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BEHAVIOUR OF FISH IN NOISY ENVIRONMENTS

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1 INTRODUCTION

We are becoming increasing aware of the importance of acoustics in the behaviour of fishes. Many different adaptations have evolved in fishes for producing sounds, and as a result, acoustic communication is commonplace, especially in nocturnal and deep sea fishes where visual communication is limited [1-7]. We now know that sound is used by potential partners for assessing quality and readiness to mate [8, 9], and a range of sounds (including FAst Repetitive Ticks!) are used to maintain shoaling or during nocturnal hunting forays [10]. We are currently looking at the calls of male damselfish on the Great Barrier Reef to study whether potential colony-mates are attracted by vocalisations (work in progress).

Most fish live in noisy environments, and whether they can vocalise or not, they have structures for detecting noises [11-15]. We have been studying the behaviour of coral reef fishes at the key life history stage where they return from a pelagic larval developmental period to settle to reef habitat. We have also conducted a broad study of reef noise at sites in the UK, Oman, Panama, Curaçao and Australia to determine whether sounds, many of which are produced by fish and invertebrates, are indicative of a particular habitat and community. Our interest comes from two angles: understanding the importance of reef noise for settlement-stage reef fishes; and mapping and determining the sources that drive the temporal and spatial heterogeneity of reef noise.

2 IMPORTANCE OF REEF NOISE FOR SETTLEMENT-STAGE REEF FISHES

2.1 Light trap studies

Light traps are commonly used to monitor larval supply near to coral reef habitats [16], and consist of a Plexiglas-sided box with entry slits illuminated by a housed fluorescent lamp, and attached to a collection bucket and moored to the seabed. They are an established tool for collecting settlement-stage reef fishes around the reefs of Lizard Island, Great Barrier Reef, Australia (e.g. [17]). To test the hypothesis that settlement-stage coral reef fishes may be attracted to reef noise as they return to reef habitat following a pelagic larval phase, we have conducted a series of experiments. In the first experiment, we compared catches of settlement-stage reef fish in light traps attached to underwater speakers playing reef sounds (recorded from a nearby reef) with those of silent traps during a summer recruitment season at Lizard Island (methods similar to [18, 19]). Our sound systems consisted of a floating barrel containing a marine battery, amplifier, and portable CD payer attached to a UW-30 (frequency response 0.1 to 10 kHz, University Sound, Buchanan) speaker in the first experiment, and to a LL964 (frequency response 0.2-20 kHz, Lubell Labs Inc., Columbus, OH) speaker in subsequent experiments.

