# Singing reefs: an investigation into the acoustic environment of the Las Perlas archipelago, Panama.

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**Submitted: September 2007**

Submitted as part assessment for the degree of Master of Science
in

Marine Resource Development and Protection

Centre for Marine Biodiversity and Biotechnology

School of Life Sciences

Heriot-Watt University

Edinburgh

“In the end we will conserve only what we love; we will love only what we understand; and we will understand only what we are taught."

Baba Dioum, 1968.

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## ABSTRACT

Coral reefs are noisy environments. Cracking snapping shrimp, rasping urchins and croaking fish are all packed into a structurally complex matrix of scleractinian corals at the highest density of biodiversity on earth. Add to this ensemble some abiotic sources of sound: rainfall, swell and breaking surf on the reef. The resulting output is a 'crackling' noise which emanates from the reef, broadcasting information far out to sea. In this study into the connectivity of the Las Perlas archipelago's patch reef system, we recorded the sounds produced by eleven reef sites and looked for associations between this broadcast sound and the resident reef fish community demographics. Other ecological factors (including rugosity and benthic data) which we thought might help explain reef sound were also examined at each site. A multiple regression analysis was performed on the collected data to identify factors that best explained the sound produced by each site.

Results demonstrated that each reef site produced a sound profile that was specific to that particular site, and different from all the other sites ($p<0.001$). Variation in sound level (i.e. intensity of noise) explained over 90% of this site disparity. Comparison of sound level with reef factors showed that it was highly correlated with the total number of fish at the site, and in particular, the abundance of *Stegastes flavilatus*, a commonly occurring damselfish species that dominated the reefs and was known to be highly soniferous. Regression analysis showed that the two best predictors of sound were the number of fish and the coral diversity. Combined, these were able to explain 97% of observed site variance in sound intensity. However, *Stegastes* spp. abundance remained an important prediction factor for sound level at all sites, and was associated with other reef variables, such as coral and fish diversity and abundance.

The results are one of the first attempts to interpret reef sound, which has been little studied. Although our findings fail to establish whether sound can be used to predict reef fish community structure, they suggest that with further development, replicates and testing the possibility exists for sound to be used as an efficient monitoring tool and rapid survey indicator of reef health. This has implications for the management of this newly designated MPA. Finally, our findings emphasise the importance of sound in Jacques Cousteau's so called "silent" world, and highlights the potential dangers of marine noise pollution.

**ACKNOWLEDGEMENTS**

I would like to thank the following people, without whom this project would not have been possible. Hamish Mair (Heriot-Watt University), my supervisor and course organiser, for his support throughout the course and his unfaltering belief in me. The staff at the Smithsonian Tropical Research Institute without whom our fieldtrip would not have been feasible: in particular Hector Guzman (STRI), for his excellent supervision and Carlos Guevara (STRI) for his help with the field research. Also Julio Agujetas, Inez Campbell and Alexis Lan (STRI) who went out of their way to make us feel at home in Panama. Steve Simpson (University of Edinburgh) for his enthusiasm, encouragement and guidance, and for lending me his sound recorder and sound analysis software and Mark Priest for his terrific assistance with the sound analysis, I am indebted to you both! Sarah Benfield for kindly loaning me her raw data from her amazing PhD, and Helena Butler (Heriot-Watt University) for her help with the GIS. Many thanks to all my coursemates, especially Katherine Nisbet and Antonin Guilbert, for their help with data collection on the fieldtrip and for their unshakable support and friendship throughout the year.

Finally, the project could not have been possible without the financial support of the Darwin Initiative, Heriot-Watt University Alumni fund and the NERC, for which I am incredibly grateful.

To all these people - and to the many more who didn’t get a mention - who helped and supported me along the way, and listened to me getting over excited about singing fish, I had brilliant fun working on this project, I learned a lot, and I am immensely grateful to you all, thank you!

# 1. INTRODUCTION

Coral reefs are noisy environments. Cracking snapping-shrimp, rasping urchins and croaking fish are all packed into a structurally complex matrix of scleractinian corals at the highest density of biodiversity on earth (Roberts *et al*, 2002). Add to this ensemble some abiotic sources of sound, such as rainfall, swell and breaking surf on the reef - even the low frequency rumbles of plate tectonics (Montgomery *et al*, 2006) - and you have a cacophony of varied noises. The resulting output is a steady 'crackling', detectable to even human ears, which emanates from the reef and broadcasts far out to sea.

This reef racket could prove useful in explaining patterns of reef larval recruitment or describing reef fish population structure, as well as having possible remote sensing and reef monitoring applications. However, with the exception of cetacean research, marine bioacoustics is a poorly explored subject - despite the well accepted fact that sound carries well underwater (travelling at 1,230 $ms^{-1}$ compared with 340 $ms^{-1}$ in air), making it an ideal medium for marine communication. It is probable that sound is a much more important cue than previously considered for marine organisms and hence potentially a very valuable feature of the marine environment to investigate. Further exploration of reef hydroacoustics could be fundamental to the unraveling of some of the many mysteries that the marine environment still holds.

Successful management of a MPA requires understanding of the marine system's inputs and outputs. The complex and dynamic nature of the marine environment means that ecosystem boundaries are not always as clear cut as in terrestrial areas, where mountain ranges, rivers and lakes form obvious confines to connectivity. This makes the pattern and scale of marine ecosystems difficult to define (Levin, 1992). A lack of definition of the scale or connectivity of marine habitats can make management and the designation of MPAs problematic.

Understanding the connectivity of marine systems is fundamental to their successful management and protection. Despite being originally considered as separately functioning systems, it is now known that availability of mangroves or seagrass beds can have striking impacts on the community structure and biomass of fish in coral reefs kilometers away (Mumby *et al*, 2004). This highlights the importance of focusing

conservation efforts on protecting connected corridors of habitat. The Las Perlas archipelago in Panama contains over two hundred islands with accompanying coral and rocky reefs and their associated populations of relatively sedentary marine species. These coral reefs are patchy environments, often separated by several kilometers of ocean. The extent to which the reef systems are connected to each other depends on the exchange of reef fish and invertebrate larvae between them. Coral reef fishes with long larval stages may be strongly interconnected over large distances, or larvae may behave to recruit back to natal reefs, decreasing reef connectivity. Understanding whether local populations on reefs around Las Perlas are functioning independently of each other, or as separated sub-units of a larger population, is of vital importance in the management of the region. The designation of the Las Perlas archipelago as a Special Management Zone in May 2007 (Law 18, 2007) require estimates of the extent and scale of connectivity – it would be important to know, for example, if reefs recruit from areas outside the protected zone.

Sound studies could be useful in helping understand connectivity, since reef fish larvae are thought to navigate between reefs using sound as a cue. The nature of the sound recorded on different reefs may also be able to provide insight into the fish communities living on these reefs, which would be useful quantifying abundance for successful fisheries management in the area.

### 1.1 Las Perlas Archipelago

The Las Perlas Archipelago of Pacific Panama (08°40’19N, 79°03’49W) is an important reef ecosystem and also forms an essential part of the Marine Biological Corridor of the Tropical Eastern Pacific (Lessios & Robertson, 2006). A group of 252 basaltic rock islands and islets with fringing patch reefs, the archipelago is situated in the Gulf of Panama, 70 km southwest off the Pacific coast of Panama City (fig. 1.1).

Las Perlas is important as it is one of only two archipelagos off the Pacific coast of the American continent (the other being the Galapagos). The islands fall within the Tropical Eastern Pacific biogeographic zone. Cold water currents and upwellings create boundaries to the north and south of this zone, and it is curtailed by deep water to the west. As a result, most reef fish within the zone are endemic to the region (Allen &

Robertson, 1994). The reef fish that live in close association with their habitat are specialised in morphology, colour, behaviour and life cycles and are one of the most

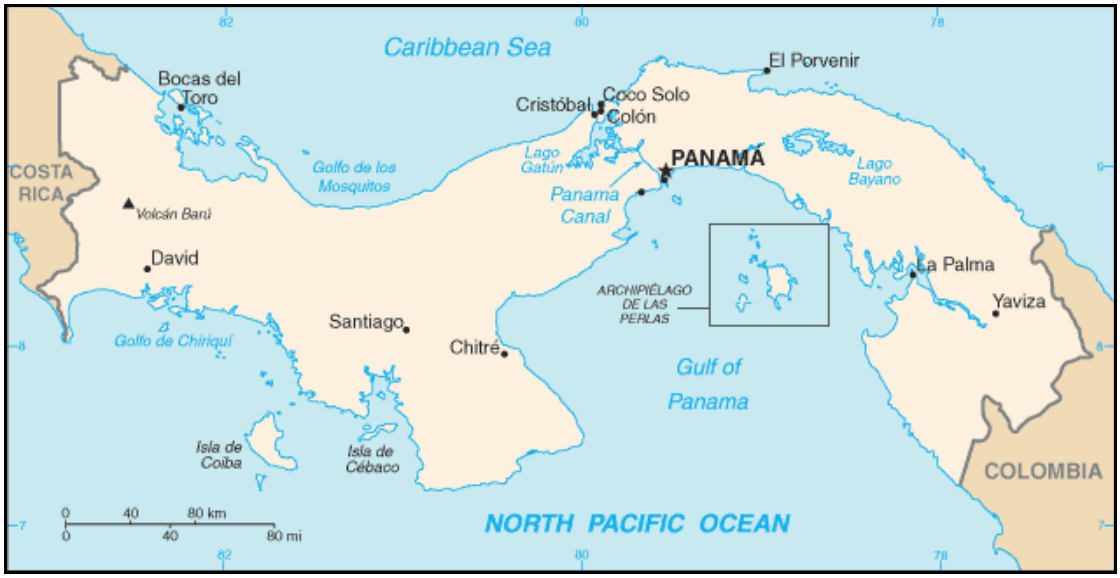



***Figure 1.1**: Map depicting the republic of Panama with political boundaries, major cities and towns. The location of the Las Perlas archipelago (Archipiélago de las Perlas) – the site of this study – is indicated by the black box in the Gulf of Panama.* Courtesy of STRI website.

complex and variable communities in nature (Sale, 1991). However there is little quantitative abundance data for tropical eastern Pacific reef fish. The coral reefs with which these fish are closely associated are relatively young compared to their Caribbean and Indo-Pacific counterparts, with the oldest corals being only 4,500 years old (Glynn & MacIntyre, 1977). Within Panama, the corals of Las Perlas have a lower vertical build up and are less diverse than those found in the neighbouring Gulf of Chiriqui (fig. 1.1), due to disruptive annual upwelling events in the Gulf of Panama (Glynn & Maté, 1996). During the dry season (January to March) the strong offshore Northern Equatorial Current causes upwelling in the Gulf of Panama, bringing colder, nutrient rich water to the surface. This results in increased productivity in the area, with phytoplankton blooms supporting zooplankton and fish, which in turn support exciting seabirds and larger predators. However, it has a negative effect on the corals, which suffer from increased competition with algae and the decreased light penetration.

The El Niño Southern Oscillation that occurs irregularly every 2-7 years reduces the upwelling of cold, nutrient rich water which makes the Gulf of Panama so productive. During El Niño events, trade winds die down, resulting in a warm current of nutrient-poor tropical water, heated by its eastward passage in the Equatorial Current, to replace

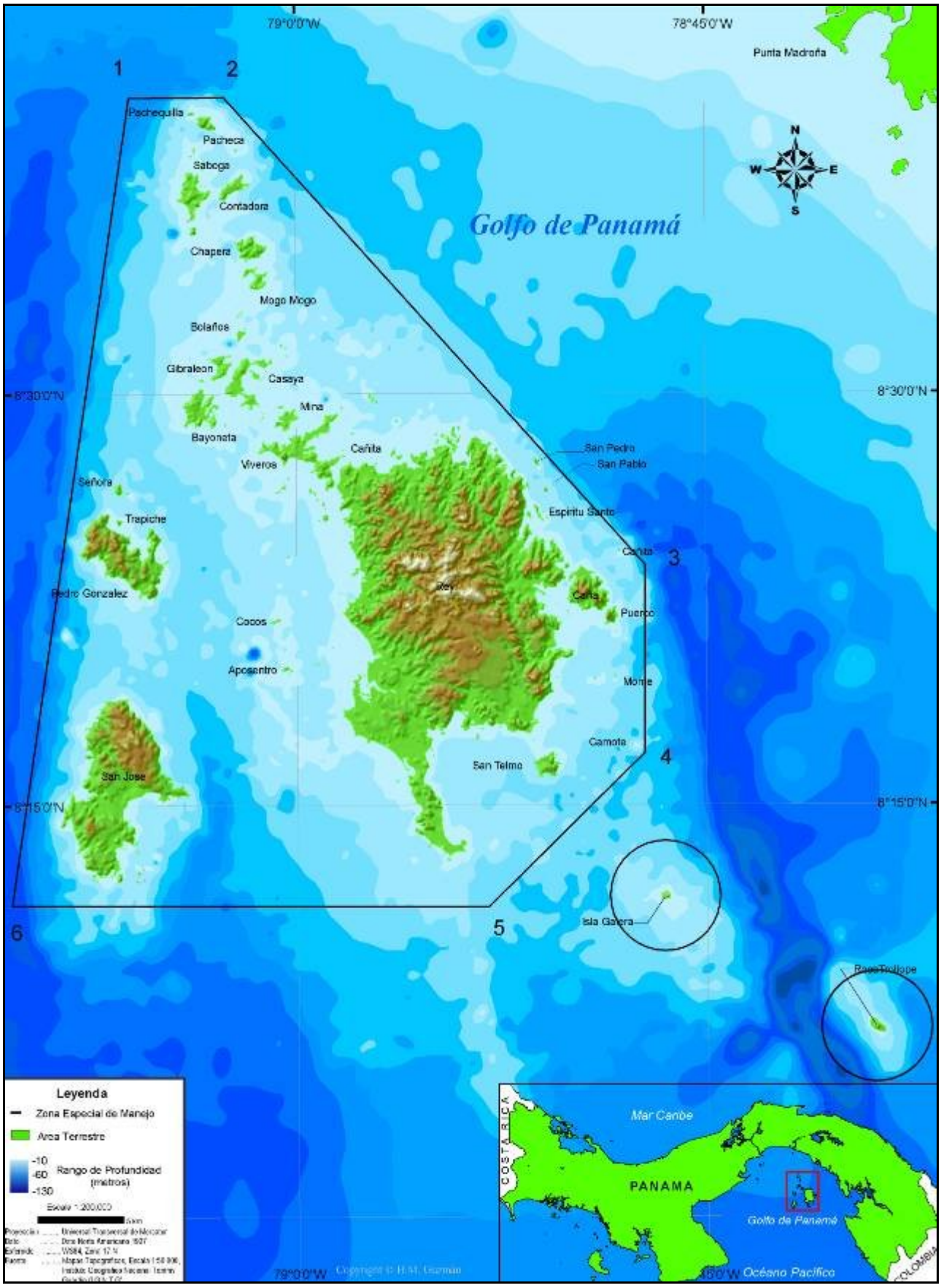



***Figure 1.2**. Map depicting the Las Perlas Archipelago and its newly designated Special Management Zone (Zona Especial de Manejo) in the Gulf of Panama.* Courtesy of Hector Guzman, STRI.

the cold, nutrient-rich surface water of the Humboldt Current. As well as limiting productivity of the area, negatively affecting fisheries, it has caused mass coral bleaching due to temperature rise in the past. The most recent El Niño event began in September 2006 and lasted until early 2007.

The islands, which are for the most part uninhabited by humans, support a wealth of pristine coral and rocky reefs, tropical forest and mangroves. Until recently, these habitats have only been lightly affected by local human activities, but as foreign investors are beginning to realise the potential for tourism in this pristine country, the health of the archipelago is becoming threatened by plans for the rapid development of new hotels, resorts and an airstrip (Guzman, pers. comm.). In May 2007, in recognition of increasing pressures from fishing and tourism all over Panama, as well as oceanwide factors such as global temperature rise and pollution, the archipelago was designated a Special Management Zone (Law 18, 2007). The zone has a total area of 168,771 hectares, including two nautical miles around the satellite zones of Isla Galera and Roca Trollope (fig. 1.2).

This study of the archipelago was a collaborative project between Heriot-Watt University and the Smithsonian Tropical Research Institute, funded by the Darwin Initiative. It builds on previous findings from the area to contribute to the mounting body of research already in this region. Its ultimate aim is to aid the development of management plans for the long term organisation of Special Management Zone.

## 2. AIMS

The overall aim of the project was to establish and then attempt to explain differing acoustic signatures of reefs around the archipelago, by recording sounds and examining reef fish communities and benthic data for comparison. Determination of whether sound recordings could be used to predict the demographics of reef fish populations, or the health of the reef, would have major implications for the use of passive sound recording as a biological monitoring tool. We believed this aim could be achieved by focusing on a few objectives.

### 2.1.1 *Objective 1*

The first objective was to compare and contrast the sounds produced by a selection of reefs across the archipelago to see if they could be distinguished from each other. Previous collections of sound recordings in the area showed reefs to have distinctive signature profiles (Simpson, in prep.). We aimed to repeat sound recordings at several sites in order to confirm this, while testing whether these sound 'profiles' stay true over longer periods of time (i.e. a year).

### 2.1.2 *Objective 2*

The second objective was to collect underwater survey data for comparison with our sound recordings. We aimed to collect detailed reef fish community data using underwater visual censuses. We were also interested in other factors that we thought might influence sound, including benthic composition, (reef fish exhibit a complex relationship with their habitat, both influencing and being influenced by it) and reef rugosity data.

Invertebrates were ignored during the study, despite the knowledge that they contribute to reef sound. Our justification for this was that their cryptic nature and penchant for disappearing deep into the Pocillioporid reef framework during the day made them too difficult to survey reliably in a non-destructive way. Invertebrates are known to be responsible for the higher frequency component of reef sound (11-12 kHz), which was not as important to us as the lower frequencies. Lower frequency sound is produced by fish, as well as detected by them, since they have a lower hearing range (0.5-2 kHz).

However, this remained a drawback to our study which we took into account when it came to analysing results.

We looked for relationships between our reef fish, benthic and rugosity data and aspects of our sound data, with the intention of highlighting the factors which were most important in explaining differences in sound. Underwater survey data was also compared to past fish and benthic community data collected in 2003 (Baxter, 2003; Benfield, 2005) to investigate whether temporal changes in a site's community structure were reflected by changes in the sound profiles.

## 2.2 Additional aims

### 2.2.1 *Aim 2: soundscape map*

An additional aim of the study was to construct a visual map of the sound around the archipelago, using ArcGIS. This involved collecting sound recordings across the entire archipelago, and then quantifying one aspect of the sound (in this case mean RMS wave pressure) to build a map of points, extrapolating between these points to estimate the extent of reef noise across out to sea. Construction of this 'soundscape' map could help explain where reefs recruit their larvae, assuming larvae use acoustic cues to navigate. This could have important implications for the protection of certain areas, such as seagrass or mangrove nursery areas which might feed onto certain reefs. This work is still in progress.

### 2.2.2 *Aim 3: genetic study*

Another additional aim was to collect data on genetic populations of fish in the area, in order to assess the connectivity of reefs by assessing gene flow between them, and comparing this to what we knew about reef sound. In the time available, it was only possible to focus efforts on one species of fish. The damselfish *Stegastes flavilatus* was chosen as a suitable candidate for the study, since previous survey work showed it to be abundant at all sites around the archipelago (Benfield, 2005); because damselfish are known to be soniferous, and because other species from the Pomacentrid family have been shown experimentally to navigate toward reef sound (Leis & Lockett, 2004). *S. flavilatus* is a demersally spawning species, meaning that it is possible larvae may imprint on natal reefs. They have a lengthy pelagic phase, allowing us to test passive

dispersion against active navigation back to natal reefs. In addition, microsatellite loci had been characterised for a similar species, *Stegastes partitus*, and primers for these loci successfully employed in seven other Pomacentrid species, making it hopeful these loci would be applicable in our species (Williams *et al*., 2003). We hoped to show that *S. flavilatus* populations around Las Perlas showed some genetic structuring, with restricted gene flow indicating self recruitment of larvae. Exploration of gene flow around the different islands could be extrapolated to help explain reef connectivity, and compared to sound recordings to look for patterns, and try and understand what aspects of sound might be influencing larval recruitment. Understanding the balance between dispersal and retention is vital for developing management strategies that operate over appropriate spatial scales. This aim eventually became a separate project due to time constraints, but is worth mentioning here since it ties in closely with this study.

# 3. LITERATURE REVIEW

## 3.1 Reef noise

Many coral reef associated animals are soniferous: consequentially reefs produce extraordinarily high levels of biological sound. The typical reef background 'crackle' is produced by the snapping of shrimps which live in the coral framework (Simpson *et al,* 2007). These snapping shrimp, from the family Alpheidae, snap shut a specialised claw which creates a captivation wave generating acoustic pressures of up to 80 kPa up to distance of 4 cm from the claw. The sound, which lasts 1 millisecond, can be 128 dB loud (Ferguson & Cleary, 2001). Snapping shrimp snaps are an important component of reef sound, and members of the Alpheidae are found on coral reefs worldwide.

A few other invertebrates, including the spiny lobster and fiddler crabs, have been shown to generate noises on the reef. The spiny lobster, *Palinurus elephas*, produces stridulatory sounds via its plectrum and file when the antennae are moved in addition to clicking sounds, thought to be part of a defensive strategy (Patek, 2001). Meanwhile fiddler crabs strike their enlarged cheliped against other body parts to create a banging sound used to signal the arrival of predators. Sea urchins (Fish, 1964) and squid (Iversen et al., 1963) are among the other reef invertebrates known to produce sound.

