A STUDY OF THE REEF FISH COMMUNITIES OF LAS PERLAS ARCHIPELAGO, PANAMA

by

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ABSTRACT

The reef-associated fish communities of Las Perlas Archipelago on the Pacific coast of Panama have been little studied, and the factors governing their structure are poorly known. In this study 39 of the reefs were surveyed using an underwater visual census technique. In total 76 species of diurnally active, non-cryptic, reef-associated fish were recorded, belonging to 25 families. There was an average density across all the reefs of 160 fish per 100m³, over 90% of which were in the families Labridae, Pomacentridae or Haemulidae. Over 94% of the fish were less than 20cm in length.

The quantitative data was analysed using Detrended Correspondence Analysis (DECORANA) and compared with the environmental variables of benthic cover, latitude and longitude. The patterns found correlated with the number of habitat types present and with latitude, explaining 25.6% of the data and 15.9% of the data respectively. There was found to be a greater abundance of fish in the west of the archipelago and with a greater amount of bottom types. The fish community structure was shown to be most different from other sites where high amounts of dead coral were present.

The trophic structure of the fish communities varied with a greater amount of planktivores and invertivores overall. A greater abundance of planktivores, invertivores and generalist feeders existed in the north and the west, whilst there was greater numbers of piscivores in the south. Piscivores were the only group to have a significant correlation with the major bottom types, having a negative correlation with percentage cover of *Pocillopora* species.

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Dedication

To Alasdair and his love of the ocean which eventually claimed him as its own.
For being my inspiration and for giving me the confidence to chase my dreams
- you will always be in my heart.

INTRODUCTION

Coral reefs are shaped by the organisms that live there, the prevailing environmental conditions and recruitment processes. They are one of the most productive and diverse habitats, with fish biodiversity as a better indicator of overall species diversity than coral biodiversity (Beger *et al*, 2003). The reef fish assemblages of Las Perlas Archipelago in the Gulf of Panama (Figures 1.1 and 1.2) are under increasing pressure from human activities such as fisheries, tourism and land based pollution. The upwelling season makes the archipelago very productive in terms of fisheries, however this, in addition to tides, sedimentation, El Nino Southern Oscillation and corallivory limit coral reef development. These reefs are simple, small enough to be studied as a unit, yet diverse. They have a wide range of interactions therefore they are an interesting object for investigations, and yet fish communities on these reefs have been poorly studied.

Figure 1.1 Las Perlas Archipelago, Gulf of Panama, Pacific.

1.1 Aims

The aim of this study is to investigate the spatial patterns of reef fish diversity and to add to the knowledge of the reef fish communities of Las Perlas Archipelago. The study will assess the differences between diversity, abundance and trophic structure of the diurnally active, non-cryptic, reef-associated fish communities of Las Perlas. Any distinct fish assemblages in the area will be identified and attempts will be made to determine some of the biotic and abiotic factors responsible for these differences.

It is expected due to the differences in oceanographic conditions (discussed in section 1.2) within the archipelago that there will be differences in the reef fish communities from the North to South and possibly the West to East of the archipelago. It is also expected that the fish will reflect changes in their habitat, due to differences in the coral composition that provide resources in terms of food and shelter. It is anticipated that different fish will respond in different ways to the variation in their environment due to different resource use and trophic groups.

The study will help to form a pre-development baseline before tourism increases further. However the well-established fisheries in the area prevent it from being an absolute baseline, as the area is no longer a pristine environment. A baseline is important in the establishment and long-term management of the proposed marine protected area in Las Perlas. This study will also help to extend the overall information available on the relationships between reef fish and their habitats.

1.2 Las Perlas Archipelago

The Isthmus of Panama separating the Pacific and the Atlantic is an active tectonic region approximately 3.5million years old (Coates *et al*, 1992). Las Perlas Archipelago is of volcanic origin and is located in the Bay of Panama approximately 70km South East of Panama City and 31km offshore of the main coast of Panama, inside the 50m isobath. It is comprised of 252 basaltic rock islands and islets, mainly uninhabited.

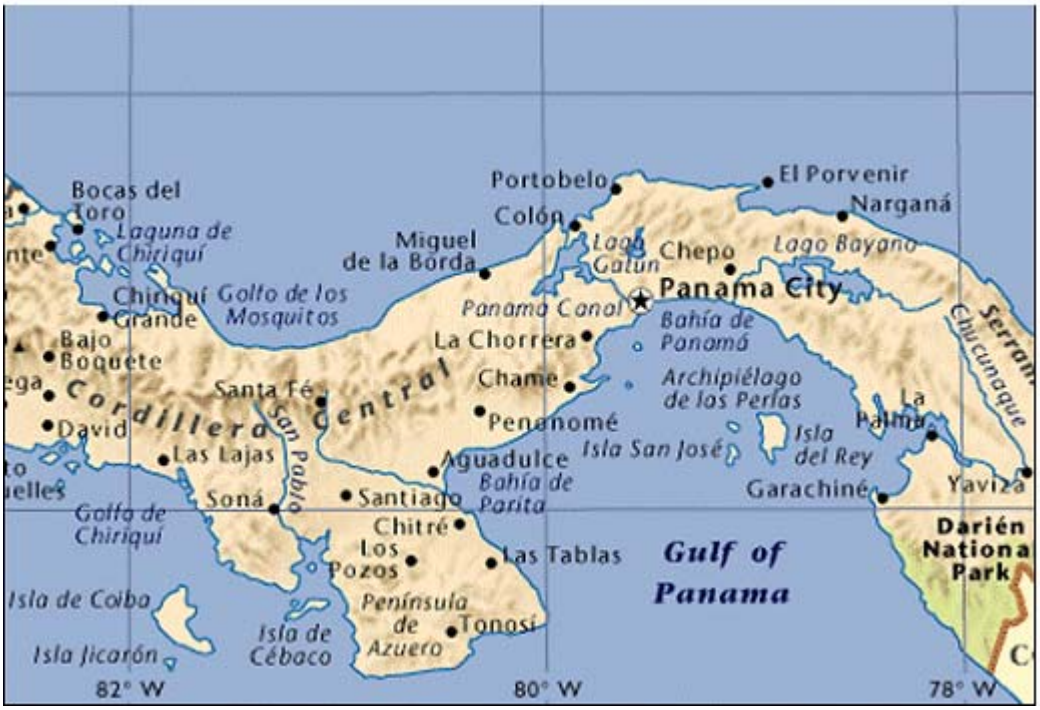

Figure 1.2: The location of Las Perlas Archipelago (Archipiélago de las Perlas) in the Gulf of Panama. The Gulf of Chiriqui (Golfo de Chiriquí) is to the West (www.sea007.com).

The Tropical Eastern Pacific is more seasonal than the Caribbean; the seawater is more turbid, less saline and slightly cooler (D'Croz and Robertson, 1997). It also has a larger watershed, greater human population and a shallow continental shelf swept by strong tides, therefore making it nutrient rich. During the dry season, between January and March, the Bay of Panama, unlike the Gulf of Chiriqui to the west (Figure 1.2), is an upwelling area due to the strong offshore North Equatorial Current of the central Pacific. Water moves into the Gulf of Panama from the southeast and exits toward the south/ southwest moving in a counter-clockwise gyre. During the dry season the south-moving currents are strong (Glynn and Maté, 1996), bringing cold nutrient rich water to the surface. This results in phytoplankton blooms, which can reduce light penetration and in turn cause high levels of zooplankton forming the basis of Las Perlas' rich fisheries, with many birds and predators feeding on baitfish, mainly anchoveta (Glynn and Maté, 1996). The seawater has an annual temperature fluctuation of to 15ºC due to this dry season upwelling (D'Croz and Robertson, 1997), with sea surface temperature dropping to below 20ºC during the upwelling. Surface salinity can drop from 30-35‰ in the dry season to 24-30‰ in the wet season (Glynn and Maté, 1996). The tidal range is quite large with tidal ranges of approximately 6m in the Gulf of Panama (Glynn and

Maté, 1996). Shallow areas of the reef flats can be exposed on medium to extreme low tides.

The El Nino Southern Oscillation (ENSO) has a profound impact in this area and causes the sea surface temperature to rise as the eastward flowing North Equatorial Counter Current speeds up, the upwelling source of cold water is cut off and the thermocline deepens. This has a significant influence on the area's coral reefs including those in Las Perlas. Extensive coral bleaching occurred during the 1982-83 ENSO when sea surface temperature rose dramatically, with mean coral mortality in the Gulf of Panama reported at approximately 85%, and several coral species suffering from local extinctions (Glynn and de Weerdt, 1991; Glynn, 1984; Glynn *et al*, 1988). The reduced upwelling due to the ENSO causes nutrient depletion in the photic zone, limiting phytoplankton, with ramifications up the food chain. During the 1982-83 ENSO birds and mammals died in large numbers (Glynn, 1988a).

There are many factors limiting coral reefs in the Bay of Panama, including high nutrients, low light penetration and high temperature and salinity variation. Also there is a high growth of macroalgae and abundance of benthic organisms that compete with coral for space, increased phosphorous levels, which may inhibit calcification in corals and a large amount of plankton that can support bioeroding organisms that limit massive coral species (Glynn and Maté, 1996). Upwelling limits the growth of corals, and subsequently growth is slower in the upwelling Gulf of Panama than in the Gulf of Chiriqui (Glynn, 1977). Typically the reefs in this area are small, shallow, patch reefs, mainly restricted to less than 10m depth, they are species-poor and patchily distributed (Glynn and Maté, 1996). The number of reef building corals on the Pacific coast of Panama is 23 (Glynn, 1996) and those around Las Perlas are nearly monotypic stands of *Pocillopora* species (80-85% live coral cover in shallow 0-6m depth), with massive corals such as *Pavona* species forming a patchy cover (approximately 18% cover) in deeper areas (6-10m depth) (Wellington, 1982).

Las Perlas Archipelago has the largest aggregations of coral reefs in the Gulf of Panama (Glynn and Maté, 1996). The oldest Carbon^{14} dated corals drilled from the Gulf of Panama are about 4,500years old and are developed on tuffaceous sandstones and calcareous sediments (Glynn and Macintyre, 1977). Fewer coral reefs, with a lower

vertical build-up and lower species diversity are present than in the non-upwelling Gulf of Chiriqui (Glynn and Maté, 1996). Some species such as the Crown of Thorns Starfish and firecorals can be found in the Gulf of Chiriqui but are absent in the Gulf of Panama. Coral reefs in the Gulf of Panama are more abundant and attain greater dimensions on the Northern and Eastern sides of the islands, these are the shores facing away from the full effect of upwelling currents (Glynn and Stewart, 1973).

The largest island of the Archipelago is Isla Del Rey, which has few reefs possibly due to the large watershed on this island and subsequent run off. The largest reef in Las Perlas Archipelago is off the northeast of Saboga Island, which has a 5.6m maximum vertical build up (Glynn and Macintyre, 1977). Contadora is one of the few populated islands in Las Perlas and contains the majority of hotels in the archipelago. It has many small patch reefs on the north coast, including the second largest reef in Las Perlas.

There are two principal reef habitats in Las Perlas Archipelago, which will form part of this study, rocky shores with a coral community growing on top and coral reefs with a *Pocillopora* framework. These different reef types are likely to support different fish communities.

1.3 Coral Reef Fish Communities

Reef fish are fish that live all their post-recruitment lives in close association with their habitat (Bellwood, 1988; Choat and Bellwood, 1991), they are specialised in morphology, colour, behaviour and life cycles and are one of the most complex and variable communities in nature (Sale, 1991). Most reef fish in the Tropical Eastern Pacific are endemic to the area and exhibit a great variety in their patterns of distribution within the region (Allen and Robertson, 1994). Many studies have been done on reef fish communities throughout the world in order to identify processes important in structuring them, though little quantitative abundance data for tropical eastern Pacific reef fish exists. Recruitment and post-recruitment processes control reef fish distribution. Many reef fish have only been described taxonomically and little information is available on their biology, therefore making it difficult to understand the processes shaping their communities. Studies have taken place to try to find the main

causes of variation in fish assemblages these have had conflicting results. Correlations between community or species distributions and environmental gradients may be useful in predicting presence or absence of fish in an area, which would be useful for management and for extrapolation over large areas to reduce field sampling requirements.

1.3.1 Recruitment Processes

Reef fish have complex lifecycles in which larvae and often eggs are pelagic (Leis, 1991) and larval dispersion and success is important in determining which fish exist in an area. The distribution of fishes can be influenced by oceanographic processes such as currents and the physical and chemical conditions of a water body, which can restrict larval supply to reefs. Fish larvae may exhibit habitat selection, which is important in determining community composition (Williams, 1991). Some reef fish are able to migrate over many kilometres, however others are not and are dependent upon larval dispersion to colonise reefs. Larvae increase their fitness by being able to find a suitable habitat upon settlement. Lincoln Smith *et al* (1991) found that the abundance of settlers was highly variable within reefs, over time and space.

1.3.2 Post-Recruitment Processes: Biological

Various habitat attributes such as substrate diversity and live coral cover have been correlated with reef fish abundance, diversity and distribution. Correlations have been found between fishes, and coral cover, some positive and some negative (Bellwood and Hughes, 2001; Russ and Alcala, 1989; Carpenter *et al*, 1981; Bell and Galzin, 1984; Sano *et al*, 1984a; Dulvy *et al*, 1995; Bohnsack *et al*, 1992), whilst other studies, such as Beger *et al*, (2003), found that there was not a close correlation. Bell and Galzin, (1984) found a highly significant positive relationship with changes in live coral cover, in sites of similar structural complexity. A change as small as 0% to <2% producing significant increases in the number of species and number of individuals of fish; many of the species were only found where there was live cover. Doherty *et al*, (1997) observed that reductions in coral cover only affected recruitment of reef fish once the coral structure was negligible (<6%). Once the coral was growing again recruitment

levels returned, suggesting that fish communities are resilient with only a weak dependence on coral cover other than by a few coral specialists.

In some instances, with some fish species, dead coral can be as important as live coral. Some species have been shown to increase with coral rubble (Russ and Alcala, 1989); this could be where the coral is an important source of shelter and not needed for food. There is the possibility that the nature of the prey alters with changes in live coral cover. Some herbivores were found to increase with live coral cover and not with, as was expected, nitrate or phosphate concentration. Also, some planktivorous fish were in greater numbers over live coral cover and were not correlated with zooplankton, in a study by Bell and Galzin (1984). Ohman and Rajasuriya (1998) however found that coral feeders did correlate with live coral cover.

The diversity or abundance of reef fishes has been found to vary with habitat complexity and relief, for example Lirman (1999) found that where there was a high topography, a different species abundance and richness occurred to where there was low topography. Luckhurst and Luckhurst (1978) found that a correlation with substrate rugosity depended upon the size of the fish and is thought to be due to the need for shelter and hiding spaces, for example Pomacentrid species use branching corals for protection, increased complexity provides more diverse shelter. Where single species coral stands exist there is not the same diversity in shelter sites therefore this will be reflected in the lower diversity of fish (Talbot, 1965). Ohman (1998) found that on coral reefs fish diversity was not influenced by live coral cover or substrate composition diversity.

Space is a limiting factor, possibly of more importance than food or predation, it is needed for hunting, hiding, courting and nesting as well as sheltering from physical stress. In reef fish if the difference in length of the fish is larger than 12% then the niches are sufficiently different to eliminate direct competition for size related resources, such as shelter (Lavett-Smith, 1978).

Correlations between structural complexity and abundance are less consistent than between structural complexity and species diversity (Ohman, 1998). This is possibly because studies are of different taxa or functional groups and use a variety of methods

for measuring structural complexity or counting fish. Differences also occur due to ecological differences between study sites and other influences on fish communities. Structural complexity has been shown to have a positive influence on fish species diversity (Risk, 1972; Luckhurst and Luckhurst, 1978; Carpenter *et al*, 1981; McCormick, 1994; McClanahan, 1994) and biomass (Carpenter *et al*, 1981; Grigg, 1994) yet the influence on total fish abundance is less consistent possibly due to many study areas containing large amounts of fish such as planktivores, which are less influenced by substrate and have a more homogenous distribution (Ohman and Rajasuriya, 1998).

Habitat structure determines the quality and quantity of various resources that fish depend upon and may affect the outcome of biological interactions for example food and predation may be influenced by the substrate type and habitat complexity. The substrate can modify the availability of resources, such as by providing a suitable habitat for prey species. Different fish and different aged cohorts of fish may respond to different components of the habitat because they have different dietary or spatial needs. This may depend upon the fish's morphology, body size, home range, behaviour, social structure, sensory limitations, and learning ability (Wainwright and Richard, 1995; Ebersole, 1980; Bruggeman *et al*, 1994a, b; Forrester, 1991; Perry and Pianka, 1997; Marcotte and Browman, 1986). Habitat complexity can partition the substrate into diverse microhabitats (Garcia-Charton and Perez- Ruzafa, 2001) therefore allowing more fish species. Ecological theory predicts that species diversity increase with increased habitat complexity or diversity and a greater number of habitat types (Ricklefs, 1973; Roughgarden, 1996), this has been shown to be the case in a study by Boecklen (1986).

More species and individuals have been found on ramose coral heads than on glomerate coral heads, in a study in the Marshall Islands by Hiatt and Strasburg (1960), probably due to a lack of hiding spaces on glomerate heads. Also the increased surface area of ramose heads gives more area for colonisation by algae and invertebrates and therefore increased food. Lirman (1999) found that the branching coral *Acropora palmata* can have a major influence on abundance and diversity of fish. Areas dominated with live *A.palmata* had more Pomacentrids, Haemulids and Lutjanidse, with Haemulids and Lutjanids almost exclusively around live or dead *A.palmata* due to its high topography.

In the same study Scarids, Labrids and Acanthurids were abundant where there was low topography and high macroalgal cover. Glynn and Maté (1996) report large aggregations of reef fish around patches of *Pavona clavus* and *Porites lobata* in Las Perlas with *Scarus ghobban* and *S.perrico* often feeding on turf algae around these.

Garcia-Charton and Perez- Ruzafa (2001) found that the most frequent species in their study showed a significant linear relationship with complexity or heterogeneity of the habitat or both. They found that habitat structure accounts for an important portion of the variability in fish assemblage structure. With habitat complexity favouring more species and greater abundance. Ohman and Rajasuriya (1998) were able to show that the multivariate pattern between habitat composition and fish community composition were correlated. The diversity of the substrate has been shown to correlate positively with fish species diversity and abundance (McCormick, 1994) although Risk (1972) found no correlation. Studies showing the relationship between fish and structural complexity have taken place in the Caribbean, South-East Asia, Great Barrier Reef and E. Africa with none apparently so far in the tropical Eastern Pacific. The strength of this correlation is thought to vary depending upon the reef type for example a study by Ohman and Rajasuriya (1998) shows that there is a strong correlation with species richness and diversity on rocky reefs but not on coral reefs in Sri Lanka. A different set of ecological processes could influence the local fish communities on rocky reefs compared with coral reefs. Possibly there could be a greater variability in the rocky reef allowing more microhabitats.

Not all species respond to all gradients in habitat structure and species may partition resources at some scales and not others. Eagle *et al* (2001) found a strong association between angelfish and habitats at some scales but not at others. Many species are not specific to habitat having a wide home range and may be associated with substratum but not confined to a specific patch (Lavett-Smith, 1978). Many have a flexible diet and resource use, therefore making them more able to adapt, conflicting with competition theory; that co-existence in diverse assemblages is from partitioning of resources (Pianka, 1966; MacArthur, 1969; Colwell, 1973). Ohman and Rajasuriya (1998) found that total abundance did not relate to any one habitat parameter but abundance of some species, families and trophic groups did, with these correlations due to food or shelter. Predictions regarding reef fishes relationship to habitat should be restricted to those

species strongly associated with the habitat (Sale, 1991; Sale and Douglas, 1984). Sale *et al* (1994) and Jones and Syms (1998) claim that failure to detect a relationship between fish and habitat does not mean that the habitat is not important in shaping the fish community, only that it is not important within the scale observed.

Fishes' relationships with each other and their habitat through trophic interactions are important; with high biodiversity it is often assumed that there is high functional redundancy and that an ecosystem is stable. However Bellwood *et al* (2003) found that the over-fishing of just one species had a high impact on the whole ecosystem despite high biodiversity. Reef fish are influenced by their habitat but also modify their habitat, therefore the relationship between the two is complex. Behaviour of the fish is an important factor and may vary over time- they may vary their habitat depending upon their age (Forrester, 1991; McCormick, 1998), hunger (Wootton, 1990), social rank (Forrester, 1991), reproductive state and the sex of the fish (Goldschmid and Kotrschal, 1981). The size of the home range that is defended by the fish may determine the density of individuals; some fish have large home ranges and others small while some of the home ranges may be mobile. By territorial behaviour smaller fish such as damselfish could inhibit the growth and numbers of larger fish (Lavett-Smith, 1978). They may also respond to environmental changes in different ways with changes in abundance, species richness, diversity, evenness or changes in species composition.

1.3.3 Post-Recruitment Processes: Physical

Some studies show the main source of variation to be the biotope (Aguilar *et al*, 2004), whilst other studies show depth to be the most important factor (Bouchon-Navaro *et al*, 1997) and others show water movement to be more important (McGehee, 1994). A high intercorrelation between the various habitat attributes, such as depth with water movement, sometimes prevents the determination of the exact effect of each factor on the fish population (Bell and Galzin, 1984; Lirman, 1999). It is thought that species segregate along more dimensions as the number of species increases (Levins, 1968).

Coral reefs contain a large number of species that may be locally rare even though they have a large geographical distribution. The type of fish assemblage present can depend upon the geographic location and type of reef; tropical reefs will be different to

temperate reefs and those separated by large water masses will have different larval supply and thus different species. Habitat breadth or niche width could account for some of the variation in the distribution and abundance of species (Falcon, 1996). Some species may increase as a function of area of the reef (Anderson *et al*, 1981; Williams, 1991); Donaldson (1996) found a correlation between locality size and fish species diversity. Adjacent reefs could have different flora and fauna, whilst some species may be associated with the same type of habitat in widely separate geographic areas (Waldner and Robertson, 1980).

There is predicted to be lower species diversity due to lower species equilibrium around small islands compared to large ones or to continental masses (MacArthur and Wilson, 1967). The distance from large islands or continental masses can also make a difference. Distance to land may influence fish populations depending upon terrestrial influences (Letourneur *et al*, 1998). Therefore, results can only be applied to the region where the study was conducted due to these geographic differences (Ebeling and Hixon, 1991). The patchiness of habitats in coral reefs allows for different habitat units at various scales with different fish associating with the different sized units from centimetres to kilometres.

Another physical factor influencing fish distribution is water motion (Hilomen and Gomez, 1988) and exposure; unless sufficient shelter exists some fish will not be found in strong currents and wave exposed areas, whilst other prefer these areas. A study by McGehee (1994) in Puerto Rico found that whilst water movement, depth and substrate do correlate, that water movement was the environmental factor most associated with reef fish distribution.

The distribution of fish can also change due to the state of the tide and the time of day (Holbrook *et al*, 1994). Connell and Kingsford (1998) found that there was little difference due to the state of the tide on grouper and snapper though this may not be the case for all fish. Time of day is important; as not all fish are diurnally active, some are nocturnal and others are crepuscular, therefore the time at which surveys take place is important. Some fish may also be migratory, therefore affected by the time of the year. They may also have different levels of abundance throughout the year, due to events such as recent recruitment, ontogenetic changes and mating activity, however Arreola-

Robles and Elorduy-Garay (2002) showed seasons of the year to have little influence on reef fish assemblages in the Gulf of California.

Many other factors can have an affect on fish species distribution on coral reefs such as water quality and depth. A study by Ohman and Rajasuriya (1998) shows that depth can influence reef fish in different ways depending upon the reef type. It can be difficult to separate a functional community from a simple random assemblage of individual species merely responding to physical factors in their environment (Lavett-Smith, 1978).

1.3.4 Post-Recruitment Factors: Disturbance

Disturbance may influence reef fish distribution and is often random, different responses to disturbance have been described. Little is known about the affects of disturbances on fish communities and the magnitude of the effect depends upon the group of fish and the type and intensity of the disturbance (Kaufman, 1983; Wellington and Victor, 1985; Williams, 1986; Robertson, 1991; McKenna, 1997). If reef fish communities are primarily influenced by competition and niche diversification then disturbance to habitats may have extreme effects (Jones and Syms, 1998) if they have overlapping habitats then it may have less effect unless the overall amount of space reduced. The intermediate disturbance model (Connell, 1978) states that at low disturbance, frequency or level, there are few dominant organisms, at high disturbance only a few adventitious species survive and at intermediate levels there is the highest diversity.

Disturbances can be beneficial for example hurricanes can remove sediment and can also be a benefit to rubble-associated species. Rubble associated species were shown to increase after a hurricane in Jamaica; there was also an increase in predators on motile soft prey (Kaufman, 1983). Bleaching events can cause an increase in certain fish such as Acanthurids, found by Robertson (1991) in a study in Panama. Whilst some species are not affected by bleaching, for example no consistent decrease in the corallivore *Arothron meleagris* was found (Guzman and Robertson, 1989) and no affect on the damselfish *Stegastes acapulcoensis* (Wellington and Victor, 1985). Las Perlas is

subjected to the disturbance of El Nino that may have an extreme impact on the fish communities.

Distribution patterns related to environmental factors have been described at various scales for whole assemblages as well as for trophic groups. There are lots of factors affecting fish community composition, therefore a single factor approach is oversimplified (Caley *et al*, 1996) and there is the need instead to assess the relative importance of the various processes together.

1.4 Reef Fish Trophic and Mobility Guilds

Different fish can be influenced in different ways by environmental factors, habitat, competition and disturbance, the ways in which they respond can be due to their mobility or due to their trophic level. A study by Arreola-Robles and Elorduy-Garay (2002) showed that the food habits of fishes were different between reefs in the Gulf of California, more planktivorous fish were at exposed sites and more herbivorous fish were at sheltered reefs. Therefore they were influenced due to their trophic level by the availability of food. Different areas in the same reef can be dominated by different fish guilds. Reef fishes are often opportunistic in their feeding with generalists thought to be unlikely to be sensitive to small or gradual changes in local environment conditions and are likely to occur in more locations.

Friedlander and Parrish (1998) found that where there was a more complex substrate there was more variability in complete assemblages, trophic guilds and mobility guilds. They separated fish into trophic guilds of herbivores, planktivores, piscivores, obligate corallivores, feeders on mobile benthic invertebrates and feeders on sessile invertebrates. They also separated them into mobility guilds of residents, transients, semi-vagile type I (moving tens of metres per day) and semi-vagile type II (moving hundreds of metres per day). Friedlander and Parrish (1998) found that the biomass of the residents and transients was low compared to both groups of semi-vagile species possibly due to the difficulties in counting these fish. Some families, such as Serranids have a relatively confined movement except when spawning (Parrish, 1987) when they aggregate at specific sites (Johannes, 1978). Other species such as some Carangids are reef associated as juveniles, but wider ranging as adults.

Smaller more sedentary herbivores may correlate with variation in the reefs (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984) such as with hole volume and rugosity, though this may not be the case with larger more mobile species, less information is available on these. Ohman and Rajasuriya (1998) showed herbivores to relate positively with coral cover and negatively with depth. Ohman (1998) showed herbivores to be more common where there were more turf algae and planktivores to have similar quantities in different reef types but with different species. Transient species were mostly piscivores or planktivores in a study by Friedlander and Parrish (1998) and they showed limited correlations with the habitat, though planktivores have been shown to correlate with depth. Coral reef fish communities are dominated numerically and in biomass by planktivores (Williams and Hatcher, 1983; Russ 1984c) therefore they can benefit from nutrient input from outside the reef.

Large predators can aggregate at small spatial scales, associated with areas or habitats of the reef though the influence of coral type on them is rarely discussed (Russ, 1991). Connell and Kingsford (1998) suggested that live sea beds such as coral are important for fisheries of Serranids and Lutjanids perhaps because there is more food and because of the structural heterogeneity.

Labrids are a dominant group of benthic carnivores on coral reefs (Williams and Hatcher, 1983); they can be generalists, feeding on a wide range of invertebrates, or specialists. Usually Labrids have large home ranges encompassing various habitat features (Roberts and Ormond, 1987); therefore it is unlikely they would have a link with the habitat at a small scale. Mobile invertebrate feeders and sessile invertebrate feeders, however, have been found to have a positive relationship with the size of holes and piscivores have been found to correlate with surface rugosity (Friedlander and Parrish, 1998).

The Scaridae are the only family of fish that consistently remove reef carbonate when feeding. Some fish such as the Chaetodontidae are coral feeders (Hobson, 1974); corallivores have been found to be positively associated with hole volume and coral cover (Friedlander and Parrish, 1998) and are inversely related to macroalgae. Ohman and Rajasuriya (1998) and Ohman (1998) found that coral feeders correlate with live coral cover whilst they were practically absent on sandstone reefs studied. Some fish

such as corallivores can profoundly affect coral reef structure (Glynn, 1976; Kaufman, 1977). *Arothron meleagris* and *A.hispidus* in the Gulf of Panama graze on adult corals such as *Pocillopora* (Hiatt and Strasburg, 1960; Glynn *et al*, 1972). *Sufflamen verres* and *Balistes polylepis* scrape the massive coral *Porites* and feed on the live coral tissues whilst *Pseudobalistes naufragium* breaks up massive corals to feed on bivalves living within them. The Pomacentrid, *Stegastes acapulcoensis,* kills coral especially the massive species such as *Pavona gigantean* in order to defend an algal mat, which it uses for food and nesting, against other herbivores and omnivores (Wellington, 1982). This enhances space monopolisation by Pocilloporids because Pomacentrids can only kill the tips of the *Pocillopora*. Less Pomacentrids occur deeper because Scaridae and Tetraodontidae graze the *Pocillopora* reducing the shelter available for the *S.acapulcoensis* (Wellington, 1982).

1.5 Human Impacts on Reef Fish Communities

There are many threats to reefs worldwide; these include over fishing, beach and coral mining, destructive fishing methods, pollution (waste, sewage, fertilisers, toxins and biocides) coastal reclamation, channel dredging, coastal development and recreational activities. There are also natural threats to reefs such as cyclones, cold-water fish kills, coral bleaching, El Nino and disease. Some natural threats are thought to be exacerbated by human activities such as El Nino and the invasion of alien species. Different threats have different impacts and magnitudes.

In order to protect reefs there is a need for education, research, legislation, available information, designation of Marine Protected Areas (MPAs), and development of management schemes with government, private and public involvement. These can include fisheries management, MPA management, and integrated coastal management. Baselines need to be established and monitoring programmes developed. Issues such as poverty and the economic value of the reefs need to be taken into consideration. The natural fluctuations need to be understood in order to assess the impacts of anthropogenic changes.

