s per capita predation rate irrespectively of prey density.

The flattening of the FR curve indicates that boat noise significantly reduced *D. emamo*'s attack rate, a key measure of a predator's efficiency

in locating prey. According to the distraction hypothesis (Chan et al., 2010), the fish may have been distracted by the boat noise, reducing their ability to find shrimp. From the perspective of animal performance and perception, this aligns with the concept of anthropogenic noise as a form of sensory pollutant, which is known to impair animal performance in noisy environments (Halfwerk and Slabbekoorn, 2015). Alternatively, and not mutually exclusive, *D. emamo* might have decreased their foraging effort in response to boat noise, as suggested by our behavioural observations. The fish tended to stay closer to the shelter when exposed to boat noise, similar to other coral reef fish species (Nedelec et al., 2016; Mills et al., 2020), likely as a protective measure from a potential threat. This supports our hypothesis of a causal relationship between attack rate and spatial occupancy, since prey encounter opportunities decrease with a predator's range of movement (Gerritsen and Strickler, 1977). Comparable findings were noted in the European minnow *Phoxinus phoxinus*, which also showed a reduced attack rate and closer proximity to conspecifics under boat noise (Hanache et al., 2020). In contrast, the round goby *Neogobius melanostomus* showed increased attack rate and swimming activity when exposed to boat noise (Fernandez-Declerck et al., 2023).

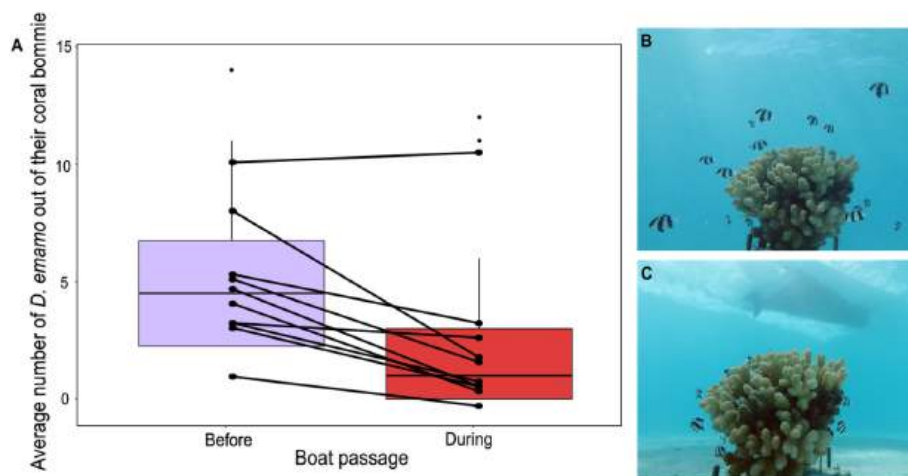


Fig. 6. A. Box plots of the mean number of whitetail damselfish *Dascyllus emamo* out of their coral bommie (*Pocillopora* sp.) observed over 5 min before (purple) and during boat passages (red) for ten different bommies ($n = 10$) at Papetoai reef. Boxes represent the first and third quartiles, thick horizontal bars the median (second quartile), whiskers the distribution range (min-max) and the small circles the outliers. Black lines and points are paired mean numbers per coral bommie. B and C. Photographs of the same pinnacle before (B) and during (C) the passage of a boat. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Boat noise significantly increased handling time, which in turn reduced the maximum feeding rate, as indicated by the substantial decrease in the magnitude of the FR curve. Handling time, traditionally defined as the average time elapsed between consecutive prey captures (Coblentz and DeLong, 2021; Li et al., 2018), generally refers to the time spent on prey processing tasks such as subduing and ingesting prey during short-term experiments (Holling, 1959b). However, in longer experiments, handling time may also include non-foraging activities such as resting (Li et al., 2018). Two non-mutually exclusive scenarios could therefore explain the increased handling time. First, consistent with the distraction hypothesis (Chan et al., 2010), boat noise may have diverted some of *D. emamo*'s attention away from prey processing. Additional experiments that directly measure handling time (as in Prosnier et al., 2024) are needed to test this hypothesis. Second, the fish might have reduced their feeding time in response to boat noise, potentially reflecting a behavioural stress response. The observed tendency for the fish to spend more time near the shelter during noise exposure aligns with extending non-foraging periods, which mathematically results in longer handling times.