Shrimp broadcasts contribute a significant amount to reef noise, but it is the fish community that characterises reef sound. Evening fish choruses can be so loud – raising noise levels by 35 dB - that they have been detected up to 15 km away from the reef (McCauley & Cato, 2000). Over 800 species of fish from 109 families worldwide are known to be soniferous, although this figure is likely to be a gross underestimation (Kaatz, 2002). Vocal fish produce sounds that commonly comprise low-frequency pulses that vary in duration, number and repetition rate. The diversity of sounds made by fish are not as remarkable as in other taxa, such as birds. Most fish show poor amplitude and frequency modulation in their vocalisations and have relatively limited acoustical repertoires; with few species able to emit more than one or two distinct sound types (Amorim, 2006). Chaetodontidae (butterflyfish) acoustic behaviours consist of low frequency pulses at less than 100 Hz, sounds with peak energy from 100 Hz to 500 Hz, and a broadband high frequency clicking at 3.6 kHz (Tricas *et al*., 2006). McCauley and Cato (2000) recorded a number of other fish producing distinctive

‘popping’, ‘trumpeting’, ‘drumming’ and ‘banging’ sounds off the Great Barrier Reef in Australia. Meanwhile several members of the Pomacentrid (damselfish) family have been shown to be capable of producing sound in the form of single pulsed lower frequency pops (100-1000 Hz) and higher frequency chirps (3400-4100 Hz) - and this is thought to be a trait applicable to the entire damselfish family (Parmentier *et al*., 2006). Many of these fish sounds are understood to be generated by the drumming of a muscle against the swim bladder – a gas-filled chamber in the abdominal cavity primarily used for buoyancy regulation (fig. 3.1). The aptly named grunts (Haemulidae), drums and croakers (Scianedae) are also known to make sounds using their swim bladders, but for many other fish - some of whom do not possess swim bladders - the mechanism of sound production is not yet fully understood.

***Figure 3.1****: Swimbladder of the toadfish,* Opsanus beta. *Sonic muscles can be seen on the lateral walls of the swimbladder. Knocking of the sonic muscle against the gas-filled bladder is the main recognised mechanism of sound production in fish.* (Courtesy of David Mann, USF).

Much noise production is associated with mating, courtship, fright, territorial or aggressive behaviours: for example the reef damselfish *Abudefduf luridus* produce low frequency growls only during competitive interactions (Santiago & Castro, 1997). Other sound production may be an unintentional byproduct of movement or feeding. Low frequency hydrodynamic sounds, for example, are produced by changes in swimming

speed large schools of fishes like the Carangidae (Jacks) during feeding frenzies. The noise made by some Scaridae (parrotfish) biting chunks of coral with their beak-like mouthparts are so loud they are often heard by divers, and a lot of high intensity underwater sound can be contributed to the stridulatory sounds of feeding fish. Although most fisheries biologists are generally aware that many fishes are soniferous, relatively few have stopped to consider the potential importance of listening to fish sounds to their fields of study.

Having established that coral reefs emit high levels of biological sound and that much of this sound is due to fish (McCauley & Cato, 2000), we aim to investigate this noise.

### 3.1.1 *Reef noise and fish communities*

Preliminary research by Simpson and Mair in 2006 (in prep.) showed that reefs around Las Perlas produced sound that, when analysed, appeared to give a sound profile that remained stable over a two minute long recording. These sound profiles were specific to individual reefs, and although some reefs produced similar sounds no two profiles were identical. Meanwhile, baseline fish community data collected by Baxter and Benfield in 2003 (Baxter, 2003; Benfield, 2005) showed different sites around the Las Perlas archipelago to have significantly differing reef fish assemblages. Investigating the fish communities of the reef might help explain why the sound produced by reef sites differed. It would be interesting to see whether noise produced from a reef could be used to predict the habitat or fish community, as this could provide the basis for the use of passive sound recording as a remote sensing technique or for biological monitoring without the need for underwater diver censuses.

As well as attributing some of the disparities in reef sound to differing biological reef components such as fish and invertebrate communities, abiotic sources of sound should also be considered in this study.

### 3.1.2 *Reef noise and the benthic habitat*

Although there is no record of corals, algae or other components of the benthos producing noise (Simpson, pers. comm.), it is important to consider the benthic habitat when trying to explain reef sound. Reef fish interact closely with their habitat, both being influenced by it and modifying it, so the relationship between the two is complex

(Benfield, 2005). Differences in benthic habitat might affect the invertebrate component of reef noise. While it is difficult to survey invertebrates, which are small, cryptic and nocturnal, their abundance may well be correlated with coral cover, which produces a complex habitat to house shrimps and urchins. The benthos may also be important in absorbing sound, altering the sound profile of the reef.

### 3.1.3 *Reef noise and rugosity*

Rugosity, or roughness factor, is an index of substrate complexity. Rugosity is often used as a measure of reef complexity, since it indicates the amount of habitat available for colonisation by benthic organisms, and shelter and foraging area for mobile organisms – including reef fish. Rugosity has been successfully used to predict reef fish species richness and abundance (Kuffner *et al*., 2007). High rugosity is often associated with healthy reefs with more fish, as it indicates the presence of more corals (a food source), which has a complex surface, and because a rugose surface will generate more turbulence leading to nutrient mixing adjacent to the reef. Spatial complexity increases habitat heterogeneity. Since reef fish and invertebrates are responsible for much sound on the reef, rugosity may also be associated with differences in sound. It also is an aspect of the reef that might affect sound, as the physical structure of the reef may well control the movement of sound waves and the nature of the sound produced. A prediction was made that higher rugosity would be associated with greater numbers of fish, coral diversity and more noisy, healthy reefs.

## 3.2 Reef noise and larval recruitment

### 3.2.1. *Open systems*

Coral reefs are widely accepted to be ‘open’ ecological systems comprised of local populations that are replenished by the recruitment of larvae from non-local reefs (Mora and Sale, 2002). This is firstly because most shallow water marine species have a bipartite life cycle, involving larvae or eggs capable of dispersal over large distances; secondly because significant gene flow occurs over large geographic distances, and thirdly because patterns of local recruitment are unpredictable and often uncorrelated with local production (Swearer *et al*., 2002). Adult reef fish are strongly site associated and often have a narrow home range. They rarely move between reef habitats, which are patchy in nature, and as a result individual reefs often have a relatively stable small

breeding community of fish (Sale, 2004). It is generally accepted that larval recruitment is one of the main controlling factors explaining this reef fish population structure (Armsworth, 2002; Booth & Wellington, 1998).

Ninety-five percent of all reef fish families undergo a larval stage out at sea, before settling onto a reef and developing into an adult (Leis & McCormick, 2002). If reefs were truly open systems, this phase would be a dispersal strategy aimed at minimising kin competition, inbreeding depression and spatio-temporal variability in environmental conditions (Leis & McCormick 2002). The pelagic larval stage typically lasts between 28 and 35 days, but can range from less than ten days in Amphiprion (clownfish) to several months in Acanthuridae and Monacanthidae, and can last up to 64 weeks in the porcupinefish family, Diodontidae (Sale, 2004). Other reef organisms, including corals and benthic invertebrates also retain a bipartite life history, with ninety percent of benthic invertebrates experiencing a pelagic phase of a week or more (Bradbury & Snelgrove, 2001).

During this time, reef larvae, typically less than 20 mm in length, may disperse several kilometres away from their natal reef before finding a new reef settle out onto (Montgomery, 2006). Until recently it was assumed that larval dispersal was largely passive and subject to oceanographic processes, with larvae drifting along in ocean currents until arriving at a suitable reef. The spatial scale above which coral reef populations become closed (because the scale is large enough to contain larval dispersal) is unknown for the Las Perlas region, but in theory could be very extensive for fish of average larval duration drifting passively on ocean currents, meaning reefs from Isla Pachequilla and Isla Galera although far apart in distance (fig. 1.2) could be closely interconnected due to larval exchange. The importance of considering larval supply rates is acknowledged by those managing reef fisheries.

### 3.2.2 *Closed systems*

The ‘open’ model of reefs has recently been criticised, since it does not explain high levels of endemism found, for example, in the Tropical Eastern Pacific. To support this theory, there is mounting evidence that instead of passive advection, some juvenile fish show behaviour that facilitates return to local reefs (Simpson *et al*., 2004; 2005). Instead of a dispersal strategy, larval development in the plankton could be a tactic to minimise

predation risk on the reef, access richer food resources or break parasite cycles (Swearer *et al*., 2002). Jones *et al.* (2005) have shown by a mass marking experiment that far from drifting randomly, panda clownfish (*Amphiprion polymnus*) larvae in Papua New Guinea return to settle out within just 100m of their birth site. Meanwhile the advent of molecular genetics has enabled demonstrations that reef populations show defined genetic structuring, with neighbouring reefs harbouring separate subpopulations (Planes *et al*., 1998). This supports the theory that larvae may be actively returning to their parental reef, causing gene flow restriction and maximising genetic differentiation between reefs observed. If larvae were solely reliant on ocean currents returning them to the reefs, dispersal would be likely to lead to much higher levels of mixing (depending on circulation patterns). Modelling of currents has shown that larvae of many marine invertebrates are also not dispersing as far as they would if dispersal was down to currents alone (Todd, 1998). The green shore crab, *Carcinus maenus*, introduced into San Fransisco Bay in 1990, has shown slow rate of spread of less than 30 km per year, which suggests a higher level of self recruitment than expected by an open system (Grosholz, 1996).

Critics question how a reef fish larva, just millimetres in length, could navigate back onto a specific reef from a distance of kilometres offshore. However, research has now shown that larvae approaching settlement stage acquire a remarkable swimming ability, with some species capable of sustained swimming speeds of between 0.04 and 0.16 $ms^{-1}$ (Fischer & Bellwood, 2002). This would allow settlement stage larvae to swim out of local currents. Leis and Carson-Ewart (2003) observed that this swimming could be directed towards reefs a kilometre away.

Settlement stage reef fish have also been shown to have sensory capabilities which would enable them to home onto reefs. Larvae could use a variety of cues, including visual and chemical cues, to help them navigate onto reefs (Montgomery *et al*. 2006). However, Stobutzki and Bellwood (1998) suggested that movement towards reefs is largely in response to reef sounds. Sound, because it travels so far underwater, is likely to be a useful orientation cue at a distance of kilometers, where light (which is absorbed and scattered by water) and chemical cues (which travel more slowly in water than in air) are not so viable. Modelling reef noise transmissions showed that larvae more than 500 m away from a reef would be able to hear it. Simpson *et al*. (2004) demonstrated in

field experiments that larvae are attracted to sound, and can localise underwater sound sources. It has been suggested that swim bladders in fish may be used to detect pressure and localise sound sources, although some larval fish and crustaceans lack air spaces in the body that could be used in this way (Montgomery, 2006).

Further experiments show that embryonic clownfish larvae in eggs on the reef may be able to imprint on the reef sound, so that they can recognise their natal reef when they reach settlement stage (Simpson *et al*., 2005). These experiments showed that larval fish were attracted to reef noise and repelled by artificial noise, but could be conditioned to respond to artificial noise, suggesting larvae have a memory for sound. This mounting evidence for a reef fish larvae's ability to detect noise, determine its direction and move towards its source, further adds to the contention that larval recruitment is far from random.

To further illustrate his point, Simpson and his colleagues carried out experiments broadcasting high (>570 Hz) and low (<570 Hz) frequency noise from artificial reefs, and collecting any fish that were attracted. Reefs emitting 'reef sounds' attracted many more fish larvae than the silent controls. Larvae from three families in particular - Apogonidae, Gobiidae and Pinguipedidae - were attracted to noisy reefs, showing that these fish use sound to locate habitat for settlement (Simpson *et al*., 2007). On the whole, reefs emitting low frequency noise were preferred to high frequency noise, although damselfish were particularly attracted to higher frequency sounds. It has long been known that acoustic cues are of major importance to many fish species (McCauley & Cato, 2000) and Simpson's work shows how sound could play a major part in reef recruitment.

The extent of the control reef larvae have over their dispersal is unknown but the fact that evidence exists for active dispersal suggests populations at ecological scales are probably less open and more subdivided than previously assumed (Leis, 2002). Investigating reef sound in Las Perlas may provide insights into the type of information being broadcast out to sea for larvae to detect, and how far out to sea these signals are propagated. It may also indicate which natural sources of sound are important to reef fish larvae, and which artificial sounds may be masking their cues. It would be interesting to see whether noise produced from a reef could be used to predict the habitat or fish community, as this would allow reef larvae to avoid or move towards

certain reefs based on information in the sound. From this, conclusions could be drawn about larval recruitment around the archipelago. This of course has important implications for how the reefs within the Special Management Zone are managed.

# 4. METHODOLOGY

## 4.1 Study Sites

Eleven sites were chosen in the northern part of the archipelago (fig 4.1), on the basis of preliminary sound work by Simpson and Mair (in prep.) of 46 sites across Las Perlas. These particular sites were selected because of their accessibility (allowing us to survey as many as possible in the time available) and because analysis had shown them to represent a diverse range of sounds. All eleven sites were on coral reefs (reefs with a Pocillopora framework) as opposed to coral communities, which had been shown to house significantly different fish assemblages (Benfield, 2005).

The first reef site, Site 1, was off the most northerly island of the archipelago, Isla Pachequilla (fig. 4.1). Preliminary work by Benfield had shown this site to be one of the healthiest in 2003, with 91% coral cover, fairly average species diversity (Shannon H $\log_{10}$) and the third highest abundance of fish.

Islote Bendico, Site 7, was on an exposed reef, with an average coral cover of 70%. This high coral cover, and a high abundance and diversity of fish (0.34) made it one of the best sites in 2003.

The third site, Site 9, was the largest reef in the archipelago. Situated to the northeast of Isla Saboga, it has been measured as having a maximum vertical build up of 5.6 meters. Nearby, Site 10 was on the northern side of Isla Contadora, one of the few populated islands in Las Perlas, which contains the majority of hotels in the archipelago. Contadora has many small patch reefs on the north coast, and Site 10 was on the second largest reef in Las Perlas. Isla Contadora and Isla Saboga had only had around 60% coral cover in the 2003 surveys, and both had poor to average numbers of fish and low species diversity (0.29).

A group of three sites were grouped on the islands of Chapera (Site 19) and Isla Mogo Mogo (Sites 21 and 22). In 2003, these had been covered by 60 and 75% coral respectively, but had fairly low fish abundance and poor diversity (0.19, 0.14).

Three more sites were positioned to the east of the largest island of the Archipelago, Isla del Rey. This island has few reefs; possibly due to the island's large watershed and

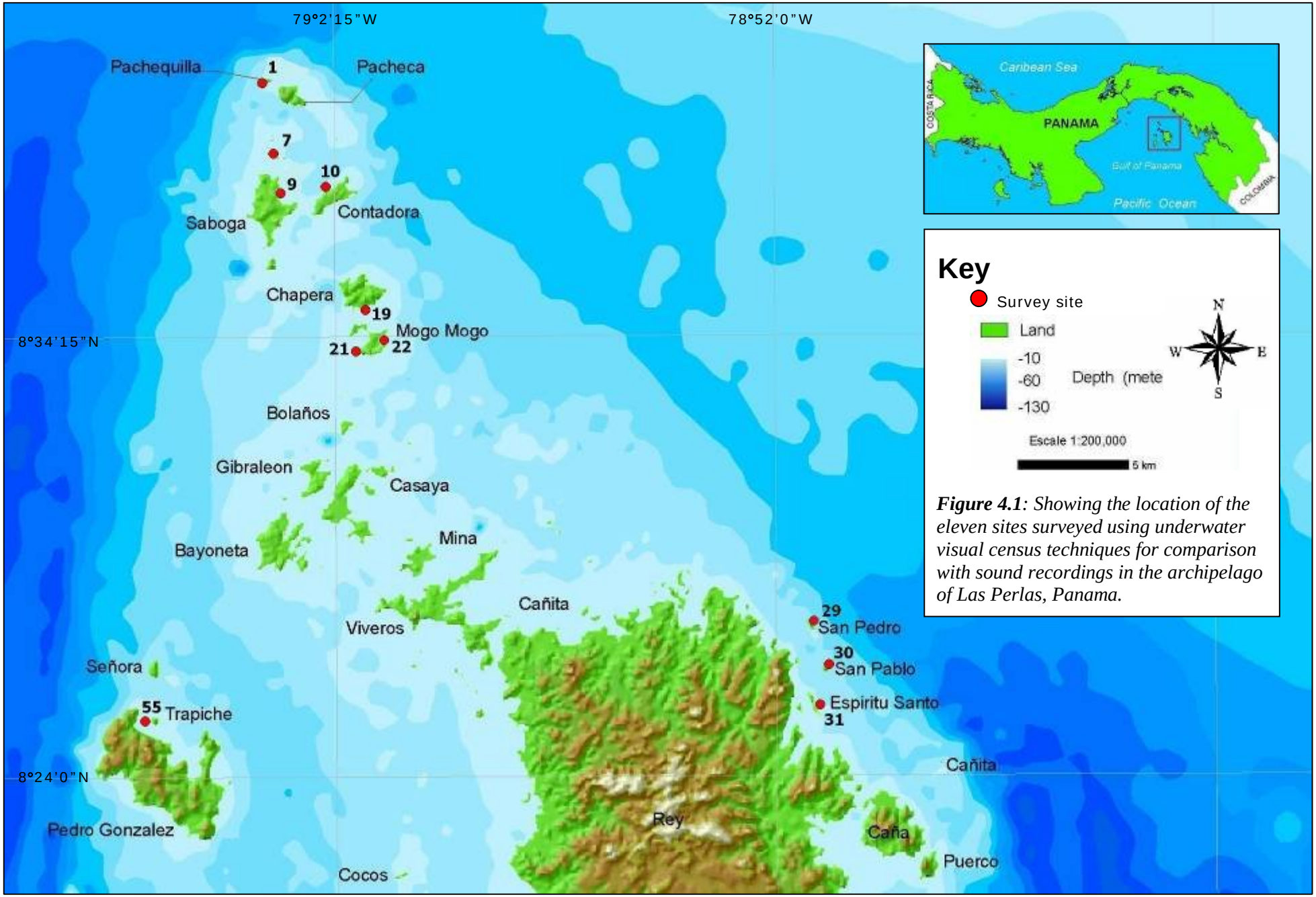



***Figure 4.1**: Showing the location of the eleven sites surveyed using underwater visual census techniques for comparison with sound recordings in the archipelago of Las Perlas, Panama.*

subsequent run off. These three sites faced east off the uninhabited series of islets San Pedro, San Pablo and Espiritu Santo (fig. 4.1). The San Pablo and Espritu Santo reefs were expected to be among the poorest, having had the lowest coral cover of all in 2003 - around 40%. San Pablo also had very low fish diversity (0.13). In contrast, the third site, San Pedro (Site 29), had one of the healthiest reefs, with a very high coral cover of 94%, and the highest diversity of fish (0.45) in 2003.

The final reef nestled off Isleta Trapiche, sheltered in the bay of larger island Pedro Gonzalez. This island, which has large areas of mangrove on it, has recently been threatened by development plans. In 2003 it was one of the better sites in Las Perlas, with the highest coral cover - in excess of 95% - but had fewer fish and a very low species diversity (0.11).

### 4.2 Sound data collection

Data was collected over ten days of fieldwork in Las Perlas. Noise from the reef was recorded from the Smithsonian's research vessel, using a hand held hydrophone. The hydrophone was connected to an EDIROL R-1 Portable 24-Bit WAVE Recorder & Player by a 25 m jacketed cable. Recordings were taken between 9 am and 5 pm, since studies have shown that sound levels on reefs increase at dusk and decrease toward sunrise because of snapping shrimp activity (Sprague *et al*., 2002). The boat was positioned over the reef, or as close as safe, and the hydrophone placed in the water column above the reef. It was only held a few meters under the water, since the top 20 m includes the most significant sources of biotic and abiotic sound, being the most productive part of the reef containing the most invertebrates and fish, as well as the noise generated by breaking waves, and because the reefs we were looking at were rarely more than 6 or 7 m deep. The hydrophone's cable was held away from the hull to minimise banging and slapping of waves against the boat (fig. 4.2).

The hydrophone works by measuring pressure fluctuations, which are converted to sound pressure level (SPL). A two minute recording was taken, interfaced to earphones so that the recording could be monitored, and stored as a WAV file. The recording concentrated on frequencies in the 'normal' acoustic range for fish between 0 and 12.5 kHz (Montgomery *et al*., 2006). Low frequency noise (less than 70 Hz) has very limited propagation in shallow water, penetrating into the seabed while frequencies above 1

Mhz are absorbed very quickly. Frequencies outside this range are rarely studied in hydroacoustics. The recording was transferred onto a hard drive at the end of each day. For each recording, notes were made of the exact GPS co-ordinates, sea state, tide and time that the recording was taken.

Back in the laboratory, recordings were run in the freely downloadable software program Audacity 1.2.6. Here, recordings could be cleaned manually to remove any non-biological noise, such as the sound of waves slapping the hull of the boat, depth sounder echoes or distant boat motors. Five cleaned 10 second samples were randomly taken from each recording. These samples were processed in bioacoustics software Avisoft-SAS Lab Pro, to give quantitative data in a text file that could be entered into an EXCEL spreadsheet for statistical analysis.