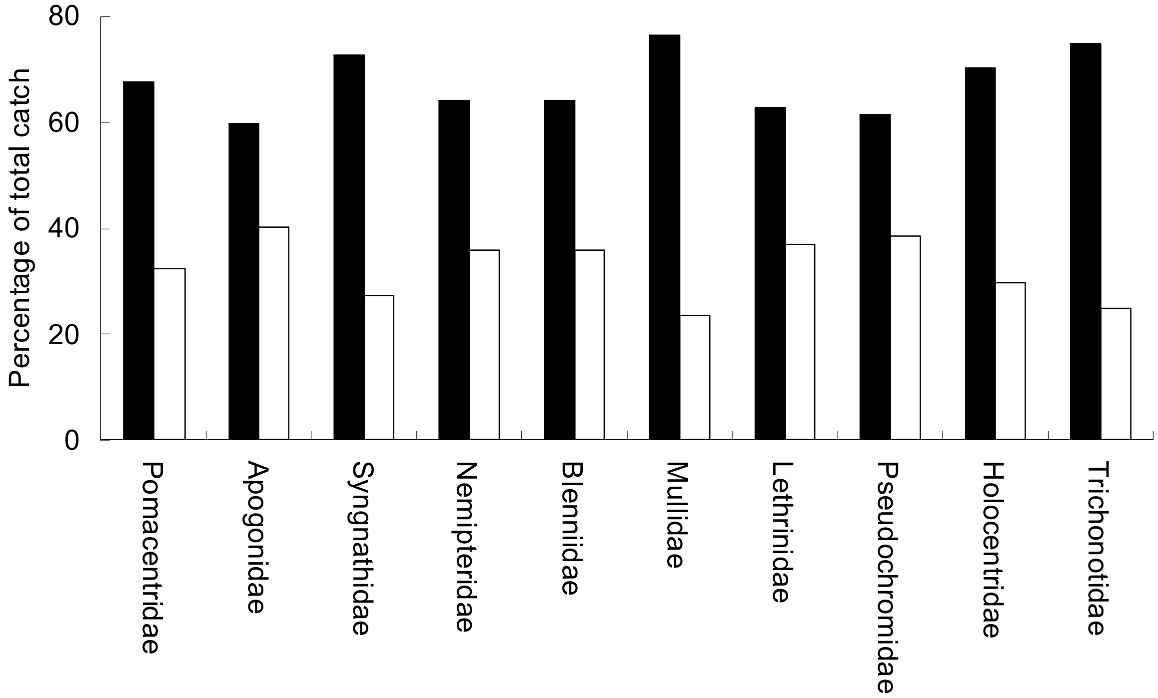

Figure 1. Percentage catch of reef fishes in light traps deployed with speakers broadcasting reef noise (filled bars) and silent traps (hollow bars) during summer months at Lizard Island. Data are shown for those families where more than 20 individuals were collected during the study (from [20]).

Of the total of 40,191 reef fishes we collected in the first study, significantly more (67%; Wilcoxon's and Binomial tests: $p<0.001$) appeared in the traps with broadcast reef noise (Fig. 1). Traps deployed with speakers also consistently caught a greater diversity of species (Wilcoxon's test: $p<0.001$, total 81 vs. 68) than did silent traps. This provided a clear demonstration that the settlement-stage of a broad range of families of coral reef fishes are attracted to reef sounds [20].

We have since followed this light trap and reef noise experiment up with a second experiment where we split the sound spectrum at 570 Hz, giving us a 'low-frequency' treatment (0-570 Hz) and a high frequency treatment (570-2000 Hz). This split gives a crude division of the reef noise within the generalist hearing range of fishes between fish vocalisation noises (low frequency) and invertebrate noises (high frequency). We found significant responses in our catches, which as yet are unpublished; I will present these results in my talk.

2.2 Patch reef studies

Light traps and sound systems provide an effective but highly unrealistic scenario for studying actual settlement behaviour. To address the question of whether the attraction to reef noise we see in several families of reef fishes would actually drive settlement patterns, we conducted two experiments using patch reefs (small piles of coral rubble) and moored sound systems [21]. In November 2003, we built 24 artificial reefs from dead coral rubble on sand flats in 3-6m water at Lizard Island, Great Barrier Reef. For six nights, we deployed submersible speakers broadcasting reef noise (at 156 dB re 1µPa at 1m; mostly the sound of snapping shrimps and fish calls) on half of these reefs, alternating the location of the speakers each night. Most settlement occurs at night, so recruiting fish were collected from the reefs early the following mornings. Of the 868 recruits we collected, most were apogonids (cardinalfish, 80%) and pomacentrids (damselfish, 15%). These two families are key members of coral reef fish assemblages around the world: the apogonids contributing up to one-quarter of all individuals on reefs and the pomacentrids up to half of the total fish biomass [22]. Analyses showed no site or date effects in our data, but both families settled in greater numbers on noisy reefs than on silent reefs (Fig. 2A). This pattern was also evident in rarer fishes, with consistently more families and taxa on reefs with broadcast noise than on reefs without (Fig. 2B).

In December 2003, the experimental field site was used to compare the settlement of fishes to reefs where we broadcast only the high (570-2000 Hz; predominantly shrimp noise) or low (0- 570 Hz; predominantly fish noise) frequency portion of reef noise with that to silent reefs. This time, nearly four times as many recruits arrived (3111 fish) compared to the previous study, but the taxonomic composition was similar. Apogonids settled on high and low frequency reefs in equivalent numbers, but pomacentrids were preferentially attracted to reefs with high frequency noise (Fig. 2C). Again, reefs without sound received much lower settlement and total numbers of families and taxa than reefs with broadcast sound (Fig. 2D).