Fishing is a threat to reefs worldwide both due to over fishing with depletion of stocks altering fish communities and due to destructive fishing methods such as dynamite

fishing, cyanide fishing and trawling which damage the habitat, reducing the structural heterogeneity and damaging organisms other than the target organism. Fishing is the most important exploitative activity on coral reefs (Russ and Alcala, 1989). Smith (1978) estimated the fisheries potential of coral reefs worldwide at $6x10^6$ tonnes/year; in 1983 the actual yield from tropical reef areas was much less at $0.48x10^6$ tonnes (Longhurst and Pauly, 1987). In Las Perlas Archipelago there are productive fisheries at a commercial, artisanal and subsistence level. There has been little research into the fisheries in the area and little is known about them and their effects on the reefs.

Selective over fishing can alter the species composition by increasing the dominance and diversity of smaller species (Baisre, 2000). Catch rates decline in areas of heavy fishing and the relative abundance of large predatory fish is reduced (Bohnsack, 1982; Russ, 1985) along with the average size of individuals of the target species. Russ and Alcala (1989) found that the largest direct effect of intense fishing was a decrease in planktivorous fish therefore changing the trophic structure.

Removal of the top predator on reefs may not, as expected, increase the prey species, as many fish are opportunists, therefore removal of one predator may cause others to switch their prey (Jennings *et al*, 1995). Competition and predation are a basis for multi-species fishery models for management but they may not be applicable on coral reefs as there are other controls on the population (Doherty and Williams, 1988). Jennings *et al* (1995) found an inverse relationship between fishing intensity and the biomass of several target species using Underwater Visual Census techniques and suggested that increased effort in an already fished area would have less impact than starting to fish an un-fished system.

When fishing began in an area that had been for a long time a reserve, in the Philippines, there was a decrease in abundance of target species, with changes in the community structure and a decrease in species richness and density. There was a decrease in small schooling planktivores and benthic feeding Chaetodonids and an increase in small Labrids and large Scarids related to the effectiveness of fishing equipment on planktivorous and herbivorous fish and a degradation of the benthic habitat.

Many reefs of the world have suffered due to the development of tourism in coastal areas; this increases pressure on the reefs by increasing pollution, runoff from developments and pressure from recreation such as scuba diving and boat moorings. Las Perlas Archipelago is underdeveloped for tourism, with hotel developments concentrated on Contadora and a hotel on San José. However this is set to change as tourism in Central America increases.

1.5.1 Marine Nature Reserves

The designation of a Marine Nature Reserve (MNR) has socio-economic, political and practical problems; there is often wide opposition. There are many reasons for designation, often primarily for the protection of resources such as fisheries into the future. They can be designated to maintain and protect biodiversity and genetic resources by conservation of habitats and biota and the protection of rare and important species, although maximising biodiversity has not played a major role in site selection (Beger *et al*, 2003). Marine species are more widely distributed with greater and more widely spread genetic variability than terrestrial species. There is the possibility of the future use of indicator groups to identify whether an area should be protected, so it is important to know which species exist there. It may be important to maintain small local populations even if the species is common elsewhere; these can be important genetic reservoirs, peripheral populations are also important. MNRs need to take into account both species and functional roles of those species (Purvis and Hector, 2000; Paine, 2002, Vanni *et al*, 2002).

If protected areas for conserving fish stocks are to be effective they must include diverse habitats to accommodate a wide range of fish species. Information on the distribution of fish stocks is important (Friedlander and Parrish, 1998) for the designation and management of reserves. The protection of spawning or nursery areas is also important for sustainable fisheries. The closing of fisheries is difficult but can be beneficial, for example a reserve in the Philippines was closed to fishing for 10years and in that time catches in a nearby fishery tripled but decreased again when the reserve reopened (Russ, 1987). Partial marine reserves may have little impact on the abundance or size of some fished species (Denny and Babcock, 2004). Kenchington (1992) has

shown MNRs to be particularly effective for species with restricted adult and larval distribution, and for those that require specific habitats during their life cycle. Some fish such as Scarids move large distances therefore small marine reserves in heavily fished areas have little positive effect on these fish stocks (Russ and Alcala, 1998).

MNRs draw attention to the problems faced by the marine environment. They can be used to promote research, education/training, and provide baselines for monitoring areas. They are used to control man's activities such as tourism and recreation, promotion of sustainable development and they may be used for the remediation of exploited areas. Coastal protection against erosion can also be an important reason to designate a MNR. Human values have an impact on the designation of these areas such as the aesthetic, historical or cultural value of an area; often MNRs are established for political reasons to fulfil international commitments or to gain status.

There are many problems in the management of MNRs, it is difficult to restrict activities and local concerns need to be linked in with national and international conservation measures. MNRs often increase visitor pressure but do allow zoning plans to reduce the impacts of this. MNRs may not help species that do not confine to specific areas, migratory species or plankton for example. Also they do not protect against widespread problems such as global warming and some pollutants.

There is the possibility of the designation of a marine protected area encompassing Las Perlas Archipelago, and with growing tourism and increased pressure from fisheries on the area this would be a good way to monitor and control activities and ensure that development is sustainable. Fish can be useful organisms for measuring environmental degradation (Fausch *et al*, 1990), therefore there is a need to describe the ecological structure and function of the reef fish assemblages of Las Perlas Archipelago in order to monitor the effects of future disturbances related to development on these populations. Data on community structure is needed to look at the magnitude and effects of impacts, including precise and repeatable estimates on length frequency and abundance of fish. This when linked with even a basic knowledge of the biology of a species may allow estimates such as recruitment and rates of recovery.

Coral reef ecosystems have economic, social and cultural importance to nations and individuals with reef fish as an important resource, reefs are important for food production, tourism, recreation, aesthetics and shoreline protection. There is inadequate information, so far, to predict the response of fish to the pressures on coral reefs. The potential value of reefs to humans can be shown in a simple example stated by Gomez (1997) for the Red Sea reefs which form a popular tourist attraction: Egyptian authorities received a $23.5million insurance payout for damage by a luxury liner to 2,000m² of coral reefs. Therefore, making these particular reefs worth $11,750/m² this value was calculated in 1996 and would be significantly higher now.

1.6 Methods of Studying Reef Fish Communities

Obtaining fisheries and biological data in many coral reef areas is difficult, coral reef fish are speciose, with a patchy distribution and are found in heterogeneous, diverse habitats. Their widespread occurrence makes it hard to determine the optimal or standard survey methods (Samoilys and Carlos, 2000). There are two basic methods of estimating the abundance of fishes on coral reefs: destructive, by poisoning or the use of explosives, and non-destructive. The most frequently used non-destructive method is the visual survey, which is relatively rapid and inexpensive and can be used for a broad spectrum of fish species.

Underwater Visual Census (UVC) techniques were first used by Brock (1954) they involve estimates of numbers of fish or numbers of species of fish, along with length estimations. They can provide rapid estimates of the relative abundance, biomass and length/frequency distributions. They may not give accurate numbers of individuals present but can be used relatively to establish patterns. For general surveys timed transects are often used (Williams, 1982, 1983; Russ 1984a, b). Other visual methods include stationary census (Thresher and Gunn, 1986) or for presence and absence data a roving diver method is used. Some surveys to find species richness survey until no additional species are recorded for 5minutes (Molles, 1978). Individual counts can address specific questions such as habitat related differences.

1.6.1 Underwater Visual Census Techniques

There are many disadvantages to the visual survey methods. Observers need to be trained and must have experience of identifying and estimating lengths accurately. The trained observers also need continual retraining in length estimation throughout the survey period (Bell *et al*, 1985; Samoilys, 1997). The most appropriate dimensions for a census are a compromise between the observer's ability to count fish rapidly and the behaviour distribution and density of the fish (Samoilys and Carlos, 2000), with narrow transects giving better counts but being inadequate for mobile species. Boundary identification errors with the problem of inclusion or exclusion of borderline fish may occur in surveys where the boundaries are not clearly marked, yet the marking of boundaries may disturb fish populations. Transect width and census duration are more likely to affect the diver's ability to count fish than the transect length (Samoilys and Carlos, 2000).

Speed may bias estimates due to observer efficiency or the presence of the diver (Lincoln-Smith, 1988; Thresher and Gunn, 1986; Fowler, 1987) standardising speed may increase errors in over counting the more mobile species (Lincoln-Smith, 1988; Samoilys, 1992). Surveys should be as rapid as possible without compromising efficiency and without counting those that enter the survey area after the census has started. Bias across species or time or space may occur and UVC has been shown to significantly underestimate cryptic fish density (Kulbicki, 1990; Ackerman and Bellwood, 2000).

The estimation of fish length underwater is complicated by the air-water interface in the divers mask, which magnifies objects by a factor of 1.3 making them appear closer to the observer. Also there is the possibility of accuracy and precision being affected by detrimental physiological effects related to SCUBA. Estimations of real fish length can be difficult due to the orientation of live fish in relation to the diver, which may not be optimal. Fish move and are at different distances from the observer, they also have morphological differences that can affect estimates. Many of the rare species are cryptic, nocturnal or wide-ranging therefore can be underestimated in this sort of survey giving lower diversity estimations. Different workers may have a bias towards different portions of the available size distribution. A 2cm change in the specified minimum size

of fish surveyed produced a change of 14.5-126% in numerical estimates in a study by Bellwood and Alcala (1988).

Harvey *et al* (2001) found that novice observers (those with little experience of fish surveys) obtained results similar to and only slightly less accurate than experienced scientific divers. They also found an improvement in accuracy when a stereo-video system was used instead of underwater visual census, however the disadvantage of this is cost and time taken to analyse the footage. Environmental factors can also affect the accuracy of the surveys, for example visibility, morphological characteristics of the reef, direction of the current, waves and wind. The alternative, destructive, methods also come with the major disadvantage of the devastation of the fish population in the area, which it is being sought to protect.

UVC methods have been shown to have a good relationship with the actual abundance, but it is dependant upon the methodology and the species of fish looked at. Sale and Douglas (1981) showed UVC methods to have a good relationship with actual abundance for some species and types of fish. Williams (1986) and Lincoln-Smith (1989) found that the techniques they used were more accurate when only a limited number of species were looked at. It is difficult for an observer to estimate visually a wide range of fish sizes especially where small fish are included (Bellwood and Alcala, 1988). Sale (1980) concluded that if cryptic species were counted then the abundance of fish was much more likely to be underestimated. The mobility of the fish relative to the census area is likely to have an impact on the accuracy of the results (Samoilys and Carlos, 2000). Accuracy for larger, more mobile species is expected to be worse (St John *et al*, 1990).

Samoilys and Carlos (2000) compared different UVC methods and found few significant differences between strip transects and stationary point counts. They found that data was highly variable (around the visual census estimates) with low precision and low power. They found that results were more accurate for smaller more sedentary species when the census area was small. Point counts were found to be much quicker than other methods. They also recommended at least 10 replicates as they found that where the sample size was too small, the power to detect differences between the means is low whereas if the sample size is too large effort is wasted.

St John *et al* (1990) compared visual estimates to destructive sampling for just 1 species; it was found that increased time, beyond 10minutes did not increase accuracy for that reef. They also found that observers have unique biases for different size classes. Biomass derived from length in this study was ~72.3% accurate, with most of the error from deriving the biomass estimates from visual estimates of numbers and length. This was due to assigning the fish to a size class, and the natural biological variability in weight length relationships, particularly where these relationships were derived from fish in a different geographic region. Estimates of size classes were good, ~86% accurate and estimates of numbers were good, ~91.6% accurate. The methodology is fairly accurate for length estimations and numbers, though the true biomass is consistently underestimated.

The fact that UVC methods mean that surveyors do not count what they do not see, has led to the assumption that UVC underestimates the true abundance (Russell *et al*, 1978). However some studies overestimated the number of fish present (St John *et al*, 1990) by an average 41.5%, this overestimation was found to be greatest when the total fish assemblages were surveyed. UVC has been used in comparison with catch per unit effort data and has been found to give very different estimates of abundance with most of the variation due to Acanthuridae and Scaridae (Connell *et al*, 1998). A few studies have tried to estimate standing stocks of commercial fish in terms of weight from UVC (Harmelin-Vivien and Bouchon-Navaro, 1981; Russ, 1985). These can be taken from length estimates but only where length weight relationships are known for that species. A biomass estimate is also valuable for considering fish distributions and ecological impact of a species with its spatial or trophic requirements and for fisheries and MNR considerations. There is a high variability in estimates of biomass for fisheries from reef fish surveys because of the schooling and clumped nature of larger individuals therefore biomass estimates will probably be inaccurate. The size of a fish is directly related to its fecundity (Alm, 1959) therefore knowledge of biomass can be important especially for looking to the future of fish communities. Size is also responsible for differences in levels of competition, predation, emigration and resource use (Jones, 1987).

Visual census methods have been developed for the Great Barrier Reef Marine Park Authority (GBRMPA) initially to detect differences between fish assemblages at

different sites and to provide baseline data for zoning management and monitoring of coral reefs (Russ and Alcala, 1989). In this method fish are placed into abundance categories on a logarithmic scale. Fish are abundant therefore statistically significant counts and replications can be done with dependable frequency (Lavett-Smith, 1978). Many reef fish are large enough to see but small enough to have small home ranges, however some cryptic fish are not amenable to observations.

1.7 Summary

This research was conducted as part of a study under the Darwin Initiative describing the marine ecology of Las Perlas Archipelago. The aim was to investigate the spatial patterns of reef fish diversity, to add to the knowledge of the reef fish communities of Las Perlas and to form a baseline for a potential protected area. This study will add to and support the work done by S.Benfield for her Ph.D thesis that will take on a more thorough investigation into the reef fish communities. The work taken on, specifically the methodology used and the data collected was carried out with support and advice from S.Benfield. The differences in diversity, abundance and trophic structure of the diurnally active, non-cryptic, reef associated fish communities are investigated in terms of their latitude and longitude and various habitat attributes. This study is in an area where reef fish have received little and at many locations, no attention and are starting to come under increased pressure due to human activities.

METHOD

2.1 Study Area

The study area was Las Perlas Archipelago, Gulf of Panama in the Tropical Eastern Pacific. Thirty-nine locations were studied in the archipelago (Figures 2.1 and 2.2); all sites were either rocky reef with coral communities or coral reef with *Pocillopora* framework. The survey took place between 16 May and 27 May 2004. Each location was accessed by boat and was studied between the hours of 08:00 and 17:00 therefore nocturnal fish were not included in the survey. The depth range was narrow with the overall maximum depth at less than 12m and most sites having a maximum depth of less than 6m. Environmental variables were recorded; water temperature (taken from diving computers), tidal state, weather, sea state, major habitat/ reef type, topography description, time and date.

Survey locations were selected based on where reefs existed, as identified by manta tow surveys of the coastline (Guzman pers. comm.) and by satellite image classification (Benfield pers. comm.). Factors affecting choice of location were the time available, accessibility and suitable weather conditions/sea state for diving. All locations were in close proximity to the shores of one of the islands or islets.

2.2 Survey Method

The survey methodology employed in this study was the Atlantic and Gulf Rapid Reef Assessment (www.coral.aoml.noaa.gov), AGRRA, methodology. This methodology is used commonly in the Caribbean and East coast of the Americas. It recommends that fish surveys take place between 10:00 and 14:00 where possible due to underwater visibility being a maximum at this time. This was not always possible due to limited survey time available, however, the proximity of Panama to the equator meant that good daylight was available from 07:00- 17:00.

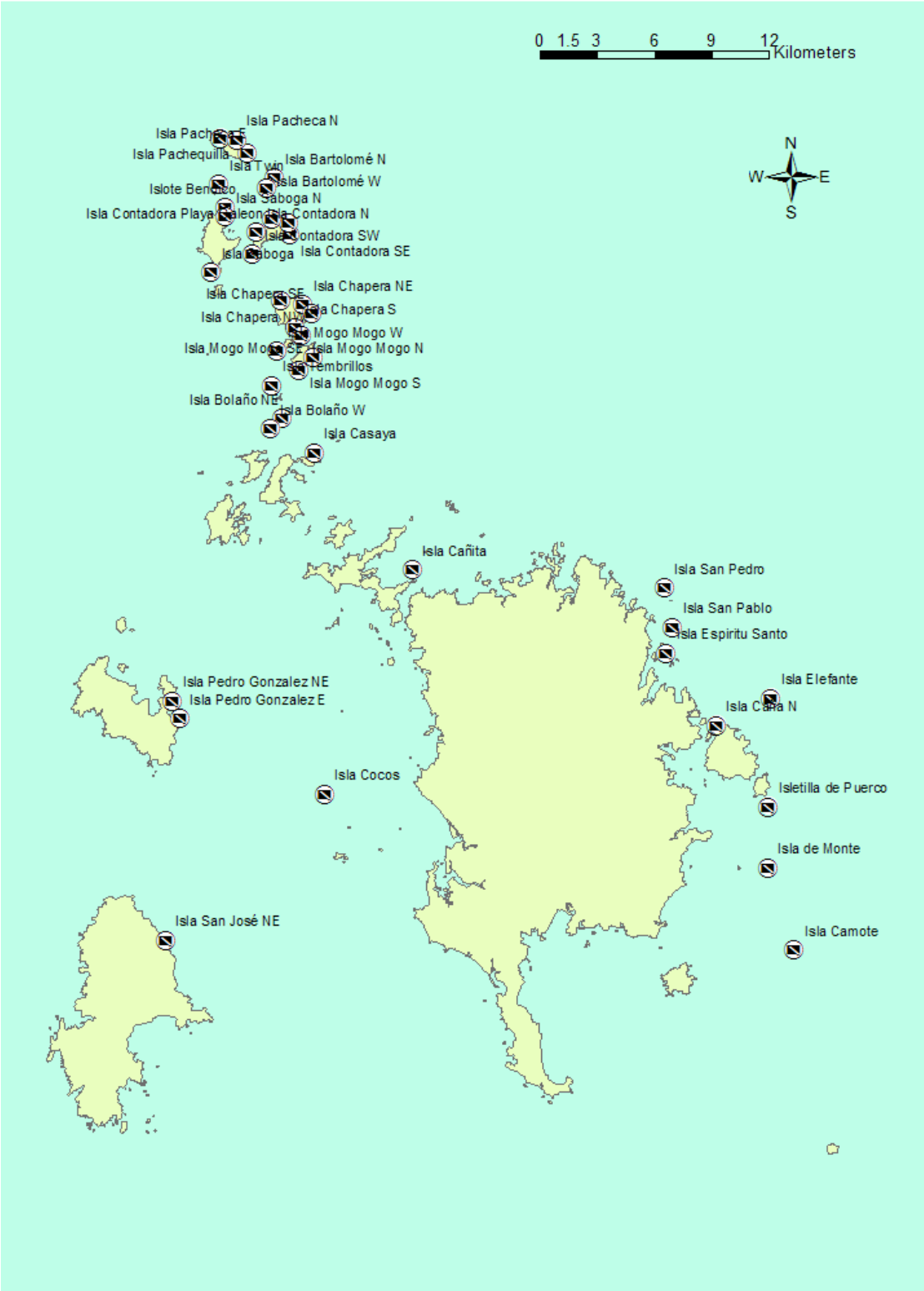

Figure 2.1: The 39 survey sites on Las Perlas Archipelago.

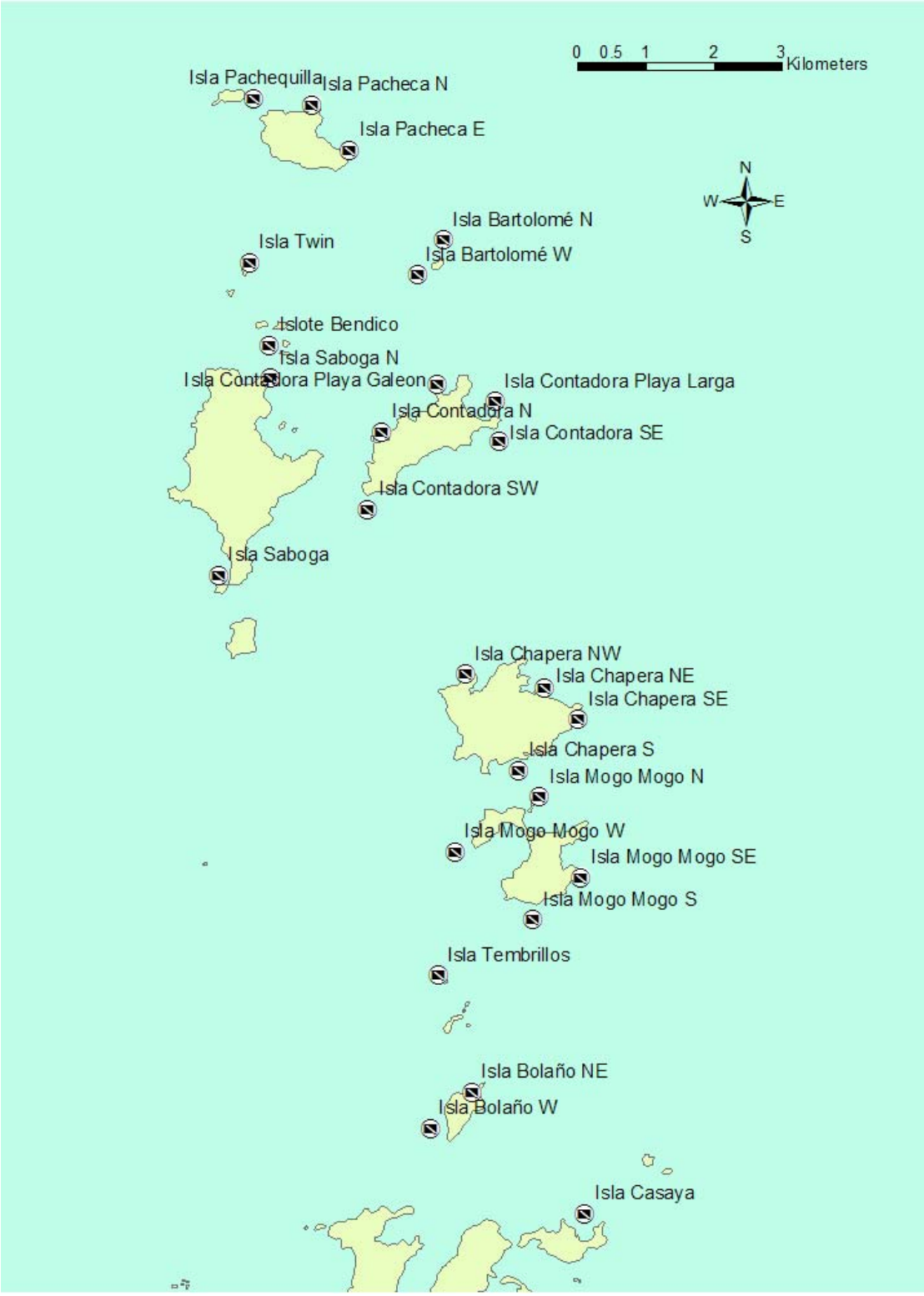

Figure 2.2: The dive sites that were surveyed on the northern cluster of Las Perlas Archipelago.

Surveys were carried out using SCUBA equipment with notes made on underwater paper data sheets (Appendix 1). Two samplers surveyed two 2m by 30m transects each at each site giving four replicate transects per site in revision to the AGRRA methodology that recommends ten. This would not be possible on many of the reefs being surveyed, due to their small, narrow size. The transect length was measured using a measuring tape, fixed to the substratum by a lead weight and attached to the diver's body. The measuring tape was deployed freely from a reel as the diver swam along the transect, which avoided prior disturbance to the fish, which would occur if the transects were laid out before surveys were conducted. After transects were complete the tape was reeled in for the next transect.

Fish were recorded in a 2m wide transect, 1m to either side of the diver, with 2m height above the substrate, and surveying fish occurring 2m ahead of the diver. Lengths were estimated using graduated, PVC t-piece, with a 60cm handle and two equal length arms with a total width across the top of 1m (www.coral.aoml.noaa.gov). Two meters is small enough for the observer to estimate the distance easily whilst allowing for a large enough sample area. Each transect took approximately 6-8 minutes and attempts were made to keep effort constant along transects by swimming at a more or less constant rate, with pauses for recording data. When schools of fish were crossing transects only those in the 2m wide strip at a given time were counted. The observer looks ahead and counts the mobile species and then on reaching the area ahead counts the sedentary species meanwhile counting the mobile species ahead and so on (Samoilys and Carlos, 2000).

Replicate transects were placed randomly but separated by a minimum of 5m (estimated by fin kicks) to prevent overlap between the fish counted. The small size of some of the reefs made it difficult to keep transects within habitats and not crossing habitats. The location of transects was decided by a preliminary assessment of the reef layout and underwater communications between the 2 divers.

All fish occurring within the transect were identified to species level, counted and placed in a size category according to their total length. Lengths were estimated using the PVC t-piece, which was carried throughout the survey. The total length of each fish

was estimated as the distance from the tip of the snout to the posterior tip of the caudal fin. The fish were recorded in size categories of 0-5, 6-10, 11-20, 21-30, 31-40 and >40cm. For those fish over 40cm estimated lengths to the nearest centimetre were also recorded. Fish in this area were not expected to avoid divers excessively as there is little influence of activities such as spear fishing. Or to be excessively attracted to them as the low tourism in the area means that there is no regular fish feeding by divers. To avoid disturbance to the fish by the boat it was usually anchored a short distance from the reef and the initial transects were done the farthest distance from the boat.

The two-metre width was used due to the amount and size range of fish being included and due to the inclusion in the survey of fish under 10cm length and the difficulty surveying these small individuals at wider transect width (Bellwood and Alcala, 1988). Where many individuals were present such as in a school, a small patch was counted and then multiplied up to the size of the school using the t-piece in order to estimate abundance. The lengths of large groups were classified into one or more size categories as necessary.

This study examined all post recruitment individuals from 1cm upwards excluding gobies and blennies, which are small, cryptic species and are too difficult to identify in the field. This was a revision of the AGRRA protocol, which recommends counts of only selected families and was developed for a different geographical location and thus different species.

Species were identified to the lowest taxon possible, with identifications based on and confirmed from the book and CD-ROM “Fishes of the Tropical Eastern Pacific” (Allen and Robertson, 1994). Test dives took place before surveying commenced in order for divers to familiarise themselves with species and equipment.

After each diver had finished their 2 transects approximately 5-10minutes was taken for a roving diver survey where any species not encountered on the transects were recorded. The gobies and blennies were still not recorded as insitu identification is difficult and the emphasis was not on them. The fish encountered on this survey were recorded as presence and absence, using categories for estimation of abundance; single, few (2-10),

many (11-100), and abundant (>100). The roving diver survey took place in the same general area as transects. This was for a much shorter time than recommended by the AGRRA methodology due to the homogeneity of the reefs in this area, with fewer overhangs and refuges in which to search for fish.

The sites selected had several distinct biotopes and the bottom composition was assessed simultaneously by a different team of divers who surveyed ninety 1m² using quadrats along transects parallel to the shore in the same areas as fish surveys were conducted. Percentage cover of scleractinian and soft coral species were recorded to species level, and the cover of sponges, macroalgae, turf algae and dead coral were also recorded. This allowed a comparison between habitat and fish communities.

Equipment used: SCUBA equipment; underwater slates, pencil and writing paper with survey template; transect tape 30m with a 2lb weight; and a graduated t-piece.

2.3 Accuracy Tests

The 2 divers S.B and L.B were trained to estimate fish lengths using laminated cardboard fish shapes, this was done on land and underwater. In both locations the t-piece was used and estimates were compared against known lengths. Divers were allowed to know how real lengths compared with estimates between training tests, in order to know whether they were under or over estimating sizes. The results of these length estimations are shown in table 2.1, each fish shape was estimated into the size categories that were used in the survey.

Table 2.1: Results of length estimation tests by the 2 divers S.B and L.B, on land and underwater.

Test	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
On land S.B	80%	60%	80%	80%	85%	90%	90%	95%	95%	95%
On land L.B	60%	80%	90%	80%	85%	90%	95%	100%	100%	
Underwater S.B	95%	95%	95%							
Underwater L.B	75%	95%	100%	95%						

Twenty estimations were done per test and both tests were continued until surveyors were able to attain >95% accuracy in estimating fish lengths consistently on land and underwater, before the survey commenced. The AGRRA protocol recommends that this calibration continue throughout survey period, however due to the limited time of the survey (10 days) this was not necessary.

In order to test the accuracy of the fish abundance counts between the divers, whilst diving the 2 observers surveyed a 30m transect simultaneously. One diver reeled out the tape and both divers attempted to swim at the same pace directly next to one another. The shallowness of the reef environment made it difficult for one diver to swim above the other as recommended by AGRRA. This was repeated 4 times at the same location. The data was then compared between the 2 divers. It was expected that the divers would have differences in their observations, due to different times at which they paused to write and differences in the fish they observed due to swimming next to one another and therefore not along exactly the same transect.

The results of the accuracy tests between the 2 observers S.B and L.B are presented in table 2.2. Some species were not observed by S.B that were by L.B, these were; *Epinephelus panamensis, Halichoeres notospilus, Halichoeres chierchiae* and *Diodon holocanthus*, L.B saw 2,2,1,1 respectively. Possibly these differences occurred due to problems associated with swimming next to one another as already discussed. For example fish could have been present at L.B's side of the transect and thus considered out of the transect by S.B, or S.B could have been pausing to write notes when these species were observed.

Table 2.2: Total fish seen, total species seen and fish seen per transect from the simultaneous transects done by the 2 divers, L.B. and S.B, together.

Observer	**Total fish over all 4 transects**	**Total species seen over all 4 transects**	**Average fish counted per transect**
L.B	604	14	151
S.B	633	10	158

Tests were done to establish whether there was a significant difference between the numbers of fish of each length estimated by the 2 observers and thus whether there was

any bias in the numbers and length of fish they noticed and recorded. The data for total fish of each length, on each transect, regardless of species, was not normally distributed according to the Anderson-Darling test, and had equal variance according to Levene's test, therefore fitting the assumptions for the non-parametric Mann-Whitney test. The Mann-Whitney test showed that the null hypothesis can be accepted that there was no significant difference between the 2 observers with W= 563.0 and P= >0.05.

To examine if there was a significant difference between the 2 samplers in the amount of species per transect seen the Moods Median test was applied to the data, as the results were normally distributed but did not have an equal variance. This gave chi-squared= 3.60 and P>0.05 and therefore there was no significant difference between the 2 samplers in terms of species seen. Hence, the two observers' data can be used together in further analyses.

2.4 Analysis

The fish abundance, number of species and diversity indices (using Shannon Wiener's diversity index) at each site was analysed using the nonparametric bivariate correlation, Spearman's Rank, with habitat variables and location. They were also subjected to multivariate Cluster Analysis, which takes all the data as a whole and groups the samples on the basis of their major features, showing any similarities in sites or species distribution.