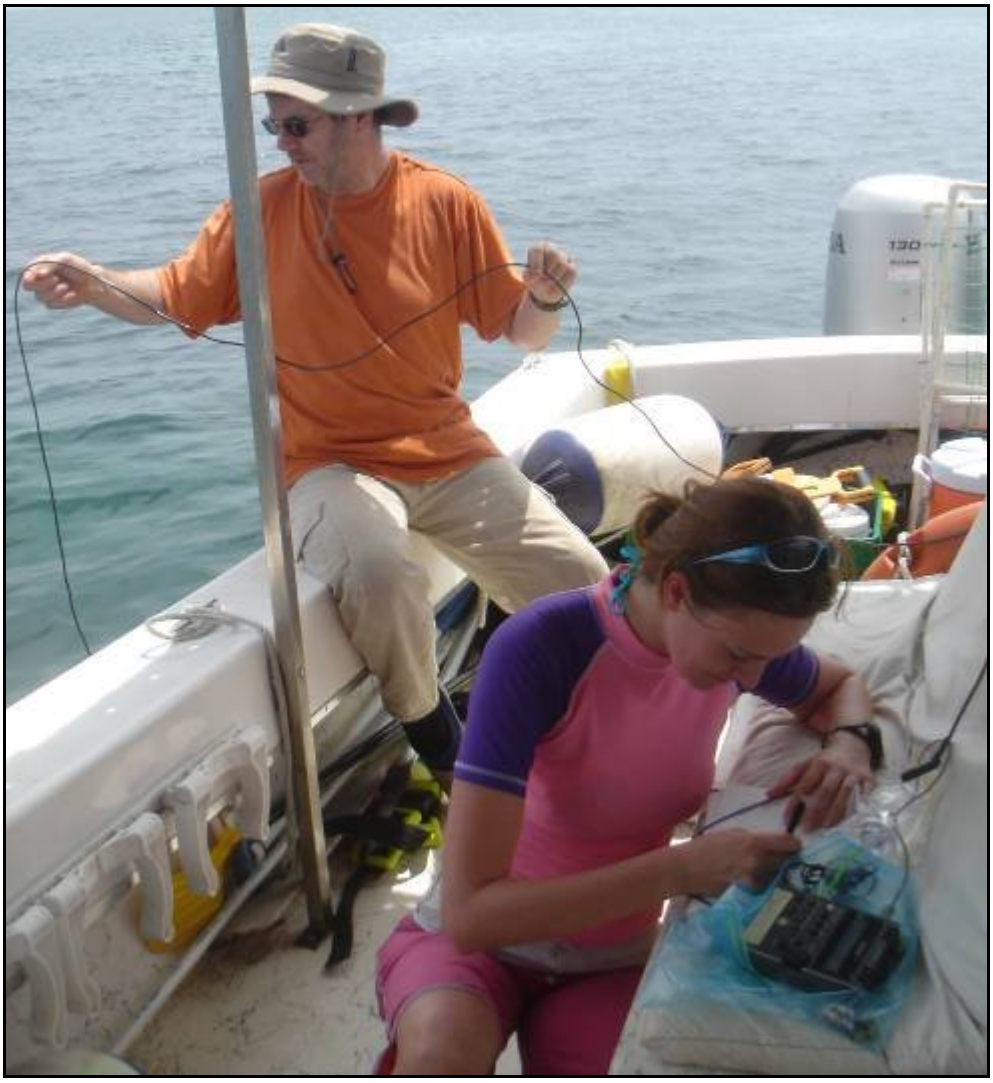


***Figure 4.2****: collecting sound recordings on the STRI research vessel, Anibal II. The hydrophone was held away from the hull of the boat to minimise rubbing.*

## 4.3 Underwater surveys

Estimating the abundance of fish on coral reefs can be done using either destructive (by poisoning or explosives) or non-destructive methods. Underwater visual census (UVC) techniques are regarded a relatively accurate and cost effective way to survey reef fish communities in a non-destructive way. Based on observers estimating the abundance of species within a given area, a UVC provides rapid estimates of the relative abundance and diversity of fish communities. Although often criticised for their lack of accuracy, with care they can be used reliably to establish relative patterns of abundance, and have been shown to correlate well with other measures of abundance (Sale and Douglas, 1981).

The belt transect method, first described by Brock (1954), was used in this study. It is simple to carry out and efficient, allowing for the synchronised collection of benthic and rugosity data. At each of the 11 sites (locations shown in fig. 4.1), transect lines were laid parallel to the shore at two levels, one deeper (3-5 m) and one shallower (1-3 m). Along each of these two lines, two 30 m fish belt transects; three 10 m benthic survey transects, and three 10 m rugosity transects were recorded, totaling 16 transects at each site. Data were collected on the number, size and species of fish; on the percentages of coral and algal species comprising the benthos, and on the rugosity of the coral reef. Additionally, at each site wave exposure, tide state, depth, visibility, topography and slope were recorded, along with the date, time and weather conditions, to allow these variables to be accounted for when examining differences between and within habitats.

### 4.3.1. *Fish surveys*

Reef fish community surveys were carried out using SCUBA equipment. The Atlantic and Gulf Rapid Reef Assessment (AGGRA) methodology was adopted (Kramer *et al*, 2005) to survey the reefs, keeping the same modifications made by Benfield and Baxter in 2003, so that data remained comparable (Baxter, 2003; Benfield, 2005). Because of the small size of most of the reefs, and to conform to previous data collection, only four 2 m by 30 m belt transects were surveyed at each site, compared to the ten recommended by AGGRA protocol. Each transect ran parallel to the shore, and wherever possible start points were randomly chosen. Where a slope was present, two

transects were run at deeper depths and two on top of the reef, although depth variation was rarely more than 5 m.

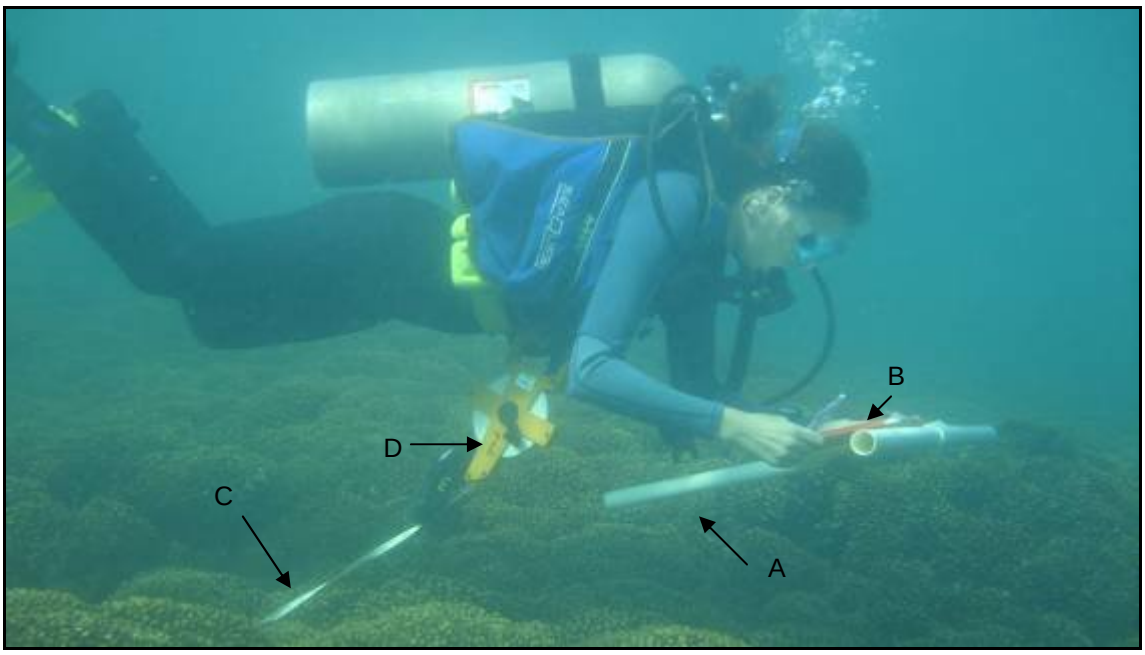



***Figure 4.2**. Photograph illustrating an observer with SCUBA equipment swimming a fish belt transect. Note the hand held PVC T-bar (a) used to estimate survey area and reef fish size, underwater slate and pencil (b) for recording species abundance and 30 m transect tape (c) on a reel (d) attached to diver, and weighted to the bottom at one end.* (Courtesy of Antonin Guilbert).

Transects were measured out by a 30 m tape attached to the observers body, which was reeled out from a spool as they swam (fig. 4.2). The species and size category (<5 cm, 5-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and >40 cm) of every fish entering a visually estimated box area 1 meter to either side of the diver and 2 m in front were recorded on underwater paper sheets (fig. 4.2). A hand-held T-bar (a PVC pipe and T connector with 60 cm handle and two equal length arms with a total length of 1m across the top) was used to help estimate the 2 x 2 m box on either side of the tape (Kramer *et al*., 2005). The T-bar was marked with 5 cm increments to help estimate fish length. Fish were measured from the tip of the snout to the posterior tip of the caudal fin. The 30 m transect was swum at a slow and steady pace, with the observer gazing directly ahead. At the end of the transect line, the survey was stopped and the tape recoiled. The next survey was begun at least five meters away (estimated by fin kicks) to prevent the same fish being sampled twice. Observers waited motionless for three minutes at the transect start point before each survey commenced, to allow disturbed fish to settle down.

Throughout the survey period great efforts were made to minimise observer error. Fish species were identified and memorised with the help of detailed guides to fish of the

tropical eastern pacific region (Robertson & Allen, 2002). Observers were trained to estimate fish lengths using cardboard fish of different lengths, following the AGGRA protocol. Surveys did not commence until >95% accuracy in fish length estimation and 100% accuracy in species identification was achieved in tests. The methodology was adhered to strictly, and the same diver carried out all the fish surveys to help standardise the sampling.

Each transect provided information on the total number of fish, size categories of fish, presence of species and the abundance of these species at each site. Species richness was counted, and fish diversity calculated using Shannon-Wiener Index and species equitability. Mean abundance for each site was calculated, as well as the overall mean abundance of species. Lengths were used to give the mean length per species per site.

4.3.2 *Benthic surveys*

Reef fish surveys were integrated with benthic sampling, with a team of two divers working together at each site. Benthic sampling also followed a modified AGGRA methodology (Kramer *et al*., 2005). The first diver began to swim the 30 m fish belt transect, followed after a period of three minutes by a trained diver from the Smithsonian Tropical Research Institute, who assessed benthic composition. Six belt transects 10 m long by 1 m wide, and 10 m apart, were assessed. Three of these were at deeper depths and three at shallower depths, and all parallel to the coastline. A one meter square PVC quadrat divided with wire into a 10 cm by 10 cm grid was used for sampling on each transect (fig. 4.3). Ten quadrats were counted along each 10 m transect, with successive placements of the frame along the shoreward side of the tape, and no space between frames. The frame was placed gently on the reef, and the grid squares counted to record the percentage cover of scleractinian and soft coral species. For each type of cover, the species was recorded on the underwater data sheet, as well as the percentage cover and the number of colonies - if there was more than one. Coral colonies less than 5 $cm^2$ (0.05 of a grid square) were considered recruits, and where one colony was covering another, only the uppermost was recorded. Sponge cover was also recorded, as well as algal cover. Algae were divided into macroalgae, algal turf, calcareous and crustose coralline algae (CCA). Areas of sand or coral rubble were also recorded.

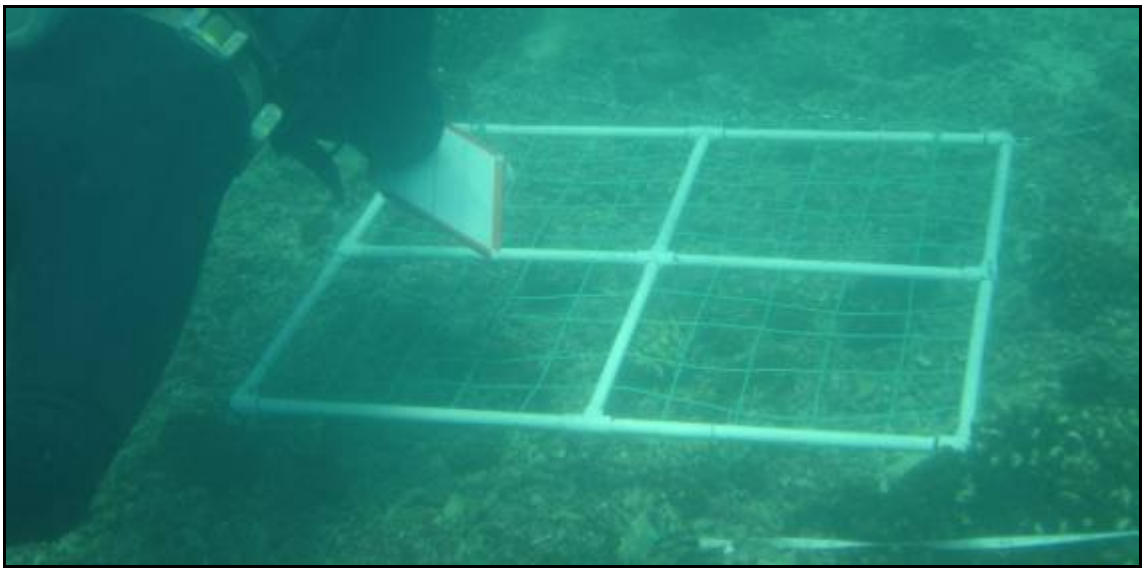


***Figure 4.3**: Photograph showing STRI scientist Carlos Guevara assessing the benthic composition using a PVC 100 cm$^2$ quadrat. Each of the 100 squares represents 1% of the quadrat, or an area of 1 dm$^2$.* (Courtesy of Antonin Guilbert).

4.3.3 *Rugosity measurements*

A ten meter long stainless steel chain was placed at the beginning of the 10 m benthic transect, and carefully spooled out along the transect line, allowing the weight of the chain to fill the contours of the reef (McCormick, 1994). This was repeated 6 times, once on each of the benthic transects. For each of the six transects, a measurement was taken of the length of transect covered by the 10 m chain. The rugosity value was calculated by the ratio of the contoured (chain) length to straight (transect) length. The higher the value, the more structurally complex the habitat is.

## 4.4 Data analysis

Data analysis was carried out in statistical software program MINITAB 13, with PCA analysis in SPSS and MS Excel. The grid soundscape map was built using ArcMAP, in the program ArcGIS.

# 5. RESULTS

## 5.1 Reef sound

In total, 106 sound recordings were collected: one at each of the 46 reef survey stations in Las Perlas (which included our 11 dive sites); plus 26 repeated recordings at different times of the day and 34 recordings at randomly picked offshore sites that we planned to use to build up a picture of noise across the archipelago for the soundscape map.

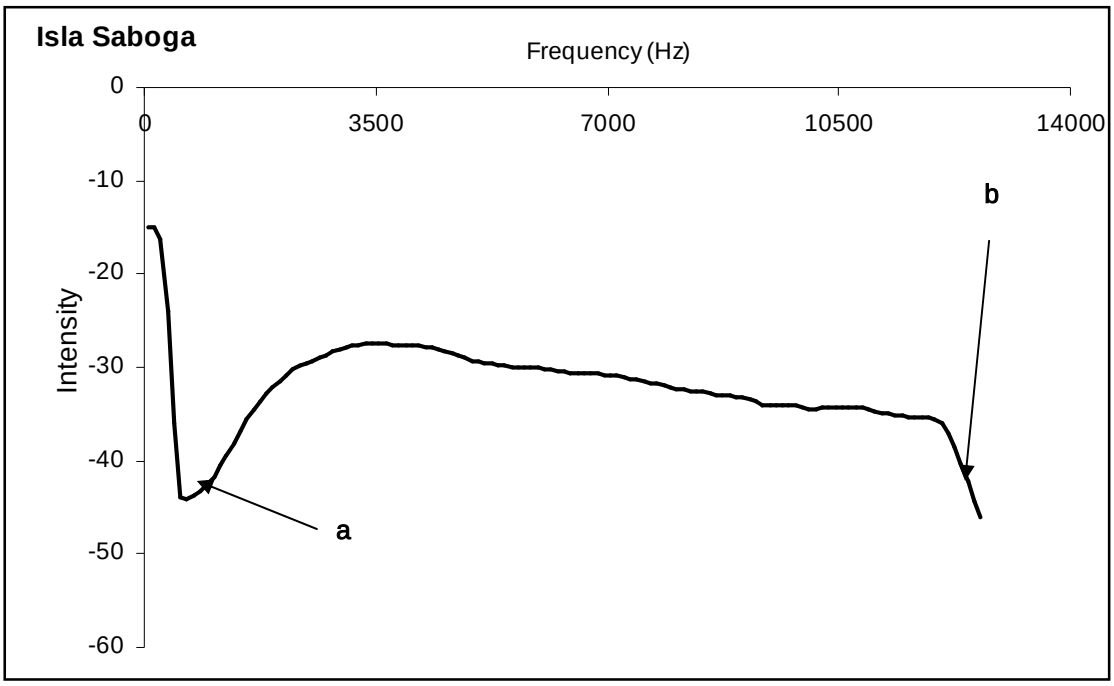



***Figure 5.1****. Example of a typical frequency-intensity graph of sound recorded from reefs in Panama. This was from Site 9, Isla Saboga. Frequency is measured in hertz, and intensity, in decibels, is a measurement proportional to the square of the acoustic pressure of the wave. The frequency-intensity curves of most of the sound recordings looked similar to this one, with two peaks of intensity, seen here at (a) and (b). This shows that reef noise is not just random noise, but has a definable structure. The first peak (a), around 50-3000 Hz, represents low frequency fish noise. The second peak (b, around 11-14 KHz) represents the often slightly louder snapping shrimp noise- although in this example the peaks have similar intensity. The sound profile of each site was characterised by these two sound sources.*

During the 212 minutes of recordings, the hydrophone sampled a multitude of sounds including banging waves against the hull, whirring boat motors, clicking and squeaking dolphins, singing whales and the croaking and grunting of individual fish – all over the often thunderous reef "crackling" that made up the bulk of the recordings. Sound recordings at all sites had a component of ambient noise with high amplitudes at frequencies 50-3000 Hz and between 11-12.5 kHz (figure 5.1). Snapping shrimp are

responsible for the broad peak in intensity centered around 11 kHz (Montgomery, 2006), represented by the loud background 'crackle' typical of coral reefs. Analysis of the sound waves showed that snapping shrimps produced a broadband – 'snap' that covered many frequencies (fig. 5.2). Because the amplitude covers a range of frequencies, it is likely that shrimps are responsible for much of the background noise on the profile, as well as for the high frequency peak in intensity. The other peak (50-3000 Hz) tended to have a lower sound level than the shrimp noise, and consisted of lower frequency chorus of pops and grunts made by reef fish (Simpson *et al*., 2007). At some sites, where the intensity of the snapping shrimp noise was lower, the ensemble of croaking and grunting was clearly audible on the recording.

### 5.1.1 *Within site variation in reef noise*

The first thing was to test the consistency of the five recorded clips over the two minute recording. Plotting frequency intensity graphs for each of the five recorded clips (fig. 5.3) appeared to show that within a two minute window, the quality of the reef noise appears to be relatively stable – the curves hold the same shape. This proves that reef sound is not just random noise: there are clear curves that remain fairly consistent in each recorded clip. However, a Friedman test showed that sound clips within each recording actually differed significantly from one another ($Q = 379.52$; $df = 4$; $p < 0.01$).

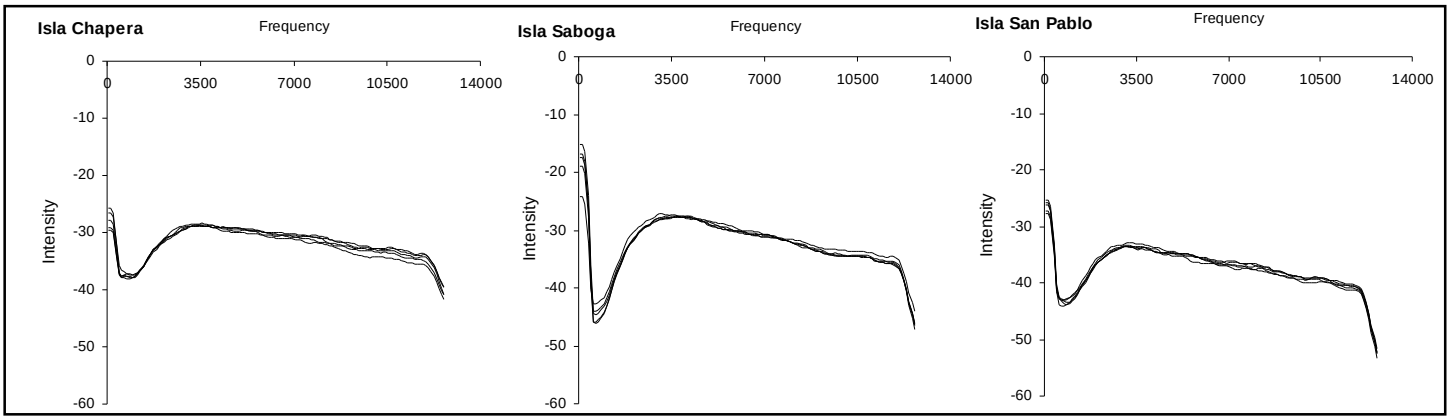



***Figure 5.3****: Sound profiles for three of the sites; Isla Chapera (site 19), Isla Saboga (site 9) and Isla San Pablo (site 30). Frequency (Hz) -intensity (dB) graphs have been plotted for the three sites. Each of the plots has five lines, representing one ten second sample clip taken from the recording. In each case, the five curves on each plot hold the same shape, indicating that the sound produced is fairly stable. These plots appear to demonstrate that reef sound stays the same for each site, but differ between sites. Note that despite differences in the curves between sites, each recording retains the two peaks (representing fish sound and snapping shrimp). For sound profiles of the remaining eight sites see Appendix 1.*

Although these differences are statistically significant they were very very small, and are most likely explained by slight changes in intensity (the curve moves up and down but the shape remains the same). In order to minimise the effects of these differences in intensity, an average of the five sound clips were used to represent noise from each site in the analysis.

5.1.2 *Between site variation in reef noise*

Next, the averaged sound recordings from each site were compared using Friedman Test. A Friedman test is the non-parametric alternative to the two way ANOVA test and the most appropriate way to test more than two related samples where the data does not conform to parametric assumptions and is, as in this case, ordinal. Tests showed that the 11 sites differed significantly in the sounds they emitted for the full spectra of recorded frequencies ($Q=1109.48$, $df=11$, $p<0.001$).