The response of *Dascyllus emamo* to boat noise exhibited a consistent pattern in both laboratory and field settings. However, the specific impact of acoustic cues compared to visual and hydrodynamic cues (Vetter et al., 2017) during the field study was not distinguished. This finding implies that *D. emamo*'s behaviour did not differ significantly between laboratory and field conditions, addressing a common issue in laboratory studies (Popper and Hawkins, 2019).

The short duration of our experiments and the higher noise levels compared to those typically experienced by *D. emamo* at Papetoai reef raise the question of whether *D. emamo* habituates to noise. Habituation, which refers to the reduction in response to repeated stimuli (Groves and Thompson, 1970), is under active consideration in noise pollution research as it is a key determinant of ecological impacts (Nedelec et al., 2016). Further FR derivation experiments could be conducted including an initial period of repeated exposure to boat noise to test for habituation (see Rojas et al., 2021, 2023 for examples of FR experiments with repeated exposure).

Although our observations did not reveal any noticeable behavioural changes in shrimps in response to boat noise, we cannot rule out the possibility of physiological or subtle behavioural changes that might have not been detectable within the constraints of our experimental protocol. However, from an ecological perspective, understanding whether the changes in interaction strength are driven by the predator or prey is less critical than understanding the wider community level consequences.

From a broader perspective, both *D. emamo* and juvenile shrimps are intricately entwined in various ecological interactions, so their behavioural and demographic responses to boat noise could reverberate throughout the community. For instance, *D. emamo* exhibits dietary plasticity, consuming a diverse range of sources including benthic and pelagic invertebrates, filamentous algae (Frédérich et al., 2010), and even ectoparasites, scales, skin, and mucus when acting as a cleaner fish (Parmentier et al., 2022a). In noisy environments, *D. emamo* may experience an overall decrease in foraging activity regardless of the food source, or it might compensate for a decreased intake of juvenile shrimps by consuming more alternative food sources. Theoretical evidence suggests that such shifts in trophic interaction strengths can have substantial implications for community stability (McCann et al., 1998; Rooney and McCann, 2012).

5. Conclusions

We investigated the behaviour of *D. emamo* and modeled its functional response (FR) – the relationship between resource consumption and resource density – while feeding on juvenile shrimp in the presence of boat noise playback. Boat noise led to a decrease in the spatial occupancy of *D. emamo*, which was associated with a reduced FR,

indicating a reduction in predation that was independent of prey density. Taken together, these noise-induced behavioural changes are likely to impact the dynamics of the predator-prey relationship and, ultimately, the fitness of both species. The combination of the ecological framework of the FR approach with behavioural metrics proves to be a vital tool for assessing the cascading effects of noise on complex ecological interactions at the community level. Nonetheless, there is an urgent need to better quantify the influence of anthropogenic noise on coral reefs.

CRediT authorship contribution statement

Lana Minier: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Frédéric Bertucci:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Tamatoa Gay:** Writing – review & editing, Investigation. **Zoé Chamot:** Writing – review & editing, Investigation. **Théophile Turco:** Writing – review & editing, Formal analysis. **Jules Schligler:** Writing – review & editing, Resources. **Suzanne C. Mills:** Writing – review & editing. **Manuel Vidal:** Writing – review & editing, Software. **Eric Parmentier:** Writing – review & editing. **Vincent Sturny:** Writing – review & editing. **Nicolas Mathevon:** Writing – review & editing, Conceptualization. **Marilyn Beauchaud:** Writing – review & editing, Conceptualization. **David Lecchini:** Writing – review & editing, Validation, Methodology, Conceptualization. **Vincent Médoc:** Writing – review & editing, Validation, Methodology, 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.

Data availability

Data will be made available on request.

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