Detrended Correspondence Analysis (DECORANA) was also used, this also analyses the data as a whole and identifies the major features of the sample by using reciprocal averaging. It improves upon other correspondence analyses by removing the arch or horseshoe problem of reciprocal averaging (whereby the second axis is a quadratic distortion of the first axis). It is a good general-purpose ordination technique, particularly for heterogeneous data sets such as this. DECORANA creates axes along which the data is spread, and forms eigenvalues that show how much of the variation in the data is explained by each axis. The option was chosen to down-weight the rare species in the DECORANA in order to minimise the problems created by outlier species. These axes were then compared, using the nonparametric Spearman's Rank

correlation, with the environmental variables of habitat and location, to show whether the trends found in the data can be explained by these parameters. They were analysed in their original form and in binary form, indicating species presence/absence for each site. They were also analysed in a broader form with the species combined into family groups.

The use of total abundances can be deceptive and may hide important information about the fish community, as it is a summary statistic. Abundances of some species, families and trophic groups may give more significant results. Therefore fish were assigned to their families and trophic guilds on the basis of information from Allen and Robertson (1994) and www.fishbase.org. These groups were then also compared to habitat and location using Spearman's rank.

RESULTS

3.1 Observations

During the survey several observations were made regarding the fish distribution. There appeared to be a greater abundance of fish aggregating around the massive coral species, dominated by different species to those around the *Pocillopora* framework, with more Balsitidae, and more *Abudefduf troschelii*, amongst others. However, the scale of these aggregations is much smaller than the scale of the transects, therefore it is unlikely this relationship will be present in the statistical analysis of the data. Where coral communities existed on rocky reefs there appeared to be a different fish community, with an increase in larger fish such as Acanthuridae and Carangidae than on the *Pocillopora* framework.

There was evidence of anthropogenic impacts on the reefs with both artisanal and commercial offshore fishing boats often close to the reefs. On many of the reefs there were stranded nets entangled, often with a small mesh size. On one reef there was even an abandoned trawling device. The families that are known to be fished in the area include the Carangidae, Lutjanidae and Serranidae. There has, as yet, been little research into the fisheries in the area and little information is available about them.

3.2 Descriptive Results

In total 39 sites across Las Perlas Archipelago were surveyed. A total of 29,876 fish were counted giving an average of 766 per site, with a standard deviation of 309 and a standard error of 49.4. This resulted in an average of 192 fish per transect, with each transect being 2m by 2m by 30m, therefore 192 fish per 120m^3.

3.2.1 Fish Species

In total 76 species of fish were recorded, 68 of these were counted on transects and the other 8 were only seen in the roving diver surveys. Appendix 2 gives a complete list of the fish found, their abundance and the sites they were present in. The species present on the roving diver surveys but not the transects were *Gymnomuraena zebra*, *Aetobatus*

narinari, *Chilomycterus reticulates*, *Aluterus scriptus*, *Gymnothorax castaneus*, *Echidna nocturna*, *Fistularia corneta* and *Haemulon sexfasciatum*.

One of the species recorded on the survey was only identified to family level; only 4 individuals of that species were seen, at only one site. The species was recorded as an unidentified member of the Carangidae. Due to its speed and orientation not enough of it was seen to identify it correctly, however enough was seen to exclude the possibility of it being the same species as any of the others identified. It only represented 0.013% of the total fish seen.

The 10 most abundant fish are shown in table 3.1. The most abundant 3 fish *Thalassoma lucasanum*, *Chromis atrilobata* and *Stegastes acapulcoensis* make up 65% of the total fish found. When *Halichoeres dispilus* and *Haemulon maculicauda* are added they make over 75% of the total number of fish counted overall.

Table 3.1: The most abundant fish species; total across all the sites and transects, percentage of the overall total number and number and percentage of sites they were counted in.

Species	**Total counted**	**Percentage of total fish found**	**Number of sites present in**	**Percentage of sites present in**
Thalassoma lucasanum	10042	33.61%	39	100%
Chromis atrilobata	5566	18.65%	31	79.49%
Stegastes acapulcoensis	3873	12.96%	38	97.44%
Halichoeres dispilus	2397	8.023%	37	94.87%
Haemulon maculicauda	1913	6.403%	12	30.77%
Haemulon steindachneri	850	2.845%	16	40.03%
Stegastes flavilatus	724	2.423%	39	100%
Abudefduf troschelii	513	1.717%	24	61.54%
Canthigaster punctatissima	344	1.151%	37	94.87%
Serranus psittacinus	342	1.145%	33	84.62%

Table 3.1 also contains the 5 fish species that were present in the most sites *Stegastes flavilatus, Thalassoma lucasanum, Stegastes acapulcoensis, Canthigaster punctatissima* and *Halichoeres dispilus* the only other that appears in more than 35 sites is *Epinephelus labriformis,* seen in 36 of the sites. Of the 68 species found on transects 17 species are present in over 20 of the sites, representing 85.3% of the fish abundance. Twelve species were only counted at 1 location, these species were only ever in very low numbers, apart from *Microlepidotus brevipinnis* of which 150 were counted at the only site they were recorded at.

3.2.2 Fish Families

The 76 species of fish encountered on the survey came from 25 families, 2 of which, the Myliobatidae and the Monacanthidae, were on the roving diver survey only and were not encountered on transects. The family with the greatest abundance was the Labridae with 13,294 counted overall; these included 7 species and made up 44.5% of all the fish seen. The next most abundant family was the Pomacentridae these also included 7 species and were 35.9% of the fish seen. The Haemulidae made up another 10.4% of all the fish seen from 8 different species. Over 90% of the fish seen were in these 3 families.

The Serranidae and the Tetraodontidae were the next most abundant families making up 2.4% and 1.2% respectively of the fish seen. Members of the Labridae, Serranidae and Pomacentridae were at all sites and the Tetraodontidae were recorded at all but one site. The Haemulidae however are a shoaling group and were only seen at 24 of the sites but often were seen in large numbers at these sites.

3.2.3 Fish Sizes

Over 44% of fish counted were in the size range 6-10 as shown in table 3.2, whilst 94.14% of the fish counted were less than 20cm and over 99% less than 31cm. The 3 most abundant species were all measured at less than 31cm, all *Chromis atrilobata* were less than 21cm. Less than 2% of these most abundant 3 species were greater than 21cm and over 75% of them were less than 10cm.

Table 3.2: The overall abundance of fish in each of the size categories.

Sizes (cm)	Total abundance of fish at this size	Percentage of total	Cumulative percentage
0-5	8733	29.23%	29.23%
6-10	13244	44.33%	73.56%
11-20	6149	20.58%	94.14%
21-30	1464	4.90%	99.04%
31-40	179	0.60%	99.64%
>40	107	0.36%	100%

3.2.4 Sites

The mean number of fish per transect at each site was calculated along with the standard deviation and standard error (Appendix 3), these show that at many of the sites there is high variability between transects. There were 5 sites with an average of over 250 fish per transect, these are shown in table 3.3 the site with the greatest abundance was Isla Contadora Southwest with 428.5 fish per transect and over 5% of the total abundance of fish counted over all the sites. The sites with the least fish counted are shown in table 3.4. The lowest abundance of fish was at Isla San Pedro with 74.5 fish per transect - only 1% of the total fish seen - followed by Isla Caña North, then Isla Elefante. These 3 sites are all in a similar location, to the east of Isla del Rey. The remainder of the sites had over 100 fish counted.

Table 3.3: The survey sites with the greatest abundance of fish; the codes allocated to them, the abundance of fish per transect and the standard deviation and standard error associated with this. The abundance as a percentage of the overall total, total number of species seen along transects at each site and the diversity indices (Shannon's H) are also shown.

Site name	Site code	Mean fish per transect	Standard deviation	Standard error	Percentage abundance	Total species	Diversity index
Isla Contadora Southwest	19	428.5	168.2	84.1	5.73	26	2.14
Isla Pedro Gonzalez East	33	360.5	265.0	132.5	4.83	25	2.86
Isla San José Northeast	31	354	278.4	139.2	4.74	39	3.04
Isla Bartolomé West	29	296.3	36.2	18.1	3.97	19	2.34
Isla Chapera Southeast	10	262.8	101.0	50.5	3.52	23	2.72

Table 3.4: The survey sites with the lowest abundance of fish; the codes allocated to them, the abundance of fish per transect and the standard deviation and standard error associated with this. The abundance as a percentage of the overall total, total number of species seen along transects at each site and the diversity indices (Shannon's H) are also shown.

Site name	**Site code**	**Mean fish per transect**	**Standard deviation**	**Standard error**	**Percentage abundance**	**Total species**	**Diversity index**
Isla San Pedro	1	74.5	30.6	15.3	1.00	16	3.04
Isla Caña North	38	77	27.2	13.6	1.03	15	1.94
Isla Elefante	3	93.8	29.1	14.6	1.26	23	3.42
Isla Casaya	12	106.8	55.7	27.9	1.43	22	3.42
Isla Chapera South	14	118	28.5	14.3	1.58	22	2.59

The mean number of species per site was 20 with a standard deviation of 5.4. The site with the most species was Isla San José Northeast with 39 species; this was also one of the top three sites in terms of abundance. There were only 5 sites with greater than 25 species observed during transects and 3 of these were also in the top 5 in terms of abundance. The site with the least species surveyed was Isla Mogo Mogo West with only 10 species, followed by Isla Bolaño West. 5 sites had less than 15 species, 4 of which are very close together in location around Isla Mogo Mogo and Isla Chapera in the mid to north of the archipelago.

The diversity index was calculated for each site using the Shannon Wiener Diversity Index, this is also shown for the sites on tables 3.3 and 3.4. This enables differentiation between a site with a few fish and of many different species and a site with many fish but of few species. The sites with the highest diversity according to Shannon's H were Isla Casaya and Isla Elefante, despite having a low abundance, these were followed by Isla Monte. The site with the lowest diversity was Bolaño West followed by Mogo Mogo Southeast then Mogo Mogo West, they were all in the same locality, in the mid to north of the archipelago all on coral frameworks. Of the 5 sites with the lowest diversity 3 of these were in the 5 sites with the lowest amount of species.

3.2.5 Habitats

The results from the bottom composition survey that took place simultaneously were available in the form of percentage cover of coral species, algae and sponge (Guzman pers. comm.). This showed that sites were either dominated by either algal turf or *Pocillopora* species or a combination of the 2 (Guzman pers. comm.).

The sites were classified as a *Pocillopora* framework or a coral community/ rocky reef. Twelve sites were classified as coral communities whilst the remainder were framework. However two of the sites, Isla Caña North and Isla Cañita, had an extremely low percentage cover of live *Pocillopora* compared to all other sites and an extremely high percentage cover of algal turf but were classified as framework sites, this was due to a large amount of dead *Pocillopora*. There were more communities in the south than in the north; this may not reflect an actual distribution in the habitats as not all areas were surveyed.

There were 10 species which only occurred on the framework, these are listed in Appendix 4, therefore 58 species occurred on transects at the coral community sites. Some species only occurred on the communities, 12 in total (Appendix 4), the total fish species occurring on the coral frame sites was 56, 2 less than at the coral communities despite the greater number of sites. It is noticeable that these are some of the larger groups of fish; Carangidae, Scaridae, Acanthuridae and Lutjanidae. Therefore a difference between these 2 types of site in relation to biomass might exist, to be discussed by Benfield (Ph.D Thesis). Many of the fish from both lists however do not occur at a lot of sites and are transient species not resident species.

3.2.6 Feeding Guilds

The fish were allocated to approximate feeding guilds according to dietary information provided by Allen and Robertson (1994) and www.fishbase.org. These guilds include those species feeding on algae, fish, invertebrates, coral or plankton; they also include those reported to eat a combination of these foods, which are classed as generalists. Also recorded were those that eat each of the above food types either as its sole food

source or as a part of a mixed diet. The numbers counted of each are shown in table 3.5 and many species are included in more than one group.

Fish that are reported to eat plankton and invertebrates are the most common numerically. It is noticeable that there are only few species making up the numbers of planktivores whilst many species contain invertebrates as all or part of their diet. The next most common are herbivorous then piscivorous fish. There are no fish from the survey that are recorded as being obligate corallivores. Over 50% of the fish have a mixed diet, they may have a different diet at different life stages, or they may be opportunistic feeders.

Table 3.5: The number of fish and number of species of fish from the survey with each feeding preference.

Feeding Guild	**Number counted**	**Number of species included**
Herbivores only	4978	10
Piscivores only	111	5
Invertivores only	4062	20
Planktivores only	5593	3
Corralivores only	0	0
Generalists	15132	38
Those eating algae as all or part of their diet	5857	20
Those eating fish as all or part of their diet	4018	29
Those eating invertebrates as all or part of their diet	19170	55
Those eating plankton as all or part of their diet	16678	13
Those eating coral as all or part of their diet	54	5

3.3 Fish Community Variation With Habitat

The mean number of individuals per site, number of species per site and the diversity indices were subjected to a bivariate correlation with the habitat variables from the benthic survey. The data was found to be nonparametric, therefore Spearman's Rank was used to see if there was a significant relationship. The habitat variables used included the number of different habitat types present, also the percentage cover of

massive coral species and the percentage cover of *Pocillopora* species. The results of these correlations are shown in table 3.6.

*Table 3.6: Spearman's Rank correlations between basic habitat variables and basic fish community variables. No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level.*

Percentage cover	**Fish diversity index**	**Mean fish per site**	**Total species of fish per site**
All algal species	--	--	--
Habitat types present	--	0.332 p=0.039 *	--
All massive coral species	--	--	--
All *Pocillopora* species	--	--	--

The only significant correlation was found between the number of different habitat types present and the number of fish per site. With an increasing diversity in habitat there is an increase in the number of fish present. The use of total abundances can be deceptive and may hide important information about the fish community. Abundances of some species, families and trophic groups provide more significant results.

3.4 Fish Community Variation With Location

The latitude and longitude of the survey sites were subjected to Spearman's Rank correlations with the total amount of fish species per site, the diversity index at each site and the mean abundance of fish at each site. The results are shown in table 3.7.

Table 3.7 shows a decrease in the abundance of fish at each site from west to east across the Archipelago. This change in abundance is not due to the greater abundance of sampling locations in the west as these differences have been removed by using the nonparametric Spearman's rank correlation as opposed to a parametric one.

*Table 3.7: Spearman's Rank correlations between basic fish community variables, the amount of habitat types present and location (longitude and latitude). No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level*

	Total species of fish per site	**Fish diversity index**	**Mean fish per site**
North-South co-ordinates	--	--	--
West-East co-ordinates	--	--	-0.401 p= 0.011 *

3.5 Family Variation with Location

Table 3.8 indicates how the different families of fish are distributed with respect to latitude and longitude using Spearman's Rank correlations. There was a correlation between Carangidae and latitude, with a greater amount in the south. This family only occurred in 6 of the sites, 15.4% of them, and only 2 of these were in the northern cluster of sites, Isla Casaya (coral frame) and Isla Contadora Southwest (coral community). There was a strong correlation between location and the amount of wrasse, Labridae, with an increased amount of Labrids to the north of the Archipelago and also to the west of the Archipelago.

The Cirrhitidae are more abundant in the west and north of the Archipelago than to the east and south. The Tetraodontidae are greater in the north than in the south. The Sygnathidae were only found at 2 sites, both of which were in the southwest, however this might be a consequence of it being a cryptic species and a rare species it was also seen on one roving diver survey in the northern group of islands.

*Table 3.8: Spearman's Rank correlations between abundance of fish of different families at each site and the location (longitude and latitude). No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level, whilst ** indicates significance at the 99% level.*

Family	**North-South co-ordinates**	**West-East co-ordinates**
Acanthuridae	--	--
Apogonidae	--	--
Balsitidae	--	--
Carangidae	-0.426 P=0.007 **	-
Chaetodontidae	--	--
Cirrhitidae	0.479 p=0.002 **	-0.675 P=0.000 **
Diodontidae	--	--
Fistulariidae	--	--
Grammistidae	--	--
Haemulidae	--	--
Holocentridae	--	--
Kyphosidae	--	--
Labridae	0.475 P=0.002 **	-0.499 P=0.001 *
Lutjanidae	--	--
Muraenidae	--	--
Pomacanthidae	--	--
Pomacentridae	--	--
Scaridae	--	--
Sciaenidae	--	--
Serranidae	--	--
Sygnathidae	-0.321 P=0.046 *	-0.382 p=0.016 *
Synodontidae	--	--
Tetraodontidae	0.347 p=0.030 *	--

3.6 Feeding Guild Variation with Location and Habitats

Table 3.9 shows the distribution of the fish relating to their diet. Piscivores show an increase from north to south. Those that are generalists, eating 2 or more of the 5 food types, are greater in the north and in the west of the Archipelago. All those that contain

invertebrates in their diet are also greater in the north and in the west as are those that contain plankton in their diet.

*Table 3.9: Spearman's Rank correlations between abundance of fish of different diets at each site and the location (longitude and latitude) and habitat variables. No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level, whilst ** indicates significance at the 99% level.*

Feeding Guild	**Habitats present**	**% *Pocillopora* species %**	**% Massive corals**	**% Algae**	**South-North**	**West-East**
Herbivores only	--	--	--	--	--	--
Piscivores only	--	-0.364 0.023 *	--	0.342 p=0.033 *	-0.441 p= 0.005 **	--
Invertivores only	--	--	--	--	--	--
Planktivores only	--	--	--	--	--	--
Generalists	--	--	--	--	0.431 P=0.006 **	-0.506 P=0.001 **
Those eating algae as all or part of their diet	--	--	--	--	--	--
Those eating fish as all or part of their diet	--	-0.415 p=0.009 **	--	0.426 p=0.007 **	--	--
Those eating invertebrates as all or part of their diet	--	--	--	--	0.356 P=0.026 *	-0.414 P=0.009 **
Those eating plankton as all or part of their diet	--	--	--	--	0.320 p=0.047 *	-0.405 P=0.011 *
Those eating coral as all or part of their diet	--	--	--	--	--	--

With less *Pocillopora* there are less piscivores, whilst greater algal cover gives a greater amount of piscivores. These are the two dominant bottom types and they appear to have a significant affect on the distribution of piscivores but not on any other fish. Whilst according to www.fishbase.org, no obligate corallivores are present those that may contain a coral component in their diet do not show a correlation with the percentage coral cover.

3.7 Multivariate Analysis of Fish Abundance

The results were analysed using multivariate methods to show differences in the fish communities as a whole between different sites. A Cluster Analysis was done on the fish data using Multivariate Statistics Package (MVSP) with Euclidean distance. The analysis was done using the average abundance per transect of each species at each site. Fish lengths were not included in this analysis. The dendrogram for the cluster analysis is shown as figure 3.1.

Figure 3.1 shows the reef at Isla Contadora Southwest to be the most different from all the other sites, it is in the middle of the northern cluster of islands. It is the only coral community in the immediate area with all the other sites around Isla Saboga, Isla Chapera, and Isla Contadora being *Pocillopora* framework. It has a very low amount of *Pocillopora* species. It has a very high amount of Labrids being over 400 individuals greater than at any other site. The average total Labridae per site is 341 whilst this site has 1,254.

Sites Isla Chapera Northeast and Southeast are in a cluster they occur in close proximity to one another, and they were surveyed on the same day as one another. The reason these stand out as a cluster may be due to large shoals of *Haemulon maculicauda* at both these sites on the day they were surveyed. Both these sites had over 500 *H.maculicauda* individuals counted whilst all other sites had less than 200, and the majority had none at all. This species often is found in large aggregations and is fairly transient (Allen and Robertson, 1994), therefore these could be visiting schools, not related to any specific environmental variables.

The next cluster of sites; Isla Comote, Isla Contadora North, Isla Pachequilla, Isla Pedro Gonzalez East, Isla San José Northeast and Isla San Pablo have the 6 highest abundances of Pomacentridae, they do not have any unique similarities in relation to habitat types or location.

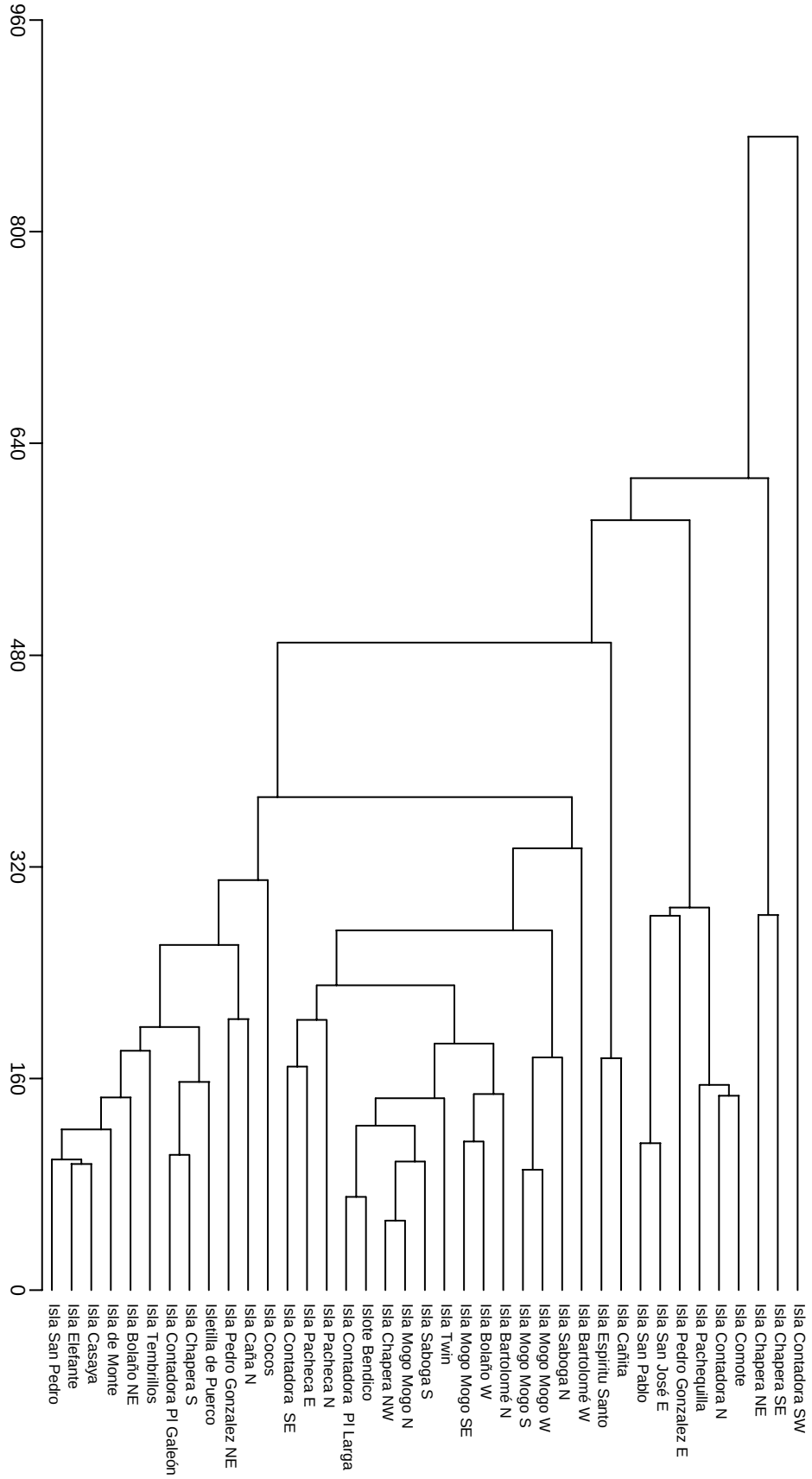

Figure 3.1: Dendrogram from a cluster analysis of the fish communities at each site, using Euclidean distance.

Sites Isla Espiritu Santo and Isla Cañita make up the next cluster, they both have low amounts of Pomacentridae, specifically *Stegastes acapulcoensis.* They also have relatively high amounts of Haemulidae, third and fourth highest of all the sites, with the highest amounts of *Haemulon steindachneri* with 353 and 315 at each site; over 250 greater than at any other site and making up 78% of the total of the 6th most abundant species on the survey.

The other sites form 2 large clusters, which are not distinctly different from one another in terms of species or habitats. Due to the significant influence of the shoaling species *H.maculicauda* and *H.steindachneri* on the arrangement of the clusters the analysis was run again using Jaccards co-efficient instead of Euclidean distance. This looks at binary data, presence and absence and the dendrogram is shown in figure 3.2.

The dendrogram for binary data (figure 3.2) does show differences due to the removal of the influence of shoaling species, which in figure 3.1 caused clusters of sites Isla Espiritu Santo and Isla Cañita and sites Isla Chapera Northeast and Southeast.

In figure 3.2 sites Isla San Pedro, Isla San Pablo and Isla Elefante form a distinct cluster and are located closely together at the northeast of Isla del Rey, along with site Isla Espiritu Santo. The reef at Isla San Pedro is a coral framework whilst Isla San Pablo and Isla Elefante are communities. Sites Isla Comote, Isla de Monte and Isletilla de Puerco form a cluster and are also close together at the southeast of Isla del Rey. They are all coral communities with similar, low amounts of *Pocillopora* and are 3 of only 7 sites with the presence of sea fans recorded (Guzman pers. comm.) They have some of the greatest amounts of crustose algae and high amounts of algal turf, therefore habitat is an important factor in this cluster. The diversity index for these sites is high for all of them and they all have an above average number of fish species per site.

Sites Isla Espiritu Santo and Isla Cañita make up the next cluster, they both have low amounts of Pomacentridae, specifically *Stegastes acapulcoensis.* They also have relatively high amounts of Haemulidae, third and fourth highest of all the sites, with the highest amounts of *Haemulon steindachneri* with 353 and 315 at each site; over 250 greater than at any other site and making up 78% of the total of the 6th most abundant species on the survey.

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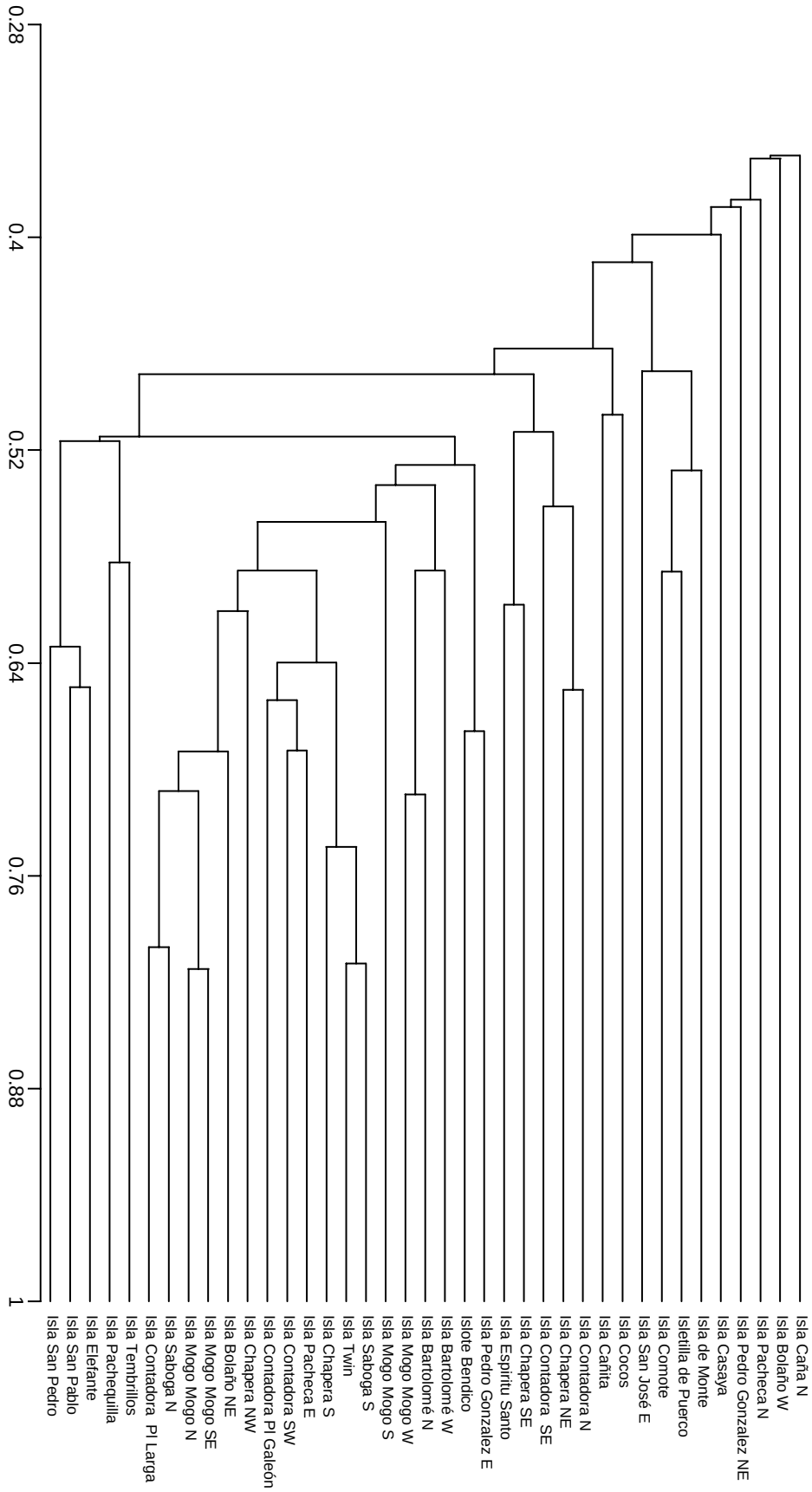


Figure 3.2: Dendrogram from a cluster analysis of the fish communities at each site, using Jaccard's co-efficient.