This site difference remained true when analysing sounds from different frequency bands that we wanted to investigate further. 0-2000 Hz, ($Q=129.34$, $df=11$, $p<0.001$), is the estimated extent of most fishes hearing (Simpson, pers comm.); 600-2000 Hz, ($Q=147.50$, $df=11$, $p<0.001$), represent the upper frequencies of fish hearing – thought to be used by larval recruits offshore, and 0-600 Hz was the lower frequencies, including most fish vocalization and anthropogenic noise ($Q=40.48$, $df=11$, $p<0.001$). This shows that sites differ not only in all the frequencies that were recorded by the hydrophone (between 0 and 12.7 kHz), but also in what fish might hear, what larvae might hear and the noises that fish produce differ between sites. This is important, since it may allow larvae to distinguish between sites when homing back onto the reef for settlement. Figure 5.4 shows how the frequency-intensity curves from different sites differ in character.

Site 10, at Contadora, showed an unusual sound profile, with dips in sound intensity around 3000 and 4500 Hz, where other sites did not, and a crest of intense sound at 7000 Hz (fig. 5.4).

A principle component analysis was run in statistical software package SPSS to extract the factors responsible for site variation. In each case, three components were extracted that were able to explain 99% of the variation. Factor 1, responsible for 92.5% of the variance, was intensity, the second factor, explaining about 4.5% of the variance was

frequency, and the third, explaining the remaining 2% was time. PCA plots were created to look for similarities between different sites. When different frequency bands were examined, the percentage of the variance explained by factors changed. For the 0-2000 Hz, factor 1 explained 79% of the variance, factor 2 a much greater 17% and factor 3 the remaining 3%. These factors were used in further analysis to represent sites.

Covariance tests showed that Factor 1 values for the 0-600 Hz frequency band were not correlated with Factor 1 values for the entire frequency range (0-12700 Hz) ($r=0.027$, $p=0.937$). This is interesting in that it shows that the intensity of sounds produced in the 0-600 Hz range may not be typical of the rest of the reef noise. All the other frequency ranges investigated (0-2000 Hz, 600-2000 Hz and 0-127000 Hz) exhibited strong positive linear associations with each other ($p=0.001$).

The only association that the Factor 1 0-600 Hz band exhibited was with factor two ($r=0.660$, $p=0.027$) – suggesting that at these lower frequencies, the actual frequency is more important in explaining site differences than the sound intensity.

RMS (root mean square) of the waveform was also calculated for each frequency bin at each site. RMS is a standard reference level so that all decibel levels will have positive values, and gives a good overall picture of sound level. RMS values were averaged for all 46 sites to give one value, which was found to range between 0.04 and 0.31 pascals ($x=0.15$p, SD 0.07, SE 0.01). A T-test confirmed that all 46 sites differed from each

a much other ($T=2.76$, $p=0.009$). In addition, 31 sites were recorded offshore. These had lower mean RMS values, averaging 0.09 p (SD 0.05, SE 0.008). This shows that reef sound is more noisy than normal ocean sound.

As expected, RMS and factor 1 values correlated highly ($r=0.882$, $p<0.001$). This was true for all frequency bands, except for 0-600 Hz band ($r=0.027$, $p=0.300$).

5.1.3 *Temporal variation in reef noise*

Having established that reefs produce noise with stable sound profiles, the final part of objective 1 was to see whether these sound profiles differed over time. Recordings collected in 2006 (by Simpson and Mair), were compared to recordings collected as part of this study. Repeated recordings taken on different days during this study were also compared.

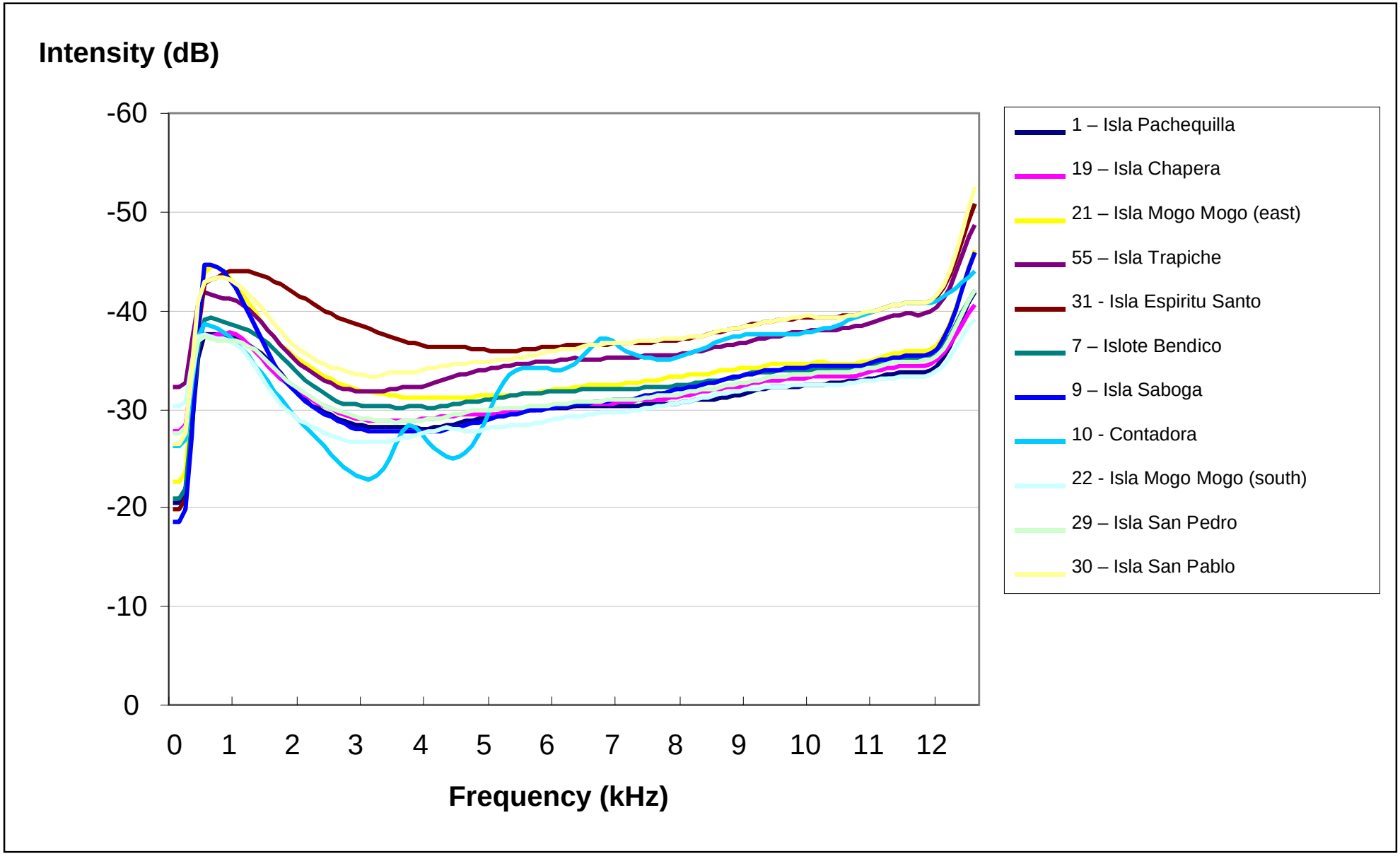



***Figure 5.3****: Frequency-intensity graph of sound, for the averaged samples for each of the 11 sites in the study. Note the profile for Contadora, which shows an unusual curve with dips in intensity around 3 and 4.5 kHz.*

After checking data for normality and homogeneity of variance, paired T-tests were used to show that overall, sound recordings at each site did not differ from those collected at the same sites during the previous years field trip (99% C.I., T=-1.78, p=0.078). In addition to there being no significant difference between factor one components for sites in 2007 and 2006, there was no difference in the intensity of sound at 1050 Hz between sites either (T=-1.69, p=0.118). When sites were analysed individually, there were no differences in sound at the 5% level, but significant differences at Islote Bendico (site 7) at the 1% level (T=2.20, p=0.05), suggesting that this site might have undergone some changes in the last year. The unusual sound profile observed at Site 10 (Contadora) did not appear in the 2006 recording at this site, which had a more typical profile.

## 5.2 Fish surveys

Eleven sites were surveyed using the AGGRA protocol. In total 44 fish belt transects were swum, 4 at each of the eleven coral reef sites, whose locations are shown in Figure 4.1. A total of 8619 fish were counted, giving an average of 784 fish per site, with a standard deviation of 251 and a standard error of 79.5. This compared with 8220 fish counted at the same sites in 2004 (over 39 surveyed sites with an average 766 per site, ± SD 309, S.E. 49.2). This gives 196 fish per 120m$^2$ transect - or a density of 160 fish per 100m$^2$ - compared to 192 fish per transect found in 2004. Between 500 and 1000 fish were found at each site, but differences between the sites was shown not to be significant (F=0.13, p=0.718).

### 5.2.1 *Fish species*

In total, 44 species were found at the sites (see Appendix 2) compared to 42 species in the previous survey of the 11 sites (Baxter, 2003). The community make up was very similar at each site, with between 10 and 25 different species recorded at each site (mean number of species 18 ± SD 4.8). There was no significant difference in the number of species recorded at each site in 2003 and 2007 (F=0.06, p=0.812), even though the type of species sometimes differed. Site 22 (Mogo Mogo south) was the least speciose, with only ten species recorded despite having the third highest abundance of fish. The greatest number of species were found at sites 1 and 7. However, a one sample

t-test showed that there was no significant difference between the number of species found at each site (t=0.13, p=0.902).

Nine species that had been found in 2004 were not spotted during project work, while eleven species were found that had not previously been spotted at this site. Three of these ten (*Hoplopagrus guentherii*, *Mugil curema* and *Epinephelus analogus* – see Appendix 2 for common names) had not been found anywhere in Las Perlas during the extensive 2003 surveys of 55 sites, although they were known to frequent the area.

The two most commonly found species were *Thalassoma lucasanum* and *Chromis atrilobata* which accounted for exactly 50% of all the fish surveyed. These were also the two most abundant fish in 2004, accounting for a slightly larger 64% of total number of fish found. In previous year's surveys, the damselfish *Stegastes acapulcoensis* was the third most abundant fish, whereas this year *Stegastes flavilatus* was more commonly found. However, a paired T-test showed that there was no significant difference between the numbers of each species found (p=0.794) in successive years.

5.2.2 *Fish families*.

Eighteen fish families were represented in the surveys, compared to twenty in 2003. Figure 5.5 shows the contribution that each family made to the total number of fish surveyed. Three families accounted for over 80% of all fish counted. The family with the greatest abundance was the Labridae (3467 counted), which was composed of six species. Seven species of Pomacentridae, the damselfish, accounted for 39% of all the fish, and Haemulidae, for which there were three species, accounted for 6%. Groupers (Serranidae) and Parrotfish (Scaridae) were the next two most abundant groups. There was no significant difference in the percentages of families between the two years (t=0.13, p=0.902) paired t test, or between sites (f=0.55, p=0.468).

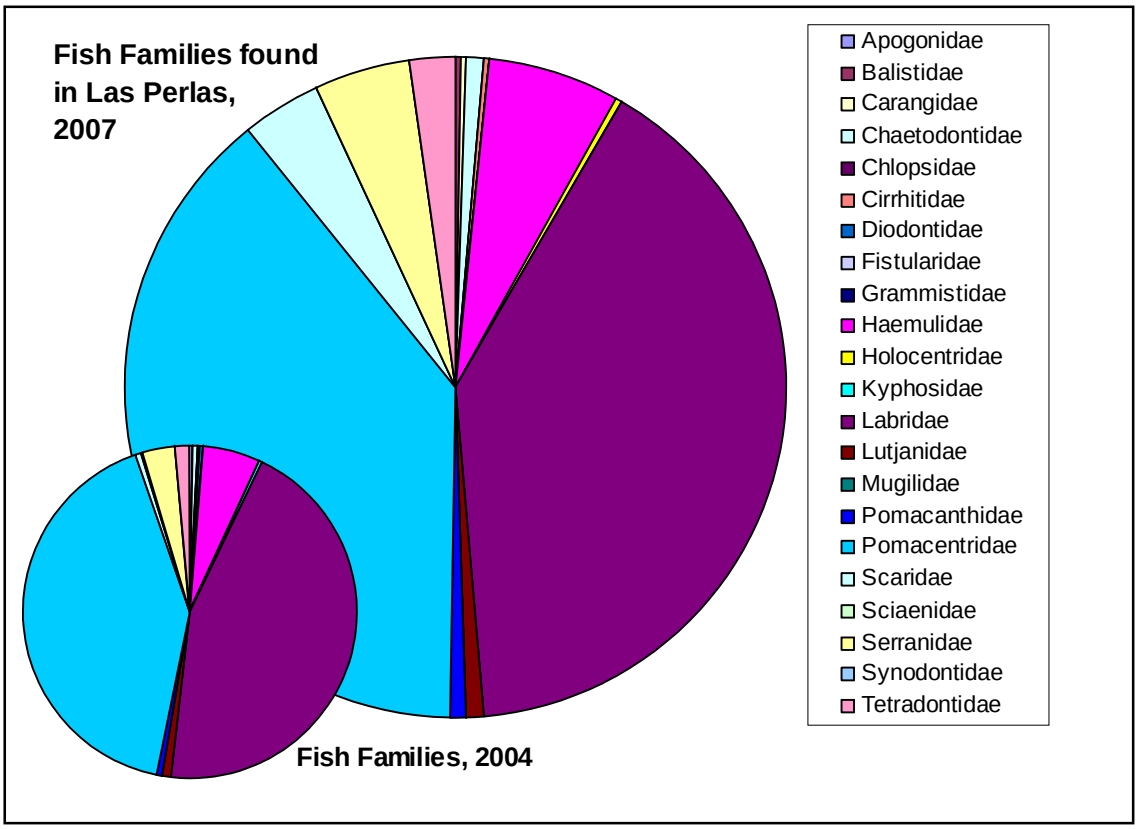



***Figure 5.5***. *Pie chart showing contribution that each family made to the total number of fish counted, compared to those surveyed at the same sites in 2004. There was no significant difference in this pattern between sites or between years. See appendix 2 for which species fall within which families.*

5.2.3 *Fish diversity*

All sites, with the exception of site 29 had shown an increase in fish diversity since 2003 (Shannon Diversity Index). However, this difference was shown not to be significant between the two years recordings at the 1% level (f=6.70, p=0.018). Although this could be significant at the 5% level, with a higher level of diversity in 2007 compared to 2003.

5.2.4 *Feeding groups.*

Fish were categorised into broad trophic groups, based on Robertson and Allen (2002). Relative abundances of these trophic groups were examined in relation to sound. A paired T-test showed no significant difference in overall feeding group composition in 2004 and 2007. Carnivores (p=0.933, t=0.09), planktivores (p=0.253, T=-1.21), corallivores (T = 1.10, p=0.298) and herbivores (T=-2.21, p=0.052) showed no difference in abundance in 2004 and 2007. However, there was a significant difference in the number of omnivores (4.24, p=0.002) with sites surveyed in 2007 having on

average of over 128 more omnivores than previously (f=10.17, p=0.005). All sites with the exception of 55 had over 50 more omnivorous fish than when last surveyed. Sites 9 and 22 showed the greatest increase, with 280 more omnivorous fish each. Site 31 had a significantly higher percentage of corallivores than all the other sites, both in 2003 and 2007. Omnivores mainly consist of Pomacentridae (damselfish) – the second biggest group of fish found. The Pomacentridae are known to be very soniferous and this finding may impact on sound (Parmentier *et al*., 2006).

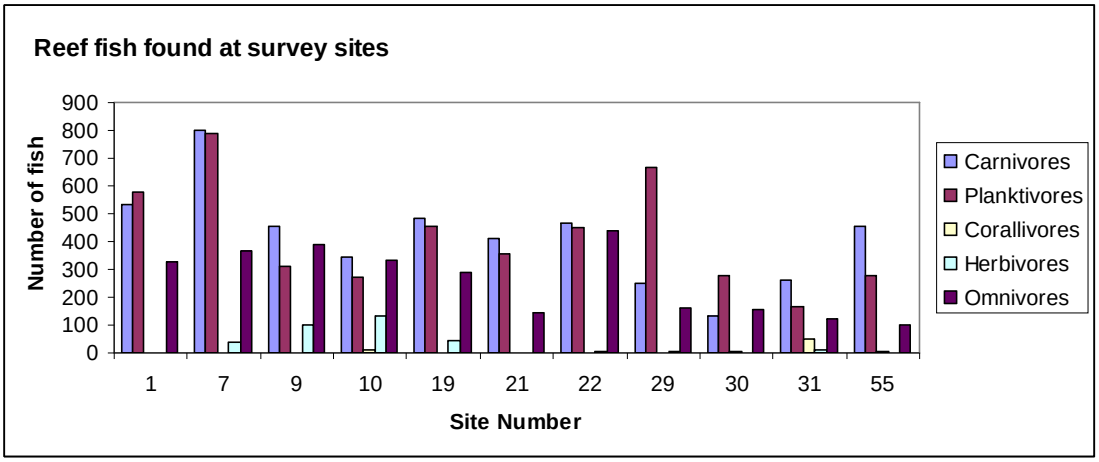



***Figure 5.5****: Bar chart showing the fish, grouped into feeding guilds, found at each site. Just as in the 2003 survey, carnivores and planktivores dominate the food chain. Site 7 had by far the greatest number of fish.*

5.2.5 *Fish size.*

During surveys, fish were categorized according to size. The fish recorded in 2007 were on average about 1 cm bigger, although this was shown not to be significant (T=0.85, p=0.415, 95%CI).

### 5.3 Benthic Surveys and Rugosity

Surveys of the benthic habitat were carried out at each site. This involved six 10 x 1 m belt transects, totalling 66 transects swum altogether. A total of 9 different coral species were found, covering 71% of the entire area surveyed. *Pocillophora damicornus* dominated the reefs, making up 63% of all the area surveyed and being present at every site but one (fig. 5.6). Two other *Pocillophora* species, *P. elegans* and *P. inflata* were also found commonly, with *P. elegans* found at 5 of the 11 sites and accounting for 9% of the area surveyed, and *P. inflata* at one other site. Other corals found included two Porites species (*P. panamensis* and *P. lobata*), and two Pavona species (*P. frondifera*

and *P. gigantea*). The final coral found was *Psammocora stellata*. The rest of the reefs were comprised of algae (28%), sand (0.28%) and sponges (0.08%) and one zooanthid.

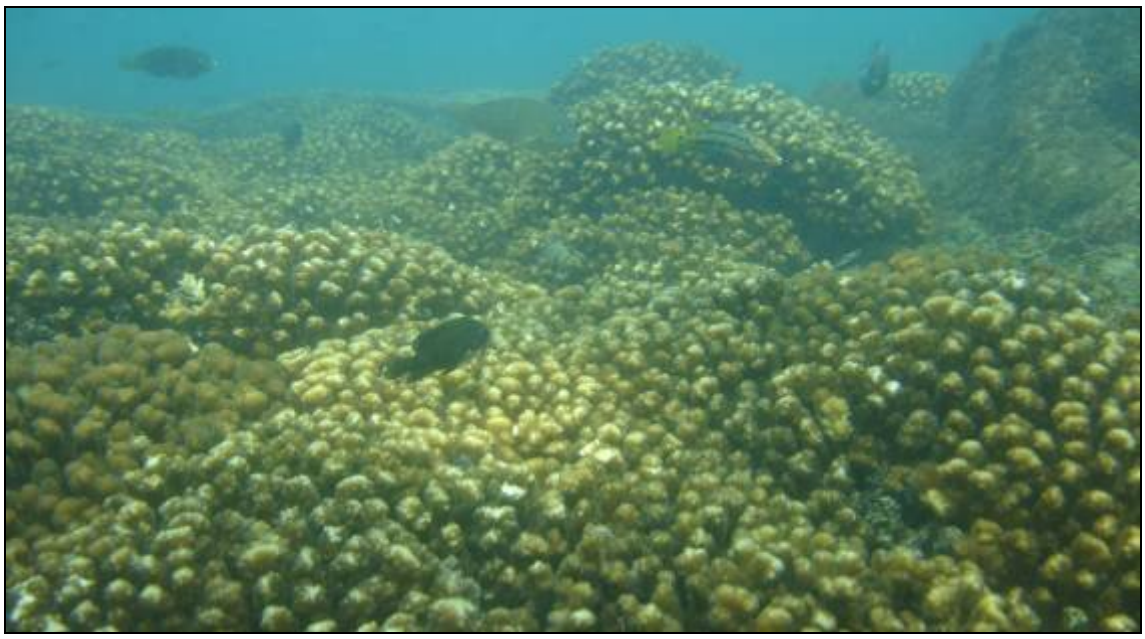


***Figure 5.6****: Photograph of the reef off Isla San Pedro (site 29).* Pocillophora *heavily dominated all the reefs accounting for 87% of the corals found.* Courtesy of Antonin Guilbert

Sites differed significantly from each other ($p<0.001$) in their benthic makeup. Pachequilla (site 1) was the 'healthiest' site with over 95% coral cover. Isleta Trapiche and Isla San Pedro also had over 90% coral cover. Espiritu Santo was the poorest site, dominated by algae (72%) with only 29% coral cover. Isla Mogo Mogo (East) only had 47% coral cover and over half algae. The remaining sites had between 60 and 80% coral cover. CCA was counted separately from the other algae as it tends to be reef building and an indicator of a healthier reef, Isla Bendico, Saboga and Contadora all had over 10% CCA, the remaining sites between 0 and 3%.

Sites had not changed significantly since being surveyed in 2003. Benthic diversity (Shannon H $\log_{10}$) was calculated for each of the sites, and was shown not to have changed significantly since 2003 with a slight decrease in average diversity ($t=1.01$, $p=0.336$). Paired t-tests also showed coral cover was not significantly different ($t=0.38$, $p=0.709$). The amount of macroalgae had not changed at each site ($t=1.26$, $p=0.237$) nor the amount of CCA ($t=1.74$, $p=0.112$).

