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Introduction

Coral reef fishes live in dangerous times due to overfishing and habitat degradation. But to sustainably exploit fisheries or conserve populations, we need to understand the fish. In particular, we need to understand what happens during the oceanic stage of their life, when they develop as larvae. A few lucky survivors make it back to the reef, grow into adults and produce offspring. Most don't.

We have now realised that luck is not the whole story. When most reef fishes are ready to recruit to reefs, they can swim far in excess of local currents for days on end. But for this ability to be of any use, the larvae must be able to interpret their environment.

Coral reefs are extremely noisy environments, with the crackle of snapping shrimps and the chatter of fish set against a backdrop of wind, rain and surf. Sound carries well underwater, and fish have great hearing.

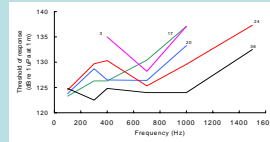
My work uses several complementary approaches to explore whether larval coral reef fishes can use the 'soundscape' to their advantage, and help tilt the balance in their favour, to find their way home.

Predicting the size of the sensory zone for settling fish detecting reef environments

For settlement-stage fishes to use reef sounds for orientation at settlement, they should be able to detect reefs acoustically long before they encounter the reefs (and their predators) physically. To address this issue, we first measured how hearing develops in larvae, using clownfish raised in captivity. We used an electrophysiological technique (ABR) to measure the brain activity as we played different sounds.



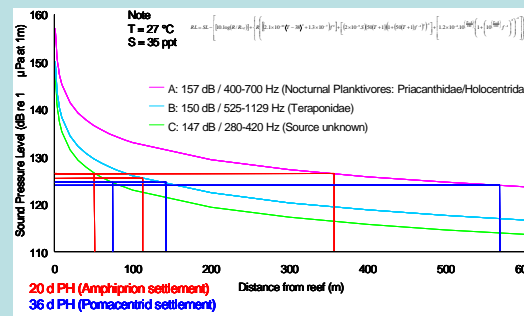
Testing larval clownfish



Larval clownfish audiogram

We found that as the larvae developed, their sensitivity to sound increased, and the frequency spectrum broadened.

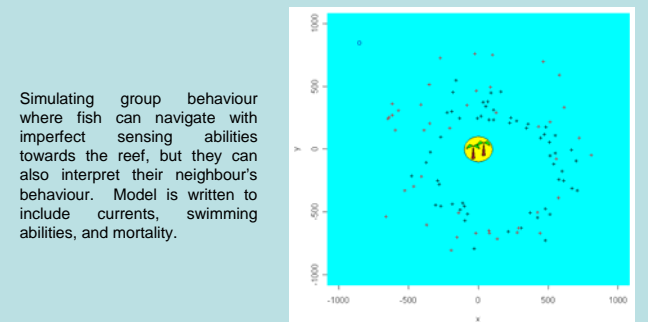
We then used oceanographic models of underwater sound to model how reef noise is transmitted, and used our thresholds to interpolate the maximum distance our larvae would detect typical reef sounds (>500 m).



Attenuation of natural sounds from reefs, with hearing thresholds predicting detection distance

Exploring group behaviour and navigation

There is evidence from genetics, trapping and chance observation that larval fishes do not act alone, but may school while at sea. Choice chamber studies suggest that groups can interpret sounds better than individuals. We are exploring this phenomenon with simulation models by adapting the 'Many Wrongs' hypothesis to reef fish navigation. This hypothesis suggests that if animals have an imperfect sensory ability, but can 'read' each other's behaviour, a 'collective' response may be superior to an individual response.

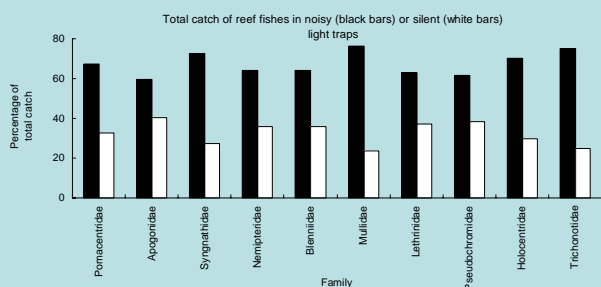


Simulating group behaviour where fish can navigate with imperfect sensing abilities towards the reef, but they can also interpret their neighbour's behaviour. Model is written to include currents, swimming abilities, and mortality.

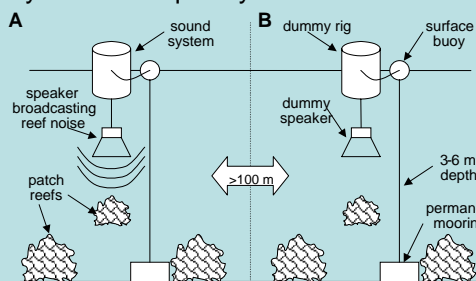
We hope to make predictions for simple rules that fish may follow to facilitate group behaviour that we can test for in lab or field experiments.