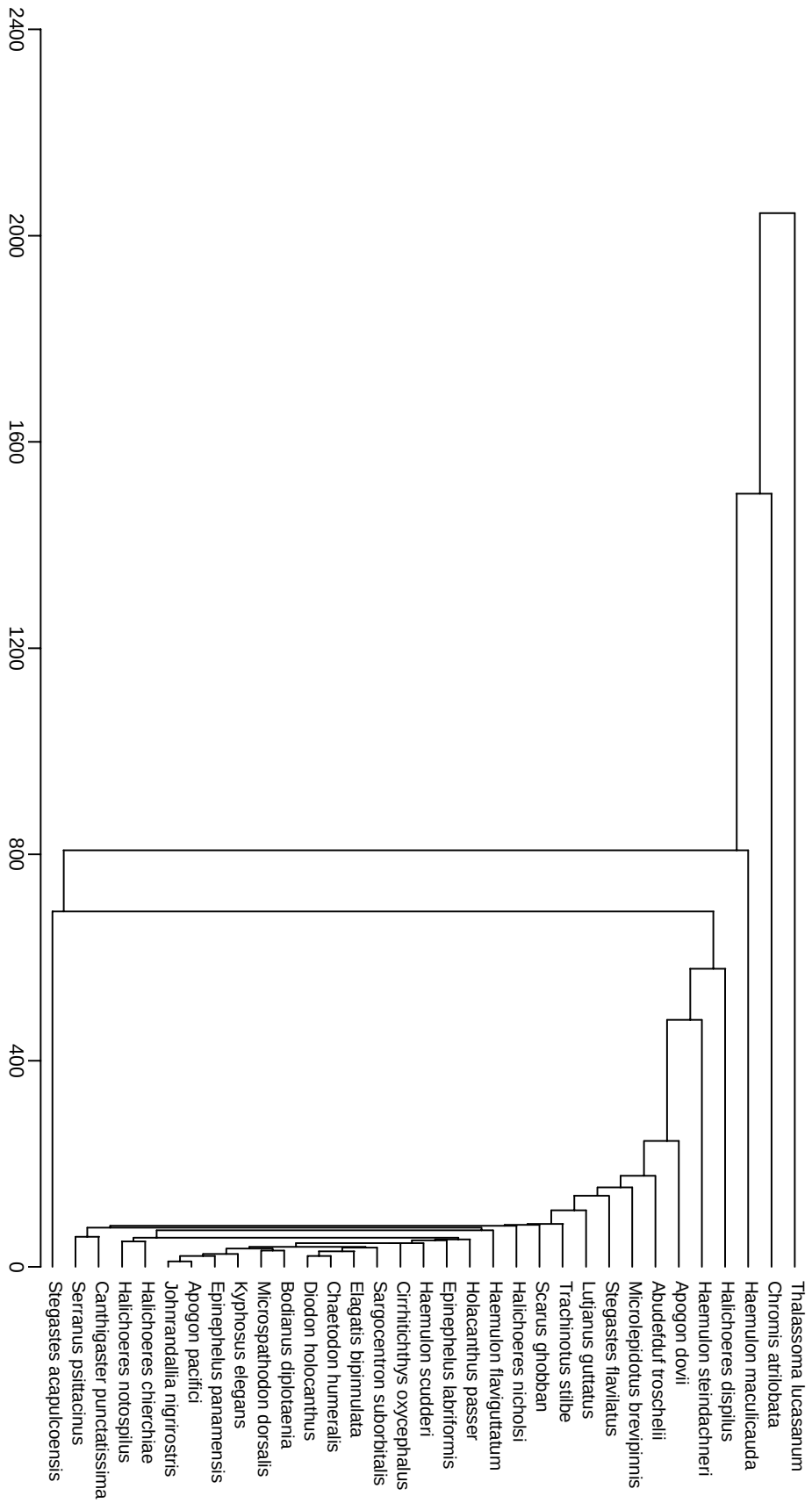


Figure 3.3: Dendrogram using Euclidean distance, of fish species making up >0.1% of the total fish species found.

Sites Isla Caña and Isla Espiritu Santo are the only sites apart from those in the 2 clusters mentioned that lie to the East of the large island, Isla del Rey; they are both coral frameworks. The reef at Isla Caña is in a sheltered location, on the dendrogram it is the most different from all the others, and is not part of a cluster. It is has been classed by the benthic survey as a framework although it has the lowest cover of live *Pocillopora* of all the sites and is 97.9% algal turf. The reason it has been classed as framework is probably due to dead coral cover, which has been colonised by algal turf. It has the second lowest abundance of fish and a low amount of species and low diversity.

A cluster analysis was also done on the fish species to see if distinct communities and associations between species existed. The dendrogram displayed in figure 3.3 does not represent all the species, just those that make up over 0.1% of the total abundance of fish found. The only fish lying away from the main cluster are *Thalassoma lucasanum*, possibly due to the much greater numbers of this species, *Haemulon maculicauda*, and *Chromis atrilobata*, possibly due to their shoaling nature giving large numbers at some sites and none at others. *Stegastes acapulcoensis* also lies away from the main cluster and is another abundant species, present at almost all the sites.

A Detrended Correspondence Analysis (DECORANA) was done using MVSP. The sites (cases) and fish (variables) were analysed using Kaisers Rule. As DECORANA is over-sensitive to rare species the rare species were down-weighted to decrease this. Fish lengths were not included in the analysis, just the quantity of each species at each site.

The eigenvalues created by the DECORANA are shown in table 3.10. The DECORANA creates axes representing trends in the data. The eigenvalues show the percentage of the variation in the fish communities that can be explained by each axis created by the analysis. Axis 1 explains 25.6% of the variation in the data and has an Eigenvalue of greater than 0.3 therefore indicating a significant trend, axis 2 explains 15.9% of the variation. The amount of variation explained by axis 3,4 and 5 is negligible, due to their low eigenvalues.

Table 3.10: The eigenvalues for each of the axis created by DECORANA for all the fish data at all the sites and the percentage of variation explained by each axis.

	Axis 1	**Axis 2**	**Axis 3**	**Axis 4**	**Axis 5**
Eigenvalues	0.318	0.197	0.095	0.052	0.020
Percentage	25.639	15.852	7.644	4.176	1.632
Cumulative Percentage	25.639	41.491	49.136	53.311	54.943

The site scores created by the DECORANA for axis 1 versus axis 2 were plotted in figure 3.4 as were the fish scores for axis 1 and 2 in figure 3.5 These 2 graphs were then plotted together as a joint plot in figure 3.6.

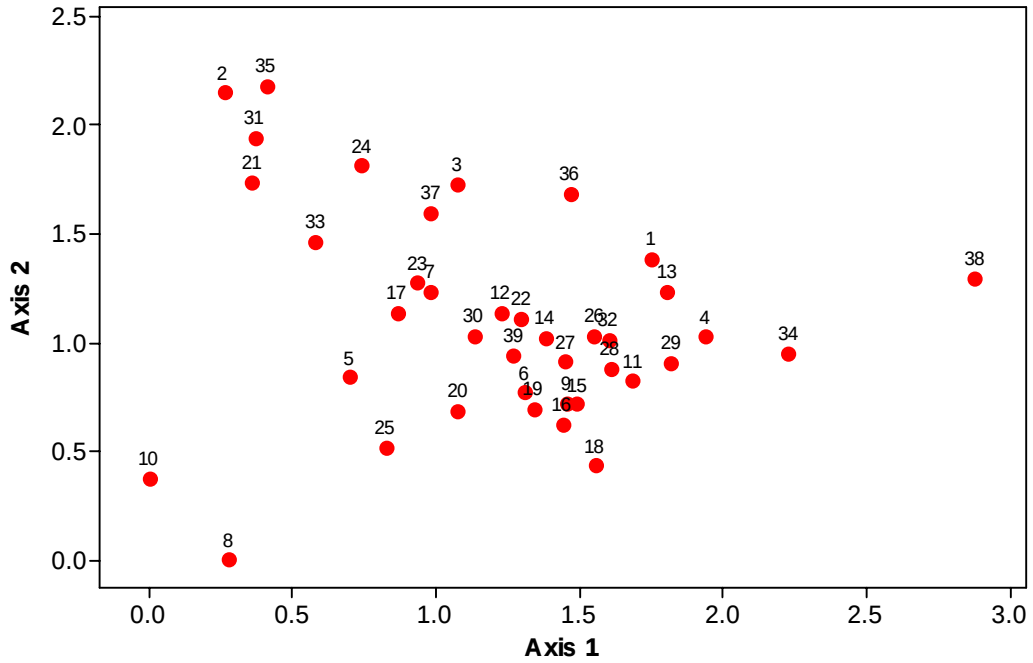


Figure 3.4: Ordination plot from the DECORANA showing the spread of sites along axis 1 and 2. Each site is numbered according to the site list in appendix 3.

Figure 3.4 shows that sites 8 and 10 representing Isla Chapera Northeast and Southeast, are different from the rest of the group as they were in the cluster analysis (figure 3.1), and are in close proximity to one another. They may be different to the other sites due to the large shoals of *H.maculicauda* at both these sites.

Site 38 which represents Isla Caña also stands away from the rest, this site is to the North of Isla Caña and is one of only 8 sites to the East of the largest island, Isla del Rey. It has virtually no live *Pocillopora* 0.056%, the lowest percentage cover of all the sites. It also had the highest percentage cover of algal turf, 97.9%, and it was noted that

this site contained a high amount of dead *Pocillopora*. This factor may have influenced the fish communities, which are noticeably different from all the other sites as it is the only site with no *Stegastes acapulcoensis*. The site with the second lowest amount of *S.acapulcoensis* is site 11 with only 17 counted in total over the 4 transects. This site also has the second lowest amount of *Pocillopora* with only 3.059% cover indicating a link between *S.acapulcoensis* and live cover of *Pocillopora*. It only had 3 individuals from the Pomacentrid family altogether, which is very low as this is one of the most abundant families with an average of 275 per site. Site 38 also had few *Thalassoma lucasanum*, the most common species overall, only 2 sites had fewer.

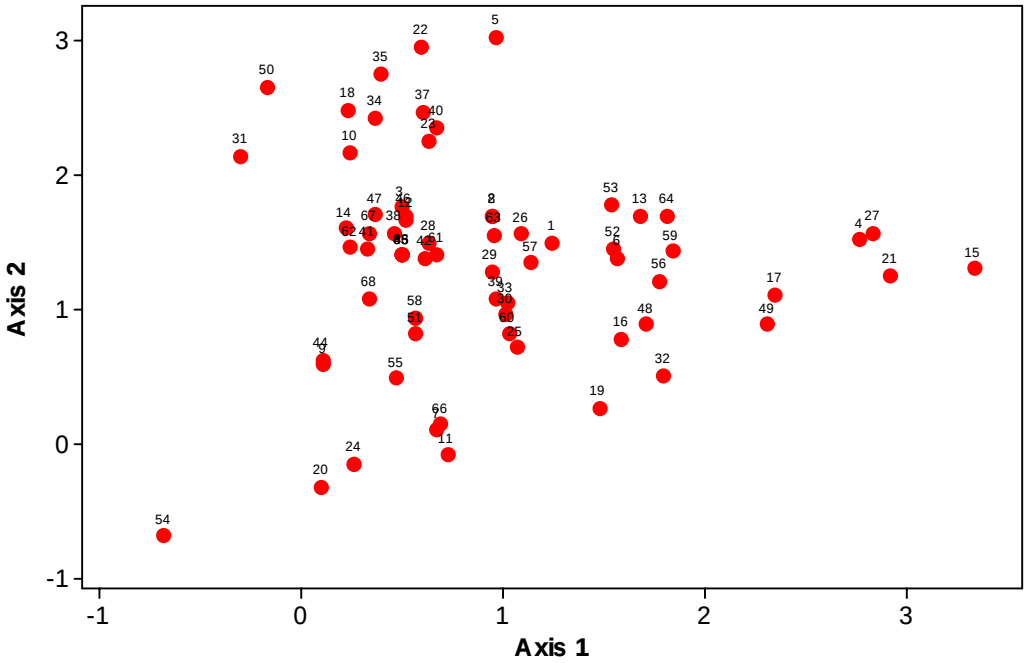


Figure 3.5: Ordination plot from the DECORANA showing the spread of species along axis 1 and axis 2. Each species is numbered according to the species list in appendix 2.

On figure 3.5 a possible outlier group away from the others along axis 1 are species 27, 4, 21 and 15, which represent *Canthingaster jathinopterous*, *Serranus psittacinus*, *Diodon holocanthus*, and *Halichoeres dispilus* respectively. These species were observed to appear in greater numbers when there is more dead coral, more rubble and less other fish.

At the same end of axis 1 are species 17 and 49, which represent *Pomacanthus zonipectus* and *Synodus lacertinus* respectively. These are also away from the main cluster but not as outlying as the group described above. *P.zonipectus* is only present in

11 sites (28% of sites) and the total amount counted was 27 individuals. They feed on benthic invertebrates and are usually associated with rocky reefs (Allen and Robertson, 1994). Whilst *S.lacertinus* is present in 2 sites (5.1% of sites) and only 3 are counted in total. This species is usually associated with sandy rubble areas near reefs (Allen and Robertson, 1994) and could be associated with dead, broken up coral. Both these are comparatively infrequently occurring species. At the opposite end of axis 1 is species number 54, which represents *H.maculicauda* and stands out from the rest of the sites. It is a shoaling fish present in only 12 sites but in large numbers with 1913 counted in total.

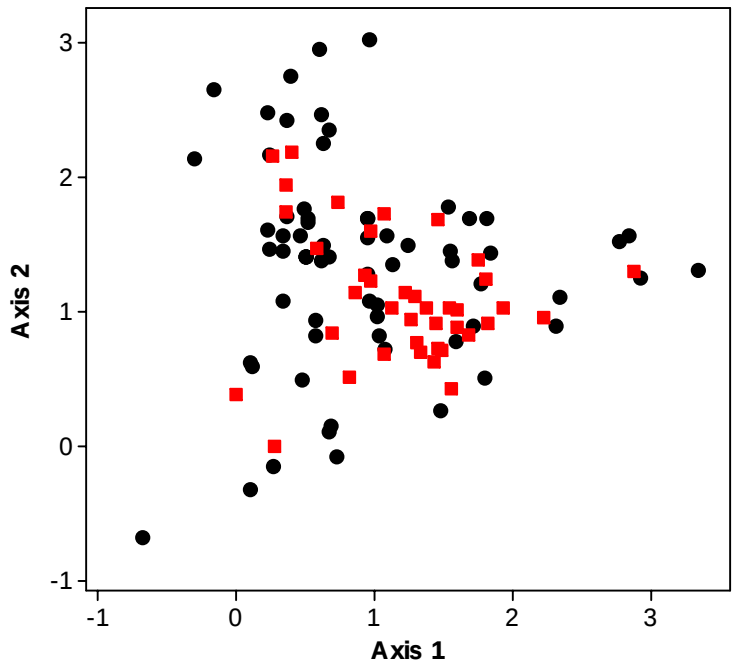


Figure 3.6: Ordination plot from the DECORANA showing a joint plot of both species and sites along axis 1 and axis 2. Species are represented by black circles and sites by red squares.

Figure 3.6 shows the trend in species along axis 1 and 2 overlaid with the trend in sites. It shows the reefs at Isla Chapera Northeast and Southeast (8 and 10) have far greater numbers of *H.maculicauda* and both the sites and the species are in the bottom left corner of figure 3.6. Other species close to these sites include *Balistes polylepis* and *Haemulon scudderi* both of which have their greatest abundance at Isla Chapera Northeast. The species *C.jathinopterous*, *S.psittacinus*, *D.holocanthus*, and *H.dispilus* are close to site 38 (Isla Caña) where a large proportion of the coral was dead and percentage algal turf cover was high.

The figures 3.4, 3.5 and 3.6, show the progression along the trends found by the DECORANA indicating which species are significant to the fish communities of that site. They may be significant by their presence or by their absence. The DECORANA site scores for axis 1 and axis 2 were subjected to nonparametric bivariate Spearman's Rank correlations with the environmental variables of habitat and location that were looked at previously. This shows whether the trends found by the DECORANA are explicable in terms of these environmental parameters and the results are displayed in table 3.11.

*Table 3.11: Spearman's Rank correlations between the DECORANA site scores for axis 1 and axis 2 and the habitat and location parameters. No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level, whilst ** indicates significance at the 99% level.*

Axis	**Habitats present**	**% *Pocillopora* species %**	**% Massive corals**	**% Algae and algal turf**	**South-North**	**West-East**
Axis 1	-0.317 p=0.049 *	--	--	--	--	--
Axis 2	--	--	--	--	-0.470 p=0.003 **	--

The diversity of habitats present may be partially responsible for the gradient along axis 1, with more habitats present at the lower values along axis 1. Whilst a statistically significant trend does exist you can see from figure 3.8, that there is a lot of variation in the data. The trend in the data represented by axis 2 and responsible according to its eigenvalue for 15.9% of the variation in the data may be explained by the distance north the sites are. However the fact that more communities were surveyed in the South may have an influence on the results with changes in fish communities possibly being a reflection of a difference in habitats surveyed and not oceanographic differences. This correlation is shown in figure 3.7, with the northern sites at the lower values on axis 2.

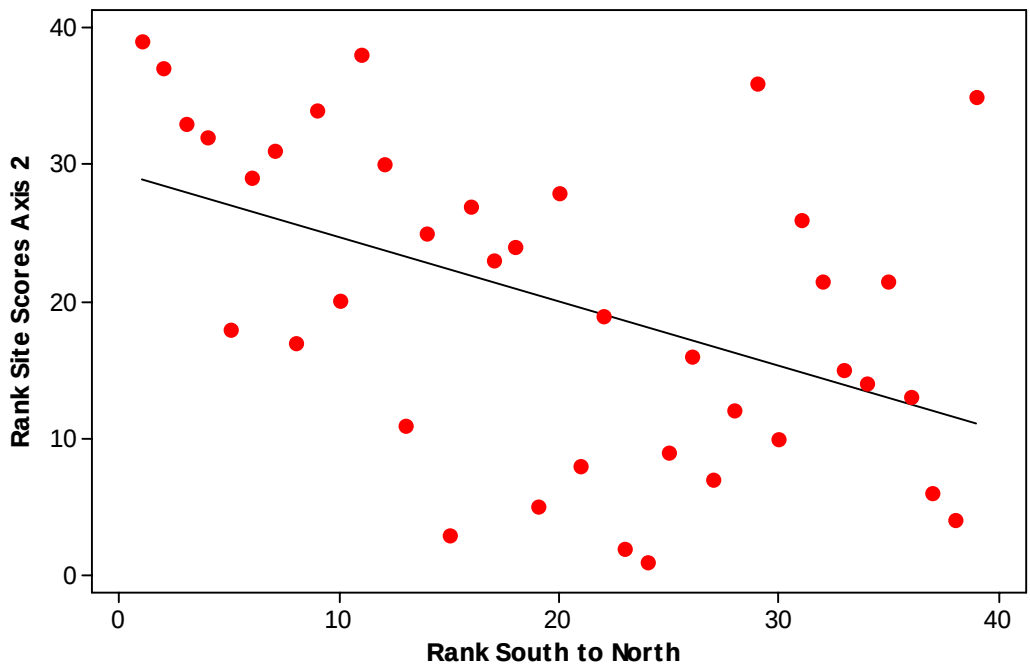


Figure3.7: Spearman's Rank correlation between the sites position south to north and the axis 2 site scores from the DECORANA, with a line of best fit.

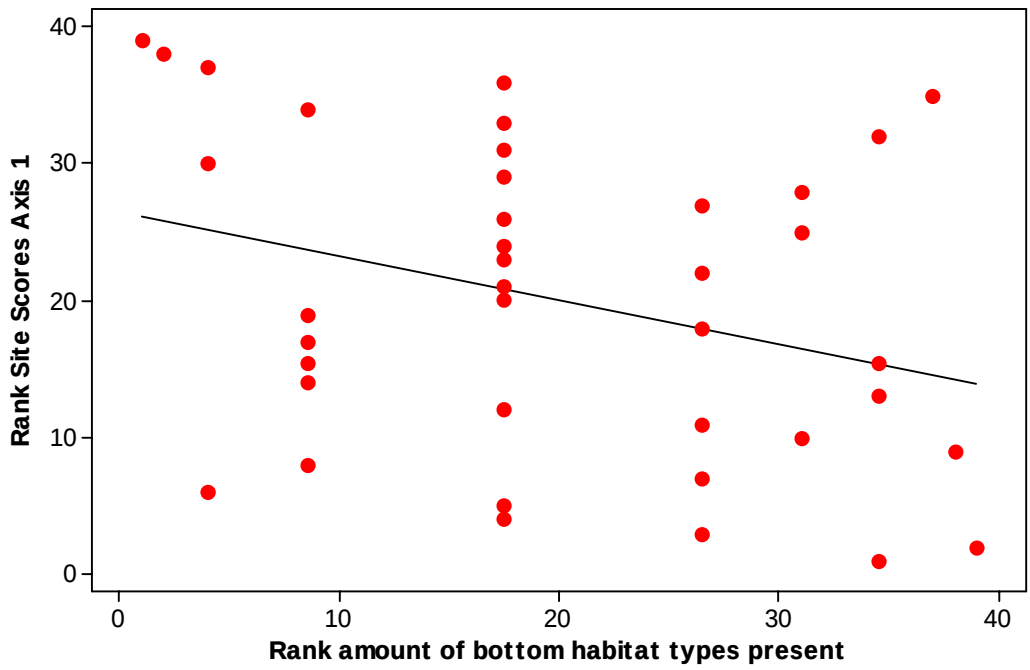


Figure 3.8: Spearman's Rank correlation between the amount of different bottom habitats present and the axis 1 site scores from the DECORANA, with a line of best fit.

DECORANA was also done using binary data, this shows whether presence and absence is important and eliminates the effects of shoaling species. The eigenvalues and their associated probabilities are shown in table 3.12. The low eigenvalues suggest that

the trends are not very significant therefore there are no significant trends in the data in terms of presence and absence of fish species and these eigenvalues were not investigated further.

Table 3.12: The eigenvalues for each of the axis created by DECORANA for the fish presence/ absence data at all the sites and the percentage of variation explained by each axis.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalues	0.100	0.069	0.050
Percentage	14.643	10.174	7.412
Cumulative percentage	14.643	24.817	32.229

Total fish abundance may hide trends associated with family groups, feeding groups, and other factors such as mobility guilds and life history stages. Cluster analysis and DECORANA were also done on the same data but combined to represent family groups. The results of this analysis are in subsection 3.7.3.

3.8 Multivariate Analysis of Family Data

A cluster analysis was done on the data for abundance of fish from each family at each site. The dendrogram is in appendix 5 and is similar to figure 3.1, which analysed all the fish species abundances. It again shows site Isla Contadora Southwest to be the most different from all the rest of the sites. It also shows a cluster of sites Isla Espiritu Santo, Isla Cañita and Isla Chapera Northeast and Southeast, which were the 4 sites with the high abundance of Haemulidae. Sites Isla Saboga North and Isla Bartolomé North and West cluster together and are in fairly close proximity to one another to the north of Isla Saboga and Isla Contadora.

Table 3.13 shows the eigenvalues for the family data. Axis 1 is significant, but axis 2 eigenvalue is very low and therefore not a significant trend. The site scores created by the DECORANA for axis1 versus axis2 were plotted in figure 3.9, as were the family scores for axis 1 and 2 in figure 3.10. These 2 graphs were then plotted together as a joint plot in figure 3.11.

Table 3.13: The eigenvalues for the axis created by DECORANA for the families of fish at all the sites and the percentage of variation explained by each axis.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalues	0.317	0.094	0.031
Percentage	50.129	14.913	4.924
Cumulative Percentage	50.129	65.043	69.984

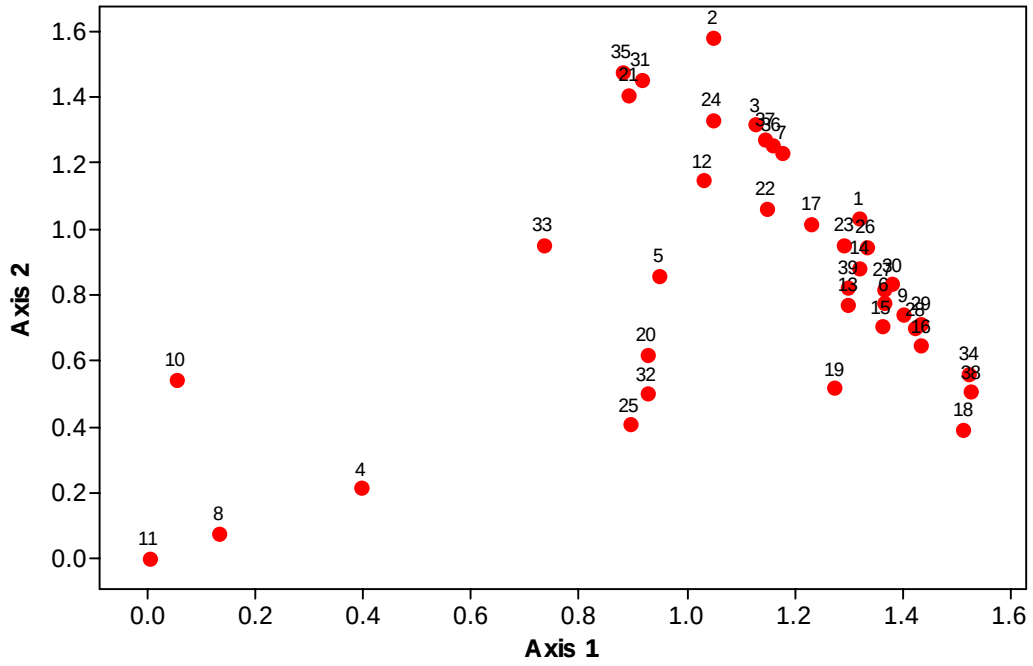


Figure 3.9: Ordination plot from the DECORANA using the family data showing the spread of sites along axis 1 and 2. Each site is numbered according to the site list in appendix 3.

Figure 3.9 shows sites Isla Espiritu Santo, Isla Cañita and Isla Chapera Northeast and Southeast (8, 10, 4 and 11) are all in a distinctly different group along axis 1 as would be expected due to the presence of large shoals of Haemulidae at these sites. Also, these 4 sites have the presence of Lutjanidae along with only 4 other sites, therefore axis 1 is possibly very heavily influenced by transient species and once Haemulidae are removed from the analysis there is very little trend at all in the data (table 3.14). The joint plot, figure 3.11 shows that these 4 reefs are influenced by Haemulidae and Lutjanidae. They also have zero of many of the same families such as Apogonidae, however they are not the only sites with zero of these fish.

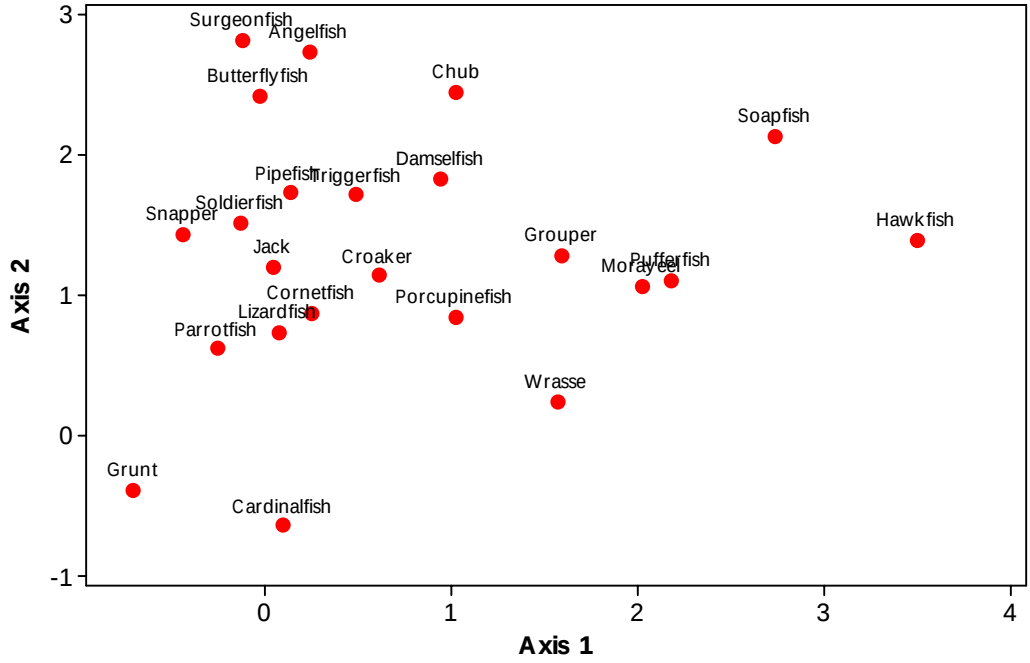


Figure 3.10: Ordination plot from the DECORANA showing the spread of families along axis 1 and axis 2.

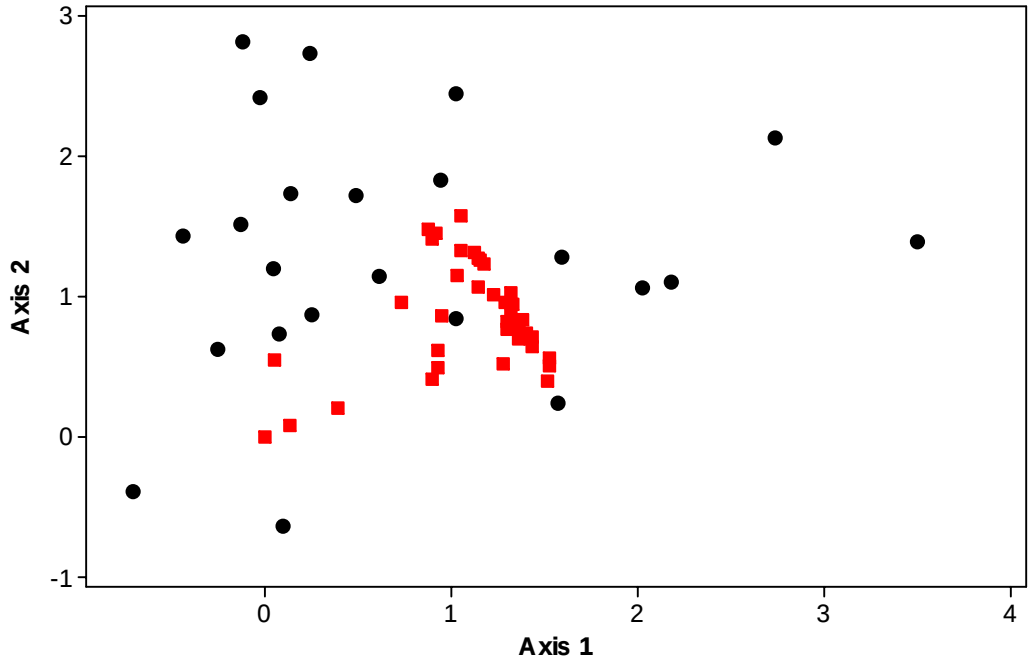


Figure 3.11: Ordination plot from the DECORANA showing a joint plot of both families and sites along axis 1 and axis 2. Families are represented by black circles and sites by red squares.

The eigenvalues for the family data but excluding the Haemulidae are in table 3.13, they show a much less significant value for axis 1. Therefore the presence of the grunts does have large influence on the trends found by the DECORANA.

Table 3.14: The eigenvalues for the axes created by DECORANA for the families of fish at all the sites excluding the Haemulidae and the percentage of variation explained by each axis.

	Axis 1	**Axis 2**	**Axis 3**
Eigenvalues	0.206	0.041	0.019
Percentage	52.944	10.402	4.776
Cumulative Percentage	52.944	63.346	68.122

3.9 Multivariate Analysis of Coral Framework Sites Only

Using the list provided by the benthic habitat survey the sites which were classed as coral communities were removed along with sites Isla Caña and Isla Cañita, which were classed as coral framework but were mainly dead coral, containing a very low percentage of live *Pocillopora* and a very high percentage of algal turf. This meant that those left had a more homogenous habitat, which should remove some of the variability in the data.