Coral diversity ($H\log_{10}$) had generally decreased since 2003. A paired t-test showed this change to be significant at the 5% level ($t=2.30$, $p=0.044$). Sites on average showed a much higher coral diversity in 2003. Sites 1, 31 and 55 were the only sites to increase

diversity. Site 55 showed the best increase (0.405) to become the second most diverse site (H=0.869), after site 31 (H=1.01). All other sites showed a drop in coral diversity, with Sites 7, 19 and 29 – the 3 most diverse sites in 2003, showing the most dramatic drop in diversity.

5.3.1 *Rugosity*

Rugosity was calculated at each site, and averaged to give a rugosity index value for each site. Sites 55 (Isleta Trapiche) and 22 (Isla Mogo Mogo) had a significantly higher level of rugosity than all other sites. At both these sites, rugosity was measured by collector HMG, while the remaining sites were measured by diver CAG. The significant difference in collectors highlights the drawbacks of this method. Sites 55 and 22 were removed from data set before analysis continued.

5.3.2 *Other variables*

Further ANOVA tests on sea state and and T-test for tide state confirmed that these variables had no significant effect on other parameters and so could be excluded from further analysis.

**5.4 Sound vs. reef variables**

To investigate the relationship between sound and reef variables, a correlation matrix was drawn up to give a broad overview of which variables might be related (fig 5.6). When dealing with such a large amount of data, correlation matrices help highlight associations for further investigation. Because some data did not conform to assumptions for parametric tests, all data was ranked prior to this analysis. A non-parametric Spearmans rank test of correlation was used.

It was important to include as many factors as possible in the matrix, since coral reefs are full of highly interrelated components. We were expecting to find a multitude of interactions within and between the fish community and the benthic environment.

*5.4.1 Sound vs. fish communities*

One of the biggest and most significant correlations found was between sound intensity and the total number of fish found at each site (r=0.809, p=0.003). A regression analysis

showed fish numbers to be useful as a predictor of sound ($r^2$=50, T=-3.36, p=0.008), explaining half the site variance (fig. 5.7). The reef at Islote Bendico (site 7) was highlight by MINITAB as an unusual observation, having an anomalously high number of fish compared to all other sites, with over 400 more fish than every other site. When site 7 was removed from the analysis, fish numbers gave an even better explanation of sound intensity ($r^2$ = 0.89, T=37.1, p<0.001) – see discussion.

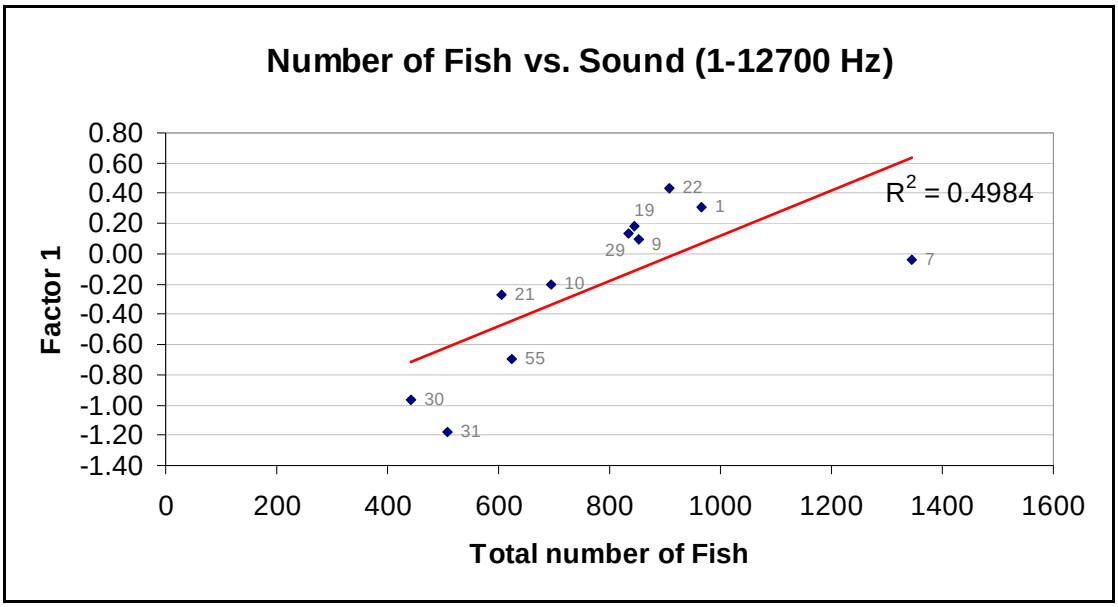



***Figure 5.7**: Graph showing the linear relationship between total number of fish found at each site and the intensity of sound. The more fish that are present, the greater the sound intensity. Site 7 could be an anomaly, with a much lower sound intensity than would be expected for the large number of fish found on this reef. Sites, represented by blue dots, are numbered.*

Because covariance tests had shown sound intensity values for the 0-600 Hz frequency range to differ from other recorded frequencies (r=0.027, p=0.937), we tested the total number of fish – a factor known to correlate with differences in intensity over the full frequency range - against sound in different frequency bands. As well as showing a strong positive relationship with the sound intensity produced at 1-27000 Hz, fish numbers were associated with sound at 0-2000 Hz (r=0.673, p=0.023) and at 600-2000 Hz (r=0.618, p=0.043). These associations were significant at the 5% level. However, there was no correlation between total fish number and changes in sound intensity for 0-600 Hz values (r=0.291, p=0.385). Factors 2 and 3 were not correlated with fish numbers either – intensity was the only aspect of sound to relate to fish numbers. A graph of regression analysis carried out on data conforming to parametic test assumptions shows this more clearly (fig. 5.8).

| | Fac1 | Fac2 | Fac3 | Fish totals | Fish species | Fish diversity (Hlog10) | Fish Species equitability | Coral cover | Algae (%) | CCA (%) | Benthic diversity (Hlog10) | Benthic species equitability | Coral diversity (Hlog10) | Coral species equitability | Rugosity | Carnivores | Planktivores | Corallivores | Herbivores | Omnivores | Acapulco gregory | Damselfish | Predators (snapper/ grouper) | Beaubrummel gregory | Scissortail chromis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fac2 | -0.364 | | | | | | | | | | | | | | | | | | | | | | | | |
| | 0.272 | | | | | | | | | | | | | | | | | | | | | | | | |
| Fac3 | -0.036 | 0.264 | | | | | | | | | | | | | | | | | | | | | | | |
| | 0.915 | 0.433 | | | | | | | | | | | | | | | | | | | | | | | |
| Fish totals | **0.809** | -0.1 | 0.191 | | | | | | | | | | | | | | | | | | | | | | |
| | **0.003** | 0.77 | 0.574 | | | | | | | | | | | | | | | | | | | | | | |
| # Fish species | 0.085 | 0.028 | 0.076 | 0.35 | | | | | | | | | | | | | | | | | | | | | |
| | 0.803 | 0.934 | 0.825 | 0.291 | | | | | | | | | | | | | | | | | | | | | |
| Fish diversity | -0.6 | 0.255 | 0.091 | -0.136 | 0.35 | | | | | | | | | | | | | | | | | | | | |
| | 0.051 | 0.45 | 0.79 | 0.689 | 0.291 | | | | | | | | | | | | | | | | | | | | |
| # Fish Species | -0.582 | 0.273 | 0.218 | -0.182 | 0.17 | **0.918** | | | | | | | | | | | | | | | | | | | |
| | 0.06 | 0.417 | 0.519 | 0.593 | 0.617 | **0** | | | | | | | | | | | | | | | | | | | |
| Coral cover | 0.109 | -0.236 | -0.036 | 0.164 | **0.908** | 0.109 | -0.027 | | | | | | | | | | | | | | | | | | |
| | 0.75 | 0.484 | 0.915 | 0.631 | **0** | 0.75 | 0.937 | | | | | | | | | | | | | | | | | | |
| % Algal cover | -0.055 | 0.236 | -0.164 | -0.264 | **-0.908** | -0.245 | -0.091 | **-0.936** | | | | | | | | | | | | | | | | | |
| | 0.873 | 0.484 | 0.631 | 0.433 | **0** | 0.467 | 0.79 | **0** | | | | | | | | | | | | | | | | | |
| % CCA | 0.264 | -0.236 | **0.618** | 0.491 | 0.284 | 0.182 | 0.173 | 0.173 | -0.373 | | | | | | | | | | | | | | | | |
| | 0.433 | 0.484 | **0.043** | 0.125 | 0.398 | 0.593 | 0.612 | 0.612 | 0.259 | | | | | | | | | | | | | | | | |
| Benthic diversity (Hlog10) | **-0.664** | 0.273 | 0.118 | -0.445 | 0.132 | 0.473 | 0.473 | 0.164 | -0.264 | -0.264 | | | | | | | | | | | | | | | |
| | **0.026** | 0.417 | 0.729 | 0.17 | 0.698 | 0.142 | 0.142 | 0.631 | 0.433 | 0.433 | | | | | | | | | | | | | | | |
| Species | 0.327 | -0.245 | 0.409 | 0.4 | -0.104 | -0.127 | -0.127 | -0.191 | 0.009 | 0.409 | -0.418 | | | | | | | | | | | | | | |
| | 0.326 | 0.467 | 0.212 | 0.223 | 0.761 | 0.709 | 0.709 | 0.574 | 0.979 | 0.212 | 0.201 | | | | | | | | | | | | | | |
| Coral diversity (Hlog10) | 0.527 | -0.491 | 0.264 | **0.627** | 0.085 | 0.018 | 0.027 | 0.018 | -0.191 | 0.482 | -0.318 | **0.827** | | | | | | | | | | | | | |
| | 0.096 | 0.125 | 0.433 | **0.039** | 0.803 | 0.958 | 0.937 | 0.958 | 0.574 | 0.133 | 0.34 | **0.002** | | | | | | | | | | | | | |
| Species | 0.183 | -0.228 | -0.146 | 0.137 | -0.059 | -0.384 | -0.557 | -0.027 | -0.046 | 0.238 | -0.429 | 0.347 | 0.064 | | | | | | | | | | | | |
| | 0.591 | 0.499 | 0.668 | 0.688 | 0.864 | 0.244 | 0.075 | 0.936 | 0.894 | 0.482 | 0.187 | 0.296 | 0.852 | | | | | | | | | | | | |
| Rugosity | -0.018 | -0.479 | -0.452 | -0.177 | -0.151 | -0.293 | -0.293 | 0.062 | -0.062 | -0.151 | -0.089 | 0.133 | 0.044 | **0.64** | | | | | | | | | | | |
| | 0.959 | 0.136 | 0.163 | 0.602 | 0.658 | 0.383 | 0.383 | 0.856 | 0.856 | 0.658 | 0.795 | 0.697 | 0.897 | **0.034** | | | | | | | | | | | |
| # Carnivores | 0.573 | 0.036 | 0 | **0.818** | 0.501 | 0.136 | 0.018 | 0.291 | -0.373 | 0.227 | -0.127 | 0.336 | 0.6 | -0.018 | -0.168 | | | | | | | | | | |
| | 0.066 | 0.915 | 1 | **0.002** | 0.116 | 0.689 | 0.958 | 0.385 | 0.259 | 0.502 | 0.709 | 0.312 | 0.051 | 0.957 | 0.957 | | | | | | | | | | |
| # Planktivores | 0.7 | 0.027 | -0.073 | **0.755** | 0.445 | -0.345 | -0.518 | 0.309 | -0.282 | 0.291 | -0.618 | 0.209 | 0.2 | 0.521 | 0.018 | 0.591 | | | | | | | | | |
| | 0.016 | 0.937 | 0.832 | **0.007** | 0.171 | 0.298 | 0.102 | 0.355 | 0.401 | 0.385 | 0.043 | 0.537 | 0.555 | 0.1 | 0.959 | 0.056 | | | | | | | | | |
| # Coralivores | -0.576 | -0.19 | -0.015 | -0.583 | -0.037 | 0.241 | 0.19 | 0.139 | -0.175 | -0.117 | 0.656 | -0.525 | -0.423 | -0.241 | -0.048 | -0.576 | -0.613 | | | | | | | | |
| | 0.064 | 0.577 | 0.966 | 0.06 | 0.915 | 0.476 | 0.577 | 0.685 | 0.607 | 0.733 | 0.028 | 0.097 | 0.195 | 0.475 | 0.887 | 0.064 | 0.045 | | | | | | | | |
| # Herbivores | 0.115 | -0.14 | 0.346 | 0.222 | -0.219 | 0.247 | 0.321 | -0.379 | 0.288 | 0.346 | -0.379 | 0.461 | 0.502 | -0.308 | -0.47 | 0 | -0.132 | -0.117 | | | | | | | |
| | 0.736 | 0.682 | 0.298 | 0.511 | 0.518 | 0.464 | 0.336 | 0.251 | 0.39 | 0.298 | 0.251 | 0.154 | 0.116 | 0.356 | 0.145 | 1 | 0.7 | 0.732 | | | | | | | |
| # Omnivores | **0.709** | -0.245 | 0.391 | **0.773** | -0.076 | -0.282 | -0.145 | -0.173 | 0.055 | 0.455 | -0.545 | **0.673** | **0.764** | 0.055 | -0.071 | 0.445 | 0.391 | -0.562 | 0.56 | | | | | | |
| | **0.015** | 0.467 | 0.235 | **0.005** | 0.825 | 0.401 | 0.67 | 0.612 | 0.873 | 0.16 | 0.083 | **0.023** | **0.006** | 0.873 | 0.836 | 0.17 | 0.235 | 0.072 | 0.073 | | | | | | |
| Acapulco | **0.811** | -0.249 | -0.129 | 0.489 | -0.078 | -0.645 | -0.489 | 0 | 0.175 | -0.028 | **-0.747** | 0.277 | 0.341 | 0.036 | 0.088 | 0.277 | 0.48 | **-0.695** | 0.156 | **0.627** | | | | | |
| | **0.002** | 0.46 | 0.705 | 0.127 | 0.819 | 0.032 | 0.127 | 1 | 0.606 | 0.936 | **0.008** | 0.41 | 0.304 | 0.916 | 0.796 | 0.41 | 0.136 | **0.018** | 0.646 | **0.039** | | | | | |
| Damselfish | **0.745** | -0.064 | 0.009 | **0.709** | 0.17 | -0.545 | **-0.609** | 0.091 | -0.055 | 0.218 | **-0.736** | 0.264 | 0.209 | 0.448 | 0.018 | 0.336 | **0.873** | -0.54 | 0.115 | **0.609** | **0.636** | | | | |
| | **0.008** | 0.853 | 0.979 | **0.015** | 0.617 | 0.083 | **0.047** | 0.79 | 0.873 | 0.519 | **0.01** | 0.433 | 0.537 | 0.167 | 0.959 | 0.312 | **0** | 0.087 | 0.736 | **0.047** | **0.035** | | | | |
| Predators (snapper/grouper) | 0.4 | 0 | -0.255 | -0.027 | -0.426 | **-0.836** | **-0.736** | -0.282 | 0.491 | -0.318 | **-0.645** | 0.018 | -0.255 | 0.393 | 0.293 | -0.291 | 0.345 | -0.416 | -0.156 | 0.155 | 0.673 | 0.555 | | | |
| | 0.223 | 1 | 0.45 | 0.937 | 0.192 | **0.001** | **0.01** | 0.401 | 0.125 | 0.34 | **0.032** | 0.958 | 0.45 | 0.232 | 0.383 | 0.385 | 0.298 | 0.204 | 0.646 | 0.65 | 0.023 | 0.077 | | | |
| Beaubrummel gregory | **0.818** | -0.218 | 0.309 | **0.891** | 0.104 | -0.327 | -0.273 | 0.018 | -0.145 | 0.445 | -0.4 | **0.627** | **0.782** | 0.164 | 0 | **0.727** | 0.555 | **-0.62** | 0.198 | **0.873** | 0.572 | 0.573 | 0.064 | -0.287 | |
| | **0.002** | 0.519 | 0.355 | **0** | 0.761 | 0.326 | 0.417 | 0.958 | 0.67 | 0.17 | 0.223 | **0.039** | **0.004** | 0.629 | 1 | **0.011** | 0.077 | **0.042** | 0.56 | **0** | 0.066 | 0.066 | 0.853 | 0.392 | |
| Scissortail chromis | -0.245 | 0.318 | -0.082 | -0.1 | 0.454 | 0.082 | -0.155 | 0.373 | -0.318 | -0.118 | 0.055 | -0.4 | -0.555 | 0.183 | -0.186 | -0.182 | 0.336 | 0.299 | -0.181 | -0.382 | -0.314 | 0.318 | 0.045 | 0.135 | -0.427 |
| | 0.467 | 0.34 | 0.811 | 0.77 | 0.161 | 0.811 | 0.65 | 0.259 | 0.34 | 0.729 | 0.873 | 0.223 | 0.077 | 0.591 | 0.584 | 0.593 | 0.312 | 0.372 | 0.594 | 0.247 | 0.348 | 0.34 | 0.894 | 0.693 | 0.19 |

***Figure 5.6**: Correlation matrix of some of the major variables. Significant linear relationships are highlighted in red. The first value represents the correlation coefficient, the second the p-value. Correlations with a p-value of less than p=0.05 are deemed statistically significant.*

*'Fac1' is variation in sound intensity, 'Fac2' is variation in sound frequency and 'Fac3' is variation in time, for frequencies between 0 and 12700 Hz.*

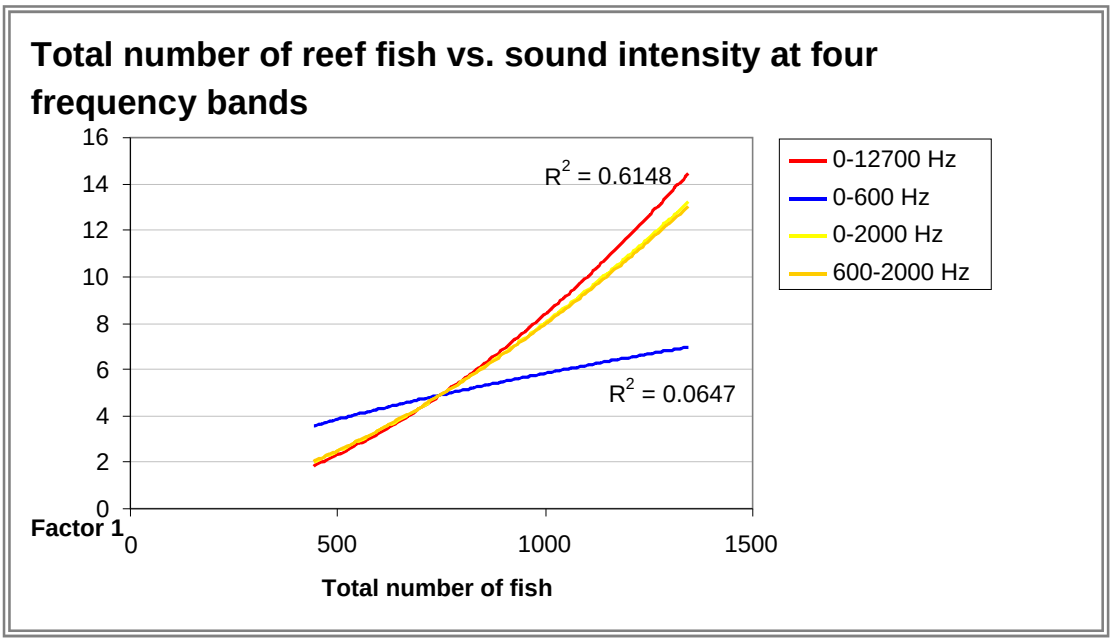



***Figure 5.8****: Regression lines for the relationship between the total number of reef fish at all 11 sites, and the sound intensity for frequencies between 0-12700 Hz, 0-2000 Hz and 600-800 Hz compared to 0-600 Hz. The 0-600 Hz frequency band does not explain the number of fish at each site ($r^2$ = 0.067), while changes in intensity at higher frequencies explain 61% of differences in total number of fish.*

Other aspects of the fish community correlated with factor 1 (intensity) variance components. Both the fish diversity and number of fish species correlated negatively (-0.6 and -0.582) with sound intensity, however in both cases this was not deemed significant (p>0.05) – see fig. 5.6. The total number of carnivores, planktivores, herbivores and omnivores all correlated with differences in sound intensity, although these associations was only statistically significant in omnivores (r=0.709, p=0.015) and planktivores (r=0.700, p=0.016).

Given that total fish numbers correlated so closely with sound intensity, it would be expected that feeding guilds associated as well: each guild represents a breakdown of the total number of fish and so is likely to show some association with it. In fact, the fish totals *were* more closely associated with the number of carnivores (r=0.818 p=0.002), planktivores (r=0.755, p=0.007) and corallivores (r=-0.583, p=0.06) than they were with sound. Because the association between feeding guilds and total number of fish were stronger and more significant than relationships between feeding guilds and sound intensity, they could be interdependent factors.

However, the fact that increased numbers planktivores and omnivores were associated with higher sound intensity, when carnivores were not, is of some significance.

Planktivores and carnivores, on average, made up the bulk of the fish community – and tended to be found in roughly equal numbers (both comprising 37%). Omnivores, including the damselfish, made up about 23% of the reefs, herbivores 3% and corallivores just 1%. If associations with intensity were due to interdependence on total numbers of fish, carnivores and planktivores would be expected to be similarly associated with sound. But planktivores and omnivores – not carnivores - showed a much stronger association with sound intensity (r=0.709 and 0.7) compared to other feeding groups (r=0.573), suggesting that fish from these feeding groups are responsible for more noise, or are more important in making noise, than predators, herbivores and corallivores.