Attraction of settlement-stage reef fishes to reef noises, and to noisy reefs

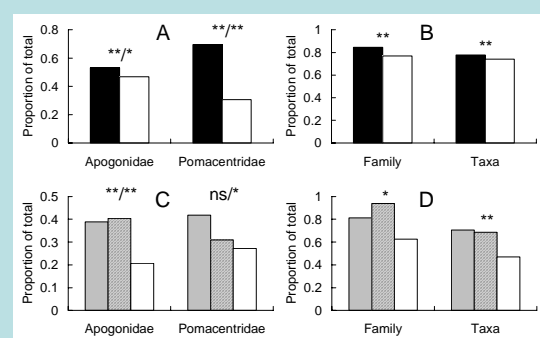
Light traps are highly attractive to many families of coral reef fishes as they come in to settle. We attached sound systems with underwater speakers replaying recordings of reefs to some light traps, and compared the catches to sister light traps with silent systems. We caught twice as many fishes from many families in the noisy traps, showing that sound is highly attractive at settlement.



We then built artificial reefs on sand flats, moored sound systems over some, and collected fish each morning that had recruited during the night. As well as noisy vs. silent reefs, we compared recruitment to high frequency vs. low frequency vs. silent reefs.



We collected many more recruits (mainly damselfishes and damselfishes), and a greater diversity of species, from 'noisy' reefs compared to silent ones. The damselfishes were especially attracted to the high frequency noises.



Black bars noisy reefs
White bars silent reefs

Grey bars high frequency
Striped bars low frequency
White bars silent

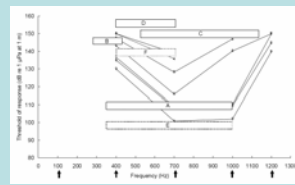
Potential for imprinting, and memory for sounds

Since many coral reef fishes spawn their eggs demersally (attached to the reef), and the embryonic stage occurs in reef habitats, there is the possibility that acoustic cues may be imprinted on fish before they head to sea to develop as larvae. This requires two processes: that embryos can detect sounds, and that behaviour is affected by acoustic experiences.

By playing sounds to embryonic clownfishes, and monitoring their heart rate, we have found that embryos would experience the sounds of local reef inhabitants during their development.



Embryonic clownfish



Detection of sound compared to natural noises

To address the issue of memory for sounds, we exposed settlement-stage damselfishes to either natural sounds, artificial noise, or no noise for 12 hours, and then monitored their directional response to these noises in choice chambers at night.

Conditioning treatment	Test treatment		
	Natural	Artificial	Silent
Natural	Positive response	Negative response	No response in 10 mins
Artificial	Positive response	Positive response	No response in 10 mins
Silent	No response in 10 mins	No response in 10 mins	No response in 10 mins

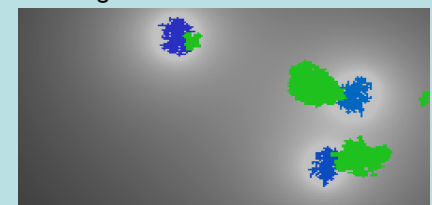
We found that fish were unwilling to respond to sound if they had spent the day in silence, whereas a noisy day elicited a response. Fish were naturally attracted to reef noise, and repelled by artificial noise, but could be conditioned to respond positively to artificial noise. This suggests a memory for sound.

The evolution of dispersal, and the effects of man

It is not obvious why almost all coral reef fishes leave the reefs, where they will live as adults, to embark on an oceanic larval stage. We have used Individual-Based Modelling (IBM) approaches to simulate reef fish dispersal over evolutionary and ecological timescales.

In theoretical landscapes, we can allow life-history characteristics to evolve in response to the reefscape, and use our results to make predictions about which species will prevail in real-world reef environments.

We are now incorporating behavioural rules into our IBMs that allow larvae to actively orientate to reefs as they develop. We have adapted our model to calculate 'soundscapes' for our reefs, based on actual recordings.



A theoretical 'soundscape' calculated from measured values of reef noise. Using IBMs, virtual fish are given certain orientation behaviours to examine the evolution of dispersal in relation to the reefscape.

Our next step is to look at behaviour in natural vs. human-impacted environments. We have started by looking at the effect of oil shipping and drilling in the Gulf of Oman.

Plans, ideas, and dreams...

Not all fish are lucky enough to live on coral reefs. I am keen to explore whether our findings can be transferred and adapted to fish in other habitats.

If the soundscape is important to fish at key life stages, we must build an understanding of what the natural sources of noise are that are important, and what conflicting noises may be masking the cues.

In order to model and manage fishes based on their ecology, we must have broader sets of data that include both key and rare families. I am keen to expand my suite of study species.

If any of these findings are to be used for 'active management' we must expand the scale on which our studies are done, and start to work at management rather than experimental scales.

Collaborators: Victoria Braithwaite, Edd Codling, Calvin Dytham, Andrew Jeffs, Rob McCauley, Jen McIlwain, Mark Meekan, John Montgomery, Jon Pitchford, Matt Wittenrich, Hong Yan

I warmly invite further interest in the work summarised here, requests for copies of papers relating to this work, interest in current collaborators as well as suggestions for future collaboration, and general discussion.

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