These framework sites only were subjected to the same bivariate nonparametric correlation as in table 3.6 and 3.7, which had revealed a trend in the total number of individual fish per site to increase with the number of habitats present and a greater number of fish in the west. With just the framework sites these relationships were no longer significant and no significant relationships were found. A cluster analysis was done on these framework sites, the dendrogram is shown in figure 3.12. This again shows the strong presence of Haemulidae with sites Isla Chapera Northeast and Southeast as a cluster and Isla Elefante alone. The cluster of sites Isla Pacheca North, Isla Saboga North, and Isla Mogo Mogo South and West are all in the northern island group, they all have high amounts of *Pocillopora*.

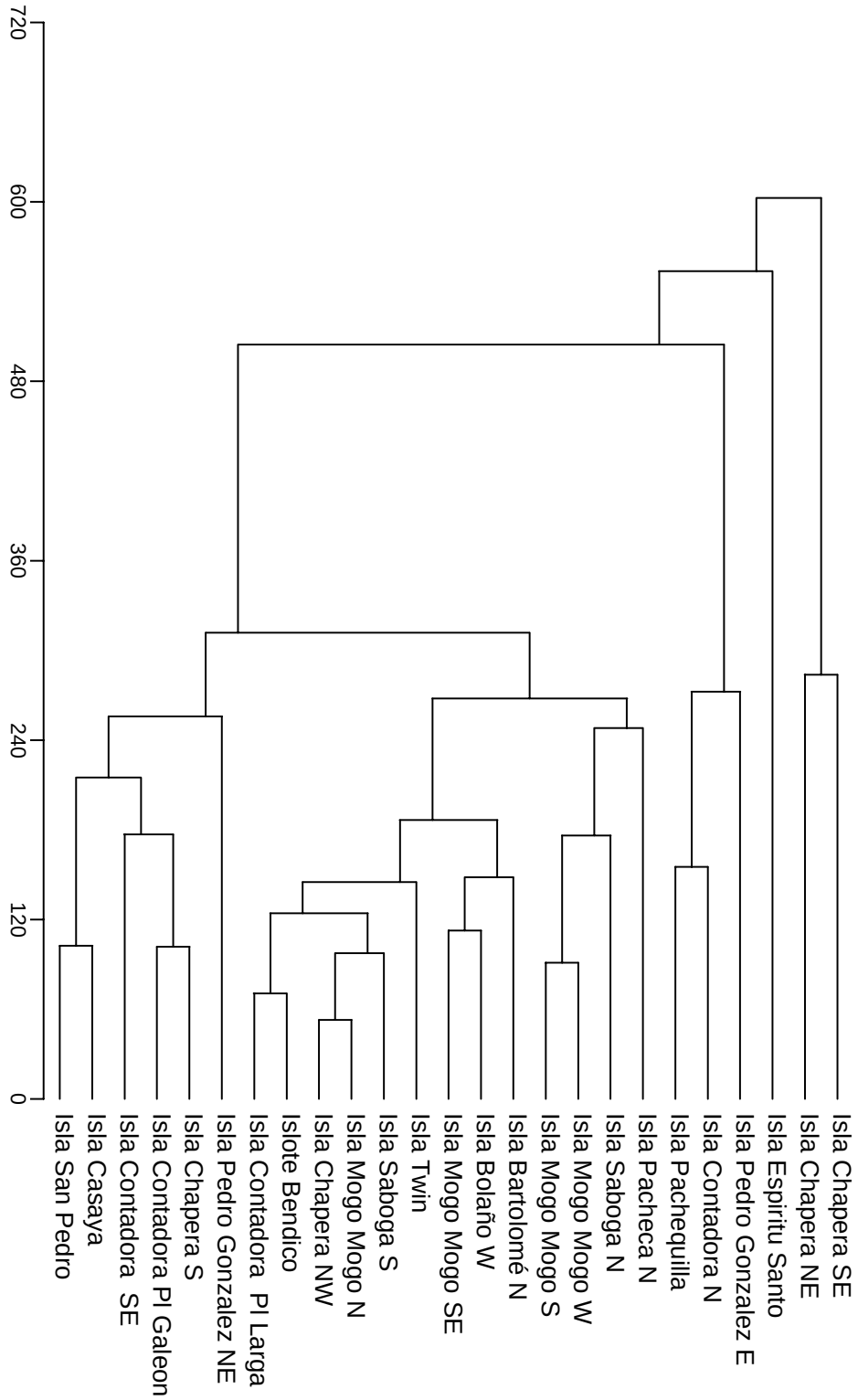


Figure 3.12: Dendrogram of coral framework site cluster analysis using Euclidean distance.

DECORANA was used giving the eigenvalues in table 3.15, which are significant for axis 1 and fairly low for axis 2. The values from the DECORANA axis 1 and 2 for sites, species and both together were plotted in figures 3.13, 3.14 and 3.15.

Table 3.15: The eigenvalues for the axes created by DECORANA for all the fish species at the framework sites only and the percentage of variation explained by each axis.

	Axis 1	Axis 2	Axis 3
Eigenvalues	0.390	0.155	0.047
Percentage	36.362	14.432	4.390
Cumulative Percentage	36.362	50.794	55.185

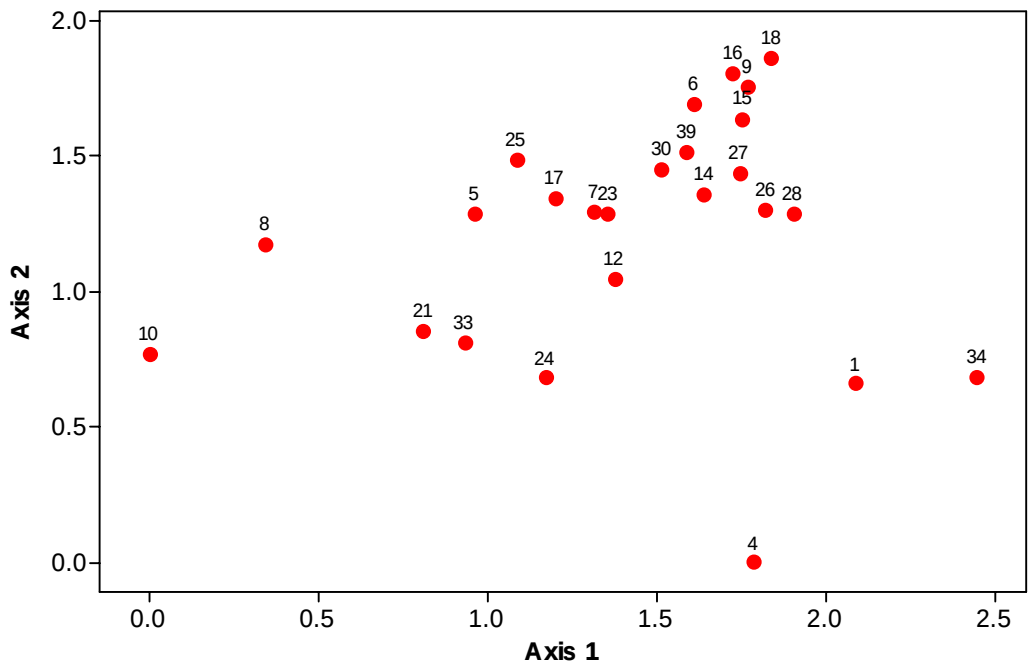


Figure 3.13: Results from the DECORANA showing the spread of the coral framework only sites along axis 1 and 2. Each site is numbered according to the site list in appendix 3.

Figure 3.13 shows sites Isla San Pedro, Isla Elefante and Isla Pedro Gonzalez Northeast, represented by 1, 4 and 34 respectively, as outliers. Site Isla Elefante is an outlier due to *H.steindachneri* abundance. Site Isla Pedro Gonzalez Northeast has the highest amount of freckled porcupine fish of any of the sites. Site Isla San Pedro has a low amount of algae and the highest amount of *Pocillopora* species of any of the sites and the lowest abundance of fish of any site. Sites 10 and 8 (Isla Chapera Northeast and Southeast) are also outliers and are due to *H.maculicauda* abundance.

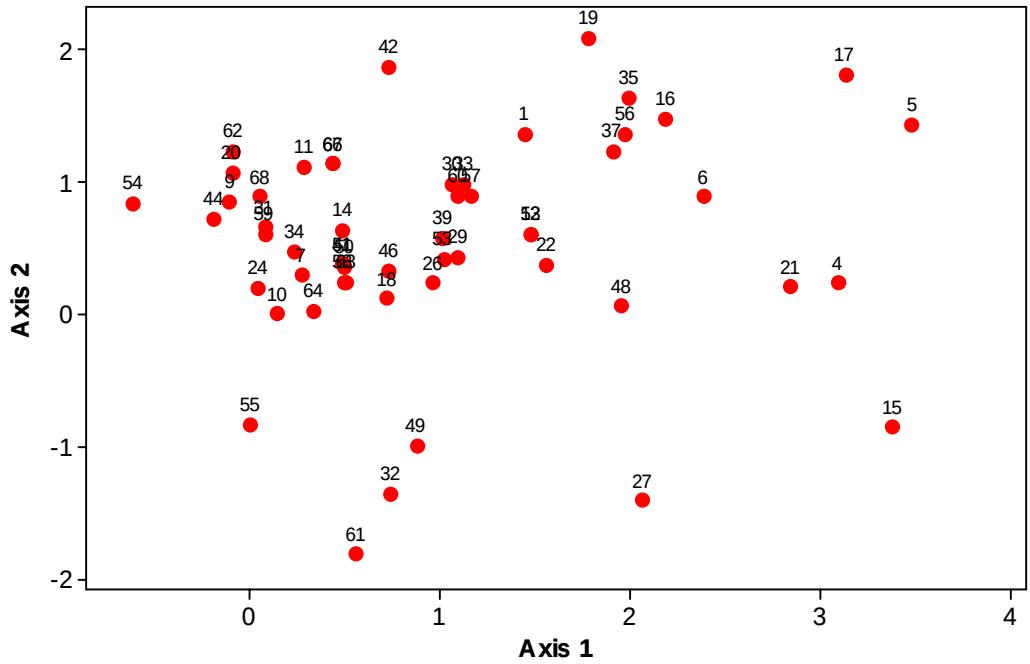


Figure 3.14: Results from the DECORANA showing the spread of the species on the coral framework only sites along axis 1 and axis 2. Each species is numbered according to the species list in Appendix 2

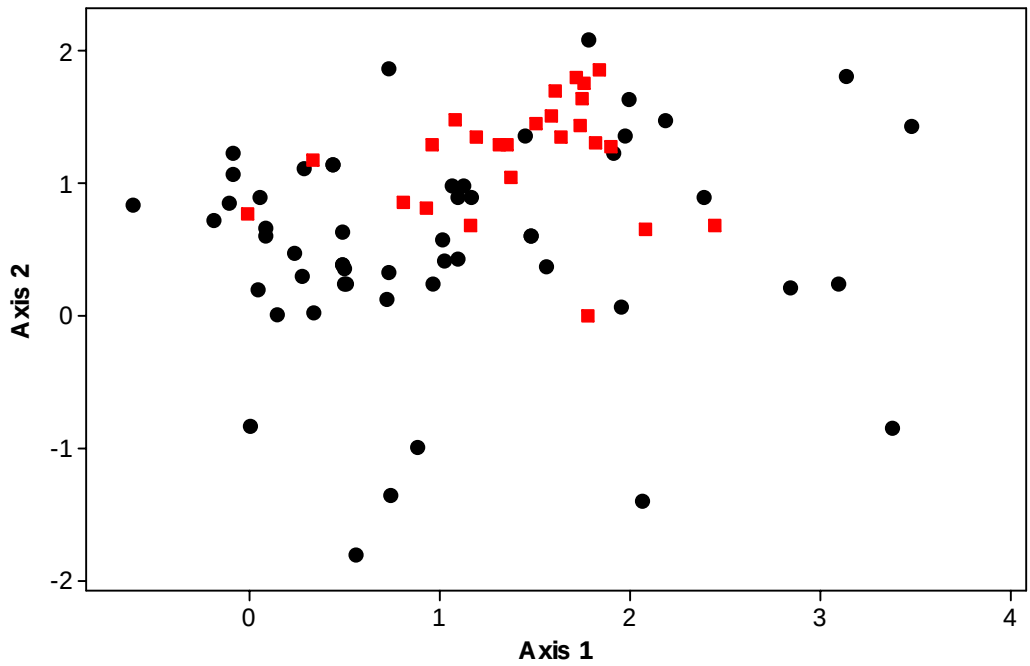


Figure 3.15: Results from the DECORANA for coral framework sites showing a joint plot of both species and sites along axis 1 and axis 2. Species are represented by black circles and sites by red squares.

Correlations were done with the environmental parameters and the results are shown in table 3.16. This shows that the north to south relationship is no longer present suggesting that this was due to the greater amount of coral communities surveyed in the South. However the relationship between the number of habitats present and the fish communities on axis 1 still exists for the frame sites alone.

*Table 3.16: Spearman's Rank correlations between the DECORANA site scores for axis 1 and axis 2 for just the coral framework sites and the habitat and location parameters. No significant correlation is indicated by –, where a significant correlation is present the correlation co-efficient is stated along with the associated probability and * indicates that it is significant at the 95% level, whilst ** indicates significance at the 99% level.*

Axis	Habitats present	All *Pocillopora* species %	All massive species %	All algae	South-North	West-East
Axis1	-0.444 P=0.026 *	--	--	--	--	--
Axis 2	--	--	--	--	--	--

DISCUSSION

4.1 Critical Overview of Methodology

Many disadvantages exist to the visual survey method, associated systematic errors have been studied by Brock (1982), Thresher and Gunn (1986) and Fowler (1987). Problems associated with Underwater Visual Census (UVC) have been discussed in section 1.6. The accuracy tests that took place before the survey commenced minimised bias due to underwater magnification, problems due to length estimation and due to differences between observers. At the depths at which our survey took place any effect on accuracy due to the detrimental physiological affects of SCUBA would be negligible. In most tropical reefs visibility is not a problem for UVC however in Las Perlas visibility can be low due to turbidity related to runoff, and this may affect the accuracy of the results. However, surveys did not take place when the visibility was considered too low.

Biases across species, time or space may occur. These are often due to difficulties in seeing fish, accurately counting or estimating length and differentiating among certain similar species (Sale, 1997). Studies comparing non-destructive visual counts to destructive counts have shown the visual surveys to have a good relationship with actual abundance for some species and types of fish (Sale and Douglas, 1981; St John *et al*, 1990), however they have been shown to be more accurate when a limited number of species are surveyed (Williams, 1986; Lincoln Smith, 1989). The aim of this study was for an overall community study, therefore all species except gobies and blennies were included; however it must be remembered that only those species that are diurnally active and are present in a calm to moderate sea state will have been included.

It has been stated that observers need to be trained and must have experience in identifying and estimating lengths accurately (English *et al*, 1994). In this survey observers had only a short time to train, little previous experience and no time to retrain throughout the survey. However, Harvey *et al*, 2001 found that novice observers (those with little experience of fish surveys) obtained results similar to and only slightly less accurate than experienced scientific divers. Visual surveys such as this can give good

relative comparisons to establish patterns but may not be accurate to real fish numbers, lengths and diversity.

Some species that were included in the counts were difficult to spot and could have been missed on some occasions. In areas where there were many fish of many species it was easier to miss smaller, more cryptic species; for example *Hippocampus ingens*, is highly camouflaged and hard to spot amongst the coral. Whereas in areas where few fish were present it was possible to be more accurate. Bellwood and Alcala (1988) found that it was difficult for an observer to estimate visually a wide range of fish sizes especially where small fish are included. *Canthigaster punctatissima*, is very small and stays very close to the reef, this was one of the more common species in small numbers, but present at 37 sites. At the scale of our survey counts of *C.punctatissima* may not be very accurate as it is likely that only those directly under the surveyor, or sufficiently disturbed by the surveyors movements may have been included, not necessarily all that are present in the transect. Some species were difficult to spot due to their behaviour, for example *Synodus lacertinus*, which hides in the rubble to ambush its prey (Allen and Robertson, 1994). Also members of the Holocentridae and the Apogonidae may have been difficult to count as they reside under overhangs to which they retreat in response to divers.

Some species are hard to identify, for example many of the Haemulidae look similar to one another and are often in large shoals, which may contain more than one species. Those that swim fast were also difficult to identify accurately such as the Carangidae, one species of which remained unidentified due to its speed and orientation. The narrow transects used give better counts, but are inadequate for these mobile species (Samoilys and Carlos, 2000). The speed at which transects were done may have caused bias in the estimates due to the observer efficiency or the presence of the diver (Lincoln-Smith, 1988; Thresher and Gunn, 1986; Fowler, 1987). Juvenile, adult and intermediate stages also makes the identification difficult, it also puts the fish into different feeding guilds making analysis of feeding groups less accurate.

There was a large variability between transects suggesting that within the reefs the fish distribution is not even. Thus there is an element of uncertainty that the survey

accurately represents the fish communities of each reef as a whole. There may be a strong influence on the fish communities by the habitat at a smaller scale than transects were at, due to the influence of microhabitats. The benthic transects were always run parallel to shore (Guzman pers. comm.) whilst the fish transects were at random. To run them in exactly the same place at the same time would have caused disturbance to the fish. The fish survey sometimes crossed more than one habitat type on the same site thus making it difficult to accurately relate the results to the habitat.

There were fewer relationships found with habitat variables than expected, this could be due to inaccuracy and bias in the methodology. It could also be due to other environmental variables that were not quantified having an effect. For example the weather and sea state may have influenced the amount of fish counted, by influencing the visibility or by causing lots of water movement, which may have caused smaller fish to find shelter. The surveys always took place when the sea state was suitable for diving, however this still encompassed a broad range of conditions.

4.2 Factors Affecting Fish Communities

Fish communities are not related to any one habitat parameter causing high variability in the data. It is thought that species segregate along more dimensions as the number of species increases (Levins, 1968). A high intercorrelation between the various habitat attributes can prevent the determination of the exact effect of each factor on the fish population (Bell and Galzin, 1984; Lirman, 1999). Many factors that were not measured in this study may affect fish communities such as water movement, size of the reef, distance between reefs, distance to land and the structural complexity of the reef. Transects were not recorded along an even depth and so this could not be used as a variable. The time of day and tidal state could affect the fish communities with different species active at different times of day and in different tidal states. Water quality and anthropogenic disturbance are also important factors, along with natural disturbance.

Different fish can be influenced in different ways by environmental factors, due to their mobility, trophic level, species and age giving them different dietary or spatial needs. Morphology, body size, home range, behaviour, social structure, sensory limitations,

and learning ability all affect their response to their environment (Wainwright and Richard, 1995; Ebersole, 1980; Bruggeman *et al*, 1994a, b; Forrester, 1991; Perry and Pianka, 1997; Marcotte and Browman, 1986). Reef fish are influenced by their habitat but also modify their habitat, therefore the relationship between the two is complex.

4.3 Fish Communities in Relation to Habitat Variables

It was expected that the fish communities would reflect changes in their habitat, due to differences in the benthic composition, which provide resources in terms of food and shelter. A failure to detect a relationship between fish and environmental variables such as habitat does not mean that they are not important in shaping the fish community, only that it is not important within the range observed (Sale *et al*, 1994; Jones and Syms, 1998). Not all species respond to all gradients in habitat structure and species may partition resources at some scales and not others. In the past both positive and negative correlations of the same relationship have been found due to different scales of surveys and different methodologies, for example fish abundance with coral cover (Bellwood and Hughes, 2001; Russ and Alcala, 1989; Carpenter *et al*, 1981; Bell and Galzin, 1984; Sano *et al*, 1984a).

Different fish may respond to different components of the habitat because of their need for resources such as shelter and food. They may also respond to habitat features in different ways such as differences in abundance, species richness, diversity, evenness or species composition. Percentage cover by *Pocillopora* species was expected to show a correlation with differences in fish community structure as it is the dominant bottom cover in many locations. It provides a completely different substrate to the rocky shores in terms of shelter and living spaces along with providing other resources to the fish such as food. However this relationship was not found with the fish community as a whole and was only found with piscivores, which have a negative correlation with *Pocillopora* cover. There may be too many other factors influencing fish distribution for any relationship to stand out.

The abundance of fish per site increased with the number of habitat types present, in agreement with results found by McCormick (1994) who also found a positive

correlation with fish species diversity, which was not the case here. A trend for fish communities as a whole to change with the amount of habitat types was found by Detrended Correspondence Analysis, explaining approximately 25% of the variation in the fish communities. However this trend was only found where all the sites were considered together and was no longer significant when just the coral framework sites were compared, indicating a difference between the fish communities at the two types of sites. The strength of this correlation between fish abundance and number of habitat types may depend upon the reef type, a study by Ohman and Rajasuriya (1998) shows a strong correlation with species richness and diversity on rocky reefs but not on coral reefs in Sri Lanka.

The diversity of habitats present did have a significant influence on the fish species distribution when analysis was done using the abundance of each species at each site, however once this was done with binary data this trend in the data became insignificant. Therefore, the amount of habitats present is not affecting species presence or absence at reefs, but it is affecting the abundance of fish found at a site.

4.4 Fish Communities in Relation to Location

The coral reefs in the Gulf of Panama are more abundant and attain greater dimensions on the Northern and Eastern sides of the islands (Glynn and Stewart, 1973), these are the shores facing away from the full effect of upwelling currents. Two of the three sites with the greatest abundance of fish were in the southwest of the archipelago, to the west side of Isla del Rey whilst the three sites with the lowest abundance of fish were to the east of Isla del Rey.

There is a greater abundance of fish in the west of the archipelago, where there are also more rocky reefs, than in the east, where there are more coral framework reefs. Therefore, fish are showing a greater abundance where they are more exposed to the effects of the upwelling. This may be due to the high productivity, and associated high levels of plankton, which would provide food for the dominant trophic group of planktivores. Whilst the fish abundance correlated with longitude, the Detrended Correspondance Analysis showed a trend due to latitude, even though no correlations were found with diversity, abundance or number of species. This suggests that location

is important to the fish communities as a whole. This trend was not apparent in presence/ absence data indicating that these differences within the archipelago are not reflected in presence/ absence of species. Where the *Pocillopora* framework reefs were looked at separately from the coral community reefs and the dead reefs, there was no longer a significant trend found by the multivariate analysis of the fish communities as a whole, due to longitude. This indicates that the greater amount of rocky reefs with coral communities surveyed in the west was responsible for the difference; to be investigated in more detail by Benfield (Ph.D Thesis).

Different families are distributed differently with respect to latitude and longitude. There are more Carangidae in the south; this family only occurred in 6 (15.4%) of the sites, and only 2 of these were in the northern cluster of sites. The same relationship was found with piscivores as a whole. Transient species were mostly piscivores or planktivores in a study by Friedlander and Parrish (1998). They may prefer the southern upwelling areas due to the high productivity, possibly benefiting from the pelagic food web and feeding on fish such as the anchoveta. They are often able to travel long distances and thus can move to shelter more easily in the more exposed conditions in the south than other less transient species. Transient species will have less need for sheltered conditions to be very close to them. The islands in the south are farther from one another to those in the north and the more transient species such as the Carangidae will be able to migrate between them.

The Sygnathidae represented by *Hippocampus ingens* were only found at 2 sites in the southwest, however it was also seen on one roving diver survey in the northern group of islands. Therefore not enough were seen for a significant trend.

There are more Labridae and Cirrhitidae in the north and the west, where there are also greater numbers of planktivores, invertivores and generalist feeders. This could be due to the predominance of rocky reefs to the west and the more exposed environment. Also where the small islands are present at the north of the archipelago there would be shorter migrating distance between the islands and between reefs for both larvae and mature fish. The west of the archipelago is influenced by the upwelling, whilst the north also has lots of framework sites providing structural complexity for shelter. The

Tetraodontidae are also in greater numbers in the north than the south though there is no trend with longitude in this group.

4.4.1 Specific Reefs

The average density of fish per reef was 192 per 120m³ transect, 160 per 100m³. The reef at Isla Contadora Southwest, in the middle of the Northern cluster of islands, is the only coral community in the immediate area and according to the cluster analysis it has a different fish community to all the others. It has a very low amount of *Pocillopora* species and a very high amount of Labridae being over 400 individuals greater than at any other site, the average total Labridae per site is 341 whilst this site has 1,254.

The sites to the northeast of Isla del Rey are similar to one another in terms of their reef fish communities indicating a locational difference. Three of the sites to the southeast of Isla del Rey also form a cluster. The reefs to the east of Isla del Rey are separated by large areas of mangrove and muddy bottom and by greater distances of deep water than between the northern islets and those to the west of Isla del Rey. The cluster to the southeast of Isla del Rey; Isla Comote, Isla de Monte and Isletilla de Puerco, are all coral communities with similar, low amounts of *Pocillopora;* they are 3 of only 7 sites with sea fans present and have high amounts of algal turf, therefore habitat is an important factor in this cluster. The diversity index for these sites is high for all of them and they all have an above average number of fish species per site.

The reef off Isla Caña to the east of Isla del Rey is very different from all the other sites; it is has been classified by the benthic survey as a framework although it has the lowest cover of live *Pocillopora* of all the sites and is 97.9% algal turf. The reason it has been classed as framework is due to dead coral cover, which has been colonised by algal turf. It has the second lowest abundance of fish and a low amount of species and low diversity. The fish community is noticeably different from all the other sites as it is the only site with no *Stegastes acapulcoensis*, it only had 3 individuals from the Pomacentridae family altogether. This is very low, as this is one of the most abundant families with an average of 275 per site. It also had few of the most common species *Thalassoma lucasanum* with only 2 sites having fewer. The site with the second lowest amount of *S.acapulcoensis* is Isla Cañita with only 17 counted in total over the 4

transects. This site also has the second lowest amount of live *Pocillopora* with only 3.059% cover and is also noted to have a large amount of dead coral, indicating a link between *S.acapulcoensis* and cover of live *Pocillopora*.

4.5 Trophic Guilds

The use of total abundances can be deceptive and may hide important trends associated with family groups, feeding groups, and other factors such as mobility guilds and life history stages. Ohman and Rajasuriya (1998) found that total abundance did not relate to any one habitat parameter but abundance of some species, families and trophic groups did, with these correlations due to different resource use. Some species appeared at many of the sites with 2 of the most abundant species appearing at all of them. This indicates a domination of fish that can be flexible in their habitat requirements, with a wide tolerance of environmental conditions.

Those with a mixed diet, generalist feeders, are thought to be unlikely to be sensitive to small or gradual changes in local environment conditions and are likely to occur in more locations. Generalists are the most common fish in the reefs of Las Perlas Archipelago, with almost two thirds of the population having a mixed diet. A flexible diet and resource use, makes them more able to adapt, to differences in their environment. Jones and Syms (1998) found that disturbance has a less extreme affect where overlapping habitats and resource use occurs, thus the high abundance of generalists may be due to the high levels of disturbance in this area due to the upwelling. On these reefs generalists are greater in the north and the west of the archipelago than in the south and east, suggesting either a response to environmental conditions across the archipelago, or a competitive advantage over those fish without such broad feeding strategies.

Many of the fish eat either plankton or invertebrates as all or part of a mixed diet. Those that eat only plankton are more common than those that eat any other specific diet. Coral reef fish communities are dominated numerically and in biomass by planktivores (Williams and Hatcher, 1983; Russ 1984c). The abundance of planktivores suggests that the common species are not totally dependant on the reefs for their food supply and that the reefs provide other resources. There is an increase in planktivores to the north and

the west, probably due to the greater influence of the upwelling bringing more plankton to the exposed west side of the archipelago. Also due to the greater amount of coral framework reefs in the north and the close proximity of the reefs to one another aiding fish dispersion. A study by Arreola-Robles and Elorduy-Garay (2002) supports this, finding more planktivorous fish at exposed sites.

Invertivores are the second most common trophic group; this group may rely on the productivity and the shelter of the reefs to provide prey organisms, and to provide them with shelter. Invertebrate feeders however, have been found to have a positive relationship with the size of holes (Friedlander and Parrish, 1998). There may be more of this particular guild in the north and west due to the productivity caused by the upwelling providing a source of food for the invertebrates on which these feed and also due to the structural complexity of the coral frameworks in the north.

Piscivores are the least most abundant group apart from obligate corallivores of which there are none (www.fishbase.org). The low abundance of predators could be due to their often transient nature and fast speed making them difficult to count. Also they are further up the food chain and due to energy loss through trophic levels have a lower biomass. They were found to increase from north to south in the archipelago as discussed in section 4.4, possibly due to the change in habitat with a greater abundance of rocky reefs in the south. The fewer piscivores in the north may be allowing the greater abundance of planktivores, invertivores and generalists by lowering the threat of predation. They are often transient and as a result have been shown to have limited correlations with the habitat (Friedlander and Parrish, 1998). However at the scale of this study they were the only group to show a correlation with the dominant bottom types. With less *Pocillopora* there are less piscivores, whilst greater algal cover gives a greater amount of piscivores. This combined with the increase in piscivores in the south indicates a difference between the habitats in the north and the south of the archipelago.

Herbivores are high in numbers yet the abundance of omnivorous species is low. Smaller, more sedentary herbivores have been found in other studies to correlate with variation in the reefs such as hole volume and rugosity (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984), which were not included as part of this study. There was no

correlation found between herbivores and cover of algal turf or coral cover as was found by Ohman and Rajasuriya (1998) who showed herbivores to relate positively with coral cover and negatively with depth. Whilst Ohman (1998) showed herbivores to be more common where there was more turf algae. Arreola-Robles and Elorduy-Garay (2002) found more herbivorous fish at sheltered reefs, however our study does not support this as there are not a greater amount of herbivores on the more sheltered east side of the archipelago.

According to www.fishbase.org, no obligate corallivores are present. Those that have a mixed diet which includes a coral component were not found to have any correlation with coral cover, unlike Ohman and Rajasuriya (1998) and Ohman (1998). This was possibly due to the mixed diet of the species found here.

The increase in generalists, planktivores and invertivores in the north and west may be responsible for an increase in fish abundance overall in the west. However, total abundance was not found to increase in the north compared with the south; this is possibly due to the decrease in piscivores in the north.

The separation of fish into feeding groups relied on the accuracy of the sources, which were not always very specific, as not enough research has been done on many of the species. Often the dietary descriptions were broad and due to the compilation of www.fishbase.org, from different sources. What one source may describe as feeding on invertebrates, another source may describe as feeding on coral or zooplankton. Also those classified as generalists may not be opportunists, they may be predominantly classed as one sort of feeder, but this was often not clear from the sources. They might also change their food over their lifetime and so may be a member of a different feeding guild depending upon age, this was not clear from the sources. However with limited information available, it has to be assumed that these sources were correct and the overall trends are valid. The multivariate analysis was not done on the trophic guilds due to the uncertainty in the classification.

4.6 Fish Species

In total 76 species were seen in Las Perlas Archipelago, the dominant reef fish species are *Thalassoma lucasanum*, *Chromis atrilobata* and *Stegastes acapulcoensis* between them making up 65% of the total fish found. The family with the greatest abundance was the Labridae, followed by the Pomacentridae then the Haemulidae; over 90% of the fish were in these 3 families.