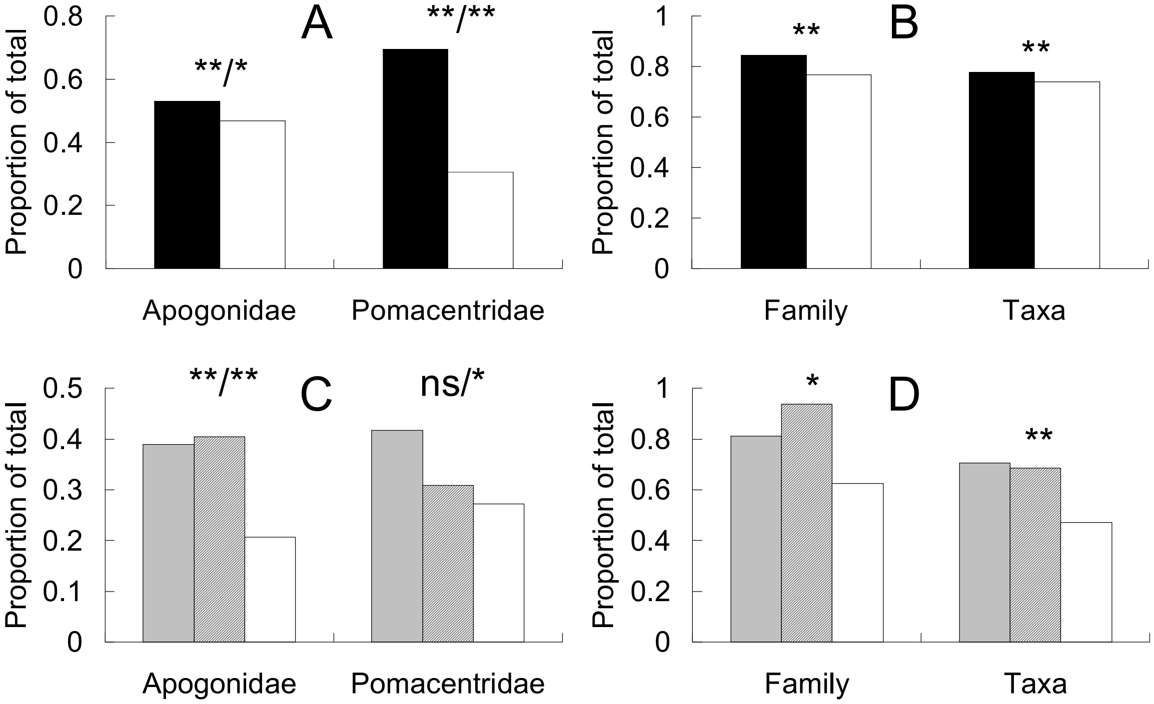

Figure 2. Proportion of total catch from reefs with different sound treatments. A & B – reefs broadcasting reef noise (black) or silent (white); C & D – reefs with high (grey) or low (diagonal hatching) frequency reef noise or silent (white). For A, statistics are: Wilcoxon's/Chi-squared; C: Friedman's/Chi-squared; B&D: Chi-squared only; **: p<0.05, *: p<0.1, ns: not significant (from [21]).

This study provided the first direct field evidence that settling reef fishes may use sounds to select and orient towards reefs, that they can localise the source, and that this cue alone is sufficient to promote recruitment. Furthermore, there was an indication that some fish groups, such as pomacentrids, may us specific components of the reef sound to guide their settlement behaviour.

More recent analysis of the catches of juvenile and adult fish at our patch reefs has shown that post-settled fishes also respond positively to reef noises, and that they have preferences for certain elements of reef noise when relocating to new habitat at night (Simpson et al., In Review, Coral Reefs). I will present this evidence in my talk.

3 MAPPING AND DETERMINING THE SOURCES THAT DRIVE THE HETEROGENEITY OF REEF NOISE

3.1 Memory for noise in settlement-stage coral reef fishes

For a settling fish, if community structure could be detected prior to settlement this would limit the number of encounters with the ‘wall of mouths’ waiting to receive them. This of course requires that the larvae can remember the sounds of several reefs and make their selection accordingly. We have conducted experiments that show that 20 day old damselfishes adjust their behaviour based on recent acoustic experiences to natural and artificial noises (unpublished). I will present these results in my talk.

3.2 Potential for imprinting in embryonic reef fishes

The preferences seen in the early life history stages of coral reef fishes may tell a far more adaptive story if the response to sounds is based on more than just their immediate experiences. There is mounting evidence that the larvae of some fishes are able to avoid dispersal [23], and even return to the reefs on which they were originally spawned [24, 25]. Evidence suggests that clownfish may imprint on olfactory cues from their host anemones during embryonic development, and that this experience later determines their settlement preferences [26, 27]. To test whether reef fish have the ability to learn about their natal environment prior to hatching through acoustic cues, we investigated the ability of embryonic clownfishes (*Amphiprion ephippium* and *A. rubrocinctus*) to detect sound during incubation in benthic nests [28]. The heart rates of embryos within eggs were monitored as the young fish were exposed to sounds in the range 100-1200 Hz at levels of 80-150 dB (re 1 μPa at 1 m) on each day of incubation. We found that from 3 d after fertilisation, heart rates of the embryos significantly increased when exposed to sound (Fig. 3). As the embryos developed, a response in heart rate was found over a broader spectra of sound (from 400-700 Hz at 3 d to a maximum of 100-1200 kHz at 9 d after fertilisation) and sensitivity also increased, with response threshold minima at 700 Hz dropping from 139.1 dB at 3 d to 88.3 dB at 9 d after fertilisation.