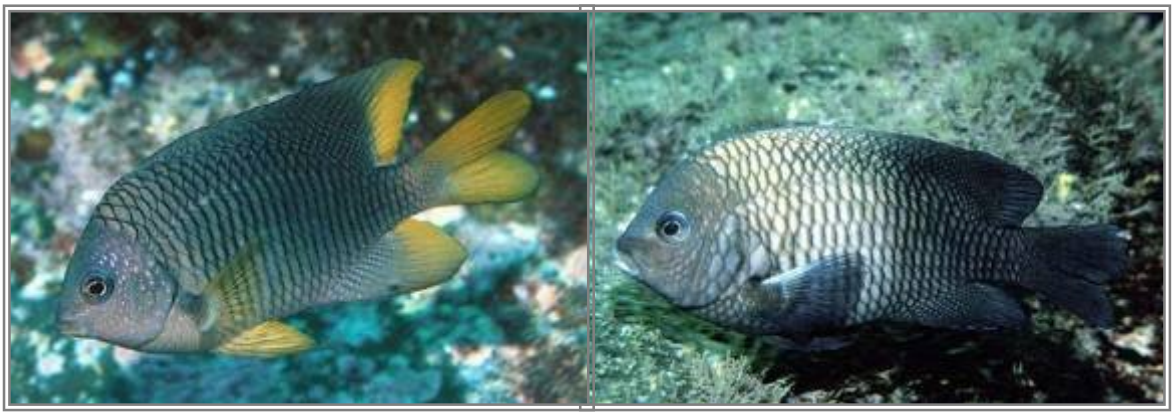


***Figure 5.9***: Stegastes flavilatus*, the Beaubrummel Gregory (left) and* Stegastes acapulcoensis*, the Acapulco Gregory (right), two of the most abundant fish on the reef, were found in numbers that are correlated with reef sound intensity.* (Robertson & Allen, 2002)

To investigate this theory we examined family groups and their association with reef noise. When looking at family groups, fish of the Pomacentridae (damselfish) stood out as showing a very strong positive association with sound intensity (r=0.745, p=0.008). There is well documented evidence for *Stegastes* and *Chromis* species ability to emit loud pops and chirps (Parmentier *et al*., 2006; Amorim, 2006). Investigation into the mean abundance of *Stegastes* spp. and the sound intensity at each site produced some interesting results. There were two species of *Stegastes* found on the Las Perlas reefs; *Stegastes acapulcoensis*, the Acapulco Gregory and *Stegastes flavilatus*, the Beaubrummel Gregory (fig 5.9). *S. acapulcoensis* showed a strong positive relationship with sound intensity (r=0.811, p=0.002), while this relationship was even stronger in the

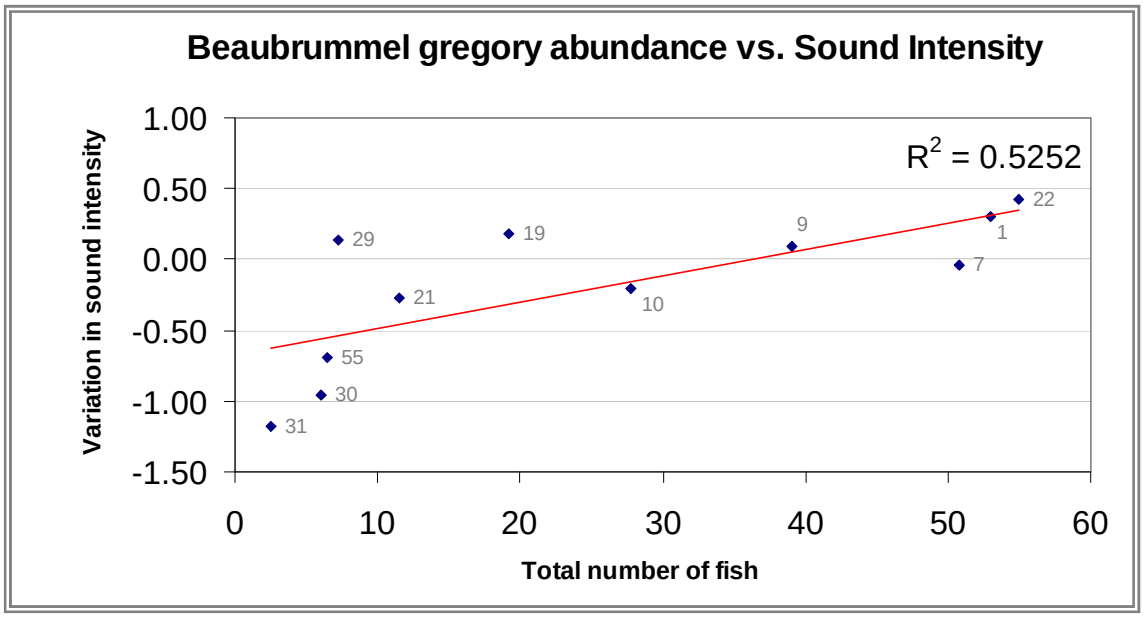



***Figure 5.10****: The relationship between mean* Stegastes flavilatus *abundance and sound intensity at each site was the strongest association highlighted by the correlation matrix. Regression showed it to explain 52% of site differences in sound intensity. This was more than any other single factor – even total fish number – unless Site 7 was excluded from the analysis.*

Beaubrummel Gregory (r=0.818 p=0.002) – fig. 5.10. This association remained true for all frequencies between 0 and 12700 Hz, with the exception of frequencies between 0 and 600 Hz (r=0.277, p=0.502). The abundance of these fish did not relate to other components of variance in sound, factors 2 (r=-0.249, p=0.460) or 3 (r=-0.129, p=0.705). Mean abundance of the commonest member of the Pomacentridae, *Chromis atrilobata* (the Scissortail Chromis) were not associated with sound (r=-0.245, p=0.467). The Pomacentridae are all omnivores: the numbers of predatory species, such as snapper and grouper, did not relate to sound differences (r=0.4, p=0.223).

*5.4.2 Sound vs. benthic communities and rugosity*

The correlation matrix showed that sound was associated with other reef factors, aside from the fish community. Spearmans rank tests showed benthic diversity to be negatively associated with sound (r=-0.664, p=0.026) – although observation this could be a result of the interactions between benthic diversity and the number of corallivores (r=-0.747, p=0.008) or damselfish abundance, which was also negatively correlated with benthic diversity (r=-0.736, p=0.010).

Ranked rugosity data showed a negative relationship with differences in sound intensity between 0 and 600 Hz ($r=-0.745$, $p=0.009$), but was not related to any other variables. The percentage of CCA found at each site was correlated with factor 3 components of variation in sound ($r=0.618$, $p=0.043$).

Within the reef, some variables were interconnected. Percentage coral cover correlated extremely positively with the number of fish species found at each site ($r=0.895$, $p<0.001$), and negatively with percentage algal cover ($r=-0.900$, $p<0.001$). The strongest reef association found was between percentage algal and coral cover. Where algal cover increases coral cover decreases ($r=-0.936$, $p<0.001$) because coral and algae compete for benthic space. Benthic diversity and fish diversity also showed a positive relationship (fig. 5.6). The number of damselfish and number of predators were negatively associated with fish diversity. Also of interest, sound intensity at 1050 Hz showed a strong negative relationship with fish diversity, but this was not deemed significant ($r=-0.691$, $p=0.019$). This would suggest that as diversity decreases, intensity of 1050 Hz noise increases – perhaps this is the noise that noisy damselfish make.

### *5.4.3 Multiple regression analysis*

A multiple regression analysis, called a General Linear Model (GLM) was used to further investigate factors affecting sound. A GLM is preferable to using lots of ANOVA tests to investigate associations, since this would not only be inefficient, time consuming and complicated to follow, but risky because repeating tests increases the chance of a type 1 error occurring.

Factor 1 and RMS Sound Levels were used as the response variables, since these explained over 78% of the difference between sites. These were tested in turn against a variety of predictor variables including total number of fish, total species, fish, benthic and coral diversity, species abundance and other factors such as exposure, slope and rugosity which could potentially explain differences in sound. Like any parametric test GLM's rely on random sampling, independence of observations, and homogeneity of variance and normality. To check the assumptions were met, a Levenes test for homogeneity of variances and Anderson-Darling normality tests were used. Data shown to be significantly different from expected ($p<0.01$) were transformed. Backwards elimination from the maximal model (containing all the predictor covariates) was used

to try and find the minimal model. Diagnostic tests and inspection of residual plots were used to confirm that the assumptions of the parametric were met.

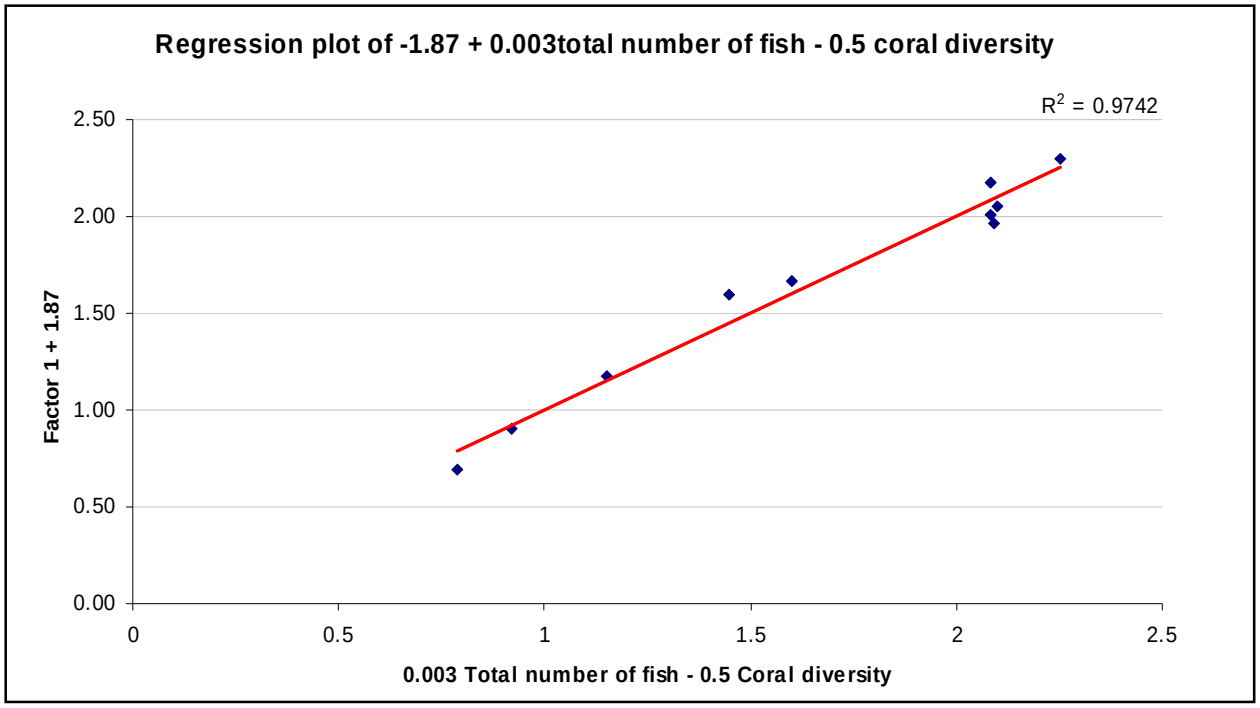



***Figure 5.11****: Plot of the regression equation used by the minimal GLM to best explain sound intensity differences between sites.*

Maximal GLM's were constructed, with 11 factors that could be used to explain between-site variations in sound intensity. When site seven was removed from the analysis, the mean abundance of *Stegastes acapulcoensis* was one of the later variables to be removed from the model, followed by the number of species (F=0.01, p=0.923), fish diversity (F=0.09, p=0.774) and finally *Stegastes flavilatus* abundance (F=0.95, p=0.368). The two remaining predictors of sound that best explained site differences in sound intensity were the total number of fish (F=148.61, p<0.001) and coral diversity (F=27.45, p=0.002). Combined, these were able to explain 97% of the variance in factor 1 (fig. 5.11).

**Factor 1= 1.87 – 0.49 Coral diversity + 0.00252 Total number of fish.**

When Site 7 *was* included in the analysis, the predictors that best explained site differences in sound were the number of *Stegastes flavilatus* (F10=9.11, p=0.017) and coral diversity (F10=6.23, p=0.037) – together explaining 73% of the variance $r^2$ =73.3, F=10.97, p=0.005).

Minimal models resulted in the same predictors for RMS values, and for Factor 1 velaues for frequency bands 0-2000 Hz and 600-2000 Hz. A separate GLM was also carried out for Factor 1 components of sound between 0 and 600 Hz. Again, fish diversity was one of the first factors to be removed (F=0.01, p=0.942, d=10), then total number of fish (F=0.02, p=0.887), omnivores (F=0.10, p=0.762), coral diversity (F=-0.54, p=0.610), *Stegastes acapulcoensis* abundance (F=1.87, p=0.221) and coral cover (F=2.23,m p=0.179) leaving two predictors: the number of *Stegastes flavilatus* (F=5.31, p=0.050), and rugosity (F=18.81, p=0.002) to explain 53% of the variance. The regression equation was

**Factor 1 = - 0.33 -0.32 Rugosity + 0.0186 *Stegastes flavilatus* abundance**

Where site 7 was left out, Stegastes flavilatus was removed from the model at a much earlier stage, leaving coral cover and the total number of species as significant predictors, explaining 50% of the variance.

# 6. DISCUSSION

## 6.1 Sound findings

Our results confirmed that all reef sites around Las Perlas emitted a specific noise. This noise is much more intense than any natural sounds found offshore – with mean RMS values of 0.15 pascals, compared to 0.09 further offshore. The majority of this noise was dominated by broadband snapping of shrimps, characterised by a peak intensity of sound around 11 kHz. A second peak of intensity occurred around 100-3000 Hz. These lower frequency noises were understood to have been produced by reef fish. All reefs, with the exception of the Site 10 reef at Contadora followed this pattern. This proves that reef noise is not just random noise. The extra peak of intensity in sound off the reef at Isla Contadora might be explained by the more developed nature of the site, which was full of boat traffic at the time of recording. These unusual peaks are in the correct range for a boat motor: a 70 horse power motor running at medium speed will produce a frequency within the range of 0.4 to 4.0 kHz (Sholik & Yan, 2002). The unusual site profile of the reef sound at Isla Contadora could represent anthropogenic disturbance, highlighting the impact of noise pollution on broadcast reef sound. The implications of this altered sound profile for marine creatures reliant on sound cues in this area are unknown.

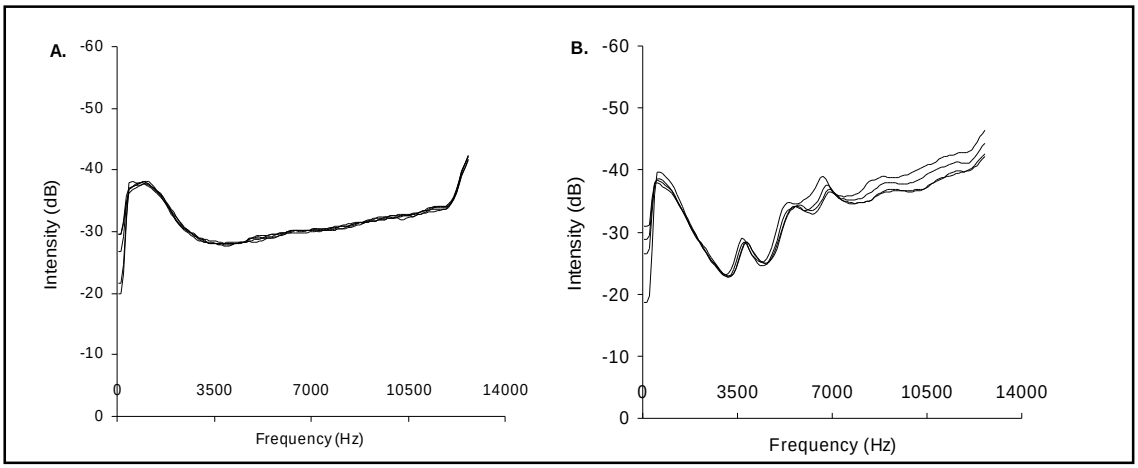



***Figure 6.1****: Frequency-intensity plots comparing noise produced by a reef at a typical site in Las Perlas (a) compared to that of a disturbed site profile (b). The plot for B was taken from recordings at Isla Contadora (site 10). At this site, development has radically altered the sound profile of the reef. Peaks in sound between 3500 and 7000 Hz might be caused by the boat traffic in the area.*

We found that each reef site produced a sound that was specific to that particular site, and significantly different from other sites ($Q=1109$, $df=11$, $p<0.001$). These sounds remained true to each site over time – not just over the period of the two minute

recording, but over an entire year (Q = 379.52; df = 7; p <0.01). Site differences were noticeable across the range of frequencies recorded – from lower frequency bands (0-600 Hz) to higher (600-2000 Hz). The implication of this is that differences in reef sounds may be available on a variety of bandwidths for detection by a series of marine organisms with different hearing ranges. Fish larvae, for example, have a higher bandwidth of hearing to adult fish which can only detect differences in sound at low frequencies. Mechanisms of hearing in benthic invertebrates and their larvae are largely unexplored.

Sound intensity, as opposed to any other component of sound, was the most important factor that distinguished reefs from each other. It was able to explain 90% of the differences between the 11 sites. This is not unexpected, since fish are known to be very limited in the sounds they are able to produce (Amorim, 2006). Between species, fish vocalisations tend to vary in duration, number and repetition rate, but fish show poor amplitude and frequency modulation and have relatively limited acoustical repertoires. As a result, different assemblages of fish at different reefs are unlikely to produce a significantly different frequency profiles that would enable us to identify the community structure or presence or absence of certain species - in the same way we can distinguish between different species of cetacean by listening to recordings. This does limit the use of passive recording as a monitoring technique. It would be difficult to listen to a recording, for example, and estimate the percentage of apex predators or abundance of corallivores.

### 6.1.1 *Low frequency noise*

One interesting finding was that the 0-600 Hz frequency band did not conform to the variation patterns of intensity of sound at different reefs. It is notable that the 0-600 Hz frequency band did not show correlations in intensity with 1-12700 Hz bands, while higher frequency bands did. This suggests that this particular range of frequencies contains slightly different information - or has a different source - to the rest of the reef.

The 0-600 Hz band intensities did, however, correlate with factor two components (0.660, p=0.027) – suggesting that at lower frequencies, the actual frequency is more important in explaining site differences than the sound intensity. Some abiotic noises, such as the slap of water against the hull, or drone of nearby boat motors, could not be

edited out of the sound samples. These noises also tend to have lower frequencies. Since higher frequency bands were closely associated with biological sources of sound, such as numbers of reef fish or *Stegastes* abundance, one explanation for the 0-600 Hz sounds being different is that they have an abiotic source. The GLM for 0-600 Hz sound factor 1 components could only explain 50% of the low frequency noise, suggesting another (possibly abiotic?) sound source.

However, part of the large peak of intensity characterising sound profiles at all sites was associated with this low frequency band, which we assumed was due to fish vocalisations. The GLM retained *Stegastes flavilatus* abundance as the second most important predictor of site variation ($F=5.31$, $p=0.05$). Studies of damselfish have shown that they produce sounds in the range 100 - 5000 Hz: the correct range for this peak in intensity. Perhaps fish producing sounds within this band are creating noises at very specific frequencies, resulting in frequency variation being more important in explaining site variation than intensity at this level.

Another reason why low frequency intensities might not correlate with changes in higher frequency intensities is that shallow water limits the propagation of low frequency sound. All reefs sites surveyed were less than 6 m in depth, and this could explain why lower frequency sound below 600 Hz did not conform to higher frequency sound patterns of intensity. The GLM minimal model retained rugosity as the most important predictor of 0-600 Hz sound intensities ($F=18.81$, $p=0.002$) suggesting that complexity of the benthic environment is very important for low frequencies.

It is important to investigate low frequency sounds further, especially since Simpson and colleague's experiments showed that sounds less than 570 Hz were the ones that attracted fish larvae (Simpson *et al*., 2007). If 0-600 Hz sounds explain a greater amount of frequency variation than intensity variation because of fish producing specific sounds, further exploration of the 0-600 Hz band and which frequencies are explaining site differences, could turn out to be a useful predictor of presence/absence data for fish at these sites.

### 6.1.2 *Sound recording problems*

The position of the hydrophone over the reefs could affect the intensity of sound. This would have implications for the study since intensity was one of the major factors that

distinguished sites from each other. An interesting example of this was shown by the recording at Site 31. Here, although the shape of the curves remained the same, the intensity changed dramatically across the five sound samples, with the first being fairly quiet and the last much more intense (fig. 6.2). Interestingly, the recording was taken on a choppy day where the boat was drifting towards the reef throughout the duration of the recording. As a result the sound clip sampled towards the end of the recording (B) shows the greatest intensity. A second recording of Site 31, with more similar sound clips, replaced this one in the analysis. The original sound recording from site 31 seen below serves as a reminder that it must always be remembered that position of the boat does have a small impact on intensity. There is the possibility that this could influence results, since intensity is the factor that explained the most differences and was used to distinguish between sites. For future projects the position of the boat is very important.