Many species have a wide home range and are not specific to habitat, they may be associated with substratum but not confined to a specific patch (Lavett-Smith, 1978). The most abundant reef fish in Las Perlas Archipelago are widely spread, apart from the Haemulidae, which are found at few sites but in large numbers. These visiting shoals have a significant impact on the data analysis but are not related to environmental conditions and are a transient group. For example *Microlepidotus brevipinnis* was only found at one site but 150 individuals were counted. *Haemulon maculicauda* is present in 12 sites but often appears in large numbers with 1913 in total counted. The 4 sites with the highest abundance of Haemulidae also have the presence of Lutjanidae along with only 4 other sites. Trends in the multivariate analysis were very heavily influenced by these transient species and when the Haemulidae were removed from the multivariate analysis' trends in the fish communities overall were insignificant. The presence of such vast quantities of Haemulidae could have made it difficult for observers to count other species and may have influenced the results.

Most of the other species appearing at few sites were in low numbers. Some species such as *Epinephelus labriformis* was a common species, at many of the sites, but was solitary and never present in large numbers.

No distinct fish communities existed, however the species, *Serranus psittacinus*, *Diodon holocanthus*, and *Halichoeres dispilus* were related to sites with a greater amount of dead coral and rubble colonised by algal turf and where there was low fish abundance and diversity, such as at Isla Caña North. This relationship is unlikely to be due to them feeding on the algal turf as none of these fish are reported to be herbivorous. They are

all fairly camouflaged species; therefore this may be a consequence of them being more visible and thus easier to count when there are less other fish present. It is possible that these species are out-competed where more live coral is present. Close to this cluster of species is *Synodus lacertinus*, which only appears in 2 sites, and only 3 individuals are counted in total. This species is usually associated with sandy rubble areas near reefs (Allen and Robertson, 1994) and could be associated with dead, broken up coral.

A strong cluster of sites are those with the 6 highest abundances of Pomacentridae; they do not have any striking similarities in relation to habitat types or location, but show that Pomacentrids have a strong impact on the multivariate analysis also.

4.7 Fisheries

More needs to be known about the fisheries in the area in order to make any sort of assessment regarding the importance of the reefs to the fisheries, which types or areas of reef are most important and also the potential effect of fisheries in the area. This study could be used for a comparison with fishery data once more is available. Competition and predation cannot be used as a basis for multi-species fishery models for management of coral reefs, as there are so many other controls on the population (Doherty and Williams, 1988).

Little data is available for local fisheries. Information based on worldwide fisheries, available from www.fishbase.org suggests that 30 of the species encountered, approximately 43% of individuals present, are not likely to be exploited at any level. Whilst the other 46 species are reported to be exploited in some part of the world and at some level, whether for aquariums, fisheries, gamefish or baitfish. However it is very unlikely that all these fish are exploited at this location. The families known to be fished in the area include Carangidae, Lutjanidae and some Serranidae.

One of the species present *Hippocampus ingens*, the Pacific Seahorse, is on the IUCN (International Union for Conservation of Nature and Natural Resources) Red List. It is listed as Vulnerable (VU A4cd) based on declines of at least 30%. These declines are caused by targeted catch, incidental capture and habitat degradation. *H. ingens* is traded for traditional medicine, curios and aquaria. They are incidentally caught, as bycatch, by

the shrimp trawl fishery and other fisheries and are and are affected by habitat degradation along the Pacific coast of Panama (www.redlist.org). *Hippocampus* was listed in Appendix II of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) in November 2002 with implementation in 2003. In Panama, *H. ingens* are included under the Ministry of Agriculture's decree 19.450, which regulates the extraction of coral reef fishes (www.redlist.org).

Over 75% of the fish surveyed were made up of just 5 species, this shows a high domination by what were all small species and would be unlikely to make profitable fisheries. Over 75% of the 3 most abundant species were <10cm, therefore not having a great contribution to biomass. Over 94% of fish overall were less than 20cm and over 99% were less than 31cm in length. This could be due to the current fisheries removing many of the larger fish. It could be that the reefs are mainly nursery grounds and the larger fish may move offshore or to different areas such as the mudflats, where they can benefit from different food types or it may be that the area supports mainly small fish. Whilst the small fish may not be of direct importance to the fisheries, they will form an important part of the food chain for fishery species.

4.8 Further Research

The roles of individuals within a community can change through their lifetime therefore life history stages of fish could be taken into account to see if there are differences within the archipelago due to nursery areas for different species. Also the different mobility guilds could be investigated to see if their distribution differs and how they respond to environmental differences within the archipelago. Further research is already underway as part of the Darwin Initiative by S.Benfield (Ph.D thesis) relating to fish habitat associations.

There are many environmental factors that could be having an impact on the fish community distribution, which were not measured as part of this study, which could be useful to measure if further work was done, such as depth, water movement and structural complexity. On many of the sites the larger massive corals were on the periphery of the framework and therefore may not have been included to a large extent in the benthic habitat survey, or indeed the fish transects. Also transects were at too

large a scale and were not specifically over one sort of habitat, often incorporating many habitats, therefore the effect of massive corals would perhaps have been diluted. A more appropriate survey to see if this observation was significant may have been a stationary diver survey over the massive coral species and over the *Pocillopora* species.

To increase the accuracy of the survey, counts could have been restricted to just the species which are expected to be influenced by the habitat as suggested by Sale (1991) and by keeping the size range of species counted to a minimum (Bellwood and Alcala, 1988). Some species may increase as a function of the area of the reef (Anderson *et al*, 1981; Williams, 1991), Donaldson (1996) found a correlation between locality size and fish species diversity. There is predicted to be lower species diversity due to lower species equilibrium around small islands compared to large ones or to continental masses (McArthur and Wilson, 1967). The distance from large islands or continental masses can also make a difference. Distance to land may influence fish populations depending upon terrestrial influences (Letourneur *et al*, 1998). Distance to land, size of the reef, and size of the adjacent island could all be investigated as potential causes of the fish community distribution, with the differences in trophic guilds between the small islands in the north and the large islands in the south indicating that this could be a factor.

CONCLUSIONS

The fish communities of Las Perlas Archipelago, Panama show a high level of dominance by just a few species, the most abundant being *Thalassoma lucasanum, Chromis atrilobata* and *Stegastes acapulcoensis.* In total 76 species were recorded with an average abundance of 192 fish per 120m³ across all the reefs. Over 94.14% of the fish counted were less than 20cm and over 99% less than 31cm. There is a trend in the fish communities for a greater abundance of fish in the west of the archipelago than in the east. There is also a trend in the fish communities to change with latitude. The dominant feeding groups in Las Perlas Archipelago are the planktivorous fish and the invertivores. There was an increased number of planktivores, invertivores and fish with a mixed diet the north and the west of the archipelago, whilst piscivorous fish are greater in the south than in the north. These locational differences can be attributed to oceanographic and habitat differences throughout the archipelago.

There is also a trend for a greater fish abundance where there is a greater amount of bottom types present indicating a link with habitat. The piscivorous fish are the only feeding group to show a link to the major bottom cover, with a negative correlation with percentage *Pocillopora* cover and a positive correlation with algal turf cover. This could also autocorrelate with the locational differences, with a positive correlation not necessarily meaning causation, and there could be many factors responsible. The reef that was the most different from the others was at Isla Caña North and this difference may be attributed to a large amount of dead coral colonised by algal turf. Species that were abundant at this site and could be linked to areas of dead coral include *Serranus psittacinus, Diodon holocanthus, Synodus lacertinus* and *Halichoeres dispilus.*

Differences do therefore exist within the reef fish communities of Las Perlas Archipelago related to both habitat and oceanography. With different groups of fish reacting in different ways to the environmental differences in the archipelago.

REFERENCES

Ackerman, J.L., Bellwood, D.R., 2000. Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Mar. Ecol. Prog. Ser*. **206**, 227-237.

Aguilar, C., González-Sansón, G., Munkittrick, K.R., MacLatchy, D.L., 2004. Fish Assemblages on fringe coral reefs of the Northern Coast of Cuba near Havana Harbor. *Ecotoxicology and Environmental Safety*. **58** (1), 126-138.

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

Alm, G., 1959. Relation between maturity, size and age in fishes. *Rep. Inst. Freshwat. Res. Dottningholm*. **40**, 5-146.

Anderson, G.R.V., Erlich, A.H., Erlich, P.R., Roughgarden, J.D., Russell, B.C., Talbot, F.H., 1981. The community structure of coral reef fishes. *Amer. Nat*. **117**, 476-495.

Arreola-Robles, J.L., Elorduy-Garay, J.F., 2002. Reef fish diversity in the region of La Paz, Baja California Sur, Mexico. *Bulletin of Marine Science*. **70** (1) 1-18

Baisre, J., 2000. Chronicle of Cuban marine fisheries (1935–1995): trend analysis and fisheries potential. *FAO Fish. Tech. Pap*. **394**.

Beger, M., Jones, G.P., Munday P.L., 2003. Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes. *Biological Conservation*. **111** (1), 53-62.

Bell, J. D., Craik, G.J.S., Pollard, D.A., Russell, B.C., 1985. Estimating length frequency distributions of large reef fish underwater. *Corals Reefs*. **4**, 41–4.

Bell, J.D., Galzin, R., 1984. Influence of live coral cover on coral-reef fish communities. *Mar. Ecol. Prog. Ser.* **15**, 265–274.

Bellwood, D.R., 1988. Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *J. Fish Biol.* **33**, 213-219.

Bellwood, D.R., Alcala, A.C., 1988. The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs*. **7**, 23-27.

Bellwood, D.R., Hoey, A.S., Choat, H.J., 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters.* **6**, 281-285.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. *Science* **292**, 1532–1534.

Boecklen, W.J., 1986. Effects of habitat heterogeneity on the species-area relationships of forest birds. *J. Biogeogr*. **13**, 59-68.

Bohnsack, J.A., 1982. Effects of piscivorous predator removal on coral reef fish community structure. In: Caillet, G.M., Simenstad, C.A., (eds) Gutshop '81. *Fish food habit studies. Washington Seagrant Publication. University of Washington, Seattle* 258-267.

Bohnsack, J.A., Harper, D.E., McClellan, D.B., Hulsbeck, M.W., Rutledge, T.N., Pickett, M.H., Eklund, A., 1992. Quantitative visual assessment of fish community structure in Biscayne National Park. *Draft Report. U.S. Dept. Comm*. 46.

Bouchon-Navaro, Y., Louis, M., Bouchon, C., 1997. Trends in fish species distribution in the West Indies. *Proc 8th Int Coral Reef Sym*. **1**, 987-992.

Brock, R.E., 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Mar. Sci*. **32**, 269-276.

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

Bruggeman, J.H., Begeman, J., Bosna, E.M., Verburg, P., Breeman, A.M., 1994a. Foraging by the stoplight parrotfish *Sparisoma viridae*. I. Food selection in different socially determined habitats. *Mar. Ecol. Prog. Ser*. **106**, 57-71.

Bruggeman, J.H., Kuyper, M.W.M., Breeman, A.M., 1994b. Comparative analysis of foraging and habitat use by the Sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Mar. Ecol. Prog. Ser*. **112**, 51-66.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* **27**, 477-500.

Carpenter, K.E., Miclat, R.I., Albaladejo, V.D., Corpuz, V.T., 1981. The influence of substratum structure on the local abundance and diversity of Philippine reef fishes. *Proc. 4th Int Coral Reef Sym*. **2**, 495-502.

Choat, J.H., Bellwood, D.R., 1991. Reef fishes: their history and evolution. In: Sale, P.F., (ed) The Ecology of Coral Reef Fishes. *Academic Press*. 39-60.

Coates, A.G., Jackson, J.B.C., Collins, L.S., Cronin, T.M., Dowsett, H.J., Bybell, L.M., Jung, P., Obando, J.A., 1992. Closure of the Isthmus of Panama: The near-shore marine record of Costa Rica and Western Panama. *Geological Society of America Bulletin*. **104**, 814-828.

Colwell, R.K., 1973. Competition and coexistence in a simple tropical community. *Am. Nat*. **107**, 737-760.

Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. *Science* **199**, 1302–1310.

Connell, S.D., Kingsford, M.J., 1998. Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. *Coral Reefs*. **17**, 49-57.

Connell, S.D., Samoilys, M.A., Lincoln Smith, M.P., Leqata, J., 1998. Comparisons of abundance of coral reef fish: Catch and effort surveys *vs* visual census. *Australian Journal of Ecology*. **23,** 579-586.

D'Croz, L.D., Robertson, D.R., 1997. Coastal oceanographic conditions affecting coral reefs on both sides of the Isthmus of Panama. *Proc. 8th Int Coral Reef Sym*. **2**, 2053-2058.

Denny, C.M., Babcock, R.C., 2004. Do partial marine reserves protect reef fish assemblages? *Biological Conservation*. **116** (1), 119-129.

Doherty, P.J., Meekan, M.G., Miller, I.R., Osborne, K., Thompson, A.A., 1997. Catastrophic loss of coral cover from reefs in the southern Great Barrier Reef and the impact on fish recruitment. *Proc. 8th Int. Coral Reef Sym.* **1**, 1005-1010.

Doherty, P.J., Williams, P.McB., 1988. The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. A. Rev*. **26**, 487-551.

Donaldson, T.J., 1996. Fishes of the remote southwest Palau islands: a zoogeographic perspective. *Pac. Sci*. **50**, 285-308.

Dulvy, N.K., Stanwell-Smith, D., Darwall, W.R.T., Horrill, C.J., 1995. Coral mining at Mafia Island, Tanzania: a management dilemma. *Ambio*. **24**, 358-365.

Eagle, J., Geoffrey, P.J., McCormick, M.I., 2001. A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae). *Mar. Ecol. Prog. Ser*. **214**, 253-265.

Ebeling, A.W., Hixon, M.A., 1991. Tropical and temperate reef fishes: a comparison of community structures. 509-563. In: Sale, P.F., (ed) The ecology of fishes on coral reefs. *Academic Press, San Diego*.

Ebersole, J.P., 1980. Food density and territory size: an alternative model and a test on the reef fish *Eupomacentrus leucosticus*. *Am. Nat*. **115**, 492-509.

English, S., Wilkinson, C., Baker, V., (eds.). 1994. Survey manual for tropical marine resources, 368 p.

Falcon, J.M., Bortone, S.A., Brito, A., Bundrick, C.M., 1996. Structure of and relationships within and between the littoral rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar. Biol*. **125**, 215-231.

Fausch, K.D., Lyons, J., Karr, J.R., Argeimeier, P.L., 1990. Fish communities as indicators of environmental degradation. *Am. Soc. Symp.* **8**, 123–144.

Forrester, G.E., 1991. Social rank, individual size and group composition as determinants of food consumption by humbug damselfish, *Dascyllys aruanus*. *Anim. Behav*. **42**, 701-711.

Fowler, A.J., 1987. The development of sampling strategies for population studies of coral reef fishes. A case study. *Coral Reefs*. **6**, 49-58.

Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *Journal of Experimental Marine Biology and Ecology* **224**, 1–30.

García-Charton, J.A., Pérez-Ruzafa, Á., 2001. Spatial pattern and the habitat structure of a mediterannean rocky reef fish local assemblage. *Mar. Biol*. **138**, 917-934.

Glynn, P.W., 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs*. **46**, 431-456.

Glynn, P.W., 1977. Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. *J. Mar. Res*. **35**, 567-585.

Glynn, P.W., 1984. Widespread coral mortality and the 1982/83 El Nino warming event. *Environm. Conserv*. **11**, 133-146.

Glynn, P.W., 1988a. El Nino-Southern Oscillation 1982-1983: nearshore population, community, and ecosystem response. *Annu. Rev. Ecol. Syst*. **19**, 309-345.

Glynn, P.W., 1996. Eastern Pacific reef coral zoogeography and faunal flux: Durham's dilemma re-visited. *8th Int. Coral Reef Sym. Abstracts*. 73.

Glynn, P.W., Cortes, J., Guzman, H.M., Richmond, R.H., 1988. El Niño (1982–1983) associated coral mortality and relationship to sea surface temperature deviations in the trophical eastern Pacific. *Proc 6th Int Coral Reef Sym*. **3,** 237–243.

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

Glynn, P.W., Stewart, R.H., 1973. Distribution of coral reefs in the Pearl Islands (Gulf of Panama) in relation to thermal conditions. *Limnol. Oceanogr*. **18**, 367-379.

Glynn, P.W., Stewart, R.H., McCosker, J.E., 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Sonderdruck aus der Geologischen Rundschau*. **61**, 483-519.

Glynn, P.W., de Weerdt, W.H., 1991. Elimination of two reef building hydrocorals following the 1982-83 El Nino warming event. *Science*. **253**, 69-71.

Goldschmid, A., Kotrschal, K., 1981. Feeding ecology of three populations of *Blennius incognitos* Bath, 1968. (Pisces: Teleostei Bleniidae) during the reproductive period and under huan influence. *Mar. Ecol.* **2**, 1-14

Gomez, E.D., 1997. Reef management in developing countries: the Philippines as a case study. *Proc. 8th Int Coral Reef Sym.* **1**, 123-128.

Grigg, R.W., 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar. Ecol. Prog. Ser.* **103**, 25-34.

Guzman, H.M., Robertson, D.R., 1989. Population and feeding responses of the corallivorous pufferfish *Arothron meleagris* to coral mortality in the eastern Pacific. *Mar. Ecol. Prog. Ser*. **55**, 121-131.

Harmelin-Vivien, M.L., Bouchon-Navaro, Y., 1981. Trophic relationships among chaetodontid fishes in the Gulf of Aquaba (Red Sea). *Proc 4th Int Coral Reef Sym.* 537-544.

Harvey, E., Fletcher, D., Shortis, M., 2001. A comparison of the precision and accuracy of estimates of reef-fish lengths determined visually by divers with estimates produced by a stereo-video system. *Fish. Bull*. **99**, 63-71

Hiatt, R.W., Strasburg, D.W., 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr*. **30**, 65-127.

Hilomen, V.V., Gomez, E.D., 1988. Distribution of fish communities in some Philippine reefs. *Proc 6th Int Coral Reef Sym*. **3**, 257–262.

Hobson, E.S., 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull*. **72**, 915-1031.

Holbrook, S.J., Kingsford, M.J., Schmitt, R.J., Stephens, J.S., 1994. Spatial and temporal patterns in assemblages of temperate reef fish. *Am. Zool*. **34**, 463-475.

Jennings, S., Grandcourt, E.M., Polunin, N.V.C., 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs*. **14**. 225-235.

Johannes, R.E., 1978. Reproductive strategies of coastal marine fishes in the tropics. *Environ. Biol. Fish*. **3**, 65-84.

Jones, G.P., 1987. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology*. **68(5)**, 1534-1547.

Jones, G.P., Syms, C., 1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. *Australian Journal of Ecology*. **23**, 287-293.

Kaufman, L.S., 1977. The three-spot damselfish: effects on benthic biota of Caribbean coral reefs. *Proc. 3rd Int. Coral Reef Sym*. **1**, 559-564.

Kaufman, L.S., 1983. Effects of hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs*. **2**, 43-7

Kenchington, R.A., 1992. *Managing marine environments*. Taylor and Francis, NY. 34-5.

Kulbicki, M., 1990. Comparisons between rotenone poisonings and visual counts for density and biomass estimates of coral reef fish populations. In: Ricard, M., (ed.) *Proceedings of the International Society for Reef Studies Congress, Noumea*. 105-112.

Lavett-Smith, C., 1978. Coral reef fish communities a compromise view. *Env. Biol. Fish*. **3(1)**, 109-128.

Levins, R., 1968. Evolution in changing environments. *Princeton Univ. Press, Princeton*. **4**, 120.

Leis, J.M., 1991. The pelagic phase of coral reef fishes: larval biology of coral reef fishes. 183-230. In: Sale. P.F., (ed). The ecology of fishes on coral reefs. *Academic Press, San Diego.*

Letourneur, Y., Kulbicki, M., Labrosse, P., 1998. Length-weight relationship of fishes from coral reefs and lagoons of New Caledonia-an update. Naga: ICLARM Q. **21**, 39-46.

Lincoln-Smith, M.P., 1988. Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. *Mar. Ecol. Prog. Ser.* **43**, 223–231.

Lincoln-Smith, M.P., 1989. Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. *Environ. Biol. Fishes* **26**, 29–37.

Lincoln Smith, M.P., Bell, J.D., Hair, C.A., 1991. Spatial variation in abundance of recently settled rocky reef fish in southeastern Australia: implications for detecting change. *Mar. Ecol. Prog. Ser*. **77**, 95-103.

Lirman, D., 1999. Reef fish communities associated with *Acropora palmata*: relationships to benthic attributes. *Bull. Mar. Sci.* **65**, 235–252.

Longhurst, A.R., Pauly, D., 1987. Ecology of tropical oceans. *Academic Press, San Diego*.

Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* **49**, 317–323.

MacArthur, R.H., 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc*. **1**, 19-30.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. *Princeton University Press, Princeton.*

Marcotte, B.M., Browman, H.I., 1986. Foraging behaviour in fishes: perspectives on variance. *Environ, Biol. Fish*. **16**, 25-33.

McClanahan, T.R., 1994. Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral reefs*. **13**, 231-241.

McCormick, M.I., 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar. Ecol. Prog. Ser.* **112**, 87–96.

McCormick, M.I., 1998. Ontogeny of diet shifts by a microcarnivorous fish, *Cheilodactylus spectabilis*: relationship between feeding mechanics, microhabitat selection and growth. *Mar. Biol*. **132**, 9-20.

McGehee, M.A., 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. *Mar. Ecol. Prog. Ser.* **105**, 243–255.

McKenna, J.E.Jr., 1997. Influence of physical disturbance on the structure of coral reef fish assemblages in the Dry Tortugas. *Caribbean J. Sci*. **33**, 82-97.

Molles, M.C., 1978. Fish species diversity on model and natural reef patches: experimental insular biogeography. *Ecol. Monogr*. **48**, 289-305.

Ohman, M.C., 1998. Aspects of habitat and disturbance effects on tropical reef fish communities. *Department of Zoology, Stockholm University, Sweden*.

Ohman, M.C., Rajasuriya, A., 1998. Relationships between habitat structure and fish communities on coral and sandstone reefs. *Env. Biol of Fishes*. **53**, 19-31

Paine, R.T., 2002. Trophic control of production in a rocky intertidal community. *Science*. **296**, 736-739.

Parrish, J.D., 1987. The trophic biology of snappers and groupers. In: Polovina, J.J., Ralston, S., (eds) Tropical snappers and groupers: biology and fisheries management. *Westview Press, Boulder, Colorado*. 405-463.

Perry, G., Pianka, E.R., 1997. Animal foraging: past, present and future. *Trends Ecol. Evol*. **12**, 360-364.

Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. *Am. Nat*. **100**, 33-46.

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature*. **405**, 212-219.

Ricklefs, R.E., 1973. Ecology. *Chiron Press. Portland*. 861.

Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull*. **153**. 1-6.

Roberts, C.M., Ormond, R.F.G., 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* **41**, 1–8.

Robertson, D.R., 1991. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panamá indicate food limitation. *Marine Biology.* **111**, 437–444.

Roughgarden, J.D., 1996. Theory of population genetics and evolutionary ecology: an introduction. *Prentice-Hall, Upper Saddle River*. 612.

Russ, G.R., 1984a. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser*. **20**, 35–44.

Russ, G.R., 1984b. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar. Ecol. Prog. Ser*. **20**, 35–44.

Russ, G.R., 1984c A review of coral reef fisheries. *UNESCO Rep. Mar. Sci*. **27**, 74-92.

Russ, G., 1985. Effects of protective management on coral reef fishes in the central Philippines. *Proc 5th Int Coral Reef Sym.* **4,** 219-224.

Russ, G., 1987. Effects of protective management on coral reef fishes in the central Philippines. *Proc. 5th Int. Coral Reef Sym*. 219-244.

Russ, G.R., 1991. Coral reef fisheries: effects and yields. In Sale. P.F., (ed). The ecology of fishes on coral reefs. *Academic Press, San Diego*. 601-635.

Russ, G.R., Alcala, A.C., 1989. Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser*. **56**, 13-27.

Russ, G.R., Alcala, A.C., 1998. Natural fishing experiments in marine reserves 1983-1993: roles of life history and fishing intensity in family responses. *Coral Reefs*. **17**, 399-416.

Russell, B.C., Talbot, F.H., Anderson G.R.V., Goldman, B., 1978. Collection and sampling of reef fishes. In: Stoddart, D.R., Johannes, R.E., (eds.) *Monographs on Oceanographic Methodology. Coral Reefs: research methods. UNESCO, Norwich*. **5**, 329-345.

Sale, P.F., 1980. Assemblages of fish on patch reefs – predictable or unpredictable? *Env. Biol. Fish*. **5,** 243–249.

Sale, P.F., (Ed.) 1991. The Ecology of Fishes on Coral Reefs. Academic Press, New York, 754.

Sale, P.F., 1991. Habitat structure and recruitment in coral reef fishes. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R., (eds) Habitat structure. *The physical arrangements of objects in space. Chapman & Hall, London*. 197-210.

Sale, P.F., 1997. Visual census of fishes: how well do we see what is there. *Proc. 8th Int. Coral Reef Sym*. **2,** 1,435-1,440.

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

Sale, P.F., Douglas, W.A., 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology*. **65**, 409–422.

Sale, P.F., Guy, J.A., Steel, W.J., 1994. Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia*. **98**, 83-99.

Samoilys, M.A., 1992. Review of the underwater visual census method developed by the DPI/ACIAR project: visual assessment of reef fish stocks. *Conference and Workshop Series QC92006, Department of Primary Industries, Brisbane*. 55.

Samoilys, M.A., 1997. Underwater visual census surveys. 16-29. In: M.A., Samoilys (ed.) *Manual for Assessing Fish Stocks on Pacific Coral Reefs, Queensland Department of Primary Industries, Townsville*.

Samoilys, M.A., Carlos, G., 2000. Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Env. Biol. of Fishes*. **57**, 289-304.

Sano, M., Shimizu, M., Nose, Y., 1984a. Changes in structure of coral reef fish communities by destruction hermatypic corals: observational and experimental views. *Pacif. Sci*. **38**, 51–79.

Smith, S.V., 1978. Coral reef area and the contributions of reefs to processes and resource's of the worlds oceans. *Nature, Lond*. **273**, 225-226.

St. John, J., Russ, G. R., and W. Gladstone. 1990. Accuracy and bias of visual estimates of numbers, size structure and biomass of coral reef fish. *Mar. Ecol. Prog. Ser*. **64**, 253–262.

Talbot, F.H., 1965. A description of the coral structure of Tutia Reef (Tanganyika Territiory, East Africa) and its fish fauna. *Proc. Zool. Soc. Lond*. **145**, 431-470.

Thresher, R.E., Gunn, J.S., 1986. Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). *Environ Biol Fish*. **17**, 93-116

Vanni, M.J., Flecker, A.S., Hood, J.M., Headworth, J.L., 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecol. Lett*. **5**, 285-293.

Wainwright, P.C., Richard, B.A., 1995. Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fish*. **44**, 97-113.

Waldner, R.E., Robertson, R., 1980. Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bull. Mar. Sci*. **30**, 171-186.

Wellington, G.M., 1982. Depth zonation of corals in the Gulf of Panama: control and facilitation by resident reef fishes. *Ecological Monographs*. **52 (3)**, 223-241.

Wellington, G.M., Victor, B.C., 1985. El Nino mass coral mortality: a test of resource limitation in a coral reef damselfish population. *Oecologia*. **68**, 15-19.

Williams, D.McB., 1982. Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs*. **1**, 35-43.

Williams D.McB., 1983. Longitudinal and latitudinal variations in the structure of reef fish communities. In: Baker, J.T., Carter, R.E., Sammarco, P.W., Stark, K., (eds) *Proceedings of the Inaugural Great Barrier Reef Conference, Townsville, Australia*. James Cook University Press, Townsville. 265-270.

Williams, D.McB., 1986. Temporal variation in the structure of reef slope fish communities (central Great Barrier Reef): Short-term effects of *Acanthaster planci*. *Mar. Ecol. Prog. Ser*. **28**, 157-64.

Williams, D.McB., 1991. Patterns and processes in the distribution of coral reef fishes. In: Sale, P.F., (ed.). *The Ecology of Fishes on Coral Reefs, Academic Press, San Diego*. 437-474.

Williams, D.McB., Hatcher, A.I., 1983. Structure of fish communities on outer slopes of inshore mid-shelf and outer-shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser*. **10**, 239-250.

Wooton, R.J., 1990. Ecology of teleost fishes. *Chapman and Hall, New York*.

Website References

http://www.coral.aoml.noaa.gov/agra/method/methodhome.htm
Atlantic and Gulf Rapid Reef Assessment: 05/05/2004

http://www.fishbase.org/search.cfm
01/07/2004

http://www.redlist.org/search/details.php?species=10072
The IUCN Red List of Threatened Species: 01/07/2004

http://www.sea007.com/Info_WorldSea/WorldSeas-Pacific-Pacific.htm
World Seas- Pacific Ocean: 24/08/2004

APPENDIX 1:
Example of data sheet.