These response curves (cf. audiograms) can be compared to noises that have been recorded from reef habitats (Fig. 4) in previous studies [29, 30]. It becomes clear from this comparison that embryonic fish will experience the noises of fish as they vocalise, but that attenuation of noises with distance from the clutch will mean that only nearby fish (hence the neighbouring community) will be detected. Whether this influences later behaviour at settlement is yet to be resolved.

3.3 The size of the ‘sensory halo’ around reefs

We have also used several approaches to explore the distance from which settling reef fish larvae can detect reefs, and have made some progress in characterising the scale at which acoustic orientation is possible. I will also present these unpublished results, as well as predictions made by other groups [31, 32], and discuss the possible interpretations to date.

3.4 Mapping reef noise heterogeneity in space and time

If habitat and community structure can be inferred from acoustic recordings, there is potentially a very valuable survey and monitoring tool which is yet to be developed. We have combined recordings with video transects and underwater visual censuses of fishes in Oman, Panama and Curaçao to test this theory, and have made some progress in identifying patterns in both space and time. I will present our unpublished findings to date in this talk.

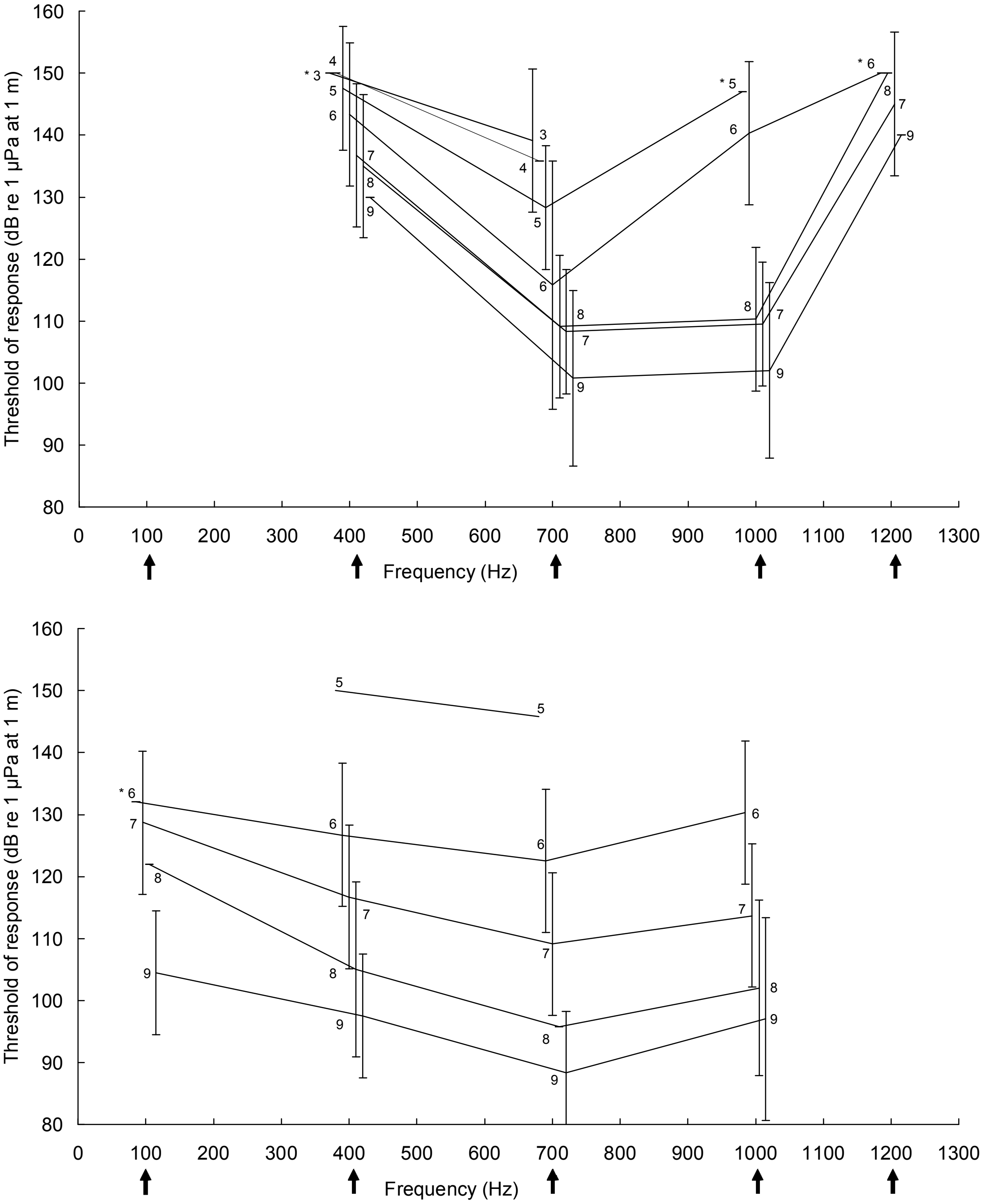

Figure 3. Development of the threshold of response to sound treatments by embryos of (a) *Amphiprion ephippium* and (b) *A. rubrocinctus* during development. Arrows indicate the test frequencies, data labels indicate the age of the embryo (days post-fertilisation), error bars show 95% confidence limits. Notice no significant response at 100 Hz for *A. ephippium* while no significant response at 1200 Hz for *A. rubrocinctus* (from [28]).