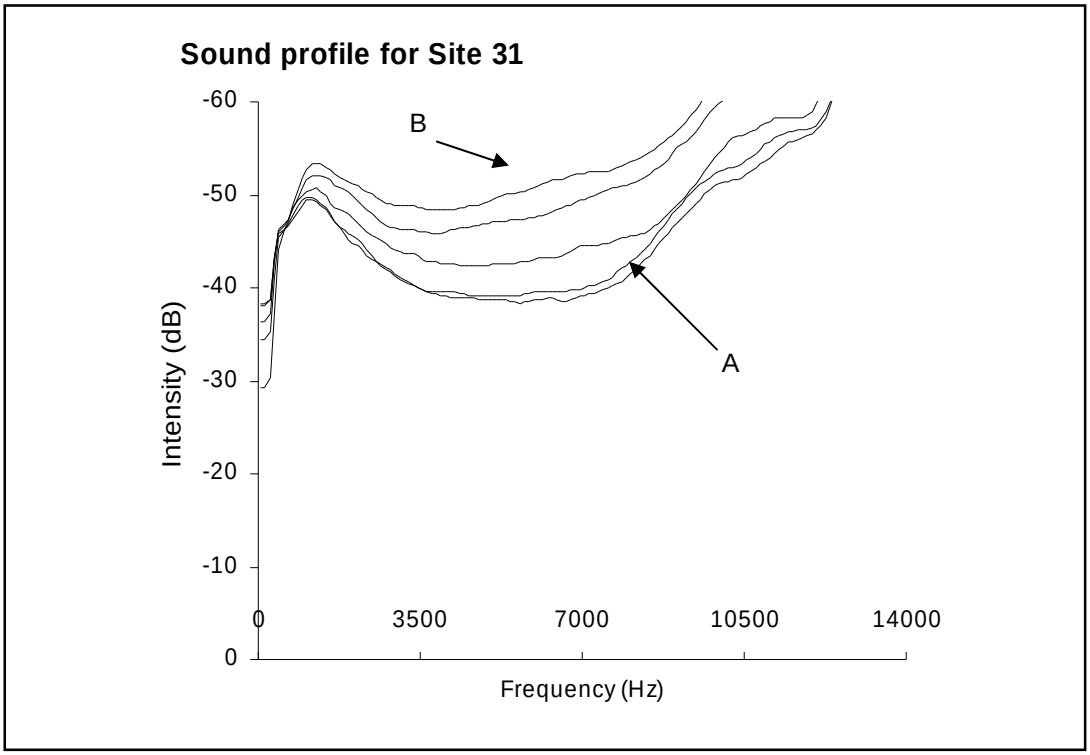



***Figure 6.2****: Sound profile for Isla Espiritu Santo (site 31). As the hydrophone gets closer to the reef, sound intensity increases from A to B.*

Sound intensity has been shown to vary with times of the day, and although sites were all sampled between 9 am and 5 pm it is possible the time of recording may have influenced our results. A comparison of recordings taken in the late afternoon with morning recordings showed that they did not differ significantly in intensity.

Although attempts were made to minimise anthropogenic sources of sound (by turning

off the engine, taking up the anchor and checking the area was clear) sound recordings were frequently interrupted by abiotic noise, such as the banging of waves against the hull of the boat, which was unavoidable unless the water was completely calm. Although a lot of this noise could be edited out using Audacity, in a few cases where the water was choppy it was difficult to delete all the interference without destroying the recording. Boat motors were also a problem, as they could be detected from a distance of kilometres (highlighting the impact of noise pollution) and especially affected recordings taken offshore, where reef noise was less intense. Many of the recordings were punctuated by a repeated clicking, occurring every tenth of a second throughout the recording. It was eventually deducted that this was caused by the research vessels depth sounder. The interruptions were easily identifiable due to their regularity and unusual wave shape, and although time consuming could be removed manually using Audacity. Other sources of sound could not always be identified and removed, although many interruptions such as surf or rainfall had natural sources and would be a normal part of reef sound for its inhabitants. Other sound recording problems included refraction scattering and reflections of sound off the sea surface and reef base, as well as production of most noise in the shallow water will lead to a complex sound field. Here, all we could do was assume that this sound field retained the critical properties of the 'reef sound'.

## 6.2 Reef-sound interactions

### 6.2.1 *Are damselfish noisy, or do they prefer noisy sites?*

The strongest association between reef sound and coral reef factors discovered was between sound intensity and mean abundance of damselfish. Damselfishes are well-known vocal species from the coral reefs, emitting pops, chirps or grunts are broadband pulsed sounds during chases and threat displays between conspecifics. We found the number of *Stegastes acapulcoensis* and *Stegastes flavilatus* showed a strong positive relationships with all frequency bands, especially 0-12.7 kHz. In fact, mean abundance of *S. flavilatus* demonstrated the strongest significant association with sound intensity identified ($r=0.818$ $p=0.002$). Sites with more *S. flavilatus* were the noisiest.

Correlation does not imply causation, so care must be taken in drawing conclusions about this finding. Work by Parmentier *et al*. (2006) showed damselfish to produce

various sounds which can range between 100 and 4000 Hz in different species. A peak of intensity was present for this band of frequencies at all sites (Appendix 1). It would make sense, therefore, to assume that the Beaubrummel Gregory is responsible for the majority of reef noise not explained by snapping shrimp. However, Simpsons work in 2007 showed that damselfish larvae were particularly attracted to higher frequency noises (>570 Hz) – so it is a possibility that reefs producing higher frequency noise at greater sound levels attract more recruiting damselfish larvae.

In fact, this explanation fits the data better, since the recorded damselfish vocalisations have been shown to protrude into the 0-600 Hz range. If damselfish were responsible for all the noise, these site variations in low frequency noise would be expected to correlate a little with damselfish abundance, whereas no correlation was found (r=0.249, p=0.460), although the GLM for 0-600 Hz retained *S. flavilatus* abundance as a predicting factor in the minimal model. In addition, all the sites had hugely increased numbers of omnivores – particularly damselfish, compared to 2003 surveys (fig 6.3), but showed little difference in reef sound between past and present recordings. Sites 9 and 22 showed the biggest increase in damselfish numbers, and had the highest mean RMS values for sound (0.23, 0.24). Meanwhile site 55, which was the only site not to increase in damselfish numbers, had a much lower RMS value (0.15). Although the sound recording and reef data were sampled in different years, and so can not be compared, a difference would support the theory that damselfish produce sound. One way to test this would be to take recordings from this particular species of *Stegastes*,

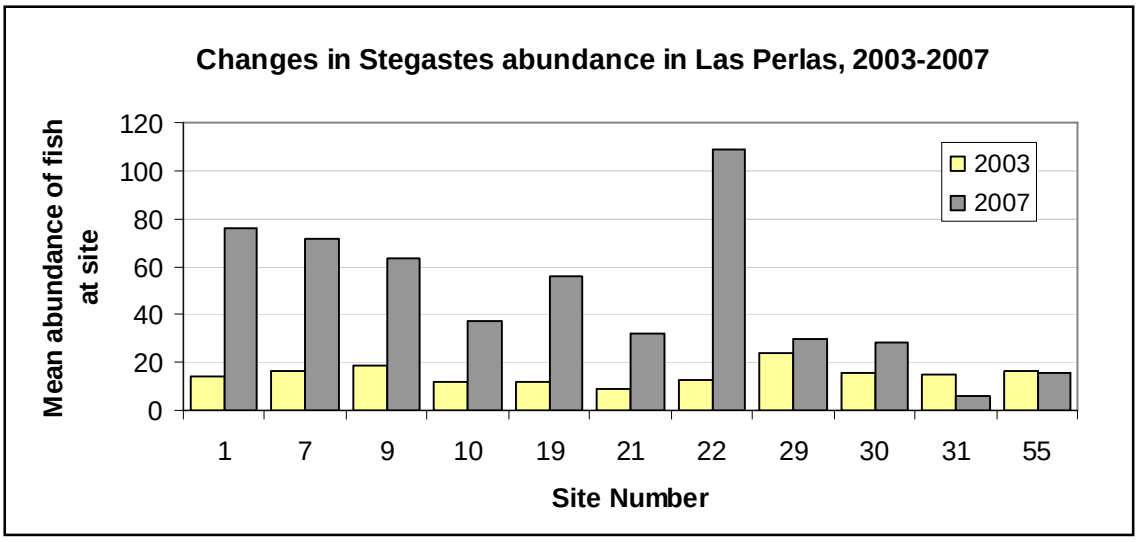



***Figure 6.3****: Histogram plot showing the mean Stegastes spp. abundance at each site in 2003 and 2007. Notice numbers of Stegastes are hugely elevated at every site.*

to determine the frequency range of its vocalisations, and then test the relationship between *Stegastes* abundance and sound intensity at these specific frequencies.

Our multiple regression model did not find *Stegastes* abundance a useful predictor of site differences in sound, although it was one of the last covariates to be removed, unless site 7 was included in the analysis. In the case of inclusion of site 7, *Stegastes* abundance *was* a predictor of sound intensity, replacing total number of fish as the most important predictor. This means that if the high Site 7 fish total was not an observation error (and we could think of no reason for it to be) *Stegastes* is a much more important predictor of sound than fish totals, although it could not explain as much variation as the model without Site 7. *Stegastes* abundance was found to be closely linked to both the total fish numbers (since it was one of the most commonly found species) and coral diversity (because it damages coral by farming algae) – two factors which ended up explaining the majority of noise in the model emitting Site 7. . Damselfish abundance was directly related to coral diversity (r=-0.747, p=0.008), where abundance was high coral diversity was decreased. The number of damselfish were also correlated negatively with fish diversity, probably because of its association coral diversity (-0.609, p=0.047). One reason why fish totals and coral diversity were shown to be important in explaining noise in the GLM was because of the influence of *Stegastes* on both these reef components.

### 6.2.2 *Other reef components*

Nine fish species that had been found in 2004 were not spotted during project work. For five of these species (Almaco Jack, Reef Lizardfish, Pacific Hamlet, Giant damselfish and Guineafowl puffer – see Appendix 2 for scientific names) only one individual had been counted in the 2004 survey, hence these species are rare in the area and unlikely to be encountered during survey work. Of the remaining four species, three, the Lined Highhat, Cortez sea chub, and Golden eye grunt were spotted in larger numbers (12, 20 and 21 respectively). However, in all three cases, all of the fish found were spotted on one transect at one site. These fish are larger schooling fish that are often found a little way off the reef, passing over to feed. Often found in large aggregations and is fairly transient (Allen and Robertson, 1994) therefore could be visiting schools, not related to specific environmental variables. Their nature means that underwater census techniques will occasionally pick up a school giving odd results. Not much can be extrapolated

about the abundance of these fish species from this result. The final fish found at 7 of the 12 sites surveyed in 2004 and none of the sites in 2007 was the Freckled Porcupinefish, *Diodon holocanthus*. Thirteen of these fish were counted during the 2004 surveys, while none were found in this years field trip. The most likely explanation is that *D. holocanthus* which is a nocturnal predator, tends to remain hidden during the day. Its main food source is snails, sea urchins and hermit crabs (fishbase.org). Another explanation might be that numbers of this fish has decreased in the area. In the past *D. holocanthus* has been shown to be susceptible to disease and parasites, and tends to accumulate toxins in its tissues, with mass mortalities occurring in Florida in 1994 (Landsberg, 1995).

Eleven species were surveyed that had not previously been found at these sites, although 9 of these 11 had been recorded at other sites around the archipelago in 2004. Of the eleven species, only one individual was recorded for five species (Barred Pargo, Burrito grunt, Spotted Cabrilla and Jewel and Panamic green morays) and two for two more (Green jack and pink cardinalfish). All of these fish are predators, usually found in small numbers on the reefs. Of the remaining three new species, 12 golden snapper were recorded, 8 mullet and 4 yellow snapper. All of these individuals were sited at site 7, Islote Bendico. Snapper are schooling piscevores that often swim off the reefs and come over to feed. Site was the deepest site and more exposed, perhaps attracting schools of larger pelagic fish like these. The stone triggerfish were also all sighted at one transect, they were very small and might have been mistaken for another triggerfish species. Mullet was a species representing a family which had not been sighted at all in the previous years surveys, although it was known to be in the area.

Other reef associations found were expected. Algae compete with coral so their negative relationship was not unusual. The number of fish species showed an extremely strong positive correlation with the percentage coral cover (0.895, $p<0.001$) and benthic diversity, since a more diverse habitat can support a greater range of species. Algae and coral cover showed a negative relationship – where algal cover increases coral cover decreases ((-0.936, $p<0.001$), this is because coral and algae compete for benthic space. Increased predators were associated with decreased fish diversity presumably because they prey on certain fish species. Damselfish numbers were correlated with decreased fish diversity since these fish are extremely territorial, and because they reduce benthic diversity by actively farming algae. Increased algal cover correlated with a lower

number of fish species, since algal reefs were dominated by algae eating damselfish, and because algae competes with coral reducing habitat niches. Also of interest, sound intensity at 1050 Hz showed a strong negative relationship with fish diversity, but this was not deemed significant (-0.691, p=0.019). This would suggest that as diversity decreases, intensity of 1050Hz noise increases – perhaps this is the noise that damselfish make.

### 6.2.3 *Reef survey problems*

The problem with fish surveys is a large sample size is necessary due to the high variability among fish populations. Many rare, cryptic or mobile species can be under reported and the power to accurately detect absolute fish abundances can be extremely low. The reason why Site 7 showed such an unusually high number of fish remains a mystery. However, a snapshot in time can not tell us about changing patterns in reef communities and changing patterns of recruitment, and there is a need to return to the site and continue to survey to get more reliable results. Repeated fish community surveys would give a better idea of reef fish communities at different sites.

Chain transect rugosity and in the past has not always correlated well with other rugosity measures, such as remotely sensed submarine data (Kuffner *et al*., 2007). Another criticism of the chain method was its destructiveness: during laying the chain would often become snagged on coral, breaking off arms unless it was recoiled incredibly carefully. Rugosity did demonstrate a relationship with sound between 0 and 600 Hz. This would fit with the theory that low frequency sound is highly influenced by reef structure, with rugosity creating a complex acoustic environment. However, because rugosity data was shown to be unreliable, and because an Anderson-Darling test showed rugosity data was not normally distributed (p>0.001)but log10, loge, log2, 1/x, arcsin, square-root, and box-cox transformations did not work, our rugosity data had to be abandoned.

# 7. CONCLUSION

Our study confirmed that the coral reefs around Las Perlas can be differentiated on the basis of the sounds they produce. These site differences in sounds could be best explained ($r^2$=97%) by the total number of fish and coral diversity: reefs with greater numbers of fish and less coral diversity were louder. In theory, this means that the number of fish and coral diversity at a reef could be roughly estimated by analysis of the reefs sounds, using the equation;

Mean RMS sound level = 0.135 – 0.08 Coral diversity + 0.0001 Total number of fish.

Firstly, this finding has management implications for Las Perlas, and raises the possibility of remote sensing as a monitoring tool. By simply putting a hydrophone over the reef for two minutes, information could be gathered about the biomass and benthic diversity of the reef site. While remote satellite image sensing has been useful in the area for mapping the region and locating areas of reef (Benfield, 2005), tools used such as LandSat and Quickbird are expensive and can not always distinguish between areas of healthy reef and dead or diseased corals, as well as being unable to determine biomass or fish density. Meanwhile, the use of indicator groups and diver surveys to monitor reefs are effort intensive and unsuitable for many remote locations. Passive sound monitoring offers a cheap and quick way to monitor biological changes over time, or even remotely survey reefs to predict fish abundance and coral diversity.

Secondly, this finding has implications for our understanding of larval fish recruitment. If larvae are able to interpret sounds broadcast from the reef far out to sea containing information about the number of fish and coral diversity of the reef, it could help them make decisions about which reef choose to navigate towards for settlement. Better understanding of larval recruitment may help with the designation and management of marine reserves (setting up reserves to include the entire area over which larvae are recruited from, or designing MPAs to increase fish with a longer pelagic larvae stage) and could provide important information on the distribution of fish stocks. Sound playback could be used to influence the movement of fish, or encourage settlement on artificial or overfished reefs for management and conservation purposes.

The main problem with this study is that the Pomacentrid *Stegastes* spp. were shown to be a defining constituent of the Las Perlas reefs, dominating fish communities, influencing benthic diversity and ultimately influencing the sound produced by the reefs. If *Stegastes* dominance is particular to Las Perlas, it may limit the application of our findings to reefs around the world. The case of Site 7 – which had a similar *Stegastes* abundance to other sites but was shown to have an atypically high number of fish and consequentially was removed from the analysis - supports the theory that *Stegastes* abundance is having a massive influence on reef sound. When Site 7 was included in the GLM, *Stegastes flavilatus* abundance was shown to be the most important predictor of sound, replacing total fish number, although it could only explain 73% of site variation. If the high fish totals at Site 7 are not an error, this shows that it is number of damselfish - and not the total number of fish - that is important in explaining reef sound. Knowledge about *Stegastes* spp. vocalisation abilities supports this, along with findings that the omnivore feeding guild (containing damselfish) was strongly associated with sound level, while carnivore and corallivore numbers were not – not all fish affect the sound profile. As a result, we conclude that total number of fish is not, in fact, a good predictor of sound: instead but *Stegastes* abundance is. In consequence, sound recordings can only be reliably used to predict the abundance of *Stegastes* at a site.

Although this is not as useful as being able to predict fish numbers, *Stegastes* numbers do give an indication of reef health and other factors, since they interact so closely with it, their abundance being correlated with the total numbers of fish and benthic diversity. Conclusions drawn from this predictor of reef sound could still be useful in monitoring changes in reefs over time, but perhaps not as useful as a remote sensing application.

Further exploration of sound is needed to assess the use of passive recordings as a remote sensing technique.

## REFERENCES


Allen, G.R. and D. R. Robertson. 1994. Fishes of the tropical eastern Pacific. *Univ. of Hawaii Press, Honolulu*.

Amorim, M. C. P. 2006. Diversity of sound production in fish. In: Ladich, F., Collin, S.P., Moller, P. and B.G. Kapoor, Editors, *Communication in Fishes* Vol. 1, Science Publishers, Enfield, New Hampshire, pp. 71–104.

Armsworth, P. R. 2002. Recruitment Limitation, Population Regulation, and Larval Connectivity in Reef Fish Metapopulations. *Ecology*, **83**(4): 1092-1104

Baxter, L. 2003. *A study of the reef fish communities of Las Perlas archipelago, Panama. Msc Thesis.* Thesis (Msc). Heriot-Watt University, Edinburgh, United Kingdom. 114 pp.

Benfield, S.L. 2005. *Mapping coral reefs and associated sublittoral habitats: A comparison of optical remote sensors and image classifiers and a study of the community structure of reef-associates fish*. Thesis (PhD). Heriot-Watt University, Edinburgh, United Kingdom. 395 pp.

Booth, D. J. and G. Wellington. 1998. Settlement preferences in coral reef fishes- what are the consequences to population structure and individual fitness? *Australian Journal of Ecology*. p. 274-279

Bradbury, I. R. and P. V. R. Snelgrove. 2001. Contrasting larval transport in demersal fish and benthic invertebrates: the roles of behaviour and advective processes in determining spatial pattern. *Canadian Journal of Fisheries and Aquatic Sciences,* **58**: 811–823.

Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. *Journal of Wildlife Management,* **18**: 297-308.

Codling, E. A., Hill, N. A., Pitchford, J. W. and S. D. Simpson. 2004. Random walk models for the movement and recruitment of reef fish larvae. *Marine Ecology Progress Series,* **279**: 215-224.

Cousteau, J. Y., and F. Dumas. 1953. *The silent world.* Perennial Library, Harper and Row, Publishers, New York.

Doherty, P. J. 2002. Variable replenishment and the dynamics of reef fish populations. In P. F. Sale (ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem*, pp. 327-355. Academic Press, San Diego.

Ferguson, B. G. and J. L. Cleary. 2001. In situ source level and source position estimates of biological transient signals produced by snapping shrimp in an underwater environment. *Journal of the Acoustical Society of America* **109**: 3031–3037.

Fish, M. P. 1964. Biological sources of sustained ambient sea noise. Pages 175-194 *in* W. N. Tavolga, ed. *Marine bioacoustics*. Pergamon Press, NY.

Fisher, R. and D. R. Bellwood. 2002. The influence of swimming speed on sustained swimming performance of late stage reef fish larvae. *Marine Biology*, **140** (4): 801-807.

Glynn, P.W. and I. G. Macintyre. 1977. Growth rate and age of coral reefs on the Pacific coast of Panama. *Proc 3rd Int. Coral Reef Sym.* **2**: 251-259.

Glynn, P.W. and J. L. Maté. 1996. Field guide to the Pacific coral reefs of Panama. *8th Int. Coral Reef Sym*. 3-33.

Grosholz, E. D. 1996. Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology*, **77**: 1680-1686.

Iversen, R. T. B., Perkins, P. J. and R. D. Dionne. 1963. An indication of underwater sound production by squid. *Nature*, **199**(4890):250-251.

Jasny, M. 1999. *Sounding the depths: Supertankers, sonar, and the rise of undersea noise*. Natural Resources Defence Council, New York.

Jones, G.P., Planes, S. and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. *Current Biology*, **15**: 1314-1318.

Kaatz, I. M. (2002). Multiple sound-producing mechanisms in teleost fishes and hypotheses regarding their behavioural significance. *Bioacoustics*, **12**: 230-233.

Kramer, P., Lang, J., Marks, K., Garza-Pérez, R. and R. Ginsburg. 2005. Atlantic and Gulf Rapid Reef Assessment Methodology v. 4.0. http://www.agrra.org/method/AGRRAv4_2005.pdf, web accessed August 20th, 2007.

Landsberg, J. H. 1995. Tropical reef-fish disease outbreaks and mass mortalities in Florida, USA: What is the role of dietary biological toxins? *Diseases of Aquatic Organisms*, **22**(2): 83-100.

Leis J. M. and M. M. Lockett. 2004. Localization of reef sounds by settlement-stage larvae of coral-reef fishes (Pomacentridae). *Marine and Freshwater Behaviour and Physiology*, **37**(2): 65-88.

Leis, J. M. and B. M. Carson-Ewart. 2003. Orientation of pelagic larvae of coral reef fishes in the ocean. *Marine Ecology Progress Series* 252: 239-253.

Leis, J.M. 2002. Pacific coral-reef fishes: the implications of behaviour and ecology of larvae for biodiversity and conservation, and a reassessment of the open population paradigm. *Environmental Biology of Fishes*, **65**: 199-208.

Leis, J.M. and M.I. McCormick. 2002. The biology, behaviour and ecology of the pelagic, larval stage of coral reef fishes. Chapter 8 (pp. 171-199) in: *Coral Reef Fishes*, P.J. Sale (ed). Elsevier Science, USA.