Date
Time
Site
Surveyor

Weather
Sea State
Temperature
Reef Type

Species	0-5cm	6-10cm	11-20cm	21-30cm	31-40cm	>40cm (list size)

Roving Diver:

Single:

Few (2-10):

Many (11-100):

Abundant (>100):

APPENDIX 2:
List of species found with common and latin names, the number allocated for the DECORANA and the number of them counted in total

Common name	Latin name	Species number	Number found
Acapulco gregory	Stegastes acapulcoensis	1	3873
Amberjack (Almaco Jack)	Seriola rivoliana	2	1
Azure parrotfish	Scarus compressus	3	4
Banded serrano	Serranus psittacinus	4	342
Banded Wrasse	Halichoeres notospilus	5	177
Beaubrummel gregory	Stegastes flavilatus	6	724
Bicolour parrotfish	Scarus rubroviolaceus	7	3
Bigeye (crevalle) jacks	Caranx sexfasciatus	8	5
Bigscale soldier fish	Myripristis berndti	9	4
Blacknose butterflyfish (Barberfish)	Johnrandallia nigrirostris	10	66
Bluechin parrottfish	Scarus ghobban	11	272
Broomtail grouper	Mycteroperca xenarcha	12	1
Bumphead damselfish	Microspathodon bairdii	13	3
Bumphead parrotfish	Scarus perrico	14	5
Chameleon Wrasse	Halichoeres dispilus	15	2397
Coral hawkfish	Cirrhitichthys oxycephalus	16	126
Cortez Angelfish	Pomacanthus zonipectus	17	27
Cortez chub	Kyphosus elegans	18	61
Cortez rainbow wrasse	Thalassoma lucasanum	19	10042
Finescale triggerfish	Balistes polylepis	20	12
Freckled porcupinefish	Diodon holocanthus	21	43
Giant damselfish	Microspathodon dorsalis	22	58
Giant hawkfish	Cirrhitus rivulatus	23	2
Golden eye grunt (Mojarra grunt)	haemulon scudderi	24	53
Golden snapper	Lutjanus inermis	25	2
Golden wrasse	Halichoeres melanotis	26	12
Green spotted sharpnose puffer	Canthingaster jathinopterous	27	8
Greybar grunt	haemulon sexfasciatum	roving only	0
Guineafowl pufferfish	Arothron meleagris	28	2
Hourglass morayeel	Muraena clepsydra	29	2
Jewel morayeel	Muraena lentiginosa	30	1
King Angelfish	Holacanthus passer	31	164
Latin grunt	Haemulon steindachneri	32	850
Lined highhat (Rock croaker)	Pareques viola	33	14
Mexican hogfish	Bodianus diplotaenia	34	153
Mottled soapfish	Rypticus bicolor	35	5
Mullet snapper	Lutjanus aratus	36	10
Orangesided triggerfish	Sufflamen verres	37	28
Pacific cornet fish	fistularia corneta	roving only	0
Pacific creolefish	Paranthias colonus	38	24
Pacific hamlet (Mutton hamlet)	Alphestes immaculatus	39	1
Pacific (panamic) night sergant	Abudefduf concolor	40	11
Pacific seahorse!!	Hippocampus ingens	41	3
Palenose morayeel	Echidna nocturna	roving only	0
Panamic graysby	Epinephelus panamensis	42	100

Panamic green morayeel	Gymnothorax castaneus	roving only	0
Panamic porkfish	Anisotremus taeniatus	43	1
Panamic sergeant major	Abudefduf troschelii	44	513
Pink cardinal fish	Apogon pacifici	45	30
Rainbow runner	Elagatis bipinnulata	46	30
Razor surgeonfish (Chancho surgeonfish)	Prionurus laticlavius	47	6
Reef cornet fish	fistularia commersonii	48	5
Reef lizardfish	Synodus lacertinus	49	3
Scissortail chromis	Chromis atrilobata	50	5566
Scrawled filefish	Aluterus scriptus	roving only	0
Shortfin grunt	Microlepidotus brevipinnis	51	150
Silver grey grunt	Anisotremus caesius	52	6
Spinster wrasse	Halichoeres nicholsi	53	293
Spotfin porcupinefish	Chilomycterus reticulatus	roving only	0
Spottail grunt	Haemulon maculicauda	54	1913
Spotted eagle ray	Aetobatus narinari	roving only	0
Spotted rose snapper	Lutjanus guttatus	55	150
Spotted sharpnosed puffer	Canthigaster punctatissima	56	344
Starry grouper (Flag cabrilla)	Epinephelus labriformis	57	262
Steel pompano	Trachinotus stilbe	58	98
Stone triggerfish (blunthead trigger)	Pseudobalistes naufragium	59	19
tailspot cardinal fish	Apogon dovii	60	275
Three banded butterflyfish	Chaetodon humeralis	61	63
Tinsel squirrelfish	Sargocentron suborbitalis	62	87
Whitespotted pufferfish	Arothron hispidus	63	15
Wounded wrasse	Halichoeres chierchiae	64	220
Unidentified Jack		65	4
Yellow snapper	Lutjanus argentiventris	66	4
Yellow spotted grunt	Haemulon flaviguttatum	67	146
Yellowfin Surgeonfish	Acanthurus xanthopterus	68	7
Zebra moray	Gymnomuraena zebra	roving only	0

APPENDIX 3:

The 39 survey sites and the codes allocated to them, the abundance of fish per transect and the standard deviation and standard error associated with this. The abundance as a percentage of the overall total. The total number of species seen along transects at each site and the diversity indexes (Shannon's H).

Site name	Site code	Mean fish per transect	Standard deviation	Standard error	Percentage abundance	Total species	Diversity index
Isla San Pedro	1	74.5	30.6	15.3	1.00	16	3.04
Isla San Pablo	2	243.3	134.5	67.3	3.26	20	1.60
Isla Elefante	3	93.8	29.1	14.6	1.26	23	3.42
Isla Espiritu Santo	4	199.8	99.8	49.9	2.67	22	2.38
Isla Contadora Southeast	5	191.3	44.4	22.2	2.56	21	2.70
Isla Contadora Playa Larga	6	170.8	45.3	22.7	2.29	18	1.89
Isla Contadora Playa Galeón	7	142	58.8	29.4	1.90	22	2.90
Isla Chapera Northeast	8	249.8	78.5	39.3	3.34	24	2.16
Isla Chapera Northwest	9	126.3	31.5	15.7	1.70	13	1.61
Isla Chapera Southeast	10	262.8	101.0	50.5	3.52	23	2.72
Isla Cañita	11	129	106.4	53.2	1.73	18	2.01
Isla Casaya	12	106.8	55.7	27.9	1.43	22	3.42
Isla Bolaño Northeast	13	143.3	13.7	6.9	1.92	15	2.89
Isla Chapera South	14	118	28.5	14.3	1.58	22	2.59
Isla Mogo Mogo North	15	121	26.3	13.2	1.62	14	2.05
Isla Mogo Mogo Southeast	16	180.3	30.7	15.4	2.41	15	1.54

Isla Mogo Mogo South	17	209.5	62.1	31.1	2.80	17	2.06
Isla Bolaño West	18	138.8	29.1	14.6	1.86	12	0.97
Isla Contadora Southwest	19	428.5	168.2	84.1	5.73	26	2.14
Isla Pacheca East	20	240	44.4	22.2	3.21	23	2.80
Isla Pachequilla	21	227.5	71.5	35.8	3.05	19	2.18
Isla Tembrillos	22	123	21.15	10.6	1.65	19	2.29
Isla Mogo Mogo West	23	195.5	58.2	29.1	2.62	10	1.59
Isla Contadora North	24	205	102.7	51.4	2.74	24	2.55
Isla Pacheca North	25	220.3	77.4	38.7	2.95	15	2.02
Isla Twin	26	179	46.1	23.0	2.40	21	2.48
Islote Bendico	27	205.8	101.2	50.6	2.75	22	2.70
Isla Bartolomé North	28	219.8	34.1	17.1	2.94	14	2.23
Isla Bartolomé West	29	296.3	36.2	18.1	3.97	19	2.34
Isla Saboga North	30	248	53.9	26.9	3.32	18	2.01
Isla San José Northeast	31	354	278.4	139.2	4.74	39	3.04
Isla Cocos	32	189.8	82.7	41.3	2.54	18	2.90
Isla Pedro Gonzalez East	33	360.5	265.0	132.5	4.83	25	2.86
Isla Pedro Gonzalez Northeast	34	146.5	44.2	22.1	1.96	18	2.42
Isla Comote	35	203.3	115.9	57.9	2.72	30	2.51
Isla de Monte	36	121.3	37.5	18.8	1.62	28	3.14

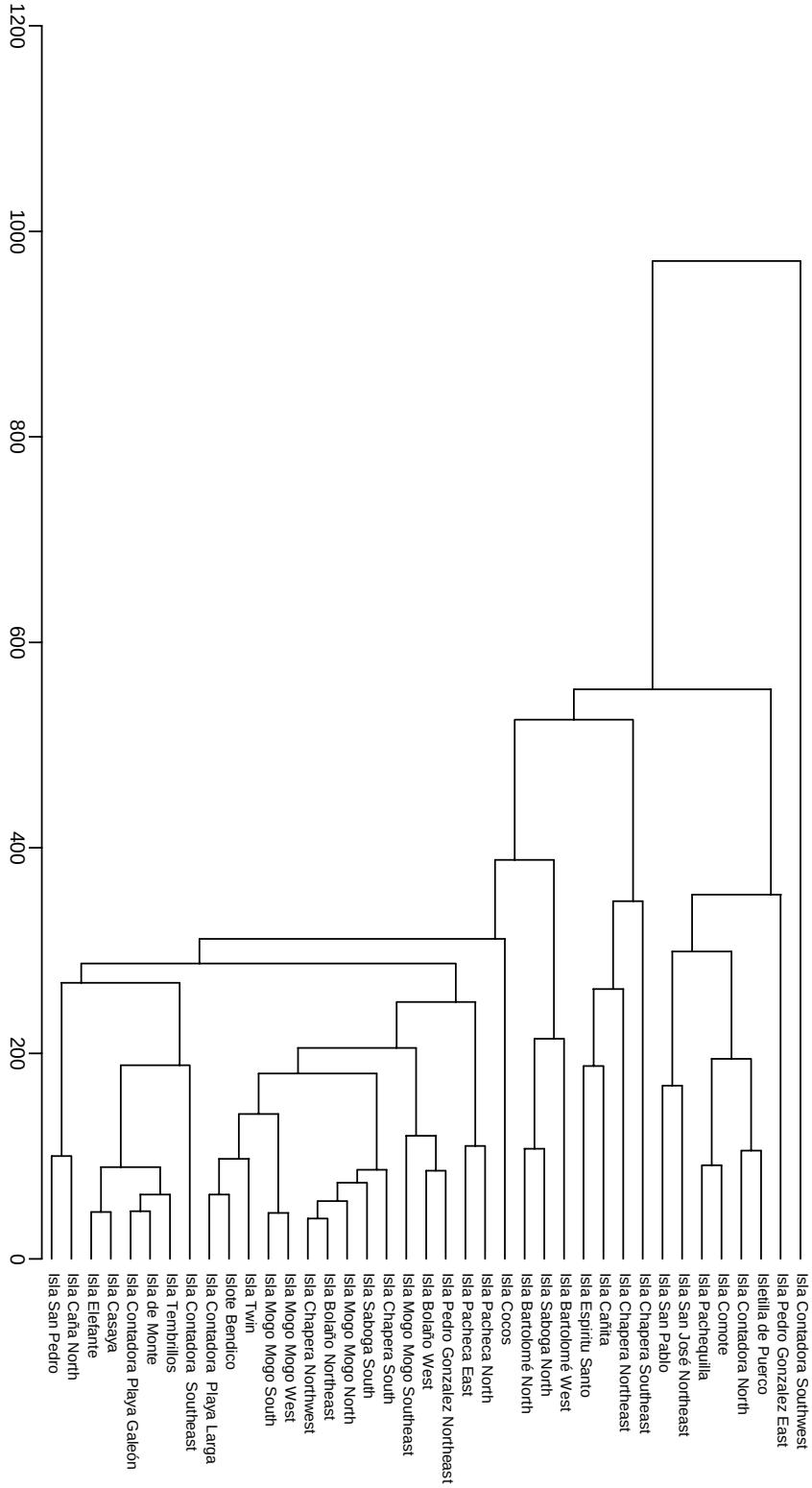
Isletilla de Puerco	37	181.3	83.6	41.8	2.43	24	2.81
Isla Caña North	38	77	27.2	13.6	1.03	15	1.94
Isla Saboga South	39	152.8	57.9	29.0	2.05	17	2.19
Mean	**-**	**192**	**-**	**-**	**-**	**20.03**	**2.39**
Standard Deviation	**-**	**77.2**	**-**	**-**	**-**	**5.44**	**-**
Standard Error	**-**	**12.4**	**-**	**-**	**-**	**0.87**	**-**

APPENDIX 4:

Species only occurring on the framework reefs;
Lutjanus inermis,
Muraena lentiginosa,
Scarus rubroviolaceus,
Alphestes immaculatus,
Muraena clepsydra,
Synodus lacertinus,
Fistularia commersonii,
Lutjanus guttatus,
Microlepidotus brevipinnis,
Lutjanus argentiventris,

Species only occurring on the communities;
Seriola rivoliana,
Scarus compressus,
Caranx sexfasciatus,
Mycteroperca xenarcha,
Cirrhitus rivulatus,
Lutjanus aratus,
Arothron meleagris,
Anisotremus taeniatus,
Paranthias colonus,
Apogon pacifici,
Prionurus laticlavius,
Unidentified Carangid.

APPENDIX 5:
Dendrogram of site cluster analysis using Euclidean distance for data on abundance of families of fish.



APPENDIX 6:
Figures showing scatter plots for all significant correlations found in the data.

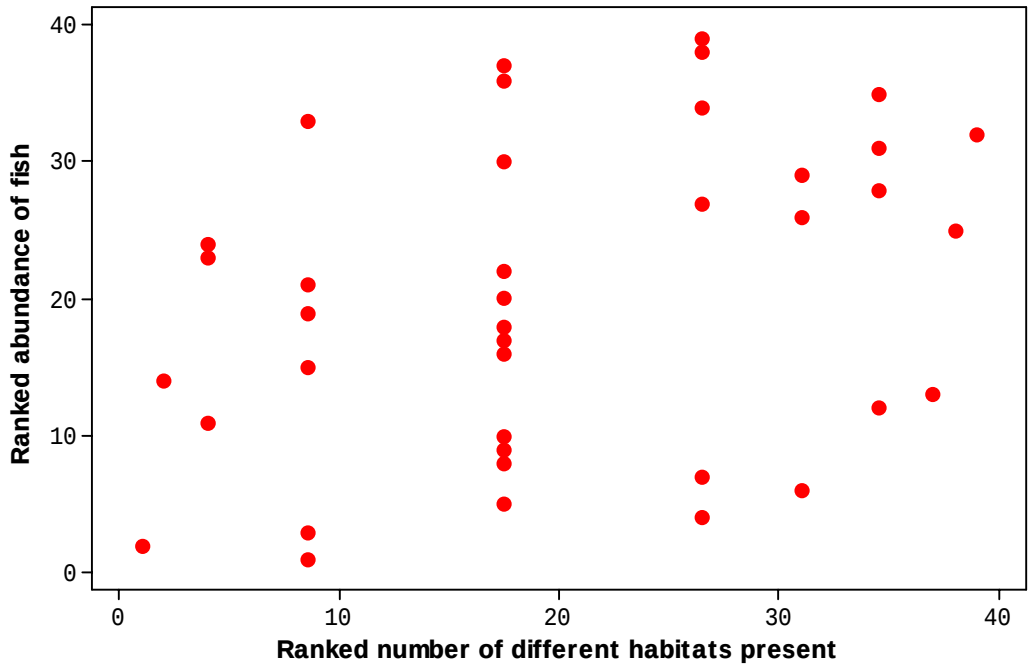


Figure A: Ranked abundance of fish versus number of bottom types present

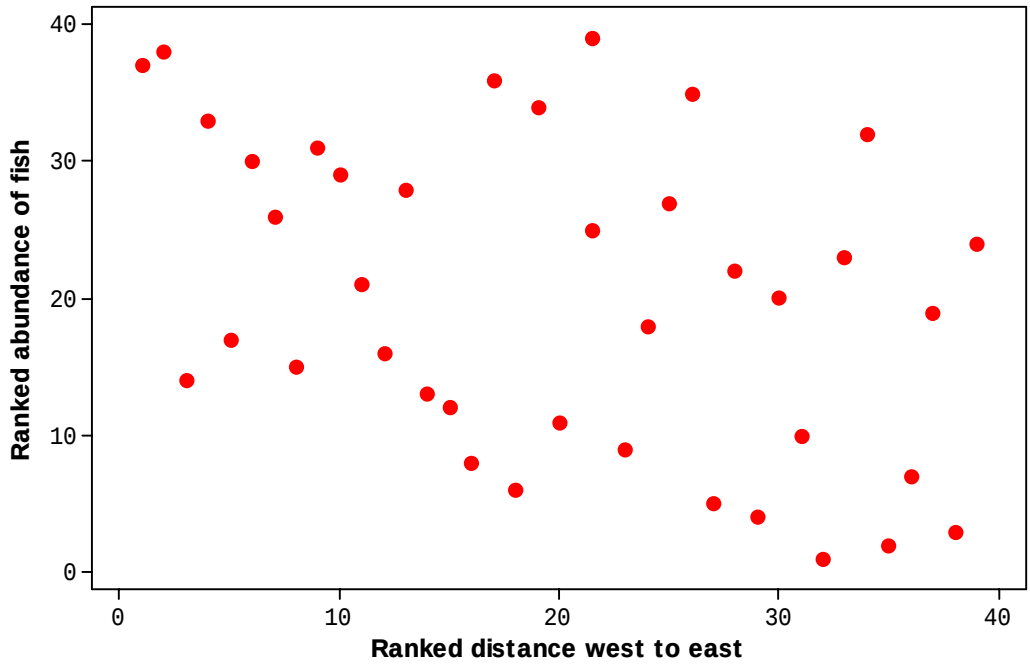


Figure B: Ranked abundance of fish versus distance west to east with the low values representing west.

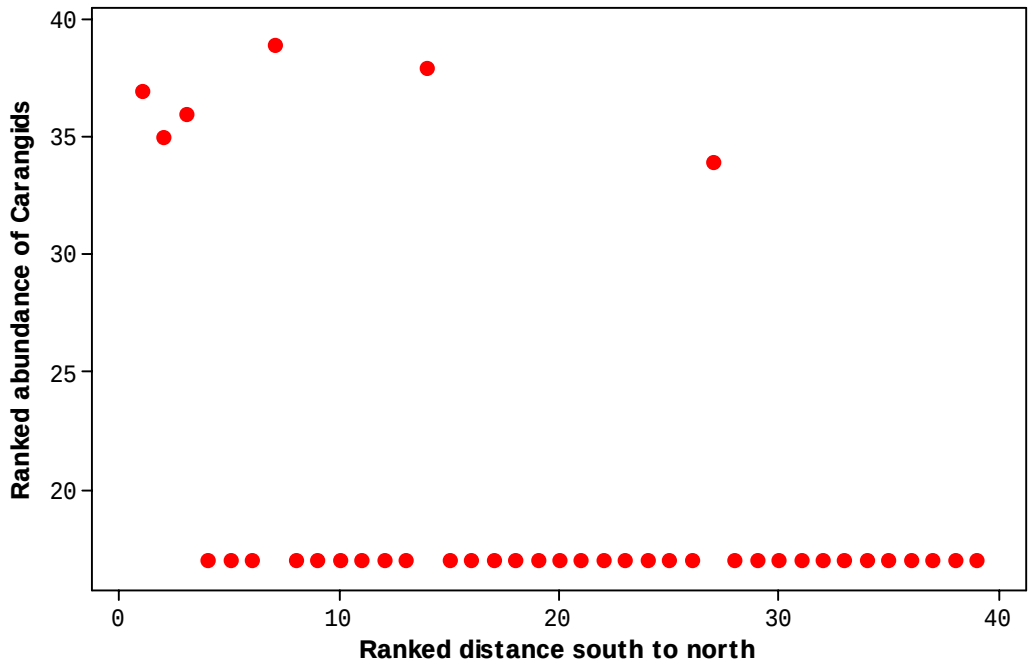


Figure C: Ranked abundance of Carangidae versus distance north to south with the low values representing south.

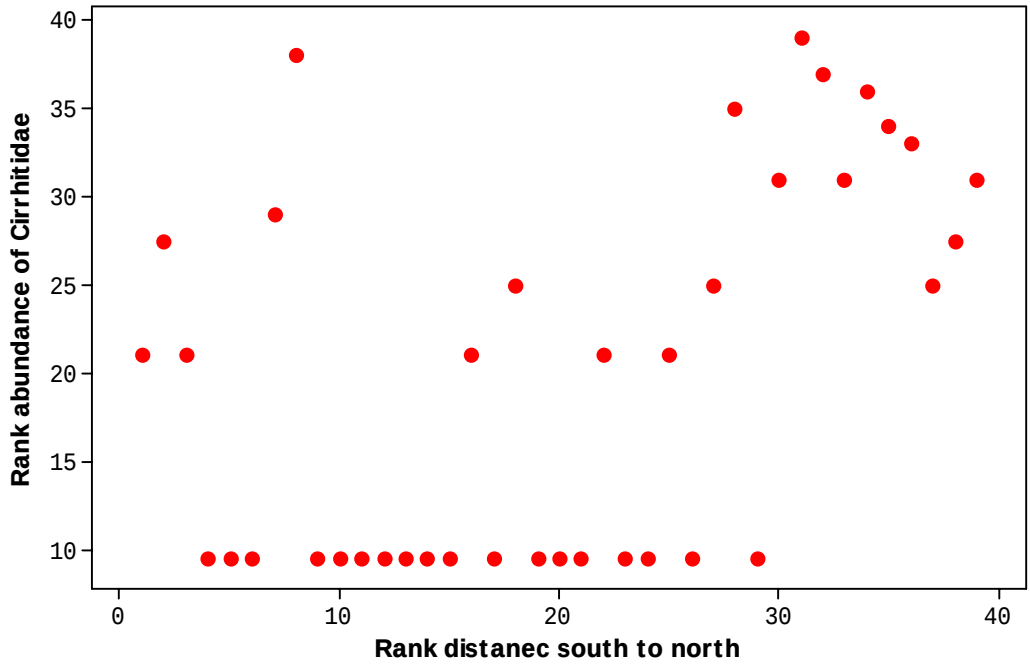


Figure D: Ranked abundance of Cirrhitidae versus distance north to south with the low values representing south.

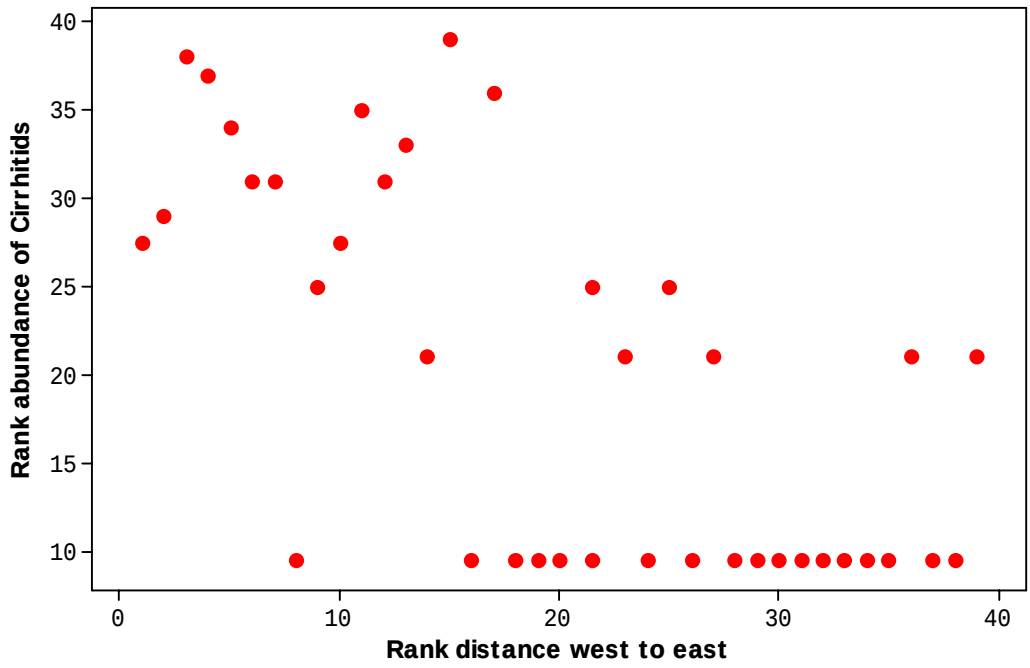


Figure E: Ranked abundance of Cirrhitidae versus distance west to east with the low values representing west.

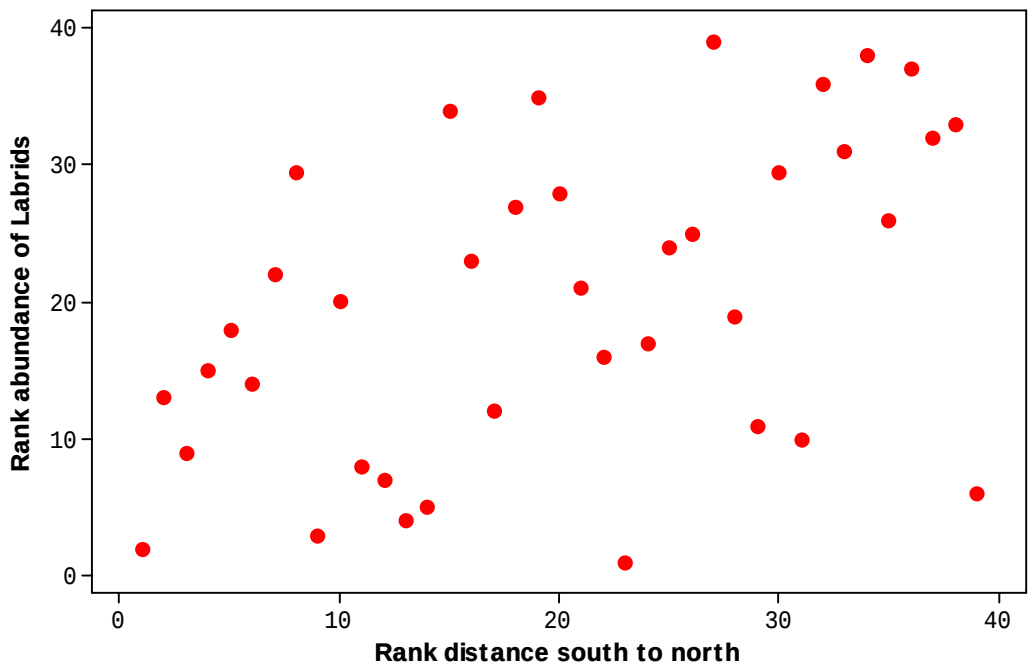


Figure F: Ranked abundance of Labridae versus distance north to south with the low values representing south.

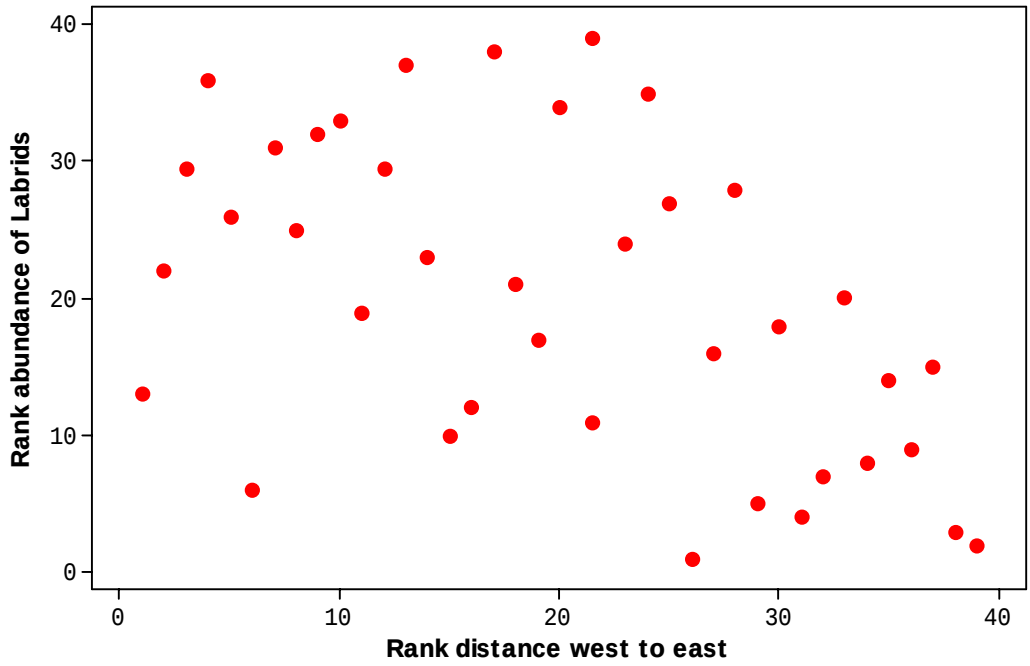


Figure G: Ranked abundance of Labridae versus distance west to east with the low values representing west.

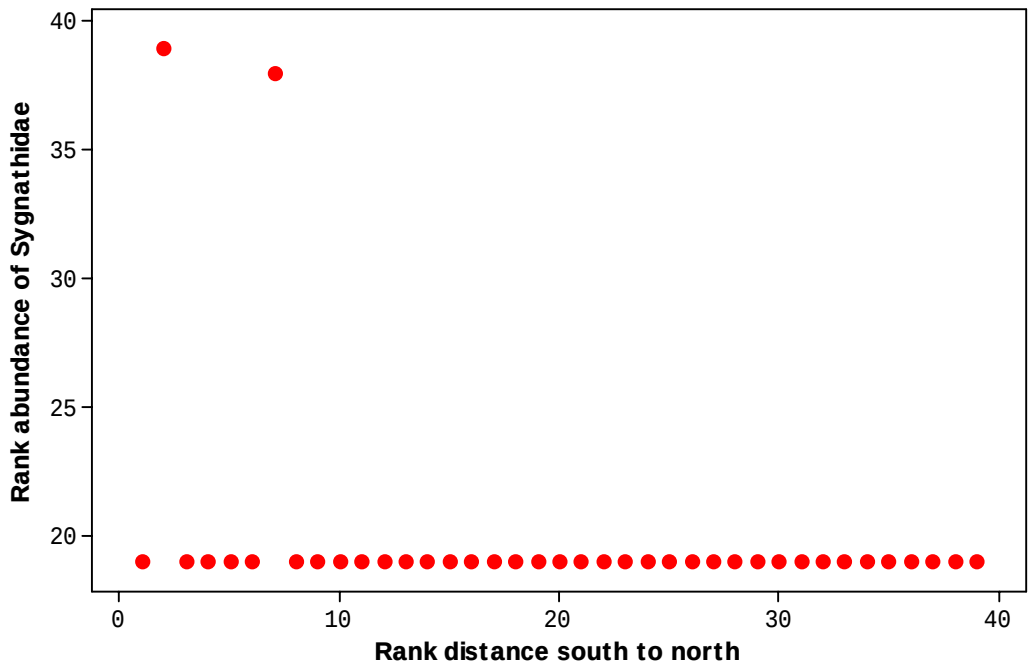


Figure H: Ranked abundance of Sygnathidae versus distance north to south with the low values representing south.