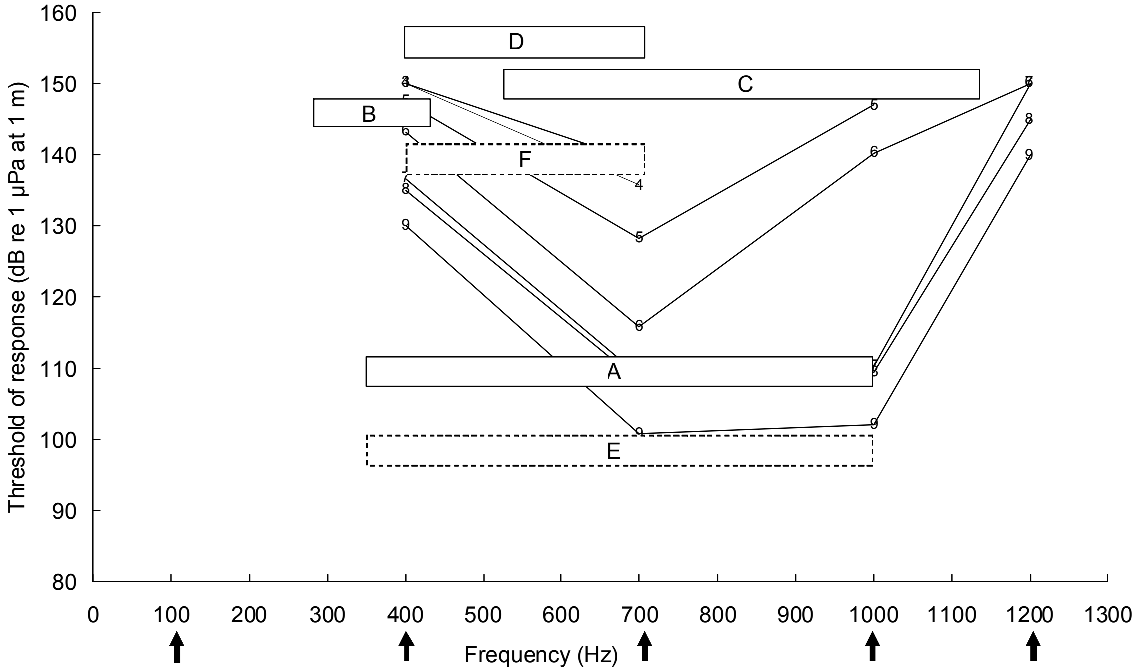

Figure 4. Development of the threshold of response to sound treatments by embryos of *Amphiprion ephippium* with sources of biological noise 'mapped' on the same axes according to the published source pressure levels (re 1 µPa at 1 m) and frequencies. A: *Pomacentrus partitus* (in [30]), B: *Terapon theraps*, C: 'banging' – source unknown, D: nocturnal planktivores (B-D in [29]), E: *P. partitus* at 10 m from source, F: nocturnal planktivores at 100 m from source (E & F calculated using A & D) (from [28]).

4 EFFECTS OF ANTHROPOGENIC NOISE POLLUTION

Finally, Man is likely producing increasing levels of anthropogenic noise in the world's oceans (e.g. [33]). This anthropogenic noise may be affecting the natural behaviour of fishes by competing with and masking natural cues, by acting as a deterrent away from natural habitats, or as an attractant towards unnatural habitats. Using Individual-Based Modelling approaches, we have simulated real-world scenarios to explore the effect of anthropogenic noise pollution on movements of larval reef fishes (e.g. shipping in the Straits of Hormuz). I will present this approach in the concluding part of my talk. This approach is easily adapted to test other scenarios on a variety of model organisms and spatial and temporal time scales. We believe this approach will ultimately advance our understanding of the effects of anthropogenic noise pollution on animals over ecological and evolutionary timescales.

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