Lessios, H. A. and D. R. Robertson. 2006. Crossing the impassable: genetic connections in 20 reef fishes across the eastern Pacific barrier. *Proceedings of the Royal Society (London) B Online*.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture *Ecology*, **73**(6): 1943-1967.

McCauley, R. D. and D. H. Cato. 2000. Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Philosophical Transactions of the Royal Society of London: Biological Sciences*, **335**(1401): 1289-1293.

McCormick, M. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Marine Ecology Progress Series* **112**: 87-96.

Montgomery, J. C., Tolimeri, N. and O.S. Haine. 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries*, **2**: 261-277.

Montgomery, J.C, Jeffs, A, Simpson, S. D., Meekan, M. and C. Tindle. 2006. Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Advances in Marine Biology*, **51**: 143-196

Mora, C. and P. F. Sale. 2002. Are populations of coral reef fish open or closed? *Trends in Ecology and Evolution*, **17**: 422-428.

Mumby, P.J., Edwards, A.J., Arias-Gonzalez, J.E., Lindeman, K.C., Blackwell, P.G., Gall, A., Gorczynska, M.I., Harborne, A.R., Pescod, C.L., Renken, H., Wabnitz, C.C.C. and G. Llewellyn. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**: 533–536.

Palumbi, S. R. and R. R. Warner. 2003. Why gobies are like hobbits. *Science*, **299**(5603): 51-52.

Parmentier, E., Vandewalle, P., Bruno, F. and M. L. Fine. 2006. Sound production in two species of damselfishes (Pomacentridae): *Plectroglyphidodon lacrymatus* and *Dascyllus aruanus* *Journal of Fish Biology*, **69**: 491-503.

Patek, S.N. 2001. Spiny lobsters stick and slip to make sound. *Nature*, **411**: 153.

Planes, S., Parroni, M. and C. Chauvet. 1998. Evidence for limited gene flow in three species of coral reef fishes in the lagoon of New Caledonia. *Marine Biology*, **130**: 361-368.

Popper, A. N, McCauley, R. D., and J. Fewtrell. 2003. High intensity anthropogenic sound damages fish ears. *Journal of the Acoustical Society of America*, **113**(1): 638-642.

Richardson, W. J., Greene, C.R., Malme, C. I. and D. H. Thomson. 1995. *Marine Mammals and Noise*. Academic Press, San Diego.

Roberts, C.M., C.J. McClean, C. J., Veron, J. E. N., Hawkins, J. P., Allen, G. R., McAllister, D. E., Mittermeier, C. G., Schueler, F. W., Spalding, M., Wells, F., Vynne, C., and T.B. Werner. 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295**(5558): 1280-1284.

Robertson, D. R. and G. R. Allen. 2002. *Shorefishes of the tropical eastern Pacific: An information system*. CD-ROM. Balboa, Panama: Smithsonian Tropical Research Institute.

Ross, D. (1993) On Ocean Underwater Ambient Noise. *Institute of Acoustics Bulletin*, St Albans, Herts, UK: Institute of Acoustics, 18.

Sale, P. F. 1980. The ecology of fishes on coral reefs. *Oceanography and Marine Biology Annual Review*, **18**: 367-421.

Sale, P.F. and W.A. Douglas. 1981. Precision and accuracy of visual census techniques for fish assemblages for coral patch reefs. *Environmental Biology of Fishes*, **6**, 333-339.

Sale, P. F. 2004. Connectivity, Recruitment Variation, and the Structure of Reef Fish Communities. *Integrative and Comparative Biology*, **44**: 390-399

Santiago, A. and J. J. Castro. 1997. Acoustic behaviour of *Abudefduf luridus*. *Journal of Fish Biology*, **51**(5): 952–959.

Sholik, A. R. and H. Y. Yan. 2002. Effects of Boat Engine Noise on the Auditory Sensitivity of the Fathead Minnow, *Pimephales promelas*. *Environmental Biology of Fishes*, **63**(2) 203-209

Simpson S.D., Meekan, M.G., McCauley, R.D. and A. Jeffs, 2004. Attraction of settlement-stage coral reef fishes to reef noise. *Marine Ecology Progress Series*, **276**: 263-268.

Simpson, S. D. 2001. Is reef-generated sound a navigation cue for settlement stage coral reef fish? *Proc 2nd Symp Underwater Bio-Sonar Systems & Bioacoustics*, p. 153-157.

Simpson, S. D., Meekan, M. G., McCauley, R. D. and A. Jeffs. 2004. Attraction of settlement-stage coral reefs fishes to ambient reef noise. *Marine Ecology Progress Series*, **276**: 263-268

Simpson, S. D., Yan H. Y., Wittenrich, M. L , and M. G. Meekan. 2005. Response of embryonic coral reef fishes (Pomacentridae: Amphiprion) to noise during development. *Marine Ecology Progress Series*, **287**:201-208

Simpson, S.D., Jeffs, A, Montgomery, J C. and R. D. McCaudley. 2007. Nocturnal relocation of adult and juvenile coral reef fishes in response to reef noise *Coral Reefs* In preparation.

Simpson, S.D., Meekan, M.G., Montgomery, J., McCauley, R.D. and Jeffs, A. (2005) Homeward sound. *Science*, **308**: 221-228.

Sprague, M. W., Luczkovich, J. J., Brainard, R. E. and K. B. Wong. 2002. Analysis of coral reef sound recordings in the Phoenix and Line Islands. *Journal of the Acoustical Society of America*, **112**(5): 2204

Stobutzki, I. C. and D. R. Bellwood. 1998. Nocturnal orientation to reefs by late pelagic stages of coral reef fishes. *Marine Ecology Progress Series*, **149**: 35-41.

Swearer, Stepehn E., Shima, J.S., Hellberg, M.E., Thorrold, S.R., Jones, G.P., Robertson, D. Ross, Morgan, S.G., Selkoe, K.A., Ruiz, G.M. and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* **70**(1): 251-272.

Tavolga, W.N. 1977. Sound Production in Fishes. *Benchmark Papers in Animal Behavior V.9. Dowden, Hutchinson & Ross, Inc*. pp10-29.

Todd, C. D. 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? *Hydrobiologia*, 375-376.

Tricas, T. C. Kajiura, S. M. and R. K. Kosaki. 2006. Acoustic communication in territorial butterflyfish: test of the sound production hypothesis *Journal of Experimental Biology* **209**, 4994-5004.

Williams, D. A., Purcell, J., Hughes, C. R. and R. K. Cowen. 2003. Polymorphic microsatellite loci for population studies of the bicolor damselfish, *Stegastes partitus* (Pomacentridae). *Molecular Ecology Notes*, **3**: 547–549

**Website references**

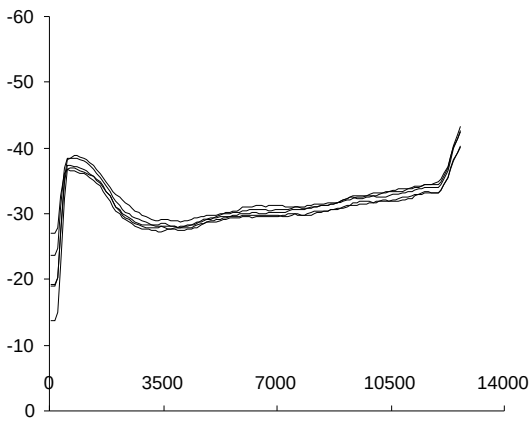
Smithsonian Tropical Research Institute, online resources
http://striweb.si.edu/maps, accessed 24/08/2007

Fish Base. Froese, R. and D. Pauly. Editors. 2007.FishBase.
World Wide Web electronic publication. http://www.fishbase.org, version (05/2007).

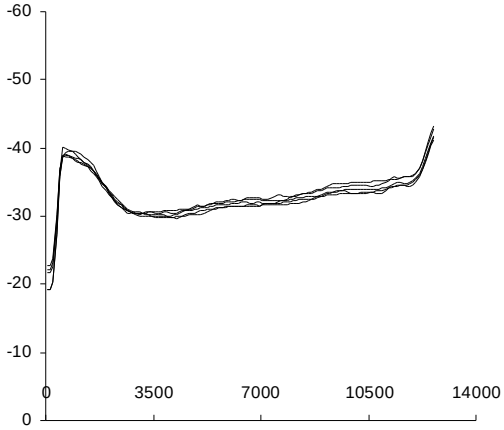
Law 18, 2007: Zona Especial de Manejo Marino-Costero, Archipiélago de Las Perlas
May 31st, 2007. Published in Panama's Gaceta Oficial, available as a PDF at http://129.171.91.238/gacetadia/gaceta.pdf.

Mann, D. 2006. University of South Florida College of Marine Science.
*http://www.marine.usf.edu/bio/fishlab/bioacoustics.htm*

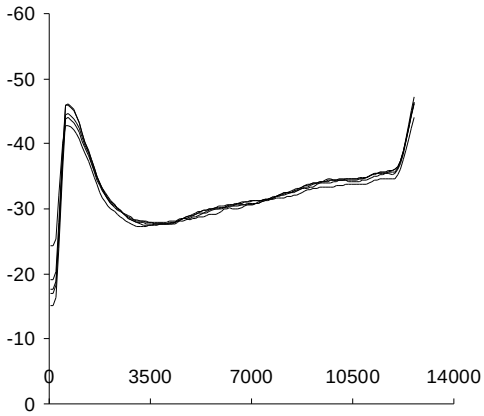
**APPENDIX 1**:
Frequency-intensity graphs for the sounds recorded over the coral reefs at each of the eleven sites around Las Perlas. The x-axis depicts frequency in hertz, and the y-axis



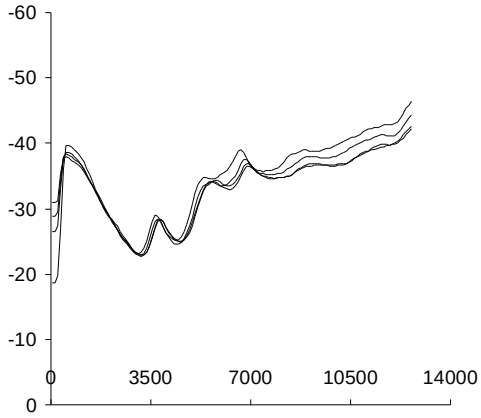

Site 1: Isla Pachequilla




Site 7: Islote Bendico

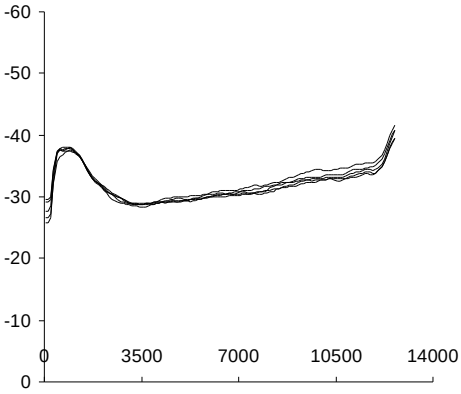



Site 9: Isla Saboga

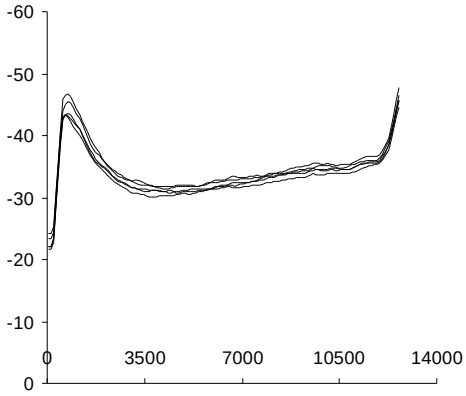



Site 10: Isla Contadora

The recordings at Contadora gave an unusual sound profile, with peaks in intensity at 4 and 7 kHz

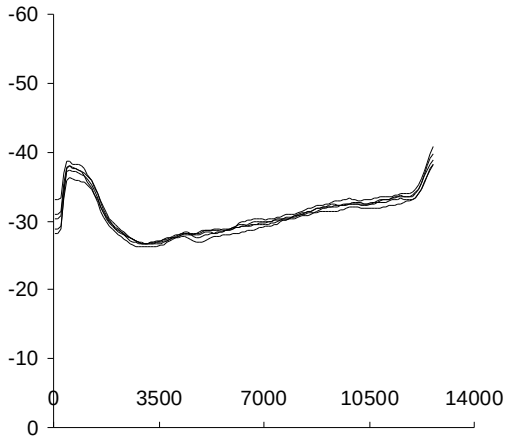



Site 19: Isla Chapera

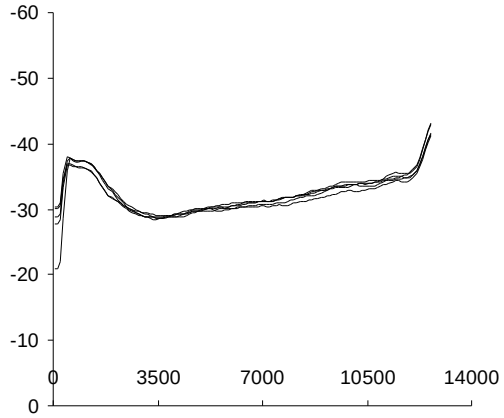



Site 21: Isla Mogo Mogo (east)

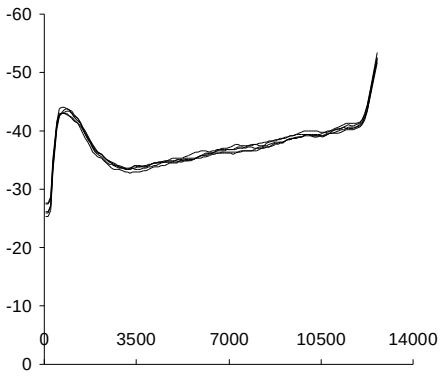
intensity in decibels.



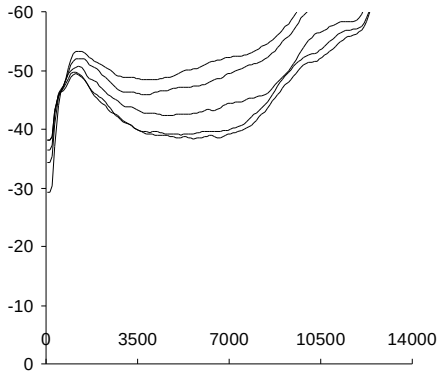

Site 22: Isla Mogo Mogo (south)




Site 29: Isla San Pedro

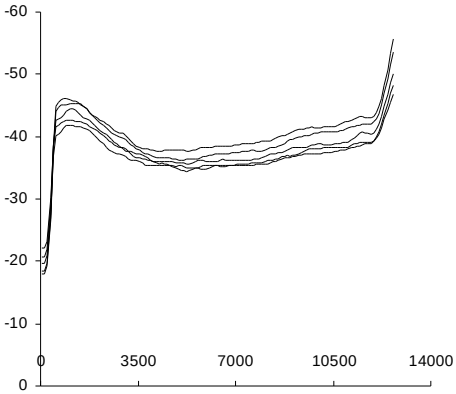



Site 30: Isla San Pablo



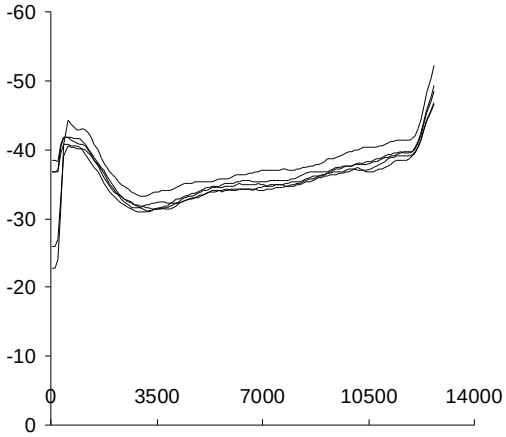

Site 31: Isla Espiritu Santo

Note how the intensity differs for each recording, especially towards the higher frequencies.




Site 31 repeat recording

econd sound recording at site 31 showed smaller erences in intensity between the samples.



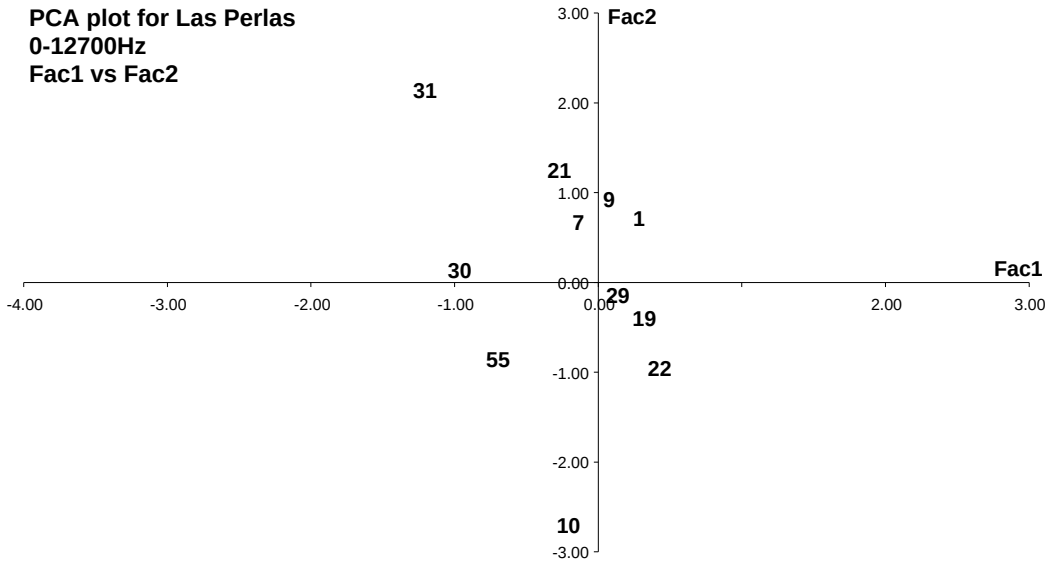

Site 55: Isleta Trapiche

**APPENDIX 2:**
List of species found during the survey, with common and latin names, and family.

| Scientific Name | Common Name | Family |
|---|---|---|
| *Apogon pacificus* | Pink cardinalfish* | Apogonidae |
| *Apogon dovii* | Tailspot cardinalfish | Apogonidae |
| *Balistes polylepis* | Finescale triggerfish | Balistidae |
| *Sufflamen verres* | Orangesided triggerfish | Balistidae |
| *Pseudobalistes naufragium* | Stone triggerfish* | Balistidae |
| *Caranx caballus* | Green jack* | Carangidae |
| *Johnrandallia nigrirostris* | Blacknose butterflyfish | Chaetodontidae |
| *Chaetodon humeralis* | Three banded butterflyfish | Chaetodontidae |
| *Muraena lentiginosa* | Jewel Moray* | Chlopsidae |
| *Gymnothorax castaneus* | Panamic Green Moray* | Chlopsidae |
| *Cirrhitichthys oxycephalus* | Coral hawkfish | Cirrhitidae |
| *Fistularia commersonii* | Reef cornetfish | Fistularidae |
| *Rypticus bicolour* | Mottled soapfish | Grammistidae |
| *Anisotremus interruptus* | Burrito grunt* | Haemulidae |
| *Haemulon steindachneri* | Latin grunt | Haemulidae |
| *Haemulon maculicauda* | Spottail grunt | Haemulidae |
| *Sargocentron suborbitalis* | Tinsel squirrelfish | Holocentridae |
| *Halichoeres notospilus* | Banded wrasse | Labridae |
| *Halichoeres dispilus* | Chameleon wrasse | Labridae |
| *Thalassoma lucasanum* | Cortez rainbow wrasse | Labridae |
| *Bodianus diplotaenia* | Mexican hogfish | Labridae |
| *Halichoeres nicholsi* | Spinster wrasse | Labridae |
| *Halichoeres chierchiae* | Wounded wrasse | Labridae |
| *Hoplopagrus guentherii* | Barred Pargo** | Lutjanidae |
| *Lutjanus inermis* | Golden snapper* | Lutjanidae |
| *Lutjanus guttatus* | Spotted rose snapper | Lutjanidae |
| *Lutjanus argentiventris* | Yellow snapper* | Lutjanidae |
| *Mugil curema* | White Mullet** | Mugilidae |
| *Pomacanthus zonipectus* | Cortez angelfish | Pomacanthidae |
| *Holacanthus passer* | King angelfish | Pomacanthidae |
| *Stegastes acapulcoensis* | Acapulco gregory | Pomacentridae |
| *Stegastes flavilatus* | Beaubrummel gregory | Pomacentridae |
| *Abudefduf concolor* | Pacific night-sergeant | Pomacentridae |
| *Abudefduf troschelii* | Panamic sergeant-major | Pomacentridae |
| *Chromis atrilobata* | Scissortail chromis | Pomacentridae |
| *Scarus ghobban* | Bluechin parrotfish | Scaridae |
| *Serranus psittacinus* | Banded Serrano | Seranidae |
| *Paranthias colonus* | Pacific creolefish | Seranidae |
| *Epinephelus panamensis* | Panamic graysby | Seranidae |
| *Epinephelus labriformis* | Flag Cabrilla/Starry Grouper | Serranidae |
| *Epinephelus analogus* | Spotted Cabrilla** | Serranidae |
| *Canthigaster punctatissima* | Spotted sharpnose pufferfish | Tetradontidae |
| *Arothron hispidus* | Whitespotted pufferfish | Tetradontidae |

* = those fish that were not found during 2003 surveys at the sites. **= those fish that were not found during 2003 surveys at all.

## APPENDIX 3:


PCA plot for Las Perlas
0-12700Hz
Fac1 vs Fac2
Fac2
Fac1
3.00
2.00
1.00
0.00
-1.00
-2.00
-3.00
-4.00
-3.00
-2.00
-1.00
0.00
2.00
3.00
31
21
9
7
1
30
29
19
55
22
10