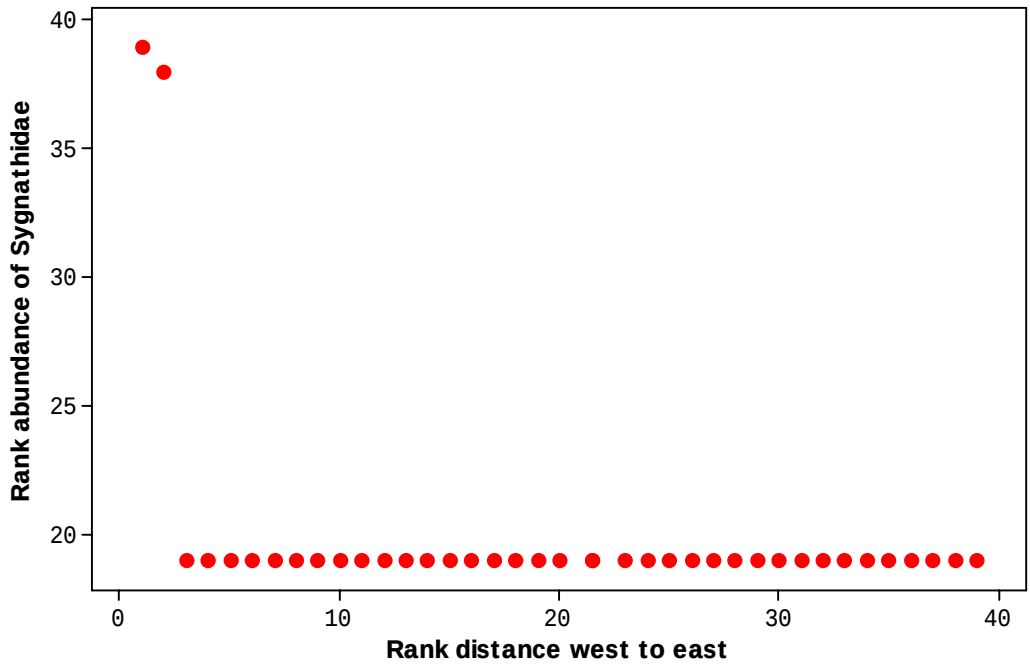


Figure I: Ranked abundance of Sygnathidae versus distance west to east with the low values representing west.

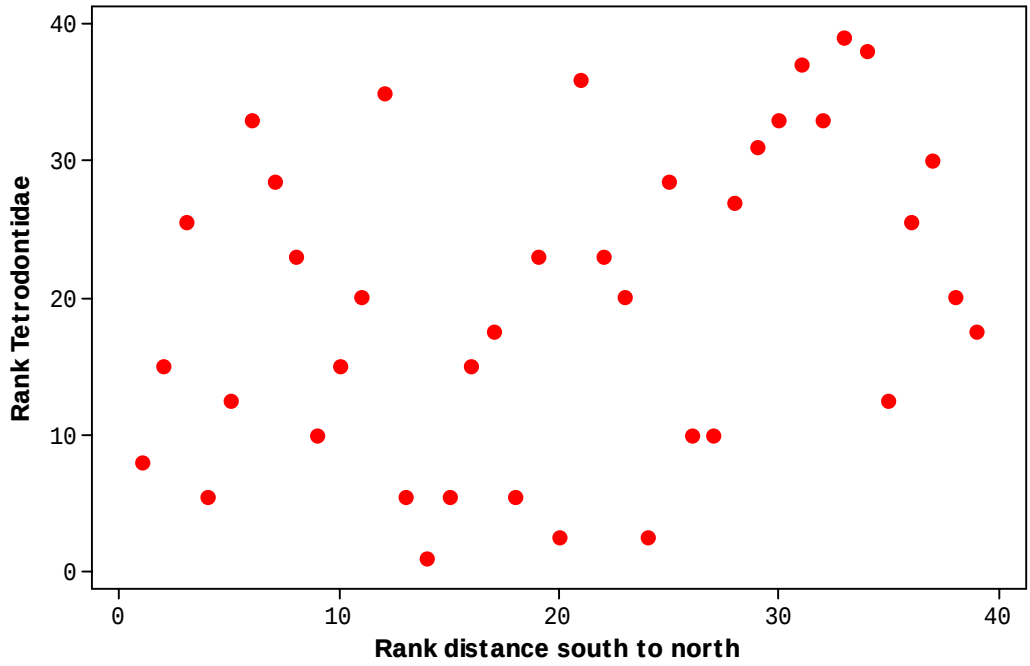


Figure J: Ranked abundance of Tetrodontidae versus distance north to south with the low values representing south.

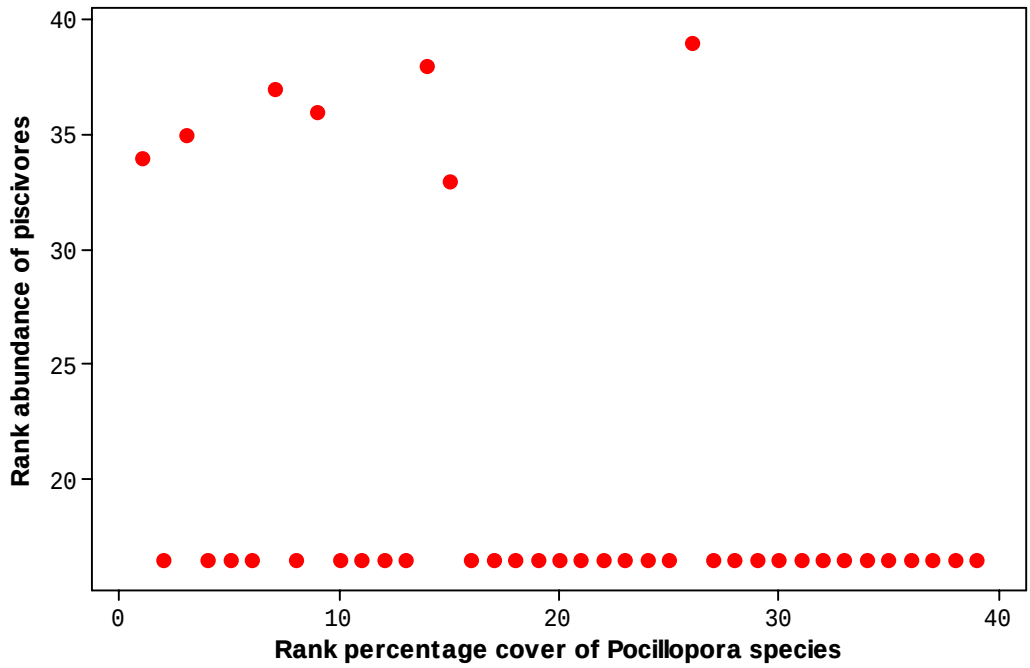


Figure K: The rank abundance of piscivorous fish versus percentage cover of *Pocillopora* species.

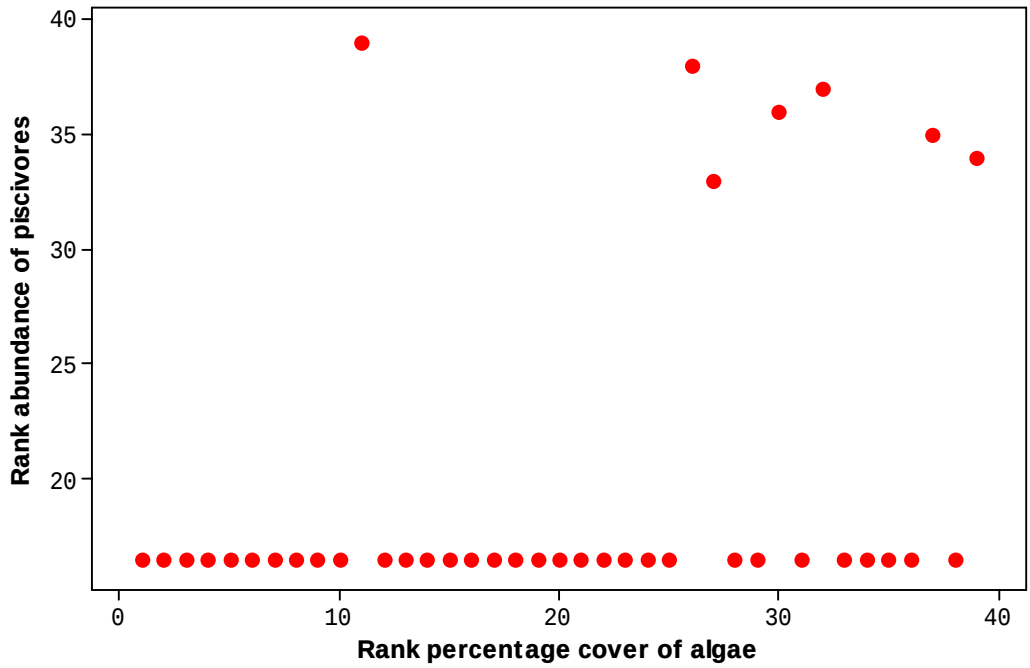


Figure L: The rank abundance of piscivorous fish versus percentage cover of algae.

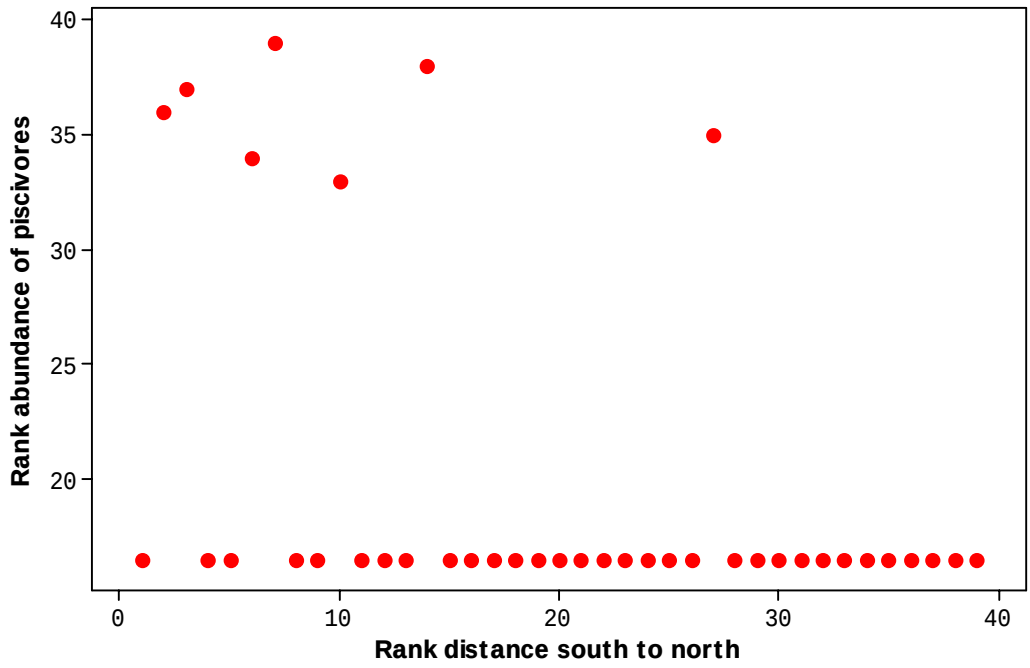


Figure M: The rank abundance of piscivorous fish versus distance north to south with low values representing south.

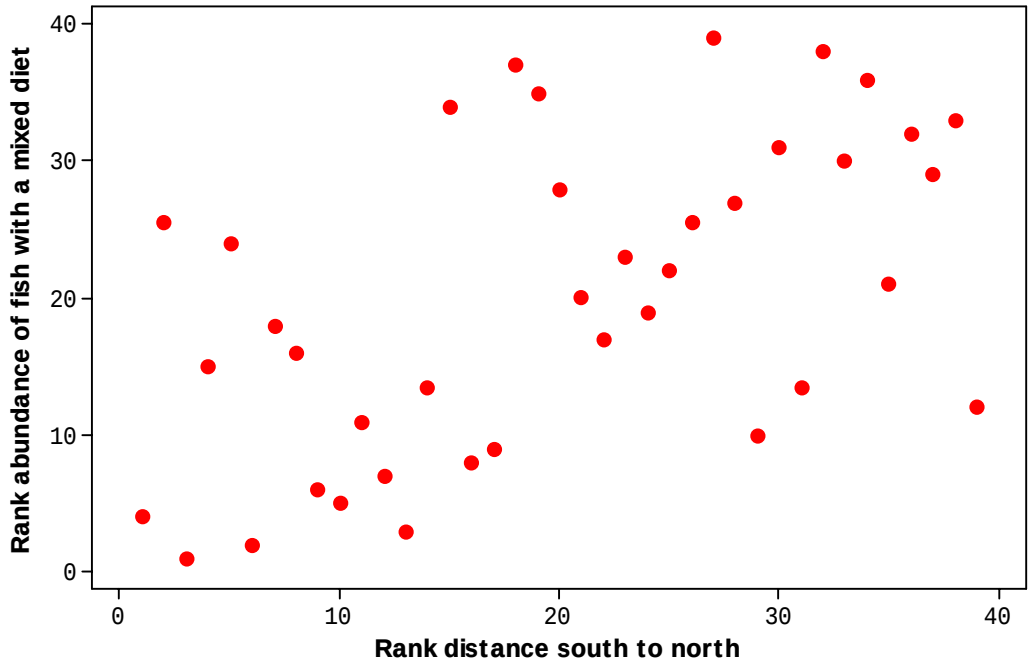


Figure N: The rank abundance of Generalist feeders versus distance north to south with low values representing south.

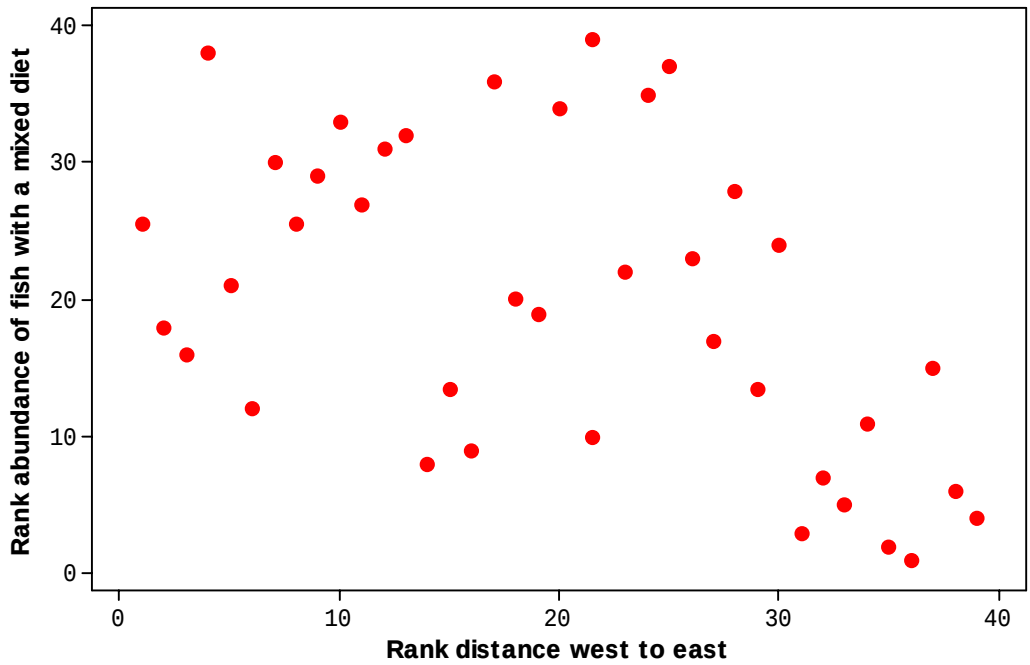


Figure O: The rank abundance of Generalist feeders versus distance west to east with low values representing west.

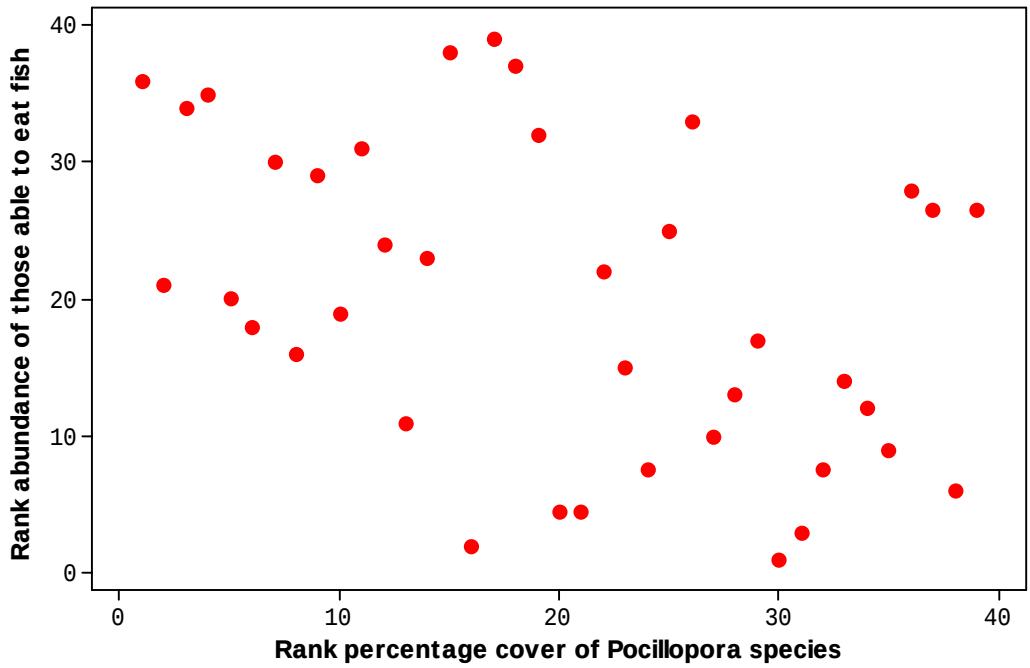


Figure P: The rank abundance of piscivorous fish and those eating fish as part of a mixed diet versus percentage cover of *Pocillopora* species.

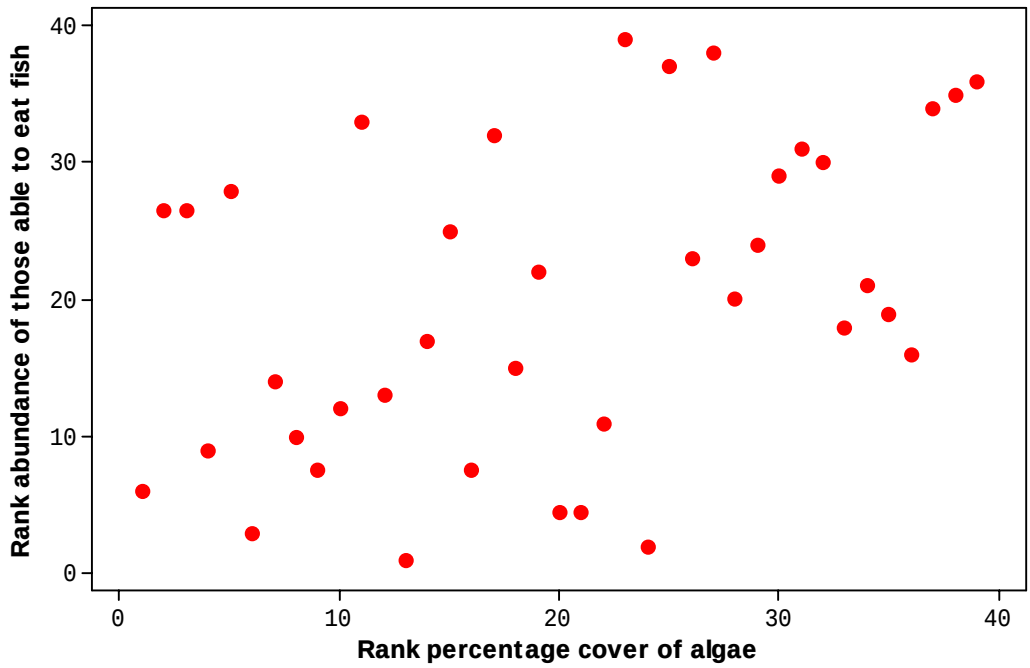


Figure Q: The rank abundance of piscivorous fish and those eating fish as part of a mixed diet versus percentage cover of algae.

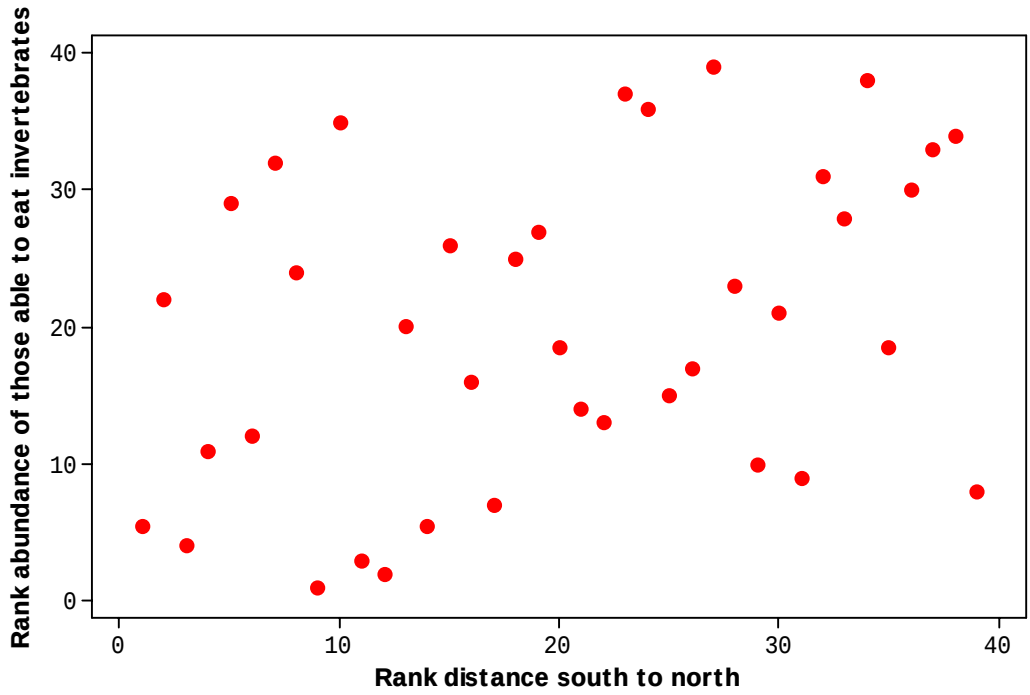


Figure R: The rank abundance of invertivores and those eating invertebrates as part of a mixed diet versus distance north to south with low values representing south.

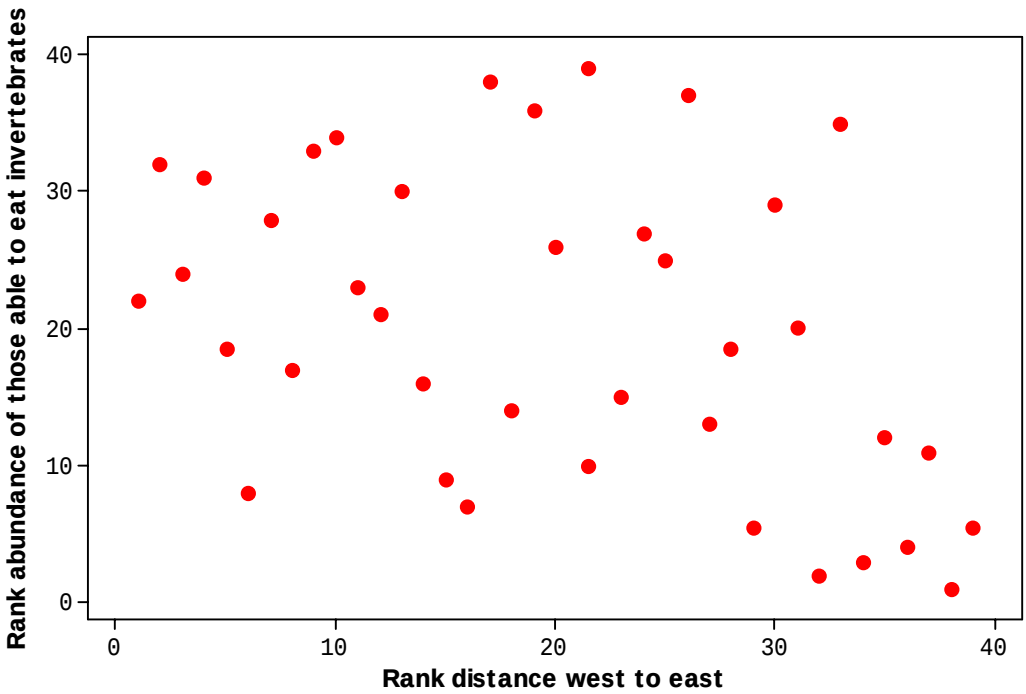


Figure S: The rank abundance of invertivores and those eating invertebrates as part of a mixed diet versus distance west to east with low values representing west.

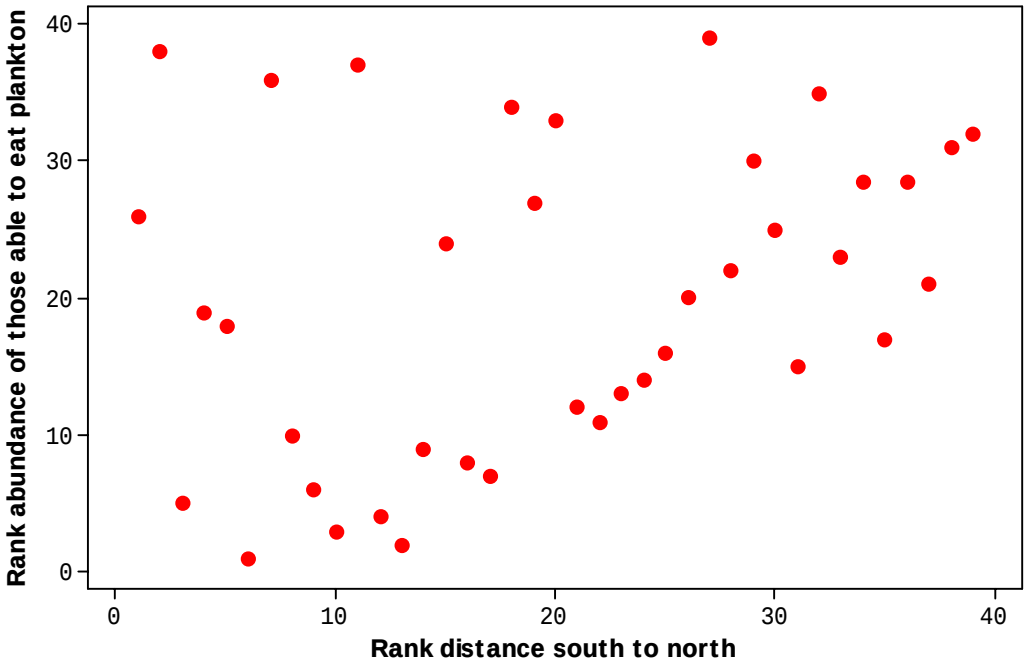


Figure T: The rank abundance of planktivores and those eating plankton as part of a mixed diet versus distance north to south with low values representing south.

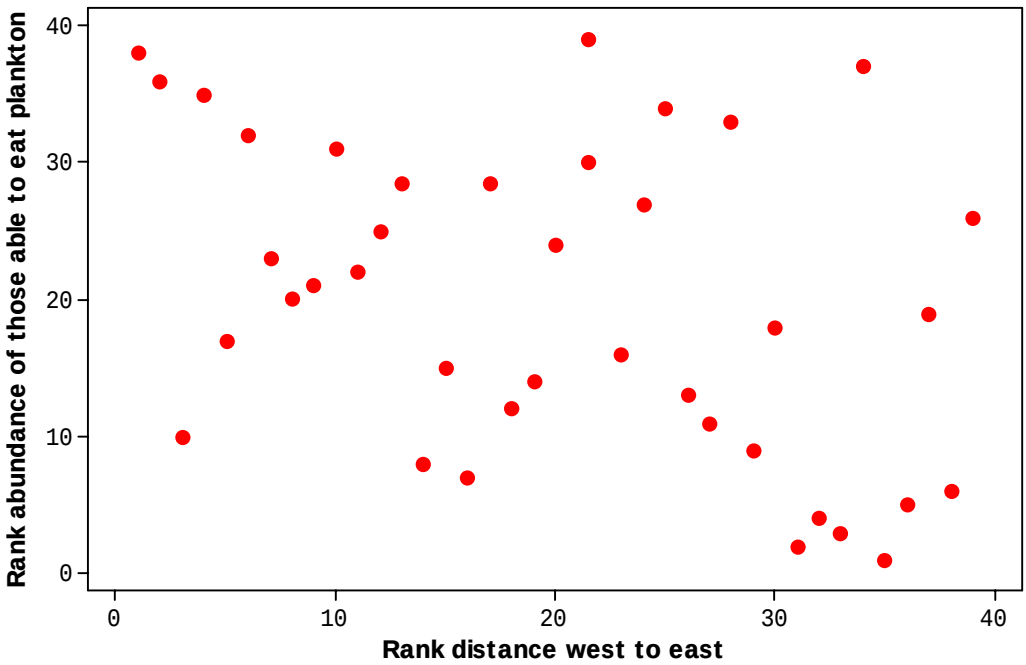


Figure U: The rank abundance of planktivores and those eating plankton as part of a mixed diet versus distance west to east with low values representing west.

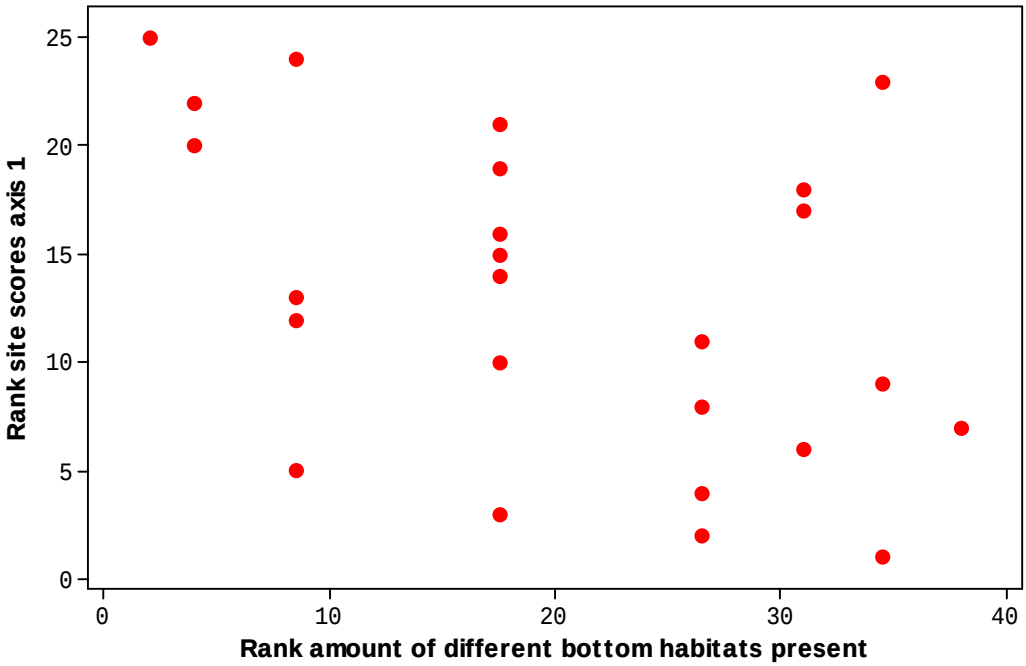


Figure V: DECORANA axis 1 site scores for the coral framework sites only, versus the amount of bottom types present at each site.